

Seasonal and interspecific variation in consumption of Ephemeroptera by brown trout in a subalpine lake

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With 2 figures and 2 tables in the text

Introduction

The subalpine lake, Øvre Heimdalsvatn, has been the subject of interdisciplinary studies under the auspices of IBP/PF. The dynamics and production of the brown trout (*Salmo trutta* L.) have been investigated and a detailed analysis of the trouts' diet throughout the year has been made (LIEN in prep.). At the same time the benthic insects, including the Ephemeroptera (BRITAIN in prep.), have been studied, therefore providing an opportunity to study the relationship between their life cycles and abundance in the benthos and their consumption by the trout.

Øvre Heimdalsvatn is situated at 1090 m a.s.l. in the Jotunheimen Mountains of southern Norway (61°25' N, 8°52' E). The lake has an area of 0.78 km², a maximum depth of 13 m and is 3 km long. It is ice covered from mid-October until the beginning of June.

Materials and methods

Between 1969 and 1972 brown trout were caught, largely by gill-netting, throughout the year. The stomachs of 1588 trout were examined for Ephemeroptera, their numbers counted and then identified to species where possible. Benthic samples were taken and emergence traps set up during the ice free period to determine Ephemeropteran abundance, life cycles and length-weight relationships. Details are given in BRITAIN (in prep.).

Results and discussion

Ephemeroptera were found in 24.6 % of the trout examined. They constituted on average 3.7 % of the trouts' total annual calorific intake (LIEN in prep.), although the proportion varied between 1.6 % in 1972 and 7.7 % in 1970. Ephemeroptera have been found to be the most important food items for brown trout in some Norwegian lakes (e. g. SCHMIDT-NIELSEN 1939; SØMME 1941), while only of minor importance in others (e. g. OLSTAD 1925; KLEMETSEN 1967). However, none of these investigations have been made at the species level. In Øvre Heimdalsvatn Ephemeroptera were consumed in all months, but there was a marked maximum during June and July and a minimum in September (Table 1). Most Ephemeroptera taken were fully-grown nymphs, although during the winter immature nymphs over about 5 mm were taken. Adults were rarely taken, probably because emergence and oviposition took place near the shore (MACAN 1966; BRITAIN in prep.).

There was little difference in the numbers of Ephemeroptera taken by the different trout size groups. The lowest numbers were taken by trout over 500 g, which fed to a greater extent than smaller fish on the crustaceans *Gammarus*

Table 1. Numbers of Ephemeroptera consumed per trout during the period 1969—1972 in Øvre Heimdalsvatn and their share of the trouts' total calorific intake each month.

	J	F	M	A	M	J	J	A	S	O	N	D
<i>L. vespertina</i>	0.16	0.28	0.55	0.45	0.30	9.83	6.30	0.21	0	0	0	0.11
<i>L. marginata</i>	0.30	0.81	0.76	0.28	0.60	2.43	0.22	0	0.01	0.05	0.04	0.33
<i>S. lacustris</i>	0	0	0	0	0	0.02	0.32	0.28	0	0.01	0	0
<i>S. aestivalis</i>	0	0.01	0	0.01	0	0.11	0.03	<0.01	0	0	0	0
<i>Siphonurus</i> spp.	0	0	0	0	0.01	0.02	0.01	0	0	0	0	0
<i>B. rhodani</i>	0	0	0	0	0	0.89	0.04	0	0	0.09	0.01	0.08
<i>B. lapponicus</i>	0	0	0	0	0	0.05	0.03	0.02	0	0	0	0
<i>B. macani</i>	0	0	0	0	0	0.05	0.17	0.07	0	0	0	0
<i>Baëtis</i> spp.	0.02	0	0.01	0	0.09	0.84	0.02	0.02	0	0.01	0	0
Total	0.48	1.10	1.32	0.74	1.00	14.24	7.14	0.60	0.01	0.16	0.05	0.52
% of trouts' total intake	1.4	1.5	1.3	1.6	2.1	12.2	12.9	1.0	<0.1	0.4	0.3	2.2

lacustris Sars and *Lepidurus arcticus* (Pallas). The trout consumed more Ephemeroptera in the western end of the lake. This was probably due to the shallowness of that part of the lake as the Ephemeroptera are more or less restricted to shallow waters in Øvre Heimdalsvatn.

The major species consumed were *Leptophlebia vespertina* (L.) and *L. marginata* (L.), which on a yearly basis accounted for 86 % of the Ephemeroptera consumed (Table 2). They have a short egg incubation period (1—2 months) and are thus present as nymphs for most of the year. On account of its larger size at all times *L. marginata* was the more important during ice cover, while *L. vespertina* dominated as soon as *L. marginata* had begun to disappear from the lake due to emergence (Table 2, Fig. 1).

Table 2. Ephemeroptera recorded in trout from Øvre Heimdalsvatn, together with relative abundance of Ephemeroptera in the benthos and their mean dry wt. immediately prior to emergence.

	Ephemeroptera consumed (total nos)	Ephemeroptera consumed (%)			Benthos (%) June—Sept. (mg)	Dry wt. at emergence
		Yearly basis	Nov.—May (ice cover)	June—Oct. (ice free)		
<i>L. vespertina</i>	2884	68.3	35.6	72.6	36.3	2.13
<i>L. marginata</i>	750	17.8	58.7	12.4	33.7	5.18
<i>S. lacustris</i>	131	3.1	0	3.5	22.4	7.26
<i>S. aestivalis</i>	24	0.6	0.2	0.6	0.9	—
<i>Siphonurus</i> spp.	8	0.2	0.4	0.2	0	—
<i>B. rhodani</i>	187	4.4	3.1	4.6	0	—
<i>B. lapponicus</i>	19	0.5	0	0.5	0	—
<i>B. macani</i>	53	1.3	0	1.4	5.3	1.29
<i>Baëtis</i> spp.	166	3.9	2.0	4.2	0	—
<i>A. inopinatus</i>	0	0	0	0	1.5	2.51

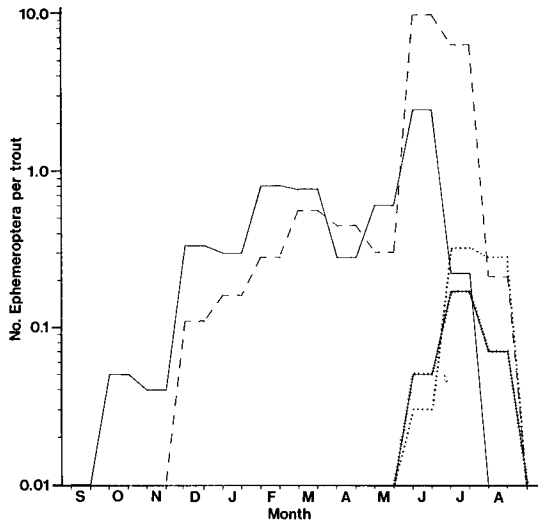


Fig. 1. The mean monthly numbers of the 4 main ephemeropteran species consumed by the trout in Øvre Heimdalsvatn, during the years 1969—72. ——— *L. marginata*, - - - *L. vespertina*, *S. lacustris*, -|-|-| *B. macani*.

Siphonurus lacustris EATON and *S. aestivalis* (EATON) were taken almost exclusively during June, July and August, as during the remaining months they were either in the egg stage or their nymphs were too small to be taken. The other lentic species consumed was *Baëtis macani* KIMMINS, which was also restricted to June, July and August as it spends the winter in the egg stage (BRITAIN 1975).

Two lotic species, *Baëtis rhodani* (PICTET) and *B. lapponicus* (BENGTSSON) were consumed by the trout, indicating either that the trout move into the streams at certain times to feed or that they feed on invertebrate drift coming into the lake. The latter seems more likely as these species were most frequent in trout stomachs during the spring spate which takes place during late May and early June. The maximum proportion of lotic species in the trouts' diet was 8.8%, which assumes that the unidentified *Baëtis* were either *B. rhodani* or *B. lapponicus*. From their life cycles around Øvre Heimdalsvatn it is clear that the *Baëtis* spp. consumed during the winter were *B. rhodani*, but during June, July and August small nymphs of the lentic *B. macani* are present. Trout which had consumed lotic species were captured in association with the inflow streams.

The maximum consumption of all species occurred immediately before or during their emergence period (Fig. 2). This is to be expected as the nymphs are largest then (Fig. 2), are largely day-active (SOLEM 1973) and are migrating towards the shore to emerge. In the two *Leptophlebia* species there was an increase in predation with increase in mean nymphal dry weight, until emergence started to reduce the number of nymphs available (Fig. 2). A similar relationship,

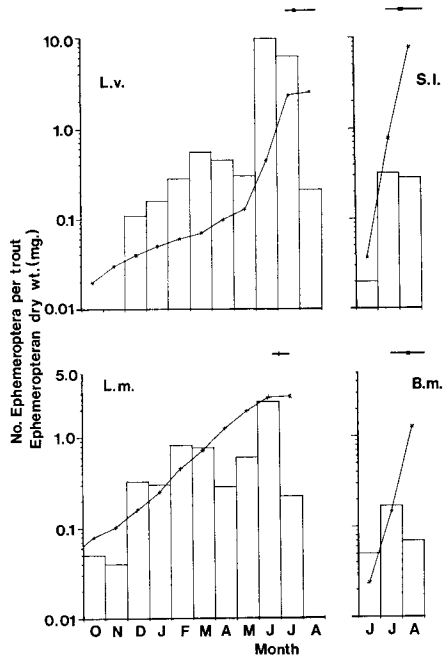


Fig. 2. Mean monthly numbers of the 4 main ephemeropteran species consumed by trout in Øvre Heimdalsvatn, based on the years 1969–72, together with the mean monthly dry weights of the species. The total emergence period and peak emergence are indicated (1971 and 1972) for each species. L. v. - *L. vespertina*, L. m. - *L. marginata*, S. l. - *S. lacustris*, B. m. - *B. macani*.

although more condensed in time, was found in *S. lacustris* and *B. macani* (Fig. 2).

The seasonal variation in species composition of the trouts' diet has been explained by differing ephemeropteran life cycles. However, their relative abundance in trout stomachs is not the same as their abundance in the benthos (Table 2). Certain investigations (e. g. NILSSON 1955; BALL 1961) have shown that trout feed on what is available with little or no selection, while others (e. g. ALLEN 1938; HUNT & JONES 1972) have shown clear selection for particular taxa. In Øvre Heimdalsvatn the trout clearly select certain taxa (LIEN in prep.). Some ephemeropteran species would also appear to be "preferred". During the ice free period *L. vespertina* is such a species as its share of consumption (73 %) is much higher than its benthic abundance (36 %) would suggest. In contrast *S. lacustris* is more abundant in the benthos than in the trouts' diet (Table 2), which is surprising as it is a large species when mature. However, it spends the winter in the egg stage or as very small nymphs and it has a very rapid summer growth. Therefore the nymphs are only over 0.05 mg dry weight during July and August. During July *L. vespertina* is still abundant and is clearly preferred, while during August the very attractive *Lepidurus arcticus* is present. It would seem that the trout become used to feeding on a particular species or genus, such as *Leptophlebia* on account of their presence throughout the winter, making the switch to *Siphonurus* more difficult.

Ameletus inopinatus EATON was not found in trout stomachs, although recorded in the benthos. It is, however, an uncommon species in Øvre Heimdalsvatn and may not reach sufficiently high numbers to be selected by the trout.

Leptophlebia spp. were one of the major items consumed by the brown trout introduced into an English moorland fishpond (MACAN 1966), although it was demonstrated that predation had little effect on the numbers attaining maturity. In contrast ELLIOTT (1967) found that in an English stream Leptophlebiidae were the only common members of the benthos and drift not recorded in trout stomachs. This suggests that there may be a hierarchy of species preferred by brown trout and that a particular species may be preferred in one locality and not in another, depending on the potential prey species present.

Summary

From 1969 to 1972 stomachs of 1588 brown trout (*Salmo trutta* L.) from Øvre Heimdalsvatn, Norway, were examined for Ephemeroptera. Emergence periods, nymphal densities, growth and length/weight regressions were determined for the Ephemeroptera, which were found in 24.6% of the trout. They constituted 3.7% of the trouts' total annual calorific intake. Ephemeroptera were most abundant and constituted a higher proportion of the trouts' calorific intake during June and July. Adults were rarely taken, most being mature nymphs. On a yearly basis *Leptophlebia vespertina* (L.) and *L. marginata* (L.) accounted for 68.3% and 17.8%, respectively of the Ephemeroptera consumed. Seasonal changes in the proportions of these species are examined in relation to their life cycles. Other significant species were *Baëtis rhodani* (PICTET) (4.4%), *Siphonurus lacustris* EATON (3.1%) and *Baëtis macani* KIMMINS (1.3%). The relative importance of ephemeropteran species was different during the ice free period (June-October) and during ice cover, largely because of their life cycles and relative sizes. Lotic species, *B. rhodani* and *B. lapponicus* (BENGTSSON), were consumed mainly during the spring spate. Comparison with benthic densities indicates that *L. vespertina* is a preferred species, while other seemingly attractive species, on account of large size and relatively high density (e. g. *S. lacustris*), were underrepresented in trout stomachs.

Acknowledgements

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