

The Lake Ecosystem of Øvre Heimdalsvatn

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The lake ecosystem of Øvre Heimdalsvatn

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The Norwegian subalpine lake, Øvre Heimdalsvatn, has a surface area of 0.78 km² and a maximum depth of 13 m. It is ice-covered for 7.5–8 months, has a marked spring spate and a mean annual renewal period of about two months. The water is poor in electrolytes. Intensive studies have been made by an interdisciplinary team of the lake's physical and chemical properties, primary production and secondary production under the auspices of IBP/PF from 1969 to 1973. Allochthonous material accounted for 1/3 of utilized plant input. The major lake predator, the brown trout, fed largely on benthic organisms and did not exploit the zooplankton biomass. On account of the long period of ice cover and the rapid rise in temperature after ice break, many organisms (both planktonic and benthic) showed synchronous development. Abiotic conditions, such as the nature of the spring spate and the temperature rise, strongly affect species and community development.

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Introduction

The subalpine lake Øvre Heimdalsvatn has been the subject of detailed interdisciplinary studies. This has largely been under the auspices of the freshwater production section (PF) of the IBP. A review and synthesis of the results of all the freshwater projects in this programme has been made (LeCren in press). Therefore in the present paper we will concentrate on the Norwegian project and only to a limited extent make comparisons with other IBP-projects.

With a background in the large amount of data obtained in the various fields, it is our aim in this paper to summarize our knowledge of the ecosystem to date and to attempt a synthesis, pointing out the major pathways and interrelationships. In addition to the data already presented in this volume we will draw upon earlier pub-

lications on Øvre Heimdalsvatn, interrelational aspects unsuitable for separate papers and data as yet unpublished. In this way we hope to present a synthesis of the lake as an aquatic ecosystem. Clearly we have been unable to measure all variables and indeed our idea of what constitute the most significant variables has changed as we became more aware of the functioning of the ecosystem. Nevertheless, we have sufficient information to be able to describe certain energy relationships into and within this ecosystem, which in several respects is typical of large numbers of mountain lakes, with their long period of ice cover, spring spate and the importance of allochthonous input. We are also able to pinpoint gaps in our knowledge of the ecosystem and suggest areas of research that should prove fruitful in the elucidation of such ecosystems.

The Lake Øvre Heimdalsvatn – a subalpine freshwater ecosystem.

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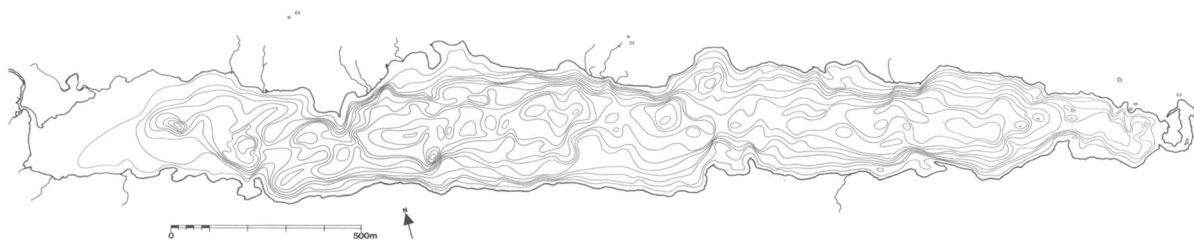


Fig. 1. Map of the lake Øvre Heimdalsvatn. Depth contours are at 1 m intervals.

Physical and chemical milieu

The 3 km long, 400 m wide and 13 m deep Øvre Heimdalsvatn (Fig. 1), situated 1090 m a.s.l. in the central mountain area of southern Norway, is in many respects a typical Norwegian mountain lake. The lake surface area is 0.78 km² and the lake volume is 3.66·10⁶ m³.

The lake is fed by a number of fast-flowing streams, of which Brurskardsbekken at the western end is the largest. The electrolyte content of these streams is low and the specific conductivity varies between 8 and 23 µS cm⁻¹. The pH is generally between 6.1 and 7.2 (Kloster 1978). The highest electrolyte concentrations occur during the winter when the streams are fed mainly by groundwater. Apart from sulphate, probably originating from melted snow, electrolyte concentrations are at a minimum during the spring spate. The lake has only one outlet, at the eastern end, which breaks through a moraine ridge and flows down into the much larger lake, Nedre Heimdalsvatn (1052 m a.s.l.) after 3 km. The period of ice cover on the lake is long, usually lasting from the middle of October to the beginning of June. The snow cover over the ice reduces light penetration. There is negligible plant production under the ice. During the thaw in May snow over the ice disappears and autochthonous plant production starts again (Tangen and Brettum 1978).

The shallowness of the lake and its situation in a windy mountain area, mean that the surface freezes in the autumn when the lake temperature is well below 4°C. Although the temperature increases during the winter, the bottom layers do not reach 4°C until the ice breaks up in June (Kloster 1978). The mean lake temperature increases during June to about 10–14°C and remains within this interval until the beginning of September when cooling commences (Fig. 2). The warming up in June was very different during the various years. During the summer, stratifications with surface temperatures up to about 17°C can occur, but usually the wind mixes the lake water producing isothermy – the general situation during the ice-free period (Kloster 1978). Surface temperatures in sheltered bays follow air temperatures more closely and can exceed 20°C during warm periods (Brittain unpubl.).

The catchment area of Øvre Heimdalsvatn is 24.4

km² which is 31 times the lake surface of 0.78 km². Although the yearly precipitation is only about 800 mm yr⁻¹ (Johannessen 1978), the lake water is theoretically renewed 6–7 times during one year. The water renewal time is very seasonally dependent (Grøterud and Kloster 1978) and is shortest during the spring spate when it reaches a minimum of 2–3 d. The renewal time increases rapidly during June and during the summer a renewal time of about 50–100 d is usual. In rainy periods the renewal time can decrease again.

The electrolyte content in the waters of Øvre Heimdalsvatn is low and the specific conductivity varied between 9 and 31 µS cm⁻¹. The pH usually lay between 6 and 7 (Kloster 1978) although extremes of 5.1 and 7.4 have been reported (Grøterud 1972).

The concentration of dissolved phosphate is low and mainly below 2 µg P l⁻¹, the limit for the analytical method used (Golterman 1969, Grøterud 1972). However, in April measurements of dissolved orthophosphate exceed this threshold. Shortly afterwards, in May, the rise in primary production starts and continues until the middle of June when it culminates. Then no detectable amounts of phosphate remain.

Dissolved nitrogen components occur in detectable amounts at some depths throughout the year, in these cases varying between 5 and about 300 µg N l⁻¹ (Kloster 1978). During the summer period the oxygen tension in all layers is generally below saturation point but above about 40% saturation (Kloster 1978). During the winter the oxygen tension decreases and in April and May anoxic conditions prevail below a depth of about 11 m.

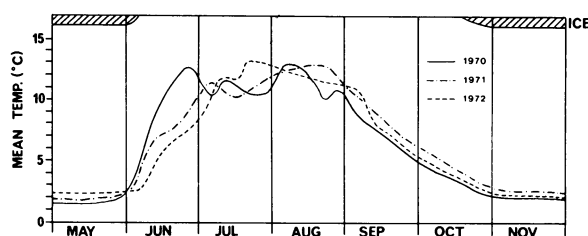


Fig. 2. Mean water temperatures in Øvre Heimdalsvatn during 1970, 1971 and 1972.

In the late winter anoxic conditions can also occur close to the bottom at other depths (Aarefjord unpubl.).

Macrophytes

The only macrophytes of quantitative importance in the lake are the submerged perennial species *Isoetes lacustris* (Pteridophyta) and *Scorpidium scorpioides* (Bryophyta) which together cover 37% of the bottom area (Brettum 1971). *I. lacustris* occupies most of the depth zone 1.0–5.5 m (32% of the bottom area). *S. scorpioides* is confined to the westernmost lake basin between 4.5 and 7 m (5% of the bottom). By the end of the growth season the total dry weight biomass of *I. lacustris* was 33900 kg and that of *S. scorpioides* 4600 kg. The average above-ground biomass (leaves) of *I. lacustris* in the autumn for the whole lake was 22.3 g m^{-2} (dry wt) of which 6.7 g m^{-2} were produced during the preceding growth season. This corresponds to an accumulation of above-ground biomass of 3.1 g C m^{-2} (conversion to carbon after Winberg 1971). Below-ground dry weight biomass of roots and stems of *I. lacustris* after the growth season was 27.9 g m^{-2} , and biomass accumulation during the growth season was 10.1 g m^{-2} which converted to carbon is 4.6 g C m^{-2} . Thus total net growth of *I. lacustris* during the ice free period (June–October) was 7.7 g C m^{-2} , which is equal to a 50.5% increase on the spring standing stock (Tangen unpubl.).

Phytoplankton

Altogether 90 pelagic and 86 tychopelagic microalgae species have been identified in the lake (Tangen et al. 1978a).

The quantitatively dominant forms are small species of Chrysophyceae (e.g. *Dinobryon* spp., *Chrysoikos skujai*, *Bitrichia chodatii*), Cryptophyceae (*Cryptomonas* spp., *Rhodomonas lacustris* and others), Dinophyceae (*Peridinium inconspicuum*, *Gymnodinium* cf. *lacustre*) and Chlorophyceae (*Dictyosphaerium simplex*, *Oocystis lacustris*, and small unidentified species). Diatoms (Bacillariophyceae) and bluegreen algae (Cyanophyceae) are of minor importance (Brettum 1972). In 1972 chrysophytes amounted to 40–50% of the total standing stock throughout the year, thus being the most important group. The dinoflagellates had a maximum in the summer, chlorophytes in the autumn, and the cryptophytes showed two maxima, one in the spring and another in the autumn. The total standing stock was low during the winter (cell volume $< 50 \text{ mm}^3 \text{ m}^{-3}$). The vernal growth started under the ice at the end of April culminating in the yearly maximum ($800 \text{ mm}^3 \text{ m}^{-3}$ in 1972) in June a couple of weeks after ice break (Tangen and Brettum 1978). The variation in phytoplankton biomass in 1972 calculated as mg dry weight m^{-3} is shown in Fig. 3. The average yearly standing crop varied by a factor of at least two (ca. $120 \text{ mm}^3 \text{ m}^{-3}$ in 1969–70, ca. $250 \text{ mm}^3 \text{ m}^{-3}$ in 1972). Primary productivity was

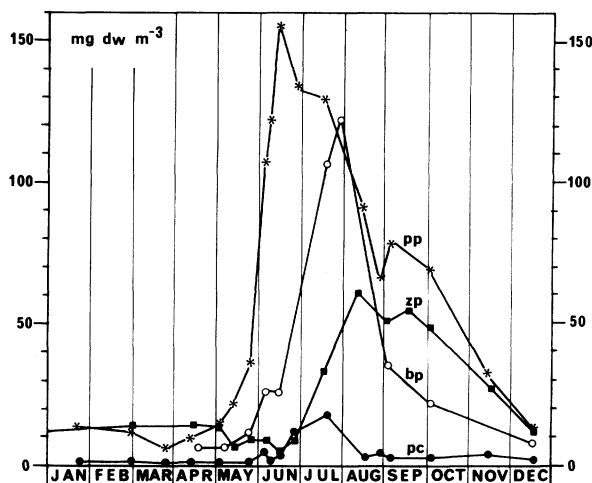


Fig. 3. Variation in biomass of phytoplankton (pp), bacterioplankton (bp), multicellular zooplankton (zp) and planktonic ciliated protozoa (pc) in Øvre Heimdalsvatn during 1972.

light inhibited in the upper 0.5 m in periods during the summer on account of too high light intensity. In 1972 the annual primary productivity for the whole lake was $10\text{--}13 \text{ g C m}^{-2}$ (Tangen and Brettum 1978).

Periphytic algae

The bottom flora (with the exception of macrophytes) is dominated by microscopic forms, mainly diatoms (*Tabellaria flocculosa*, *T. fenestrata* and *Gomphonema acuminatum*), some desmids (Brettum 1970) and small filamentous green algae (e.g. *Zygnema* spp., *Spirogyra* spp.) (Tangen et al. 1978a). The periphyton "net" primary productivity during August in the depth zone 0–2 m was low, less than $10 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Müller 1973). In the inflow stream, Brurskardsbekken, the periphyton biomass was dominated by diatoms, although during June and July there were more species of green algae (mainly desmids) at some stations (Tangen et al. 1978a). The drifting microalgae had a distinctly different species composition to that of the periphyton, and an important fraction probably originated from the lacustrine habitats in the watercourse (Tangen et al. 1978a).

Allochthonous organic matter

A significant part of the organic material occurring in the lake was found to be of terrestrial origin (Larsson and Tangen 1975). In the lower parts of the catchment area, up to about 1250 m a.s.l., bushes of *Salix* spp. (dwarf willow) and *Betula nana* (dwarf birch) and trees of *Betula tortuosa* (mountain birch) are abundant (Øst-hagen and Egelie 1978). Fragments of these plants are the dominant fractions in the imported particulate organic matter.

The yearly input of particulate organic carbon (POC) via the inflow streams was estimated to be 22 g C m^{-2} of lake surface. On the basis of preliminary studies and observations, airborne allochthonous material seemed to be unimportant, with the possible exception of the region adjacent to land. The yearly output of POC from the lake was found to be 8 g C m^{-2} lake surface. The output was a mixture of allochthonous and autochthonous material (Larsson and Tangen 1975), but since the highest output was found simultaneously with the highest input of POC, most of the POC output was probably of allochthonous origin and thus the net import into the lake was about 14 g C m^{-2} . Dissolved organic carbon (DOC) was not measured routinely but measurements of KMnO_4 consumption were made (Grøterud 1972). Caution must be exercised in converting KMnO_4 consumption to g C m^{-3} . However, Gjessing (1976) compared the ratio between organic carbon (mg C l^{-1}) and consumption of KMnO_4 (mg O l^{-1}) and found it fairly stable, between 1.05 and 1.21. Using the KMnO_4 values from Øvre Heimdalsvatn, the average amount of dissolved organic carbon in the lake would be about 0.3 g C m^{-3} and the maximum values in the main inlet during the spring spate about 1.4 g C m^{-3} . These values are surprising since they are less than the particulate organic carbon. This is a very uncommon situation; usually the concentration of dissolved organic carbon completely dominates the particulate being 2–18 times higher (Jordan and Likens 1972, Efford and Hall 1975). Further measurements of DOC in Øvre Heimdalsvatn are necessary to verify this unusual result. The following discussion is therefore limited to various fraction of POC.

Particulate organic detritus (POD)

In 1972 the standing crop of organic seston showed a minimum in late April (ash-free dry wt 0.2 g m^{-3}), a maximum in early June ($1.0\text{--}1.2 \text{ g m}^{-3}$), a summer minimum in Aug/Sep (ca. 0.5 g m^{-3}) and a maximum again in October ($0.7\text{--}0.8 \text{ g m}^{-3}$) (Fig. 4) (Larsson and Tangen 1975). A similar annual cycle was observed in 1971. The maximum in June was caused by the large amounts of allochthonous organic material carried into the lake by the inlet streams during the spring spate. The maximum in October was produced by strong westerly winds leading to resuspension of bottom material on account of strong water turbulence. The standing crop of POD has been deduced by subtracting the biomass of bacterioplankton, phytoplankton and zooplankton from the total seston. The ratio POD/plankton (in terms of dry weight) varied between 10 (during winter) and 1 (in July–August). POD concentrations were lowest in late spring (dry weight less than 0.2 g m^{-3}) and highest in June (ca. 0.8 g m^{-3}). There was also a minimum in the summer (ca. 0.25 g m^{-3} in July–August) and another maximum in October (ca. 0.5 g m^{-3}). The average annual standing crop of POD in terms of dry weight was 0.3 g m^{-3} , which when converted to carbon gives 0.16 g C m^{-3} (Tangen unpubl.).

Sediments

In the middle of the lake the sediments are about 2 m thick and the deepest parts were found to be about 8000 yr old. It is difficult to estimate the yearly sedimentation exactly since it varies among the different parts of the

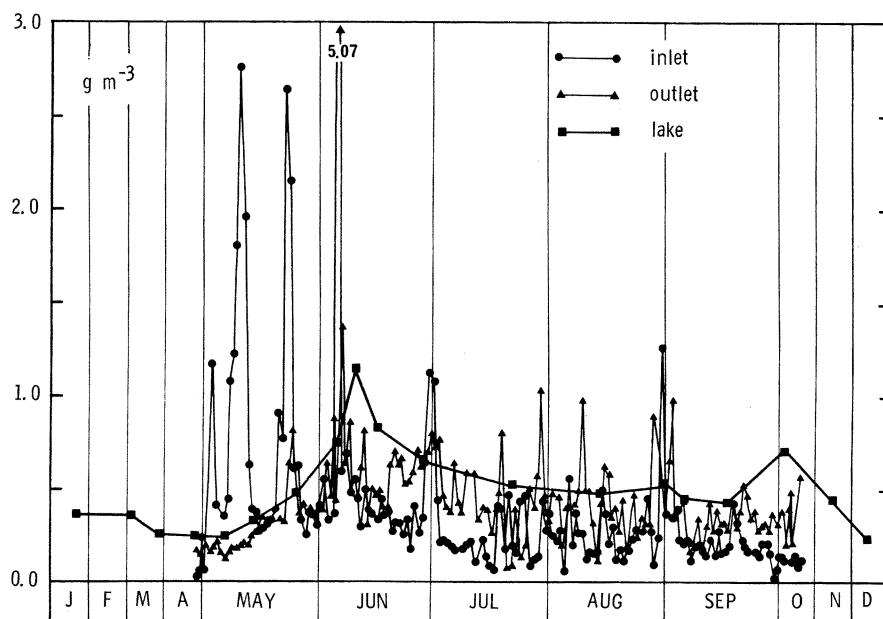


Fig. 4. Øvre Heimdalsvatn – seston concentrations in the inlet, the lake itself and in the outlet during 1972.

lake, but is probably on average about 0.2 mm. The carbon content in the sediments which are well mixed up with inorganic components did not exceed 20% of the dry weight (Kloster and Hongve 1978). The estimated yearly sedimentation of organic matter is $3 \text{ g C m}^{-2} \text{ yr}^{-1}$.

Bacterioplankton

The bacterioplankton is composed mainly of short rods and cocci. Although no effort have been made to discriminate between different types in the counting procedure, these morphological groups seem to dominate throughout the year (Tangen 1973). There are only small vertical variations in the size of the standing crop in the pelagic zone, except in a thin layer above the bottom where cell numbers are comparatively high. In 1972 the standing crop was small during late winter ($<0.1 \text{ mill cells mL}^{-1} = \text{ca. } 5 \text{ mg dw m}^{-3}$) and reached a maximum in July (average concentration $1.6 \text{ mill cells mL}^{-1} = \text{ca. } 120 \text{ mg dw m}^{-3}$ (Fig. 3)). Converted to carbon (according to Hobbie et al. 1972) the average annual standing crop was 13 mg C m^{-3} . High numbers of bacteria, of which a considerable fraction probably was soil species, were observed in the inlet water during the spring spate, whereas during other seasons concentrations were lower than in the lake. Throughout the year the concentration of bacteria in the outlet water was similar to the surface water in the lake. The vertical distribution of bacterioplankton with very high concentrations near the bottom in the macrophyte belt, indicates that the macrophytes and the benthic microphytes might be important contributors of DOC for bacterial growth in Øvre Heimdalsvatn.

Zooplankton

Although 47 multicellular invertebrates have been identified in water and net samples from the lake and inflow and outflow streams, only 7 were of quantitative importance in the lake pelagic (Larsson 1978).

The two cladocerans *Holopedium gibberum* and *Bosmina longispina* dominated both the biomass and production. They were purely summer and autumn forms overwintering as resting eggs. During the summer *H. gibberum* had 3–4 generations while *B. longispina* had 4–5 generations. Their respective maximum biomass from 1969 to 1973 varied between 0.24 and 0.27 g dw m^{-2} , and 0.12 and 1.7 g dw m^{-2} lake surface. The production of *H. gibberum* varied between 0.9 and $1.7 \text{ g dw m}^{-2} \text{ yr}^{-1}$ and the production of *B. longispina* between 0.4 and $1.2 \text{ g dw m}^{-2} \text{ yr}^{-1}$. Together they accounted for 84–92% of the measured multicellular zooplankton production.

The two copepod species of quantitative importance were *Cyclops scutifer* and *Heterocope saliens*. Both have

one generation per year. *Cyclops scutifer* is perennial while *H. saliens* overwinters as resting eggs. Their respective maximum biomass varied between 0.04 and 0.11 g dw m^{-2} , and between 0.01 and 0.07 g dw m^{-2} . The production of *C. scutifer* varied between 0.10 and $0.12 \text{ g dw m}^{-2} \text{ yr}^{-1}$ and the production of *H. saliens* between 0.05 and $0.10 \text{ g dw m}^{-2} \text{ yr}^{-1}$. The copepods contributed 5–8% of the measured production of multicellular zooplankton.

The three main rotifer species were *Conochilus unicornis*, *Polyarthra vulgaris* and *Kellicottia longispina*. *Kellicottia longispina* was perennial while the others were facultatively perennial and appeared during winter time only in certain years. Maximum rotifer biomass varied between 0.01 and 0.02 g dw m^{-2} and the yearly production between 0.10 and $0.16 \text{ g dw m}^{-2} \text{ yr}^{-1}$. The rotifer share of the total zooplankton production was about 3–8%.

The development of the biomass of the multicellular zooplankton during 1972 is shown in Fig. 3. The total production was found to vary between 2.0 and $3.1 \text{ g dw m}^{-2} \text{ yr}^{-1}$. The protozoan production is not included in this estimate owing to insufficient information about these forms to estimate their production. However, the maximum biomass of ciliated protozoans was found to vary between 0.02 and 0.08 g dw m^{-2} (Fig. 3) (Brettum 1972, Larsson 1978, Tangen and Brettum 1978) and the relatively high biomass of such short-lived forms showed that the total zooplankton production was obviously much higher.

Zoobenthos

It was found convenient to divide the bottom areas into three different zones based on the distribution of the aquatic macrophytes (Aarefjord et al. 1978). The exposed zone is the bottom area above the macrophytic vegetation, from the shoreline down to a depth of 1–2 m. The macrophytic zone is the belt with submerged macrophytes generally between 1–2 m and 5–5.5 m (Brettum 1971). In some places, particularly in the sheltered bays this zone reached the lake shore, and here helophytes also occurred. The non-macrophytic zone is the remaining bottom area below the macrophytes.

The major taxa in the exposed zone are Ephemeroptera, *Gammarus lacustris*, Trichoptera, Chironomidae, Plecoptera, Coleoptera and Oligochaeta. Emergence forms an integral part of the life cycle of nearly 70% of the macrofauna. The insect emergence from the exposed zone represented nearly 1.5 kJ m^{-2} or 0.07 g dw m^{-2} total lake surface (Brittain and Lillehammer 1978). Using a production/emergence ratio of 5.4 (see Brittain 1978a) the total insect production in the exposed zone was in the order of $0.4 \text{ g dw m}^{-2} \text{ yr}^{-1}$ in terms of total lake area. However, fish predation is probably considerable in Ø. Heimdalsvatn (Tabs 1, 3), so the ratio of

Tab. 1. Benthic invertebrates – estimated average annual production and average annual amount consumed by the trout. Trout consumption is the average for the period 1969–1972 (Lien 1978a). Units: $\text{KJ m}^{-2} \text{ yr}^{-1}$ ($\text{g dw m}^{-2} \text{ yr}^{-1}$). P = Production, B_E = Biomass at emergence, B = Mean biomass. Terrestrial insects are included, but their share is less than 1%. In estimating production of “other benthic invertebrates” allowance has been made for differences in the energy content per g dw of different food organisms (Lien 1978a).

Taxa	Period of estimation for production	Method for calculation of production	Production	Consumption
<i>Gammarus</i>	1969–1972	Cohort level. (Allen 1951)	8.7 (0.47)	9.1 (0.49)
<i>Lepidurus</i>	1969–1972	Trout consumption (Lien 1978a)	5.5 (0.28)	5.5 (0.28)
Plecoptera, Ephemeroptera, Trichoptera 50% } Chironomidae	1971–1972	Emergence $P/B_E = 5.4 \text{ yr}^{-1}$ (Brittain 1978a)	8.8 (0.37)	4.8 (0.20)
	1970–1972	$P/B = 2.0 \text{ yr}^{-1}$	10.5 (0.44)	4.1 (0.17)
Sub-total			33.5 (1.56)	23.5 (1.14)
Zooplankton				0.2 (0.03)
Other benthic Invertebrates		54(61)% of sub-total	18.1 (0.95)	12.6 (0.70)
Grand total			51.6 (2.51)	36.3 (1.87)

Tab. 2. Selected components of an energy budget for Øvre Heimdalsvatn during 1972 (see text for further explanation).

Energy source	Energy value $\text{KJ m}^{-2} \text{ yr}^{-1}$	Notes
Total solar radiation	3970000	Measured
Net input of solar energy (annual total)	1510000–2300000	Estimated
Phytoplankton production	420–540	Measured
Production of periphytic and benthic algae	210–290	Few measurements
Macrophytes	330–380	<i>Isoëtes</i> measured + 10% for <i>Scorpidium</i>
Total autochthonous plant production	960–1210	
Input of particulate allochthonous organic matter	920	Measured
Total input of allochthonous and autochthonous particulate organic matter	1880–2130	
Export of particulate organic matter	330	Measured
Net input	1550–180	
Permanently sedimented	130	Calculated from cores
Particulate organic matter utilized in the lake	1420–1670	
Zooplankton production	46	Measured and calculated excl. protozoa
Benthic production	51	Measured and calculated excl. protozoa average 1969–1972 (See Tab. 1)
Invertebrate production	97	Excl. protozoa/bacteria
Trout production	7	Measured and estimated

5.4 may be too low. Emergence is also a minimum value as certain species, particularly among the Chironomidae and Trichoptera do not emerge solely at the shore, but also in open water.

The major Ephemeroptera in Ø. Heimdalsvatn are

Leptophlebia vespertina, *L. marginata* and *Siphonurus lacustris*. The first two species are present throughout the winter while *S. lacustris* is primarily a summer species (Brittain 1978a). The dominant plecopteran is *Diura bicaudata*, a carnivore, while the most abundant

herbivorous plecopteran is *Nemoura avicularis* (Lillehammer 1978a). *Limnephilus nigricreps*, *Mystacides azureus*, and *Polycentropus flavomaculatus* are the most common Trichoptera in Ø. Heimdalsvatn (Lillehammer 1978b). Among the Coleoptera, *Deronectes alpinus* occurred in highest densities, but *Platambus maculatus* was the major contributor to the biomass (Brittain 1978b).

The stony and rocky substrata in the exposed zone and the long period of ice cover made biomass estimation difficult (Brittain and Lillehammer 1978). However, estimates were made for Ephemeroptera (Brittain 1978a) and Coleoptera (Brittain 1978b). The ephemeropteran biomass at emergence was about 0.02 g dw m⁻², giving a production in the order of 0.1 g dw m⁻² yr⁻¹. On account of the high larval densities in deeper waters, the mean coleopteran biomass for the whole lake was approximately 0.02 g dw m⁻².

In the deeper water of Ø. Heimdalsvatn the benthos was dominated by *Gammarus lacustris* and Chironomidae. The former usually occurred in greatest densities in the macrophytic zone (Aarefjord unpubl.). For the whole lake the mean biomass was 0.17 g dw m⁻², which represented about 40% of the benthic biomass on the soft bottom. The annual production of *G. lacustris* was about 9.0 KJ m⁻² (Aarefjord unpubl.).

In the exposed zone Mollusca were uncommon. The main species were the gastropods, *Gyraulus acronicus* and *Lymnaea peregra* (Brittain 1978c). The numbers of gastropods decreased with depth, although they were found in the deepest parts of the lake. The Bivalvia occurred in highest densities on soft substrata in the deepest parts of the lake (Brittain 1978c).

Sixty-two chironomid species have been identified from Ø. Heimdalsvatn, a surprisingly high number considering the altitude of the lake (Aagaard 1978). This may be due to the exposed nature of the lake enabling colonisation by both lentic and lotic forms. Orthocladiinae accounted for 52% of the species and 74% of the specimens taken in the emergence traps in the exposed zone were Orthocladiinae. In the exposed zone *Corynoneura lacustris* was the most abundant chironomid (Aagaard 1978). In the lake as a whole *Procladius* was the major genus, accounting for 25% of the biomass.

The mean total chironomid biomass was 0.22 g dw m⁻² (Aarefjord unpubl.).

The most common oligochaetes were *Pelosclex ferox* and *Eiseniella tetraedra* (Aarefjord et al. 1973). The notostracan *Lepidurus arcticus* was also a member of the deep water benthos, although despite it being a major component in the diet of the trout, especially in August (Lien 1978a), very few were taken in benthic samples.

At certain times of the year some of the insects associated with the exposed zone were also present in deeper waters. For example, *Nemoura avicularis* (Plecoptera) occurred down to 9 m during the winter, although emerging at the shore in June (Lillehammer 1978a).

Small Crustacea were common in the parts of the lake where the macrophytes extended to the shore. *Eurycerus lemallatus*, *Sida crystallina*, *Ophryoxus gracilis*, *Polypheumus pediculus* and *Megacyclops gigas* were among the most common. They were not sampled quantitatively but since they occupied small areas in relation to the whole lake their production was probably negligible compared to the planktonic species.

The measured mean benthic biomass, excluding *Lepidurus arcticus*, was 0.48 g dw m⁻². Adding 25%, the share accounted for by *L. arcticus* in the trout's diet, a value of 0.60 g dw m⁻² is obtained. This gives a biomass value of 4–6 g ww m⁻². This lies within the range compiled by Økland (1963) for 13 Norwegian oligotrophic lakes but well below the value given for the mesotrophic Norwegian lake Lille Jonsvatn studied by Solem (1973). However, if the molluscs are excluded the biomasses are more comparable.

Fish

Brown trout *Salmo trutta* was the main fish species in the lake. A small population of minnow *Phoxinus phoxinus* was also observed in increasing numbers during the study period (1969–1973). The fish studies were restricted to the trout, although an investigation of the minnow population is now in progress. The respective annual production of the trout during 1969 and 1970, including spawning, was estimated to 6.77 KJ m⁻² yr⁻¹ and 11.13 KJ m⁻² yr⁻¹ (lake surface) or 0.26 and 0.48 g dw m⁻² lake surface (Lien 1978a).

Tab. 3. The relationship between the energy content (weight in parentheses) of insects (in terms of total lake area) emerging from the exposed zone in Øvre Heimdalsvatn and the amounts consumed by the trout.

Insect taxa	Emergence		Consumed		Emergence/ Consumed	
	1971	J m ⁻² yr ⁻¹ (g dw m ⁻² yr ⁻¹)		1972	1971	1972
		1972	1971			
Chironomidae	904 (0.041)	280 (0.013)	2960 (0.130)	996 (0.044)	0.31	0.28
Ephemeroptera	456 (0.021)	418 (0.019)	916 (0.042)	611 (0.028)	0.50	0.68
Plecoptera	406 (0.017)	67 (0.003)	774 (0.034)	268 (0.012)	0.52	0.25
Trichoptera	335 (0.014)	126 (0.005)	4720 (0.195)	4520 (0.186)	0.07	0.03

The amount of food consumed by the trout population varied between 25.5 and 43.1 KJ m⁻² yr⁻¹ for the period 1969–1972 (Lien 1978a). The most important food items were *Gammarus lacustris*, *Lepidurus arcticus*, Trichoptera and Chironomidae. These groups accounted for 2/3 of the total consumption (Lien 1978a). The rate of food absorption was measured to between 42 and 53% (Lien 1978a). The remainder was returned to the lake as faeces and was then available for decomposers.

Energy studies of prespawning, spawning and spent trout showed energy loss of almost 50% for both sexes during spawning (Lien 1978a). This value includes shedding of roe and milt, reduction of body weight and an additional decrease of specific energy content. However, due to the small number of spawning trout, only 4.5–13% of the total fish production was removed from the lake during the annual spawning.

Production studies of the trout parasites showed that the two cestodes *Cyathocephalus truncatus* and *Proteocephalus* sp. were the most important. However, parasite production only accounted for between 0.1 and 0.2% of the total trout production (Lien 1978a).

Ducks

A total of 10 different duck species were identified on the lake during 1970–1972. Based on duck surveys together with metabolic rate and assimilation efficiency given in literature, the approximate values of food consumption were estimated to 1.26, 0.75 and 0.88 KJ m⁻² yr⁻¹ lake surface in 1970, 1971 and 1972 respectively (Lien 1978b).

Food web

The brown trout is the only organism in Øvre Heimdalsvatn for which we have a detailed knowledge of its diet both in different age classes and during different seasons (Lien 1978a).

The amount of information obtained from other taxa is very variable, owing largely to the following difficulties:

- (1) Most of the animals consumed a wide spectrum of foods. Few were strictly herbivores, detritivores or carnivores.
- (2) Faecal pellets were often reingested by the same individual, the same species and also by other species.
- (3) Gut contents (e.g. soft-bodied organisms) could not always be identified.
- (4) Only a small fraction of the detritus ingested may be assimilated.
- (5) The diet of many species changed with season and age.

Nevertheless, a summary of existing observations from Øvre Heimdalsvatn is given in Fig. 5.

Wetzel (1975) pointed out that dead organic matter was the main energy source for lake's heterotrophic organisms. In an ecosystem such as Ø. Heimdalsvatn with a relatively large input of allochthonous organic matter and a short period for autochthonous primary production, the pool of dead organic matter probably plays an even greater role than is usually the case.

Fine particulate organic matter dominated the seston biomass in the lake (Larsson and Tangen 1975). One of

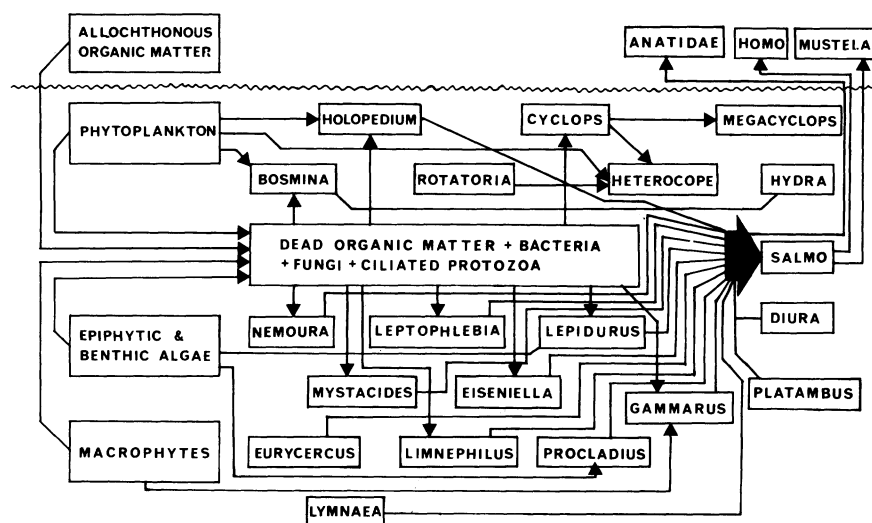


Fig. 5. Selected pathways in the food web documented for Øvre Heimdalsvatn. The primary produced material is grouped into allochthonous organic matter, phytoplankton, epiphytic and benthic algae and macrophytes, while the secondary producers are generally taken to the generic level. The lake surface is indicated and planktonic organisms are placed nearer the surface than the typically benthic organisms.

the two major zooplankton species, *Bosmina longispina*, fed largely on this as demonstrated by microscopical examination of the guts. Laboratory experiments also showed that the species was able to grow and reproduce solely on dead allochthonous particles together with the attached bacteria and protozoa (Larsson unpubl.). The guts of the other major zooplankton species, *Holopedium gibberum*, contained mainly algae, showing that algae were the other important food source in the pelagic zone. It is likely, due to their somewhat non-selective feeding mechanism, that both species ingest both detritus and algae, although clearly in different proportions.

When the upper part of the lake sediments was examined under the microscope it gave the impression that the individual particles were in fact the faecal pellets of invertebrates. Benthic invertebrates, including *Lepidurus arcticus*, chironomids, plecopterans and oligochaetes have been observed to ingest these sedimentary particles (Borgström unpubl., Lillehammer unpubl.) in laboratory studies. Growth in Plecoptera has also been demonstrated on a laboratory diet of their own faecal pellets (Lillehammer unpubl.).

Gammarus lacustris is an important species both as a member of the benthos and as a food organism for the trout. It is known to have a broad spectrum of possible food items (Anderson and Raasveldt 1974). In Øvre Heimdalsvatn, much of its food consisted of macrophytic fragments of both terrestrial and aquatic origin, although epiphytic algae and small crustaceans were also recorded (Borgström unpubl.). The major trichopteran species in Øvre Heimdalsvatn are either detritivores or omnivores (Lillehammer 1978b). *Polycentropus flavomaculatus* an important omnivorous species in the exposed zone consumes detritus. Recently Monk (1976) demonstrated weak cellulase activity in *P. flavomaculatus* and *G. lacustris*, so it is possible that certain members of the lake benthos may be able to utilise dead organic matter directly without it being attached by bacteria or fungi.

Another group for which allochthonous matter is important, is the herbivorous Plecoptera. Several species have their main growth during the winter when dead organic matter is the sole source of plant material (Lillehammer 1978a). Many of the herbivorous Plecoptera in Ø. Heimdalsvatn have been reared in the laboratory through their complete life cycle on a diet of the leaves of terrestrial trees and bushes (Lillehammer 1975b, Saltveit 1977).

The Ephemeroptera in Ø. Heimdalsvatn are herbivorous (Brittain 1978a). The species present as nymphs during the winter as well as during the summer fed mainly on finely divided detritus, although diatoms, other algae and fragments of vascular plants were also present. The species confined as nymphs largely to the ice free period utilised more diatoms and vascular plant material, although detritus was still accounting for about 50% of the gut contents. Although detritus is a major food source for the Ephemeroptera, they do not

accomplish the primary breakdown of terrestrial leaves as do the Plecoptera.

Whereas the gastropods are surface dwellers, grazing on benthic and epiphytic algae, the bivalves burrow in soft substrate filtering out detritus, bacteria, algae and probably Protozoa (Monakov 1972). Therefore bivalves are more common in deeper waters where soft substrata predominate (Brittain 1978c).

There is no doubt that the brown trout was the most important predator in the lake. Almost all animals larger than 0.5 mm occurred in its diet. Only *Hydra* sp. and the minnow *Phoxinus phoxinus* did not appear to be eaten. However, in quantitative terms the trout consumed almost entirely benthic animals, particularly the larger forms. The four main groups were the crustaceans *Gammarus lacustris* and *Lepidurus arcticus*, Trichoptera larvae (mainly *Mystacides azureus* and *Limnephilus nigriceps*) and Chironomidae larvae. These groups accounted for 60–70% of the biomass consumed. In comparison only 2.0% of the diet consisted of zooplankton (Lien 1978a). Trout consumption in relation to invertebrate production will be considered further in the section on dynamics and energy budget.

In the pelagic community two invertebrate predators occurred: *Heterocope saliens* and *Cyclops scutifer*. The calanoid copepod *H. saliens* lived mainly on rotifers and nauplii of cyclopoids during the copepodite stage although diatoms were also frequently found in the guts. *Cyclops scutifer* has been regarded as a facultative carnivore and in Ø. Heimdalsvatn the adults are presumed to eat *Heterocope saliens* nauplii in June.

Megacyclops gigas is a copepod species in which the nauplii are pelagic while the copepodite stages are semibenthic. It is more strictly carnivorous at least in later stages. Copepodite stage V and adults feed on *Cyclops scutifer* copepodites during late winter. This has been documented both from gut analyses and laboratory studies (Larsson 1978). On a single occasion *M. gigas* was found with a half-eaten chironomid in its mouth.

Examples of other benthic predators are the *Platambus maculatus* (Coleoptera) (Brittain 1978b), *Diura bicaudata* (Plecoptera) (Lillehammer 1978a), *Sialis lutaria* (Megaloptera), certain species of Chironomidae (Aagard 1978) and *Hydra* sp.

Vertebrate predation, besides the trout predation, also takes place to some extent e.g. ducks (Lien 1978b). The main predator of the trout is man, although fish-eating American mink *Mustela vison* have been observed by the lake (Lien 1978c).

The benthic communities of the streams-around Øvre Heimdalsvatn were dominated by insects. The species diversity changed with different vegetation zones, decreasing from the subalpine, through the low-alpine to the mid-alpine where only a few species remained, thus reflecting the amount and diversity of allochthonous input (Lillehammer and Brittain 1978). The composition of the benthos in the main inlet and the lake outlet also

reflected the type and amount of food supply available. In the inlet stream winter growing detritivores dominated whereas in the outlet summer growing species several of which were filter feeders, dominated (Lillehammer and Brittain 1978). The presence of filter feeders in the outflow and the fact that it is the main nursery area for the lake trout means that a certain amount of the lake production lost via the outflow is returned in the form of fish biomass. The material not captured by the filter feeders sediments out in the first 500 m of the outflow stream and thus also enters the benthic ecosystem of which the young trout are a part.

Seasonal development

All the individual studies in Ø. Heimdalsvatn showed that there were marked annual patterns in the succession of the organisms throughout the year although recognizable variability in numbers, biomass, growth and production of the various organisms was recorded in the various years. The organisms seemed well adapted to a short but fairly warm summer and eight months of winter and ice cover. The climate also produced distinct seasonal changes with a corresponding response in the ecosystem communities. The rapid change from winter in early May to summer in the middle of June made the development of the individuals in many populations very synchronous.

When the snow cover disappeared from the ice during May, sufficient light penetrated the ice to start primary production. Plant nutrients accumulated during the winter by all the decomposing processes (Kloster 1978) and from May until the middle of June an increasing phytoplankton production was observed. A sudden rise in the phytoplankton production occurred when the ice disappeared at the beginning of June. A similar growth pattern in the other plant communities is probable.

Simultaneously with increasing phytoplankton production in May there was also an increase in the individual growth rate of *Cyclops scutifer* and an increasing reproduction rate in *Kellicottia longispina*. Both were perennial species, which were "on the spot" when the increased primary production commenced. However, the waterflow through the lake also increased during May and a large proportion of the plankton populations were washed out of the lake by the spring spate (Larsson 1978).

The overwintering benthic animals also showed an increase in individual growth during May and early June. This was found for *Gammarus lacustris* (Aarefjord unpubl.) and several insects (Brittain unpubl.).

The course of events in June strongly affect the subsequent development of the ecosystem during the following months. Jensen (1977) found that individual growth rate of trout was best correlated with June temperatures during the various years. In the zooplankton community high and low June temperatures and variations in the severity of the spring spate produced vari-

ations in the initial summer populations and in growth rates. It also affected the number of zooplankton generations (Larsson 1978).

The ice usually breaks up during the first or second week of June at the same time as the spring spate culminates. During the rest of the month there is an increase in water temperature and a decrease in waterflow. Simultaneously with the break up of the ice the resting eggs of the zooplankton hatch. The number of individuals is small and probably does not seriously affect phytoplankton numbers. There seems to be excess food for the zooplankton; the algal biomass is increasing very rapidly, and the standing stock of POD has its annual peak during this period. On a yearly basis the cladocerans are the main predators on the phytoplankton. However, they have very low concentrations in June since only small numbers of resting eggs survive the winter, and they need 3–4 wk of growth before they can reproduce.

In the last half of June the decreasing amounts of nutrients seem to limit phytoplankton growth; and the second cladoceran generation hatches during this period causing a marked increased grazing pressure. This results in a decrease in phytoplankton biomass and production (Fig. 3). Maximum bacterioplankton standing stock occurs a couple of weeks before the zooplankton maximum. Although the biology of the bacterioplankton has not been treated in detail it is obvious that the increase in bacteria is due to increased temperature and the relatively large amounts of available organic material in the water.

Ciliated protozoa also have a rapid increase in biomass during June (Fig. 3) possibly related to the increased bacterial growth. The decrease between the middle of July and beginning of August might have been caused by predation from the second generation of Cladocera.

In the pelagic community there is a stagnation and subsequent decrease in production from the middle of July to the middle of August (Fig. 3). Then, however, there is an increase both in phytoplankton production and in zooplankton reproduction, which may be interpreted as a result of the recycling of plant nutrients. From the middle of September the biomass of all plankton groups usually decreases, and some species from overwintering stages. Only *Cyclops scutifer* showed marked growth in the late autumn months.

In the benthic community major growth both in plants and animals occurred during the ice free period. The largest amounts of epiphytic and benthic algae and macrophytes were found in August/September. Unfortunately there were insufficient measurements to determine at what time in the summer the benthic plant production was highest.

The crustaceans *Lepidurus arcticus* and *Gammarus lacustris* had their main growth during the summer (Lien 1978a, Aarefjord unpubl.) *Lepidurus arcticus* hatched from resting eggs in mid June (Borgstrøm and

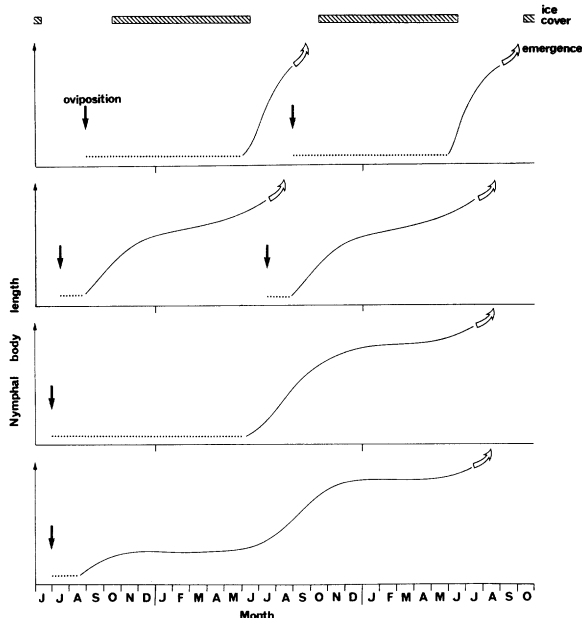


Fig. 6. The four main types of life cycle strategy in the lentic Ephemeroptera and Plecoptera of mountain areas in southern Norway. The dotted lines indicate the egg stage, while the solid lines indicate the nymphal stage.

Larsson 1974) and became adult during August. *Gammarus lacustris* which had a two year life cycle had its main growth during its second and third summer (June–October) (Aarefjord unpubl.).

Among the benthic insects there are several species which spend the winter in the egg stage or in a state of quiescence, and these species grow rapidly during the summer (e.g. *Baetis macani* – Ephemeroptera). However, the growth and production of the benthic insects is not restricted to the ice free period. Certain species, such as *Ameletus inopinatus*, *Leptophlebia marginata* (Ephemeroptera), and *Capnia atra*, *Diura bicaudata* (Plecoptera) have most of their growth during the period of ice cover (Brittain 1978a, Lillehammer 1978a). Their growth is slow during winter, but on account of the long duration (8 months) of the winter the major part of their growth takes place under the ice. Several winter growing species are specialist feeders on allochthonous material, particularly the leaves of terrestrial bushes, and are thus able to obtain sufficient food despite the virtual absence of autochthonous primary production.

The univoltine life cycle predominated among the benthic insects in Ø. Heimdalsvatn. No case of multivoltine life cycle (i.e. more than 1 generation per year) has been definitively documented, probably because of the short ice free period and the low summer temperatures. Only one possible case of a multivoltine life cycle has been found. The emergence pattern of *Corynoneura lacustris* (Chironomidae) suggests that it can have two generations, a winter one and a rapid summer genera-

tion (Aagaard 1978). Semivoltine life cycles were, however, fairly common and examples are known from among the Chironomidae, Trichoptera and Plecoptera.

Emergence characterized the major part of the exposed zone fauna (Brittain and Lillehammer 1978). It was limited to the ice free period, from June to early October. Most emergence had taken place by early September, thus leaving a safety margin in the event of an unusually late season. There were two main peaks in emergence, one soon after the disappearance of the ice composed of winter-growing species and one during late July and August composed of summer-growing species. Both at the order and species level there was a succession in emergence during the ice free period (Lillehammer 1975a, Aagaard 1978, Brittain and Lillehammer 1978, Brittain 1978a, Lillehammer 1978a, b, Brittain 1978e). The emergence of a particular species could occur at different times from year to year, largely as a result of differences in water temperatures in the exposed zone (Brittain 1978e). However, the succession was always maintained. This is of importance for predators such as trout, providing a more or less constant food supply. Insects were most available immediately prior to emergence on account of their increased activity and large size. The amount of insects consumed by the trout appeared to change in response to that available (Tab. 3), indicating the importance of studies encompassing more than one year in such mountain biotopes.

Among the Ephemeroptera and Plecoptera of Norwegian mountain lakes such as Ø. Heimdalsvatn four main types of life cycle strategy can be distinguished (Fig. 6). Two of these are univoltine cycles, while two are semivoltine life cycles. The first strategy, represented by the mayfly *Baetis macani* and several other aestival species, spend the period of ice cover in the egg stage and/or as very small nymphs (Brittain 1974, 1975, 1978a, Lillehammer 1975b, 1976, 1978a). Then nymphal growth, emergence and oviposition all take place during the ice free period. The second type of strategy is the most common and is again a univoltine life cycle. However, the egg incubation period is much shorter, about 1–8 wk. If emergence occurs early in the summer there may be some nymphal growth before ice formation. Nymphal growth then continues throughout the period of ice cover, although often at a much reduced rate. There may be another short burst of growth after ice break before emergence begins. Among the species that have adopted such a strategy are *Leptophlebia vespertina*, *L. marginata* (Ephemeroptera) and *Nemoura avicularis* (Plecoptera) (Brittain 1974, 1978a, Lillehammer 1978a). The stonefly *Diura bicaudata*, like the mayfly *B. macani*, has a long egg incubation period. However, nymphal growth is not completed during the ice free period, but continues throughout the following winter. Thus the total life cycle takes two years (Lillehammer 1978a).

The final type of strategy is illustrated by the stonefly

Nemurella pictetii. Above the tree line the egg incubation period is only slightly longer than species with a strategy of the second type. However, nymphal growth is much slower and takes almost two years (Brittain 1978d). This semivoltine strategy in *N. pictetii* shows that certain species are capable of adopting different strategies under different environmental conditions, as below the tree line including in Ø. Heimdalsvatn itself, *N. pictetii* has a univoltine life cycle that fits into the second category. The ability to change strategies clearly enables the species to colonise a much wider range of habitats than would otherwise be possible within the restraints of a fixed life cycle strategy.

All the Ephemeroptera in Ø. Heimdalsvatn are univoltine, but both the first two types of strategy are represented. *Siphonurus lacustris* and *Baëtis macani* are typical aestival species, while both *Leptophlebia* species have a short egg incubation period and are present as nymphs throughout the winter. As all four species occur in the same habitat there must be advantages and disadvantages in both strategies. The *Leptophlebia* species have the advantage of being able to utilize the autumn and winter for growth, enabling them to emerge early. On the other hand they are more susceptible to trout predation by virtue of their presence throughout the winter and because the trout become conditioned to feeding on them and are slow to switch over to *S. lacustris* and *B. macani* when these appear. In addition, other more attractive food items, such as *Lepidurus arcticus* become available during the summer (Lien 1978a). Many mayflies appear to have an emergence threshold temperature below which they do not emerge. This is probably related to the fact that air temperatures have to be above a certain level before the complex mating flights can take place. Therefore, species such as *Baëtis macani* run the risk that temperatures may fall below the emergence threshold before their emergence is complete.

The two *Leptophlebia* species are both hiemal species, but even their strategies are separated in time. In Ø. Heimdalsvatn *Leptophlebia marginata* was always larger and emerged earlier, thus reducing any possible interspecific competition for food or emergence sites (Brittain 1978a).

During the period of ice cover those insects present as nymphs or larvae occur in two main areas of the lake. There are those more or less restricted to stony substrata in the exposed zone and those found on soft substrata in the deeper parts of the lake. The latter have the advantage of water temperatures 3–4°C higher than in the exposed zone (Brittain unpubl.). However, they are more susceptible to trout predation as the trout prefer higher temperatures and also have difficulty in penetrating the narrow zone of free water in the exposed zone (Lien 1978a). *Mystacides azureus* (Trichoptera) and *Nemoura avicularis* (Plecoptera) are common species on soft bottom in the deeper parts of Ø. Heimdalsvatn during the winter and thus figure extensively in the

trout's diet (Lillehammer 1978a, b). It appears that these two species are dependant on the higher temperatures in order to complete their development. In fact, *N. avicularis* is rarely found above the tree line (Brittain 1974, Lillehammer 1974). In contrast to these two species, *Polycentropus flavomaculatus* (Trichoptera) and *Diura bicaudata* (Plecoptera) are more or less restricted to the exposed zone during the period of ice cover and are therefore rarely taken by the trout. Both these species occur widely at higher altitudes (Brittain 1974, Lillehammer 1974). *Diura bicaudata* also has a semivoltine life cycle in Ø. Heimdalsvatn (Lillehammer 1978a) and the same appears to be true of *P. flavomaculatus*. Therefore the lower temperatures in the exposed zone are probably of less importance for these two species.

Trout spawning took place in September/October chiefly in the outlet, although also in the main inlet stream. The fry hatched the following spring and the young trout stayed on average three years in the streams. No concentrated seasonal migration of young trout from the streams into the lake took place during the ice free season (Lien 1978a). Trout were sampled throughout the whole year, although most of the annual catch was taken during August and September when conditions for gill-netting were most favourable.

The rate of food consumption of trout varied throughout the year with a peak in July and August, although a considerable amount of food was also consumed during the winter (Lien 1978a). The consumption of many of the food items showed distinct seasonal variation during the years 1969–1972. *Lepidurus arcticus* was the dominant food during August with decreasing importance during the autumn and total absence from January to June when in the egg stage. *Gammarus lacustris* was present in the lake throughout the whole year, but was eaten to a lesser degree during the summer than in the rest of the year, probably on account of the greater availability of other food items, such as the insects. The two other major food groups, the Trichoptera and Chironomidae, also showed seasonal variation within the different years studied, but no clear seasonal pattern emerged for the whole four years.

Dynamics and energy budget

Measurements of total radiation and light penetration into the water, estimates of net production of various organisms in the lake, measurements of the input and output of particulate organic matter and estimates of the yearly sedimentation (Tab. 2) provide a basis for a discussion concerning the energy pathways in the lake although a full energy budget cannot be presented.

The phytoplankton production was found to vary between 10 and 13 g C m⁻² yr⁻¹. The production of epiphytic and benthic algae was only measured on a couple of occasions, but was found to be much lower than that of phytoplankton. The total algal production was presumably about 15–20 gC m⁻² yr⁻¹. A similar

situation exists for the macrophytes. *Isoetes* production (biomass accumulation) was measured and found to be $7.7 \text{ gC m}^{-2} \text{ yr}^{-1}$ in 1972, while only biomass data for the end of the growing season are available for the moss *Scorpidium*. The *Scorpidium* biomass was about 15% of that of *Isoetes*. Since the moss was situated deeper than *Isoetes*, a *Scorpidium* production of about 10% of the *Isoetes* production seems reasonable. Thus total macrophytic production was estimated to be about $8\text{--}9 \text{ gC m}^{-2} \text{ yr}^{-1}$. Total primary production would then be about $25\text{--}30 \text{ gC m}^{-2} \text{ yr}^{-1}$, or equivalent to about $960\text{--}1210 \text{ KJ m}^{-2} \text{ yr}^{-1}$.

The total radiation onto the lake was measured continuously using a star pyranometer and found to be close to four million $\text{KJ m}^{-2} \text{ yr}^{-1}$ ($3966000 \text{ KJ m}^{-2} \text{ yr}^{-1}$ in 1972). However, the net input of solar radiation was less and Johannessen (1978) estimated this to be between $1500\,000$ and $2300000 \text{ KJ m}^{-2} \text{ yr}^{-1}$. Thus about 0.5–0.8% of this was converted into plant material available for heterotrophic organisms. This is less than the 1% given as a world mean by Odum (1971). The total amount of primary production is, however, of normal order of magnitude for alpine and arctic lakes (Likens 1975).

In Ø. Heimdalsvatn the additional input of allochthonous organic matter almost doubled to loading of organic particles in the lake. If the amount of outflowing organic particles and the amount of sedimented organic matter is subtracted, the total amount of plant particles utilized by the heterotrophic organisms is about $1420\text{--}1670 \text{ KJ m}^{-2} \text{ yr}^{-1}$.

The multicellular zooplankton contributed $2\text{--}3 \text{ g dw m}^{-2} \text{ yr}^{-1}$ (about $40\text{--}60 \text{ KJ m}^{-2} \text{ yr}^{-1}$, in 1972 $46 \text{ KJ m}^{-2} \text{ yr}^{-1}$) to the secondary production taking place in the lake. From the biomass estimates of the ciliated Protozoa, it might be reasonable to expect a protozoan production of about 50% of the multicellular production. Thus the total zooplankton production would be between 60 and $90 \text{ KJ m}^{-2} \text{ yr}^{-1}$.

An estimate of the total benthic production is given in Tab. 1. Due to various difficulties the production was calculated in different ways. The best estimate was found for *Gammarus lacustris* by calculating production according to cohort development (Boysen Jensen 1919, Allen 1951). For the period 1969–1972 the *Gammarus lacustris* production was on average $0.47 \text{ g dw m}^{-2} \text{ yr}^{-1}$ or $8.7 \text{ KJ m}^{-2} \text{ yr}^{-1}$ (Aarefjord unpubl.). The production of *Lepidurus arcticus* had to be calculated from the trout consumption since it was almost exclusively found in trout stomachs. However, $5.5 \text{ KJ m}^{-2} \text{ yr}^{-1}$ must be an underestimate since production obviously occurred in addition to the part accounted for by trout predation.

The production of the insects emerging from the shore, namely the Plecoptera, Ephemeroptera and some Trichoptera, but minus Chironomidae, was estimated to be $8.8 \text{ KJ m}^{-2} \text{ yr}^{-1}$ by a method by which the emerging biomass was multiplied by a constant of 5.4 (Brittain 1978a).

The largest uncertainty is connected to the estimated chironomid production. Their annual mean biomass was 0.22 g dw m^{-2} or 5.2 KJ m^{-2} . Various P/B ratios have been reported in the literature for chironomids (Mason 1977). However, a P/B ratio of about 2 seems realistic and was used on the results from Ø. Heimdalsvatn. Thus the chironomid production would then be about $10.5 \text{ KJ m}^{-2} \text{ yr}^{-1}$.

In addition there is the production of Nematoda, Oligochaeta, Mollusca, the Trichoptera emerging in open water, Megaloptera, benthic or semi-benthic Cladocera and Copepoda and the benthic microfauna of Rotatoria and Protozoa. In the sampled biomass they represented less than 10% of the other taxa. However, they were not adequately sampled and their share must be greater. In trout stomachs these taxa minus the microfauna represented about 35% of the total diet in terms of calorific content. Although the trout is a selective feeder, not “sampling” representatively, the latter percentage seems more realistic and thus 54% of the sub-total is added to the benthic production figures in Tab. 1 to give the total production of $50.6 \text{ KJ m}^{-2} \text{ yr}^{-1}$. The total multicellular invertebrate production was found to be about $97 \text{ KJ m}^{-2} \text{ yr}^{-1}$. Lien (1978a) found differences in the energy content per gram dw for different food organisms. This has been incorporated into Tab. 1, giving a different percentage (61%) for “other benthic invertebrates” when given in dry weights.

The relationship between production and respiration has been considered by among others McNeill and Lawton (1970), McLusky and McFarlane (1974), Rigler (1975). For Ø. Heimdalsvatn, the results of Rigler (1975) from the arctic Char Lake probably provide the best basis for comparison. The production of zooplankton and zoobenthos should then be multiplied by about 8 and 3 respectively to give total invertebrate assimilation in the lake. This rough estimate of total assimilation gives figures of about $850 \text{ KJ m}^{-2} \text{ yr}^{-1}$. Thus the multicellular invertebrates in Ø. Heimdalsvatn assimilate approximately 1/3 of the organic matter utilized in the lake. The remaining 2/3 is broken down by the benthic protozoa, the bacteria and the fungi in the lake.

The calorific value of the invertebrates consumed by the trout was found to vary between 28.7 and $43.1 \text{ KJ m}^{-2} \text{ yr}^{-1}$ with $36.3 \text{ KJ m}^{-2} \text{ yr}^{-1}$ being the average for the period 1969–1972 (Lien 1978a). The trout consumption was found to be 70% of the estimated production of the benthic invertebrates. Too much cannot be drawn from this situation since the total invertebrate production figure was partly based on the trout consumption. However, looking at the various taxa separately, including those estimated independently of fish consumption (Tab. 1), the fish predation was considerable.

The production of *Gammarus lacustris* was calculated independently of fish consumption and was found to be very similar to the fish predation. *Lepidurus arcticus* was very rarely found outside the trout stomachs, thus indicating very hard predation.

P/B ratios from the literature have been used for the insect's production. The P/B ratios are probably very sensitive to fish predation and it is uncertain as to what degree they are valid for Ø. Heimdalsvatn. However, in this case production and consumption also coincide to some extent (Tab. 1).

A relationship was found between the amount of insects emerging and their consumption by the trout (Tab. 3). For all insect groups lower numbers emerged in 1972 than 1971, at the same time as less insects were consumed by the trout in 1972 than in 1971. This may indicate that the P/B ratios are not very variable. The higher ratios emergence/trout consumption were found in the Ephemeroptera and Plecoptera (Tab. 3). These two groups emerged almost exclusively from the shoreline in Ø. Heimdalsvatn, while a large proportion of the Chironomidae and Trichoptera emerged in open water. Despite this fact, it seems apparent that Trichoptera are selected by the trout in preference to the other insect groups. The figures for Ephemeroptera and Plecoptera indicate that about twice as many nymphs are consumed by trout as manage to emerge from the lake. The selectivity of trout has also been shown at the species level. For example, the mayfly *Leptophlebia vespertina* is clearly a preferred species (Brittain and Lien 1978). However, at certain times for example during the spring spate 1978 which carries with it insect drift, trout may become opportunists (Brittain and Lien 1978).

In 1957 when the trout studies started in Ø. Heimdalsvatn it was an overpopulated lake with stagnation in individual growth (Jensen 1977, 1978). This stagnation was obviously due to a deficit in the amount of acceptable food objects. It is an interesting feature that the population still seems to optimally exploit the benthic invertebrates. The difference is, however, that more of the food intake now goes to fish growth while previously more went into respiration by the larger and heavier population and to more reproductive tissues which is characteristic of overstocking (Sømme 1941).

It might be possible that during overpopulation the trout also exploited invertebrate groups which today are more or less untouched. For instance in the present situation zooplankton predation is very low. In the overpopulated lake zooplankton might have been exploited to a greater degree. However, the question needs more study and trout consumption in an overpopulated, optimal and underpopulated situation should be compared.

If the fish population were reduced to a size where the benthic animals were not fully exploited, interesting results might appear. Would less favourable food items go free of trout predation, or would the predation pressure on the whole benthic community be reduced? Another question would be to what extent invertebrate predators would increase?

After this discussion and speculation some concluding remarks can be made. In a lake where there is such low primary production and the waterflow is so dominant,

the input of organic matter from the surroundings is of overwhelming importance. Only the particulate organic matter have been investigated and with the dissolved organic matter in addition the results would be even more conclusive.

The major part of the plant material synthesized in or permanently brought into the lake is utilized there. The multicellular animals utilize a large proportion, possibly as much as one third. However, the bacteria, fungi and protozoans are probably the most important decomposers in the lake.

The fish in the lake prey effectively on the benthic invertebrates, but the zooplankton, representing more than the half of the invertebrate production, is left almost untouched. Only *Daphnia longispina* might be an exception. This species was extremely abundant in the trout stomachs compared with the lake (Larsson 1978, Lien 1978a). The low densities of *D. longispina* might well be due to fish predation.

If one considers the lake as an isolated system without allochthonous input, the total efficiency of the Øvre Heimdalsvatn ecosystem is reflected in the fact that a total solar radiation of about $4.10^6 \text{ KJ m}^{-2} \text{ yr}^{-1}$ gives rise to a fish production of $6\text{--}11 \text{ KJ m}^{-2} \text{ yr}^{-1}$. An even lower efficiency would be obtained if one took into account the allochthonous input.

Not only does the lake receive seston input from the inflow streams, but also contributes to the outflow ecosystem (Fig. 7). The outflowing seston forms a continuous stream of potential food flowing past the benthos and fish. Filter feeding benthos are particularly able to exploit this food supply. On the basis of drift, benthic and fish studies in the outflow we are able to present a preliminary energy flow diagram for the lake outflow during August (Fig. 7). There were 1688 crustaceans m^{-3} in the outflow water, which fell drastically to 46 m^{-3} after 500 m. Converting to biomass, we find that 770 g dw d^{-1} runs out of the lake, of which 747 g disappears during the first 500 m of the stream. Drifting insects are negligible in the outflow itself, but 500 m downstream about 10 g dw d^{-1} was present. Using the phytoplankton biomass values from the lake, between 1000 and 2500 g dw flows out of the lake daily. In the same way the bacterial biomass was estimated to be 4000 g dw d^{-1} . Knowing the outflow of total seston, we calculated the daily flow of dead particulate organic matter (detritus) to be $6500\text{--}7000 \text{ g dw d}^{-1}$. After 500 m the total seston was reduced to about $10000 \text{ g dw d}^{-1}$. Estimation of benthic biomass is difficult because only semi-quantitative data are available. Therefore, despite August being a month in which much of the insect community is in the egg stage, the estimated benthic production of 30 g dw d^{-1} is clearly a considerable underestimate. During August the benthic algal production is near its maximum and the biomass was between 6.6 and 16.6 g dw m^{-2} . Using the P/B ratio from the lake periphyton this gives a gross production in the first 500 m of the outflow of 750 g dw d^{-1} . The outlet stream is the best spawning

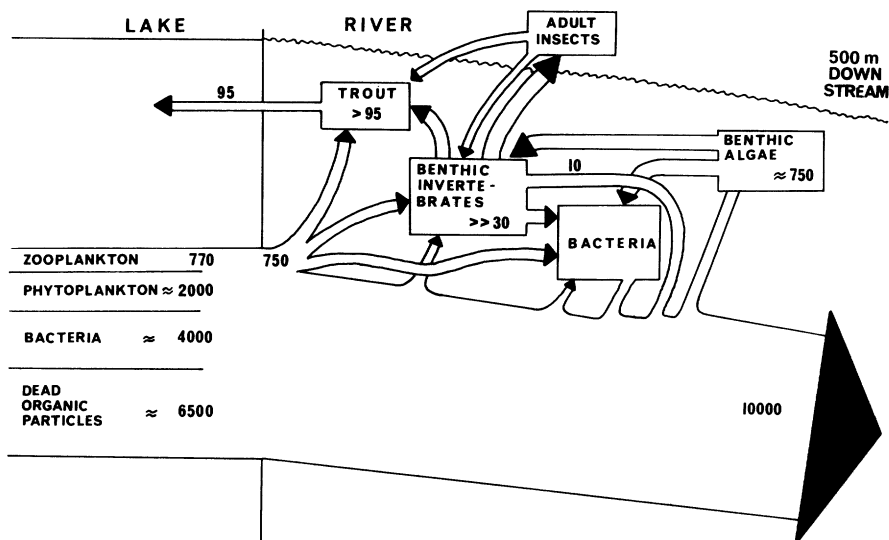


Fig. 7. An energy flow diagram for the first 500 m of the outflow of Øvre Heimdalsvatn during August. Figures are given in g dw d⁻¹.

locality around Øvre Heimdalsvatn and an estimated 26000 g dw yr⁻¹ of young trout enter the lake from the outlet (Lien 1978a). Taking into account seasonal variation in growth rate the average daily input of trout into the lake during August was 175 g dw. Then dividing by the total area over which this is produced, the share of the first 500 m is about 95 g dw d⁻¹.

Regulating factors

The small amounts of plant nutrients, the lake morphology and the cold climate with eight months of ice cover are obviously the dominant factors determining the nature of the lake ecosystem. However, on top of these main regulatory factors other factors modify particular aspects of the system. Of particular significance is the lake hydrology in combination with the terrestrial plant community of the catchment area. The very rapid water renewal in the spring gives the lake a river like nature during this period. The lake receives large amounts of organic material (Larsson and Tangen 1975) simultaneously with the strong removal of the perennial zooplankton species (Larsson 1978). The former makes more food available for the heterotrophic organisms while the removal of the carnivorous copepodite V and adults of *Cyclops scutifer* provides the possibility of a switch to *Heterocope saliens* during the first critical period after hatching from resting eggs.

The temperature development during June was particularly variable from year to year and this variation was found to be of importance for many organisms in the lake. The individual growth rate of trout was higher in years with higher June temperatures (Jensen 1977, 1978). Most of the zooplankton species showed more rapid development in the years when June was warmer and this seemed to be translated into a larger maximum

summer biomass (Larsson 1978). In the insects both June and July temperatures affected the timing of emergence, although in different ways in different orders (Brittain and Lillehammer 1978). Within an order, however, the species succession was maintained from year to year despite different temperature conditions (Brittain 1978a, Lillehammer 1978a, b). The phytoplankton biomass maximum was reached before the end of June and the effect of temperature on this was uncertain (Tangen and Brettum 1978).

The fact that trout was the only fish of importance probably influenced the fauna of the lake. The zooplankton community was left almost untouched by the trout (Lien 1978a) and might have had another structure if there had been a plankton feeding fish in addition. A lower stock of trout might have also given larger populations of *Lepidurus arcticus* and *Daphnia longispina*.

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