for artificial lures used by anglers. Anglers collect some kinds of freshwater invertebrates for use as live bait, while some kinds are even harvested and sold in bait shops. Because invertebrates are important in the diets of many fishes, fisheries biologists must be able to identify them and understand their biology in order to manage populations of sport and commercial fishes.

Because freshwater invertebrates are easy to collect and observe, they are very useful in education programs. This ranges from formal instruction in life sciences in schools and colleges to outreach activities by museums, zoos, science centers, conservation organizations, and government agencies. Freshwater invertebrates fall within subject areas such as zoology and ecology for teaching life sciences. In addition, freshwater invertebrates have been the subjects for artists, authors, poets, and historians, so they can be effectively included in interdisciplinary teaching. Because freshwater invertebrates live in many different environments and play important roles in ecosystems, they can be used easily in outreach programs concerned with conservation, biodiversity, natural resource management, and environmental stewardship.

Classification of Freshwater Invertebrates

There are more than a million species of animals in the world, and 95% of them are invertebrates. Within the insects alone, about 900,000 species have been described and scientists estimate that there is an equivalent number of species that have not been discovered. Obviously, the study of organisms requires a scheme for classifying them. Classification means organizing living things into groups of similar organisms that can be distinguished from other groups of organisms. The main categories of the groups used for classifying living things are kingdom, phylum, class, order, family, genus, and species. These categories are hierarchical, which means they have been conceived and organized in a graded or nested series. It is customary to list them in sequence, beginning with the highest category that includes the most categories below it. The species is the lowest and most fundamental category in the classification system. A species is defined as a group of organisms in nature that are similar in structure and capable of successfully producing offspring, but reproduction does not occur with other such groups. The classification system for animals is illustrated below for a terrestrial insect that is familiar to everyone — the house fly.

Kingdom: Animalia (animals)
Phylum: Arthropoda (arthropods)
Class: Hexapoda (hexapods)
Subclass: Insecta (insects)
Order: Diptera (true flies)
Family: Muscidae (muscid flies)
Genus: *Musca*
Species: *domestica*

The subject of classification (systematics) stimulates much controversy among the scientists who study it. Classification is supposed to represent the relationships of organisms according to their evolution (phylogeny), but this is always speculative. Scientists propose classification schemes chiefly by comparing the body structure of modern species to that of fossils of extinct species. It is a daunting task to solve such intriguing mysteries with very little evidence. As a result, classification schemes are constantly changing and there is never complete agreement on how organisms should be classified. This is illustrated above in the example of the classification of the house fly. At one time everyone thought that all invertebrates with six legs were a separate class known as insects (Insecta). Now, most scientists think that there are two distinct groups of invertebrates that have six legs, so the insects have been put into a subclass category, and the class of all invertebrates with six legs has been renamed as hexapods (Hexapoda). The intricate details of classification and the complex scientific names that they produce are beyond the purpose of this guide. Users just need to be aware that the many different kinds of invertebrates are organized in a system of categories within categories based on evolution, but the system will always be undergoing improvements.

The term that scientists use when referring generally to any category in the classification system is taxon (pleural = taxa); in this usage, for example, family, genus, or species are each a taxon and collectively are taxa. In this guide, I use the word "kind" as a less

technical substitute for "taxon." My use of kind is based on the accepted evolutionary classification scheme presented above, but I use the word interchangeably for family, genus, and species.

The following is a list of the common names of the major groups of freshwater invertebrates that users of this guide are likely to encounter, along with the classification category and scientific name that is most widely accepted at this time.

- Flatworms (Phylum Platyhelminthes, Class Turbellaria)
- Segmented worms (Phylum Annelida)
  - Aquatic earthworms (Class Oligochaeta)
  - Leeches (Class Hirudinea)
- Mollusks (Phylum Mollusca)
  - Snails (Class Gastropoda)
  - Mussels, clams (Class Bivalvia)
- Arthropods (Phylum Arthropoda)
  - Arachnids (Subphylum Chelicerata, Class Arachnida)
    - Water mites (a group of unrelated freshwater mites, usually assigned the name Hydracarina or Hydrachnidia)
  - Crustaceans (Subphylum Crustacea, Class Malacostraca)
    - Aquatic sowbugs (Order Isopoda)
    - Scuds, sideswimmers (Order Amphipoda)
    - Crayfishes, shrimps (Order Decapoda)
  - Insects (Subphylum Atelocerata, Class Hexapoda, Subclass Insecta)
    - Mayflies (Order Ephemeroptera)
    - Dragonflies, damselflies (Order Odonata)
    - Stoneflies (Order Plecoptera)
    - True bugs (Order Hemiptera)
    - Dobsonflies, fishflies, alderflies (Order Megaloptera)
    - Water beetles (Order Coleoptera)
    - Caddisflies (Order Trichoptera)
    - True flies (Order Diptera)

The biology of organisms within a category becomes more uniform the lower you proceed in the hierarchy. For example, the organisms included within the subclass of insects eat very different foods, live in different habitats, have different life histories, etc., while organisms belonging to the house fly species are almost identical in regard to their biological characteristics. Unfortunately, accurate identification becomes more difficult the lower one goes in the hierarchy. Anyone can distinguish an insect from a spider (six legs versus eight, respectively), but species level identification of invertebrates requires a high quality microscope and formal training in the subjects of morphology and taxonomy. This guide emphasizes identification at the family level, which is a good compromise between identification difficulty and biological uniformity. Many of the common freshwater invertebrates can be identified to family by eye, or with no more magnification than a simple hand lens. In some instances, the guide distinguishes organisms only to class or order, if they are difficult to identify but there is reasonable biological uniformity at the higher levels. Users should always remember that the illustrations in this guide show common species that are representative of a family, order, or class, but there may be some slight differences in the appearance of the invertebrates that they find. There are two reasons for this. There is natural variability within species over the geographic areas where they occur, and other closely related species in the group may also be commonly collected.

Fundamentals of Freshwater Ecology

Ecology is the study of the relationship between organisms and their environment. It comes from two Greek words: *oikos*, meaning "the family household," and *logy*, meaning "study of." It is important that users of this guide know something about the household where freshwater invertebrates live in order to understand the biology of the different kinds of invertebrates. As the science of ecology teaches us, it is impossible to separate the study of organisms from the study of their environment. However, freshwater ecology is a broad and complex science, and the scope of this guide only allows for a brief overview of the most pertinent elements. References for more detailed information on freshwater ecology are provided at the end of this part. This brief overview concentrates on the ecological factors that determine where and when invertebrates occur and how abundant they are. It is useful to consider these according to three types of ecological factors: physical, chemical, and biological.

Physical Factors

The most important physical factors that affect freshwater organisms are temperature, light, water current, and composition of the bottom materials (substrate). The metabolic rate of animals varies according to temperature, with higher temperature producing higher metabolism. All enzyme activity and oxidation of carbohydrates are affected. Invertebrates are commonly referred to as being "cold blooded," which means that they cannot regulate their body temperature. Individual species are adapted to a certain range of temperatures. If temperatures are consistently outside the acceptable range for a species, reproduction and survivorship become reduced until the species can no longer exist at that location. Temperature also affects the amount of oxygen that can dissolve in water, with cold water holding more oxygen than warm water. Since most aquatic invertebrates use dissolved oxygen for breathing, water temperature determines if there is sufficient dissolved oxygen for their needs.

Light has some direct effects on the behavior of aquatic invertebrates, in that some organisms hide during the day and become active at night. However, the main effects of light on aquatic invertebrates are indirect. The amount of light reaching the water affects its temperature. More importantly, the amount of light reaching the water and how far it penetrates in the water determines how much photosynthesis takes place in aquatic plants, including flowering plants, moss, and algae. Photosynthesis by aquatic plants produces food and dissolved oxygen for invertebrates. A very important feature of aquatic environments is the relative amount of plant biomass produced within the system (autochthonous) versus the amount of plant biomass produced outside the system (allochthonous), such as tree leaves and needles that fall into the water. Light is, therefore, the primary determining factor of whether the food base for a given community is live green plants growing in the aquatic environment or decaying plant matter that originated in the terrestrial environment. The proportion of the food base that comes from these two sources is a primary determinant of what kinds of invertebrates live in an aquatic environment. The abundant plant life that develops in aquatic environments with ample light produces good habitat for invertebrates in addition to food.

Water current affects aquatic invertebrates in many direct and indirect ways, and it is interrelated with most of the other ecological factors. Current can be a direct benefit to invertebrates by bringing them suspended particles of plant matter for food and by refreshing

the surfaces of their gills with water that is saturated with dissolved oxygen. However, moving water exerts a tremendous force. Small invertebrates are susceptible to being dislodged, which makes them easy prey for fish, or having their delicate body structures, such as gills, damaged by the abrasive sand that is being transported by the flowing water. Macroinvertebrates that live in swift streams or the wave-washed shores of lakes must have special adaptations to deal with the force exerted by the currents. Current also influences the composition of bottom sediment, and, in turn, the size of the mineral particles composing the bottom of aquatic environments has a profound influence on the distribution of aquatic invertebrates.

Substrate is the base on which an organism lives. In aquatic environments, substrate includes everything on the bottom or sides or projecting out into the aquatic environment. The nature of the substrate is probably the most important factor that determines the kinds of invertebrates that live in an aquatic environment and their distribution and abundance within that environment. Substrate has numerous direct and indirect effects on invertebrates, and it is interrelated with many other ecological factors. The substrate can be composed of mineral material, which ranges from large boulders to fine particles of clay, or diverse types of organic material, such as fallen trees, living rooted plants, filamentous algae, or detritus. Invertebrates depend upon it for attachment sites and hiding places. For stream-dwelling organisms, the size and arrangement of the substrate create very small refuges with a range of current velocities, so that different species all have the velocity that is appropriate for them. Substrate is also related to the food of invertebrates. Algae that grow attached to solid objects (periphyton) require firm, stable surfaces for their existence. Detritus accumulates around large pieces of substrate, such as rocks or logs, especially in flowing waters. The substrate is where nearly all invertebrates reside most of the time, so its importance cannot be overstated.

Chemical Factors

The most important chemical factors that affect freshwater invertebrates are oxygen, acidity, alkalinity, hardness, and nutrients. Like all animals, the metabolic activities of invertebrates require that they obtain oxygen and get rid of carbon dioxide. The scientific term for this physiological process is respiration. Sometimes muscular action is used to increase the rate of respiration, such as when we enlarge our chest to take in a deep breath, and that is called ventilation. In this guide, it will suffice to use the simple term breathing for all processes related to obtaining oxygen. Most aquatic invertebrates breathe oxygen that is dissolved in the water. Unfortunately, the chemical properties of water are such that it does not hold much oxygen in solution. The air that we breathe is about 21% oxygen, but less than 15 parts of oxygen will dissolve in 1 million parts of water (0.0015%) at the temperature just above freezing. Water contains only about half as much dissolved oxygen at warmer temperatures that are common in the summer under natural conditions. The oxygen requirements of invertebrates vary considerably among the different kinds, and the amount of available dissolved oxygen is a limiting factor for many of them. Species with high oxygen requirements are often restricted to places where the water remains cool, where splashing puts more oxygen in solution, or where there is sufficient current to constantly deliver oxygen and keep the organism saturated with the oxygen that is available.

The acidity of water is a reflection of the concentration of hydrogen ions in solution. When hydrogen ion concentration is high the water is acidic, whereas when hydrogen ion concentration is low, bicarbonate and carbonate ions prevail and the water is alkaline. The measure of acidity is pH, which is the hydrogen ion concentration. A pH value of 7 is neutral, below 7 is acid, and above 7 is alkaline. Most invertebrates are adapted for water that remains close to neutral. The pH scale is logarithmic to base 10, so a change of 1 pH unit represents a tenfold increase or decrease in hydrogen ion concentration. In general, pH values below 5 and above 9 are

harmful to most aquatic organisms.

The alkalinity of water is the concentration of all the compounds that can shift the pH into the alkaline range. In natural inland waters, alkalinity usually comes from bicarbonate, carbonate, and hydroxide ions. Alkalinity provides buffering capacity, which is the ability of water to neutralize hydrogen ions and thereby avoid becoming acidic.

Hardness is another commonly measured chemical property of water. It is a measure of all positively charged ions (cations) in solution. The main cations found in freshwater are calcium, sodium, magnesium, and iron. Water with high concentrations of these cations is called "hard," and water with low concentrations is called "soft." As a general rule, there are more kinds of invertebrates in moderately hard waters. The specific benefits of living in water containing additional cations are not completely understood, but scientists have observed that invertebrates living in hard waters are more resistant to stress, especially from certain toxic chemicals.

The primary nutrients in surface waters are the negatively charged ions (anions) of nitrogen and phosphorus, especially nitrate and phosphate. These chemicals do not directly affect invertebrates, but they do cause important indirect effects by stimulating the growth of all types of aquatic plants, including microscopic algae and large flowering plants. Moderate increases in the concentrations of nutrients are sometimes beneficial to invertebrates because slight increases in plant growth increase the amounts and types of useable food and habitat. However, an overabundance of nutrients leads to the condition known as eutrophication, which is always detrimental to invertebrates. Eutrophication occurs when extra nutrients act like fertilizer and cause too much plant growth. This upsets the balance in the aquatic environment. Overly abundant floating algae can cause the water to be soupy, which blocks sunlight from penetrating down in the water where other plants would normally live. Solid substrates can become coated with a thick layer of slimy algae, which prevents invertebrates from attaching. In addition, the kinds of algae that come with eutrophication are undesirable for food and are avoided by invertebrates. Consequently, many invertebrates will disappear from aquatic environments affected by eutrophication because of the loss of important food sources and places to attach. Rooted flowering plants can become so thick that they clog the aquatic habitat. When these copious amounts of plants die and decompose the concentration of dissolved oxygen can become very low, or nonexistent. Thus, nitrogen and phosphorus have a direct bearing on the quality of the aquatic environment, which, in turn, determines the kinds and numbers of invertebrates that are able to live there.

Biological Factors

The biological factors that affect the occurrence and abundance of invertebrates are even more complex than the physical and chemical factors. There are so many kinds of plants and animals in freshwater environments and they interact with the environment and themselves in such diverse ways, there are countless subtle effects on invertebrates. Biological factors are especially important to invertebrates in three ways: their influence on the organic substrate, food, and relationships among species. Plants and plant materials, either living or dead, can serve as organic substrate for invertebrates. As is true of the mineral substrate, the organic substrate provides a base for organisms to live on. Typical dead plant materials that function as substrate are logs, limbs, twigs, and leaves. Live aquatic plants that are inhabited by invertebrates are usually flowering plants with complex structures, such as leaves, stems, stalks, and roots. Sometimes tangles of live filamentous algae provide substrate that can be used by invertebrates. As a general rule, the more complex the substrate the more different kinds of invertebrates will live there. Substrate complexity creates more places to hide from predators and more small spaces where different kinds of invertebrates can find the specific conditions that suit their needs. Organic materials are an excellent habitat because they

provide complex substrate.

All animals are consumers, so food is always a very important biological factor that influences an organism's success in its environment. Some of the most important features of food that different kinds of freshwater invertebrates are specialized for include whether the food item is plant or animal, whether it is living or dead, where it originated, the size of the pieces, and where it is located in the water. Each one of these features, or combinations of them, make the food usable by only certain kinds of invertebrates. The only live plants that are eaten to a great extent by invertebrates are algae. Live aquatic vascular plants often have natural chemicals that make them taste bad. The microscopic cells of algae occur either floating in the water or attached to the surfaces of solid objects, especially large stones or vascular plants. Decaying plant material is called detritus, and this is a major food resource for many invertebrates. Much of the detritus in aquatic environments, especially streams, comes from trees and shrubs that grow on shore and drop their leaves, flowers, and twigs into the water. Scientists call this type of material allocthonous detritus. Detritus is also available from plants that lived in the water then died, or else their foliage died back for the winter. Detritus from plants that grew in the aquatic environment is called autochthonous detritus. Autochthonous detritus can come from flowering plants, mosses, or algae, and it is often more nutritious for invertebrates than allochthonous detritus, which tends to have a lot of unusable components such as cellulose. Size and location are other important features of detritus that affect its use as food by invertebrates. Pieces of detritus that are larger than 1 mm, such as fallen leaves, are called coarse detritus. Detritus particles that are smaller than 1 mm are referred to as fine detritus. Coarse detritus is usually located on the bottom or wedged against solid objects, whereas, fine detritus may be on the bottom or suspended in the water. Invertebrates have very different adaptations that make them specialized for acquiring and consuming the different kinds and sizes of detritus in various locations. In addition to plants, other animals are food for some invertebrates. Most invertebrates that eat animals eat them alive, but a few consume dead animal matter, which is called carrion.

When some invertebrates feed, they have a beneficial effect on the supply of food for other kinds of invertebrates, including the size and quality of the food as well as its location. Algae grow more and contain more nutrition in response to moderate levels of grazing by invertebrates. Invertebrates scrape off the top layer of cells and prevent the algae from shading itself from the sun, much like when we mow our lawn in the summer and the grass responds by becoming greener and growing more. Invertebrates that feed on large pieces of detritus, especially dead leaves from trees on shore, make small particles available to other organisms. The invertebrates that feed on large detritus have sloppy eating habits. A considerable amount of food falls out of their mouths after it has been shredded into smaller pieces, which are called orts. In addition, the feces that they eliminate become small particles of detritus that are useful food for other invertebrates. As a result of invertebrate feeding, large pieces of detritus in one location become small particles that are suspended in the water or drop to the bottom in another location in the aquatic environment.

The relationship among invertebrates in the natural environment is another important biological factor. There are many kinds of freshwater invertebrates and some kinds build up high population numbers in the aquatic environment. Living in close association makes it inevitable that invertebrates will experience some sort of relationship with each other. Competition and predation are the two types of relationships among freshwater invertebrates that are most commonly observed. Competition occurs when two or more organisms need some resource, such as food or space, and there is not enough of that resource to go around. Competition can occur between individuals of the same species (intraspecific) or between individuals belonging to different species (interspecific). Competition is always detrimental to all organisms involved and leads to

increased death or decreased birth, or both. Intraspecific competition between individuals of the same species is usually more intense than interspecific competition. Predation occurs when one organism becomes food (prey) for another organism (predator). Predation is always beneficial to the predator and detrimental to the prey. Neither competition nor predation usually eliminates any kind of organism under natural conditions in relatively undisturbed environments. Long ago, the competitors, predators, and prey arrived at a balance within the environment where they lived. Usually the organisms on the receiving end of the detrimental effects are reduced in numbers and their distribution is restricted within their environment, but they are not eliminated. Competition and predation are beneficial processes that increase diversity and productivity. It is usually only when humans are involved that competition or predation eliminates species. Examples are when alien species are introduced into aquatic environments, or when pollution adds too much stress to the hardships already produced by competition or predation.

As can be seen from this brief review of freshwater ecology, there are many complex factors that affect where and when invertebrates occur and how abundant they are. Sometimes these factors are readily apparent to our eyes, but scientific measurements must be taken in some situations to explain why certain invertebrates occur in a particular place or why they are absent.

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Fundamentals of Freshwater Invertebrate Biology

Freshwater invertebrates lead complex lives and there are many differences in the biology of the various kinds. In an effort to simplify this complexity, this guide emphasizes six of the most important biological characteristics of these invertebrates: habitat, movement, feeding, breathing, life history, and stress tolerance. An explanation of these six major biological characteristics will be useful for persons who are just beginning to study freshwater invertebrates. This awareness will also facilitate the use of Section 3 — Information About Different Kinds.

Habitat

A simple definition of habitat is the place where an organism naturally lives and grows. Habitat is mostly determined by the physical and chemical conditions that exist at a particular place, but organic substrates, such as live plants, logs, or detritus, can also be important biological components of habitat. Potentially, many, many different habitats could be created from the various combinations of physical, chemical, and biological factors identified in the preceding subsection. Scientists have attempted to make it easier to study freshwater ecology by organizing the many different habitats into a few categories that share some of the most important ecological factors. These habitat categories are important because unique assemblages of various kinds of invertebrates live in each type of habitat.

Freshwater habitats are divided into two broad categories: running waters and standing waters. The ecological term for running waters is lotic, and for standing waters it is lentic. There are also many common names for lotic and lentic habitats.

Some examples of common names for running waters are seeps, springs, brooks, branches, creeks, streams, and rivers. There is no standard scientific definition of these terms according to the size or other features, but they are commonly distinguished by the following subjective descriptions.

Seep and spring usually refer to the smallest flowing waters that occur where groundwater first emerges to flow in a channel. If the water emerges boldly and flows with a distinct current, it is probably called a spring. If the water merely trickles out of the ground without any noticeable current, it is a seep. Springs usually flow through cracks in impervious underground rock strata, whereas seeps flow through loose soil.

Brook, branch, creek, and stream often refer to intermediate size flowing waters that can be waded from one side to the other. Of these terms, the best one to use in freshwater ecology is stream.

River is usually used for larger flowing waters that are too deep to wade across.

Some examples of common names for standing waters are bogs, marshes, swamps, ponds, and lakes. Different depths, chemistry, and plant communities distinguish these standing-water habitats, although, like the names for flowing waters, there are no standard scientific definitions. Standing water bodies are commonly distinguished by the following subjective descriptions.

Bogs are very shallow, with little open water, because they have dense growths of *Sphagnum* mosses. The water is lacking in nutrients and is acidic, with $pH < 4.5$. The bottom is covered with a thick layer of decaying organic matter, known as peat.

Marshes have a bit more water depth and open water than bogs. Emergent vegetation, such as rushes, reeds, and sedges are present, rather than mosses. The water is rich in nutrients because marshes are connected to adjacent bodies of water and receive inputs of nutrients during times of flooding. Marsh waters may be slightly acidic, and the bottom may have a thin layer of peat.

Swamps are similar to marshes, except they are somewhat deeper and have much more open water. The main difference between marshes and swamps is the dominant vegetation. Large shrubs and trees that are adapted to grow in the water, such as cypress trees in the southeastern United States, dominate swamps.

Ponds and lakes are different from the previous types of lentic habitats by being much deeper. They are confined in distinct basins, whereas bogs, marshes, and swamps are spread out. Ponds are usually thought of as being smaller than lakes, but it is difficult to differentiate between a large pond and a small lake. Some scientists distinguish ponds from lakes by the depth that light penetrates and the resulting growth of rooted plants. In this scheme, lakes are bodies of standing water in which rooted plants do not grow across the entire width of the basin, because the middle is too deep for light to penetrate to the bottom. Ponds are considered to be bodies of standing water that are shallow enough to support the growth of rooted plants across their entire bottom, because everywhere in the basin is shallow enough for light to penetrate to the bottom.

Lotic and lentic habitats are further subdivided into zones. A zone is not defined exactly in freshwater ecology, but it is generally used to describe broad areas in which the major features of a habitat are alike, but different from the major features of other broad areas in the same habitat. For our purposes, a rule-of-thumb might be that zones extend for at least several meters and perhaps as much as several hundred meters. The concept of a zone is explained better by considering the following two examples.

Lotic habitats are divided into two zones: erosional and depositional. Another name for a lotic-erosional zone is riffle. This is the zone where streams at normal flow (not just during floods) have sufficient power to pick up fine sediments, keep them in suspension, and transport them downstream. The power of the stream in a particular zone depends on the gradient (slope) and width of the channel. A lotic-depositional zone is the area where the stream does not have sufficient power at normal flow to keep fine sediments in suspension, so the small particles in transport settle out on the bottom. Another name for a lotic-depositional zone is pool.

Lentic habitats are divided into three zones: pelagic, littoral, and profundal. Pelagic refers to all of the open water, from the surface down to the bottom, but not including the bottom. The upper part of the pelagic zone is often distinguished separately as the limnetic zone. The lower boundary of the limnetic zone is the maximum depth that enough light penetrates for photosynthesis by green plants, which is usually about 1% of the available surface light. The depth of the limnetic zone varies in different lentic habitats according to the clarity of the water. The littoral and profundal zones refer to areas of the bottom. The littoral zone is the area of bottom that extends from shore down to the point of light penetration. The profundal zone is the area of bottom that begins at the depth where light no longer penetrates and extends to the maximum depth of the lake.

Zones of lotic and lentic habitats are further subdivided into microhabitats, which are the specific places where organisms reside. A rule-of-thumb about size might be that different microhabitats could be found within an area of approximately 1 square meter. Examples of microhabitats in lotic-erosional and lentic-littoral zones

are illustrated in Figures 1 and 2, respectively. For invertebrates, the primary feature of microhabitats is the substrate. Substrate is either mineral or organic. The most important characteristic of mineral substrate related to freshwater invertebrates is the size of the individual pieces. Scientists have developed a standard scale (Wentworth scale) for size categories of mineral substrate, along with names for the different sizes. These are:

Boulder	> 256 mm (Figure 1F)
Cobble	64–256 mm (Figure 1G)
Pebble	16–64 mm (Figure 1H)
Gravel	2–16 mm (Figure 1H)
Sand	0.0625–2 mm (Figures 1I, 2G)
Silt	0.0039–0.0625 mm (Figure 2G)
Clay	< 0.0039 mm (Figure 2G)

In addition to the size of mineral pieces described in the Wentworth scale, the substrate can be bedrock, which is also called rock outcrop. This is the continuous solid rock bottom that occurs where flowing water has eroded the channel down to the underlying geological formations.

Invertebrate microhabitats can also be created by organic substrate, which is either live plants or detritus. Live aquatic plants that serve as microhabitats include flowering plants, moss, and filamentous algae. There are many kinds of each of these types of plants, a few of which are illustrated in Figures 1 and 2. Different species of flowering plants can protrude upright above the water surface (cattail, Figure 2A), lie mostly on the surface of the water (water lily, Figure 2B), or have the entire plant beneath the water surface (water-starwort, Figure 1B; moss, Figure 1C; pondweed, Figure 2C; elodea, Figure 2D). These are referred to as emergent, floating, and submerged aquatic plants, respectively. Another microhabitat is created by vascular plants when their roots become exposed in the water from erosion by currents in streams or by waves washing the shores of lakes. These tangles of roots are commonly called root wads. Often the root wads come from terrestrial trees and shrubs growing at the edge of the water body.

The other type of organic substrate is detritus. In addition to being food for many invertebrates, coarse detritus, such as leaves, flowers, stems, and twigs, makes very effective substrates for invertebrates to live on. Leaf packs form a preferred microhabitat for many kinds of invertebrates in lotic-erosional zones (Figure 1E). Leaf packs form when the current jams a bunch of leaves and other plant parts on a rock or dead tree limb. In lentic-littoral zones, the coarse detritus merely lies on the bottom, often in clumps (Figure 2F). Some kinds of invertebrates eat the coarse detritus while they dwell there, but others merely use it as a place to hang on and hide. Very large and stable pieces of detritus, such as logs and branches that fall into the water from trees on shore, are also used extensively as substrates by invertebrates. This material is simply called woody debris (Figures 1D, 2E).

The greatest diversity of invertebrates in lotic habitats occurs in erosional zones where the mineral substrate is predominantly loose cobbles and pebbles, with a few boulders (Figure 1). The size and irregular composition of this material provide an infinite array of hiding places, attachment sites, current velocities, surfaces for algae to grow, edges to catch coarse detritus and woody debris, and openings where fine detritus settles.

The loose composition of mineral substrate in lotic-erosional zones often extends below the stream bottom for a meter or more. This area, called the hyporheic zone, has practically no perceptible current, but there is sufficient flow to keep the water supplied with oxygen. Many invertebrates spend at least part of their lives here, where they are safe from large predators. Aquatic biologists know very little about invertebrate life in the hyporheic zone because it is so difficult to sample this area. It is speculated that some stream species are rarely collected because they spend much of their lives in this mysterious zone below the stream bottom.

The greatest diversity of invertebrates in lentic habitats occurs in littoral zones (Figure 2). Plants are the primary habitat feature responsible for this. The many species of aquatic plants, with their different shapes and structures, provide a wide variety of places to live, in the same way that mineral substrates provide assorted opportunities in lotic-erosional zones.

In this guide, the format for presenting habitat information for the various kinds of freshwater invertebrates is to first state the categories and zones where they occur (for example, lotic-erosional). Then the different sizes and types of those habitats are presented using the common names described above (for example, springs and small streams). Finally, the specific microhabitats preferred by the kinds of invertebrates are given (for example, cobble and pebble mineral substrate as well as woody debris).

Movement

Most freshwater invertebrates have specialized body shapes and behaviors that enable them to be in a place that meets their essential requirements for acquiring food and oxygen, avoiding competition with other invertebrates, and hiding from predators. Some invertebrates stay in or near one place as much as possible, while others roam around freely. This feature of their biology is referred to as locomotion, habits, or modes of existence. The categories of movement used in this guide are explained in the following paragraphs. Examples of most categories are shown in the illustrations of riffle and pond habitats (Figures 1 and 2, respectively).

Clingers are organisms with bodies that are highly modified in order to maintain a relatively fixed position on firm substrates in current. This is a challenging feat for small organisms because water exerts a strong force when it is moving. Invertebrates have several different mechanisms for being effective clingers. Some have a flat shape that offers little resistance to flowing water (flatheaded mayflies, Figure 1Q, Plate 55; water pennies, Figure 1S, Plate 78). Others have sucker-like structures that create a vacuum to hold on to the substrate (black flies, Figure 1N, Plate 90). Several kinds produce silk, which is sticky and is used to glue them to the substrate in current (common netspinner caddisflies, Figure 1P, Plates 73, 74). Almost all clingers occur in lotic-erosional habitats. Most live on coarse mineral substrate (bedrock, boulders, cobbles, pebbles), but some inhabit large pieces of woody debris, and a few attach to live plants in current. There are a few kinds that use the clinger habit to live on the wave-swept, rocky shores of lakes.

Climbers are adapted to dwell on live aquatic plants or accumulations of plant debris. They have elongate bodies with thin, spindly legs that extend down from the body (narrowwinged damselflies, Figure 2K, Plate 36). This body form allows them to maneuver up and down stalks and through dense tangles of plants and debris. They are often a greenish color, sometimes with mottled patterns, to make them camouflaged. They can usually swim, but only do so if they need to move across a short stretch of open water. Almost all climbers live in lentic-littoral and lotic-depositional habitats because that is where suitable beds of aquatic plants and accumulations of plant debris occur.

Crawlers are somewhat like clingers and climbers in that they require a firm substrate, free of fine sediment. However, they do not have special features like clingers to hold on in swift current, nor do they have elongate bodies with thin legs to climb in plants. Crawlers seek small, protected places among loose stones (boulder, cobble, pebble, gravel), woody debris, coarse detritus (especially leaves), exposed roots, and at the bases of plants that grow in tangles (especially moss). They move around slowly, using just their legs and tarsal claws. The latter provide traction. Crawlers are most common in lotic-erosional habitats, but within specific places where they are sheltered from fast currents. Examples of crawlers that live in riffles are common stoneflies and hellgrammites in loose rocks (Figure 1L, Plate 43; Figure 1O, Plate 60), giant stoneflies in leaf packs (Figure 1J, Plate 42), and spiny crawler mayflies in moss (Figure 1M, Plate 54). Some kinds also live in lotic-depositional and

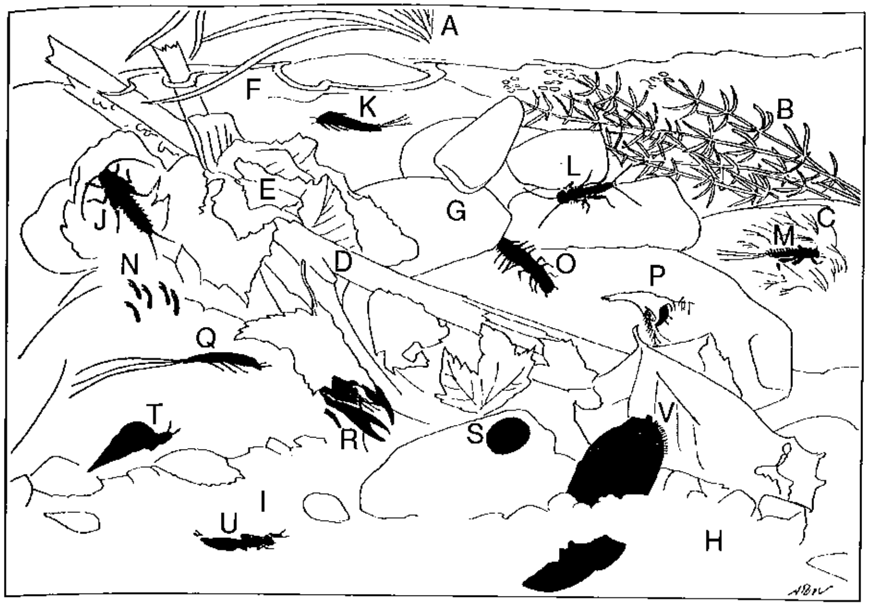

Figure 1A. Key to color figure on following two pages of a typical riffle habitat in a stream (lotic-erosional zone), illustrating the primary components of the habitat (A–I), common invertebrates that live there (J–V), and some of the biological features of those organisms, such as movement and feeding. (A) Terrestrial grass. (B) Submerged flowering aquatic plant (water-starwort, *Callitriche* sp.). (C) Submerged aquatic moss (*Fontinalis* sp.). (D) Woody debris. (E) Leaf pack. (F) Boulder. (G) Area of cobbles. (H) Area of pebbles and gravel. (I) Area of sand. (J) Giant stonefly (crawler, shredder-detritivore). (K) Ameletid minnow mayfly (swimmer, collector-gatherer). (L) Common stonefly (crawler, engulfer-predator). (M) Spiny crawler mayfly (crawler, collector-gatherer). (N) Black flies (clinger, collector-filterer). (O) Hellgrammite (crawler, engulfer-predator). (P) Common netspinner caddisfly (clinger, collector-filterer). (Q) Flatheaded mayfly (clinger, scraper). (R) Crayfish (crawler, omnivore). (S) Water penny (clinger, scraper). (T) Pleurocerid snail (clinger, scraper). (U) Clubtail dragonfly (burrower, engulfer-predator). (V) Mussel (burrower, collector-filterer).

Figure 1. A typical riffle habitat in a stream.

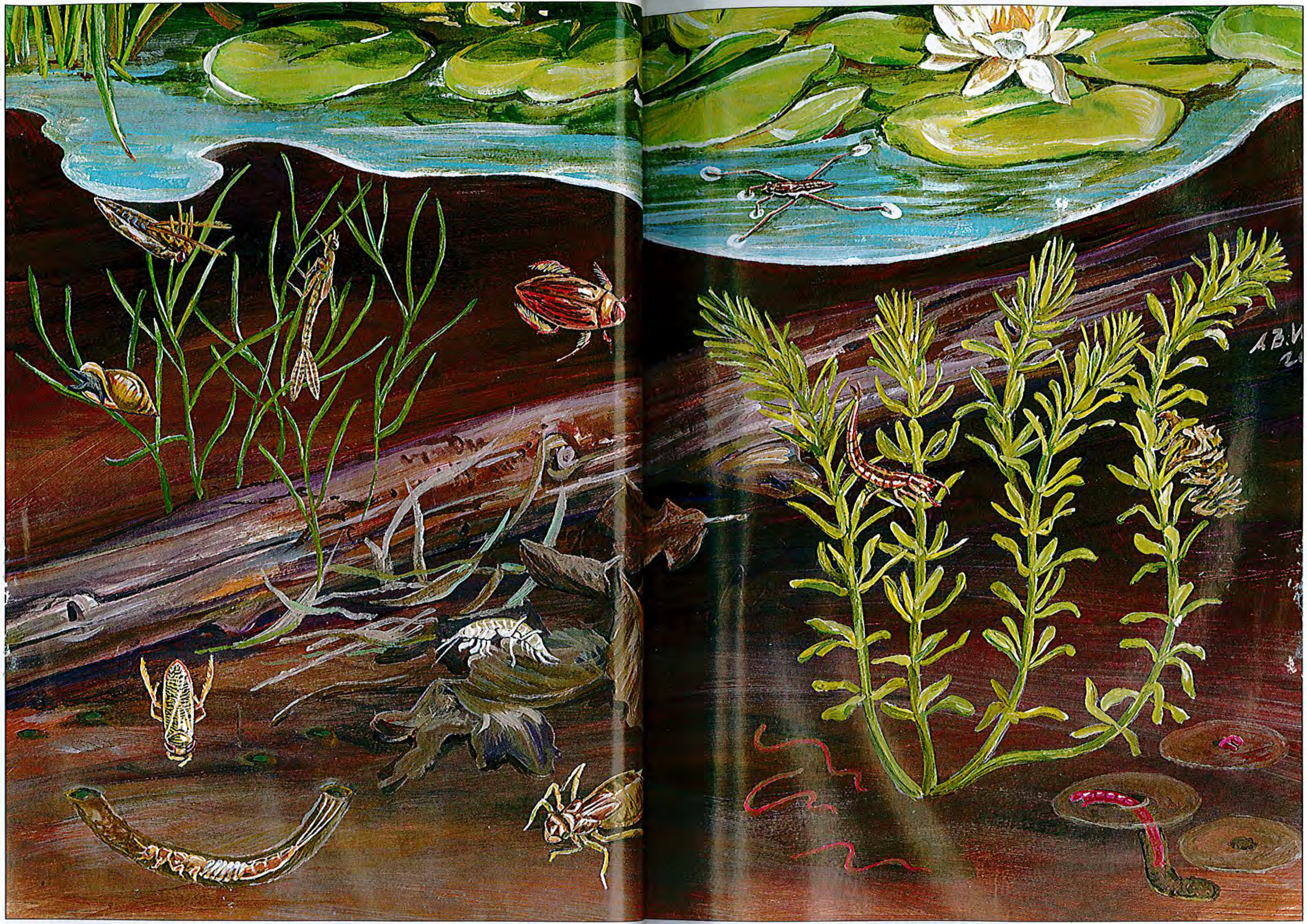

Figure 2. A typical habitat in the shallow water at the edge of a pond.

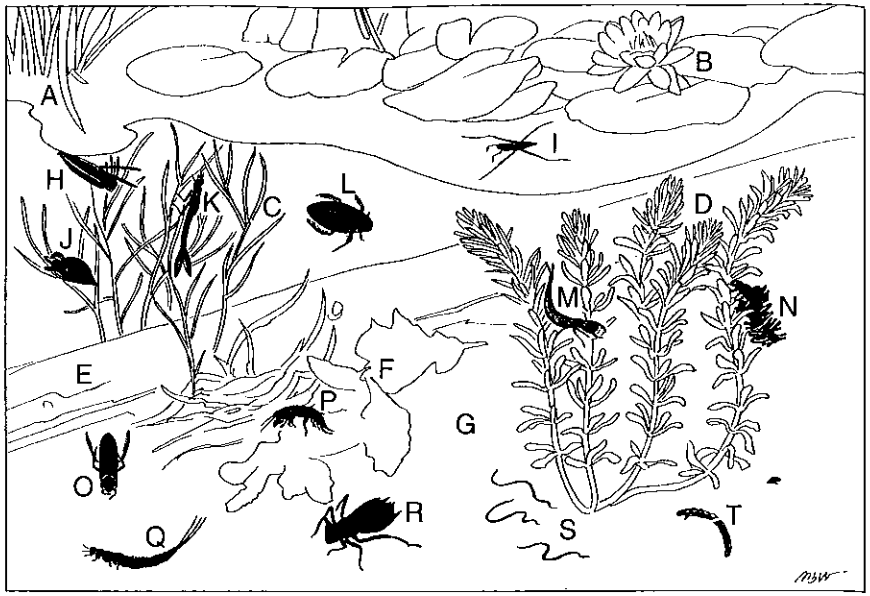

Figure 2A. Key to color figure on two preceding pages of a typical habitat in the shallow water at the edge of a pond (lentic-littoral zone), illustrating the primary components of the habitat (A–G), common invertebrates that live there (H–T), and some of the biological features of those organisms, such as movement and feeding. (A) Emergent flowering aquatic plant (cattail, *Typha* sp.). (B) Floating flowering aquatic plant (water lily, *Nymphaea* sp.). (C) Submerged flowering aquatic plant (pondweed, *Potamogeton* sp.). (D) Submerged flowering aquatic plant (elodea, *Elodea* sp.). (E) Woody debris. (F) Accumulation of dead tree leaves and aquatic plant detritus lying on bottom. (G) Bottom composed of mixture of sand, silt, clay. (H) Backswimmer (swimmer, piercer-predator). (I) Water strider (skater, piercer-predator). (J) Lymnaeid snail (clinger, scraper). (K) Narrowwinged damselfly (climber, engulfer-predator). (L) Predaceous diving beetle adult (swimmer, engulfer-predator). (M) Predaceous diving beetle larva (climber, piercer-predator). (N) Northern case maker caddisfly (climber, shredder-herbivore). (O) Water boatman (swimmer, collector-gatherer). (P) Scud (crawler, omnivore). (Q) Common burrower mayfly (burrower, collector-gatherer). (R) Skimmer dragonfly (sprawler, engulfer-predator). (S) Aquatic earthworms (burrower, collector-gatherer). (T) Non-biting midges (burrower, collector-gatherer).

lentic-littoral habitats (scuds, Figure 2P, Plate 18).

Sprawlers are adapted to live in places where the bottom consists of fine sediments (sand, silt, clay). Sprawlers have body shapes or other mechanisms to stay on top of the soft, fine sediment, rather than getting down into the sediment. In order to maintain this position, they usually have somewhat flattened bodies and legs that extend out to the sides, away from the body (skimmer dragonflies, Figure 2R, Plate 40). Sprawlers usually lie still and do not change their location very often. The body is often modified in various ways to protect the delicate gills from abrasion and clogging. Most sprawlers live in lentic-littoral and lotic-depositional habitats. Some occur in lotic-erosional habitats, but they are restricted to specific places where sand and silt accumulate, such as in eddies behind large stones and logs or near shore.

Burrowers, like sprawlers, are adapted to live in microhabitats where the bottom consists of fine sediments (sand, silt, clay). However, burrowers are adapted to dig down and reside in the soft, fine sediment, rather than lying on top. The bodies of burrowers often have special modifications for digging, such as scoop-like front legs or pointed projections on the head (common burrower mayflies, Figure 2Q, Plate 50). Others simply have elongate, pointed, flexible bodies that are effective for wiggling through the sediment (aquatic earthworms, Figure 2S, Plate 3). Some construct a distinct tunnel with walls that do not collapse (non-biting midges, Figure 2T, Plate 91), while others move through loose sediment that surrounds and touches them. Some are more stationary and simply wiggle their bodies and legs until they are almost covered by the sediment (clubtail dragonflies, Figure 1U, Plate 37). Often there are special mechanisms for obtaining dissolved oxygen from the water above them. Most burrowers live in lentic-littoral, lentic-profundal, and lotic-depositional habitats. Some occur in lotic-erosional habitats, but they are restricted to specific places where sand and silt accumulate, such as in eddies behind large stones and logs or near shore.

Swimmers are adapted for actively moving themselves through the water. They do this in two ways. Some swimmers move their entire body to propel themselves (ameletid minnow mayflies, Figure 1K, Plate 58). This is similar to how fish swim. Most fish swim by flexing their bodies from side to side, whereas most swimming invertebrates flex their bodies up and down. Invertebrates that swim with their body are usually streamlined, without projecting hairs, gills, or other structures that would provide resistance to the water. They sometimes have long tails on the end of the body to help push them along. Other kinds of invertebrates swim by moving their legs, which is analogous to using paddles or oars to move a boat. Legs are modified for swimming (natatorial) by being flat, at least on the ends. Dense brushes of long hairs also make legs more efficient for pushing through the water. Examples of invertebrates that swim by means of modified legs are predaceous diving beetle adults (Figure 2L, Plate 32), water boatmen (Figure 2O, Plate 21), and backswimmers (Figure 2H, Plate 22). Swimmers inhabit all types of lentic and lotic habitats. Some swimmers are so efficient that they can move through very swift lotic-erosional habitats where it is difficult for us to walk. However, members of this group only swim in short bursts. Most of the time, they remain perched on solid substrates, such as rocks, pieces of wood, live plants, or coarse detritus.

Skaters are adapted to remain on the surface of water without breaking through the film created by surface tension. They usually have small bodies and very long, thin legs (water striders, Figure 2I, Plate 26). The secret to staying on the surface film usually involves special hairs on the ends of the legs and sometimes on the body. Glands at the bases of these fine hairs secrete an oily substance that keeps the hairs from becoming wet, thus they spread out on top of the surface film rather than poking through. Most skaters are capable of moving nimbly on the surface in pursuit of food. Although a few kinds of skaters are conspicuous on aquatic habitats, this habit is not common among invertebrates. Skaters are usually found in lentic and lotic-depositional habitats, but they venture out

on the surface of lotic-erosional areas if the current is moderate.

Planktonic organisms lack the ability for sustained, directed locomotion. They can adjust their buoyancy to slowly rise and fall in the water, but for lateral movements they depend on the prevailing water currents produced by the wind (phantom midges, Plate 88). There is an abundant and diverse assemblage of planktonic animals in lakes and ponds, but it is composed almost entirely of microscopic organisms, especially rotifers and crustaceans such as water fleas (Cladocera). This habit is rare among the larger invertebrates that are the subject of this guide. These are usually found only in lentic habitats, but they may occur in large lotic-depositional habitats that have practically no current.

In this guide, the format for presenting information on the movements of the various kinds of freshwater invertebrates is to first state the categories that fit them (for example, mostly clingers, some crawlers). Then, further descriptions of their movements and any unique adaptations in their behavior or structure of their body are given.

Feeding

There are two ways that scientists usually consider invertebrate feeding, either the type of food that is consumed or how the food is obtained. Typical foods of freshwater invertebrates are detritus (coarse and fine particles), wood, algae, live vascular plants, and other animals. One problem with considering only the type of food consumed is that most invertebrates eat several types of food (omnivores) during their life. They tend to be opportunistic and eat whatever is most readily available. Freshwater invertebrates are much more consistent about how they obtain their food. Some scientists have found it more useful to summarize the diverse and variable information on types of food eaten by the many individual kinds of invertebrates into a handful of categories based on the body structures and behavioral mechanisms that they use to acquire their food. The term for these broad categories is functional feeding groups.

This guide emphasizes functional feeding groups, but in some cases the types of foods are also mentioned. The functional feeding groups used in this guide are explained in the following paragraphs. The illustrations of riffle and pond habitats (Figures 1 and 2, respectively) help explain some of the ways that invertebrates obtain their food.

Shredders chew on intact or large pieces of plant material. Shredders have basic mouthparts, without any special modifications. Basic mouthparts include two jaw-like structures (mandibles) for cutting and grinding and often an upper lip (labrum) and a lower lip (labium) to help keep the food inside the mouth. There are two types of shredders, based on whether the plant material is alive or dead. Shredder-detritivores feed on detritus, which is dead plant material in a state of decay (giant stoneflies, Figure 1J, Plate 42). The detritus that they consume is in large pieces (> 1 mm), often referred to as coarse detritus or coarse particulate organic matter (CPOM). Leaves, needles, flowers, and twigs that fall from trees and shrubs on shore are the most common foods of shredder-detritivores. Shredder-herbivores feed on living aquatic plants that grow submerged in the water (northern casemaker caddisflies, Figure 2N, Plate 69).

Collectors acquire and ingest very small particles (< 1 mm) of detritus, often referred to as fine detritus or fine particulate organic matter (FPOM). Collectors are divided into two types according to where the fine detritus is located in the habitat. Collector-filterers use special straining mechanisms to feed on fine detritus that is suspended in the water. Usually this involves nets they spin from silk (common netspinner caddisflies, Figure 1P, Plates 73, 74), hairs on their heads (black flies, Figure 1N, Plate 90), or hairs on their legs (brush legged mayflies, Plate 51). Some collector-filterers can use parts of their bodies to create water current for their feeding (mussels, Figure 1V, Plate 12). Collector-gatherers eat fine detritus that has fallen out of suspension and is lying on the bottom or is mixed within bottom sediments. They do not have any special adaptations to acquire their food. They either position themselves on the bottom and eat the fine detritus from the top of the sediment (non-biting midges, Figure 2T, Plate 91), or they burrow through the bottom and unselectively swallow the sediment and fine detritus as they go (aquatic earthworms, Figure 2S, Plate 3). Finger-like projections from some of the mouthparts (palps) usually help them gather the fine particles of food.

Scrapers (also called grazers) are adapted to remove and consume the thin layer of algae that grows tightly attached to solid substrates in shallow waters. These microscopic plants are very nutritious (sort of an aquatic salad bar), but invertebrates must have special adaptations to remove this material. The jaws of aquatic insect scrapers have sharp, angular edges. When these mouthparts move, the action is something like using a putty knife or paint scraper to remove old paint or varnish. After the attached algae have been loosened, the material is swept into the mouth by finger-like projections from other mouthparts. Snails scrape algae by means of a rough, tongue-like structure that works like a rasp. Examples of invertebrates that graze on attached algae are flatheaded mayflies (Figure 1Q, Plate 55), water pennies (Figure 1S, Plate 78), and snails (Figure 1T, Plate 7; Figure 2J, Plate 10).

Piercers have their mouthparts, or sometimes their entire head, elongated and protruding as modifications to puncture their food and bring out the fluids contained inside. It is informative to divide the piercers into two types, according to whether their food is plants or animals. Piercer-herbivores penetrate the tissues of vascular aquatic plants or individual cells of filamentous algae and suck the liquid contents. This is not a common functional feeding group in aquatic environments, even though it occurs extensively on land. Most aquatic piercer-herbivores simply have a small, narrow head that can be inserted into the hole that they nibble in plants (crawling water beetle adults, Plate 28; microcaddisflies, Plate 63). Piercer-predators subdue and kill other animals by removing their body fluids. These are very common in aquatic environments. Most have their mouthparts modified into one or two hard, sharp, hollow tubes that they stab into their prey, much like a medical syringe (water scorpions, Plate 23; predaceous diving beetle larvae, Figure 2M, Plate 82). They usually have other mechanisms to help with subduing their prey, such as enlarged front legs (raptorial) and poisonous saliva. Most of them pump digestive enzymes into their unfortunate prey to dissolve the internal organs into a fluid that can be sucked out through the mouthparts, similar to using a straw. When they have finished feeding, they discard the empty carcasses of their prey. Piercer-predator aquatic invertebrates usually feed on other invertebrates, but some prey on vertebrates such as fish and tadpoles. Their prey is often much larger than themselves.

Engulfer-predators feed upon living animals, either by swallowing the entire body of small prey or by tearing large prey into pieces that are small enough to consume. They typically have large jaws with pointed ends and sharp, tooth-like projections for attacking and devouring their prey. Many kinds of engulfer-predators have their mouthparts arranged to project in front of the head (prognathous) in order to maximize their effectiveness (common stoneflies, Figure 1L, Plate 43; hellgrammites, Figure 1O, Plate 60).

In this guide, the format for presenting feeding information for the various kinds of freshwater invertebrates is to first state the functional feeding groups that they belong to (for example, mostly scrapers, some collector-gatherers). Then, additional information on the specific foods that they consume and any unique adaptations in their behavior or structure of their body for feeding are given.

Breathing

Most kinds of freshwater invertebrates depend upon oxygen dissolved in the water for their breathing. Oxygen enters the organisms either through their general body surface or through gills that are specialized for this purpose, or both. This is referred to as a closed breathing system. Whether gills or body surface, dissolved oxygen passes through the skin of the organism by simple diffusion.

Some kinds of invertebrates have behavioral mechanisms, such as wiggling the body, to increase the rate of oxygen diffusion. This works by keeping the body constantly in contact with water that is completely saturated with dissolved oxygen. It is common for invertebrate gills to have muscles attached to them so they can be moved in the water, which works the same way as wiggling the body to increase the rate of oxygen diffusion.

Quite a few aquatic insects breathe oxygen from the atmosphere, reflecting their close relationship to terrestrial insects. Terrestrial insects have holes in their bodies, called spiracles, that let air in. This is called an open breathing system. All of the adult insects that live in the water, and some larvae, have open breathing systems. There are two basic ways that insects can live in the water and still breathe air by means of an open breathing system. Some kinds can attach a quantity of air to their body, commonly called an air store, and take it underwater to breathe from. The air store can be in the form of a bubble or a thin layer. The aquatic insects that carry an air store underwater hold it in a location on their body where spiracles are located, and simply breathe from the air store. These kinds of air-breathing aquatic insects usually have modifications to some of their body structures to help them hold the bubble or layer of air. The modifications include special features of their wings, legs, or hairs. The other way that some insects breathe air is to have spiracles or some type of extension on the end of their body that they push up to the surface to reach the atmosphere. The extensions for breathing this way are called breathing tubes or siphons. These kinds of insects usually rest near the surface where they can breathe continuously. When they need to go below the surface, they fill up the tubes and cavities inside their body with air and go under until they use up the oxygen. Aquatic insect larvae that obtain dissolved oxygen by means of closed breathing systems, do so in the same ways as other freshwater invertebrates.

In this guide, the first thing that is stated about how the different kinds of invertebrates breathe is whether they obtain oxygen from the water or air. If they obtain dissolved oxygen from the water, the guide explains whether they do this over their overall body surface or with gills. Then any special behaviors or structural modifications are described.

Life History

Life history is a term that scientists use to cover all of the biological events in an organism's life from birth to death. Some of these events are covered under the preceding biological aspects. In this guide, the part on life history is used to present any unique information about reproduction, growth, and development of the individual organisms. It is impossible to avoid using some specialized terms for this topic, so they are explained in this introduction.

Reproduction by invertebrates usually involves mating by a male and female of the same species. In some species, mature males and females look different (sexual dimorphism). One sex may differ from the other by having certain body structures conspicuously enlarged (usually the males) or the two sexes may be different colors or have different patterns of pigmentation. There are also numerous examples of asexual reproduction among freshwater invertebrates. The simplest type of asexual reproduction is budding or fission, in which an organism merely divides into two organisms. Fission is not common in the invertebrates that are the subject of this guide, but some flatworms do this. Parthenogenesis is a type of asexual reproduction in which egg development occurs without fertilization. This happens in some of the snails and insects. Hermaphroditic describes an individual that contains both male and female reproductive organs. This situation occurs commonly in the flatworms, aquatic earthworms, leeches, snails, and mussels. In most cases, these hermaphroditic organisms mate with another individual of their species, but self-fertilization does occur in some kinds.

Eggs result from all types of reproduction except fission. Most invertebrate females are oviparous, which means they lay their eggs somewhere outside of their body. In a few kinds of invertebrates

the females retain their eggs and allow them to hatch within their body, at which time they release free-living offspring. This type of egg laying is called ovoviviparous.

After hatching from the egg, invertebrates begin life as small, immature forms that must undergo the processes of growth and development. Growth refers to increasing in size, while development refers to the changes that make them capable of reproducing. While young invertebrates are growing and developing, they are called larvae, juveniles, or just immatures. After they have reached their final stage with functional reproductive organs and external structures for mating and laying eggs, they are called adults. These topics are very important when studying freshwater invertebrates because many of the organisms that are discovered will be immature forms that are undergoing growth and development.

Growth is relatively simple in the flatworms, aquatic earthworms, and leeches because they are not impeded by any type of external protective structure. They just continuously get larger until they become adults. However, a hard, non-living, protective covering made of a complex protein (chitin) is characteristic of all arthropods. The scientific term for this outer layer is exoskeleton, but in this guide it is referred to as "skin" for simplicity. The skin of an arthropod does not grow after it has been produced. Since it is rigid, it prevents the growth of the organism inside. Thus, arthropods must periodically shed their skin (molt) in order to increase in size. When it is time to molt, much of the old skin is dissolved from the inside and the chemical components are reabsorbed by the invertebrates, sort of like recycling. At this time a new and larger skin is produced below the old one. The new skin is larger because it is soft and highly folded, thus it fits in the old, smaller skin. Arthropods break open the old skin by swallowing air or water to create internal pressure, then they climb out and swallow more air or water to enlarge their new skin that is still soft and folded. This enlargement process is kind of like ironing out the wrinkles in recently washed clothes. After the new skin has been stretched to a larger size that will accommodate the arthropod's growing body, it remains soft for a period of time. Arthropods in this soft condition after molting are referred to as being teneral. In addition to being soft, teneral arthropods also lack color. They are pale, almost white. The hardening of the new skin is caused by a chemical process called tanning, which also produces the normal color of the arthropod. Different kinds of aquatic arthropods shed their skin from as few as 3 times to as many as 45 times.

Mollusks are also enclosed in non-living protective covers produced by the organism, which are commonly called shells. The shells of mollusks are made of protein and calcium carbonate. Mollusks can enlarge their shells by producing successively larger growth rings, something like tree trunks. Thus, the bodies of mollusks can grow without shedding their shells.

The appearance of some invertebrates changes considerably between the time they hatch from the egg until they become adults. The changes that take place during development are called metamorphosis. This word comes from Greek meaning "change in form." The most dramatic examples of metamorphosis occur with the insects and mites in the arthropods and with mussels and clams in the mollusks. The metamorphosis of those groups will be described in their respective parts of Section 3.

Generation refers to a population of organisms going from the egg to the adult stage. The number of generations that different kinds of freshwater invertebrates produce in 1 year is important ecological information. Scientists can use this information to predict such things as how many fish can be supported in a body of water or how long it will take a stressed aquatic environment to recover. The overall duration of a single generation for different kinds of freshwater invertebrates ranges from as short as a few weeks to as long as several years. Thus, the number of generations produced by different kinds of aquatic insects commonly ranges from many generations each year to only one generation every several years. Specific information on the number of generations per year is presented for the individual kinds of invertebrates in Section 3.

It is also important to know if organisms remain continuously active during their life history. Some kinds of freshwater invertebrates seem to disappear from a habitat for several months or longer, then suddenly become abundant again. Usually the abrupt disappearance of organisms is a result of natural interruptions in life history. Dormancy is the broad term that is used for any period of inactivity, but there are several types of dormancy — including diapause, hibernation, and aestivation.

Diapause is a condition when invertebrates in any stage of development before the adult, including the egg stage, become dormant and cease their growth and development. Diapause is genetically determined. Some species are "programmed" to enter diapause when certain environmental conditions provide the proper cues. A combination of temperature and length of daylight in relation to darkness are common cues that trigger diapause. After diapause is initiated, it can only be broken by another set of environmental factors that have been "programmed" into the organism. The purpose of diapause is for invertebrates to avoid adverse conditions that occur regularly on a seasonal basis. Some of the naturally unsuitable conditions that invertebrates escape by means of diapause are water temperature being too hot or too cold, low flow (or no water), or not enough dissolved oxygen. Each species usually diapauses in the same stage and at the same time of year.

Hibernation and aestivation are two other types of dormancy, but they are not genetically programmed and occur irregularly, or not at all, during the larval or adult stages of invertebrates. Hibernation is a temporary response to cold, while aestivation is a temporary response to heat. These types of dormancy are much simpler and usually occur for shorter durations than diapause. If the environment where an organism lives becomes too cold for its normal activities, the organism will hibernate until the environment warms up. If the environment where an organism lives becomes too hot for its normal activities, the organism will aestivate until the environment cools off. Freshwater invertebrates must hide themselves in protected locations within their habitat before any type of dormancy is initiated. Common locations for dormancy are down in the bottom substrate, within accumulations of detritus, or in living plant tissue. If individual kinds of invertebrates commonly undergo any type of dormancy, that information is presented in the life history parts of Section 3.

Stress Tolerance

This term refers to the ability of organisms to withstand disturbances in their environment. There are many different types of disturbances that can occur in freshwater environments. Some are caused by human activities, while others are the result of the forces of nature. Pollution is the term that is most often associated with disturbances caused by human activities, but its meaning is actually restricted to substances or energy that are released into water and bring about undesirable changes. Environmental stress is a broader term that is used for any action that brings about undesirable changes. Some examples of environmental stress that do not fit the strict definition of pollution are removing water for irrigation or municipal supplies, impounding (damming) a stream, and deforestation that eliminates shade and leaf fall. However, this broad concept of environmental stress is not limited to human activities. Natural events such as floods, forest fires, and volcanoes also disturb aquatic environments.

Different kinds of freshwater invertebrates vary widely in their ability to cope with environmental stress. Professional aquatic biologists take advantage of this situation when they conduct biomonitoring to assess environmental health. If samples of the living assemblages in a body of water contain many kinds of organisms that are known to be sensitive to stress, then that indicates a healthy environment. If samples reveal just a few kinds of organisms, all of which are known to be tolerant to stress, that indicates an unhealthy environment. There are many intermediate conditions

between these two extremes in which samples contain a mix of tolerant and sensitive organisms. Professional aquatic biologists derive mathematical indices from equations that incorporate numerical tolerance scores for each kind of invertebrate. However, this numerical approach is usually only applicable for a particular geographic region and requires many years of research by professional aquatic biologists to develop. This guide provides subjective information based on many years of field research on pollution and environmental stress that I have conducted, as well as that reported by other scientists. The various kinds of organisms are placed into the following categories:

Very sensitive — usually found only in nearly pristine environments; quickly eliminated if any disturbance occurs; do not occur in high numbers anywhere.

Somewhat sensitive — similar to facultative; will be in pristine environments but can also withstand a limited amount of disturbance; usually do not occur in high numbers.

Facultative — occur in environments with conditions ranging from pristine to moderate levels of disturbance; often occur in high numbers under conditions of moderate disturbance.

Somewhat tolerant — similar to very tolerant but they cannot survive in severely disturbed environments; occur in high numbers but they do not dominate the community as completely as the very tolerant kinds.

Very tolerant — seldom found in pristine environments; occasionally found in moderately disturbed environments; exceptionally high numbers in environments with severe disturbance; can withstand almost anything; flourish where conditions are so bad that they probably have only one or two competitors, or none.

If lower taxonomic units (genus or species) within the higher group that is presented in the guide (usually family) are known to vary in their tolerance to stress, then the range of stress tolerance categories within the family is also given. Many kinds of freshwater invertebrates have different levels of tolerance for particular types of disturbance. For example, a kind of invertebrate might be tolerant of the poisonous effects of a particular chemical but very sensitive to fine sediment that clogs their gills. Such distinctions between the effects of different types of pollution or environmental stress are beyond the scope of this guide. The categories of stress tolerance that are used in this guide are generalizations about a group's overall tolerance to stress from all types of disturbance. In some instances, descriptive statements are added about some kinds of organisms that are widely known to be exceptionally sensitive or exceptionally tolerant to particular types of disturbance.

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