

# CHAPTER 11-3

## AQUATIC INSECTS: BRYOPHYTE HABITATS AND FAUNA

---

### TABLE OF CONTENTS

Aquatic Bryophyte Habitat and Fauna .....	11-3-2
Streams.....	11-3-4
Streamside.....	11-3-7
Artificial Bryophytes.....	11-3-7
Preference Experiment .....	11-3-8
Torrents and waterfalls.....	11-3-9
Springs .....	11-3-9
Bogs and Fens .....	11-3-13
Collembola – Springtails.....	11-3-14
Coleoptera – Beetles .....	11-3-17
Odonata – Dragonflies and Damselflies.....	11-3-20
Diptera – Flies.....	11-3-22
Other Insects .....	11-3-23
Lakes and Ponds.....	11-3-24
Arctic and Alpine .....	11-3-26
Disturbance .....	11-3-27
Retention .....	11-3-28
Colonization .....	11-3-28
Pollution Effects.....	11-3-30
Geographic Differences.....	11-3-30
Summary .....	11-3-31
Acknowledgments .....	11-3-32
Literature Cited .....	11-3-32

# CHAPTER 11-3

## AQUATIC INSECTS: BRYOPHYTE HABITATS AND FAUNA



Figure 1. *Sphagnum* blanket bog. Photo through Creative Commons.

### Aquatic Bryophyte Habitat and Fauna

Insect distribution and abundance depend on freedom from predation, interspecific competition, and physical disturbance (McAuliffe 1983). Bryophytes offer a refuge from all three of these dangers. Aquatic insect biodiversity depends on gradients in habitat size and acidity (Harrison & Agnew 1962; Heino 2009). Bryophytes can contribute to the acidity, particularly in *Sphagnum* (Figure 1) habitats, and add to both habitat size diversity and complexity. Thus, bryophytes can increase the diversity of insects in streams, lakes, bogs, and springs by creating more niches for occupation.

Moon (1939) summarized his study of aquatic insects as evidence that the substrate provides mechanical support for the fauna and is the surface on which food grows or is

deposited. Bryophytes can contribute greatly to the available substrate, growing periphyton, and trapping detritus. For carnivorous insects, the bryophytes also harbor animal food organisms. Others have reported similar advantages of the moss substrate: increased substrate area (Glime & Clemons 1972), increased algal cell counts (Gurtz & Wallace 1984), replacing scour or sediment-buried algal cover (Hains 1981), protection from scour (Gurtz & Wallace 1984), filtering and trapping detritus (Gurtz & Wallace 1984), providing high prey density (Gurtz & Wallace 1984). The mosses also permit the insects to gain a hold in areas of high velocity where the insects may be able to reduce ventilation needed to gain oxygen, thus saving energy (Johnson 1978; Gurtz & Wallace 1984).



Gurtz and Wallace (1984) found that after a clearcut in the southern Appalachians, USA, the insect fauna increased in density more on the moss-covered (mostly *Hygroamblystegium tenax* – Figure 2) rock faces than on other stream substrates. It was primarily the collector-gatherers and scrapers that increased, whereas shredders declined. They considered that the mosses contributed to the biological stability of their substrates. They were most important in areas of rapid, shallow, turbulent flow. These habitats not only replenished the CO<sub>2</sub> and nutrient supply for the mosses, but provided the flow needed for the net-spinning caddisfly *Parapsyche* (Figure 3).



Figure 2. *Hygroamblystegium tenax*, where insect fauna increased after a forest clearcut in the southern Appalachians, USA. Photo by Barry Stewart, with permission.



Figure 3. *Parapsyche apicalis* larva, a net-spinning caddisfly that lives on mosses. Photo by Donald S. Chandler, with permission.

By experimenting on colonization of *Fontinalis neomexicana* (Figure 4), Maurer and Brusven (1983) found that collector-gatherers were the most numerous (74% of the density), with shredders, collector-filterers, engulfers, and scrapers making up the remainder. Arrival of *Brachycentrus* sp. (Figure 5), a collector-filterer, and *Hydroptila* sp. (Figure 6), a scraper, both caddisflies, changed these percentages after three weeks. Maurer and Brusven believed that fine particulate matter and epiphytic algae may have facilitated the rapid recolonization.



Figure 4. *Fontinalis neomexicana*, home to many collector-gatherers. Photo by Belinda Lo, through Creative Commons.



Figure 5. *Brachycentrus appalachia* (larger), a common bryophyte dweller that colonized after three weeks. Photo by Bob Henricks, with permission.



Figure 6. *Hydroptila* in case, one of the smallest caddisflies, and a colonizer on *Fontinalis neomexicana* (Figure 4). Photo by Bob Henricks, with permission.

In a Nepalese river system, altitude was an important determinant of the bryophytes and associated fauna (Ormerod *et al.* 1994). Not only did the substrate change, with bryophytes being more common at higher altitudes, but attached diatoms were more common among higher altitude streams. The high altitude springs supported dense



cover of bryophytes, but bryophytes were not well supported by the cold streams of ice and glacial melt.

Ward (1986) studied altitudinal relationships in the Rocky Mountains, USA. As in the Nepalese system, aquatic tracheophytes were absent in the high mountain sites. Rather, bryophytes dominated in the headwaters. The **zoobenthos** (animals that live on the bottom) density experienced a 3-fold to 6-fold increase from the tundra to the plains at lower elevations. Vinson and Hawkins (2003) likewise found that diversity of genera decreased as elevation increased, with only **Plecoptera** (stoneflies; Figure 25) being an exception.

Like altitude, latitude affects stream insect richness. Vinson and Hawkins (2003) examined data on **Ephemeroptera** (mayflies; Figure 8-Figure 9), **Plecoptera** (stoneflies; Figure 25), and **Trichoptera** (caddisflies; Figure 6) from 495 published studies on richness. **Ephemeroptera** showed three richness peaks (~30°S, 10°N, 40°N) with the highest near 5-10°N and 40°N latitude. **Plecoptera** richness was distinctly highest at ~40°N latitude and similarly at 40°S latitude. **Trichoptera** richness showed less latitudinal variation than the other two orders, although it was slightly higher near the equator and at 40°N and S latitude than at other latitudes.

In a study of mosses growing on filter beds, Hussey (1982) found that growth of mosses [*Leptodictyum riparium* (Figure 7) was most common] changed the macroinvertebrate community. Even the thickness of the moss will cause differences among communities (Macan & Worthington 1951). The mayflies *Baetis* (Figure 8) and *Ephemerella* (Figure 9), **Plecoptera** (Figure 25), and the scud *Gammarus* prefer not-so-thick moss, whereas thick moss harbors abundant **Chironomidae** (Figure 15). Macan and Worthington found that of the 431,941 animals per sq m of thick moss, 75% were **Chironomidae**. Despite the small size of the moss inhabitants, they found that rooted plants and attached mosses provide the greatest productivity of fish food organisms. That probably refers to the kinds of organisms that fish eat, not to organisms among the mosses that are actually eaten as these may be unavailable unless they enter the drift. (See Chapter 11-2, Bryophyte Roles as Insect Habitats – Food.)



Figure 7. *Leptodictyum riparium*, a moss whose growth changed the macroinvertebrate community. Photo by Jan-Peter Frahm, with permission.



Figure 8. *Baetis rhodani*, a common bryophyte inhabitant. Photo by J. C. Schou, with permission.



Figure 9. *Ephemerella dorothea* on moss (*Platyhypnidium riparioides* or *Hygrohypnum* sp.). Photo by Donna Bennett, with permission.

## Streams

Streams can be rich habitats for aquatic fauna. In the Åland Islands of Finland, Autio and Salmela (2010) collected 104 **Diptera** species from 19 sites, using Malaise traps. These sites included open mires, wooded mires, rich fens, Baltic shore meadows, ditches, and a grove. These **Diptera** included the semiaquatic families **Limoniidae**, **Tipulidae**, **Pediciidae**, **Cylindrotomidae**, **Ptychopteridae**, **Psychodidae**, and **Dixidae**. But the species richness was less than that in other parts of Finland, a phenomenon that Autio and Salmela attributed to the absence of brooks and springs.

In a Victorian Australia upland stream the habitats included mossy stones and the tracheophyte *Ranunculus fluitans*, with number of species reaching 19 among mosses compared to 5 in stony riffles (McKenzie-Smith 1987). The densities among the bryophytes were greater than that McKenzie-Smith could explain on the basis of greater surface area, so he concluded that they offered more than just space.

In Appalachian Mountain streams, I found that the insect communities on the leafy liverwort *Scapania undulata* were most similar to those on *Fontinalis dalecarlica* (Figure 16) (Glime 1968). These seem like strange similarities because these two bryophyte species



were the most different from each other structurally. However, they did tend to occur in the same streams, suggesting that conditions of flow, nutrients, and temperature may have been more important for the insects. *Scapania undulata* provided a unique habitat where insects were able to hide within the folded leaves. The large, streaming moss *Fontinalis dalecarlica* may have offered a similar advantage by having a leaf that was somewhat rolled, making it tubular and providing good shelter for the very small.

In many northern streams the bryophytes remain throughout the year, providing a habitat for insects when the tracheophytes disappear. But in English rivers, *Fontinalis antipyretica* (Figure 10), *Fissidens crassipes* (Figure 11), and *Leptodictyum riparium* (Figure 7) decline considerably during winter (Wehr & Whitton 1983; Kelly & Whitton 1987).



Figure 10. *Fontinalis antipyretica*, a species that declines in English winters. Photo by Bernd Haynold, through Wikimedia Commons.



Figure 11. *Fissidens crassipes*, a moss that diminishes in English rivers in the winter. Photo by Michael Lüth, with permission.

As noted earlier, bryophytes in streams increase the heterogeneity of the habitat, increasing the available niches for insects (Allan 1975; Williams 1980). And size matters – sometimes (Bourassa & Morin 1995). Although the taxonomic composition differs among streams, the size distribution is quite similar. But substrate composition in nine Canadian streams did affect overall abundance – more

than it did their size. Eutrophic sites favored higher abundance, but only for organisms larger than 1 mm (approximately 1  $\mu$ g dry mass). These small organisms contribute to less than 3% of the respiration of the stream ecosystem, contrasting with the results of Smith-Cuffney (1987 – see above). Does this mean that bryophytes, with their fauna of the smallest organisms, contribute little to the stream ecosystem? I think not, because it is these small organisms that become big ones, and without the shelter of bryophytes they are more likely to be food for predators.

In a Tennessee, USA, springbrook, Stern and Stern (1969) found that the highest number of insects on bryophytes and algae occurred in winter. In February they found 768 individuals per 0.1 m<sup>2</sup>, whereas in July they found only 43 per 0.1 m<sup>2</sup> (Figure 12). **Diptera** comprised 84.4% of the fauna, Trichoptera 9.6%, **Plecoptera** 3.1%, and **Ephemeroptera** 2.8%. **Coleoptera** comprised only 0.1%.

Following logging in a southern Appalachian, USA, stream, Gurtz and Wallace (1984) found that the stonefly *Amphinemura wui* (Figure 13) increased in numbers, a response they attributed to the particulate accumulation by bryophytes. Baetid mayflies and the spiny crawler mayfly *Ephemerella* (s.l.) (Figure 9) increased most among mosses, correlating with a similarly high increase in diatoms among mosses. And as one might expect, the **Orthocladinae** (**Chironomidae** – midges, Figure 15) increased in response to the increased sediment among the mosses.

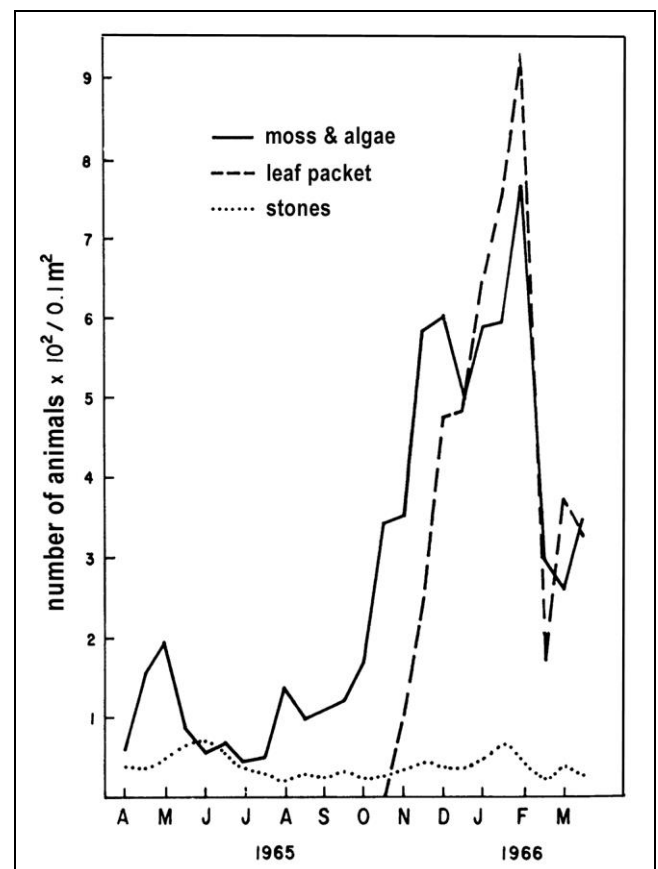


Figure 12. Seasonal distribution of invertebrates on three substrate types in a springbrook in Tennessee, USA. Redrawn from Stern & Stern 1969.



Figure 13. *Amphinemura wui* adult, a species that lives among mosses in its naiad state and feeds on detritus. Photo by Donald S. Chandler, with permission.

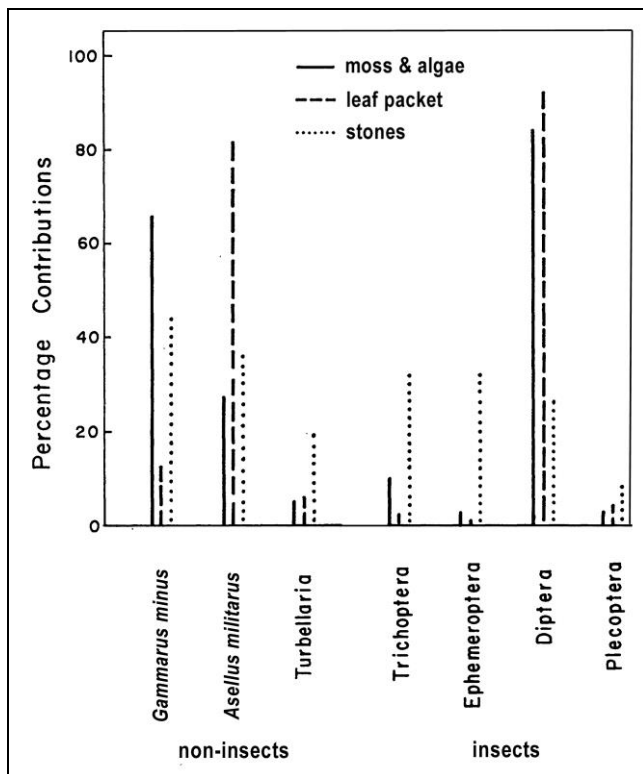


Figure 14. Comparison of insects and other invertebrates among mosses and algae, leaf packets, and stones in a Tennessee springbrook. Redrawn from Stern & Stern 1969.

One of the uses of bryophytes in stream studies could be to serve as **surrogates** – indicators of the habitat and the organisms one might expect to find there. But it seems that bryophytes do not make very reliable surrogates (Paavola 2003; Paavola *et al.* 2003, 2006). Paavola and coworkers, using 101 boreal stream sites, found that within stream areas, the insect communities correlate primarily with stream size, pH, and water color. Bryophytes, on the other hand, correlate with nutrient levels and habitat heterogeneity, whereas fish correlate with oxygen levels, depth, and substrate size. But the surrogate role is not as dismal as it may seem. At the level of ecoregions, all three respond to acidity and depth as well as spatial coordinates

and the community concordance is much smaller than it is on the level of a single stream or stretch of stream. Nevertheless, these three taxonomic groups had low predictive value. When Virtanen *et al.* (2009) examined bryophyte correlations in 138 boreal springs, temperature was a major driver of communities. The **EPTC** insects [**Ephemeroptera** (Figure 8-Figure 9), **Plecoptera** (Figure 25), **Trichoptera** (Figure 6), and **Coleoptera** (Figure 41-Figure 43), *i.e.* major orders on bryophytes and in fast streams] were not good surrogates for the bryophytes, nor were the **Chironomidae** (Figure 15). Concordance between bryophytes and **Chironomidae** was a little better than with the EPTC group.



Figure 15. **Chironomidae** larva, a common bryophyte inhabitant that is not a good surrogate for bryophytes. Photo by Jason Neuswanger, with permission.

In their study of *Fontinalis dalecarlica* (Figure 16) communities, Cattaneo *et al.* (2004) found that depth was an important contributor to differences in invertebrate biomass. Shallow mosses supported lower invertebrate biomass than did the deeper ones, possibly due to frequent exposure of the shallow mosses.



Figure 16. *Fontinalis dalecarlica*, a moss able to occupy a wide range of depths that affect the composition of the insect communities. Photo by Kristoffer Hylander, with permission.



## Streamside

The streamside habitat is one of changing water levels, providing a moisture gradient and a place to leave behind the naiad or pupal stage and crawl to the terrestrial environment for adulthood. Lindegaard *et al.* (1975) examined four zones related to the fauna on the moss *Cratoneuron* (Figure 17). Underlying the moss they found a detritus zone, with numerous flies and earthworms. Above it was a zone of water-covered mosses. The **madicolous** zone occurred just above the water surface and the moss remained constantly wet by splash and capillary water. This madicolous zone and the water zone were suitable for caddisflies, flies, and molluscs. Above that the moss was dry, occupied by springtails, beetles, spiders, and predaceous mites.



Figure 17. *Cratoneuron filicinum*, member of a genus that creates faunal zones. Photo by Barry Stewart, with permission.

## Artificial Bryophytes

Artificial substrata provide important information on the role of the moss in the association with invertebrates (Cox 1988). Suren (1988) used mosses constructed from nylon twine woven into squares. These artificial mosses were colonized by the stoneflies *Zelandoperla* (Figure 18) and *Zelandobius* (Figure 19), midges, nematodes, mites, copepods, and ostracods.



Figure 18. *Zelandoperla pennulata* adult from the Takitimu Mountains, N Z. Photo by Brian Patrick, with permission.



Figure 19. *Zelandobius illiesi*, a stonefly that colonized artificial mosses in New Zealand. Photo by Stephen Moore, Landcare Research NZ, with permission.

Glime and Clemons (1972) found that aquatic insects may only colonize mosses as a place to live. In their experiments, insects on artificial string mosses (Figure 20) formed similar communities to those on *Fontinalis* (Figure 16), but the number of species on mosses made of polyethylene strips was more limited.



Figure 20. Artificial string moss used in study by Glime & Clemons (1972). Photo by Janice Glime.

Suren (1987, 1988) found that artificial mosses in high alpine streams of New Zealand provided habitat similar to that of mosses, but some taxa, for example **Collembola**, were not restored due to lack of suitable food. Others can be absent due to lack of suitable materials for building their "houses." Suren did find that these surrogate mosses did develop abundant periphyton in one stream, but in another they collected primarily detritus and silt. For substitute mosses, the right kind of artificial structure must be found to also house the needed food. This most likely would require longer for the dependent organisms to colonize.

Suren (1991b) also found that colonization of artificial bryophytes was rapid, reaching a peak in abundance after only 4 weeks. After two months, the density and richness resembled that of the natural bryophytes. Nevertheless, some taxa did not reach normal levels, with larvae of **Empididae** (Diptera; Figure 21) and the crane fly *Limonia hudsoni* (see Figure 22) having lower numbers. Taxa that were characteristic of riffles, *e.g.*, the mayflies *Deleatidium* sp. (Figure 23) and *Nesameletus* sp. (Figure 24), or stoneflies *Stenoperla prasina* (Figure 25) and *Zelandobius* sp. (Figure 19), did not colonize the "stems" of artificial



bryophytes very well but did colonize the bases of these and the bedrock beneath. TWINSPAN identified a strong similarity between the artificial mosses and the real mosses, but the fauna of the artificial substrates were different from that of the riffles.



Figure 21. **Empididae** larva, a dipteran group that did not reach normal numbers on artificial mosses. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 22. **Limonia** larva, a genus with lower numbers on artificial mosses than on the real ones. Photo from State Hygienic Laboratory, University of Iowa, with permission.



Figure 23. **Deleatidium** sp., a riffle stonefly that colonized the bases, but not the stems, of artificial mosses. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 24. **Nesameletus** naiad, a riffle mayfly that colonized the bases, but not the stems, of artificial mosses. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 25. **Stenoperla prasina** naiad, a stonefly that colonized the bases, but not the stems, of artificial mosses in New Zealand. Photo by Kanji Saito, with permission.

Suren and Winterbourn (1992) experimented with artificial bryophytes in shaded and unshaded New Zealand portions of an alpine stream. The artificial mosses consisted of pieces of nylon twine woven into 4 mm pores of nylon mesh cut into 0.01 m<sup>2</sup> squares. They found that at the unshaded site seven taxa preferred substrata with high detrital and periphytic biomass. Of the 22 taxa there, 8 were influenced by periphyton biomass, three by detrital biomass, and two by exposure time. At the shaded site, only two taxa had a relationship with these food groups. Exposure time was the most important variable for four of these taxa.

### Preference Experiment

Corona (2010) experimented with substrate choice of wood, cobble, sand, and moss to help explain the distributions of **Ephemeroptera** (Figure 8-Figure 9), **Plecoptera** (Figure 25), and **Trichoptera** (Figure 6) in streams in the San Bernardino National Forest (SBNF) in Southern California. She placed three of these preference samplers (615 cm<sup>2</sup> Plexiglass trays) in each of the three streams to determine where the insects chose to live. The actual stream had the leafy liverwort **Porella** sp. (Figure 26), but moss with a similar 3-d structure was chosen



because it was available commercially. Of the possible combinations of substrata, only two pairs were significantly different: large gravel vs sand and sand vs moss. The majority of species had greater species abundance in the liverwort and experimental moss compared to other microhabitats. Species diversity was greater in the experimental moss habitat compared to the sand habitat (Table 1). Corona suggested this could be a response to the greater food source that accumulated in the more complex structure of the mosses. In the stream, *Drunella grandis* (Figure 27) characterized the *Porella* habitat. Other species seemed to be influenced by habitat availability, with *Plecoptera* sp. 1 characterizing sand in the natural habitat, but characterizing the moss in the experimental preference habitat.



Figure 26. *Porella pinnata*. This genus provides a suitable habitat for *Drunella grandis* in California, USA, streams. Photo by Jan-Peter Frahm, with permission.



Figure 27. *Drunella grandis*, a stonefly naiad that inhabits *Porella pinnata*. Photo by Bob Newell, with permission.

### Torrents and Waterfalls

The precipice nears and the clump of mosses soon finds itself in a freefall, wet, and being carried by the pounding water and convection currents. Soon it will rejoin the stream below, bumping along until it gets pinned behind a log or rock.

In that same freefall are insects, dwellers of the water, giving in to the strong movement of the water, then drifting with the stream. Like the moss, they await a place where they can lodge. But for them, that lodging place might be the moss itself, a haven out of the torrent that takes them to

unknown destinations. A haven where they can lay their eggs and find algae, bacteria, fungi, or smaller insects to eat. A haven where they can rest safe from larger hungry predators. A place to be until that day when they must climb to the water's surface and take their maiden flight, free from the rushing torrent that made their life so tenuous.

Table 1. Field Tray Results for species contributors with a cut-off at 90% contribution characterizing microhabitats across all depths.

	Moss	Large Gravel	Sand	Wood
<b>Lower Barton Creek</b>				
<i>Baetis tricaudatus</i>	8.24	59.89	100	24.85
<i>Diphetero hageni</i>	28.15	34.76		45.08
<i>Micrasema</i>	8.01			
Nemouridae immature	9.30			
Plecoptera sp. 1	8.01			
<i>Zapada cinctipes</i>	9.61			
<b>Santa Ana</b>				
<i>Baetis tricaudatus</i>	51.87	18.45	74.47	31.99
<i>Ephemerella dorothea</i>	6.51	27.95	12.77	12.52
<i>Lepidostoma errigenum</i>	23.92	25.69	12.77	15.99
<i>Paraleptophlebia</i>	12.12	27.91		35.49
<b>Upper Barton Creek</b>				
<i>Baetis tricaudatus</i>				57.14
<i>Psychoglypha</i>	100			42.86

Thomas (1980) successfully reared the torrential dweller *Porricondyla ramadei* (Diptera: Cecidomyiidae), taken from submerged bryophytes in the turbulent water of a mountain stream in the Pyrénées. There were also hundreds of other strictly torrential invertebrates in the sample. Wallace and Ross (1971) described a new species of caddisfly, *Pseudogoera singularis* (Odontoceridae) from mosses in waterfalls of the Southern Appalachians, USA.

### Springs

Virtanen *et al.* (2009) investigated bryophyte inhabitants in 138 boreal springs. They found that water chemistry and temperature determined bryophyte assemblages. By contrast, Ilmonen (2009) found that the macroinvertebrate assemblages correlated with physical habitat but not with changes in chemistry.

Chironomids likewise responded to temperature, but water chemistry had little effect on them in 138 springs in Finland; physical habitat was somewhat important in their distribution (Virtanen *et al.* 2009). The **Chironomidae** (Figure 15) had a closer correspondence with **Ephemeroptera** (Figure 27), **Plecoptera** (Figure 25), **Trichoptera** (Figure 6), and **Coleoptera** (Figure 41-Figure 43) than with the bryophytes. Hence, as in stream habitats, spring bryophytes and insects are relatively poor surrogates for each other. Even when the insect assemblages were similar, the environmental characters differed. As in streams, better concordance occurred when larger geographic areas were included.

Hurny *et al.* (2005) found that springs in the Arctic separated from other stream types based on nutrient concentrations and likelihood of freezing. Glacier and



mountain streams separated from both springs and tundra streams on substrate instability and likelihood of freezing.

Lindegaard *et al.* (1998) concluded that the high variability of substrate within a spring accounted for the low variation among Danish streams. This same variability also made it impossible for Lindegaard and coworkers to correlate environmental variables with fauna. They classified the macroinvertebrates associated with springs and springbrooks into seven groups: (1) **cryobiotic** species restricted to the spring area, (2) **crenophilous** species with maximum abundances in springs, (3) **lotic** species also living in the spring area, (4) **lentic** species found in **limnocrenes**, (5) **ubiquitous** species, (6) **madicolous** species, and (7) **terrestrial** species.

Thorup (1963) described insects from Danish springs. Although I don't know how they correlated with the bryophytes, the genera and some of the species mentioned are known from bryophytes: *Baetis rhodani* (Figure 8), *Brachyptera risi* (Figure 28), *Nemurella picteti* (Figure 29), *Leuctra hippopus* (Figure 30), *Leuctra fusca* (Figure 31), *Agapetus fuscipes* (Figure 32), *Crunoecia irrorata* (Figure 33), *Pericoma* cf. *blandula* (Figure 34), and *Simulium ornatum* (Figure 35).



Figure 28. *Brachyptera risi* naiad, a bryophyte inhabitant in Danish springs. Photo by Guillaume Doucet <[www.guillaume.doucet.free.fr](http://www.guillaume.doucet.free.fr)>, with permission.



Figure 29. *Nemurella picteti* adult, a stonefly whose naiads live in Danish springs. Photo by Pete Hillman, with online permission.



Figure 30. *Leuctra hippopus* naiad, a stonefly that lives in Danish springs. Photo by Niels Sloth, with permission.



Figure 31. *Leuctra fusca* naiad, a stonefly that lives in Danish springs. Photo by James K. Lindsey, with permission.



Figure 32. *Agapetus fuscipes* larva in its case, an insect that inhabits Danish springs. Photo by J. C. Schou, with permission.



Figure 33. *Crunoecia irrorata* larva in its case, an insect inhabiting Danish springs. Photo by Niels Sloth, with permission.





Figure 34. *Pericoma blandula* adult, a species whose larvae live in Danish springs. Photo Copyright by Nick Upton <www.naturepl.com>, with permission.



Figure 35. *Simulium ornatum / intermedium / trifasciatum* complex adult, a species group the lives in Danish springs as larvae. Photo by Malcolm Storey, through Discover Life online permission.

Unlike other studies on surrogates, Ilmonen (2009) found that a rare spring-dwelling caddisfly (*Crunoecia irrorata*) was a good surrogate for springs that had a high conservation value. These springs had high overall species diversity, including other rare (red-listed) species. But as in other studies cited herein, these relationships held on a regional, but not within-spring system basis. Ilmonen and Paasivirta (2005) found that while there were differences in relative abundances among types of springs, the most common taxa were the same in all of them. The insects were somewhat more abundant in moss carpets and less abundant in sites that were pools. The strongest separators related to water flow and minerogenic substrate, a relationship supported by studies in Spain (Barquin & Death 2009).

Depth is an important factor for some insects. At the Puppu Springs, NZ, the invertebrates on the moss *Cratoneuropsis relaxa* (Figure 36) were 20 times more abundant at 0.6 m depth than at 4.3 m depth (Michaelis 1977). Such depth differences can relate to temperature, oxygen availability, and photosynthetic organisms (algae)

for food. Boulders with bryophytes had more invertebrates than those at similar depths with no bryophytes.



Figure 36. *Cratoneuropsis relaxa*, a moss where depth matters to the insects. Photo by Tom Thekathyl, with permission.

Bottazzi *et al.* (2011) found that springs with mosses served as home for predominately **Chironomidae** (Figure 15) and **Plecoptera** (Figure 29-Figure 31), as well as the crenophilic microcrustaceans in **Harpacticoida** and **Ostracoda**. Only pH and temperature explained the diversity pattern, factors demonstrated as important by (Virtanen *et al.* 2009). Nevertheless, the presence of mosses increased the species diversity of the springs.

Seepage areas differ from other springs by having small flow rates in which the source water has filtered into permeable earth. These are often suitable habitats for bryophytes. In England, these seepage areas provide habitat for the crane fly *Tipula cheethami* (Figure 37) larvae living among the moss *Platyhypnidium riparioides* (Figure 38) and the snipefly *Spania nigra* (Figure 39) larvae on the liverwort *Pellia neesiana* (Figure 40) (Boyce 2002). On cliff seepages, one might find the tiny beetle *Sphaerius acaroides* (Figure 41-Figure 42) among the mosses. *Ochthebius poweri* (Figure 43) (**Coleoptera: Hydraenidae**) live in these seeps, eating the algae there. Some caddisflies occur there as well.



Figure 37. *Tipula abdominalis* larva, member of a genus that is found among *Platyhypnidium riparioides* in seepage areas of England. Photo by Tom Murray, through Creative Commons.





Figure 38. *Platyhypnidium riparioides*, a moss home for insects in seepage areas in England. Photo by David T. Holyoak, with permission.



Figure 39. *Spania nigra* adult, a snipefly whose larvae are known from the liverwort *Pellia neesiana* in seepages. Photo by Marko Mutagen, through Creative Commons.



Figure 40. *Pellia neesiana*, home for the snipefly *Spania nigra* in seepages. Photo by Jan-Peter Frahm, with permission.



Figure 41. *Sphaerius acaroides* adult, an inhabitant of mosses on cliff seepages. Photo by David Maddison, through Creative Commons.



Figure 42. *Sphaerius acaroides* larva, an inhabitant of mosses on cliff seepages. Photo by David Maddison through Creative Commons.



Figure 43. *Ochthebius exaratus* adult, an inhabitant of mosses in seepage cliffs, where it eats algae. Photo by Udo Schmidt through Creative Commons.



Ward and Dufford (1979) found that mosses and water cress (tracheophyte) had similar macroinvertebrate biomass in a Colorado springbrook-pond system. The tiny caddisfly *Hydroptila* (Figure 6) developed its largest populations on the moss. The crane fly *Limonia* (Figure 22) was present in large numbers and was restricted to mosses; *Euparyphus* (Stratomyiidae; Figure 44), another dipteran, was the second most abundant organism. Surprisingly, the *Coleoptera* (Figure 41) were the most diverse on mosses.



Figure 44. *Euparyphus* sp. larva, a genus that was restricted to mosses in a Colorado springbrook-pond system. Photo from EPA, through public domain.

Bryophytes in springs provide a continuous gradient from land to water, both vertically and horizontally (Lindegaard *et al.* 1975; Thorup & Lindegaard 1977; Bottazzi *et al.* 2011). Thus they provide a wide range of niches that promote a high invertebrate diversity. This transition furthermore makes an easy transition area for insects emerging from their aquatic stage into adults.

### Bogs and Fens

Bogs and fens are dominated by bryophytes at the ground level, creating unique and generally favorable habitats for invertebrates. Bogs have a wide temperature range within a single day (Gerson 1969). At the surface, the temperature can have a 30°C span in a single day while the stem layer experiences only a 5°C temperature span. Similarly, the surface humidity can range 40-100% while the stem layer remains at 100%. The pH ranges widely from acid bogs to rich fens, having a strong influence on some members of the insect assemblages.

Bogs have been widely studied for their unusual plant assemblages, but invertebrates have received much less attention, an omission known for a long time (Jewell & Brown 1929). Muttkowski (1912) summarized the insects in trout bogs in Yellowstone National Park, USA. These included *Ephemeroptera* (rare), *Odonata* (rare), *Hemiptera* (few), *Trichoptera* (rare), *Chironomidae* (Figure 15) (common), *Psychodidae* (common), and *Tipulidae* (frequent).

Many insects live in peatlands because of the diversity of habitats present there. For example, Bordoni (1972) found 179 species of beetles (Coleoptera) in a Tuscan fen, but only a few were actually bryophilous. Members of the *Staphylinidae* are known to feed on mosses (Mani 1962) and were well represented in that Tuscan fen. The *Sphaeriidae* (minute bog beetles) live among mosses (Arnett 1971).

A member of the insect order *Grylloblattodea* (crickets and grasshoppers) lays its eggs among mosses (Gerson 1969; Richards & Davies 1977). Crickets and grasshoppers in peatlands even feed on *Sphagnum* (Figure

1) (Vickery 1969). Uvarov (1977) suggested that these insects may eat the mosses to obtain water. Paasivirta *et al.* (1988) found that aquatic sites had greater insect emergence than semi-terrestrial sites in a boreal raised bog of central Finland.

As the hummocks and hollows build, the *Sphagnum* species change. *Sphagnum* (Figure 1) bogs undergo succession and their fauna changes as the *Sphagnum* species change (Murphy 1955). This succession of species is true for oribatid mites (Tarras-Wahlberg 1952-53) and pselaphid beetles (Reichle 1966). The fauna often occupy a specific position relative to the water table, presumably due to a preferred moisture level. Murphy (1955) found that the springtail *Sminthurides malmgreni* (Figure 45) became associated with the most humid hollow and pool species, *Sphagnum cuspidatum* (Figure 46) and *S. subsecundum* (Figure 47). When the mosses *S. papillosum* (Figure 48) and *S. magellanicum* (Figure 49), typical hummock mosses, become available, the springtails *Folsomia brevicauda* (see Figure 50) and *Isotoma sensibilis* (see Figure 51) are likely. Still others are present in the dry *Calluna* (Figure 52) and *Cladonia* (probably *Cladina*) habitat.



Figure 45. *Sminthurides malmgreni*, a bog dweller in hollows and pools. Photo by Jan van Duinen, with permission.



Figure 46. *Sphagnum cuspidatum*, a hollow and pool species where one can find *Sminthurides malmgreni*. Photo by Jonathan Sleath, with permission.





Figure 47. *Sphagnum subsecundum*, a bog hollow and pool species where one can find *Sminthurides malmgreni*. Photo by Michael Lüth, with permission.



Figure 48. *Sphagnum papillosum*, a hummock species that is home to *Folsomia brevicauda* and *Isotoma sensibilis*, with sundew. Photo by Michael Lüth, with permission.



Figure 49. *Sphagnum magellanicum*, a hummock species that is home to the springtails *Folsomia brevicauda* and *Isotoma sensibilis*. Photo by Michael Lüth, with permission.



Figure 50. *Folsomia fimetaria*, a springtail that lives in hummocks of bogs. Photo by Andy Murray, through Creative Commons.



Figure 51. *Isotoma* sp., a genus found in hummocks of *Sphagnum papillosum* and *S. magellanicum*. Photo by Anki Engström at <[www.krypinaturen.se](http://www.krypinaturen.se)>, with permission.



Figure 52. *Calluna vulgaris* heath on drier hummocks in the Outer Hebrides. Photo by Alan Silverside, with permission.

Bryophytes play a major role in the fauna of bogs. That fauna is often shared with fauna of surrounding habitats, but some unique organisms prefer that habitat, and others use it seasonally.

### Collembola - Springtails

Whereas **Collembola** are not common among submerged bryophytes, a number of species occur among bryophytes, especially *Sphagnum* (Figure 1, Figure 46-Figure 49), in bogs. Ussinger (1974) suggests collecting these bog taxa by submersing the moss in water until the **Collembola** float.

Bright (2002) reported 15 springtail species in Michigan bogs. These included *Bourletiella arvalis*



(Figure 53), *Folsomia prima* (Figure 54), *Heteraphorura subtenuis*, *Hydroisotoma schaefferi* (Figure 55), *Hypogastrura nivicola* (Figure 56), *Isotoma viridis* (Figure 57), *Neelus minutus* (see Figure 58), *Orchesella albosa* (Figure 59), *Sminthurides aquatica* (Figure 60-Figure 61), *Sminthurides malmgreni* (Figure 62), *Sminthurides occultus*, *Sminthurides penicillifer* (Figure 63), *Sminthurinus aureus* (Figure 64), *Sminthurinus bimaculatus* (Figure 65), and *Tomocerus flavescens* (Figure 66).



Figure 53. *Bourletiella arvalis*, a tiny bog-dwelling springtail. Photo by Jan van Duinen, with permission.



Figure 54. *Folsomia* sp.; *F. prima* is a bog dweller. Photo by Jan van Duinen, with permission.



Figure 55. *Hydroisotoma schaefferi* male, a species that can be found with *Sphagnum* (Figure 1, Figure 46-Figure 49) in bogs. Photo by Tom Murray, through Creative Commons.



Figure 56. *Hypogastrura nivicola*, a bog inhabitant. Photo by Scott Justis, with permission.



Figure 57. *Isotoma viridis*, a species that occurs in bogs. Photo by Jan van Duinen, with permission.



Figure 58. *Neelus murinus* with eggs – a bog inhabitant. Photo by Frans Janssens, with permission.





Figure 59. *Orchesella cincta*, member of a genus with bog inhabitants. Photo by Malcolm Storey, through Creative Commons.



Figure 60. *Sminthurides aquatica*, a bog-dweller. Photo by Andy Murray, through Creative Commons.



Figure 61. *Sminthurides aquatica* on frog's eye, demonstrating its small size. Photo by Kim Fleming, through Creative Commons.



Figure 62. *Sminthurides malmgreni*, a bog dweller. Photo by Jan van Duinen, with permission.



Figure 63. *Sminthurides* cf. *penicillifer* female. Photo by Andy Murray, through Creative Commons.



Figure 64. *Sminthurinus aureus*. Photo by Andy Murray, through Creative Commons.



Figure 65. *Sminthurinus bimaculatus*. Photo by Andy Murray, through Creative Commons.





Figure 66. *Tomocerus flavescens*, a bog dweller. Photo by Royce Bitzer, with permission.

### Coleoptera - Beetles

*Crenitis punctatostrata* (Hydrophilidae; Figure 67) is a true **bryobiont** (animal exclusively associated with bryophytes) that lives its entire life among *Sphagnum* (Figure 1) and is known from the Jura Mountains (Matthey 1977). This species lays its eggs among the mosses and the larvae remain there. The pupa lives in a cell formed from the bryophytes.

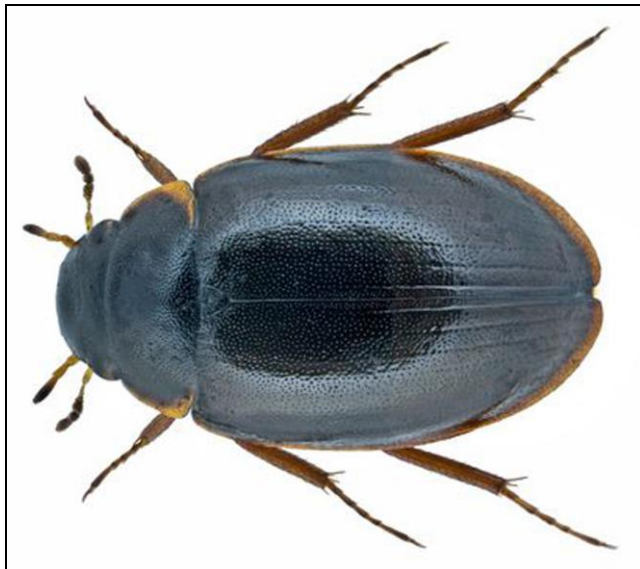


Figure 67. *Crenitis punctatostrata* adult, a species that lays its eggs among mosses and the larva develop there. Photo by Udo Schmidt, through Creative Commons.

For some *Sphagnum* (Figure 1)-associated insects, this moss provides a safe haven during unfavorable seasons. One of the more unusual of these is the tiny water beetle *Hydroporus morio* (quick silver diver; Figure 68) (Jackson 1956 in Gerson 1982). This beetle lives in *Sphagnum* pools in Europe and is sensitive to heat. When these pools dry out in summer, the exposure to heat on a sunny *Sphagnum* mat can be dangerous for *H. morio*. To survive, the beetle bores small round holes into the damp *Sphagnum* in the "dried" pool and **aestivates** (summer equivalent of hibernates) in that protected (and insulated)

location until the rains return. In the southern parts of its range, it is disappearing, apparently due to climate warming (Anderson 2015).



Figure 68. *Hydroporus morio* adult, an insect that lives in *Sphagnum* pools, then bores holes into the mat to aestivate when the pools dry. Photo by Niels Sloth, with permission.

Others find bryophytes a suitable place to survive the winter (Reichle 1966). More than 20 species of beetles in the **Pselaphidae** live in *Sphagnum* (Figure 1) bogs, where they can find a microclimate similar to that of their early postglacial ancestors. Among these are beetles that overwinter as adults in the interstitial spaces of frozen moss mats.

Larson and House (1990) found that small pools were dominated by oligochaetes, beetles, and mosquitoes. Hebauer (1994) listed **Coleoptera** (Figure 68) species he considered to be **tyrphophils**, *i.e.*, living among *Sphagnum* (Figure 1), in middle Europe. These included *Ilybius erichsoni* (Figure 69), *Agabus congener* (Figure 70), *I. wasastjernai* (Figure 71), *Bidessus grossepunctatus* (Figure 72), *Hygrotus novemlineatus* (Figure 73), *Colymbetes paykulli* (Figure 74), *C. striatus*, *Enochrus affinis*, *E. coarctatus*, *E. ochropterus* (Figure 75), *Hydrochus brevis* (Figure 76), *H. megaphallus*, *Hydroporus brevis* (Figure 77), *H. melanarius* (Figure 78), *H. memnonius* (Figure 79), *H. scalesianus* (Figure 80), *H. tristis* (Figure 81). Underground springs with *Sphagnum* housed *Hydroporus ferrugineus* (Figure 82), *H. obsoletus*, and *H. longicornis* (Figure 83). Leng (1913) reported **Parnidae** and **Elmidae** (Figure 84) in *Sphagnum* (Figure 1) bogs.



Figure 69. *Ilybius erichsoni* adult, a tyrphophil, on *Sphagnum*. Photo by Niels Sloth, with permission.



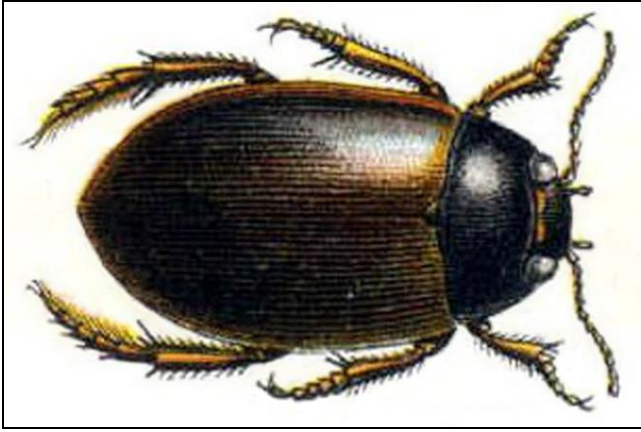


Figure 70. *Agabus congener* adult, a *Sphagnum* dweller. Image through Creative Commons.

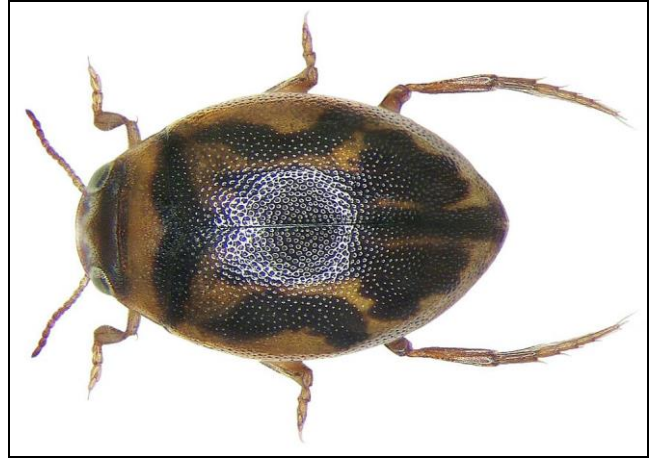


Figure 73. *Hygrotus inaequalis* adult, a *Sphagnum* dweller. Photo by Udo Schmidt, with permission.



Figure 71. *Ilybius wasastjernai* adult, a *Sphagnum* dweller. Photo by Niels Sloth, with permission.



Figure 74. *Colymbetes paykulli* adult, a *Sphagnum* dweller. Photo by Niels Sloth, with permission.



Figure 72. *Bidessus unistriatus* adult, a *Sphagnum* dweller. Photo by Udo Schmidt, through Creative Commons.



Figure 75. *Enochrus ochropterus* adult, a *Sphagnum* inhabitant. Photo by Niels Sloth, with permission.





Figure 76. *Hydrochus brevis* adult, a *Sphagnum* inhabitant. Photo by Christoph Benisch <kerbtier.de>, with permission.



Figure 77. *Hydroporus brevis* adult, a *Sphagnum* inhabitant. Photo by Niels Sloth, with permission.



Figure 78. *Hydroporus melanarius*, a bog dweller, on moss. Photo by Niels Sloth, with permission.



Figure 79. *Hydroporus memnonius* adult, a bog dweller, on moss. Photo by Niels Sloth, with permission.



Figure 80. *Hydroporus scalesianus* adult on leaf litter. Photo by Niels Sloth, with permission.



Figure 81. *Hydroporus tristis* adult on moss. Photo by Wolfram Sondermann, through Creative Commons.



Figure 82. *Hydroporus ferrugineus*, an inhabitant of underground springs with *Sphagnum*. Photo by Roger S. Key, with permission.



Figure 83. *Hydroporus longicornis* adult on moss, an inhabitant of underground springs with *Sphagnum*. Photo by Niels Sloth, with permission.





Figure 84. *Elmidae* larva, a *Sphagnum* bog dweller. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Reichle (1967) considered temperature and humidity to be the most important variables influencing the pselaphid beetles in bogs. These beetles respond to saturated humidities of 95-100%, and these match the conditions found among the interstices created by the mosses. The temperature stratification created by the mosses could explain the differences in species at different **seral stages** (stages in succession).

For the five species of pselaphids Reichle (1967) studied, these preferences were *Bythinopsis tychoides*, mean  $21.5 \pm 0.81$ , range  $25.9-15.3^{\circ}\text{C}$ ; *Decarthron defectum*,  $28.5 \pm 0.55$ ,  $31.4-24.0$ ; *Pselaphus bellax* (Figure 85),  $19.5 \pm 0.86$ ,  $24.7-13.0$ ; *Reichenbachia borealis* (Figure 86),  $21. \pm 0.99$ ,  $26.2-14.4$ ; and *Rybaxis clavata* (Figure 87),  $28.3 \pm 0.41$ ,  $29.9-25.1$ . These preferences correlated well with the natural conditions of the microhabitats where they resided in the New York bog.

To these species, a report from the New York Entomological Society (Anonymous 1925) added the pselaphid *Pselaphus erichsoni* and the staphylinid *Boreaphilus henningianus*, cohabiting in a New York, USA, bog with *Bythinopsis tychoides*. Mr. Nicholay, at that same meeting, recommended using sifting to locate the **Coleoptera** in such habitats.



Figure 85. *Pselaphus bellax* adult, a *Sphagnum* bog dweller. Photo by Yann Gobeil, through Creative Commons.



Figure 86. *Reichenbachia borealis* adult, a *Sphagnum* bog dweller. Photo by Tom Murray, through Creative Commons.



Figure 87. *Rybaxis* female adult, a *Sphagnum* bog dweller. Photo by Tom Murray, through Creative Commons.

### Odonata – Dragonflies and Damselflies

The **Odonata** are commonly seen flying about bogs. These strong fliers can easily migrate there. Boudot and Jacquemin (2002) identified 20 species of **Odonata** as tyrphobionts in France. Larson and House (1990) found that **Odonata** dominated, along with **Chironomidae** (**Diptera**; Figure 15), in the large, stable, vegetated pools. With two or more years in their naiad stage, the **Odonata** are important consumers in this habitat and may be a major factor in the insects that survive there. These dragonflies included *Aeshna subarctica* (Figure 88), *Somatochlora arctica* (Figure 89), *Leucorrhinia dubia* (Figure 90), and *Somatochlora alpestris* (Figure 91). The bog habitat influences these dragonflies by its strong *pH* fluctuations, low secondary productivity, few vertical plant structures (needed for emergence), and the isolation of bogs from each other (Dreyer 1988). Goffart and Fichet (2003) observed female *Aeshna subarctica* laying eggs (Figure 88) by inserting them into *Sphagnum* (Figure 1) at the water surface. Sahlén *et al.* (2004) found that *Aeshna subarctica elisabethae* from central and eastern Europe was "strictly" related to *Sphagnum* habitats.





Figure 88. *Aeshna subarctica* laying eggs in *Sphagnum*. Photo by Guillaume Doucet <[www.guillaume.doucet.free.fr](http://www.guillaume.doucet.free.fr)>, with permission.



Figure 89. *Somatochlora arctica* adult male; females lay eggs in *Sphagnum*. Photo by Piet Spaans, through Creative Commons.



Figure 90. *Leucorrhinia dubia*, a prominent predator in bogs. Photo by L. B. Tettenborn through Creative Commons.

Michiels and Dhondt (1990) observed dragonflies (*Sympetrum danae* – Figure 92) during their egg-laying activities in bogs. This species typically oviposits in flight while still paired in copulation. This behavior seems to make them subject to frog predation – those that were post-

tandem were attacked less frequently by the frogs. The females seemed to prefer *Sphagnum* (Figure 1) as a substrate for their eggs. They avoided warmer sites and often chose sites that already had ovipositing females on them. Michiels and Dhondt reported several threatened and potentially threatened *Odonata* species living in these diminishing habitats. These included *Nehalennia speciosa* (Figure 94), *Coenagrion johanssoni* (see Figure 93), *Aeshna caerulea* (Figure 95), *A. crenata*, *A. subarctica elisabethae* (Figure 88), *Somatochlora arctica* (Figure 89), and *S. alpestris* (Figure 91). In northern Europe where the habitat is common, these species, except *N. speciosa* and *A. crenata*, are likewise common.



Figure 91. *Somatochlora alpestris* adult, a prominent predator in bogs. Photo by Gilles San Martin, through Creative Commons.



Figure 92. *Sympetrum danae* female adult, a species that lays her eggs in bogs. Photo by L. B. Tettenborn, through Creative Commons.



Figure 93. *Coenagrion hastulatum* adult. Photo by L. B. Tettenborn, through Creative Commons.





Figure 94. *Nehalennia speciosa* mating damselfly adults. These bog dwellers lay their eggs in bogs. Photo by Guillaume Doucet <<http://guillaume.doucet.free.fr/>>, with permission.



Figure 95. *Aeshna caerulea* adult emerging. Photo by Guillaume Doucet <[guillaume.doucet.free.fr](http://guillaume.doucet.free.fr/)>, with permission.

The ground cricket *Pteronemobius* sp. (Figure 96) not only eats bryophytes, but also punctures *Sphagnum* leaves with its ovipositor to place its eggs in the resulting cavity (Vickery 1969).



Figure 96. *Pteronemobius heydenii*, a genus of cricket that eats bryophytes and punctures *Sphagnum* leaves to lay its eggs. Photo through Flickr Creative Commons.

### Diptera – Flies

If you have ever walked through a forest surrounding a bog on a humid summer evening, you probably have not forgotten the experience of blood-giving. Mosquitoes are not typical bryophyte fauna, but in bogs *Aedes excrucians* (Figure 97) occurs in bog pools and occasionally among the *Sphagnum* (Figure 1) mosses there (Elgmork & Sæther 1970).



Figure 97. *Aedes excrucians* larvae, bog pool dwellers. Photo by Donald S. Chandler, with permission.

The **Tipulidae** (Figure 98) often deposit eggs and live as larvae and pupae among the peat mosses. *Tipula* (Coulson 1962; Freeman 1968) and *Dolichopeza* (Byers 1961) also feed on the mosses. The moss-mimicking tipulid *Phalacrocer replicata* feeds on *Sphagnum* spp. (Clymo & Hayward 1982). Other tipulid species burrow into *Sphagnum* (Figure 1) spp.

But bogs often attract human traffic for berry picking and other interests. This traffic can be detrimental to these developing **Diptera**. *Molophilus ater* (Figure 99) (**Limoniidae**) numbers are lower among the peat along a path than in adjacent areas (Duffey 1979). These limoniid crane fly adults seem to spend more time where there is vegetation than on bare ground, although they seem to prefer the bare ground for laying eggs. This same preference for egg laying is not true for large bare areas. Unfortunately, larvae are often crushed along the paths, especially those near the surface.





Figure 98. **Tipulidae** adult, a common family in bogs. Photo by Bob Armstrong, with permission.



Figure 99. **Molophilus ater** adult, a species negatively affected by bog traffic. Photo by James K. Lindsey, with permission.

As in most aquatic moss habitats, **Chironomidae** (Figure 15) are important contributors to the fauna (Muttkowski 1912; Larson & House 1990). Smirnov (1961) did not find any abundant species in *Sphagnum* (Figure 1) bogs to specialize on a food group, but one chironomid, *Psectrocladius psilopterus*, was the only species to eat submerged *Sphagnum*; even so, it ate primarily algae.

### Other Insects

The moisture available within a *Sphagnum* habitat, perhaps made safer by the antibiotic properties of the moss, provides a suitable habitat for nests of *Myrmica ruginodis* (Figure 100-Figure 101) and *Formica picea* (Figure 102) (Matthey 1971). These ants also feed on the mosses (Plitt 1907) and become major predators when the bog dries up (Grdović & Sabovljević 2008).



Figure 100. **Myrmica ruginodis** pupa among mosses. Photo by James K. Lindsey, with permission.



Figure 101. **Myrmica ruginodis** adult amid mosses. This species makes its nest of *Sphagnum* fragments. Photo by James K. Lindsey, with permission.



Figure 102. **Formica picea** adult, a species that makes nests of *Sphagnum*. Photo by April Nobile <[www.antweb.org](http://www.antweb.org)>.

On one fortunate adventure into a Michigan, USA, fen I had the privilege of watching ants on one of their nests on a windy day (Figure 103). The light-weight *Sphagnum* pieces were flying off the nest faster than they could grab new ones and repair the nest. This of course created great activity among the ants (Figure 104).





Figure 103. Ant nest in *Sphagnum* in a Michigan fen. Photo by Janice Glime.



Figure 104. Close view of ants repairing nest of *Sphagnum* in a Michigan fen as its bits of *Sphagnum* are being scattered by wind. Photo by Janice Glime.

A number of terrestrial insect types can be found in bogs and fens as well, including crickets and grasshoppers (Vickery 1969), caterpillars of moths (Chapman 1894), and aphids in the genera *Myzodium* (Figure 105) and *Muscaphis* (Figure 106) (Gerson 1969). But aquatic and semi-aquatic types occur there as well, including the biting midge *Forcipomyia* (Figure 107) (Oldroyd 1964) and mayfly naiads (Richardson 1981).



Figure 105. *Myzodium mimulicola*, aphids that live in bogs. Photo by Andrew Jensen, through Creative Commons.



Figure 106. *Muscaphis utahensis*, a bog-dwelling aphid. Photo from Biodiversity Institute of Ontario, through Creative Commons.



Figure 107. *Forcipomyia* sp. larvae, a biting midge that lives among mosses in bogs. Photo by Tom Murray, through Creative Commons.

Although some of the insects eat *Sphagnum*, Danks and Rosenberg (1987) report that most species in Canadian bogs are generalists. Flannagan and Macdonald (1987) likewise found the **Ephemeroptera** and **Trichoptera** of Canadian peatlands to be generalists. They suggested that the ability for some insects to survive in temporary pools provided adaptations that also permitted them to live in other wet habitats such as peatlands. Mayfly naiads even use *Sphagnum* species for "nests" (Richardson 1981).

## Lakes and Ponds

Floating bryophytes can be abundant in small lakes and ponds. The thallose liverwort *Riccia fluitans* (Figure 108) can form dense 3-d mats that provide a protective network. The spaces formed house numerous invertebrates in these floating habitats (Armstrong 2014).

Needham (1901) found layers of shed exuviae of the dragonfly *Gomphus exilis* (Figure 109), with *G. spicatus* mixed in, among mosses on logs at the edge of Little Clear Pond, suggesting the mosses created a preferred site for emergence.





Figure 108. *Riccia fluitans*, home for numerous insects in the floating mats. Photo by Jan-Peter Frahm, with permission.



Figure 109. *Gomphus exilis* female, a species that uses mosses for emergence. Photo by Sheryl Pollock, with permission.

One of the unusual habitats at the edge of lakes is the **moss ball**. Moss balls generally begin on a small pebble that gets moved back and forth across the shoreline as the water gets blown onto the shore and recedes. These are able to develop a special fauna of *Asellus aquaticus* oligochaetes, and leeches on balls formed by *Fontinalis antipyretica* (Figure 10) and *Drepanocladus sendtneri* (Figure 110), but insects were not mentioned (Luther 1979 in Gerson 1982).



Figure 110. *Drepanocladus sendtneri*, a moss-ball former that is inhabited by invertebrates. Photo by Michael Lüth, with permission.

Floating plants provide a habitat that is constantly wet, yet does not require breathing under water. Plants such as those in the flowering plant family Lemnaceae (duckweeds) have their own fauna of insects. And in some lakes and ponds, the floating thallose liverwort *Ricciocarpus natans* (Figure 111) may occur with the duckweeds. In these habitats one might find the springtail *Sminthurides aquaticus* (Figure 112) that eats from the surface, the beetle *Tanysphyrus lemnae* (Figure 113) that completes its entire life cycle in only two weeks on *Lemna* (Figure 113), but it is not yet known from *Ricciocarpus*, and *Mesovelis mulsanti* (Figure 114), a bug known as the water treader, crawling on the surface and in depressions on the surface of this floating habitat (Scotland 1934). The liverwort *Ricciocarpus natans* is also capable of rearing the dipteran *Phytoliriomyza mesnili* (Agromyzidae) (Spencer 1990), but it can pupate on more occasionally inundated species such as *Riccia beyrichiana* (Figure 115) and feed on this and other terrestrial bryophytes (Hering 1966).



Figure 111. *Ricciocarpus natans*, home for springtails and other surface dwellers. Photo by Jan-Peter Frahm, with permission.



Figure 112. *Sminthurides aquaticus*, a springtail that lives on *Ricciocarpus natans*. Photo by Andy Murray, through Creative Commons.





Figure 113. *Tanysphyrus lemnae* on *Lemna*. Note the holes chewed in the leaves by these weevils. Photo by Aydin Örstan through, Creative Commons.



Figure 114. *Mesovelis mulsanti*, a surface dweller. Photo by Matt Bertone, through Creative Commons.



Figure 115. *Riccia beyrichiana*, site for pupation of *Phytoliriomyza mesnili* when the thallus is inundated. Photo by Jan-Peter Frahm, with permission.

## Arctic and Alpine

In investigating alpine streams of New Zealand, Suren (1993) found that streambed stability strongly influenced the bryophyte distribution. These communities are dominated by **Nematoda**, **Oligochaeta**, **Copepoda**, and **Chironomidae** (Figure 15). These differed in fauna from bryophytes outside New Zealand, particularly certain families of **Ephemeroptera**, **Plecoptera**, and **Trichoptera** (EPT) that are also present elsewhere in New Zealand. Nevertheless, the invertebrate densities within the bryophytes are higher above treeline than below. The invertebrate densities are higher among bryophytes that have a high periphyton component compared to those with a higher detrital component.

In the alpine area of the South Island of New Zealand, Suren (1988) found that the dominant bryophyte dwellers are the stoneflies *Zelandoperla* (Figure 18) and *Zelandobius* (Figure 19) and the midges (**Chironomidae**, Figure 15). The mosses had 5-15 times as many invertebrates as the rocky areas, but these moss-dwelling invertebrates also include nematodes, mites, copepods, ostracods, and other non-insect invertebrates. The most common mayflies are restricted to rocky areas.

In the Southern Alps of New Zealand, Cowie and Winterbourn (1979) found 44 species of invertebrates among the mosses. These are mainly immature stages of insects, with the fauna varying by moss; the moss species reflects differences in habitat. *Fissidens rigidulus* (Figure 116) grows in the torrential middle channel of the stream and supports *Zelandoperla fenestrata* (**Plecoptera**; see Figure 18), *Zelolessica cheira* (**Trichoptera**; see Figure 117-Figure 118), *Empididae* (**Diptera**; Figure 21) and the ever-present **Chironomidae** (Figure 15). Among the clumps of *Pterygophyllum quadrifarium* (Figure 119) in the saturated inner spray zone Cowie and Winterbourn found *Austroperla cyrene* (**Plecoptera**), and **Helodidae** (**Coleoptera**) as the most abundant species, along with the flatworm *Neppia montana*. *Cratoneuropsis relaxa* (Figure 36), in the outer spray zone, was not a good insect habitat, housing primarily the isopod *Styloniscus otakensis*. Water Saturation, flow rates, and available detritus as a food source seem to have the greatest influence on the locations of these insects.



Figure 116. *Fissidens rigidulus*, a moss that grows in the torrential mid-channel where **Plecoptera** and **Diptera** are common. Photo by Bill & Nancy Malcolm, with permission.





Figure 117. *Zelolessica* sp., prevalent among *Fissidens rigidulus* midstream in Southern Alps of New Zealand. Photo by Stephen Moore, Landcare Research NZ, with permission.



Figure 118. *Zelolessica* sp., prevalent among *Fissidens rigidulus* midstream in the Southern Alps of New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 119. *Pterygophyllum quadrifarium*, a moss that houses insects in the spray zone of torrential channels in New Zealand. Photo by Bill and Nancy Malcolm, with permission.

Robinson *et al.* (2001) studied the glacial streams of the Swiss Alps. These streams experience strong seasonal changes in water chemistry resulting from the seasonal changes in glacial melt, especially in water turbidity, particulate phosphorus, and conductivity. The macroinvertebrates likewise vary seasonally, with winter macroinvertebrate taxon richness being 2-3 times as high as that in summer. These same differences are also reflected in higher numbers and biomass in winter. Although taxa are not delimited by substrate in this study, many of the dominant taxa are species known as common bryophyte inhabitants.

**Diptera**, common among temperate streams, are even more common in Alaskan streams (Oswood 1989). **Plecoptera** and **Ephemeroptera** are next in abundance, but **Trichoptera** are somewhat rare. The **Hemiptera**, **Odonata**, **Megaloptera**, **Coleoptera**, net-spinning caddisflies, burrowing mayflies, and the stoneflies **Pteronarcyidae**, **Peltoperlidae**, and **Perlidae** are rare or absent. On the other hand, the ever present **Chironomidae** (**Diptera**; Figure 15) and **Nemouridae** (**Plecoptera**) actually increase from south to north in the northern hemisphere.

A similar predominance of **Chironomidae** (Figure 15) is seen in the European Central Alps – comprising 90-95% of the emergence (Füreder *et al.* 2005). As in Oswood's (1989) Alaskan study, **Ephemeroptera**, **Plecoptera**, and **Trichoptera** comprised much fewer numbers. Füreder *et al.* (2001) considered seasonal shifts from harsh summers to less severe autumn and winter conditions in the Tyrolean Alps, Austria, to affect the insect life history patterns and maintain a relatively high insect diversity and productivity in glacier-fed streams. As in glacial streams, the individual alpine streams of the French Pyrénées seem to differ greatly in diversity, displaying distinct benthic macroinvertebrate communities. Within a stream, the 15 most abundant taxa were consistently more stable and persistent from one year to the next than was the entire stream community (Brown *et al.* 2006).

Miller and Stout (1989), working in Alaska, suggested that to be so successful the dipterans that compose the most numerous and variable taxa in the Arctic must have variable **diapause** (period of suspended development; state of physiological dormancy), ability to grow in cold waters, and good dispersal powers.

## Disturbance

Disturbance greatly reduces the number of invertebrates, and in some cases the bryophytes, on stones in streams (Englund 1991; Parker & Huryn 2006). Small stones rarely have bryophytes (Slack & Glime), except when they are embedded in the substrate (Englund 1991). Rock size likewise affects the diversity of stream insects (Hart 1978). In Englund's study, following disturbance, several invertebrate taxa increased their density on moss-covered undersides of over-turned stones. The undisturbed moss-covered rocks acquired increased density of invertebrates as a result of the disturbance. On the other hand, on disturbed rocks recovery of lost mosses [*Fontinalis dalecarlica* (Figure 16), *Hygrohypnum* (Figure 120-Figure 121)], and hence invertebrate inhabitants, was poor even 14 months after the stones were overturned.



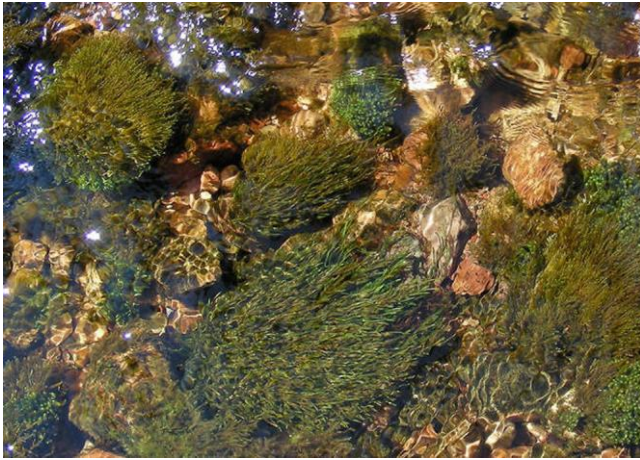


Figure 120. *Hygrohypnum ochraceum* habitat, a genus that can have poor recovery after disturbance, resulting in loss of insects. Photo by Dick Haaksma, with permission.



Figure 121. *Hygrohypnum ochraceum*, home to many insects. Photo by Michael Lüth, with permission.

In an Alaskan stream, Parker and Huryn (2006) attributed the high macroinvertebrate density in a spring stream to the density of bryophytes there. That biomass was more than 1000 times the density of the mountain stream where disturbance among the loose rocks was great during spring melt.

Disturbance can take the opposite form as well. During the dry season, aquatic insects must find a place of refuge that provides sufficient moisture, or go dormant. In a first-order stream in the Atlantic Forest, Brazil, Rosa *et al.* (2011) found that Chironomidae dominate in both the rainy and dry seasons, but that in the rainy season the Ceratopogonidae are second, whereas in the dry season it is the annelid family Naididae that is second. Rosa and coworkers concluded that the bryophyte habitat provides refuge during spates, minimizing downstream movement of the invertebrate fauna. The density of the fauna is much greater during the rainy season, but the diversity is similar.

## Retention

Restoration is not always friendly to mosses. In a headwater stream, the moss cover declined dramatically following restoration (Muotka & Laasonen 2002). This resulted in increases of insects only among the algae-eating scrapers. The mosses were an important retentive feature

for macroinvertebrates, but the restoration techniques knocked them loose from numerous locations, favoring the growth of algae.

## Colonization

The rapidity of invertebrate recolonization of mosses can be amazing. Maurer and Brusven (1983) found that insects colonized insect-free *Fontinalis neomexicana* (Figure 4) to capacity within one week. The moss substrate had 5-30 times the densities of insects compared to the mineral substrate. As in many streams, larvae of midges (Chironomidae, Figure 15) were most abundant. Thienemann (1936), in his enumeration of alpine Chironomidae, commented on the importance of mosses as a habitat.

Korsu (2004) found that the restoration procedure in one Finnish stream destroyed almost half of the bryophytes and invertebrate densities plummeted. But recolonization was rapid. The disturbed area was recolonized within two weeks and peak numbers were reached within one month. Korsu found that recovery was especially fast in winter, with bryophytes playing a major role. It is interesting that the density of insects on bryophytes was higher after the restoration than before. The mayfly *Baetis* (Figure 8) had a negative correlation with the bryophytes before restoration, but afterwards (within 1 day!) it had a positive correlation. A similar response occurred for *Hydropsyche siltalai* (Figure 122). Korsu concluded that bryophytes provided refugia during the disturbance and remained a shelter long afterwards.



Figure 122. *Hydropsyche siltalai* larva, a species that increased in numbers after restoration of a stream in Finland. Photo by Urmas Kruus, with permission.

Experimental studies on colonization of mosses are relatively rare. Some of these have been discussed earlier under Artificial Mosses (Chapter 11-1). Maurer and Brusven (1983), however, designed a study using live *Fontinalis neomexicana* (Figure 4) in an Idaho, USA, river. After removing all the insects, they trimmed the moss clumps into 40 X 15 cm plots and arranged them in a natural streambed in five staggered rows with three clumps per row, as well as two comparative samplings. After three weeks of colonization, moss clumps were collected in nylon organdy net (250 µm mesh) to keep insects intact. Insects were removed by washing and hand picking. It



took only one week for insects to reach carrying capacity of the mosses (compared to controls)! The caddisfly *Micrasema* sp. (Figure 123) and mayfly *Dipheter hageni* (= *Baetis parvus*; Figure 124) were especially prevalent among moss clumps during the study. At the same time, the moss cover did not change the insect densities in the underlying hyporheic zone.



Figure 123. *Micrasema charonis* larva with a case made from moss parts. Photo by Bob Henricks, with permission.



Figure 124. *Dipheter hageni* naiad, common among *Fontinalis neomexicana* in Idaho. Photo by Donald S. Chandler, with permission.

Maurer and Brusven (1983) found that the **Ephemeroptera** were the most abundant in both test and control clumps, with **Diptera**, **Trichoptera**, **Coleoptera**, and **Plecoptera** following in that order. The **Chironomidae** (Figure 15) made up ~94% of the **Diptera**. The riffle beetle *Cleptelmis ornata* (Figure 125) was a slow colonizer, reaching carrying capacity only after 4-6 weeks.

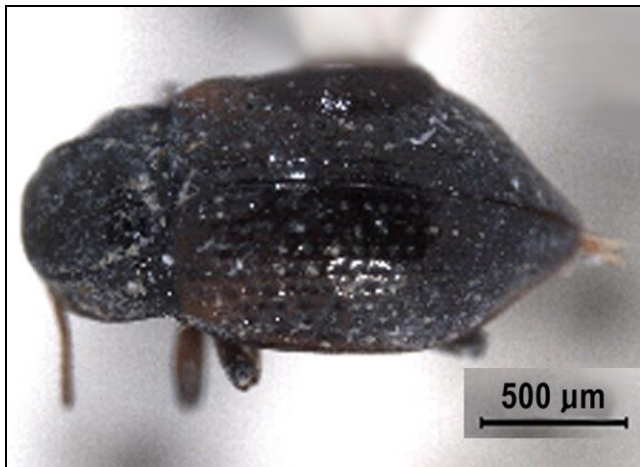


Figure 125. *Cleptelmis ornata* adult, a slow colonizer of bryophytes. Image modified from Biodiversity Institute of Ontario, through Creative Commons.

Mackay and Waters (1986) found that mosses provided suitable sites for the **Hydropsychidae** (net-spinning caddisflies; Figure 3) downstream of impoundments. They suggested that the mosses and algae provided suitable sites for attachment of their nets and the location benefitted from the settling effect of the impoundment on abrasive sand.

Streams suffer natural disturbance. In two North Swedish woodland streams nearly 17% of the moss-covered stones were overturned in just a few years (Englund 1991). In experiments, overturning rocks with mosses resulted in a reduction of both ash-free dry weight and diversity. On the other hand, three out of 16 taxa actually increased density on the underside of the overturned stones, living among the buried mosses. All the other taxa decreased in density. Even after 14 months the mosses and invertebrate populations had not recovered.

As already noted, Gurtz and Wallace (1984) found that presence of mosses increased the density of taxa following clear cutting surrounding a southern Appalachian Mountain stream. But disturbance resulting from the insecticide fenitrothion on bogs did not have as favorable a result (Fairchild & Eidt 1993). The poison caused a reduction in insect emergence for the next 6-12 weeks, with the **Chironomidae** (Figure 15) and **Ceratopogonidae** (Figure 126) experiencing more than 50% reduction for at least 1 month after the treatment. Since bog pool insects carry the nutrients to land, this nutrient transfer diminished and more nutrients accumulated in the bog pools.



Figure 126. *Bezzia* larva, in a family (**Ceratopogonidae**) that is quickly reduced by fenitrothion in bogs. Photo from <www.dfg.ca.gov>, through public domain.

It is interesting that in a study of Swedish streams, Malmqvist and Hoffsten (2000) found a negative correlation between macroinvertebrate richness and moss (*Fontinalis* – Figure 10) coverage. In a glacial river in Iceland, Gislason *et al.* (2001) found that distance from glacier, altitude, bryophyte biomass, and Pfankuch Index of channel stability explaining 31% of the variability in the macroinvertebrate data. The **Chironomidae** (Figure 15) predominated, but **Simuliidae** (Figure 35), **Plecoptera** (Figure 28-Figure 31), and **Trichoptera** (Figure 123) were present in low numbers.

In New Zealand alpine streams, bryophytes were confined to stable substrates (Suren 1991a). Suren (1988) found a negative effect on **Collembola** (Figure 45) when real mosses were replaced by artificial mosses in the high



alpine streams of the South Island of New Zealand. Among those moss-inhabited substrates, *Limonia hudsoni* (see Figure 22) and *Zelandoperla* sp. (Figure 18) were typically associated with bryophytes (Suren 1991a).

Not all bryophyte growths bring a positive recovery of the insect fauna. In the Kuparuk River, Alaska, USA, fertilization by phosphorus encouraged the growth of mosses after eight years of increased phosphorus. Persistence of the mosses had both positive and negative effects on the insect populations. It prevented the recovery of *Ephemerella* (Figure 9) (Slavik *et al.* 2004) and midge (*Chironomidae*, Figure 15) taxa, including the tube-building *Orthocladus rivulorum* (Figure 127-Figure 128) that had been affected by the shifts in primary producers. This shift included the loss of epilithic algae due to human activity, but they subsequently returned within 2-3 years. Once the bryophytes became established, they persisted, changing the morphology of the stream bottom.



Figure 127. *Orthocladus rivicola* larva, an insect that did not recover from phosphorus fertilization that caused an increase in moss growth in an Alaskan river. Photo from Stroud Water Research Center, through Creative Commons.



Figure 128. Orthoclad in silt tube. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Disturbances that remove mosses can greatly affect the invertebrate fauna. Gurtz and Wallace (1984) found that moss (*Hygroamblystegium tenax* – Figure 2) density and leaf detritus were the most important characters determining abundance of aquatic insects following a disturbance. Following clearcutting, the greatest increase in taxon density in the stream that drained the clear-cut watershed occurred in the moss-covered rock face compared to any other substrate. Moss habitats experienced increases of the shredder stonefly *Amphinemura wui* (Figure 13), a response that Gurtz and Wallace attributed to the accumulation of particulate matter

by the moss. The *Baetidae* mayflies likewise increased, experiencing their greatest increase among mosses where there was also the greatest increase in number of diatoms. But the chironomid *Eukiefferiella* spp. (Figure 129) showed the sharpest increase among the insects, occupying mosses on the rock face.



Figure 129. *Eukiefferiella* (arrow) on *Nesameletus ebop-ohaupapa*. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Forestry practices for logging and drainage often have considerable impact on the bryophytes and their inhabitants. In a small headwater stream where *Fontinalis dalecarlica* (Figure 16) formed the dominant habitat in riffles, forestry disturbances by ditch construction changed these mossy habitats to sand riffles (Vuori & Joensuu 1996). Transplanted mosses in the disturbed sites accumulated considerably more inorganic matter than did undisturbed controls. Subsequently, the invertebrate richness was significantly lower as well. The mosses at the control site supported a dominance of shredder stoneflies whereas the disturbed site was dominated by blackflies (*Simuliidae*; Figure 35).

## Pollution Effects

In addition to physical disturbances of flooding and human activities, pollution affects both the bryophytes and their fauna. Winterbourn *et al.* (2000) looked for effects on the food chain in New Zealand streams where mosses were a significant component. Despite the lowering of pH and increases in aluminium and iron in the water, there was not a biomagnification effect in the food web. The metal concentrations in the invertebrates was considerably lower than that in the mosses. It is possible that the bryophytes were able to sequester the metals, thus protecting the invertebrates from those that might have increased in their algal and detrital food.

## Geographic Differences

If one were to examine bryophytes in New Zealand streams, the fauna would be significantly different from that of bryophytes in the North Temperature Zone. In New Zealand, instead of the typical mayflies, stoneflies, and caddisflies, the fauna is dominated by nematodes, oligochaetes, and copepods, with the only abundant insect being *Chironomidae* (Figure 15) (Suren 1993). In fact, other types of insects comprise less than 2% of the



invertebrate fauna. This is not due to a difference in bryophytes, but rather the absence of families that typically inhabit the North Temperate bryophyte habitat.

By contrast, Egglisshaw (1969) found that mayflies occupied up to 16% of the invertebrate fauna of Scottish streams. Suren (1993 – updated in Table 2) reviewed studies from other parts of the world and found that the most important bryophyte insects were **Plecoptera** (**Nemouridae**, **Perlodidae**, **Leuctridae**, **Chloroperlidae**),

**Ephemeroptera** (**Baetidae**, **Heptageniidae**, **Ephemerellidae**), and **Trichoptera** (**Brachycentridae**, **Glossosomatidae**, **Lepidostomatidae**, **Limnephilidae**, and **Sericostomatidae**). These families mesh well with my own studies in bryophytes of Appalachian Mountain streams, eastern USA, except for **Perlodidae**, **Heptageniidae**, and **Sericostomatidae**. Others (**Baetidae**, **Lepidostomatidae**, **Limnephilidae**) were uncommon in the Appalachian streams.

Table 2. Percentages of the contributions by invertebrate taxa > 0.1% of the total invertebrate density in ten studies on invertebrate fauna of stream bryophytes: 1) Percival & Whitehead 1929 from a) thin moss & b) thick moss; 2) Percival & Whitehead 1930; 3) Frost 1942; 4) Egglisshaw 1969; 5) Stern & Stern 1969; 6) Glime & Clemons 1972; 7) Lindegaard *et al.* 1975; 8) Cowie & Winterbourn 1979; 9) McKenzie-Smith 1987; 10) Smith-Cuffney 1987 from a) unshaded and b) shaded streams; 11) Suren 1991a from a) unshaded and b) shaded streams; 12) Vlčková *et al.* 2002; - = not reported with abundances > 0.1% total density. (from Suren 1993). The last two columns indicate the number of studies presented here in which the taxon was represented by >0.1% and the average percent of the community the taxon represented.

	1a	1b	2	3	4	5	6	References			10a	10b	11a	11b	No. Studies	Av % Comp
Turbellaria	-	-	-	0.4	-	0.3	-	-	-	-	1.6	-	-	-	0.26	3
Nematoda	-	-	-	-	-	-	-	-	-	-	1.8	2.8	22.1	12.5	14.65	4
Oligochaeta	3.6	3.3	24.1	0.4	-	-	-	10.3	-	2.9	6.0	1.4	-	-	0.57	8
Tardigrada	-	-	-	-	-	-	-	-	-	-	-	-	2.4	-	0.59	1
Amphipoda	1.2	1.1	0.1	-	-	4.8	-	6.9	-	42.5	-	-	-	-	6	4.0
Copepoda	-	-	57.8	2.5	-	-	-	-	-	-	-	4.0	9.0	1.5	0.47	5
Ostracoda	-	-	-	-	-	-	-	-	-	-	-	-	-2.8	0.7	0.13	2
Isopoda	-	-	-	-	-	1.9	-	-	-	-	-	-	-	-	1	0.2
Hydracarina	3.3	3.0	3.6	1.0	-	0.1	-	6.3	-	-	2.7	7.0	1.1	5.9	0.73	10
Collembola	-	-	-	-	-	-	-	4.2	-	-	1.2	-	-	-	2	0.9
Ephemeroptera	15.9	6.5	-	4.0	4.2	2.6	2.0	-	-	5.46	15.2	1.8	-	-	0.88	9
Plecoptera	-	-	-	-	44.6	2.9	5.7	16.7	22.5	5.4	3.1	8.2	2.1	2.5	0.01	10
Diptera	1.3	1.5	0.1	2.3	2.3	-	12.6	-	21.2	-	1.1	6.1	1.5	7.7	1.96	11
Chironomidae	54.3	40.9	9.2	83.0	34.1	77.9	71.7	33.2	33.7	21.6	54.0	53.0	57.7	63.4	33.81	14
Coleoptera	6.2	4.2	3.6	2.0	-	0.1	2.9	0.7	-	2.3	-	-	-	-	0.15	8
Trichoptera	4.0	0.3	0.1	3.7	1.4	9.1	3.4	-	23.6	13.4	6.2	7.9	-	-	0.29	11

## Summary

Bryophytes increase the number of niches for occupancy by aquatic insects. They increase surface area, culture algae, collect detritus, provide high prey density, and provide a refugium against the current. At the same time they permit the insects to live in the greater oxygen provided by the rapid flow, saving them ventilation energy. Feeding groups of these insects include collector-gatherers, scrapers, shredders, collector-filterers, and engulfer, with collector-gatherers typically being most abundant.

Altitude and latitude are important determinants of both the bryophytes and the associated fauna. Thickness of the moss mat also is important in determining the fauna, with thicker mats creating more niches.

The most common orders of moss dwellers in streams are **Ephemeroptera** (mayflies), **Plecoptera** (stoneflies), **Trichoptera** (caddisflies), and **Diptera** (flies). Streams in the Arctic and alpine habitats lack most of the **Trichoptera** (caddisflies), but otherwise have similar order representation among stream bryophytes, with even more **Chironomidae**. The associations of insects with the species of bryophytes may be a consequence of both needing similar conditions, as exemplified by the similarities of insect

communities on the moss *Fontinalis dalecarlica* and the liverwort *Scapania undulata*, two species that often occur side-by-side. Nevertheless, bryophytes do not make good surrogates for the stream inhabitants, correlating primarily with nutrient levels and habitat heterogeneity, whereas insects correlate more with stream size, pH, and water color. In fact, clumps of string and other artificial mosses seem to attract communities similar to those on real mosses. On the other hand, the presence of bryophytes will usually indicate a high density of insects.

The bryophytes may serve as a refuge for insects in winter when non-bryophyte plants are absent and the bryophytes are common in fast water where freezing is less common. The bryophytes furthermore serve as a location of collected detritus and a site for winter diatoms.

Within the clump of bryophytes of a stream one can find a detritus zone with little or no flow, a water zone within the moss clump, and a **madicolous** zone just above the water surface but where the bryophytes are still wet. And at the surface of the moss, but submerged, the highest water velocity and therefore the most oxygen exist.

Waterfalls may have specialists that live among the wet mosses, avoiding the torrent itself. Springs often have dense bryophyte cover. **Chironomidae** here



respond to temperature; many insects also respond to nutrient concentrations or pH. Depth of streams, pools, and springs can influence insect community composition, in part because of temperature and oxygen gradients. Bogs and fens have both pool and dry hummock conditions, contributing a wide range of niches that differ in moisture, temperature, and light. Consequently, there is a wide variety of insects, and even flying adults make use of the mosses for egg deposition, mating, and resting. More **Collembola** (springtails) are found in bogs and fens than in most aquatic habitats. **Coleoptera** (beetles) and **Odonata** (dragonflies and damselflies) likewise are common in these habitats. **Hymenoptera** (ants, bees) are absent from streams and lakes, but in bogs and fens ants build nests from the *Sphagnum*. Little seems to be published about insects associated with lake bryophytes. Some of the beetles are associated with floating *Riccia fluitans* and *Ricciocarpos natans* in shallow lakes. In one case, the latter is inhabited by the leaf miner *Phytoliriomyza mesnili*.

Disturbance immediately reduces the number of invertebrates, but if mosses remain or are replaced, they are quickly recolonized by remaining drifting organisms or from egg-laying. Attempts at restoration can cause the bryophytes to break loose and reduce the insect fauna.

If one compares the bryophyte fauna around the world, differences in relative abundance of the orders are apparent. These differences are often the result of evolutionary and distributional differences. For example, the families of the insects are different in Australia and New Zealand from those in North America.

## Acknowledgments

My gratitude goes to my sister, Eileen Dumire, for her candid suggestions for improvement of this chapter. I appreciate all the photographers who have kindly given me permission to use their images and to those who have contributed their images to Creative Commons.

## Literature Cited

- Allan, J. D. 1975. The distribution ecology and diversity of benthic insects in Cement Creek, Colorado. *Ecology* 56: 1040-1053.
- Anderson, Roy. 2015. *Hydroporus morio* – quicksilver diver. Northern Ireland Priority Species. Accessed 9 January 2015 at <<http://www.habitas.org.uk/priority/species.asp?item=7549>>
- Armstrong, W. P. 2014. Bryophyta. Accessed 18 September 2014 at <<http://waynesword.palomar.edu/bryophl.htm>>.
- Arnett, R. H. Jr. 1971. The Beetles of the United States. American Entomological Institute, Ann Arbor, MI.
- Autio, O. and Salmela, J. 2010. The semi-aquatic fly fauna (Diptera) of wetlands of the Åland Islands. *Mem. Soc. Fauna Flora Fenn.* 86: 43-53.
- Barquín, J. and Death, R. G. 2009. Physical and chemical differences in karst springs of Cantabria, northern Spain: Do invertebrate communities correspond? *Aquat. Ecol.* 43: 445-455.
- Bordoni, A. 1972. *Boll. Ass. romana Entomol.* 27: 9-25.
- Bottazzi, E., Bruno, M. C., Pieri, V., Disabatino, A., Silver, L., Carolli, M., and Rossetti, G. 2011. Spatial and seasonal distribution of invertebrates in Northern Apennine rheocene springs. *J. Limnol.* 70(suppl. 1): 77-92.
- Boudot, J. P. and Jacquemin, G. 2002. Les Odonates des tourbières et lacs acides du massif vosgien: bilan de 10 années de prospection. Actes des 1ères et 2ndes Rencontres odonatologiques de France, Soc. Fr. d'Odonatologie, Martinia, numéro hors-série 4: 27-38.
- Bourassa, N. and Morin, A. 1995. Relationships between size structure of invertebrate assemblages and trophy and substrate composition in streams. *J. N. Amer. Benthol. Soc.* 14: 393-403.
- Boyce, D. C. 2002. A review of seepage invertebrates in England. *English Nature Research Reports* #452.
- Bright, Ethan. 2002. Semiaquatic Collembola (Springtails) of Michigan. *Aquatic Insects of Michigan*. Last updated 4 November 2013. Accessed 2 September 2014 at <[http://insects.ummz.lsa.umich.edu/~ethanbr/aim/sp/Collembola/sp\\_collemb.html](http://insects.ummz.lsa.umich.edu/~ethanbr/aim/sp/Collembola/sp_collemb.html)>.
- Brown, L. E., Milner, A. M., and Hannah, D. M. 2006. Stability and persistence of alpine stream macro-invertebrate communities and the role of physico-chemical habitat variables. *Hydrobiologia* 560: 159-173.
- Byers, G. W. 1961. The crane fly genus *Dolichopeza* in North America. *Bull. Univ. Kans. Sci.* 42: 665-924.
- 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.
- Chapman, T. A. 1894. Some notes on the microlepidoptera whose larvae are external feeders, and chiefly on the early stages of *Eriocephala calthella* (Zygaenidae, Limacodidae, Eriocophalidae). *Trans. Entomol. Soc. London* 42: 335-350.
- Clymo, R. S. and Hayward, P. M. 1982. The ecology of *Sphagnum*. In: Smith, A. J. E. (ed.). Chapter 8. Bryophyte Ecology. Chapman & Hall, New York, pp. 229-289.
- Corona, E. M. 2010. Ephemeroptera, Plecoptera and Trichoptera microhabitat distributions in streams. Ph.D. dissertation, California State University, Long Beach, 76 pp.
- Coulson, J. C. 1962. The biology of *Tipula subnodicornis* Zetterstedt, with comparative observations on *Tipula paludosa* Meigen. *J. Anim. Ecol.* 31: 1-21.
- 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.
- Cox, R. J. 1988. A study of the invertebrate communities associated with real and artificial bryophytes in lotic ecosystems. Unpublished PhD thesis, University of Tennessee, pp. 163.
- Danks, H. V. and Rosenberg, D. M. 1987. Aquatic insects of peatlands and marshes in Canada: Synthesis of information and identification of needs for research. *Mem. Entomol. Soc. Can.* 119: 163-174.
- Dreyer, W. 1988. Zur Ökologie der Hochmoorlibellen. *Bonn Zool. Beitr.* 39: 147-152.
- Duffey, E. 1979. Some effects of trampling on *Molophilus ater* (Meigen) (Diptera, Tipulidae). *Biol. Conserv.* 16: 219-232.
- Egglishaw, H. J. 1969. The distribution of benthic invertebrates on substrata in fast flowing streams. *J. Anim. Ecol.* 38: 19-33.



- Elgmork, K. and Sæther, O. R. 1970. Distribution of invertebrates in a high mountain brook in the Colorado Rocky Mountains. Univ. Colorado Stud. Ser. Biol. 31: 1-55.
- Englund, G. 1991. Effects of disturbance on stream moss and invertebrate community structure. J. N. Amer. Benthol. Soc. 10: 143-153.
- Fairchild, W. L. and Eidt, D. C. 1993. Perturbation of the aquatic invertebrate community of acidic bog ponds by the insecticide fenitrothion. Arch. Environ. Contam. Toxicol. 25: 170-183.
- Flannagan, J. F. and Macdonald, S. R. 1987. Ephemeroptera and Trichoptera of peatlands and marshes in Canada. Mem. Entomol. Soc. Can. 119: 47-56.
- Freeman, B. E. 1968. Studies on the ecology of adult Tipulidae (Diptera) in southern England. J. Anim. Ecol. 37: 339-362.
- Frost, W. E. 1942. River Liffey survey IV. The fauna of submerged "mosses" in an acid and an alkaline water. Proc. Roy. Irish Acad. Ser. B13: 293-369.
- Füreder, L., Schütz, C., Wallinger, M., and Burger, R. 2001. Physico-chemistry and aquatic insects of a glacier-fed and a spring-fed alpine stream. Freshwat. Biol. 46: 1673-1690.
- Füreder, L., Wallinger, M., and Burger, R. 2005. Longitudinal and seasonal pattern of insect emergence in alpine streams. Aquat. Ecol. 39: 67-78.
- Gerson, U. 1969. Moss-arthropod associations. Bryologist 72: 495-500.
- Gerson, U. 1982. Bryophytes and invertebrates. In: Smith, A. J. E. (ed.). Bryophyte Ecology. Chapman & Hall, New York, pp. 291-332.
- Gislason, G. M., Adalsteinsson, H., Hansen, I., Olafsson, J. S., and Svavarsdottir, K. 2001. Longitudinal changes in macroinvertebrate assemblages along a glacial river system in central Iceland. Freshwat. Biol. 46: 1737-1751.
- 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. and Clemons, R. M. 1972. Species diversity of stream insects on *Fontinalis* spp. compared to diversity on artificial substrates. Ecology 53: 458-464.
- Goffart, Philippe and Fichet, Violaine. 2003. *Aeshna subarctica*. Accessed on 10 March 2009 at <[http://biodiversite.wallonie.be/especes/ecologie/libellules/Aeshna\\_subarctica03.html](http://biodiversite.wallonie.be/especes/ecologie/libellules/Aeshna_subarctica03.html)>.
- Grdović, S. and Sabovljević, M. 2008. An ecological approach to bryophytes of beehive yards: Is there a bee-moss relationship? Acta Vet. (Beograd) 58: 287-294.
- Gurtz, M. E. and Wallace, J. B. 1984. Substrate-mediated response of stream invertebrates to disturbance. Ecology 65: 1556-1569.
- Hains, J. J. 1981. The response of stream flora to watershed perturbation. M.S. Thesis, Clemson University, Clemson, S. C., 81 pp.
- Harrison, A. D. and Agnew, J. D. 1962. The distribution of invertebrates endemic to acid streams in the western and southern Cape Province. Ann. Cape Prov. Mus. 11: 274-291.
- Hart, D. D. 1978. Diversity in stream insects: Regulation by rock size and microspatial complexity. Internat. Verein. Theoret. Angew. Limnol. Verhand. 20: 1376-1381.
- Hebauer, F. 1994. Entwurf einer Entomosoziologie aquatischer Coleoptera in Mitteleuropa (Insecta, Coleoptera, Hydradeephaga, Hydrophiloidea, Dryopoidea). Lauterbornia 19: 43-57.
- Heino, J. 2009. Biodiversity of aquatic insects: Spatial gradients and environmental correlates of assemblage-level measures at large scales. Freshwat. Rev. 2: 1-29.
- Hering, E. M. 1966. Minierfliegen in Lebermoosen II (Dipt., Agromyzidae). Dt. Entomol. Z. 13: 231-235.
- Huryn, A. D., Slavik, K. A., Lowe, R. L., Parker, S. M., Anderson, D. S., and Peterson, B. J. 2005. Landscape heterogeneity and the biodiversity of Arctic stream communities: A habitat template analysis. Can. J. Fish. Aquat. Sci. 62: 1905-1919.
- Hussey, B. 1982. Moss growth on filter beds. Water Res. 16: 391-398.
- Ilmonen, J. 2009. Benthic Macroinvertebrate and Bryophyte Assemblages in Boreal Springs: Diversity, Spatial Patterns and Conservation. Ph. D. Dissertation, University of Oulu, Oulu Yliopisto, Oulu, Finland.
- Ilmonen, J. and Paasivirta, L. 2005. Benthic macrocrustacean and insect assemblages in relation to spring habitat characteristics: Patterns in abundance and diversity. Hydrobiologia 533: 99-113.
- Jackson, D. J. 1956. The capacity for flight of certain water beetles and its bearing on their origin in the western Scottish Isles. Proc. Linn. Soc. London 167: 76-96.
- Jewell, M. E. and Brown, H. W. 1929. Studies on northern Michigan bog lakes. Ecology 10: 427-475.
- Johnson, T. 1978. Aquatic mosses and stream metabolism in a north Swedish river. Internat. Verein. Theor. Angew. Limnol. Verhand. 20: 1472-1477.
- Kelly, M. G. and Whitton, B. A. 1987. Growth rate of the aquatic moss *Rhynchostegium riparioides* in northern England. Freshwat. Biol. 18: 461-468.
- Korsu, K. 2004. Response of benthic invertebrates to disturbance from stream restoration: The importance of bryophytes. Hydrobiologia 523: 37-45.
- Larson, D. J. and House, N. L. 1990. Insect communities of Newfoundland bog pools with emphasis on the Odonata. Can. Entomol. 122: 469-501.
- Leng, C. W. 1913. Aquatic Coleoptera. J. N. Y. Entomol. Soc. 21: 32-42.
- Lindegaard, C., Brodersen, K. P., Wiberg-Larsen, P., and Skriver, J. 1998. Multivariate analyses of macrofaunal communities in Danish springs and springbrooks. In: Botosaneanu, L. (ed.). Studies in Crenobiology. The Biology of Springs and Springbrooks. Backhuys Publishers, Leiden, The Netherlands, pp. 201-219.
- Lindegaard, C., Thorup, J., and Bahn, M. 1975. The invertebrate fauna of the moss carpet in the Danish spring Ravnkilde and its seasonal, vertical and horizontal distribution. Arch. Hydrobiol. 75: 109-139.
- Luther, H. 1979. Aquatic moss balls in southern Finland. Ann. Bot. Fenn. 16: 163-172.
- Macan, T. T. and Worthington, E. B. 1951. Life in Lakes and Rivers. Collins, London, 272 pp.
- Mackay, R. J. and Waters, T. F. 1986. Effects of small impoundments on hydrosychid caddisfly production in Valley Creek, Minnesota. Ecology 67: 1680-1686.
- Malmqvist, B. and Hoffsten, P.-O. 2000. Macroinvertebrate taxonomic richness, community structure and nestedness in Swedish streams. Arch. Hydrobiol. 150: 29-54.
- Mani, M. S. 1962. Introduction to High Altitude Entomology. Methuen, London.
- Matthey, W. 1971. Ecologie des insectes aquatiques d'une tourbière du Haut-Jura. Rev. Suisse Zool. & Mus. Hist. Nat. Geneve 78: 367-536.



- Matthey, W. 1977. Observations sur *Crenitis punctatostrata* (Letzn.) (Col., Hydrophilidae) dans les tourbières jurassiennes: Comportement reproducteur, cycle de développement et facteurs de mortalité des adultes. [Observations on *Crenitis punctatostrata* (Letzn.) (Col. Hydrophilidae) in the peat bogs of the Jura Mountains: Reproductive behavior, developmental cycle and mortality factors of the adults.]. Mitt. Schweiz. Entomol. Ges. 50: 299-306.
- Maurer, M. A. and Brusven, M. A. 1983. Insect abundance and colonization rate in *Fontinalis neo-mexicana* (Bryophyta) in an Idaho batholith stream, USA. Hydrobiologia 98: 9-15.
- McAuliffe, J. R. 1983. Competition, colonization patterns, and disturbance in stream benthic communities. In: Barnes, J. R. and Minshall, G. W. (eds.). Stream Ecology. Application and Testing of General Geological Theory. Plenum Press, New York, pp. 137-156.
- McKenzie-Smith, F. 1987. Aquatic bryophytes as habitat for invertebrates in a Victorian upland stream. Unpublished B.Sc. (Honors) Thesis, Monash University, Melbourne Australia, 104 pp.
- Michaelis, F. B. 1977. Biological features of Pupu Springs. N. Z. J. Marine Freshwat. Res. 11: 357-373.
- Michiels, N. K. and Dhondt, A. A. 1990. Costs and benefits associated with oviposition site selection in the dragonfly *Sympetrum danae* (Odonata: Libellulidae). Anim. Behav. 40: 668-678.
- Miller, M. C. and Stout, J. R. 1989. Variability of macroinvertebrate community composition in an arctic and subarctic stream. Hydrobiologia 172: 111-127.
- Moon, H. P. 1939. Aspects of the ecology of aquatic insects. Trans. Soc. Brit. Entomol. 6: 39-49.
- Muotka, T. and Laasonen, P. 2002. Ecosystem recovery in restored headwater streams: The role of enhanced leaf retention. J. Appl. Ecol. 39: 145-156.
- Murphy, D. H. 1955. Long-term changes in collembolan populations with special reference to moorland soils. In: McE. Kevan, D. K. (ed.). Soil Zoology. Butterworths, London, pp. 157-166.
- Muttkowski, R. A. 1912. The ecology of trout streams in Yellowstone National Park. Roosevelt Wild Life Ann. 2: 154-240.
- Needham, J. G. 1901. Aquatic insects in the Adirondacks. N. Y. State Museum Bull. 47: 383-612.
- Oldroyd, H. 1964. Diptera from Nepal. Asilidae. Bull. Brit. Mus. (Nat. Hist.) Entomol. 15: 237-254.
- Ormerod, S. J., Rundle, S. D., Wilkinson, S. M., Daly, G. P., Dale, K. M., and Juttner, I. 1994. Altitudinal trends in the diatoms, bryophytes, macroinvertebrates and fish of a Nepalese river system. Freshwat. Biol. 32: 309-322.
- Oswood, M. W. 1989. Community structure of benthic invertebrates in interior Alaskan (USA) streams and rivers. Hydrobiologia 172: 97-110.
- Paasivirta, L., Lahti, T., and Peraetie, T. 1988. Emergence phenology and ecology of aquatic and semi-terrestrial insects on a boreal raised bog in central Finland. Holarct. Ecol. 11: 96-105.
- Paavola, R. 2003. Community Structure of Macroinvertebrates, Bryophytes and Fish in Boreal Streams - Patterns from Local to Regional Scales, with Conservation Implications. Unpublished Ph. D. thesis. University of Jyväskylä, Jyväskylä University Printing House, Finland, 35 pp.
- Paavola, R., Muotka, T., Virtanen, R., Heino, J., and Kreivi, P. 2003. Are biological classifications of headwater streams concordant across multiple taxonomic groups? Freshwat. Biol. 48: 1912-1923.
- Paavola, R., Muotka, T., Virtanen, R., Heino, J., Jackson, D., and Mäki-Petäys, A. 2006. Spatial scale affects community concordance among fishes, benthic macroinvertebrates, and bryophytes in streams. Ecol. Appl. 16: 368-379.
- Parker, S. M. and Huryn, A. D. 2006. Food web structure and function in two Arctic streams with contrasting disturbance regimes. Freshwat. Biol. 51: 1249-1263.
- Percival, E. and Whitehead, H. 1929. A quantitative study of the fauna of some types of stream-bed. J. Ecol. 17: 282-314.
- Percival, E. and Whitehead, H. 1930. Biological survey of the river Wharf. II. Report on the invertebrate fauna. J. Ecol. 18: 286-295.
- Plitt, C. C. 1907. *Webera sessilis* and ants. Bryologist 10: 54-55.
- Reichle, D. E. 1966. Some pselaphid beetles with boreal affinities and their distribution along the postglacial fringe. Syst. Zool. 15: 330-344.
- Reichle, D. E. 1967. The temperature and humidity relations of some bog pselaphid beetles. Ecology 48: 208-215.
- Richards, O. W. and Davies, R. G. 1977. Imm's General Textbook of Entomology, 10th edn. Chapman and Hall, London.
- Richardson, D. H. S. 1981. The Biology of Mosses. Chapter 8, Mosses and micro-organisms. John Wiley & Sons, Inc., New York, pp. 119-143.
- Robinson, C. T., Uehlinger, U., and Hieber, M. 2001. Spatio-temporal variation in macroinvertebrate assemblages of glacial streams in the Swiss Alps. Freshwat. Biol. 46: 1663-1672.
- Rosa, B. F., Silva, M. V. da, Oliveira, V. C. D., Martins, R. T., and Alves, R. D. G. 2011. Macroinvertebrates associated with Bryophyta in a first-order Atlantic Forest stream. Zoologia (Curitiba) 28: 351-356.
- Sahlén, G., Bernard, R., Rivera, A. C., Ketelaar, R., and Suhling, F. 2004. Critical species of Odonata in Europe. Internat. J. Odonatol. 7: 385-398.
- Scotland, M. B. 1934. The animals of the *Lemna* association. Ecology 15: 290-294.
- Slavik, K., Peterson, B. J., Deegan, L. A., Bowden, W. B., Hershey, A. E., and Hobbie, J. E. 2004. Long-term responses of the Kuparuk River ecosystem to phosphorus fertilization. Ecology 85: 939-954.
- Smirnov, N. N. 1961. Food cycles in sphagnum bogs. Hydrobiologia 17: 175-182.
- Smith-Cuffney, F. L. 1987. Ecological interactions in the moss habitat of streams draining a clearcut and a reference watershed. Unpublished Ph.D. thesis, University of Georgia, 174 pp.
- Spencer, K. A. 1990. Division Bryophyta. In: Host Specialization in the World Agromyzidae (Diptera) series Entomologica, vol. 45. Kluwer Academic Publishers, Springer, Netherlands, pp. 1-3.
- Stern, M. S. and Stern, D. H. 1969. A limnological study of a Tennessee cold springbrook. Amer. Midl. Nat. 82: 62-82.
- Suren, A. M. 1987. The ecological role of bryophytes in high alpine streams of New Zealand. In: Sladeczek, V. (ed.). Proceedings of the Conference (23) Congress in New Zealand, Hamilton, NZ, 8 Feb 1987.
- 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. 1991a. Bryophytes as invertebrate habitat in two New Zealand alpine streams. Freshwat. Biol. 26: 399-418.



- Suren, A. M. 1991b. Assessment of artificial bryophytes for invertebrate sampling in two New Zealand alpine streams. *N. Z. J. Marine Freshwat. Res.* 25: 101-112.
- 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. 1992. The influence of periphyton, detritus and shelter on invertebrate colonization of aquatic bryophytes. *Freshwat. Biol.* 17: 327-339.
- Tarras-Wahlberg, N. 1952-53. Oribatids from the Åkhult-Mire. *Oikos* 4: 166-171.
- Thienemann, A. 1936. Alpine chironomiden. *Arch. Hydrobiol.* 30: 167-262.
- Thomas, A. G. B. 1980. Dipteres Torrenticoles Peu Connus 7. Les Cecidomyiidae Porricondylinae du Sud-Ouest de la France (Nematocera). [Poorly known torrential Diptera. 7. Cecidomyiidae Porricondylinae (Nematocera) from South-West of France.]. *Ann. Limnol.* 16(3): 225-231.
- Thorup, J. 1963. Growth and life-cycle of invertebrates from Danish springs. *Hydrobiologia* 22: 55-84.
- Thorup, J. and Lindegaard, C. 1977. Studies on Danish springs. *Folia Limnol. Scand.* 17: 7-15.
- Usinger, R. L. 1974. *Aquatic Insects of California*. University of California Press, Berkeley.
- Uvarov, B. 1977. Grasshoppers and Locusts, a Handbook of General Acridology, Vol. 2. Centre for Overseas Pest Research, London.
- Vickery, V. R. 1969. Two species of *Pteronemobius* previously unreported in Quebec (Orthoptera: Ensifera: Grylloidea: Nemobiinae). *Ann. Soc. Entomol. Quebec* 14: 22-24.
- Vinson, M. R. and Hawkins, C. P. 2003. Broad-scale geographical patterns in local stream insect genera richness. *Ecography* 26: 751-767.
- Virtanen, R., Ilmonen, J., Paasivirta, L., and Muotka, T. 2009. Community concordance between bryophyte and insect assemblages in boreal springs: A broad-scale study in isolated habitats. *Freshwat. Biol.* 54: 1651-1662.
- Vlčková, Š., Linhart, J., and Uvíra, V. 2002. Permanent and temporary meiofauna of an aquatic moss *Fontinalis antipyretica* Hedw. *Acta Univ. Palacki. Olomuc* 39/40: 31-40.
- Vuori, K.-M. and Joensuu, I. 1996. Impact of forest drainage on the macroinvertebrates of a small boreal headwater stream: Do buffer zones protect lotic biodiversity? *Biol. Conserv.* 77: 87-95.
- Wallace, J. B. and Ross, H. H. 1971. Pseudogoerinae: A new subfamily of Odontoceridae (Trichoptera). *Ann. Entomol. Soc. Amer.* 64: 890-894.
- Ward, J. V. 1986. Altitudinal zonation in a Rocky Mountain stream. *Arch. Hydrobiol. Suppl.* 74: 133-199.
- Ward, J. V. and Dufford, R. G. 1979. Longitudinal and seasonal distribution of macroinvertebrates and epilithic algae in a Colorado springbrook-pond system. *Arch. Hydrobiol.* 86: 284-321.
- Wehr, J. D. and Whitton, B. A. 1983. Accumulation of heavy metals by aquatic mosses. 3. Seasonal changes. *Hydrobiologia* 100: 285-291.
- Williams, D. D. 1980. Some relationships between stream benthos and substrate heterogeneity. *Limnol. Oceanogr.* 25: 166-172.
- Winterbourn, M. J., McDiffett, W. F., and Eppley, S. J. 2000. Aluminium and iron burdens of aquatic biota in New Zealand streams contaminated by acid mine drainage: Effects of trophic level. *Sci. Total Environ.* 254(1): 45-54.

