MAYFLY STRATEGIES IN A NORWEGIAN SUBALPINE LAKE

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ABSTRACT

Mayfly ecology was studied in the lake, Øvre Heimdalsvatn, 1090 m a.s.l. in the Jotunheimen Mountains. Life cycle, winter growth, biomass, nutrition, predation, emergence and fecundity are considered. The four main species have adopted different strategies - *Baetis macani* has opted for low mortality and rapid summer growth, *Siphlonurus lacustris* for large size and high biomass, *Leptophlebia vespertina* for high density and *L. marginata* for winter growth. Each strategy has its disadvantages, but they enable coexistence in spite of the environmental restrictions imposed by a long period of lake ice cover and a short summer.

INTRODUCTION

The ecology of mayflies (Ephemeroptera) was studied in the subalpine lake, Øvre Heimdalsvatn as part of multidisciplinary ecosystem study under the auspices of IBP/PF. Some data have been published earlier on Ephemeroptera of this lake (Brittain 1974, 1978, 1979; Brittain and Lien 1978, Brittain and Lillehammer 1978, and Larsson *et al.* 1978). The aim of the present paper is to consider the life cycle strategies employed by the major ephemeropteran species in Ø. Heimdalsvatn by synthesising data from the above studies supplemented by new information on fecundity.

There are four major species in the lake: *Leptophlebia marginata* (L.), *L. vespertina* (L.), *Siphlonurus lacustris* Eaton and *Baetis macani* Kimmins. *Siphlonurus aestivalis* Eaton, *Ameletus inopinatus*

Eaton and *Baetis rhodani* (Pictet) have also been recorded. However, they have not been considered here as they only constitute 1-4% of the emerging mayflies (Brittain 1978).

HABITAT DESCRIPTION

Øvre Heimdalsvatn is siutated at 1090 m a.s.l. in the Jotunheimen Mountains of central southern Norway. It has a surface area of 0.78 km^2 a maximum depth of 13 m and is ice-covered from October until early June. During June there is a relatively rapid rise in temperature and lake temperatures generally remain between 10 and 14°C during the latter part of June, and in July and August. During this period the shallow waters of the lake, where Ephemeroptera are most abundant, can reach 20°C.

METHODS

Field sampling of nymphs and adults, together with a description of sampling sites and laboratory methods treated in this paper are described in detail in Brittain and Lillehammer (1978). Methods used in the predation analysis are given in Brittain and Lien (1978).

Fecundity, defined as the total number of eggs per female, was estimated from subimago material using a Sedgewick-Rafter cell (Clifford and Boerger 1974). One quarter of the total field was counted, except for *B. macani* where all eggs were counted. Subimago material was taken within two days of peak emergence for the species in question. Densities and fecundities are expressed in terms of total lake area in m^2, in order to compare values with other ecosystem components. However, the Ephemeroptera are more or less restricted to the shallow waters of Øvre Heimdalsvatn which only account for about 18% of the total lake area (Aarefjord *et al.* 1978). Therefore, when comparing values with other studies, especially those carried out in lotic habitats, this fact should be taken into account.

RESULTS AND DISCUSSION

All four major species are univoltine, but their strategies differ markedly (Fig. 1, Table 1). There is a progression from *L. marginata* in which nymphs are present for about 10 months of the year and in which nearly 60% of total nymphal growth is accomplished during the period of ice cover, to *B. macani* where nymphal growth is restricted to 2-3 months during the summer. *L. vespertina* has a similar life cycle to *L. marginata*, although emerging later and having only about 30% of its growth under the ice. *S. lacustris*, despite its more or less delayed egg hatching, is primarily a summer species, most of its nymphal growth being accomplished between ice break and

Table 1. Selected parameters of the ephemeropteran populations in Øvre Heimdalsvatn.

	L. marginata	*L. vespertina*	*S. lacustris*	*B. macani*
% of growth under ice	58	30	23	0
Consumed by trout (nos/m^2/year)	2.97	11.39	0.52	0.22
Av. indiv. wt at maturity (mg dw)	5.2	2.1	7.3	1.3
Nymphal biomass prior to emergence (mg dw/m^2)	4.34	6.94	7.86	1.03
C.V. of body length in pre-emergence popln.	15.1	14.1	27.7	17.1
Emergence peak 1971	3 Jul.	29 Jul.	9 Aug.	12 Aug.
1972	29 Jun.	23 Jul.	1 Aug.	10 Aug.

emergence in August.

These differences in nymphal growth strategy are reflected in emergence periods (Table 1). There is a succession in emergence of all the ephemeropterans in Øvre Heimdalsvatn (Brittain 1978). This succession is maintained from year to year despite changes in lake temperature (Brittain 1979).

The biometric variation in the pre-emergence nymphal populations can provide further information on strategies (Ulfstrand 1975). The delayed hatching in *S. lacustris* is clearly reflected in the high coefficient of variation in body length (Table 1). Maintenance of a coherent cohort in *B. macani* is perhaps not surprising as it has such a short period of nymphal growth and ice break-up appears to be the factor associated with egg hatching in this species (Brittain 1975). In the two *Leptophlebia* species the reduction in growth rate during the winter may operate in a regulatory manner.

The differences in nymphal growth periods are also reflected in their nutrition. All four species are herbivores. However, while detritus dominated in the two *Leptophlebia* species, vascular plant material in *S. lacustris* and diatoms in *B. macani* were almost as important as detritus.

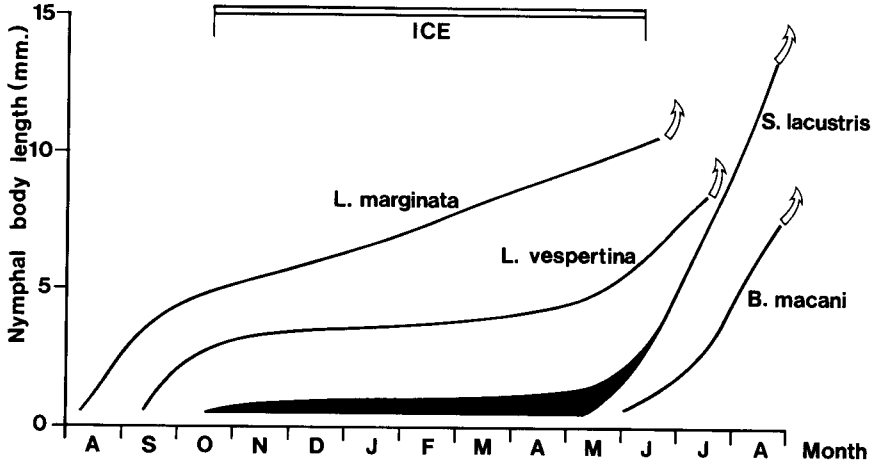

Figure 1. Nymphal growth of the major mayfly species in Øvre Heimdalsvatn. Emergence of each species and the period of lake ice cover are indicated.

Size is an important factor in ecological segregation. In Ø. Heimdalsvatn the four main species differ in their size at maturity and also throughout their nymphal lives (Fig. 1). *S. lacustris* is by far the largest of the four with a mean individual dry weight at maturity of 7.3 mg. In contrast nymphs of *B. macani* weigh only 1.3 mg. Such differences in nymphal size are important when considering biomass. For instance the nymphal biomasses of *S. lacustris* and *B. macani* prior to emergence were 7.86 and 1.03 mg/m^2 dry weight respectively (Table 1). By virtue of its large size, *S. lacustris* has a similar biomass to *L. vespertina*, the most abundant ephemeropteran in Ø. Heimdalsvatn.

The number of eggs required to produce an adult insect is also a measure of success and gives an indication as to whether the species inhabits a favourable environment (Clifford and Boerger 1974). The four main species in Ø. Heimdalsvatn differ in their fecundity and the subsequent survival of the eggs and nymphs (Tables 2 and 3). Clifford and Boerger (1974) and Benech (1972) showed that adult size is a major factor determining fecundity. Therefore it is not surprising to find that *S. lacustris* has the highest and *B. macani* the lowest fecundity of the four species. Degrange's (1960) data for *S. lacustris* and *L. vespertina* are similar to the values from Ø. Heimdalsvatn, although the range is greater in the present material. The fecundity of *B. macani* is exceptionally low, even when its small size is taken into account. The other three species produce about 120-130 eggs per mm body length, while *B. macani* produces only 30 eggs per mm body length.

However, if the number of eggs required to produce one adult is considered, the picture changes radically. Mortality from egg to imago is far greater in *S. lacustris* than in *B. macani* with the two *Leptophlebia* species occupying an intermediate position (Table 3).

Table 2. Fecundity and body length in mayfly subimagos (10 of each species examined) from Øvre Heimdalsvatn.

	Fecundity		Av. body length (mm)	No. eggs/mm body length
	Range	Av. no.		
L. marginata	600-2020	1380	10.7	129.0
L. vespertina	640-1832	1079	8.7	124.0
S. lacustris	624-2792	1740	13.2	131.8
B. macani	129-258	201	6.8	29.6

The oviposition behaviour in *Baetis* in which the female lays her eggs on the substratum rather than scattering them over the water surface may considerably reduce egg mortality. Also, *B. macani* by its presence as a nymph for only a short period largely avoids trout predation (Table 1). It is also able to utilise the peak biomass of benthic and epiphytic algae while the two *Leptophlebia* species are in the egg stage. Unlike the other three species *B. macani* is not at or near its altitudinal limit. The *Leptophlebia* species are rare above the subalpine vegetation belt and *S. lacustris* usually occurs in low numbers in the low alpine (Brittain 1974). In contrast *B. macani* can occur in high densities in both low and mid-alpine localities (Brittain 1974, 1975). Nevertheless, if one compares these values with Clifford and Boerger's data (1974) all four major species in Ø. Heimdalsvatn can be considered to be living in a more or less favourable environment.

Thus, in summary, the four main species in the subalpine lake Øvre Heimdalsvatn, appear to have adopted different approaches: *B. macani* has opted for low mortality and rapid summer growth, *S. lacustris* for large size and high biomass, *L. vespertina* for high density and *L. marginata* for winter growth. Each strategy carries with it disadvantages, but the adoption of differing strategies enables these four species to coexist in spite of the environmental restrictions imposed by a long period of ice cover and a short summer.

Table 3. Egg and adult mayfly densities in Øvre Heimdalsvatn.

	Av. no. eggs per female	Total no. females emerging /m^2/year	Total no. eggs /m^2/year	Total no. males and females emerging /m^2/year	No. eggs required to produce 1 adult
L. marginata	1830	0.380	524.4	0.833	630
L. vespertina	1079	1.382	1491.2	3.232	461
S. lacustris	1740	0.576	1002.2	1.077	931
B. macani	201	0.409	82.2	0.797	103

RESUME

L'écologie des éphéméroptères a été etudiée dans le lac Øvre Heimdalsvatn, situé a 1090 m d'altitude. Le cycle saisonnier, la croissance en hiver, la biomasse, la nourriture, la prédation, l'emergence et la fécondité ont tous été considerés. Les quatres espèces les plus importantes ont adopté des stratégies individuelles: *Baetis macani* a choisi la mortalité basse et la croissance rapide en été, *Siphlonurus lacustris* la grande taille et la biomasse importante, *Leptophlebia vespertina* la grande densité et *L. marginata* la croissance en hiver. Chacune de ces stratégies ont des désavantages, tout en permettant la coexistence malgré les restrictions du milieu imposées par de longues periodes de gel et des étés courts.

ZUSSAMENFASSUNG

Die Ökologie der Eintagsfliegen im See Övre Heimdalsvatn 1090 m ü.m. im Gebirge Jotunheimen, wurde studiert. Lebenslauf so wohl als Winterwachstum, Biomasse, Ernährung, Predation, Auftauchen und Fecunditet wurden in Betracht gezogen. Vier Arte von Eintagsfliegen haben verschiedene Strategien entwickelt um zu überleben. *Baetis macani* hat niedrige Mortalitet und raschen Sommerwachstum, *Siphlonurus lacustris* hat Grösse und viel Biomasse, *Leptophlebia vespertina* hat hohe Densitet und *L. marginata* hohen Winterwachstum. Jede dieser Strategien hat ihre Nachteile, aber sie erlauben Koexistence trotz der Restrictionen der Umgebung; lange Eisperioden und kurzer Sommer.

REFERENCES

Aarefjord, F., J.E. Brittain and A. Lillehammer. 1978. The benthos of Øvre Heimdalsvatn. *Holarct. Ecol.* 1: 219-220.

Benech, V. 1972. La fécondité de *Baetis rhodani* Pictet. *Freshwat. Biol.* 2: 337-354.

Brittain, J.E. 1974. Studies on the lentic Ephemeroptera and Plecoptera of southern Norway. *Norsk ent. Tidsskr.* 21: 135-154.

Brittain, J.E. 1975. The life cycle of *Baetis macani* Kimmins (Ephemerida) in a Norwegian mountain biotope. *Ent. scand.* 6: 240-244.

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

Brittain, J.E. 1979. Emergence of Ephemeroptera from Øvre Heimdalsvatn, a Norwegian subalpine lake. p. 115-123. *In:* K. Pasternak and R. Sowa ed. Proceedings of the Second International Conference on Ephemeroptera, August 23-26, 1975. Panstwowe Wydawnictwo Naukowe, Warszawa.

Brittain, J.E. and L. Lein. 1978. Seasonal and interspecific variation in consumption of Ephemeroptera by brown trout in a subalpine lake. *Int. Ver. theor. angew. Limnol. Verh.* 20: 728-733.

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

Clifford, H.F. and H. Boerger. 1974. Fecundity of mayflies (Ephemeroptera), with special reference to a brown-water stream of Alberta, Canada. *Can. Entomol.* 106: 1111-1119.

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

Larsson, P., J.E. Brittain, L. Lien, A. Lillehammer and K. Tangen. 1978. The lake ecosystem of Øvre Heimdalsvatn. *Holarct. Ecol.* 1: 304-320.

Ulfstrand, S. 1975. Diversity and some parameters of Ephemeroptera and Plecoptera communities in subarctic running waters. *Arch. Hydrobiol.* 76: 499-520.