

CHAPTER 11-2

AQUATIC INSECTS: BRYOPHYTE ROLES AS HABITATS

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CHAPTER 11-2

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Figure 1. Habitat for stream bryophyte dwellers, Wolf Brook, NY, USA. Photo by Jason Neuswanger, with permission.

Potential Roles

Ulfstrand (1967) astutely stated that aquatic insects select their habitats on the basis of factor combinations. While some minimal levels of factors are important – oxygen, temperature, space, stability – the most important factor determining location within this medley of minimums is usually food. And that food works in two directions: enough food to maintain nutrition and avoidance of becoming food themselves. To satisfy both food factors, Ulfstrand found that substrate is especially important; bryophytes are often important choices among those substrates.

Bryophytes are major components in several types of ecosystems, including peatlands, mountain streams (Figure 1), high latitudes, and boreal forest floor. Many researchers have found that bryophytes are important substrata for insects (Percival & Whitehead 1929). Arnold and Macan (1969) found the greatest species richness and number of individuals among mosses, citing their role as cover and source of food by trapping particles.

Bryophytes, both mosses and liverworts, often form extensive cover in rocky and stony reaches of streams (Macan & Worthington 1951). These can have profound effects on the fauna by providing footholds against the current. Mosses with moderate thickness are suitable for the mayflies *Baetis* (Figure 2) and *Ephemerella* (Figure 3) and **Plecoptera** (stoneflies; Figure 20). Fish benefit as well, with the greatest production of fish-food organisms where there are either rooted plants or mosses. For example, **Chironomidae** (Figure 9) are in greatest numbers among thick mosses. And fish certainly eat **Chironomidae** (Mousavi *et al.* 2002). Based on gut contents, Frost (1939) considered moss-dwelling insects to be an important constituent of the diet of trout (Frost 1939) and young salmon (Frost & Went 1940) in the River Liffey, Ireland. Likewise, Minnows appear to crop the moss fauna (Frost 1942). On the other hand, Brusven *et al.* (1990) found that at least in the daytime when salmonid fish feed, the insects drifting in the moss-covered channel (*Fontinalis neomexicana* – Figure 4) did not provide any greater biomass for fish food than in channels where mosses were absent and insect faunal density was much less. Bowden *et*

al. (1999) likewise questioned whether fish actually benefit from the increased abundance of insects in streams where bryophytes are present, citing a lack of evidence.



Figure 2. *Baetis rhodani* on sand, a mayfly that also lives among mosses. Photo by J. C. Schou, with permission.

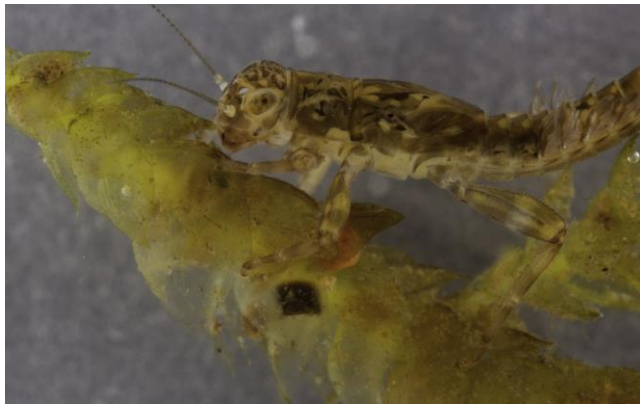


Figure 3. *Ephemerella dorothea* on moss (*Platyhypnidium riparioides*) in Virginia, USA. Photo by D. N. Bennett, with permission.



Figure 4. *Fontinalis neomexicana*, a slightly amphibious species that provides shelter for moss dwellers. Photo by Belinda Lo, through Creative Commons.

I am aware of no study that demonstrates quantitatively that the increase in number of insects in moss mats benefits fish. It appears that insects may have evolved to drift at night precisely to avoid predation by day-feeding

fish. Bryophytes are a difficult place for fish to locate and catch the insects, perhaps reducing the catchable food from what might have been available if rock-dwelling insects were present instead. The hypothesis that bryophyte dwellers increase available fish food needs to be tested.

Corona (2010) suggested that immature insects in streams stayed together because that behavior would increase survival, a concept already suggested for vertebrates by Elgar (1986), Robinette *et al.* (1995), and Brown and Brown (2004). Bryophytes that provide a stable, protected habitat would facilitate such behavior.

Nearly fifty years after Macan and Worthington (1951) expressed the profound contribution of bryophyte-dwelling insects, Bowden *et al.* (1999) summarized that bryophytes "can profoundly influence both the abundance and community structure of stream invertebrates." But they further stated that "the number of fundamentally important roles of bryophytes in stream ecosystems remain unexamined." I will attempt to pull together what various scattered studies around the world have revealed about the roles of stream bryophytes.

Paddling a Kayak to gain first-hand information, Yamamura (2009) observed the adaptations of aquatic insects to various flow regimes in the rivers of Idaho, following up on studies by Rosentreter (1984). In their studies, Yamamura and Rosentreter found that aquatic insects benefit by having aquatic bryophytes because:

1. Bryophytes **decrease stream velocity** on the rock's surface layer.
2. Bryophytes **trap more detritus** (Figure 5; product of disintegration, especially organic matter produced by the decomposition of organisms) than smooth rock (food for shredder insects).
3. Bryophytes provide hiding cover (**refuges**) from predators.
4. Bryophytes provide better background coloration for **camouflage**.
5. Bryophytes provide **greater surface area**, providing a greater amount of habitat area.
6. Bryophytes provide **more food** since algae can grow upon the greater surface area created by the three dimensions of the moss surface.
7. Bryophytes provide greater **algae retention** and protection when stream flow regimes are low enough to create dry surfaces. The bryophytes **retain water longer** than other substrata in the stream, permitting the algae to dry slowly and acclimate to the encroaching desiccation.
8. Perennial bryophytes such as *Scouleria aquatica* (Figure 6) can provide **long-term stability** to an ephemerally dry rock surface, permitting survival of algae, insect larvae, and eggs.

Yamamura (2009) concluded that insect larval data support the interpretation that larvae in spring-fed streams (streams containing aquatic moss) are larger compared to those in runoff-dominated streams (streams that lacked mosses). He concurred with Rosentreter (1984) that spring-fed (mossy) streams have three cohorts present while most run-off (non-mossy) streams have two cohorts. This raises the question, do mosses in runoff-dominated streams benefit insects enough to produce larger larvae and another generation (cohort) per year? Perhaps the insects benefit

from the added cover of bryophytes – insect predators in Idaho streams include other insects, fish, shore birds, and the American dipper. Mosses provide cover in which to hide from all these predators.

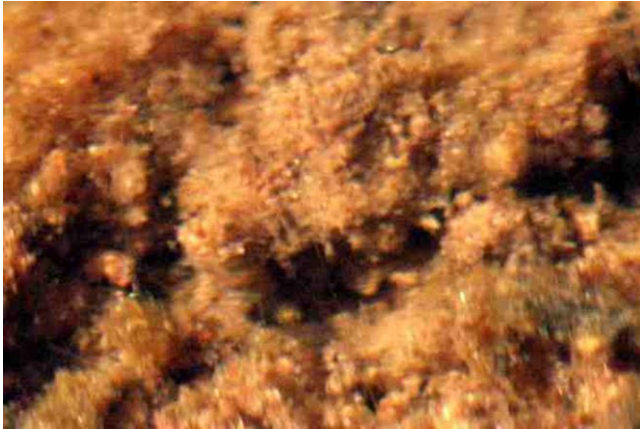


Figure 5. **Detritus**, a common food for aquatic insects and typically accumulated at plant and leaf bases among bryophytes. Photo by James K. Lindsey, with permission.



Figure 6. *Scouleria aquatica* on rock near stream water. Photo by Matt Goff, with permission.

Refuge

Bryophytes serve as refuges in both moving water and lentic systems such as lakes and ponds. In streams, they provide a refuge against the torrents of rapidly flowing water, permitting insects to live where they can take advantage of the higher oxygen and suspended food sources available in flowing water while remaining safely anchored within the moss or clinging to its surface. In both habitats, the bryophyte provides a hiding place from predators, especially fish, but also larger insects, crayfish, and birds.

The importance of bryophyte-dwelling insects as fish food is a subject for speculation. While the bryophytes provide homes for numerous insects, there is no direct evidence that these insects are available as increased fish food. Greig and McIntosh (2008) examined the effect of brown trout (*Salmo trutta*) predation on the caddisfly *Zelandopsycha ingens*, a bryophyte dweller in New Zealand. They determined that these trout can have

positive effects on the size and fecundity of the adult caddisflies by reducing competition among the larvae through predation. The striking revelation of this study was that despite the detritus-based diet of these caddisflies, reduction in the number of larvae still had a positive effect on the adults of the species when compared to those in fishless streams. The adults were larger and the females had 33% more eggs, but the egg size was unchanged. Nevertheless, the increase in number of eggs did not compensate for the loss of larvae.

The study by Greig and McIntosh (2008) suggests that fish have an impact on insects that typically live among the bryophytes, many of whom are detritus feeders. Thus, the bryophyte cover potentially increases the number of insects surviving and the number of adults reproducing, but we are left with the question of whether the bryophytes ultimately produce more available fish food.

Habitat Diversity and Substrate Variability

Habitat diversity offers more niches, hence making the area suitable for more species. Clenaghan *et al.* (1998) identified ecological factors that contribute to macroinvertebrate community composition. Local ecological factors include acidic water, moss, shading, agricultural runoff, longitudinal trends in stream physico-chemistry (distance from headwaters, geology, land use) and season (related to life history patterns of the invertebrates). In their study of a conifer-afforested catchment in Ireland, macroinvertebrate density and richness increased with the distance from the headwaters and the concomitant increases in pH, water hardness, and available nutrients.

Douglas and Lake (1994) demonstrated that habitat diversity was important in increasing species richness in streams. Bryophytes not only add to that diversity, but increase available surface area. Based on a review of the literature, Smith-Cuffney (1987) reported that stream mosses in low order, high elevation streams have a structurally unique community. Measured as respiration rates, the communities among *Fontinalis* (Figure 4) had three times the rates found in the stone community and five times that of the **hyporheic** community. Arnold and Macan (1969) found the largest number of species and individuals of insects inhabited mosses in a Shropshire Hill stream in the UK, where the mosses provided both shelter and trapped food.

Pardo and Armitage (1997) demonstrated the importance of environmental variables in the spatial distribution of aquatic insects based on eight mesohabitats. They found that water velocity and flow dynamics, together with the nature of the substrate were the major determinants of **benthic** (bottom) communities. Heino (2009) looked at the environmental variables somewhat differently, attempting to explain why such things as the influence of altitude varied with geography. He found pH, stream size, and moss cover were the most important variables, with functional diversity increasing with moss cover. These two approaches are not that different, with pH and water velocity both influencing moss cover and moss cover providing safe sites in areas of high flow rates.

Špoljar *et al.* (2012) likewise found that flow velocity and pH had the greatest effect on community structure. In two springs in Papuk Nature Park, Croatia, the

macroinvertebrate taxa numbered only 25. Where the bryophyte cover was dense (90% cover), the community structure was most affected by flow velocity and pH; macroinvertebrate diversity and abundance were higher than in the stream with only 50% bryophyte cover. In the latter stream, algae, protozoa, and **meiofauna** (minute animals living in small spaces in soil or aquatic sediments) reached higher abundance, apparently resulting from suspended organic matter and epiphytes.

Bryophyte communities exemplify the species-area relationship (Gleason 1922). Increased bryophyte cover means an increase in available substrate due to its three-dimensional structure. Heino and Korsu (2008) found a strong relationship between species richness and number of individuals, and both of these were significantly related to the bryophyte biomass. They attributed the relationship to the increased cover provided by greater bryophyte coverage. Heino *et al.* (2005) found that despite the highest congruence between bryophytes and macroinvertebrates among the stream biological groups, that congruence was nevertheless weak. This seems to relate to differences in the stream factors that determine bryophyte locations. Bryophyte diversity followed water color, habitat stability, and stream size, in that order. Macroinvertebrate diversity instead was determined in the order of stream size, water color, and acidity.

Nutrients

Nutrients can affect moss growth in some cases and limit it due to competition for light by encrusting algae in others. In their study of the Kuparuk River, Alaska, USA, Lee and Hershey (2000) found that fertilization with phosphorus increased the growth of mosses (*Hygrohypnum* – Figure 7), but that insects did not respond as extensively as one might expect. Invasion by mosses resulted in an increased density of the mayfly *Ephemera aurivillii* (Figure 8) and **Chironomidae** (midges; Figure 9), but had no effect on densities of the mayfly *Baetis* spp. (Figure 2) or **Simuliidae** (blackflies; Figure 22). Both *Baetis* and *Ephemera* grew larger in fertilized areas, but Lee and Hershey suggested that this was most likely due to the increase in epiphytic diatoms. Only *Ephemera* seemed to be affected by substrate type (bare rock, natural moss, artificial moss), with the greatest densities among the mosses, presumably due to increased habitat complexity. Clenaghan *et al.* (1998) compared several factors and found that mosses were one of the factors explaining the diversity of insects in a catchment stream in Ireland, and that both density and richness increased with moss weight. Voelz and McArthur (2000) likewise concluded that habitat complexity was one of the most important factors in determining species richness in streams.

In my own culturing studies, I have found that enrichment was often detrimental to the mosses. These mosses lost their green color and were covered by algae that presumably intercepted the light – and CO₂. While the bryophytes remained intact, even if dead, this enrichment could benefit the insects by increasing food sources, but such enrichment most likely would make establishment of new mosses or increased coverage by existing ones less likely.



Figure 7. *Hygrohypnum alpinum*, home of many aquatic insects. Photo by Michael Lüth, with permission.



Figure 8. *Ephemera aurivillii* naiad, a species whose density increases when there are mosses. Photo by Tom Murray, through Creative Commons.



Figure 9. **Chironomidae** larva, an insect that increases in abundance when greater moss growth occurs. Photo by Bob Henricks, with permission.

Substrate Size

The biodiversity of macroinvertebrates typically increases linearly with the substrate suitability index [suitability of sediment, **periphyton** (freshwater organisms attached to or clinging to plants, but also used to include other objects projecting above the bottom sediments; *Aufwuchs*), and benthic organic materials] (Duan *et al.* 2009). In large rivers in China (Yangtze River, Yellow River, East River, Juma River), Duan *et al.* found that the macroinvertebrate community was not dependent upon macroclimatic conditions or latitude, but rather responded to the commonality of instream habitat conditions of substrate composition and flow conditions in these rivers.

They found that taxa richness was highest on cobble covered with hydrophytes, high on moss-covered bedrock, and low on clay or cobble where there were no plants. Sandy beds were unstable and thus devoid of benthic macroinvertebrates. As in many stream studies, the EPT insects [**Ephemeroptera** (Figure 8, **Plecoptera** (Figure 20), **Trichoptera** (Figure 13)] dominated the cobble, gravel, and moss-covered bedrock. But contrasting with most stream studies (see Chapter 11-9, Holometabolous Insects – **Diptera**), the **Chironomidae** larvae (Figure 9) reached greatest dominance in the clay beds.

But substrate size apparently does not act alone and importance differs among types of insects (see for example Ulfstrand 1967). Contrasting with other studies, Wise and Molles (1979) found that small substrates supported more insect individuals than did the larger stones. And mixed sizes supported numbers between the small and large sizes.

Stability

I love the expression "A rolling stone gathers no moss," because it so perfectly describes the situation of stability. This expression can be traced to Erasmus' Adagia, first published around 1500, and has since taken on wide usage with somewhat conflicting interpretations. Nevertheless, in the context of a stream, its meaning is clear.

Bryophytes themselves indicate a stable substrate (Yamamura 2009). Such stable areas are present due to stream channel geometry. Rapids can focus the ice scraping at the center of the river, away from the sides where bryophyte populations are able to grow. Hence, some invertebrates may live in those mossy areas simply because they, too, only survive where the substrate is stable and the water has a reduced shearing effect.

Stability is most important for eggs and many pupae that cannot move to a more favorable location when the need arises. Bryophytes will only become well established on stable rocks and boulders, so they signal a stable habitat. Furthermore, as water levels recede, bryophytes maintain water content well beyond the time that a rock can do so, creating a moisture stability. And when the young insects hatch from the eggs, these tiny animals are not only easy prey for larger animals, but they are poor swimmers unable to navigate in the flowing water. The bryophytes provide cover and protection in their small-chambered labyrinth that prevents entry to predators such as fish and large insects and that reduces the flow to near-pool conditions (Glime 1978).

pH Relationships

The **depauperate** (lacking in numbers or variety of species) fauna of some bryophytes may relate more to the preferred habitats of the bryophytes than to the bryophytes themselves. For example, in Wales, Ormerod *et al.* (1987) found that in streams with low pH the bryophytes [liverworts *Scapania undulata* (Figure 10) and *Nardia compressa* (Figure 11)] had few insects; 60% of the *S. undulata* sites had fewer than 20 macroinvertebrate taxa. The pH where Ormerod *et al.* found these liverworts growing was 5.2-5.8. On the other hand, less than 5% of the sites with the red alga *Lemanea* (Figure 12) (pH 5.5-8.5) were so impoverished. In particular, *Hydropsyche*

(Figure 13) was absent at sites with *S. undulata* and *N. compressa*, but present in streams with *Fontinalis squamosa* (Figure 14).



Figure 10. *Scapania undulata*, a leafy liverwort that can serve as food for the mayfly *Ecdyonurus*. Photo by Michael Lüth, with permission.



Figure 11. *Nardia compressa*, a leafy liverwort that can be eaten in some streams by the mayfly *Ecdyonurus* sp. Photo by Des Callaghan, with permission.



Figure 12. *Lemanea* sp. covered with blackflies. Photo by Janice Glime.



Figure 13. *Hydropsyche* larva, a net-spinning caddisfly that frequents *Fontinalis antipyretica* (Figure 18) and *Platyhypnidium riparioides*. Photo by Guillaume Doucet <<http://guillaume.doucet.free.fr/>>, with permission.



Figure 14. *Fontinalis squamosa* above and below water on rocks, home to several stonefly genera. Photo by Janice Glime.

Research by Willoughby and Mappin (1988) suggests that the insect avoidance of the two leafy liverworts that Ormerod *et al.* (1987) observed may not have been a response to pH, but rather the result of the liverwort terpenes and terpene alcohols in the oil bodies. On the other hand, some insects such as the mayfly *Ecdyonurus* (Figure 15) feed on such acid-tolerant bryophytes as *S. undulata* (Figure 10), but are unable to live in the acid streams at the lower end of the pH tolerance range of this liverwort. Ormerod and coworkers (1987) considered that these mayflies are therefore physiologically restricted from acid streams.



Figure 15. *Ecdyonurus venosus* naiad, a mayfly genus in which some members feed on *Scapania undulata* (Figure 10) when the pH is not too low. Photo by Guillaume Doucet <<http://guillaume.doucet.free.fr/>>, with permission.

Other factors may affect the choices of many insects to avoid colonizing these acid-tolerant bryophytes. For example, one possibility that Ormerod *et al.* (1987) considered was that the diatom *Eunotia* (Figure 16) that grows in the leaf axils of leafy liverworts (acid-loving) is inaccessible to grazing *Baetis* (Figure 2), whereas the diatom *Cocconeis* (Figure 17) grows on the leaf lamina of the moss *Hygrohypnum* (Figure 7; growing at a higher pH) where it is easily grazed (Sutcliffe *et al.* 1986).



Figure 16. *Eunotia* sp., a diatom that grows in leaf axils of leafy liverworts where *Baetis* is unable to reach it. Photo by Janice Glime.

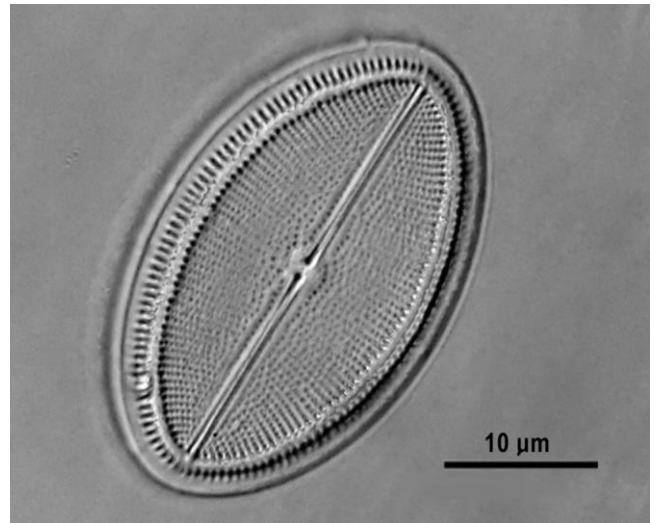


Figure 17. *Cocconeis placentula*, an epiphytic diatom that cements itself to aquatic bryophyte leaves. Photo by Ralf Wagner at <<http://www.dr-ralf-wagner.de/>>, with permission.

Heino (2005) likewise found that functional richness of macroinvertebrates increased with increased pH, with total nitrogen, water color, and substrate particle size also varying with moss cover in 111 boreal headwater streams in Finland. The functional structure depended on these same variables with its dominant pattern being related to increase of shredder-sprawlers and decrease of scraper-swimmers in acidic conditions.

Frost (1942) compared the fauna on the mosses in acid and alkaline streams in her survey of River Liffey, Ireland. *Chironomidae* (Figure 9) constituted 40-54% of the fauna in these streams. In the carboniferous limestone sites,

Fontinalis antipyretica (Figure 18) and *Platyhypnidium riparioides* (Figure 19) dominated in a pH range of 7.4 to 8.4. The stonefly fauna of these mosses was comprised of predominantly *Isoperla* (Figure 20). The dominant caddisfly genus was *Hydropsyche* (Figure 13). Mayflies included *Ephemere*llidae (Figure 8) (mean 533 per sample of 200 g wet weight), *Baetis* (Figure 2), and *Caenis* (Figure 21). The blackfly *Simulium* (Figure 22) was common. In the acid streams (peat bog drainage), the pH ranged 4.4-6.8, and the bryophytes were dominated by *Fontinalis squamosa* (Figure 14) with a small coverage by the leafy liverwort *Scapania undulata* (Figure 10). The stonefly fauna was comprised of *Protonemura* (Figure 104), *Amphinemura* (Figure 105), *Leuctra* (Figure 49), and *Chloroperla* (Figure 23). *Polycentropus* (Figure 24) was the predominant caddisfly.



Figure 18. *Fontinalis antipyretica*, home to the stonefly *Isoperla* and net-spinning caddisfly *Hydropsyche*. Photo by Andrew Spink, with permission.

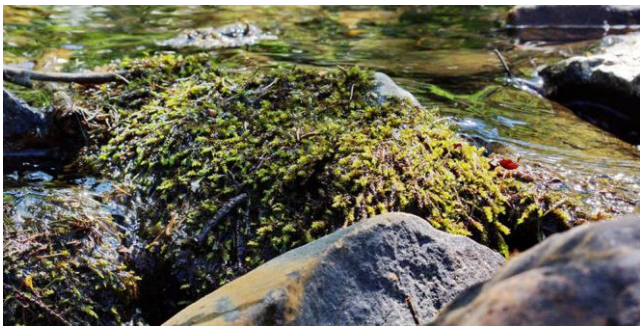


Figure 19. *Platyhypnidium riparioides*, home to the stonefly *Isoperla* and net-spinning caddisfly *Hydropsyche*. Photo by Andrew Spink, with permission.



Figure 20. *Isoperla similis* naiad, member of a genus that inhabits *Fontinalis antipyretica* (Figure 18) and *Platyhypnidium riparioides*. Photo by Donald S. Chandler, with permission.



Figure 21. *Caenis youngi* naiad, member of a genus that sometimes inhabits *Fontinalis antipyretica* (Figure 18) and *Platyhypnidium riparioides*. Photo by Bob Newell, with permission.



Figure 22. *Simulium* (blackfly) larvae showing the large numbers that can occupy one rock – or moss. Photo by F. Christian Thompson, through USDA public domain.



Figure 23. *Chloroperlidae* naiad, a detritus inhabitant, including mosses. Photo by Bob Henricks, with permission.



Figure 24. *Polycentropus* larva, a dominant caddisfly among *Fontinalis* in acid streams. Photo by Jason Neuswanger, with permission.

In a similar study, Willoughby and Mappin (1988) found that growth of the mayfly *Serratella ignita* (Figure 25) was similar when fed on food from acid or alkaline streams. In acid streams they fed on the leafy liverwort *Nardia compressa* (Figure 11) with the filamentous alga *Klebsormidium subtile* (Chlorophyta; see Figure 26), whereas in the alkaline streams they ate the moss *Platyhypnidium riparioides* (Figure 19) with the epiphytic diatom *Cocconeis placentula* (Figure 17). But if the alga *Klebsormidium subtile* was absent in the acid streams, they were unable to subsist on the liverworts alone.



Figure 25. *Serratella ignita* naiad, a mayfly species that can subsist in both acid and alkaline streams, feeding on bryophytes and associated algae. Photo by J. C. Schou, with permission.



Figure 26. *Klebsormidium flaccidum*, a green alga associated with *Nardia compressa* in acid streams, providing food for *Serratella ignita*. Photo by Sarah Kiemle, with permission.

Bryophyte Structure

Not all bryophytes are created equal, despite their frequent treatment as one entity in ecological studies. Their structures can differ greatly, and this has a strong influence on which organisms can live there. This structure is seldom considered in describing the habitat and the influences of the bryophytes on the inhabitants. Let's consider a few and the differences they offer.

Scapania undulata

This is a leafy liverwort whose chemical components of terpenoids have already been mentioned. Its growth form is somewhat layered (Figure 27), and its leaves are **conduplicate** (Figure 28). That is, the leaf is folded over so that the smaller portion is on top. This fold provides a protected area where several small insects such as the stoneflies *Leuctra* (Figure 49) and *Nemoura* (Figure 40) like to hide (Glime 1968). Its layered effect makes it somewhat more open to the water, permitting predators to penetrate more deeply in search of prey, a problem that is avoided by the small insects that can hide within the folds of the leaves.



Figure 27. *Scapania undulata* showing layered effect. Photo by Hermann Schachner, through Creative Commons.



Figure 28. *Scapania undulata* showing folded leaves with smaller lobes on top. Photo by Florent Beck, through Creative Commons.

Hygroamblystegium spp.

This genus, including *Hygroamblystegium fluviatile* and *H. tenax*, forms thick mats on rocks (Figure 29). Its extensive branching provides an array of spaces within the mat, affording protection from both the current and most larger insects and fish. The leaf has a strong costa (Figure 30) that is used by some caddisflies in the construction of their cases (to be discussed later in the **Trichoptera** subchapter). Its small leaves and branches afford small spaces unavailable to larger insects, thus limiting the species and life stages that can live there.



Figure 29. *Hygroamblystegium tenax* in a dry stream bed. Photo by Janice Glime.



Figure 31. *Platyhypnidium riparioides*, home to many kinds of aquatic insects. Photo by Michael Lüth, with permission.



Figure 30. *Hygroamblystegium fluviatile* showing cupped leaves and strong costa used by some caddisflies in construction of their cases. Photo by Hermann Schachner, with permission.

Platyhypnidium riparioides

This species occurs in many of the same streams as those of *Hygroamblystegium fluviatile* (Figure 30). It is a widespread species that forms a chambered mat. It has somewhat larger leaves than *H. fluviatile* but creates a similar habitat with many species in common. It is not unusual to find these two species on the same rock, often intermixed. *Platyhypnidium riparioides* (Figure 31-Figure 32) affords somewhat larger spaces within the mat. Its costa is reduced and much thinner than that of *Hygroamblystegium* species and does not seem to be particularly useful for case building.

Fissidens grandifrons

Fissidens grandifrons (Figure 33) tends to prefer alkaline streams. It is a large moss with flat branches that are layered somewhat like those of *Scapania undulata* (Figure 27-Figure 28), an inhabitant of acid streams. It occurs in very cold water and waterfalls, both conditions that provide it access to more CO₂ than would be available in un-aerated warmer water. I never searched this moss for insects, but my collections of it did not reveal any conspicuous fauna. It is a stiff moss and its preference for torrential water may discourage them.



Figure 32. *Platyhypnidium riparioides*, showing leaves where many kinds of insects are able to hide. Photo by John Hribljan, with permission.

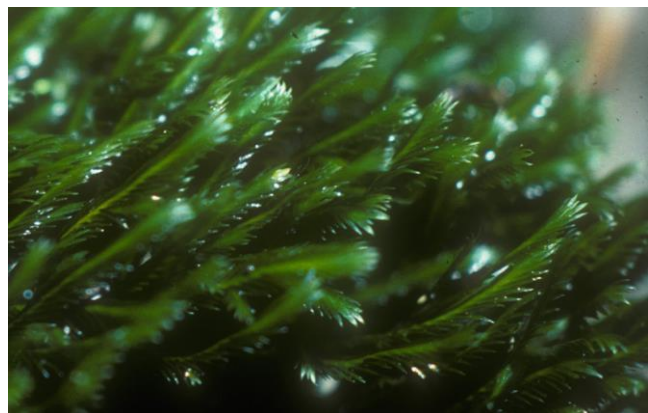


Figure 33. *Fissidens grandifrons* showing the flat branches and accessible spaces between them. Photo by Janice Glime.

***Fontinalis* spp.**

Fontinalis species are large mosses (Figure 34). They have a **streamer** growth form in which all stems dangle in the same direction as the flow of water, at least where there is a distinct flow. The end portions of the stems are

exposed, harboring **Simuliidae**. The leaf structure varies among species, thus providing differing suitability for the insects. *Fontinalis antipyretica* (Figure 35) has large, keeled leaves that form a 3-sided branch with well protected interior space. However, this space may be somewhat difficult for many insects to enter due to the close **appression** (state of being pressed close to) of leaves. *Fontinalis hypnoides* (Figure 36) has narrow, more or less flat leaves that do not provide much enclosed space. In between these two extremes are various degrees of enclosure and access to that enclosure. The flat surface of the branch of *F. antipyretica* would be ideal for blackfly larvae, but this *Fontinalis* species is often not successful in the very fast flow needed by these larvae. If the moss is in fast flow, the keel is easily worn away and the leaves become tattered. However, in cool streams there is usually sufficient oxygen for both the moss and blackflies to survive.



Figure 34. *Fontinalis dalecarlica*, a refuge for invertebrates during low water levels. Photo by Kristoffer Hylander, with permission.



Figure 35. *Fontinalis antipyretica* demonstrating the folded, overlapping leaves that give little accessibility to the interior leaf space. Photo by David T. Holyoak, with permission.

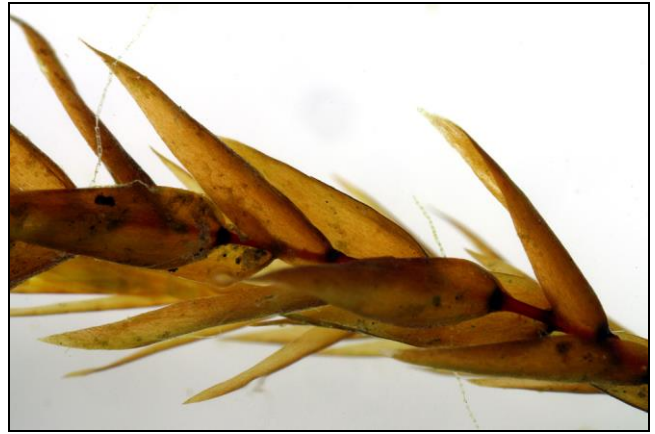


Figure 36. *Fontinalis hypnoides* showing flattened, narrow leaf. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Fontinalis squamosa (Figure 37), a European species, is one of the several intermediate species. Its leaves are concave and provide hiding places within the concavities. Like all *Fontinalis* species, it lacks a costa. This species has been indicated as home to numerous insects in many European stream studies.



Figure 37. *Fontinalis squamosa* showing concave leaves. Photo by Michael Lüth, with permission.

Flow Regimes

Flow regimes provide another limitation for bryophyte inhabitants. Many bryophytes live in areas of high flow that is too abrasive for the establishment of **tracheophytes** (plants with lignified vascular tissue, *i.e.*, all plants that are not bryophytes). At the same time, many insects require protection from the rapid flow. Furthermore, insects drift in streams for various reasons – searching for food, making a false move that puts them in the current, overpopulation, finding a site for pupation, and dislodgment due to changes in flow.

Baker *et al.* (1996) found that the hydraulic stability of streams over multiple years determined whether a site was dominated by periphyton, bryophytes, or tracheophytes. Variations within the year can control periphyton biomass, with low velocities favoring both periphyton and tracheophytes that serve as additional substrate for them. Bryophytes, on the other hand, are often restricted to areas of high velocity; these same high velocities restrict colonization and accumulation of detritus.

Bryophytes modify the internal flow of water. The arrangement of sedimentary deposits and fauna below the leaves of submerged stream bryophytes supports this concept of internal current modification (Devantery 1995). Using *Platyhypnidium riparioides* (Figure 19) and colored liquid, Devantery was able to demonstrate that a single leaf of this moss caused symmetrical twirling behind it. Between the leaves he observed a retrocurrent in the direction of the leaf. This current was slowed progressively and directed the water toward the leaf insertion, explaining the accumulation of detritus there. The same hydrodynamics also occurred in a second species of bryophyte that had a different leaf morphology.

Certain insects take advantage of refugia, especially during periods of high flow (Lancaster & Hildrew 1993). Bryophytes are able to provide such refugia and are likely to be especially important for such species as *Nemurella pictetii* (Figure 38) and larger naiads of *Leuctra nigra* (Figure 39), both stoneflies known from bryophytes. Lancaster and Hildrew found that seasonal flow conditions affected the distribution of these two species in streams after high-flow events, but that these seasonal differences in flow seemed to have little effect on the *Chironomidae* or the young instars (instar is developmental stage between molts of an insect) of *Leuctra nigra*.



Figure 38. *Nemurella pictetii* naiad, a species that uses bryophytes as refugia. Photo by Urmas Kruus, with permission.



Figure 39 *Leuctra nigra* naiad, a species that uses bryophytes as refugia. Photo by J. C. Schou, with permission.

Flow Rates

One possible role of bryophytes as a habitat for insects and other invertebrates is their ability to provide a refuge with multiple current velocities (Madaliński 1961; Elliott 1967a; Gurtz & Wallace 1984; Suren 1992a, b; Glime 1994). Hence, organisms can migrate within the bryophyte mass to locate the current velocity that meets their needs.

Macan and Worthington (1951) suggested that mosses can "profoundly influence the fauna by providing a foothold for animals which otherwise could be swept away by the current."

Devantery (1987) reminds us of the importance of flow in contributing to the accumulation of food resources in the bryophyte mat. With regard to the moss *Platyhypnidium riparioides* (Figure 19), Devantery considers that the moss increases the spatial uniformity, a perspective that seems to be in contrast with those who consider the moss to increase the complexity of the habitat (Dražina *et al.* 2011). The flow serves as an antagonist with the danger that it can dislodge the bryophytes.

Flow rates approaching the bryophytes influence the insects that make those bryophytes home. The *Chironomidae* (Figure 9) are reduced by higher flow velocities associated with *Fontinalis antipyretica* (Figure 18), whereas the smallest of the *Simuliidae* larvae (Figure 22) are positively influenced (Linhart *et al.* 2002a, b). This may relate to available food, with the Simuliidae trapping fine particles with their head fans and *Chironomidae* living among the detritus that has been trapped by the moss.

Overturned Rocks

The famous statement, "a rolling stone gathers no moss," applies in its literal sense as well as the figurative. Bryophytes cannot grow under an overturned rock, and rolling is abrasive, damaging new stems and knocking off older clumps. For stream ecosystems, these dangers prevail. Englund (1991) found that 16.7% of the moss-covered stones in North Swedish woodland streams had been overturned in the last few years. Small stones rarely had mosses (See also Slack & Glime 1985), a factor most likely related to their instability. But when stone size exceeded more than 12 cm, mosses were abundant even on rocks that were not embedded into the substrate.

Englund (1991) experimented on the effects of overturning not only on the mosses, but also on their invertebrate fauna. Overturning, as expected, reduced both diversity and abundance of fauna as well as reducing the dry weight of mosses. Nevertheless, 3 out of 16 invertebrate taxa increased, predominantly on the moss-covered underside. For the remaining taxa, peak densities occurred on the upper moss-covered sides of control stones, and these densities decreased on the overturned stones. Despite the introduction of insects through stream drift (see below), recovery was still weak 14 months later, probably because of the slow recovery of the mosses.

Life History and Flow

For insects living in streams, the habitat is likely to be too fast at times and too dry at others. Yamamura (2009) concluded that the variability of the flow regime can limit the distribution and the life history traits of aquatic insects.

Some have solved this transient habitat problem by life cycle stages that either are dormant or that do not require water. Among these, the egg stage is a suitable stage for surviving drought in some stoneflies, mayflies, and dipterans (Ward 1992). In the case of the stonefly *Nemoura* (s.l.) (Figure 40), a common moss dweller, in a Welsh stream, the adults emerge at the end of the drought (Hynes 1958; Ward 1992). In their short adult life stage,

they may take advantage of newly formed pools in the stream for oviposition before the stream returns to normal flow.



Figure 40. *Nemoura* naiad, a common bryophyte dweller. Photo by Bob Henricks, with permission.

Mosses may often play an important role in providing moist sites for the aquatic insects during fluctuating conditions, but their role at such times has scarcely been investigated. In a Welsh mountain stream, severe flooding transported large quantities of gravel (Hynes 1968). Gravel-dwelling insects were greatly reduced, and the moss cover was reduced by 80%. But the fauna living among the remaining mosses was not significantly decreased. The stoneflies, caddisflies, and **Elmidae** (riffle beetles; Figure 41) recolonized the area before any reproduction could have contributed to their recovery. Hynes hypothesized that these insects migrated to deep within the benthic zone (away from abrasion) during the flood and then reappeared after the water level returned to normal.



Figure 41. **Elmidae** adult, a rapid colonizer of bryophytes. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Water Level

Water level changes bring problems of not only hydration but also food availability for aquatic insects. Open-water carnivores can easily move and will most likely still have access to smaller insects and other

invertebrates for food. But those that feed on periphyton, and most likely on high quality detritus, may depend on the chambered bryophyte clumps for their dinner. Fortunately, these bryophytes help to provide both hydration and food for herbivores and detritus feeders. As the water level decreases, bryophytes can act like a filter to trap detrital matter from the slow water. In a Québec, Canada, stream, Cattaneo *et al.* (2004) found that many of the invertebrates moved to or remained among mosses (*Fontinalis dalecarlica*; Figure 34) at low water levels. Water depth explained 50-80% of the variation in the invertebrate biomass among the mosses and the biomass was lower on shallow mosses that had more frequent exposure. Grazers were more common in the moss habitat than in the gravel, but carnivores such as **Plecoptera** and **Odonata** were in the gravel.

Stream Drift

Stream drift is a natural occurrence among stream fauna, especially insects (Anderson & Lehmkuhl 1968). Waters (1972) emphasized that this is an episodic event and not a continuous phenomenon. The drift organisms are bottom and vegetation organisms. When stream discharge is reduced by seasonal events, **catastrophic drift** can occur. Two primary organisms in such drift in Oregon, USA, are *Simulium* sp. and *Baetis tricaudatus*, both bryophyte dwellers (Corrarino & Brusven 1983).

Catastrophic drift (Minckley 1964) occurs from a physical disturbance such as flooding, **anchor ice** (ice anchored to bottom) (O'Donnell & Churchill 1954), pollution (Coutant 1964), drought, and high temperatures (Wojtalik & Waters 1970; Reisen & Prins 1972 for *Simulium* - Figure 22). **Behavioral drift** occurs at a particular time of day or night; it may result from crowding, competition, need for food, predation, making a new case, or attempting to reach land at emergence time (Waters 1972). **Constant drift** is comprised of small numbers that are always present as organisms move about and become dislodged from their substrates (Waters 1972).

Most drift occurs at night (Bishop 1969; Elliott 1965, 1968; Holt & Waters 1967), and it always moves the drifters downstream, at least initially. This night-time drift typically has two peaks: one just after darkness begins and one just before dawn (Waters 1972). But in some species, younger individuals may drift in the daytime and older, larger individuals at night (Anderson & Lehmkuhl 1968). Light often suppresses drifting in night drifters (Holt & Waters 1967); a full moon on a clear night can suppress it (Anderson 1966; Bishop & Hynes 1969).

Brusven (1970) found that the riffle beetle *Optioservus seriatus* (Figure 42) was much more likely to drift as an adult compared to its larval form. This species demonstrated the complexity of the drift phenomenon, with drift relating closely to density in one stream but not in the other in this study.

Larimore (1974) studied a very different kind of stream in the Salt Fork Basin, Illinois, USA. This stream ran through farmland where farm runoff was common and rooted macrophytes and bryophytes were absent. Only **Chironomidae** (Figure 9) among the drift organisms matched those found in cooler streams with rocky bottoms discussed above.



Figure 42. *Optioservus seriatus* adult, an insect more likely to drift as an adult than as a larva. Photo from ISUInsects.org, through Creative Commons.

Drift distances are usually not far. McLay (1970) found that the maximum drift in a New Zealand stream was 45.7 m, with a mean of only 10.7 m. Waters (1965) found that *Baetis tricaudatus* (Figure 43) travelled 50-60 m, but Elliott (1971a) showed that this strong swimmer was also capable of dropping out of the drift rapidly. Elliott (1967a) found that when dense macrophyte vegetation was present the maximum drift distance was only about 10 m. Nevertheless, this is sufficient to redistribute the insects and reduce local population competition.



Figure 43. *Baetis tricaudatus* naiad, a drifter that can travel 50-60 m in the drift, or drop out rapidly. Photo by Bob Henricks, with permission.

Many of the species enter the drift as young naiads and larvae, permitting them to disperse and to reduce population competition (Anderson 1967; Elliott 1967a, b; Waters 1969). But more frequently it is the larger stages later in the life cycle that enter the drift (Anderson 1967; Elliott 1967a; Müller 1966; Ulfstrand 1968). While drifting permits macroinvertebrates in streams to seek a more favorable location and to colonize new habitats, it poses its own set of threats (Brittain & Eikeland 1988). The insects may fall prey to predatory fish or fail to stop at a favorable habitat before reaching a quiet area of the stream where drift can no longer help them to relocate.

Some insects enter the drift to avoid or escape from predators. In experiments the net-spinning caddisfly *Ceratopsyche bronta* (Figure 44) moved from one area to another in an artificial stream when the predator stonefly *Acroneuria lycorias* (Figure 45) was present (Michael & Culver 1987). However, it did not exhibit the same drift response to the predator megalopteran *Corydalus cornutus* (Figure 46). Michael and Culver suggested that the caddisfly might have been unable to detect the megalopteran.



Figure 44. *Ceratopsyche bronta* larva, an insect that drifts in response to the presence of the predator stonefly *Acroneuria lycorias*. Photo by Bob Henricks, with permission.



Figure 45. *Acroneuria lycorias* naiad, predator on the caddisfly *Ceratopsyche bronta* larvae. Photo by Tom Murray, through Creative Commons.



Figure 46. *Corydalus cornutus* larva, a stream predator. Photo by Alan Cressler, with permission.

Researchers were curious about how the upstream positions got repopulated. Elliott (1971b) marked insects and found that some immature insects were able to move upstream on the stream bottom, especially small naiads of stoneflies and mayflies, small larvae of true flies, and beetle larvae. In winter, upstream movement was about 30% of downstream drift; in spring and summer it fell to only 7-10%. Madsen *et al.* (1973) examined upstream movement in adult mayflies and stoneflies and found that the representative of the common moss-dwelling stonefly genus *Nemoura* (Figure 40) did not move upstream, whereas the mayflies *Caenis rivulorum* (Figure 47), *Baetis rhodani* (Figure 2), *B. vernus* (Figure 48), and *Serratella ignita* (Figure 25) all moved upstream; all three of these mayfly genera are known from bryophytes. Furthermore, females migrated upstream more than males.



Figure 47. *Caenis rivulorum* naiad, a mayfly whose adults move upstream to lay eggs. Photo by Urmas Kruus, with permission.



Figure 48. *Baetis vernus* adult, a species in which females fly upstream to lay eggs. Photo by Walter Pfliegler, with permission.

Elliott (1971a) divided the drift invertebrates into three groups based on their ability to return to a substrate. The first group apparently had no control over their return to a substrate and did so at the same rate as dead organisms. This group included the *Chironomidae* (Figure 9). The second group includes several bryophyte dwellers, including *Leuctra* (Figure 49) and *Simulium* (Figure 22). These insects travelled shorter distances and were able to return to the substrate more quickly than dead ones at low velocities (10-12 cm sec⁻¹) but not at faster velocities (≥ 19 cm sec⁻¹). The third group, which included bryophyte dwellers such as *Serratella ignita* (Figure 25), *Hydropsyche* spp. (Figure 13), and *Baetis rhodani* (Figure 2), returned to the substrate significantly faster and drifted significantly shorter distances at all velocities tested; *Baetis* and *Simulium* are usually the insects with the highest numbers in the drift (Waters 1972). Caddisflies with cases fall out of the drift very quickly.



Figure 49. *Leuctra* sp. naiad. Photo by Guillaume Doucet <<http://guillaume.doucet.free.fr/>>, with permission.

Elliott (2003) examined dispersal in nine genera of aquatic invertebrates, most of which occur among bryophytes. He found that dispersal of invertebrates in the streams was not density dependent. Rather, it was a constant percentage of the initial number of each species. The most rapid dispersers, with 70-91% dispersing within 24 hours, were the carnivores *Perlodes* (Figure 50), *Rhyacophila* (Figure 116), and *Isoperla* (Figure 20), travelling up to 13.5 m per day. *Protonemura* (Figure 104) and *Rithrogena* (Figure 51) exhibited about 50% dispersal within 24 hours and travelled only about 8 m per day. The third group, *Ecdyonurus* (Figure 15), *Hydropsyche* (Figure 13), *Gammarus* (Figure 52), and *Baetis* (Figure 2, Figure 48), only had about 33-40% dispersal in 24 hours and travelled only 5.5-7 m per day. All of these genera dispersed upstream. These examples do not answer the question of why drift, but they suggest that some of that downstream drift is compensated by upstream movement.



Figure 50. *Perlodes microcephala* naiad, a genus in the high dispersing insects of Elliott 2003. Photo by Niels Sloth, with permission.



Figure 51. *Rithrogena impersonata* naiad, a genus with 50% dispersal in 24 hours. Photo by Donald S. Chandler, with permission.



Figure 52. *Gammarus pulex*, a genus in the dispersing invertebrates of Elliott 2003. Photo by Niels Sloth, with permission.

Lehmkuhl (1969) found that the six mayfly species in his study, including the sometimes moss-dweller *Baetis tricaudatus* (Figure 43), were displaced by winter flooding. He found that in these species drift was not related to habitat. Two of the species that were abundant in the riffle areas were scarce in the drift. In the lab, drift rate did not correlate with ability of a species to hold to its substrate.

Lehmkuhl and Anderson (1972) demonstrated that drift of individual species is seasonal. Within the four species of **Ephemeroptera** studied, some species had peak drift in October and others in May. Winter floods accounted for lesser peaks in drift. Periods of low drifting occur when a species is in its egg state, suggesting that life cycle stages are among the determinants of who is drifting.

Some insects enter the drift at the time of emergence, not by choice, but because they must at that time break through the water-air interface and penetrate the surface tension. If there is no suitable emergent rock or vegetation, this becomes a nearly impossible task. Bryophyte-covered rocks can afford a better place to climb out than a smooth rock. However, there is thus far no study to determine if any insect group might seek out bryophytes as opposed to just rocks for this dangerous endeavor.

The behaviors of the *Hydropsyche* spp. (Figure 13) are worthy of note. This net-spinning caddisfly must live near the water surface where it can trap food in its nets (Edington 1968). When released into the water, larvae would swim with side-to-side movements toward the surface (Edington 1965; Elliott 1971a). When the velocity was slow, they returned to the bottom (Elliott 1971a). When they encountered mosses in swift-flowing areas they made "firm contact." It appears that bryophytes may have a role in catching these drifters.

Elliott (1967a) suggested that aquatic plants served as a natural net for drifting insects. Previously Elliott (1965) examined invertebrate drift in a Norwegian mountain stream where bryophytes formed a dense bottom cover. He did not show a direct link between the bryophyte fauna and drift, but did list the dominant insects in both. Using 400 cm² samples, he found *Baetis* sp. (Figure 2), *Simulium* spp. (Figure 22), *Rhyacophila* sp. (Figure 79), **Polycentropidae** (Figure 24), and **Plecoptera** (Figure 49). When he

calculated those insects in the water column above a square meter of bottom at any time, he found that the values were extremely low, although all the insects among the top taxa in the mosses except **Polycentropidae** were also in the drift.

At least some of the bryophyte dwellers are drift organisms, including *Simulium* (Figure 22), *Isoperla* (Figure 20), and *Ephemerella* (s.l.) (Figure 8) (Minshall & Winger 1968). In these three genera, the drift is suppressed by light, including that of a full moon on a clear night. Density may play a role in the number of individuals entering the drift, as in **Capniidae** (Figure 109), *Ephemerella* sp., and *Hydropsyche* sp. (Figure 13) in a South Carolina, USA, stream (Reisen & Prins 1972; see also Waters 1962, 1966). And, to my surprise, Minshall and Winger (1968) found that reductions in flow cause an increase in drift. The latter may relate to the need for a new location to gain suspended food or oxygen. To this end, *Simulium* larvae may drift at least 100 m (Carlsson 1967). Elliott (2002) calculated the rate of drift and found that most of the organisms had a very constant amount of time spent in a drifting event. For *Serratella ignita* (Figure 25) the mean drift time was 28.8 s, whereas for *Baetis rhodani* (Figure 2) it was 9.4 s, the same drift time as for the amphipod *Gammarus pulex* (Figure 52). For the blackfly *Simulium* it was only 6.4 s, with their choice of rapid water accounting for the 100 m drifting they can accomplish.

In Oregon, USA, Anderson and Lehmkuhl (1968) likewise found known moss dwellers in the drift: the mayflies *Paraleptophlebia* (Figure 53) and *Baetis* (Figure 2), the stoneflies *Nemoura* (Figure 40), *Capnia* (Figure 109), and possibly *Leuctra* (Figure 49) (small *Capnia* and *Leuctra* are difficult to distinguish), dipterans **Chironomidae** (Figure 9) and **Simuliidae** (Figure 22). Dendy (1944) likewise found *Baetis*, *Nemoura*, **Simuliidae**, **Chironomidae**, and **Hydropsychidae** (Figure 13) in the drift in a stream in Michigan, USA, but added significant numbers of the mayfly *Ephemerella* (s.l.) (Figure 8) and caddisfly *Brachycentrus americanus* (Figure 54) to those found by Anderson and Lehmkuhl. To these, Reisen and Prins (1972) added the stoneflies *Isogenus* (probably now *Isogenoides*; Figure 55) and *Isoperla* (Figure 20).



Figure 53. *Paraleptophlebia bicornuta* naiad, a moss-dweller genus that enters the drift. Photo by Bob Newell, with permission.



Figure 54. *Brachycentrus americanus* larva, moss dweller that enters the drift. Photo by Donald S. Chandler, with permission.



Figure 55. *Isogenoides frontalis* larva, a moss-dweller that enters the drift. Photo by Donald S. Chandler, with permission.

Bryophytes may provide safe sites for drifting organisms, primarily insects. There is a periodicity in stream drift, with light, even strong moonlight, suppressing activity (Albrecht 1968). Numerous organisms, particularly stoneflies, mayflies, and caddisflies, become detached from their substrate and join the water current (Bishop & Hynes 1969). Diptera are day-active and contribute significant numbers to daytime drift. Lest they travel ultimately to a lake or even the distant sea, these drifting organisms must find a suitable substrate where they can cling against a sometimes raging current. Furthermore, it is during these excursions that they are most visible and vulnerable to predation by birds and especially fish.

Bryophytes would seem to provide an ideal location for regaining their composure and taking a more leisurely approach to locating a suitable settling place. The 3-d surface of the bryophyte provides numerous "handles" for hanging on in the current and gives the insects either an instant home or one that can be traversed while maintaining a safe hold to something permanent. On the other hand, one theory for the cause of drift is to decrease population numbers (Müller 1954; Waters 1961, 1962; Pearson & Franklin 1968; Bishop & Hynes 1969). If such is the case, a rock with both smooth surface area and bryophyte cover

would support such loss by forcing at least some individuals to the smooth rock as the bryophyte itself becomes overpopulated. This would seem to eventually provide a selection factor against those organisms that did not do their nightly foraging among the mossy safe site. Is there really a selection factor involved in moss-seeking behavior?

Glime and Clemons (1972) set out to determine the relative importance of bryophytes in catching such insects and constructed artificial mosses to determine how the new colonizers compared to the organisms in the drift. Clemons (unpubl data; Glime & Clemons 1972) used string mosses to determine the use of substrata similar to mosses as a catching net for drifting organisms and compared this substrate to that of real mosses and Visqueen (polyethylene plastic sheeting) strips. In the 24 hours following the placement of 7 of these artificial mosses, insects were found on the strings. These included the mayfly *Baetis* sp. (Figure 2), stoneflies *Amphinemura nigritta* (= *Nemoura venosa*) (Figure 56) and *Leuctra* sp. (Figure 49), blackflies *Cnephia* sp. (Figure 57) and *Prosimulium mixtum* (Figure 58), midges *Chironomidae* (Figure 9), and the caddisfly *Lepidostoma* sp. (Figure 59) occurring in more than one of the string habitats. The Visqueen strips had a smaller and less diverse fauna. While this experiment provides evidence that insects can settle on such substrates rather quickly from the drift, much more study is needed to determine the importance of bryophytes in providing safety nets for drifting insects. Gurtz and Wallace (1984) found that following a major disturbance that dislodged many of the insects, it was moss-covered rock faces that increased in insect density more than any other substrate. Furthermore, they considered that the mosses may enhance the stability of the substrate on which they reside.



Figure 56. *Amphinemura nigritta* naiad, a rapid bryophyte colonizer. Photo by Donald S. Chandler, with permission.



Figure 57. *Cnephia* adult, a genus that sometimes lives among bryophytes and enters the drift. Photo by Sam Houston, with permission.



Figure 58. *Prosimulium mixtum* larva, a blackfly that lives among bryophytes and enters the drift. Photo by Tom Murray, through Creative Commons.



Figure 59. *Lepidostoma* larva, a drifting caddisfly that sometimes lives among bryophytes. Photo by Jason Neuswanger, with permission.

In alpine streams the drift pattern may differ. Hieber *et al.* (2003) found no night-day differences in these streams. They found that **Chironomidae** (Figure 9) were the dominant drifting organisms, so one might look at this group in alpine streams as creating more food for fish in streams with mosses than in those without.

The complex structure of bryophytes may not only catch drift, but it may also deter stream drift. Holomuzki *et al.* (1999) found that resettlement choices after drifting by hydropsychid caddisfly larvae depended on the complexity of the algal community. Drift entry of hydropsychids due to stonefly predation increased on rocks with a biofilm, but not on rocks with a thick periphyton mat or macroalgae such as *Cladophora* (Figure 60), with drift inversely related to the amount of *Cladophora* on the rocks. Since bryophytes are even more complex in structure, it is reasonable to assume that they reduce drift.



Figure 60. *Cladophora crispata*, a filamentous alga that keeps **Hydropsychidae** from entering the drift in the presence of predatory stoneflies. Photo by Yuuji Tsukii, with permission.

It is interesting that when Perić *et al.* (2014) sampled the invertebrate drift in a moss-rich **karst** (landscape underlain by limestone that has been eroded by dissolution, producing characteristic landforms) stream system, they did not find the **Chironomidae** (Figure 9) (3.9%) to be the most abundant. Rather, the most abundant insects were the beetles in **Elmidae** (Figure 41) (13.2%) and blackflies **Simuliidae** (Figure 58) (12.2%).

So let's revisit the possibility that other bryophyte dwellers besides **Chironomidae** do not enter the drift as readily as insects on other substrates. Brusven *et al.* (1990) found that in a channel of the South Fork Salmon River, Idaho, USA, the 20% moss-covered portion (*Fontinalis neomexicana*, Figure 4) had 1.6-7.2 times the diversity of the moss-free channel and 1.4-6.1 times the biomass. But the mossy portion did not have any greater numbers in the drift than did the moss-free channel. This, however, does not offer us much on which to base a conclusion because the study only included daytime drift. Their drift organisms were more than 50% **Chironomidae** (Figure 9), a group that drifts equally in day and night (Anderson & Lehmkuhl 1968). The implications for fish are that the bryophytes do not benefit them because the food organisms they house do not increase the daytime drift, at least in this one example.

Safe Sites

For many insects, the mosses offer a safe site, a pool-like environment in which they can forage for food without danger of being swept away by rapidly flowing water. Beetles (**Coleoptera**), scuds (*Gammarus*; Figure 52) and mites occupy only sheltered niches and mosses in the Welsh Dee (Badcock 1949). On vertical faces of waterfalls, the dipteran *Limnophora* (Figure 61) can be found only in moss (Badcock 1949).



Figure 61. *Limnophora* larva, sometimes a bryophyte dweller. Photo by Stephen Moore, Landcare Research, NZ, with permission.

In aquatic habitats, fish are a major predator on insects. The result is that fishless lakes have a higher insect species richness and diversity than lakes inhabited by fish, as demonstrated for chironomids (midge larvae) (Mousavi *et al.* 2002). Bryophytes are typically inhabited by many **Chironomidae** (Figure 9) and when present in lakes or streams they can provide safe sites with loads of detrital food.

Several studies have alluded to the possibilities of bryophytes in providing a **refuge**, a location in the stream where the small organisms can escape predation by larger ones. For example, Parker *et al.* (2007) found twice as many insects on *Fontinalis novae-angliae* (Figure 62) as on *Podostemum ceratophyllum* (Figure 62). One possibility is that the insects are avoided because the moss provides an unpalatable location – an **enemy-free space**. Parker *et al.* (2007) remind us that a number of studies have shown that small herbivores that use plants as both a habitat and a food source may be protected by living on hosts that are chemically defended against wood-be insect consumers. Aquatic mosses may be just such safe sites. To test this hypothesis, Parker and coworkers observed the feeding habits of the Canada goose (*Branta canadensis*, Figure 63-Figure 64) and a crayfish (*Procambarus spiculifer*, Figure 65). In a riverine system where both the riverweed *Podostemum ceratophyllum* (Figure 62) and the moss *Fontinalis novae-angliae* (Figure 62) occurred, both animals consumed riverweed in preference to the moss. This was despite the fact that the moss comprised 89% of the plant biomass. At the same time, there were twice as many macroinvertebrates among the mosses as associated with the riverweed. Examination of the moss chemistry revealed the presence of C₁₈ acetylenic acid, octadeca-9,12-dien-6-ynoic acid, a compound that deterred the crayfish from eating it. Some invertebrates, on the other hand, had different connoisseurial preferences; the amphipod *Crangonyx gracilis* (Figure 66) and the isopod *Asellus aquaticus* (Figure 67) rejected the riverweed, but consumed significant quantities of *Fontinalis novae-angliae*. For periphyton-consuming insects, the same chemical deterrents could protect them without affecting their food source.

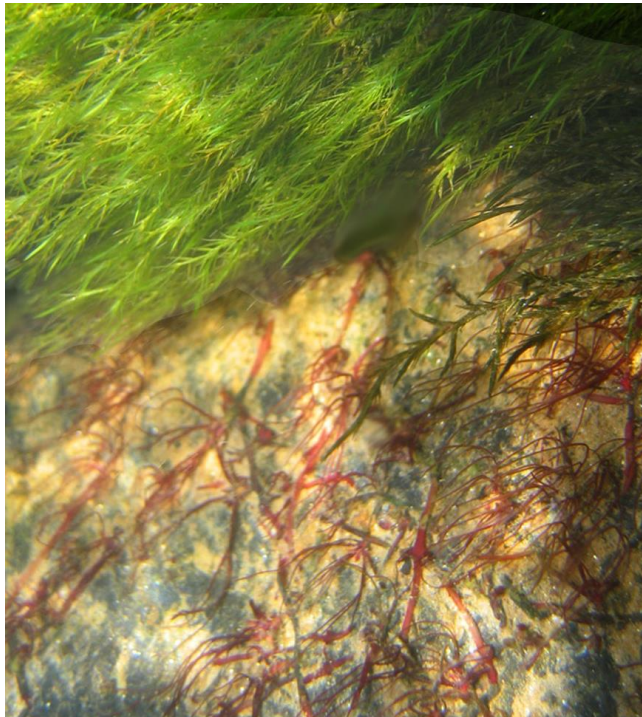


Figure 62. *Podostemum ceratophyllum* (red) and *Fontinalis novae-angliae*, the latter protecting invertebrates from grazing by geese. Photo by John Parker, with permission.



Figure 63. Canada Goose (*Branta canadensis*) searching for food. Photo by Eileen Dumire, with permission.



Figure 64. Canada Geese (*Branta canadensis*) grazing on *Podostemum ceratophyllum*. Photo by John Parker, with permission.

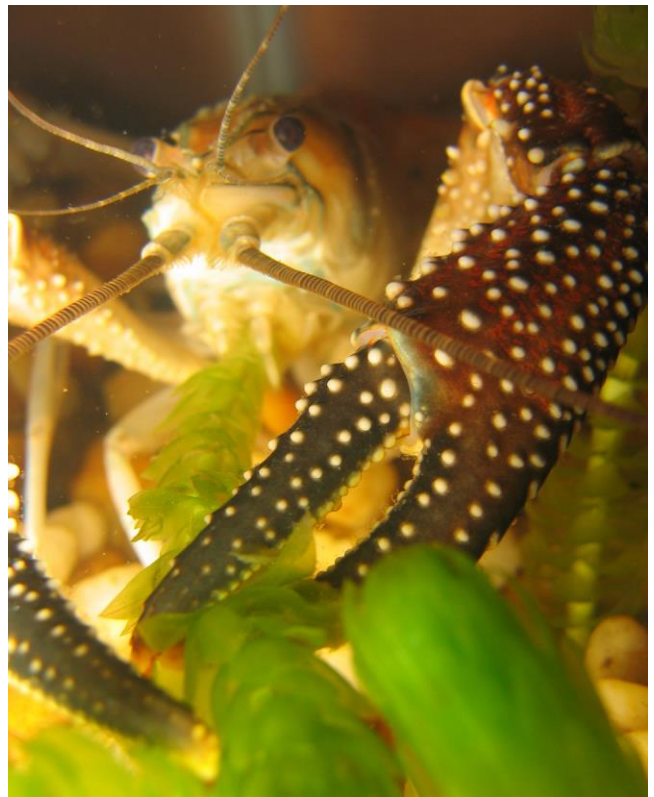


Figure 65. *Procambarus spiculifer* eating *Egeria*. Photo by John Parker, with permission.



Figure 66. *Crangonyx* sp., an amphipod *Fontinalis* consumer. Photo from Biodiversity Institute of Ontario, through Creative Commons.



Figure 67. *Asellus aquaticus*, an isopod *Podostemum* avoider and *Fontinalis* consumer. Photo by Niels Sloth, with permission.

But bryophytes are not always selected for their provision of shelter. Using experimental reduction of bryophyte stem density in New Zealand alpine streams, Suren and Winterbourn (1991b) found that only two out of 22 taxa of invertebrates selected the bryophytic home based on shelter as the primary factor in the shaded site; none of them selected it based primarily on its offer of shelter in the sunny site. Rather, periphyton or detrital biomass were the primary influencing factors.

Winterbottom *et al.* (1997) cleverly tested the importance of refugia against the effect of reduction of shear stress during periods of peak flow by creating artificial refugia using cages of different mesh sizes to restrict the flow within cages. They compared a 1.1 mm mesh size that created a reduced flow within the cage with that of a 15 mm mesh size that did not restrict flow. They found that during periods of high flow the invertebrates accumulated more in the flow-restricted refugia than they did there during low-flow periods or in the unrestricted cages. By contrast, in a second stream with lower flow rates generally and during the experimental period, the number of invertebrates did not increase in the refugia during natural spates of increased flow (but less flow than in the first stream), suggesting that the reduced flow in the 1.1 mm mesh cages enabled them to serve as refugia in the first stream during periods of rapid flow. However, the researchers were unable to determine if the accumulation of invertebrates was by active movement to the refugia or by passive collection. Nevertheless, this experiment

demonstrates that bryophytes with different mesh sizes could provide differential refugia for insects during periods of high flow rates.

Biomass and Richness

Many insects hang out among the riffles, taking advantage of the flowing water that brings food and oxygen. Dodd (2011) found that in a river community 516 out of 521 individuals collected occurred among riffles and mosses. These are the sites where biomass and richness usually reach their peaks.

Clenaghan *et al.* (1998) concluded that macroinvertebrate density and richness increased with moss weight. Wulforst (1994) compared the biomass of insects among mosses with those in the interstitial spaces of the substrate (Figure 68). In general, they were orders of magnitude higher (100's of times) in biomass among the mosses. These included **Ephemeroptera**, **Plecoptera**, **Trichoptera** and **Coleoptera** (EPTC).

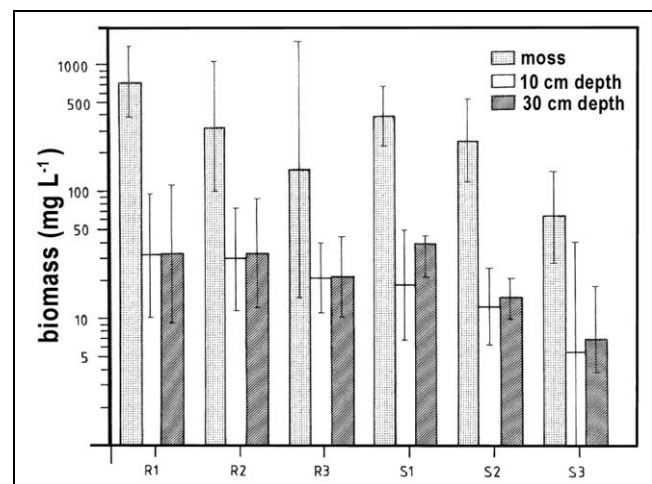


Figure 68. Combined biomass (mg L⁻¹) of **Ephemeroptera**, **Plecoptera**, **Trichoptera**, and **Coleoptera** at six stations of two brooks in the Harz Mountains in mosses and interstitial spaces of the hyporheic zone at 10 and 20 cm depth. Bars show 95% CI. N = 14 for mosses, 28-36 for interstitial spaces. Redrawn from Wulforst 1994.

Linhart *et al.* (2002a, b) examined the **meiobenthos** (meiofauna; between .1 mm and 1 mm in size) of two low-order streams (*i.e.*, small feeder streams) and found that these bryophytes harbored ten times as many organisms as the surrounding mineral bed. In this case, the **Chironomidae** (midge larvae, Figure 9) were the dominant organisms, but a number of other aquatic insects and other invertebrates call this location home, at least in the early stages of their lives.

Brusven *et al.* (1990) studied the effect of bryophyte biomass on macroinvertebrate density in the South Fork of the Salmon River, Idaho, USA. They compared the insect densities on sand, pebbles, cobbles, and the moss *Fontinalis neomexicana* (Figure 4). Insect densities in moss clumps were 4-18 times as great as those in adjacent mineral substrata. Although mosses occupied only 20% of the channel, insect density was 1.6 to 7.2 times as great, with 1.4 to 6.1 times as much insect biomass as the moss-free channel, thus accounting for nearly 50% of the insects in the stream. Midges (**Chironomidae**, Figure 9) typically comprised over 50% of the insect community, whereas

annelids were the primary non-insect invertebrates. The moss seemed to provide a safe site, at least during the day, because despite the greater number of insects present, daytime drift was not greater. Hence, the salmonid fish that feed primarily on drifting invertebrates during the day derive little benefit from the increased numbers in the bryophytes.

On the other hand, Tada and Satake (1994) found that in a cool mountain stream in Japan macroinvertebrates from *Platyhypnidium riparioides* (Figure 19) had 11-13 taxa (species), whereas bare rock bottoms had 13-14. Nevertheless, the caddisfly *Micrasema* sp. (Figure 69) exceeded 100,000 individuals per m² of mosses in November, a level that ranged 2.8-16.3 times as high as that on the bare rock bottom.



Figure 69. *Micrasema charonis* larva, a common genus on bryophytes. Photo by Robert G. Henricks, with permission.

Chantha *et al.* (2000) found that the invertebrate communities of bryophytes and algae in a Quebec, Canada, stream were dominated by **Chironomidae** (especially **Orthocladinae**; Figure 9). The algae and invertebrates formed stable communities during the summer, even sustaining during strong mid-summer flooding. Like many other northern streams, the **Ephemeroptera** and **Coleoptera** were important components. The relative importance of the various taxa changed with the seasons as sizes and life cycle stages changed. Moss biomass explained 43% of the algal spatial variation, but surprisingly the periphyton did not increase proportionally with increase in moss biomass. The epiphytes were less dense per unit of bryophyte biomass as the bryophyte biomass increased in density. Insects in this system became more abundant, but smaller, as the moss biomass increased, with a net result of little change in insect biomass per moss biomass. This may be a function of decreased light for algal growth and decreased oxygen for insects in deeper parts of the moss mat.

Matthaei *et al.* (2006) found that runoff from land use could reduce both aquatic mosses and invertebrate density. The greatest decrease in richness occurred in **Ephemeroptera**, **Plecoptera**, and **Trichoptera**, the three most abundant moss-dwelling orders that move among the open spaces of the bryophyte mats.

Food Sources

Bryophytes harbor a wide variety of invertebrates that can serve as food for the larger members of the bryophyte fauna. Dražina *et al.* (2011) reported 100 taxa of meiofauna among bryophytes in a European study. For example, rotifers averaged 219 individuals per cm³.

Bryophytes are usually predominate in the upper reaches of streams where the flow rate is greater and the stream is shaded. Shredders likewise predominate among the bryophytes in these reaches. Hawkins and Sedell (1981) found that functional groups characterized different stretches of the river continuum. Upstream in shaded reaches the shredders were dominant. Scrapers were most important in the intermediate sections. Collectors increased in importance progressively downstream. Predators were represented equally throughout the stream.

Mosses seem to afford ideal feeding locations for some kinds of insects. In particular, filterers and scrapers can be more common there than elsewhere in streams, showing a positive correlation with such habitats, whereas shredders are negatively correlated, *i.e.*, are moss avoiders (Ely 2005). On the other hand, Zalewski *et al.* (2001) found a significant correlation between **CPOM** (coarse particulate organic matter), bryophytes, and shredders. Smith-Cuffney (1987) found that mosses in streams of a clearcut community supported collector-gatherers, whereas in the forested streams the shredders formed a much larger proportion of the moss fauna.

Cattaneo *et al.* (2004) found that in a Québec stream grazers were more abundant in mosses than among gravel, suggesting that they used the periphyton. The reduction of periphyton when shallow water mosses are exposed may explain why deeper mosses might house more invertebrates.

Wallace *et al.* (1988) found that the mosses retained large amounts of detritus, providing abundant food for collector-gatherers. Like Ely, they found that scrapers reached greatest abundance on cobbles and pebbles that were free of mosses. Smith-Cuffney (1987) found that in a southern Appalachian Mountain stream, mosses in a clearcut community of a forested watershed supported predominantly collector-gatherers with shredders as a minor component. Shredders were a much larger component in the stream that drained the clearcut. Scrapers were more common in the clearcut system where periphyton were abundant. Collector-filterers such as *Parapsyche cardis* (see Figure 70) benefited from the physical environment provided by the mosses.

Although aquatic mosses are seldom eaten by their inhabitants (Haefner & Wallace 1981), they can provide a rich food source through the other inhabitants. Fontaine and Nigh (1983) considered the periphyton (Figure 71) on bryophytes to be an important food source. In New Zealand, periphyton and detritus were primary food sources (Suren 1993). Unfortunately, bryophytes tend to be shade plants and periphyton tends to prefer the sun, so the periphyton is not at its max. Nevertheless, invertebrate densities were higher among mosses containing periphyton than among those with detritus, most likely reflecting the higher food quality of periphyton. Ogbu and Akinya (2001) likewise found that mosses in Nigeria provided a suitable substrate for periphytic algae, especially diatoms.



Figure 70. *Parapsyche apicalis* larva, member of a genus known to seek shelter in bryophytes. Photo by Donald S. Chandler, with permission.



Figure 71. Stream mosses in Tucquan Creek, Lancaster County, Pennsylvania, USA, laden with a detrital-periphyton complex. It is likely that the schist bedrock is contributing to the light color. Photo by Keith Williams, with permission.

McWilliam-Hughes *et al.* (2009) found *Fontinalis* sp. (Figure 4) abundant in headwater streams and *Drepanocladus* (*s.l.*) sp. (Figure 72) abundant in low-order streams. The scrapers living in low-order streams seemed to depend more on *Fontinalis* as a food source than did scrapers in high-order streams depend on *Drepanocladus* (*s.l.*). They suggested that in low-productivity, nutrient-limited rivers primary consumers might switch to marginal food sources such as bryophytes when more preferred food is limited or unavailable.

The feeding guilds change with the seasons. Habdija *et al.* (2004) found that current velocity and food supply affected the composition of insects inhabiting bryophytes in karst streams. Those inhabiting the bryophytes were predominantly small forms of oligochaetes, **Diptera** (Figure 58), and **Coleoptera** (Figure 41), comprising 64.1-98.7% of the total macroinvertebrate individuals. **Collector-gathers** dominated in spring and summer, whereas in autumn it was **collector-filterers**, and in winter

scrapers reached their maximum. Gregg and Rose (Gregg 1981; Gregg & Rose 1985) found that among the **tracheophytes** (plants with lignified vascular tissue, *i.e.*, all plants that are not bryophytes), shredders, scrapers, and predators were the primary guilds in the autumn and that all guilds had their highest abundances in spring. Bryophytes offer the advantage of being present year-round, and their extensive periphyton growths provide a good winter food source for those insects that remain active in the winter. It is interesting that Gregg found that *Hydropsyche* (Figure 13), *Simulium* (Figure 22), *Baetis tricaudatus* (Figure 43), *Glossosoma velona* (Figure 73), and *Helicopsyche borealis* (Figure 74) avoided macrophytes, whereas all of these genera are known from bryophytes (though *Helicopsyche* is rare there). One problem for these insects was that the tracheophytes reduced the velocity, creating problems for these high-oxygen taxa. The advantage in the presence of tracheophytes seemed to be that of increasing heterogeneity, an advantage also offered by bryophytes.



Figure 72. *Drepanocladus exannulatus*, a less desirable food source than *Fontinalis* for insect scrapers. Photo by Michael Lüth, with permission.



Figure 73. *Glossosoma* sp. larvae, a tracheophyte avoider that lives among bryophytes. Photo by Jason Neuswanger, with permission.



Figure 74. *Helicopsyche* sp. larva & case. *Helicopsyche borealis* avoids tracheophytes, but the genus is known from bryophytes. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Thus, we have seen that the reduced water velocity within a bryophyte mat (Devantery 1987; Suren 1991) makes the bryophytes suitable safe sites not only for insects, but also for the periphyton and detrital food components, as shown in New Zealand (Suren 1991), as well as for the insect prey species, as shown in the North Temperate Zone (Elliott 2005).

Bryophytes as Food

Early reports indicated that bryophytes were ingested, but the food value remained in question. Nevertheless, *Fontinalis* (Figure 4) was found in gut contents (Gaevskaya 1969). Jones (1949, 1950) found *Fontinalis* in the guts of the stoneflies *Amphinemura* (Figure 105), *Chloroperla* (Figure 23), *Dinocras* (Figure 75), *Leuctra* (Figure 49), and *Protonemura* (Figure 104), the mayflies *Ecdyonurus* (Figure 15) and *Ephemerella* (s.l.) (Figure 8), as well as in the caddisflies *Hydropsyche* (Figure 13) and *Philopotamus* and the beetle *Oreodytes* (Figure 76).



Figure 75. *Dinocras cephalotes* naiad, a stonefly genus that eats mosses. Photo by Guillaume Doucet <www.guillaume.doucet@yahoo.fr>, with permission.

Jones (1951) considered *Fontinalis antipyretica* (Figure 18) to be one of the main foods for herbivorous insects in his study of the River Towy, Wales. But Dangles (2002) cautions us against categorizing food habits by

generic or higher levels. In his study of four streams in northeastern France he found that two species in the same genus with very similar mouthparts had different diets, one feeding on bryophytes and the other on detritus, including leaf litter.



Figure 76. *Oreodytes septentrionalis*, a genus including bryophyte consumers. Photo by Brian Eversham, with permission.

Caddisflies *Pycnopsyche guttifera* (Figure 77) and *Philocasca alba* both feed on mosses. In an interesting study, Mutch and Pritchard (1984) found that the late-instar larvae of *Philocasca alba* had significantly higher growth rates if their diet of detritus or leaf litter was supplemented with mosses.



Figure 77. *Pycnopsyche guttifera* larva, a consumer of mosses. Photo by Donald S. Chandler, with permission.

Tada and Satake (1994), working with insects on mats of the moss *Platyhypnidium riparioides* (Figure 19) in a cool mountain stream in Japan, found the mayflies *Baetis* (Figure 43) and *Ephemerella* (s.l.) (Figure 8), the stoneflies *Acroneuria* (Figure 45) and *Isoperla* (Figure 20), and the caddisflies *Micrasema* (Figure 69), *Rhyacophila* (Figure 79), and *Palaeagapetus rotundatus* not only live among the bryophytes, but also feed on the leaves of the leafy liverwort *Chiloscyphus polyanthos* (Figure 78) and *Scapania undulata* (Figure 10). Interestingly, they do not feed on leaves of the moss *Platyhypnidium riparioides*, suggesting the possibility of antifeedant compounds in that species.



Figure 78. *Chiloscyphus polyanthos* in the fluctuating water level zone where several kinds of insects eat the leaves. Photo from <www.aphotofauna.com>, with permission.

Even the free-living carnivore caddisfly *Rhyacophila dorsalis* (Figure 79) apparently eats mosses (Slack 1936). One out of nine had *Fontinalis antipyretica* (Figure 18) leaves in the gut. For the mayfly *Ephemerella* (s.l.) (Figure 8), *Fontinalis* is a common food (Jones 1949). *Ephemerella* (s.l.) feeds on the green alga *Ulothrix* when it is available, but feeds on the ever-present moss when the alga is scarce or absent (Jones 1949). On the other hand, in a different study, Jones (1950) found that beetles and mayflies did not eat *Fontinalis* (Figure 18), but the moss was in the gut of *Chloroperla* (Figure 23), *Leuctra* (Figure 49), *Protonemura* (Figure 104), and *Amphinemura* (Figure 105), all stoneflies, and in the gut of the net-spinning caddisfly *Hydropsyche* (Figure 13) – a genus that traps its food with a net. In addition to using the moss for housing, the caddisfly *Micrasema* (Figure 69) eats mosses and associated periphyton (Chapman & Demory 1963; Decamps & Lafont 1974). Chapman and Demory (1963) found that in its preferred food was *Platyhypnidium riparioides* (Figure 19). It is possible that many insects eat the mosses primarily for their associated periphyton, but for *Micrasema* it appears that the primary target is the mosses themselves. Even the filter-feeding blackflies such as *Simulium tuberosum* (Figure 80) will feed on aquatic mosses (Jones 1949), but we need to check to see if they are really digested.



Figure 79. *Rhyacophila dorsalis* larva, a moss consumer. Photo by Walter Pfliegler, with permission.



Figure 80. *Simulium tuberosum* larva, known to have mosses in its gut. Photo by Tom Murray, through Creative Commons.

Most members of the caddisfly genus *Rhyacophila* (Figure 79) are carnivores, although some of these bryophyte dwellers eat bryophytes. Perhaps more importantly is their ability to hide among the mosses to ambush their prey at dusk and dawn [e.g. *Baetis* (Figure 43), *Gammarus* (Figure 52)]. Elliott (2005) found most of the *Rhyacophila dorsalis* (Figure 79) among clumps of the leafy liverwort *Scapania* (Figure 10) and the mosses *Platyhypnidium riparioides* (Figure 19) and *Fontinalis antipyretica* (Figure 18). Although most of the *Rhyacophila* species are carnivores, most of their guts had fragments of bryophytes, but these appeared to be undigested, exhibiting chlorophyll. Older individuals fed primarily at night and diatoms occurred in 29% of the guts of 4th instars; bryophytes occurred in 25%. However, in the 5th instar, only 9% contained diatoms and 7% contained bryophytes. The *Rhyacophila* larvae would disappear into the moss colony to search for food, then return to the bryophyte surface to eat it. These observations suggest that the bryophytes may have been eaten inadvertently when capturing prey.

The inadvertent consumption of bryophytes by carnivores is a likely occurrence in a number of insects. For example, Jones (1950) found *Fontinalis* (Figure 14) in the guts of *Plecoptera* [*Chloroperla* (Figure 23), *Leuctra* (Figure 49), *Protonemura* (Figure 104), *Amphinemura* (Figure 105)] and *Trichoptera* (*Hydropsyche*, Figure 13), but these could have resulted from bits of the moss mixed in with their typical food. *Hydropsyche* is a filter feeder, spinning its own nets to trap food, but bits of drifting moss may get trapped in the net. Nevertheless, Jones did not find any *Fontinalis* in guts of either *Coleoptera* (beetles) or *Ephemeroptera* (mayflies) in these same collections.

Nutritional and Antifeedant Properties

Few protein values are published for aquatic mosses, so we cannot judge if any relationship to protein content is typical. However, it has been a common view among biologists that mosses are avoided as food because of their low food value, among other reasons. Nevertheless, Winterbourn and co-workers (1986), using C^{13} ratios, found bryophytes to be important sources of carbon for the benthic fauna in two British rivers.

Suren and Winterbourn (1991a) examined the gut contents of 23 invertebrate taxa that dwell among bryophytes in two New Zealand alpine streams. Fourteen of these taxa had bryophytes in the guts, but the researchers found that only the tipulid larvae of *Limonia hudsoni* (Figure 81) and caddisfly larvae *Zelandopsycha ingens* (Figure 82) and *Oeconesus similis* (Figure 83) regularly consumed the bryophytes. They found that the bryophytes contained more refractory and indigestible compounds than other riparian plants and were thus less nutritious for the animals. They suggested that the bryophytes might also contain **antifeedant** compounds (compounds that discourage herbivory). Such compounds do exist in aquatic bryophytes, including *Fontinalis* (Liao 1993; LaCroix 1996). But we must keep in mind that modifications of digestive systems and their pH and enzymes make these "indigestible" foods digestible to some specialists (see discussion in Chapter 10-3 on *Asellus*).



Figure 81. *Limonia* larva; some species are regular consumers of bryophytes. Photo courtesy of State Hygienic Laboratory, University of Iowa, with permission.



Figure 82. *Zelandopsycha* larva & case; some species include bryophytes in their regular diet. Photo by Stephen Moore, Landcare Research, NZ, with permission.

But sometimes the consumed mosses carry with them associated periphyton that might be the real food source, as in *Micrasema* (Figure 69) of the Pyrénées (Decamps & Lafont 1974). Dudley (1988) likewise considered that the real food might be the associated periphyton. Suren (1988) similarly concluded that the mosses were not an important food source, citing the similarity of faunal communities on

artificial mosses that became colonized with periphyton. But separating assimilation of moss tissue vs periphyton is a challenging endeavor.

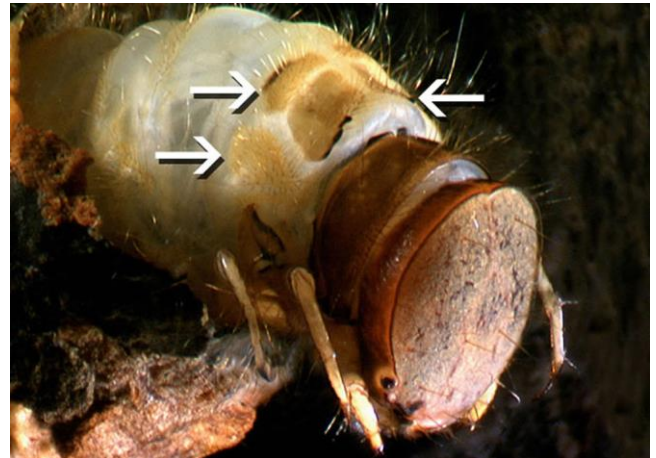


Figure 83. *Oeconesus* larva head; *O. similis* frequently eats bryophytes. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Modern methods have made it somewhat easier to determine the diets of aquatic insects. Using $\Delta^{13}\text{C}$, Winterbourn *et al.* (1986) demonstrated the importance of bryophytes as important food sources. It is surprising that so many invertebrates eat aquatic mosses. Pritchard and Berté (1987) found that the aquatic moss *Leptodictyum* (Figure 84) had the lowest protein content of the five foods tested (wheat flakes, alder, burreed, willow leaves, *Leptodictyum*). Wheat flakes and alder had the most, burreed and willow leaves were next. Nevertheless, Pritchard and Berté (1987) found that despite the low nutritional value in *Leptodictyum*, the caddisfly *Limnephilus externus* (Figure 85) chose mosses second out of the five choices, and the caddisfly *Nemotaulius hostilis* (Figure 86) chose mosses third among these choices. As the larvae grew, they increased their intake of moss, preferring it over alder or willow. Their preference for burreed over moss varied and was sometimes equal. Nevertheless, *N. hostilis* grew more slowly on mosses than on alder or burreed.



Figure 84. *Leptodictyum riparium*, an aquatic moss with lower protein content than several tracheophytes, but still eaten by the caddisfly *Limnephilus externus*. Photo by David T. Holyoak, with permission.



Figure 85. *Limnephilus externus* larvae, consumers of the moss *Leptodictyum*. Photo by Bob Newell, with permission.



Figure 86. *Nemotaulius hostilis* larva in case. This species chooses mosses third compared to tracheophyte choices. Photo by Donald S. Chandler, with permission.

Tracing Bryophytes in the Food Chain

If identification of assimilated bryophytes is a challenge, the identification of the role of bryophytes in the food chain is an even greater challenge. To what degree is the assimilated carbon from bryophytes passed upward to predators and top carnivores? Or is it simply stored in the insect tissues and unavailable to them? Or is it mostly lost through **egestion** (process of ridding the body of undigested or waste material; defecation; not to be confused with elimination of nitrogenous waste such as that in urination)?

Identification of unique acetylenic fatty acids in bryophytes, including *Fontinalis antipyretica* (Figure 18) (Anderson & Gellermann 1975; Dembitsky & Rezanka 1995; Sushchik *et al.* 2007), has enabled us to use these fatty acids as markers. These unique acetylenic fatty acid markers are absent in tracheophytes, algae (*e.g.* Sushchik *et al.* 2007), and bacteria, providing us with a tool to trace bryophytes in their consumers (Dembitsky & Rezanka 1995). When testing five aquatic bryophytes, Dembitsky and Rezanka determined that acetylenic fatty acids occurring in the triacylglycerols of bryophytes comprised from 6.6% of the fatty acids in the moss *Calliergon cordifolium* (Figure 87) to 80.2% in the thallose liverwort *Riccia fluitans* (Figure 88). Identification of these unique acetylenic fatty acids opened the possibility of determining if the bryophytes were actually assimilated into tissues of their consumers (Kalachova *et al.* 2011).



Figure 87. *Calliergon cordifolium*, a moss in which acetylenic fatty acids comprise 6.6% of the triacylglycerols. Photo by Michael Lüth, with permission.



Figure 88. *Riccia fluitans*, a thallose aquatic liverwort that contains 80.2% acetylenic fatty acids in its triacylglycerols. Photo by Jan-Peter Frahm, with permission.

Torres-Ruiz *et al.* (2007) used fatty acid content to identify the food groups eaten by several aquatic invertebrates. They found the aquatic primary producers had a higher EFA content for 18:2 ω 6 and 18:3 ω 3 in green algae, 20:5 ω 3 in diatoms, and 20:4 ω 6 in bryophytes. Furthermore, they identified specific markers for diatoms (20:5 ω 3 [eicosapentaenoic acid], 16:1 ω 7, 16:4 ω 4s, 16C-polyunsaturated FAa [PUFAa]), green algae (18:3 ω 3 [α -linolenic acid], 18:2 ω 6 [linoleic acid], 16C-PUFAB), and bryophytes (20:4 ω 6, 20:3 ω 3), permitting them to identify aquatic primary producers as the primary food source for the moss-dwelling mayfly *Ephemerella* (*s.l.*) (Figure 3, Figure 8) and caddisfly *Hydropsyche* (Figure 13). Gladyshev *et al.* (2012) used stable isotope composition of fatty acids to trace a food web from periphyton and mosses, to consumers, including **Trichoptera**, and finally to the secondary consumer fish, the grayling, in the Yenisei River in Siberia.

Kalacheva *et al.* (2009) and Kalachova *et al.* (2011) used similar logic to determine the use of *Fontinalis antipyretica* (Figure 18) as a food source in the Yenisei River. In addition to the differences among fatty acids listed above by Torres-Ruiz *et al.* (2007), green algae and Cyanobacteria synthesize high amounts of α -linolenic acid

(18:3 ω 3); bacteria synthesize odd-numbered, branched fatty acids (Kalacheva *et al.* 2009; Kalachova *et al.* 2011). Bryophytes differ from these and from tracheophytes not only by having highly specific acetylenic fatty acids, but also the levels in the bryophytes maintain a high level of these fatty acids throughout the year (Kalacheva *et al.* 2009).

Kalacheva *et al.* (2009) used fatty acid and stable isotope analyses in a 4-year study on the food sources of macroinvertebrates in the Yenisei River. Using the highly specific biomarkers of acetylenic acids in *Fontinalis antipyretica* (Figure 18), they determined that the lipids of gammarids, **Ephemeroptera**, **Trichoptera**, and **Chironomidae** (Figure 9) all demonstrated the presence of these acetylenic acids in their fatty acids. In some cases, these were seasonal. For example, the amphipod *Eulimnogammarus viridis* exhibited maximum levels of the *F. antipyretica* biomarker in winter and minimum levels in summer. In particular, *Serratella ignita* (Figure 25) and *S. setigera* had the highest level of acetylenic acids A18 and A20 when analyzed. On the other hand, the **Chironomidae** *Prodiamesa olivacea* (Figure 89) and *Pseudodiamesa branickii* (Figure 90) and **Trichoptera** *Apatania crymophila* (Figure 91) had the lowest. The researchers concluded that for most of the aquatic insects the *Fontinalis antipyretica* in the Yenisei River played only a minor role in assimilation. On the other hand, the aquatic insects seemed to have a more depleted ^{13}C content than the biofilms, an indication that the consumption of *F. antipyretica*, which likewise has a lower $\delta^{13}\text{C}$ value than biofilms, contributed to their assimilation. Although the moss was consumed as a minor supplement year-round, consumption in general increased in winter when food sources such as epilithic biofilms were greatly reduced.



Figure 89. *Prodiamesa* sp. larva. *Prodiamesa olivacea* had low levels of bryophyte-derived acetylenic fatty acids, indicating little or no consumption of bryophytes. Photo by Peter Cranston, with permission.

Kalachova and coworkers (2011) raised the question of whether the moss was consumed directly or transferred up the food pyramid by consumption of invertebrates that had eaten it. They concluded that it was direct consumption because of lack of the marker fatty acids in the invertebrates lower in the food pyramid. Perhaps the most important conclusion is that these mosses were assimilated

into the tissues of the mayfly *Serratella* (Figure 25) species and others, a conclusion that cannot be supported by gut analysis alone. This line of research is worth pursuing further in other systems to determine the importance of bryophytes in the food web.



Figure 90. *Pseudodiamesa branickii*, a species that had low levels of bryophyte-derived acetylenic fatty acids, indicating little or no consumption of bryophytes. Photo from <Benthos.narod.ru>, with online permission.



Figure 91. *Apatania crymophila* larva, a caddisfly with low levels of acetylenic acid. Photo from Omnilexicon, through Creative Commons.

Macroinvertebrates can be flexible in their choices of food. In four acid streams of northeastern France, only 24-36% of the biomass consumed by shredders was comprised of leaf fragments; 44% of their diet was benthic algae and bryophytes (Dangles 2002). Some taxa such as the stonefly *Brachyptera seticornis* (Figure 92) and caddisfly *Chaetopterygopsis maclachlani* (Figure 93), specialized on benthic algae and bryophytes. Even though the caddisfly *Pycnopsyche guttifera* (Figure 77) is a classical shredder, it eats algae and is known to eat even terrestrial mosses (Williams & Williams 1982).



Figure 92. *Brachyptera seticornis* naiad, stonefly that specializes in eating algae and bryophytes. Photo from <<http://www.nebudbaiduzhym.com>>.

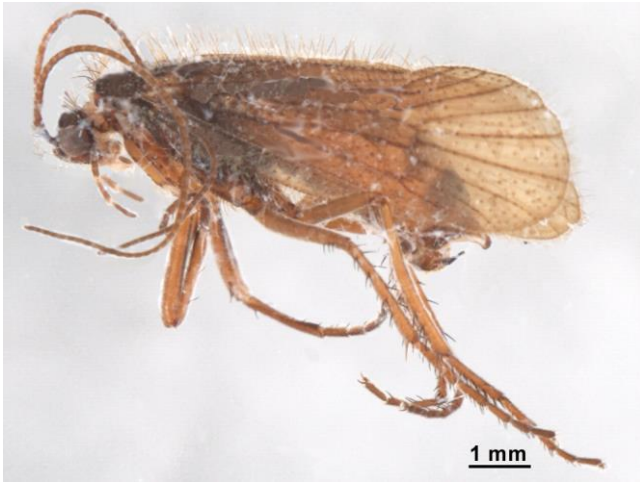


Figure 93. *Chaetopterygopsis maclachlani* adult. The larvae specialize on bryophytes as food. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Few preference experiments have been done with aquatic mosses as a choice. Leberfinger and Bohman (2010) gave detritivores *Limnephilus bipunctatus* (caddisfly, Figure 94) and *Nemoura* sp. (stonefly; Figure 40) the choice of shrubby cinquefoil, birch, Swedish whitebeam, dead and fresh grass, aquatic moss, and algae. Both insects preferred leaves of shrubby cinquefoil; *Nemoura* sp. also ate algae. The dead grass was the least preferred food. The shrubby cinquefoil had the highest nutritional value among the detritus choices. Leberfinger and Bohman considered the high carbon to nitrogen content of the fresh foods to be a contributing factor in their choice.



Figure 94. *Limnephilus bipunctatus* larva in case, a species that preferred aquatic mosses over grass, but less than shrubby cinquefoil. James K. Lindsey, with permission.

The **Tipulidae** (craneflies) are known from both terrestrial and aquatic habitats. In the terrestrial realm they typically live in wet habitats such as cedar swamps. *Tipula oropezoides* (Figure 95) is one such species. And it feeds on both mosses and liverworts. Wyatt and Stoneburner (1989) observed the larvae feeding on the moss *Rhizomnium punctatum* (Figure 96). It would strip the one-cell-thick lamina from the thick costa and leaf borders.



Figure 95. *Tipula* larva, a genus that is common among bryophytes and leaf litter and is known to feed on both mosses and liverworts. Photo by J. C. Jones, through Creative Commons.



Figure 96. *Rhizomnium punctatum*, food for *Tipula oropezoides*. Photo by Jan-Peter Frahm, with permission.

Food when Food Is Scarce

Bryophytes are often considered to be emergency foods for aquatic insects (Dangles 2002; McWilliam-Hughes *et al.* 2009; Kalachova *et al.* 2011). They can be particularly important as a winter food source when other foods become scarce (Kalachova *et al.* 2011). Even within the growing season, the abundance of insects changes and this changes their impact on the bryophytes they consume (Figure 97) (Dangles 2002).

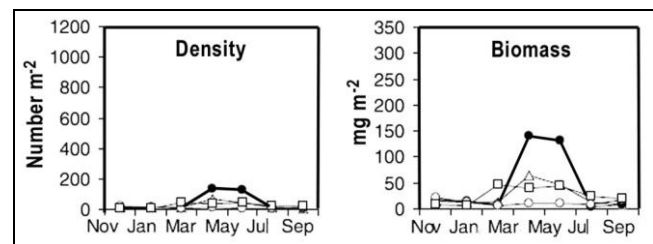


Figure 97. Density and biomass of insect shredders feeding on bryophytes in four streams in four replicate study streams (shown by 4 different symbols and lines) in Vosges Mountains (northeastern France). Modified from Dangles 2002.

Bryophytes can also serve as food in areas of a stream where other food sources are scarce (McWilliam-Hughes *et al.* 2009). Based on $\delta^{13}\text{C}$ values, McWilliam-Hughes and coworkers determined that scrapers in low-order streams were more dependent on *Fontinalis* sp. (Figure 23) than scrapers in high-order streams depended on the *Drepanocladus* sp. (Figure 72) that was dominant there. In fact, 98% of the scraper $\delta^{13}\text{C}$ values were enriched relative to bryophyte $\delta^{13}\text{C}$ values and those two measures correlated well ($r=0.53$). When the values from pool habitats were removed, the correlation increased to $r=0.76$. McWilliam-Hughes and coworkers suggested that in low-productivity rivers, primary consumers might switch to alternative marginal food sources such as *Fontinalis* sp.

Epiphytes and Meiofauna of Bryophytes

In aquatic habitats, bryophytes are typically covered with periphyton. This periphyton coating can serve as food for many kinds of insects. The most common of these are diatoms (Ward 1994; pers. obs.). Amos (1999) found diatoms, desmids, and filamentous algae associated with *Fontinalis* (Figure 62). In New Zealand, Suren (1988) found that as day length increased the mosses were covered with flocculent masses of the diatom *Diatoma* sp. (Figure 98) and the filamentous green alga *Ulothrix* sp. (Figure 99) **Cyanobacteria** included *Placoma* (Figure 100), *Tolypothrix* (Figure 101), and *Chamaesiphon* (Figure 102). Suren (1992b) found that the bryophytes provided an abundant and persistent food source for invertebrates, one that was more stable than that on plain tiles. The bryophytes grew a high biomass of the filamentous diatom *Diatoma hiemale* (Figure 98) in the unshaded site and the crustose diatom *Epithemia sorex* (Figure 103) at the shaded site. The masses of filamentous diatoms were of short duration because they were easily washed away.

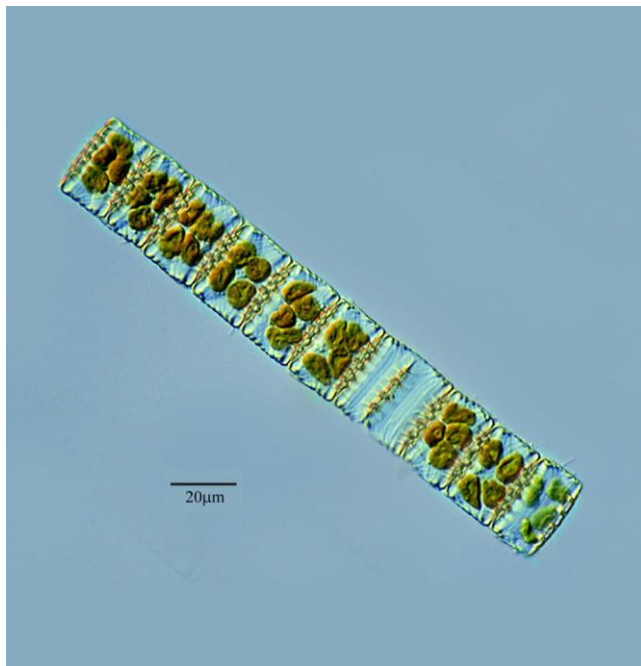


Figure 98. *Diatoma hiemale*, a common diatom on bryophytes at unshaded sites in New Zealand. Photo from Proyecto Agua, with permission.

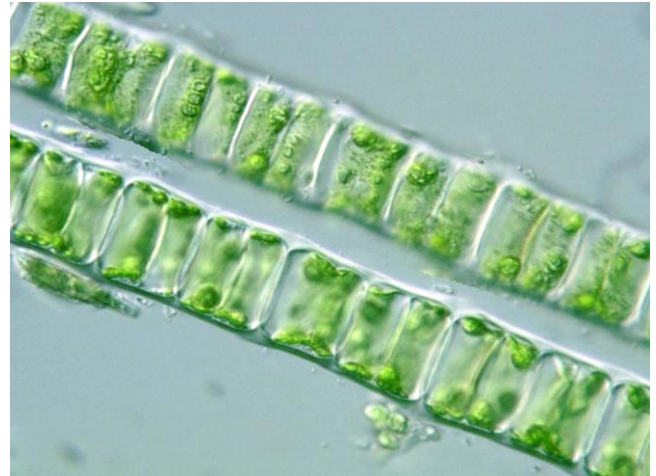


Figure 99. *Ulothrix*, a filamentous green alga that covers stream mosses as days grow longer in spring. Photo by Yuuji Tsukii, with permission.

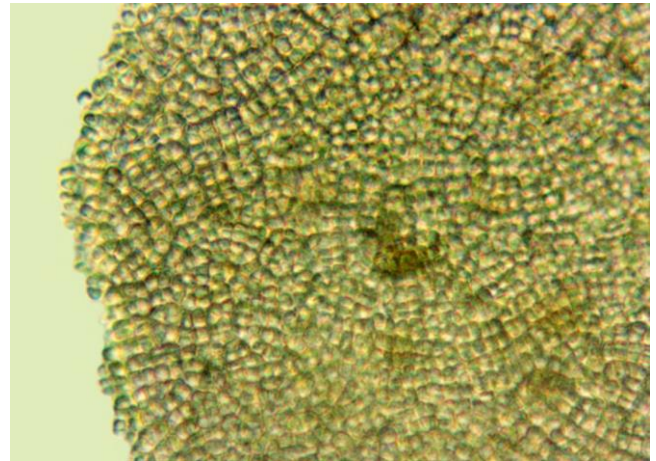


Figure 100. *Placoma* sp., a member of **Cyanobacteria** that covers stream mosses as days grow longer in spring. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 101. *Tolypothrix tenuis*, a member of **Cyanobacteria** that covers stream mosses as days grow longer in spring. Photo by Yuuji Tsukii, with permission.



Figure 102. *Chamaesiphon* sp., member of **Cyanobacteria** that covers stream mosses as days grow longer in spring. Photo by Stephen Moore, Landcare Research, NZ, with permission.

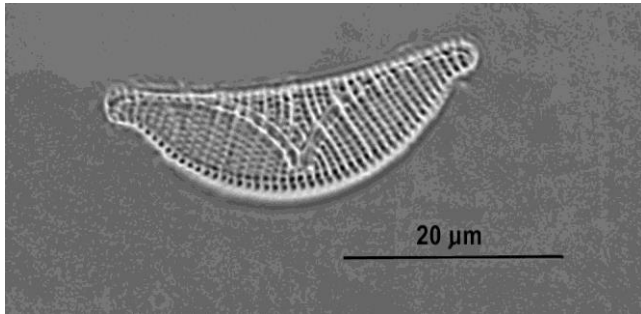


Figure 103. *Epithemia sorex*, a common inhabitant on bryophytes in shaded streams of New Zealand. Note the **puncta** (holes) in the cell wall. Photo by Ralf Wagner, with permission.

Diatoms (**Bacillariophyta**) at first appear to be indigestible boxes with glass shells of SiO_2 . However, Ogilvie and Clifford (1986) reported that insects can digest the cytoplasm of diatoms through the tiny holes (**puncta**; Figure 103) in the cell wall. Diatoms and detritus are important foods for the tiny insect inhabitants of bryophytes. But meiofauna, intolerant of high water velocity (Winner 1975), can also reside there, seeking refuge from the high velocity of water on rocks and other substrata in the area.

As already noted, Chantha *et al.* (2000) found that as the moss biomass increased in a Quebec, Canada, stream, the invertebrates became more abundant but smaller. Clumps of moss with greater depth provided more spaces for invertebrates, but the algae did not increase proportionally, presumably due to diminishing light deeper into the mat. Both the algal biomass (5-fold) and invertebrate density (10-fold) was much greater on mosses compared to the nearby rocks, but the overall invertebrate biomass was similar on these two substrates because of the much greater area of bare rock.

Trapping Detritus

The ability of bryophytes to trap detritus (Butcher 1933; Cowie & Winterbourn 1979; Gurtz & Wallace 1984; Suren & Winterbourn 1992a, b) as well as other food resources (Devantery 1987) undoubtedly plays an important role in feeding many kinds of inhabitants. Bryophytes trap **CPOM** (coarse particulate organic matter), **FPOM** (fine particulate matter), and **UFPOM** (ultra fine particulate organic matter) (Habdija *et al.* 2004). The fine particulate matter may be particularly important for the

meiofauna, including such small insects as the **Chironomidae** (Figure 9) (Aguila-S. 1998). Trapping is possible due to the reduced flow within the bryophyte mat, and this same slower flow provides a refuge from flow for stream insects (Madaliński 1961; Elliott 1967a, b; Gurtz & Wallace 1984; Suren 1992a, b; Glime 1994).

Hury and Wallace (1987) found that in mountain stream areas where bedrock outcrops are covered with mosses, collector-gatherers consume the FPOM (fine particulate organic matter) collected by the moss colony. Some probably also eat the dung that accumulates there from the many inhabitants (Fisher & Gray 1983).

Cherchesova *et al.* (2012) suggested that small and medium stoneflies living among mosses and other locations where **detritus** (Figure 5) is common probably eat detritus. These include *Protonemura aculeata* (see Figure 104), *Amphinemura trialetica* (Figure 105), *Taeniopteryx nebulosa* (Figure 106), *Taeniopteryx caucasica*, *Brachyptera transcaucasica* (see Figure 107), *Chloroperla* sp. (Figure 23), *Nemoura cinerea* (Figure 108), *Capnia nigra* (Figure 109), *Leuctra fusca* (Figure 110), and *Leuctra hippopus* (Figure 111), all in genera that commonly live among mosses.



Figure 104. *Protonemura meyeri* naiad, seen here amid a bed of detritus. Photo by James K. Lindsey, with permission.



Figure 105. *Amphinemura* naiad, a stonefly that blends well with detritus. Photo by Bob Henricks, with permission.



Figure 106. *Taeniopteryx nebulosa* naiad, a detritus dweller. Photo by Niels Sloth, through Creative Commons.



Figure 107. *Brachyptera risi* naiad. Photo by Guillaume Doucet <www.guillaume.doucet.free.fr>, with permission.



Figure 108. *Nemoura cinerea* naiad, a moss and detritus dweller. Photo by James K. Lindsey, with permission.



Figure 109. *Capnia* sp. naiad, a detritus dweller. Photo by Jason Neuswanger, with permission.



Figure 110. *Leuctra fusca*, a probably detritus feeder. Photo by Louis Boumans, through Creative Commons.



Figure 111. *Leuctra hippopus* naiad, a probably detritus feeder. Photo by Niels Sloth, with permission.

Suren (1992b) found that bryophytes increase the periphyton and detritus through increased habitat stability, acting much like debris jams in forested North American streams, but on a micro scale. The variation of periphyton among the bryophytes was much lower than that of plain tiles, suggesting that this food source is more stable than that on rocks. Thus the bryophyte periphyton and detritus provide persistent food sources for the bryophyte inhabitants.

Linhart *et al.* (2002a, b) found that **Chironomidae** (Figure 9) and rotifers responded negatively to flow velocity, but correlated positively with the fine detrital matter trapped within the moss clump. Within *Fontinalis antipyretica* (Figure 18), the amount of trapped fine matter was dependent on the local flow velocity. Egglishaw (1969) found that detritus was the most important factor determining the structure of the community.

The moving waters provide a continuous renewal of organic particles that serve as food items. This permits the filter feeders among the Trichoptera and the Simuliidae to form large populations there (Galdean *et al.* 2001).

Macan and Worthington (1951) found that the fauna on different bryophyte growth forms differed. The not-so-thick moss housed the mayflies *Baetis* (Figure 43) and *Ephemerella* (*s.l.*) (Figure 8), stoneflies, and the scud *Gammarus* (Figure 52). Thick mosses supported great numbers of **Chironomidae** (Figure 9) (75% of the individuals). These mosses support some of the greatest productivity of the fish food organisms.

In Appalachian headwater streams, Wallace *et al.* (1988) found that thick mats of moss on the bedrock were important in retaining large amounts of organic matter. This seemed to account for the 48% collector-gatherers (insects) in the stream with dense mosses compared to 31% in the one with mostly cobbles and pebbles that were free of mosses. Haddija *et al.* (2000) found a positive correlation between flow velocity and the deposition rate of CPOM in moss mats, the location where most of the CPOM was deposited in an alkaline stream. Miliša *et al.* (2006) found similar relationships in the Plitvice Lakes of Croatia.

It is interesting that some folks in the UK have proposed that the increase of aquatic bryophytes downstream of sheep-dip (insecticide & fungicide mix) or heavy metal mines may be evidence that invertebrates are a major factor controlling aquatic bryophyte abundance (Richard Lansdown, Bryonet 13 January 2008). I wonder if the metals, at least, reduce the growth of periphyton, reducing competition and permitting higher productivity among the bryophytes. On the other hand, it is possible that sheep feces provide a food source, as suggested by Fisher and Gray (1983) in regard to macroinvertebrates living in a moss matrix in a desert stream.

Seasonal fluctuations in water level can present a challenge to stream macroinvertebrates. Wood *et al.* (2016) examined the role of trapped organic matter among the inundated clumps of the leafy liverwort *Porella pinnata* in the Middle Oconee River, GA, USA. This liverwort is generally above the water level, but during periods of high flow it becomes inundated. They found a significant increase in macroinvertebrate biomass, insect density, and organic matter among the *P. pinnata* than on adjoining

bare rock. Thus, the presence of bryophytes explained the additional organic matter, insect biomass, and density. Among these opportunistic insects were the **Diptera** and **Plecoptera** as the most abundant. I would suggest that additionally, the liverworts may have provided "landing sites" for insect that were caught up in the high-water flow.

Detrimental Effects?

But the encroachment of bryophytes is not good for all members of the stream community. Bryophytes displace epilithic algae that would otherwise occupy the rocks. These diatoms and other algae serve as food for the scrapers, some of whom cannot carry out the same feeding strategy on the bryophytes. The soft structure and irregular surface of bryophytes sometimes requires a different scraping apparatus from that used on a rock. Slavik *et al.* (2004) found that added phosphorus in an Alaskan stream increased epilithic algae initially, but that after eight years of fertilization the bryophytes replaced the diatoms as primary producers. This increased moss growth altered ammonia uptake rates, benthic gross primary productivity, habitat structure, insect abundance, and faunal species composition.

The detrimental effects of bryophyte encroachment was apparent in a South African stream when managers chose to transplant *Fontinalis* (Figure 18) into the stream to increase habitat for insects and ultimately increase fish production (Richards 1947). While the idea sounded good, the mosses took over the rock surfaces that had been inhabited by scrapers and insects adapted to clinging to smooth rock surfaces and displaced the native fauna. Unfortunately, I don't know the long-term outcome, which may indeed have increased the number of insects once the bryophyte-adapted species were able to colonize.

Bryophytes vs Tracheophytes

It is clear that bryophytes house numerous aquatic insects. And we know that aquatic insects serve as fish food. But do the insects that live among the bryophytes achieve that role? Bowden *et al.* (1999) found that such a role was unclear. As will soon be seen, bryophytes serve as safe sites for the insects. On the other hand, tracheophytes usually provide a more open habitat than the small chambers of bryophytes. And the tracheophytes can house larger individuals, sheltering fish that seek food there.

Macroinvertebrate biomass, insect density, and organic-matter content were significantly greater in patches of *P. pinnata* than on adjacent bare rock. Bryophyte biomass explained additional variation in organic matter, insect biomass, and density. The most abundant insects in *P. pinnata* patches were Dipterans and Plecopterans.

A legitimate comparison between the bryophyte fauna and that of tracheophytes is difficult because these two plant groups tend to occupy different habitats. In lakes the bryophytes are able to extend into deeper water where there is less light than that needed to support the more rapidly growing tracheophytes. The greater depth furthermore coincides with lower temperatures and less temperature fluctuation. Nutrients and dissolved O₂ also differ. And the meshlike nature of the bryophyte more easily traps detritus that can serve as a food source.

In streams, most tracheophytes are unable to tolerate the rapid flow regime that bryophytes can withstand. Since bryophytes occupy greater flow, their surface interface can have a higher oxygen concentration. And since the bryophytes tend to occupy upstream reaches that are steeper and more rocky, they coincide with a different group of insects adapted to faster water, sometimes lower temperatures, some drying in summer, and different species of predators, especially fish. With such limitations on the comparisons, it should be no surprise that studies designed to compare the inhabitants between bryophytes and tracheophytes are rare.

Harrod (1964) found that in a UK chalk stream four aquatic tracheophytes [*Ranunculus fluitans* (Figure 112), *Callitriche platycarpa* (Figure 113), *Veronica beccabunga* (Figure 114), and *Carex* sp. (Figure 115)] had some inhabitants, present on all four species, that are also known bryophyte inhabitants: *Baetis rhodani* (mayflies; Figure 2) (Frost 1942), *Rhyacophila dorsalis* (free-living caddisflies; Figure 116) (Slack 1936), and *Chironomidae* (midges; Figure 9) (Hynes 1961). *Hydropsyche* sp. (net-spinning caddisflies; Figure 13) and *Ephemerella* (s.l.) spp. (mayflies; Figure 3, Figure 8, Figure 25) preferred *C. platycarpa*. *Simulium ornatum* (blackflies; Figure 117) dominated both *Carex* sp. and *R. fluitans* (Harrod 1964).



Figure 112. *Ranunculus fluitans* with flower, a species where *Simulium ornatum* is dominant. Photo by Rasbak, through Creative Commons.



Figure 113. *Callitriche platycarpa*, a preferred substrate for *Hydropsyche* and *Ephemerella*. Photo by J. C. Schou, with permission.



Figure 114. *Veronica beccabunga* with flowers. Photo by Jacopo Werther, through Creative Commons.



Figure 115. *Carex hystricina* with flowers, a species where *Simulium ornatum* is dominant. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 116. *Rhyacophila dorsalis* larva, a bryophyte inhabitant that also occurs on aquatic tracheophytes. Photo by Walter Pfliegler, with permission.

Krecker's (1939) model contends that invertebrate abundance varies with macrophyte biomass, but also with plant species. Those plants with finely dissected leaves have more inhabitants than do plants with broad leaves. Cyr and Downing (1988) tested this assumption with macrophytes and found that the dissected *Myriophyllum* spp. (Figure 118) harbored significantly ($p < 0.01$) more epiphytic invertebrates than did the broad-leaved taxa of *Potamogeton amplifolius* (Figure 119), *P. robbinsii* (Figure 120), or *Vallisneria americana* (Figure 121). But they also

found more invertebrates on the large *P. amplifolius* than on the other two broad-leaved species. The numbers of **Trichoptera** (caddisflies; Figure 91) and **Chironomidae** (midges; Figure 90) varied based on plant species. Interestingly, they found that plants with dissected leaves (*Ceratophyllum demersum* (Figure 122) and *Myriophyllum* spp.) did not usually support more invertebrates than did species with large leaves, attesting to the importance of surface area.



Figure 117. *Simulium ornatum* / *intermedium* / *trifasciatum* adult, a blackfly species complex whose larvae are common on both *Ranunculus fluitans* and *Carex*. Photo by Malcolm Storey, through Discover Life online permission.



Figure 118. *Myriophyllum* sp., a tracheophyte with intermediate densities of insects, inferior to that of mosses. Photo by Alison Fox through USDA, with permission.



Figure 119. *Potamogeton amplifolius*, a broad-leaved aquatic plant that harbors fewer insects than those found among dissected leaves. Photo by Jean Pawek, with online permission.



Figure 120. *Potamogeton robbinsii*, a broad-leaved aquatic plant that harbors fewer insects than those found among dissected leaves. Photo by Barre Hellquist, through Creative Commons.

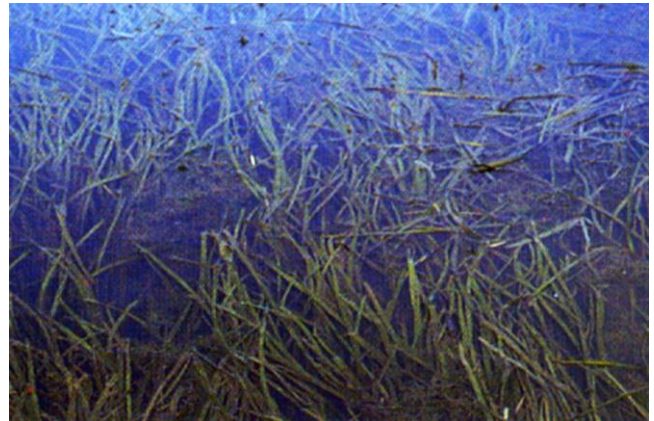


Figure 121. *Vallisneria americana* showing its dense habit of growth. Photo by William & Wilma Follette, through Creative Commons.



Figure 122. *Ceratophyllum demersum*, an aquatic plant with dissected leaves that does not support as many invertebrates as macrophytes with large leaves. Photo from DoralBio5 website, through Creative Commons.

Epele *et al.* (2012) conducted a similar study on **Chironomidae** (midge) assemblages in Patagonia. They recorded 35 taxa of **Chironomidae**. The most abundant subfamilies were **Orthoclaadiinae** (20), **Chironominae** (7), and **Podonominae** (4). The five most abundant species represented five genera: *Parametriocnemus* (Figure 123), *Parapsectrocladius*, *Paratrichocladius* (Figure 124), *Pseudochironomus*, and *Rheotanytarsus* (Figure 125) most abundant taxa. *Myriophyllum quitense* (Figure 126) is structurally complex and was inhabited by 11 taxa. *Isoetes savatieri*, a structurally simple plant, hosted only 5 taxa. Among the bryophytes in areas of rapid flow they found **Podonominae**, *Eukiefferiella* spp., *Parapsectrocladius* sp. They found that stability of the substrate was important, with boulders, cobbles, and rooted plants supporting more **Chironomidae** abundance, richness, and diversity than did sand/gravel. They concluded that more complex substrates supported greater diversity.

generally had the highest density of **Chironomidae** (larvae per sq cm on wood or per gram dry weight on all others). On 11 June the density among mosses was more than double that among filamentous algae, with the others having only 1/6 or less density than that among the mosses. But on 21 June, *Hippuris* had 457 midge larvae compared to 268 on mosses; the algae had none, and the other plants had much lower densities than the mosses. By 11 July, the density among the mosses was nearly double that on *Hippuris* with all others trailing behind. Similar results persisted on 31 July, but on 20 August no insects were reported for the mosses! On 1 October the moss inhabitants reached their highest density (1817 per gram), nearly twice that on *Hippuris*. Differences in surface area are likely to account for the generally higher habitation among mosses (Table 1). Could the low numbers on 20 August have been movement of larvae from mosses to a better food source during low flow?



Figure 123. *Parametriocnemus* sp., a common genus on aquatic plants in Patagonia. Photo by Gillian Martin, Biodiversity Institute of Ontario, through Creative Commons.



Figure 124. *Paratrichocladius skirwithensis* pupa, a genus that is common on macrophytes in Patagonia. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.

Boerger *et al.* (1982) compared the **Chironomidae** (midge larvae; Figure 9) fauna on several aquatic plants and the moss *Drepanocladus revolvens* (Figure 127) in the North Fork of the Bigoray River, Alberta, Canada, on several sampling dates. When compared to *Sparganium* (Figure 128), *Potamogeton* (Figure 129), *Hippuris* (Figure 130), sponge, filamentous algae, and wood, the moss



Figure 125. *Rheotanytarsus*, a genus that is common on macrophytes in Patagonia. Photo by Jason Neuswanger <Troutnut.com>, with permission.



Figure 126. *Myriophyllum quitense*, home to 11 taxa of **Chironomidae** in Patagonia. Photo from Jardín Botánico Nacional, through Creative Commons.



Figure 127. *Drepanocladus revolvens*, a moss with higher density of **Chironomidae** when compared with nearby aquatic tracheophytes. Photo by Kristian Peters, with permission.



Figure 128. *Sparganium angustifolium* with flowers, a tracheophyte with fewer **Chironomidae** than that on mosses. Photo by Barbara Studer, through Creative Commons.



Figure 129. *Potamogeton perfoliatus*, a plant with fewer fauna than found on nearby mosses. Photo by Donald Cameron, through public domain.

Table 1. Comparison of surface area and volume per weight of three tracheophytes, *Drepanocladus revolvens* (Figure 127), filamentous algae, and willow leaves. From Boerger *et al.* 1982.

Plant type	n	area/wt cm ² g ⁻¹	vol/wt cm ³ g ⁻¹	area/vol cm ² g ⁻¹
<i>Sparganium</i>	8	707±13	19.7±1.2	37.6±2.4
<i>Potamogeton</i>	10	1028±116	14.0±0.9	73.6±7.2
<i>Drepanocladus revolvens</i>	10	1526±136	15.2±1.5	103±9.4
<i>Hippurus</i>	9	2549±638	20.9±2.2	122±9.6
Filamentous algae	5	—	23.5±5.6	—
Willow leaves	9	250±9		

In UK lakes and rivers, Macan and Worthington (1951) found that thick mosses on stones and boulders had a mean of 431,941 animals per square meter, whereas *Potamogeton perfoliatus* (pondweed; Figure 129) had only 243,972 and bare rocks had only 4600. Both rooted plants and mosses increased the food used by fish. Percival and Whitehead (1929) likewise found that bryophytes in UK streams had greater insect densities, with intermediate densities on the alga *Cladophora* (Figure 131) and loose mosses, but with the highest densities on thick moss and river weed (Podostemaceae?).



Figure 130. *Hippuris vulgaris*, a tracheophyte with only half the insect density found on mosses. Photo through Creative Commons.



Figure 131. *Cladophora crispata*, member of a genus that is home to aquatic insects. Photo by Yuuji Tsukii, Protist Information Server, with permission.

In Doe Run, Kentucky, USA, Minckley (1963) found intermediate densities on the vascular plants *Nasturtium* (Figure 132), *Myriophyllum* (Figure 118), and *Myosotis* (Figure 133), with the highest densities on mosses. Gregg (1981) found that when the insects were counted on available surface area (3-d, not stream bed), the bare substrate had significantly more insects than did the tracheophytes *Ranunculus* (Figure 134) or *Rorippa* (Figure 135). It seems that the most important role of these tracheophytes was to increase available substrate. It is likely that bryophytes have that role as well.



Figure 132. *Nasturtium officinale* with flowers, an emergent plant with lower insect densities than that found on mosses. Photo by Matt Lavin, through Creative Commons.



Figure 133. *Myosotis scorpioides*, an emergent tracheophyte that had fewer insect inhabitants than mosses. Photo by Les Mehrhoff, through DiscoverLife <<http://www.discoverlife.org>>.



Figure 134. *Ranunculus aquatilis*, a tracheophyte genus that had even fewer insects than bare substrate in a Kentucky, USA, stream. Photo by Teun Spaans, through Wikimedia Commons.



Figure 135. *Rorippa palustris*, an emergent tracheophyte genus that has fewer insects than the bare substrate in a Kentucky, USA, stream. Photo by Mel Harte, through DiscoverLife <www.discoverlife.org>.

Unlike the bryophytes that trap large quantities of detritus, the tracheophytes tend to be somewhat cleaner because they have fewer pockets in which to trap things. Soszka (1975) used both laboratory and field experiments to examine how insects in a Polish lake used the tracheophytes. He found that only the larvae of Lepidoptera depended on the tracheophytes for food. Rather, most of the insects ate the epiphytic algae and detritus.

Nearly 60% of the invertebrate taxa associated with macrophytes studied by Krull (1970) occurred on only three or fewer species of macrophytes and 33 invertebrate taxa were associated with only one species. **Odonata** (Figure 136) are relatively common among macrophytes (Corbet 1962) but nearly totally absent among bryophytes (see Chapter 11-4 of this volume). The reasons remain to be explored, but the **Odonata** are large and tend to occur in quiet water where they can lie in wait for prey, whereas bryophytes are more common in rapid water.



Figure 136. A head-on view of the dragonfly *Tanypteryx hageni* naiad lying in wait for its prey. Photo by Greg Courtney, with permission.

The morphology of the plant appears to be of a major importance. Kreckler (1939) found that the lowest number of insects occurred on *Vallisneria* (Figure 121), a plant with smooth, linear leaves. On the other hand, *Myriophyllum* (Figure 118) species (Figure 118) are divided and provide a large surface area. *Potamogeton crispus* (Figure 137) has very wavy leaves and had high faunal densities. Harrod (1964) considered the colonization of aquatic macrophytes to depend on four factors: morphology, position in stream, epiphytes present, and chemical nature. Habitat permanence may be important in lakes (Hargeby 1990). (Hutchinson 1975) suggested that chemical defenses were not well developed in aquatic macrophytes compared to terrestrial plants. Presumably they are also less well developed than in bryophytes.



Figure 137. *Potamogeton crispus* showing dense growth. Photo by J. C. Schou, with permission.

Despite the open nature of most macrophytes, Tarzwell (1936) found more organisms on the tracheophytes than on the mosses in Michigan, USA, streams. Using a relative scale in which 1.0 represented the numbers on sand, he reported individuals on the tracheophytes *Ranunculus* (Figure 134) (194), *Rorippa* (Figure 135) (301), and *Elodea* (Figure 138) (452) to be greater than those on mosses on gravel (111) or mosses on gravel and rubble (140). Similarly, Percival and Whitehead (1929) found that fauna

on a square decimeter of the tracheophyte *Potamogeton* (Figure 129) (2405) exceeded that of both loose moss (709) and thick moss (2140).



Figure 138. *Elodea canadensis* flowering. Note detrital accumulation on substrate but little at leaf bases. Photo by Christian Fischer, through Creative Commons.

The ability to colonize tracheophytes vs bryophytes often depends on the suitability of the morphology. Although bryophytes have a large surface area, most of it is below the interface with flowing water, hence creating surfaces that may be lacking in sufficient oxygen as well as being unsuitable for filter feeders that depend on the flow. This appears to be the case for blackflies. Niesiolowski (1980) found a greater number of blackflies on *Potamogeton* (Figure 137) than on *Fontinalis* (Figure 62). He attributed this to the differences in leaf size and setting. *Potamogeton* leaves are all exposed to the current whereas only tips of bryophyte branches that interface with the water flow are available for these filter-feeding larvae.

Clearly the relationships between aquatic insects and bryophytes are complex and may be indirect. They serve as refuges and food sources, but these roles may change as the seasons change. Their importance in increased diversity is certain, but their role in overall productivity of the habitat is still elusive.

Summary

Bryophytes provide a stable habitat with lots of surface area, a variety of internal spaces with oxygen and flow gradients, a place to hide from predators or escape from flow (enemy-free space/refuges/safe sites), a trap for algae and detritus to serve as food, and a place to hunt for smaller organisms while hiding from larger predators. Bryophytes can also serve as a moist refuge and a place to find food during times of low water. Hence, a rich bryophyte fauna exists to take advantage of these benefits, increasing the functional diversity. The bryophytes provide habitats for insects in streams, rivers, lake margins, deep waters of lakes, ponds, bogs, and fens.

Two strong determinants of the bryophyte faunal composition are velocity and pH. Nutrients can change the dynamic, in some cases increasing moss cover and fauna, but in others increasing algal dominance and reducing bryophyte cover due to competition for light and CO₂.

Some insects specialize on parts of the mosses, with some in leaf axils, some in liverworts, some on the leaf lamina. Morphology of the bryophyte may help to define the faunal community. Other insects specialize on the food types that grow on the mosses – diatoms, Cyanobacteria, filamentous green algae. Some preferences for bryophyte species may relate to the preference of the bryophyte for a particular pH range, flow, or other conditions. Bryophytes can also serve as a trap for drifting insects while helping others to avoid the drift altogether. The bryophytes seem to keep at least some species from joining the drift at emergence by providing a substrate where they can climb out of the water.

Artificial string mosses are colonized by the same dominant insects as are mosses, but Visqueen strips have a smaller, more selective fauna.

New methods using fatty acids have supported the gut analyses that reveal bryophytes in the diets of a number of insects. These fatty acids have been used as tracers to implicate the movement of bryophyte carbon upward in the food pyramid. Antiherbivore compounds may keep some insects from eating the bryophytes; in other cases they keep predators from attacking the insects because they prefer eating among plants that lack these compounds. But it appears that trapped detritus and adhering periphyton may play the most important role in determining bryophyte insect inhabitants.

Although macroinvertebrate density and richness increase with moss weight, lower reaches within the mat may be unacceptable habitats for many, so that area covered is more important. And in some cases, encroachment by bryophytes can eliminate insects adapted to smooth rocks.

Bryophytes offer different advantages compared to those of tracheophytes. They occur in rapid water of streams where tracheophytes are unable to survive, they provide enclosed, protective spaces, they trap more detritus, and they persist year-round. But large-leaved tracheophytes provide better habitats for such taxa as **Simuliidae** because more of their surface area is in direct flow where these blackflies can filter out their food.

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Literature Cited

Albrecht, M.-L. 1968. Die Wirkung des Lichtes auf die quantitative Verteilung der Fauna im Fließgewässer. *Limnologica* (Berlin) 6: 71-82.

- Amos, William H. 1999. Life in the torrent - the moss *Fontinalis* and its tiny inhabitants. Microscopy UK, Accessed on 16 April 2008 at <<http://www.microscopy-uk.org.uk/mag/indexmag.html?http://www.microscopy-uk.org.uk/mag/artsep99/bamoss.html>>.
- Anderson, N. H. 1966. Depressant effect of moonlight on activity of aquatic insects. *Nature* (London) 209: 319-320.
- Anderson, N. H. 1967. Biology and downstream drift of some Oregon Trichoptera. *Can. Entomol.* 99: 507-521.
- Anderson, N. H. and Lehmkuhl, D. M. 1968. Catastrophic drift of insects in a woodland stream. *Ecology* 49: 199-206.
- Anderson, W. H. and Gellermann, J. L. 1975. Acetylenic acids from mosses. *Lipids* 10: 501-502.
- Arnold, F. and Macan, T. T. 1969. Studies on the fauna of a Shropshire Hill stream. *Field Stud.* 3(1): 159-184.
- Badcock, R. M. 1949. Studies in stream life in tributaries of the Welsh Dee. *J. Anim. Ecol.* 18: 193-208.
- Baker, R. G., Bettis, E. A. III., Schwert, D. P., Horton, D. G., Chumbley, C. A., Gonzalez, L. A., and Reagan, M. K. 1996. Hydraulic habitat of plants in streams. Holocene paleoenvironments of northeast Iowa. 1. International Symposium on Habitat Hydraulics Tondheim, Norway, 18-20 Aug. 1994 Biggs.
- Bishop, J. E. 1969. Light control of aquatic insect activity and drift. *Ecology* 50: 371-380.
- Bishop, J. E. and Hynes, H. B. N. 1969. Downstream drift of the invertebrate fauna in a stream ecosystem. *Arch. Hydrobiol.* 66: 56-90.
- Boerger, H. J., Clifford, H. F., and Davies, R. W. 1982. Density and microdistribution of chironomid larvae in an Alberta brown-water stream. *Can. J. Zool.* 60: 913-920.
- Bowden, W. B., Arscott, D., Pappathanasi, D., Finlay, J., Glime, J. M., LaCroix, J., Liao, C.-L., Hershey, A., Lampella, T., Peterson, B., Wollheim, W., Slavik, K., Shelley, B., Chesterton, M. B., Lachance, J. A., LeBlanc, R. M., Steinman, A., and Suren, A. 1999. Roles of bryophytes in stream ecosystems. *J. N. Amer. Benthol. Soc.* 18: 151-184.
- Brittain, J. E. and Eikeland, T. J. 1988. Invertebrate drift – a review. *Hydrobiologia* 166: 77-93.
- Brown, C. R. and Brown, M. B. 2004. Group size and ectoparasitism affect daily survival probability in a colonial bird. *Behav. Ecol. Sociobiol.* 56: 498-511.
- Brusven, M. A. 1970. Drift periodicity of some riffle beetles (Coleoptera: Elmidae). *J. Kans. Entomol. Soc.* 43: 364-371.
- Brusven, M. A., Meehan, W. R., and Biggam, R. C. 1990. The role of aquatic moss on the community composition and drift of fish-food organisms. *Hydrobiologia* 196: 39-50.
- Butcher, R. W. 1933. Studies on the ecology of rivers: I. On the distribution of macrophytic vegetation in the rivers of Britain. *J. Ecol.* 21: 58-91.
- Carlsson, G. 1967. Environmental factors influencing blackfly populations. *Bull. World Health Org.* 37: 139-150.
- Cattaneo, A., Cloutier, L., and Méthot, G. 2004. The response of invertebrates in moss and in gravel to water level fluctuations in a Québec stream. *Arch. Hydrobiol.* 161: 21-43.
- Chantha, S.-C., Cloutier, L., and Cattaneo, A. 2000. Epiphytic algae and invertebrates on aquatic mosses in a Quebec stream. *Arch. Hydrobiol.* 147: 143-160.
- Chapman, D. W. and Demory, R. L. 1963. Seasonal changes in the food ingested by aquatic insect larvae and nymphs in two Oregon streams. *Ecology* 44: 140-146.
- Cherchesova, S. K., Shioloshvili, M. N., Yakimov, A. V., Nemno, E. V., Lvov, V. D., and Kovilyaeva, N. E. 2012. Stoneflies

- (Insecta, Plecoptera) of Kabarda-Balkarian Republic (The Central Caucasus). *Illiesia* 8(19): 174-181.
- Clenaghan, C., Giller, P. S., O'Halloran, J., and Hernan, R. 1998. Stream macroinvertebrate communities in a conifer-afforested catchment in Ireland: Relationships to physico-chemical and biotic factors. *Freshwat. Biol.* 40: 175-193.
- Corbet, P. S. 1962. A biology of dragonflies. Witherby, London.
- Corona, E. M. 2010. Ephemeroptera, Plecoptera and Trichoptera microhabitat distributions in streams. Ph.D. dissertation, California State University, Long Beach, 76 pp.
- Corrarino, C. A. and Brusven, M. A. 1983. The effects of reduced stream discharge on insect drift and stranding of near shore insects. *Freshwat. Invert.* 2: 88-98.
- Coutant, C. C. 1964. Insecticide Sevin: Effect of aerial spraying on drift of stream insects. *Science* 146: 420-421.
- Cowie, B. and Winterbourn, M. J. 1979. Biota of a subalpine springbrook in the Southern Alps. *N. Z. J. Marine Freshwat. Res.* 13: 295-301.
- Cyr, H. and Downing, J. A. 1988. The abundance of phytophilous invertebrates on different species of submerged macrophytes. *Freshwat. Biol.* 20: 365-374.
- Dangles, O. 2002. Functional plasticity of benthic macroinvertebrates: Implications for trophic dynamics in acid streams. *Can. J. Fish. Aquat. Sci.* 59: 1563-1573.
- Decamps, H. and Lafont, M. 1974. Cycles vitaux et production des *Micrasema* Pyreneennes dans les mousses d'eau courante. *Ann. Limnol.* 10: -32.
- Dembitsky V. M. and Rezanka T. 1995. Distribution of acetylenic acids and polar lipids in some aquatic bryophytes. *Phytochemistry* 40: 93-97.
- Dendy, J. S. 1944. The fate of animals in stream drift when carried into lakes. *Ecol. Monogr.* 14: 335-357.
- Devantery, P. 1987. Action des courants sur la faune d'une mousse immergée: *Platyhypnidium riparioides* (Bryophyta). [Effects of the current on the fauna of submerged mosses: *Platyhypnidium riparioides* (Bryophyta)]. Unpublished Ph. D. thesis, Univ. Claude Bernard, Lyon, France, 291 pp.
- Devantery, P. 1995. Étude expérimentale des rétrocourants sous-foliaires dans les bryophytes immergées: Implications écologiques. [Experimental study of sub-foliar retrocurrents in underwater bryophytes: Ecological implications.]. *Ann. Limnol.* 31: 157-167.
- Dodd, J. A. 2011. Long-term Change in River Invertebrate Communities. Ph.D. Dissertation, University of Glasgow, Scotland.
- Douglas, M. and Lake, P. S. 1994. Species richness of stream stones: An investigation of the mechanisms generating the species-area relationship. *Oikos* 69: 387-396.
- Drazina, T., Spoljar, M., Primc-Habdija, B., and Habdija, I. 2011. Small scale patterns of meiofauna in bryophytes. In: 7th Symposium for European Freshwater Sciences, 27 June - 1 July 2011 in Girona, Spain.
- Duan, X., Wang, Z., Xu, M., and Zhang, K. 2009. Effect of streambed sediment on benthic ecology. *Internat. J. Sediment Res.* 24: 325-338.
- Dudley, T. L. 1988. The roles of plant complexity and epiphyton in colonization of macrophytes by stream insects. *Verh. Internat. Verein. Limnol.* 73: 1153-1158.
- Edington, J. M. 1965. The effect of water flow in populations of net-spinning Trichoptera. *Mitt. Internat. Verein. Theor. Angew. Limnol.* 13: 40-48.
- Edington, J. M. 1968. Habitat preferences in net-spinning caddis larvae with special reference to the influence of water velocity. *J. Anim. Ecol.* 37: 675-692.
- Egglishaw, H. J. 1969. The distribution of benthic invertebrates on substrata in fast flowing streams. *J. Anim. Ecol.* 38: 19-33.
- Elgar, M. A. 1986. The establishment of foraging flocks in house sparrows: Risk of predation and daily Temperature. *Behav. Ecol. Sociobiol.* 19: 433-438.
- Elliott, J. M. 1965. Invertebrate drift in a mountain stream in Norway. *Norsk Entomol. Tidsskr.* 13: 97-99.
- Elliott, J. M. 1967a. Invertebrate drift in a Dartmoor stream. *Arch. Hydrobiol.* 63: 202-237.
- Elliott, J. M. 1967b. The life histories and drifting of the Plecoptera and Ephemeroptera in a Dartmoor stream. *J. Anim. Ecol.* 36: 343-362.
- Elliott, J. M. 1968. The life histories and drifting of Trichoptera in a Dartmoor stream. *J. Anim. Ecol.* 37: 615-625.
- Elliott, J. M. 1971a. The distances travelled by drifting invertebrates in a Lake District Stream. *Oecologia* 6: 350-379.
- Elliott, J. M. 1971b. Upstream movements of benthic invertebrates in a Lake District stream. *J. Anim. Ecol.* 40: 235-252.
- Elliott, J. M. 2002. Time spent in the drift by downstream-dispersing invertebrates in a Lake District stream. *Freshwat. Biol.* 47: 97-106.
- Elliott, J. M. 2003. A comparative study of the dispersal of 10 species of stream invertebrates. *Freshwat. Biol.* 48: 1652-1668.
- Elliott, J. M. 2005. Contrasting diel activity and feeding patterns of four instars of *Rhyacophila dorsalis* (Trichoptera). *Freshwat. Biol.* 50: 1022-1033.
- Ely, D. T. 2005. Long-term response of stream invertebrates to catchment logging. M. S. Thesis, University of Georgia, Athens.
- Englund, G. 1991. Effects of disturbance on stream moss and invertebrate community structure. *J. N. Amer. Benthol. Soc.* 10: 143-153.
- Epele, L. B., Miserendino, M. L., and Brand, C. 2012. Does nature and persistence of substrate at a mesohabitat scale matter for Chironomidae assemblages? A study of two perennial mountain streams in Patagonia, Argentina. *J. Insect Sci.* 12: 68.
- Fisher, S. G. and Gray, L. J. 1983. Secondary production and organic matter processing by collector macroinvertebrates in a desert stream. *Ecology* 64: 1217-1224.
- Fontaine, T. D. and Nigh, D. G. 1983. Characteristics of epiphyte communities on natural and artificial submersed lotic plants: Substrate effects. *Arch. Hydrobiol.* 96: 293-301.
- Frost, W. E. 1939. River Liffey survey II. The food consumed by the brown trout (*Salmo trutta* Linn.) in acid and alkaline waters. *Proc. Royal Irish Acad. B* 45, No. 7.
- Frost, W. E. 1942. River Liffey survey IV. The fauna of submerged "mosses" in an acid and an alkaline water. *Proc. Royal Irish Acad. Ser. B* 13: 293-369.
- Frost, W. E. and Went, A. E. J. 1940. River Liffey Survey III. The growth and food of young Salmon. *Proc. Royal Irish Acad. B* 46, No. 4.
- Gaevskaya, N. S. 1969. The role of higher aquatic plants in the nutrition of the animals of freshwater basins. 3 Vols. National Lending Library of Science and Technology, Yorkshire, England, 629 pp.
- Galdean, N., Callisto, M., and Barbosa, F. A. R. 2001. Biodiversity assessment of benthic macroinvertebrates in

- altitudinal lotic ecosystems of Serra Do Cipó (MG, Brazil). *Re. Brasil. Biol.* 61: 239-248.
- Gladyshev, M. I., Sushchik, N. N., Kalachova, G. S., and Makhutova, O. N. 2012. Stable isotope composition of fatty acids in organisms of different trophic levels in the Yenisei River. *PloS one* 7(3): e34059.
- Gleason, H. A. 1922. On the relation between species and area. *Ecology* 3: 158-162.
- Glime, J. M. 1968. Aquatic Insect Communities Among Appalachian Stream Bryophytes. Ph.D. Dissertation, Michigan State University, East Lansing, MI, 180 pp.
- Glime, J. M. 1978. Insect utilization of bryophytes. *Bryologist* 81: 186-187.
- Glime, J. M. 1994. Bryophytes as homes for stream insects. *Hikobia* 11: 483-497.
- Glime, J. M. and Clemons, R. M. 1972. Species diversity of stream insects on *Fontinalis* spp. compared to diversity on artificial substrates. *Ecology* 53: 458-464.
- Gregg, W. W. 1981. Aquatic macrophytes as a factor affecting the microdistribution of benthic stream invertebrates. Unpubl. M. S. thesis, Idaho State University, Pocatello, ID, 163 pp.
- Gregg, W. W. and Rose, F. L. 1985. Influences of aquatic macrophytes on invertebrate community structure, guild structure, and microdistribution in streams. *Hydrobiologia* 128: 45-56.
- Greig, H. S. and McIntosh, A. R. 2008. Density reductions by predatory trout increase adult size and fecundity of surviving caddisfly larvae in a detritus-based stream food web. *Freshwat. Biol.* 53: 1579-1591.
- Gurtz, M. E. and Wallace, J. B. 1984. Substrate-mediated response of stream invertebrates to disturbance. *Ecology* 65: 1556-1569.
- Habdija, I., Meštrović, M., Matoničkin, R., Primc Habdija, B., and Cindrić, Z. 2000. Current velocity and retention degree of detritus in moss mats as factors affecting the distribution of macroinvertebrates on the travertine barriers in karstic waters. *Limnol. Reports* 33: 245-250.
- Habdija, I., Primc Habdija, B., Matonickin, R., Kucinic, M., Radanovic, I., Milisa, M., and Mihaljevic, Z. 2004. Current velocity and food supply as factors affecting the composition of macroinvertebrates in bryophyte habitats in karst running water. *Biologia-Bratislava* 59: 577-594.
- Haefner, J. D. and Wallace, J. B. 1981. Production and potential seston utilization by *Parapsyche cardis* and *Diplectrona modesta* (Trichoptera: Hydropsychidae) in two streams draining contrasting southern Appalachian watersheds. *Environ. Entomol.* 10: 433-441.
- Hargeby, A. 1990. Macrophyte associated invertebrates and the effect of habitat permanence. *Oikos* 57: 338-346.
- Harrod, J. J. 1964. The distribution of invertebrates on submerged aquatic plants in a chalk stream. *J. Anim. Ecol.* 33: 335-348.
- Hawkins, C. P. and Sedell, J. R. 1981. Longitudinal and seasonal changes in functional organization of macroinvertebrate communities in four Oregon streams. *Ecology* 62: 387-397.
- Heino, J. 2005. Functional biodiversity of macro-invertebrate assemblages along major ecological gradients of boreal headwater streams. *Freshwat. Biol.* 50: 1578-1587.
- Heino, J. 2009. Biodiversity of aquatic insects: Spatial gradients and environmental correlates of assemblage-level measures at large scales. *Freshwat. Rev.* 2: 1-29.
- Heino, J. and Korsu, K. 2008. Testing species-stone area and species-bryophyte cover relationships in riverine macroinvertebrates at small scales. *Freshwat. Biol.* 53: 558-568.
- Heino, J., Paavola, R., Virtanen, R., and Muotka, T. 2005. Searching for biodiversity indicators in running waters: Do bryophytes, macroinvertebrates, and fish show congruent diversity patterns? *Biodiv. Conserv.* 14: 415-428.
- Hieber, M., Robinson, C. T., and Uehlinger, U. 2003. Seasonal and diel patterns of invertebrate drift in different alpine stream types. *Freshwat. Biol.* 48: 1078-1092.
- Holomuzki, J. R., Pillsbury, R. W., and Khandwala, S. B. 1999. Interplay between dispersal determinants of larval hydropsychid caddisflies. *Can. J. Fish. Aquat. Sci.* 56: 2041-2050.
- Holt, C. S. and Waters, T. F. 1967. Effect of light intensity on the drift of stream invertebrates. *Ecology* 48: 225-234.
- Hurny, A. D. and Wallace, J. B. 1987. The exopterygote insect community of a mountain stream in North Carolina, USA: life histories, production, and functional structure. *Aquat. Ins.* 9: 229-251.
- Hutchinson, G. E. 1975. A Treatise on Limnology, Vol. III. Wiley, N. Y.
- Hynes, H. B. N. 1958. The effect of drought on the fauna of a small mountain stream in Wales. *Verh. Internat. Verein. Limnol.* 13: 826-833.
- Hynes, H. B. N. 1961. The invertebrate fauna of a Welsh mountain stream. *Arch. Hydrobiol.* 57: 344-388.
- Hynes, H. B. N. 1968. Further studies on the invertebrate fauna of a Welsh mountain stream. *Arch. Hydrobiol.* 65: 360-379.
- Jones, J. R. E. 1949. A further ecological study of calcareous streams in the Black Mountain district of South Wales. *J. Anim. Ecol.* 19: 142-159.
- Jones, J. R. E. 1950. A further ecological study of the River Rheidol: The food of the common insects of the main-stream. *J. Anim. Ecol.* 19: 159-174.
- Jones, R. R. E. 1951. An ecological study of the River Towy. *J. Anim. Ecol.* 20: 68-86.
- Kalacheva, G. S., Sushchik, N. N., Gladyshev, M. I., and Makhutova, O. N. 2009. Seasonal dynamics of fatty acids in the lipids of water moss *Fontinalis antipyretica* from the Yenisei River. *Russ. J. Plant Physiol.* 56: 794-806.
- Kalachova, G. S., Gladyshev, M. I., Sushchik, N. N., and Makhutova, O. N. 2011. Water moss as a food item of the zoobenthos in the Yenisei River. *Central Eur. J. Biol.* 6: 236-245.
- Krecker, F. H. 1939. A comparative study of the animal population of certain submerged aquatic plants. *Ecology* 20: 553-562.
- Krull, J. N. 1970. Aquatic plant-macroinvertebrate associations and waterfowl. *J. Wildlf. Mgmt.* 34: 702-718.
- LaCroix, J. J. 1996. Phenolics from *Fontinalis antipyretica* Hedw. and Light as Causes of Differential Distribution of *Asellus militaris* Hay in Gooseneck Creek. Unpubl. M. S. Thesis, Mich. Tech. Univ., Houghton, MI, 47 pp.
- Lancaster, J. and Hildrew, A. G. 1993. Flow refugia and the microdistribution of lotic macroinvertebrates. *J. N. Amer. Benthol. Soc.* 12: 385-393.
- Larimore, R. W. 1974. Stream drift as an indication of water quality. *Trans. Amer. Fish. Soc.* 1974: 507-517.
- Leberfinger, K. and Bohman, I. 2010. Grass, mosses, algae, or leaves? Food preference among shredders from open-canopy streams. *Aquat. Ecol.* 44: 195-203.
- Lee, J. O. and Hershey, A. E. 2000. Effects of aquatic bryophytes and long-term fertilization on Arctic stream insects. *J. N. Amer. Benthol. Soc.* 19: 697-708.

- Lehmkuhl, D. M. 1969. Biology and Downstream Drift of some Oregon Ephemeroptera. Dissertation Abstracts International 30(6): 2 pp.
- Lehmkuhl, D. M. and Anderson, N. H. 1972. Microdistribution and density as factors affecting the downstream drift of mayflies. *Ecology* 53: 661-667.
- Liao, C.-L. 1993. Chemical defence in bryophytes with high apparency. In: Glime, J. M. *Ecology Column. Bryol. Times* 75: 1-4.
- Linhardt, J., Fiurásková, M., and Uvira, V. 2002a. Moss- and mineral substrata-dwelling meiobenthos in two different low-order streams. *Arch. Hydrobiol.* 154: 543-560.
- Linhardt, J., Vlcková, S., and Uvira, V. 2002b. Moss-dwelling meiobenthos and flow velocity in low-order streams. *Acta Universitatis Palackianae Olomucensis Facultas Rerum Naturalium (2001-2002) Biologica* 39-40: 111-122.
- Macan, T. T. and Worthington, E. B. 1951. *Life in Lakes and Rivers*. Collins, London, 272 pp.
- Madaliński, K. 1961. Moss dwelling rotifers of Tatra streams. *Polsk. Arch. Hydrobiol.* 9: 243-263.
- Madsen, B. L., Bengston, J., and Butz, I. 1973. Observations on upstream migration by imagines of some Plecoptera and Ephemeroptera. *Limnol. Oceanogr.* 18: 678-681.
- Matthaei, C. D., Weller, F., Kelly, D. W., and Townsend, C. R. 2006. Impacts of fine sediment addition to tussock, pasture, dairy, and deer farming streams in New Zealand. *Freshwat. Biol.* 51: 2154-2172.
- McLay, C. 1970. A theory concerning the distance travelled by animals entering the drift of a stream. *J. Fish. Res. Bd. Canada* 27: 359-370.
- McWilliam-Hughes, S. M., Jardine, T. D., and Cunjak, R. A. 2009. Instream C sources for primary consumers in two temperate, oligotrophic rivers: Possible evidence of bryophytes as a food source. *J. N. Amer. Benthol. Soc.* 28: 733-743.
- Michael, D. I. and Culver, D. A. 1987. Influence of plecopteran and megalopteran predators on *Hydropsyche* (Trichoptera: Hydropsychidae) microdistribution and behavior. *J. N. Amer. Benthol. Soc.* 6: 46-55.
- Miliša, M., Habdija, I., Primc-Habdija, B., Radanović, I., and Kepčija, R. M. 2006. The role of flow velocity in the vertical distribution of particulate organic matter on moss-covered travertine barriers of the Plitvice Lakes (Croatia). *Hydrobiologia* 553: 231-243.
- Minckley, W. L. 1963. The ecology of a spring stream Doe Run, Meade Co., Kentucky. *Wildl. Monogr.* 11: 1-126.
- Minckley, W. W. 1964. Upstream movements of *Gammarus* (Amphipoda) in Doe Run, Meade County, Kentucky. *Ecology* 45: 195-197.
- Minshall, G. W. and Winger, P. V. 1968. The effect of reduction in stream flow on invertebrate drift. *Ecology* 49: 580-582.
- Mousavi, S. K., Sandring, S., and Amundsen, P.-A. 2002. Diversity of chironomid assemblages in contrasting subarctic lakes: Impact of fish predation and lake size. *Arch. Hydrobiol.* 154: 461-484.
- Müller, K. 1954. Investigations on the organic drift in North Swedish streams. *Rept. Inst. Freshwat. Res. Drottningholm* 35: 133-148.
- Müller, K. 1966. Die Tagesperiodik von Fließwasserorganismen. *Z. Morphol. Oekol. Tiere* 56: 93-142.
- Mutch, R. A. and Pritchard, G. 1984. The life history of *Philocasca alba* (Trichoptera: Limnephilidae) in a Rocky Mountain stream. *Can. J. Zool.* 62: 1282-1288.
- Niesiołowski, S. 1980. Studies on the abundance, biomass and vertical distribution of larvae and pupae of black flies (Simuliidae, Diptera) on plants of the Grabia River, Poland. *Hydrobiologia* 75: 149-156.
- O'Donnell, D. J. and Churchill, W. S. 1954. Certain physical, chemical and biological aspects of the Brule River, Douglas County, Wisconsin. *Trans. Wisc. Acad. Sci. Arts Lett.* 43: 201-255.
- Ogbogu, S. S. and Akinya, T. O. 2001. Distribution and abundance of insect orders in relation to habitat types in Opa Stream-Reservoir System, Nigeria. *J. Aquat. Sci.* 16: 7-12.
- Olgive, G. A. and Clifford, H. F. 1986. Life histories, production, and microdistribution of two caddisflies (Trichoptera) in a Rocky Mountain stream. *Can. J. Zool.* 64: 2706-2716.
- Ormerod, S. J., Wade, K. R., and Gee, A. S. 1987. Macro-floral assemblages in upland Welsh streams in relation to acidity, and their importance to invertebrates. *Freshwat. Biol.* 18: 545-557.
- Pardo, I. and Armitage, P. D. 1997. Species assemblages as descriptors of mesohabitats. *Hydrobiologia* 344: 111-128.
- Parker, J. D., Burkepile, D. E., Collins, D. O., Kubanek, J., and Hay, M. E. 2007. Stream mosses as chemically-defended refugia for freshwater macroinvertebrates. *Oikos* 116: 302-312.
- Pearson, W. D. and Franklin, D. R. 1968. Some factors affecting drift rates of *Baetis* and Simuliidae in a large river. *Ecology* 49: 75-81.
- Percival, E. and Whitehead, H. 1929. A quantitative study of the fauna of some types of stream-bed. *J. Ecol.* 17: 282-314.
- Perić, M. S., Dražina, T., Špoljar, M., Radanović, I., Primc, B., and Habdija, I. 2014. Meiofauna constitute a considerable portion of invertebrate drift among moss-rich patches within a karst hydrosystem. *Biologia* 69: 363-380.
- Pritchard, G. and Berté, S. B. 1987. Growth and food choice by two species of limnephilid caddis larvae given natural and artificial foods. *Freshwat. Biol.* 18: 529-535.
- Reisen, W. K. and Prins, R. 1972. Some ecological relationships of the invertebrate drift in Praters Creek, Pickens County, South Carolina. *Ecology* 53: 876-884.
- Richards, P. W. 1947. The introduction of *Fontinalis antipyretica* Hedw. into South Africa and its biological effects. *Trans. Brit. Bryol. Soc.* 1: 16.
- Robinette, K. W., Andelt, W. F., and Burnham, K. P. 1995. Effect of group size on survival of relocated prairie dogs. *J. Wildl. Mgmt.* 59: 867-874.
- Rosentreter, R. 1984. The zonation of mosses and lichens along the Salmon River in Idaho. *Northwest Sci.* 58: 108-117.
- Slack, H. D. 1936. The food of caddis fly (Trichoptera) larvae. *J. Anim. Ecol.* 5: 105-115.
- Slack, N. G. and Glime, J. M. 1985. Niche relationships of mountain stream bryophytes. *Bryologist* 88: 7-18.
- Smith-Cuffney, F. L. 1987. Ecological Interactions in the Moss Habitat of Streams Draining a Clearcut and a Reference Watershed. Unpubl. Ph.D. thesis, University of Georgia, 174 pp.
- Soszka, G. J. 1975. Ecological relationships between invertebrates and submerged macrophytes in the lake littoral. *Ekol. Pol.* 23: 393-416.
- Špoljar, M., Dražina, T., Ostojić, A., Miliša, M., Udovič, M. G., and Štafa, D. 2012. Bryophyte communities and seston in a karst stream (Jankovac Stream, Papuk Nature Park, Croatia). *Ann. Limnol.-Internat.* 48: 125-138.

- Suren, A. M. 1988. Ecological role of bryophytes in high alpine streams of New Zealand. *Internat. Ver. Theor. Angew. Limnol.* 23: 1412-1416.
- Suren, A. M. 1991. Bryophytes as invertebrate habitat in two New Zealand alpine streams. *Freshwat. Biol.* 26: 399-418.
- Suren, A. 1992a. Meiofaunal communities associated with bryophytes and gravels in shaded and unshaded alpine streams in New Zealand. *N. Z. J. Marine Freshwat. Res.* 26: 115-125.
- Suren, A. M. 1992b. Enhancement of invertebrate food resources by bryophytes in New Zealand alpine headwater streams. *N. Z. J. Marine Freshwat. Res.* 26: 229-239.
- Suren, A. 1993. Bryophytes and associated invertebrates in first-order alpine streams of Arthur's Pass, New Zealand. *N. Z. J. Marine Freshwat. Res.* 27: 479-494.
- Suren, A. M. and Winterbourn, M. J. 1991a. Consumption of aquatic bryophytes by alpine stream invertebrates in New Zealand. *N. Z. J. Marine Freshwat. Res.* 25: 331-343.
- Suren, A. M. and Winterbourn, M. J. 1991b. The influence of periphyton, detritus and shelter on invertebrate colonization of aquatic bryophytes. *Freshwat. Biol.* 27: 327-339.
- Suren, A. M. and Winterbourn, M. J. 1992a. Bryophytes as invertebrate habitat in two New Zealand alpine streams. *Freshwat. Biol.* 26: 327-339.
- Suren, A. M. and Winterbourn, M. J. 1992b. The influence of periphyton, detritus and shelter on invertebrate colonization of aquatic bryophytes. *Freshwat. Biol.* 17: 327-339.
- Sushchik, N. N., Gladyshev, M. I., Kravchuk, E. S., Ivanova, E. A., Ageev, A. V., and Kalachova, G. S. 2007. Seasonal dynamics of long-chain polyunsaturated fatty acids in littoral benthos in the upper Yenisei River. *Aquat. Ecol.* 41: 349-365.
- Sutcliffe, D. W., Carrick, T. R., Charmier, A. C., Gledhill, T., Jones, J. G., Marker, A. F. H., and Willoughby, L. G. 1986. Acidification problems of freshwaters. In: Commission of the European Communities. *Effects of Air Pollution on Aquatic Eco-systems, Workshop on Reversibility of Acidification*, Grimstad, Norway, pp. 75-77.
- Tada, M. and Satake, K. 1994. Epiphytic zoobenthos on bryophyte mats in a cool mountain stream, Toyamazawa. *Rikusuizatsu [Jap. J. Limnol.]* 55: 159-164.
- Tarzwel, C. M. 1936. Experimental evidence on the value of trout stream improvement in Michigan. *Trans. Amer. Fish. Soc.* 66: 177-187.
- Torres-Ruiz, M., Wehr, J. D., and Perrone, A. A. 2007. Trophic relations in a stream food web: Importance of fatty acids for macroinvertebrate consumers. *J. N. Amer. Benthol. Soc.* 26: 509-522.
- Ulfstrand, S. 1967. Microdistribution of benthic species (Ephemeroptera, Plecoptera, Trichoptera, Diptera: Simuliidae) in Lapland streams. *Oikos* 18: 293-310.
- Ulfstrand, S. 1968. Benthic animal communities in Lapland streams. *Oikos Suppl.* 10: 120 pp.
- Voelz, N. J. and McArthur, J. V. 2000. An exploration of factors influencing lotic insect species richness. *Biodiv. Conserv* 9: 1543-1570.
- Wallace, J. B., Gurtz, M. E., and Smith-Cuffney, F. 1988. Long-term comparisons of insect abundances in disturbed and undisturbed Appalachian headwater stream. *Verh. Internat. Verein. Limnol.* 23: 1224-1231.
- Ward, J. V. 1992. *Aquatic Insect Ecology. 1. Biology and Habitat.* John Wiley & Sons, Inc., N. Y., 438 pp.
- Ward, J. V. 1994. Ecology of alpine streams. *Freshwat. Biol.* 32: 277-294.
- Waters, T. F. 1961. Standing crop and drift of stream bottom organisms. *Ecology* 42: 532-537.
- Waters, T. F. 1962. A method to estimate the production rate of a stream bottom invertebrate. *Trans. Amer. Fish. Soc.* 91: 243-250.
- Waters, T. F. 1965. Interpretation of invertebrate drift in streams. *Ecology* 46: 327-334.
- Waters, T. F. 1969. Diel patterns of aquatic invertebrate drift in streams of northern Utah. *Proc. Utah. Acad. Sci. Arts Lett.* 46: 109-130.
- Waters, T. F. 1972. The drift of stream insects. *Ann. Rev. Entomol.* 17: 253-271.
- Williams, D. D. and Williams, N. E. 1982. Morphological and dietary variations in a riverine population of *Pycnopsyche guttifer* (Trichoptera: Limnephilidae). *Aquat. Ins.* 4: 21-27.
- Willoughby, L. G. and Mappin, R. G. 1988. The distribution of *Ephemerella ignita* (Ephemeroptera) in streams: The role of pH and food resources. *Freshwat. Biol.* 19: 145-155.
- Winner, J. M. 1975. Zooplankton. In: Whitton, B. A. (ed.). *River Ecology.* Blackwell Scientific Publications, Oxford, pp. 155-169.
- Winterbottom, J. H., Orton, S. E., Hildrew, A. G., and Lancaster, J. 1997. Field experiments on flow refugia in streams. *Freshwat. Biol.* 37: 569-580.
- Winterbourn, M. J., Rounick, J. S., and Hildrew, A. G. 1986. Patterns of carbon resource utilization by benthic invertebrates in two British river systems: A stable carbon isotope study. *Arch. Hydrobiol.* 107: 349-361.
- Wise, D. H. and Molles, M. C. Jr. 1979. Colonization of artificial substrates by stream insects: Influence of substrate size and diversity. *Hydrobiologia* 65: 69-74.
- Wojtalik, T. A. and Waters, T. F. 1970. Some effects of heated water on the drift of two species of stream invertebrates. *Trans. Amer. Fish. Soc.* 99: 782-788.
- Wood, J., Pattillo, M., and Freeman, M. 2016. Organic-matter retention and macroinvertebrate utilization of seasonally inundated bryophytes in a mid-order Piedmont River. *Southeast. Nat.* 15: 403-414.
- Wulforst, J. 1994. Selected faunal elements of the hyporheos and in submerged moss clumps (bryorheal) along an acidification gradient in two brooks in the Harz Mountains, West Germany. *Internat. Verein. Theoret. Angew. Limnol. Verhand.* 25: 1575-1584.
- Wyatt, R. and Stoneburner, A. 1989. Bryophytophagy of *Rhizomnium punctatum* by larvae of the crane fly *Tipula oropezoides*. *Bryologist* 92: 308-309.
- Yamamura, A. M. 2009. *Aquatic Insect Adaptations to Different Flow Regimes.* Unpubl. Ph. D. Dissertation, Oregon State University, Corvallis, WA.
- Zalewski, M., Bis, B., Frankiewicz, P., Lapinska, M., and Puchalski, W. 2001. Riparian ecotone as a key factor for stream restoration. *Ecohydrol. Hydrobiol.* 1: 245-251.

