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The invertebrate fauna of the moss carpet in the Danish spring Ravnkilde and its seasonal, vertical, and horizontal distribution

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With 12 figures and 11 tables in the text

Abstract

The moss fauna of the spring Ravnkilde was sampled every three months for one year. It was found to differ quantitatively and qualitatively from the moss fauna in larger water courses, probably due to different temperatures and food conditions. Fluctuations in total number of individuals throughout the year agreed well with life cycles of the dominating species. Species with slow larval development dominated the fauna. A vertical zonation of the moss fauna is described. A horizontal zonation was noted but influence of a neighbouring stone fauna was not important on the moss fauna's composition. Differences in current velocity and detritus deposits were felt responsible for the horizontal distributional differences.

Introduction

In an earlier paper THORUP (1966) stressed the importance of substrate in delimitating bottom fauna communities in running waters, particularly in springs. Faunal composition of a certain substrate type was demonstrated to be homogeneous with the transition zone (ecotone) between neighbouring substrate types in most cases being very narrow in springs.

The purpose of the present study is to describe the fauna of a moss substrate throughout the year in the spring Ravnkilde. Further, the variation in horizontal faunal composition of a moss carpet, especially as influenced by the adjacent stone fauna, will be analysed.

The spring, Ravnkilde, a large helocrene, is situated in the northern part of Jutland, Denmark. According to NIELSEN's (1942) description of the spring, the area covered by moss seems to have been larger thirty years ago than it is now. Further, a comparison of an outline made in 1966 (THORUP 1966, Fig. 7) and Fig. 1 indicates that a reduction in the moss area is in progress. A short description of the spring flora is given by BENGTSSON (1967).

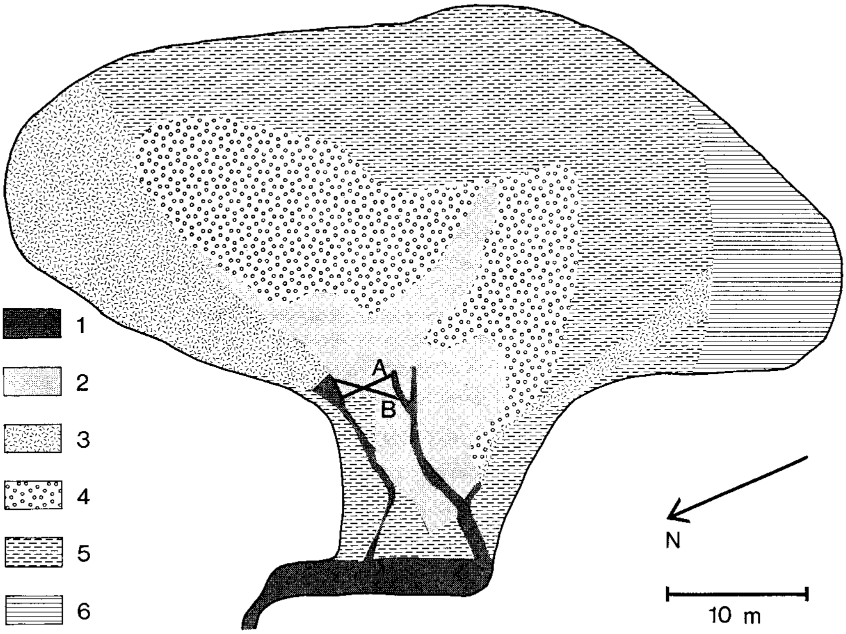

Fig. 1. Outline of the spring Ravnkilde with sampling lines A and B. Substrate types: 1 stony bottom; 2 moss carpet; 3 madicolous localities; 4 moss and higher vegetation; 5 emergent higher vegetation; 6 dead beech leaves.

NIELSEN (1941) stressed the richness of the spring fauna in Himmerland, the part of Denmark where Ravnkilde is situated. Still only a few studies, most of which deal with the biology of individual species and particular ecological problems (e.g., NIELSEN 1942, 1950 a, b, 1951, THORUP 1963, 1970) have appeared. A few papers consider the physiography and flora of the springs (BERG 1951, BENGTSSON 1967).

The present paper deals only with the fauna of a small part of Ravnkilde, viz. the area covered with emergent mosses. This type of vegetation is not to be confused with the moss growth described in previous running water studies (e.g., THIENEMANN 1912, PERCIVAL & WHITEHEAD 1929, FROST 1942, HYNES 1961, MINCKLEY 1963). In the latter studies the moss growth is primarily characterized by floating submerged in the water often in the presence of high current velocity. In Ravnkilde the mosses emerge through the water surface and the current is slow. Only a few studies deal with a substrate (plant growth) comparable to this (e.g., NADIG 1942).

Description of the moss carpet

The moss carpet constitutes a rather large and unbroken area (Figs. 1 and 2). On two sides it is well defined by stony bottomed rills. On the two other sides a gradual change to a substrate of higher vegetation is found. A reduction of the area covered with moss is demonstrated by the fact that the area presently occupied by moss and higher vegetation (Fig. 1) was earlier all moss. Two species, *Cratoneuron commutatum* and *C. filicinum,* dominate the moss flora.

The moss carpet (Figs. 3 and 4) is about 8 cm thick, and of this the lower 4—5 cm is surrounded by water seeping through the moss. Below the moss is a layer of stones. The lowermost 1—1.5 cm of the moss is dead and surrounded by detritus. In the upper submerged part some detritus collects in the axils. The lower section of the emergent portion constitutes a madicolous zone and the upper section a dry zone. Water movement through the moss carpet is faster close to the border and thus detritus deposits are smaller there. In places temporary rills occur in the moss carpet.

Hydrographic notes

No hydrographic measurements were made during this study so the following information derives from the literature or measurements carried out later.

The water flow of Ravnkilde varies between 54 and 88 l/sec. (BERG 1951). Current rate in the rills is about 40 cm/sec., being a little higher in the right rill than in the left. Flow through the moss mat is about 10 cm/sec., and up to 30 cm/sec. in small, temporary rills. Water temperature in the marginal rills is practically constant throughout the year at about 7.5 °C. In the moss carpet

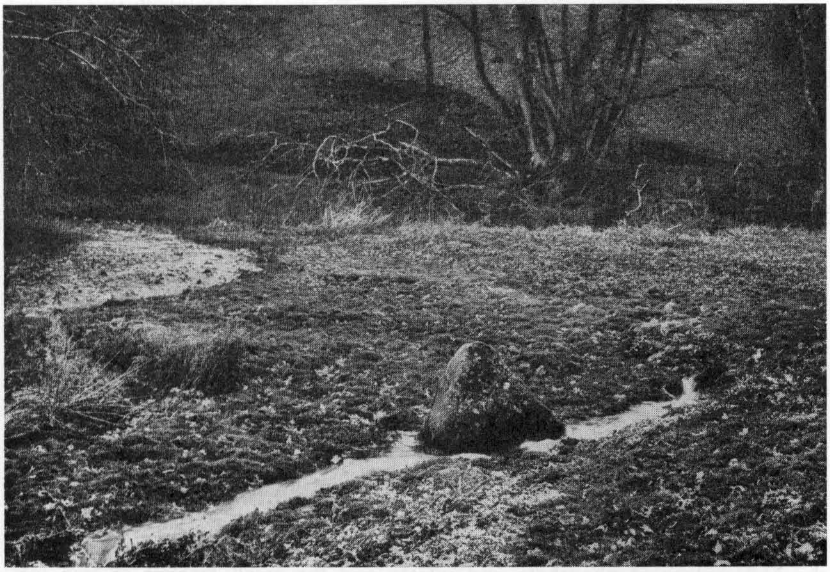

Fig. 2. Ravnkilde (facing east). The area of study is just behind the boulder and between the rills.

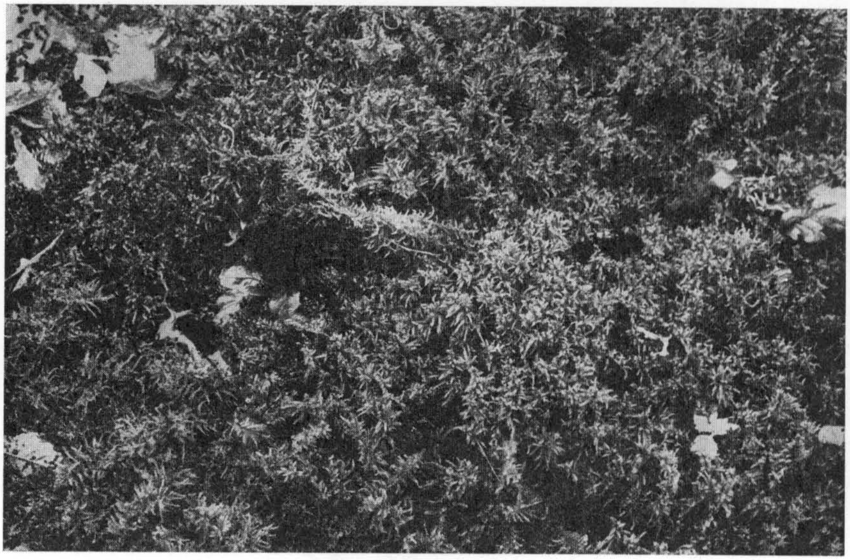

Fig. 3. Close-up of the moss carpet showing the structure of the dry upper zone inhabited mainly by terrestrial animals.

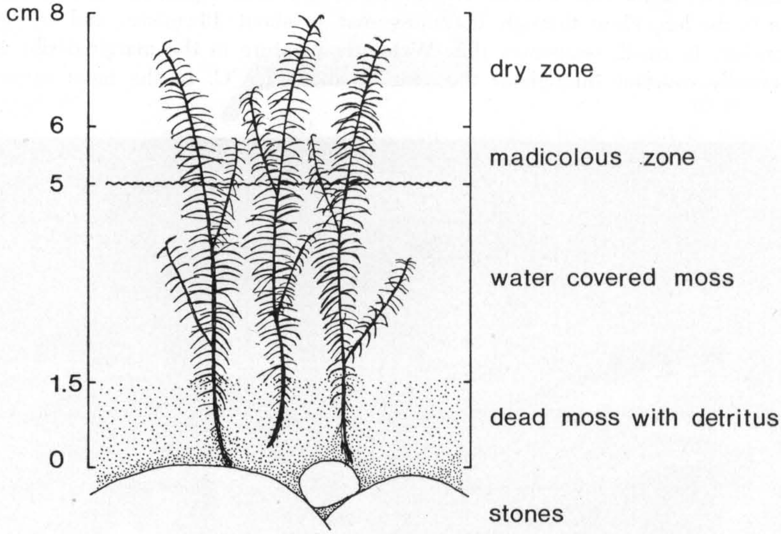

Fig. 4. Vertical zonation of the moss carpet.

7.3 °C was measured in February and 8.6 °C in May as the lowest and highest temperatures, respectively.

Chemical analyses were made in June and November 1973 (Table 1). Note the high values of phosphate and nitrate and the small amount of iron (cfr. Nielsen 1950 a). The latter is indicated further by the fact that no part of the spring or the springbrook has ochre deposits. According to Iversen (1973) no chemical parameter shows seasonal trends in a neighbouring spring. The oxygen content of water taken from the lower part of the moss carpet is high (nearly 100 % saturation) and only a little lower than water from the rills.

Table 1. Chemical data from the spring Ravnkilde.

		June 73	Nov. 73
pH		7.8	8.0
O_2 (rills)	mg O_2/l	—	11.8
O_2 (moss carpet, bottom)	mg O_2/l	—	11.6
NH_4^+	mg N/l	—	0.002
NO_3^-	mg N/l	3.01	6.45
PO_4^{3-}	mg P/l	0.075	0.081
Si	mg/l	—	9.32
$Fe^{2+} + Fe^{3+}$	mg Fe/l	—	<0.001
alkalinity	meq/l	2.39	1.91

Sampling procedure

Two transects were established (Fig. 1) between the marginal rills. Ten samples, close to one another at the border and with increasing distance between samples towards the middle of the moss carpet (cfr. Figs. 5—12), were taken along each transect. Due to stones under the moss dredge could not be used. Therefore, samples were collected by hand to fill a jar holding 375 cm³, an amount corresponding to about 65 cm² of moss carpet surface.

Samples taken every three months from May 1969 to May 1970 were fixed in 4 % formalin. Since detritus was removed by washing the sample in a sieve with a mesh size of 200 μ, the smallest animals (e.g., most ostracods, the first instars of most insects) were lost. The remaining organisms were sorted by hand from the moss without use of magnification.

Species found and relations to moss as substrate

In total 131 species were found in the samples. They are listed in Table 2 with numbers/m² and percentage distribution also indicated. Of the 131 species 29 are identified only to genus or a higher taxa. In several of these taxa more than one species is included.

Of the most common species listed in Table 3, 14 are found in numbers exceeding 1,000/m² and total 86.5 % of all individuals. Thirty species are as dense as 100 to 1,000/m², (10.6 % of the total number). Thus, the 44 most common species make up 97.1 %, and the remaining 87 species only 2.9 % of the total number. The average number of close to 100,000/m² of moss surface is uncertain due to method difficulties. However, the order of magnitude is thought to be correct.

Table 2. Species found in the moss carpet of the spring Ravnkilde during the sampling period.

	no./m²	%
Coelenterata		
Hydra sp.	194	0.2
Turbellaria		
Dugesia gonocephala (Dugès)	278	0.3
Oligochaeta		
Nais elinguis Müller	7,520	7.6
Lumbriculus variegatus (Müller)	38	< 0.1
Enchytraeidae	2,685	2.7
Eiseniella tetraedra (Savigny)	615	0.6
Entomostraca		
Ilyodromus olivaceus (Brady et Norman)	23	< 0.1
Potamocypris wolfi Brehm	38	< 0.1
Malacostraca		
Gammarus pulex L.	6,819	6.9
Trichoniscus pusillus Brandt	9	< 0.1
Collembola		
Isotomurus palustris (Müller)	4,182	4.2
Entomobrya nicoleti (Lubbock)?	3	< 0.1
Lepidocyrtus cyaneus Tullberg	2	< 0.1
Tomocerus minor (Lubbock)	205	0.2
Sminthurides malmgreni (Tullberg)	6	< 0.1
Sminthurides parvulus (Krausbauer)	22	< 0.1
Ephemeroptera		
Baëtis rhodani Pictet	178	0.2
Plecoptera		
Protonemura hrabei Raušer	122	0.1
Amphinemura sulcicollis (Stephens)	11	< 0.1
Amphinemura standfussi Ris	2	< 0.1
Nemoura flexuosa Aubert	3	< 0.1
Nemurella picteti Klapálek	16,561	16.7
Leuctra hippopus (Kempny)	155	0.2
Leuctra nigra (Olivier)	23	< 0.1
Leuctra sp. juv.	12	0.1
Heteroptera		
Velia caprai Tamanini	9	< 0.1
Hemiptera terr.	3	< 0.1
Trichoptera		
Rhyacophila fasciata Hagen	3	< 0.1
Agapetus fuscipes Curtis	8	< 0.1
Plectrocnemia conspersa (Curtis)	97	0.1
Potamophylax nigricornis Pictet	14	< 0.1
Halesus digitatus (Schrank)	3	< 0.1

Table 2 (continued)

	no./m²	%
Chaetopteryx sp.	2	< 0.1
Crunoecia irrorata (CURTIS)	25	< 0.1
Sericostoma personatum SPENCE	23	< 0.1
Beraea maurus (CURTIS)	6	< 0.1
Coleoptera		
Hydrophilidae		
Limnebius truncatellus THUNBERG (adults)	3	< 0.1
Helophorus aquaticus L. (adults)	8	< 0.1
Helophorus flavipes FABRICIUS (adults)	3	< 0.1
Helophorus guttulus MOTSCHULSKY (adults)	98	0.1
Helophorus minutus FABRICIUS (adults)	14	< 0.1
Coelostoma orbiculare FABRICIUS (adults)	2	< 0.1
Cercyon convexiusculus STEPHENS (adults)	2	< 0.1
Anacaena globulus PAYKULL (adults)	5	< 0.1
Enochrus coarctatus GREDLER (adults)	2	< 0.1
Staphylinidae		
Quedius auricomus KIESENWETTER (adults)	34	< 0.1
Stenus spp. (adults)	72	0.1
Oxytelus sp. (adults)	6	< 0.1
Staphylinidae (larvae)	91	0.1
Helodidae		
Helodes minuta L. (larvae)	291	0.3
Chrysomelidae		
Phaeodon cochleariae FABRICIUS (adults)	5	< 0.1
Chrysomelidae (adults)	2	< 0.1
Curculionidae		
Apion sp. (adults)	26	< 0.1
Curculionidae (larvae)	11	< 0.1
Diptera		
Tipulidae		
Tipula cheethami EDWARDS	254	0.3
Tipula spp.	62	0.1
Limoniidae		
Dicranomyia sp.	2	< 0.1
Pedicia rivosa L.	80	0.1
Dicranota spp.	511	0.5
Limoniidae	3	< 0.1
Psychodidae		
Pericoma blandula EATON	12,867	13.0
Pericoma fuliginosa (MEIGEN)	551	0.6
Pericoma mutua EATON or *pilularia* TONNOIR	11	< 0.1
Pericoma neglecta EATON or *subneglecta* TONNOIR	22	< 0.1
Pericoma pseudexquisita TONNOIR	492	0.5

Table 2 (continued)

	no./m²	%
Pericoma pulchra EATON	8	< 0.1
Pericoma sp. juv.	100	0.1
Pericoma sp. pupae	69	0.1
Dixidae		
Dixa spp.	657	0.7
Chironomidae		
Macropelopia notata (MEIGEN)	180	0.2
Krenopelopia binotata (WIEDEMANN)	3,434	3.5
Trissopelopia longimana (STAEGER)	454	0.5
Brillia modesta (MEIGEN)	105	0.1
Heterotrissocladius marcidus (WALKER)	17	< 0.1
Eukiefferiella bavarica GOETGHEBUER	2	< 0.1
Eukiefferiella brevicalcar EDWARDS	2	< 0.1
Eukiefferiella claripennis LUNDBECK	2	< 0.1
Eukiefferiella minor EDWARDS	289	0.3
Eukiefferiella verralli EDWARDS	485	0.5
Rheocricotopus fuscipes (KIEFFER)	4,356	4.4
Rheocricotopus foveatus (EDWARDS)	51	0.1
Chaetocladius laminatus BRUNDIN	9,600	9.7
Chaetocladius sp. cfr. *acuticornis* PAGAST	612	0.6
Limnophyes prolongatus EDWARDS	501	0.5
Metriocnemus fuscipes MEIGEN	178	0.2
Metriocnemus hygropetricus KIEFFER	611	0.6
Metriocnemus terrester PAGAST	14	< 0.1
Metriocnemus sp.	57	0.1
Parametriocnemus stylatus (KIEFFER)	6,906	7.0
Paraphaenocladius impensus EDWARDS	608	0.6
Pseudorthocladius curtistylus (GOETGHEBUER)	2	< 0.1
Pseudorthocladius sp. cfr. *filiformis* (KIEFFER)	8	< 0.1
Parakiefferiella bathophila (KIEFFER)	9	< 0.1
Corynoneura lobata EDWARDS	15	< 0.1
Micropsectra atrofasciata KIEFFER *Micropsectra attenuata* REISS *Micropsectra praecox* MEIGEN	3,334	3.4
Ceratopogonidae		
Atrichopogon alveolatus NIELSEN	38	< 0.1
Dasyhelea sp.	2	< 0.1
Culicoides spp.	48	< 0.1
Palpomyia-Bezzia group spp.	376	0.4
Thaumaleidae		
Thaumalea spp.	14	< 0.1
Simuliidae		
Eusimulium costatum (FRIEDERICHS)	283	0.3
Eusimulium latipes (MEIGEN)	34	< 0.1

Table 2 (continued)

	no./m²	%
Stratiomyiidae		
Beris clavipes (L.)	11	< 0.1
Empididae		
Hemerodromia sp.	32	< 0.1
Atalanta sp.	31	< 0.1
Ephydridae		
Ephydridae	22	< 0.1
Sciomyzidae		
Sciomyzidae	2	< 0.1
Cyclorrapha	23	< 0.1
Araneae		
Lycosa sp.	22	< 0.1
Pirata piraticus (CLERK)	155	0.2
Gnathonarium dentatum (WIDER)	3	< 0.1
Lophomma punctatum (BLACKWALL)	9	< 0.1
Savignia frontata BLACKWALL	8	< 0.1
Diplocephalus permixtus (O. P.-CAMBRIDGE)	166	0.2
Erigone sp.	14	< 0.1
Erigonidae	8	< 0.1
Linyphiidae	31	< 0.1
Erigonidae juv. + Linyphiidae juv.	1,038	1.0
Acarina		
Panisus michaeli KOENIKE	63	0.1
Sperchon glandulosus (KOENIKE)	278	0.3
Sperchon setiger (THOR)	2	< 0.1
Sperchon squamosus KRAMER	6	< 0.1
Sperchon sp.	2	< 0.1
Lebertia lineata THOR	14	< 0.1
Lebertia sefvei (WALTER)	71	0.1
Lebertia stigmatifera (THOR)	23	< 0.1
Pergamasus sp. cfr. *brevicornis* BERLESE	1,604	1.6
Platyseius sp. (? *neocorniger* (ODUMS))	545	0.5
Mucronothrus nasalis (WILLMANN)	4,640	4.7
Gastropoda		
Galba truncatula (MÜLLER)	1,247	1.3
Radix peregra (MÜLLER)	5	< 0.1
Ancylus fluviatilis MÜLLER	5	< 0.1
Succinea pfeifferi ROSSMÄSSLER	200	0.2
Total (131 species)	99,186	

Table 3. Species found in numbers exceeding 1,000/m² and between 100 and 1,000/m². Numbers are means of 5 series sampled between May 1969 and May 1970. Species are arranged according to no./m².

	no./m²	%
1. *Nemurella picteti*	16,561	16.7
2. *Pericoma blandula*	12,867	13.0
3. *Chaetocladius laminatus*	9,600	9.7
4. *Nais elinguis*	7,520	7.6
5. *Parametriocnemus stylatus*	6,906	7.0
6. *Gammarus pulex*	6,819	6.9
7. *Mucronothrus nasalis*	4,634	4.7
8. *Rheocricotopus fuscipes*	4,356	4.4
9. *Isotomurus palustris*	4,182	4.2
10. *Krenopelopia binotata*	3,434	3.5
11. *Micropsectra* spp.	3,334	3.4
12. Enchytraeidae	2,685	2,7
13. *Platyseius* sp. (? *neocorniger*)	1,604	1.6
14. *Galba truncatula*	1,247	1.3
14 species exceeding 1,000/m²	85,749	86.5
15. *Dixa* spp.	657	0.7
16. *Eiseniella tetraedra*	615	0.6
17. *Chaetocladius* sp. cfr. *acuticornis*	612	0.6
18. *Metriocnemus hygropetricus*	611	0.6
19. *Paraphaenocladius impensus*	608	0.6
20. *Pericoma fuliginosa*	551	0.6
21. *Pergamasus* sp. cfr. *brevicornis*	545	0.5
22. *Dicranota* spp.	511	0.5
23. *Limnophyes prolongatus*	501	0.5
24. *Pericoma pseudexquisita*	492	0.5
25. *Eukiefferiella verralli*	485	0.5
26. *Trissopelopia longimana*	454	0.5
27. *Palpomyia-Bezzia* group spp.	376	0.4
28. *Helodes minuta*	291	0.3
29. *Eukiefferiella minor*	289	0.3
30. *Eusimulium costatum*	283	0.3
31. *Dugesia gonocephala*	278	0.3
32. *Sperchon glandulosus*	278	0.3
33. *Tipula cheethami*	254	0.3
34. *Tomocerus minor*	205	0.2
35. *Succinea pfeifferi*	200	0.2
36. *Hydra* sp.	194	0.2
37. *Macropelopia notata*	180	0.2
38. *Baëtis rhodani*	178	0.2
39. *Metriocnemus fuscipes*	178	0.2
40. *Diplocephalus permixtus*	166	0.2
41. *Pirata piraticus*	155	0.2
42. *Leuctra hippopus*	155	0.2

Table 3 (continued)

	no./m²	%
43. *Protonemura hrabei*	122	0.1
44. *Brillia modesta*	105	0.1
30 species with between 100 and 1,000/m²	10,529	10.6
87 species found in numbers less than 100/m²	2,908	2.9

Compared to many running water studies the number of individuals per m² is high. In the Suså River the greatest number measured by Jónasson (1948) was 32,000/m² at a locality with dense vegetation. Albrecht (1953) found in Die Plane, on a bottom covered with vegetation, less than 8,500/m². However, these substrates are not comparable to the moss carpet in Ravnkilde.

Percival & Whitehead (1929, 1930) studied the fauna in submerged thick moss in streams and calculated numbers as high as 431,941 and 1,464,770/m² in the two papers, respectively. Hynes (1961) found about 265,500/m² at a locality corresponding to those of Percival & Whitehead. Minckley (1963) reported about 102,000/m² in *Fissidens* beds in a spring stream which is very close to the number found in Ravnkilde.

These moss localities are not comparable to the moss growth in Ravnkilde either since they are characterized by swift water flow and are mostly situated farther downstream where the amount of dispensed food particles in the water is probably larger. Also the thickness of the moss carpet may influence the number of individuals. In Ravnkilde the thickness amounts to 8 cm but only about 5 cm are submerged. In the studies referred to, the thickness is not stated, but this factor alone could be responsible for the differences.

In the moss carpet of Ravnkilde a very rich species variation occurs as well. Compared to Nadig's (1942) studies on Swiss springs with comparable substrate where 41 species were found, Ravnkilde yielded 131 species. It must, however, be stressed, that not only is the oxygen content in Nadig's locality very low, varying between 10.3 and 71.0 % saturation, but also the temperature fluctuates more than it does in Ravnkilde. More importantly deposits of ochre characterize Nadig's locality and such deposits are known to reduce the fauna conspicuously (Thorup 1966).

From the present study it is difficult to decide to what extent a species is typical of the biotope in question. Several earlier works have detailed the fauna associated with mosses (Thienemann 1912, Hubault 1927, Percival & Whitehead 1929, Beyer 1932, Frost 1942, Nadig 1942, Dittmar 1955, Hynes 1961). A direct comparison with these studies is not possible,

Table 4. Species mainly associated with moss substrates according to: (1) THIENEMANN 1912, (2) HUBAULT 1927, (3) PERCIVAL & WHITEHEAD 1929, (4) BEYER 1932, (5) FROST 1942, (6) NADIG 1942, (7) DITTMAR 1955, (8) HYNES 1961. Parentheses denote references to related species.

	1	2	3	4	5	6	7	8	Others
Nais elinguis			×				(×)	(×)	
Ilyodromus olivaceus				×		×			
Potamocypris wolfi				×			×		
Isotomurus palustris				(×)					STRENZKE 1949, GISIN 1960
Tomocerus minor				(×)					STRENZKE 1949, GISIN 1960
Amphinemura sulcicollis			×	(×)	×		×	×	
Nemurella picteti						×	×		
Gammarus pulex	×	×	×	(×)	(×)				
Plectrocnemia conspersa	×			×	×	×		×	
Limnebius truncatellus	×					×			
Helodes minuta	×			×		×	×		
Pedicia sp.		×		×	×	×	×		
Dicranota sp.	×	×		×	×	×	×	×	
Pericoma blandula		×			×				
Pericoma fuliginosa		×			×		×		
Pericoma pseudexquisita		×			×				
Dixa sp.		×					×		
Krenopelopia binotata									THIENEMANN 1954, FITTKAU 1962
Brillia modesta							×		LEHMANN 1971
Eukiefferiella claripennis									LEHMANN 1971
Eukiefferiella minor									THIENEMANN 1954, LEHMANN 1971
Rheocricotopus fuscipes	×								
Chaetocladius laminatus						(×)			LEHMANN 1971
Limnophyes prolongatus									STRENZKE 1950, THIENEMANN 1954
Metriocnemus fuscipes									STRENZKE 1950
Metriocnemus hygropetricus									STRENZKE 1950, THIENEMANN 1954, LEHMANN 1971
Metriocnemus terrester									STRENZKE 1950
Parametriocnemus stylatus							×		THIENEMANN 1954, LEHMANN 1971
Paraphaenocladius impensus									STRENZKE 1950, LEHMANN 1971
Atrichopogon alveolatus									NIELSEN 1951
Pirata piraticus									NØRGAARD 1951
Diplocephalus permixtus									LOCKET & MILLIDGE 1953
Panisus michaeli		×							VIETS 1936

Table 4 (continued)

	1	2	3	4	5	6	7	8	Others
Sperchon glandulosus							×		
Lebertia lineata							×		
Lebertia sefvei							×		
Lebertia stigmatifera							×		VIETS 1936
Pergamasus brevicornis									MICHERDZIŃSKI 1969
Mucronothrus nasalis									HAMMER 1965
Galba truncatula		×				×			

as the fauna has not been determined to the same extent as in the present one, and because many of the studies deal with streams where major ecological factors (e.g., temperature, oxygen, current rate) deviate from what they are in Ravnkilde. Many species occur in Ravnkilde due to preference for ecological conditions met with in springs (crenophilous and crenobiontic species), and some species are absent because they cannot exist in springs. In no case are more than twenty of the species found in the moss of Ravnkilde (Table 2) listed in any of the studies referred to above. By examining the species lists from moss and supplementing these with information from papers dealing with individual groups, it is possible to pick out a number of organisms which often occur in mosses (Table 4). Together with the species attaining large individual-numbers (Table 3) they characterize the fauna of the moss carpet in Ravnkilde.

Crenobiontic and crenophilous species characterize the fauna in comparison with the moss fauna from streams (e.g., *Ilyodromus olivaceus, Potamocypris wolfi, Nemurella picteti, Krenopelopia binotata, Panisus michaeli, Lebertia sefvei*). The fauna is further distinguished by the absence of species often found in large numbers in stream moss (e.g., *Ephemerella ignita, Hydropsyche* spp., Helmidae, *Hydraena gracilis, Limnophora riparia*).

Seasonal variations

Dominant species at each sampling period are listed in Table 5. With few exceptions the same species dominate the fauna at all sampling dates. Such a species may be absent at certain times because it is in a stage that does not live in the locality or is so small that it is not retained by the sampling procedure (e.g., *Chaetocladius laminatus, Rheocricotopus fuscipes, Krenopelopia binotata*).

The total number of individuals is subject to large variations through the sampling period. The lowest value, recorded in May 1969, is less than half the number found in May 1970 but procedural differences are partly responsible as specimens of terrestrial origin (e.g., *Mucronothrus, Isotomurus, Pergamasus*) were not sorted from the May 1969 samples. All the difference cannot be accounted for in this way, however, as most all species occurred in much smaller number in 1969. Yearly fluctuations in population size do occur, therefore, although we do not know what ecological factors are responsible. HYNES (1970, Table XXII, 3) also demonstrated unaccountable variations in numbers over the years in River Derwent, England.

The February 1970 samples show a small number of individuals compared to August and November 1969 and May 1970. Undoubtedly responsible is a decrease in population size of many species through the winter. Thus, *Nais elinguis*, which in the previous months played an important role in the fauna, in February is of minor importance because of cessation of reproduction during winter (PERCIVAL & WHITEHEAD 1929). As many spring invertebrates begin reproduction very early in the year (e.g., *Gammarus pulex, Nais elinguis, Chaetocladius laminatus*, Table 6) an increase in total number is already apparent by May even though several species occur in even smaller numbers in this month than in February. Such findings are in agreement with those of FROST (1942) and HYNES (1961), although the winter minimum in their streams persists well into May.

The greatest number of individuals is found in November. At this time the breeding season is terminated and many species attain their largest populations. The studies of FROST (1942) and HYNES (1961) also substantiate the November peak although the former found a great maximum in July, too, but this was primarily due to a maximum of Helmidae larvae, which do not occur in Ravnkilde.

In all sampling periods four species are so numerous that together they total more than 50 % of the fauna. *Nemurella picteti* and *Pericoma blandula* belong to this group, the former being most prominent in August, November, and February. In May *Chaetocladius laminatus* dominates, making up about 30 % of the fauna in both years.

The number of species varies a great deal through the year, being highest in November when 102 taxa were recorded. The lowest number, 70 taxa, was found in May 1969 but this low number is partly because terrestrial forms were not included on that date. Therefore, it seems probable that 88 taxa, recorded from February 1970 samples, represents the true minimum. If so, the number of taxa recorded follows the same trend as the number of individuals.

Organism density fluctuates in agreement with the curve given by HYNES (1970, Fig. XIV, 5) for a fauna dominated by insects, showing a large maximum in late autumn. Whether a smaller peak occurs in midsummer as supposed by HYNES is unknown due to lack of samples from this

Table 5. Density and percentage distribution of species which constitute more than 1 % of the total number in one sampling series, and the total number of species found at each sampling date.

	May 1969		Aug. 1969		Nov. 1969		Feb. 1970		May 1970	
	no./m²	%	no./m²	%	no./m²	%	no./m²	%	no./m²	%
Nemurella picteti	4,977	10.6	29,292	24.7	21,138	16.5	16,785	19.2	10,638	9.3
Pericoma blandula	4,823	10.2	20,215	17.0	16,777	13.1	13,392	15.3	9,146	8.0
Chaetocladius laminatus	13,808	29.3	415	0.4	15	< 0.1	200	0.2	33,577	29.3
Nais elinguis	838	1.8	13,069	11.0	14,362	11.2	2,061	2.4	7,269	6.3
Parametriocnemus stylatus	3,931	8.3	4,200	3.5	13,515	10.5	9,923	11.4	2,969	2.6
Gammarus pulex	3,331	7.1	5,685	4.8	7,762	6.1	7,200	8.2	10,131	8.8
Mucronothrus nasalis	23	< 0.1	1,846	1.5	5,877	4.6	7,323	8.4	8,131	7.1
Rheocricotopus fuscipes	5,254	11.1	7,869	6.6	38	< 0.1	29	< 0.1	8,600	7.5
Isotomurus palustris	323	0.7	4,908	4.1	8,177	6.4	5,046	5.8	2,462	2.1
Krenopelopia binotata	2,615	5.5	254	0.2	4,546	3.5	4,215	4.8	5,545	4.8
Micropsectra spp.	708	1.5	5,100	4.3	438	0.3	6,654	7.6	3,769	3.3
Enchytraeidae	600	1.3	2,431	2.1	8,869	6.9	577	0.7	954	0.8
Platyseius sp. (? *neocorniger*)	262	0.6	385	0.3	2,869	2.2	3,285	3.8	1,464	1.3
Galba truncatula	400	0.8	3,538	3.0	1,454	1.1	585	0.7	262	0.2
Dixa spp.	192	0.4	1,277	1.1	731	0.6	823	0.9	262	0.2
Eiseniella tetraedra	500	1.1	777	0.7	608	0.5	500	0.6	692	0.6
Chaetocladius sp. cfr. *acuticornis*	—	—	600	0.5	2,462	1.9	—	—	—	—
Metriocnemus hygropetricus	54	0.1	1,907	1.6	754	0.6	262	0.3	77	0.1
Paraphaenocladius impensus	23	< 0.1	115	0.1	2,423	1.9	431	0.5	46	< 0.1
Pericoma fuliginosa	531	1.1	215	0.2	685	0.5	631	0.7	692	0.6
Limnophyes prolongatus	—	—	1,462	1.2	992	0.8	38	< 0.1	15	< 0.1
Pericoma pseudexquisita	—	—	1,969	1.6	431	0.3	62	0.1	—	—
Trissopelopia longimana	285	0.6	92	0.1	123	0.1	584	0.7	1,185	1.0
Remaining species	3,675	7.8	10,948	9.2	13,077	10.2	6,709	7.7	6,883	6.0
Total	47,154		118,569		128,123		87,315		114,769	
Total number of species	70		96		102		88		91	

period. The February minimum corresponds to HYNES' minimum in spring, the variations being primarily due to life cycles of the dominating species.

Life cycles

In HYNES' (1961) analysis of community structure in Afon Hirnant he grouped the species according to length of life cycle and time of hatching or breeding. In his textbook (HYNES 1970, p. 294—299) he describes these different life cycles.

Table 6. Occurrence by month of pupae or adults of insects which have larval stages inhabiting the moss carpet.

	F	M	A	M	J	J	A	S	O	N
Nemurella picteti				×			×			
Leuctra hippopus				×						
Plectrocnemia conspersa				×						
Potamophylax nigricornis	×						×			
Crunoecia irrorata				×						
Beraea maurus				×						
Tipula cheethami							×			
Pedicia rivosa				×						
Macropelopia notata							×			
Krenopelopia binotata							×			
Trissopelopia longimana				×			×			
Brillia modesta	×		×				×			
Eukiefferiella bavarica				×						
Eukiefferiella brevicalcar			×	×						
Eukiefferiella claripennis				×						
Eukiefferiella minor				×						
Eukiefferiella verralli			×	×			×			
Rheocricotopus fuscipes				×			×			
Chaetocladius laminatus	×		×	×						
Chaetocladius sp. cfr. *acuticornis*							×			×
Limnophyes prolongatus			×	×	×		×			
Metriocnemus fuscipes				×			×			
Metriocnemus hygropetricus			×	×			×			
Parametriocnemus stylatus				×						
Paraphaenocladius impensus				×						
Parakiefferiella bathophila				×						
Corynoneura lobata				×	×					
Micropsectra atrofasciata			×	×						
Micropsectra attenuata				×	×					
Micropsectra praecox				×			×			
Eusimulium costatum				×			×			
Eusimulium latipes				×						

As the Ravnkilde samples were only taken every three months, it is difficult to make out the exact life cycle of a species. However, on the basis of figures in Table 5 and information on emergence periods in Table 6, it is possible to determine, for the dominating species, HYNES' life cycle types with tolerable certainty. The N-group, consisting of species with no seasonal change in size distribution or numbers, includes species, the life cycle of which cannot be determined from the present material. They could for example be species with slow life cycles and long breeding periods or species with fast life cycles and many overlapping generations.

In his 1961 paper, HYNES further described the importance of each species by means of an index figure calculated as the sum of each species' percentage of 11 selected samples.

In the present study an index figure is calculated for each dominant species as the sum of percentages in all samples except May 1969 which is not included because the terrestrial animals were not sorted out and the percentages of the remaining species, therefore, are too high. Furthermore, two May samples would overemphasize certain life cycles. In Table 7 the dominant species are arranged according to their type of life cycle (HYNES 1961) and the index figure for each species is given. In bivoltine species the indexes have been divided between the two generations in proportion to their numerical importance which appears in Table 5.

The dominant type of life cycle is one with a long growth period ending in May. The preponderance of species with such slow life cycles could be due to low temperatures year around at the locality.

Compared to the long life cycle the sum of index numbers for the fast seasonal cycles is small but note that the group which finish its life cycles in late winter or early spring (F0) attains a relatively high index. The latter consists of bivoltine species, the second generation of which finish life cycles in summer (F3) or autumn (F4).

To compare these results with those of HYNES (1961) the index figures in both studies are divided by the number of samples included in the index (i.e., Ravnkilde 4, HYNES 11) (Table 8). In both studies slow life cycles are the most important, but attain higher index figures in our study than in HYNES'. The opposite is the case with fast cycles indicating better growth conditions in HYNES' locality than in ours. This is also to be expected as summer temperatures are higher in Afon Hirnant than in Ravnkilde and so promote species with fast summer life cycles. Also, HYNES' locality is situated farther downstream where better food conditions exist, especially better possibilities for algal feeders and filter feeders. The latter groups are responsible for about two thirds of the index number of the F-group in HYNES' study whereas they are unimportant in Ravnkilde.

Table 7. Dominant species of the moss carpet arranged by type of life cycle (Hynes 1961, 1970). The index figures are the sum of the percentages at the four sampling dates from August 1969 to May 1970. Further explanation in text.

		index figure
N	(non seasonal, i.e., no seasonal change in size distribution nor in numbers)	
	Nais elinguis	30.9
	Gammarus pulex	27.9
	Enchytraeidae	10.5
	Eiseniella tetraedra	2.4
	N total	71.7
S1	(slow seasonal cycle; early spring adults)	
	Metriocnemus hygropetricus	2.6
	Limnophyes prolongatus	2.0
	S1 total	4.6
S2	(slow seasonal cycle; late spring adults)	
	Nemurella picteti	69.3
	Pericoma blandula	53.4
	Parametriocnemus stylatus	28.0
	Dixa spp.	2.8
	Paraphaenocladius impensus	2.5
	S2 total	156.0
S3	(slow seasonal cycle; summer adults)	
	Mucronothrus nasalis	21.6
	Isotomurus palustris	18.4
	Krenopelopia binotata	13.3
	Platyseius sp. (? *neocorniger*)	7.6
	Galba truncatula	5.0
	Pericoma fuliginosa	2.0
	S3 total	67.9
F0	(fast seasonal cycle; late winter adults)	
	Chaetocladius laminatus	29.9
	Micropsectra spp.	6.6
	Trissopelopia longimana	0.6
	F0 total	37.1
F1	(fast seasonal cycle; early spring adults)	
	Pericoma pseudexquisita	2.0
	Rheocricotopus fuscipes	0.0
	F1 total	2.0
F2	(fast seasonal cycle; late spring adults)	
	none	

Table 7 (continued)

		index figure
F3	(fast seasonal cycle; summer adults)	
	Rheocricotopus fuscipes	14.1
	Trissopelopia longimana	1.3
	Chaetocladius laminatus	0.0
	F3 total	15.4
F4	(fast seasonal cycle; autumn adults)	
	Micropsectra spp.	8.9
	Chaetocladius sp. cfr. *acuticornis*	2.4
	F4 total	11.3

Table 8. Index figures of the different life cycles from Ravnkilde and Afon Hirnant (HYNES 1961) and index figures corrected for comparability. Further explanation in text.

Life cycle	Ravnkilde	Afon Hirnant	Ravnkilde with all Chironomidae in N	Afon Hirnant moss samples only
N	17.9	27.8	46.0	83.0
S1	1.2	1.0	—	0.1
S2	39.0	42.7	31.4	6.8
S3	17.0	1.9	13.7	—
S total	57.2	45.6	45.1	6.9
F0	9.3	—	—	—
F1	0.5	6.6	0.5	0.8
F2	—	0.6	—	0.3
F3	3.9	2.4	—	0.3
F4	2.8	13.6	—	6.7
F total	16.5	23.2	0.5	8.1
Total	91.6	96.6	91.6	98.0

The above comparisons are made on the assumption that species are grouped in the same way in both studies. However, such is not the case in all respects. HYNES did not separate the Chironomidae into species hence, all were placed in the N-group. In contrast, chironomids are placed in several groups in the present study, especially the F-groups. Further, HYNES' index was based on samples from both stony bottoms and mosses, the last substrate being represented by two out of eleven samples. To make a better comparison, our index figures were corrected by transferring all chironomids to the N-group and HYNES' by calculating the index for the two moss samples alone. The corrected figures, also seen in Table 8, show the same trend as described above.

Vertical distribution

As seen in Fig. 4 various zones with quite different ecological conditions occur enabling animals with different biological and ecological requirements to live in the biotope. Zonation was not investigated in this study, but our knowledge about the single species allows us to list more of them by zone (Table 9).

The dry zone is not wetted directly by spring water, but air spaces between the mosses must be very humid due to evaporation and little air circulation.

Species belonging to terrestrial groups are often found in large numbers in the dry zone. Several are known to live in humid places *(Tomocerus minor, Entomobrya nicoleti, Lophomma punctata, Diplocephalus permixtus, Succinea pfeifferi)*, in terrestrial moss *(Entomobrya nicoleti, Lophomma punctata, Diplocephalus permixtus)*, or in moss in or at brooks and streams *(Isotomurus palustris, Sminthurides malmgreni, Quedius auricomus, Pergamasus brevicornis, Platyseius neocorniger, Pirata piraticus, Gnathonarium dentatum)*. VAILLANT (1955) listed terrestrial species found on madicolous habitats. He included all species we listed for the dry zone in Table 9, except *Succinea pfeifferi*.

The madicolous zone (sensu VAILLANT 1955) occurs just above the water surface where the moss is constantly wetted by capillary water. The fauna of such localities was described by THIENEMANN (1909) as "fauna hygropetrica" and was thoroughly investigated by VAILLANT (1955) under the designation "faune madicole". VAILLANT further distinguished between three types of madicolous habitats, among which the locality described here is most closely allied to his "l'habitat bryomadicole". However, there are only a few similarities between the fauna in the madicolous zone of Ravnkilde and the "fauna bryomadicole" as described by VAILLANT. Two species *(Limnophyes prolongatus, Paraphaenocladius impensus)* were listed as "petrimadicole et bryomadicole" and two *(Pericoma neglecta, Eiseniella tetraedra)* as "limimadicole et bryomadicole". The mentioned chironomids (except *Chaetocladius* spp.) were further found in wet moss by STRENZKE (1950). Nevertheless, most of the species listed in Table 9 (madicolous zone) were found by VAILLANT to be "espèces eumadicole" or "espèces madicole preferentielle".

Although only two species *(Chaetocladius laminatus, Galba truncatula)* listed for this zone in Table 9 exceed $1000/m^2$, all the species show morphological or physiological adaptations or both to madicolous habitats.

Table 9. Vertical zonation of species in the moss carpet. Species marked with "?" are not strictly connected with one zone.

Dry zone

Isotomurus palustris
Tomocerus minor and other Collembola
Quedius auricomus
Stenus spp.
Pirata piraticus
Diplocephalus permixtus and other Araneae
Pergamasus sp. cfr. *brevicornis*
Platyseius sp. (? *neocorniger*)
Succinea pfeifferi

Total 20 species comprising 8.4 % of all individuals

Madicolous zone

? *Crunoecia irrorata*
Beraea maurus
Helodes minuta
Pericoma pulchra
Pericoma fuliginosa
Dixa spp.
? *Chaetocladius laminatus*
? *Chaetocladius* sp. cfr. *acuticornis*
Limnophyes prolongatus
Metriocnemus fuscipes
? *Metriocnemus hygropetricus*
Metriocnemus terrester
Paraphaenocladius impensus
Pseudorthocladius curtistylus
Atrichopogon alveolatus
Thaumalea spp.
? *Panisus michaeli*
Galba truncatula

Total 18 species comprising 15.1 % of all individuals

Water covered moss (only species exceeding $100/m^2$ are included)

Hydra sp.
Dugesia gonocephala
Gammarus pulex
Baëtis rhodani
Protonemura hrabei
Nemurella picteti
Tipula cheethami
Pericoma blandula
Pericoma pseudexquisita
Krenopelopia binotata
Brillia modesta
Eukiefferiella minor

Table 9 (continued)

	Eukiefferiella verralli
	Rheocricotopus fuscipes
	Parametriocnemus stylatus
?	*Micropsectra* spp.
	Palpomyia-Bezzia group spp.
	Eusimulium costatum
	Sperchon glandulosus
?	*Mucronothrus nasalis*
	Total 82 species comprising 64.0 % of all individuals
Detritus zone	
?	*Nais elinguis*
	Lumbriculus variegatus
	Eiseniella tetraedra
	Leuctra hippopus
	Pedicia rivosa
	Dicranota spp.
	Macropelopia notata
	Trissopelopia longimana
	Heterotrissocladius marcidus
	Total 8 species comprising 9.6 % of all individuals
Zone unknown	
	Enchytraeidae
	Trichoniscus pusillus
	Tipula spp.
	Total 3 species comprising 2.8 % of all individuals

So, many species' respiration is dependent on at least temporary contact with the atmosphere (*Helodes minuta, Pericoma pulchra, P. fuliginosa, Dixa* spp., *Atrichopogon alveolatus, Thaumalea* spp., and perhaps *Galba truncatula*). The trichopterans found have reduced gills and no lateral line, which are adaptations for living in humid places (NIELSEN 1942).

Below the madicolous zone is a section characterized by being constantly submerged but free of extensive detritus deposits. This zone is richest in both number of species and individuals as more than half of each is classed as living here.

The large majority of the species are rheophilous or even rheobiontic, although most of them avoid faster currents and, therefore, normally occur in vegetation, especially mosses, in brooks and streams. Several species prefer springs as habitat and are seldom found farther downstream in the North and Central European plain. To this group belong *Nemurella picteti, Pericoma blandula, Krenopelopia binotata, Brillia modesta, Parametriocne-*

mus stylatus, Micropsectra attenuata, M. praecox, Sperchon glandulosus, and *Mucronothrus nasalis.*

Only a few species (e.g., *Baëtis rhodani, Eusimulium costatum*) show adaptations for living in rapidly running waters and, as will be discussed later, they are primarily found at the boundary between the moss substrate and stony bottom with its faster water flow. A few *(Tipula cheethami, Pericoma blandula, P. pseudexquisita)* are to some extent dependent on contact with the atmosphere for respiration. These species perhaps should have been classed with madicolous forms, but due to their size and occurrence at other types of localities they seem to require deeper water than is found in madicolous habitats.

Except for the carnivores and filter feeders the great majority of species in the water-covered-moss zone are dependent on detritus as food. It can be difficult, therefore, on the basis of the species' feeding biology, to ascertain whether it should be placed in this group or in the dead-moss-with-detritus zone. However, many of these species are normally found in places without detritus deposits and some (*Nemurella picteti, Pericoma* spp.) are equipped with long bristles which prevent detachment from the vegetation by the current (STEINMANN 1907).

Also difficult to compare is the faunal composition of Ravnkilde's water-covered-moss zone with those in other running water localities. Many species are primarily bound up to the complex of ecological conditions met with in springs and, therefore, do not occur farther downstream. Nevertheless, a number of species are known to be associated with vegetation especially moss, in springs (e.g., *Nemurella picteti, Pericoma blandula, Mucronothrus nasalis, Krenopelopia binotata, Brillia modesta, Parametriocnemus stylatus)* or in brooks and streams (*Eukiefferiella* spp., *Rheocricotopus fuscipes*).

The lowermost part of the moss is composed of dead stems enclosed by deposits of rather coarse detrital particles allowing burrowing species *(Eiseniella tetraedra, Leuctra hippopus, Pedicia rivosa, Dicranota* spp., *Macropelopia notata, Trissopelopia longimana*) to live here. However, due to the loose nature of the detritus, species which are adapted for living among plants and prefer places rich in organic material also occur (*Nais elinguis,* chironomid larvae). Therefore, whether a species lives in the detritus or among the moss stems above is often difficult to decide.

Most of the species in this group are typical of springs and small brooks. A conspicuous exception is *Nais elinguis* which is found in nearly all types of fresh and even brackish water. In the moss carpet of Ravnkilde it is one of the most numerous species.

Horizontal distribution

A purpose of this investigation was to see how far into the moss carpet species from the neighbouring stony bottom would occur. Quite a number of species not belonging to the moss fauna occurred in the samples (Table 10), but with a few exceptions these were only found in samples taken not more than 10—20 cm from the border and only in small numbers. The great majority of these species is typical of stony bottoms.

Table 10. Species mainly associated with stones in the rills and only occasionally found in the moss carpet borders.

Dugesia gonocephala	*Pericoma neglecta* or *subneglecta*
Baëtis rhodani	*Brillia modesta*
Protonemura hrabei	*Eukiefferiella minor*
Amphinemura sulcicollis	*Eukiefferiella verralli*
Nemoura flexuosa	*Eusimulium costatum*
Velia caprai	*Eusimulium latipes*
Rhyacophila fasciata	*Panisus michaeli*
Agapetus fuscipes	*Lebertia lineata*
Potamophylax nigricornis	*Radix peregra*
Halesus digitatus	*Ancylus fluviatilis*

An analysis of density distribution reveals that some species prefer the area close to the borders (border species; Figs. 5—9), whereas others are most numerous in the interior of the moss carpet (interior species; Figs. 10—12).

More individuals are found at the borders than in the middle. About the same total number occur at the two borders (Fig. 5). *Gammarus pulex*, *Nemurella picteti*, *Pericoma blandula* and *Rheocricotopus fuscipes* are most numerous at the borders. *Nemurella picteti* is found in about the same number at the two borders (Fig. 7). *Gammarus pulex* and *Pericoma blandula* attain their highest abundance at the right border (Figs. 6 and 8), whereas *Rheocricotopus fuscipes* is most numerous at the left border (Fig. 7). The differences in numbers at the two borders can be due to differences in current velocity, which is stronger at the right border than the left. *Isotomurus palustris*, *Krenopelopia binotata* and *Parametriocnemus stylatus* are most numerous in the interior and clearly avoid the borders (Figs. 10—12).

Figs. 5—8. Distribution across the moss carpet of the total fauna, *Gammarus pulex*, *Nemurella picteti* and *Pericoma blandula*. Station 1 is situated at the right border and Station 10 at the left border looking downstream.

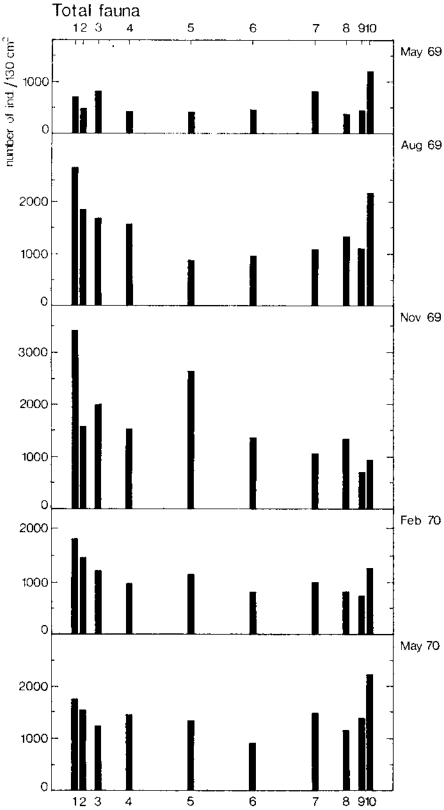

Fig. 5

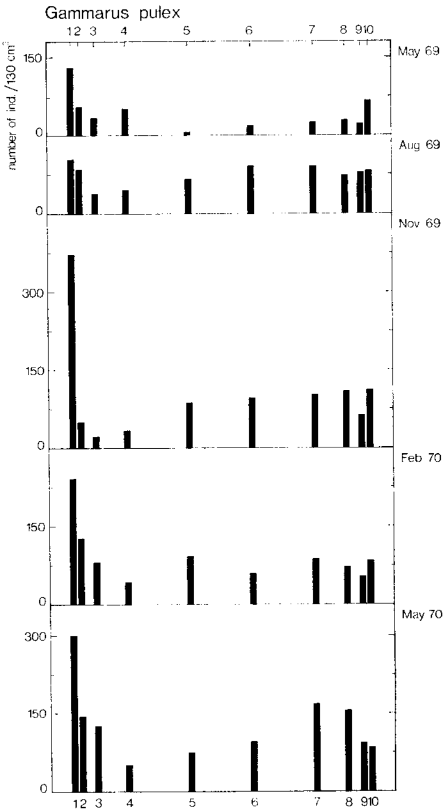

Fig. 6

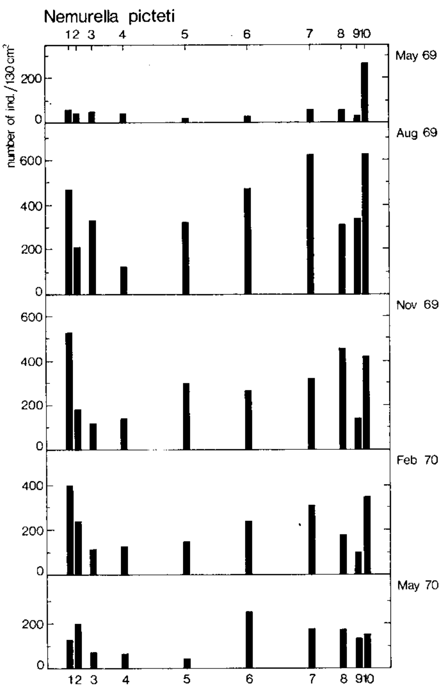

Fig. 7

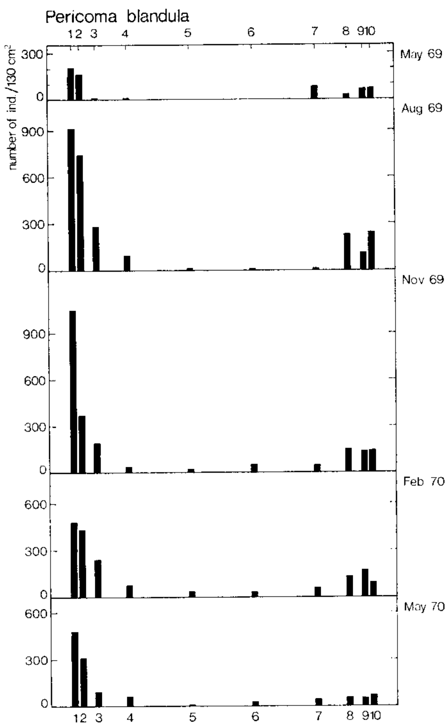

Fig. 8

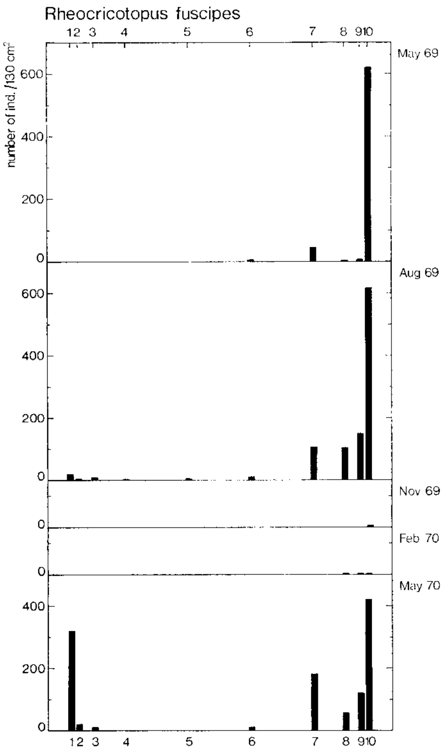

Fig. 9

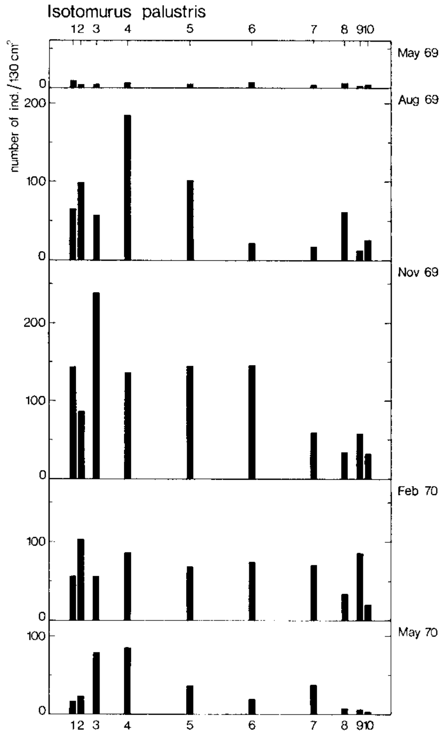

Fig. 10

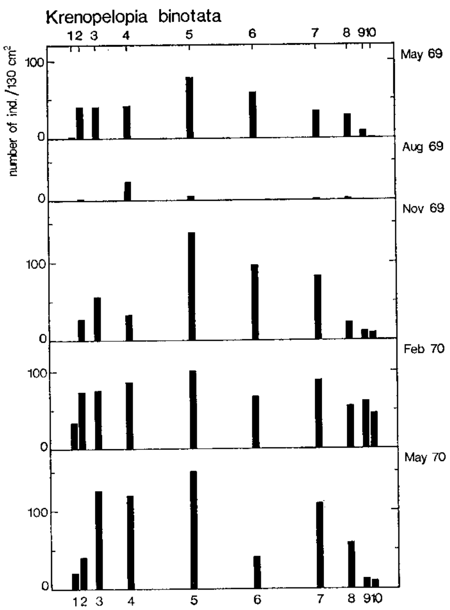

Fig. 11

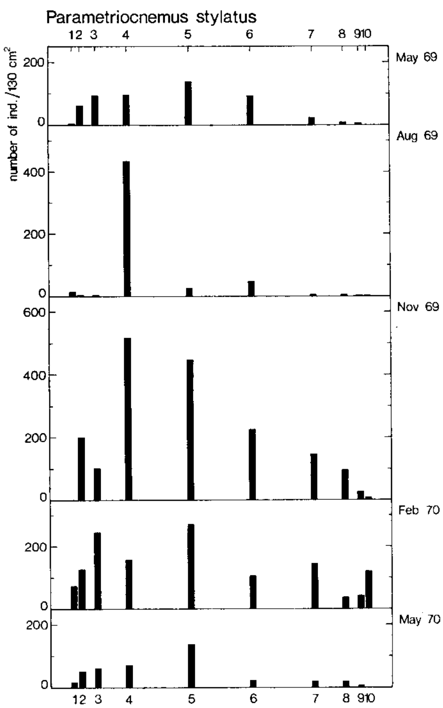

Fig. 12

To persue this analysis further a comparison is made between the mean of the outermost samples and the remaining eight samples from each sampling line at all sampling dates (Table 11). The border samples, taken 10—20 cm within the moss carpet, contain about $1^1/_2$ times the individuals as the intermediate samples. Several species are more than twice as numerous at the border than in the interior. They are classified as border species. The latter group also includes some species with the proportion

Table 11. Analysis of border and interior moss carpet preference by species which constitute more than 1 % of the total number in one sampling series. "B" is average number found in border samples. "I" is average number found in interior samples. Further explanation in text.

	B	I
Border species		
Nais elinguis	93	38
Gammarus pulex	78	36
Nemurella picteti	169	92
Pericoma blandula	185	58
Rheocricotopus fuscipes	99	11
Chaetocladius sp. cfr. *acuticornis*	17	0
Micropsectra spp.	44	15
Interior species		
Enchytraeidae	11	19
Eiseniella tetraedra	1	5
Isotomurus palustris	19	29
Krenopelopia binotata	4	27
Limnophyes prolongatus	1	4
Parametriocnemus stylatus	11	49
Paraphaenocladius impensus	0	5
Platyseius sp. (? *neocorniger*)	6	12
Mucronothrus nasalis	12	35
Galba truncatula	4	9
Indifferent species		
Pericoma fuliginosa	3	4
Pericoma pseudexquisita	3	3
Dixa spp.	7	4
Chaetocladius laminatus	59	63
Metriocnemus hygropetricus	5	4
Trissopelopia longimana	4	3
Total fauna	914	564

Figs. 9—12. Distribution across the moss carpet of *Rheocricotopus fuscipes, Isotomurus palustris, Krenopelopia binotata* and *Parametriocnemus stylatus.* Station 1 is situated at the right border and Station 10 at the left border looking downstream.

between border and interior samples < 2 due to a single exceptional sample. Using the same criteria some species are listed as interior species. The remaining species seem to be indifferent to variations within the moss carpet.

The main reason for distributional differences is undoubtedly variation in current velocity, the greatest of which is along the border. A higher current velocity implies smaller detritus deposits and so the substrate and food conditions are altered towards the border. We have not been able to measure current velocities in the moss carpet, but now and then places with more open moss growth were observed during the sampling period. In such places current velocity is increased locally and is undoubtedly responsible for some of the irregularities in horizontal distribution of species as seen in February and May samples from Station 5 in several of the Figs. 5—12.

The majority of border species are vertically distributed in water covered moss. Species associated with the dry or madicolous zones would risk being carried away with the flow and species associated with the detritus zone would find poorer substrate and food conditions here.

Of those preferring the interior of the moss carpet only three are associated with water covered moss. Species associated with the dry and madicolous zones play the important roles here.

All interior species except two have slow seasonal life cycles. The two exceptions are classified with the non seasonal group due to lack of knowledge about their life cycles. In contrast, only two border species have slow seasonal cycles, two are non seasonal and the rest have fast seasonal cycles. It is uncertain whether this difference is of biological significance, though it could be explained by better ecological conditions due to increased current flow along the border.

Summary

The moss carpet and the fauna associated with this biotope in Ravnkilde is described. Faunal samples were collected at intervals of three months from May 1969 to May 1970. 131 taxa were identified, 102 to species level. The total number of individuals averaged approximately 100,000/m^2 with 14 species representing 86.5 % of total number. Compared to other running water studies, the fauna in Ravnkilde must be regarded as rich, although greater densities have been found in moss from streams.

Ravnkilde's moss carpet is further characterized by the occurrence of crenophilous and crenobiontic species and the lack of several forms often found in large numbers further downstream.

Large variation in numbers occurs throughout the year, the maximum of 128,123/m^2 being found in November and the minimum, 87,315/m^2, in February. With few exceptions the same species dominate the fauna throughout the year.

The fluctuation in numbers of individuals agrees well with the life cycle of the dominant species.

A classification according to type of life cycle shows that species with long-lasting life cycles dominate the fauna quantitatively. Low summer temperatures and poor food conditions, especially for algal and filter feeders, are felt responsible.

Based on knowledge of the individual species' biology a vertical zonation of the fauna into four zones with quite different ecological conditions and faunal composition is described.

Although rills with stony bottoms border the moss carpet, the influence of the stone fauna on the moss fauna is unimportant. Species from the former group are only occasionally found in the mosses and then only very close to the border. However, a horizontal variation in the fauna does occur, some species being more numerous close to the border, others to the interior. Variation in current velocity and the amount of detritus among the moss stems is thought to be responsible for this trend.

Zusammenfassung

Die Moosdecke von Ravnkilde und ihre Fauna werden beschrieben. Die Proben der Fauna wurden vom Mai 1969 bis zum Mai 1970 mit Intervallen von drei Monaten gesammelt. 131 Taxa wurden identifiziert, 102 davon bis zu den Arten. Die Gesamt-Individuenzahl lag durchschnittlich nahe bei 100.000/m². 14 Arten machten 86,5 % der Individuen aus. Mit anderen untersuchten Wasserläufen verglichen, muß die Fauna in Ravnkilde als reich betrachtet werden, obwohl höhere Individuenzahlen im Moos größerer Wasserläufe vorkommen.

Die Fauna ist weiter durch das Vorkommen von krenophilen und krenobionten Arten charakterisiert, sowie auch durch den Mangel an mehreren Arten, die oft in größerer Zahl im unteren Wasserlauf zu finden sind.

Im Laufe des Jahres variiert die Anzahl der Individuen sehr, das Maximum wurde mit 128.123/m² im November und das Minimum mit 87.315/m² im Februar gefunden. Mit wenigen Ausnahmen dominieren die gleichen Arten während des ganzen Jahres. Die Fluktuationen in der Anzahl der Individuen stimmen mit dem Lebensrhythmus der dominierenden Arten gut überein.

Eine Klassifizierung nach diesen Rhythmen zeigt, daß Arten mit langem Lebenslauf quantitativ dominieren. Niedrige Sommertemperaturen und schlechte Ernährungsbedingungen werden als Ursachen dafür hervorgehoben, insbesondere für Algenfresser und für filtrierende Arten.

Aufgrund der Kenntnis der Biologie der einzelnen Arten wird eine vertikale Zonierung der Fauna aufgestellt. Es gibt vier Zonen mit ganz verschiedenartigen ökologischen Verhältnissen und Zusammensetzungen der Fauna.

Obwohl Rinnsale mit Steinboden begrenzend auf die Ausbreitung der Moosdecke wirken, ist der Einfluß der Steinfauna auf die Moosfauna ohne Bedeutung. Arten der ersteren Gruppe kommen in der Moosdecke nur zufällig und nur am Rande vor. Es gibt aber eine horizontale Variation in der Fauna, indem einige Arten dicht am Rande und andere im inneren Teil der Moosdecke zahlreich sind. Variationen in der Strömungsgeschwindigkeit und die Menge von Detritus unter den Moosstengeln werden für diese Tendenz verantwortlich gemacht.

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