Studies on the lentic Ephemeroptera and Plecoptera of Southern Norway

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The Ephemeropteran and Plecopteran faunas of lentic habitats ranging from 9 to 1448 m a.s.l. in four areas of southern Norway – Finse, Heimdalen, Vassfaret and the Oslo region – were investigated with respect to species composition and abundance. Environmental parameters, such as water chemistry and temperature, are considered in relation to the observed distributions. In addition, life-cycle data are presented for *Ameletus inopinatus, Siphlonuru slacustris, Baëtis macani, Centroptilum luteolum, Cloëon dipterum, C. simile, Heptagenia fuscogrisea, Leptophlebia marginata, L. vespertina, Caenis horaria* and *C. moesta* (Ephemeroptera), and for *Amphinemura sulcicollis, Nemoura avicularis, N. cinerea, Nemurella picteti* and *Leuctra fusca* (Plecoptera).

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The aim of this study was primarily twofold; to study the distribution and abundance of lentic Ephemeroptera and Plecoptera in contrasting areas of southern Norway, and to obtain information on the life cycles of different species. In addition, since little ecological work has been published on the Norwegian lentic Ephemeropteran and Plecopteran faunas, it is hoped that the present investigation will provide a basis for further studies and possibly indicate aspects worthy of more detailed investigation.

A number of taxonomic studies, distribution records, and check lists have been published concerning the Norwegian species (e.g. Bengtsson 1909, 1928, Brekke 1938, 1965, Lillehammer 1967, 1972, 1974a, Brittain 1972a and Dahlby 1973). During the last ten years a number of ecological studies from lotic habitats, principally in western Norway, have been carried out (Elliott 1965, Lillehammer 1965, 1966, 1974b, Larsen 1968 and Steine 1972). From lentic habitats there has been little published information. One of the few studies is that of Grimeland (1966a, b), who investigated the mayfly fauna of a group of freshwater habitats in the county of South Trøndelag with special reference to their distribution and the length of the adult stages. Some data are also available from wider limnological studies (e.g. Økland 1964). Lillehammer (1974b) surveys Plecoptera recorded from lentic localities in different parts of Norway.

STUDY AREAS

The geographical position of the four contrasting study areas – Finse, Heimdalen, Vassfaret and the Oslo region – is shown in Fig. 1. Scientific investigations under the auspices of the International Biological Programme (IBP) were already in progress in the first three areas and the present studies were carried out in co-operation with these projects. In the fourth area, the Oslo region, a number of the localities were or had been under investigation, some in connection with limnological studies, others being the subject for parasitological research.

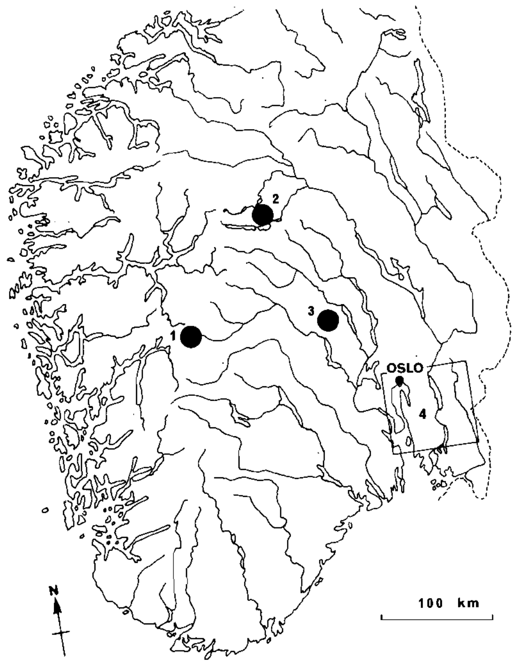

Fig. 1. The location of the four study areas. 1. Finse, 2. Heimdalen, 3. Vassfaret, 4. Oslo region.

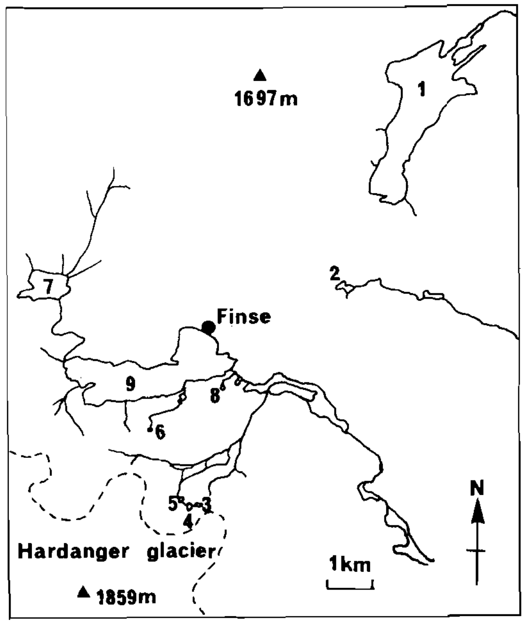

Fig. 2. The Finse area. Investigated localities are numbered.

Finse

The Finse area (Fig. 2), situated on the northwest side of the Hardanger glacier (Hardangerjøkulen), lies mainly within the Ulvik district of the county of Hordaland. Altitudes within the study area range from 1200 to nearly 1900 m a.s.l. At lower levels the bedrock is granite, which is slow to weather and poor in nutrients. Above this, especially on the north side of the main valley, there are schists which provide more nutrient conditions. The schists are in turn overthrust by granite, forming the Hallingskarvet massif and the higher parts of the Hardangerjøkul. In addition there are extensive areas of moraine material. The area is situated on the watershed between east and west. Precipitation is therefore high, in the region of 1200 mm per year, and this together with cool summers (mean temperature of 8°C for July and August) results in a short ice-free period. The whole area lies in the alpine region.

Heimdalen

Heimdalen and its surroundings (Fig. 3) lie on the eastern edge of the Jotunheim mountains in the county of Oppland. Within the area altitudes range from 1000 to 1843 m a.s.l. The bedrocks are basic but resistant to weathering, and are composed of intrusives and sparagmite from the thrust masses of the Caledonian and pre-Ecocambrian ages (Holtedahl 1960). Moraines are widespread, but there is no present glacial activity within the area.

The climate is drier and less severe than the Finse area. At the level of Øvre Heim-

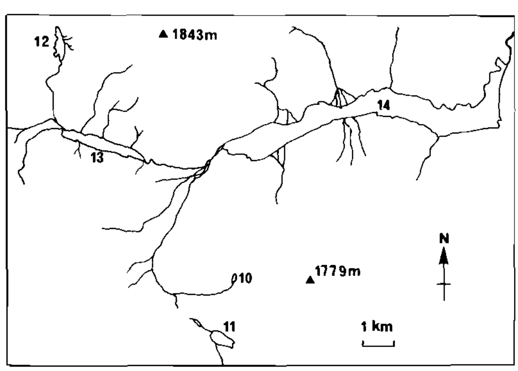

Fig. 3. Heimdalen and surroundings. Investigated localities are numbered.

dalsvatn annual precipitation is in the region of 700 mm and the yearly mean temperature is approximately 0°C. This results in a somewhat longer ice-free period than Finse, especially at lower altitudes. The lower localities (below 1100 m a.s.l.) are situated in the subalpine region, while the others lie in the alpine region. Intensive studies have been carried out on Øvre Heimdalsvatn under the auspices of IBP/PF.

Vassfaret

The Vassfaret area (Fig. 4) lies on the border between the counties of Buskerud and Oppland about 100 km north-west of Oslo. It comprises a forest area up to about 900 m a.s.l. and a mountain plateau area above this where an altitude of 1285 m a.s.l. is reached. The slowly eroding gneiss and granite which make up the bedrock of the area are covered by a thin layer of glacial gravel (Holmsen 1955, Smithson 1963). The area has an inland climate with cold winters and relatively warm summers, although precipitation is in the order of 1000 mm per year. However, there are quite large differences within the area between the valley bottom at 500–600 m and the mountain plateau at 1200 m a.s.l. Spruce (*Picea abies*) dominates the forest parts, with birch (*Betula pubescens*) and pine (*Pinus sylvestris*) occurring sporadically, particularly on and around boggy areas and around the tree line. The mountain plateau area lies in the middle alpine region.

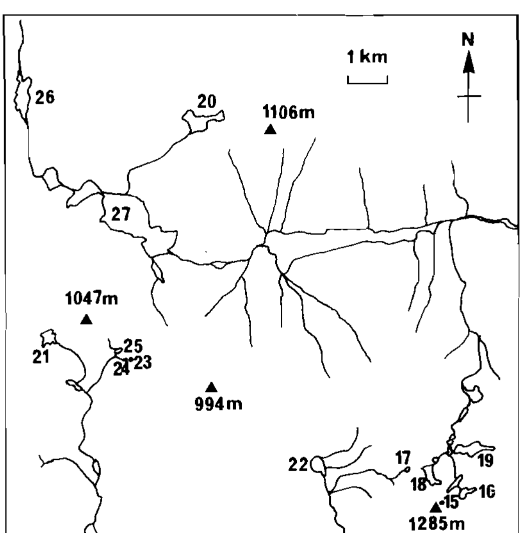

Fig. 4. Vassfaret. Investigated localities are numbered.

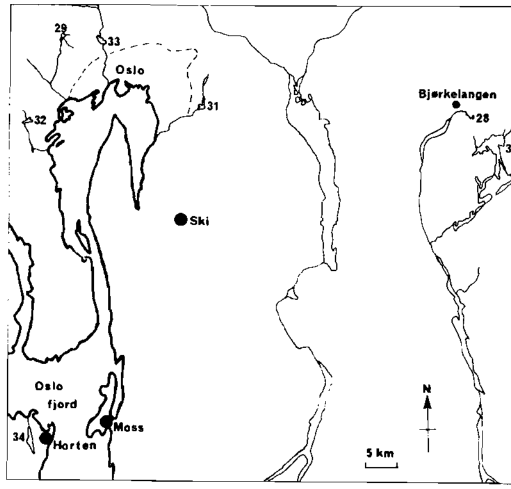

Fig. 5. The Oslo region. Investigated localities are numbered.

Oslo region

The region around Oslo (Fig. 5) has an extremely varied and complicated geology. In the east, granite and gneiss dominate, while to the west, Permian eruptives, together with Cambro-Silurian sediments, form the major part. Deposits of marine clay are common near the coast (Holtedahl 1960). The climate varies within the region, the degree of continentality increasing as one goes further north and further from the fjord. In Oslo, the annual mean temperature is 5.8°C and the yearly precipitation is 740 mm (based on values 1931–1960). Most of the region is covered by coniferous forest, although at lower altitudes large areas are devoted to agricultural and urban development.

METHODS

The four areas were sampled every 6–7 weeks during the ice-free period, thus enabling the registration of the major species in the different localities. In addition, especially in the more lowland localities where the ice-free period was longer and insect numbers higher, life-cycle data could be obtained. With only one, or even two, sampling visits, some major species could quite easily be absent from collections. For example, the mayfly *Baëtis macani* only occurs in collections from the end of July to the end of September while the stonefly *Capnia atra* is absent from collections for several weeks during the summer. The greater part of the field work was carried out during 1971, but in certain localities some sampling was carried out during 1972, largely to obtain more detailed information on the life cycles of certain species. As a large number of localities, often some distance from the road, were sampled with such a frequency, it was necessary to employ a relatively simple and rapid method. In addition, variation in substratum in the littoral and the difficulties of sampling substrata composed of large stones imposed limitations. However, the same methods were used throughout the study, thus making the results comparable within the scope of the investigation.

Two main types of sampling were used in each locality. First, for a period of 5 minutes, stones were picked up from the bottom by hand and examined for Ephemeroptera and Plecoptera. At the same time as the stones were picked up a net was held underneath to obtain those nymphs that swam away when disturbed (Macan & Maudsley 1968). Secondly, a 'kick' method was used, modified from its use in running-water studies (Hynes 1961, Frost et al. 1971), whereby the substratum was disturbed by kicking and a net passed once over the area. A total of five kicks was made. In some of the more productive lakes, where littoral vegetation was abundant, five net sweeps were made through the vegetation (Macan 1964). The net used in the investigations was circular, with a diameter of 20 cm and netting with 15 meshes/cm. With the exception of the largest and most varied localities where three stations were taken, two stations were sampled in each locality on each sampling visit. Stations were chosen to be representative of that locality and were sited away from inflow and outflow streams as such areas were considered to have a different faunal composition.

A search for adults was made in the vicinity of each station, but species only found as adults are indicated in Tables I–IV by 'I', there being the possibility that they did not originate from the habitat in question.

Nymphal collections were preserved in 3 % formalin, and adult specimens initially in 70 % alcohol and subsequently in 3 % formalin. The body lengths of the nymphs were measured, to the nearest 0.03 mm, from the tip of the head to the base of the cerci.

At each station air and water temperatures were measured. Water temperature was measured in the littoral zone at a depth of approximately 20 cm. To determine whether these spot temperature readings were representative of the maximum temperatures reached, maximum-minimum thermometers were placed in eight localities during the summer of 1971. The presence and extent of ice cover was also noted and the ice-free period given in the results is a composite value based on the conditions of 1971–1973.

A water sample for subsequent chemical analysis was taken from the shallow littoral in every locality on each sampling occasion. Calcium and magnesium values were obtained by titration with E.D.T.A. (the Schwarzenbach method). Specific conductivity was determined using a Philips direct-reading conductivity meter and values given as μmhos at 18°C ($\varkappa_{18}$) while pH was measured by a Radiometer pH meter 26. The consumption of $KMnO_4$ was determined as described by Werescagin (1931). For the chemical parameters mean values for the whole ice-free period were determined for each locality and it is these values that are given in the results tables.

From the summation of the results of the two methods of sampling the nymphal populations, an abundance index was calculated for all the species in each locality. In view of the variation in life cycle, whereby some species were present throughout the ice-free period while others occurred only briefly, maximum abundance rather than mean abundance formed the basis of the index. The abundance index for a locality was the maximum number of specimens of that species taken on any single sampling occasion divided by the number of sampling stations. Actual values ranged from 0.1 to 246. To simplify the appreciation of the relative abundance between localities, and as the methods are subject to a certain amount of

Table I. Physical, chemical and faunistic parameters of the investigated localities in the Finse area

										Ephem.		Plecoptera			
Locality	m a.s.l.	Area, ha.	Ice free, months	Max. temp., ° C	Ca, mg/l	Mg, mg/l	$\varkappa_{18}$, µmhos	pH	$KMnO_4$, mg/l	*Baëtis macani*	*Siphlonurus lacustris*	*Capnia atra*	*Diura bicaudata*	*Nemoura cinerea*	*Nemurella picteti*
1. Flakavatn	1448	334	3.25	5.2	1.7	0.8	12.0	6.7	0.4			+++			
2. Lake 1430	1430	8.0	3	6.7	2.3	0.9	15.0	7.0	0.5			+++			
3. Lake 6	1365	0.7	3.25	8.8	14.1	2.5	71.9	7.4	0.4			+++			
4. Lake 5	1363	1.4	3.5	8.7	10.2	2.0	59.3	7.1	<0.1						
5. Lake 4	1353	1.1	3.5	7.8	7.1	1.1	43.4	7.2	<0.1			++			
6. Lake 8	1330	0.5	3.5	10.0	4.1	1.2	25.1	7.2	0.4	++					
7. Sandaavatn	1262	52	3.5	7.7	3.3	1.0	21.2	6.9	<0.1			++			+
8. Lake 13	1225	0.6	3.5	8.2	1.2	0.6	9.5	6.8	3.0	I					
9. Finsevatn	1214	283	3.75	9.2	2.7	0.8	17.3	6.7	0.9		++	++	++	+	I

variation, the indices were grouped into the following four categories:

0.1–0.9	+	rare
1.0–9.9	++	common
10.0–99.0	+++	moderately abundant
>100	++++	abundant

DISTRIBUTION AND ABUNDANCE

Finse

A summary of the results from the Finse area is given in Table I. During the summer of 1971 the highest temperatures recorded by maximum-minimum thermometers in place throughout the ice-free period in Lake 8 and Sandaavatn were 13.7°C and 8.8°C respectively. Spot values from other localities reinforce this view, with spot maximum temperatures ranging from 5.2° C for Flakavatn to 10.0° C for Lake 8. The ice-free period for the lakes in the Finse area is correspondingly short, between 3 and 4 months.

The concentration of dissolved minerals shows considerable variation, with particularly high values in areas of recent glacial activity such as Lakes 4, 5, and 6 which show increasing specific conductivity with decrease in distance from the glacier front of Blåisen. Values of pH range from 6.7 to 7.4, the higher values again being found near Blåisen. The high pH values are due to the ability of glaial material to absorb H^+ions (Strøm 1956). The $KMnO_4$ consumption is extremely low with the exception of Lake 13, which is partly surrounded by peat bog and has a small catchment area.

The fauna of lentic localities at Finse is poor in species, particularly Ephemeroptera. Only two species of Ephemeroptera are present, *Baëtis macani* Kimmins and *Siphlonurus lacustris* Eton. The former occurs up to over 1300 m and is often abundant in outlet streams. iFnsevatn is the sole lentic habitat in which *S. lacustris* has been found, conditions probably being too severe in the other localities. However, *S. lacustris* has been found recently in trout from Lengjedalsvatn (7 km east of Finse), situated 1305 m above sea level (Lien, personal communication), so altitude in itself is not limiting. Both species are aestival forms, growing rapidly during the course of the summer and emerging at the end of the summer.

The dominant and often the sole species of Plecoptera is *Capnia atra* Morton, which occurs even in the most extreme habitats such as Flakavatn and Lake 1430. Also it has the capacity to invade relatively recently created habitats such as Lake 6 which was covered by glacier until about 1920 (Andersen & Sollid 1971). Investigation of a small lake near Blåisen, exposed only since 1955, indicated that *C. atra* was absent, probably owing to the lack of suitable substratum rather than

Table II. Physical, chemical and faunistic parameters of the investigated localities in the Heimdalen area

										Ephemeroptera					
Locality	m a.s.l.	Area, ha.	Ice free, months	Max. temp., ° C	Ca, mg/l	Mg, mg/l	$\varkappa_{18}$, μmhos	pH	$KMnO_4$, mg/l	*Baëtis macani*	*Ameletus inopinatus*	*Siphlonurus lacustris*	*Leptophlebia vespertina*	*L. marginata*	*Siphonurus aestivalis*
10. Blåtjern	1465	3.5	3.75	12.3	0.9	0.9	8.7	6.6	1.8						
11. Urektjern	1365	28	3.75	11.7	1.0	0.6	8.6	6.6	1.7			+	+		
12. Brurskardtj.	1308	18	3.75	10.8	1.1	0.7	9.9	6.6	2.0	++					
13. Ø. Heimdalsvn.	1090	78	4.25	14.7	1.2	0.7	12.7	6.7	4.0	+++	I	+++	++	++	I
14. N. Heimdalsvn.	1052	770	4.5	10.0	1.4	0.7	12.0	6.8	8.2		++	+++	++	+	

colonising ability. Three other species, *Diura bicaudata* (L.), *Nemoura cinerea* (Retzius), and *Nemurella picteti* Klapalek, are restricted to Finsevatn and the surrounding pools.

Although Finsevatn has the most species, their numbers are low. During the last 40 years considerable changes have occurred in Finsevatn (Strøm 1956, Borgstrøm 1972). During the 1930s it was strongly affected by glacial ooze, but owing to the reduction of glacial activity and the redirection of an outlet stream of the Hardanger glacier the waters have become much clearer and the pH has fallen. The increased transparency would be expected to increase the productivity of the lake. However, since 1965 Finsevatn has been regulated for hydro-electric power with a height of 3.3 m, thus retarding any increase in littoral productivity.

Heimdalen

The results from Heimdalen and its surroundings are given in summary form in Table II. Maximum water temperatures are higher than at Finse, in the region of 10–15° C. As a result of bedrocks that are slow to weather the concentrations of dissolved minerals are generally low. The consumption of $KMnO_4$ increases with decreasing altitude, reflecting the increase in the supply of allochthonous organic matter from terrestrial vegetation as one goes from the mid-alpine, through the low alpine and into the sub-alpine region.

Blåtjern lies above the limit for strictly lentic Ephemeroptera, although both *B. macani* and *Ameletus inopinatus* Eton occur in the outflow stream. Urektjern and Brurskardtjern support extremely low mayfly populations, only isolated specimens being taken. However, once in the subalpine region the picture changes, with more species and a considerable increase in numbers.

Plecoptera are more widely distributed,

Table III. Physical, chemical and faunistic parameters

Locality	m a.s.l.	Area, ha.	Ice free, months	Max. temp., ° C
15. Trig. Pool	1245	0.5	4	11.3
16. Lake 1220	1220	6.0	4	11.7
17. Pool 1205	1220	1.0	4	8.7
18. Lake 1205	1205	9.0	4.25	10.9
19. Lake 1171	1171	19	4.25	11.0
20. Fjellvatn	994	28	4.5	19.2
21. Raufjellvatn	855	9.8	5	13.5
22. Damtjern	845	12	5	13.3
23. Cabin pond A	795	0.2	5	11.5
24. » » B	795	0.6	5	11.7
25. Lille Damtjern	792	2.0	5	11.5
26. Suluvatn	602	23	5.25	23.8
27. Nevlingen	572	147	5.5	20.4

Plecoptera						
Capnia atra	*Diura bicaudata*	*Nemurella picteti*	*Nemoura cinerea*	*N. avicularis*	*Amphinemura standfussi*	*Isoperla obscura*
+++	++	++				I
+++	++		++			I
++	+	++	+++			
	+++	++	++	+++	+++	I
++++	++	++	++	+++	++	

although there is an increase in both species and abundance as one comes into the sub-alpine zone. Adults of *Isoperla obscura* (Zetterstedt) were taken near most localities, but as no nymphs were taken it is indicated by 'I' in Table II. This species is probably common around the outflows. More information on the Plecoptera of the Heimdalen area, both lentic and lotic, is given in Lillehammer (1974b).

Vassfaret

Table III summarises the results from Vassfaret. All localities are especially low in dissolved minerals owing to the fact that hard, acidic rocks predominate in the area. The water chemistry of the localities around 1200 m is remarkably constant, whether they be pools or lakes. In the forest area there is more variation, mostly explained by differences in size and altitude. The smaller habitats have a lower pH and a higher $KMnO_4$ consumption, while calcium, magnesium, and specific conductivity decrease with altitude. These general conclusions are substantiated by Eie (1974).

Despite an increase in the ice-free period and in summer temperatures, especially at lower altitudes, the lentic Ephemeropteran and Plecopteran faunas are surprisingly poor, both in species and in total numbers when compared with Heimdalen. This is probably the result of extremely low mineral content, low pH, and in the forest area a high degree of humification. The two Nemourids, which for practical purposes are the sole species of either Ephemeroptera or Plecoptera in the mountain habitats, are present in fairly large numbers. This is probably the result of the absence of fish and the lack of competition

of the investigated localities in the Vassfaret area

					Ephemeroptera						Plecoptera		
Ca, mg/l	Mg, mg/l	$\varkappa_{18}$, µmhos	pH	$KMnO_4$, mg/l	*Leptophlebia marginata*	*L. vespertina*	*Siphlonurus linnaeanus*	*S. lacustris*	*Heptagenia fuscogrisea*	*Centroptilum luteolum*	*Nemoura cinerea*	*Nemurella picteti*	*Nemoura avicularis*
0.4	0.4	8.3	5.2	2.8							+++	+	
0.3	0.4	7.6	5.3	1.1							+++	+++	
0.4	0.3	7.6	5.3	2.7							+++		
0.3	0.4	8.1	5.1	1.4	+						+++	+++	
0.4	0.4	7.4	5.3	2.1		+					++	+++	
0.5	0.4	7.9	5.5	6.7	++	+++					+++	+	
0.7	0.5	9.4	5.3	5.1	++	++	+				++		++
0.5	0.5	9.7	5.1	12.4	++	+++					+++	+	++
0.9	0.7	10.0	5.1	42.9		+							
0.7	0.6	11.8	4.8	38.3		++							
0.9	0.6	11.5	5.3	23.9		+++							
1.3	0.8	11.8	6.0	9.8	+++	++		++	++	+	++		++
1.2	0.5	10.7	6.3	15.1	++	+++			++		++		+++

Table IV. Physical, chemical and faunistic parameters of the investigated localities in the Oslo region

										Ephemeroptera			
Locality	m a.s.l.	Area, ha.	Ice free, months	Max. temp., °C	Ca, mg/l	Mg, mg/l	$\varkappa_{18}$, μmhos	pH	$KMnO_4$, mg/l	*Leptophlebia vespertina*	*L. marginata*	*Centroptilum luteolum*	*Caenis horaria*
28. Røytjern	227	30	6	17.0	4.4	1.8	35.1	6.6	12.7	++++	++		++
29. Burudvann	217	50	6.25	18.5	6.5	1.9	39.6	7.2	17.9	+++	+++	+	++
30. Setten	167	1250	7.75	19.7	2.8	1.6	28.7	6.7	22.8	++++	++	+++	+++
31. Nøklevann	163	73	6.5	18.5	4.1	2.2	36.4	7.0	14.7	++++	+++	+	++
32. Semsvann	144	76	6.5	21.0	13.8	2.4	74.4	7.6	15.2	+++	+++	+++	+++
33. Bogstadvann	135	100	6.5	19.1	4.4	2.1	31.7	6.9	19.6	++++	+++	+	+++
34. Borrevann	9	208	7.75	25.0	13.2	4.7	134	8.8	18.1		+	++	++

for the available food owing to the general paucity of the fauna.

Apart from sporadic occurrences, the Ephemeroptera have their upper limit in the subalpine region. *Leptophlebia vespertina* (L.) is the sole mayfly or stonefly in the three most humic localities. This widespread species obviously owes part of its success to its ability to survive in a wide range of chemical and physical environments, including low pH and oxygen concentration (Brittain, unpubl. data). The lakes Suluvatn and Nevlingen have a more diverse mayfly fauna than the other localities. They both have a higher electrolyte content, pH, and temperature. Of the two, Suluvatn has the more species, possibly because of the greater regulation of Nevlingen in connection with earlier timber floating. In addition, Suluvatn is generally much shallower and thus has a larger littoral area in proportion to its total area than Nevlingen.

The Plecopteran community is uniformly poor in species. It is surprising that both *C. atra* and *D. bicaudata* are absent since suitable habitats are present in the higher parts of Vassfaret. In addition both species are present in the outflow of the large lake, Sperillen, which is situated only about 25 km from the investigated localities in Vassfaret (Lillehammer, personal communication). *Nemoura cinerea* is the dominant stonefly species. It occurs together with *Nemurella picteti* above the tree line and with *Nemoura avicularis* at lower altitudes. In only one locality, Damtjern, are all three species present. Therefore, owing to the difficult conditions in Vassfaret, there may be interspecific competition between *N. avicularis* and *N. picteti* in the forest region, restricting the latter species to the montane areas. In other areas *N. avicularis* is not found above the subalpine region (c.f. Heimdalen), but *N. picteti* occurs in lowland localities when conditions are more favourable. The relationships between these three Nemourids deserve further attention.

Oslo region

The data from the lakes in the Oslo region are given in Table IV. They are ice free longer than localities in the other three areas. Setten and Borrevann are free of ice for nearly 8 months, Setten because of its large size and Borrevann because of its low altitude and proximity to the Oslo Fjord. Complete ice cover is rare on these lakes before December/January. Water temperatures in the Oslo region are correspondingly higher during the summer months.

Røytjern, Setten ,and Nøklevann, lying on hard acid rocks and surrounded by coniferous forest, have lower electrolyte values. The catchment areas of Bogstadvann and Burudvann are largely composed of slow weathering eruptive rocks, so that their electrolyte content is not as high as Semsvann, which lies

							Plecoptera		
C. moesta	*Siphlonurus linneanus*	*S. aestivalis*	*Ephemera vulgata*	*Cloëon dipterum*	*C. simile*	*Heptagenia fuscogrisea*	*Nemoura cinerea*	*Nemoura avicularis*	*Leuctra fusca*
+++			+	+	++				++
I			+			++	+		
	+		+	+	++	+++		++	+
+++		I	+	++	+		++		++
++++			++	+++	+		++		I
	++			+++	++	++	++		++
+++				+++		+			

partly on basic Cambro-Silurian sediments. In addition, more farming is carried on around Semsvann.

Borrevann is situated below the post-glacial marine boundary, which has resulted in the deposition of large amounts of marine clay in the area. This, together with the high level of farming practised around the lake, has produced a lake which is among the most eutrophic in Norway. The levels of $KMnO_4$ consumption in the localities from the Oslo region are remarkably similar, with values ranging from 12.7 to 22.8 mg/l O_2. However, the origin and nature of the organic sub-seances probably vary considerably.

The Ephemeropteran fauna is rich in both species and numbers. It includes a number of species more or less restricted to lowland localities, such as *Cloëon dipterum* and *Caenis horaria.* The restriction of such species to lowland habitats is likely to be a combination of temperature, substratum and the availability of food. However, the most abundant species is the widespread *Leptophlebia vespertina.*

The regulation of Nøklevann, in connection with its use as a source of drinking water for the city of Oslo, seems to have had little effect on the mayfly and stonefly fauna. However, the increased use of the water from Borrevann for drinking purposes has been a contributary factor to its increasing eutrophication. In Borrevann conditions are obviously not suitable for some mayfly species, such as *L. vespertina* and *Heptagenia fuscogrisea,* which are either absent, or present in very small numbers.

The following additional species were recorded by Økland (1964) from Borrevann: the Ephemeroptera, *Ephemera vulgata, Siphlonurus aestivalis* and *Caenis nocturna,* and the Plecoptera *N. cinerea* and *N. picteti.* Both stoneflies and *S. aestivalis* were extremely rare and only isolated specimens were taken during the whole period of Økland's intensive study. *Ephemera vulgata* and *C. nocturna* were also uncommon and were more usual on substrata types other than those investigated in this study, namely mud and sand especially at greater depths than sampled. There is also the possibility that the composition of the littoral community has changed in the last 10 years in response to the accelerating rate of eutrophication (Morgan 1970).

The Plecopteran fauna of the lentic localities in the Oslo region is poor, suggesting that few species are successful in the more productive lowland habitats except where they are large in size.

LIFE CYCLES

Owing to their small numbers in samples the following species recorded in this study are not discussed in respect to their life cycles: *Siphlonurus aestivalis, S. linneanus, Ephemera vulgata* and *Isoperla obscura.*

EPHEMEROPTERA

Ameletus inopinatus Eaton

This species is present in small numbers in the lower lentic habitats in Heimdalen. Previous investigations (Gledhill 1959, Larsen 1968, and Ulfstrand 1968) concluded that the species is univoltine with a long emergence period. The present results do not diverge from this, emergence reaching a peak in Øvre Heimdalsvatn in the first week in July, but mature nymphs are still found as late as September. Growth appears to take place under the ice as most nymphs are almost fully grown shortly after ice break.

Siphlonurus lacustris Eaton

In a Welsh stream (Hynes 1961) nymphs of *S. lacustris* were small throughout the winter, grew rapidly during March, April, and May and emerged in June. Small nymphs appeared again a month later, but hatching was spread over several months, some overwintering in the egg stage. A wide variation in incubation period was also found experimentally by Degrange (1960). In Heimdalen and around Finse the life cycle is essentially similar, but the timing is different. By ice break in June most nymphs are only 2–4 mm in length. Growth is then rapid, and emergence reaches a peak in Heimdalen at the beginning of August, and at Finse 3–4 weeks later, no doubt owing to later ice break and lower temperatures. In Swedish Lappland the emergence period extends from mid-July to early September, with a peak at the end of July (Ulfstrand 1969). More detailed studies on the life cycle of *S. lacustris* in Øvre Heimdalsvatn will apear in a future paper.

Baëtis macani Kimmins

The life cycle of *B. macani* will form the subject of a separate publication. Briefly, its life cycle is one of extremely rapid growth during the first half of the ice-free period followed by emergence during the second half. Thus at Finse, emergence reaches a peak in September, whereas in Heimdalen it occurs in August.

Centroptilum luteolum (Müller)

The life cycle of *C. luteolum* has been the subject of some discussion in respect of whether it is multivoltine or just a case of an extended emergence period (Bretschko 1965, Macan & Maudsley 1968 and Lavandier & Dumas 1971). The general consensus is that there are two generations per year, a slow growing winter one and a rapidly growing summer one. The data from Semsvann (Fig. 6) suggest that there are two generations per year, a winter generation emerging in June and a summer generation which emerges in August. In June most of the population is ma-

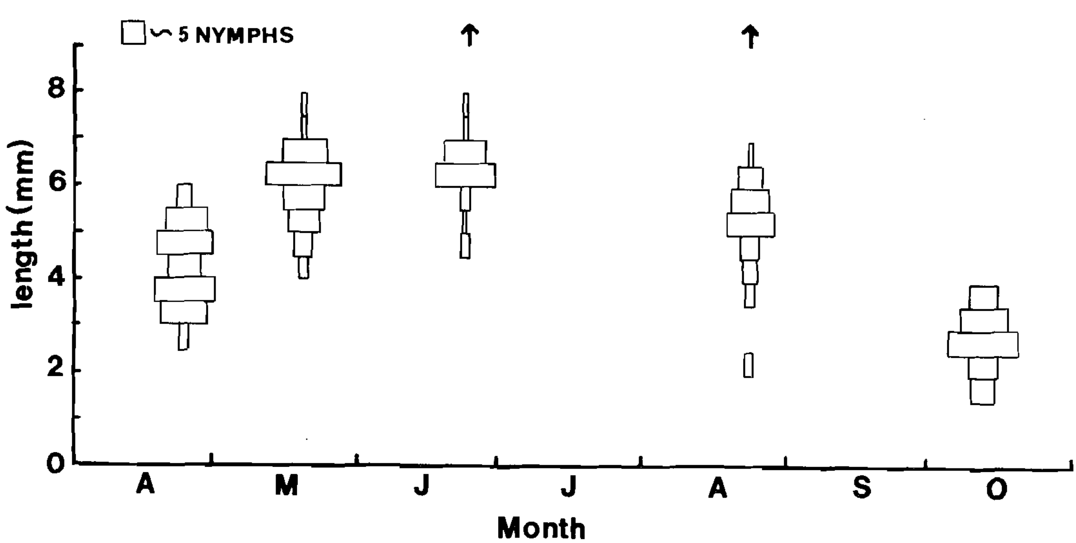

Fig. 6. Life cycle of *Centroptilum luteolum* in Semsvann (loc. 32). ↑ indicates adults were taken.

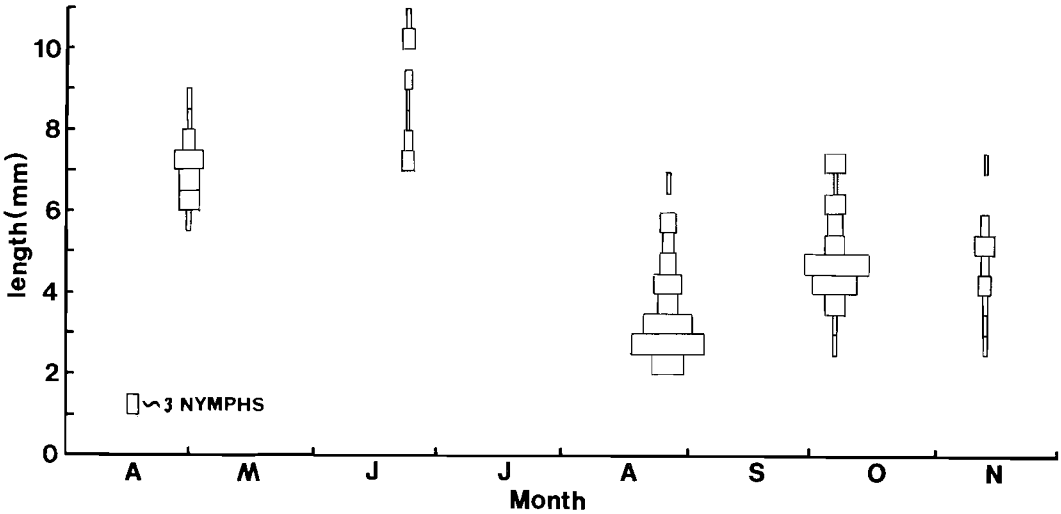

Fig. 7. Life cycle of *Cloëon dipterum* in Bogstadvann (loc. 33).

ture and none are less than 4.5 mm, while in August more than half the population is below 5.5 mm, thus indicating that a new generation has hatched during July. Data from Setten and Borrevann are compatible with the species being multivoltine. Grimeland (1966a) records the flight period of *C. luteolum* in South Trøndelag as from mid-June to the end of August, without any major break. Therefore, even if multivoltine, there is probably a great deal of overlap between the two generations.

Cloëon dipterum (L.)

Previous studies on the life cycle of *C. dipterum* (Brown 1961, Macan 1961, Kjellberg 1973) have shown it to be predominantly univoltine, although in some summers a second rapidly growing generation occurs. In both Bogstadvann and Borrevann *C. dipterum* is univoltine, the nymphs reaching maximum size and emerging during July (Fig. 7). Growth of the next generation is fairly rapid during August and September, reaching 4–5 mm by early October. Growth continues during the period of ice cover, and by the end of April a length of 6–8 mm is attained.

Cloëon simile Eaton

In Britain, *C. simile* has two generations per year, one emerging in May and June and the other during September (Macan 1961). Grimeland (1966a) gave two flight periods for this species in South Trøndelag, June/July and August. In Bogstadvann only one generation is apparent, emerging in August after *C. dipterum*, but sample numbers are low so the species may well be multivoltine in Bogstadvann.

Heptagenia fuscogrisea (Retzius)

The growth and life cycle of *H. fuscogrisea* has been studied by Bengtsson (1968) in northern Sweden, where it was univoltine and emerged during June and July. Most growth occurred during the autumn and early spring. In the Vindelälven area of northern Sweden Ulfstrand (1969) captured adults during July and early August. In both Setten and Røytjern, for which most data are available, emergence occurs in June (Fig. 8). By the end of July small nymphs of the next generation are already present in collections. After hatching, growth is more rapid in Røytjern than in Setten, possibly owing to the higher average temperatures in the smaller Røytjern. Scattered results from Vassfaret and Bogstadvann differ little from the situation in Setten and Røytjern.

Leptophlebia marginata (L.) and
L. vespertina (L.)

The life cycle of these two species, which are best treated together, has been well docu-

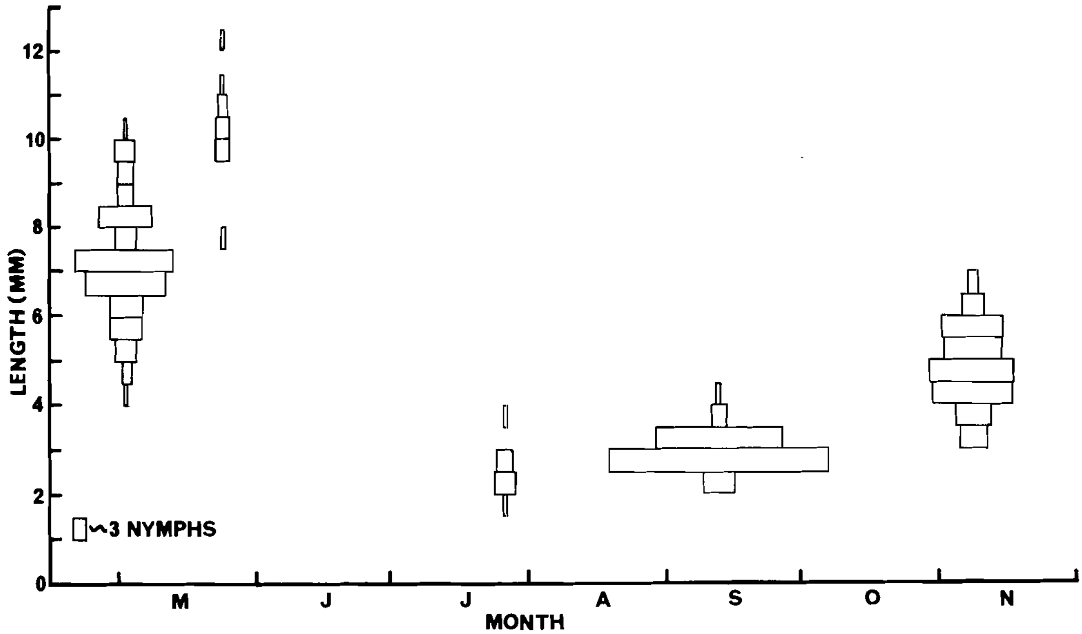

Fig. 8. Life cycle of *Heptagenia fuscogrisea* in Setten (loc. 30).

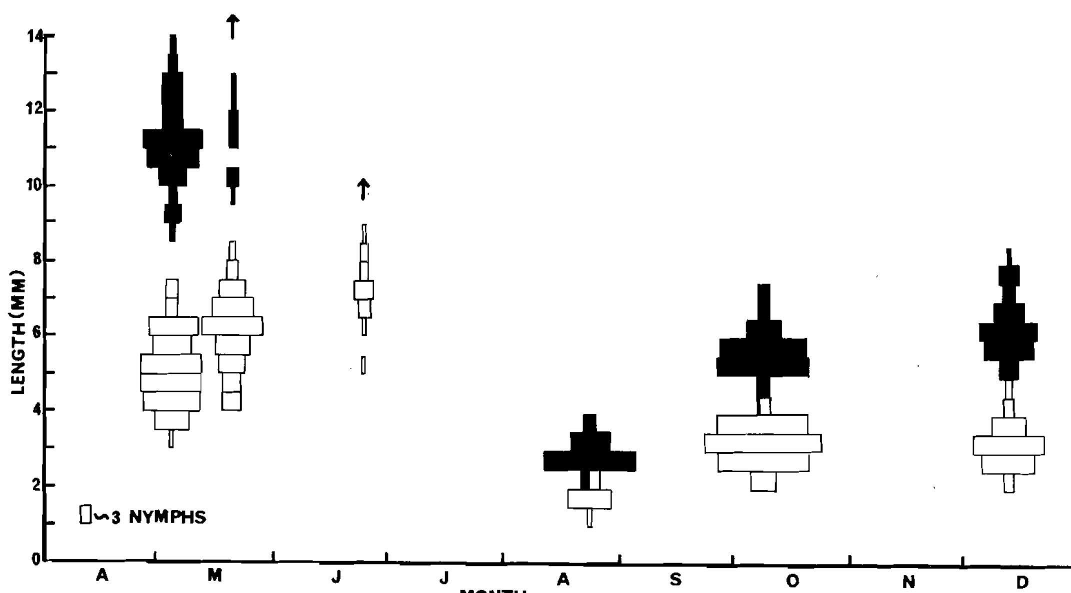

Fig. 9. Life cycles of *Leptophlebia marginata* (shaded) and *L. vespertina* (unshaded) in Burudvann (loc. 29). Arrows indicate the presence of adults of the respective species.

mented in Britain (Moon 1938, Macan 1961, 1965, and Brittain 1972b). In Sweden, *L. vespertina* has been studied by Kjellberg (1972, 1973) and *L. marginata* by Bengtsson (1968). Both species are univoltine, with the possible exception of the Swedish mountains

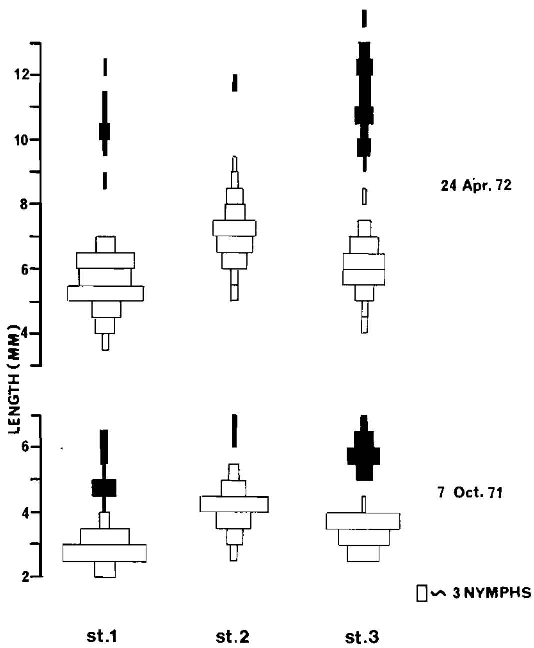

Fig. 10. Size difference between *Leptophlebia marginata* (shaded) and *L. vespertina* (unshaded) at 3 sampling stations around Bogstadvann (loc. 33).

(Kjellberg 1973), *L. marginata* being larger at a given time and emerging earlier than *L. vespertina.* Emergence of both species takes place later in Scandinavia than in Britain because of lower water temperatures and the presence of a cover of ice until May/June. In the present study the limits recorded for the flight period of *L. marginata* were 24 April to 15 July and for *L. vespertina* from 24 May to 9 September. Generally the peak emergence of *L. marginata* varied from May in lowland localities to June/July in the higher regions, while that of *L. vespertina* was in most cases approximately one month later. A major factor determining the time of emergence of these two species is temperature (Macan & Maudsley 1966, Brittain, in press) so it is to be expected that emergence will take place later at higher altitudes. Nymphal growth in a lowland locality, Burudvann, is shown in Fig. 9.

The absolute size of each species at a given time can also vary within the same lake. For example, in Bogstadvann size differences are apparent between the three sampling stations (Fig. 10). Stations 1 and 3 are stony shores, while station 2 is a shallow bay with emergent vegetation where both temperature and primary production are generally higher. In addition, station 2 has a smaller population of *L. marginata* which would reduce any possible interspecific competition.

Caenis horaria (L.)

In a study of what was at the time thought to be a population composed solely of *C. horaria.* but may have been a composite population of *C. horaria* and *C. moesta* (Moon 1938), it was found that no growth occurred during the winter months. The species was univoltine, emerging in June and July and small nymphs appearing again by the end of July.

Essentially the same situation as Moon (1938) found in the English Lake District was

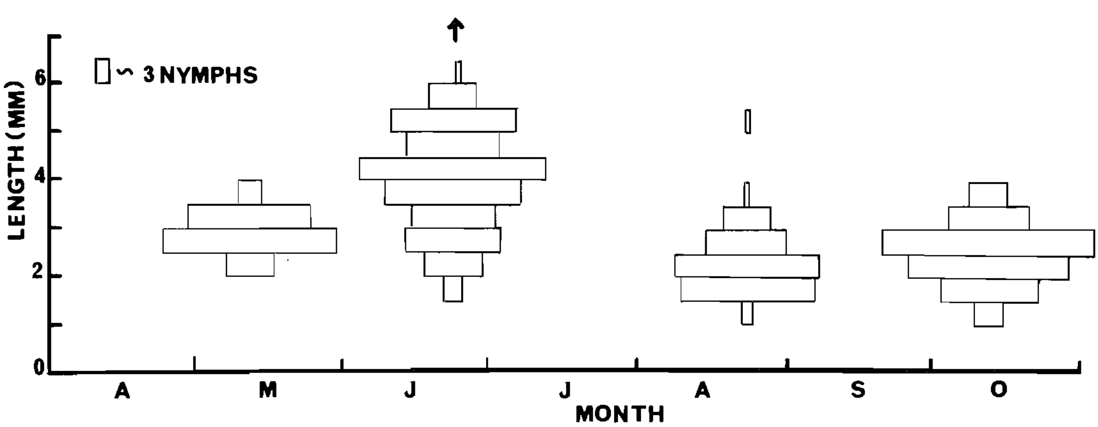

Fig. 11. Life cycle of *Caenis horaria* in Semsvann (loc. 32). ↑ indicates adults present.

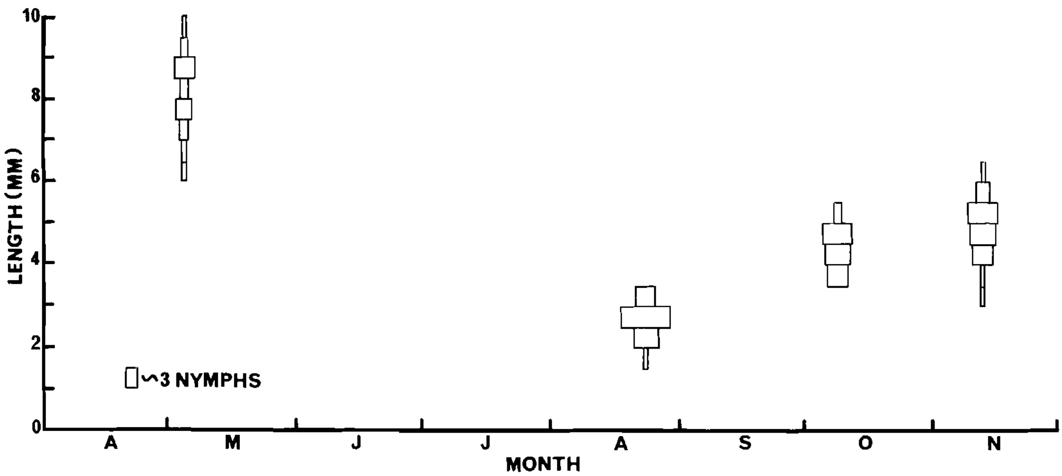

Fig. 12. Life cycle of *Nemoura avicularis* in Burudvann (loc. 29).

found in the Oslo region (Fig. 11). Small nymphs appeared in August and had reached a length of 2.5–3.0 mm by October. From October until May there was virtually no growth, the second period of growth taking place in the month or so before their emergence during June and July.

Caenis moesta Bengtsson

From the data available the life cycle of *C. moesta* is very similar to that of *C. horaria*. There are only small differences in mean size and size distribution of the two species. This may be a reason for the absence of bimodality in Moon's (1938) results for '*C. horaria*'.

PLECOPTERA

Amphinemura standfussi Ris

Amphinemura standfussi is a univoltine species which emerges later than many other lentic stoneflies. In Heimdalen emergence is concentrated in the month of August and most growth takes place in the two months prior to emergence.

Brinck (1949) and Benedetto (1973) record a similar situation from the mountainous and northern parts of Sweden, while in southern Sweden (Brinck 1949) the species is more hiemal. From northern Norway Tobias & Tobias (1971) registered adults during August.

Nemoura avicularis Morton

This species has a one-year life cycle in a wide range of localities. Its life cycle has been studied in a number of countries and reviewed by Brittain (1973). In the lentic habitats investigated emergence took place soon after ice break, during May and June. The nymphs of the next generation are first found in collections during August and growth is then fairly rapid during the autumn, a length of 5–6 mm being attained by the beginning of November (Fig. 12).

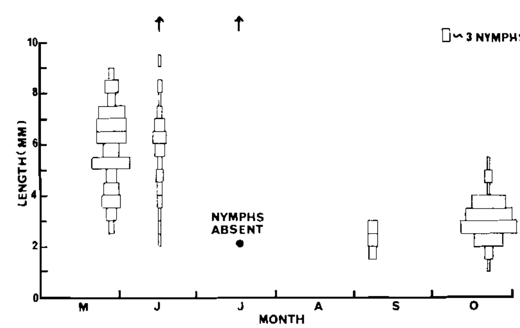

Fig. 13. Life cycle of *Nemoura cinerea* in Damtjern (loc. 22). ↑ indicates adults taken.

Nemoura cinerea (Retzius)

Field studies of *N. cinerea* (Brinck 1949, Hynes 1961, Svensson 1966, and Benedetto 1973) have reported this species to be univoltine with a long emergence period and often a large spread in nymphal size. However, from laboratory studies, Khoo (1964) concluded that *N. cinerea* was semivoltine and demonstrated the presence of extended egg hatching and nymphal dormancy.

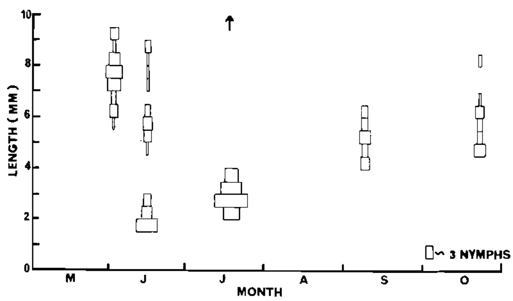

Fig. 14. Life cycle of *Nemoura cinerea* in Lake 1205 (loc. 18). ↑ indicates adults taken.

In lentic localities around Oslo emergence began by the end of May. At 850 m in Vassfaret adults were common at the end of June, whereas in the mountain localities adults were most abundant during July. In the lowland localities up to and including Damtjern in Vassfaret, *N. cinerea* showed a clear univoltine life cycle. For example, in Damtjern (Fig. 13) emergence began 2–3 weeks after ice break and continued well into July. Small nymphs appeared in September and reached an average length of 3 mm by the middle of October. By the spring there was considerable spread in population size, resulting in a relatively long emergence period. Above the tree line, however, the pattern became rather different. Emergence did not commence until the end of June, reached a peak during July, and continued as late as September. Small nymphs were already present in June, at the same time as mature nymphs. This bimodality was especially noticeable in Lake 1205 (Fig. 14).

Eggs of *N. cinerea* from Lake 1205 were incubated in the laboratory at 10° C where they hatched after 25–26 days. The earliest emergence which could have physically taken place in Lake 1205 was, owing to the cover of ice, the beginning of June. Even at a temperature of 10° C, which is higher than present in the field at that time, small nymphs would not appear in collections until early July. However, by this time the average length of the nymphs in the field was nearly 3 mm (Fig. 14), having been present in collections since mid-June. The obvious conclusion is therefore that *N. cinerea* takes at least two years to complete its life cycle in such habitats. Thus little growth takes place during the first 9–10 months after oviposition. Most growth occurs during the following summer, from approximately 2 to 6 mm in length.

If the species were univoltine in all localities it would be difficult to explain the larger mean size of populations during September and October in the higher situated localities where temperatures and also probably available food are lower. It is unlikely that temperatures in a habitat such as Damtjern reach values that are inhibitive to growth for any significant period. In fact, maximum–minimum thermometers were located in Damtjern and Lake 1205 during the period 17 July to 8 September 1971. For this period the maximum and minimum temperatures were for Damtjern, 17.2° C and 9.8° C, and for Lake 1205, 15.1° C and 5.5° C. A median temperature more than 3° C higher in Damtjern would explain the shorter incubation period and the more rapid initial growth, enabling it to complete its life cycle within a year.

The nymphs, originating from the eggs hatched in the laboratory from Lake 1205, were kept at 10° C for a period. By the middle of November their mean length was 3.3 mm, a length which corresponds well with the length in Damtjern, rather than that in Lake 1205. Therefore it appears that the two life cycle types are determined primarily by environmental factors, of which temperature is of major importance. Nutritional factors are also probably of importance.

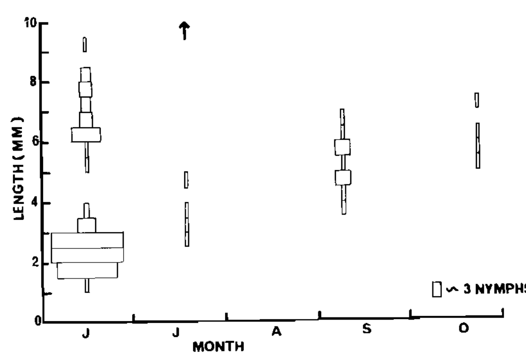

Fig. 15. Life cycle of *Nemurella picteti* compiled from the summation of results from Lakes 1171, 1205 and 1220 (locs. 19, 18 and 16, respectively). ↑ indicates adults taken.

Nemurella picteti Klapalek

In common with *N. cinerea, N. picteti* is recorded as having a long flight period and being univoltine (Hynes 1941, Brinck 1949, Khoo 1964, Ulfstrand 1969 and Lavandier & Dumas 1971). However, as was the case with *N. cinerea,* there is evidence that the species takes two years to complete its life cycle in the mountain localities in Vassfaret and at Finse. As numbers were small, results from Lakes 1171, 1205 and 1220 were combined in Fig. 15. In addition the results of hatching eggs and rearing the nymphs from Lake 1220 at a temperature of 10° C showed that even at 10° C the nymphs did not attain the size of the field population during the autumn, indicating that the field population probably hatched before ice break. In a Pyrenean stream, Lavandier & Dumas (1971) found that the population of *N. picteti* was bimodal prior to emergence in February, but they postulated that the smaller nymphs emerged the same year, in October and November. Such a long emergence period is impossible above the tree line in Norway owing to the long duration of ice cover. Also water temperatures are lower in the Norwegian mountains.

The presence of a life cycle taking more than one year is a fairly common feature in the Setipalpia, but previous studies of the Filipalpia have shown them to be almost solely univoltine. Only three species, *Nemoura cinerea* (Khoo 1964), *Leuctra nigra* (Khoo 1964), and *L. ferruginea* (Harper 1973) have been reported as being semivoltine. However, if a longer life cycle were to exist in the European Filipalpia, *N. picteti* and *N. cinerea,* both widespread species with long emergence periods and often with considerable size variation within a single population, would be obvious candidates.

Leuctra fusca L.

Previous investigations (Hynes 1941, Brinck 1949, and Ulfstrand 1968) have shown that in *L. fusca* most growth is accomplished during the summer months, and it is therefore a typical aestival species (Brinck 1949). Data from Setten fit in well with these earlier studies, mature nymphs occurring at the end of July, whereas no nymphs were found in May or September.

Capnia atra Morton

As small nymphs are present during the autumn and emergence takes place at or immediately prior to ice break, considerable growth must occur under the ice. There is, however, according to previous investigations (Brinck 1949, Svensson 1966 and Benedetto 1973) a pause in growth during the middle of the winter.

Around Finse, imagines and mature nymphs occurred during June and the first half of July. By the end of August small nymphs, 2–3 mm long, were present in Sandaavatn, Lake 1430, and Flakavatn, but it was not until the end of September that nymphs of similar size were present in the other Finse localities, by which time nymphs from the three former localities were nearly 5 mm long. This difference in nymphal growth rate and/or egg incubation period may be a function of temperature and the length of the ice-free period, but this point needs further investigation before a definite judgement can be made. Even in the most extreme habitats, *C. atra* was univoltine. A female from Lake 1430 laid eggs which hatched over a period of 7–13 days at 4° C (Lillehammer, personal communication). Imagines were present in the field long after emergence had taken place, up to 6 weeks in some cases.

Diura bicaudata (L.)

Early investigations suggested that *D. bicaudata* was univoltine with a very short egg incubation period (Hynes 1941, Brinck 1949), but later investigations combining laboratory and field studies (Khoo 1968, Schwarz 1970) have shown that it may have both one and two-year life cycles, depending on the presence or absence of diapause in the egg stage. In the localities investigated in the present study a two-year life cycle is the most likely, small nymphs being present in collections at the same time as or shortly after emergence of the adults.

GENERAL DISCUSSION

Within each area and also generally there was a correlation between the concentrations of calcium and magnesium. The correlation coefficient (r) for all the localities taken to-

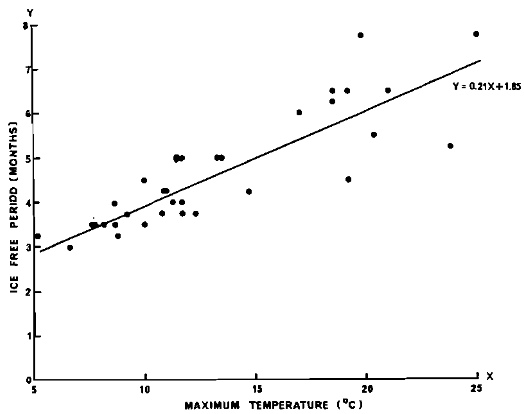

Fig. 16. The relationship between the length of the ice-free period and the maximum temperature recorded in the locality during sampling.

gether was 0.86. As may be expected the correlation was stronger within the three smaller, more geologically homogeneous areas, than in the larger and more varied Oslo region. Calcium concentrations and conductivity were also correlated (r = 0.93), although as with calcium and magnesium the regression coefficients for each area had somewhat different values as a result of variations in the proportion of the various chemical components. Therefore in future investigations of this nature, especially within a particular area, it may be necessary to measure only one of the three factors, calcium magnesium and conductivity, rather than all three. The calcium and pH values show a similar relationship to that found for total hardness and pH by Økland (1969) from a survey of several hundred lakes over the whole of Norway.

The length of the ice-free period plays an important role in the temperature regime of a freshwater habitat. In the present investigation there was a strong correlation between the length of the ice-free period and the maximum temperature recorded in the locality (r = 0.86) (Fig. 16). The temperature values are, however, the maximum of several spot readings, but the placement of maximum-minimum thermometers in eight localities during the summer of 1971 showed that as the maximum spot temperature increased, so the absolute maximum rose. The relationship between them was good (r = 0.96). The length of the ice-free period varied from as little as three months at Finse to nearly eight months in some lowland localities. The actual period is determined by a combination of factors, of which size, altitude, and winter precipitation are important.

The number of species and their abundance varies for both Ephemeroptera and Plecoptera with changes in vegetation. That the subalpine region is especially important in this respect is well seen in the Heimdalen area (Table II). The mean number of Ephemeropteran species in the different vegetation regions of the four study areas was as follows: high alpine zero, mid-alpine 0.2, low alpine 0.7, subalpine 3.3 and boreal 4.8 species. Thus the limit for lentic Ephemeroptera was in the mid-alpine region and even in the mid-alpine and low alpine regions there were very few species capable of colonising lentic localities. These are principally summer growing species, such as *Baëtis macani* and *Siphlonurus lacustris*. However, once in the subalpine there was a considerable increase both in species and abundance. For example, in the same water course in Heimdalen there was a fourfold increase in the number of species and approximately a hundredfold increase in the number of Ephemeropteran nymphs from the low alpine to the subalpine. There was a further increase in the boreal zone, especially in the more lowland localities where 8 or 9 species were often present. The dramatic change in the subalpine region is no doubt a result of a combination of biotic and abiotic factors, of which tempera-

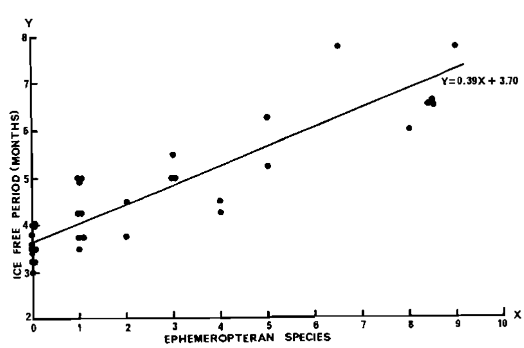

Fig. 17. The relationship between the length of the ice-free period and the number of Ephemeropteran species recorded from the locality.

ture and the increased supply of allochthonous matter are clearly important. There is a good correlation between the number of Ephemeropteran species and the duration of the ice-free period (r = 0.88) (Fig. 17), indicating the importance of temperature and possibly also the length of the period of autochthonous primary production.

The number of Plecopteran species also showed changes with different vegetation regions. Lentic Plecoptera were found as far up as the high alpine region, but again there was an increase in the number of species as the supply of allochthonous matter increased. Leaves, especially those of *Salix* spps, form a major food source for many Plecoptera in subalpine and alpine areas (Lillehammer, personal communication). Plecoptera appear to be less successful in lowland lentic habitats; both species number and abundance have low values. There are few characteristically lowland lentic Plecopteran species like *Cloëon dipterum* and *Ephemera vulgata* among the Ephemeroptera. The Plecopteran species most commonly encountered in lowland lentic habitats are more widespread species such as *Nemoura cinerea, N. avicularis* and *Nemurella picteti.* However, Plecoptera are more abundant in lotic habitats and around the outflows of large lakes (Lillehammer, personal communication). Possibly temperature, substratum, and interspecific competition play a role here.

Increased eutrophication can also lead to the disappearance of some species of Ephemeroptera (Morgan 1970). Such a situation may occur or may indeed have occurred in Borrevann and a number of other Norwegian lakes artificially enriched by agricultural, domestic, and industrial products. Lowland Plecoptera may be equally or even more threatened by such changes.

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