HOLARCTIC ECOLOGY 1: 239–254. Copenhagen 1978

The Ephemeroptera of Øvre Heimdalsvatn

John E. Brittain

Zoological Museum, University of Oslo

Brittain, J. E. 1978. The Ephemeroptera of Øvre Heimdalsvatn. – Holarct. Ecol. 1: 239–254.

The species composition, distribution, seasonal variations in abundance, life cycles, emergence periods, length-weight relationships and biomass of the Ephemeroptera of Øvre Heimdalsvatn were investigated. Detritus was a significant factor in explaining the variation in total ephemeropteran numbers around the lake. Numbers in the exposed zone reached a maximum during July due to emergence activity. The ephemeropteran biomass at emergence, to which *Leptophlebia vespertina* (L.), *L. marginata* (L.) and *Siphlonurus lacustris* Eaton were the main contributors, was estimated to be 0.02g dw m^{-2}. Other species recorded from the lake were *Baëtis macani* Kimmins, *B. rhodani* Pictet, *Siphlonurus aestivalis* Eaton and *Ameletus inopinatus* Eaton. All species were univoltine, but differences in ability to grow during ice cover and in life cycle timing resulted in a succession in emergence during the ice free period.

J. E. Brittain, Zoological Museum, Sarsgt. 1, Oslo 5, Norway.

1. Introduction

These studies were instigated in connection with the Norwegian contribution to the freshwater section of the IBP. Øvre Heimdalsvatn, the subalpine lake selected for these studies, is typified by its rapid flow through rate especially during the spring spate, its short ice free period and the importance of allochthonous input (Larsson and Tangen 1975, Vik 1978). No detailed information has been published on the Ephemeroptera of such lakes. Similar investigations were made of other taxa in the exposed zone of Øvre Heimdalsvatn and therefore the methods employed and the sampling stations used are grouped together in a separate paper (Brittain and Lillehammer 1978).

A number of taxonomic studies, distribution records and check lists have been published concerning the Norwegian Ephemeroptera. Ecological studies are less common and many concern lotic habitats in Western Norway (Elliott 1965, Larsen 1968, Steine 1972). Those concerning lentic habitats, such as Grimeland's study of *Caenis horaria* (L.) (1966) and the wider limnological studies of Økland (1964) and Solem (1974) have been undertaken in lowland lakes. In Sweden the mayfly fauna of a forest tarn has been well studied (Kjellberg 1972, 1973) and a number of watercourses in northern Sweden have been investigated by Ulfstrand (1968a, b, 1969). Paasivirta (1975) has recently published a study of insect emergence from an oligotrophic lake in southern Finland. The author had surveyed a large number of lentic habitats in southern Norway, ranging from eutrophic lowland lakes to pools in the vicinity of a glacier (Brittain 1974) and thus the IBP project provided the opportunity to study the Ephemeroptera of a single lake in detail, both in terms of the ephemeropteran community and in relation to the other members of the aquatic community. Most of the data from the study are given here, but certain aspects are presented in other papers in this volume (e.g. Brittain and Lillehammer 1978) or have been published elsewhere (Brittain 1974, 1975, 1978).

The Lake Øvre Heimdalsvatn – a subalpine freshwater ecosystem.
Contribution no. 17.
Accepted 17 May 1978
© HOLARCTIC ECOLOGY

Tab. 1. Intraspecific seasonal variation in ephemeropteran numbers in Øvre Heimdalsvatn expressed as a percentage of the total numbers of that species and the relative importance of the various species in the benthic samples and in the emergence traps, also expressed as a percentage.

	Benthic samples-1972					Emergence traps	
	Jun	Jul	Aug	Sep	Jun–Sep	1971	1972
Leptophlebia vespertina	32.4	66.9	0.6	0.2	36.3	49.4	56.7
Leptophlebia marginata	80.9	18.2	0.1	0.9	33.7	10.4	17.2
Siphlonurus lacustris	10.8	65.5	20.3	3.5	22.4	29.4	4.6
Baëtis macani	0	70.5	29.5	0.3	5.3	6.6	20.1
Siphlonurus aestivalis	25.0	69.6	0	5.4	0.9	3.0	0.1
Ameletus inopinatus	25.6	72.2	1.1	1.1	1.5	0	0.6
Baëtis rhodani	0	0	0	0	0	1.2	0.7
All species	39.6	52.4	6.7	1.3			

2. The ephemeropteran community

2.1. Distribution, numbers and species composition

Ephemeroptera are an important group in the shallow waters of Øvre Heimdalsvatn in terms of numbers and biomass. More specimens were taken in the benthic samples than any other macroinvertebrate group. On average they constituted 27.1% of the macroinvertebrate fauna of the exposed zone (Brittain and Lillehammer 1978). The two sampling methods employed (Brittain and Lillehammer 1978) had similar efficiencies as regards Ephemeroptera and therefore the unadjusted percentage differed little from the above values. Numbers varied considerably throughout the ice free

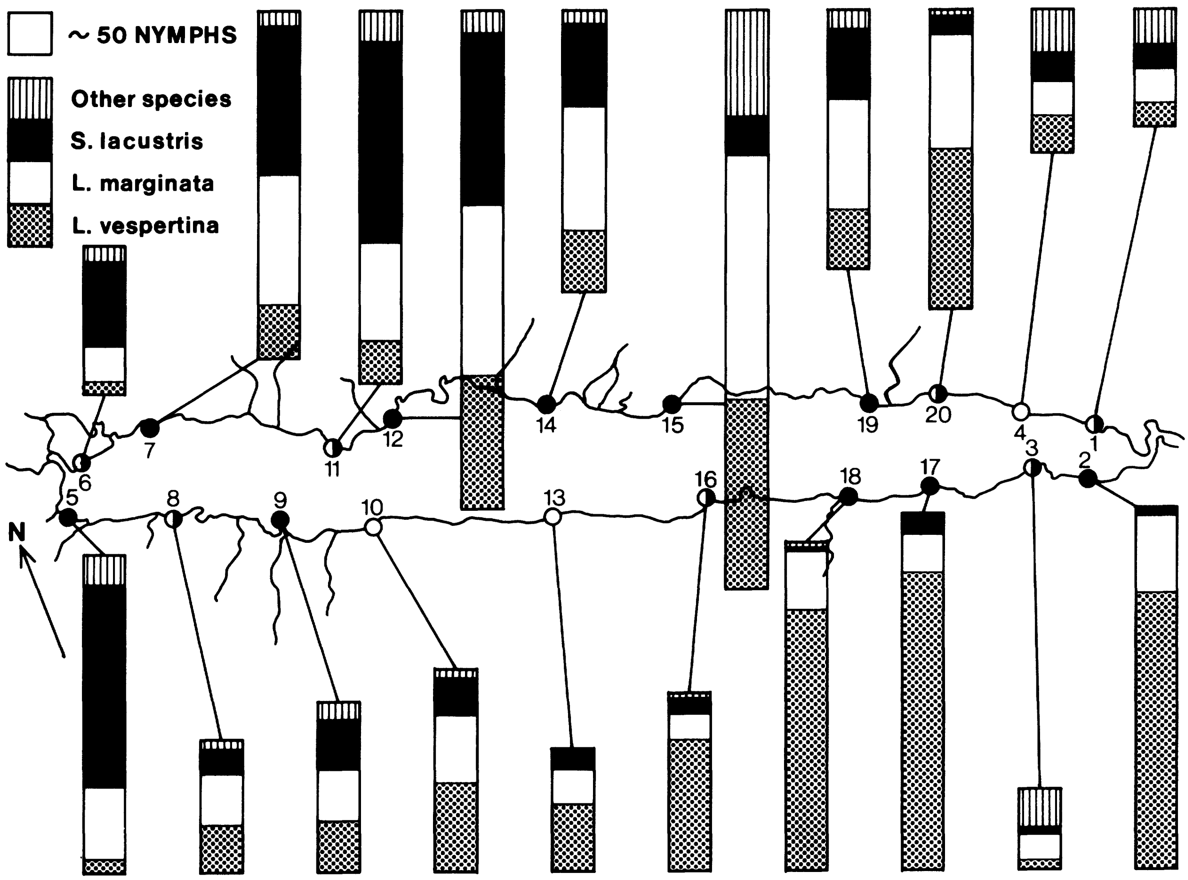

Fig. 1. Distribution and abundance of Ephemeroptera in the exposed zone of Øvre Heimdalsvatn during the ice free period of 1972. The amount of detritus present at the stations is indicated by the degree of shading, the open circles representing the least amount.

period (Tab. 1). Their maximum abundance was in July (52.4% of total numbers), followed by June (39.6%). The increase in numbers in July did not represent recruitment per se, but a movement to and a concentration in the shallow water prior to emergence (Macan and Maudsley 1968, Brittain 1971). By the end of August, however, most species had emerged and the majority were the egg stage. Even by September few nymphs of the new generation were present in collections and the eggs of some species do not hatch until the following spring or summer. Numbers of Ephemeroptera at the 20 stations are given in Figs 1 and 2. The amount of detritus at the various sampling stations (Brittain and Lillehammer 1978) was a significant factor determining the variation in total ephemeropteran numbers around the lake ($P < 0.01$, Mann-Whitney U-test). The physical substratum had no direct influence on numbers, although there was often more detritus associated with the more unstable, smaller substrata (Brittain and Lillehammer 1978).

Ephemeroptera occurred predominantly in the 0–3 m zone in Øvre Heimdalsvatn. On mud substrata, mean densities in the 1–3 m zone were 11.7 m^{-2} compared with 2.0 m^{-2} in the 5–7 m zone. The 'summer' species *Siphlonurus lacustris* and *Baetis macani* were not recorded deeper than 1 m, but the 'winter' species *Leptophlebia vespertina* and *L. marginata* were present in low densities as deep as 7 m. The highest densities below 1 m of these two species were recorded during the winter, before the movement towards the shore associated with emergence had commenced.

The following species were recorded:

Leptophlebia vespertina (L.)
L. marginata (L.)
Siphlonurus lacustris Eaton
S. aestivalis Eaton
Ameletus inopinatus Eaton
Baëtis macani Kimmins
B. rhodani (Pictet)
Heptagenia sp.

B. rhodani was only taken in the emergence traps and not in the benthic samples, while only a single nymph of *Heptagenia* sp., probably originating from a nearby stream, was taken at st. 5 in August. The proportions of the different species taken in the emergence traps and in the bottom samples are given in Tab. 1. Although the general pattern is similar, there are a number of differences, most of which can be explained by the relationship between the time of sampling and the time of peak emergence of the species concerned. Thus if the benthic fauna was sampled when emergence of a particular species was at a peak, more nymphs of that species were taken as they were concentrated in shallow water prior to emergence. Therefore, although few in number, the emergence traps probably gave a more reliable picture of the relative importance of the various species.

2.2. Nutrition

All ephemeropteran species in Øvre Heimdalsvatn are herbivores and finely divided detritus generally dominated the guts of nymphs of the two *Leptophlebia* species and *A. inopinatus*. However, diatoms, other algae,

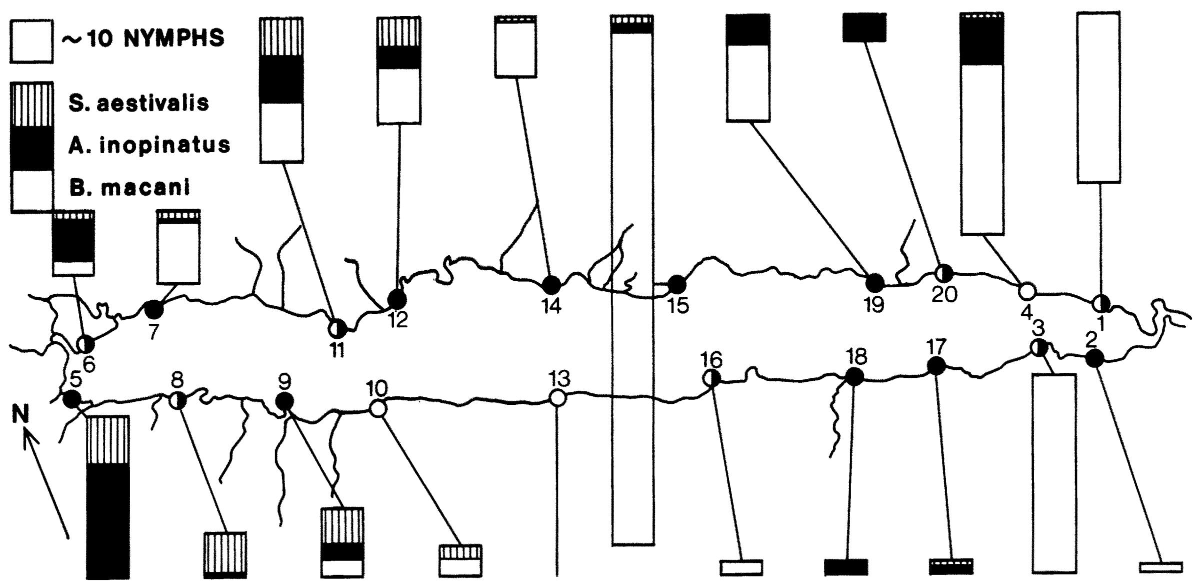

Fig. 2. Distribution and abundance of the minor species of Ephemeroptera in Øvre Heimdalsvatn during the ice free period. The amount of detritus present at the stations is indicated by the degree of shading.

vascular plant fragments and mineral matter were also present. Vascular plant material was almost as frequent as detritus in the two *Siphlonurus* species, while in *B. macani* diatoms were equally common. Nutrition varied somewhat from place to place and from season to season. Benthic and epiphytic algae are much commoner during the ice free period, especially during its latter half (Müller 1973), and this is probably exploited by the Ephemeroptera, particularly *B. macani.* During the winter, when there is little primary production, detritus composed of both autochthonous and allochthonous elements probably forms the major food source, although in contrast to some of the Plecoptera they do not accomplish the primary breakdown of terrestrial leaves. Previous studies on the nutrition of the species found in Øvre Heimdalsvatn (e.g. Moon 1938, Jones 1950, Brittain 1971, Kjellberg 1972) are generally in agreement with the above conclusions.

2.3. Predation

During the latter part of June and the whole of July, Ephemeroptera were common in the stomachs of trout from Øvre Heimdalsvatn (Lien 1978a). The following species have been recorded in trout stomachs: *L. vespertina, L. marginata, S. lacustris, S. aestivalis, B. macani, B. rhodani* and *B. lapponicus*. The first two species occurred most frequently and in greatest numbers. The presence of *B. rhodani* and *B. lapponicus* nymphs, both primarily lotic species, indicates that some of the trout may take mayfly drift in the vicinity of the inflow streams.

Nymphs are particularly vulnerable to predation prior to emergence on account of increased activity, especially during daylight (Solem 1973). Few adults were recorded from the fish stomachs. Although greatest numbers of Ephemeroptera were taken during June, July and August, they were recorded during all months. The two *Leptophlebia* species were almost the only species taken during the winter because the other major species were either in the egg stage or present as small nymphs. The seasonal and interspecific variation in the predation of the Ephemeroptera by the trout is documented and discussed in Brittain and Lien (1978).

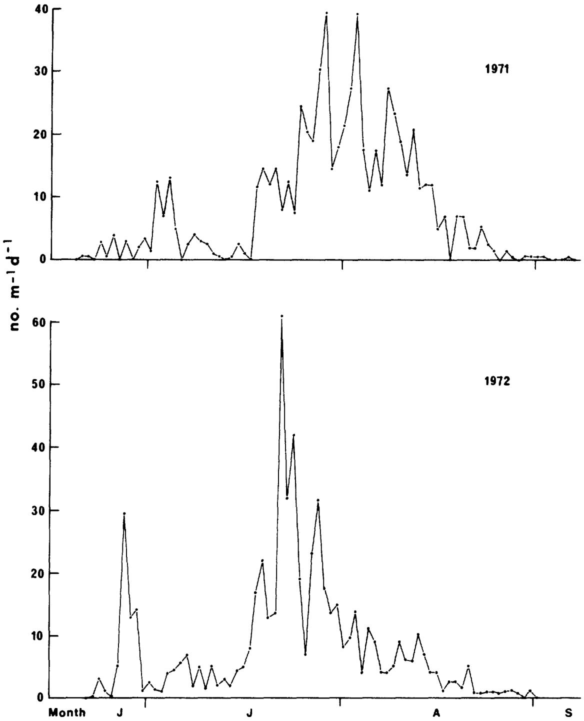

Fig. 3. Daily emergence (per metre shoreline) of Ephemeroptera from Øvre Heimdalsvatn during 1971 and 1972.

2.4. Emergence

The emergence of Ephemeroptera commences at the end of June, continues throughout July and August and terminates, apart from a few sporadic cases, in early September (Fig. 3). The emergence pattern is characterised by two peaks, one at the end of June due to the emergence of *L. marginata* and a much higher peak during the second half of July and the first half of August due to the emergence of *L. vespertina, S. lacu-*

Tab. 2. Emergence of Ephemeroptera from Øvre Heimdalsvatn during 1971 (2 traps) and 1972 (3 traps)

	1971				1972					1971+1972	
	F.2	F.3	Total no.	%	A	B	C	Total no.	%	Total no.	%
Leptophlebia vespertina	537	104	641	49.4	178	274	553	1005	56.7	1646	53.6
Leptophlebia marginata	105	30	135	10.4	157	36	111	304	17.2	439	14.3
Siphlonurus lacustris	183	199	382	29.4	22	25	35	82	4.6	464	15.1
Baëtis macani	44	41	85	6.6	167	87	103	357	20.1	442	14.4
Siphlonurus aestivalis	14	25	39	3.0	0	1	0	1	0.1	40	1.3
Ameletus inopinatus	0	0	0	0	5	0	6	11	0.6	11	0.4
Baëtis rhodani	7	9	16	1.2	7	2	4	13	0.7	29	0.9
Total	890	408	1298		536	425	812	1773		3071	

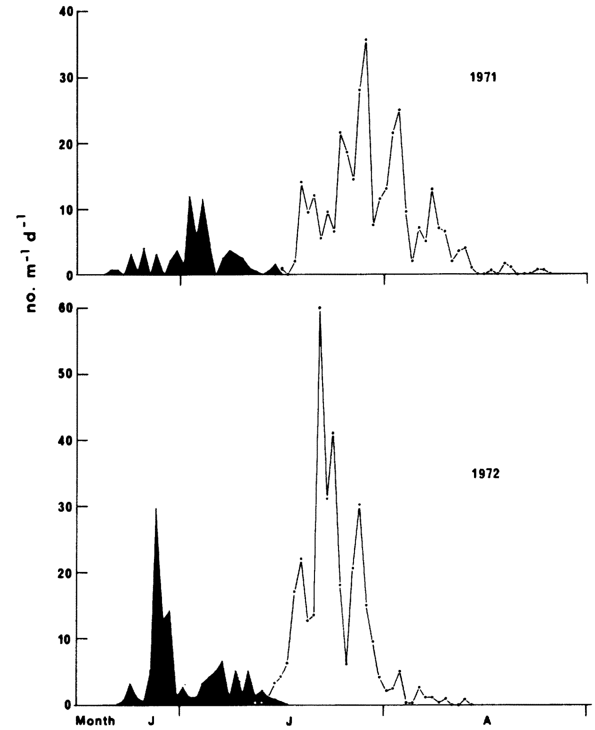

Fig. 4. Daily emergence (per metre shoreline) of *Leptophlebia marginata* (shaded) and *L. vespertina* from Øvre Heimdalsvatn during 1971 and 1972.

stris and *B. macani* (Figs 4, 5, 6). The numbers of the various species taken in the emergence traps are given in Tab. 2. The species succession and the emergence patterns of the individual species are considered in Brittain (1978).

Temperature is of importance in determining when emergence actually takes place once maturation is completed (Macan and Maudsley 1966, Brittain 1972, 1976a, 1978). Much of the daily variation in the number of Ephemeroptera emerging can be explained by reference to the daily maximum air temperature and daily irradiance (Brittain 1978). The former is considered to give a good indication of temperatures in the exposed zone of Øvre Heimdalsvatn during the major part of the ice free period (cf. Szumiec 1973). Temperature can also be of importance over longer periods. The emergence periods of the various species, together with the date on which 50% had emerged, are given for 1971 and 1972 in Tab. 3. If the two years are compared, it can be seen that emergence generally occurred earlier in 1972 than in 1971. This reflects the temperature conditions because during the major part of July 1971 lake temperatures at 0.5 m were markedly lower than in 1972 (Fig. 7). Air temperatures were also higher during July 1972.

2.5. Length – weight relationships

The most reliable estimate of ephemeropteran numbers was obtained from the emergence traps. Therefore to obtain a figure for biomass at that time, nymphal samples were taken during or immediately prior to emergence. Additional samples of some species were also taken earlier during the ice free period to see whether the length – weight relationship differed in immature nymphs compared with mature, pre-emergence nymphs. Individual wet, dry and ash weights were determined as described in Brittain and Lillehammer (1978). The mean weights of the different millimetre size groups are given in Tab. 4. Length – weight regres-

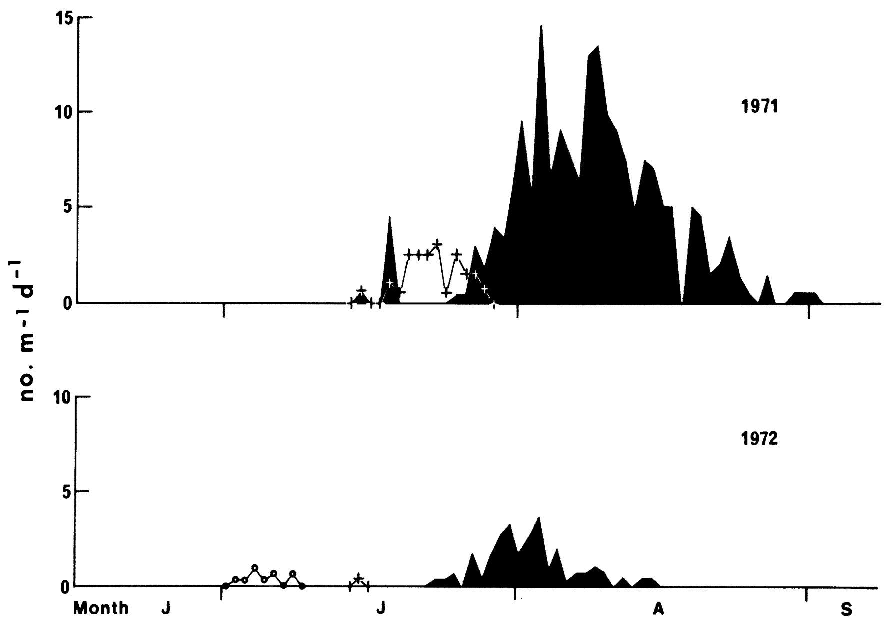

Fig. 5. Daily emergence (per metre shoreline) of *Siphlonurus lacustris* (shaded), *S. aestivalis* (+–+) and *Ameletus inopinatus* (0–0) from Øvre Heimdalsvatn during 1971 and 1972.

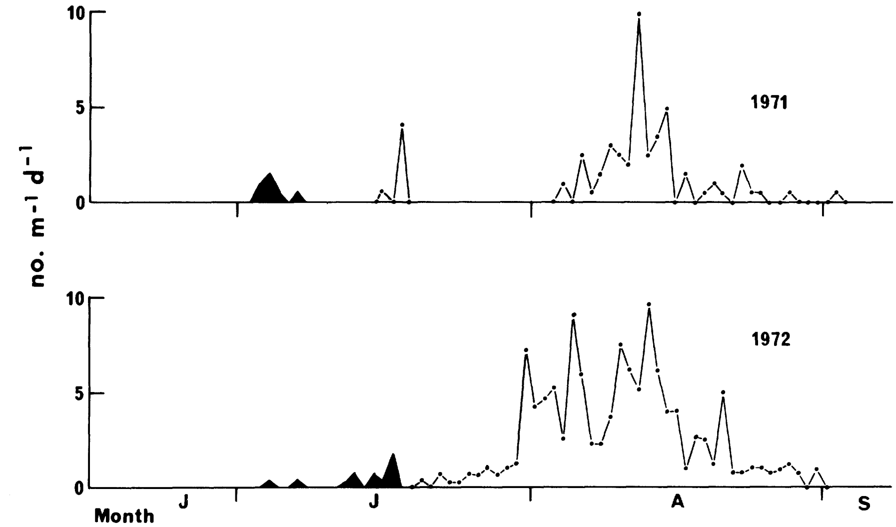

Fig. 6. Daily emergence (per metre shoreline) of *Baëtis rhodani* (shaded and *B. macani* from Øvre Heimdalsvatn during 1971 and 1972.

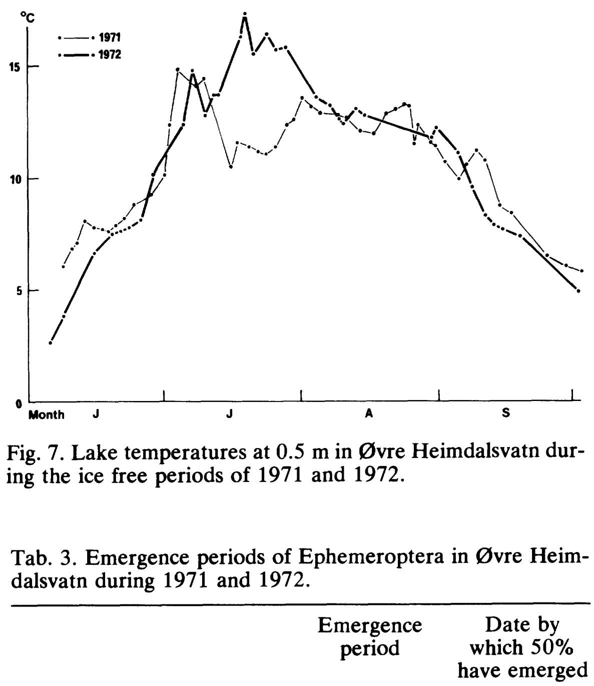

Fig. 7. Lake temperatures at 0.5 m in Øvre Heimdalsvatn during the ice free periods of 1971 and 1972.

Tab. 3. Emergence periods of Ephemeroptera in Øvre Heimdalsvatn during 1971 and 1972.

		Emergence period	Date by which 50% have emerged
Leptophlebia	1971	20 Jun–15 Jul	3 Jul
marginata	1972	22 Jun–16 Jul	29 Jun
Ameletus			
inopinatus	1972	26 Jun– 8 Jul	4 Jul
Baëtis	1971	3 Jul –18 Jul	16 Jul
rhodani	1972	4 Jul –17 Jul	15 Jul
Siphlonurus	1971	15 Jul –28 Jul	22 Jul
aestivalis	1972	15 Jul	15 Jul
Leptophlebia	1971	16 Jul –25 Aug	29 Jul
vespertina	1972	12 Jul –21 Aug	23 Jul
Siphlonurus	1971	15 Jul – 6 Sep	9 Aug
lacustris	1972	23 Jul –15 Aug	1 Aug
Baëtis	1971	18 Jul – 2 Sep	12 Aug
macani	1972	21 Jul –31 Aug	10 Aug

sions, both for wet and dry weight, have been calculated and the results summarized in Tab. 5.

Regression lines are plotted for *L. vespertina, L. marginata* and *S. lacustris* using individual measurements (Figs 8–11). Dry weight, expressed as a percentage of wet weight, ranged from 7 to 9% for the immature nymphs of *L. vespertina* and *lacustris*, but from 13 to 17% for the mature nymphs of the same species (Tabs 6, 7). There was also a tendency towards a reduction in relative ash content with increase in size, but this was not so constant. There was little difference in the correlation coefficients for wet and dry weights, suggesting that both gave equally reliable estimates. Ash weights, because of their small magnitude, were probably less reliable and this may explain inconsistencies in the reduction of relative ash content with increase in length.

2.6. Biomass

The exposed zone survey and the setting up of emergence traps was not planned with a view to provide biomass data, but it is possible to estimate the biomass of Ephemeroptera at a specific point in time, i.e. at the beginning of the emergence period. A combination of the numbers emerging and the size-weight distributions at the beginning of emergence can be used. The emergence trap data for the individual ephemeropteran species are given in Tab. 2, while Tab. 8 summarizes the biomass figures. The total ephemeropteran biomass at emergence was greater in 1971 than 1972, largely on account of the higher numbers of *S. lacustris* in 1971. The biomass of *S. lacustris* decreased from 86.5 mg m^{-2} in 1971 to only 12.4 mg m^{-2} in 1972. The biomass of *B. macani* showed an increase from 1971 to 1972, but it did not have such a large effect on total biomass on account of its low individual weight. In both years the two *Leptophlebia* species, together with *S. lacustris*, ac-

Tab. 4. Wet, dry and ash weights ± 95% confidence limits in mg for ephemeropteran nymphs in Øvre Heimdalsvatn, arranged in mm size groups. The number of measurements is given in parentheses. '*' indicates each measurement was not from single individual, but several weighed together to obtain a measurable weight. Where no number is given, it is the same as for wet weight.

	Length (mm)	Wet weight (mg)		Dry weight (mg)		Ash weight (mg)	
Leptophlebia vespertina							
17–20 Jun 1973	4	1.45	(2)	0.10		0.01	(1)*
	5	2.04±0.49	(8)	0.17 ±0.06		0.01	(1)*
	6	2.95±0.41	(8)	0.32 ±0.07		0.02	(1)*
	7	4.39	(3)	0.49		0.03	(1)*
17 Aug 1973	7	8.56	(2)	0.99		–	
	8	11.30±1.73	(5)	0.96 ±0.42		0.03	(1)
	9	15.47±0.97	(22)	2.10 ±0.17		0.11±0.02	(12)
	10	18.44±1.50	(15)	2.62 ±0.40		0.15±0.04	(11)
	11	22.57	(1)	3.64		0.18	(1)
Leptophlebia marginata							
17 Jun 1973	9	15.65	(1)	1.20		0.17	
	10	18.29	(3)	2.37		0.20	
	11	24.05±2.65	(8)	3.64 ±0.48		0.27	(3)
	12	28.88±2.05	(21)	4.63 ±0.53		0.35±0.09	(15)
	13	36.64±3.75	(17)	7.31 ±0.94		0.45±0.10	(8)
Ameletus inopinatus							
17–23 Jun 1973 and 23 Jun 1975	7	4.81	(1)	0.47		0.02	
	9	11.74	(1)	2.28		0.55	
	10	10.96±3.77	(4)	1.47 ±0.87		0.29±0.27	
	11	17.70±1.48	(8)	2.72 ±0.70		0.49±0.26	
	12	21.35±2.14	(9)	2.83 ±0.46		0.39±0.27	
	13	26.13	(3)	3.13		0.33	
Siphlonurus lacustris							
17 Jun 1973	3	0.36±0.04	(23)	0.025±0.004	(14)	0.005	(1)*
	4	0.62±0.33	(25)	0.045±0.007	(16)		
18 Aug 1973	9	16.67	(1)	1.81		0.15	
	10	23.14	(2)	2.58		0.21	
	12	38.99±2.98	(9)	5.82 ±0.75		0.34±0.14	(6)
	13	44.96±1.79	(18)	7.13 ±0.48		0.32±0.07	(7)
	14	49.11±4.34	(14)	7.99 ±0.85		0.42±0.11	(10)
	15	60.61±4.64	(5)	10.55 ±3.44		0.48	(3)
	17	70.00	(1)	10.92		0.49	
Baëtis macani							
17 Aug 1973	8	8.82±1.20	(8)	1.18 ±0.21		0.05±0.03	(7)
	9	10.95	(3)	1.40		0.05	
	10	12.18	(1)	1.89		0.12	

Tab. 5. Regression data for the relationship between length (l) and weight (w) in Ephemeroptera from Øvre Heimdalsvatn. The relationship is expressed by the equation: $w=al^b$ or $\log w=\log a+b \log l$, in which 'a' is the intercept of the regression line on the Y-axis, 'b' the regression coefficient, 'r' the correlation coefficient and 'n' the number of measurements.

		Wet weight				Dry weight			
		a	b	r	n	a	b	r	n
Leptophlebia vespertina	– Jun	0.070	2.09	0.82	21	0.0013	3.00	0.79	21
	– Aug	0.143	2.12	0.82	45	0.0012	3.55	0.74	45
Leptophlebia marginata	– Jun	0.062	2.48	0.76	50	0.0001	4.35	0.82	50
Siphlonurus lacustris	– Jun	0.048	1.81	0.70	49	0.0028	1.97	0.71	30
	– Aug	0.180	2.14	0.90	50	0.0039	2.91	0.87	50
Baëtis macani	– Aug	0.281	1.65	0.66	12	0.0441	1.57	0.61	12
Ameletus inopinatus	– Jun	0.021	2.79	0.92	26	0.0030	2.82	0.77	26

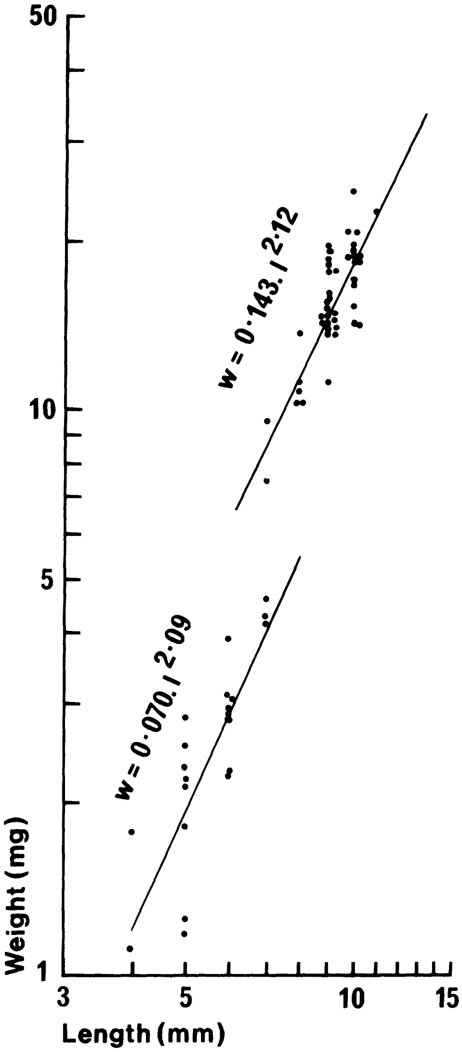

Fig. 8. Relationship between body length and wet weight in *Leptophlebia vespertina* from Øvre Heimdalsvatn in August (upper) and June (lower). The relationship is expressed by the equation: $w = al^b$, where a and b are constants (see also Tab. 5).

counted for approximately 90% of the ephemeropteran biomass at emergence. *B. macani* and *S. aestivalis* accounted for most of the remainder, *A. inopinatus* and *B. rhodani* representing under 1% of the total.

The mean total ephemeropteran biomass at emergence for the years 1971 and 1972 was estimated to be 0.14 g wet wt m^{-2} or 0.021 g dry wt m^{-2} in terms of the whole lake. In terms of the exposed zone, the area where this is produced, values of 0.77 g wet wt m^{-2} and 0.12 g dry wt m^{-2} are obtained.

3. Autecology

3.1. Leptophlebia vespertina

L. vespertina was the most abundant ephemeropteran in Øvre Heimdalsvatn, accounting for on average 53.6% of the Ephemeroptera taken in the emergence traps and 36.3% of those taken in the benthic samples (Tab. 1). The benthic value is lower as the bottom samples were outside the main emergence period, during which nymphs are concentrated in the exposed zone.

L. vespertina occurred at all sampling stations around Øvre Heimdalsvatn, although there were differences in various parts of the lake (Fig. 1). Numbers were low in the western end, while being especially high in the south-eastern parts and along the northern shoreline. The relationship between the amount of detritus at the

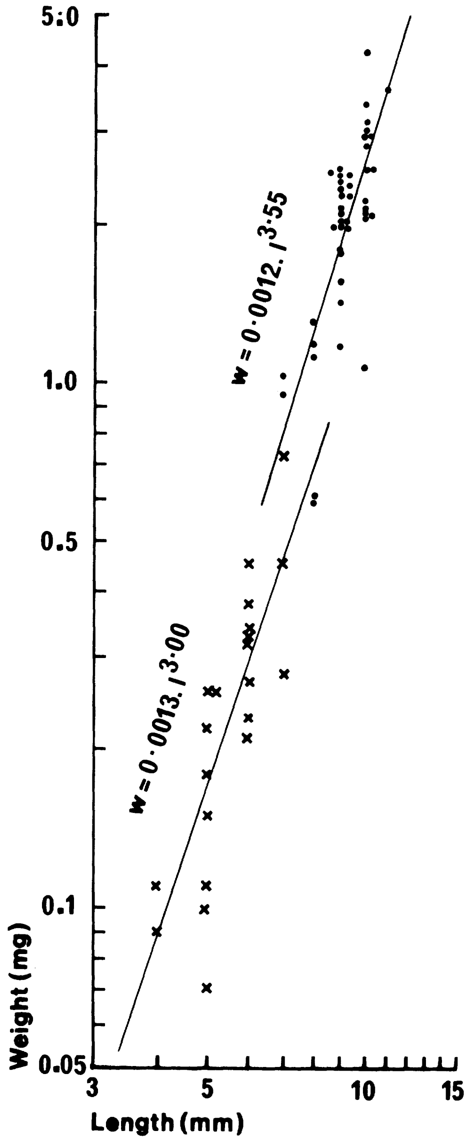

Fig. 9. Relationship between body length and dry weight in *Leptophlebia vespertina* nymphs from Øvre Heimdalsvatn in August (upper) and June (lower). The relationship is expressed by the equation: $w = al^b$, where a and b are constants (see also Tab. 5).

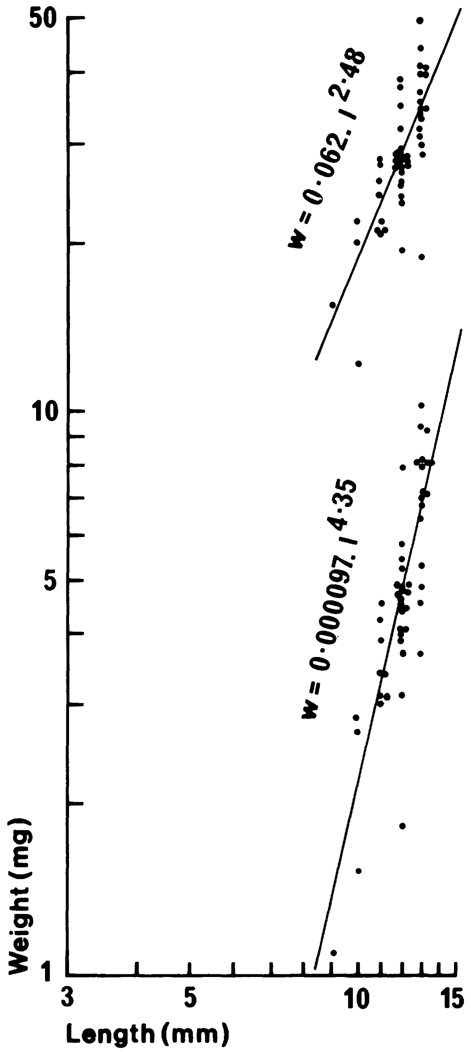

Fig. 10. Relationship between body length and wet and dry weights in *Leptophlebia marginata* nymphs from Øvre Heimdalsvatn during June. The relationship is expressed by the equation: w = al^b, where a and b are constants (see also Tab. 5).

stations and nymphal numbers was significant ($P < 0.05$, Mann-Whitney U-test), indicating the role of detritus in the nutrition of this species. There was considerable variation in numbers of *L. vespertina* in the individual emergence traps, from 104 to 553, reflecting the different location of the traps around the lake.

In most localities *L. vespertina* is univoltine (Moon 1938, Macan 1961, Brittain 1972, Kjellberg 1973), the only exception so far known being the Swedish mountains where it is semivoltine (Kjellberg 1973). On the basis of egg incubation data (Brittain 1976b) and the emergence period in Øvre Heimdalsvatn (Tab. 3), hatching takes place during September and October (Fig. 12). By June the mean length of the nymphs (± 95% C. L.) had reached 4.87 ± 0.12 mm, indicating that growth had taken place during the period of ice cover (Tab. 9). The growth rate was, however, slow on account of the low temperatures, and after ice break at the beginning of June the growth rate increased. Emergence commenced in the middle of July, the main emer-

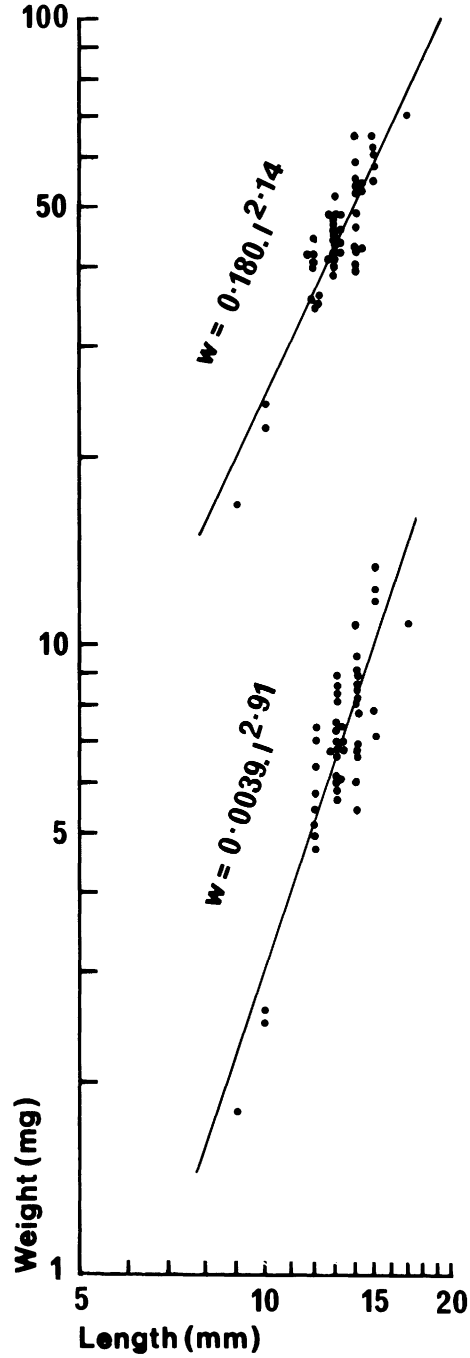

Fig. 11. Relationship between body length and wet and dry weights in *Siphlonurus lacustris* nymphs from Øvre Heimdalsvatn during August. The relationship is expressed by the equation: w = al^b, where a and b are constants (see also Tab. 5).

Tab. 6. Relationship between wet weight, dry weight and ash weight, expressed as a percentage, for Ephemeroptera in Øvre Heimdalsvatn. Means are given ± 95% confidence limits when based on 5 or more measurements.

		DW/WW	AW/DW
Leptophlebia vespertina	– Jun	9.45±1.31	7.21±2.98
	– Aug	13.13±0.82	5.20±0.55
Leptophlebia marginata	– Jun	16.76±0.93	7.43±1.34
Ameletus inopinatus	– Jun	14.11±1.72	14.52±3.57
Siphlonurus lacustris	– Jun	7.06±0.57	7.07
	– Aug	15.67±0.70	5.57±0.26
Baëtis macani	– Aug	13.37±1.09	4.33±0.79

Tab. 7. Relationship between wet weight, dry weight and ash weight, expressed as a percentage, for a sample of *Siphlonurus lacustris* taken during August. Means are given ± 95% confidence limits when based on 5 or more measurements. The number of measurements is given in parentheses.

Length (mm)	DW/WW		AW/DW	
9	10.86	(1)	8.29	(1)
10	11.17	(2)	8.22	(2)
12	14.90±1.35	(9)	6.01±2.47	(6)
13	15.83±0.66	(18	4.55±0.92	(7)
14	16.38±1.52	(14)	5.43±1.17	(10)
15	17.29±4.84	(5)	5.27	(3)
17	15.60	(1)	4.49	(1)

gence extending to mid-August, although adults were also recorded as late as 20 September. A few mature nymphs were also taken in bottom samples during late August and September.

In 1971, 50% emergence occurred around 20 July, while in 1972 it was 5–6 d earlier. Emergence also commenced earlier in 1972 (Tab. 3). These differences can be explained by the low temperatures during much of July 1971 (Fig. 7, Brittain 1978). There was a significant excess of males emerging from Øvre Heimdalsvatn ($P < 0.01$) (Tab. 10), agreeing with Kjellberg's results from Sweden (Kjellberg 1972). There was also a tendency for males to emerge before females (Brittain 1978). The number of *L. vespertina* in the benthos at different times (Tab. 1) are in agreement with the life cycle data. High numbers were present in June and July, whereas only 1% of total numbers were taken in August and September, months during which the egg stage predominated.

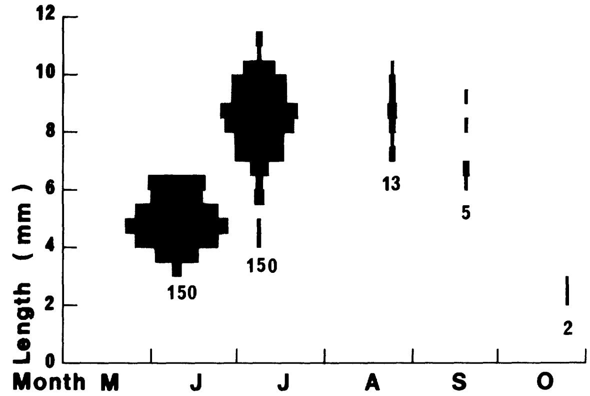

Fig. 12. Nymphal size distribution of *Leptophlebia vespertina* in Øvre Heimdalsvatn during the ice free period of 1972. Sample sizes are given.

Length-weight data for *L. vespertina* are given in Tabs 4, 5 and Figs 8, 9. Mature nymphs of *L. vespertina* are larger and heavier in Øvre Heimdalsvatn than in the forest tarn studied by Kjellberg (1972). In southern Norway mature nymphs of *L. vespertina* are generally larger in high boreal and subalpine localities than in lowland lakes (Brittain 1974, unpubl.). The reason for this is uncertain, but the longer time spent in the nym-

Tab. 8. Mean individual weights (in mg) and biomass estimates (in mg m^{-2}) for Ephemeroptera at emergence in Øvre Heimdalsvatn. Estimates for *Siphlonurus aestivalis* and *Baetis rhodani* are calculated from the individual weights of *Siphlonurus lacustris* and *Baetis macani,* respectively. Values are given in terms of the whole lake.

	Wet weights				Dry weights			
	Mean indiv. wt	Biomass			Mean indiv. wt	Biomass		
		1971	1972	Mean 71–72		1971	1972	Mean 71–72
Leptophlebia vespertina	15.84	50.50	52.64	51.57	2.13	6.79	7.08	6.94
Siphlonurus lacustris	45.67	86.50	12.37	49.44	7.26	13.75	1.97	7.86
Leptophlebia marginata	29.85	19.98	30.00	24.99	5.18	3.47	5.21	4.34
Baëtis macani	9.63	4.06	11.37	7.72	1.29	0.54	1.52	1.03
Siphlonurus aestivalis	–	8.83	0.14	4.49	–	1.40	0.02	0.71
Baëtis rhodani	–	0.76	0.41	0.59	–	0.10	0.05	0.08
Ameletus inopinatus	18.17	0	0.67	0.34	2.51	0	0.09	0.05
Total		170.63	107.60	139.12		26.05	15.94	21.01

Tab. 9. Percentage of total growth (length increase) during different periods for 6 ephemeropteran species in Øvre Heimdalsvatn.

	Ice free (Jun-Oct)		
	Prior to emergence	After emergence	Ice cover (Oct-Jun)
Ameletus inopinatus	4.5	0.0?	95.5
Leptophlebia marginata	0.6	41.1	58.3
Leptophlebia vespertina	45.8	24.3	29.9
Siphlonurus lacustris	76.9	0	23.1
Siphlonurus aestivalis	78.3	0	21.7
Baëtis macani	100	0	0

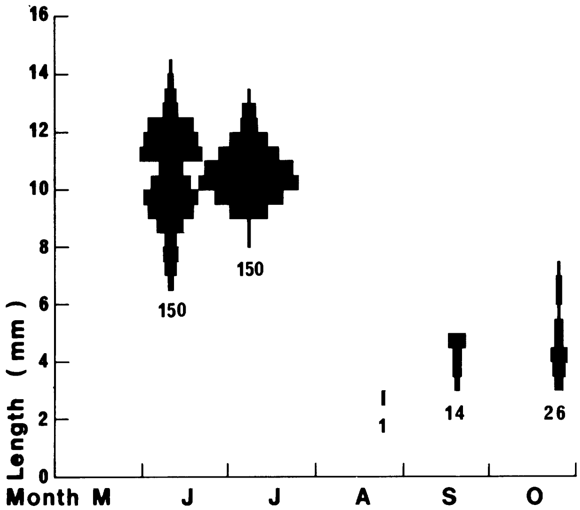

Fig. 13. Nymphal size distribution of *Leptophlebia marginata* in Øvre Heimdalsvatn during the ice free period of 1972. Sample sizes are given.

phal stage on account of the later emergence in the higher localities may be the reason.

L. vespertina and *L. marginata* in Øvre Heimdalsvatn had similar weights at a given length, reflecting their close morphological similarity. The larger, more mature, nymphs of *L. vespertina* contained proportionally less water (Tab. 6), probably because of the development of reproductive products and wing buds combined with increased chitinisation. Although having a lower mean individual weight than either *L. marginata* or *S. lacustris, L. vespertina* still retained its important position in terms of biomass at emergence (Tab. 8). It accounted for 37% of the wet weight biomass and 33% of the dry weight biomass at emergence.

3.2. Leptophlebia marginata

L. marginata was one of the major species in Øvre Heimdalsvatn, accounting for 33.7% of the Ephemeroptera in the benthic samples taken in the exposed zone and between 10.4 and 17.2% in the emergence traps (Tab. 1). In contrast to *L. vespertina* benthic samples were taken during the main emergence period of *L. marginata,* thus giving a relatively higher percentage in the benthic samples.

As with *L. vespertina,* there were higher numbers of *L. marginata* at stations with greater amounts of detritus ($P < 0.01$, Mann-Whitney U-test) (Fig. 1). However, although at low densities numbers of the two species increased concomitantly, at high densities the increase of one species appeared to be at the expense of the other.

As *L. marginata* and *L. vespertina* are often present in the same locality, several authors (e.g. Moon 1938, Macan 1965, Brittain 1972) have considered both species together. Generally *L. marginata* is larger at a given time and emerges earlier. The situation in Øvre Heimdalsvatn is no exception (Figs 12, 13). Small nymphs were present for the first time in August. Growth then continued throughout the autumn and winter until by the beginning of June the major part of the population was at the size necessary for emergence. In northern Sweden growth also continued throughout the winter (Bengtsson 1968). Emergence in Øvre Heimdalsvatn did not take place until the end of June, probably on account of the low temperatures around ice break (Fig. 7). Macan and Maudsley (1966) postulated that *L. marginata* and *L. vespertina* have a temperature threshold of about 11°C for emergence. In Øvre Heimdalsvatn emergence of *L. marginata* started when surface temperatures over the deepest parts of the lake were 7–8°C (Fig. 7). However, temperatures in the exposed zone were probably higher and followed air temperatures more closely. Maximum air temperatures rose from around 5°C to around 10°C immediately prior to emergence (Brittain 1978). Emergence of *L. marginata* continued into the first half of July, there being little overlap between the two *Leptophlebia* species (Fig. 4, Tab. 3). The numbers of *L. marginata* in the benthos were greatest in June prior to emergence as the July samples were taken towards the end of the emergence period (Tab. 1). As with *L. vespertina* there was an excess of males ($P < 0.05$) (Tab. 10).

Numbers per trap varied from 30 to 157. Numbers were slightly less in 1971, although there was considerable variation from trap to trap during the same year (Tab. 2).

Length-weight data for *L. marginata* in June are given in Tab. 4 and Fig. 10. As mentioned earlier weights at a given length were similar for the two *Leptophlebia* species. Nymphs in the June samples of *L. marginata* contained the least amount of water, probably as they were taken during the emergence period.

In terms of biomass at emergence *L. marginata* made

Tab. 10. Sex ratios of Ephemeroptera emerging from Øvre Heimdalsvatn (1971 and 1972)

	♂	♀	♂/♀
Leptophlebia vespertina	945	701	1.35
Leptophlebia marginata	244	195	1.25
Siphlonurus aestivalis	20	19	1.05
Baëtis macani	214	227	0.94
Siphlonurus lacustris	217	247	0.88
Ameletus inopinatus	5	6	0.83
Baëtis rhodani	3	26	0.12

up 18.0% by wet weight and 20.7% by dry weight of the total ephemeropteran biomass at emergence, a slight increase in the proportion obtained using numbers emerging due to their relatively high mean weight at maturity (Tab. 8).

3.3. Siphlonurus lacustris

S. lacustris accounted for 22.4% of the Ephemeroptera in the benthic samples taken in the exposed zone, and from 4.6 to 29.4% of the emerging Ephemeroptera, and thus is an important member of the ephemeropteran community. Numbers in the emergence traps were consistently higher in 1971 (Tab. 2).

Numbers of *S. lacustris* were higher in the northern and western parts of Øvre Heimdalsvatn (Fig. 1). At high densities of *S. lacustris,* numbers of *L. vespertina* were low and vice versa, with the exception of st. 12 which supported an especially rich fauna. There was therefore no significant relationship between detritus and numbers (Mann-Whitney U-test). Gut analyses indicated that macrophyte material formed a larger part of its diet than of either of the *Leptophlebia* species. The northern and western areas of the lake are most sheltered from strong winds, thus permitting the establishment of shallow water macrophytes and the accumulation of their decaying parts.

S. lacustris had the major part of its growth during the ice free period (Tab. 9). Previous laboratory and field studies (Degrange 1960, Hynes 1961) have shown wide variation in the egg incubation period and that some overwinter as eggs and others as small nymphs. In Øvre Heimdalsvatn little growth occurred before ice break as nearly 80% of the June sample were under 4 mm in length (Fig. 14). There was, however, a great deal of size variation, suggesting that at least some could have overwintered as nymphs. After ice break growth was rapid and emergence started in mid-July (Figs 5, 14). It reached a peak at the beginning of August and terminated at the beginning of September. As with most other species emergence took place later in 1971 (Tab. 3). In contrast to the *Leptophlebia* species, there was a slight excess of females (Tab. 10), but numbers were not significantly different from 1:1 ratio.

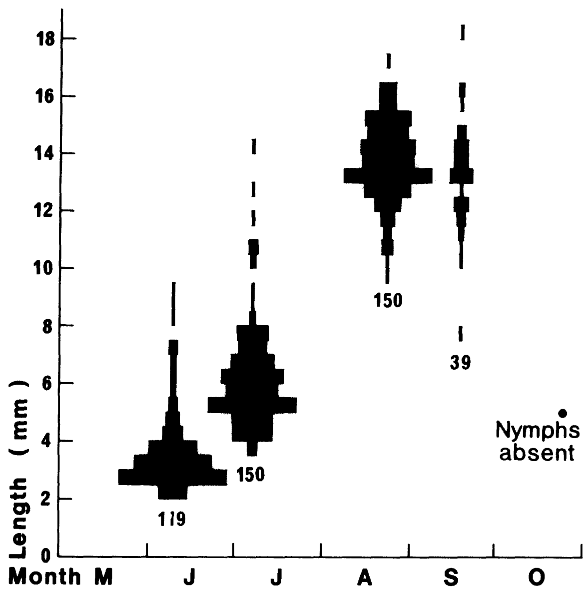

Fig. 14. Nymphal size distribution of *Siphlonurus lacustris* in Øvre Heimdalsvatn during the ice free period of 1972. Sample sizes are given.

Small nymphs of *S. lacustris* and *S. aestivalis* in Øvre Heimdalsvatn were indistinguishable, so the June sample of "*S. lacustris*" used for obtaining weights (Tab. 4) undoubtedly contained a few nymphs of *S. aestivalis.* However, numbers of *S. aestivalis* were very low, only 4–9% of total *Siphlonurus* numbers. In addition, the two species are morphologically similar, giving similar weights for a given length (cf. *Leptophlebia* spp). Therefore it was considered reasonable to refer to the June sample of *Siphlonurus* as *S. lacustris* in the subsequent tables and figures concerning length – weight relationships.

Owing to differences in body form the ephemeropteran species had varying body weights at a given length. For example, 10 mm long nymphs of *S. lacustris,* a robust, wide-bodied species, weighed nearly twice as much as 10 mm long nymphs of the streamlined *B. macani.* Nymphs of *S. lacustris* attained both the greatest body length and body weight of the species weighed, with mature specimens of 15 mm weighing 60 mg wet weight. In terms of biomass at emergence, *S. lacustris* became more important than in terms of numbers on account of its high individual weight. It constituted 35.5% of wet weight biomass and 37.4% of dry weight biomass at emergence.

3.4. Baëtis macani

B. macani was one of the common species in Øvre Heimdalsvatn, accounting for 6.6–20.1% of Ephemeroptera in the emergence traps (Tab. 1). Mean nymphal

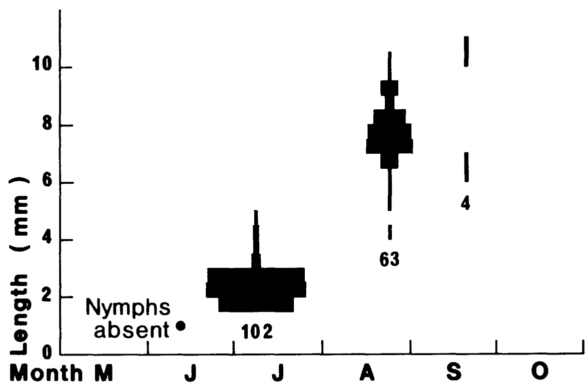

Fig. 15. Nymphal size distribution of *Baëtis macani* in Øvre Heimdalsvatn during the ice free period of 1972. Sample sizes are given.

numbers in the exposed zone were low as they were only present for 2–3 months during the ice free period. Numbers in the emergence traps were higher in 1972, the opposite of *S. lacustris*.

In contrast to most other species, *B. macani* often occurred in higher numbers where there was less detritus in the substratum and the substratum itself was more stable (Fig. 2). This could be the result of competition from other species as the absence of mountain species such as *B. macani* at lower altitudes is often attributed as much to their inability to compete with other species as to any abiotic feature of the environment. Densities were also especially high at st. 15 and around the outflow. In fact, *B. macani* often occurs in high numbers in and around lake outflows (Brittain 1974, 1975).

B. macani completes its numphal development even more rapidly than *S. lacustris*. No nymphs were taken in the June samples, in July their mean length was 2.22 ± 0.08 mm (± 95% C. L.), and by mid-August their emergence peak was reached with a mean nymphal length of 7.67 ± 0.24 mm (Fig. 15). Thus in 6 wk their mean length increased nearly 4 times. The emergence period itself was moderately long, extending from mid-July to late September (Fig. 6). The sex ratio of emerging adults was close to 1:1 (Tab. 10).

Of the Ephemeroptera weighed, *B. macani* was the lightest at maturity, with a mean individual weight of 9.63 mg wet weight (Tab. 8). Therefore its share of total ephemeropteran biomass at emergence was only about 5%.

3.5. Siphlonurus aestivalis

In terms of numbers *S. aestivalis* was one of the minor species in Øvre Heimdalsvatn. Numbers in the emergence traps were highest in 1971 when it made up 3% of the total Ephemeroptera (Tab. 2). In the benthic samples, taken during 1972, 0.9% of the Ephemeroptera were *S. aestivalis* (Tab. 1). *S. aestivalis* is a lentic species, but obviously conditions in Øvre Heimdalsvatn were unsuitable for a larger population. Competition from *S. lacustris* could possibly be important, although they were both common in the western end of the lake (Figs 1, 2).

S. aestivalis has a similar life cycle to *S. lacustris*, although *S. aestivalis* emerged first (Tab. 3, Fig. 5). Similar numbers of males and females were taken in the emergence traps (Tab. 10).

Weight data were not available for *S. aestivalis* nymphs, so for the purpose of estimating biomass they were assumed to have the same length-weight relationship as *S. lacustris*. On the basis of this assumption *S. aestivalis* accounted for about 3% of the ephemeropteran biomass at emergence.

3.6. Baëtis rhodani

B. rhodani was not taken in the benthic samples (Tab. 1). It is a species more typical of lotic habitats, and constituted almost 40% by numbers of the Ephemeroptera taken in the emergence trap situated in the outflow stream of Øvre Heimdalsvatn. It is possible that the adults in the lake traps (Fig. 6, Tab. 2) were artifacts, and that they did not emerge from the lake, but were either washed in from nearby streams or entered while ovipositing. Around Øvre Heimdalsvatn *B. rhodani* probably has only one generation per year as only one emergence period was recorded, which extended from late June to mid-July. There was a large excess of females both in the traps in the lake and in the outflow (Tab. 10).

For the purpose of estimating biomass at emergence the length-weight data for *B. macani* were used. No comparative data are available for these two *Baëtis* species but any differences would have little influence on total ephemeropteran biomass on account of the very low numbers of *B. rhodani*.

3.7. Ameletus inopinatus

A. inopinatus although typically a lotic species is often common around lake inflows and outflows. In Øvre Heimdalsvatn, *A. inopinatus* was most common around the main inflow, the outflow and the exposed st. 11 (Fig. 2).

No small nymphs were taken in Øvre Heimdalsvatn prior to ice formation, but in Nedre Heimdalsvatn (1052 m a.s.l.) two small nymphs were taken in late September. In the River Aurland, western Norway, Larsen (1968) found small nymphs during October and November. Therefore hatching probably took place in Øvre Heimdalsvatn from October onwards. By June the nymphs were more or less fully grown and emergence took place late June and early July (Fig. 5, Tab. 3). *A. inopinatus* was only recorded in the emergence traps during 1972 (Tab. 2). Despite low numbers there were similar numbers of males and females emerging (Tab. 10). Body weight was quite variable in *A. inopinatus,* due partly to mature nymphs being generally heavier in 1975 than in 1973 (Tab. 4). In terms of biomass at emergence, *A. inopinatus* was one of the minor species, constituting only 0.2% of the total (Tab. 8).

4. Discussion

Øvre Heimdalsvatn is situated near the upper boundary of the subalpine zone. Above this zone densities and species number decrease considerably (Brittain 1974). Thus Øvre Heimdalsvatn has a richer ephemeropteran fauna both in terms of numbers and species than the above-lying lakes and pools.

All species in Øvre Heimdalsvatn are univoltine. However, different species have adapted their life cycles in different ways to suit the mountain environment with its short summer. Two main categories are present in Øvre Heimdalsvatn; those whose growth is largely or totally restricted to the ice free period, e.g. *B. macani* and *S. lacustris,* and those who have a significant part of their growth during the period of ice cover, e.g. *Leptophlebia* spp. and *A. inopinatus.* These fit into Landa's (1968) categories of respectively summer and winter species. It is interesting that one of each type, *B. macani* and *A. inopinatus,* are the species most common at higher altitudes than Ø. Heimdalsvatn (Brittain 1974).

The ephemeropteran communities of northern Fennoscandian lakes (Ulfstrand 1969, Brittain unpubl.) contain more north-easterly elements such as *Metretopus borealis* (Eaton) and *Heptagenia joernensis* (Bengtsson). *B. macani* is the only species in Øvre Heimdalsvatn that is restricted to northern Europe (Illies 1978).

Data on ephemeropteran densities, biomass and production in the stony littoral of lakes are sparse, although some studies have been made on sand/mud substrata, with or without macrophytes (e.g. Dvořak 1970, Alimov et al. 1972, Hudson and Swanson 1972). Problems of methodology are undoubtedly the reason. Several investigations have also been carried out in running waters (e.g. Ulfstrand 1968b, Zelinka 1969, Illies 1971, Pearson and Kramer 1972, Waters and Crawford 1973). Returning to lakes, Dunn (in Hunt and Jones 1972) found densities of 50–2250 m^{-2} for *L. marginata* in the stony littoral of Llyn Tegid, Wales, while in two other Welsh lowland lakes ephemeropteran densities of 48–1964 m^{-2} were recorded in the littoral zone (Brittain 1971).

In a Swedish forest tarn *L. vespertina* had a biomass at emergence of 2.24 g wet wt m^{-2}, equivalent to a mean density of about 400 m^{-2} (Kjellberg 1972). In another Swedish forest habitat, Lake Vitalampa, the mean biomass of *L. vespertina* was 0.14 g wet wt m^{-2} and the naximum biomass, which was recorded just before emergence, was 0.3 g wet wt m^{-2} (Erikson et al. 1974). Data are also available from two lowland Norwegian lakes, Borrevann (Økland 1964) and Lille-Jonsvann (Solem 1974). In the former lake, where *Caenis* species dominated, the ephemeropteran density at a depth of 0.2 m on the stony shore was 1416 m^{-2}, which gave a biomass of 5 g wet wt m^{-2}. In Lille-Jonsvann, on soft bottom down to 2 m, maximum densities were about 100 m^{-2} and the biomass was up to 0.6 g wet wt m^{-2}. Compared with a mean biomass at emergence in the exposed zone of Øvre Heimdalsvatn of about 0.7 g wet wt m^{-2}, equivalent to a density of 34 m^{-2}, the above values, especially for biomass, are similar even though they are all from lowland localities which are not directly comparable with Øvre Heimdalsvatn. Densities were often higher in lowland lakes because of abundance of *Caenis* spp., which have a lower individual weight than many other genera, such as *Leptophlebia* and *Siphlonurus.*

The annual production of *L. vespertina* in the two Swedish localities was 4–5 g wet wt m^{-2} (Kjellberg 1972) and 0.43 g wet wt m^{-2} (Eriksson et al. 1974). In both studies the production/biomass ratio was about 3. Speir and Anderson (1974) suggested that emergence data could be used to estimate the annual production of aquatic insects. Kjellberg (pers. comm.) found a production/emergence ratio of 5.4 for *L. vespertina* on the dominant shore type. If this ratio were to be applied to the ephemeropteran biomass at emergence in Øvre Heimdalsvatn, production figures of about 0.8 g wet wt m^{-2} yr^{-1} or 0.1 g dry wt m^{-2} yr^{-1} would be obtained for the whole lake. In terms of the exposed zone, the values would be 4.2 g wet wt m^{-2} and 0.6 g dry wt m^{-2} yr^{-1}. Clearly there are differences between the two localities and populations so these figures should be only regarded as estimates, for order of magnitude calculations.

Using the calorific determinations of Lien (1978a), which gave a value of 5.2 cal/mg dry wt for *L. vespertina,* it is possible to estimate the energy value of ephemeropteran emergence. For the years 1971 and 1972 it amounted to approximately 100 cal m^{-2} yr^{-1} (Brittain and Lillehammer 1978).

Paasivirta (1975) studied insect emergence in an oligotrophic lake, Pääjärvi, in southern Finland. In the littoral zone (0–4.5 m) he recorded 262 ephemeropterans emerging per m^2, which gave a biomass of 356 mg m^{-2}. For the exposed zone of Øvre Heimdalsvatn, the equivalent values were 34 m^{-2} and 110 mg m^{-2}. The biomass value is proportionally greater in Øvre Heimdalsvatn, where the mean individual weight is greater due to the greater abundance of larger species such as *S. lacustris* and *L. marginata. Caenis horaria* and *Centroptilum luteolum* (Müller), both small species, were among the most common Ephemeroptera in Pääjärvi.

The emergence of lentic Ephemeroptera has been studied in two small water bodies in Britain (Morgan and Waddell 1961, Macan 1965). In the former study data are presented from a shallow Scottish loch rich in macrophytes. They found, as in Øvre Heimdalsvatn, differences from trap to trap and from year to year. In a shallow Lake District tarn (Macan 1965) *L. vespertina* and *L. marginata* were among the most numerous organisms. Actual densities, almost 2000 m^{-2} in September, were much higher than in Øvre Heimdalsvatn, probably because the tarn was almost entirely covered by aquatic vegetation, with *Myriophyllum alterniflorum* the major species. In a subsequent paper (Macan and Maudsley 1966) the commencement of emergence of *Leptophlebia* spp. was related to the date on which water temperatures reached 11°C. As discussed earlier this hypothesis fits in with the situation in Øvre Heimdalsvatn.

The relative importance of the various species in Øvre Heimdalsvatn differs to some degree depending on the measure used, whether number in the benthic samples, numbers emerging, or the biomass at emergence. *L. vespertina* is clearly the most abundant ephemeropteran in the lake, but the biomass of *S. lacustris* at emergence is as great as that of *L. vespertina* on account of its greater individual mean weight. *L. marginata* and *B. macani* are also common species in Øvre Heimdalsvatn, but the low individual weight and the short duration of the nymphal stage of *B. macani* reduce its importance in respectively the biomass at emergence and the proportion in the benthos. The remaining species, *S. aestivalis, B. rhodani* and *A. inopinatus* are uncommon in the lake. Of these three species, *S. aestivalis* has the highest biomass at emergence, although still only 3% of the total.

The four major species in Øvre Heimdalsvatn are *L. marginata, L. vespertina, S. lacustris* and *B. macani.* They show a progression in their life cycles from *L. marginata,* in which nearly 60% of the total growth takes place during the period of ice cover, via *L. vespertina* and *S. lacustris,* to *B. macani* in which growth is restricted to the ice free period. They also have different emergence periods. This life cycle separation probably contributes to their co-existence in relatively high numbers for a subalpine lake. It also means that Ephemeroptera of different sizes and at different stages are present during much of the year, enabling them to make best use of the resources available. This variation, producing a succession in for example emergence, is also important for predatory organisms, such as fish and birds (Lien 1978a, b).

Acknowledgements – I thank R. Borgstrøm, P. Larsson, L. Lien and A. Lillehammer for constructive discussion. A. Lillehammer, F. Smedstad and the technical staff of IBP assisted with the field work. E. Vastaberg carried out the preliminary sorting, M. Basberg the weighing and R. Samuelsen the typing of the MS. Financial support was received from the Norwegian Research Council for Science and the Humanities, the International Biological Programme and the Royal Society (London). The provision of facilities at the Zoological Museum, Oslo, and the encouragement of Prof. R. Vik are gratefully acknowledged.

References

Alimov, A. F., Boullion, V. V., Finogenova, N. P., Ivanova, M. B., Kuzmitskaya, N. K., Nikulina, V. N., Ozeretskovskaya, N. G. and Zharova, T. V. 1972. Biological productivity of lakes Krivoe and Krugloe. – In Kajak, Z. and Hillbricht-Ilkowska, A. (ed.) Productivity problems of freshwaters. Polish Scientific Publishers, Warszawa, pp. 39–56.

Bengtsson, B. E. 1968. Tillväxten hos några Ephemerider i Rickleån under vinterhalvåret (in Swedish). – Unpubl. thesis, Univ. Umeå.

Brittain, J. E. 1971. The biology and distribution of *Leptophlebia vespertina* (L.) (Ephemeroptera) and *Nemoura avicularis* Morton (Plecoptera) in some North Wales lakes. – Ph. D. thesis, University of Wales, Bangor.

– 1972. The life cycles of *Leptophlebia vespertina* (L.) and *L. marginata* (L.) in Llyn Dinas, North Wales.-Freshwat. Biol. 2: 271–277.

– 1974. Studies on the lentic Ephemeroptera and Plecoptera of Southern Norway. – Norsk ent. Tidsskr. 21: 135–154.

– 1975. The life cycle of *Baëtis macani* Kimmins (Ephemerida) in a Norwegian mountain biotope. – Ent. scand. 6: 240–244.

– 1976a. The temperature of two Welsh lakes and its effect on the distribution of two freshwater insects. – Hydrobiologia 48: 37–49.

– 1976b. Experimental studies on growth in *Leptophlebia vespertina* (L.) (Ephemeroptera). – Freshwat. Biol. 6: 445–449.

– 1978. Emergence of Ephemeroptera from Øvre Heimdalsvatn, a Norwegian subalpine lake. – Proc. 2nd int. Conf. Ephemeroptera, 1975, Krakow (in press).

– and Lien, L. 1978. Seasonal and interspecific variation in consumption of Ephemeroptera by brown trout in a subalpine lake. – Verh. int. Verein. theor. angew. Limnol. 20: 728–733.

– and Lillehammer, A. 1978. The fauna of the exposed zone of Øvre Heimdalsvatn: Methods, sampling stations and general results. – Holarct. Ecol. 1: 221–228.

Degrange, C. 1960. Recherches sur la réproduction des Ephéméroptères. – Trav. Lab. Hydrobiol. Piscicult. Grenoble 51: 7–193.

Dvořak, J. 1970. A quantitative study on the macrofauna of stands of emergent vegetation in a carp pond of south-west Bohemia. – Rozpr. čsl. Akad. Věd. Řada mat. přírod. Věd 80: 63–114.

Elliott, J. M. 1965. Invertebrate drift in a mountain stream in Norway. – Norsk ent. Tidsskr. 13: 97–99.

Eriksson, F., Johansson, J.-A., Mossberg, P., Nyberg, P., Olofsson, H. and Ramberg, L. 1974. Ekosystemets struktur i sjön Vitalampa. – Klotenprojektet rapport 4. Scripta limnol. upsal. 10 (370): 1–95.

Grimeland, G. 1966. [Flying activity in *Caenis horaria* (L.)]. – K. norske Vidensk. Selsk. Mus. Årb. 1966: 7–23.

Hudson, P. L. and Swanson, G. A. 1972. Production and standing crop of *Hexagenia* (Ephemeroptera) in a large reservoir. – Stud. nat. Sci. East. New Mexico Univ. 1: 1–42.

Hunt, P. C. and Jones, J. W. 1972. The effect of water level fluctuations on a littoral fauna. – J. Fish. Biol. 4: 385–394.

Hynes, H. B. N. 1961. The invertebrate fauna of a Welsh mountain stream. – Arch. Hydrobiol. 57: 344–388.

Illies. J. 1971. Emergenz 1969 im Breitenbach. – Arch. Hydrobiol. 69: 14–59.

– (ed.) 1978. Limnofauna Europa. 2nd ed. – Fischer, Stuttgart.

Jones, J. R. E. 1950. A further study of the river Rheidol: The food of the common insects of the main stream. – J. Anim. Ecol. 19: 159–174.

Kjellberg, G. 1972. Autekologiska studier över *Leptophlebia vespertina* (Ephemeroptera) i en mindre skogstjärn 1966–1968. – Ent. Tidskr. 93: 1–29.

– 1973. Growth of *Leptophlebia vespertina* L., *Cloëon dipterum* L. and *Ephemera vulgata* L. (Ephemeroptera) in a small woodland lake. – Ent. Tidskr. 94: 8–14.

Landa, V. 1968. Developmental cycles of central European Ephemeroptera and their interrelations. – Acta ent. bohemoslov. 65: 276–284.

Larsen, R. 1968. The life cycle of Ephemeroptera in the lower part of Aurland river in Sogn and Fjordane, Western Norway. – Norsk ent. Tidsskr. 15: 49–59.

Larsson, P. and Tangen, K. 1975. The input and significance of particulate terrestrial organic carbon in a subalpine freshwater ecosystem. – In: Wielgolaski, F. E. (ed.), Fennoscandian tundra ecosystems. Part I. Plants and microorganisms. (Ecological studies, vol. 16). Springer, Berlin, pp. 351–359.

Lien, L. 1978a. The energy budget of the brown trout population of Øvre Heimdalsvatn. – Holarct. Ecol. 1: 279–300.

– 1978b. The vertebrates of the Øvre Heimdalen valley. – Holarct. Ecol. 1: 107–110.

Macan, T. T. 1961. A key to the nymphs of British species of Ephemeroptera. – Sci. Publs Freshwat. biol. Ass. 20: 1–68.

– 1965. The fauna in the vegetation of a moorland fishpond. – Arch. Hydrobiol. 61: 273–310.

– and Maudsley, R. 1966. The temperature of a moorland fishpond. – Hydrobiologia 27: 1–22.

– and Maudsley, R. 1968. The insects of the stony substratum of Windermere. – Trans. Soc. Br. Ent. 18. 18: 1–18.

Moon, H. P. 1938. The growth of *Caenis horaria* (L.), *Leptophlebia vespertina* (L.) and *L. marginata* (L.) (Ephemeroptera). – Proc. Zool. Soc. Lond. 108: 507–512.

Morgan, N. C. and Waddell, A. B. 1961. Insect emergence from a small trout loch and its bearing on the food supply of fish. – Freshwat. Salmon Fish. Res., Edinburgh 25: 1–39.

Müller, C. 1973. Periphyton. – IBP i Norge. Årsrapp. 1972: 425–431.

Økland, J. 1964. The eutrophic lake Borrevann (Norway) – an ecological study on shore and bottom fauna with special reference to gastropods, including a hydrographic survey. – Folia limnol. scand. 13: 1–334.

Paasivirta, L. 1975. Insect emergence and output of incorporated energy and nutrients from the oligotrophic lake Pääjärvi, southern Finland. – Ann. zool. fenn. 12: 126–140.

Pearson, W. D. and Kramer, R. H. 1972. Drift and production of two aquatic insects in a mountain stream. – Ecol. Monogr. 42: 365–385.

Solem, J. 1973. Diel rhythmic pattern of *Leptophlebia marginata* L. and *L. vespertina* L. (Ephemeroptera). – Aquilo, ser. Zool. 14: 80–83.

– 1974. The bottom fauna of lake Lille-Jonsvann, Trøndelag, Norway. – Norw. J. Zool. 21: 227–261.

Speir, J. A. and Anderson, N. H. 1974. Use of emergence data for estimating annual production of aquatic insects. – Limnol. Oceanogr. 19: 154–156.

Steine, I. 1972. The number and size of drifting nymphs of Ephemeroptera, Chironomidae and Simuliidae by day and night in the River Stranda, Western Norway. – Norsk ent. Tidsskr. 19: 127–131.

Szumiec, M. 1973. Determination of water temperature in shallow water bodies. – Acta Hydrobiol. 15: 247–257.

Ulfstrand, S. 1968a. Life cycles of benthic insects in Lapland streams (Ephemeroptera, Plecoptera, Trichoptera, Diptera Simuliidae). – Oikos 19: 167–190.

– 1968b. Benthic animal communities in Lapland streams. – Oikos Suppl. 10: 1–120.

– 1969. Ephemeroptera and Plecoptera from the river Vindelälven in Swedish Lapland. – Ent. Tidskr. 90: 145–165.

Vik, R. 1978. The lake Øvre Heimdalsvatn – a subalpine freshwater ecosystem: Introduction. – Holarct. Ecol. 1: 84–88.

Waters, T. F. and Crawford, G. W. 1973. Annual production of a stream mayfly population; a comparison of methods. – Limnol. Oceanogr. 18: 286–296.

Zelinka, M. 1969. Die Eintagsfliegen (Ephemeroptera) in Forellenbäcken der Beskiden. 1. Abundanz und Biomasse. – Folia Fac. sci. nat. Univ. Purkynianae Brno, Biol. 25: 157–168.