Aquatic Insect Ecology

I. Introduction

The ecology of aquatic insects has been intensively studied from various perspectives, reflecting their abundance, diversity, and important role in the communities and ecosystems they inhabit. Aquatic insects are abundant in most freshwater habitats and often exhibit high diversity. In aquatic food webs, they serve as food items for nearly the full range of vertebrate and invertebrate predators, and many function as predators themselves. Considerable information is available on insect responses to a variety of environmental conditions, including factors that operate at the landscape level. Thus, insect responses often are used as indicators of water quality conditions in freshwater systems. Longitudinal trends in insect functional feeding groups are an important component of the River Continuum Concept (see Chapter 2, Section II.A.1.b and II.D), a major paradigm in the discipline of stream ecology. Although the ecological literature on aquatic insects is extensive, most has been produced within the last 30 years, reflecting current interest in the topic. In spite of this extensive body of work, the enormous diversity of insects combined with their widespread distribution dictates that much remains to be learned.

This chapter provides a brief overview of: constraints on aquatic insect species diversity, life history, and community structure; the role of aquatic insects in ecosystem processes; the impact of land use, climate change, and disturbances on their communities; and the utility of aquatic insects in biomonitoring studies. The review encompasses both lentic and lotic habitats, as well as a brief coverage of saline habitats. The discussion is placed in the context of how physical and life history factors constrain the distribution and abundance of aquatic insects, thereby altering communities and ecosystem function.

II. Aquatic Insect Communities

A. Insect Taxonomic Diversity

Insects are the most species-rich and often the most abundant group of substrate-dwelling macroinvertebrates, and have successfully invaded virtually all aquatic habitats. Although there are many specialized habitats, most aquatic insects are found either in lotic or lentic habitats (Table 17.1)
<table>
<thead>
<tr>
<th>Order</th>
<th>Estimated NA species</th>
<th>Primary (and secondary) habitat</th>
<th>Generation time (yr)</th>
<th>Primary feeding mode (FFG)</th>
<th>Examples of common NA genera</th>
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<tr>
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<td>40</td>
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<td>≤1</td>
<td>Collector-gatherers</td>
<td>Podura, Sminturides</td>
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<td>≤1</td>
<td>Collector-gatherers, collector-filterers, scrapers</td>
<td>Baetis, Hexagenia</td>
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<tr>
<td>Odonata</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>≥1</td>
<td>Predators</td>
<td>Aeshna, Comphus, Libellula</td>
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<tr>
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<td>120</td>
<td>Lentic + lotic</td>
<td>≥1</td>
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<tr>
<td>Orthoptera</td>
<td>40</td>
<td>Water margin; semiaquatic</td>
<td>≥1</td>
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<td>Conocephalus</td>
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<tr>
<td>Plecoptera</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>6 families</td>
<td>330</td>
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<td>≥1</td>
<td>Shredders</td>
<td>Pternarcys, Capnia</td>
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<td>Neuroptera</td>
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<td>Piersers</td>
<td>Sisyra</td>
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<tr>
<td>Trichoptera</td>
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<td>All major FFGs</td>
<td>Rhyacophila, Hydropsyche, Glossosoma, Neophylax</td>
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<td>Lepidoptera</td>
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<td>≤1</td>
<td>Shredders, scrapers</td>
<td>Petrophila</td>
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<tr>
<td>Coleoptera</td>
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<td>≤1 (some &gt;1)</td>
<td>All major FFGs</td>
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<td>Diptera</td>
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<td>Shredders, predators</td>
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<td>Collector-filterers, scrapers</td>
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<td>≤1</td>
<td>All major FFGs</td>
<td>Chironomus, Polypedilum, Tanytarsus</td>
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<td>≤1</td>
<td>All major FFGs</td>
<td>Chaoborus, Chrysops, Ephydra</td>
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<td>Internal parasites</td>
<td>≤1</td>
<td>Parasites</td>
<td>Apsilops, Trichogramma</td>
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</tbody>
</table>
and are constrained to one or the other habitat by physiological adaptations (see below). In our discussions, we will follow the classification used in Chapter 16. The orders Ephemeroptera (mayflies), Odonata (dragonflies and damselflies), Plecoptera (stoneflies), Trichoptera (caddisflies), and Megaloptera (fishflies and alderflies) are considered to be strictly aquatic in their immature stages. Other insect orders are partially aquatic (in the immature stage), including Collembola (semiaquatic springtails), Neuroptera (spongillaflies), Heteroptera (aquatic and semiaquatic bugs), Coleoptera (water beetles), Diptera (aquatic flies and midges, especially Suborder Nematocera but some Brachycera), and Lepidoptera (aquatic caterpillars). All of these latter groups have important aquatic representatives as immatures. Even several species of Orthoptera (grasshoppers) are found in association with aquatic habitats. These aquatic insect orders are treated taxonomically in Chapter 16. Generic level keys to aquatic insects of North America can be found elsewhere.

Species diversity in many of the aquatic insect orders is very high. A pristine stream may contain well over 100 species of insects, including many that are difficult or impossible to identify in the immature aquatic stages. Ponds, lakes, and wetlands can also exhibit very high diversity, depending on water quality conditions, littoral development, and substrate characteristics. Due to taxonomic problems associated with this high diversity, the role of aquatic insects in aquatic ecosystems is often difficult to study. To minimize this problem, aquatic insects have been categorized into a smaller number of functional feeding groups, as discussed in more detail later in this chapter.

B. Physical Constraints on Aquatic Insects

The physical environment of aquatic ecosystems exerts substantial control over the population abundances and hence community composition of insects (see Chapter 2). Still, it is remarkable that virtually every North American freshwater environment has been colonized by aquatic insects, ranging from alpine lakes to desert hot springs, oligotrophic streams to sewage treatment lagoons, and tree holes to the extreme depths of large lakes. Within these habitats, the physical factors of particular importance to aquatic insects include: dissolved oxygen concentration, water temperature, water chemistry, type of substrate, and hydrodynamics.

1. Dissolved Oxygen

As aerobic organisms, all insects must obtain sufficient oxygen to drive their metabolic machinery. This presents a particular challenge for aquatic insects because water, even when saturated, contains much less oxygen than terrestrial environments (a maximum of about 15 ppm oxygen in water compared to over 200,000 ppm in the air). Seasonal and spatial variation in oxygen concentration greatly restricts the types and diversity of insects found in aquatic environments. Dissolved oxygen concentrations are highly variable over time and space, and oxygen may be totally lacking from some aquatic habitats (“anoxic”). Oxygen concentrations in lentic systems change with depth because lakes thermally stratify during the summer under ice, which prevents reaeration with the atmosphere for part or all of the lake (Fig. 17.1a,c). Solubility is also temperature dependent, and oxygen production and demand differ between oligotrophic and eutrophic lakes, and among depth strata of a lake (Fig. 17.1). Most cold-water oligotrophic lakes remain oxygenated throughout the year because solubility increases as water temperature decreases (Fig. 17.1a,c), and oxygen demand is relatively low in deep bottom waters. The likelihood of under-ice anoxia increases with productivity due to proportionally increasing respiratory requirements but decreases with depth due to high oxygen storage in the hypolimnion (Fig. 17.1c). This condition is temporarily alleviated during spring and fall mixing events, when reaeration with the atmosphere recharges the entire water column with oxygen. In warmer climates, lakes may mix for several months of the year, stratifying only in summer, and may become permanently stratified in the tropics. The water column...
of shallow ponds and wetlands can become anoxic due to respiratory oxygen demands under ice even in relatively unproductive systems. Because the vast majority of aquatic insects are substrate dwellers, this represents a potential physiological constraint.

No insect can complete its life cycle in a completely anoxic environment, but some can cope with temporary anoxia. For example, the chironomid midge *Chironomus* and related Chironomini (Diptera: Chironomidae) contain a hemoglobin-like pigment (hence the common name bloodworm) that allows them to store oxygen and thus survive short-term or even seasonal anoxia. The phantom midge *Chaoborus* (Diptera: Chaoboridae) is also found in anoxic sediments but uses a different strategy than do bloodworms. *Chaoborus* migrates vertically at night toward the surface both to obtain oxygen and to hunt for prey. During the day, it returns to the deep, dark sediments to evade its own predators. Shallower environments (e.g., ponds and marshes) that experience oxygen depletion contain a more diverse array of insects because they can obtain oxygen in a myriad of ways. Some insects, including many heteropterans, carry air stored as a bubble on their body that they occasionally replenish by swimming to the water surface (Fig. 17.2a). Others maintain a semipermanent connection to the atmosphere through a breathing tube, as exemplified by mosquito larvae (Diptera: Culicidae) and rat-tailed maggots (Diptera: Syrphidae). Yet other insects, such as some beetle larvae (Coleoptera) and one genus of mosquito (Fig. 17.2b), use specialized spiracles to pierce the vascular tissues of rooted aquatic plants and thus “steal” their oxygen.

In most unimpacted streams, dissolved oxygen concentrations generally are near saturation and thus oxygen rarely limits insect diversity. We often see the greatest diversity of aquatic insects in small streams, due in part to the abundance of oxygen. However, insects requiring a connection to atmospheric air are typically in low numbers, because flow would quickly displace these taxa far downstream. Thus, most lotic insects obtain their oxygen by diffusion through the body wall, often aided by tracheal gills, which are thinly sclerotized evaginations of the body wall designed to increase surface area (Fig. 17.2c). Most representatives of the insect orders that are wholly aquatic (e.g., Ephemeroptera, Plecoptera, and Trichoptera) possess such tracheal gills in the larval, aquatic state and achieve their highest diversity in flowing waters. Gills, however, rely on abundant dissolved oxygen for diffusion into the body, and thus gilled larvae can experience stress at low oxygen concentrations. Exposure to low oxygen can occur in larger rivers with low turbulence (and therefore low reaeration), especially at night when photosynthesis turns off or where municipal or industrial pollutants deplete oxygen due to high respiratory demand downstream of their input (Fig. 17.3). In these cases, the aquatic insect fauna will more closely mimic that found in oxygen-poor standing waters (many dipterans, for example). Some behavioral adaptations allow insects to survive periods of low oxygen in flowing water. For example, perlid stoneflies perform “push-ups” when oxygen declines, presumably to move more oxygenated water across their ventral thoracic gills. Burrowing mayflies of the genus *Hexagenia* undulate their body to draw water, and thus food and oxygen, through their burrows.

![Figure 17.2](image1.png)

**Figure 17.2** Respiratory structures of aquatic insects: (A) ventral air bubble of the backswimmer *Neoplea* (Heteroptera: Pleidae); (B) longitudinal section of postabdominal respiratory siphon of the mosquito larva *Taeniorhynchus* (Diptera: Culicidae), used to pierce plant air stores; (C) abdominal filamentous tracheal gills of the caddisfly *Anabolia* (Trichoptera: Limnephilidae).

![Figure 17.3](image2.png)

**Figure 17.3** Oxygen features in streams. Oxygen “sag” in a river receiving a point discharge of municipal waste. BOD, biological oxygen demand; COD, chemical oxygen demand; PPr, primary production.
2. Water Temperature

Water temperature also imposes constraints on aquatic insects. Temperature directly affects insects by regulating metabolic rates and thus development from egg to adult, and indirectly, by influencing such things as fluid dynamics, gas saturation constants, and primary productivity rates\[144\]. Water temperature fluctuates both spatially and temporally. For example, stratified lakes show marked temperature gradients from top to bottom (Fig. 17.1), while rivers can show horizontal (bank to bank) and longitudinal (source to estuary) gradients in temperature. Low- to mid-order streams also may exhibit pronounced diel temperature fluctuations, especially on sunny days. Shallow unshaded wetlands also exhibit large diel temperature fluctuations, ranging from subfreezing to tepid in northern wetlands. Thus, temperature variation imposes fundamental constraints on insect life histories in many aquatic habitats.

Some aquatic insects prefer a narrow range of temperature, usually cool water (cold stenotherms), whereas others can tolerate a broader range of temperatures (eurytherms). Consequently, temperature fluctuation can limit the types of insects found within a habitat. Any significant change in water temperature, as may result from thermal pollution or climate change, will likely alter the species composition of aquatic insects. Considerable variation in temperature tolerance occurs within the orders of aquatic insects, and so temperature preferences should be examined on a species-specific basis.

The upper lethal limit for all but the most specialized species is between 30°C and 40°C\[173,281\], although most temperate aquatic habitats do not approach such temperatures. However, thermally destabilized habitats, such as cooling water reservoirs, have temperatures which may approach this limit intermittently or seasonally, and abundance and richness of most taxa are negatively affected\[358\]. Types of insects that can tolerate and even thrive in hot water include various beetles and true flies, although species diversity declines with increasing temperature. For example, in a survey of hot springs, 60 species of Coleoptera were recorded at 30°C, but only two species occurred at 45°C\[54\]. At the other extreme, many species exhibit growth decline at temperatures only a few degrees above freezing in both lentic\[62\] and lotic systems\[304\].

Aquatic insects have multiple strategies for surviving subfreezing conditions, including morphological, behavioral, life history, and physiological adaptations\[210\]. Many aquatic insects can supercool to tolerate subfreezing temperatures in the range of −5°C to −7°C without forming antifreeze compounds\[115\]. Antifreeze compounds produced by some species also prevent freezing of bodily fluids to several degrees below 0°C\[94,104\]. Other species actually tolerate freezing of extracellular tissues, which provides some protection against intracellular freezing\[94,391,418\]. Cocoons and diapausing eggs are important life history strategies to prevent ice damage\[173\]. In arctic ponds that freeze solid, some insect species overwinter several times as larvae\[62\]. Because water and snow cover provide some degree of thermal buffering, even streams and ponds in the arctic do not drop more than several degrees below freezing. In north temperate regions, where terrestrial temperatures may reach −35°C, stream temperatures typically do not drop below −1°C in pools and −2°C in riffles\[163\] (Fig. 17.4). Thus, aquatic insects only need mechanisms that provide them with a few degrees of thermal buffering. In some streams, avoidance of ice scour may be a more serious problem for benthic insects than subfreezing temperatures, and many insects accomplish this behaviorally by migrating to areas that do not freeze\[261\]. Prior to the formation of surface ice, anchor ice attached to the streambed may form at night due to cooling associated with back radiation\[20\]. As the stream warms during the day, anchor ice lifts off the bottom, scouring the streambed.

Temperature, and its variation, can influence aquatic insect diversity in any freshwater habitat. For streams, the River Continuum Concept\[369\] predicts that biological diversity should be highest in mid-order (medium-sized) streams, in part because temperature variation is highest, thereby providing the most temperature “niches” for insects. The literature on this topic, however, is mixed. Insect faunal diversity can be high in cold streams, which are thought to be the ancestral habitat for aquatic insects\[174\]. For example, over 325 species of aquatic insects were cataloged in a cool Oregon stream\[111\]. On the other hand, over 500 species of aquatic insects were found in a warmer coastal South Carolina stream\[247\]. Over 20 species of mayflies alone were collected from wood snags in the warm Ogeechee River in\[33\], suggesting that aquatic insects can be diverse at a variety of temperatures.

3. Water Chemistry

Many aspects of water chemistry can restrict the occurrence or abundance of aquatic insects, including pH, salinity, and concentrations of specific ions or elements. Generally, it is the extremes in any of these parameters that result in change to aquatic insect communities, while levels around the mean have less direct impact. Low pH, as is found in acidified lakes and streams of pH <5 (due to acid deposition, mine drainage, organic acids, or poor buffering), can alter community composition such that only acid-tolerant taxa are found\[174\]. Several taxa of Ephemeroptera declined at pH below 5.5 in Ontario lakes, but odonates and chironomids increased, possibly due to the absence of fish predators\[68\]. However, it is unclear whether it is the low pH itself that adversely affects insects or some related factor. For example, iron can precipitate under acidic conditions with an associated reduction in oxygen. Acidic waters can also leach metals from soils and rock, especially
aluminum, which can increase drift and possibly have toxic effects on aquatic insects\textsuperscript{[137]}. Regardless, some aquatic insects thrive in acid streams and lakes\textsuperscript{[174]}. Salinity gradients that form in coastal estuaries, along saline lakes, and even from runoff after road salting, can affect insects, most of which are salt-intolerant. However, some insects such as brine flies (Diptera: Ephydridae) thrive in warm, saline water, where they have few competitors. Many other chemical features, such as calcium concentration and total ionic strength, have potential importance to aquatic insects, but little is known about the requirements of specific taxa.

4. Substrate and Flow

At the scale of local habitat, substrate and hydrodynamics are probably the most important factors determining the types and abundance of aquatic insects present. Swift currents in streams, wave action along shorelines, wind-generated turbulent mixing, and tidal action all present significant hydrodynamic challenges to insects. Most aquatic insects spend at least part, if not most, of their life cycle associated with the substrate, and hydrodynamic forces interact strongly with substrate type to produce the habitat experienced by the insect fauna. Hydrodynamic and substrate influences on aquatic insects are discussed in more detail in the sections below on lentic and lotic insect communities.

Eight categories of aquatic insect habits have been recognized\textsuperscript{[91]}, primarily based on the substrate or habitat they occupy. The first four groups remain associated with the substrate for most of their lives. Burrowers and sprawlers inhabit fine sediments where they either tunnel into the

![Graph showing temperature changes in French River, Minnesota](image-url)
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sediments or remain on top of the sediments, respectively. **Climbers** move along the stems of vascular macrophytes or pieces of detritus. **Clingers** attach themselves to the surfaces of substrates exposed to water movement, such as rocks in streams or along wave-swept lakeshores. The final four groups spend part, or most, of their lives moving through or on the water. **Swimmers** periodically propel themselves through the water to change location, although they mostly remain attached to a substrate. **Divers** split their time among swimming to the surface, diving back through the water, and clinging to submerged objects. **Skaters** are adapted for life on top of the water surface, where they use hydrophobic body parts to move over water. **Planktonic** forms float or swim about in open water.

1. **Littoral Communities**

Littoral areas of ponds and lakes are typically better oxygenated, structurally more complex, and afford more abundant and diverse food resources than do profundal sediments. All these factors lead to a high diversity of insects and very complex trophic interactions (see Section IV.C). Littoral communities generally have aquatic insect representatives from most aquatic orders (Table 17.2), including nearly all the morphological and trophic types as well as the full size range of aquatic species. Large taxa such as dragonflies, damselflies, many of the lentic mayflies, aquatic beetles and bugs, and caddisflies are important members of littoral zone communities, and are typically uncommon in profundal zones (Table 17.2).

Aquatic insects also show considerable spatial variability within the littoral zone[390]. Many species use macrophytes as habitat, while others are characteristic inhabitants of inorganic and organic sediments and periphyton in rocky areas. Macrophyte habitats usually have higher density and species diversity of insects, including many of the larger taxa mentioned above, than less structurally complex habitats because foraging efficiency of fish predators is reduced[86,121,150,360]. Patchiness of early instar larvae in littoral zones is at least partially determined by female oviposition behavior; a study in the United Kingdom showed that while adults were associated with riparian trees and early instar larvae with shaded microhabitats under the trees, food resources for larvae were more abundant in unshaded areas[140]. Many highly mobile species, particularly members of the Coleoptera and Heteroptera,

| Table 17.2 Aquatic insect communities in lentic habitats. |
|-----------------|-----------------------------------------------|-----------------------------------------------|----------------|
| Habitat type    | Habitat characteristics                      | Typical insect community                       | References     |
| Littoral        | High O₂, macrophytes, rock, sand, or silt substrata | Ephemeroptera (esp. Siphlonuridae, Baetidae, Heptageniidae, Caenidae, Leptophlebiidae), Odonata (representatives from most families), Diptera (many families but esp. diverse Chironomidae), Trichoptera (esp. Phryganeinae, Limnephilidae, Leptoceridae), Plecoptera (some Perlidae and Perlodidae), Hemiptera (most aquatic families), Megaloptera (few genera), Neuroptera (both aquatic genera), Coleoptera (adults and larvae of many families), Hymenoptera (parasitoids only) | 232, 390       |
| Eutrophic profundal | Low O₂, soft mineral and organic sediments | Chironomidae (esp. Chironomus, Procladius) | 166, 182, 232  |
| Oligotrophic profundal | High O₂, soft mineral sediments | Chironomidae (esp. Tanytarsini and Orthocladiinae) | 308            |
| Wetlands        | Variable hydrology, variable O₂, organic sediments, macrophytes | High diversity of most lentic orders. Diptera and Coleoptera are especially well represented. | 23, 162, 301   |
swim in the water column (plankton), or use the upper or lower surface of the air–water interface (epineuston and hyponeuston, respectively). Gyrid beetles, referred to as whirligig beetles because they swim in whirling swarms on the water surface, are especially well adapted for their habitat; they have dorsal and ventral compound eyes permitting them to see above and below the water surface simultaneously. The burrowing mayfly, Hexagenia, is often very abundant in littoral and sublittoral sediments of lakes, but is particularly sensitive to anoxia\textsuperscript{[26,285]}. A few Plecoptera (stoneflies) are found in erosional lentic habitats\textsuperscript{[401]}, reflecting the high oxygen requirements of members of this order. Smaller species, especially representing the dipteran family Chironomidae, also are usually very diverse and present in high densities. Despite the rich diversity and habitat complexity found in littoral areas, or perhaps because of it, the ecology of aquatic insects in littoral zones has attracted somewhat less study than in many other aquatic habitats.

2. Profundal Communities

Profundal zones of lakes have quite different communities than do littoral zones (Table 17.2). In both oligotrophic and eutrophic lakes, chironomids most often dominate the insect fauna. However, in eutrophic lakes, where the profundal zone is typically anoxic during much of the summer (Fig. 17.1a), Chironomus and Procladius may be the only insect genera present\textsuperscript{[166,308]}. Procladius is a free-living chironomid, most often characterized as a predator, but it also ingests a variety of sediment-dwelling algal diatoms and desmids\textsuperscript{[183,372]}. Although ubiquitous in lentic habitats, Procladius also is tolerant of low-oxygen conditions where Chironomus dominates. Chironomus switches from burrow construction and deposit feeding to construction of elevated U-shaped chimneys through which they pump water from the oxygenated zone, while also obtaining food particles\textsuperscript{[336]}. When filter feeding, feces are deposited on the sediment surface, forming mounds. At high density, this feeding mechanism can be important in returning phosphorus to the water column\textsuperscript{[67,117]}. However, the trophic ecology of Chironomus is much more complex than suggested by the filter-feeding model (Fig. 17.5). Recent studies have shown that methane-derived carbon is an important resource for Chironomus larvae. Methane is produced by two major groups of methanogenic bacteria, which are obligate anaerobes\textsuperscript{[421]}. One group utilizes acetate derived from the dissolved organic carbon (DOC) pool, while a second group utilizes hydrogen (H\textsubscript{2}) and carbon dioxide (CO\textsubscript{2}) to produce methane (CH\textsubscript{4}). CH\textsubscript{4} produced from either pathway is utilized by methane-oxidizing bacteria (which are aerobes). Recent studies have shown that utilization of these bacteria by Chironomus is often trophically significant\textsuperscript{[107,129,130,131,153]}. Furthermore, the role of methanogenic carbon in Chironomus diets is greater in lakes that are more subject to anoxia in the profundal zone\textsuperscript{[153]} (Fig. 17.5).

In oligotrophic lakes, the chironomid community in the profundal zone is more diverse than in eutrophic lakes, but still depauperate compared to littoral zones. The presence of Chironomus spp. is indicative of lake trophic conditions. Indeed, an elaborate key to lake typology which recognizes several categories of trophic conditions has been developed based on the occurrence of chironomid genera and species\textsuperscript{[308]}, and lake classification has a long history based on chironomid assemblages\textsuperscript{[52,57]}. Because the habitat of profundal zones is much less structurally complex than littoral zones, and oxygen is not limiting in deep oligotrophic lakes, direct effects of fish predators appear to be much stronger than in littoral zones (see Section IV.C).

3. Wetland Communities

The various types of wetlands afford a variety of habitats for aquatic insects. Many wetlands support similarly species-rich insect communities as do littoral zones of lakes. But unlike lake littoral zones and most other aquatic habitats, the dipteran suborder Cyclorapha can be very common\textsuperscript{[186]}. Also similar to littoral zones, insect biomass is positively associated with emergent vegetation\textsuperscript{[189,329]}. However, water level is highly variable in wetlands, by definition, and many wetland types are subjected to periods of desiccation. Desiccation provides a variety of challenges for aquatic insects, and results in somewhat different communities than are found in more permanent lentic ecosystems\textsuperscript{[398]}. Insect emergence was greatest from wetlands with an intermediate hydroperiod, reflecting trade-offs between desiccation stress and the presence of fish in permanently inundated areas\textsuperscript{[309]}. Hydroperiod is likely, therefore, to be the most important factor affecting
wetland insect communities\textsuperscript{[23,162,317,398,402]}. Insect species in ephemeral wetland habitats exhibit either desiccation-resistance or drought-avoidance strategies\textsuperscript{[402]}. Desiccation-resistant insects, especially many Diptera, and some odonates, caddisflies, and beetles, deposit drought-resistant eggs or lay eggs in plant stems, which then hatch to reestablish the habitat following the return of hydric conditions\textsuperscript{[23,402]}. Insects that avoid desiccation have several different strategies. Some migrate to more permanent habitats to complete one or more generations, which may be especially important for large predatory species\textsuperscript{[403]}. Wing polymorphism (i.e., long- and short-winged individuals of the same species) associated with this strategy is not uncommon and is particularly well studied in water striders\textsuperscript{[328]} and some beetles\textsuperscript{[173]}. Other insects have long flight periods as adults and thus will spend the drought cycle in the terrestrial environment\textsuperscript{[402]}. This strategy is also used by chironomids and mosquitoes, as well as some dragonflies and limnephilid caddisflies\textsuperscript{[402,413]}. These general strategies interact with life history such that wetland insect communities exhibit a succession following the drought cycle with dominance shifting from mosquitoes and chironomids to larger taxa such as beetles, odonates, heteropterans, and caddisflies\textsuperscript{[23]}. The extreme of this cycle is that prolonged drought results in very low density of insects\textsuperscript{[162]}. Under these conditions, the wetland fauna is characterized by high abundance of molluscs and annelids and low abundance and species richness of insects, but it becomes more and more dominated by a rich insect fauna with prolonged inundation\textsuperscript{[162]} (Fig. 17.6). Although wetland insect communities have received somewhat less study than other aquatic habitats, it is apparent that the species diversity and trophic complexity of these habitats reflect the life history variability of the various species and the complexity of the habitats, superimposed on a highly variable hydroperiod.

### D. Lotic Insect Communities

Lotic insect communities are functionally and structurally quite different from lentic communities due to the different physical and chemical challenges of the lotic environment. At a local scale in stream ecosystems, substrate and current velocity are probably the most important physical factors determining the community structure of aquatic insects. The stream substrate has obvious importance because the vast majority of stream insects spend most of their lives attached to substrates. Lotic substrates can be broadly divided into inorganic substrates (geologic material ranging from silt to boulders) and organic substrates (fine organic particles up to logs). The particle size of inorganic matter has a large influence on insect community structure. Coarser bed materials (e.g., gravel, cobble, and boulders) generally provide more interstitial habitat for insects than do finer sediments (e.g., sand and silt). For example, water penny beetles (family Psephenidae), hellgrammite larvae (Megaloptera: Corydalidae), and perlid stoneflies (Plecoptera) frequently are found in interstitial spaces on the undersides of rocks. Sedentary filter-feeding insects require the space between particles both to operate their filtration device (e.g., nets, specialized body parts) and to allow water flow to carry food items to them. Many case-building caddisflies pupate in dense aggregations on
Flow affects many aspects of insect biology, including body form, food acquisition, and movement. Taxa found in the swift currents of streams usually are streamlined (e.g., *Baetis* mayflies), dorsoventrally compressed (e.g., heptageniid mayflies and psephenid water penny beetles), possess suctorial disks (e.g., blepharicerid flies), use rock ballast in their cases to resist the flow (e.g., *Glossosoma* caddisflies), or are small enough to fit almost entirely within the sheltered boundary layer (e.g., chironomid midges). Many insects take advantage of swift flow by allowing current to transport food items to them. Examples include caddisflies of the family Hydropsychidae that construct silken nets to capture suspended food particles, blackflies (Simuliidae) that filter food with specialized mouthparts (Fig. 17.7A), and *Brachycentrus* caddisflies that capture particles on the setae (hairs) of their front legs (Fig. 17.7B). Filter-feeding insects also can be found along the wave-swept shores of lakes or on stable substrates (e.g., wood debris) of large rivers, where similar hydrodynamic forces are experienced. Many insects prefer low water movement, such as found in quiescent stream pools and along stream protected faces of cobbles and boulders where interstitial water flow carries the dissolved oxygen needed for metamorphosis, but they are more dispersed in the larval stage. A lower diversity of insects is typically found in fine sediments because the tight packing of particles restricts physical habitat and the trapping of detritus, and can limit the availability of oxygen. However, taxa adapted to such habitats (e.g., chironomid midges, oligochaete worms, certain mayflies) may be abundant. For example, densities of chironomid midges were found to exceed 80,000/m² in the sand substrate of an Alberta river. Organic substrates such as large woody debris or leaf packs often are “hot spots” for invertebrate activity because they provide both substrate and nutritional resources. In a survey of Oregon streams, 56 invertebrate taxa were found closely associated with wood, and another 129 taxa were determined to be facultative associates of wood. The more specialized moss habitat typically supports a high density of chironomids and other flies (e.g., moth flies, family Psychodidae) and a different assemblage of species than found on adjacent mineral substrates.

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margins. In these habitats, organic matter is deposited by gravity and thus can be gathered and ingested. These taxa often are more wormlike than swift-water forms.

Variation in flow (floods to desiccation) is the major cause of natural disturbance in streams (see Section V.A) and is responsible for large, usually temporary, reductions in macroinvertebrate abundance and diversity. The hyporheic zone and the undersurfaces of rocks provide refugia during flood events (Fig. 17.8). During drought, the deep hyporheic zone is especially important, but is usually accessible only to smaller invertebrates (typically about 1–5 mm in length). The spatial extent of the hyporheic zone varies with local geomorphology. In bedrock-dominated reaches, it is virtually nonexistent, whereas in the Flathead River, MT, the hyporheic zone may extend tens of meters vertically and up to 3 km laterally from the river, supporting relatively large stoneflies several millimeters in length. Finally, recolonization by egg-laying adults or by individuals drifting from upstream (Table 17.3) serves to reintroduce taxa that become locally extinct during drought, flood, or other disturbance events.

1. Functional Feeding Groups

Rather than focusing on the species as the ecological unit in streams, aquatic insect ecologists often consider the insect community in terms of functional feeding groups. The functional feeding group approach categorizes stream consumers according to their mode of feeding, or functional role, rather than taxonomic groups. From an ecosystem perspective, this approach reduces the number of groups to be considered by 1–2 orders of magnitude compared to the species approach. Thus, rather than studying dozens or hundreds of specific consumers, a smaller number of groups of organisms can be studied collectively from the perspective of their function in the stream ecosystem. This categorization also has utility in other aquatic ecosystems, and has recently been applied to all North American aquatic insects regardless of habitat.

Commonly recognized functional feeding groups are: (1) scrapers (grazers), which remove and consume attached algae and associated periphytic material; (2) shredders, which ingest coarse particulate organic matter (CPOM), as decomposing leaf litter, living macrophyte tissue, or dead wood; (3) predators, which eat living animals; and (4) collectors, which consume decomposing fine particulate organic matter (FPOM). The last group can be further divided into collector-gatherers, which collect FPOM from the sediments, and collector-filterers, which collect FPOM from the water column (Fig. 17.9). Two other, less common functional feeding groups among insects are the macrophyte-piercers, which pierce the tissues of macroalgae and rooted hydrophytes, and parasites, which develop on or in aquatic insects, generally killing them. Because groups of insect species can be studied collectively to unravel major avenues of organic matter processing, the functional feeding group approach greatly simplifies the study of insect function in aquatic ecosystems. It also provides a strong basis for comparative studies of the biomass and productivity of consumer groups across ecosystems, whereas it is much more difficult (and often less informative) to make such comparisons on a species-by-species basis.

**Figure 17.8** Channel cross section of a stream, showing position of hyporheic zone relative to surface water and groundwater.
TABLE 17.3 Mechanisms of insect recolonization of stream reaches\[^{158}\].

<table>
<thead>
<tr>
<th>Mechanism</th>
<th>Time scales</th>
<th>Example</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Downstream drift</td>
<td>Nocturnal, constant, episodic, dispersal stages of some invertebrates</td>
<td>Many insects</td>
<td>394</td>
</tr>
<tr>
<td>Drift from tributaries</td>
<td>Nocturnal, constant, episodic, dispersal stages of some invertebrates</td>
<td>Many insects</td>
<td>64</td>
</tr>
<tr>
<td>Upstream flight</td>
<td>Seasonal, depending on emergence period</td>
<td><em>Baetis</em> mayflies</td>
<td>161</td>
</tr>
<tr>
<td>Flight from other watersheds</td>
<td>Seasonal, depending on emergence period</td>
<td>Many insects, <em>Baetis</em> mayflies</td>
<td>316, 383</td>
</tr>
<tr>
<td>Upstream swimming</td>
<td>Seasonal</td>
<td><em>Leptophlebia cupida, Paraleptophlebia</em> mayflies</td>
<td>43, 148</td>
</tr>
<tr>
<td>Upstream crawling</td>
<td>Daily</td>
<td><em>Dicosmoecus</em> caddisflies, <em>Juga</em> snails</td>
<td>44, 141</td>
</tr>
<tr>
<td>Movement from hyporheic refuge</td>
<td>Episodic, seasonal</td>
<td>Many early instar insects; overwintering stages of many insects in cold climates; many residents of intermittent streams</td>
<td>96, 163, 319</td>
</tr>
</tbody>
</table>

FIGURE 17.9 Simplified food web for a hypothetical North American forested stream, showing major energy inputs and use by different macroinvertebrate functional feeding groups.\[^{198,425}\]. Macroinvertebrate examples are: shredders (*Peltoperla* stonefly, *Tipula* cranefly, *Hydatophylax* caddisfly); collector-filterers (*Hydropsyche* caddisfly, *Simulium* blackfly); grazers (*Glossosoma* caddisfly, *Juga* snail); predators (*Calineuria* stonefly, *Orohermes* hellgrammite). Broken lines indicate fate of fecal matter.
Although implementation of this approach has been an important precedent for the development of other major paradigms of aquatic ecology (e.g., the River Continuum Concept[369]), the functional feeding group concept is not without limitations. First, assignment of individual organisms from aquatic samples to a functional feeding group generally requires identification of the organism to family or genus. This can be a very time-consuming task, although a shortcut approach using an illustrated key is effective for many taxa[233]. Second, feeding ecology can vary within a genus, and even within a species depending on habitat or food availability. Thus, published functional group designations for the generic level are not always reliable[238]. In fact, many aquatic insects are known to change feeding habit with growth and development[78,283]. For example, the large limnephilid caddisfly Dicosmoecus gilvipes begins larval life as a collector-gatherer, feeds primarily as a scraper of periphyton during the middle instars, and finally becomes partly predaceous in the final instar[123,211]. Other insects are omnivorous throughout their lives. Filter-feeding caddisflies of the genus Hydropsyche will consume virtually anything that becomes entrapped in their nets, including FPOM, living algae, and small animals[35], thus making them potential members of several functional feeding groups.

Some orders of aquatic insects, or the aquatic representatives within an order, perform mostly as a single functional feeding group, whereas others show great diversity in feeding (Table 17.1). Generally, the more primitive orders of aquatic insects show more limited diversity in feeding mode. For example, aquatic collembolans are exclusively collector-gatherers, odonates are strictly predaceous, and stoneflies (Plecoptera) are either shredders or predators, generally depending on family. Less speciose orders also tend to show less feeding diversity, as one might expect. For example, megalopterans are entirely predaceous, neuropterans pierce either animals or plants, and aquatic hymenopterans are mostly parasites. In contrast, more derived orders such as Trichoptera, Diptera, and Coleoptera show considerable diversity in feeding mode, in part due to their large number of aquatic species. The Diptera and Trichoptera, in particular, have been enormously successful in freshwater ecosystems. Chironomid midges alone may equal the species diversity of all other insects combined in a typical aquatic ecosystem. In any specific stream, it is usually possible to find caddisflies represented in all functional feeding groups, and often dominating the biomass of those groups. Beetles possibly occupy the broadest range of aquatic habitats, ranging from ice fields to seashores, and can be very speciose.

2. Longitudinal Patterns in Functional Feeding Groups

Functional feeding groups are thought to vary in predictable ways from headwaters to large rivers, as predicted by the River Continuum Concept (RCC)[369], an important paradigm in stream ecology. The RCC predicts that small, heavily shaded streams will have high inputs of detritus (allochthonous CPOM) from adjacent riparian zones. Due to this abundant detritus, shredders will dominate the macroinvertebrate community. Both collector-filterers and collector-gatherers also will be abundant because high-quality FPOM will be produced as CPOM is fragmented. In medium-sized streams, light inputs increase and thus benthic algal production will increase. The shredders are replaced by scrapers, while collectors remain abundant. In large rivers, benthic algal production and direct riparian inputs decline. Food resources for macroinvertebrates are dominated by FPOM in suspension; collectors dominate the macroinvertebrate community. In all streams, predators comprise a small but fairly stable proportion of the fauna. These predictions were tested for the McKenzie River drainage in Oregon, which consisted of streams ranging in size from first to seventh order[147]. Functional feeding group distributions were found to be generally consistent with predictions of the RCC (Fig. 17.10). These longitudinal shifts were more pronounced than were seasonal fluctuations in community structure in the individual Oregon streams. Not all studies of functional feeding groups have shown the same degree of conformance to the RCC[241,412]. Some groups, such as shredders, predictably decline with increasing stream size, whereas other groups, such as scrapers, do not fit tightly with RCC expectations. In evaluating conformance to the RCC, abundance and biomass have often been considered as currency. However, some researchers have argued that production rather than biomass is a more appropriate currency as it is a better measure of transfer of energy between trophic levels[29,30,132]. Large rivers, at least in their natural state, likely have more complex energy inputs than implied by the RCC. The Riverine Productivity Model[157] was developed, which suggested that riparian inputs and benthic primary production are quite important to insect production in large rivers. This is contrary to predictions of the RCC. A preliminary test of the model in the Ohio River suggested that the shallow edges of large rivers function similarly (and have similar insect communities) as mid-order streams, because they receive riparian litterfall and also have substantial periphyton production. Riparian canopy highly influenced functional feeding group composition in six small streams in Oregon[146], but the absence of canopy increased the abundance of all functional feeding groups possibly because both autotrophic (on-site) and heterotrophic (from upstream) inputs were received. Hence, insect consumers responded to the abundance and composition of the available food resources. This notion of energy transfer via both autotrophic and heterotrophic food webs underpins the lotic ecosystem model[228], which postulates a hierarchical organization to stream food webs and a central role for aquatic insects.
3. Insect Drift

Drift is the downstream transport of organisms in the current (usually expressed as number/m$^3$), and is a unique property of stream ecosystems. Because drift provides insects with a unidirectional transportation system, it has the potential to be important to the distribution and ecology of stream insects. At any given time, the proportion of fauna in the drift, compared to that on the substrate, is typically very small (0.01–0.5%)\cite{362,394}. Some insect species and groups have a much greater propensity to drift than others. Mayflies, especially $Baetis$, and larval chironomids are perhaps the most common insect drifters, but most other aquatic insect groups are also well represented in the stream drift. Stream drift has been well characterized for a wide range of stream types, and there is reasonable understanding of mechanisms determining drift entry and the consequences of drifting (Fig. 17.11). Because many fish feed on drifting insects either partially or exclusively, many drift studies have also focused on the importance of drift in supporting fish production\cite{282}.

Insects that entered the drift were once thought to be essentially lost from the system. Although estimates of drift distance vary widely, most experimental studies in small- to mid-sized streams have shown that insects drift only a short distance (a few meters or less) during any drift event\cite{6,409}. However, in a high-order blackwater river with an important but widely dispersed snag habitat, insects drifted kilometers between snags\cite{31}. 

![Figure 17.10](image1.png) Longitudinal changes in relative abundance of macroinvertebrate functional feeding groups at different seasons within an Oregon, USA, river system\cite{147}. Collectors, collector-gatherers; Filterers, collector-filterers. Stream size increases along the x-axis; DCC, Devilsclub Creek; MACK, Mack Creek; LOKC, Lookout Creek; MZER, McKenzie River. Note the general conformance to the predictions of the River Continuum Concept\cite{369}.

![Figure 17.11](image2.png) Conceptual model of the colonization cycle of aquatic insects\cite{425} illustrating that mechanisms underlying the downstream component of the cycle are relatively well understood compared to upstream component of the cycle.
Insects may drift passively or inadvertently if they are dislodged, such as might occur during a very high discharge event or in response to an anthropogenic disturbance. However, most experimental studies have suggested that most drift is active, or a behavioral response to some stimulus. This can occur catastrophically in response to stressors such as chemical spills or high levels of UVB radiation, or on a smaller scale in response to depleted food resources or the presence of a predator. Drift was hypothesized to be density dependent, such that drifting insects represented a portion of the population exceeding the carrying capacity of the stream. However, empirical studies of drift have yielded little support for the density-dependent hypothesis.

In most streams, drift densities are much higher at night than during daylight hours. Because fish feed heavily on drifting invertebrates, nighttime drift behavior provides invertebrates with more protection from fish predation. Because many macroinvertebrates forage more on the upper surfaces of rocks at night, it was once thought that dislodgment was simply more likely at night. However, it has been found that well-fed Baetis foraged only at night on tops of stones, while starved nymphs foraged during both day and night but drifted similarly to fed nymphs. Thus, activity during foraging was not related to drift (i.e., they were not accidentally dislodged) and drift entry was active.

Clearly, drift is an important mechanism for invertebrate dispersal, especially for early larval instars. It is also an important means for recolonizing reaches impacted by natural or anthropogenic disturbance. However, if there were no upstream movement of macroinvertebrates, downstream drift potentially could result in a net displacement of populations, net depletion of upstream reaches, and loss of invertebrate-mediated ecosystem functions in depleted areas. One proposed colonization cycle stated that insects displaced downstream as larvae later fly upstream as adults to oviposit, thereby repopulating depleted areas. However, it has also been argued that upstream compensation is not necessary for population persistence.

Upstream flight has been observed for some taxa and quantified using a stable isotope tracer for a Baetis mayfly population in arctic Alaska (Fig. 17.12) and a Leuctra stonefly population in New York. Upstream flight is clearly also an important mechanism for recolonizing headwater reaches that have experienced catastrophic disturbances. Upstream movement of aquatic larvae has also been observed, and is an additional mechanism that may compensate for downstream drift. However, genetic studies of rainforest streams revealed limited downstream displacement of aquatic insects, and upstream reaches were populated by offspring of a few individuals. More research is needed on the topic of directional upstream dispersal; despite a relatively good understanding of drift behavior, an upstream flight component of the colonization cycle appears to differ considerably among taxa, but is certainly less well understood than is the phenomenon of downstream drift (Fig. 17.11).

**E. Saline Habitats**

Insects have enjoyed only limited success in colonizing the marine environment, and the only truly oceanic taxa are surface-dwelling, water striders of the genus Halobates. The reasons for this are unclear but have variously been attributed to physiological stresses associated with respiration and osmoregulation, physical stress...
of wave action, competition for habitat and resources with established species, and predation\textsuperscript{173,390}. Because several species of beetles, true flies, and caddisflies have successfully colonized intertidal zones and brackish waters, it seems unlikely that physiological stresses alone have hindered radiation into the marine realm. Chironomidae, Culicidae, and Ceratopogonidae are very common in salt marshes\textsuperscript{119}. With increasing saltwater inundation in estuaries, Chironomidae dominate the insect fauna and may be important in the diets of estuarine fishes\textsuperscript{406,408}. A damselfly actually grew faster at intermediate salinity than in freshwater, but high salinity was lethal\textsuperscript{185}. Across a salinity gradient, however, insects tend to decline proportionally, while crustaceans increase\textsuperscript{46}. Similarly, physical stress also seems unlikely to be a major hindrance both because many low-energy marine habitats exist and because many insects inhabit wave-swept lakeshores and stream riffle habitats. These considerations suggest that competitive and predatory pressures from marine phyla, which have been established in marine habitats much longer, are the most likely mechanism that has precluded high insect diversity in marine habitats\textsuperscript{173,363,390}. Alternatively, insects may be in the early stages of invading marine systems, such that they may yet become established there after many more millennia\textsuperscript{405}.

F. Specialized Habitats

Aquatic insects have invaded many specialized microhabitats. The species that comprise these communities often have morphological, behavioral, and life history adaptations which are unique to those habitats and reflect the remarkable phenotypic plasticity of the Insecta. Some of the better-studied examples of these habitats include tree holes, hot springs, pitcher plants, and caves and other subterranean environments\textsuperscript{390}.

Mosquitoes are particularly well adapted to specialized ephemeral habitats such as tree holes, tires, rain gutters, and other containers that catch rainwater\textsuperscript{234}. Filter feeding is the most common mechanism for acquiring food in such habitats, but detrital and bacterial particles may also be gleaned from leaf and bark surfaces, and a few species are predatory\textsuperscript{234}. In tree hole habitats, a combination of leaf litter quality, litter quantity, and stemflow nutrients influence mosquito productivity\textsuperscript{69,70}, but field experiments\textsuperscript{373} found no evidence that quantity of leaf detritus was limiting.

Aquatic insects inhabiting subterranean habitats, including cave pools and streams, underground rivers, and extensive hyporheic zones, share some morphological characteristics. These insects, like many other subterranean invertebrates, lack pigment, have reduced or absent compound eyes and ocelli, and possess reduced wings\textsuperscript{390}. Diptera and Coleoptera are perhaps the best represented among subterranean insects although representatives of other groups also have been reported\textsuperscript{390}. The trophic ecology of these insect communities is dependent on organic matter imported from surface ecosystems. Most common among these nutritional sources are flocculated DOM, entrained FPOM, bacteria (which utilize DOM), and bat guano.

Geothermal springs are another specialized habitat that has been exploited by some insects. Hot springs tend to have representatives from the Diptera, Coleoptera, and Odonata\textsuperscript{390}. In addition to the high temperatures, these habitats also have high mineral content, which may pose toxicity problems for some species. However, thermal effects were more important than chemistry in limiting insect diversity in a northern California stream receiving natural hot spring inputs\textsuperscript{203,205} (Fig. 17.13).

III. AQUATIC INSECT LIFE HISTORIES

Aquatic insects show tremendous diversity in their life history patterns, including differences in reproductive and dispersal strategies, life cycle length, growth rate, developmental strategies, and phenology of the various life history stages. This great variety serves to separate taxa seasonally and spatially, thus providing the basis for the varied and dynamic nature of aquatic insect community composition.

Developmentally, most insects can be categorized as either \textit{hemimetabolous} or \textit{holometabolous} (Fig. 17.14). Collembola, considered \textit{ametabolous}, have a developmental pattern that is distinctive from other insects and is phylogenetically primitive. This has led some entomologists to exclude it from the Insecta\textsuperscript{48}. The insect orders Ephemeroptera, Odonata, Heteroptera, and Plecoptera are \textit{hemimetabolous}. The aquatic immature forms, with few exceptions, respire using gills, and although they may differ considerably from adults, they are clearly insect-like.
The immature stages are referred to as nymphs or larvae. A newly hatched larva is referred to as a first instar, and larval development proceeds through a series of instars. The number of instars varies widely among families, but variability also may occur at the species level depending on environmental conditions[48]. Most aquatic insects are holometabolous, which means they undergo complete metamorphosis (Fig. 17.14). The immature instars are referred to as larvae and do not resemble the adults. Larval appearance is variable, but is usually not insect-like. Commonly, larvae are described as wormlike, grub-like, or caterpillar-like. A pupal stage that follows the last larval instar is characterized by development of the adult form in a protected habitat or cocoon. The insect does not feed during this stage and appears quiescent. However, metabolic activity is very high as larval tissues are reorganized to form the morphologically and physiologically different adult form.

Virtually all aquatic insects have an aerial adult phase. Copulation usually occurs outside of the aquatic environment, and eggs are laid on or in the water for most species. Typically, the larval stage dominates the life cycle; the adult stage is very short and does not always involve feeding. Notable exceptions to this rule are the Odonata (dragonflies and damselflies), which are long-lived and voracious predators as aerial adults, and aquatic Hemipteran and Coleoptera, in which the adult as well as the larval forms are also typically aquatic and long-lived. Many dipterans also feed as adults. Mosquitoes and blackflies are notorious pests, but are also vectors of diseases such as malaria, encephalitis, dengue, Rift Valley Fever, river blindness, West Nile virus, and many others that infect and kill millions of people worldwide[178,187,287]. With climate change, the geographic distribution of these diseases is increasing[56,344].

For many aquatic insects, the adult phase is often important to dispersal between lentic habitats, and permits upstream oviposition (Fig. 17.11), and oviposition between watersheds[383] in lotic habitats. Surprisingly, despite the tremendous evolutionary and ecological importance of oviposition behavior, it is poorly studied relative to other aspects of aquatic insect life histories[288]. Even though aquatic beetles and bugs have aquatic adult forms, dispersal still is accomplished by the adult stage, which is usually winged. Dispersal varies tremendously among insects and has been studied thoroughly for only a few taxa. For example, Baetis mayflies in a tundra river in arctic Alaska have been shown to fly approximately 2 km upstream to lay eggs[161]. Larval insects also can move substantial distances, aside from drift. For example, late instar larvae of the grazing caddisfly Dicosmoecus gilvipes can crawl up to 25 m per day in search of algal food[141]. Nymphs of
the lotic mayfly *Leptophlebia cupida* move upstream at an average rate of 10 m per hour during seasonal migrations between habitats[148]. The frequency with which an organism completes its life cycle is referred to as *voltinism*. Depending on environmental constraints, especially temperature and nutrition, as well as evolutionary factors, aquatic insects may be univoltine (one generation per year), multivoltine (more than one generation per year; e.g., bivoltine = 2/yr and trivoltine = 3/yr), semivoltine (2-year life cycle), or merovoltine (3- or more-year life cycle). Generally, larger insects will have longer life cycles than smaller species. For example, in the Kuparuk River in Arctic Alaska, the relatively small *Baetis* mayflies are univoltine, but the larger *Brachycentrus* caddisflies are merovoltine[154]. Univoltine development is by far the most common, especially in temperate regions[173]. However, even in arctic streams, where the streambed is frozen for almost 9 months, most species are univoltine[154]. Arctic lakes have chironomid populations with life cycles ranging from 1–4 years, but univoltine development predominates[151]. One arctic pond species of chironomid has a 7-year life cycle[62]. Temperate regions display similar variation. The wood-boring aquatic beetle *Lara avara* has about a 5-year life cycle, likely due to the low nutritional value of wood[12]. At the other extreme, some herbivorous chironomid midges in warm desert streams can complete their life cycle in as little as 2 weeks, a distinct advantage in desert streams where floods scour organisms and resources[112].

Variation in growth rate is also important in distinguishing insect species, separating cohorts, and providing structure to aquatic insect communities. Within physiological constraints, temperature and food are the major factors affecting growth for most taxa. These factors vary widely within and between lentic and lotic ecosystems, as well as geographically.

In cool climates, many aquatic insects have life cycles with synchronized development. Environmental factors, especially temperature and photoperiod, as well as evolutionary factors serve as proximal cues that synchronize life cycles[63]. For example, many insects will overwinter in the egg stage and hatch in the spring. Others may overwinter as larvae, emerging in the spring when the appropriate temperature and/or photoperiod cues are present. Although multiple evolutionary and environmental mechanisms can contribute to synchronous development, and contributing factors vary among species[63], individuals in a cohort, or age class, of the same species will emerge during a very short interval, enhancing the probability of mating success. Synchrony occurs through two general paths. Larval hatching and growth may be timed such that all individuals within a cohort are of identical or nearly identical size throughout their development and emerge together. This is common in many caddisflies, such as the widely distributed *Helicopsyche borealis*[294] and the large limnephilid *Dicosmoecus gilvipes*[202]. Alternatively, hatching and larval development may not be synchronous but instar-specific growth rates still may result in synchronized emergence[217].

Within a community, co-occurring species typically exhibit a variety of patterns of voltinism and synchrony. For example, 14 species of dragonflies in a temperate pond were found to have several different developmental patterns[413]. *Epitheca cynosura* was univoltine with synchronous development; *E. princeps* was synchronized but semivoltine; and another congener, *E. simplicollis*, was sometimes bivoltine. Asynchronous univoltine development occurred in *Libellula lydia*, while other species showed different combinations of synchrony, asynchrony, and mixed voltinism[413].

### IV. INSECT-MEDIATED PROCESSES

Insects are important consumers and important prey items in virtually all aquatic habitats, and thus are intimately involved in the flows of matter and energy that occur in these ecosystems. Insects also exert top-down controls on nutrient cycles, primary productivity, decomposition, and translocation of materials, and affect relative abundances of other consumers in lentic as well as lotic ecosystems. Specific relationships between insects and aquatic resources that are of particular interest include detritivory, grazing, and predation. Processes that integrate one or more of these specific relationships include secondary production and stream drift. All these processes are shaped by physical habitat and life history constraints.

#### A. Detritivory

Detritivory, the feeding on decaying organic matter, is a major insect-mediated process in both lentic and lotic systems, although it has received more attention in lotic studies. The relative importance of allochthonous versus autochthonous detritus in aquatic ecosystems is widely variable, and size of the water body is the major determining factor. Consumer resources in small lentic systems and low-order streams are typically dominated by allochthonous inputs, whereas large lakes and middle-order streams[369] are more likely to be dominated by autochthonous production. When detritus is plentiful, however, insect detritivory is usually important to ecosystem function.

Detritus forms a major habitat for aquatic insects in ponds and many wetlands. The coarseness of the detrital substrate provides habitat for large aquatic insects, such as odonate nymphs, which prey on small detritivorous chironomids, mayflies, and microcrustaceans. For some large insects, detritus serves as a food source, although
availability of detritus seldom limits wetland insect abundance or production, and microbial decomposition appears to be more important than insect-mediated decomposition in many wetlands\textsuperscript{[23]}.

Low-order streams are strongly influenced by the input of terrestrial organic matter from adjoining ecosystems. In temperate streams, much of this detritus enters as a seasonal (autumnal) pulse of leaves, which is then processed in the stream by microbial and macroinvertebrate communities, and serves as the major energy source for many stream consumers (Fig. 17.9). Life cycles of many detritivorous insects are cued to this seasonal pulse of leaves such that they develop through the fall and winter when their food resource also is plentiful. Microbes, which colonize the detritus, form an integral part of the CPOM complex and are nutritionally important to shredders\textsuperscript{[12,90]}. Dominant shredder taxa vary according to stream type and biogeography. Shredders are found in many of the aquatic insect orders (Table 17.1). Some of the more conspicuous insect shredders are pteronarcid and capniid stoneflies, larval craneflies, and several families of caddisflies. Low-order streams often have 30–50% shredders in their macroinvertebrate communities (Fig. 17.10), as was found in Oregon streams\textsuperscript{[147]}, by virtue of their closed canopy and high input of CPOM per unit of stream surface\textsuperscript{[369]}.

In a first-order mountain stream, an ecosystem-level experiment (litter exclusion by suspending a net over a small stream) was used to demonstrate that terrestrial litter supported the vast majority of insect secondary production in the stream\textsuperscript{[375]}. Interestingly, insects and other consumers occupying a moss microhabitat in the stream did not respond to litter exclusion, suggesting that moss inhabitants comprised a food web that was independent of that supported by terrestrial detritus\textsuperscript{[375]}. In a different study, experimental reduction of shredders in a stream using an insecticide resulted in lower CPOM decomposition (20–40% that of a reference stream) and 5–15-fold lower FPOM transport\textsuperscript{[384]}. Clearly, insects are of critical importance to CPOM processing in streams.

Formation of FPOM from CPOM by shredders during their feeding is an important process. FPOM is also formed by several other mechanisms and is dynamic in stream food webs. All consumers produce feces, which are an important component of FPOM\textsuperscript{[160,320]}. Bacteria use DOM, thereby incorporating it into bacterial biomass, which itself constitutes a portion of the FPOM pool\textsuperscript{[236]}. Bacteria produce extracellular materials, which are sloughed into the FPOM pool\textsuperscript{[417]}. FPOM is produced by flocculation of DOM due to a variety of physical and chemical processes\textsuperscript{[93,271,389,417]}. The mass of FPOM usually exceeds that of nonwoody CPOM by about an order of magnitude\textsuperscript{[379]} and turns over much more rapidly. Insect collector-filterers and collector-gatherers that use this resource are important components of the macroinvertebrate community in all streams\textsuperscript{[147,369]} (Fig. 17.10). However, because FPOM is formed by many processes, it varies widely in quality; some FPOM is highly labile but much is refractory\textsuperscript{[157]}. Its retention in streams is also high but varies considerably due to physical and/or chemical characteristics of the particles\textsuperscript{[239]}. The variety of collectors that use FPOM also is very high (Table 17.1).

DOM is generally considered to be the exclusive resource of stream microbes, which assimilate labile components of DOM into microbial biomass\textsuperscript{[214,236]}. However, larval blackflies also ingest DOM\textsuperscript{[416]} (Fig. 17.15), and this process can be important to the size and quality of the FPOM pool downstream of blackfly aggregations\textsuperscript{[160]}. DOM ingestion by blackflies includes some labile material, such as bacterial exopolymers\textsuperscript{[83]}, and thus such feeding may be a nontrivial source of nutrition for these aquatic insects. Although direct DOM ingestion by stream insects is not thoroughly understood, its importance is likely limited to a few taxonomic groups.

Large woody debris (LWD) often forms an important pool of detritus in stream ecosystems\textsuperscript{[12,42,346,365]}. Wood may cover over 25% of the beds of small streams in
old-growth forests\cite{12}. However, only very specialized insects use this material as food, and these likely do not ingest quantities that are significant to wood decomposition\cite{173}. LWD is important as macroinvertebrate habitat. In a southeastern blackwater stream, much of the secondary production was found to be associated with woody snags\cite{341}. In addition, the insect community on the snags was distinct from other substrates. LWD also serves an important mechanism for retaining CPOM and FPOM resources that are used by insects\cite{341}. In addition, LWD is a major factor defining pool and riffle habitat within a stream, which determines many aspects of macroinvertebrate community structure. Wood itself has low nutritional value, but the microorganisms that coat submerged wood (e.g., algae, bacteria, fungi, protozoans) provide a rich food resource for macroinvertebrates.

A few invertebrates (wood gougers, a special group of shredders) are adapted to feed directly on the wood and include the cranefly larva Lipsothrix and the elmid Lusta avara\cite{12,173}. These taxa bore into and feed strictly on wood and have very long life cycles (3–6 yr) as a result of the low nutritive value of their food. Examining a piece of water-logged wood will reveal the tunnels of these borers and often the insects themselves. Wood is also used by some larval caddisflies for case construction. Heteroplectron californicum, a caddisfly that can be found in shallow pools, hollows out twigs to construct portable cases (Fig. 17.16). When the larvae move, their cases appear to be moving twigs, and the larvae themselves are not visible.

**B. Grazing**

Benthic primary production is a major process in virtually all shallow aquatic ecosystems\cite{195}. As a consequence, grazing insects functioning as primary consumers can be found in nearly all of those ecosystems except for perhaps where extreme physical conditions predominate\cite{201}. Aquatic primary producers include algae, rooted macrophytes, and bryophytes (mosses and livorworts). Benthic algae frequently are the dominant plants in streams and along rocky, wave-swept littoral zones, whereas rooted macrophytes become more important in the finer sediments of lakes and large rivers where they are exploited for both habitat and food by insects. Fine sediments may also be covered with a layer of algal epipelon, which is readily grazed by insects. Mosses can be locally important, especially in streams; and because of their fibrous texture and long-lived nature, they provide excellent habitat for a variety of insects\cite{122,343}. Where mosses line the rock walls and spray zones of waterfalls, a specialized insect fauna (torrenticolous insects) often develops. In the discussion below, we will mostly concern ourselves with grazers of periphyton and macrophytes.

Scrapers can be found in six orders of aquatic insects (Table 17.1), and for several of those orders (Ephemeroptera, Trichoptera, and Lepidoptera), algal consumption is a major way of life. Grazers often possess elaborate mechanisms to remove periphyton (attached algae, microbes, and associated organic matter) from surfaces\cite{196}. Many species of mayflies bear stout bristles on the labial or maxillary palps, which are effective in removing periphyton from cracks and crevices. These bristles increase in length with successive instars, thereby allowing older larvae to remove larger particles while younger larvae remove smaller particles, effectively partitioning the resource by age. Many caddisfly larvae have robust or scoop-shaped mandibles for transferring periphyton to their mouths. Some limnephilid caddisflies, such as Dicosmoecus, also use tarsal claws to gather algae into small piles for ingestion\cite{196}. Orthocladius chironomids have stout mandibles lined with 4–5 teeth, which wear down over time\cite{312} but are replaced during the molt process. Even presumed shredders, such as cranefly larvae (Tipulidae), possess setae on the cutting surfaces of their mandibles that may help to collect algae from leaf surfaces, thereby allowing these insects to function as facultative grazers\cite{280}. For shredders, the microorganisms, including algae, which grow on decaying leaves may be the most nutritional component of the leaves\cite{202}.

**FIGURE 17.16** Wood cases of the caddisfly Heteroplectron californicum next to shredded alder leaves. Note the opening chewed by caddisflies at upper end of twigs; larva resides inside the twig within a silk-lined tunnel\cite{38}.
a small, heavily shaded New Hampshire stream whose energy base was previously thought to be almost totally detrital. Still, periphyton is often limiting to the growth of insect grazers, and competition for algal resources has been demonstrated. Among stream insects, caddisflies and mayflies tend to be highly conspicuous grazers although small chironomid midges may be equally important herbivores due to their ubiquity, high densities, and short generation times. As individual species or groups of taxa, insect grazers can exert large effects on the abundance, productivity, and community structure of benthic algae. Often, a single species can be the primary regulator of periphyton. For example, Helicopsyche borealis caddisflies consumed >95% of the algal standing crop in a northern California stream. Experimental exclusion of these caddisflies produced a mat of filamentous algae almost 30 mm thick (Fig. 17.17). In another study, the large caddisfly Dicosmoecus gilvipes consumed about 60% of benthic algal production, and most of the remaining algae were dislodged and washed away by the grazing activities of these sloppy feeders. Furthermore, these large grazers can negatively affect other benthic invertebrates, which they bulldoze and thereby displace as they harvest periphyton.

Tightly evolved associations between plants and herbivores are well documented in terrestrial ecosystems. In aquatic ecosystems, however, there are few examples of host-specific associations between aquatic insects and benthic algae, for reasons that are still unclear. One possible example from North American streams is a mutualistic relationship that may exist between the chironomid midge Cricotopus nostocicola and the blue-green alga Nostoc parmelioides. The first-instar midge larva finds and enters a small, globular colony of Nostoc and begins feeding on Nostoc cells, in the process changing the colony morphology to an earlike form about 1 cm diameter (Fig. 17.18). These dark-green colonies often are quite obvious on rocks, and the single larva can be seen clearly within the colony. The midge grows and pupates within the colony, finally emerging as an adult. The association also may benefit the colony, which has a higher photosynthetic rate when the fly is present. Amazingly, the midge will reattach to the colony if it becomes dislodged from the substrate during a disturbance, which doubtless benefits both the colony and larva. Another example, although probably not mutualistic, is the association between the micro-caddisfly Dibusa angata and the freshwater red alga Lemanea australis. Larval instars 1–4 of Dibusa are found among the basal holdfasts of Lemanea, where they consume epiphytic diatoms. Fifth-instar larvae construct cases made of Lemanea and consume only Lemanea tissue. There is no known benefit of this association to the alga.

Many insects consume living macrophyte tissue, a generally understudied and underappreciated process. Unlike for algae, insects and aquatic macrophytes are often
closely associated, perhaps because the large size of rooted plants makes specialization more feasible than for microscopic algae. The major insect orders involved in macrophyte grazing are the Trichoptera, Lepidoptera, Coleoptera, and Diptera. It is perhaps not surprising that rooted hydrophytes are eaten by the more advanced insect orders, as their terrestrial insect relatives are also mainly plant eaters. Indeed, it has been speculated that over evolutionary time terrestrial insects followed their host plants as they gradually invaded the water to eventually become true hydrophytes. Furthermore, parasitoids of those insects may have followed their hosts, as evidenced by the hymenopterans that now parasitize aquatic lepidopterans. Insect grazers can consume up to 100% of the standing stock of macrophytes, although the damage is usually much less\textsuperscript{215}. It is more common to see the grazing scars of insects, such as beetles and moths, on the surfaces of floating leaves and other plant structures. Lepidopterans feed on aquatic plants in numerous ways, including leaf mining, stem or root boring, foliage feeding, and flower or seed consumption\textsuperscript{1325}. Coleopterans likewise exhibit a wide variety of feeding modes; leaf beetles (Chrysomelidae) are particularly common herbivores of water lilies, where their larval galleries are obvious on the floating leaves\textsuperscript{85}. Even though beetles may not consume large amounts of leaf tissue, their feeding activity can increase nutrient uptake and primary production by the plant and accelerate decomposition\textsuperscript{382}.

C. Predator–prey Interactions

Many aquatic insects function as predators, and predators are found in nearly all major aquatic insect groups. A few groups, notably the Odonata, aquatic Heteroptera, and Megaloptera, are strictly predators, whereas other groups are more heterogeneous in their trophic affiliations but may have important subdivisions that are predators. For example, among the Plecoptera, most members of the families Perlidae, Perlodidae, and Chloroperlidae are primarily predators\textsuperscript{1335}. Within the Trichoptera, Rhyacophilidae are free-roaming predators. Many of the sedentary, net-spinning Hydropsychidae are facultative predators\textsuperscript{35}, and some larval Limnephilidae become opportunistic predators in later instars\textsuperscript{91}. Many Coleoptera and Heteroptera function as aquatic predators in both the immature and adult forms.

Predators acquire prey using different behavioral strategies\textsuperscript{269}. Many predators, such as stoneflies, actively search for their prey (hunters). Ambush or sit-and-wait predators wait until a prey item is within range before striking. Odonate larvae often use this strategy. Once the prey is captured, predators may engulf their prey intact, in bites, or may feed only on the internal fluids. Fluid feeders use specialized piercing (haustellate) mouthparts for injecting enzymes into their prey and sucking out the partially digested bodily fluids. Clearly, the relative sizes of predators and prey, as well as the mode of feeding used by the predator, are important mechanical constraints governing predator–prey interactions. Engulfing predators are limited to prey small enough to be subdued and swallowed intact, whereas piercing predators have access to a broader variety of prey sizes that are large enough to be handled and to accommodate the piercing mouthparts.

Predation can be very important in regulating aquatic insect communities in lentic ecosystems, but predator effects interact strongly with habitat complexity (see Fig. 17.19). Wetland, pond, and lake littoral zones often have a structurally complex habitat of dense macrophyte beds. Predatory fish often exhibit top-down control of aquatic insect communities in areas where macrophytes are absent, but are not very effective in dense macrophyte beds\textsuperscript{86,100,121,150,356}. When fish are absent, predatory insects may control the abundance and diversity of their prey (Fig. 17.19). For example, odonates in littoral zones potentially control zooplankton abundance, and, like fish, they are less effective predators when macrophytes are very dense\textsuperscript{611}. The presence or absence of fish within a water body has a major impact on community structure, with large mobile taxa being far less common in lakes that historically lack fish\textsuperscript{351,355,398}. Fish are often size-selective predators, typically eliminating large predatory taxa, thereby indirectly affecting diversity and relative abundance of smaller taxa (Fig. 17.19). Fish and predatory insects interact to increase the effect on prey compared to when either is present alone\textsuperscript{180}.

Control of community structure in lentic habitats has been characterized as falling along a gradient of physical and biotic control, with two major transitions\textsuperscript{398}. Temporary ponds and deep lakes provide two extremes along a habitat size and permanence gradient, and two major transition thresholds occur along this permanence gradient, which provide the template for interaction of physical factors and predator control of insect communities\textsuperscript{398}. A permanence transition along the gradient controls predator presence or absence. In highly ephemeral habitats (Fig. 17.20), most predatory insects are excluded\textsuperscript{23,398}. As a result, predator–prey interactions are relatively unimportant and the insect community is controlled by physical factors\textsuperscript{398}, primarily drought cycles\textsuperscript{162} (see Fig. 17.6). Once the permanence transition is crossed, predatory insects become abundant and control various aspects of prey community composition\textsuperscript{22}. Permanent habitats tend to have the highest diversity of insect species\textsuperscript{23}. A predator transition occurs when habitats are large enough and deep enough to support fish\textsuperscript{398}. An elegant set of experiments examined the role of these two transitions in structuring an assemblage of \textit{Lestes} damselflies and showed how permanence and predator transitions interacted with damselfly life history variation to produce the observed assemblages\textsuperscript{337}. 
Predator–prey interactions involving stream insects have been studied from similar perspectives. As in lentic systems, experimental studies of fish control of aquatic insect communities have not always led to the same conclusions. Aquatic insect diversity and density were not affected when trout were experimentally removed from a rocky mountain stream\[3\] or excluded from cages in a North Carolina Piedmont stream\[286\]. However, in

**FIGURE 17.19** Predator and habitat control of aquatic insect communities. In lentic ecosystems that support fish, fish exercise strong top-down control of aquatic insect communities in low complexity habitats (A), resulting in low abundance and diversity of predatory and nonpredatory insects, and dominance of small-bodied, nonpredatory species. When habitat complexity is high (B), fish do not effectively control predatory species, which can achieve high abundance and diversity, but diversity and abundance of nonpredatory species is also high. When fish are absent and habitat complexity is low (C), high abundance and diversity of predatory insects results in top-down control of nonpredatory species, and dominance of large-bodied predators. In structurally complex habitats that do not support fish (D), diversity and abundance of both predators and nonpredators is high, and the community exhibits a wide range of body sizes. Thus, the presence or absence of fish has little effect on aquatic insects in structurally complex habitats.

**FIGURE 17.20** Temporary and permanent aquatic ecosystems: (A) ephemeral ponds dry during the summer, restricting aquatic invertebrate diversity to those species that are either drought tolerant or have dispersal mechanisms that permit them to emigrate when conditions are unfavorable; such habitats generally exclude fish (photograph by R. M. Northington); (B) lakes represent a permanent aquatic environment, where fish may or may not be present, and which often have littoral regions with macrophytes and profundal regions that have little structural complexity (photograph by A. E. Hershey).
California’s Eel River, fish control predatory invertebrates (especially damselflies), which in turn control the abundance of larval chironomids, affecting both algal biomass and the physical appearance of the algal mat in the river\(^{278}\). This study is an example of food web control via cascading trophic interactions\(^{72}\) (see Fig. 17.21a), which have been well studied for pelagic systems. Although it is not clear how common trophic cascades are in stream ecosystems, it is clear that fish do not control insect abundance in all streams.

Aquatic insects respond to predators through morphological, behavioral, and life history adaptations with important consequences for aquatic insect communities. For example, *Ephemera* mayflies are morphologically armored against stonefly predators\(^{270}\) and *Baetis* mayflies adopt a “scorpion posture” when attacked by stoneflies\(^{268}\). In stream habitats where *Hydra* are abundant, long hairs on the midge larva *Cricotopus sylvestris* decrease predation risk relative to short-haired species, such as *C. bicinctus*, as well as to individuals of *C. sylvestris* whose hairs have been experimentally shortened\(^{155}\) (Fig. 17.22). Many aquatic insects construct tubes or cases which provide varying levels of predator defense\(^{152,278}\). Behavioral responses to predators can be very complex. For example, among coexisting *Coenagrion haustellatum* damselflies, individuals were more active when predators were absent, but there was also a genetic component to activity level\(^{155}\). Furthermore, more active individuals grew faster, resulting in a life history trade-off between activity and growth\(^{155}\). The alternative strategies used by fish and invertebrate predators provide contrasting selective environments for prey. In some lakes where dragonfly predation is important, *Enallagma* damselflies have larger caudal lamellae which enhance swimming speed, whereas in lakes with fish, *Enallagma* caudal lamellae are smaller and associated with a cryptic strategy for predator avoidance\(^{230}\). Predator impact on feeding behavior may also affect important ecosystem functions, such as shredding activity\(^{220}\). Alteration of growth rates may or may not have implications for prey demographics, depending on whether adult fecundity is a function of body size, as it is in *Baetis* mayflies but not in *Enallagma* damselflies\(^{230}\). Predator effects on prey depend on the feeding mode of the predators as well as predator avoidance by prey, such that the effects of coexisting predators may be nonadditive and result in interference and/or facilitation effects on predator consumption\(^{259}\).

Recent studies have shown that aquatic insects are an important prey resource for terrestrial predators. Aquatic insects provide a significant food source for some terrestrial arthropods\(^{262,263,311}\); although for spiders, the aquatic insect subsidies appear to decrease with spider size\(^{11}\). Aquatic insects also provide an important subsidy to some terrestrial vertebrates\(^{307}\). Such subsidies are reciprocal. Terrestrial invertebrates are important to some stream fishes\(^{224,260}\), and the timing of terrestrial subsidies to aquatic systems compared to aquatic subsidies to terrestrial systems may result in stabilizing the temporal availability of energy to vertebrate predators in both ecosystems\(^{254}\). Alteration of

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**FIGURE 17.21** Examples of potential cascading effects of predators on aquatic insects in habitats of low structural complexity\(^{72}\). (A) When piscivorous fish are present, they control the density of insectivorous fish, which then do not have sufficient numbers to control predatory insects. Predatory insects become abundant enough to control nonpredatory insects. (B) In the absence of piscivorous fish, insectivorous fish can control predatory insects, releasing nonpredatory insects from top-down control. (C) In habitats where fish are absent, predatory insects may control the biomass of nonpredatory insects. Note that structural complexity may interact with predators (Fig. 17.19) to prohibit cascading effects.

**FIGURE 17.22** Long hairs provide *Chironomus sylvestris* with protection against *Hydra*, compared to short-haired *C. bicinctus* or *C. sylvestris* with experimentally shortened hairs. *Hydra* is a freshwater cnidarian that preys on chironomids and other aquatic invertebrates\(^{155}\).
the stream predator community can destabilize reciprocal subsidy relationships and restructure food webs: invasion by exotic rainbow trout interrupted the flow of terrestrial subsidies to native Dolly Varden[241], altering the stream insect community and insect control of algal biomass.

Over half a century of research has revealed that predator–prey interactions involving insects have varying impacts on insect abundances, distributions, and behavior, and have been important in selecting for morphological adaptations for predator defense. Recent studies have revealed that aquatic insects also serve as an important link between adjacent riparian systems, and that such interactions are bidirectional. The highly diverse and complex array of responses of aquatic insects to predators are a reflection of the high diversity of aquatic insects, the broad array of predation threats imposed upon them, and the evolutionary plasticity of the Insecta.

D. Insects as Conduits for Energy Flow in Aquatic Food Webs

Insects provide a critical linkage in energy flow from microbial to vertebrate populations in aquatic ecosystems, and between aquatic and terrestrial ecosystems[254,263,311,375]. Food web studies have been used to understand these linkages and thereby integrate organic matter processing with community interactions[568,82]. Two goals of a food web study are to identify organic matter sources for the various consumers and to elucidate the trophic structure of the web. In most aquatic ecosystems, either three or four trophic levels are present including: (1) primary producers and detritus; (2) primary consumers, including detritivores (shredders and collectors) and grazers (scrapers); (3) secondary consumers (predators); and (4) tertiary consumers (vertebrate predators which consume invertebrate predators). These designations are oversimplifications because omnivory is common such that many consumers occupy more than one trophic level[195].

In stream ecosystems, the relative importance of the detritivore food chain compared to the grazer food chain is a matter of some debate[240], but this varies as a function of stream order and riparian conditions[92,128,147]. The food web in any particular aquatic ecosystem will reflect the combination of factors altering resource and invertebrate abundance and distribution. Thus, wide variation in food web structure occurs. Gut analyses are often used to delineate trophic structure[1156]. However, some food items are difficult or impossible to recognize, while others may be overlooked due to rarity or temporal variability. The gut analysis approach is impractical for studies involving fluid-feeding predators because sclerotized parts are not ingested and thus prey identity cannot be determined.

In recent years, stable isotopes have been used to study food web relationships in both lotic and lentic systems[116,156,277,367,368] and linkages between stream and riparian ecosystems[262]. One useful aspect of carbon stable isotopes is that the various organic matter sources for consumers often have different relative abundances of the two stable isotopes of carbon, 13C and 12C. Because the relative abundances of these isotopes change only slightly as the organic matter is processed by various consumers, the difference between the ratio 13C:12C in a consumer and a standard (or δ value, expressed as parts per thousand, or “per mil”) can be used to infer the consumer’s food source. Stable isotopes can also be experimentally manipulated. 13N has been used extensively in enrichment studies of lotic ecosystems to serve as a tracer of consumer food sources as well as nitrogen distribution through the system[153,161,248,295,349,415]. 15N also is used in trophic studies. 13N and 14N change as food is processed by consumers because the various metabolic processes use, or fractionate, these isotopes differently. The net result is that with each trophic level, consumers become enriched (by about 3 per mil in many cases) in 15N relative to 14N, as 15N is retained in the tissues and 14N is excreted. Thus, consumers in a food web can generally be assigned to a trophic level even if their precise food resource is not known[116,272]. However, the δ15N value of the base of the web may vary between systems, and thus should be measured for each system where δ15N is being studied in consumers[277,366].

When organic matter sources in a stream are isotopically distinct, a combination of δ13C and δ15N analyses can yield considerable insight into a stream food web. Such an analysis was performed for the dominant consumers and their food resources of Lookout Creek in Oregon[116] (Fig. 17.23). In Lookout Creek, the δ13C values revealed that macroinvertebrates were trophically distinct from two predatory vertebrates studied, whereas the δ13C values showed that consumers relied more heavily on stream algae than on terrestrial detritus. The macroinvertebrate scrapers studied (the snail Juga and the caddisfly Dicosmoecus gilvipes) appeared to consume algae, whereas the shredding caddisfly Heteroplectron californicum apparently ate terrestrial detritus. The stonefly Calineuria californica, a presumed predator, occupied a trophic level close to primary consumers and thus may have consumed some plant matter along with small invertebrates that were not measured. The endosymbiotic midge larva Cricotopus nostocicola (described earlier) was positioned over its algal host Nostoc parmelia. Cutthroat trout, Oncorhynchus clarki, and Pacific giant salamanders, Dicamptodon ensatus, consumed invertebrates, as shown by their vertical positioning over the δ13C of their food and a 3–4 per mil difference in δ15N (Fig. 17.23). Gut contents of trout revealed a variety of invertebrates, whereas salamanders had exclusively snails in their guts[404]. Stable isotopes provide a means with which to trace organic matter sources for insect consumers in freshwater...
ecosystems that receive runs of anadromous Pacific salmon (Oncorhynchus spp.). Adult salmon provide energy and nutrients through excretion while alive, and in their eggs and carcasses after spawning. Salmon-derived nutrients (e.g., N, P) may be taken up by stream algae[50,242,318], which are then fed upon by aquatic insect grazers [76,190]. In addition, salmon carcasses can provide a high-quality source of CPOM for shredders[77,190]. Stable isotopes of N and C provide a powerful method to quantify the importance of salmon nutrients and energy to freshwater food webs[76,190]. Salmon spawners have an isotopic signature that reflects their position in the marine food web, and thus are enriched in both 15N because they feed on fish and zooplankton, and in 13C because they exploit marine sources of carbon (both isotopes are more abundant in the ocean than in freshwater). By comparing the isotopic signature of insects in freshwater habitats where salmon spawn with those where salmon are absent, the proportion of marine or salmon-derived N and C in the insect community can be estimated. These studies suggest that aquatic insects can derive from <10% to >90% of their carbon or nitrogen from salmon sources[76,190].

Salmon have been introduced to many areas outside their natural range, where they can have a profound influence on the aquatic insect fauna of freshwater ecosystems[97,165]. For example, in a Lake Superior tributary stream, the 15N signature of heptageniid mayfly grazers suggested about 30% reliance on salmon-derived N from Lake Superior[318] (Table 17.4). Stable isotopes demonstrating the incorporation of salmon nutrients into freshwater food webs, when combined with other studies[75,242], suggested that salmon spawners can stimulate freshwater productivity. However, the enriching effects of salmon nutrients are balanced by the benthic disturbance caused by migration and spawning behavior[245,559]. Benthic aquatic insects are therefore exposed to both scour

<table>
<thead>
<tr>
<th>Material</th>
<th>δ15N (‰)</th>
<th>δ13C (‰)</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Upstream</td>
<td>Downstream</td>
<td>Upstream</td>
<td>Downstream</td>
</tr>
<tr>
<td>Salmon</td>
<td></td>
<td>8.9</td>
<td>−22.8</td>
<td></td>
</tr>
<tr>
<td>CPOM</td>
<td>−0.2</td>
<td>−28.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hydropsyche</td>
<td>3.1</td>
<td>4.1</td>
<td>−29.1</td>
<td>−28.9</td>
</tr>
<tr>
<td>Heptageniidae</td>
<td>1.6</td>
<td>4.0</td>
<td>−29.2</td>
<td>−28.9</td>
</tr>
</tbody>
</table>

**TABLE 17.4** δ15N and δ13C values for food web components and source materials in a Lake Superior tributary stream. Salmon spawning occurs in the downstream reach of the river, but not the upstream reach. The stable isotope values show that salmon-derived N but not salmon-derived C is incorporated into collector (Hydropsyche) and especially grazer (Heptageniidae) food web components[318].
and food resources provided by salmon. The availability of salmon tissue can increase the growth rates of aquatic insects, especially those of detritivores and shredders\(^\text{[77]}\). However, scour of sediments by spawning salmon can greatly deplete benthic insects\(^\text{[245]}\). Certain aquatic insects, especially chironomid midges, often predominate after disturbance because their life history strategies enable them to rapidly recolonize\(^\text{[75]}\). The relative role of enrichment and disturbance for aquatic insect communities represents an area ripe for investigation in both native and introduced ranges of Pacific salmon.

### E. Secondary Production

Secondary production is the amount of animal biomass that is produced in a given area over a given time period, usually expressed in g m\(^{-2}\) yr\(^{-1}\). For a cohort, this measurement integrates both individual growth rate and survivorship of individuals within the cohort\(^\text{[28,32]}\). In a food web context, secondary production is the summation of the amount of biomass that is potentially available to be consumed by the next trophic level over some period of time. Thus, an estimate of secondary production expresses energy or material flow through the consumer compartments of the ecosystem, and is useful for identifying major pathways of energy flow in an ecosystem\(^\text{[18,36,324]}\).

Estimation of secondary production often provides insights that are not apparent from biomass or abundance measurements alone\(^\text{[32]}\). This is especially true for organisms of small body size if they exhibit rapid growth rates. For example, high secondary production was measured for snag-dwelling chironomids in a high-order blackwater river despite their low biomass, which was due to very high biomass turnover rates of these small-bodied organisms\(^\text{[30]}\). Even for large-bodied insects, measurement of production may provide surprising insights. A study of secondary production revealed that *Hydropsyche benti* and *Cheumatopsyche analis* had a previously unrecognized trivoltine life cycle in Upham Brook, Virginia, a consequence of an upstream impoundment supplying food resources necessary for faster turnover rates and high production\(^\text{[2]}\). Another production study revealed a multivoltine life cycle in the mayfly *Caenis latipennis* in an Oklahoma creek\(^\text{[352]}\). For a neotropical stream insect, production was low despite rapid growth rates due to a combination of high abundance of noninsect macroconsumers and scouring of benthic resources by flooding\(^\text{[284]}\).

Stream secondary production is very often dominated by insects, and insect secondary production in streams has received considerable study. However, crustacean and mollusc production may also be quite important\(^\text{[265,338,370]}\). Meiofaunal production, which is typically overlooked, can also contribute significantly to secondary production\(^\text{[134,315,332]}\).

Because different habitats vary markedly in abundances and community composition of their insect fauna, calculation of secondary production on a habitat-specific basis is needed to reveal the spatial complexity of insect-mediated pathways of energy flow in aquatic ecosystems. In addition, failure to consider some habitats may grossly underestimate secondary production. In high-order rivers, snag habitats are very important sites of secondary production, reflecting the paucity of stable substrates and the success of both mayflies and chironomids in utilizing the amorphous detritus associated with that habitat\(^\text{[30,33]}\). Similarly, debris dams are critical areas for insect production in intermittent streams\(^\text{[74]}\). Variability in secondary production within and among stream sites likely reflects a combination of patchy distribution of resources, temperature differences, and substrate heterogeneity\(^\text{[108]}\).

Fisheries managers often use secondary production to assess the capacity of a stream reach to support fish. Early studies suggested that stream invertebrate production was insufficient to support the observed fish production, a problem referred to as Allen’s paradox\(^\text{[7]}\). This may be due to underestimates of the production-to-biomass ratio (P/B) for individual species\(^\text{[30]}\), or perhaps failure to consider the production of chironomid midges\(^\text{[37,171]}\). In a New Zealand stream, trout consumed nearly all benthic macroinvertebrates (mostly insects), and additional resources, such as terrestrial invertebrates, were needed to balance the production budget\(^\text{[170]}\).

Although a wealth of literature exists for lotic secondary production, as noted above, the same is not true for lentic systems. Table 17.5 summarizes many of the studies of whole-lake benthic secondary production found in a literature search. As indicated, most of these lakes exist outside of North America, and whole-lake estimates for North America were all for shallow, oligotrophic lakes where whole-lake estimates could be easily calculated. Production estimates, regardless of method, entail lengthy calculations for each taxon represented, with area-based corrections for each depth sampled. The amount of time needed to accurately produce reliable estimates makes the calculation of whole-lake productivity a very difficult task. Therefore, studies of larger lakes in North America, such as the Great Lakes, are limited in scope, with most focusing on the zebra mussel, *Dreissena polymorpha*\(^\text{[19,80,98,179]}\), rather than on insects. The paucity of current literature on this subject indicates a need for more whole-lake studies in a variety of North American ecoregions to enhance our understanding of the productivity of all aquatic systems.

Although conceptually very useful, secondary production is time-consuming and expensive to measure at the community level. The various techniques for measuring secondary production\(^\text{[28,32]}\) involve sampling efforts that quantify consumer standing stocks at several points in the growing season, at least a trophic level understanding of the various consumers, and some knowledge of life histories...
of the dominant consumers (Table 17.6). However, in the process of measurement, considerable insight is gained into the insect community, which sheds light on which consumers play key roles in various aquatic ecosystem processes.

V. ROLE OF DISTURBANCE AND HUMAN IMPACTS ON AQUATIC INSECT COMMUNITIES

A “disturbance” has been defined as any discrete event that disrupts population, community, or ecosystem structure, usually by changing resource abundance or the physical environment. Many types of natural and human-induced disturbances can disrupt the habitat, resources, or population densities of aquatic insects. Large-scale natural disturbances that can affect insects include: (1) hydrologic events such as floods, ice, or wave action that scour or remove substrates; (2) droughts that lead to drying of aquatic habitats; (3) watershed disturbances, such as wildfire, that can disrupt nutrient and sediment inputs to streams and lakes for decades; and (4) seasonal events, such as summer or winter oxygen depletion, that can lead to insect mortality and major changes in community structure (Fig. 17.24). Naturally, many small-scale disturbances can also affect local insect populations. Human-related disturbances of aquatic insect habitats are at least as important and include nominally: (1) point and nonpoint source pollutants that enter aquatic ecosystems from the land, connected water, or the atmosphere; (2) water withdrawal, diversion, and storage; (3) modifications of river channel geomorphology and destruction of wetlands; (4) watershed disruptions, such as logging and other land uses; and (5) introduction and establishment of exotic species. All these mechanisms, singly and in combination, can alter population densities and community structure of insects, sometimes for decades or centuries as in the case of watershed land use change. In general, however, natural disturbances tend to be episodic, and, if the habitat returns to its original state, insect communities recover quickly. Human disturbance, by contrast, tends to be chronic and thus insect communities may not recover until the disturbance ceases or the habitat is restored. In response to the recognition that both structure and function of aquatic ecosystems have suffered greatly due to human-induced disturbance, there has been considerable recent interest in ecosystem restoration, especially restoration of wetland and stream ecosystems.

A. Disturbance

Variation in flow (floods to desiccation) is the major cause of natural disturbance in streams and is responsible for large, usually temporary, reductions in insect abundance and diversity. Stream insects have evolved various mechanisms to deal with such flow variation, including life history adjustments to minimize the presence of vulnerable stages during times of peak flows, behavioral movement into more protected hyporheic (interstitial) and lateral habitats during floods, and high reproductive rates to compensate for losses. Despite these adaptations, severe flood disturbance will still remove large proportions of the insect fauna. During drought, refuge provided by the deep hyporheic zone is especially important, but its accessibility to insects will depend on its grain size. Other insects may survive drought via resistant life stages, such as diapausing eggs or cocoons. Insects can recolonize streams from several sources: (1) egg laying by adults, usually aerial in the case of insects, (2) drift from upstream areas, and

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**TABLE 17.5** Studies of whole-lake secondary production in lakes varying in trophic status around the world.

<table>
<thead>
<tr>
<th>Organism</th>
<th>Location</th>
<th>Trophic status</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zoobenthos</td>
<td>Alderfen Broad, Norfolk, UK</td>
<td>Eutrophic</td>
<td>223</td>
</tr>
<tr>
<td>Zoobenthos</td>
<td>Upton Broad, Norfolk, UK</td>
<td>Eutrophic</td>
<td>223</td>
</tr>
<tr>
<td>Zoobenthos</td>
<td>Lake Mývatn, Iceland</td>
<td>Eutrophic</td>
<td>213</td>
</tr>
<tr>
<td>Zoobenthos</td>
<td>Hjarbæk Fjord, Iceland</td>
<td>Eutrophic</td>
<td>213</td>
</tr>
<tr>
<td>Zoobenthos</td>
<td>Lake Pääjärvi, Finland</td>
<td>Oligotrophic</td>
<td>313</td>
</tr>
<tr>
<td>Zoobenthos</td>
<td>Mirror Lake, USA</td>
<td>Oligotrophic</td>
<td>339</td>
</tr>
<tr>
<td>Zoobenthos</td>
<td>Thingvallavatn, Iceland</td>
<td>Oligotrophic</td>
<td>212</td>
</tr>
<tr>
<td>Zoobenthos</td>
<td>Lake Brunsee, Germany</td>
<td>Oligotrophic</td>
<td>39</td>
</tr>
<tr>
<td>Zoobenthos</td>
<td>Crampton Lake, USA</td>
<td>Oligotrophic</td>
<td>17</td>
</tr>
</tbody>
</table>
movement along the bed from upstream, downstream, hyporheic, or lateral habitats[322].

In general, aquatic insect communities recover rapidly from natural disturbance. A Cascade Mountain stream that experienced an extreme disturbance was studied to address the ability of stream macroinvertebrate community to recover [199]. A debris flow, which is an episodic mass movement of sediment and debris through the stream channel (usually triggered by a landslide), devastated about a 1-km reach of Quartz Creek, Oregon, and partially disturbed areas downstream (Fig. 17.25). More than 99% of the macroinvertebrates were removed by the debris flow. An associated flood alone in an upstream reach removed >90% of the invertebrates, so that instream sources of

<table>
<thead>
<tr>
<th>Method</th>
<th>Data needed</th>
<th>Comments</th>
<th>Other references</th>
</tr>
</thead>
<tbody>
<tr>
<td>Allen curve</td>
<td>Density (no./m²) for several dates spanning the development of a cohort; mean individual mass for each date (often obtained from length × weight regressions [Smock, 1980]).</td>
<td>Graphical presentation of density versus mean individual mass. The area under the curve corresponds to the secondary production of a population. This method was developed prior to the widespread availability of electronic calculators and computers.</td>
<td>7</td>
</tr>
<tr>
<td>Increment summation</td>
<td>Density (no./m²) for several dates spanning the development of a cohort; mean individual mass for each date (often obtained from length × weight regressions [Smock, 1980]).</td>
<td>Production (P) between sampling dates is calculated as the product of mean density (N) and change in mean individual mass (W): P = NW. Annual production is the summation of these incremental measurements for a year.</td>
<td>395, 396</td>
</tr>
<tr>
<td>Removal summation</td>
<td>Density (no./m²) for several dates spanning the development of a cohort; mean individual biomass for each date (often obtained from length × weight regressions [Smock, 1980]).</td>
<td>Production lost between sampling dates is the product of the change in density and the mean individual mass: P = WN. Annual production is the sum of all production losses over a year.</td>
<td>395</td>
</tr>
<tr>
<td>Instantaneous growth</td>
<td>Growth rate; mean biomass</td>
<td>Production between sampling dates is the product of growth rate and mean biomass, where growth rate is determined in laboratory experiments or from field samples of distinct cohorts, and biomass is determined from field samples: P = g × B. Growth is temperature- and size-dependent, so the accuracy of this method depends on making measurements under the appropriate conditions. Annual production is: P = Σ(gi)Bi, where the i are the production intervals.</td>
<td>143, 305</td>
</tr>
<tr>
<td>Size frequency</td>
<td>Mean annual density; size distribution of individuals throughout year; mean mass for each size category; cohort production interval (mean development time from hatching to emergence).</td>
<td>This method is widely used and does not depend on the presence of distinct cohorts in field populations. The mean size frequency distribution, which is skewed toward smaller size categories due to mortality, represents an average cohort. For populations where distinct cohorts are known, this method gives a similar result as the increment summation method. P = ΣWiΔNi, where i is the number of size classes. This estimate of secondary production needs to be corrected for the CPI: (multiply P by 365/CPI).</td>
<td>27</td>
</tr>
</tbody>
</table>
insects clearly were low. Yet, in both the flood-impacted and debris flow–impacted reaches, macroinvertebrate species richness and total abundance recovered within 1 year of the disturbance to normal levels (Fig. 17.25). In another example, the eruption of Mt. St. Helens (southwestern Washington) eliminated the entire biota from entire drainage systems, which included streams, lakes, and wetlands. Many stream channels were completely rerouted by topographic changes. Yet, in the first year after the eruption, 98 species of macroinvertebrates (mostly insects) were found in one devastated stream [10]. Five years after the eruption, 141 species were found in the same stream, although nearly half of these were the ubiquitous chironomid midges. These examples attest to the remarkable resilience of stream insects and other invertebrates to natural disturbance.

Episodic natural events contrast, however, with chronic anthropogenic disturbance, such as inputs of chemical and thermal pollutants or prolonged watershed disturbance. Prolonged point-source pollution can have devastating effects on aquatic insects. Low concentrations (0.2 ppm) of the insecticide dieldrin in a factory effluent reduced benthic insect densities by over 90% in a South Carolina stream, and the remaining invertebrates had high tissue concentrations (up to 100 ppm) of dieldrin [374]. Wallace and coworkers later explored the structural and functional significance of reduced insect populations in streams by conducting an experimental release of insecticide (methoxychlor) in an Appalachian Mountain stream. Insecticide application resulted in massive drift of insects, and reduction of benthic densities by over 85% [380,384]. The remaining benthic invertebrates were composed of an impoverished fauna of mostly noninsects (e.g., oligochaetes) and chironomid midge larvae. Furthermore, important ecological processes in the stream were altered. For example, leaf litter decomposition declined drastically because an important shredding caddisfly, Lepidostoma, was eliminated by the insecticide treatment [400]. When treatment ceased, Lepidostoma recolonized rapidly and leaf litter processing recommenced, again pointing to the resilience of aquatic insect communities. However, human chronic disturbance of aquatic ecosystems and their watersheds tends to preclude recovery of insect communities to predisturbance conditions. Watershed disturbances such as forest logging, agriculture, and urbanization can have long-term impacts on aquatic insect communities by altering energy inputs, thermal regimes, and sediment composition [127,197,378].

B. Land Use
Changes in land use often lead to large and persistent disturbance of adjacent aquatic ecosystems, disrupting insect communities as well as ecosystem function. Because aquatic insects are sensitive to physical and chemical conditions in their environment as well as to top-down and bottom-up
Biotic controls, their communities also reflect changes in land use on both geological and ecological time scales as well as on multiple spatial scales. For both lotic and lentic ecosystems, nutrient loading from either nonpoint or point sources, changes in hydrology, timber harvesting, construction, and riparian or shoreline development are among the most important land use alterations that affect insects.

Lentic insect responses to land use disturbances are seen through indirect effects of physical and chemical changes in littoral macrophyte zones and chemical changes in profundal zones. Nutrient loading results from many land use changes, including: (1) nutrients associated with sediments derived from construction and tillage; (2) fertilizer from agriculture, suburban and urban runoff; and (3) waste water and industrial inputs. These inputs are derived from both inflow streams and land uses on lake shorelines. Nutrient inputs enhance macrophyte growth and/or phytoplankton productivity. Since macrophytes support a high diversity of aquatic insects as well as affording refuge from fish predators, (Fig. 17.19), land use changes altering macrophytes have strong indirect effects on littoral insects. However, if macrophyte growth becomes too dense, anoxia may be a problem, especially at the sediment/water interface. Sedimentation may negatively affect macrophytes, thereby indirectly negatively affecting insect abundance and diversity. Nutrient inputs also enhance phytoplankton production, and at high level this often leads to bottom water anoxia and associated low insect diversity and changes in insect community structure.

Invertebrate populations in wetlands are affected by vegetational and water management practices and by water quality and plant physical structure. However, direct effects of land use on wetland invertebrates were few in urban playa wetlands, although invertebrate abundances were positively associated with macrophyte growth. Similar to littoral areas of lakes, macrophyte beds respond to land use surrounding the wetlands. Water level fluctuation in wetlands, often associated with land use changes,
has considerable influence on invertebrate community structure and the balance between insect and noninsect invertebrates\cite{8,162}. Wetland insects and other invertebrates are a major source of food for migratory and resident waterfowl\cite{121,347,354}, thus wetland loss and associated loss of invertebrate food resources and habitat have had a major impact on wetland bird species\cite{300}.

Noel Hynes first articulated the importance of employing a landscape perspective for understanding stream ecosystem structure and function\cite{175}. The realization of this linkage between the stream and its terrestrial setting was a critical development in stream ecosystem theory\cite{241}, and aquatic insects have been central to this perspective because of their role in processing allochthonous inputs. This aquatic–terrestrial relationship is well appreciated qualitatively but poorly understood quantitatively. Local geomorphology, vegetation, and climate determine the quality and quantity of organic matter entering a stream. These processes and disturbance history at a site determine the spatial and temporal patterns of riparian zone characteristics that dictate the physical characteristics of the stream habitat\cite{128}. Thus, riparian processes and natural disturbances, or disturbances due to changes in land use, will alter insect habitats in the stream channel. These disturbances operate over temporal scales ranging from geologic alterations of landform, to ecological succession of the riparian forest, as well as over spatial scales spanning watersheds, to local patchiness of algal growth on individual rocks within the channel\cite{128}. Aquatic insect abundance and diversity respond to all of these perturbations.

Stream insect communities reflect land use within the watershed because changes in land use alter stream habitat and water quality\cite{81,127,235}. As discussed previously, insect communities are sensitive to predominant sources of organic matter, dictated largely by stream order, local geomorphology, and riparian vegetation\cite{250,252,360}. Biogeography\cite{159,289} and water quality factors\cite{197,299} also constrain insect communities. Use of geographic information systems (GIS) science has facilitated landscape-level analyses and land use studies of stream insect communities. In Minnesota North Shore tributaries to Lake Superior, insect community structure and substrate characteristics within a stream are correlated with agricultural and residential land uses in the watersheds\cite{297}. The types of alterations seen will depend on the nature and intensity of the land use change\cite{69}, but local geomorphology modifies some of the effects of land use change, as well as constraining land cover and dictating what land uses might occur in a watershed\cite{128,251}. In an extensive study of a 45-catchment river basin in central Michigan, geology and land use were found to be of approximately equal importance in determining invertebrate communities in streams\cite{298}.

Land use changes that alter large woody debris (LWD) have large impacts on insect communities. Logging is one of the major such land uses. Logging has greatly altered the size and amount of LWD that enters stream channels\cite{341}. Removal of riparian trees changes inputs of LWD for centuries, altering substrate stability and insect habitat\cite{250}, but recent changes in forest practices in some states now offer some protection to the riparian zone from excessive harvest\cite{126}. Streams that lack LWD sources due to past logging are candidates for rehabilitation, which now emphasizes the input of logs in natural volumes and arrangements to improve stream habitat and to augment the food base. In addition to removing LWD and thereby altering detrital inputs and channel structure, logging also removes vegetative cover within the watershed. This results in increased sedimentation into the stream, reduced infiltration which decreases ground water recharge, and increased runoff which increases the magnitude of stream discharge change following storm events\cite{128,250}.

Other land uses, including urban, agricultural, and industrial development, may follow timber harvest. Agriculture has a large effect on sedimentation in a stream reach\cite{95}, but stream buffers are more important than the whole catchment in determining sediment-related habitat variables in agricultural basins\cite{298}. Road construction is usually associated with all types of human land use. Road construction often destabilizes hillside, leading to landslides and sometimes debris flows in stream channels downslope\cite{199,345}, which constitute a major disturbance to the stream ecosystem (see below).

The growth of urban and suburban areas throughout the United States has had wide-ranging detrimental effects on streams, including altered hydrology, greater discharge volume, and poor water quality\cite{95,256,267}. Many of these effects are magnified by the lack of vegetated riparian zones, which would normally be able to retain and process nutrients flowing in from the landscape\cite{348}. The impervious surfaces characterizing high percentages of urban landscapes act as conduits of nutrient-rich runoff directly into unprotected streams. For example, when impervious surface cover was greater than 6%, urban streams in Maine experienced increased nutrients, total suspended solids, and declines in dissolved oxygen and aquatic invertebrates\cite{246}. Increasing runoff over impervious surfaces also adds bacterial and heavy-metal contamination to receiving streams, causing greater detriment to aquatic communities\cite{15}. The highly erosive forces of stormwater flows during rain events can greatly increase sedimentation\cite{361} and lead to a loss of habitat structure and the creation of homogenous streambeds, which are very detrimental to aquatic insects.

These anthropogenic factors affecting urban systems have devastating impacts on stream communities, leading to significant losses in biodiversity, a decrease in stress-intolerant invertebrate species, and a decrease in stream biotic integrity\cite{49,114,299,306}. A loss of habitat structure in conjunction with land use changes and increased impervious
surface cover in the watershed of the Provo River, Utah, showed the presence of more tolerant organisms such as leeches, oligochaetes, and tolerant caddisflies and a decrease in overall diversity of aquatic biota. In addition, studies of several major cities showed a significant negative relationship between the total number of invertebrate taxa and an index of urban intensity of heavily impacted stream systems. In California, a benthic community dominated by the presence of filterers, such as hydropsychid caddisflies and Corbicula sp., were indicative of heavily impacted systems.

These changes in land use dramatically alter watershed hydrology and hence stream hydrology. As discussed previously, insect communities are strongly affected by stream hydrology, but are also sensitive to the various forms of pollution that result from many land uses. Thus, insect communities are intimately linked to land use in the watershed as well as to local conditions in the stream channel.

C. Restoration

Ecological restoration can be defined as assisting the recovery of a degraded, damaged, or destroyed ecosystem. Aquatic ecosystems and their biota are subject to human-induced degradation from multiple sources, but perhaps the most prominent are chemical pollutants, physical habitat modification, invasive species, and land use changes. All these impacts can deleteriously affect aquatic insect communities. Ecosystem restoration may be the key to aquatic insect recovery to preimpact conditions. Recently, stream restoration research has begun to focus on urban and agricultural landscapes, but restoration of streams draining forested landscapes has a longer history.

Many urban stream restoration projects typically involve some combination of approaches such as increasing the sinuosity of straightened channels, increasing the complexity to the channel through additions of large woody debris, addition of engineered structures, stabilization of riparian zones, and land acquisition. The effectiveness of such restoration efforts on aquatic insects are poorly known because most projects do not involve pre- or postrestoration monitoring. Furthermore, ecological benefits may occur on decadal time scales, thus long-term monitoring is necessary to evaluate the success of a project. Despite the considerable expense that has been invested in urban stream restoration, failure to mitigate stormwater drainage into streams may negate any positive effects of restoration on urban stream hydrology, thereby also limiting the opportunity for recovery of aquatic insect communities. Research has not only reinforced the usefulness of riparian forest buffers and reforestation of riparian areas for stream restoration, but has also provided other novel approaches to restoring streams and their aquatic insect fauna. For example, restoration has demonstrated the importance of reestablishing natural flow regimes, especially to relocate and resort sediments. Additional approaches include redesigning stormwater drainage systems to minimize thermal and chemical pollution, and the use of sediment traps to reduce the downstream movement of fine sediments, although with equivocal results. Some agencies are attempting to reestablish native macroinvertebrate fauna, such as dragonflies and mussels. Restoration strategies implemented at the reach scale, however, may be overwhelmed by impacts at the watershed or regional scale, including impoundments that disrupt ecological connectivity and aerial deposition that produces acidic streams, both with detrimental impacts on aquatic insect communities.

Research in forested streams has demonstrated a strong link between organic matter standing stocks and higher trophic levels, including aquatic insect secondary production. Restoration strategies, in part, seek to reestablish energy inputs and flow that have been lost or modified in the impacted system. Unimpacted forested streams generally rely on allochthonous (i.e., externally derived) organic matter to fuel biological production, and such inputs generally exceed those from autochthonous (i.e., internally derived) sources. As a result, forested stream ecosystems are dominated by shredder and collector aquatic insects, with some predators and scrapers also present. Furthermore, aquatic insect abundance, productivity, and biomass are often higher in wood-created debris dams than on streambed sediments. Past logging may have removed near-stream trees that provide a source of both allochthonous matter such as leaves and large wood to the stream. Large woody debris increases the retention and storage of particulate organic matter, thereby providing critical habitat and food resources for stream organisms, especially benthic insects. Accumulations of organic matter provide additional surface area for colonization by microbial biofilms, which may increase nutrient uptake and encourage consumption by insects. Without sufficient instream retention structures provided by large woody debris, this organic matter moves downstream more readily, and thus is unavailable to local stream food webs. Hence, impacted streams can become energy-limited because of a lack of sufficient retentive structures and inputs of allochthonous matter, and often exhibit declines in shredder and collector aquatic insects as well as predators that feed on both these groups. Large wood additions hold considerable promise as a restoration approach for degraded forested streams by providing organic matter retention and habitat that benefit aquatic insects and other biota. Indeed, studies have demonstrated short-term changes in aquatic insect abundance and diversity.
D. Climate Change

The influence of natural and human-induced climate variation on biological communities is not a new study topic, especially with insects\textsuperscript{[133]}. However, recent recognition of the potential ecological impacts of global climate change resulting from human activities\textsuperscript{[387]} has led to a huge number of relevant publications\textsuperscript{[266]}. Indeed, significant ecological impacts of anthropogenic climate change have been forecasted for most of the world’s ecosystems\textsuperscript{[176]}. For aquatic ecosystems, climate-induced changes in broad-scale weather patterns (e.g., North Atlantic Oscillation [NAO], Pacific Decadal Oscillation [PDO]) may alter both system hydrology\textsuperscript{[25]} and water temperature\textsuperscript{[51]}—arguably the most fundamental features of those ecosystems. Already at northern and southern latitudes, changes in the extent of snowpack and subsequent timing and intensity of spring snowmelt have been documented over the last century. This information, combined with modeling efforts\textsuperscript{[120]}, suggests several important consequences for aquatic ecosystems and associated fauna\textsuperscript{[110,237,275]}. However, specific information about the influence of climate variation on lotic ecosystems, especially for aquatic insects, is limited\textsuperscript{[105]} compared with wetland\textsuperscript{[411]} and lentic ecosystems\textsuperscript{[410]}.

Climate variation can alter the magnitude and predictability of key environmental variables\textsuperscript{[120]}, causing more pronounced disturbance events, such as floods, or modifications in the timing of seasonal events, such as spring snowmelt. The influence of climate variation on aquatic insects has already been noted. In lakes, for example, increases in the average water temperature has been linked to changes in macroinvertebrate taxonomic composition\textsuperscript{[60]}, while British Odonata have exhibited a pronounced advance in phenology over the last 40 years consistent with climate trends\textsuperscript{[142]}. In streams, growth of mayfly nymphs increased during warm phases of the NAO because of warmer winter water temperatures\textsuperscript{[51]}, while macroinvertebrate taxonomic composition and abundance have been shown to be sensitive to interannual rainfall variability\textsuperscript{[25]}.

Specific responses of aquatic insects to variation in climate and associated hydrologic conditions can be difficult to identify, especially separating these direct responses from biotic interactions (e.g., predation and competition) that can themselves be modified by abiotic factors\textsuperscript{[229]}. Furthermore, other aspects of environmental change, such as sedimentation and acidification, may override climatic effects on macroinvertebrates\textsuperscript{[105]}. This complexity emphasizes the importance of long-term datasets on aquatic insect abundance and composition\textsuperscript{[177]}. Unfortunately, such datasets are rarely of sufficient duration to make predictions about climate change, which may be manifest over periods of 50 years or more. Despite difficulties in making predictions, studies of terrestrial insects suggest that evolutionary responses are unlikely to provide sufficient adaptation to prevent local species extinctions under climate change\textsuperscript{[266]}. The situation may be especially acute with aquatic insects because of their phenological dependency on environmental cues (e.g., to break egg dormancy) and increasing isolation of their rearing habitat due to altered hydrology\textsuperscript{[110,275]}. On the other hand, aquatic insects can have exceptional dispersal abilities and high tolerance of extreme conditions, which may buffer them from some of the predicted consequences of climate change. Providing definitive answers to how aquatic insects will respond to climate change will require more research, especially given the many uncertainties evident in the scientific literature.

VI. AQUATIC INSECTS IN BIOMONITORING STUDIES

Biomonitoring studies are used to measure response and recovery of aquatic communities to disturbances, protect biodiversity, evaluate compliance, and improve understanding of the relationship between physical, chemical, and biological components\textsuperscript{[133]}. Many federal and state biomonitoring programs exist throughout North America. For example, the USGS National Water Quality Assessment (NAWQA) program seeks to evaluate water quality from national to local spatial scales\textsuperscript{[133]}, while Alaska’s Water Quality Assessment & Monitoring Program (WQAMP) addresses expectations for state water quality stewardship set out in the federal Clean Water Act. Such biomonitoring programs have historically emphasized the measurement of chemical and physical parameters, but use of aquatic organisms has become more prominent in the last several decades\textsuperscript{[66]}. This is due, in part, to the recognition that chemical and physical measurements provide information on instantaneous conditions but may not accurately reflect long-term conditions associated with a particular water body. By contrast, organisms function as better sensors of environmental quality\textsuperscript{[216]} by, for example, integrating past and current conditions over a larger spatial scale.

Many freshwater organisms have been used in biological monitoring, including bacteria, algae, vascular plants, macroinvertebrates, and fish. Of these organisms, macroinvertebrates, including molluscs, crustaceans, annelids, and insects, are frequently recommended for biomonitoring programs because of their diversity, ease of collection, and ease of identification to levels needed for bioassessment\textsuperscript{[47,149]}. For example, a recent review noted that 49 of the 50 U.S. states use macroinvertebrates in their water quality monitoring programs (and the 50th is poised to), whereas about two-thirds of the programs use fish, and only one-third use algae\textsuperscript{[73]}. Indeed, aquatic insects are considered sensitive indicators of environmental perturbations because of their abundance, biomass, and diversity in many freshwater ecosystems\textsuperscript{[47]}.

Aquatic insects have been particularly useful in biomonitoring of streams but have also been used in lentic
studies to assess changes in lake water quality and productivit\[52,393\]. For example, insects, especially chironomid midges, have been used in paleolimnological studies to reconstruct changes in land use surrounding a lake\[392\]. Stream macroinvertebrates, especially insects, offer several advantages in biomonitoring studies\[334\]. The small size and limited mobility of macroinvertebrates renders them relatively easy to sample and reflective of local conditions. Macroinvertebrates are also known to be sensitive to a variable of pollutants. Furthermore, since insects absorb or transform chemical pollutants, measures of their abundance provide a more ecologically meaningful measure of pollution than do direct chemical analyses. Insects also integrate environmental quality over a longer period than do static measures of water quality. Biomonitoring, therefore, integrates ecology, life history, physiology, and taxonomy into a single management and assessment tool. Although valuable and widely used, aquatic insects also present a few disadvantages in these studies\[334\]. For example, spatial and temporal variation in abundance of aquatic life history stages must be taken into account. Thus, biomonitoring sampling designs must be stratified to reflect as much spatial and temporal variability as possible\[169\], especially in terms of underlying geology\[241,298\]. Furthermore, aquatic insect identification is time-consuming and requires trained personnel, while errors in taxonomy can lead to misleading conclusions\[208,303\].

Current biomonitoring approaches that use aquatic insects span the range of biological organization, from the gene to the ecosystem\[302,303\]. Such approaches include: (1) molecular and cellular measures of biochemical and physiological activity, collectively known as biomarkers\[181\]; (2) attributes at the organism level, such as changes in morphology, behavior, and life history parameters that can be used as indices of pollution\[222\], or use of “sentinel organisms” that bioaccumulate toxic materials and can then be analyzed\[65\]; (3) population-level responses, such as the occurrence or abundance of indicator species, used as a measure of sensitivity to a pollutant; (4) community-level approaches that integrate many types of data into summary responses to pollutants; and (5) ecosystem-scale studies that assess effects of stressors on ecological processes and function.

Of these different approaches, those at the community level are probably in most widespread use, and may be either qualitative or quantitative. Rapid assessment methods are generally qualitative and permit the assessment of a large number of streams with a reasonable degree of effort\[208\]. Quantitative approaches are also very common, and the choice between qualitative and quantitative techniques depends on the objectives of the study. Several different metrics of aquatic insect communities are typically used\[303\] in part because different groups of insects have been classified by their tolerance to pollution\[73\]. Many parameters of communities and their constituent populations have been used for this purpose, including population densities, species diversity, evenness, and richness, and various indices based on specific groups of insects.

Taxa richness is widely used, but is difficult to compare across studies because different levels of resolution tend to be used by different investigators and for different taxonomic groups. EPT richness (combined richness of Ephemeroptera, Plecoptera, and Trichoptera taxa) takes advantage of the relative ease with which these insects can be identified and their sensitivity to pollution\[73,207,273\]. This index does vary longitudinally but is robust to seasonal and interannual fluctuations\[334\]. Since chironomids are considered pollution tolerant while EPT taxa are not, the ratio of EPT to chironomids is another popular community-level metric. Diversity and similarity indices afford the advantage of being readily comparable among sites, and biotic indices offer a readily interpretable score\[167\]. Functional attributes of insects also have utility in biomonitoring\[118,331\]. Such attributes focus on life history characteristics (i.e., species traits) of insects including functional feeding group, mobility, fecundity, and longevity\[232,274,276\]. Since such measures rely on functional rather than taxonomic information, they bridge community- and ecosystem-level approaches to biomonitoring.

Increasingly, multimetric and multivariate approaches are being recommended over a single metric for assessment in biomonitoring studies\[118,208,208,303,333\]. Multimetric approaches can combine the strengths of individual metrics to minimize the chance of an incorrect assessment, and often several metrics can be calculated from the same dataset. Multivariate statistical approaches permit partitioning of variance due to different factors, thus providing more useful information than a single measure. Furthermore, such approaches are less subjective than univariate approaches. The utility of several different biomonitoring approaches that use benthic macroinvertebrates has been demonstrated\[73\], which has also stressed the importance of combining information on both physical habitat quality and macroinvertebrate composition when assessing water quality.

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