5

Habitat, Life History, and Behavioral Adaptations of Aquatic Insects

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INTRODUCTION

The observed patterns of distribution and abundance of aquatic insects indicate successful adaptations to a wide variety of habitats. To demonstrate how organisms adapt to particular niches of the freshwater community, examples of species using certain environments are presented in this chapter and the life cycle is used as a framework for describing diverse modes of coping with environmental characteristics.

Factors that influence utilization of a particular habitat can be grouped into four broad categories: (1) physiological constraints (e.g., oxygen acquisition, temperature effects, osmoregulation; (2) trophic considerations (e.g., food acquisition); (3) physical constraints (e.g., coping with habitat); and (4) biotic interactions (e.g., predation, competition). However, these categories are so interrelated that detailed analysis of each factor is not appropriate. Aquatic insect respiration is covered in detail in chapter 4, but it is considered here because activities related to oxygen acquisition are central to behavioral and morphological features associated with most other activities.

The traditional division of freshwater systems into standing (lentic) and running (lotic) waters is useful for indicating physical and biological differences. Most insects are adapted to either a lentic or a lotic habitat, but overlaps are common. For example, insects inhabiting pools in streams have "lentic" respiratory adaptations, whereas those on wave-washed shores of lakes are similar to stream riffle inhabitants in both oxygen requirements and clinging adaptations.

Despite their success in exploiting most types of aquatic environments, insects are only incompletely or secondarily adapted for aquatic life. With very few exceptions, aquatic insects are directly dependent on the terrestrial environment for part of the life cycle. Even Hemiptera and Coleoptera with aquatic adults may require access to surface air for respiration. This dependence on the terrestrial environment probably contributes to the prevalence of insects in shallow ponds and streams as compared with deep rivers or lakes and to their virtual absence from the open sea.

ADAPTATION TO HABITAT

Osmoregulation

Aquatic insects need to maintain a proper internal salt and water balance. Body fluids usually contain a much higher salt concentration than does the surrounding water and water tends to pass into the hypertonic (higher osmotic pressure) hemolymph. The insect integument, especially the wax layer of the epicuticle, appears to be especially important in preventing flooding of the tissues (Chapman 1982). Some freshwater insects take in large quantities of water during feeding. Their feces contain more water than the frass of terrestrial counterparts since many aquatic insects excrete nitrogenous wastes as ammonia, which is generally toxic unless diluted with large quantities of water (Chapman 1982). The production of a hypotonic urine (lower osmotic pressure, or more dilute than the body fluids) is an important osmoregulatory mechanism in aquatic insects. Specialized areas of the hindgut reabsorb ions before wastes are eliminated.

In contrast, saltwater and terrestrial insects produce a rectal fluid that is hypertonic to the hemolymph (Stobbart and Shaw 1974). For example, the dipteran *Ephydra cinerea*, which occurs in Great Salt Lake (salinity > 20% NaCl), maintains water and salt balance by drinking the saline medium and excreting rectal fluid that is more than 20% salt.

Concentrations of freshwater ions vary tremendously. Many insects absorb salts directly from the surrounding water by active transport across specialized regions of the body. Such regions include the rectal gills of the mosquito, *Culex pipiens;* the rectal gills are larger in larvae reared in water with low ionic concentrations, which increases the surface area available for absorption of chloride ions (Wigglesworth 1938). Specialized areas of the integument, including the gills and anal papillae in larvae[1] of Ephemeroptera, Plecoptera, and Trichoptera, facilitate uptake of ions from the hypotonic external media (Wichard and Komnick 1973, 1974; Wichard et al. 1975; Wichard 1976, 1978). In the mayfly *Callibaetis* sp. the number of cells involved with chloride uptake decreases as the salinity of the environment increases, an adaptation to the increasing salinity of drying temporary ponds (Wichard and Hauss 1975; Wichard et al. 1975).

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1. Throughout this chapter we use the term "larva" for the immature stages of all orders of insects.

Temperature

Virtually all facets of life history and distribution of aquatic insects are influenced by temperature. Aquatic insects occur at temperatures ranging from zero to about 50°C. Metabolism, growth, emergence, and reproduction are directly related to temperature, whereas food availability, both quantity and quality, may be indirectly related (Anderson and Cummins 1979). The thermal death point of most freshwater invertebrates is between 30 and 40°C (Pennak 1978), so species such as the ephydrid fly, *Scatella thermarum*, found at 47.7°C in Icelandic hot springs (Tuxen 1944), have developed considerable thermal acclimation.

In contrast to the limited number of species found at high temperatures, a diverse fauna exists at the freezing point and many lotic species can grow at winter temperatures. Hynes (1963) and Ross (1963) suggest that this is an adaptation to exploit the seasonal pulse of leaf input in the autumn. The ancestral aquatic habitat of many insects is postulated to be cool streams; Hynes (1970a, 1970b) comments that the extant taxa of Plecoptera, Ephemeroptera, Trichoptera, Corydalidae, and nematocerous Diptera occur in cool streams and these are survivors of primitive groups.

Shallow lentic waters will generally reach higher summer temperatures than streams of the same area, resulting in a greater algal food supply and faster insect growth rates. However, oxygen may become a limiting factor because O_2 concentration is inversely proportional to temperature and high algal respiration during darkness may deplete the available O_2. Thus, a greater proportion of lentic than lotic species utilizes atmospheric O_2 or has developed other more efficient respiratory devices.

Life cycle adaptations have evolved that enable species to utilize favorable periods for growth, coupled with appropriate timing for aerial existence. This may involve diapause or quiescent periods in a resistant life stage for avoiding inclement periods of excessively high or low temperatures. Asynchronous larval cohorts and extended emergence periods occur in springs, where temperature is uniform year around. Cold springs can also be refugia for species normally found in colder climates, e.g., arctic insects in temperate region springs.

Sweeney and Vannote (1978) and Vannote and Sweeney (1980) suggest that an optimal thermal regime exists for a given species and that deviations into warmer (southern) or cooler (northern) waters adversely affect fitness by decreasing body size and fecundity. Alteration of thermal regimes, for example by removal of riparian vegetation or by hypolimnionic release from dams, will obviously affect insect life cycles or species composition (Lehmkuhl 1972a; Ward 1976).

Lotic Habitats

The velocity of moving water influences substrate particle size. Substrates may range from large boulders to fine sediments in a relatively short reach, resulting in a wide range of microhabitats. Flowing water continuously replenishes water surrounding the body and turbulence provides reaeration; thus, dissolved oxygen is rarely limiting to stream inhabitants. The transport of inorganic and organic materials by the current may be either detrimental (e.g., scouring action) or beneficial (as a food source).

The range of current velocities associated with a rubble or cobble substrate also increases habitat diversity, and various taxa are adapted for maintaining position at different velocities. Filter-feeding collectors exploit the current for gathering food with minimal energy expenditure. Other fast-water forms feed by predation, scraping the periphyton-detrital film, or gathering fine particles that collect in crevices.

An important microhabitat for the stream biota is the "boundary layer" on stones (Ambühl 1959; Hynes 1970a). Current velocity is greatly reduced due to frictional drag and, as the layer extends for 1–4 mm above the surface, many insects are small or flat enough to live within it. Bournaud (1963) provides a discussion of problems and methods of measuring velocity in microsites actually occupied by stream-dwelling organisms. Recent studies by Statzner and Holm (1982) using laser doppler anemometry indicate that velocity patterns around the body of benthic invertebrates are much more complicated than is suggested by the currently accepted boundary layer concept.

Morphological and Behavioral Adaptations to Current: A general flattening of the body and smooth, streamlined dorsum are typical of many rheophilic (current-loving) insects: e.g., heptageniid mayflies, perlid stoneflies, and psephenid beetles. Many mayflies and stoneflies have legs that project laterally from the body, thereby reducing drag and simultaneously increasing friction with the substrate. In some caddisflies (e.g., Glossosomatidae), the shape of the case rather than the insect modifies turbulent flow to a laminar sublayer.

True hydraulic suckers are apparently found only in the larvae of the dipteran family Blephariceridae (fig. 21.11). A V-shaped notch at the anterior edge of each of the six ventral suckers works as a valve out of which water is forced when the sucker is pressed to the substrate. The sucker operates as a piston with the aid of specialized muscles. In addition, a series of small hooks and glands that secrete a sticky substance aid sucker attachment (Brodsky 1980). Blephariceriids move in a "zigzag" fashion, releasing the anterior three suckers, lifting the front portion of the body to a new position, and reattaching the anterior suckers before releasing and moving the posterior ones to a new position. The larvae are commonly found on smooth stones, and Hora (1930) attributes their absence from certain Indian streams to the presence of moss or roughened stones that would interfere with normal sucker function.

Several aquatic insects have structures that simulate the action of suckers. The enlarged gills of some mayflies (e.g., *Epeorus* sp. and *Rhithrogena* sp.) function as a friction pad, and *Drunella doddsi* has a specialized abdominal structure for the same purpose. Brodsky (1980) describes a "pushing-proleg" in some chironomids; it has a circlet of small spines that function as a false sucker when pressed to the substrate. Mountain midge larvae (Deuterophlebiidae) possibly use a similar mechanism to attach their suckerlike prolegs.

Larval black flies (Simuliidae) use a combination of hooks and silk for attachment. The thoracic proleg resembles that of chironomids and deuterophlebiids, described above, and the last abdominal segment bears a circlet of hooks. The larva spreads a web of silk on the substrate to which it attaches either the proleg or posterior hooks. The larva moves forward in an inchwormlike manner, spins silk over the substrate, and attaches the proleg and then the posterior circlet of hooks to the silken web.

Silk is used for attachment by a number of caddisflies (e.g., Hydropsychidae, Philopotamidae, and Psychomyiidae), which build fixed nets and retreats. Some case-making caddisflies (e.g., *Brachycentrus* sp.) also use silk for attaching their cases to the substrate in regions of fairly rapid flow, and free-living caddisflies may use "security threads" as they move over the substrate in fast currents. The line is used in combination with their large anal prolegs, which are employed as grapples. Many chironomid larvae construct fixed silken retreats for attachment, and black fly pupae are housed in silken cases that are attached to the substrate. Other morphological adaptations to running water are given in table 7A.

Despite the fact that unidirectional current is the basic feature of streams, the majority of lotic insects have not adapted to strong currents but instead have developed behavior patterns to *avoid* current. Very few lotic insects are strong swimmers, probably because of the energy expenditure required to swim against a current; downstream transport requires only a movement off the substrate to enter the current. Streamlined forms, such as the mayflies *Baetis* sp., *Isonychia* sp., and *Ameletus* sp., are capable of short rapid bursts of swimming, but most lotic insects move by crawling or passive displacement. The benthic fauna chiefly occurs in cracks and crevices, between or under rocks and gravel, within the boundary layer on surfaces, or in other slack-water regions. Presumably, much of the benthic population seeks refuge deeper in the substrates during floods; insects are difficult to find at such times, but normal population levels are found soon after the flows subside.

The *hyporheic* region is the area below the bed of a stream where interstitial water moves by percolation. In gravelly soils or glacial outwash areas it may also extend laterally from the banks. An extensive fauna occurs down to one meter in such substrates (Williams and Hynes 1974; Williams 1981b). Most orders are represented, especially those taxa with slender flexible bodies or small organisms with hard protective exoskeletons. Stanford and Gaufin (1974) report that some stoneflies spend most of their larval period in this subterranean region of a Montana River. They collected larvae in wells over 4 m deep, located 30–50 m from the river.

Drift. Downstream drift is a characteristic phenomenon of invertebrates in running waters. Despite the adaptations for maintaining their position in the current or avoiding it, occasional individuals could be expected to lose attachment or orientation and be transported downstream. However, the large numbers of some taxa that drift indicate that this is more than a passive activity. Waters (1965) divided drift into three categories: (1) *catastrophic,* resulting from physical disturbance of the bottom fauna, e.g., by floods, high temperatures, and pollutants; (2) *behavioral,* indicated by characteristic behavior patterns resulting in a consistent diel periodicity (usually at night); and (3) *constant,* the continual occurrence of low numbers of most species. Mayflies of the genus, *Baetis* consistently exhibit high behavioral drift rates with a night-active periodicity. Other mayflies, stoneflies, caddisflies, black flies, and the amphipod *Gammarus* sp. are frequently abundant in drift. Drift is important to stream systems in the recolonization of denuded areas, as a dispersal mechanism, and particularly as a food source for visual predators. Many fish, especially salmonids, select and defend territories best suited for the interception of drift (Waters 1972).

Irrespective of its causes, drift results in a net downstream displacement of some portion of the benthic population. Whether drift losses from upstream areas represent excess production or whether compensatory upstream movements are required is not known. Müller (1954) proposed that upstream flight of adults could be the mechanism to complete the "colonization cycle," and upstream migrations of some mayflies and amphipods in the slow water near shore have been recorded (e.g., Neave 1930; Minckley 1964; Hayden and Clifford 1974). However, the relative importance of upstream movement, or even its necessity for most taxa, remains an open question. Several workers (Bishop and Hynes 1969; Waters 1972; Müller 1974, Williams 1981a) have reviewed the extensive literature on the significance of drift to production biology, population dynamics, and life histories.

Unstable Substrates. Sandy substrates of rivers and streams are poor habitats because the shifting nature of the bed affords unsuitable attachment sites and poor food conditions. An extreme example of this instability is the Amazon River, where strong currents move bedload downstream as dunes of coarse sand reaching 8 m in height and up to 180 m in length, largely preventing the establishment of a riverbed fauna (Sioli 1975). Despite substrate instability, some sandy streams are quite productive. Blackwater streams of the Southeast have extensive areas of sand with an average standing stock, primarily small Chironomidae less than 3 mm in length, exceeding $18000/m^2$. Though their biomass is small, rapid growth rates result in a significant annual production and an important food source for predaceous invertebrates and fish (Benke et al. 1979).

The inhabitants of sandy or silty areas are mostly sprawlers or burrowers (table 6B), with morphological adaptations to maintain position and to keep respiratory surfaces in contact with oxygenated water. The predaceous mayflies *Pseudiron* sp. and *Analetris* sp. have long, posterior-projecting legs and claws that aid in anchoring the larvae as they face upstream. Some mayflies (e.g., Caenidae and Baetiscidae) have various structures for covering and protecting gills, and others (e.g., Ephemeridae, Behningiidae) have legs and mouthparts adapted for digging. The predaceous mayfly *Dolania* sp. burrows rapidly in sandy substrates of Southeastern streams. The larva utilizes its hairy body and legs to form a cavity underneath the body where the ventral abdominal gills are in contact with oxygenated water.

Many dragonflies (e.g., *Cordulegaster* sp., *Hagenius* sp., Macromiidae, and many Libellulidae) have flattened bodies and long legs for sprawling on sandy and silty substrates. They are camouflaged by dull color patterns and hairy integuments that accumulate a coating of silt. The eyes, which cap the anteriolateral corners of the head, are elevated over the surrounding debris. Many gomphid larvae actually burrow into the sediments using the flattened, wedge-shaped head, and fossorial tibiae. The genus *Aphylla* (Gomphidae) is somewhat unusual in that the last abdominal segment is upturned and elongate, allowing the larvae to respire through rectal gills while buried fairly deep in mucky substrate.

Wood-Associated Insects. Wood debris provides a significant portion of the stable habitat for insects in small streams where water power is insufficient to transport it out of the channel. In addition to the insect component using wood primarily as a substrate, a characteristic xylophilous fauna is associated with particular stages of degradation. These include: chironomid midges and scraping mayflies (*Cinygma* sp. and *Ironodes* sp.) as early colonizers; the elmid beetle, *Lara* sp., and the caddisfly, *Heteroplectron* sp., as gougers of firm waterlogged wood; and the tipulids, *Lipsothrix* spp., in wood in the latest stages of decomposition (Anderson *et al.* 1978; Dudley and Anderson 1982). Wood debris is most abundant in small forested watersheds, but it is also an important habitat in larger streams with unstable beds. Cudney and Wallace (1980) found that submerged wood in the Coastal Plain region of the Savannah River was the only substrate suitable for net-spinning caddisflies, but that high standing crops and production could be supported in a relatively small space because the caddisflies were exploiting the food resource transported to them by the current. Benke *et al.* (1979) reported that snags in a small Southeastern blackwater river were highly productive, not only for net-spinning caddisflies, but also for filter-feeding Diptera and other typical "benthic" insects. Even in the Amazon situation mentioned above, large logs in the lee of dunes are heavily colonized by chironomid midges (Sioli 1975).

Lentic Habitats

Standing-water habitats range from temporary pools to large, deep lakes. They tend to be more closed than are lotic environments, with recycling occurring within the lake basin. The physical environment is governed by the climate and geology of the area and the shape of the basin. The habitats for insects are illustrated in a typical cross section from the surface film, through open waters, to the shallow and deep benthos (fig. 5.1). Similar habitats occur in lotic situations so many of the insects discussed below can also be found in lotic environments.

Surface Film. The unique properties of the water surface constitute the environment for the *neuston* community. Water striders (Gerridae), whirligig beetles (Gyrinidae), mosquito larvae (Culicidae), and springtails (Collembola) are common examples. The surface film results from the attractive forces among water molecules. Within the body of water the forces are equal on all sides, but at the surface the attraction is less between air and water than on the other three sides. This results in a slight pull toward the center of the water mass and the surface acts as if it were a stretched elastic membrane. "To an organism of small size, this air-water interface can be an impenetrable barrier, a surface on which to rest, or a ceiling from which to hang suspended" (Usinger 1956a).

Water striders and bugs of the related family Veliidae have preapical claws that enable them to move about without breaking the surface film and a velvety hydrofuge hair pile on the venter that is nonwettable. The skating motion of gerrids is more accurately described as rowing. The weight causes a slight dimpling of the surface film (easily seen in the shadow cast on the bottom of clear shallow waters). The long tarsi of the middle legs are pressed against the depression in the film for propulsion while the hind legs are held outstretched behind as rudders for steering.

The gerrids also exploit the surface film by detecting vibrations from surface ripples with sensors located between the tarsal segments on the meso- and metathoracic legs. The
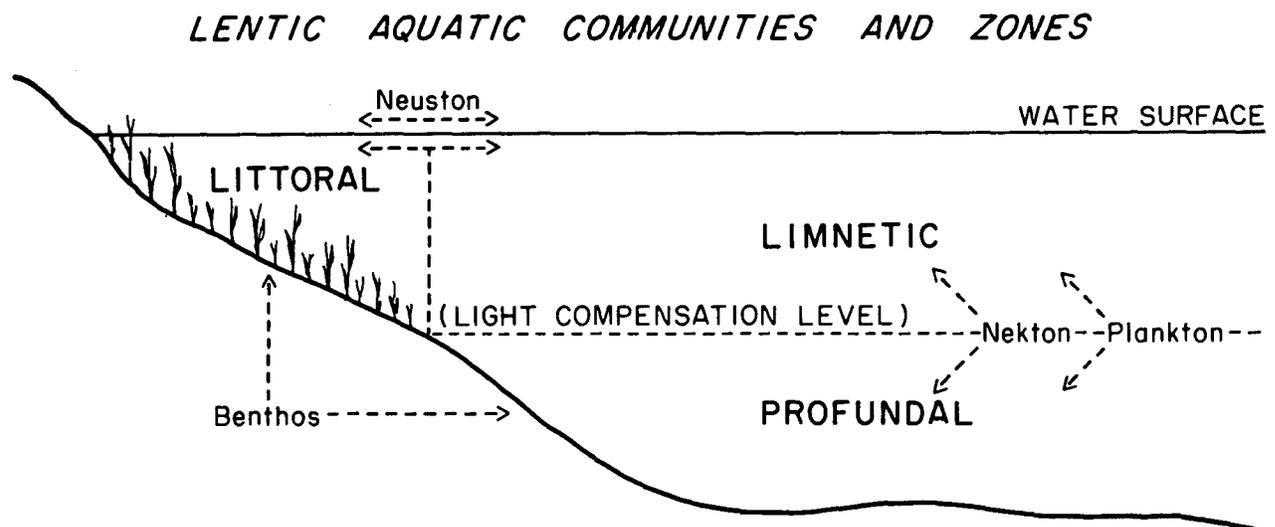
LENTIC AQUATIC COMMUNITIES AND ZONES

Figure 5.1. Diagram of lentic zones *(capital letters)* and aquatic communities *(lower case letters).*

sequence in which these sensors perceive an oncoming ripple tells the insect how much to turn to face the disturbance caused, for example, by a potential prey. The strider turns by moving its rowing legs in opposite directions much as an oarsman would turn a boat. At this juncture, a combination of visual and vibratory information allows the strider to choose between approaching the disturbance or fleeing from it. If the former, it rows forward, pausing between each stroke to evaluate further ripple signals (Milne and Milne 1978). Some gerrids also use vibrations of the surface film for communication in courtship and mating (Wilcox 1979).

Some semiaquatic insects have developed chemical propulsion mechanisms for a quick return to shore. The beetles *Dianus* sp. and *Stenus* sp. (Staphylinidae) can skim across the surface at a rate of 60–70 cm/sec. Glands at the tip of their abdomens discharge a secretion that lowers the surface tension behind the abdomen so that the insect is being drawn forward by the normal surface tension of the water in front (Jenkins 1960).

Whirligig beetles have divided eyes; the lower part detects events under the water and the upper part detects events on or above the water surface. Glands keep the upper portion of the body greased to repel water, whereas the lower surface and lower eyes are wettable. Whirligig gyrations on the surface are effected by rapid propulsion with paddle-shaped swimming legs. The hind legs are unique in that the segments can be folded up during the forward stroke and spread apart like a fan for the powerful backward stroke. In addition to propulsion, the swimming activity causes a series of ripples or bow waves that, when reflected back by obstacles, are detected by the antennae touching the surface film, allowing quick course correction even in the dark (Milne and Milne 1978).

Neuston insects are potentially vulnerable to predation by visual aquatic predators because they are silhouetted against the sky; however, both gerrids and gyrinids seem to be avoided by fish, apparently because secretions produced by repugnatorial glands make them distasteful.

Hydrofuge structures are important adaptations for obtaining atmospheric air through the surface film. The openings of terminal spiracles have glands that discharge a waxy secretion on the cuticle; contact with the surface film repels the water exposing the spiracles to the air. The waxy lining of the tracheae prevents water from running into them by capillarity. Some insects (e.g., *Culex* sp., *Limonia* sp., *Stratiomys* sp.) can hang from the surface film supported by a crown of semihydrofuge hairs around the spiracles. The semihydrofuge hair will lie in the water surface, half wetted and half exposed. When a stratiomyiid larva submerges, the crown is lifted off the water and envelops an air bubble that is used as an air store.

Feeding adaptations associated with neuston specialization are exemplified by mosquito larvae. Though the mouthparts are basically of the primitive chewing type, the larvae have brushes arising from the labrum that sweep floating or suspended material toward the mouth. *Anopheles* sp. larvae lie beneath the surface film supported by tufts of float hairs on each segment. The larva rotates its head so that the mouth brushes are uppermost and sets up a current that draws the microbial-rich layer of water along the underside of the surface film and into the mouth.

Limnetic Zone. In open waters, to the depth of effective light penetration, a broad distinction is made between *nektonic* and *planktonic* organisms: nekton are swimmers able to navigate at will (e.g., Coleoptera, Hemiptera, some Ephemeroptera), whereas plankton are floating organisms whose horizontal movements are largely dependent on water currents.

The phantom midge *Chaoborus* sp. is the most common insect plankter; it is abundant in many eutrophic (nutrient-rich) ponds, lakes, and some large rivers. *Chaoborus* sp. exhibits vertical migrations, occurring in benthic regions during the day but migrating vertically into the water column at night. These migrations are dependent on light and oxygen concentrations of the water (LaRow 1970). Larvae avoid predation by being almost transparent except for two crescent-shaped air-sacs or buoyancy organs (fig. 21.30); they lie horizontally in the water, slowly descending or rising by adjusting the volume of the air-sacs. Their prehensile antennae are used as accessory mouthparts to impale zooplankton and deliver them to the mouth.

Many lentic insects are strong swimmers but relatively few are nektonic. They pass through the limnetic zone when surfacing for emergence, but the vast majority of lentic insects occurs in shallow water with emergent plants. As mentioned previously, the scarcity of insects in limnetic areas may be a consequence of the secondary adaptations for aquatic life. There are no resting supports in the limnetic zone so maintaining position requires continuous swimming or neutral buoyancy.

Littoral Zone: The littoral zone, the shallow region with light penetration to the bottom, is typically occupied by macrophytes (macroalgae and rooted vascular plants). It contains a diverse assemblage of insects with representatives of most aquatic orders. Habitats include benthic and plant surfaces, the water column, and the surface film (table 6A); occupants include burrowers, climbers, sprawlers, clingers, swimmers, and divers (table 6B). Morphological and behavioral types in the littoral zone are similar to those in slow-moving or backwater regions of lotic habitats. The diversity and abundance of littoral species results in biological factors (e.g., competition and predation) assuming importance in shaping community structure.

The biomass and diversity of invertebrates associated with aquatic macrophytes in lentic or lotic habitats may exceed that of the fauna in the sediments at the same location. The impact of herbivorous insects on many living plants is low, and it has been suggested that aquatic macrophytes produce secondary plant substances that serve as chemical defenses against herbivores (Otto and Svensson 1981b), or that they may be deficient in some essential amino acids (Smirnov 1962). However, herbivore-chewers (shredders-herbivores), miners, and stem borers (see chap. 6) feed on macrophytes, and these include pests of economic importance such as the weevil *Lissorhoptrus simplex* (Curculionidae) on rice (Leech and Chandler 1956), and the caddisfly *Limnephilus lunatus* (Limnephilidae) on watercress (Gower 1967). Berg (1949)

and McGaha (1952) recorded a diverse fauna feeding on *Potomogeton* sp. and other aquatic plants. Such feeding adaptations may be recent because only the more advanced orders (Lepidoptera, Trichoptera, Coleoptera, and Diptera) are represented.

Insects may also use macrophytes as a substrate rather than as food. For example, macrophytes in both lentic and lotic habitats may harbor a number of filter-feeding Ephemeroptera, Trichoptera, and Diptera. Many species found in weed beds are green in color and blend in with their surroundings. Dragonflies of the family Aeshnidae often have contrasting bands of pale and dark green or light brown that adds to the effectiveness of the camouflage. Some species in most orders utilize macrophytes as oviposition sites. Larvae of some Coleoptera and Diptera rely on the intracellular air spaces for respiration and are thus limited in their distribution by that of their macrophyte "host."

Profundal Zone: The number of taxa of aquatic insects occurring below about 10 m is limited, but the few species that do occur there may be very abundant. This area includes the sublittoral and profundal regions. The latter is the zone below which light penetration is inadequate for plant growth. The deep water is a stable region because water movement is minimal and temperature varies only slightly between summer and winter. Periodic depletion or absence of dissolved oxygen may occur, especially in eutrophic situations. Substrates are usually soft or flocculent and offer little in the way of habitat diversity or cover. The inhabitants are mostly burrowers that feed on suspended or sedimented materials and are capable of tolerating low dissolved oxygen or even anaerobic conditions. Typical deep-water insects are ephemerid mayflies (e.g., *Hexagenia* sp., *Ephemera* sp.) and many genera of Chironomidae (e.g., *Chironomus, Tanytarsus*). Predaceous deep-water insects include *Sialis* sp. (Megaloptera) and *Chaoborus* sp. (Diptera).

Dense populations of the midge *Chironomus* are characteristic of profundal sediments. The larvae build U-shaped tubes with both openings at the mud-water interface. Body undulations cause a current of water, providing oxygen, and particulate food in the form of phytoplankton and fine detritus with its accompanying microbes to be drawn through the tube. Hemoglobin serves as an oxygen store during periods of low dissolved oxygen, but the larvae become quiescent under anaerobic conditions. The life cycle of profundal *Chironomus* typically requires two years, compared with a year or less for the same species in shallow waters. This is due to the slow growth at cold temperatures, low food quality, and to extended periods of quiescence when the water is anoxic (Jonasson and Kristiansen 1967; Danks and Oliver 1972).

The profundal chironomid community has been used extensively as an indicator of the nutrient conditions or productivity status of lakes. Saether (1980b) lists about twenty genera of chironomids that are characteristic of particular oxygen-nutrient-substrate combinations, which, in conjunction with other noninsect assemblages, can be used in lake typology classifications. Warwick (1980) documented over 2500 years of land-use practices around Lake Ontario using the subfossil chironomid head capsules in a sediment core; changes in species composition of midges were associated with various periods of eutrophication, deforestation, sedimentation, and contamination.

LIFE CYCLE ADAPTATIONS

Diverse life history patterns have evolved to enable species to exploit foods that are seasonably available, to time emergence for appropriate environmental conditions, to evade unfavorable physical conditions (e.g., droughts, spates, and lethal temperature), and to minimize repressive biotic interactions such as competition and predation. Typically, a seasonal succession of species can be cataloged at a given location by determining the emergence and flight periods of adults or by studying the larval growth periods. However, comparison of a given species at different sites may indicate considerable flexibility in life histories. Some important adaptations include: (1) responses to temperature and oxygen levels; (2) use of daylength or temperature as environmental cues to synchronize life stages; (3) resting stages to avoid unfavorable conditions; and (4) extended flight, oviposition, or hatching periods to spread the risk in coping with environmental conditions that cannot be avoided entirely.

The duration of aquatic insect life cycles ranges from less than two weeks (e.g., some Culicidae and Chironomidae) to 4–5 years (e.g., some Megaloptera and Odonata), but in the north temperate zone an annual cycle is most common. Hynes (1970a) distinguished three main types of life cycles for insects in a temperate stream: slow seasonal, fast seasonal, and nonseasonal cycles. In seasonal cycles a distinct change of larval size occurs with time, i.e., the progression of growth by cohorts can be discerned by periodic sampling of field populations. In nonseasonal taxa, individuals of several ages are present at all times. The three types are illustrated by three species of glossosomatid caddisflies, all collected from one emergence trap (fig. 5.2).

Slow-seasonal cycles are common in cool streams and typified by some Plecoptera, Ephemeroptera, and Trichoptera. Eggs hatch soon after deposition, and larvae grow slowly, reaching maturity nearly a year later. In many species, an extended hatching period results in recruitment over several months. Larvae grow during winter and most species have a flight period early in the year.

Fast-seasonal cycles are those in which growth is rapid after a long egg or larval diapause or after one or more intermediate generations. The caddisfly *Agapetus bifidus* has an egg diapause of 8–9 months and a larval growth period of only 2–3 months (fig. 5.2). Various fast-seasonal cycles reach full term in spring, early and late summer, and fall. Two or more fast cycles may be exhibited by the same species when rapid generations succeed one another, as in the mayfly *Baetis* sp. and the black fly *Simulium* sp. Individuals that grow rapidly at warm temperatures tend to be much smaller than those of the earlier, slow-growing generation (Hynes 1970b; Ross and Merritt 1978; Sweeney 1978; Cudney and Wallace 1980; Georgian and Wallace 1983).

In nonseasonal cycles, individuals of several stages or size classes are present in all seasons. This may be because the life cycle spans more than a year as in some large Plecoptera and Megaloptera, or because a series of overlapping generations occurs, or for other unexplained reasons. Chironomidae often exhibit nonseasonal patterns probably because two or more species have not been distinguished or because short life cycles result in overlapping cohorts.
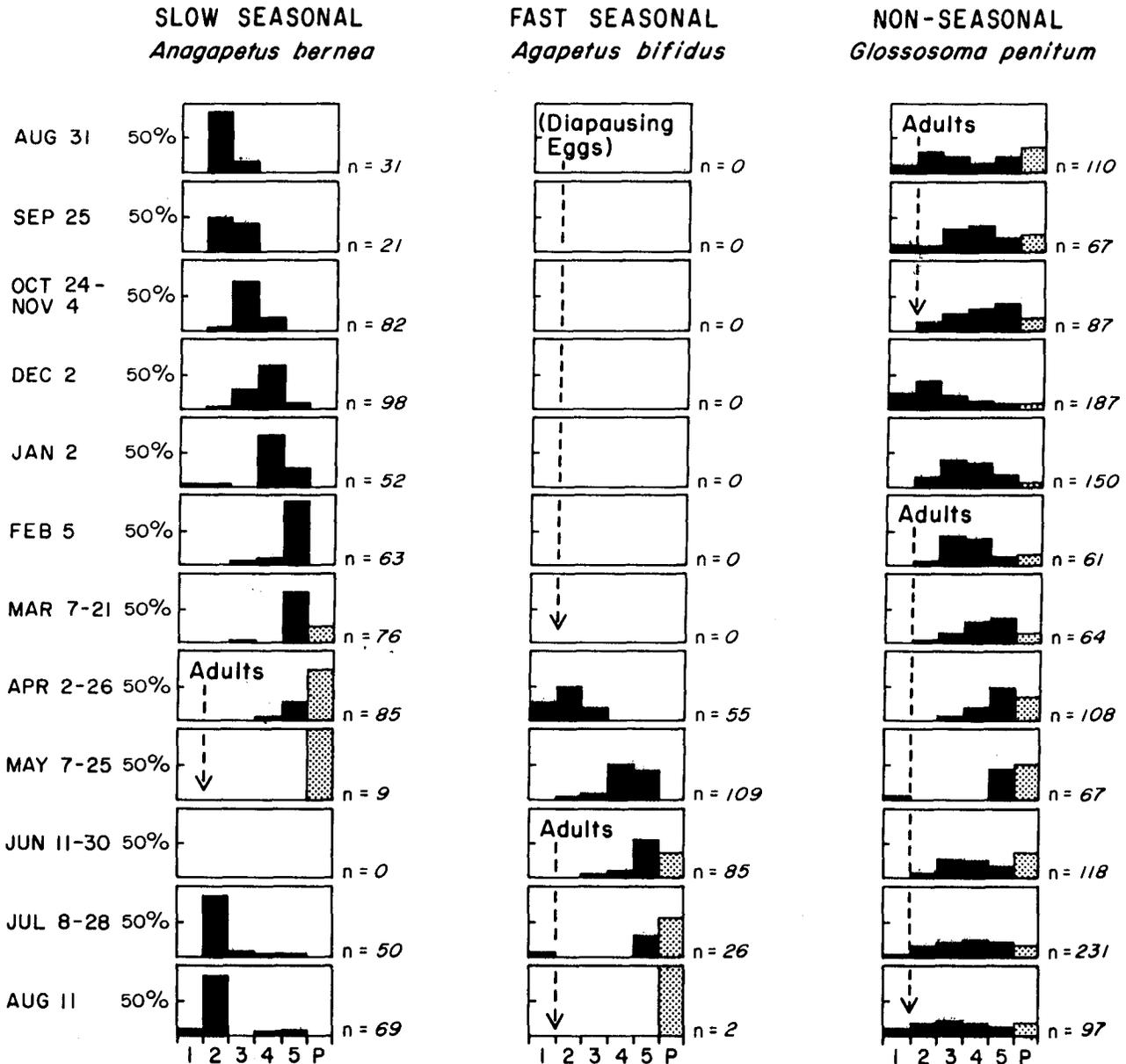
SLOW SEASONAL
Anagapetus bernea

FAST SEASONAL
Agapetus bifidus

NON-SEASONAL
Glossosoma penitum

Figure 5.2. Age distribution of three glossosomatid caddisflies, illustrating life cycles. Field data are expressed as percentage composition per month for each instar. There are five larval instars; P = prepupa + pupa; n = number per sample. Flight period of adults is also indicated. (Data from Anderson and Bourne [1974].)

Poorly synchronized life cycles would be expected to occur in situations where limiting factors for growth or reproduction (e.g., temperature, food, and moisture) are not seasonally dependent. Thus in the tropics the unvarying temperature and light conditions could result in continuous periods of growth and reproduction. It is somewhat surprising that aquatic insects in the southern hemisphere are predominantly of the nonseasonal type in contrast to the situation in the north temperate zone (Winterbourn 1974, 1978; Hynes and Hynes 1975; Corbet 1978; Towns 1981).

Habitat Selection

On a gross level, habitat selection is primarily the province of the mated females as deposition of eggs determines where the larvae will initially occur. The chain of behavioral cues leading to oviposition has rarely been elucidated but habitat selection may involve visual, tactile, and chemosensory cues. Coleoptera and Hemiptera detect water while in daytime flight apparently from the reflective surface so they are attracted to ponds, swimming pools, and other shiny surfaces. For most aquatic insects, oviposition occurs near the location from which the adult emerged, but dispersal flights are common especially in species from temporary habitats.

Species that overwinter as adults (e.g., Coleoptera, Hemiptera) may have a fall dispersal flight to overwintering sites, and also a spring flight for oviposition.

The widespread tropical dragonfly, *Pantala flavescens* (Libellulidae), an obligate migrant that breeds in temporary ponds, exhibits long-distance dispersal in search of oviposition sites. The adults fly upward at emergence and are then transported by the wind to places where rain will later fall. Wind may transport the adults over 1400 km across the Indian Ocean toward the cold front produced by monsoons (Corbet 1963).

Caddisflies from temporary streams (*Hesperophylax* sp., *Grammotaulius* sp.) and ponds *(Limnephilus indivisus)* (table 5A) deposit eggs in damp channels or depressions before the habitat fills with autumnal rains or snow. A similar selection of habitat before it is suitable for the larva occurs with snow-pool mosquitos *(Aedes)*, which deposit diapausing eggs in depressions, and hatching occurs the following spring when eggs are wetted by the melting snow.

Males are responsible for habitat selection in many odonates; they establish territories, over ponds or streams depending on the species, and actively court females to oviposit within that locale. A male in tandem flight may even remain coupled while the female is ovipositing below the surface. Belostomatid bugs, which incubate eggs on the back of the male (table 5A), are another instance of male influence on habitat selection. Movement by the male through swimming or overland crawling to nearby pools will determine the site in which the larvae develop.

In general, taxa with specialized habitat requirements might be expected to exhibit the greatest degree of habitat selection by the ovipositing female. Insect parasitism (which is rare in aquatic insects) requires habitat specialization. The Palaearctic wasp, *Agriotypus* sp., crawls into the water enveloped by a film of air and seeks out a mature larva or pupa of the caddisflies *Silo* sp. or *Goera* sp. (Goeridae). An egg is then deposited within the caddisfly case so that the *Agriotypus* sp. larva can develop as a parasite of the pupal stage of the caddisfly (Clausen 1931).

Oviposition and Eggs

The diversity of oviposition strategies is illustrated in table 5A. Hinton (1981) provides a comprehensive treatment of insect eggs. Much of the life cycle can be deduced from the timing and habits of oviposition and the location of the eggs, but this aspect of natural history frequently receives less attention than it deserves. Elliott and Humpesch (1980) point out that information on fecundity, oviposition behavior, and hatching is essential for: (1) interpretation of life cycles; (2) identification of larval cohorts; (3) study of spatial patterns and movements; (4) construction of life tables; and (5) estimation of growth rates, mortality, and production.

The number of eggs varies greatly among taxa and among individuals of a species. Within the Ephemeroptera, *Dolania* sp. deposits about 100 eggs (Peters and Peters 1977), whereas the fecundity of *Ecdyonurus* sp. is 5000–8000 eggs per female (Elliott and Humpesch 1980). The number of eggs

produced by *Baetis rhodani* ranges from 600 to 2400 per female (Elliott and Humpesch 1980). The within-species variation in fecundity is related to size of the female, which in turn is associated with growth conditions of the larvae. In taxa in which feeding by adults is required for egg maturation, fecundity will depend not only on food availability but also on appropriate oviposition conditions, because eggs may be resorbed if conditions are unsuitable for oviposition.

The eggs of some insects mature in the pupa or last larval stage (e.g., Megaloptera, Ephemeroptera, some Plecoptera) and are ready to be laid soon after emergence and mating. At the other extreme (e.g., Odonata, Hemiptera, some Plecoptera, and Coleoptera), adults emerge with undeveloped ovaries, require a feeding period before oviposition (or overwintering), and deposit eggs over an extended period or in discontinuous clutches. Potential fecundity can be estimated by dissection of newly emerged females if eggs mature all at one time. However, when egg maturation is a continuing process or when successive clutches are produced, total egg production depends on the length of life of individual adults.

The egg is potentially a vulnerable stage because it lacks mobility. However, in many instances the egg is the most resistant stage of the life cycle and spans periods of cold, heat, drought, or food shortages. The hatching period may extend for several months, which spreads the risk over a range of environmental conditions. Extended hatching may be due to irregular rates of development of individual embryos, to irregular breaking of diapause, or to extended oviposition periods.

Larval Growth and Feeding

Differences in duration of the larval stage and in growth patterns provide for much of the variation in life histories. The examples presented below illustrate food acquisition strategies and larval growth patterns that adapt species to particular environments.

Though the fauna of temporary habitats is quite limited, most orders of aquatic insects are represented and these exhibit extreme seasonal regulation of life cycles. Wiggins *et al.* (1980) describe several life-cycle patterns for temporary ponds, depending on the timing of adult colonization and kind of resistant stage. The prime requisite for all species is rapid larval development during the wet phase. Many mosquitoes are temporary-habitat breeders; under optimum conditions some species can complete their growth in five days. Rapid growth implies adaptation to warm waters as even the species that emerge early in snow-melt pools (e.g., limnephilid caddisflies) will be exposed to high temperatures when water volume diminishes. The timing of recruitment in temporary pools is correlated with feeding behavior. The earliest larvae are detritivores, either shredders (e.g., limnephilid caddisflies) or fine-particle feeders (e.g., siphlonurid mayflies, *Aedes* sp. mosquitoes, Chironomidae); then algal feeders (e.g., *Callibaetis* sp. mayflies, haliplid beetles) and finally predators (e.g., Odonata, Hemiptera, dytiscid and gyrinid beetles) are recruited coinciding with abundant prey resources.

Table 5A. Summary of data for oviposition and egg stage of selected aquatic insects.

Taxon	Preoviposition Period	Oviposition Season	Oviposition Site	Oviposition Behavior
EPHEMEROPTERA				
Baetidae				
Baetis spp.	1 day (including subimago)	extended (spring–fall)	Shallow riffles, under-side of stones	♀ folds wings along abdomen walks into water and selects site
Callibaetis floridanus	5–7 days (including subimago)	entire year	Lentic, often temporary habitats	♀ lands on water and extrudes milky mass; dies on site
Ephemeridae				
Hexagenia spp.	2–4 days (including subimago)	May–Sept	Lakes, large rivers	♀♀ plummet to water and extrude 2 egg packets; on contact with water, eggs separate and sink. Some ♀♀ can take off and repeat
Leptophlebiidae				
Leptophlebia cupida	2 days (including subimago)	mid May–early July	Mainstream of slow-moving rivers	♀ dips abdomen in water, releases a few eggs at a time; completed in 5 min; flies up or down stream, daytime only
Ephemerellidae				
Ephemerella ignita	2 days (including subimago)	late June–Sept	Turbulent streams, in moss	♀ flies upstream with extruded egg ball; contact with water releases ball, and eggs then separate
Heptageniidae				
Epeorus pleurialis	3 days (including subimago)	Mar–May	Streams, fast water	♀ touches water several times, washes eggs off in batches
ODONATA				
Lestidae				
Lestes congener	3 wk	Aug	Temporary ponds; only in dry stems of *Scirpus* sp., 5–30 cm above water	♂ + ♀ in tandem; eggs inserted singly in incisions 2 cm apart
Archilestes grandis	—	mid June–late July	Lentic; in branches or petioles up to 13 m above water	♂ + ♀ in tandem; oviposition during daytime. Endophytic oviposition; 2 eggs per incision in petioles but about 10 in pithy stems
Aeshnidae				
Anax imperator	11–14 days	early June–early Aug	Ponds; warmest area	♀ alights on floating plants and deposits eggs endophytically; egg may penetrate leaf; 1 egg per incision
Corduliidae				
Tetragoneuria spp.	1 wk	mid May–July (ca. 1 mo at a site) (individuals live 2 wks)	Lotic, ca. 10 or more feet from shore	♀ makes 2 passes to select a site; on 3rd pass she drags abdomen through water trailing egg string until it adheres to solid object. Several ♀♀ add to egg-string aggregations on same day

Description of Egg or Egg Mass	Number of Eggs*	Incubation and Hatching Period	Comments	Geographic Area	Reference
contiguous rows of yellow, spherical eggs, form a flat semicircular plate	B. rhodani, winter generation up to 2500; summer generation up to 1200	B. rhodani, start of hatching 17 wks @ 3°C, 1 wk @ 22°C. Hatching interval 34 days @ 3°C, 3 days @ 22°C	Hatching period is variable for species and site. Delayed hatch of some eggs for 40 wk	Europe North America	655, 1181 415
viscous, reddish brown egg mass on venter of abdomen; mass is released and eggs separate when abdomen touches water	450–500	Hatch in 5–10 sec (ovoviviparous)	Adapted for temporary habitats. ♀♀ mate, and embryonic development complete before oviposition	Florida	170, 2474
eggs ellipsoid, .16–.19 × .28–.32 mm; sticky surface results in eggs adhering in clumps	2260–7684; x̄ = 4000 for average-size ♀♀ (24–25 mm)	11–26 days; 2 wk @ summer temp	Both low temp. and low D.O. will delay incubation (Fremling 1967)	Midwest	800, 801, 1154
ovoid, .23 × .12 mm; eggs anchored by peg-like structures that spring out after wetting	x̄ (mean-sized ♀), 2959; *Fecundity, F = 2.02 L³·⁰⁴	Hatching started in 10–14 days @ 20°C; 50% emerge on day 1, hatching continues for 43 days	Latitude effect on oviposition period and fecundity. 1072–2065 eggs per ♀ in Penn.	Alberta Pennsylvania	416, 2385
greenish egg ball; eggs have polar anchoring mechanism to attach to substrate	eggs per mass, 156–603; x̄ = 322	112–392 days @ 8.2°C; 56–294 days @ 15.8°C. In stream, 10% hatch by 100 days, 90% by 300 days	Extended hatching period. Temp. > 14.5°C delays hatching; egg diapause in some populations	England, Lake District	657
cream colored; ellipsoid, .08–.09 × .13–.15 mm; adhere firmly to substrate	2000–6000, x̄ = 4260 (dissected ♀♀)	Estimated 7 mo in field @ 11–14°C	Extended hatching period, with peak of small larvae in Feb	Kentucky	1678
elongate, 1.2 mm long; soft and greyish when deposited; cuticle then hardens and darkens	87–297 (x̄=205) mature oocytes; no. of egg clutches per ♀ not determined	Prediapause development for 1 wk; 3 mo diapause; 6–7 wk postdiapause; synchronous hatching (1 wk, in May)	Diapause occurs under snow cover; postdiapause embryogenesis triggered by snowmelt. Hatching threshold is 5°C	Saskatchewan	2165
white with dark anterior end; 1.9 × .3 mm	up to 149/♀; 70–180 (Smith and Pritchard 1956)	15 days; eggs hatch without wetting	At emergence, prolarva "jumps" to water; use of deciduous petioles for egg site possible because eggs do not overwinter	Oklahoma	191
elongate cylinder, .2 × .4 mm, with anterior bladelike projection to anchor egg in leaf	no data; can mature successive batches of eggs	Direct development; at field temp., 22–26 days; in lab, range of 28–51 days @ 15–20°C	Long oviposition period results in many larval size classes overwintering; thus, synchrony required in final instar	Southern England	436, 439, 441
oval, brown eggs, .7 × .4 mm, within a string of gelatinous matrix that swells to 3.5 mm wide × 11 cm long	up to 1000 per string. Egg-string aggregation averages 250 thousand eggs; exceptionally large mass contained over 1 million	Individual strings in lab, hatching began @ 2 wk, 50% complete by 3 wk, continues for 7 wk	Hatching of eggs within large aggregations is retarded and thousands fail to hatch	Michigan	1344

*Fecundity of many mayflies conforms to power law: $F = aL^b$, where L = body length, and a and b are constants (Elliott 1972; Clifford and Boerger 1974).

Table 5A.—Continued

Taxon	Preoviposition Period	Oviposition Season	Oviposition Site	Oviposition Behavior
PLECOPTERA				
Nemouridae				
Nemoura trispinosa	2–3 wk (feeding required)	mid June–early July	Lotic, midstream	Extruded as mass; flying ♀ dips abdomen into water; mass "explodes" when jelly expands
Amphinemura nigritta	as above	June	As above	As above (?)
Perlodidae				
Hydroperla crosbyi	2–5 days	Feb–Mar	Lotic, head of riffle	♀ alights on water, extrudes egg mass. Mass separates and eggs sink
Perlidae				
Paragnetina media	< 1 day	June (synchronous emergence)	Lotic	Extruded as mass
HEMIPTERA				
Gerridae				
Gerris spp.	several mo (adults overwinter)	spring and summer	Pools and running water	♀ glues eggs to floating objects or at water's edge, at or below waterline; deposited in parallel rows
Corixidae				
Ramphocorixa acuminata	—	early spring–fall; some eggs overwinter	Ponds, stock watering holes	Preferentially on crayfish (*Cambarus* sp.); also on other smooth surfaces. Several ♀♀ oviposit on one crayfish
Notonectidae				
Notonecta undulata	(*Buenoa* sp. = 16 days; Bare 1926)	early spring through summer	Lentic, widespread (clear pools to slimy ponds)	Eggs glued to submerged plants and other objects; irregular spacing
Belostomatidae				
Abedus herberti	—	nonseasonal	Warm streams and ponds	Starting at apex of wings and moving forward, ♀ deposits a solid mass of eggs on dorsum of ♂
MEGALOPTERA				
Corydalidae				
Dysmicohermes crepusculus	few days	July–early Sept	Above lotic waters; bridges, trees, rocks	♀ deposits rows of eggs; she may add 3–4 smaller tiers on top of the base layer
Sialidae				
Sialis rotunda	1 day	late Apr–June	On vegetation or other objects overhanging lentic waters	♀ secretes adhesive, then deposits upright rows of eggs forming a tight mass

Description of Egg or Egg Mass	Number of Eggs	Incubation and Hatching Period	Comments	Geographic Area	Reference
sticky coating attaches eggs to substratum	114–833/batch; $\bar{x}$ = 514	Immediate development @ 10°C. Incubation minimum of 3 wk, 80% by 6 wk; continues to 12 wk	In field, hatching from mid July to mid Sept	Ontario	972
—	90–188/batch; $\bar{x}$ = 121	4-mo embryonic diapause (germ disk stage)	In lab, hatching began @ 12°C in Sept; continued to Nov with temp. decrease from 12 to 8°C	Ontario	972
brown, oval, triangular cross section. Gelatinous coating glues eggs to substratum	172–330 eggs/mass; up to 3 masses/♀; 442–1418, $\bar{x}$ = 787 (dissected ♀♀)	7 mo egg diapause to Sept–Oct	Synchronous hatching with decreasing temp. from 25 to 19°C	Texas	1831
—	3–7 batches; 1207–2929 egg/♀ (dissected ♀♀)	At 20°C, 32 days; continues for 58 days	Partial hatch in fall, remainder in spring. Some parthenogenesis	Ontario	971
elongate, cylindrical, 3 × 1 mm; white, turning amber brown before hatching	—	2 wk incubation	♂ of *Rhagadotarsus* calls ♀ with wave patterns; defends oviposition territory (Wilcox 1979)	Kansas	1140
elongate, oval, .9 × .4 mm, with apical nipple. Egg attached by elastic pedestal and disk with strong glue	up to 22 mature eggs in abdomen at one time; successive batches are matured	5–10 day incubation	Continuous reproduction and asynchronous incubation. Synchrony of oviposition induced by freezing or recolonization. Oviposition on crayfish gives protection, aeration, and solid, non-silted, attachment surface	Kansas	920
elongate, oval, 1.7 × .6 mm; with small tubular micropyle; rough surface with hexagonal sculpturing	—	5–14 day incubation	Continuous oviposition in summer and overlapping broods. Some notonectids insert eggs into plants	Kansas, and New York	1140
oval with rounded top; yellow, darkening to tan. Egg swells during development from 3.1 × 1.7 mm to 5.0 × 2.0 mm	one ♀ produced 4 masses in 13 mo, total = 344 eggs	Incubation in lab @ 18°C=21–23 days	♂ aerates eggs by raising and lowering wings. Encumbered ♂♂ occur throughout the year	Arizona	2262
oblong mass, 30 × 25 mm. Eggs, 1.0 × .5 mm, with micropylar projection; greyish yellow, becoming reddish at hatching	1000–1700 eggs/mass $\bar{x}$ = 1500	In field, 26–63 days, $\bar{x}$=43 days; in lab (20°C), 25 days	Synchronous hatching within a mass	Oregon	688
cylindrical, rounded at top with micropylar tubercle; .7 ×.3 mm; white when laid, turning dark brown before hatching	300–500 eggs/mass; ♀ may deposit a second, smaller mass	8–12 days	Synchronous hatching within a mass, usually at night. Larvae drop from egg mass into the water	Oregon	77, 78

Table 5A.—Continued

Taxon	Preoviposition Period	Oviposition Season	Oviposition Site	Oviposition Behavior
TRICHOPTERA				
Glossosomatidae				
Agapetus fuscipes	few days	Apr–Oct	Chalk streams, slow flow over clean gravel	♀ swims underwater and oviposits on rock, then places "capstone" of small gravel on egg mass before cement is dry; submerged for 15–20 min
Agapetus bifidus	—	July–early Aug	Streams, in crevices on cobble	♀ probably swims to substrate
Hydropsychidae				
Hydropsyche sp. *Cheumatopsyche* sp.	few days	May–Sept	Large rivers, on submerged objects	♀ swims underwater, deposits egg mass on firm surface. Masses concentrated 3–5 ft below surface
Limnephilidae				
Limnephilus indivisus	several wk (ovarial diapause over summer)	early fall	Dry basin of temporary pool	♀ attaches gelatinous egg mass under log or to other protected site
Limnephilus lunatus	variable: 2–3 wk in fall; > 3 mo in spring	fall	Chalk streams, attached to watercress	♀ deposits egg mass on plants above water. Mass absorbs water and swells to 10 mm in diameter
Clistoronia magnifica	2 wk (in lab)	July–Aug	Lentic, attached to submerged logs or plants, or loose in littoral benthos	In lab, ♀ observed to enter water for 5 min and attach egg mass. May also oviposit on surface and egg mass sinks to substrate
Calamoceratidae				
Heteroplectron spp.	few days? (pupae contain mature eggs)	early summer	Small streams; loosely attached masses near waterline; also in drop zones not attached	Some ♀♀ may oviposit underwater, but site of eggs suggests that most oviposit at the waterline
Leptoceridae				
Ceraclea spp.	< 1 day	spring, or spring and mid-late summer	Lentic and lotic	♀ oviposits on surface. Mass floats until it absorbs water, then sinks and adheres to submerged objects
Chathamiidae				
Philanisus plebeius	few wk	summer–fall	Marine; in starfish (*Patiriella*) in tidepools	♀ probably inserts ovipositor through pores on aboral surface of starfish to deposit eggs in coelom

Description of Egg or Egg Mass	Number of Eggs	Incubation and Hatching Period	Comments	Geographic Area	Reference
round, .2–.25 mm in diameter, creamy white; deposited in single-layered, compact mass	eggs/mass = 12–94, $\bar{x}$ = 27. In lab, 12 ♀♀ deposited 70 masses	Direct development. At 12°C, hatching starts @ 1 mo, and continues for 3 wk	In cold springbrook, eggs hatched from early May—Oct	Southern England	51
mass, firm matrix, 1.2 × 1.6 mm. Eggs round, .2–.3 mm in diameter	30–100 eggs/mass	7 mo to hatching	Eggs overwinter in obligatory diapause	Oregon	56
concentric rows of closely packed eggs (Badcock 1953)	*Hydropsyche*, dissected ♀♀ = 331–465 eggs (Fremling 1960a). 820 deposited in 50 min by a ♀ (Badcock 1953)	In lab, 8–11 days	—	England, Iowa	82, 799
—	—	Larvae hatch in few wk, but remain in matrix until flooded	Emergence from egg mass dependent on time of flooding; may be in fall or the following spring	Ontario	2670, 2678
dome-shaped mass, opaque yellow when deposited. When swollen, jelly is colorless with eggs in rows. Eggs bluntly elliptical, .4 × .3 mm	270–636/mass	Duration of egg stage (room temp.) averages 17 days	Fall oviposition synchronized by decreasing duration of ovarial diapause as summer progresses	Southern England	905
spherical colorless mass, up to 3 cm in diameter, takes 8 hr to achieve full size. Eggs greenish, arranged in lines	200–300 eggs per mass; ♀ may deposit a second smaller mass	2–2½ wk @ 16°C; larvae continue to emerge from a mass for 1 wk	Field oviposition period extended by long flight period. May be 2–3 mo ovarial diapause in spring	Oregon, British Columbia	54, 2728
egg mass spherical, 7–15 mm, coated with silt, jelly very fluid; eggs yellowish, arranged in rows	132–348 eggs per mass, $\bar{x}$ = 209. Dissected ♀♀ contain 300–400 eggs	At 20°C, hatching @ 12 days; 15 days @ 15°C; larvae remain in matrix 2–9 days	Short, synchronous oviposition period. Eggs above waterline require 100% humidity; larvae remain in mass until inundated, then all emerge in ca. 1 min	Pennsylvania Oregon	1868 R. Wisseman (unpublished)
mass, dark green, ca. 1 mm sphere when deposited. Eggs, spherical, green yolk, transparent chorion; eggs swell from .1 mm to .2 mm in diameter by time of hatching	100–300 eggs per mass	In lab, 1–3 wk	Direct embryonic development	Kentucky	2017
eggs spherical, .4 mm, yellow-yellowish gray; single or in small clumps in coelomic cavity of host	dissected ♀♀ contain up to 400 mature eggs, $\bar{x}$ = ca. 160. Variable numbers in starfish: mostly < 10, but up to 112	At least 5 wk incubation @ 16–18°C	Extended incubation and hatching periods as eggs were found in starfish throughout the year	New Zealand	2732

Table 5A.—*Continued*

Taxon	Preoviposition Period	Oviposition Season	Oviposition Site	Oviposition Behavior
COLEOPTERA				
Gyrinidae				
Dineutus spp.	—	May–Aug	Ponds, on underside of *Potamogeton* sp. leaves	Deposited in clusters; each egg glued separately to leaf
Haliplidae				
Peltodytes sp., *Haliplus* sp.	—	May–early July	Lentic, in beds of *Chara* sp. and *Nitella* sp.	*Peltodytes*, eggs glued to macrophytes or algae. *Haliplus*, ♀ chews hole in hollow stems and deposits several eggs within
Dytiscidae				
Agabus erichsoni	—	May–June	Temporary woodland pools	Eggs deposited in clumps of 2–3 among root fibers or moss on bottom of pond
Colymbetes sculptilis	—	late Mar–April	Temporary woodland pools	Eggs firmly attached to submerged vegetation or to edge of rearing container
Hydrophilidae				
Hydrophilus triangularis	—	early–mid summer	Eutrophic ponds, with some vegetation	♀ spins a silken egg case; ellipsoidal shape with elongate "mast." Construction takes > 1 hr
Psephenidae				
Psephenus falli	1 day? (mature ovaries at emergence)	early May–mid Aug	In riffles, under rocks	♀ crawls down a rock and remains submerged for life (1–3 days)
Elmidae				
Stenelmis sexlineata	—	May–Aug	Lotic, in riffles, on sides and bottom of rocks	Submerged ♀ selects depressions or cracks on rocks; deposits group of eggs usually touching each other; each egg pressed against surface for 10–20 sec to glue it down
LEPIDOPTERA				
Pyralidae				
Nymphula sp.	1 day	July–Aug	Lentic, underside of floating *Potamogeton* sp. leaves	♀ generally does not enter water but extends tip of abdomen to attach egg mass on underside near margin of leaf. Oviposition occurs at night
HYMENOPTERA				
Agriotypidae				
Agriotypus sp.	few days	May–July	Lentic or lotic; in cases of goerid or odontocerid caddisflies	♀ crawls down a support into water and searches for a host. Eggs only deposited on prepupa or pupa. ♀ may stay underwater for several hr, enveloped in air bubble

Description of Egg or Egg Mass	Number of Eggs	Incubation and Hatching Period	Comments	Geographic Area	Reference
white, elongated ellipsoid, 1.9 × .6 mm; cluster arranged diagonally @ 45° angle from midrib	7–40 eggs per cluster (Wilson 1923b); 12–17 eggs per ♀ per day (Istock 1966)	5–6 days	Synchronous hatching of clusters; extended oviposition period of the population	Iowa, Michigan	1188, 2722
Peltodytes, oval, with projecting plug, .5 × .3 mm, yellowish brown; *Haliplus*, oval, .4 × .2 mm, whitish	30–40 eggs within a wk	8–10 days @ 21°C	♀♀ live over 1 yr, so several batches of eggs are matured	Michigan	1045, 1570
short oval; pale cream becoming light brown with age; 1.7 × 1.1 mm	♀♀ contain 14–31 eggs at one time; ovaries continue to develop eggs	8–9 mo; some embryonic development before pond drys up, then diapause; hatching occurs the following spring	Eggs from dry pond bottom were chilled for 3 mo @ 0°C, then flooded and larvae emerged within a few hr	Ontario	1215
elongate oval, somewhat kidney-shaped; pale yellow with smooth chorion; 1.8 × .7 mm	—	6 days @ 19°C; longer in field as oviposition occurs at < 14°C	Apparently a short incubation and hatching period, as 1st-instar larvae only found for 3 wk in April	Ontario	1215
egg case is yellow, turns brown; eggs, elongate ellipsoid, 4.4 × 1 mm; bright yellow	10–130 eggs per case; ♀ probably matures more than 1 batch	—	Egg case floats and eggs do not hatch if case turns over; mast assumed to aid in stabilizing the case	Iowa	2721
spherical, lemon yellow eggs, deposited in compact, single-layered mass	ca. 500 eggs per ♀; several may oviposit together, forming masses of over 2000 eggs	16–17 days @ 23°C	Apparently synchronous hatching within a mass, but extended oviposition period	Southern California	1750
oblong; whitish-yellow; .55–.62 mm long	—	6–10 days @ 22–25°C	Protracted oviposition period; adults live underwater for > 1 yr	Kentucky	2639
elliptical eggs, .45 × .6 mm; light grey or whitish; about 20 eggs/mass	♀ of *N. badiusalis* laid 441 eggs in one night	6–11 days	Direct development of eggs; synchronous hatching within a mass	Michigan	159
elongate, .9 × .2 mm; tapered to a stalk which is inserted into the host's integument	—	In lab, 5–8 days	Several eggs may be deposited on one host but only one larva can develop per host	Japan, France	407, 917

Table 5A.—*Continued*

Taxon	Preoviposition Period	Oviposition Season	Oviposition Site	Oviposition Behavior
DIPTERA				
Tipulidae				
Tipula sacra	< 1 day	June–July	Lentic, in soil or algae mats near shore	♀♀ emerge during the day; mate and begin ovipositing immediately
Lipsothrix nigrilinea	< 12 hr	Mar–Aug; peak in May–June	In saturated wood in streams	♀ searches for suitable site on wood near waterline with ovipositor. Deposits egg ca. 1 mm deep in soft wood or crack; then moves to make another insertion
Ptychopteridae				
Ptychoptera lenis	< 1 day	late May–June	Lentic, stagnant water	Mating and oviposition occur shortly after emergence. Eggs occur loose on substrate, so probably scattered at pond surface and sink to substrate
Simuliidae				
Simulium spp.	variable; blood meal may be required for egg maturation	spring and summer; multivoltine	Lotic; various sites (wetted vegetation, dam faces, debris, etc.)	Variable even within a species; may oviposit in flight, but more commonly on solid surface in masses or strings, at or below waterline
Culicidae				
Aedes aegypti	variable; blood meal required for egg development	nonseasonal	artificial containers: cisterns, cans, old tires	Eggs deposited singly, at or near waterline
Culex pipiens	variable; blood meal required, except in autogenous strains; some overwinter as nulliparous ♀♀	spring–late autumn	Lentic; small catchments and pools with high organic content	♀ lands on water and deposits eggs in raftlike masses. Oviposition usually at night
Chironomidae				
Chironomus plumosus	2–5 days	mid May, July–Sept	Lentic; on water or on flotsam	♀ flies over water (sometimes several mi); extrudes egg mass between hind tibiae and deposits it on first surface that she touches
Tabanidae				
Tabanus atratus	1 wk	June–Oct	On plants, near or over water	♀ faces head downward while depositing egg mass on vertical portion of plant
Ephydridae				
Dichaeta sp. (=*Notiphila*) (Mathis 1979a)	5–15 days	throughout summer	Marshy areas with accumulation of decaying vegetation	♀ scatters eggs along shore or on floating detritus. Eggs not glued to substrate but many in crevices
Sciomyzidae				
Sepedon spp.	4–24 days	—	Lentic; on emergent vegetation, from 5 cm to > 1 m above water	♀ in head downward position, deposits eggs in vertical row

Description of Egg or Egg Mass	Number of Eggs	Incubation and Hatching Period	Comments	Geographic Area	Reference
shining black, elongate, convex on one side; 1.0 × .4 mm; posterior filament uncoils when wetted as anchoring device	dissected ♀♀, x̄ = 925, range, 500–1600 eggs	In lab, few days; in field, < 1 mo	Direct development of eggs; hatching period from early July–mid Aug	Alberta	1953, 1958
cream colored, elongate, smooth; no anchoring device	dissected ♀♀, x̄ = 185, range, 106–380 eggs	About 3 wk @ 16°C	Direct development, but extended hatching period because of long flight period	Oregon	605
elongate oval; whitish yellow; longitudinal reticulations on chorion; .8–.9 mm long	dissected ♀♀ contain 530–806 eggs	In field, 14–20 days	Egg maturation occurs during pharate adult stage	Alberta	1094
oval to triangular .25 × .14 × .13 mm; whitish, turning brown as they mature.	300–600 eggs per ♀. Eggs may occur in large aggregations (72 000/ft²)	5 days @ 23°C	Successive generations in summer; overwinter often as diapausing eggs	Ontario	517
elongate oval	average about 140 eggs when fed on humans; may be 2 or more egg cycles	Highly variable; embryonic development completed in 2–4 days after flooding	Direct development in water but eggs withstand desiccation for at least 1 yr	Southeastern states	1001
cylindrical, tapered	100–400 eggs per mass; ♀ lays 2–4 masses	1–3 days	First batch of eggs may mature without a blood meal. Size of later masses depends on blood meals. Several generations per yr.	Holarctic	1001
egg mass is dark brown, tear-shaped; swells to 25 × 5 mm. Eggs, cream colored, oval, .5 × .2 mm	eggs per mass: x̄ = 1676, range, 1154–2014	3 days @ 24°C; 14 days @ 9°C	Egg mass floats and larvae remain in it for 1 day after hatching. 2 generations per yr	Wisconsin	1053
egg mass is subconical, oval at base, with 4–5 tiers of eggs, 5–25 mm × 2–10 mm. Eggs white when laid, then darken	500–800 eggs per mass	4–12 days	—	Florida	1256
egg ellipsoidal, convex on venter; longitudinally ridged; white; .9 × .3 mm	—	1–2 days @ 21–25°C	Eggs float when marsh floods and have plastron for underwater respiration	Ohio, Montana	617
eggs lie horizontal touching preceding one. Egg elongate with coarse, longitudinal striations; white, becoming colored during development	Up to 25 eggs per row; ♀ probably deposits several rows	3–5 days		USA	1788

Fast development is characteristic of temporary inhabitants of water, but larval diapause or quiescence may extend the life cycle to several years. Corydalidae (Megaloptera) larvae in intermittent streams burrow into the streambed when surface water dries up; growth only occurs during the wet cycle so larval duration may be 3–4 years, depending on the annual duration of stream flow. The extreme example of tolerance of drought is the chironomid, *Polypedilum vanderplanki*, from ephemeral pools in Africa. The larvae can withstand complete dehydration and exist in a state of suspended metabolism, or cryptobiosis. The dehydrated larvae can survive immersion in liquid helium and heating to over 100°C (Hinton 1960). In their natural habitat, they can survive several years in sun-baked mud and rehydrate when wetted (McLachlan and Cantrell 1980). They are normally the first invaders of small pools and can inhabit the shallowest and most ephemeral pools with virtually no competitors.

Many stream insects are adapted to a narrow range of cool temperatures (cold stenothermy). Hynes (1970b) attributes winter growth not only to use of leaf detritus as a food base, but also suggests that this growth pattern may have been selected for because predation by fish would be less at low temperatures. Larval diapause to avoid high summer temperatures occurs in some early-instar Plecoptera (e.g., Capniidae, Taeniopterigidae) and in mature larvae or prepupae of some limnephilid caddisflies (e.g., *Dicosmoecus* sp., *Neophylax* sp., *Pycnopsyche* sp.).

Habitat partitioning may be effected by segregation by functional feeding groups. Thus, in addition to shredders, the winter-growing stream species include scrapers (e.g., heptageniid mayflies, glossosomatid caddisflies), filter-feeders (e.g., Simuliidae), and deposit feeders (e.g., several mayflies, some Chironomidae). Within a group, coexistence may be based on differential responses to food and temperature. For example, three coexisting species of the caddisfly genus *Pycnopsyche* are all shredders and winter growers, but the food resource is partitioned by the species having different timing of rapid growth intervals and also some differences in microhabitat preferences (Mackay 1972).

Elaborate and specialized feeding adaptations occur in the filter-feeding Ephemeroptera, Trichoptera, and Diptera (Wallace and Merritt 1980). The adaptations include specialized anatomical structures (e.g., leg setae in *Isonychia* spp. mayflies and *Brachycentrus* spp. caddisflies, mouth brushes in mosquitoes, head fans in *Simulium* spp.), and silk nets in many caddisflies and some chironomid midges. Habitat partitioning within the filter-feeding guild occurs along the water velocity gradient. Also, there is some selectivity in feeding habits. Georgian and Wallace (1981) demonstrated that the hydropsychid caddisflies that build large-meshed nets filter larger volumes of water than do those species with small nets and mesh size; the former will select for animal or algal foods rather than detritus.

Black fly larvae select areas where the current is fast and the boundary layer is thin so that the cephalic fans reach into the current. They show no selectivity with respect to food quality and will readily ingest inorganic as well as organic materials. Their food includes detritus, bacteria, diatoms, and animal fragments. The particle size of ingested material ranges from colloidal to 350 μm; a mucuslike secretion on the fans aids in trapping the minute particles (Ross and Craig 1980). Though they do not select for food quality, the type of food available will affect growth rates. Carlsson *et al.* (1977) found that black fly larvae at lake outfalls occurred in very dense aggregations and had exceptionally high growth rates associated with the availability of colloidal-sized organic material washed into the river at ice melt.

The above examples are primarily winter-growing lotic taxa. Most stream species respond to increasing temperatures in the spring by increasing their rate of growth. Multivoltine stream taxa include *Baetis* sp., *Glossosoma* sp., some hydropsychid caddisflies, and several black fly species. Though typical life cycles are univoltine, the duration and timing are more indeterminate than is usually suggested. Pritchard (1978) cites examples of cohort splitting in which individuals of the same cohort may have 1-, 2-, or even 3-year life cycles, depending on food availability and environmental conditions.

Aquatic insect predators include large conspicuous species with relatively long life cycles compared with those of their prey and have a range of morphological specializations and behavior patterns. Some are ambush or "sit-and-wait" predators, whereas others actively pursue their prey. The Hemiptera and some Coleoptera (e.g., Dytiscidae, Gyrinidae) are aquatic predators both as larvae and adults, whereas all others (e.g., Odonata, Megaloptera, some Diptera) are aquatic only as larvae.

Some of the most specialized predators are larval Odonata; the hinged prehensile labium, or mask, is unique to this order. The mask is projected forward by elevated blood pressure induced by abdominal muscles. Prey are impaled by hooks or setae on the labial palpi. The food is then returned to the mouth when the labium is folded back by adductor muscles. Prey perception involves receptor organs on the antennae and tarsi as well as use of the eyes. Sight is more important in later instars and in climbing species that live on vegetation than in bottom-sprawling or burrowing forms (Corbet 1963). In mature larvae of visual hunters, such as *Anax* sp., prey capture involves a highly integrated binocular vision, resulting from stimulation of certain ommatidia in each eye that enables the distance of the prey to be accurately judged. Feeding behavior of odonates is influenced by factors such as degree of hunger, time since the last molt, and the density, size, and movement of potential prey. As larvae grow, individual prey items become larger and more varied because larger larvae can also consume small prey (Corbet 1980).

Preoral digestion is a feature of hemipteran and some beetle predators. Salivary secretions are injected to immobilize prey and to liquefy tissues with hydrolytic enzymes. In Hemiptera the mouthparts are modified into a 3- or 4-segmented beak that is used to pierce the prey and suck the fluids. Dytiscid beetle larvae have chewing mouthparts, but their long sickle-shaped mandibles are grooved for fluid feeding. Larvae of some hydrophilid beetles (e.g., *Tropisternus* sp. and *Hydrophilus* sp.) are unusual in that the prey is held out of the water. In this position, the prey juices flow down the mandibles and into the oral opening rather than being lost into the surrounding water.

Territoriality and intraspecific competition were shown by Macan (1977) to be important factors affecting growth rate and life cycle of the damselfly *Pyrrhosoma* sp. In years when the larvae were abundant and prey populations were low, two size classes existed at the end of the summer. Macan attributed this to cohort splitting; larvae in superior feeding territories grew rapidly whereas those occupying poorer feeding sites grew slowly and would either require an extra year or die of starvation. Furthermore, Macan suggests that fish predation was selective for the larger specimens, which led to vacancies in the superior feeding sites, and that these were then readily filled by smaller larvae. Thus, predation by fish did not greatly reduce the numbers of damselflies reaching maturity because elimination of large larvae allowed smaller ones to exploit the food resource.

The prevalence of insect predators suggests that predation may be a dominant biotic factor influencing aquatic insects. Selective pressures due to predation have produced behavioral responses by prey species. For example, mayfly prey may react to predators by drifting or displaying scorpionlike threat postures (Peckarsky 1980; Peckarsky and Dodson 1980). The mayflies can apparently detect predators by noncontact chemical cues, and they may be able to distinguish between predaceous and detritivorous stoneflies that have a similar body form.

Metamorphosis and Eclosion

Molting during the larval stages results in a larger insect of essentially the same body form, whereas the final molt produces a more complete change associated with the development of wings and other adult structures. These are considered two distinct types of physiological differentiation, and Chapman (1982) suggests that the term *metamorphosis* be restricted to the latter. Molting and metamorphosis are mediated by hormones. There is no fundamental physiological difference between the metamorphosis of hemimetabolous and holometabolous insects; the difference is a matter of degree rather than kind. The pupal instar may be regarded as the equivalent of the last larval instar of hemimetabolous insects (Gillott 1980).

Control of molting involves the interaction of a molting hormone (ecdysone) and a juvenile hormone. The latter exerts an influence on development only in the presence of the former. When the concentration of juvenile hormone in the blood is high, the next molt will be larval-larval. At intermediate concentrations, a larval-pupal molt occurs, and when there is little or no circulating juvenile hormone (due to inactivity of the corpora alata) an adult insect will emerge at the next molt (Gillott 1980).

The primary morphological difference between hemimetabolous (Exopterygota) and holometabolous (Endopterygota) insects is the external development of the wings in the former and the delayed eversion of wings in the latter (Hinton 1963). The gradual development of adult structures is apparent in hemimetabolous insects by the progressive development of external wing pads and rudiments of the genitalia. Changes also occur in the last larval instar of the Holometabola, but these are internal and major differentiation is constrained by lack of space. During the pupal instar,

the wings are evaginated to outside of the body; this makes room for development of the indirect flight muscles and the reproductive system. The pupal instar is usually of short duration. In the strict sense, the insect becomes an adult immediately after the apolysis (separation) of the pupal cuticle and the formation of the adult epicuticle to which the musculature is now attached (Hinton 1971a). Thus, in most instances, locomotion and mandibular chewing are activities, not of the pupa, but of the *pharate* adult that is enclosed within the pupal exuviae.

The final event in metamorphosis is *eclosion,* or emergence, which is the escape of the adult from the cuticle of the pupa or last larval instar. See chapter 8 for a further discussion of aquatic insect metamorphosis.

The development of a pupal stage has permitted the great divergence of larval and adult forms in the Holometabola. Larvae exploit environments and food resources that result in growth, whereas the activities of the adult center on dispersal and reproduction. If the number of species is considered to be a measure of biological success, complete (holometabolous) metamorphosis is a prime contributor to the success of insects. Hinton (1977) states that this is a focal point of insect evolution because about 88% of the extant insect species belong to the Endopterygota.

Metamorphosis in hemimetabolous aquatic insects differs in detail among the various taxa but the behaviors involved are mostly associated with switching from an aquatic to a terrestrial mode of life (especially respiration and flight) and overcoming the abiotic and biotic hazards during an especially vulnerable stage. Data from Corbet (1963) for Odonata illustrate both morphological and behavioral changes occurring during metamorphosis and eclosion.

The onset of metamorphosis in some dragonflies can be detected several weeks before emergence when the facets of the adult compound eye begin to migrate to the top of the head. Respiration rate also increases prior to metamorphosis associated with increased metabolic requirements. Behavioral changes characteristically involve movement to shallow water or up the stems of plants towards the surface. In *Anax imperator,* histolysis of the labium occurs and feeding stops several days before emergence.

Nearly all Odonata have a diurnal rhythm of emergence. The timing is presumably to restrict emergence to an interval when weather conditions are favorable and when predation is least likely to occur. The major predators are birds or mature adult dragonflies that hunt by sight, so night is the safest time to leave the water. In the tropics, most of the large dragonflies emerge after dusk; they eclose, expand their wings, and are then ready to fly before sunrise. In the temperate regions or at high altitudes where nocturnal temperatures are low, odonates tend to emerge in early morning or during the daytime. Mortality during emergence of *Anax imperator* may amount to 16% of the annual population (Corbet 1963). The individuals are immobile and defenseless for several hours during eclosion and while the wings expand and harden. Cold and wind increase mortality by prolonging ecdysis or by postponing emergence and thereby exposing more individuals to

predation. Overcrowding is common in species that have mass emergences; competition for emergence supports is so intense that the first larva to climb a support may be used as a platform by others that follow. Although overcrowding is an ecological disadvantage of mass emergence, this type of synchronization is apparently adaptive, perhaps because it satiates predators and affords the appropriate synchronization of males and females.

Adaptations of pupae pertain to respiration, protection, and emergence from the water. These factors also operate on the pharate adult, so it is convenient to discuss the two stages together. This is usually a quiescent stage, but mosquito pupae (tumblers) are relatively active swimmers, and Hinton (1958a) demonstrated that some black fly pupae both feed and spin a cocoon. Pupation occurs out of water in Megaloptera, Neuroptera, most Coleoptera, and many Diptera. Larvae construct a chamber in the soil (e.g., Megaloptera, Coleoptera) for metamorphosis, and eclosion may occur within the chamber (Coleoptera) or after the pharate adult has worked its way to the soil surface (Megaloptera).

Many nematocerous Diptera have aquatic pupae, some of which are active swimmers (e.g., Culicidae, Dixidae, Chaoboridae) throughout the pupal stage, whereas others (e.g., Chironomidae, some Tipulidae) only swim to the surface for emergence. In taxa in which the pupa is glued to a substrate (e.g., Blephariceridae, Deuterophlebiidae, Simuliidae), the adult emerges underwater and rises to the surface enveloped in a gas bubble. These adults expand their wings and are capable of flying immediately after reaching the surface. Species with swimming pupae will emerge using the exuviae as a platform at the water surface. All Chironomidae emerge in this manner, and the cast skins remain trapped in the surface film for some time. Collections of exuviae are useful for taxonomic purposes and also as a rapid method of sampling the entire chironomid fauna of a water body (Wartinbee and Coffman 1976; also see chap. 25).

Respiration in most aquatic Diptera pupae differs from that of the larvae in which the terminal abdominal spiracles are generally the most important. The pupae have respiratory horns or other extensions of the prothoracic spiracles. Depending on the species, these may be used for breathing at the surface, in the water column, or even to pierce the tissues of submerged plants.

The case-making caddisflies illustrate several morphological and behavioral adaptations in the pupal stage. The mature larva selects a protected site, such as under a stone or in a crevice in wood, and attaches the case with silk. Then the case is shortened, and the ends are closed with mineral or detrital particles and a silk mesh that allows for water flow.

Metamorphosis occurs within the case. The pupa (pharate adult) is active within the case, maintaining a flow of water for respiratory purposes by undulating the body. The pupa has elongate bristles on the labrum and on anal processes that are used for removing debris from the silk grating at either end of the case. The back-and-forth movement within the case is effected by the dorsal hook-plates on the abdomen. The pharate adult has large mandibles used for cutting an exit hole at emergence. It then swims to the surface or crawls to shore where eclosion occurs.

CONCLUDING COMMENTS

The critical importance of systematics to basic life-history studies has been emphasized on numerous occasions (e.g., Wiggins 1966; Ross 1967a; Waters 1979a, 1979b). Excellent progress has been made for several aquatic insect groups in North America (e.g., Edmunds et al. 1976; Wiggins 1977); however, eggs and all instars of immatures cannot always be identified. Studies of aquatic insect life histories require that individual investigators develop reliable methodologies for separating early instars of closely related species (e.g., Mackay 1978). It is unfortunate that life histories of so many aquatic insect species remain unknown. In some quarters, the mistaken impression still persists that such efforts are unfashionable and of little value. Ecosystem-level studies are often directed to studies of the processing of organic matter by various groups of animals, and insects are frequently the most abundant group considered. The integration of production, feeding habit, and bioenergetic data can yield a much better understanding of the role of individual species in ecosystems. Benke (1979), Benke et al. (1979), and Waters (1979a, 1979b) have emphasized that a knowledge of basic life histories is mandatory for reasonable estimates of production. Waters has pointed out that voltinism and length of aquatic life (=CPI, or Cohort Production Interval [Benke 1979]) are two of the most important life history features influencing secondary production estimates. The "once-per-month" sampling program of most studies is not adequate for many estimates of aquatic insect secondary production, and sampling schedules need to be tailored to the life histories of the organisms being studied (Cummins 1975; Waters 1979a).

Both temperature and food may influence life-history patterns; however, data on the potential combined effects of temperature and food quality on life histories of various groups of aquatic insects are too meager for any broad generalizations as yet. All students are encouraged to develop an appreciation for the importance of systematics, life histories, secondary production, and bioenergetics as interconnecting links toward the basic understanding of the structure and function of aquatic communities.