APPLIED FRESHWATER BIOLOGY

John S. Richardson, Ph.D.

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INTRODUCTION

Water is essential for all life and sustains freshwater ecosystems around the world. In addition to the myriad life-forms that freshwater ecosystems support, these ecosystems provide us with water and food, as well as opportunities for recreation and personal reflection. Unfortunately, our freshwaters have become seriously impacted and degraded by various stressors. Throughout my career I have witnessed some of this degradation firsthand and have been able to incorporate case studies into aquatic ecosystem courses I have taught.

This book began as an outcome of teaching aquatic ecosystems courses for over 25 years, along with the need to provide students with a comprehensive volume containing practical applications of the lessons learned in freshwater biology. Being unable to find a book that fit the way I want to approach these subjects, I was inspired to write one that follows many of the key themes from my courses. Each chapter addresses relevant environmental issues affecting freshwater ecosystems and provides a solutions-based approach to help mitigate these stressors.

It would be difficult, however, for any one textbook to address all the topics that are important to the protection and conservation of freshwater ecosystems. I have tried to include most current issues, but admittedly there are more. Where appropriate, I have included examples from most types of freshwaters, but some threats are specific to particular ecosystems. For example, I have not addressed groundwater ecosystems in any substantive way. Some freshwaters are less frequently considered in the literature, such as temporary waters, tree holes, springs of all sorts, and others, and this book reflects that dearth of studies in having few mentions of such ecosystems.

The first two chapters of this book are intended as a review of freshwater biology, hydrology, and freshwater ecosystems but will not constitute a full course on these subjects. I assume the student has some previous background in ecology and freshwater biology. If not, an excellent text for freshwater ecology is Dodds and Whiles (2019). There are many other good books on freshwater ecosystems, and those should be consulted for a thorough grounding in the basics of the field—for instance, Hynes (1970), Hutchinson (1983), Allan et al. (2021), Jones and Smol (2023), Hildrew and Giller (2023), as well as others on specific topics and taxa.

Chapters 3 to 14 are each set up to explore different stressors affecting freshwater ecosystems. The first half of each chapter provides background and a summary of the impacts of a particular class of stressors and how they can also interact with other stressors to compound problems. The second half of each chapter is designed to consider the range of solutions currently available to remedy the impacts of these stressors. Chapters 15 and 16 pull together key concepts that were previously discussed to focus on the restoration of freshwater ecosystems and the importance of monitoring these restoration projects. Importantly, these chapters all contain relevant case studies as well as student activities. While each chapter could very easily be expanded to be a book on its own, the materials are intended to fit a one-term course. Examples are all referenced so that a reader who is interested in further exploration of a topic has entry points to the current literature.

While much of this book deals with the practical application of science to mitigate impacts that degrade water and watersheds, it is important to understand that use of this science is governed by policy and law enacted by governments that have the legal authority to set rules, objectives, targets, and limits. Watershed management and policy differs globally, and that is a broad topic covered in political science, law, engineering, and other fields and not primarily the domain of scientists. In an ideal world, scientists working in freshwater ecosystems are actively sought after for their advice on how to align policy with practice and outcomes, from the local government level on up.

Today we need trained practitioners who have the understanding to protect and restore our freshwater ecosystems for both human and nonhuman use around the world. It is my sincere hope that this book will be a valuable resource to meet this end. The intended audience includes students in upper-level classes and graduate classes in biology, environmental sciences, and environmental engineering (as well as practitioners in these respective fields). Each chapter is intended to provide material for approximately two consecutive class periods. Although I have used case studies throughout, instructors may wish to augment the examples in the text with local cases to amplify certain topics. Instructors may also want to elaborate on specific examples included and use figures from the original articles for classroom instruction.

ABOUT THE AUTHOR

John S. Richardson, Ph.D., was born and raised in Toronto, Canada, and earned his first degree from the University of Toronto (B.Sc. 1979). From there, his academic career took him west as he earned degrees from the University of Alberta (M.Sc. 1983) and the University of British Columbia (Ph.D. 1989). Dr. Richardson spent three years at Simon Fraser University as a post-doctoral fellow before landing a faculty position at the University of British Columbia. He counts himself as very fortunate to have been at UBC all these years. Dr. Richardson has had many roles, including faculty member, Head of Department, member of the Peter Wall Institute for Advanced Studies, and a member of the editorial boards of several high-ranking journals. He has also been on many panels dealing with endangered species, riparian regulations, and other applications of his research.

Photo credit: UBC Brand and Marketing/Martin Dee

Richardson's research has focused on freshwater and riparian area ecology, primarily as a population, community, and ecosystem ecologist. Science can ask basic questions to provide for generalization, and at the same time use applied problems and systems as the specific context to give relevance to our studies. The application of science requires the best science available, as that is where we put our understanding to the test. He has successfully mentored many excellent graduate students and post-doctoral fellows who have been his great pleasure to work with. He adds that working in a global community of scholars with many outstanding colleagues has been a treat, and there is not space to name them all, but it will be obvious from his publication record that he has been fortunate to work with many outstanding people.

Beyond the academy, John enjoys travel. Many of his excursions have been to kayak or hike in other parts of the world. When not traveling, he enjoys cycling and running. Music has also been one of his hobbies throughout his life.

ACKNOWLEDGMENTS

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I am extremely grateful to Gwen Eyeington (J. Ross Publishing) for seeding the idea of making this book, her very thoughtful and thorough editorial work in making it become a reality, and for her guidance and patience throughout this process. Thank you, Gwen!

My parents, Kathleen and Ronald Richardson, were great supporters, and I am grateful for all their guidance. I have been fortunate to have excellent academic mentors who have taught me and supported me throughout my career, especially in my early years—most notably, Rosemary Mackay and Bill (W.E.) Neill.

This work is dedicated to my wife, Daphne Richardson.

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1

HYDROLOGY AND FRESHWATER BIOLOGY

There has always been a dance between water and living organisms, with life being ever dependent on water. Most of the earth's water is contained in our oceans, seas, and coastal marshes as saltwater. Of the freshwater on the planet, most is locked up in glaciers (about 68.7%) and groundwater (about 30.1%) and therefore not available for species living on the earth's surface. That leaves only about 1.2% of freshwater for lakes, streams, wetlands, and other freshwater ecosystems (source: United States Geological Survey). Lakes and streams cover an estimated 2.3% of the nonglaciated land surface of the world, and very much less of the planet's total surface, and yet support about 9% of the world's animal species (Balian et al. 2008; Allen and Pavelsky 2018; Reid et al. 2019). Freshwater species are more than twice as likely to be in decline as species in marine or terrestrial ecosystems (WWF 2022). These are important statistics that demonstrate that the relation between freshwater and life is delicately balanced. The way water moves through ecosystems falls under the science of hydrology, and the way plants, animals, and microorganisms use freshwater is addressed in the science of freshwater biology. It is important to briefly review key concepts of both disciplines before moving forward.

HYDROLOGY

Hydrology is the study of the movement of water—from evaporation through to precipitation, pathways of water flows, and runoff generation (see Figure 1.1). Hydrology is a science of its own, and there are full courses and degree programs devoted to this topic (one suggested text is Dingman 2015). Hydrology of any particular region is influenced by climate, geology, topography, and biology; and hydrology provides one of the primary controls on the kinds of freshwater ecosystems you could encounter.

One basic spatial unit for studying freshwater ecosystems is the watershed or catchment, which is the area that contributes water to a stream, lake, or wetland (also known as contributing area). Watershed is commonly used in North America, whereas the term *catchment* is more typical in Europe, where the word *watershed* usually means the point at which water is shed one direction or the other. Water moves from higher to lower elevations, due to the force of gravity. Water flows on the surface in the form of streams and rivers or below the surface in the form of groundwater. The difference in elevation that water could move through is also known as the gravity head or hydraulic head, and indicates a potential amount of energy per unit weight of water if it falls over that distance, which we will return to in Chapter 7 where we consider

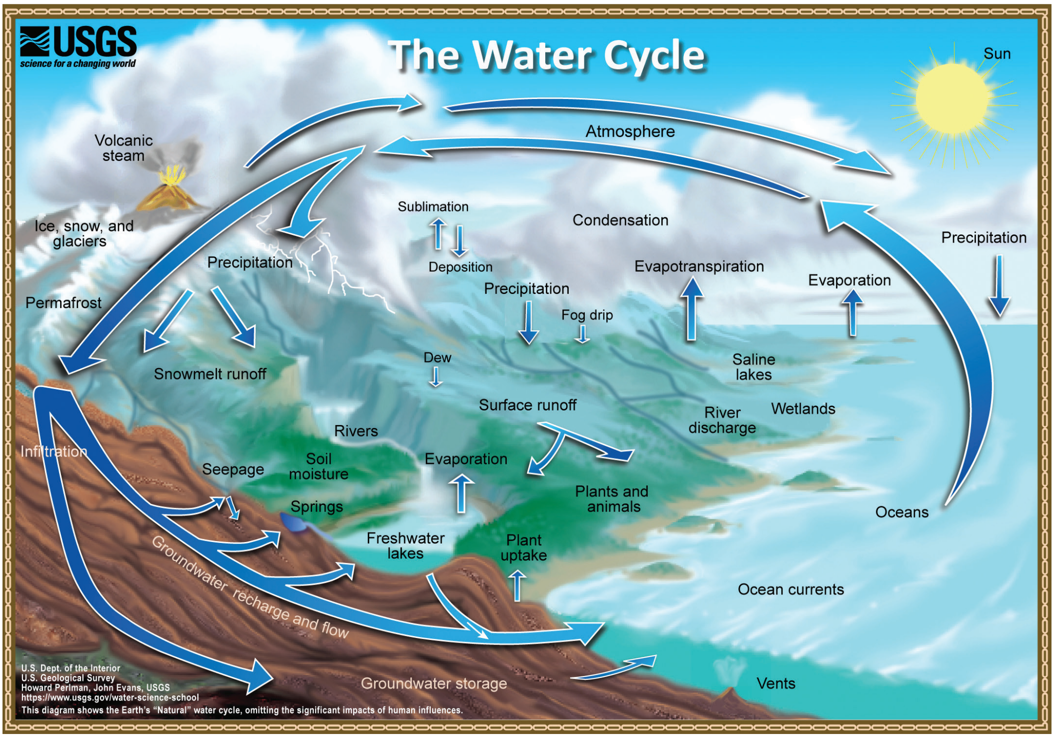

Figure 1.1 The water cycle. This shows the different pathways by which water moves around the planet and where it comes from, thereby creating the freshwater ecosystems that we study. *Source*: United States Geological Service; Howard Perlman and John Evans.

hydroelectric power production. The topography may be a good indicator of the direction that water movement might take, although in relatively flat regions with porous soils, groundwater may not follow the slope at the earth's surface. In some places, especially with little topography, the surface may not indicate the direction of water flow beneath the ground since water flow is also affected by the conductivity of the ground and how deep the soils are.

Water moves in other ways as well. It can be deposited from the atmosphere as precipitation in the form of rain, snow, or hail, and it can also condense as water droplets on various surfaces. In forests (especially cloud forests) and on other structures, condensation may be substantial (Berland et al. 2017), although this input may not be measurable directly as precipitation. These inputs from precipitation and condensation flow with gravity into the ground or overland. When water percolates below the earth's surface it is known as groundwater (deep or shallow) or the water table, and then it is referred to as the phreatic zone or the saturated zone. As water moves through the groundwater it re-emerges at lower points on the surface as run-off generation to springs, streams, lakes, and wetlands. Groundwater may percolate slowly, depending on the pore size of the materials it is working through, with it being slower through finer materials. Water stored in the ground may reside there (in *storage*) for time periods ranging from minutes to hours or days, and even sometimes up to many centuries. Hydrologists can age water to determine its residence time. In some cases, macropores develop in the soils as water erodes away particles or moves through earthworm burrows or spaces left by decaying roots to create preferential flow paths with lower resistance, which allows for faster movement of water through the ground (Sidle et al. 2000). In some cases, rock can be dissolved by slightly acidic water and particularly in limestone areas, underground streams can develop, and develop karst systems.

Water generally enters a stream from groundwater where the water table elevation is higher than the stream, and there may be preferential flow paths, as noted in the previous discussion about macropores. These can create focused areas of groundwater inflow, such as springs. As water reaches low points in the local environment, flow accumulates at the surface creating streams or filling areas such as lakes or wetlands. As streams flow downhill, they accumulate water from adjacent areas. Along a channel, there can be exchanges of surface flow with water underneath the channel in the gravel or sand bed, which is called *hyporheic* flow. The area beneath the stream bed is the hyporheic area where specific organisms are primarily found since the area can be used as a refuge from flooding. There is also parafluvial flow, a type of hyporheic exchange which is flow that is moving through gravel bars and sand bars at the edges or bends of a stream.

Water accumulates at the surface in streams, lakes, and wetlands and moves downhill toward the sea. Along the way, a large component of the net loss of water is through evaporation and transpiration (water that is taken up by plants and released through their leaves). Some estimates suggest that 55 to 67% of water is lost back into the atmosphere through transpiration by plants in temperate and boreal forests (Schlesinger and Jasechko 2014). Typically, as streams flow, they gain water. However, there can be *losing* stretches of a stream where the water table may be lower in elevation than the stream (due to extraction or change in geology) and where water leaves a stream and enters the groundwater, thereby reducing the stream's volume. A common example of this is where streams leave an area that is rocky and enter an area where soils are more permeable, such as desert areas where the water table may be much deeper and more permeable than the source areas.

There are many tools and methods specific to the study of hydrology. Two important measures are the inputs (precipitation, condensation) and outputs of water to a watershed or catchment. Inputs are often measured as rainfall using a gauge. However, precipitation can accumulate as snow. There are ways to figure out the snowpack water equivalent (depth of water resulting from melting the snow) based on the mass of water in the snow, which can be measured from a snow core or the mass of snow on top of pressure sensors on the ground beneath the snow (*pillows*). We also mentioned that inputs through condensation (usually included within the precipitation term) require special measurement methods.

Outputs from a known area via flow in a stream channel is usually measured as discharge (often L/s or m^3/s) past some point. These estimates need to be calibrated from the depth of water impounded upstream of a weir (the *pond*) (see Figure 1.2) or from the depth of the water at a known cross section to calculate discharge. Weirs are typically found in smaller streams, and often in a research context. Both measures are usually based on a pressure transducer, which records the height of the water surface above the sensor. In some instances, particularly larger rivers (throughout this book we will mostly use the term *stream* for all moving waters), the water level known as *stage height* is measured against a kind of ruler that stands at the stream's edge. Whether with a stage gauge or pressure transducer, the measurement is just of water depth, which needs to be converted into discharge.

There are a few methods that can be used to create a calibration that will convert depth measures into discharge, also called a rating curve. One of those methods is an estimate of

Figure 1.2 A V-notch weir used to measure the height of the water surface; in this case, from a very small watershed. Water slows in the pond that was dammed just upstream of the weir, and the height of the water can be recorded on a pressure transducer, which measures the elevation of the water surface above it. Higher flows result in deeper water in the pond. The actual discharge in L/s still needs to be calibrated through a rating curve that relates the height of water to the flow, and this can be done by using a couple of methods, based on depth and current velocity profiles, or salt-dilution gauging. The calibration depends on getting a regression of discharge against the pressure reading. In very simple systems, there may be a staff gauge, which is often a big ruler that someone must read directly for water depth, but still needs calibration.

velocities and depths across a stream. In this case, a cross section of a stream is broken into vertical segments of a given width, and for each segment, the width and depth (area) and velocity can be multiplied to get the rate of flow for that vertical segment. One can then integrate all the verticals across the channel to get an estimate of instantaneous discharge. The selection of a point in the stream to measure is often associated with a natural narrowing of the stream width. Another method to calibrate the discharge is timing how long it takes to fill a bucket of known volume, which only works on very small streams. Yet another method is salt dilution gauging, where a known quantity of salt (either dry or dissolved in a brine) is injected at a point along the stream, and the salt concentration (usually measured as change in electrical conductivity) is recorded at a specific point that is a sufficient distance downstream where the salt has been fully mixed across the channel (BC Government 2018). Discharge is computed by the degree of dilution of the injected salt (lower concentration indicates higher dilution and thus, higher discharge). Stage height or pressure can be measured periodically by a direct reading of gauges, but are more commonly measured continuously given the widespread availability of data loggers. Discharge is a measure of total rate of water passing a point based on the rating curve developed from stage gauges. However, it may be useful to estimate the volume per second per unit area, the latter known as unit discharge, which accounts for the watershed area. Continuous records of flows can provide a very detailed understanding of discharge.

One tool used in hydrology to understand land-use effects is known as the paired-catchment approach; we will explore the results from such studies in later chapters. In this case, two (or more) catchments (hence paired) are matched for similarities in area, climate, vegetation cover, elevation, etc., and are measured for discharge for some period of time before a landscape-scale manipulation, such as forest harvesting or another land disturbance. By establishing the relationship of one watershed against the other (regression analysis) before the disturbance, we end up with a prediction of what the discharge would be from the watershed in the absence of a disturbance (see Chapter 8, Box 8.1). These studies usually involve alteration of one of the study watersheds through forest harvesting, pesticide application, agricultural expansion, or some other kind of land use (Moore et al. 2005). Such studies have been instrumental in advancing our understanding of how land-use practices affect the quantity and timing of flows, and often additional measures are taken, such as water quality (including temperature).

In summation, the movement of water in the study of hydrology is illustrated by the water balance equation. This equation is based on conservation of mass and has inputs and outputs (see Figure 1.1). The equation is usually shown as $P = Q + ET + \Delta S$, where P = precipitation, Q = discharge (streamflow), ET = evapotranspiration, and ΔS is the change in storage (such as in groundwater and aquifers). Water input to watersheds comes from the atmosphere (precipitation) in the form of rain or snow, and it can also condense as water droplets on various surfaces. In forests (especially cloud forests) and on other structures, condensation may be substantial (Berland et al. 2017); however, this input may not be measurable as precipitation and typically requires specialized sampling equipment and not simply a rain gauge.

IMPORTANT PARAMETERS OF WATER QUALITY

Water Temperature—The “Master Variable”

Temperature is an important physical property of water; it determines chemical reactions, water movements, and biological responses. Water is an unusual substance in several ways, but one that is tremendously important is that water *as a liquid* reaches its most dense state at ~4°C, and then gets lighter (less dense) again toward freezing. This means water that is about to freeze is at the surface, and hence, ice forms primarily from the top of lakes, wetlands, and streams, so that liquid water remains below and allows life to avoid being frozen. If this were not true, ice would form from the bottom and eventually an entire lake or wetland would be solid, leaving little to no refuge for life from freezing. This is not an issue in many parts of the world, but in north and south temperate regions, and at certain elevations, it is critical to how freshwater ecosystems change seasonally. In Chapter 2, we will explore more about how these patterns of water temperatures affect habitats.

The physics of thermal regimes is similar for all surface waters. However, the relative importance of each process for gaining and losing heat energy varies. These processes include gains and losses of short- and long-wave radiation, groundwater inputs, latent and sensible heat exchanges, and advection of water from upstream (see Figure 1.3). The relative rates of these processes differ with stream (or lake) size, climate, and other factors, but the physical processes involved are universal. A good introduction to stream temperature processes is Leach et al. (2023).

Flowing water does not easily crystalize to ice, and so under such conditions water can supercool to below 0°C. This supercooled water can crystalize around objects in the water, such as rocks on the bottom as the friction at the surface of an object slows water down sufficiently to crystalize, creating what is sometimes referred to as anchor ice. As ice accumulates on objects below the surface, it can create layers of ice that can break free from below the surface, float to the top of the water as small patches of ice, potentially contributing to *pancake ice*. Water can also freeze rapidly at the water's surface as air temperatures fall far below freezing—usually known as *frazil ice*—which can block flows and cause local flooding or block intake pipes.

In some parts of the world, lakes can stratify. For example, the surface water may be warmer and hence, less dense than deeper water, at least in summer, which many people will have experienced from swimming in lakes. As water heats from the surface by inputs of solar radiation, the ability of that warm water to mix throughout a lake is limited by either conduction (a slow transfer mechanism) or convection if there is enough wind at the surface. However, as the difference in temperatures diverges between surface and deeper waters, the difference in

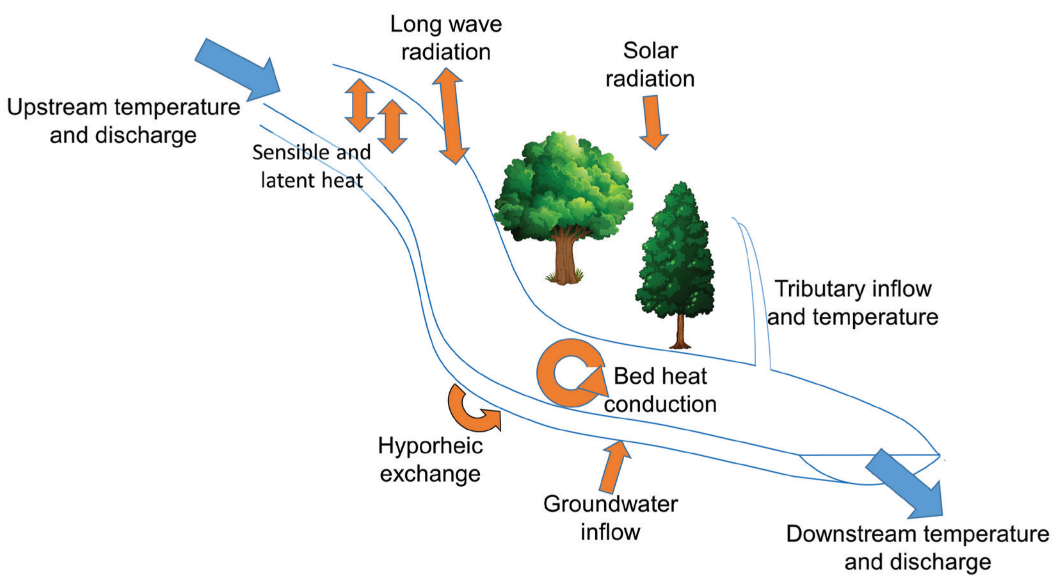

Figure 1.3 A schematic of the main thermal exchanges (inputs and outputs) with surface waters; redrawn after Moore et al. (2005). Blue arrows indicate direction of flow, and therefore inputs and outputs of water of a given temperature, which will be modified by the volume of water. In the case of a stream, the rate of heating is inversely related to discharge (more water takes more energy to heat). Orange arrows are the heat exchanges showing directions of gains or losses of thermal energy to the water.

density of the water along that gradient begins to require more and more wind energy to mix, which may not be present. Eventually, only the warmer surface water can be mixed (relatively similar density), leading to layering or stratification of a lake with a warm surface layer (epilimnion) and a cooler bottom layer (hypolimnion). Once stratified, a lake can resist deeper mixing unless there is an enormous storm that stirs the lake to depth, or more commonly, when the surface waters lose their heat energy as weather cools in the autumn. This process—called *turnover*—is when lake water mixes and thereby averages out temperatures, nutrients, and oxygen concentrations. In winter there can be a reversed stratification; that is, as the surface water loses its heat from the top and water cools to around 4°C, the 4°C water (most dense) will be on the bottom while the surface continues to lose its heat energy and form a colder surface layer. When turnover occurs twice a year, the lake is considered dimictic. However, some lakes never stratify and some stratify once per year (monomictic) if there is insufficient temperature difference between the surface and deeper water or if there is enough wind energy to mix the water to the bottom. Some lakes are permanently stratified (meromictic), which is often a consequence of a chemical gradient in density (such as salty water forming the bottom layer) causing stratification (Overmann et al. 1991).

Temperature is sometimes referred to as a controlling variable or even the *master variable* because of its large role in metabolic rates of organisms. Given that most species living in water are poikilothermic (or ectothermic), their body temperatures are determined by their environmental surroundings. Generally, biological activity is very low (or nearly zero) when the temperature is zero, although some organisms can tolerate and function with temperatures *at or below zero* by having high concentrations of solutes in their bodies, which reduces the point at which water freezes. Biological activity increases with increasing temperatures, although the slope of this relationship differs by organism and activity measured. However, biological responses do not continue increasing without bounds as temperatures increase, and at some point (optimal growth temperature), growth rates reach a maximum (see Figure 1.4). Beyond that maximum temperature, growth rates generally decrease as organisms' physiology (such as cardiac scope or energy intake) cannot cope with higher temperatures; eventually, temperatures may reach a point at which they are lethal.

There are many aspects of biology that modify the particular shape of the temperature-response curves. The specific shape and endpoints of these curves obviously differ by species, and by the particular measure (for instance, growth, activity, or metabolism) being plotted. Moreover, the details of these curves can differ between populations of a species because there is local genetic adaptation of populations, as seen in sockeye salmon (*Oncorhynchus nerka*) for example (Eliason et al. 2011). The shapes may also vary depending on the density of a population, the particular activities they are engaged in, and how much food they are getting. Often more stress (such as higher densities, less food, lots of predators) reduces the scope for activity and the threshold for peak activity.

The viscosity and density of water get lower as temperature rises—water becomes only 64% as viscous as temperature increases from 4 to 20°C. For organisms of a larger size, such as a fish, the water's viscosity relative to their mass is reduced only slightly. However, for a very small organism, such as an algal cell or a copepod (a small crustacean), the water is like molasses. The reason for this is that a small organism has very low mass and therefore little momentum, so that with each movement of something like a copepod, it stops after each stroke of its antennae, which act like paddles. Thus, temperature-dependent changes in viscosity can have a large effect in a small organism's ability to escape predators or chase their own prey. Reynold's number

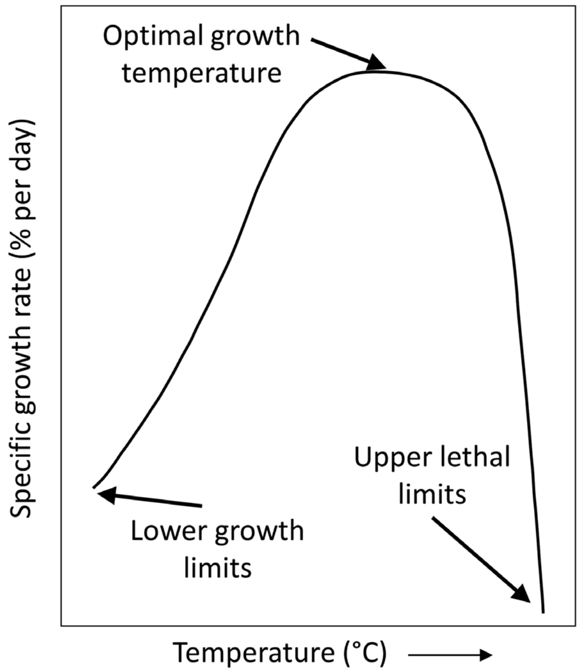

Figure 1.4 An idealized temperature-growth curve (or temperature-activity curve) for poikilothermic organisms.

and other means for scaling these mass-momentum relationships are helpful when trying to understand the way organisms use their aquatic environment and how much control they have over their movements relative to directional and turbulent flow of water. We will not address this topic further here, but for reference, an excellent source is Vogel (1996).

The Force of Flow

Flows of water exert forces, which can move materials in its way, reshaping the morphology of the environment, known as geomorphology (Church 2015). This erosive power of water is referred to as tractive force or shear stress for which there is a specific equation. In general, tractive force, *tau*, is denoted by its Greek letter, τ, for flowing waters. Without specifying the precise equation, there is an approximation that will simplify that relation:

$$\tau \propto average\ surface\ slope, water\ depth$$

Force from moving water can be found in stream flows, wave action, or even ice flows (as ice breaks up in spring). The majority of the force is exerted during high flows, such as floods, and the higher the discharge, the more work that can be done in rearranging morphology. The resulting geomorphology depends on the sizes of materials available to move and their specific gravity (Church 2002). For instance, small particles (sand, gravel) will move at lower tractive forces than large particles (cobbles, boulders). Lighter particles, such as wood and leaves, will move more easily than mineral particles. Movements of materials typically result in wave formations, such as dunes, which with bigger materials, look like riffle-pool sequences in streams. These will be described further in Chapter 2.

Oxygen Content

Oxygen concentrations in freshwater are on average about 0.0045% of that in the air. Solubility of oxygen is a function of temperature, and saturation concentrations decline as water warms. Consequently, while biological activity increases with higher temperature, available oxygen concentrations decline from about 14.6 mg/L (or ppm) at 0°C to ~8.2 mg/L at 25°C (at standard pressure). Oxygen enters through the air-water interface by diffusion or mixing by aeration by wave action or turbulent flows, and then moves through the water by diffusion and mixing. In most surface waters there is mixing of water that moves oxygen and other solutes through much of the water (however, see Chapter 2 on lake stratification). Oxygen is also produced through photosynthesis during daylight by algae or vascular plants, but then, during the dark, all organisms use up oxygen, so there can be pronounced day-night cycles in oxygen concentrations.

Oxygen in freshwater systems can be consumed through biological and chemical processes. Biological oxygen demand (BOD) is the amount of oxygen required by all organisms, including microorganisms that break down and decompose organic materials on lake or wetland bottoms. Chemical oxygen demand (COD) is the amount of oxygen used by nonbiological processes, including oxidation of breakdown products. As the amount of BOD and COD in a system increases, it can result in less oxygen available in the water if demand exceeds the renewal rate of oxygen. These low oxygen concentrations are a challenge to most organisms in water (in extreme cases, managers may resort to artificial aeration). One problem for life occurs when lakes or wetlands are covered in ice. With little or no diffusion of oxygen from above the ice, the remaining oxygen is used by active BOD organisms, including decomposers breaking down organic matter, and COD; thereby, oxygen can be depleted (anoxia). This depletion can result in *winter kill* where extremely low concentrations of oxygen are insufficient to support many species, and large numbers of individuals die, which is most often observed as dead fish. Similarly, anoxic conditions can occur when nighttime respiration rates (and no oxygen renewal from primary production) in productive waters can use up most of the oxygen. This can be common at outfalls of wastewater treatment plants (treated domestic or industrial water) or industrial sources of organic materials.

Oxygen can limit the activity rates of an individual, and concentrations might even be insufficient for an organism to survive in some environments. A large fraction of animals living in freshwater have gills, an expansion of surface area over which oxygen exchange (and other osmoregulatory exchanges) can take place. Most people are familiar with gills in fish, but gills are found in many animals. Some species rise to the water's surface to refresh air carried in specialized chambers, plastrons, and other mechanisms. Some species ventilate their bodies to create a flow of water to enhance oxygen availability, such as cased caddisfly larvae (Trichoptera).

Some groups of bacteria and archaea can function without oxygen using an alternate electron donor in respiration, and are responsible for anaerobic metabolism, which can generate methane and participate in denitrification. These anaerobic processes can occur in the organic sediments of wetlands and lakes, in large accumulations of organic matter in other freshwaters, and even in groundwater and hyporheic areas. Anaerobic processes often affect the forms of different chemical compounds, that is, going from oxidizing to reducing conditions.

Nutrients

All organisms require an external source of energy to survive. Primary producers primarily depend on solar energy. Other organisms require some form of fixed energy, either from the consumption of living primary producers, dead plant tissues such as leaves, or prey. Beyond energy, it is also critical to get nutrients from the environment or their food, primarily nitrogen (N), phosphorus (P), and potassium (K). Nitrogen is one of the building blocks for protein and enzymes. Phosphorus is part of DNA, adenosine triphosphate (ATP), bone, teeth, cell membranes, and serves other biological roles. Potassium is needed for nerve cell transmission, electrolyte balance, stomatal control in vascular plants, etc. These three nutrients are often considered to be the most limiting of elements for freshwater organisms, but are not the only substances required by life.

In addition to the previously mentioned nutrients, there are elements that are needed in small amounts. Calcium is needed for bones, nerve signaling, exoskeletons, etc. As humans, we are familiar with our need for iron (Fe) in hemoglobin, such that shortage results in anemia, but excessive amounts are toxic. Iron is similarly needed by all other vertebrates for hemoglobin, which is the mechanism for transporting oxygen to cells within the body. Iron is also needed in trace amounts for other functions in most other organisms. Copper is the basis of the molecule haemocyanin, which is used as an oxygen carrier in some freshwater invertebrates, just as the iron-based hemoglobin is used in vertebrates. Diatoms are a group of photosynthetic protists that require silica from the environment to construct frustules around themselves as protection (like shells) and are characteristic for taxonomic identification (see Behrenfeld et al. [2021] for an alternative hypothesis for the evolution of frustules). Organisms need other elements in addition to the aforementioned nutrients (for example, iodine and boron are needed by most organisms), and although other elements may be needed in only trace amounts, they are still essential.

Consideration of how ratios of different elements may be required for an individual organism to function, can be determined through a pillar of chemistry known as *stoichiometry* (Sterner and Elser 2002). One such stoichiometric ratio is known as the Redfield ratio, which states that on average, the molar (atom for atom) ratio of N:P in organisms is about 16 (there is a lot of variation between species). This can also be used as a quick check as to which nutrient is most in short supply in water; such as, if the ratio is >16, then P is probably limiting, and if it is <16, then N is probably limiting. This is not so exact that one can use this without additional information, but it is a good starting point. In general, organisms do not need *extra* nutrients, and so are most often limited by whatever nutrient or trace element is in the shortest supply—sometimes called Liebig's law of the minimum. However, organisms may be able to make trade-offs to maintain function. Phosphorus can often be in short supply in freshwaters, and if an organism cannot get all the P it requires, it may be able to compensate slightly by investing lower concentrations in some organs and even some proteins, although this ability is usually quite limited (Sterner and Elser 2002). Some species can also store nutrients, for example diatoms have a large vacuole to store materials, in what is sometimes called *luxury* uptake.

Nutrient status of a body of water can also affect the size spectrum of the species there. For instance, in very oligotrophic (nutrient poor) waters, it gives an advantage to small-bodied algae with a larger surface-to-volume ratio, and may favor picoplankton and nanoplankton (*pico* and *nano* being an indication of body sizes), whereas more nutrient-rich waters would likely not provide such a size advantage and one might expect larger-bodied primary producers (Stockner and Shortreed 1989).

In one study, Stockner and Shortreed (1989) showed that nutrient status could affect the numbers of trophic levels, and they compared some oligotrophic lakes to some lakes with higher nutrient concentrations. In their oligotrophic lakes, there were more steps required to go from the tiny primary producers to slightly larger species like protozoa, then crustaceans, then bigger species large enough to be consumed by young sockeye salmon. Remember that picoplankton are one million times smaller than the microplankton at the base of the food web in more nutrient-rich lakes. At each trophic level in a food web, energy is lost because the consumer uses a lot of energy for respiration, and thus the transfer of energy through each step may be only 10 to 50% of the energy entering each trophic level. In the oligotrophic lakes there was less primary production to begin with because of the limits to nutrients, and more trophic steps to reach the size of prey eaten by young sockeye salmon, and therefore there was less energy overall for the sockeye, meaning fewer and smaller salmon. Later on in this chapter, we will explore the roles of nutrient status and the numbers of trophic levels on ecosystem productivity.

Acidity

One measure of water acidity is pH. Rain is naturally at a pH slightly below neutral (pH of 7) due to carbonic acid in precipitation. There are a range of ion exchanges that occur in soils and in water that affect pH. The underlying geology of a catchment is one factor that can strongly affect pH. A lot of base cations, such as Ca^{2+}, can result in a basic or alkaline pH (greater than 7), whereas a lack of such ions and a high concentration of H^+ results in more acidic water pH (less than 7). The level of pH matters as organisms have to maintain ion exchanges to maintain their internal pH, often using calcium to buffer acids, which can deplete calcium from bones and exoskeletons. Other vital functions can also be affected if pH is strongly acidic. Experimental lake acidification demonstrated the range of impacts that acidity in water can have (Schindler et al. 1985) (see Chapter 4, Box 4.1). The pH of water also affects the ways ions behave, which in turn affects nutrient and other solute availability. In the 1970s, the northern hemisphere experienced decades of acid rain, caused by pollutants such as sulfur (as sulfuric acid) and nitrogen (nitric acid) transported into the atmosphere from industrial and agricultural sources, which we will learn more about in Chapter 4.

There are a number of other measures related to acidity, such as alkalinity, buffering capacity, and conductivity. Alkalinity is a measure of the capacity of water to buffer against changes in pH, and thus is equivalent to buffering capacity. Conductivity is a measure of the capacity of water to conduct an electrical charge (measured as μS/cm or mS/cm), and very solute-poor water may have conductivities of 10 μS/cm, while freshwaters in catchments with a lot of sedimentary rock may have conductivities in the 1000s of μS/cm.

Turbidity

Turbidity is one way to measure the concentrations of fine, suspended sediments, and is an important measure used to describe and monitor water quality. Turbidity is an estimate of the ability of particles to block light and is generally proportional to the concentrations of suspended particles. It is measured in a standardized way as NTUs (nephelometric turbidity units). However, turbidity measures are affected by the types of particles—whether they are organic or inorganic—their sizes, and even the *color* of the water created by the colored dissolved organic matter (similar in color to iced tea or coffee). Comparable measures include total suspended solids (TSS), which is generally reported as the dry mass of suspended particles per L. We will discuss turbidity further in Chapter 3.

Light

Light is essential for photosynthetic organisms, provides for visually oriented organisms, and also brings long-wave and short-wave radiation that heats water. The amount and quality of light reaching a water surface depends on latitude, solar angle (varies across days and seasons), the elevation of the water surface, any kind of cover such as forest canopies, cloud cover and vapor in the atmosphere, as well as any other particulates in the air, like smoke from forest fires. There are models available that can provide the predicted amount of incoming radiation for a given latitude and day of the year. Different wavelengths of light are attenuated with water depth, with red and infrared being absorbed faster than other wavelengths. The rate of attenuation and how it affects each wavelength is affected by whatever is in the water, such as color and suspended particles. Turbidity, as discussed before, affects transmission of light and absorbance of particular wavelengths.

Because light is critical to photosynthesis, we often speak of photosynthetically active radiation (PAR), which is the range of wavelengths corresponding to the main photosystems—generally 300 to 700 nm and depending on photopigments involved such as chlorophyll a, chlorophyll b, carotenoids, xanthophylls, and so forth. In limnology, there is a concept of *compensation depth*, which is the depth at which only 1% of incoming light remains, and it is sometimes considered the maximum depth from which rooted plants can grow. As discussed previously, the attenuation of light depends on a number of properties of water, so in reality, this depth is not quite so absolute, but rather, is a useful generalization.

Altitude and latitude can also affect the quality of light since some wavelengths are attenuated depending on the thickness of the atmosphere that light passes through or the solar angle. As a component of sunlight, ultraviolet radiation—especially ultraviolet B radiation (UVB)—intensity varies, with higher fluxes closer to the equator and at higher elevations. UVB can be harmful to life as it can cause genetic damage. Some organisms are more tolerant of UVB than others, but for some it can be fatal; for instance, it can cause deformities in amphibian and fish larvae (Blaustein et al. 1997; Alves and Agustí 2020). Dissolved organic matter (DOM) in water can also act as a bit of a sunblock from UVB, especially colored DOM (tea or coffee colored that is produced from leaching of soluble molecules from organic matter) as it absorbs energy from UVB, which lyses the molecules. However, as in most things the quantity matters, as UVB is also essential in small amounts to many vertebrates to produce vitamin D, which is essential in calcium uptake.

BIOLOGY OF FRESHWATER ORGANISMS

Freshwater is scarce and only makes up about 3% of all water on the planet (most is seawater), and only about 1.2% of that freshwater is actually available to support humans and freshwater ecosystems. However, estimates of the numbers of species globally suggests that even though freshwaters cover less than 1% of the earth's surface (or about 2.3% of the nonglaciated land), about 10% of species are exclusive to freshwaters—making freshwaters a key ecosystem in terms of biodiversity (Dudgeon 2020). It is not possible to cover all of freshwater biology here, so I provide suggestions for sources of information in the following paragraphs, but I also advise taking a course in the biology of freshwaters.

In freshwaters there are hundreds of thousands of species, and that count does not include most micro-organisms. Organisms come from all kingdoms of life, although some groups are better characterized than others. There are viruses, archaea, bacteria, cyanobacteria, algae of many kinds, vascular plants and mosses, protists, invertebrates (at least 12 phyla), and fish, along with other vertebrates. It has been estimated that there are at least 126,000 species of freshwater animals and 2,600 species of macrophytes (Balian et al. 2008). One estimate is that there are at least 13,000 species of freshwater fish (Lévêque et al. 2007). Groups such as protists, bacteria, and archaea lack good estimates of numbers of species. However, the tree of life is not as simple as once characterized in kingdoms such as animals, plants, fungi, bacteria, etc. For an example of relations between organisms see Wikipedia's entry for *tree of life* (*biology*). Evidence from many kinds of genetic analyses have shuffled what was known and indicates that organisms we once may have called protists are not monophyletic, and may be in completely separate clades of eukaryotes (organisms with a nuclear membrane). Keep in mind that there are many versions of the tree of life, with different names used for some major groupings. One conception of a modern tree of life for eukaryotes (see Figure 1.5) shows that even groups that we typically call algae are more distant from each other than animals are from fungi (after Keeling 2004). An examination of the bigger tree of life will reveal that eukaryotes are a relatively small component of total biological diversity.

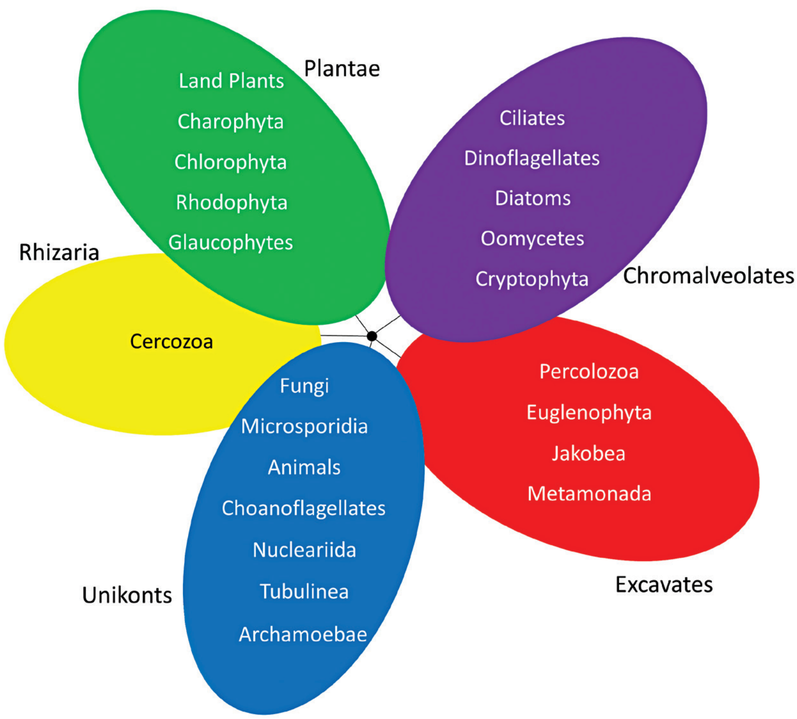

Figure 1.5 One modern conception of the relationships of major taxonomic groupings of eukaryotes based on genetic sequencing (following Keeling 2004).

There are many books on the biology of freshwater organisms (Dodds and Whiles 2019), and some of those include keys and general biology. Some of the best taxonomic keys, which also have great background information include Merritt et al. (2019) for North American freshwater insects, Tachet et al. (2010) for European freshwater invertebrates, and for freshwater invertebrates (other than insects) in North America there is Thorp and Rogers (2014) and Thorp et al. (2016). For algae, Wehr et al. (2015) is a good guide. There are an enormous number of guides for fish identification and biology in different parts of the world. In the following table, I provide a quick review of the kinds of organisms found in freshwaters of the world. For the purposes of this book, we will use an old system that may not reflect the true evolutionary relations among groups as previously noted. We will consider these as viruses, bacteria, protists, fungi, plants, and animals (see Table 1.1).

Table 1.1 List of the six taxonomic groupings (kingdoms) used in this book.

Kingdom	Characteristics	Nuclear Membrane
Virus	Only able to reproduce within a living host using host's gene replication machinery; generally considered parasites, but may be more influential in evolution of life than previously thought	None; a segment of RNA surrounded by a protein coat
Bacteria (including Cyanobacteria) and Archaea	Single celled; includes a range of decomposers, pathogens, and even photosynthetic form	Procaryote (no membrane around DNA genetic material)
Protists	Large polyphyletic group; some predatory and some photosynthetic	Eucaryote (genetic material [DNA] contained within a membrane, separated from the rest of the cell)
Fungi	Mostly decomposers and pathogens; a few taxa are considered mutualists	Eucaryote
Plants and algae	Typically photosynthetic, but some are non-photosynthetic parasites of other plants; single-cells, colonial, or multicellular. Now thought of as a polyphyletic group	Eucaryote
Animals	Multicellular; heterotrophic	Eucaryote

Micro-Organisms

We often lump viruses, archaea, bacteria, and fungi together as small organisms or *microbes*—mostly due to their size. Viruses are ubiquitous and yet there are relatively few studies of them in freshwaters. Bacteria are important decomposers of organic matter, and can also include pathogenic species. One group of bacteria, the cyanobacteria, are often called blue-green algae even though they are actually photosynthetic prokaryotes.

Freshwater fungi are generally referred to as aquatic hyphomycetes, but in fact, this grouping includes representatives of many taxonomic groups of fungi (Bärlocher 2012). Fungi, along with bacteria, are major decomposers of organic matter, while some species are pathogens of particular host species. One group of aquatic fungi that have become well-known is the chytrid fungi (*Batrachochytrium dendrobatidis*, *B. salamandrivorans*) that have afflicted many amphibian species around the world. They grow in the skin of amphibians, causing chytridiomycosis, which sometimes leads to death.

Algae and Plants

What we call algae includes several diverse groups of photosynthetic eukaryote organisms that may be distinct at the kingdom or phylum level (see Figure 1.5). For instance, as mentioned before, the so-called blue-green algae are, in fact, photosynthetic bacteria. Most other *algae* are predominantly single-celled, photosynthetic organisms, although some can be colonial or chained, thereby creating something beyond single cells. In one modern classification, many algae are single-celled species of the kingdom Plantae, including green algae (Chlorophyta) and red algae (Rhodophyta). However, diatoms (Bacillariophyceae) are in a separate kingdom in this classification. While most algae are single-celled, some are in chains (such as *Cladophora*) and some even form erect structures as in the stoneworts (Charophyta: *Chara* spp.). For more on algal biology see Stevenson et al. (1996) or Wehr et al. (2015).

Multicellular plants or vascular plants (sometimes called macrophytes or hydrophytes) are grouped in various ways, and make up about 1 to 2% of all angiosperms (Chambers et al. 2008). One way of grouping them is in terms of whether they are rooted or not, and also whether they are floating, emergent, or submerged. Duckweeds (Lemnaceae) are floating plants. Most freshwater plants are rooted in lake, wetland, or stream bottoms and have flowers that reach the water surface, as their flowers need to be pollinated (for instance, pondweeds, milfoil, lily pads). The depth to which plants can root is determined by the amount of light reaching the bottom, and the *photic zone*, defined on average as where light is only 1% of incident light at the water surface. However, there are some plants that can tolerate less light and some need more. The actual depth of the 1% limit varies depending on the various factors that limit light penetration such as turbidity and colored dissolved organic carbon (DOC). Many plants are found around the edges of freshwaters, including cattails (*Typha* spp.) and sedges (*Carex* spp.), which are not fully aquatic, since they cannot survive being permanently submerged.

Animals

Invertebrates are represented by at least 12 phyla in freshwaters, although a few phyla have only a small number of species (for example Cnidaria—*Hydra*; Porifera—sponges) whereas phyla such as the Arthropoda (insects, crustaceans) are represented by tens of thousands of species. Other phyla include the Annelida (worms), Mollusca (snails, clams, limpets), Bryozoa (moss animals), Nematoda (roundworms), Gastrotricha (hairy bellies), Rotifera (wheel animals), Platyhelminthes (flatworms), Nematomorpha (horsehair worms), and Tardigrada (water bears).

Freshwater fishes may number more than 13,000 species. Most of these species are in the tropics, and the carp order (Cypriniformes) is considered to have the most species at ~4,250 species, followed by the catfishes (Siluriformes) with an estimated 3,000 species globally. Fishes can be found in almost all freshwaters. They are limited primarily by access, such as waterfalls and other impassible barriers and water permanence. Fish are rare in temporary waters, but even then, there are some that can make do, such as lungfish, snakeheads, and others that can breathe air and are able to move themselves across terrestrial landscapes.

Among the vertebrates associated with freshwaters, some groups breathe air for oxygen (birds, mammals, reptiles), while fish and many amphibians depend on gas exchange across their gills or skin for oxygen. Of course, there are some fish that are capable of breathing air and certain amphibians may use different methods depending on their developmental stage (larvae versus adults). Some of these are almost exclusively aquatic, such as river dolphins and crocodilians (alligators, crocodiles, caiman, gharial). Mammals such as beavers, muskrats, coypu, platypus, and otters spend most of their time in water. Some other species such as Desmans of Eurasia (*Galemys pyrenaicus* and *Desmana moshata*) or water shrews (*Sorex* spp.) forage exclusively in the water, but mostly live on shorelines. The same association exists for many birds that feed on fish or other aquatic organisms, nest near water, or use water as escape habitats. There are many organisms that are associated with water and interact with freshwater food webs, whether we would say they are an aquatic species or not. We would say many of these species are riparian dependent; that is, they must be near water for parts of their life cycle. This includes organisms of all sorts (Richardson et al. 2005; Ramey and Richardson 2017).

Beyond taxonomy, we can consider organisms in other ways that are more easily comparable across geography and ecosystems, including total biomass, biomass size structure, feeding groups (trophic levels), and other groupings. This is referred to as trait analysis (Statzner and Bêche 2010; Verberk et al. 2013). For instance, we would expect that two streams in different parts of the world that look the same (same gravel-cobble bottom and same size) would probably have similar types of organisms (feeding groups, trait groups), even if the actual species are different.

Food Resources

We often refer to the food resources at the base of any food web as basal resources. Two primary categories are primary producers and detrital materials (dead organic matter, such as leaf litter or wood). Primary producers, including a diverse set of photosynthetic organisms such as algae, protists, cyanobacteria, mosses, and vascular plants, use the energy of sunlight to fix CO_2 into complex carbohydrates and take up nutrients to form proteins and other internal chemistry. Primary producers are also known as *autotrophs*. There are also *chemoautotrophs*, which are widespread globally, but not common. For instance, iron bacteria oxidize ferrous iron (Hildrew and Townsend 1976) and purple-sulfur bacteria use hydrogen sulfide under reducing conditions (Overmann et al. 1991). Because primary producers are within the aquatic realm, we refer to that as *autochthonous* production, that is, from within. Detrital materials are the remnants of primary production outside of the system (terrestrial) and therefore called *allochthonous* materials. Sometimes these two categories are referred to as the green part of the food web (primary production) and the brown part (detritus).

Most of the organic materials that enter freshwater from the terrestrial realm are referred to as detritus, as they are often the dead, senescent tissues of plants. Detrital materials can include leaf litter, seeds, flowers, branches, and whole trees (wood), etc. These are generally referred to by particle size: coarse particulate organic matter (CPOM, >1 mm diameter), fine particulate organic matter (FPOM, <1 mm, >0.63 μm), and dissolved organic matter (DOM, <0.63 μm). Most DOM is not technically dissolved, but is operationally defined as particles that pass through a glass fiber filter paper, nominally with pore size ~0.63 μm. DOM is also essentially the same as DOC, except one is based on the entire molecule (DOM) and the other is solely the mass of carbon (DOC).

Detrital processing is one term given to the decomposition of organic matter. Much of the organic matter from plants is cellulose based, and animals do not independently have the ability to digest cellulose. Therefore, it is up to fungi and bacteria to digest organic matter—the actual process of decomposition—making it more available for animals by converting it into consumable microbial biomass and by partially digesting plant matter. The surfaces of decomposing leaves, wood, and animal matter are covered by a biofilm of these fungal and bacterial decomposers, and it is often this biofilm that constitutes the food of many detritus consumers. Some animals that eat plants or plant detritus have symbiotic microbes that help with the digestion of cellulose; such microbes are found in other kinds of herbivorous animals, for example, termites and ruminants. Detritus-consuming animals include many kinds of invertebrates, as well as amphibian larvae and some fish species.

Fungi as a decomposer needs detrital particles large enough for them to develop their mycelia (*roots*) on, and hence, the division between particles greater than one mm in area and those particles that are even less. CPOM can support fungi and bacteria, whereas smaller particles are digested by bacteria.

This dichotomy between primary producers and detritus is too simple, as there are complex interactions between resource types. For instance, algae can produce excess molecules of organic carbon and lead to the *priming* of decomposition of organic matter by enhancing microbial growth through the extra energy provided by *leaky* algae (Halvorson et al. 2020).

Allochthonous inputs include detritus as just discussed, but it also includes living organisms, such as invertebrates falling from the surrounding land, and it might also include seeds and fruits that fall from vegetation nearby (Richardson and Sato 2015). Another kind of allochthonous input can include organisms like salmon, eels, and other species that return to freshwater and die, thereby importing large amounts of energy and nutrients gained in the marine environment (Wipfli and Baxter 2010). These flows of energy and nutrients across ecosystem boundaries are known as cross-ecosystem resource subsidies. Such flows are the basis of the concept of meta-ecosystems, that is, separate ecosystems linked by these flows of energy and nutrients.

FOOD WEBS

Food webs are one way of describing the feeding relations and flow of energy between organisms. Organisms are typically divided into trophic levels or feeding levels. After the *autotrophs* or primary producers, such as autotrophic plants and algae, most other organisms get their energy and nutrients by eating other organisms or parts of other organisms; such consumers are referred to as *heterotrophs*. Furthermore, primary consumers are those that eat primary producers, secondary consumers are those that consume primary consumers, etc. We sometimes refer to top predators as those consumers at the apex of the food web, which typically are large-bodied species. Each of these groupings constitute a trophic level.

Trophic levels are not always tidy and discrete, since there are predators that feed on a range of prey sizes and types; this is called omnivory. Omnivory includes organisms that feed on different combinations of food. Some organisms consume detritus and animals, others detritus and plants, plants and animals, or other combinations of a range of tropic levels. Also,

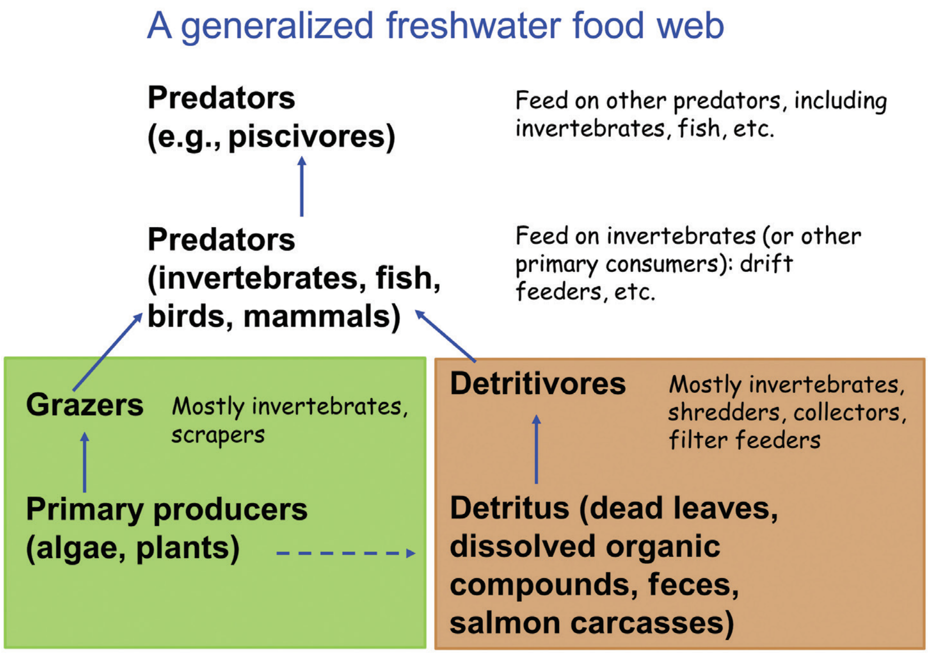

Figure 1.6 A generalized food web from freshwater ecosystems. Arrows indicate the flow of energy and nutrients upward from basal resources. There is a greater emphasis on detrital-based pathways of energy flows and less structural biomass from woody tissue than in most terrestrial ecosystems. We often refer to the green side of the food web as primary production and grazers, as opposed to the brown side of the food web which is based on detrital materials and detritivores—note the two distinct colored boxes at the base of the food web.

organisms can exhibit *life history omnivory* where different life stages of a single species feed at different trophic levels.

Food webs are structured with basal resources at the bottom, primary consumers that feed on those resources, and several levels of predatory animals (see Figure 1.6). Thus, there can be primary consumers feeding on autochthonous production (the *green* side of the food web), grazing on algae, or feeding on plants. Primary consumers feeding on detrital materials (the *brown* side of the food web) are known as detritivores (Zou et al. 2016). This detrital-based part of the food web has many similarities to food webs in organic soils. Organic materials that constitute detritus can include wood, leaf litter, and even dissolved organic matter. The quantitative contribution of detritus varies depending on the size of the waterbody, how much it is covered by vegetation, and other characteristics of the watershed. Heavily shaded streams or forested wetlands can be mostly dependent on detritus, and large, deep depositional areas such as deltas can also be based on detritus. Lakes and wetlands also receive a large amount of dissolved carbon from groundwaters and inflow streams, and while there are debates about the relative amounts, it is still significant.

Freshwater food webs can be further complicated by organisms that do not fit nicely into a particular trophic category, such as predatory plants and photosynthetic animals. Some non-plants in freshwater are photosynthetic due to symbiotic algae, mostly via the green algae *Chlorella* that can exist as cellular inclusions (Venn et al. 2008). These organisms include some

Figure 1.7 A freshwater sponge growing on rocks in a stream; notice the green photosynthetic tissue that comes from symbiotic algae within the sponge.

single-cell species, such as *Euglena* spp., and sponges such as *Spongilla lacustris* (see Figure 1.7). Thus, these species can be both heterotrophic and autotrophic. Predatory plants, such as bladder wort (*Utricularia* spp.), are typically associated with oligotrophic (low nutrient) environments. *Utricularia* have small traps, or *bladders*, that capture bacteria, protists, or small animals in a manner much like the terrestrial Venus fly trap (*Dionaea muscipula*). The edges of low nutrient lakes and bogs often have other partly carnivorous plants, including pitcher plants (*Sarracenia* spp.) and sundews (*Drosera* spp., in the same family as the Venus fly trap).

COMMUNITY ECOLOGY

The interaction of species within an ecosystem can include more than consumption and predation found within food webs. These interactions include competition, facilitation, and mutualism. Moreover, food webs rarely include the study of feedbacks, such as how predators may deplete their prey and result in density-dependent feedbacks to the predator's reproductive rates, as in predator-prey dynamics. All of these dynamical relations are the domain of community ecology.

In terms of the dynamics of food webs in freshwaters, there are a number of general processes described that have largely developed from studies in freshwaters. One idea is the concept of top-down or bottom-up effects. Bottom-up effects are largely due to more energy entering the base of the food web, leading to overall greater productivity and often greater taxonomic diversity (more species as rarer species get included). Top-down effects are largely a consequence of top predators (or even intermediate-level predators) often being capable of suppressing the abundance and productivity of their prey populations. Top-down control can have an outcome that is especially obvious in freshwater food webs through trophic cascades, where a high-level predator can depress numbers of its prey, which might free up the prey of that first prey (Carpenter et al. 1985; Shurin et al. 2006). A trophic cascade is a community response where a top predator has effects on at least two trophic levels below, hence cascading from the top of the food web down through the web.

Life history omnivory was previously discussed, but organisms can also switch habitats and feeding behaviors dramatically throughout their life history. Some obvious examples include amphibians and aquatic insects that spend their larval stages in water and adult stages out of water. However, these life-cycle transitions between habitats can also include using different features of freshwaters at different stages of their life cycles. A good example would be the bluegill sunfish (*Lepomis macrochirus*), where in the presence of largemouth bass (*Micropterus salmoides*), which is predaceous on small bluegills, the young bluegills remain in among the macrophytes in order to reduce predation risk and forgo eating planktonic crustaceans. Then, when they are large enough to not be eaten by the largemouth bass, they switch habitats and food choices (Carpenter et al. 1985).

ECOSYSTEM PROCESSES

Ecosystem processes occur when biological and nonbiological components of the ecosystem interact. Nonbiological components include nutrients, inorganic sediments, etc. Some examples of ecosystem processes include production (primary and secondary), decomposition, ecosystem metabolism, and nutrient cycling and mineralization.

We often refer to the amount of living tissue in an ecosystem at any given time as standing crop or biomass, usually in units of g/m^2. Depending on the question, biomass might be wet mass, dry mass, or even ash-free dry mass (AFDM). However, biomass is not the same thing as productivity, which is a rate that is expressed as the change in biomass through time, such as $g\ C/m^2/y$ or in smaller time units like per day or minute. Production is different yet, and is the net carbon produced over an interval; but there may actually be very little biomass present if a lot of it is eaten, so production includes productivity and losses. Even a species with low current biomass, such as algae or bacteria, may have high production and also high turnover (essentially how quickly biomass is being replaced), so the biomass is getting replaced at a high rate such that productivity and consumption may be balanced (Carpenter et al. 1985).