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The fauna of the exposed zone of Øvre Heimdalsvatn: Methods, sampling stations and general results

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Twenty stations were sampled monthly during the ice free period (June-September) in 1972. Emergence traps, emptied daily, were also employed. The major macroinvertebrates in the exposed zone were Ephemeroptera, *Gammarus lacustris*, Trichoptera, Chironomidae, Plecoptera and Coleoptera, and these constituted over 90% of total numbers. Densities of *G. lacustris*, Ephemeroptera, Tipulidae and Plecoptera showed a positive correlation with detritus. No significant relationship was found for the other taxa. Nearly 70% of the fauna emerged, and did so during the period from June to September. Chironomidae, Ephemeroptera, Plecoptera, Trichoptera and Tipulidae accounted for nearly all emergence and their total average annual emergence was 372 cal m^{-2}. Of this total, Chironomidae constituted 28%, Ephemeroptera 28%, Plecoptera and Trichoptera 15% each and Tipulidae 4%.

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Introduction

The exposed zone, for those secondary consumers able to exploit it, presents a rich supply of both autochthonous and allochthonous matter, and during the summer months a high temperature. Attention was concentrated on the macroinvertebrates of this zone, down to a depth of about 1 m, in terms of the composition of the benthos and the numbers of emerging insects. The bottom sampling was restricted to the ice free period, which extends from early June to early October. Emergence from the exposed zone took place almost exclusively during this period. The only known exception was *Capnia atra* Morton (Plecoptera) whose emergence period started at the end of May, the nymphs crawling up through cracks in the ice. The insects emerge from the aquatic system to reproduce, and despite the return of a number of females to the lake for oviposition, it undoubtedly represents a considerable energy loss for the system.

In this paper all the methods and sampling stations used in the exposed zone studies are described together as they were the same for most taxa. However, only the more general results from the different taxa are presented here. Detailed results are given in Aagaard 1978 (Chironomidae), Brittain 1978a (Ephemeroptera), 1978b (Coleoptera), 1978c (Mollusca), Lillehammer 1978a (Plecoptera), and 1978b (Trichoptera). The fauna of the surrounding streams is described in Lillehammer and Brittain (1978).

Methods and sampling stations

The variety of substrata present in the shallow waters of Øvre Heimdalsvatn presented sampling problems. Owing to this variation it was desirable to sample as many sites as possible during the ice free period. The main aim was a relative presentation of the various stations. Emergence trap data were also available for comparison.

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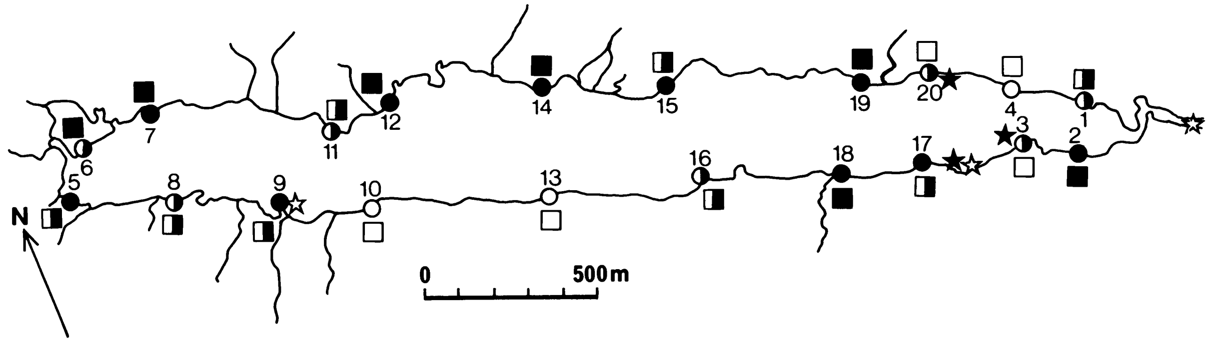

Fig. 1. The location of sampling stations and emergence traps used in the studies of the exposed zone of Øvre Heimdalsvatn. The circles represent the amount of detritus present at each station, those completely shaded having the greatest and those unshaded the least amount of detritus. The squares indicate the type of substratum, those completely shaded having the most unstable substrata with small particle size and those unshaded the most stable substrata with large particle size. For further explanation see text. The stars indicate the positions of the emergence traps, open for 1971 and shaded for 1972.

In the sampling of the benthic fauna two techniques, both time based, were used as different methods have varying efficiencies as regards different taxa. Firstly, for a period of 3 min, stones were picked up from the bottom by hand and placed in plastic bowls on the lake side. As the stones were lifted from the bottom a net was passed underneath to obtain those animals that either swam away when disturbed or fell to the bottom (Moon 1935, Macan and Maudsley 1968). The stones were then brushed to remove the animals clinging to them. All the animals, including those in the net, were preserved in 3% formalin. The second method was a "kick" technique modified from its use in running waters (Macan 1958, Hynes 1961, Frost et al. 1971, Ar-

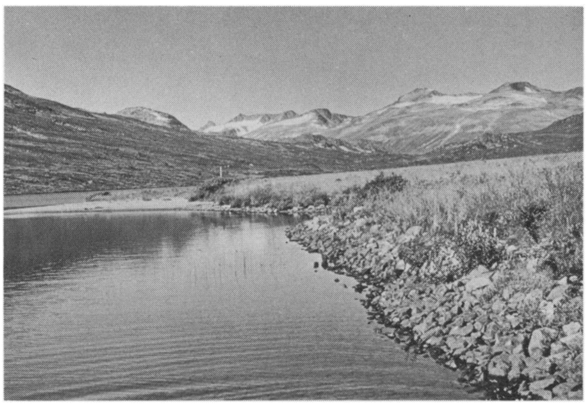

Fig. 2. General view of station 15 taken during August.

Fig. 3. The substratum at station 15.

Fig. 4. The substratum at station 7.

Fig. 5. The substratum at station 20.

mitage et al. 1974), whereby for a 3 min period the substratum was disturbed by kicking while a net was passed forwards and backwards over the area. The net contents were then sorted and placed in 3% formalin. The net used for both methods was triangular with sides of 36 cm and netting of mesh size 0.5 mm.

Both methods were used twice, thus providing four samples at each station. Such techniques were also employed by Eie (1973), Brittain (1974) and Lillehammer (1974). Twenty stations (Fig. 1) were sampled approximately monthly during the ice free period. The actual periods during which samples were taken in 1972 were: 6–13 June, 6–9 July, 23–25 August and 18–20 September. In addition, limited sampling was carried out on 25 October, shortly after ice formation.

Stations were chosen to cover all sectors of the lake and to provide a representative selection of the major substrata in the exposed zone of Øvre Heimdalsvatn. The stations were grouped according to substratum type and the amount of detritus present. Substratum was divided into three categories ranging from stable substrata, usually composed of large stones and rocks to unstable substrata composed of small stones and gravel (Figs 2–5). A measure of the amount of detritus, that is plant material of both autochthonous and allochthonous origin, was obtained by noting the amount of such material in the kick samples. Stations were initially assigned to one of three categories: high, medium and low detrital content. For certain statistical analyses those stations with the most detritus were compared with the remaining stations. The small areas with macrophytic vegetation were excluded, as were areas in the immediate vicinity of the inflows and the outflow. The latter areas probably support a fauna intermediate between that of the lake and the streams. On contrasting substrata the area of bottom sampled by the two methods was estimated. It was clear that the kick method sampled a greater area and the more unstable the substratum the larger this area became (Tab. 1). Therefore the totals were adjusted to take account of these discrepancies, converting all samples to the same area. This area was approximately 8.4 m^2 at each station on each sampling occasion. For Ephemeroptera the sampling efficiency calculated from a comparison of emergence data and nymphal numbers prior to emergence, was of the order of 80%, i.e. the area sampled being equivalent to about 7 m^2.

The two sampling methods employed in the exposed zone of Øvre Heimdalsvatn were more or less selective for certain groups (Tab. 2). Rapid swimmers, such as *G. lacustris* and Coleoptera, were taken in higher numbers in the kick samples, as also were Tipulidae, which occur down in the substratum. The reverse was true of Mollusca, and of Chironomidae which were associated more with stone surfaces than with interstitial spaces.

Emergence traps were set up in the lake, two in 1971 and three in 1972. In addition a trap was placed over the outflow stream in 1971. Their location is shown in Fig. 1. The traps were put in place shortly after the ice break and taken in prior to ice formation in the autumn. Each trap was emptied daily throughout the season, usually around 0900 a.m. The catches were preserved in 70% alcohol. The traps were of the box type (Davies 1950) with sides 1 m. Fine netting covered all sides and the top, while a clasp system enabled the collector to gain access to the trap. The trap was placed such that all the insects emerging along a 1 m stretch of shore were collected. The majority of the insects of the exposed zone emerge at the shore, but much of the deep water fauna emerges in open water and were thus not collected in the traps.

In the laboratory nymphal body lengths were measured to the nearest 0.1 mm, from the tip of the head to the base of the cerci. In the consideration of the life cycle of the various species they were grouped into 0.5 mm size categories.

Samples for determination of wet, dry and ash free weights were deep frozen in excess water immediately after collection in the field. After a few months the samples were thawed in the laboratory and wet weight determined after removal of excess water. The samples were then dried for at least 3 h at 70°C in a vacuum before dry weight was measured. Ash content was determined by burning samples at 500°C for at least 2 h in a muffle furnace. In trial runs it was found that there was no significant weight change after the time periods specified above. All weighings were carried out with a Mettler ME 22 balance, usually to the nearest 0.01 mg, although 3 decimal places were sometimes measured

Tab. 1. Area (±95% confidence limits) in m^2 covered by the two sampling methods used in the exposed zone of Øvre Heimdalsvatn. Data are given from three stations which represent the three substratum categories given in the text. Means are based on six values for the area sampled.

	1 min kick sample	1 min stone sample
Unstable (small stones/gravel)	0.70±0.07	0.21±0.05
Moderately stable (stones)	0.48±0.08	0.21±0.02
Stable (large stones)	0.41±0.10	0.21±0.05

Tab. 2. Ratio between numbers, after conversion to the same area, taken in the kick samples and those taken by plucking stones from the bottom in the exposed zone of Øvre Heimdalsvatn.

Tipulidae	5.0
Gammarus lacustris	4.4
Coleoptera	2.6
Ephemeroptera	2.0
Hydracarina	2.0
Plecoptera	1.7
Trichoptera	1.0
Mollusca	0.8
Chironomidae	0.5

when ash weights were especially low. All specimens were weighed individually except when dry weights were less than 1 mg, in which case they were grouped together into convenient samples for burning. In the Trichoptera (Lillehammer 1978b) weights were determined from alcohol fixed material in which evaporation was monitored and standardised.

Results and discussion

On account of the emerging aquatic insects forming an important part of the macrofauna of the exposed zone, total numbers fluctuate a great deal during the ice free period (Tab. 3). The predominance of the univoltine life cycle among these aquatic insects is the reason for total numbers reaching a maximum during July. During September, when most groups have emerged, total numbers are at a minimum. In addition the early instars were underestimated by the sampling methods used. Numbers of *G. lacustris* also varied. The more or less permanent population of the exposed zone was supplemented during July and August by mature individuals migrating to the shallow waters from the deeper parts of the lake to reproduce, and by their offspring (Aarefjord unpubl.). There was variation in numbers at the different sampling stations around Øvre Heimdalsvatn (Fig. 6). No significant relationship (Kruskal-Wallis one-way

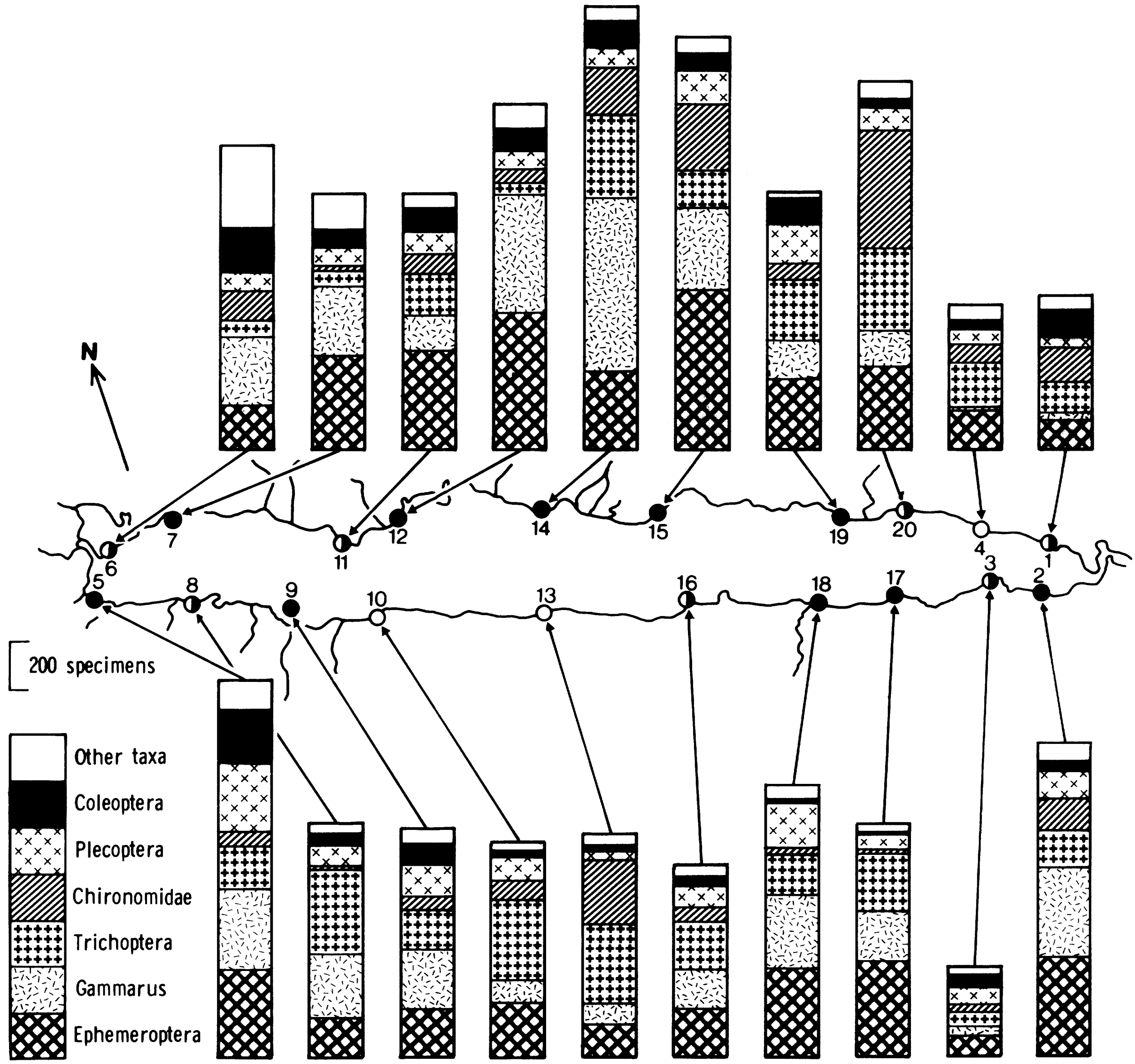

Fig. 6. Total numbers of the different taxa (adjusted totals) taken during the survey of the exposed zone. The stations are divided into three categories, indicating the amount of detritus. Stations with high levels of detritus are completely shaded while those with low levels are unshaded.

Tab. 3. Seasonal abundance of the most common taxa in the benthic samples taken in the exposed zone of Øvre Heimdalsvatn. Values are expressed as a percentage of the total numbers of each taxa.

	Jun	Jul	Aug	Sep
Ephemeroptera	40.3	51.9	6.3	1.5
Gammarus lacustris	11.1	47.4	31.3	10.3
Trichoptera	7.1	31.9	33.1	28.0
Chironomidae	3.0	68.2	13.5	15.4
Plecoptera	38.3	6.8	23.9	31.0
Coleoptera	34.3	39.0	13.1	13.6
Hydracarina	9.4	65.5	13.4	10.5
Tipulidae	12.0	15.1	34.9	38.1
All taxa	22.2	43.8	20.7	13.3

Tab. 4. Values of U_1 and U_2 and significance levels in the Mann-Whitney U-test on the relationship between numbers and the amount of detritus in the exposed zone of Øvre Heimdalsvatn.

	U_1	U_2	Probability values
Gammarus lacustris	8	92	<0.001
Ephemeroptera	14	86	<0.01
Tipulidae	25	75	<0.05
Plecoptera	26.5	73.5	<0.05
Coleoptera	39.5	60.5	Not significant
Hydracarina	40.5	59.5	Not significant
Trichoptera	59	41	Not significant
Chironomidae	62.5	37.5	Not significant
Mollusca	70	30	Not significant
Total fauna	17	83	<0.01

analysis) was found between total macroinvertebrate numbers and the type of physical substratum. However, the amount of detritus was significantly related to numbers ($P < 0.01$, Kruskal-Wallis one-way analysis). Mean values and 95% confidence limits for total numbers at stations in three original detritus categories: low, medium and high were 853 ± 434, 994 ± 371 and 1364 ± 236, respectively. For subsequent analysis using the Mann-Whitney U-test the first two categories were grouped together, giving two groups of 10 stations, The difference in total numbers between the two groups was highly significant ($P < 0.01$) (Tab. 4). Values for the individual taxa are also given in Tab. 4. *Gammarus*, Ephemeroptera, Tipulidae and Plecoptera all showed a significant relationship with detritus. The remaining groups did not show any significant relationship. The possible reasons for these relationships are discussed in the papers on the individual taxa.

The supply of allochthonous material appears to be an important contribution to the detritus pool as macroinvertebrate numbers were highest at stations 5, 12, 14, 15 and 20, which are in receipt of the material carried into the lake by the major inflow streams. These stations are also sheltered from the strong westerly and northwesterly winds, thus permitting accumulation.

The six taxa, Ephemeroptera, *G. lacustris*, Trichoptera, Chironomidae, Plecoptera and Coleoptera constitute about 92% of the total numbers (Tab. 5). With the addition of the Hydracarina and the Tipulidae this figure rises to 98%. Thus, the remaining seven taxa only constitute approximately 2% of the total. If one considers biomass instead of numbers, the Hydracarina are of even less importance. This also applies to some extent to the chironomids, but their numbers were underestimated by the sampling method used on account of their small size. This opinion is reinforced by their dominance of the emergence trap material (Figs 7, 8). In addition they can occur in significant numbers in the hyporheic zone, at least in lotic biotopes (Williams and Hynes 1974).

Emergence is an important feature of the exposed zone of Øvre Heimdalsvatn during the ice free period and forms an integral part of the life cycle in nearly 70% of the sampled macrofauna (Tab. 5). These include the insect groups Chironomidae, Ephemeroptera, Plecoptera and Trichoptera, each of which has a characteristic emergence period and pattern (Figs 7 and 8).

The Chironomidae, which dominate the emergence trap material in terms of numbers, have 2–3 major peaks encompassing the period from late June to the end of August (for details see Aagaard 1978). The Plecoptera emerge early, mainly during June and the first half of July. The duration of the emergence periods of the individual stonefly species is given in Lillehammer (1974, 1978a). Two main emergence periods characterise the Trichoptera, the first during July and the second between the end of August and the beginning of September (Lillehammer 1978b). The Ephemeroptera emerge from late June to the end of August. They differ from other taxa in their response to the different thermal conditions of 1971 and 1972 (Brittain 1978a). Whereas ephemeropteran emergence was brought forward in 1972, the emergence of the other taxa tended to be later, as well as there being fewer emerging, during 1972.

Tab. 5. Percentage composition of the bottom fauna in the exposed zone of Øvre Heimdalsvatn, during the ice free period.

Ephemeroptera	27.1
Gammarus lacustris	21.6
Trichoptera	17.4
Chironomidae	10.6
Plecoptera	9.7
Coleoptera	6.3
Hydracarina	2.7
Tipulidae	2.7
Mollusca	0.8
Oligochaeta	0.3
Hemiptera	0.3
Other Diptera	0.2
Sialis lutaria	0.1
Hirudinea	0.1
Lepidurus arcticus	<0.1

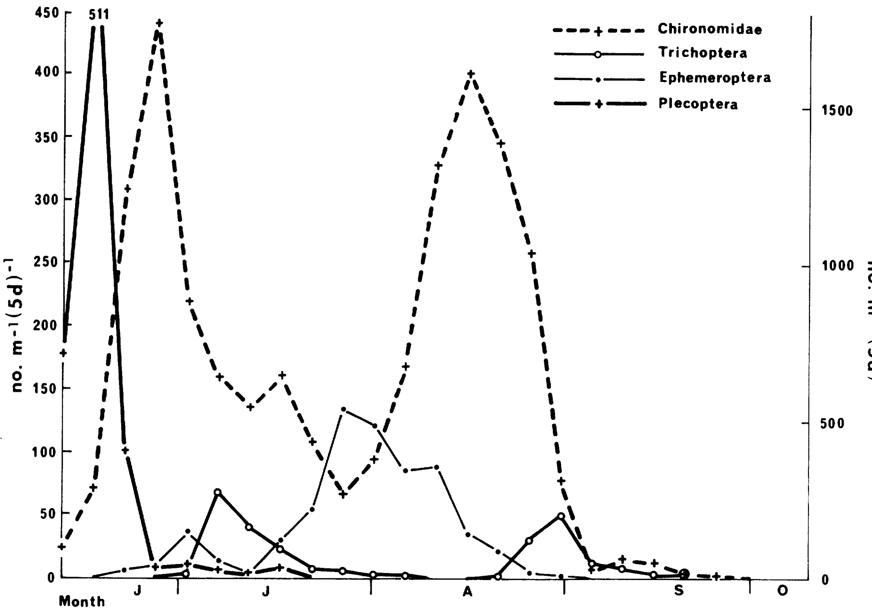

Fig. 7. Emergence from Øvre Heimdalsvatn during 1971 in terms of 5-d totals per m shoreline. The right-hand scale applies to the Chironomidae, while the left-hand scale applies to all other taxa.

Emergence from Øvre Heimdalsvatn begins at ice break and the major part is over by the beginning of September. Thus there is little emergence activity during the month prior to ice formation. This could provide a safety valve in the event of a cooler summer delaying emergence. Chironomids dominate in terms of numbers, but their individual biomass and calorific value are lower than those of the other major insect groups, the Ephemeroptera, Plecoptera, Trichoptera and Tipulidae. The emergence of the major insect groups in Øvre Heimdalsvatn represented on average 372 cal m^{-2} during the summers of 1971 and 1972 (Tab. 6). Of this total Chironomidae accounted for about 38%, the Ephemeroptera for 28%, and the Plecoptera and Trichoptera both for 15%. Therefore in terms of energy (cal m^{-2}), rather than density (no./m shoreline) where Chironomidae accounted for almost 90% of the total, there was a significant contribution from each of the different insect groups. Because the groups peaked at different times, this meant that there was a more constant supply of available food energy throughout the ice free period for the predatory members of the aquatic community, especially the trout (Lien 1978a), and for the terrestrial fauna of the lake's surroundings (Lien 1978b).

In Lille-Jonsvann (Solem 1973) at 0.2 m, Oligochaeta, Insecta, Mollusca and *G. lacustris* were the major taxa. Within the Insecta, Chironomidae were dominant with Trichoptera also forming an important part. In Øvre Heimdalsvatn Oligochaeta were important, although poorly represented in the sampled material. However, the greater importance of Mollusca in the

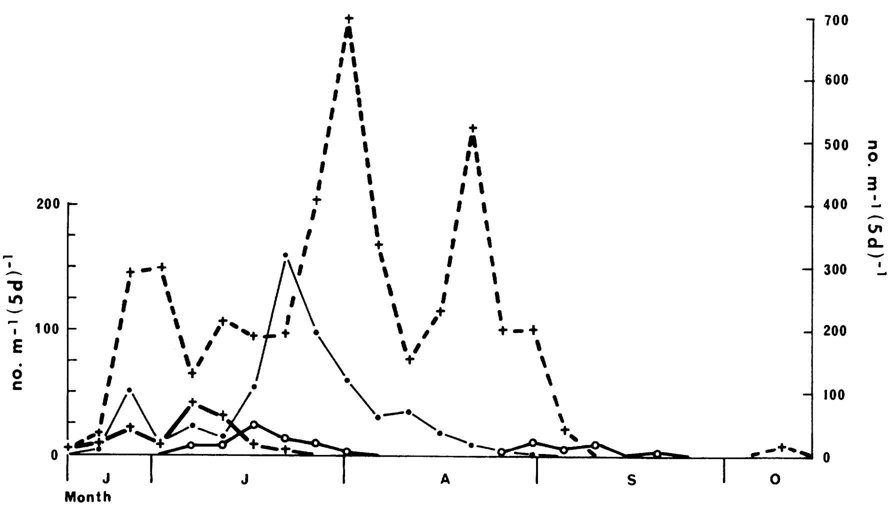

Fig. 8. Emergence from Øvre Heimdalsvatn during 1972 in terms of 5-d totals per m shoreline. Scales and symbols as in Fig. 7.

Tab. 6. Densities, mean weights and energy values of the major insect groups emerging from the shore of Øvre Heimdalsvatn. Densities are given per metre shoreline (approx. 10^2 times no. m^{-2}). In addition to the authors' own data, weights and calorific values from the following sources were used: Cummins and Wuycheck 1971 (calorific values for Trichoptera), Hofsvang 1973 (weight and calorific values for Tipulidae), Lien 1978a (weights and calorific values for Chironomidae and Plecoptera), Ricker 1968 (calorific data for Ephemeroptera and Trichoptera).

	No. emerging /m shoreline				Mean individual dry wt (mg)	Cal per individual	Emerging in cal m^{-2}			
	1971	1972	Mean 1971–1972	%			1971	1972	1971–72	%
Chironomidae	13615	4188	8901.5	87	0.3	1.6	216	170	141.5	38
Ephemeroptera	649	591	620	6	3.3	17.0	109	100	104.5	28
Plecoptera	839	137	488	5	2.0	11.7	97	16	56.5	15
Trichoptera	279	103	191	2	5.0	29.0	80	30	55	15
Tipulidae	36	3	19.5	<0.5	13.8	77.0	27	2	14.5	4
Total	15418	5022	10220				529	215	372.0	

shallow waters of Lille-Jonsvann compared with Øvre Heimdalsvatn, can probably be ascribed to substratum differences and the mesotrophic nature of Lille-Jonsvann. Borrevann, investigated by Økland (1964), has an even higher trophic status than Lille-Jonsvann. Økland presented data from the stony lake shore where the Ephemeroptera dominated in terms of numbers. Other important groups were Trichoptera, Gastropoda and Chironomidae. Although Ephemeroptera were the most numerous macroinvertebrates in both Borrevann and Øvre Heimdalsvatn, the major species were different (Brittain 1978a). *G. lacustris* was also absent from Borrevann, and, as in Lille-Jonsvann, Mollusca were more important members of the shallow water community.

The two Norwegian lake considered, Borrevann and Lille-Jonsvann, are both quite different from Øvre Heimdalsvatn largely on account of their higher trophic status and their lower altitude. The only detailed study of the exposed zone of a mountain lake is that of Gjende (Eie 1973). Gjende, situated at 984 m a.s.l. and only 10 km NW of Øvre Heimdalsvatn, has an area of 13.8 km^2 and a maximum depth of 149 m. Insecta made up most of the macroinvertebrate fauna of the exposed zone of Gjende. The main difference between the two lakes was the low numbers of *G. lacustris* in Gjende. In Øvre Heimdalsvatn *G. lacustris* was most abundant at less exposed stations with unstable substrata and accumulated detritus, a habitat uncommon in Gjende.

Similar differences to those between the Norwegian lakes Borrevann, Lille-Jonsvann, Øvre Heimdalsvatn and Gjende can also be seen in the littoral fuana of lakes in the English Lake District (Macan and Maudsley 1969) and in North Wales (Brittain 1971). With increasing productivity the fauna changed from one dominated by insects to one of more varied character, where groups such as Mollusca, Tricladida, Crustacea and Hirudinea were major components. In addition, certain insect groups, such as Plecoptera, decreased in numbers.

Paasivirta's (1975) study from Pääjärvi in Finland, is a detailed one of total insect emergence from an oligotrophic lake. As in Øvre Heimdalsvatn, Chironomidae dominated in terms of numbers, with the Ephemeroptera and Trichoptera the next most abundant taxa. Compared with Øvre Heimdalsvatn, Trichoptera were more numerous and Plecoptera less so in Pääjärvi. This may be due to the much greater development of shallow-water macrophytes in Pääjärvi. In studies of emergence from lentic water bodies outside Fennoscandia (e.g. Judd 1953, Mundie 1957, Morgan and Waddell 1961, Learner and Potter 1974) Chironomidae were usually the most numerous, followed in differing order by the other main groups, Trichoptera, Ephemeroptera and Plecoptera.

These four groups also accounted for over 90% of the insect biomass emerging from a small German stream (Illies 1975), one of the few studies where emergence biomass data are given. In this study it was demonstrated that emergence data can aid the understanding of the metabolic processes of productivity in an aquatic ecosystem. The total annual biomass of emerging adults varied between 2.7 and 6.3 g m^{-2}. If we compare this with the biomass emerging/m shoreline from Øvre Heimdalsvatn, and not with the biomass m^{-2} which includes large areas not covered by the emergence traps and where insect production is probably lower, the values are similar. In Øvre Heimdalsvatn the annual emerging dry weight biomass/m shoreline of the five major insect groups (Tab. 6) was 9.8 g in 1971 and 4.0 g in 1972.

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