

# CHAPTER 11-1

## AQUATIC INSECTS: BIOLOGY

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# CHAPTER 11-1

## AQUATIC INSECTS: BIOLOGY



Figure 1. *Rhyacophila carolina* larva, a free-living caddisfly that occurs commonly on bryophytes. Photo by Bob Henricks, with permission.

### Aquatic Insects

Cascading waterfalls, silt-laden torrents, lurking predators, limited oxygen, unpredictable water levels, icy winters – all these dangers face the insects (Figure 1) that call lakes, and especially streams, their homes. So why do the insects choose to live there, and how do bryophytes help to make life in such unfriendly conditions possible?

The relationship between aquatic insects and bryophytes is a topic dear to my heart. When I was working on my M.S. project on the bryophytes, my roommate was working on aquatic insects. Never passing up an opportunity for a field trip, I accompanied her on all her collecting trips. We both soon realized that in her rocky mountain streams of northern West Virginia, USA, there were typically more insects among the bryophytes than in any other microhabitat in these streams. It was this discovery that led me to my Ph. D. research topic on the insects associated with Appalachian stream bryophytes and the many studies I have done on ecology of aquatic mosses since then.

These wonderful bryophyte-insect communities are not a new discovery. Stream ecologists in particular have observed the importance of mosses as cover for aquatic insects and other aquatic invertebrates and even fish (Thienemann 1912; Carpenter 1927; Percival & Whitehead 1929, 1930; Humphries & Frost 1937; Jones 1941, 1948, 1951; Frost 1942; Badcock 1949; Illies 1952; Hynes 1961; Minckley 1963; Egglisshaw 1969; Arnold & Macan 1969; Lindgaard *et al.* 1975; Hawkins 1984; McKenzie-Smith 1987; Suren & Winterbourn 1992a, b; Gislason *et al.* 2001; Linhart *et al.* 2002; Paavola 2003).

In Idaho, USA, Maurer and Brusven (1983) found that *Fontinalis neomexicana* (Figure 2) housed 5-30x the densities of insects found associated with the mineral substrates; biomass, however, was only 2x as great. The moss did not alter insect densities in the underlying **hyporheic** zone (saturated zone beneath the bed of a river or stream that can support invertebrate fauna). The diversity of functional groups was greater among mosses, but the species richness was similar to that of the mineral substrate.



Figure 2. *Fontinalis neomexicana*, a moss that greatly increases the density of stream insects. Photo by Belinda Lo, through Creative Commons.

The numbers of insects among bryophytes can be extensive (Figure 3). Minckley (1963) found that mosses had the highest densities of insects compared to sand, stones, and tracheophytes in a Kentucky, USA, stream. Lillehammer (1966) found that moss-covered stones had 606 individuals m<sup>-2</sup> compared to 471 m<sup>-2</sup> on stones with no mosses.



Figure 3. This branch of *Palustriella commutata* demonstrates the variety and density of aquatic insects that can occur on aquatic mosses. Photo by Dan Spitale.

When more sophisticated statistical methods became available, bryophyte biomass emerged as one of the factors accounting for the variation in insect fauna among streams, and as we might expect, it has a positive influence on the insect fauna (Gislason *et al.* 2001). Furthermore, bryophytes can occupy deeper waters, forming a zone that is lower than that of tracheophytes, and this zone is able to support fauna that could not otherwise live at those depths (Blackstock *et al.* 1993).

Minshall (1984) considered bryophytes to be a major factor in increasing insect numbers because of the increased surface area offered by them. Egglishaw (1969) found that most species of invertebrates, including insects, were less aggregated in clumps among the mosses than they were under stones. One might interpret that this is due to the complex nature of the mosses and the large space in which they can be distributed. On the other hand, it would seem that the stone habitat would be more homogeneous and thus one might expect less clumping. Another mystery.

Table 1. Orders of insects and their abundances among bryophytes in various locations around the world. NR refers to not recorded, which may mean the researcher(s) didn't look at the group.

	sample size	Collembola	Odonata		Diptera		Coleoptera		Reference
		Ephemeroptera	Plecoptera		Trichoptera				
Straffan, River Liffey, Ireland	200 g	NR	533	NR	22	11446	492	262	Frost 1942
Ballysmuttan, River Liffey, Ireland	200 g	NR	16	NR	310	10482	148	1095	Frost 1942
Cold Springbrook, TN, USA	0.1 m <sup>2</sup>	NR	7.1	NR	8	215	24.6	0.4	Stern & Stern 1969
Bystřice, Czech Republic	10 g dry	NR	1103	NR	18	44762	359	184	Vlčková <i>et al.</i> 2001-2002
Mlýnský náhon, Czech Republic	10 g dry	NR	176	NR	0	11035	13	5	Vlčková <i>et al.</i> 2001-2002
Welsh Dee Tributary, Wales	~300 cm <sup>2</sup>	NR	9.7	NR	513	82.8	0.4	7.4	Hynes 1961
Mouse Stream, Alpine, NZ	1 m <sup>2</sup>	NR	NR	NR	540	61270	730	0	Suren 1991a
Tim's Creek, Alpine, NZ	1 m <sup>2</sup>	NR	NR	NR	270	24580	260	90	Suren 1991a
West Riding, Yorkshire, UK – loose moss	%	NR	13.42	NR	154	65.3	3.1	6.7	Percival & Whitehead 1929
West Riding, Yorkshire, UK – thick moss	%	NR	8.03	NR	0.65	42	8	4.4	Percival & Whitehead 1929
alpine unshaded stream, NZ	%	NR	NR	NR	2.1	581.8	NR	NR	Suren 1991b
alpine shaded stream, NZ	%	NR	NR	NR	2.5	69.9	NR	NR	Suren 1991b
River Sawdde, Wales		rare	NR	NR	very rare	NR	NR	very rare	Jones 1949

## Life Cycle Stages

Life cycle stages play a major role in the occupancy of water habitats by insects. Most of these orders of insects have poor ability to survive freezing, so escape into water can maintain their temperatures above freezing. The flowing part of water generally remains at ~1°C throughout the winter, and lakes and ponds that don't freeze to the bottom have water just above 0 up to 4°C.

Because of the importance of water in the life cycle of the major groups of aquatic insects, we must understand the types of life cycles among them before we can begin a discussion of the biology and ecology of these groups. There are two major groups of classification among the insects, based on life cycles and their developmental stages.

## Collembola

The **Collembola** (Figure 4), or springtails, long considered to be insects, have been kicked out of the **Insecta** by cladistics, due to linkages shown by their DNA and supported by their morphology. Because they have much of their ecology in common with insects, and their earlier inclusion among Insecta, they will be discussed among these aquatic insect subchapters.

The **Collembola** have the simplest life cycle, one in which the hatchling is a miniature of the adult. The immature stage is known as a **nymph**. Their life cycle consists of **egg/embryo**, **nymph**, and **adult**. The **Collembola** hatch from their egg casing and look like the adults, perhaps in somewhat different proportions; they



continue to increase in size without changing their basic form as they become adults.



Figure 4. *Collembola Arthropleona oruarangi*, a group of "pre-insects" that are born looking like little adults. Photo by Stephen Moore, Landcare Research, NZ, with permission.

## Hemimetabolous Insects (Hemimetabola)

### Nymphs

Among the aquatic insects, this group includes the true bugs (order **Hemiptera**), a group that lacks gills in all stages. The **Hemiptera** are **hemimetabolous** insects and thus lack the pupal stage (familiar to most people as the chrysalis of butterflies). Instead, they have only the **egg/embryo** (Figure 8), **nymph** (including **naiads** in the other hemimetabolous orders), and **adult**. [The **holometabolous** insects, on the other hand, have an **egg/embryo**, **larva**, **pupa**, and **adult (imago)**.]

### Naiads

Those orders with obligate aquatic immature stages that do not resemble the adults, but that do not pass through a second stage as a pupa before becoming an adult, have an aquatic stage known as a **naiad**. The **naiad** is a specialized nymph stage known only among aquatic insects and occurs in the orders **Plecoptera** (Figure 5, Figure 73, Figure 74, Figure 77), **Ephemeroptera** (Figure 6), and **Odonata** (Figure 7). The naiad usually differs from the adult in having some form of gills to aid in gaining oxygen in the aquatic environment. When it is time for the adult to emerge, these insects climb to the surface or out of the water, often on an emergent plant, and often hang vertically while they climb out of their naiad **exoskeleton** (Figure 5). The shed exoskeleton is the **exuvia** (pl. **exuviae**; Figure 5). In the **Ephemeroptera**, the emergent stage is a subadult known as a **subimago** (Figure 6). This subimago goes through one additional moult to become the adult (**imago**).

## Holometabolous Insects (Holometabola)

The remaining orders of aquatic insects are **holometabolous** and have what is known as **complete metamorphosis**. These insects have four life cycle stages: **egg/embryo** (Figure 8), **larva** (Figure 1), **pupa** (Figure 9), **adult (imago)** (Figure 10). The larva stage looks nothing like the adult. It is familiar to most people in the moths and butterflies as the caterpillar. The larva is a worm-like

creature, with or without legs, or in some cases with prolegs that are of soft tissues. The aquatic larvae have gills in many taxa, but not in others. Some have fleshy legs with hooks at the posterior end.



Figure 5. **Plecoptera** exuvia. Photo by Jason Neuswanger at <Troutnut.com>, with permission.



Figure 6. *Baetis* male subimago emerging to adult. Photo by Jason Neuswanger at <Troutnut.com>, with permission.



Figure 7. *Enallagma* damselfly naiad. Photo by Tom Murray, through Creative Commons.

The **pupa** is usually a stationary phase (known as a chrysalis in butterflies). As the pupa develops, the larva develops a chitinous outer covering that has the imprint of parts like wings and antennae. The insect is likely to be dormant or in **diapause** (in insects, period of suspended development, especially during unfavorable environmental

conditions) during its pupal stage, providing it reprieve from winter's cold or tropical drought. But during this time the insect goes through a number of changes in both form and physiology. When the insect has matured into an adult and conditions are right for its emergence, it breaks out of the pupa. In most cases, those that spend their larval lives in the water emerge into the atmosphere, spending their adult lives as terrestrial organisms (except in most of the beetles).



Figure 8. Emerald dragonfly with eggs. Photo by Bob Armstrong, with permission.



Figure 9. **Chironomidae** (midge) pupa. Photo by Bob Henricks, with permission.



Figure 10. **Chironomidae** adult male. Photo by Roger S. Key, with permission.

The holometabolous insect orders that live among bryophytes include **Coleoptera**, **Trichoptera**, **Megaloptera**, **Neuroptera**, and **Diptera**.

## Adaptations to Aquatic Bryophyte Life

Bryophyte dwellers might benefit from several behavioral and structural adaptations to make life among the bryophytes easier. They need to be able to gain sufficient oxygen (Hynes 1970), to move about freely, to avoid being pulled out if a predator catches a tail or leg, to avoid being swept away by the current, and to eat the available food. In streams where the water level varies a lot or dries up, they need to have a means to avoid desiccation.

## Life Cycle Strategies

Although I would normally discuss structural adaptations first, the life cycle adaptations appear to be the most important ones among the insects. Differing requirements among life cycle stages permit insects to survive from year to year in changing environmental conditions.

Blackstock *et al.* (1993) found the insects in a clear sequence of bryophyte to herbaceous swamp to woody plant community occupying different depth zones in the basin of Pant-y-llyn, Wales. These changes, on a large scale, require a degree of mobility on the part of the insect inhabitants as the habitat changes from aquatic to terrestrial seasonally. But even more permanent aquatic habitats have their down times. Success for an aquatic insect means having a strategy to survive during stages when the habitat is dry (Blackstock *et al.* 1993), too cold, or too hot.

To understand the role of bryophytes in the life of their insect inhabitants, one must understand these life cycles. Only twelve orders of insects plus the **Collembola** (Figure 4) are generally considered to have aquatic members, but even these aquatic members typically live out of the water during part of their lives (Thorp & Covich 1991; Ward 1992). Since most of the aquatic insects live in the water in immature stages, an understanding of these stages is necessary to understand fully how bryophytes are so important for them.

Danks (1991) points out that we can understand insect life cycle adaptations best by understanding the options. These include the choices (evolutionarily) to develop or to enter **diapause** (period of suspended development) and to grow rapidly or grow slowly. These developmental options respond to photoperiod and temperature, among other things (Danks 1991; Zwick 1996). Because of dependency on these cues, eggs of some stoneflies are able to remain in the sediments for years, providing a "seed bank" (Zwick 1996). The choices that have been programmed into the life cycle impact the life span of the insect.

Eggs (Figure 8) are an important stage for insects with a terrestrial adult stage and aquatic immature stage(s). The term egg is used somewhat loosely, referring to both the unfertilized egg and the embryonic stage that remains within the egg "shell," indicated herein as **egg/embryo**. Most of these insects lay their eggs in the water, so a substrate that anchors and protects them from both flowing water and predation is important. Even such free-swimming insects as the dragonfly *Sympetrum* (Figure 11) in the **Odonata** sometimes lay their eggs in plates on moss



growths, securing the eggs and hatchlings (Figure 12) (Wesenberg-Lund 1943).



Figure 11. *Sympetrum sanguineum* mating. Photo by Qartl through Creative Commons.



Figure 12. *Sympetrum striolatum* egg-laying among grasses and mosses. Photo by Hugh Venables through Creative Commons.

Some of the aquatic insects live in immature stages in the water for more than one year (Danks 1992; Ulfstrand 1968b). These extended lives may result from slow

development, long or repeated dormancy, or adults that live a long time (Danks 1991, 1992). Others, in particular the mayflies (**Ephemeroptera**), may live for only one day as adults (Figure 13), just long enough to mate and lay eggs, but can spend about one year in the naiad stage in the water. The long life cycles are usually coupled with several factors, including cold, unpredictable temperatures, unreliable or low quality food supplies, natural enemies, and large adult size. Life cycle traits relate strongly to the predictability of the environment where the insect lives and the environmental signals that are provided (Danks 2006). But Danks cautions that much more detail is needed to understand these life cycle patterns in insects.



Figure 13. *Callibaetis ferrugineus* subimago. Photo by Jason Neuswanger, with permission.

Radford and Hartland-Rowe (1971) examined the life cycles of stream insects from Alberta, Canada. Several of these represent genera [*Nemoura*/*Zapada*/*Prostoia* (Figure 14), *Ephemerella*/*Drunella* (Figure 15)] that are common among bryophytes. Of these, *Prostoia* (= *Nemoura*) *besametsa* (see Figure 16) and *Drunella* (= *Ephemerella*) *coloradensis* (Figure 17) are characterized as fast seasonal types. But in the same family, *Zapada* (= *Nemoura*) *cinctipes* (Figure 18), *Z. columbiana* (Figure 19), *Z. oregonensis* (Figure 20-Figure 21), and *Drunella doddsii* (Figure 22) are slow seasonal types. None of these species has more than one brood per year except *Zapada cinctipes*, which has two. Temperature is important in determining growth rate in these species.



Figure 14. *Nemoura* sp. naiad, a genus with both fast and slow development. Photo by Bob Henricks, with permission.





Figure 15. *Ephemerella invaria* naiad, a genus with both fast and slow development. Photo by Bob Henricks, with permission.



Figure 16. *Prostoia* naiad, a common bryophyte dweller. Photo by Jason Neuswanger, with permission.



Figure 17. *Drunella coloradensis* naiad, having a fast seasonal type of development. Photo by Bob Henricks, with permission.



Figure 18. *Zapada cinctipes* naiad. Photo by Bob Armstrong, with permission.



Figure 19. *Zapada columbiana* adult on snow, emerging in winter. Photo by Jason Neuswanger, with permission.



Figure 20. *Zapada oregonensis* naiad showing gills. Photo by Jim Moore, through Creative Commons.



Figure 21. *Zapada oregonensis* adult. Photo by Jim Moore, through Creative Commons.





Figure 22. *Drunella doddsii* naiad, having a slow seasonal type of development. Photo by Bob Henricks, with permission.

Since insects have little tolerance for low temperatures (Dunman *et al.* 1991; Moore & Lee 1991), they must spend winter in a way that avoids the dangers of freezing (Ramløv 2000), as will be discussed in more detail below. It is this need to avoid freezing that forces some insects to spend part of their lives in the water. Bryophytes provide a habitat that helps them to cope with this watery habitat.

As Danks (1991) points out, the life cycle strategies provide options that facilitate survival: develop or enter diapause; grow rapidly or grow slowly. These are typically under the control of such environmental parameters as temperature and photoperiod.

### Life Cycle Cues

As already stressed, changes in life cycle phases are often necessary to survive changing weather conditions as the seasons change. Danks (1999) pointed out that life cycles are influenced by climate severity, seasonality, unpredictability, and variability. Some insects solve the unpredictability and variability problems by having flexible life cycles. These modifications can be determined by factors such as food availability and temperature. Danks (1991) points out that various stages in the life cycle are used in combination to adapt the insects to the changes of the seasons in nature.

In cold environments, some of the **Chironomidae** (*Diamesa incallida*; Figure 23) may produce 8-10 generations in a single year, with egg-laying occurring throughout the year (Nolte & Hoffmann 1992). *Diamesa incallida* is a hot-spring-dwelling midge that lives in water at 76-80°C, a community where we are not likely to find bryophytes, but it demonstrates the role of temperature and the wide range of capabilities in a family that is common among bryophytes. Some Arctic **Chironomidae** solve the problem of finding a sexually mature mate by negating the need for mating and being **parthenogenetic** (producing offspring without fertilization) (Langton 1998).



Figure 23. *Diamesa* (Diptera) pupal exuvium, a genus that may produce 8-10 generations in a single year. Photo by Will Bouchard, with permission.

Shama and Robinson (2009) demonstrated that an alpine caddisfly (*Allogamus uncatus*, a bryophyte dweller) in Switzerland responded to late season photoperiod cues by accelerating development, but the species showed adaptive plasticity in response to season length, making responses different among populations with only small geographic differences. Furthermore, the responses of the two sexes can differ (Shama & Robinson 2006).

On the other hand, the bryophyte-dwelling caddisfly *Limnephilus externus* (Figure 24-Figure 26) did not make developmental adjustments in response to diet supplementation, although it did grow to a larger size (Jannot *et al.* 2008). Furthermore, this caddisfly was unable to adjust to pond drying, responding by reduced growth rates and delayed development. This indicates the danger of an unpredictable environment for the aquatic insects.



Figure 24. *Limnephilus externus* larva in case. Photo by Wendy Brown <Gunnison Insects>, with permission.



Figure 25. *Limnephilus externus* adult, a caddisfly that does not adjust its development in response to food supplements. Photo by Jason Neuswanger, with permission.





Figure 26. *Limnephilus externus* larva showing abdominal gills. Photo by Wendy Brown <Gunnison Insects>, with permission.

In unpredictable or unstable environments, flexibility in the life cycle is important (Brittain & Saltveit 1989). Knispel *et al.* (2006) found that the bryophyte-dwelling mayfly *Baetis alpinus* (Figure 27) in the Swiss floodplains has synchronous egg development with high hatching success. By developing faster in warmer habitats it is able to hatch when conditions are favorable in the autumn. Long development time and delayed hatching permit success in unpredictable habitats in the cold glacial conditions. The mayfly *Rhithrogena nivata* (see Figure 28) has a long incubation period; the timing of hatching and glacial discharge conditions determine the success of development. This plasticity permits it to live in the very unstable, cold habitats that are limiting to other species.



Figure 27. *Baetis alpinus* naiad, a mayfly with synchronous egg development that promotes high hatching success. Photo by Andrea Mogliotti, with permission.

Many insects have developmental cues similar to those of plants. These include degree-days (calculated by taking the average of the daily maximum and minimum temperatures compared to a base temperature necessary for growth by the species). As in many plants, degree days may be important in determining the rate of development. For example, the mayfly *Leptophlebia cupida* (Figure 29) in the Bigoray River, Alberta, Canada, has only one reproductive period each year (Clifford *et al.* 1979). Clifford *et al.* (1979) found that degree days of water

temperature was more important than number of days for development, with 34 instars being produced in the laboratory at 20°C. That number is most likely plastic in response to environmental conditions.



Figure 28. *Rhithrogena impersonata* naiad, a genus in which some species have life cycle plasticity that depends on local weather. Photo by Donald S. Chandler, with permission.



Figure 29. *Leptophlebia cupida* naiad, a species with only one reproductive cycle per year. Photo by Jason Neuswanger, with permission.

For aquatic insects, the temperatures are much more tempered than in the terrestrial environment. In a study of 95 aquatic species, Pritchard *et al.* (1996) found that only 4 of 92 possible comparisons among **congenerics** (members of same genus) demonstrated significant differences in degree of cold adaptation. All **Odonata** (damselflies and dragonflies), 71% of **Diptera** (true flies), and 81% of **Ephemeroptera** (mayflies) had significant slopes indicating that they were warm adapted. They suggested that the **Plecoptera** are cold-adapted species that may use the egg stage to survive when the temperatures are too high.

In the stonefly family **Leuctridae**, commonly represented among bryophytes, the length of the naiad stage depends on the temperature. In *Leuctra ferruginea* (Figure 30) those individuals living in the coolest streams required two years for their life cycle, whereas those in the warmest waters were able to complete the life cycle in one

year (Harper 1973). The **Leuctridae** (Figure 30) and **Nemouridae** (Figure 14) are both common at the cooler upstream stations in Southern Ontario. Six species of the stonefly **Isogenoides** (Figure 31) from Colorado, USA, a genus also known from mosses, varied in hatching time both among the species and within some species (Sandberg & Stewart 2004). In one species the eggs hatched over an extended period of time, stopped hatching for the winter, then resumed hatching in May-June the following year. Some eggs even survived and hatched two years later. In one species, a summer diapause was needed before the eggs would hatch. Members of the genus required three months to four years before hatching.



Figure 30. *Leuctra ferruginea* naiad, a stonefly that has modified its life cycle to suit the climatic conditions. Photo by Tom Murray at BugGuide.



Figure 31. *Isogenoides hansonii* naiad, in a genus with moss-dwelling members in which life cycles vary both between and within species. Photo by Bob Henricks, with permission.

### Temperature Relations

As already noted, temperature plays an important role in determining when life cycle stages occur. Freezing, desiccation, and anoxia are all lethal among aquatic insects, from egg to adult (Lencioni 2004). When in the aquatic habitat, these three factors are related, with ice preventing the renewal of oxygen, and ice crystals drawing water from the cells, causing desiccation. Some of the aquatic insects enter **diapause** during winter. This usually requires storage of food as glycogen and lipids, hormonal control, and depression or suppression of oxidative metabolism with mitochondrial degradation.

But the mosses themselves seem to present a relatively constant temperature. Thorup (1963) considered the

temperature among mosses in springs to be so constant that it would not provide the developmental temperature point needed to trigger changes in stages. Correlated with the moss habitats in springs was an insect life cycle with only one generation per year.

### Overwintering

Duman *et al.* (1991) defined two physiological mechanisms by which insects survive winter: freeze tolerance and freeze avoidance or freeze resistance (see also Ramløv 2000). Aquatic insects have only limited ability to survive at temperatures below freezing (Moore & Lee 1991). They can supercool to only  $-3$  to  $-7^{\circ}\text{C}$  and only some members in the order **Diptera** are known to be freeze tolerant. The adults seem to be somewhat more cold tolerant. Thus this is a group of insects for which aquatic habitats that do not freeze provide them with an escape to suitable temperatures for the winter. What is fascinating is the plasticity of their responses. Duman *et al.* (1991) found that not only do different populations of the same species exhibit different overwintering mechanisms, but that even the same population may change its overwintering mechanism from year to year.

Because of their need for warmer temperatures in immature stages than that needed by terrestrial insects, most of the aquatic insects spend their egg and immature stages in the water. In fact, warm-water insects avoid the freezing dangers of winter by surviving as eggs. This is particularly true for the blackflies (**Simuliidae**; Figure 51-Figure 53) (Hynes 1970).

Insects rarely spend their entire lives in the water, but some spend larval stages there, pupal stages on land, then return to the water as adults, as in many **Coleoptera** (beetles). Others, particularly some of the **Trichoptera** (caddisflies) overwinter as adults. In fact, some even emerge mid-winter in cold climates. And the adult stonefly *Zapada cinctipes* (**Nemouridae**; Figure 18) re-enters the water when air temperatures drop below freezing (Tozer 1979). However, the stream chironomid *Diamesa mendotae* (Diptera; Figure 32-Figure 33) does things quite differently – its freeze tolerance is actually greater in the larval (stream) stage (Figure 33). Although it has a larval super-cooling-point (SCP) temperature of  $-7.4^{\circ}\text{C}$  and pupal SCP of  $-9.1^{\circ}\text{C}$ , compared to  $-19.7^{\circ}\text{C}$  for the adults (Bouchard *et al.* 2006), the larvae of *D. mendotae* are freeze tolerant, with a lower lethal temperature (99% dead) of  $-25.4^{\circ}\text{C}$ ,  $\sim 10^{\circ}\text{C}$  lower than their minimum super cooling point ( $-15.6^{\circ}\text{C}$ ). They change from freeze tolerant as larvae to freeze intolerant as adults! Nevertheless, the adults are able to tolerate cold temperatures sufficiently to mate on the snow (Ferrington *et al.* 2010). Furthermore, they can survive under the snow for extended periods of time (Anderson *et al.* 2013).

The often moss-dwelling *Serratella ignita* (Figure 60) overwinters from late summer until late the next spring as an egg (Arnold & Macan 1969). On the other hand, the mayfly *Ameletus inopinatus* (Figure 34) and stonefly *Leuctra hippopus* (Figure 35), a stony bottom dweller, do the most developing in the naiad stage while their stream is iced over, at least in northern Sweden (Ulfstrand 1968b). The low temperatures slow, but usually do not stop, development and growth.





Figure 32. *Diamesa mendotae* adult on snow. Permission to reproduce given by Leonard Ferrington on behalf of the Chironomidae Research Group at the University of Minnesota.



Figure 33. *Diamesa mendotae* larvae alive in Petri dish after freezing. Permission to reproduce given by Leonard Ferrington on behalf of the Chironomidae Research Group at the University of Minnesota.



Figure 34. *Ameletus ludens* naiad, member of a genus where some species develop under the ice in streams. Photo by André Wagner, with permission.

It is interesting that in alpine streams that have snow cover for 6-9 months of the year, taxa richness and abundance of the insects seems to have no seasonal pattern. Nevertheless, the species composition differs significantly from summer to winter. Schütz *et al.* (2001) found two strategies for larval survival. The insects either had to be adapted to the extreme conditions of summer or avoid these by developing during the winter (typical of **Ephemeroptera** and **Plecoptera**).



Figure 35. *Leuctra hippopus*, a stonefly that develops in Sweden while the stream is iced over. Photo by Niels Sloth, with permission.

But ice is also a good insulator, so those insects living on the bottom of lakes and ponds are usually able to avoid lethal low temperatures there. Such insects as the **Chironomidae** (Figure 90) typically live in sediments where oxygen content is low. Cold water holds more oxygen, and since these organisms are adapted to low oxygen conditions, there is sufficient oxygen in the cold water. Some **Chironomidae** and **Trichoptera** (Figure 83) actually occur in ice and frozen sediment, as noted in a north Swedish river (Olsson 1981). Olsson found that 80-100% of these frozen insects survived thawing. **Chironomidae** survived exposure to  $-4^{\circ}\text{C}$  for five months. Danks and Oliver (1972a) found that in the Arctic **Chironomidae** that overwinter are mature larvae and are ready to emerge as soon as the winter season is over. They take advantage of the warm sun by emerging in the middle of the day when the water temperature is highest (Danks & Oliver 1972b).

It is interesting that **Plecoptera**, **Ephemeroptera**, **Trichoptera**, **Diptera**, and **Coleoptera** have all been recovered alive from **anchor ice** (submerged ice anchored to the bottom; Figure 36). Anchor ice can encase bryophytes as well, and when it breaks loose, it can take the entire patch of bryophytes with it. Hence, it would likewise take all the insect inhabitants as well, moving them downstream to a new location.

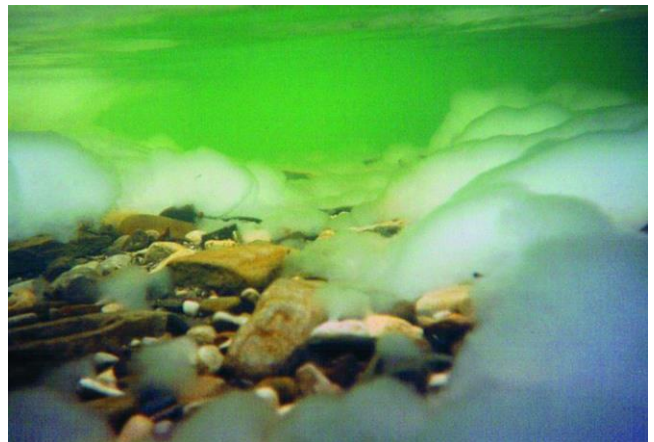


Figure 36. Anchor ice, Alberta, Canada, visible here as cloud-like mounds of ice attached to the rocks under water. Courtesy of Pacific Northwest National Laboratory.



## Structural

Hynes (1970) summarized the adaptations of stream insects to include flattening, streamlining, friction discs, close application to the surface of stones, and in some the presence of hydraulic suckers. But many of these adaptations pertain to a life on rocks or other relatively smooth substrate. Such characters as flattening, friction discs, close application to the surface, and hydraulic suckers are of little value among the chambers of a bryophyte mat. This leaves us with only one adaptation from his list, that of streamlining (Figure 37), present in the stoneflies [Plecoptera: **Leuctridae** (Figure 37), **Capniidae** (Figure 38), **Chloroperlidae** (Figure 39), and some **Gripopterygidae** (Figure 40)], and mayflies [Ephemeroptera: **Leptophlebiidae** (Figure 41) and **Baetidae** (Figure 45)] – all known from bryophytes. Others have retained the dorsi-ventral flattening, but it is better described as compressing (Figure 42) since these insects do not quite fit the definition of flat. And compression is useful among bryophytes. Other bryophyte adaptations include small size, attachment hooks, and gill covers or gills absent (Glime 1968).



Figure 39. **Chloroperlidae** naiad. Photo by Bob Henricks, with permission.



Figure 37. **Leuctra laura** naiad showing streamlining. Photo by Tom Murray at BugGuide, through Creative Commons.



Figure 40. **Zelandobius illiesi**, a stonefly naiad with streamlining. Photo by Stephen Moore, Landcare Research NZ, with permission.



Figure 38. **Allocapnia** sp. naiad showing streamlining. Photo by Bob Henricks, with permission.



Figure 41. **Paraleptophlebia mollis** naiad, a mayfly illustrating streamlining. Photo by Tom Murray through Creative Commons.





Figure 42. *Ephemerella* naiad showing dorsi-ventral compression. Photo by Bob Henricks, with permission.

Bryophyte-dwelling insects therefore do not necessarily have the same adaptations as stream insects in general. Streamlining helps, but does not need to be as severe. Steinmann (1907, in Muttkowski 1929) found that about 30% of the bryophyte-dwelling taxa were streamlined. But in the streams of the Appalachian Mountains, streamlining was not common (Glime 1994). For example, the common bryophyte-dwelling mayfly *Ephemerella* (Figure 42) is neither flattened nor streamlined (Arnold & Macan 1969), but has a shape more like a terrestrial insect – it is dorsiventrally compressed.

Small size is also an advantage and seems to be the most important characteristic of bryophyte dwellers. Bryophytes provide small spaces where invertebrates can hide, but these same small spaces limit the sizes of the organisms that can occur there. This explains why bryophytes tend to harbor small species and hatchling insects (Figure 43).



Figure 43. *Taeniopteryx* naiad on the edge of a Syracuse watch glass, demonstrating the small size of this bryophyte dweller. Photo by Bob Henricks, with permission.

Dudley (1988) suggested that while the complex structure of bryophytes might interfere with attachment by larger larvae, it reduces frequency of encounter between such predators and the small insect inhabitants. In the Appalachian, USA, streams 70% of the bryophyte dwellers were less than 6 mm long (Glime 1994). Egglishaw (1969) found that a higher proportion of smaller animals occurred on mosses than on stones or riffles. In *Leuctra inermis* (see Figure 37, Figure 44), *Baetis rhodani* (Figure 45), and *Isoperla grammatica* (Figure 46) it was the young (small) stages that occurred among the bryophytes.



Figure 44. *Leuctra inermis* adult, a species whose early naiad instars live among mosses in riffles. Photo by James K. Lindsey, with permission.

Frost (1942) remarked that because of the very young and thus small specimens, identification was both difficult and questionable, forcing identification to genus or subfamily only. Glime (1994) found that *Baetis* sp. was present among mosses (10 per gram) in summer, but were absent in later stages when the larger naiads were present among rocks in the stream bed. Others that moved out of the bryophytes when they got larger were the crane fly *Limonia* (Figure 47), stonefly *Taeniopteryx* (Figure 48), and caddisflies *Lepidostoma* (Figure 49) and *Neophylax* (Figure 50). Similar migration of older stages occurs in Europe (Thienemann 1912; Carpenter 1927; Egglishaw 1969).



Figure 45. *Baetis rhodani*, a mayfly that starts its life among bryophytes, but moves out as it grows larger. Photo by J. C. Schou through Creative Commons.



Figure 46. *Isoperla grammatica* naiad showing dorsiventral compression. Photo by Dragiša Savić, with permission.



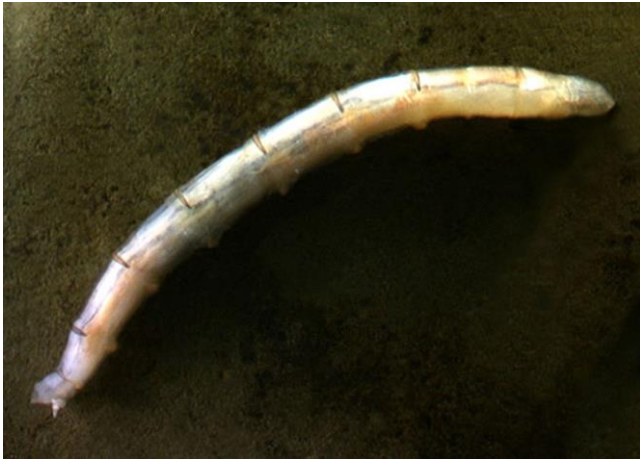


Figure 47. *Limonia* sp., an insect that lives among bryophytes until it gets too large; then it moves out. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 50. *Neophylax atlanta* larva and case, a caddisfly that moves from bryophytes to other substrates as it grows. Photo by Bob Henricks, with permission.



Figure 48. *Taeniopteryx* sp. naiad, a moss-dwelling stonefly that moves to substrates with more space when it gets larger. Photo by Bob Henricks, with permission.



Figure 49. *Lepidostoma* larva and case, a caddisfly that moves out of the bryophytes as it grows. Photo by Bob Henricks, with permission.

### Attachment

While torrents bring much-needed oxygen, they also are treacherous, dislodging the insects and sweeping them downstream. Black flies (**Simuliidae**; Figure 51-Figure 53) are among the best adapted of the aquatic insects for surviving this torrential onslaught, living on the upper surface of the bryophyte mats (Niesiolowski 1979). On both rocks and mosses, they are able to anchor themselves with a circle of hooks on the rear of the abdomen (Figure 51) (Arnold & Macan 1969). Furthermore, they manufacture a silken thread that they lay down on their substrate surface as an anchor. When they do become dislodged by chance or choice, they have a tether that prevents them from travelling too far and helps them to gain a "foothold" on their new downstream substrate. Those hooks, on both the abdomen and the single proleg foot (Figure 52), enable blackfly larvae to grab onto the silken mat (Figure 53) they have made. They are able to use these same two sets of hooks to move along their silken mat like inch worms.



Figure 51. **Simuliidae** larva showing anal hooks. Photo by Bob Henricks, with permission.





Figure 52. *Prosimulium mixtum* larva showing single proleg. Photo by Tom Murray at BugGuide, through Creative Commons.



Figure 55. *Rhyacophila fuscata* larva showing anal hooks that serve as anchors. Photo by Jason Neuswanger, with permission.



Figure 53. Simuliidae larvae on leaf where silken threads form a mat, aiding in attachment. Photo by Bob Henricks, with permission.

The net-spinning caddisflies (**Hydropsychidae**) accomplish anchorage by a pair of hooks on the posterior end (Figure 54), a modification of many caddisflies for pulling themselves into their cases. But among the free-living caddisflies like the **Hydropsychidae** and **Rhyacophilidae** [e.g. *Rhyacophila dorsalis* (Badcock 1949)], these hooks (Figure 55) serve as anchors among the bryophytes. Other insects have hooked claws that help them to clamber among the bryophytes, including the beetles (e.g. **Elmidae**, Figure 56) and some mayflies (e.g. **Ephemerellidae**, Figure 60) and stoneflies [e.g. *Nemoura* (Figure 57) and *Acroneuria* (Figure 58)]. Others, like the **Chironomidae**, achieve anchorage by nestling at the leaf bases (Figure 59) where little flow occurs.



Figure 54. *Hydropsyche* larva showing posterior prolegs with hooks that provide anchorage. Photo by Bob Henricks, with permission.



Figure 56. **Elmidae** adult showing clawed feet that help it climb among mosses. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 57. *Nemoura* sp. naiad showing hooked claws. Photo by Bob Henricks, with permission.





Figure 58. *Acroneuria abnormis* naiad showing hooked claws. Photo by Tom Murray, through Creative Commons.

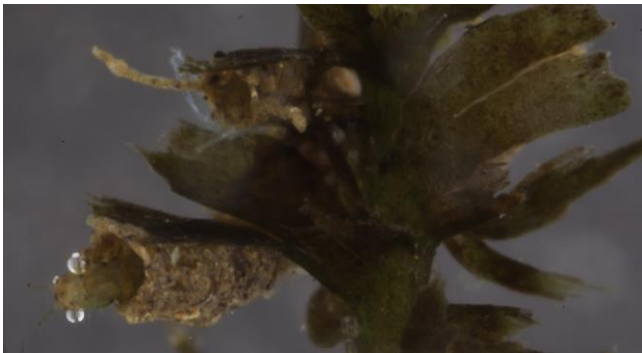


Figure 59. *Rheotanytarsus exiguus* (Chironomidae) group nestled in leaf bases. This species makes a tube where it lives. Photo by D. N. Bennett, with permission.

Hora (1930) and Ward (1992) suggested that backward pointing dorsal spines (Figure 60-Figure 64) of some moss dwellers, e.g. the **Gripopterygidae** (Figure 61), are adaptations to reduce chances of being swept downstream. Illies (1961) reported large dorsal spines on a moss-dwelling stonefly from Chile. Similar (but smaller) spines are known on the common moss-dwelling mayfly *Ephemerella ignita* (Figure 60; Hynes 1970). Even **Diptera** larvae [e.g. **Psychodidae** (Figure 62), **Tipulidae** (Figure 63-Figure 64)] can have backward-directed spines. But the tipulid larvae of *Phalacrocer* (Figure 63) and *Triogma* (Figure 64-Figure 65) have such projections and live mostly among semiaquatic mosses where there is no flow to dislodge them. This suggests the spines may serve either as camouflage or as trapping devices to prevent would-be predators from pulling them out of the moss mat.



Figure 60. *Serratella ignita* naiad showing spinelike structures on the dorsal side of the abdomen. Photo by J. C. Schou through Creative Commons.



Figure 61. *Zelandobius illiesi* (Gripopterygidae) showing backward-pointing dorsal spines. Photo by Stephen Moore at Landcare Research, NZ, with permission.



Figure 62. *Clogmia albipunctata* (Psychodidae) larva with backward pointing spines. Photo by Ashley Bradford through Creative Commons.



Figure 63. *Phalacrocer replicata* larva showing green color and projections that help to camouflage it among mosses. Photo from Wikimedia Commons.





Figure 64. *Triogma* larva showing backward pointing spines. This larva also has cryptic coloration that makes it difficult to detect among the bryophytes. Photo by Janice Glime.



Figure 65. *Triogma trisulcata* larva among *Sphagnum* showing appendages that mimic moss leaves. Photo by Walter Pfliegler, with permission.

**Gill covers** help to keep silt from accumulating among the gills, since the mosses often reside where they collect large amounts of silt. The gill covers can also be used to fan the fills, hence moving the water and facilitating oxygen exchange. Gill covers are common among the **Ephemeroptera**, especially in the **Ephemerellidae** (Figure 66-Figure 67) and **Caenidae** (Figure 68).



Figure 66. *Drunella grandis* naiad showing raised gill covers and fimbriate gills. Photo by Bob Newell, with permission.



Figure 67. *Serratella* gills showing gill covers and fibrillate gills on successive abdominal segments. Photo by Bob Henricks, with permission.



Figure 68. *Caenis latipennis* naiad showing large gill covers over the dorsal abdomen. Photo by Donald S. Chandler, with permission.

## Behavioral

Behavior often permits organisms to change their locations, providing the best location available to them as the season changes and required resources are in new locations. Behavioral adaptations can help them capture prey, avoid being prey themselves, gain sufficient oxygen, avoid being swept away by the current, and escape cool or freezing temperatures.

Bryophytes provide a series of zones (Figure 69) that permit insects to live in the flow regime they require. As will be seen, oxygen can be a limiting factor, requiring some insects to live near the surface of the bryophyte where torrential waters trap oxygen from the air. Hence, these insects require a means of anchorage lest they themselves become part of the torrent. Others are well adapted to the low oxygen levels and live at the base where detritus accumulates and predators seldom venture. But it is advantageous that they can move about and seek the zone within the stream or lake and within the bryophyte community that best meets their needs.

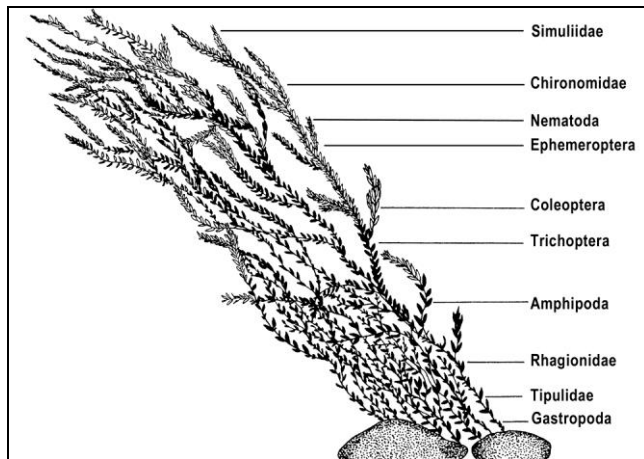


Figure 69. *Fontinalis* zonation of insects. Redrawn from Niesiolowski 1979.

Aquatic insects tend to avoid light, exhibiting negative phototaxis (Moon 1940; Shelford 1945). Mayflies, in particular, demonstrate a negative phototaxis, preferring darker locations (Wodsealek 1911; Gros 1923; Percival & Whitehead 1926). This may account for the presence of some taxa among the darker spaces of mosses, particularly in rapid water where rock surfaces may be highly exposed to light. Others may avoid light to be less conspicuous to their prey. On the other hand, *Baetis harrisoni* (Figure 70) chose illuminated stones 112 times compared to 14 for shaded stones, exhibiting strong positive phototaxis (Hughes 1966).



Figure 70. *Baetis harrisoni* naiad, a mayfly that prefers illuminated stones. Photo by Helen James through Creative Commons.

Insects often escape adverse conditions in their environments by modifying the environments themselves. Such modifications may include making shelters (Figure 71), excavating, aggregating (Figure 53), forming colonies, and parental actions (Danks 2002). Although all of these actions may be found among aquatic insects, not all of these occur among those living among bryophytes. The bryophyte itself sometimes makes such actions as excavating and making shelters unnecessary. For example, several families of caseless caddisflies live among bryophytes. But the very tiny **Hydroptilidae** may take advantage of the bryophytes for case-building materials.



Figure 71. *Helicopsyche* case, made by the caddisfly as a shelter. Photo by Mike Quinn, through Creative Commons.

### Oxygen Conditions

Ponds can become quite anoxic in winter when the surface is frozen (Nagell & Brittain 1977). Streams are less likely to become anoxic, but within the bryophyte mat water can be quite quiet and oxygen can be used up quickly by decaying organisms. However, insects have a wide array of adaptations to help them through places and times of anoxia (Hoback & Stanley 2001). For example, 10 Arctic species of **Collembola** (springtails) are known to survive anoxia at 5°C for up to 36 days (Hodkinson & Bird 2004). The mayfly *Cloeon dipterum* (Figure 72) is able to survive 3-4 months in anoxic ponds, and naiads survived up to 155 days at 0°C in the lab (Nagell 1977).



Figure 72. *Cloeon dipterum*, a mayfly that can survive 3-4 months in anoxic pond water. Photo by Malcolm Storey, through Creative Commons.

As is obvious from previous studies, oxygen relations in the insects are dependent on temperature (Jacob & Walther 1981). More oxygen can dissolve at low temperatures. In fact, oxygen limitations due to temperature are so important that they set the thermal limits in at least some species of aquatic insects (Verberk & Bilton 2011). Furthermore, since smaller insects use less oxygen, large insects may have been an adaptation to excess oxygen in the Carboniferous Era (Verberk & Bilton 2011). Oxygen limitations may explain in part the presence of small insects among the bryophytes, whereas



the larger stages move to rock faces where flow is uninterrupted and able to replenish the oxygen more easily.

Knight and Gaufin (1966) measured oxygen consumption as a function of temperature in two stonefly naiads that associate with bryophytes: *Hesperoperla pacifica* (Figure 73) and *Pteronarcys californica* (Figure 74). These insects followed the general trend of consuming more oxygen at higher temperatures. This relationship is problematic because gasses are lost from the water at higher temperatures, thus limiting the most available oxygen to winter.



Figure 73. *Hesperoperla pacifica* with its pompom-like gills peeking out from the ventral thorax. Photo by Arlen Thomason, with permission.



Figure 74. *Pteronarcys californica*, probably the largest insect inhabitant of bryophytes. Photo by Bob Henricks, with permission.

Among the common bryophyte dwellers, the mayflies (**Ephemeroptera**) are the least tolerant of low oxygen (Gaufin *et al.* 1974), making them good indicator organisms. These are followed by stoneflies (**Plecoptera**), then caddisflies (**Trichoptera**), flies (**Diptera**), and damselflies (**Odonata**) in that order. Of course there are exceptions within the orders.

Insects living in low oxygen conditions may be adapted by developing enlarged respiratory organs (Figure 75) (Dodds & Hisaw 1924), including enlargement of tracheal gills (Figure 76) (Golubkov *et al.* 1992). Behavior can play an important role, with most species moving away from the anoxic sediments when oxygen becomes limiting (Kolar & Rahel 1993). But moving is not always a good choice because it can result in being swept into the current and usually means becoming more visible, hence being more obvious to predators. The movement itself attracts attention through the excellent vision in the well developed eyes of other arthropods and fish.

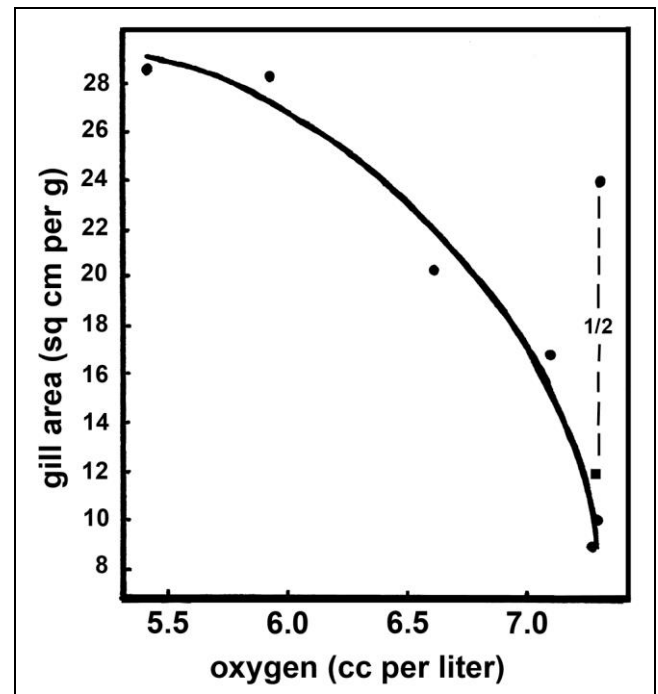


Figure 75. Relationship of gill size in seven species of **Ephemeroptera** to oxygen availability in aquatic systems. The outlier species on the right is the genus *Iron*, a genus for which the gills form a suction cup, preventing one side of the gills from functioning in oxygen uptake. Its position when only half the area is used is shown by the square at the base of the dotted line on the right. Redrawn from Dodds & Hisaw 1924.

Gills are a common adaptation to low oxygen, especially in **Ephemeroptera** (Figure 76), **Plecoptera** (Figure 77-Figure 79), and **Trichoptera** (Figure 80). These are placed in almost every position (*e.g.* Figure 78), depending on the genus or family, and are useful taxonomic characters in some groups. But they also tend to be protected, between legs or under gill covers. Others have cutaneous breathing – providing the expanse of the insect's surface and avoiding the danger of collecting sediments.



Figure 76. *Leptophlebia nebulosa* showing abdominal (tracheal) gills. Photo by Don S. Chandler, with permission.



Figure 77. *Nemoura* sp. naiad showing clusters of white thoracic gills at the "neck." Photo by Bob Henricks, with permission.

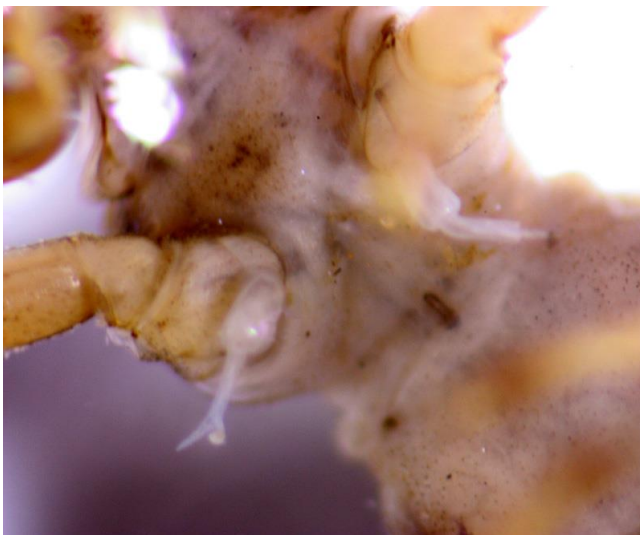


Figure 78. Coxal gills on a winter stonefly. Photo by Bob Henricks, with permission.



Figure 79. *Acroneuria carolinensis* naiad showing gills on the ventral thorax. Photo by Tom Murray, through Creative Commons.



Figure 80. *Hydropsyche* sp. larva showing gills on ventral side. Photo by Bob Henricks, with permission.

As early as 1907, Babak and Foustka concluded that as the oxygen concentration in the water decreased, movement of the gills of mayflies increased. Dodds and Hisaw (1924) showed a relationship between gill area and oxygen concentration in mayflies. But in the mayfly *Baetis* (Figure 45, Figure 70) used for testing, the gills never beat and it seems that they do not use their gills for oxygen consumption in the range of 5.0 to 8.0 cc L<sup>-1</sup> (Wingfield 1939). Rather, these mayflies live in rapid streams where oxygen concentrations are usually above 4 cc L<sup>-1</sup> and rapid flow keeps fresh, oxygenated water flowing over the gills. Under these conditions their cuticular respiration is sufficient. Macan (1962) reported on the work of Ambühl (1959). He found that *Baetis vernus* was scarce when the current speed was below 10 cm sec<sup>-1</sup> and increased in relative numbers up to 40 cm sec<sup>-1</sup>. *Ephemera ignita* (Figure 60) was most common at current speeds of 10-30 cm sec<sup>-1</sup>.

Movements of another type – undulating the body (Figure 81) or fanning the gills (Figure 82) – can increase the rate of oxygen movement across the gills. Undulations typically begin as oxygen levels are low and are also used for swimming, a second way to gain more oxygen. These undulations are easily seen when high-oxygen-requiring mayflies are brought to the lab and put in quiet water. **Ephemere**llidae species accomplish water movement over their gills by moving the gill covers (Figure 82) up and down, fanning the gills. **Trichoptera** (caddisflies) are able to pump water through their cases (Figure 83) to renew oxygen. Humps and projections maintain space between the larva and its case, permitting water (and oxygen)



movement through the case. But these activities require energy and the insects cannot sustain prolonged use of these behaviors (Hynes 1970).



Figure 81. *Baetis tricaudatus* naiad showing the tail and abdomen flipped up in an undulation. Photo by Bob Henricks, with permission.



Figure 82. *Ephemerella subvaria* naiad showing four gill covers on each side. Photo by Tom Murray, through Creative Commons.



Figure 83. *Limnephilus* sp. showing spacer hump just behind the thorax. Photo by Jason Neuswanger, with permission.

Most of the bryophyte dwellers do not carry oxygen in the air bubble of a **plastron** (Figure 84) or other form of

bubble (Figure 85), as done by a number of free-swimming species. However, the plastron mechanism is useful to some of the **Elmidae** (Figure 84), tiny beetles that clamber among the bryophytes (Arnold & Macan 1969). The plastron is much like a diving bell. The insect traps a bubble of air and carries it beneath the water surface. As the insect breathes, it exchanges its  $\text{CO}_2$  for the  $\text{O}_2$  in the plastron. Oxygen in the water will diffuse into the bubble as the oxygen is depleted, but as the nitrogen leaves the bubble, the bubble shrinks. The same mechanism applies to other types of bubbles such as the one in Figure 85. Eventually the concentration of oxygen in the bubble is too low and the insect must resurface to grab another bubble, or grab one from a photosynthesizing plant, including bryophytes. The collection of bubbles on plants under water is known as **pearling** (Figure 86).



Figure 84. *Stenelmis crenata* showing plastron (white area under ventral side). Photo by M. J. Hatfield through Creative Commons.



Figure 85. *Lancetes angusticollis* adult from South Georgia clinging to moss. Note the anal air bubble used like a diving bell. Photo by Roger S. Key, through Creative Commons.

### Obtaining Food

Feeding strategies include shredders, gatherers, scrapers, and detritus feeders. Venturing away from the protective bryophyte substrate is dangerous because the insects can easily be swept away by the current in streams. Thus, it is not any surprise that many of the insects have adapted strategies that permit them to obtain food without venturing away from their safe site. Many are detritus

feeders, and if they have adaptations to get enough oxygen, they can live in the silt or sand. Others such as the net-spinning caddisflies (Figure 87) and the blackflies (Figure 88-Figure 89) trap their food as it flows by them. The very effective anchorage permits the **Simuliidae** (blackflies) to hang from the rear and expose the head fans (Figure 89) into the current to trap organic particles, including diatoms, for food. Some eat their surrounding homes – the bryophytes.



Figure 86. *Riccia fluitans* with pearling. Photo through Creative Commons.

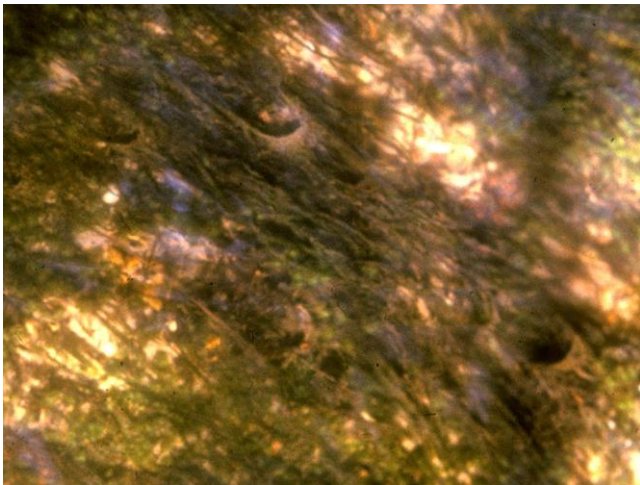


Figure 87. *Cheumatopsyche* nets on *Fontinalis*, trapping detritus and algae that flow by. Photo by Janice Glime.

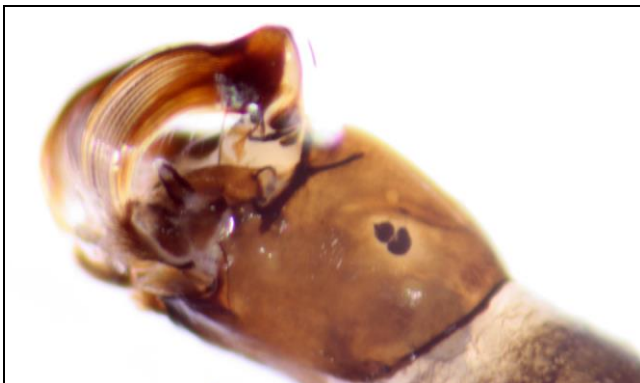


Figure 88. Simuliidae larva head fans closed. Photo by Bob Henricks, with permission.



Figure 89. **Simuliidae** larva showing head fans that are used to capture food. Photo by Bob Henricks.

Others, including some of the net-spinning **Hydropsychidae** (Figure 87), let the bryophytes do the trapping and eat the periphyton and detritus within the bryophyte mat. I base this assumption on finding many more larvae than nets among the mosses. The **Chironomidae** (Figure 90) live in leaf bases where detrital matter accumulates, obtaining both protection and food. In any case, the diet of the aquatic stage is usually quite different from that of the adult.

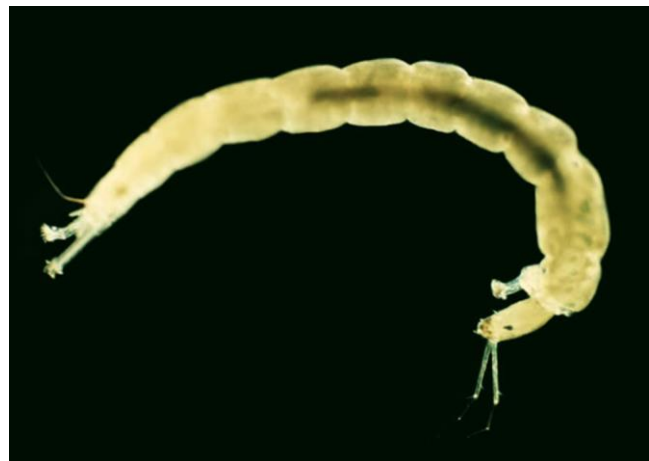


Figure 90. *Coryneura* sp. (**Chironomidae**). Photo by Stephen Moore, Landcare Research, NZ, with permission.

## Who Lives There?

Aquatic bryophytes in mountain streams typically are replete with insects, crawling about and dining on the detritus and algae in the milieu. They find themselves safely out of the torrent above and tucked away from the view of fish and other predators. It seems like they should have a pretty cushy life.

When I began my studies on insects living among bryophytes in Appalachian Mountain, USA, streams, few studies were available for comparison, and most of those



were from Europe. Like the development of keys for bryophytes, the development of keys for aquatic insects lagged way behind what was needed. To further complicate the problem, many of the insects had been described from adults, but studies to link the immature aquatic stages to their adults were lacking for many. It was the insect version of the early *Takakia* classification problem.

As I delved into the many more recent papers to prepare this chapter, I found many unfamiliar names of genera, only to discover that those familiar genera from nearly 50 years ago had gone through reclassification and were now represented under multiple new names, especially at the generic level. To further complicate these changes in generic concepts, the insects, like the bryophytes, comprise many microspecies. Limited dispersal distances for short-lived adult stages, mountain and land barriers, and disconnected stream or lake systems all contributed to the isolation needed for development of differences in physiology, behavior, phenology, and morphology (see for example Hughes *et al.* 1999; Monaghan *et al.* 2002). As bryologists we are well aware of these problems in classifying things separated by great distances, but for these insects the microspecies differences can be manifest over much shorter distances, a phenomenon that has been recognized in some aquatic bryophytes as well (Glime 1987; Shaw & Allen 2000). Nevertheless, there are lessons to learn from the orders, families, and even the genera as we examine who lives among the bryophytes – and why.

Drozd *et al.* (2009) used pitfall traps to compare invertebrate inhabitants related to bryophytes in the mountain areas (384-1200 m asl) of the Czech Republic. In most cases, the **Collembola** were the most abundant group except for the high number of ants at Podolánky. The numbers differed by bryophyte and moisture level (Figure 92). Insects were highest in the dry litter control (within 2

m of moss area). The lowest numbers were in wet *Sphagnum fallax* (Figure 91).



Figure 91. *Sphagnum fallax* with capsules, the species with the lowest number of **Collembola** among bryophytes in the mountainous areas of the Czech Republic. David T. Holyoak, with permission.

Drozd and coworkers (2009) considered several caveats in interpreting their results. Some of the invertebrates move about little and would therefore be poorly represented in the pitfall traps. Others that do move about would move easily between the bryophytes and litter, possibly only passing over the bryophytes in their search for food. Others may reside among the bryophytes as transient visitors, seeking escape from a predator or avoiding the desiccation common in more open areas, but returning to the litter habitat when that environment was safe. In any case, insects that met all their needs within the bryophyte mat would be under-represented in the pitfall traps.

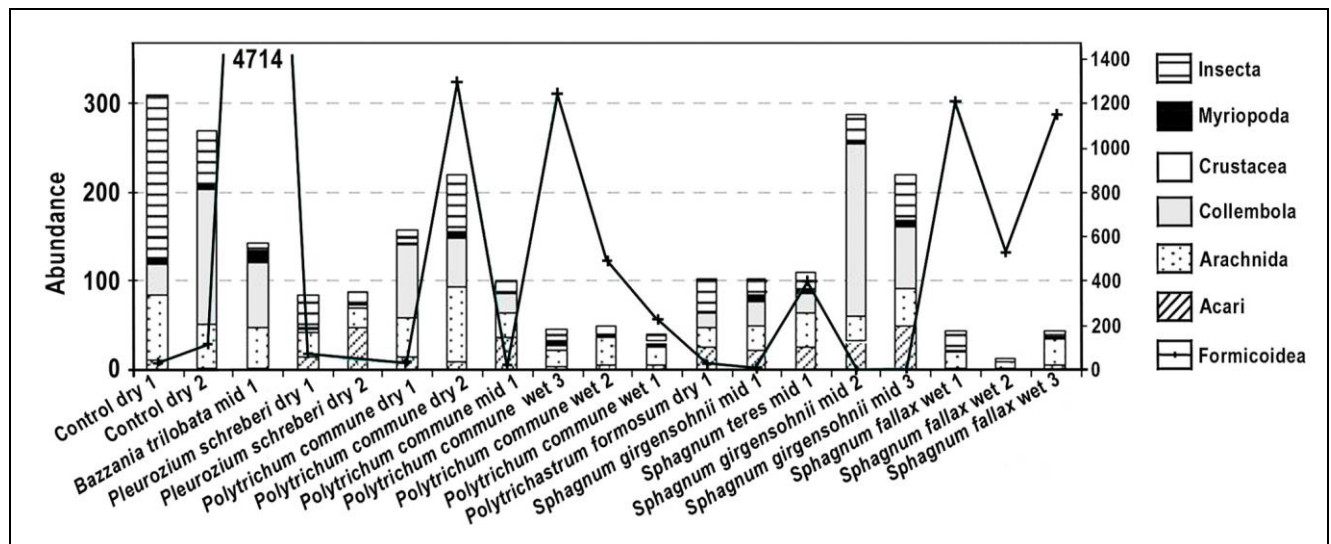


Figure 92. Abundance of taxonomical groups in pitfall traps associated with several species of bryophytes in dry, moist, and wet conditions at five locations in mountains of the Czech Republic. The scale at right is for ant data (**Formicoidea**) from Podolánky. Redrawn from Drozd *et al.* 2009. Controls are litter areas

The insects found among the mosses in streams are mostly **Ephemeroptera** (mayflies), **Plecoptera** (stoneflies), **Trichoptera** (caddisflies), **Diptera** (flies), and

**Coleoptera** (beetles) (Needham & Christenson 1927; Wesenberg-Lund 1943; Cowie & Winterbourn 1979; Glime 1994; Gislason *et al.* 2001). But moving about



among stems and leaves of mosses is not easy for the weak-legged or swimming insects in the small spaces. Hence, as already noted, most of the inhabitants are small (Thienemann 1912; Glime 1994; Amos 1999; Drazina *et al.* 2011). This also means that young, immature naiads of **Ephemeroptera** and **Plecoptera** are common (Stern & Stern 1969).

Many species overwinter as eggs on the mosses, then begin their immature lives there. Among the **Diptera**, *Dicranota* (Figure 93), *Atherix* (Figure 94), and *Simulium* (Figure 51-Figure 53) are common at this time; likewise, young **Elmidae** (larvae; Figure 95) are common among the mosses (Thienemann 1912).



Figure 93. *Dicranota* larva, a common stream moss inhabitant. Photo by Tom Murray, through Creative Commons.



Figure 94. *Atherix* sp. larva, a common dweller among stream bryophytes. Photo by Jason Neuswanger, with permission.



Figure 95. **Elmidae** larva, a common beetle larva among stream bryophytes. Photo by Stephen Moore, Landcare Research, NZ, with permission.

In a New Zealand stream, Cowie and Winterbourn (1979) found 44 species of invertebrates, mainly immature stages of insects. The moss *Acrophyllum* sp. (Figure 96) hosted the stonefly *Austroperla cyrene* (Figure 97), a species of beetle in the **Helodidae** (Figure 98), and a triclad, *Neppia montana* (Figure 99); the moss *Fissidens* sp. (Figure 100) hosted the stonefly *Zelandoperla fenestrata* (see Figure 101), the caddisfly *Zelolessica cheira* (Figure 102), a fly in the family **Empididae** (Figure 103), and several species of midges (**Chironomidae**; Figure 90); . The moss *Cratoneuropsis* (Figure 104) had only one common taxon, a terrestrial isopod, *Styloniscus otakensis*, suggesting that the streamside *Cratoneuropsis* habitat is more terrestrial than aquatic. In addition to water saturation and flow rates, the ability of mosses to trap detritus was important in determining invertebrate inhabitants.



Figure 96. *Acrophyllum quadrifarium* from New Zealand, home to beetles in **Helodidae**. Photo by Bill & Nancy Malcolm, with permission.



Figure 97. *Austroperla cyrene* from NZ. Photo by Steve Pawson, permission pending.



Figure 98. **Helodidae** adult, member of a family that lives among leaves of the moss *Acrophyllum* sp. Photo from <www.pybio.org>, with permission.





Figure 99. *Neppia*, an inhabitant of the moss *Acrophyllum* sp. Photo by Stephen Moore, Landcare Research, NZ., with permission



Figure 100. *Fissidens fontanus* with Amano shrimp in an aquarium. Photo through Creative Commons.



Figure 101. *Zelandoperla* sp., an inhabitant of *Fissidens* in New Zealand. Photo by Stephen Moore, Landcare Research NZ, with permission.

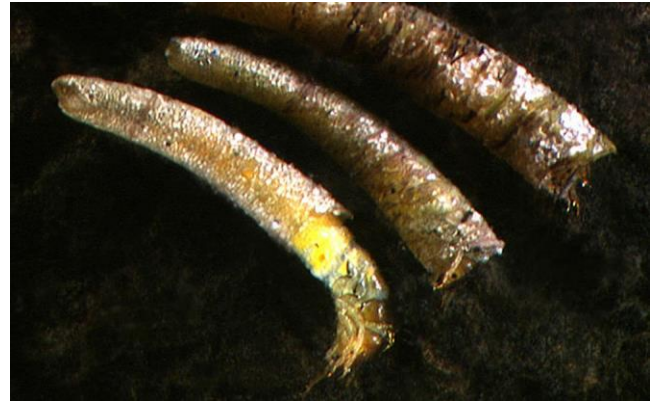


Figure 102. *Zelolessica* sp., an inhabitant of aquatic *Fissidens* in New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 103. **Empididae** larva, an inhabitant of aquatic *Fissidens* in New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 104. *Cratoneuropsis relaxa*, in a genus that commonly houses isopods but few insects in New Zealand. Photo by Tom Thekathyl, with permission.

Suren (1988) examined faunal assemblages in New Zealand alpine streams, with the stoneflies (**Plecoptera**) *Zelandoperla* (Figure 101) and *Zelandobius* (Figure 105) and midge larvae (**Chironomidae**; Figure 90) being dominant. The mosses supported 5-15 times as many invertebrates as did the rocky habitats. In addition to these dominant insects, several non-insect invertebrates were dominant.





Figure 105. *Zelandobius illiesi*, a stonefly genus that is common among alpine stream mosses in New Zealand. Photo by Stephen Moore, Landcare Research NZ, with permission.

One of the interesting questions about bryophyte fauna is whether any species has a unique fauna. So far we have seen little specificity among the other invertebrates. Nevertheless, differences may exist dependent upon the niches of the bryophytes themselves. Some bryophytes occupy fast flow, some occupy areas where they spend part of the year above water, some are deep, and certainly differences exist among growth forms that create differences in the protection they afford. And some **Trichoptera** use liverworts or mosses to construct their cases, forcing them to live with certain species. Coinciding with these differences are the kinds of food the bryophyte habitats provide, again affecting who can survive there.

Paavola (2003) examined the concordance among the macroinvertebrates, bryophytes, and fish to look for possible **surrogates** to describe the system and its state of health. **Surrogates** are groups of organisms that can be used to assess suitability of a habitat for another group of organisms such as fish. When considered across drainage systems, there was strong concordance, but within a single river system that concordance was weak.

Bryophyte locations in the Paavola (2003) study were mainly related to nutrient levels and in-stream complexity, whereas macroinvertebrates correlated with stream size and fish correlated with oxygen levels, depth, and substrate size. But macroinvertebrates also relate to in-stream complexity (Allan 1975; Hart 1978; Trush 1979; Wise & Molles 1979; Williams 1980; Vinson & Hawkins 1998) and to substrate texture (Glime & Clemons 1972). And bryophytes add to that complexity. Some of the genera that inhabit bryophytes are also common in leaf packs – a substrate that provides cover and detritus for food. These include *Baetis* (Figure 45), *Leuctra* (Figure 30), and **Chironomidae** (Figure 90) (Robinson *et al.* 1998).

Due to differences in growing season, ice-free season, winter severity, available food, and flow regime changes from year to year, the fauna assemblage can also change from year to year. This can result in the temporary disappearance of an entire species, or even an entire order (Milner *et al.* 2006). This disappearance is particularly true for **Plecoptera**. Channel stability is important in determining faunal stability, but a normally stable channel can suffer from heavy rains or flooding during snow melt.

And channel stability likewise determines the stability of bryophytes, hence playing a role in the bryophyte fauna.

In my study of the insects inhabiting the bryophytes of mid-Appalachian Mountain streams, I identified 141 species occurring among 10 species of bryophytes in 28 streams, and that does not include the species of the **Chironomidae** (Figure 90), which were identified only to family (Glime 1994). The smallest of the insects occurred on the leafy liverwort *Scapania undulata* (Figure 106) and the largest could be found on various species of *Fontinalis* (Figure 107). As in many other studies, the most abundant insects were midges (**Chironomidae**), the stoneflies *Leuctra* (Figure 30) and *Isoperla bilineata* (Figure 108), and the blackflies (*Simulium tuberosum*; Figure 109).



Figure 106. *Scapania undulata*, home for the smallest aquatic insects. Photo by Michael Lüth, with permission.



Figure 107. *Fontinalis antipyretica*, a large moss that houses the largest moss dwellers. Photo by Bernd Haynold Wikimedia Commons.



Figure 108. *Isoperla bilineata*, a common stream moss dweller in the Appalachian Mountains, USA. Photo by Bob Henricks, with permission.





Figure 109. *Simulium tuberosum*, a common inhabitant of bryophytes in Appalachian Mountain streams. Photo by Tom Murray, through Creative Commons.

Heino and Korsu (2008) questioned the species-area concept in aquatic systems, examining rocks and bryophyte cover in two river sites. They found only a weak species-area relationship on stream stones. On the other hand, bryophyte biomass was important both in supporting species richness and in increasing number of individuals of stream macroinvertebrates. They suggested that cover was important in increasing number of individuals and that the species richness was a subsequent passive response. The bryophyte biomass can be expected to increase with time, whereas the area of stones will not. The mechanisms that promote these species-area relationships need to be demonstrated experimentally. These could involve food relationships, sampling methods, niche space, flood disturbance, predation refugia, or flow regime.

### Specificity

Many streams have only one dominant bryophyte, and others have the species intermingled. These conditions complicate any attempts to determine insect preference. Nevertheless, some specificity seems to exist, but keep in mind that it might be a preference of both insect and bryophyte for the same stream conditions. The caddisfly *Rhyacophila* cf. *invaria* (Figure 110) was present in 36% of the collections (Figure 118) of *Platyhypnidium riparioides* (Figure 111) in mid-Appalachian Mountain, USA, streams, but totally absent among *Hygroamblystegium fluviatile* (Figure 112), despite the frequent occurrence of these two mosses in the same streams, often on the same rocks (Glime 1994). *Rhyacophila carolina* (Figure 1) reached its greatest abundance in clumps of the leafy liverwort *Scapania undulata* (Figure 106; Figure 118).

Less distinct preferences occurred in the elm mid beetle larva *Optioservus* sp. (Figure 113; Figure 118) [36% of *Hygroamblystegium fluviatile* (Figure 112), 7% of *Platyhypnidium riparioides* (Figure 111)] (Glime 1994). The stonefly *Pteronarcys proteus* (Figure 114) occurred in 24% of the *H. fluviatile*, 7% of the *P. riparioides*, and never in any of the other species, including *Scapania undulata* (Figure 106), *Fontinalis dalecarlica* (Figure 115), and *Hygrohypnum* spp. (Figure 116) (Figure 118).



Figure 110. *Rhyacophila invaria* larva, a common free-living caddisfly among *Platyhypnidium riparioides* in Appalachian Mountain, USA, streams. Photo by Donald S. Chandler, with permission.



Figure 111. *Platyhypnidium riparioides*, a common moss in Appalachian Mountain, USA streams. Photo by David T. Holyoak, with permission.



Figure 112. *Hygroamblystegium fluviatile*, a common moss for insect fauna in Appalachian Mountain, USA, streams. Photo by Michael Lüth, with permission.





Figure 113. *Optioservus* sp., a common beetle larva among *Hygroamblystegium fluviatile* and *Platyhypnidium riparioides* in Appalachian Mountain, USA, streams. Photo by Arlo Pelegrin, with permission.



Figure 114. *Pteronarcys proteus*, a stonefly that seems to have some selection in bryophytes it will inhabit. Photo by Jason Neuswanger, with permission.



Figure 115. *Fontinalis dalecarlica*, a large moss but that did not house *Pteronarcys proteus* in Appalachian Mountain, USA, streams. Photo by Kristoffer Hylander, with permission.

The liverwort *Scapania undulata* (Figure 106) has a different form from that of any of the mosses. This flattened habit seems to favor the fast-water members of *Simuliidae*, with *Prosimulium hirtipes* (Figure 117) in

58% of the collections and *Simulium tuberosum* (Figure 109) in 75% of the collections (Figure 118) of this liverwort in mid-Appalachian Mountain, USA, streams (Glime 1994). But *S. tuberosum* also occurred in 78% of the *Fontinalis dalecarlica* (Figure 115) collections (Figure 118).



Figure 116. *Hygrohypnum luridum*, a moss that is not suitable habitat for the large *Pteronarcys* in the streams of the Appalachian Mountains, USA. Photo by Michael Lüth, with permission.



Figure 117. *Prosimulium hirtipes*, a common blackfly on the liverwort *Scapania undulata*. Photo by Janice Glime.

Diversity differs little among bryophyte species (Figure 119), although richness can be higher in the larger *Fontinalis* (Figure 115) species (Glime 1968, 1994). *Fontinalis* species are also the only ones that typically house larger insects. *Scapania* (Figure 106), on the other hand, housed the smallest insects in the Appalachian Mountains, USA, streams.



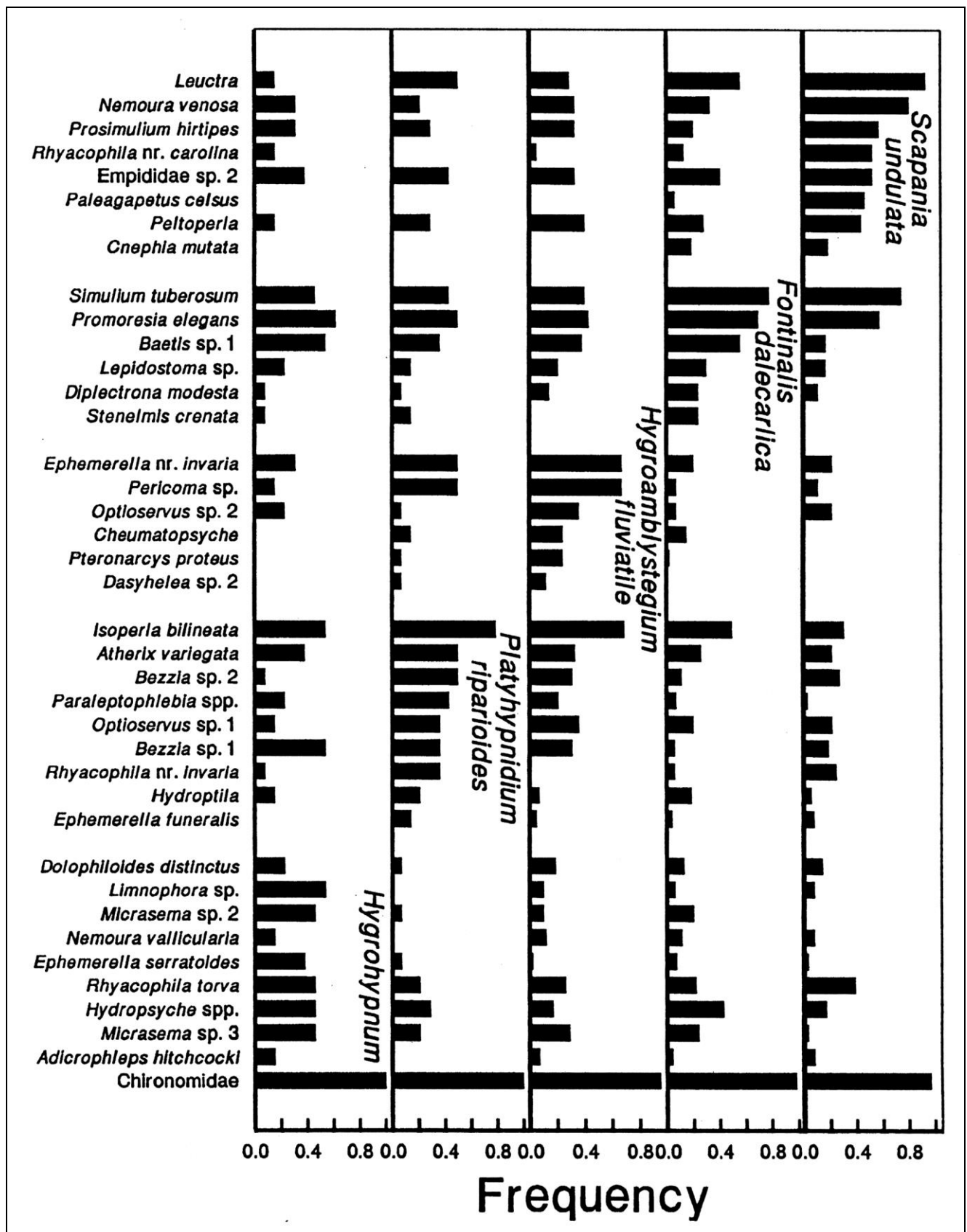


Figure 118. Frequencies of insects on five bryophyte species sampled in 28 streams in the middle Appalachian Mountains, USA. Only insects with at least 10% frequency on at least one species of bryophyte are included. The bryophyte name appears by the group of species that was most abundant on that bryophyte; the name applies to all groups in that frame. From Glime 1994.

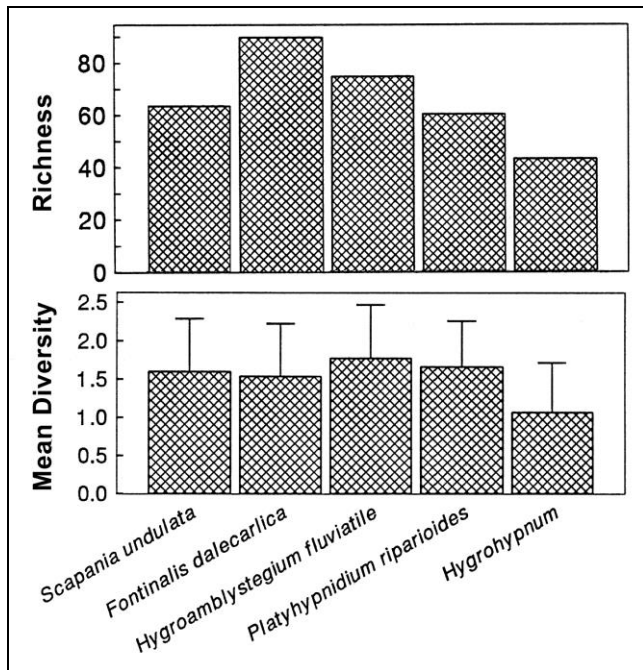


Figure 119. Comparison of mean insect richness and Shannon diversity on a leafy liverwort (*Scapania undulata*) and four species of mosses in 28 mid Appalachian Mountain streams, USA. Redrawn from Glime 1994.

Perhaps the greatest specificity is among some of the case-making caddisflies (**Trichoptera**). Several species in the **Hydroptilidae** make their cases exclusively from bryophytes, including *Palaeagapetus celsus* from leafy liverworts (Flint 1962; Glime 1978, 1994). The flat leaves of *Scapania undulata* seem to be ideal for their method of cutting nearly circular pieces that they cement together for the cases, apparently causing these larvae to live almost exclusively among leafy liverworts (Glime 1978, 1994). Likewise, in the **Brachycentridae** *Adicropheps hitchcocki* (Figure 120) uses bits of *Fontinalis* (Figure 107) leaves or other mosses to construct its cases (Flint 1965; Glime 1994). When it uses *Hygroamblystegium fluviatile* (Figure 112) it may use only costae to make the case, sometimes leaving the ends of the costae dangling from the case (Glime 1994). The **Chironomidae** (Figure 90), as a family, was present in 98-100% of the collections of all species (Figure 118), but these comprised multiple species that could have differed among bryophytes and streams.

The acidity may affect the inhabitants, causing an appearance of bryophyte specificity. Frost (1942) found that the **Plecoptera** and **Coleoptera** were less important in the calcareous stream than in the acid stream, whereas the **Ephemeroptera** and **Trichoptera** reached their greatest density in the more calcareous stream.

### Seasons

One reason for insects to live among bryophytes is to escape the cold of winter. To this end, some insects are more abundant in streams in the winter, but many spend the winter as pupae or eggs.

Thienemann (1912) found that young fauna were especially common among mosses in summer. Seasons can

partition niches, with different sizes of insects occupying different niches. This means that larger members of a genus or family can occupy the same moss clump as younger members of other species in that family feeding group because they have different feeding niches. In some cases this niche partitioning is done by a seasonal migration to a different substrate. Hildrew and Edington (1979; see also Muotka 1990) found that early instars of *Hydropsyche siltalai* (Figure 121) and *H. pellucidula* (Figure 122) occupied the same rocks. However, in spring *H. siltalai* migrates to moss beds, but *H. pellucidula* was totally absent among the mosses at that time.



Figure 120. *Adicropheps hitchcocki* showing case made with *Hygroamblystegium*. Note costae protruding near opening. Photo by Bob Henricks, with permission.



Figure 121. *Hydropsyche siltalai*, a caddisfly larva that moves to moss beds as it gets older, avoiding competition with *H. pellucidula*. Photo by Urmas Kruus, with permission.



Figure 122. *Hydropsyche pellucidula*, a net-spinning caddisfly that avoids niche competition with *H. siltalai* by avoiding moss beds when the latter migrates there. Photo by Niels Sloth, with permission.



In the Appalachian Mountain streams, the total numbers diminish in the winter (Glime 1968), but some insects, like the blackfly *Prosimulium hirtipes* (Figure 51-Figure 53; Figure 123), hatch in late fall and spend the winter in the water, emerging as adults in spring.

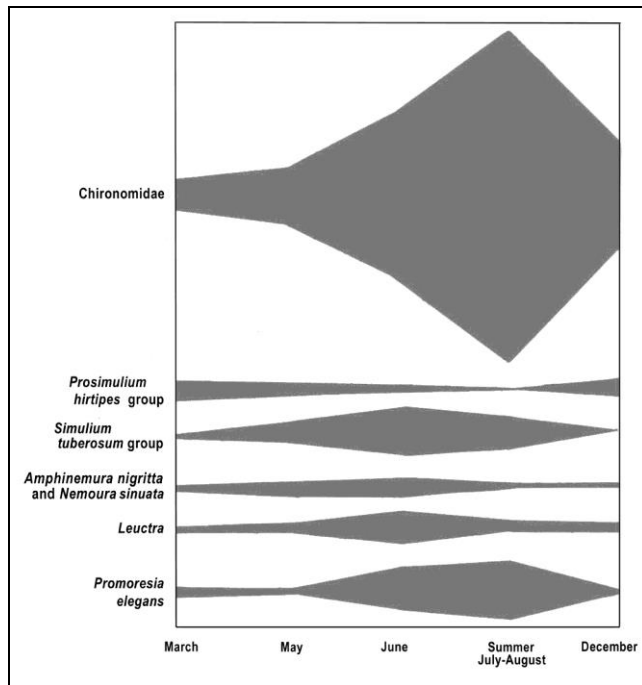


Figure 123. Relative abundance of the six most common insects among bryophytes in five collecting seasons in Appalachian Mountain, USA, streams. Based on Glime 1968.

In these Appalachian streams, counts do not always track diversity and richness (Figure 127; Glime 1994). What is more interesting is that **Shannon diversity** (following Patten 1962) and species richness do not always agree. This may be the result of the differences in counts, which are reflected in the **Shannon diversity**:

$$H' = -\sum_{i=1}^R p_i \log_2 p_i$$

where  $p_i$  = the proportion of individuals belonging to the  $i$ th type, or count of the species divided by total count of all species

$R$  = richness, or total number of species

**Richness**, on the other hand, is simply the number of species present. In these streams, Shannon diversity was highest in March, but richness was highest in July. It is also interesting that these seasonal differences can be different among bryophyte species (Figure 124-Figure 127).

The ever-present **Chironomidae** (Figure 90) often peak among the mosses in winter (Frost 1942), but in the Appalachian Mountain, USA, streams the peak is mid-summer (Figure 123) (Glime 1968). Whitehead (1935) suggested that this might be a behavioral attribute in which the insects seek shelter among the mosses to avoid or respond to the ravages of flooding. But clearly the insects differ among orders, families, and seasons, as seen in these Appalachian Mountain streams (Figure 125-Figure 126).

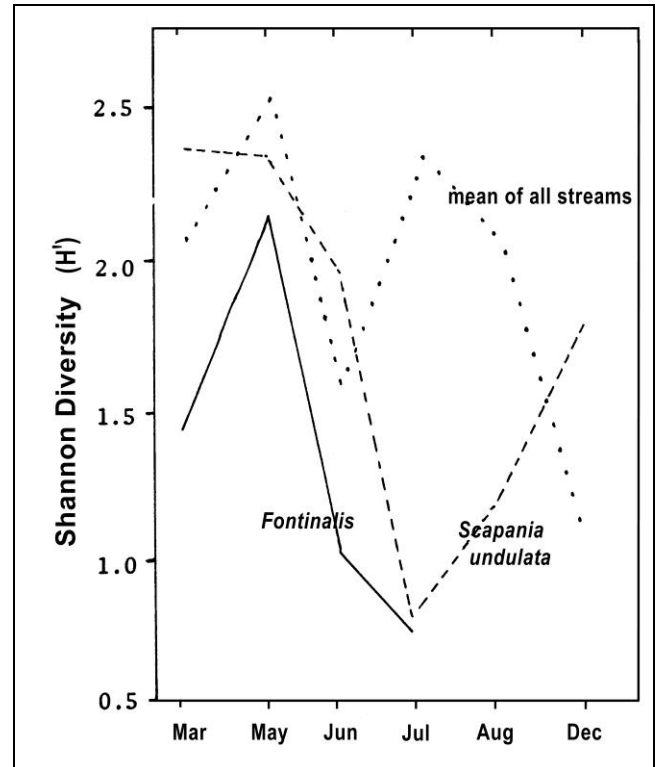


Figure 124. Seasonal changes in species diversity ( $H'$ ) among mosses (*Fontinalis* spp. —) and liverworts (*Scapania undulata* --) in Appalachian Mountain, USA, streams.

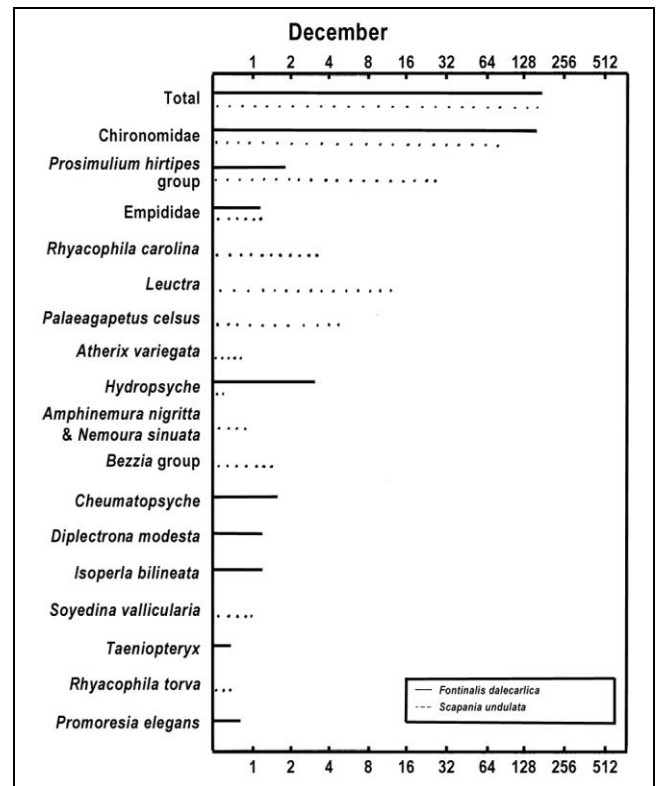


Figure 125. Relative numbers of the most abundant species (>3 occurrences) of insects per gram dry weight of bryophyte in December in Appalachian Mountain, USA, streams. Frequencies appear at right end of each bar. Based on Glime 1968.

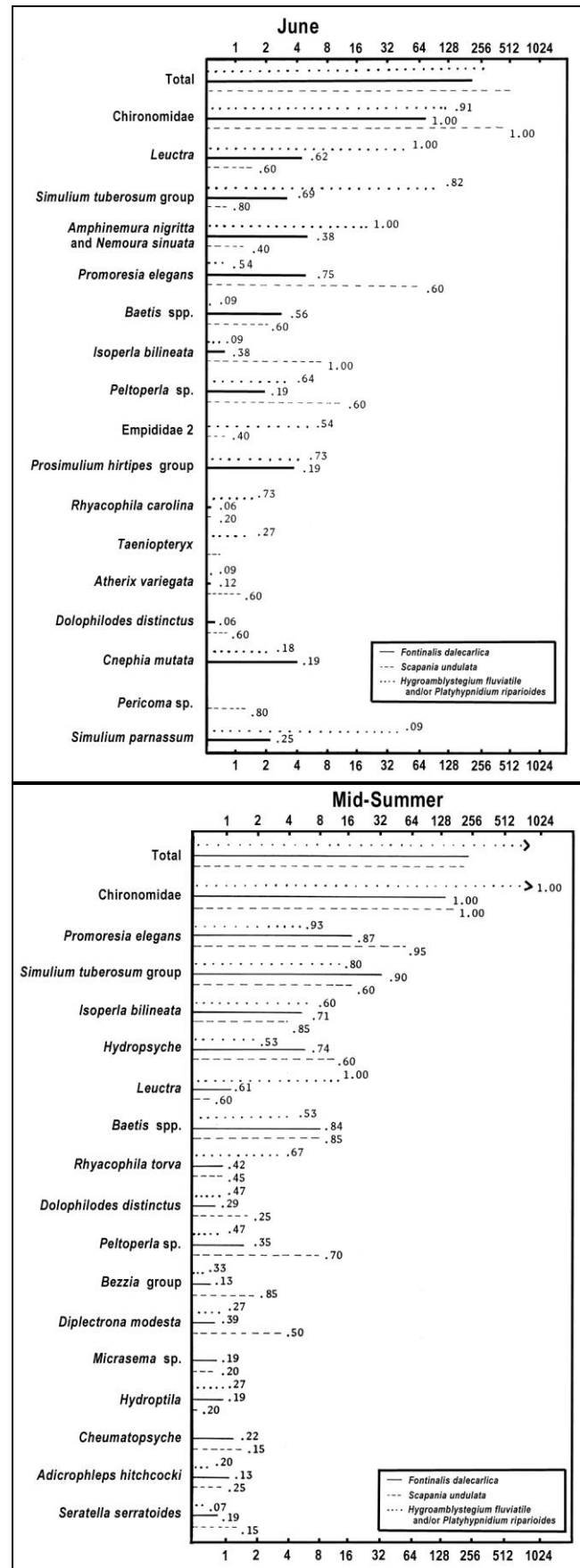
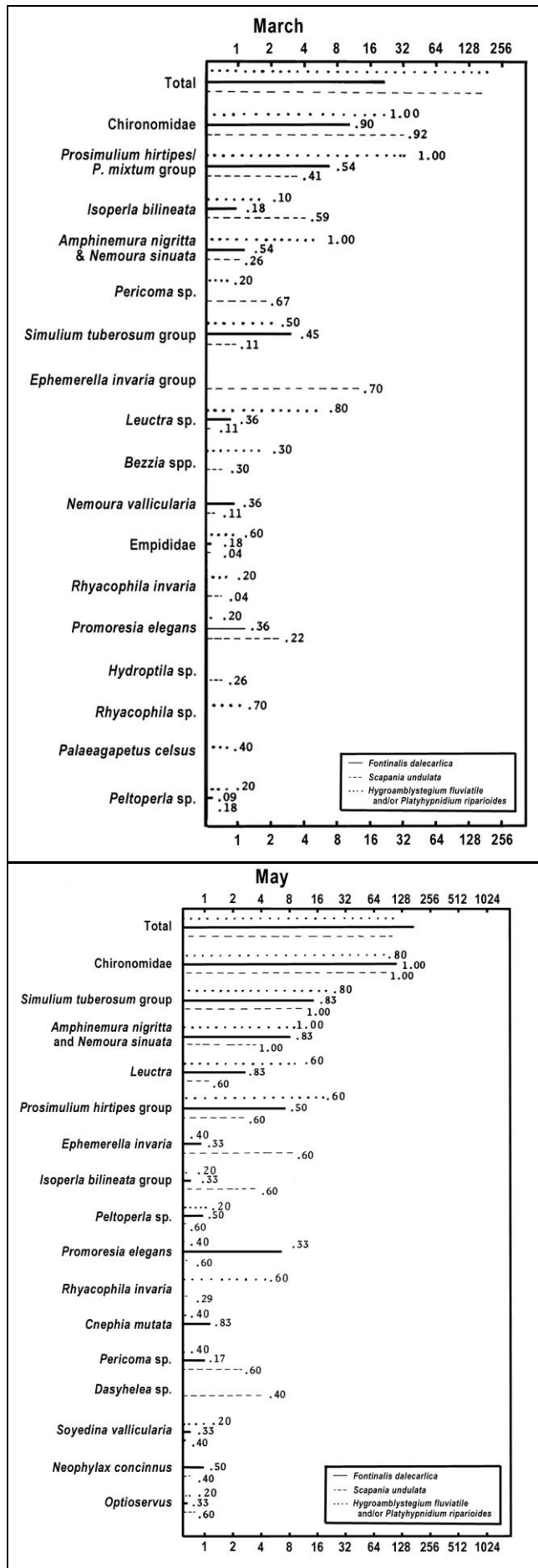


Figure 126. Seasonal relative numbers of the most abundant species (>3 occurrences) of insects per gram dry weight of bryophyte in Appalachian Mountain, USA, streams. Frequencies appear at right end of each bar. Based on Glime 1968.



Table 2. Common genera of bryophyte-dwelling aquatic insects. Numbers refer to references: (1) Percival & Whitehead 1930 (UK); (2) Glime 1994 (Appalachian Mountains, USA); (3) Thienemann 1912 (North Rhine-Westphalia); (4) Suren 1988 (alpine NZ); (5) Muttkowski & Smith 1929 (Yellowstone USA); (6) Frost 1942 (UK); (7) Tada & Satake 1994 (Japan); (8) Krno 1990 (Slovakia). Only studies that included all insect groups are included; note that most studies did not identify genera of the Chironomidae.

<b>COLLEMBOLA</b>	2	<b>Pediciidae – <i>Dicranota</i></b>	3,6
<b>Isotomidae – <i>Isotoma</i></b>	2	<b>Psychodidae – <i>Pericoma</i></b>	2,3,6,8
<b>EPHEMEROPTERA</b>	1,2,3,5,6,7,8	<b>Simuliidae</b>	2,6,7,8
<b>Baetidae</b>	1,2,3,6,7,8	<i>Cnephia</i>	2
<i>Baetis</i>	1,2,3,6,7,8	<i>Odagmia</i>	8
<b>Baetiscidae – <i>Baetisca</i></b>	2	<i>Prosimulium</i>	2,8
<b>Caenidae – <i>Caenis</i></b>	6,8	<i>Simulium</i>	2,6
<b>Ephemerellidae</b>	1,2,5,6,7,8	<b>Tipulidae</b>	1,2,6,7
<i>Drunella</i>	5,7	<i>Hexatoma</i>	1,2
<i>Ephemerella</i>	1,2,6,7,8	<b>Limnobiinae</b>	6
<i>Torleya</i>	8	<i>Limnophora</i>	2
<b>Heptageniidae</b>	1,5,7,8	<i>Tipula</i>	2,6
<i>Cinygmula</i>	7	<b>COLEOPTERA</b>	1,2,3,6,8
<i>Heptagenia</i>	1,5	<b>Dytiscidae – <i>Ilybius</i></b>	2
<i>Rhiithrogena</i>	8	<b>Elmidae</b>	1,2,3,6,8
<i>Stenacron</i>	2	<i>Dubiraphia</i>	2
<b>Leptophlebiidae</b>	2,6,8	<i>Elmis</i>	1,8
<i>Habroleptoides</i>	8	<i>Esolus</i>	3,6
<i>Leptophlebia</i>	6	<i>Limnius</i>	3,6
<i>Paraleptophlebia</i>	2,6	<i>Optioservus</i>	2
<b>ODONATA</b>	2	<i>Promoresia elegans</i>	2
<b>Gomphidae – <i>Gomphus</i></b>	2	<i>Stenelmis crenata</i>	2
<b>PLECOPTERA</b>	1,2,4,5,6,7,8	<b>Gyrinidae – <i>Gyrinus</i></b>	6
<b>Chloroperlidae – <i>Chloroperla</i></b>	6,7	<b>Hydraenidae</b>	3
<i>Chloroperla</i>	6	<i>Hydraena</i>	3
<b>Gripopterygidae</b>	4	<i>Limnebius</i>	3
<i>Zelandobius</i>	4	<b>TRICHOPTERA</b>	1,2,3,5,6,7,8
<i>Zelandoperla</i>	4	<b>Brachycentridae</b>	2,3,7,8
<b>Leuctridae – <i>Leuctra</i></b>	1,2,6,8	<i>Adicrophleps</i>	2
<b>Nemouridae</b>	1,2,4,5,6,7,8	<i>Brachycentrus</i>	5,8
<i>Amphinemura</i>	6,7,8	<i>Micrasema</i>	2,3,7
<i>Nemoura</i>	2,8	<b>Hydropsychidae</b>	1,2,3,8
<i>Protonemura</i>	6,7,8	<i>Arctopsyche</i>	7
<b>Perlidae</b>	5	<i>Cheumatopsyche</i>	2
<i>Acroneuria</i>	5	<i>Diplectrona</i>	2
<b>Perlodidae</b>	2,6,7,8	<i>Hydropsyche</i>	1,2,3,6,8
<i>Megarcys</i>	7	<i>Parapsyche</i>	2
<i>Isoperla</i>	2,6,7,8	<b>Hydroptilidae</b>	1,2
<b>Peltoperlidae – <i>Peltoperla</i></b>	2	<i>Agapetus</i>	1,6
<b>Pteronarcidae – <i>Pteronarcys</i></b>	2,5	<i>Agraylea</i>	2
<b>Taeniopterygidae – <i>Taeniopteryx</i></b>	2,6	<i>Hydroptila</i>	1,2,3,6
<b>HEMIPTERA</b>	2	<i>Ithytrichia</i>	1,2,3,6
<b>Veliidae – <i>Microvelia</i></b>	2	<i>Oxyethira</i>	2,3,6
<b>DIPTERA</b>	1,2,3,4,6,7,8	<i>Paleagapetus</i>	2
<b>Athericidae – <i>Atherix</i></b>	2,3	<b>Leptoceridae – <i>Leptocerus</i></b>	1,6
<b>Ceratopogonidae</b>	2,8	<b>Lepidostomatidae – <i>Lepidostoma</i></b>	1,2,6
<i>Bezzia</i>	2	<b>Limnephilidae</b>	7,8
<i>Dasyhelea</i>	2	<i>Allogamus</i>	8
<b>Chironomidae</b>	1,2,3,4,6,7	<i>Drusus</i>	8
<i>Corynoneura</i>	3	<i>Parachiona</i>	8
<i>Cricotopus</i>	3	<i>Pseudostenophylax</i>	7
<i>Dactylocladius</i>	3	<b>Philopotamidae</b>	1,2,3
<i>Diamesa</i>	3	<i>Chimarra</i>	2,6
<i>Orthocladius</i>	3,7	<i>Dolophiloides</i>	2
<i>Tanytarsus</i>	3	<i>Philopotamus</i>	1,3
<i>Thienemanniella</i>	3	<b>Polycentropodidae – <i>Polycentropus</i></b>	1,2,6
<b>Empididae</b>	2	<b>Psychomyiidae – <i>Psychomyia</i></b>	1,6
<i>Clinocera</i>	6	<b>Rhyacophilidae – <i>Rhyacophila</i></b>	1,2,3,6,7,8
<i>Hemerodromia</i>	6	<b>Uenoidae</b>	2,5
<b>Limoniidae – <i>Antocha</i></b>	7	<i>Neophylax</i>	2
<b>Muscidae – <i>Limnophora</i></b>	1,3,6	<i>Thremma</i>	5

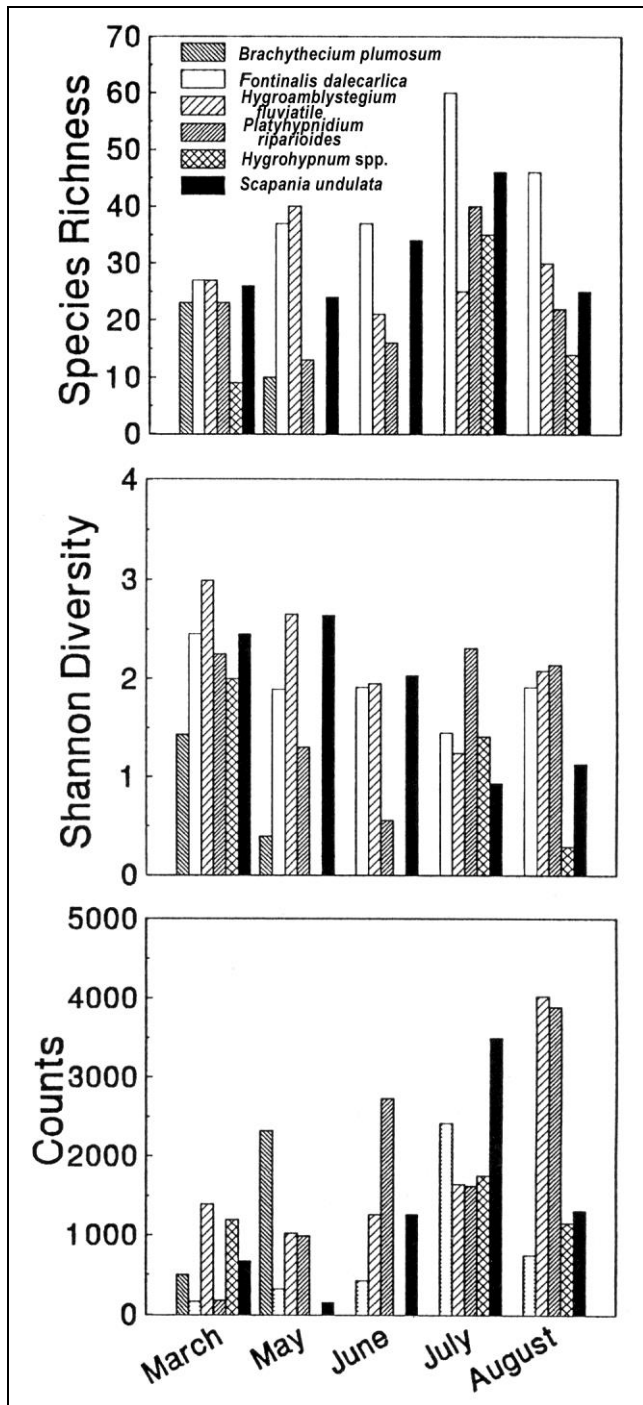


Figure 127. Bryophyte-dwelling insect seasonal richness, species diversity, and counts from handful samples. Redrawn from Glime 1994.

## Sampling

Sampling of the fauna of aquatic bryophytes can be a time-consuming process. And sampling used for most terrestrial or stream habitats can introduce strong biases for these sheltered species.

My own methods were to use hand grabs, then determine the dry weight of the bryophytes after the fauna had been removed. This sampling kept the internal fauna intact, and to test for surface losses, I initially placed a net just downstream from my collections. Very few

invertebrates landed in the net, so I proceeded with my hand collections. These were placed in baby food jars with 95% alcohol and a few drops of glycerine added to prevent predation and decay until the jars reached the lab. I removed the insects with microforceps while systematically searching through a dissecting microscope at 10 X.

Frost (1942) was one the early surveyors of bryophyte fauna. Her sample size was 200 g of wet moss. Kamler (1967) cut 10x10 cm samples under water. Maurer and Brusven (1983) were particularly careful. They surrounded the moss with a nylon organdy net of 250  $\mu$ m mesh while removing the moss from the stream, then used several washes and hand picking to extract the insects.

Armitage (1961) used the modified square foot sampler, similar to the Surber sampler (Figure 128) used by Gurtz and Wallace (1984), to catch insects from rocks, mosses, sticks, and under rubble in streams. However, most bryophyte dwellers are adapted to clinging to the bryophyte and require more than a little disturbance to free them. This leads to underestimates of the bryophyte fauna relative to those among the rubble of the stream bottom and also to species bias. Wulforst (1994) modified this method slightly, using a box sampler to cut a square of 14  $\text{cm}^2$  to sample mosses in an acid stream. The moss samples were quantified by volume using displacement of water in a graduated cylinder.

In his New Zealand studies, Suren (1988) likewise used a Surber sampler (Figure 128) with 100  $\mu$ m mesh to sample 0.01  $\text{sq m}$ . Rocky areas were sampled with a 0.02  $\text{sq m}$  sampler that had a thick foam flange around the bottom to provide a seal with the substrate. Mosses were scraped into the sampler with a razor blade. This method permitted the same area to be sampled in both rock and moss areas.



Figure 128. Surber sampler being used as drift net for winter stream drift sampling. Photo by Janice Glime.



## Preservative

It is important to understand the role of the preservative. Not only does it keep the organisms from decaying and being eaten by cohabitants during the period until the sample can be examined, but it increases the extraction efficiency for flotation techniques (discussed below), at least in a sucrose solution of 1.12 specific gravity (Pask & Costa 1971). In samples preserved for 14 days in 10% formalin compared to those not preserved but examined the same day, the preserved insects had a recovery of 91% whereas those with no preservation had only an 83% recovery rate.

Since any collection of bryophytes will bring significant water with it, it is necessary to use a higher concentration than that used when preserving just insects. I added 95% alcohol to my bryophyte collections (with insects), hoping to achieve a concentration of around 70%.

## Extraction

The least bias in extraction can be achieved by careful hand picking while observing through a dissecting microscope. When I first tried to publish my Ph. D. work, the reviewer wanted to know what method I had used to "estimate" the numbers of **Chironomidae**, which could reach thousands in a single handful of moss. But I had removed and counted every single one of them at 10X magnification! Gurtz and Wallace (1984) also hand-picked invertebrates from the mosses at 7X under a dissecting microscope, using a count per dry weight of moss.

There are simpler and less time-consuming methods for those who don't want to spend three years searching among the bryophytes with a microscope. But, these each have their biases. The Tullgren funnel (Andrew & Rodgers 1999) creates a temperature gradient over the sample, typically with a tungsten light bulb above it. Mobile organisms will move away from the higher temperatures and fall into a collecting vessel with alcohol or mixed preservative. But not all insects move quickly, and some may die from the heat and desiccation before falling to their death in the alcohol below. Furthermore, some will die before reaching the lab due to the reduced oxygen.

Fairchild *et al.* (1987) developed a behavioral method for extracting invertebrates from *Sphagnum* (Figure 91). The method includes a vertical temperature gradient coupled with dissolved oxygen gradients in a column of water containing the *Sphagnum* sample. They determined the overall extraction to be 85% efficient ( $n=4$ ). I do have concerns about bias in the species extracted.

Teskey (1969) developed a method especially for sampling the small flies of the family **Tabanidae**. He used a combination of a specially designed sieve with a multiple Berlese funnel (similar to the Baermann funnel in Figure 129) or by using hand searching to sample these larvae. But to identify the larvae, as in many of the aquatic taxa, they had to be reared to adults. Cochrane (1913) used sieves to collect larvae of *Culicoides furensoides* (Diptera: Ceratopogonidae) from *Sphagnum* (Figure 91).

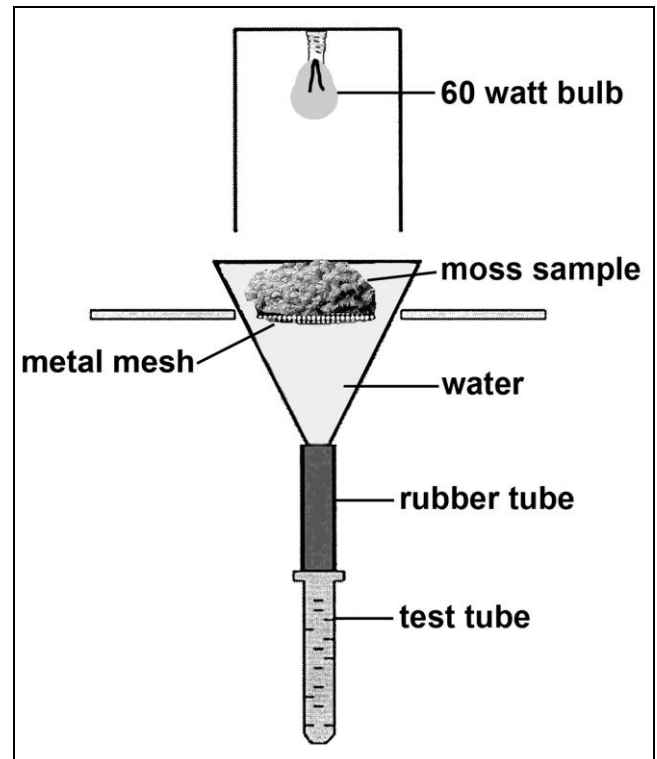


Figure 129. Baermann funnel using moss sample and modified from the Berlese funnel setup, using water instead of air. Modified from Briones 2006.

## Flotation

Any flotation technique requires that the density of the flotation liquid be greater than that of the insects but less than that of the debris (Lackey & May 1971). The 1.12 specific gravity sucrose solution of Pask and Costa (1971) works well in this regard. The kerosene phase separation extracts more total individuals than those extracted by sugar flotation or the Tullgren funnel, particularly more **Acari** (mites) and **Collembola** (springtails) (Andrew & Rodgers 1999).

Fast (1970) pointed out that calling the flotation techniques "flotation" was a misnomer. While the sugar solution is important, many of the organisms remain lodged at leaf bases or caught among the leaves and stems. He preserved samples with 10% formalin. To separate the organisms, he used 360 g sucrose per liter of water and gave the samples only one immersion in the sugar solution. He then sorted at 3.5X magnification. One problem I found with the flotation method was that tiny creatures like the Chironomidae got trapped in the surface tension. They were almost impossible to pick up, so they needed to be trapped on a filter. By the time you have then picked them off the filter, you might as well sort them directly from the moss and learn about their hideouts and spatial relationships at the same time.

Hribar (1990) reviewed ten methods for sampling biting midge larvae. Some of these will work for aquatic bryophytes. Hribar was successful in extracting larvae of **Ceratopogonidae** (*Alluaudomyia*, *Atrichopogon*, *Bezzia*, *Culicoides*, *Dasyhelea*, and *Forcipomyia*) from *Fontinalis*

(Figure 107) and aquatic liverworts by using a Berlese funnel (see Figure 129). He found that sugar flotation and salt flotation provided similar results, but the sugar flotation caused less mortality. Magnesium sulfate is a slower process but results in fewer deaths than salt solutions. Nevertheless, he considered agar extraction and salt flotation to be the most effective for collecting larvae. Sieving, sieving plus salt flotation, and Berlese funnels worked well for mosses.

In short, unbiased sampling to determine numbers of insects living among bryophytes requires time and patience.

## Artificial Mosses

Several researchers have attempted to explain the role of aquatic bryophytes by using artificial mosses. Glime and Clemons (1972) used strips of plastic and bundles of string (Figure 130) as artificial mosses. The plastic permitted colonization by **periphyton** (attached organisms) but lacked the chambering found among mosses; only 13 species occurred on the 33 samples. The string offered a soft substrate with limited chambers; 23 species of aquatic insects occurred on the 35 samples, some of which were not present on the real mosses. The real mosses [*Fontinalis novae-angliae* (Figure 131) & *F. dalecarlica* (Figure 115)] had 25 species among the 46 samples, differing little in overall richness from that of the string mosses. It appeared that density of insects was higher among real mosses, but there was no common base upon which to compare them. It is interesting that the Shannon diversity differed little among the three substrata (1.8 on moss, 1.9 on string, and 1.7 on plastic). Nevertheless, the Shannon diversity (d) on plastic was significantly different from that on mosses or strings. The lack of complexity and smaller surface area of the plastic may have accounted for the limited diversity.



Figure 130. Artificial mosses made of cotton string. Photo by Janice Glime; see Glime & Clemons 1972.

Suren (1988) used nylon twine (5 cm long, 1 mm thick) to weave squares 0.01 m<sup>2</sup> thick with a pore size of 4

mm. He found no differences in the fauna between artificial and real mosses in a New Zealand stream. The artificial mosses even had abundant periphyton growth [especially *Epithemia* (Figure 132) in winter and spring], but their accumulation of detritus and silt was sparse. This perhaps explains the significantly lower numbers of detritus feeders such as **Acarina** (mites), **Collembola** (springtails), **Tardigrada** (water bears), **Dorylaimoidea** (nematodes), and **Ostracoda** (seed shrimp) on the artificial mosses.

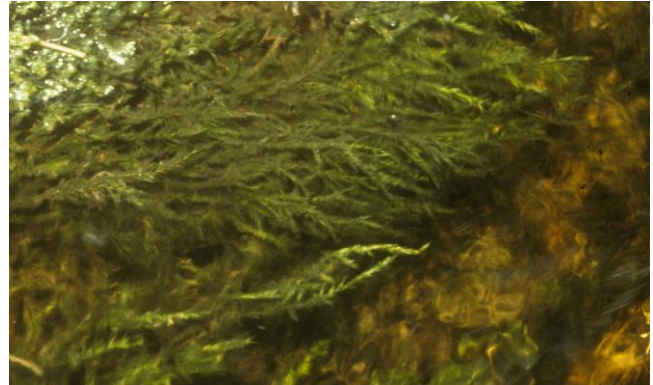


Figure 131. *Fontinalis novae-angliae*, a moss with around 25 species of insects in a New Hampshire, USA, stream. Photo by Janice Glime.



Figure 132. *Epithemia* sp., a common diatom genus on mosses, on a filamentous alga. Photo by Jason Oyadomari, with permission.

## Summary

Aquatic insects are those insects that spend part of their life cycles in the water, usually as a means of escaping the harsher environment on land during one or more seasonal conditions. For most, the immature stages are those requiring such an escape.

Aquatic bryophyte dwellers include the **Collembola** (no longer considered to be insects) that look like miniature adults when born. The **hemimetabolous** insects include the **nymphs** of **Hemiptera** that look like their parents from birth and simply grow larger. The **naiads** of **Ephemeroptera**, **Odonata**, and **Plecoptera** are likewise hemimetabolous, but the naiads often differ from the adults in having gills, different mouth parts, and wing



pads instead of wings. Their life cycle goes from egg/embryo to naiad to adult. The **holometabolous** insects have four distinct stages in the life cycle – **egg/embryo**, **larva**, **pupa**, and **adult**. These orders, among bryophytes, include **Coleoptera**, **Neuroptera**, **Megaloptera**, **Trichoptera**, and **Diptera**. Some have gills as larvae but not as adults.

As an escape from unfavorable conditions, the life cycle stages often respond to environmental cues, including photoperiod, temperature, or available food. Aquatic insects are especially sensitive to temperature, and many of them are in the water for winter to escape the below-freezing temperatures in the terrestrial environment. Some overwinter as dormant eggs or pupae, others as active larvae, naiads, or adults.

Structural adaptations include streamlining, small size, gills, hooks or silk for anchoring, gill covers, and cases or tubes. They move about in the bryophyte clumps to achieve the best oxygen and flow conditions, often leaving as they grow larger. Oxygen may be obtained through gills, cuticle, or a **plastron** that carries an air bubble from the surface or from photosynthesizing plants or algae. Bryophyte dwellers include shredders, gatherers, scrapers, and detritus feeders that prey upon smaller organisms, including periphyton, or eat the detritus gathered by the bryophytes. Some eat the bryophytes. Some make nets to trap food. A few species have a specific requirement for bryophytes for case building, but most simply need a refuge with adequate oxygen, food, and cover.

Sampling is often done with nets, but is best by hand grabs and hand sorting. The faster methods such as nets are commonly used, but they have biases against interior and clinging organisms. Sorting by flotation or Berlese funnels has similar biases. Artificial mosses can sample colonizers but they may not provide the food sources needed and require somewhat lengthy colonization times.

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