The Life Cycle of *Baëtis macani* Kimmins (Ephemerida) in a Norwegian Mountain Biotope

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Abstract

The life cycle and aspects of the biology of *Baëtis macani*, a species restricted to Fennoscandia, are described from a small lake and its outflow at 1330 m a.s.l. near Finse, Norway (60°36′ N, 7°30′ E). Additional data are presented from Øvre Heimdalsvatn, a subalpine lake in the Jotunheim mountains (61°26′ N, 8°52′ E). At Finse the ice free period lasts only 3 1/2 months

during which time nymphal development and emergence occur. It is probable that after winter diapause egg hatching occurs at the end of June in connection with the rise in temperature at ice break. Nymphal growth is rapid. Emergence begins in mid-August, reaches a peak during early September and continues until the beginning of October, shortly before ice forms again.

Introduction

Baëtis macani Kimmins was collected by Bengtsson as early as 1907 (Müller-Liebenau 1969), but it was not until 1957 that the species was described (Kimmins 1957, Macan 1957). Subsequently both nymphs and adults have been studied from a taxonomic viewpoint and included in the key to the European species of Baëtis (Müller-Liebenau 1969). Baëtis macani is closely related to B. vernus Curtis and the imagos differ little, it only being in the nymphs that there are significant differences. Baëtis macani also appears to have affinities with the recently described Canadian species B. bundyi (Lehmkuhl 1973). The two species can be distinguished in the nymphal stage, the only one so far described for B. bundyi, by differences in the labial palps and in body length (Lehmkuhl — personal communication).

Distribution

Baëtis macani is restricted to Fennoscandia and it has not hitherto been recorded south of 59°45′ N. It has been found as far north as Utsjoki (69°45′ N) in northern Finland (Bagge 1965). It occurs over 1000 m in the mountains of southern Norway (Brittain 1974), but further north and east it has been found at much lower altitudes, almost down to sea level. It occurs in both lentic and lotic habitats

throughout the greater part of its range, often with the greatest densities in and around lake outflows.

Habitat description

The life cycle and biology of B. macani was investigated in a small lake (lake 8 in Brittain 1974) and its outflow stream at an altitude of 1330 m a.s.l. near Finse, Norway (60°36' N, 7°30' E). The Finse area lies on the northern edge of the Hardanger glacier (Hardangerjøkulen) and experiences a climate strongly influenced by its proximity to Norway's western seaboard. Precipitation is about 1200 mm per year and combined with the cool summers (Fig. 1) results in a short ice free period. The habitat studied is situated just within the maximum glacial extension of 1750 and its formation is probably the result of processes associated with the formation of the terminal moraine. Today it is about 850 m from the nearest arm of the glacier. The catchment area of the lake is extremely small as it lies on a ridge and most of the inflowing water originates from snow beds in the immediate vicinity.

Although the lake lies in the middle alpine region, scattered bushes of dwarf willow (Salix) occur around the lake. Parts of the outflow are covered by cotton grass (Eriophorum). The substratum is variable on account

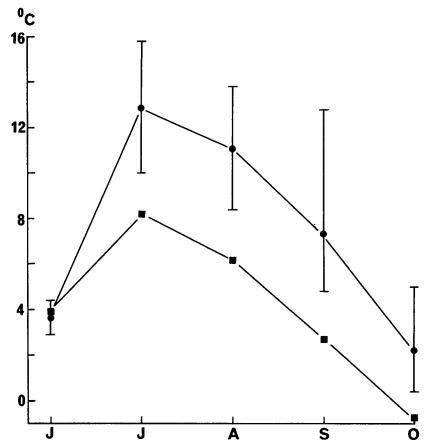


Fig. 1. Mean monthly temperatures at Finse (1224 m a.s.l.) during period 1971—73 (\blacksquare — \blacksquare) and range and mean of daytime spot water temperature readings in the investigated lake and outflow (\blacksquare — \blacksquare)

of the differential deposition of clay and silt.

The lake is ice free for about 3 1/2 months a year and during this period mean values for the following chemical parameters were: Ca⁺⁺ 4.1 mg/1, Mg⁺⁺ 1.2 mg/1, κ_{18} 25.1 μ mhos, pH 7.2 and KMnO₄ consumption 0.4 mg/l (Brittain 1974).

Methods

The pool and the outflow area were sampled from July 1971 to October 1973 during the ice free periods. The first two years' sampling only yielded half grown and older nymphs, although much adult material was obtained. In 1973 samples were taken fort-

nightly during the ice free period in order to follow nymphal development more closely.

Samples were taken using a hand net (mesh 0.5 mm) either by sweeping through the aquatic vegetation or by "kicking" the substratum. The net contents were then sorted in the field and the nymphs preserved in 3% formalin. Imagos and sub-imagos were collected under stones by the water's edge where they congregate and from the adjacent vegetation by sweep netting. On each sampling occasion water temperature was measured and the values obtained are summarised in Fig. 1.

Nymphs and adults were measured in the laboratory to the nearest 0.1 mm. Body length was taken from the front of the head to the

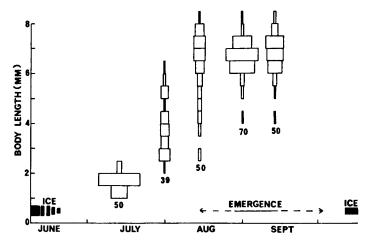


Fig. 2. Nymphal growth and emergence of *B. macani* at Finse. Nymphs are in 0.5 mm size groups and the number measured on each occasion is given. The ice free period is also indicated.

base of the cerci, while wing length was from the tip of the wing to its base on the thorax.

Results and discussion

The eggs of *B. macani* are similar to those described for other *Baëtis* species (Degrange 1960, Bohle 1969). The eggs from Finse were larger than those of the closely related *B. vernus* (Bohle 1969). They were oval in shape and had mean dimensions of $190 \times 250 \ \mu m$. In addition the eggs were covered by a transparent gelatinous layer 80 μm thick, presumably for attachment to the substratum.

Attempts to rear the eggs of B. macani have so far proved unsuccessful and so the egg incubation period must be deduced from other sources. Bohle (1969) found that the eggs of B. vernus did not hatch below a temperature of 3.6°C. The eggs also displayed a degree of freezing tolerance, which may be necessary for the eggs of B. macani at Finse. Thus if such a temperature control exists in B. macani, hatching would not take place at Finse until the ice begins to break up at the end of June. Throughout the winter temperatures probably lie near 0°C. and certain areas in the outlet stream may even freeze. If the nymphal growth curve (Fig. 2) is extrapolated backwards, hatching would have occurred in association with ice break. Thus it appears likely that some embryonic development occurs immediately prior to ice formation in the autumn and the winter is then spent largely either in a stage of diapause or of retarded development (Bohle 1969). With the onset of the rise in temperature associated with ice break development begins again and the eggs hatch soon afterwards.

Nymphs first appeared in collections during the middle of July, 3-4 weeks after ice break. At that time most of the population was between 1 and 2 mm in length. Growth then proceeded rapidly during the following month, with emergence beginning in mid-August. The rate of growth expressed as a percentage of the final length was greatest during the second half of July and the first half of August, the period with the highest air and water temperatures (Fig. 1). Although air temperatures were recorded 2.5 km from the lake it appears that the spot daytime water temperature readings are more indicative of maximum than mean temperatures in the lake and its outflow. Availability of food could also be important for growth. Preliminary gut analyses indicate that B. macani is a herbivore and that detritus, vascular plant material and diatoms form the major part of its diet. Detritus is no doubt present throughout the ice free period, but vascular plant material, both from terrestrial and semi-aquatic vegetation, will be most abundant immediately after ice break. Algae are, however, generally most abundant in Au-

Table 1. Body lengths and v	wing lengths of	adult B.	macani from I	Finse.
All lengths are in mm.				

		Sub-imagos		Imagos	
		♂	P	♂"	P
Body length	$ar{\mathbf{x}}$	6.21	6.58	6.43	6.69
	S.D.	0.59	0.77	0.54	0.65
	Range	5.0-7.4	5.5-8.3	4.8—7.6	5.5—8.1
	n	27	40	31	17
Wing length	x	6.60	6.80	6.85	7.32
	S.D.	0.47	0.70	0.54	0.54
	Range	5.6—7.4	5.9-8.3	6.07.8	6.7—8.3
	n	27	40	31	17

gust (Strøm 1926). Nevertheless, the absence of other mayfly species and the general paucity of the fauna may result in there being no significant competition for food.

At Finse emergence extends from mid-August to the beginning of October reaching a peak during early September. Emergence is curtailed by the formation of ice around the middle of October. However, few, if any, nymphs of *B. macani* do not succeed in emerging before this deadline. Emergence does not seem to be restricted by low water temperatures as emergence was observed when the water temperature was only 3.5°C. This is perhaps a necessary adaptation in the event of a colder than average summer.

Table 1 gives the body lengths and wing lengths of adults collected from Finse during the period 31 August—2 September 1972. It can be seen that the females are on average longer, both in the sub-imaginal and imaginal stage. The wing length of the females is also greater than that of the males. The sex ratio differs little from 1: 1. In a stream in northern Sweden emergence occurred around midday and egg laying mainly in the evening (Thomas 1970). Observations at Finse indicate a similar pattern.

Data on the life cycle of B. macani are also available from Øvre Heimdalsvatn, $(61^{\circ}26' \text{ N}, 8^{\circ}52' \text{ E})$, a subalpine lake at 1060 m in the Jotunheim mountains (Brittain 1974). The climate around Øvre Heimdalsvatn is not as severe as at Finse and the ice free season extends from the beginning of June to the middle of October. The growth pattern is

similar to that at Finse, but the whole life cycle is moved forward, no doubt as a result of the earlier ice break. By the 6—9 July the mean length in Øvre Heimdalsvatn was 2.22 ± 0.38 mm (S.D.), compared with a mean length at Finse on 13 July of 1.58 ± 0.26 mm. Emergence also commenced earlier from Øvre Heimdalsvatn, extending from late July to the beginning of September with a peak during the first half of August. In northern Sweden emergence has been recorded during July and August (Ulfstrand 1969, Thomas 1970).

Thus *B. macani* is able to complete the major part of its life cycle, nymphal growth and development, within 3 months. Temperatures during the period of ice cover are probably too low to permit nymphal growth so use must be made of the short ice free season. The related Canadian species *B. bundyi*, an inhabitant of tundra ponds, has a similar life cycle (Lehmkuhl 1973). A short developmental cycle utilizing the relatively high temperatures prevailing during the short ice free period is clearly of advantage and enables *B. macani* to colonize habitats where other mayfly species are unable to survive.

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