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NORSK ENTOMOLOGISK FORENING

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Oxygen consumption, caloric values, water and ash content of some dominant terrestrial arthropods from alpine habitats at Finse, south Norway

SIGMUND HÅGVAR & EIVIND ØSTBYE

Hågvar, S. & Østbye, E. 1974. Oxygen consumption, caloric values, water and ash content of some dominant terrestrial arthropods from alpine habitats at Finse, south Norway. *Norsk ent. Tidsskr.* 21, 117–126.

Caloric values, water and ash content, and oxygen consumption are given for some dominant invertebrate species (mostly Coleoptera) from alpine habitats at Finse, south Norway, about 1200–1400 m a.s.l. Mean caloric values ranged from 5228 to 6365 cal/g dry weight, and the ash content varied from 2.9 to 6.3 % of the dry weight. In several Coleoptera species, the water percentage decreased markedly with increasing dry weight. The water weight in mg per animal first increased, then decreased, with increasing dry weight. It is anticipated that these changes are caused by a higher percentage of fat being accumulated with increase in dry weight. Oxygen consumption was measured at 5°, 10°, 15°, and 20° C. Active specimens in some cases showed an oxygen consumption several times higher than resting specimens. Different stages in the development (eggs – larval stages – pupae – imagines) can show very different levels of oxygen consumption. Therefore, temperature variations in the natural habitat, the length of each developmental stage, and the activity pattern must be taken into consideration when calculating the respiration of a specimen of a given species under natural conditions.

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To get a picture of the energy flow through alpine communities, the main factors in the energy budget of the dominant species must be studied. This work presents data on oxygen consumption, caloric values, and water and ash content of some dominant alpine invertebrate species in south Norway. The animals were collected in different alpine habitats between 1200 and 1400 m a.s.l. at Finse, situated in the north-western part of the Hardangervidda mountain plateau (60°36'N – 7°30'E).

This paper is part of an analysis of a high mountain ecosystem. The authors shared the planning of this study and the sampling of the material. The treatment of the data and the main task of writing was the responsibility of the first author.

MATERIAL AND METHODS

Animals used for measuring oxygen consumption were either collected immediately before the experiment or stored at outdoor tempera-

tures for one or a few days. Measurements were made at 5°, 10°, 15° and 20°C, the temperature being kept within $\pm 0.1^\circ\text{C}$ by submerging the respirometers into a 50 l water/glycerol bath containing a cooler and a thermomixer. In most of the experiments, a modified type of volumetric respirometers was used (Scholander & Iversen 1958). A constant pressure respirometer (Engelmann 1963) was used for some measurements of respiration at different developmental stages of *Zygaena exulans* Hochw. at 20°C. When using this type, a control respirometer without animals was run at the same time to record effects due to changes in the atmospheric pressure during the experimental time.

During the experiments, the activity of the animals was noted. The data presented in the following figures and tables refer to animals which showed very little or no movement at all during the experiments. Animals which were clearly active often showed a much higher respiration, and these are treated separately in this presentation.

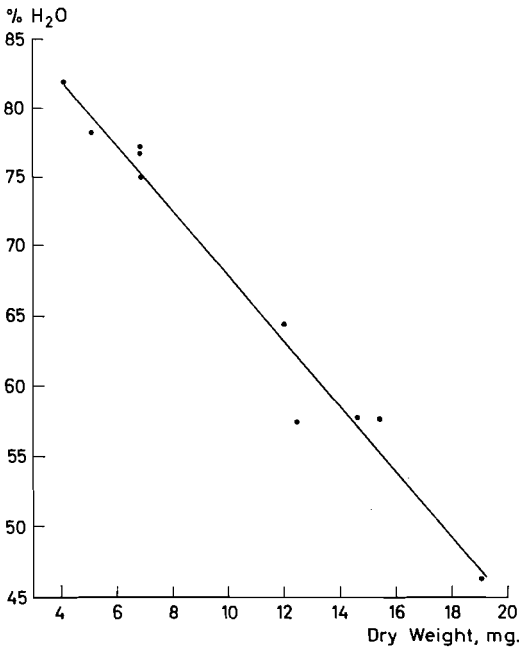


Fig. 1. Correlation between dry weight and water percentage in *Nebria gyllenhalii*. Regression line: $Y = 91.53 - 2.35 \times (r = 0.986)$.

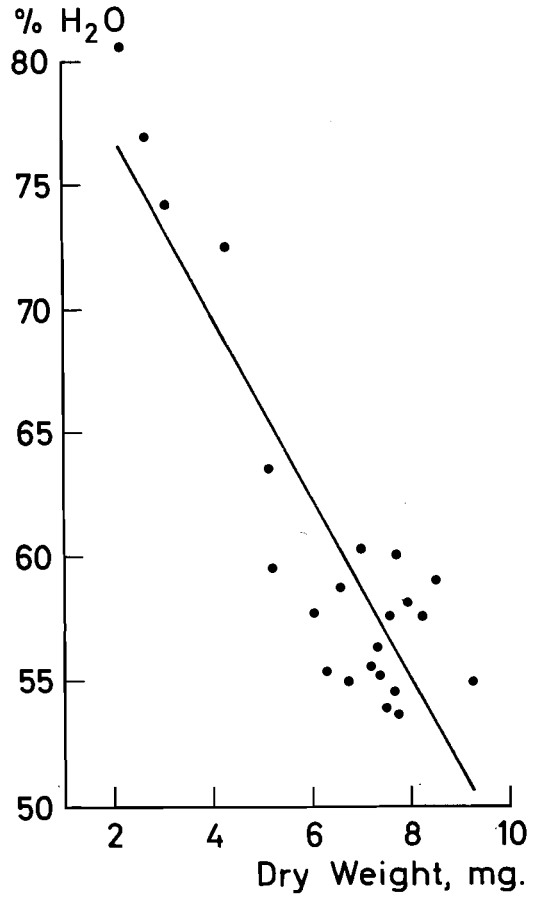


Fig. 3. Correlation between dry weight and water percentage in *Patrobus assimilis*. Regression line: $Y = 84.35 - 3.67 \times (r = 0.889)$.

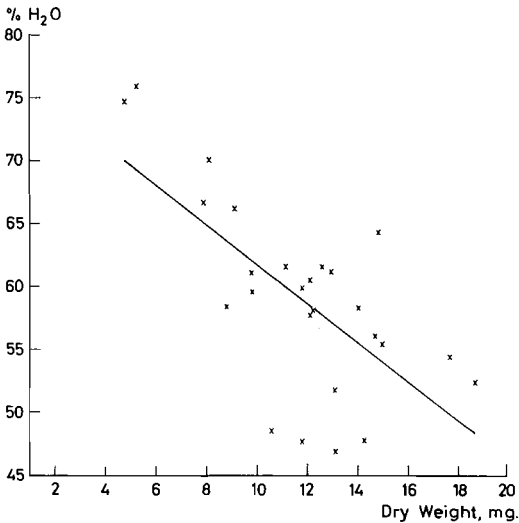


Fig. 2. Correlation between dry weight and water percentage in *Nebria nivalis*. Regression line: $Y = 77.58 - 1.57 \times (r = 0.678)$.

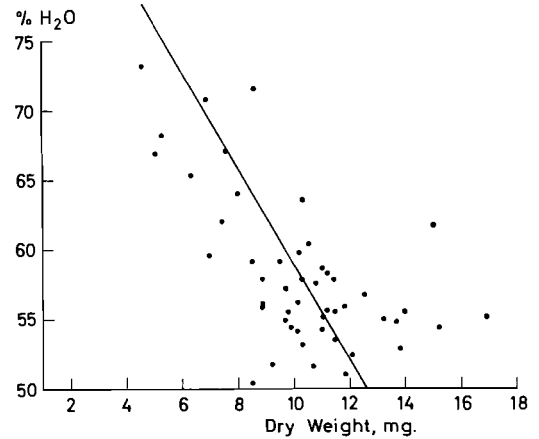


Fig. 4. Correlation between dry weight and water percentage in *Patrobus septentrionis*. Regression line: $Y = 93.90 - 3.49 \times (r = 0.610)$.

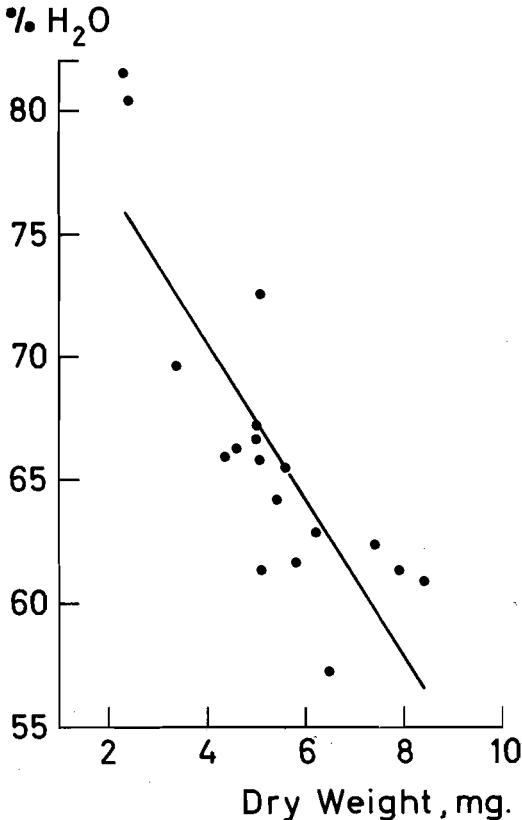


Fig. 5. Correlation between dry weight and water percentage in *Calathus melanocephalus*. Regression line: $Y = 83.35 - 3.21 X$ ($r = 0.820$).

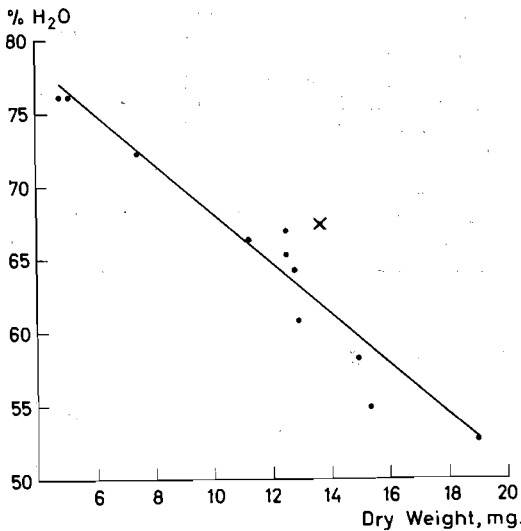


Fig. 6. Correlation between dry weight and water percentage in *Otiorrhynchus dubius*. X marks mean value of four animals treated together. Regression line: $Y = 85.20 - 1.70 X$ ($r = 0.943$).

The oxygen consumption is given as ml O_2 per g fresh weight per hr. In this study the body weight *before* the experiment is used.

Animals used for determination of water content and caloric values were weighed and frozen at Finse. Only animals weighed before freezing could be used for the determination of water content, because animals lost water while frozen.

Caloric values were achieved by using a microbomb-calorimeter (Phillipson 1964) connected to a recording potentiometer with copper-constantan thermocouples. Before measuring, the apparatus was calibrated using benzoic acid of known caloric value. 43 measurements gave a standard deviation (SD) which was 3.3% of the mean value. The animals were dried and homogenized, and small pills of dried material, mostly 10–20 mg, were completely burned.

Ash content, given as per cent of the dry weight, was achieved by completely burning larger samples of dried animals (100–200 mg) at 500°C.

RESULTS

Figs. 1–9 illustrate the correlation between water percentage and dry weight for imagines of the following species of Coleoptera: *Nebria gyllenhali* Schnh., *N. nivalis* Payk., *Patrobis assimilis* Chd., *P. septentrionis* Dej., *Calathus melanocephalus* L. (Carabidae), *Otiorrhynchus dubius* Ström (Curculionidae) and larvae, pupae and imagines of *Zygaena exulans* Hochw. (Lep.). In all cases, except imagines of *Z. exulans*, water percentage decreased with increasing dry weight, this trend being especially pronounced among the Coleoptera. The water percentage also decreased with increasing fresh weight, although this correlation may be less pronounced.

One sample of about 550 eggs from *Z. exulans* contained 76.8% water. This percentage is similar to that of larvae.

Fig. 10 shows the relation between dry weight and water weight in the Coleoptera investigated, based upon the regression lines in Figs. 1–9. This figure reveals that when dry weight increases, the water weight first increases, then decreases.

Table I gives a survey of the ash content

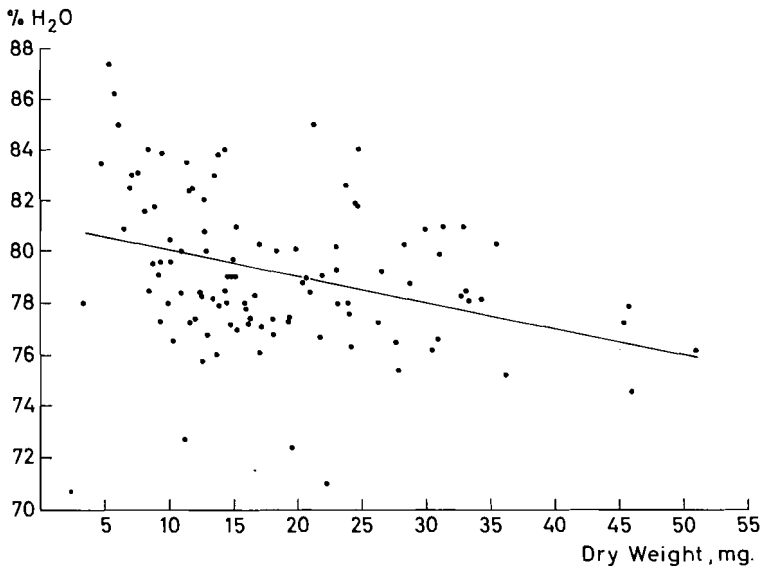


Fig. 7. Correlation between dry weight and water percentage in larvae of *Zygaena exulans*. Regression line: $Y = 81.07 - 0.10 \times$ ($r = 0.341$).

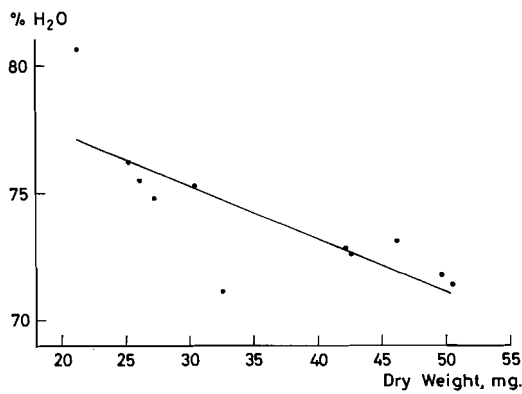


Fig. 8. Correlation between dry weight and water percentage in pupae of *Zygaena exulans*. Regression line: $Y = 81.44 - 0.21 \times$ ($r = 0.789$).

Table I. Ash content in per cent of dry weight for some dominant invertebrate species. n = number of samples. When there are two or more samples, the mean value, SD and minimum- and maximum values are given.

	n	\bar{X}	SD	Min/Max
<i>Mitopus morio</i>	1	5.35		
<i>Nebria gyllenhali</i>	1	3.92		
<i>Nebria nivalis</i>	2	2.89	0.07	2.84/2.94
<i>Patrobis septentrionis</i>	1	3.25		
<i>Calathus melanocephalus</i>	2	4.45	1.06	3.70/5.20
<i>Melasoma collaris</i>	8	4.61	0.96	3.30/6.24
<i>Otiorrhynchus dubius</i>	1	4.24		
<i>Zygaena exulans</i>				
larvae	3	4.79	0.55	4.24/5.33
pupae	1	6.25		
imagines ♂	2	5.66	0.91	5.02/6.30
imagines ♀	7	4.77	0.57	4.30/5.56

of some species. The coleopterous species had the lowest ash content, while *Mitopus morio* Fabr. (Opiliones) and larvae, pupae, and imagines of *Z. exulans* showed the highest values.

Table II shows caloric values for different species. Most values are given both as cal/g dry weight and as cal/g ash-free dry weight. All the mean values of the first category, except eggs of *Z. exulans*, lie between 5000

and 6000 cal/g. However, as seen from the maximum and minimum values, there can be a considerable variation between samples within the same species.

Oxygen consumption at different temperatures is listed in Table III. The mean values may differ considerably between imagines of different species at the same temperature. The mean values of different developmental stages within the same species may also differ

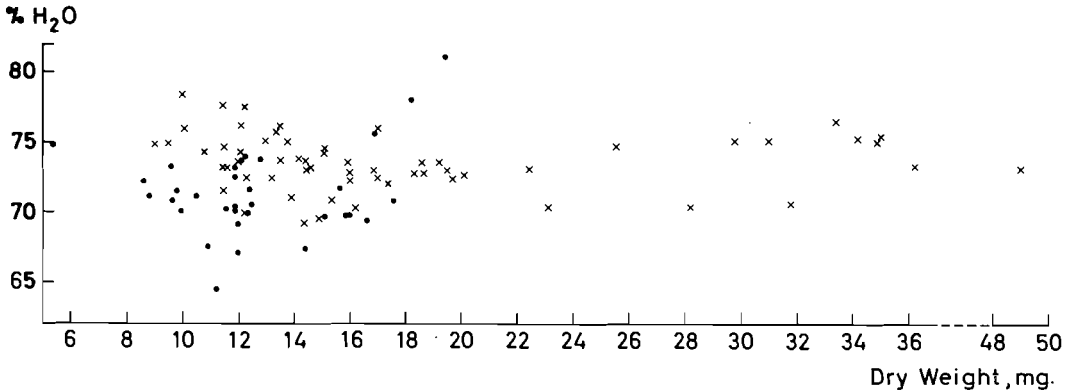


Fig. 9. Correlation between dry weight and water percentage in imagines of *Zygona exulans*. X = females, dots = males.

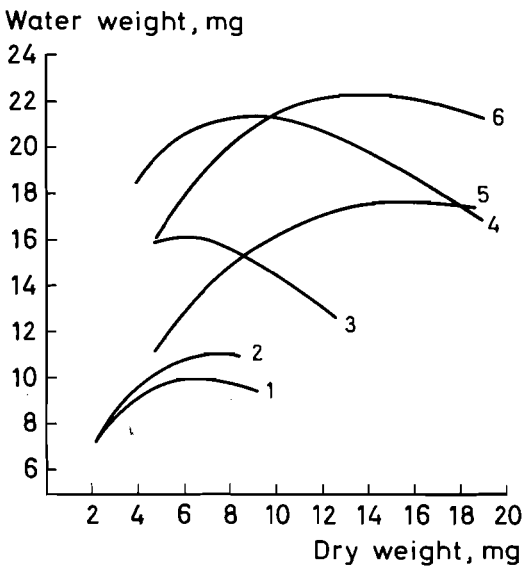


Fig. 10. Correlation between dry weight and water weight in six species of Coleoptera. The curves are based upon the regression lines in Figs. 1-6. 1 = *Patrobis assimilis*, 2 = *Calathus melanocephalus*, 3 = *Patrobis septentrionis*, 4 = *Nebria gyllenhalii*, 5 = *Nebria nivalis*, 6 = *Otiorrhynchus dubius*.

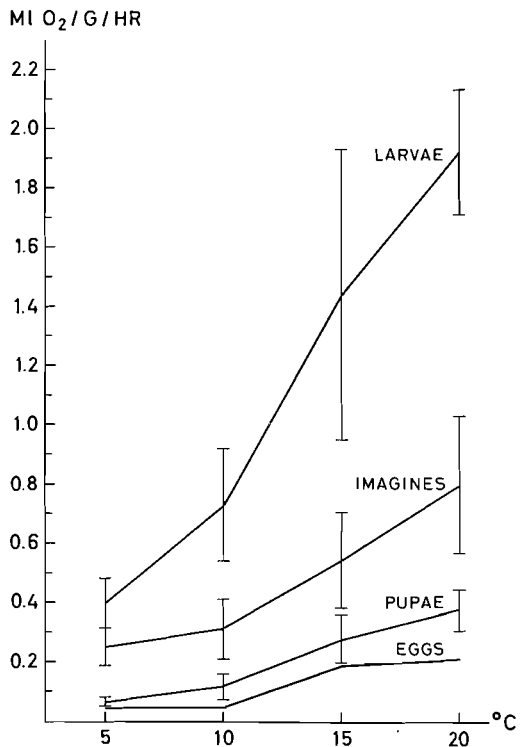


Fig. 11. Respiration rates in different developmental stages of *Melasoma collaris*, measured at 5, 10, 15 and 20°C. The mean values together with the SD values are given. Table III gives the exact values.

widely. This is visualized for *Melasoma collaris* L. (Col., Chrys.) and *Z. exulans* in Figs. 11 and 12. Mean values for imagines of all species at different temperatures are depicted in Fig. 13, thus comparisons between species can easily be made.

Animals which were active during the experiments in some cases showed a much higher oxygen consumption than the highest

Table II. Caloric values per g dry weight and per g ash-free dry weight for some dominant invertebrate species n = number of samples. Mean values are given together with SD values and minimum- and maximum values

Species	n	cal/g dry weight			cal/g ash-free dry weight		
		\bar{X}	SD	Min/Max	\bar{X}	SD	Min/Max
<i>Mitopus morio</i>	10	5342	137	5086/5474	5650	150	5452/5814
<i>Nebria gyllenhali</i>	10	5913	133	5629/6039	6155	138	5860/6287
<i>Nebria nivalis</i>	15	5633	241	5179/6037	5827	214	5368/6217
<i>Patrobis septentrionis</i>	6	5408	363	5001/5889	5590	375	5171/6087
<i>Calathus melanocephalus</i>	3	5335	23	5308/5348	5584	24	5555/5597
<i>Melasoma collaris</i>	10	5685	280	5271/6201	5960	294	5526/6501
<i>Otiorrhynchus dubius</i>	7	5228	197	5000/5467	5459	206	5220/5707
<i>Zygaena exulans</i>							
eggs	2	6365	47	6331/6398			
larvae, 3-15 mg dry	5	5573	83	5483/5684			
larvae, 15-30 mg dry	5	5637	162	5390/5818			
larvae, 30-51 mg dry	5	5828	209	5632/6145			
larvae, total	15	5679	186	5390/6145	5965	195	5661/6454
pupae	11	5521	314	4958/5880	5890	335	5289/6271
imagines	10	5795	134	5571/6078	6114	141	5878/6413

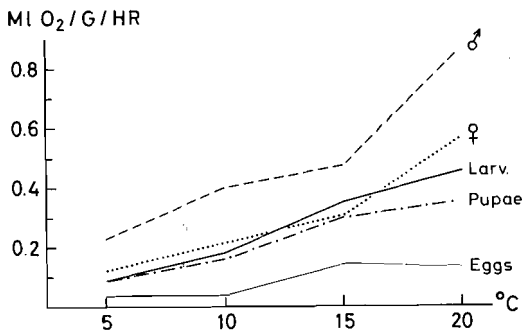


Fig. 12. Respiration rates in different developmental stages of *Zygaena exulans*, measured at 5, 10, 15 and 20°C. Only the mean values are drawn. Table III gives more information.

values listed at each temperature in Table III. Such high recorded values are listed in Table IV.

DISCUSSION

The caloric values of the species investigated lie within the range of most earlier investigations among invertebrates (e.g. Golley 1961, Slobodkin & Richman 1961, Willner 1972, Hofsvang 1973). For some of the species the difference between the lowest and the highest value is rather large. As the caloric value of dried animal tissue is mainly dependent on

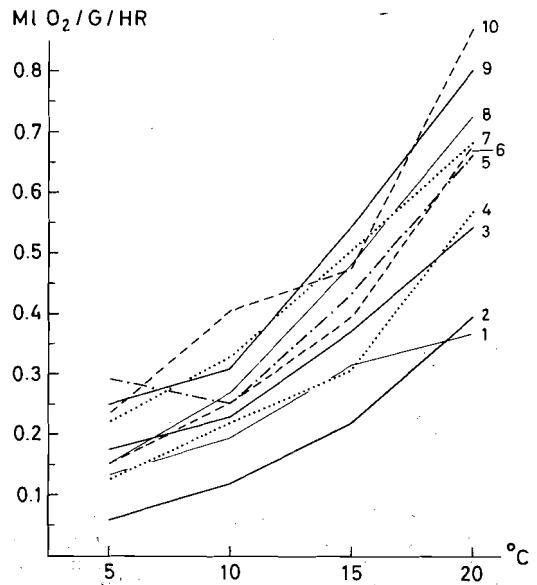


Fig. 13. Mean values of oxygen consumption for imagines of different invertebrate species at 5, 10, 15 and 20°C. 1 = *Otiorrhynchus dubius*. 2 = *Amara alpina*. 3 = *Nebria nivalis*. 4 = *Zygaena exulans* ♀. 5 = *Calathus melanocephalus*. 6 = *Patrobis septentrionis*. 7 = *Nebria gyllenhali*. 8 = *Mitopus morio*. 9 = *Melasoma collaris*. 10 = *Zygaena exulans* ♂.

the fat content (Skar et al. 1972), it is reasonable that the caloric value will vary according to age, sex, and season. These factors

Table III. Oxygen consumption given in ml/g/hr of different invertebrate species at 5°, 10°, 15° and 20° C. n = number of animals. The mean values are given together with the standard deviation (SD) and the minimum and maximum values recorded. All animals were inactive during the experiments.

Species	5° C				10° C				15° C				20° C			
	n	\bar{X}	SD	Min. Max.	n	\bar{X}	SD	Min. Max.	n	\bar{X}	SD	Min. Max.	n	\bar{X}	SD	Min. Max.
<i>Mitopus morio</i>	12	0.154	0.045	0.100 0.247	12	0.270	0.050	0.168 0.382	11	0.477	0.078	0.365 0.611	6	0.729	0.096	0.618 0.865
<i>Nebria gyllenhali</i>	20	0.221	0.088	0.107 0.391	23	0.330	0.144	0.123 0.675	22	0.504	0.137	0.325 0.874	16	0.684	0.240	0.373 1.304
<i>Nebria nivalis</i>	19	0.175	0.066	0.058 0.316	26	0.229	0.087	0.087 0.455	25	0.371	0.066	0.277 0.543	22	0.543	0.220	0.278 1.130
<i>Patrobus septentrionis</i>	18	0.152	0.071	0.027 0.272	18	0.253	0.062	0.114 0.350	24	0.397	0.139	0.175 0.706	20	0.679	0.230	0.359 1.236
<i>Calathus melanocephalus</i>	7	0.294	0.082	0.137 0.365	5	0.251	0.032	0.200 0.283	7	0.434	0.109	0.263 0.548	7	0.665	0.166	0.530 1.015
<i>Amara alpina</i>	6	0.059	0.037	0.032 0.131	9	0.120	0.028	0.083 0.180	10	0.219	0.062	0.148 0.342	12	0.396	0.103	0.284 0.689
<i>Melasoma collaris</i> , imago	8	0.251	0.058	0.183 0.343	20	0.312	0.101	0.196 0.590	9	0.546	0.158	0.304 0.774	6	0.803	0.231	0.523 1.161
<i>M. collaris</i> , pupae	9	0.062	0.014	0.038 0.086	12	0.113	0.041	0.047 0.154	13	0.274	0.082	0.172 0.448	13	0.373	0.073	0.288 0.462
<i>M. collaris</i> , larvae	10	0.393	0.084	0.263 0.508	9	0.730	0.191	0.470 1.092	8	1.440	0.490	0.730 1.991	6	1.922	0.213	1.544 2.140
<i>M. collaris</i> , eggs	100 ¹	0.041			100 ¹	0.043			100 ¹	0.189			100 ¹	0.210		
<i>Otiorrhynchus tubius</i>	7	0.135	0.032	0.088 0.173	10	0.193	0.046	0.130 0.260	6	0.316	0.124	0.213 0.552	7	0.371	0.099	0.228 0.496
<i>Zygaena exulans</i> , ♂	8	0.232	0.081	0.153 0.388	13	0.404	0.234	0.213 0.944	10	0.473	0.162	0.284 0.759	11	0.868	0.316	0.342 1.399
<i>Z. exulans</i> , ♀	15	0.125	0.041	0.071 0.209	20	0.218	0.053	0.136 0.317	10	0.306	0.058	0.222 0.386	18	0.570	0.151	0.333 0.791
<i>Z. exulans</i> , pupae	4	0.084	0.010	0.071 0.092	4	0.158	0.013	0.138 0.165	4	0.299	0.039	0.260 0.350	10	0.356	0.112	0.175 0.496
<i>Z. exulans</i> , larvae	13	0.084	0.045	0.023 0.174	12	0.183	0.066	0.088 0.288	5	0.351	0.159	0.174 0.603	22	0.453	0.175	0.184 0.825
<i>Z. exulans</i> , eggs	150 ¹	0.037			150 ¹	0.036			150 ¹	0.144			325 ²	0.129	0.041	0.086 0.198

¹ One sample

² Four samples

Table IV. Oxygen consumption given in ml/g/hr at 5°, 10°, 15° and 20° C for some active specimens of different invertebrate species

Species	5° C	10° C	15° C	20° C
<i>Nebria glylhenhali</i>	0.520, 0.672	0.873	1.035	1.328
<i>N. nivalis</i>	0.430, 0.840 0.857			
<i>Patrobis septentrionis</i>		0.521	0.770	
<i>Calathus melanocephalus</i>		0.394	0.600	
<i>Amara alpina</i>	0.172	0.272, 0.350	0.446, 0.576	
<i>Otiorrhynchus dubius</i>				0.499, 0.609 0.791 2.283
<i>Melasoma collaris</i> , larva				
<i>M. collaris</i> imago	0.501			
<i>Zygaena exulans</i> ♂			0.914, 1.287 2.229, 2.264	1.503, 1.568 1.745, 2.049 2.429, 2.603 2.885, 3.282
<i>Z. exulans</i> ♀		0.447		

were not taken into consideration during the sampling of the material presented here. The high caloric content in eggs of *Z. exulans* indicates a high fat content.

The ash content is lower than that found in bird species (Ricklefs 1967, Myrcha & Pinowski 1969, Skar et al. 1972). This difference is probably caused by the presence of bone tissue and feathers in birds. The order of magnitude of the ash content in the present material corresponds to earlier studies among invertebrates (Wiegert 1965, Klekowski et al. 1967, Hofsvang 1973).

All the coleopterous species investigated (imagines) showed a clear decline in the water percentage with increasing dry weight. According to Szwykowska (1969), Skar (1969), and Skar et al. (1972), a correlation exists between a high fat content and a low water percentage in animal tissue. It must be anticipated that the increase in dry weight of adult Coleoptera is correlated with an increased percentage of fat, relatively little new water being added. Correspondingly, Klekowski et al. (1967) found that in the last larval instars of *Tribolium castaneum* (Hbst.), an increase in caloric content was correlated with a decrease in water percentage.

As shown in Fig. 10, the marked decline in water percentage when dry weight increases results in a decreasing water weight when the dry weight exceeds a certain value. In larvae and pupae of *Z. exulans*, however, the decline in water percentage is so small that a similar effect is not achieved.

Imagines of *Z. exulans* showed a very stable water percentage even though the dry weight varied markedly. This is probably explained by the fact that the body weight of this species does not increase after hatching, and no fat reserves are built up. On the contrary, the body weight of both males and females decreases markedly after hatching. Evidently the animals only ingest small amounts of food (probably nectar), keeping the water percentage constant and keeping the body weight above a certain value. These conditions are easily explained by the life cycle, the population hatching almost simultaneously on warm days, swarming, copulating, and laying new eggs within a few days. There is no need for this species to build up a fat reserve, contrary to coleopterous species which depend on a certain amount of activity to allow the sexes to meet, and probably also to develop their reproductive organs. Furthermore, many coleopterous species hibernate as adults and need to build up a fat reserve before hibernation.

The very small reduction in water percentage among larvae of *Z. exulans* when dry weight increases indicates that the fat content does not increase much during the larval development. This is verified through the caloric values for larvae of different dry weight groups (Table II). There is a slight increase in caloric content when dry weight increases, but the difference is significant only between the first and third group (t -test, $0.95 < p < 0.98$). At least this holds for the

summer season. According to Tullgren et al. (1941), it is possible that *Z. exulans* has a two-year life cycle. This would imply one or two hibernations for the larvae, perhaps including an accumulation of fat before winter.

It is reasonable that pupae should also show a slight decrease in water percentage with increasing dry weight, representing fully developed larvae of different weights. However, after hatching, the water percentage becomes remarkably stable for different weight groups. There is no clear difference between the sexes – the males perhaps have slightly lower values.

The oxygen consumption increases markedly from 5° to 20°C, in most cases following a slightly exponential trend. The variation within each temperature may be considerable for a given species. This is mainly probably caused by differences in the physiological state of animals, as only animals which are motionless or show very little movement during the experiment were used for calculations of the mean values. The listing of values for clearly active animals shows that respiration may increase manyfold during activity. In *N. nivalis*, very active animals at 5°C might have an oxygen consumption almost five times higher than animals at rest. This fact shows that when calculating the oxygen consumption of an individual during natural conditions, both temperature variations in the habitat, the length of each developmental stage, and the activity pattern of the animal must be taken into consideration.

The mean values recorded for resting animals at different temperatures correspond mainly with earlier data from arctic arthropods (e.g. Scholander et al. 1953).

In a study on the aerobic and anaerobic metabolism of the carabid beetle *Pelophila borealis* Payk. at Finse, Conradi-Larsen & Sømme (1973) found a respiration rate in summer that was similar to the values we have recorded for *A. alpina*. In an earlier work, Østbye (1963) recorded twice as high respiration rates for *N. nivalis* as found in this study. The rates for *N. gyllenhalii* in his study were similar to those recorded here, except for those at a temperature of 10°C, where he found the values doubled.

Both beetles in his study showed the same

pattern of oxygen uptake with little or no increase in consumption rate in the temperature range between 10° and 20°C. Their optima of temperature preference were found to be within the same temperature range, thus indicating a stabilizing mechanism for metabolism in this range. Schmidt (1956) observed corresponding regulation levels in oxygen uptake in experiments on transpiration, oxygen consumption, and preferred temperatures in some *Carabus* species. These regulation levels, however, were relatively small. In the present study, such regulation levels may have been overlooked, because of too large intervals between the temperatures at which the respiration rates were measured.

Respiration data from eggs, pupae, larvae and imagines in *M. collaris* and *Z. exulans* show that the oxygen consumption per gram and hour may vary markedly during development.

In both species eggs have the lowest respiration rate at all temperatures. The two species differ much concerning the oxygen consumption of larvae. The mean value for *M. collaris* larvae at 5°C is higher than the mean value of *Z. exulans* larvae at 15°C. At all temperatures, larvae of the former species have a respiration about four times higher than the latter. This difference can be explained by the difference in life cycle. The larvae of *M. collaris* grow very fast and have a larval period of about 12 days at 20°C. Larvae of *Z. exulans* kept in culture at the same temperature changed their weight very little during 10 days. The loss of weight during ecdysis seemed to be considerable, and observations indicate that the larvae do not eat for several days during ecdysis, contrary to larvae of *M. collaris*. In *Z. exulans* the larval period makes up the greatest part of the life cycle, which, as mentioned earlier, perhaps lasts for two years. In *M. collaris* the imaginal stage covers the main period of the life cycle, there is a new generation every year, and the larval period lasts only a few weeks.

The respiration of pupae is clearly lower than for imagines of *M. collaris*. In *Z. exulans* the pupal respiration is similar to that of larvae and females. Males have a somewhat higher respiration, probably making them better suited for swarming activity. The values are similar to those of adult *M. collaris*. In this species no distinction was made

between the sexes during the respiration experiments.

One might have expected a higher respiratory rate developed in species living in cold habitats close to glaciers (especially *N. nivalis*) than in species active mainly on warm and sunny days (*Z. exulans*). However, no good correlation seems to exist between the respiratory rate and the type of habitat preferred by different species.

Experiments on the temperature preference of beetles, among them *N. nivalis* and *N. gyllenhalii*, living on the border of glaciers and snowfields, seemed to reveal a eurytherm preference (Krogerus 1960, Østbye 1963). As the optima of their preferred temperature ranges were around 5° to 20°C, they could be classified as 'cold-loving eurytherm' species.

Scholander et al. (1953) found that terrestrial insects from arctic and tropical areas revealed little or no difference in oxygen consumption at the same temperatures. Only in the range of 10–20°C, the arctic species showed a somewhat higher respiration. Among aquatic organisms, however, arctic species showed a clear metabolic adaption to lower temperatures.

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We wish to express our sincere gratitude to the late Mrs. Jadwiga Hagen for conscientiously performing most of the laboratory work, Mr. Dag Svalastog and Mr. Johan Schmidt for their laboratory work, Cand. real. Arne Hagen and Cand. real Hans-Jørgen Skar for valuable advice, master mechanic Odvar Iversen for the construction of respirometers, and Mrs. Margaret Espeland for improving the English. This work is part of the Hardangervidda IBP/PT-UM project.

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Anurophorus atlanticus n.sp. A new species of Collembola (Isotomidae) from Western Norway

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Fjellberg, A. 1974. *Anurophorus atlanticus* n. sp. A new species of Collembola (Isotomidae) from Western Norway. *Norsk ent. Tidsskr.* 21, 127-130.

The new species was collected under rotten bark on dead trees in an oceanic *Betula/Pinus* wood near Bergen. It is related to *A. septentrionalis* Palissa, 1966, but is recognized by 1 + 1 ventral setae of Th. II, claws with a distinct inner tooth, smaller PAO, and different dorsal chaetotaxy and cuticula structure. Some remarks on the ecology and distribution of *A. septentrionalis* and *A. laricis* Nic. are made.

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TYPE MATERIAL

Holotype. Male, 0.8 mm labelled: 'Norway. Hordaland: Os. Hauglandsdalen, 14.V.1972. Under bark on dead *Betula odorata*. A. Fjellberg leg.' Deposited in alcohol at Zoological Museum, Department of Entomology, Bergen, Norway.

Allotype. Female, 0.9 mm. Labelled and deposited as holotype.

Paratypes. Material from the type locality deposited as follows: 70 specimens in alcohol together with other types in Bergen, 33 specimens in alcohol and 2 on slides at British Museum (Natural History), Department of Entomology, London, and 339 specimens in alcohol in my own collection.

DESCRIPTION

Total body length 0.7-1.0 mm. Colour greyish, pigmentation rather scattered. Microsculpture of cuticula distinctly coarser at tip of abdomen, otherwise fine and uniform. Head with 8 + 8 eyes. PAO elliptical, 2.0-2.4 as high as broad and 1.5-1.7 as high as diameter

of nearest ocellus (Figs. 7 and 10). Tenent hairs of feet: 2,3,3. Ventrally: 1,1,0. Claws

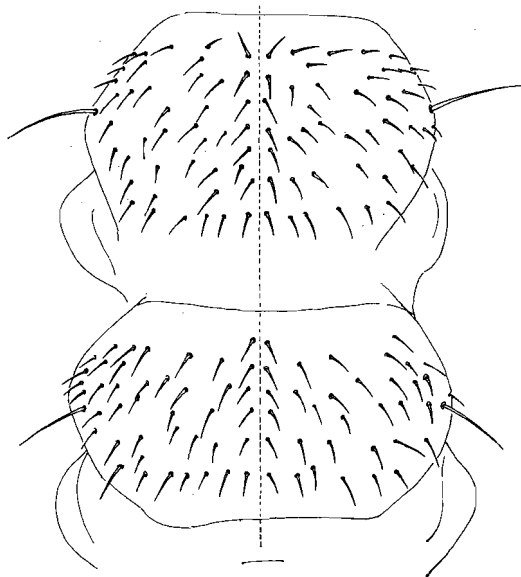


Fig. 1. *A. atlanticus* n. sp. Dorsal chaetotaxy of Th. II-III.

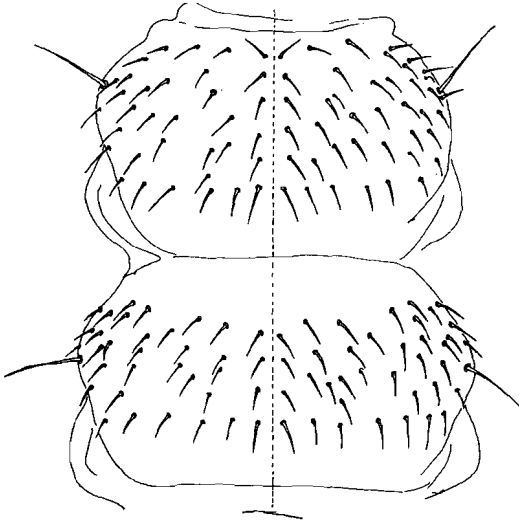


Fig. 2. *A. septentrionalis*. Dorsal chaetotaxy of Th. II-III.

with a distinct tooth at the middle of inner edge. Empodium sharply pointed, approximately $\frac{1}{4}$ of inner length of claw (Fig. 9). Macrochaeta of thorax and abdomen well differentiated, thorax. Some of the curved setae of Abd. V-VI (the segments are fused) distinctly serrated. Number of setae along dorsal median line of Th. II - Abd. III of adults (variation in parenthesis): 7 (6-9), 6 (4-7), 5 (3-6), 5 (4-6), 5 (6). Th. II with 1 + 1 setae along linea ventralis (abnormally one may be lost or doubled), Th. III with 3 - 5 setae at each side of linea ventralis (highly variable) (Fig. 3). Head with 4 + 4 setae along linea ventralis. Ventral tube with 4 caudal and 3 + 3 lateral setae. Ant. IV with numerous curved sensorial hairs.

AFFINITIES

The new species is related to *A. septentrionalis* Palissa, 1966, but is immediately recognized by the 1 + 1 ventral setae of Th. II, which are not present in *A. septentrionalis*. Also the PAO is slightly smaller and more roundish, the cuticula structure is finer, and the dorsal clothing of setae is richer (Figs. 1

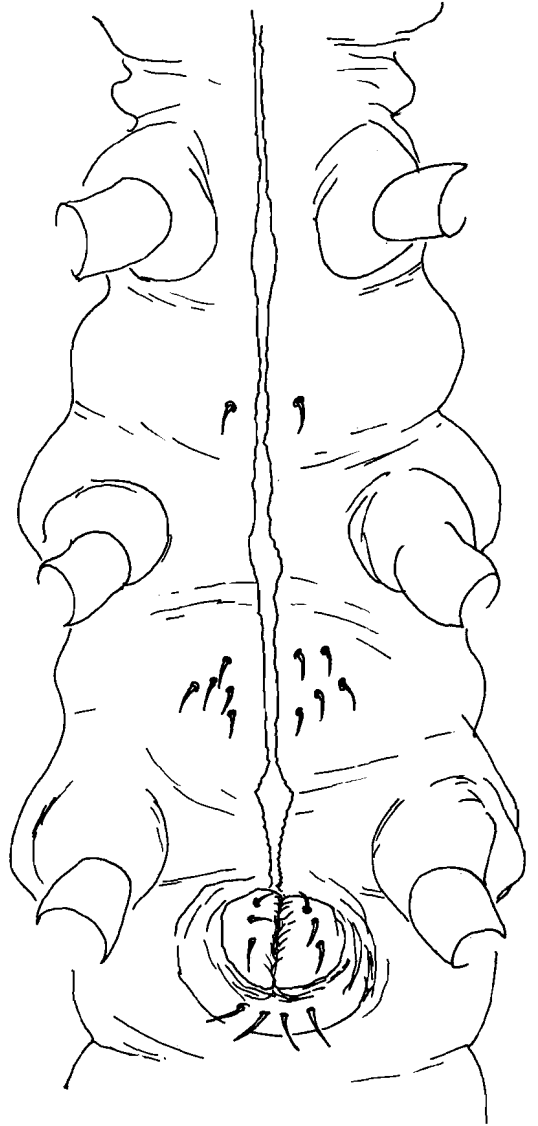
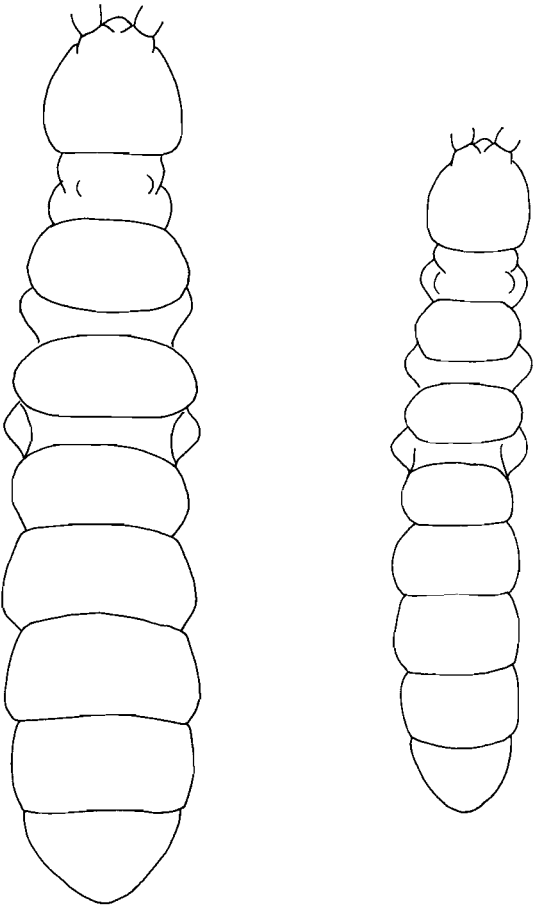


Fig. 3. *A. atlanticus* n. sp. Ventral chaetotaxy of Th. I - Abd. I.

and 2). *A. septentrionalis* has never more than 4 + 4 setae along dorsal median line of Abd. I, whereas *A. atlanticus* usually has 5 + 5. The inner edge of claws is untoothed in *A. septentrionalis*. *A. atlanticus* is a smaller, more parallel species (Figs. 4 and 5). The specimens collected in May, which are reproductive adults, measure 0.7-1.0 mm. Equivalent specimens of *A. septentrionalis* measure 0.8-1.3 mm.



Figs. 4 and 5. General shape of *A. septentrionalis* (4) and *A. atlanticus* n. sp. (5).

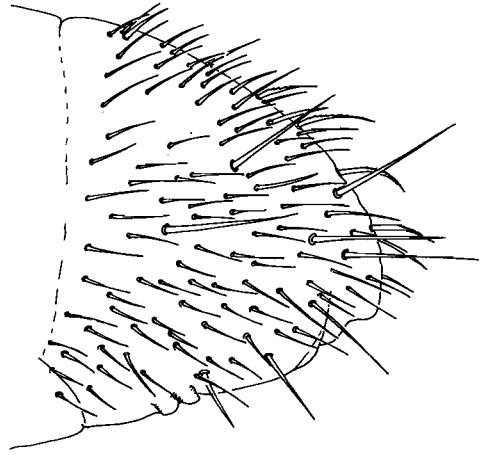


Fig. 6. *A. atlanticus* n. sp. Lateral view of Abd. V + VI.

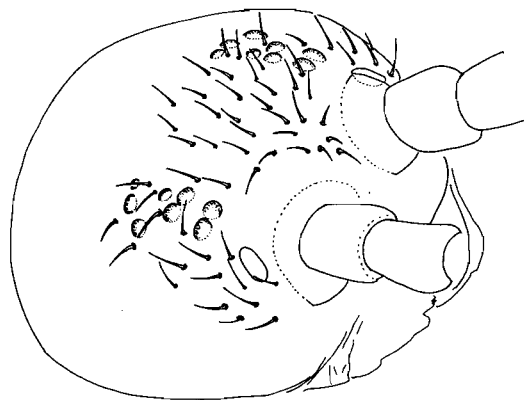
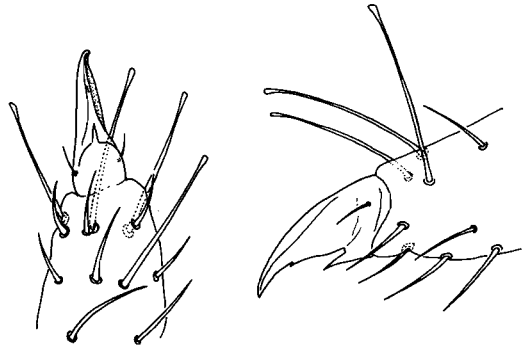
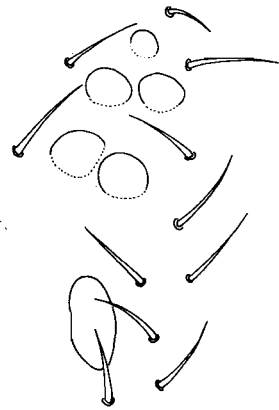


Fig. 7. *A. atlanticus* n. sp. Head with PAO, ocelli, and adjacent setae.



Figs. 8, 9 and 10. *A. atlanticus* n. sp. Left tibiotarsus II, ventral (8), right tibiotarsus III, lateral (9), and detail of left PAO and nearest ocelli (10).

HABITATS

Until now *A. atlanticus* has only been collected at one single locality in Western Norway, approx. 15 Km ESE of Bergen. It is a typical oceanic *Betula odorata*/*Pinus silvestris* wood with rich undergrowth of *Juniperus communis*, moss, and heather. The specimens were collected in large numbers under rotten bark and dead stems of birch and pine (both standing and fallen) in association with *Xenylla boernerii* Axelson, *Hypogastrura purpurescens* (Lubbock), *Onychiurus absoloni* (Börner), *Proisotoma clavipila* (Axelson), *Vertagopus cinerea* (Nicolet), etc.

The related species *A. laricis* Nicolet is common in the same area, but is usually found at drier habitats (moss and lichens on stones, under bark scales on living tree trunks). *A. septentrionalis* is not seen in Western Norway yet, but is common in the eastern, continental part of the country (Fjellberg unpubl.). Palissa (1966) assumed that *A. septentrionalis* and *A. laricis* are geographically vicarious, the latter not being present

in Fennoscandia. As I have collected the two species at the same locality both in Swedish Lappland (Abisko) and Eastern Norway (Tjøme and Høyjord in Vestfold County), this does not seem to be correct. But the two species seem to be well separated ecologically. Until now I have only found *A. septentrionalis* in pine litter, while *A. laricis* prefers drier, more exposed habitats (see above). The xerophilous nature of the latter is possibly reflected by its much darker pigmentation.

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The overwintering of *Pelophila borealis* Payk III.

Freezing tolerance

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Sømme, L. 1974. The overwintering of *Pelophila borealis* Payk. III. Freezing tolerance. *Norsk ent. Tidsskr.* 21, 131-134.

The freezing tolerance of adult *Pelophila borealis* Payk. (Col., Carabidae), acclimated at 0°C, were studied at three sub-zero temperatures in the laboratory. All beetles frozen at -10°C died within a few minutes. At -5°C about 50 percent survived 16 days storage in frozen condition, and 5 percent survived 48 days. At -3°C most of the beetles survived more than two months storage. Survival rates of frozen beetles could be increased by previous acclimation to -5°C in a supercooled state. Beetles collected in early autumn were killed by short exposures at -5°C in frozen condition, but their freezing tolerance increased during the autumn, and was highest in the middle of the winter.

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For many insects, ice formation in their tissues is fatal, and during overwintering the harmful effect of freezing is usually avoided by supercooling. Larvae and pupae of several species, however, are able to tolerate freezing, in a few cases even at temperatures as low as -190°C (Asahina 1969). Few cases of freezing tolerance are known from adult insects, but Miller (1969) found that adults of the carabid *Pterostichus brevicornis* survived 5 hrs at -87°C. Other insects are killed by freezing at much higher temperatures. Several adult Coleoptera and Hymenoptera, studied by Ohyama & Asahina (1972), are freezing-tolerant at temperatures above -10°C, but die at lower temperatures. Besides temperature, the time spent in frozen condition is of importance for the survival of freezing-tolerant insects. In frozen pupae of the slug caterpillar (*Monema flavescens*) increasing mortality occurs with increased storage time at -10°C or -20°C (Asahina 1969).

At Finse, on the mountainous plateau of Hardangervidda in South Norway, adults of *Pelophila borealis* Payk. overwinter in the soil of a sedimentation flat at about 1200 m

a.s.l. (Østbye & Sømme 1972). During the winter the flat is occasionally flooded by the adjacent river, resulting in a layer of ice in which the beetles are enclosed. Due to their anaerobic metabolism, the beetles are not killed by oxygen deficiency during ice enclosure (Conradi-Larsen & Sømme 1973). Because of a thick layer of snow, mid-winter temperatures at the overwintering sites rarely drop below -1°C or -2°C. In the autumn, however, temperatures as low as -8°C have been recorded (Østbye & Sømme 1972), although this appears to be an exception.

When an insect is cooled below the freezing point in contact with moisture, the ice may rapidly penetrate the cuticle, leaving the insect itself frozen (Salt 1963). Since overwintering *P. borealis* may become completely enclosed by ice, it is highly probable that inoculative freezing occurs in their natural habitats. Survival under these conditions must depend on the freezing tolerance of the beetles. In dry surroundings overwintering *P. borealis* may be supercooled to more than -20°C (Østbye & Sømme 1972), although higher supercooling points were recorded in

the autumn. The preliminary results of Østbye & Sømme (1972) suggest that part of the beetles may survive freezing if this takes place at temperatures above -10°C .

The purpose of the present investigation was to study the freezing tolerance of adult *P. borealis* at various temperatures, and survival rates after various storage times in frozen condition. It was also of interest to see if the degree of freezing tolerance changes with season and with previous acclimation temperatures.

METHODS

Adult beetles were collected at Finse in the autumns of 1972 and 1973, and stored in plastic boxes at their overwintering sites (Conradi-Larsen & Sømme 1973). From these sites the boxes could be dug up at any time during the winter. Following removal, the beetles were stored at 0°C until freezing experiments could be carried out at -10° , -5° , and -3°C . Since the beetles usually have supercooling points lower than -10°C (Østbye & Sømme 1972), freezing had to be accomplished by inoculation (Salt 1963). This was done by placing individual beetles in a drop of water at the bottom of a one litre glass beaker. The beaker was partly submerged in a cooling bath, which previously had been adjusted to the desired temperature. Since it is impossible to feel or to judge by sight if a beetle is frozen or not, the actual time of freezing was recorded by a copper-constantan thermocouple connected to a recording potentiometer. The thermocouple was placed in contact with the abdomen of the beetle. To assure a larger area of contact between moisture and cuticula, more water was added as soon as the first drop was frozen. Subsequently the beetle was left to be gradually cooled to the temperature of the cooling bath.

Under these experimental conditions the beetles were supercooled until instantaneous freezing occurred. The liberation of heat during freezing was registered by the potentiometer as a rebound. With the cooling bath set at -10° , freezing took place during cooling when the temperature of the beetles had reached about -7° to -8°C . At -5°C freezing usually occurred 5 to 60 min after

the beetle had reached this temperature. At -3°C the rebound was too weak to be registered with certainty. For this reason beetles to be stored at -3°C were frozen at -5°C and transferred to the -3°C incubator shortly afterwards.

Beetles frozen at -5°C , together with the ice by which they were partly surrounded, were placed in one dram vials and transferred to incubators at -3° or -5°C , both with an accuracy of $\pm 0.2^{\circ}\text{C}$. The vials contained two to five beetles each, and were left in the incubators for various time intervals. Beetles frozen at -10°C were left in the cooling bath for the appropriate time.

After exposure the beetles were thawed at room temperature and their survival rates recorded after one to three days. Only beetles able to walk were registered as alive. Those falling on their sides and backs, or only able to move legs or antennae, were counted as dead together with beetles showing no movements.

To study the effect of temperature acclimation on freezing tolerance, some beetles were incubated at -5°C for to to 3 weeks prior to freezing. Since contact with water was avoided, the beetles remained supercooled during this period.

RESULTS

The mortality of frozen beetles stored at -10° , -5° , and -3°C is shown in Table I. The experiment was based on beetles removed from their overwintering sites during the winter of 1973/74. Between removal and freezing they were kept at 0°C , which approximately corresponds to the temperature of their habitat, for up to three weeks.

From Table I it clearly appears that the freezing tolerance of *P. borealis* is both temperature and time dependent. All beetles were registered as dead after short exposures to -10°C , although some of them showed small movements of legs and antennae. High survival rates were found in beetles frozen and stored at -5°C . All beetles were alive after 4 days at this temperature, but the number of dead and moribund increased with increasing exposure time. A few beetles only survived 48 days exposure. Still higher survival rates were found at -3°C . No beetles

Table I. Mortality at -10° , -5° , and -3° C of frozen adults of *P. borealis* previously acclimated at 0° C

Temp. $^{\circ}$ C	Storage time	n	Percent mortality
-10°	10 min.	5	100
	1 hr	19	100
-5°	4 days	6	0
	8 »	13	15.3
	12 »	5	20.0
	16 »	24	45.8
	32 »	12	75.0
-3°	48 »	19	94.7
	16 days	7	0
	32 »	12	0
	64 »	8	25.0

Table II. Mortality at -5° C of frozen adults of *P. borealis* previously acclimated at -5° C for two to three weeks

Time at -5°	n	Percent mortality
8 days	7	14.2
12 »	4	0
16 »	11	18.2
32 »	12	33.3
48 »	13	69.2

were dead after 32 days, and 25 per cent only were dead or moribund after 64 days at this temperature.

Table II presents the mortality of beetles acclimated in a supercooled state for 2 to 3 weeks at -5° C before being frozen at this temperature. The beetles were removed from their overwintering sites at the same time as those used in the experiments described above. Compared to beetles kept at 0° C (Table I), higher survival rates were found in beetles acclimated at -5° C. In the last group more than 65 percent survived 32 days in frozen condition at -5° C, and about 30 percent survived 48 days.

Finally, some experiments were performed to see if the freezing tolerance of the beetles changed with the time of the year. The results are presented in Table III. Large differences were found between beetles collected in early and late autumn. Those collected in September were killed by short exposures at -5° C, while those collected in the end of October showed relatively high survival rates. Although the results are based on a small

Table III. Mortality at -5° C of frozen adults of *P. borealis* collected at various times of the year

Date of collection	Time at -5° C	n	Percent mortality
4 Sept. 1972	1 hr	5	100
	2 hrs	8	100
23 Oct. 1972	4 days	4	0
	8 »	8	38
	20 »	7	100
17 Dec. 1972	8 days	4	0
	16 »	4	50
27 Jan. 1973	8 days	6	0
	24 »	12	75
23 March 1973	12 days	4	25
	20 »	8	63
	26 »	3	66

number of beetles, the degree of freezing tolerance appeared to be still higher in beetles removed from their overwintering sites in December, January and March.

DISCUSSION AND CONCLUSIONS

From the present study it is concluded that adults of *P. borealis* can survive freezing at least at temperatures down to -5° C, while all beetles die at -10° C. The survival rates are not only dependent on temperature, but also on the time spent in frozen condition. Thus most of the beetles were dead after one month at -5° C, while most of them survived two months at -3° C. The degree of freezing tolerance changes with the time of the year, and may also increase if the beetles are exposed to sub-zero temperatures in a supercooled state.

In the spring, survival rates of about 90 percent have been found in beetles that have overwintered in their natural habitats (Conradi-Larsen & Sømme 1973). The low mortality may partly be explained by the ability of the beetles to supercool (Østbye & Sømme 1972), and partly by their ability to survive freezing. While lowest ground temperatures are recorded in the autumn before a thick snow cover is accumulated, the soil remains relatively dry. Under these conditions the beetles probably remain unfrozen, thus avoiding the harmful effects of freezing at low temperatures. Even if freezing occurs, the beetles have a fair chance of survival, at least at temperatures down to about -5° C.

The greatest risk of freezing apparently occurs later in the season. At this time, the overwintering sites may be flooded, but since the ground is covered by a thick layer of snow, ground temperatures rarely drop below -1° or -2°C . At these temperatures the beetles can probably survive for several months, even in a frozen condition.

In general very little is known about freezing tolerance of insects at temperatures slightly below the freezing points of their haemolymph. Because of ice inoculation, the risk of freezing will be higher in insects overwintering in moist habitats, than in insects from dry surroundings. As appears to be the case with *P. borealis*, the survival of many species may depend on their freezing tolerance at temperatures likely to occur in their natural habitats.

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Studies on the lentic Ephemeroptera and Plecoptera of Southern Norway

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The Ephemeropteran and Plecopteran faunas of lentic habitats ranging from 9 to 1448 m a.s.l. in four areas of southern Norway – Finse, Heimdalen, Vassfaret and the Oslo region – were investigated with respect to species composition and abundance. Environmental parameters, such as water chemistry and temperature, are considered in relation to the observed distributions. In addition, life-cycle data are presented for *Ameletus inopinatus*, *Siphonuru slacustris*, *Baëtis macani*, *Centropetillum luteolum*, *Cloëon dipterum*, *C. simile*, *Heptagenia fuscogrisea*, *Leptophlebia marginata*, *L. vespertina*, *Caenis horaria* and *C. moesta* (Ephemeroptera), and for *Amphinemura sulcicollis*, *Nemoura avicularis*, *N. cinerea*, *Nemurella picteti* and *Leuctra fusca* (Plecoptera).

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The aim of this study was primarily two-fold; to study the distribution and abundance of lentic Ephemeroptera and Plecoptera in contrasting areas of southern Norway, and to obtain information on the life cycles of different species. In addition, since little ecological work has been published on the Norwegian lentic Ephemeropteran and Plecopteran faunas, it is hoped that the present investigation will provide a basis for further studies and possibly indicate aspects worthy of more detailed investigation.

A number of taxonomic studies, distribution records, and check lists have been published concerning the Norwegian species (e.g. Bengtsson 1909, 1928, Brekke 1938, 1965, Lillehammer 1967, 1972, 1974a, Brittain 1972a and Dahlby 1973). During the last ten years a number of ecological studies from lotic habitats, principally in western Norway, have been carried out (Elliott 1965, Lillehammer 1965, 1966, 1974b, Larsen 1968 and Steine 1972). From lentic habitats there has been little published information. One of the few studies is that of Grimeland (1966a, b), who investigated the mayfly fauna of a

group of freshwater habitats in the county of South Trøndelag with special reference to their distribution and the length of the adult stages. Some data are also available from wider limnological studies (e.g. Økland 1964). Lillehammer (1974b) surveys Plecoptera recorded from lentic localities in different parts of Norway.

STUDY AREAS

The geographical position of the four contrasting study areas – Finse, Heimdalen, Vassfaret and the Oslo region – is shown in Fig. 1. Scientific investigations under the auspices of the International Biological Programme (IBP) were already in progress in the first three areas and the present studies were carried out in co-operation with these projects. In the fourth area, the Oslo region, a number of the localities were or had been under investigation, some in connection with limnological studies, others being the subject for parasitological research.

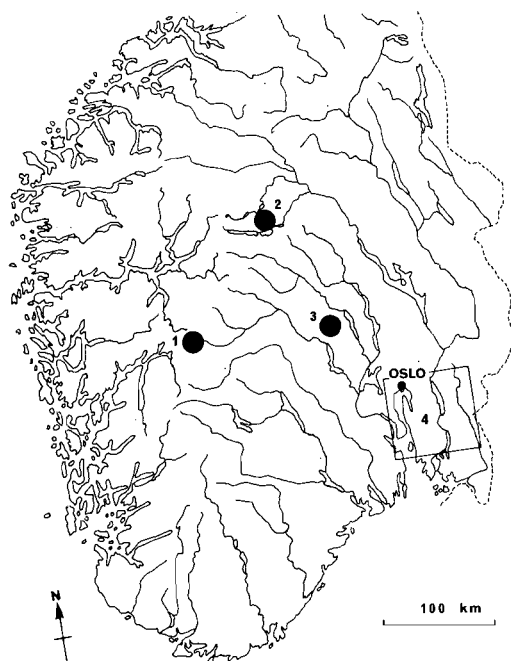


Fig. 1. The location of the four study areas. 1. Finse, 2. Heimdalen, 3. Vassfaret, 4. Oslo region.

Finse

The Finse area (Fig. 2), situated on the north-west side of the Hardanger glacier (Hardangerjøkulen), lies mainly within the Ulvik district of the county of Hordaland. Altitudes within the study area range from 1200 to nearly 1900 m a.s.l. At lower levels the bedrock is granite, which is slow to weather and poor in nutrients. Above this, especially on the north side of the main valley, there are schists which provide more nutrient conditions. The schists are in turn overthrust by granite, forming the Hallingskarvet massif and the higher parts of the Hardangerjøkul. In addition there are extensive areas of moraine material. The area is situated on the watershed between east and west. Precipitation is therefore high, in the region of 1200 mm per year, and this together with cool summers (mean temperature of 8°C for July and August) results in a short ice-free period. The whole area lies in the alpine region.

Heimdalen

Heimdalen and its surroundings (Fig. 3) lie on the eastern edge of the Jotunheim moun-

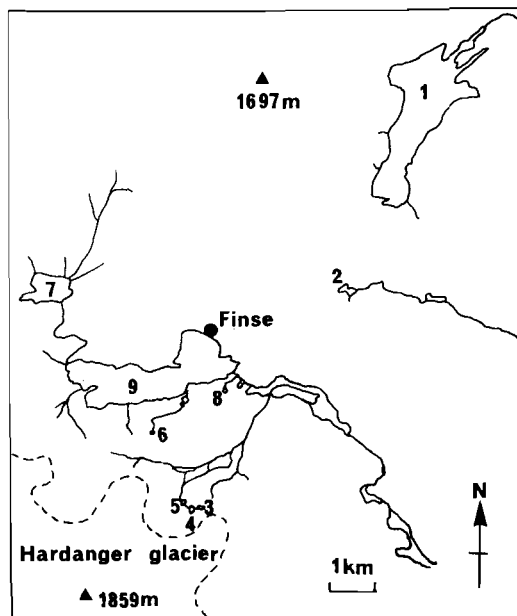


Fig. 2. The Finse area. Investigated localities are numbered.

tains in the county of Oppland. Within the area altitudes range from 1000 to 1843 m a.s.l. The bedrocks are basic but resistant to weathering, and are composed of intrusives and sparagmite from the thrust masses of the Caledonian and pre-Ecocambrian ages (Holdedahl 1960). Moraines are widespread, but there is no present glacial activity within the area.

The climate is drier and less severe than the Finse area. At the level of Øvre Heim-

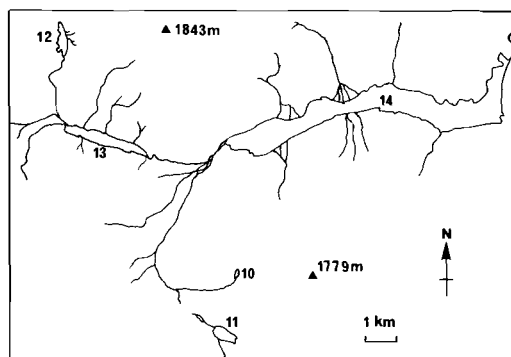


Fig. 3. Heimdalen and surroundings. Investigated localities are numbered.

dalsvatn annual precipitation is in the region of 700 mm and the yearly mean temperature is approximately 0°C. This results in a somewhat longer ice-free period than Finse, especially at lower altitudes. The lower localities (below 1100 m a.s.l.) are situated in the subalpine region, while the others lie in the alpine region. Intensive studies have been carried out on Øvre Heimdalsvatn under the auspices of IBP/PF.

Vassfaret

The Vassfaret area (Fig. 4) lies on the border between the counties of Buskerud and Oppland about 100 km north-west of Oslo. It comprises a forest area up to about 900 m a.s.l. and a mountain plateau area above this where an altitude of 1285 m a.s.l. is reached. The slowly eroding gneiss and granite which make up the bedrock of the area are covered by a thin layer of glacial gravel (Holmsen 1955, Smithson 1963). The area has an inland climate with cold winters and relatively warm summers, although precipitation is in the order of 1000 mm per year. However, there are quite large differences within the area between the valley bottom at 500–600 m and the mountain plateau at 1200 m a.s.l. Spruce (*Picea abies*) dominates the forest parts, with birch (*Betula pubescens*) and pine

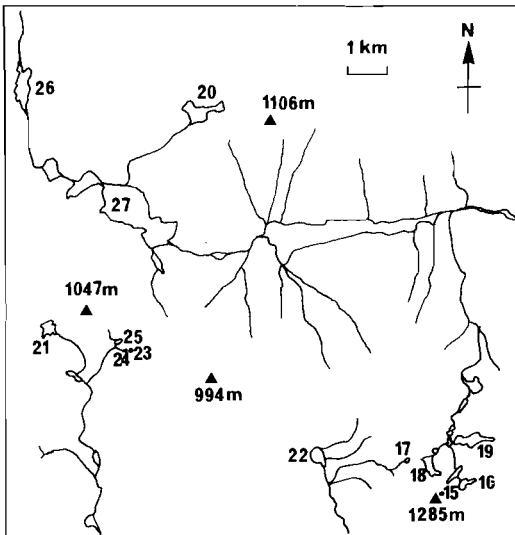


Fig. 4. Vassfaret. Investigated localities are numbered.

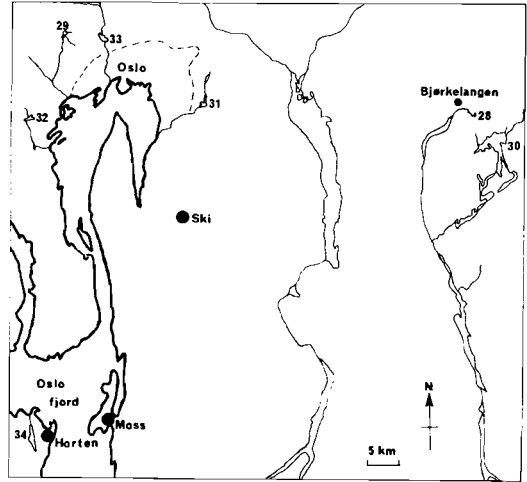


Fig. 5. The Oslo region. Investigated localities are numbered.

(*Pinus sylvestris*) occurring sporadically, particularly on and around boggy areas and around the tree line. The mountain plateau area lies in the middle alpine region.

Oslo region

The region around Oslo (Fig. 5) has an extremely varied and complicated geology. In the east, granite and gneiss dominate, while to the west, Permian eruptives, together with Cambro-Silurian sediments, form the major part. Deposits of marine clay are common near the coast (Holtedahl 1960). The climate varies within the region, the degree of continentality increasing as one goes further north and further from the fjord. In Oslo, the annual mean temperature is 5.8°C and the yearly precipitation is 740 mm (based on values 1931–1960). Most of the region is covered by coniferous forest, although at lower altitudes large areas are devoted to agricultural and urban development.

METHODS

The four areas were sampled every 6–7 weeks during the ice-free period, thus enabling the registration of the major species in the different localities. In addition, especially in the more lowland localities where the ice-free

period was longer and insect numbers higher, life-cycle data could be obtained. With only one, or even two, sampling visits, some major species could quite easily be absent from collections. For example, the mayfly *Baëtis macani* only occurs in collections from the end of July to the end of September while the stonefly *Capnia atra* is absent from collections for several weeks during the summer. The greater part of the field work was carried out during 1971, but in certain localities some sampling was carried out during 1972, largely to obtain more detailed information on the life cycles of certain species. As a large number of localities, often some distance from the road, were sampled with such a frequency, it was necessary to employ a relatively simple and rapid method. In addition, variation in substratum in the littoral and the difficulties of sampling substrata composed of large stones imposed limitations. However, the same methods were used throughout the study, thus making the results comparable within the scope of the investigation.

Two main types of sampling were used in each locality. First, for a period of 5 minutes, stones were picked up from the bottom by hand and examined for Ephemeroptera and Plecoptera. At the same time as the stones were picked up a net was held underneath to obtain those nymphs that swam away when disturbed (Macan & Maudsley 1968). Secondly, a 'kick' method was used, modified from its use in running-water studies (Hynes 1961, Frost et al. 1971), whereby the substratum was disturbed by kicking and a net passed once over the area. A total of five kicks was made. In some of the more productive lakes, where littoral vegetation was abundant, five net sweeps were made through the vegetation (Macan 1964). The net used in the investigations was circular, with a diameter of 20 cm and netting with 15 meshes/cm. With the exception of the largest and most varied localities where three stations were taken, two stations were sampled in each locality on each sampling visit. Stations were chosen to be representative of that locality and were sited away from inflow and outflow streams as such areas were considered to have a different faunal composition.

A search for adults was made in the vicinity of each station, but species only found as

adults are indicated in Tables I-IV by 'T', there being the possibility that they did not originate from the habitat in question.

Nymphal collections were preserved in 3% formalin, and adult specimens initially in 70% alcohol and subsequently in 3% formalin. The body lengths of the nymphs were measured, to the nearest 0.03 mm, from the tip of the head to the base of the cerci.

At each station air and water temperatures were measured. Water temperature was measured in the littoral zone at a depth of approximately 20 cm. To determine whether these spot temperature readings were representative of the maximum temperatures reached, maximum-minimum thermometers were placed in eight localities during the summer of 1971. The presence and extent of ice cover was also noted and the ice-free period given in the results is a composite value based on the conditions of 1971-1973.

A water sample for subsequent chemical analysis was taken from the shallow littoral in every locality on each sampling occasion. Calcium and magnesium values were obtained by titration with E.D.T.A. (the Schwarzenbach method). Specific conductivity was determined using a Philips direct-reading conductivity meter and values given as μmhos at 18°C (χ_{18}) while pH was measured by a Radiometer pH meter 26. The consumption of KMnO_4 was determined as described by Werescagin (1931). For the chemical parameters mean values for the whole ice-free period were determined for each locality and it is these values that are given in the results tables.

From the summation of the results of the two methods of sampling the nymphal populations, an abundance index was calculated for all the species in each locality. In view of the variation in life cycle, whereby some species were present throughout the ice-free period while others occurred only briefly, maximum abundance rather than mean abundance formed the basis of the index. The abundance index for a locality was the maximum number of specimens of that species taken on any single sampling occasion divided by the number of sampling stations. Actual values ranged from 0.1 to 246. To simplify the appreciation of the relative abundance between localities, and as the methods are subject to a certain amount of

Table I. Physical, chemical and faunistic parameters of the investigated localities in the Finse area

Locality	m a.s.l.	Area, ha.	Ice free, months	Max. temp., °C	Ca, mg/l	Mg, mg/l	χ_{18} , μ mhos	pH	KMnO ₄ , mg/l	Ephem.		Plecoptera				
										<i>Baëtis macani</i>	<i>Siphonurus lacustris</i>	<i>Capnia atra</i>	<i>Diura bicaudata</i>	<i>Nemoura cinerea</i>	<i>Nemurella picteti</i>	
1. Flakavatn	1448	334	3.25	5.2	1.7	0.8	12.0	6.7	0.4			+++				
2. Lake 1430	1430	8.0	3	6.7	2.3	0.9	15.0	7.0	0.5			+++				
3. Lake 6	1365	0.7	3.25	8.8	14.1	2.5	71.9	7.4	0.4			+++				
4. Lake 5	1363	1.4	3.5	8.7	10.2	2.0	59.3	7.1	<0.1							
5. Lake 4	1353	1.1	3.5	7.8	7.1	1.1	43.4	7.2	<0.1			++				
6. Lake 8	1330	0.5	3.5	10.0	4.1	1.2	25.1	7.2	0.4	++						
7. Sandaavatn	1262	52	3.5	7.7	3.3	1.0	21.2	6.9	<0.1			++				+
8. Lake 13	1225	0.6	3.5	8.2	1.2	0.6	9.5	6.8	3.0	I						
9. Finsevatn	1214	283	3.75	9.2	2.7	0.8	17.3	6.7	0.9		++	++	++	+	+	I

variation, the indices were grouped into the following four categories:

0.1–0.9	+	rare
1.0–9.9	++	common
10.0–99.0	+++	moderately abundant
>100	++++	abundant

DISTRIBUTION AND ABUNDANCE

Finse

A summary of the results from the Finse area is given in Table I. During the summer of 1971 the highest temperatures recorded by maximum-minimum thermometers in place throughout the ice-free period in Lake 8 and Sandaavatn were 13.7°C and 8.8°C respectively. Spot values from other localities reinforce this view, with spot maximum temperatures ranging from 5.2°C for Flakavatn to 10.0°C for Lake 8. The ice-free period for the lakes in the Finse area is correspondingly short, between 3 and 4 months.

The concentration of dissolved minerals shows considerable variation, with particularly high values in areas of recent glacial activity such as Lakes 4, 5, and 6 which show increasing specific conductivity with decrease in distance from the glacier front of Blåisen. Values of pH range from 6.7 to 7.4, the higher values again being found near Blåisen. The high pH values are due to the

ability of glacial material to absorb H⁺ ions (Strøm 1956). The KMnO₄ consumption is extremely low with the exception of Lake 13, which is partly surrounded by peat bog and has a small catchment area.

The fauna of lentic localities at Finse is poor in species, particularly Ephemeroptera. Only two species of Ephemeroptera are present, *Baëtis macani* Kimmins and *Siphonurus lacustris* Eton. The former occurs up to over 1300 m and is often abundant in outlet streams. Finsevatn is the sole lentic habitat in which *S. lacustris* has been found, conditions probably being too severe in the other localities. However, *S. lacustris* has been found recently in trout from Lengjedalsvatn (7 km east of Finse), situated 1305 m above sea level (Lien, personal communication), so altitude in itself is not limiting. Both species are aestival forms, growing rapidly during the course of the summer and emerging at the end of the summer.

The dominant and often the sole species of Plecoptera is *Capnia atra* Morton, which occurs even in the most extreme habitats such as Flakavatn and Lake 1430. Also it has the capacity to invade relatively recently created habitats such as Lake 6 which was covered by glacier until about 1920 (Andersen & Solli 1971). Investigation of a small lake near Blåisen, exposed only since 1955, indicated that *C. atra* was absent, probably owing to the lack of suitable substratum rather than

Table II. Physical, chemical and faunistic parameters of the investigated localities in the Heimdalen area

Locality	m a.s.l.	Area, ha.	Ice free, months	Max. temp., °C	Ca, mg/l	Mg, mg/l	χ_{10} , μ mhos	pH	KMnO ₄ , mg/l	Ephemeroptera					
										<i>Baëtis macani</i>	<i>Ameletus inopinatus</i>	<i>Siphonurus lacustris</i>	<i>Leptophlebia vespertina</i>	<i>L. marginata</i>	<i>Siphonurus aestivalis</i>
10. Blåtjern	1465	3.5	3.75	12.3	0.9	0.9	8.7	6.6	1.8						
11. Urektjern	1365	28	3.75	11.7	1.0	0.6	8.6	6.6	1.7			+		+	
12. Brurskardtj.	1308	18	3.75	10.8	1.1	0.7	9.9	6.6	2.0	++					
13. Ø. Heimdalsvn.	1090	78	4.25	14.7	1.2	0.7	12.7	6.7	4.0	+++	I	+++	++	++	I
14. N. Heimdalsvn.	1052	770	4.5	10.0	1.4	0.7	12.0	6.8	8.2		++	+++	++	+	

colonising ability. Three other species, *Diura bicaudata* (L.), *Nemoura cinerea* (Retzius), and *Nemurella picteti* Klapalek, are restricted to Finsevatn and the surrounding pools.

Although Finsevatn has the most species, their numbers are low. During the last 40 years considerable changes have occurred in Finsevatn (Strøm 1956, Borgstrøm 1972). During the 1930s it was strongly affected by glacial ooze, but owing to the reduction of glacial activity and the redirection of an outlet stream of the Hardanger glacier the waters have become much clearer and the pH has fallen. The increased transparency would be expected to increase the productivity of the lake. However, since 1965 Finsevatn has been regulated for hydro-electric power with a height of 3.3 m, thus retarding any increase in littoral productivity.

Heimdalen

The results from Heimdalen and its surroundings are given in summary form in Table II. Maximum water temperatures are higher than at Finse, in the region of 10–15° C. As a result of bedrocks that are slow to weather the concentrations of dissolved minerals are generally low. The consumption of KMnO₄ increases with decreasing altitude, reflecting the increase in the supply of allochthonous organic matter from terrestrial vegetation as one goes from the mid-alpine, through the low alpine and into the sub-alpine region.

Blåtjern lies above the limit for strictly lentic Ephemeroptera, although both *B. macani* and *Ameletus inopinatus* Eton occur in the outflow stream. Urektjern and Brurskardtjern support extremely low mayfly populations, only isolated specimens being taken. However, once in the subalpine region the picture changes, with more species and a considerable increase in numbers.

Plecoptera are more widely distributed,

Table III. Physical, chemical and faunistic parameters

Locality	m a.s.l.	Area, ha.	Ice free, months	Max. temp., °C
15. Trig. Pool	1245	0.5	4	11.3
16. Lake 1220	1220	6.0	4	11.7
17. Pool 1205	1220	1.0	4	8.7
18. Lake 1205	1205	9.0	4.25	10.9
19. Lake 1171	1171	19	4.25	11.0
20. Fjellvatn	994	28	4.5	19.2
21. Raufjellvatn	855	9.8	5	13.5
22. Damtjern	845	12	5	13.3
23. Cabin pond A	795	0.2	5	11.5
24. » » B	795	0.6	5	11.7
25. Lille Damtjern	792	2.0	5	11.5
26. Suluvatn	602	23	5.25	23.8
27. Nevlingen	572	147	5.5	20.4

Vassfaret

Table III summarises the results from Vassfaret. All localities are especially low in dissolved minerals owing to the fact that hard, acidic rocks predominate in the area. The water chemistry of the localities around 1200 m is remarkably constant, whether they be pools or lakes. In the forest area there is more variation, mostly explained by differences in size and altitude. The smaller habitats have a lower pH and a higher $KMnO_4$ consumption, while calcium, magnesium, and specific conductivity decrease with altitude. These general conclusions are substantiated by Eie (1974).

Despite an increase in the ice-free period and in summer temperatures, especially at lower altitudes, the lentic Ephemeropteran and Plecopteran faunas are surprisingly poor, both in species and in total numbers when compared with Heimdalen. This is probably the result of extremely low mineral content, low pH, and in the forest area a high degree of humification. The two Nemourids, which for practical purposes are the sole species of either Ephemeroptera or Plecoptera in the mountain habitats, are present in fairly large numbers. This is probably the result of the absence of fish and the lack of competition

Plecoptera						
<i>Capnia atra</i>	<i>Diura bicaudata</i>	<i>Nemurella picteti</i>	<i>Nemoura cinerea</i>	<i>N. avicularis</i>	<i>Amphinemura standfussi</i>	<i>Isoperla obscura</i>
+++	++	++				I
+++	++		++			I
++	+	++	+++			
++++	+++	++	++	+++	+++	I
++++	++	++	++	+++	++	

although there is an increase in both species and abundance as one comes into the sub-alpine zone. Adults of *Isoperla obscura* (Zetterstedt) were taken near most localities, but as no nymphs were taken it is indicated by 'I' in Table II. This species is probably common around the outflows. More information on the Plecoptera of the Heimdalen area, both lentic and lotic, is given in Lillehammer (1974b).

of the investigated localities in the Vassfaret area

Ca, mg/l	Mg, mg/l	$\chi_{1.8}$, $\mu mhos$	pH	$KMnO_4$, mg/l	Ephemeroptera					Plecoptera			
					<i>Leptophlebia marginalis</i>	<i>L. vespertina</i>	<i>Siphonurus linnaeanus</i>	<i>S. lacustris</i>	<i>Heptagenia fuscogrisea</i>	<i>Centropilum luteolum</i>	<i>Nemoura cinerea</i>	<i>Nemurella picteti</i>	<i>Nemoura avicularis</i>
0.4	0.4	8.3	5.2	2.8							+++	+	
0.3	0.4	7.6	5.3	1.1							+++	+++	
0.4	0.3	7.6	5.3	2.7							+++	+++	
0.3	0.4	8.1	5.1	1.4	+						+++	+++	
0.4	0.4	7.4	5.3	2.1		+					++	+++	
0.5	0.4	7.9	5.5	6.7	++	+++					+++	+	
0.7	0.5	9.4	5.3	5.1	++	++	+				++		++
0.5	0.5	9.7	5.1	12.4	++	+++					+++	+	++
0.9	0.7	10.0	5.1	42.9		+							
0.7	0.6	11.8	4.8	38.3		++							
0.9	0.6	11.5	5.3	23.9		+++							
1.3	0.8	11.8	6.0	9.8	+++	++	++	++	+		++		++
1.2	0.5	10.7	6.3	15.1	++	+++			++		++		+++

Table IV. Physical, chemical and faunistic parameters of the investigated localities in the Oslo region

Locality	m a.s.l.	Area, ha.	Ice free, months	Max. temp., °C	Ca, mg/l	Mg, mg/l	χ_{18} , μ mhos	pH	KMnO ₄ , mg/l	Ephemeroptera			
										<i>Leptophlebia vespertina</i>	<i>L. marginata</i>	<i>Centroptilum luteolum</i>	<i>Caenis horaria</i>
28. Røytjern	227	30	6	17.0	4.4	1.8	35.1	6.6	12.7	++++	++		++
29. Burudvann	217	50	6.25	18.5	6.5	1.9	39.6	7.2	17.9	+++	+++	+	++
30. Setten	167	1250	7.75	19.7	2.8	1.6	28.7	6.7	22.8	++++	++	+++	+++
31. Nøklevann	163	73	6.5	18.5	4.1	2.2	36.4	7.0	14.7	++++	+++	+	++
32. Semsvann	144	76	6.5	21.0	13.8	2.4	74.4	7.6	15.2	+++	+++	+++	+++
33. Bogstadvann	135	100	6.5	19.1	4.4	2.1	31.7	6.9	19.6	++++	+++	+	+++
34. Borrevann	9	208	7.75	25.0	13.2	4.7	134	8.8	18.1		+	++	++

for the available food owing to the general paucity of the fauna.

Apart from sporadic occurrences, the Ephemeroptera have their upper limit in the subalpine region. *Leptophlebia vespertina* (L.) is the sole mayfly or stonefly in the three most humic localities. This widespread species obviously owes part of its success to its ability to survive in a wide range of chemical and physical environments, including low pH and oxygen concentration (Brittain, unpubl. data). The lakes Suluvatn and Nevlingen have a more diverse mayfly fauna than the other localities. They both have a higher electrolyte content, pH, and temperature. Of the two, Suluvatn has the more species, possibly because of the greater regulation of Nevlingen in connection with earlier timber floating. In addition, Suluvatn is generally much shallower and thus has a larger littoral area in proportion to its total area than Nevlingen.

The Plecopteran community is uniformly poor in species. It is surprising that both *C. atra* and *D. bicaudata* are absent since suitable habitats are present in the higher parts of Vassfaret. In addition both species are present in the outflow of the large lake, Sperillen, which is situated only about 25 km from the investigated localities in Vassfaret (Lillehammer, personal communication). *Nemoura cinerea* is the dominant stonefly species. It occurs together with *Nemurella picteti* above the tree line and with *Nemoura avi-*

cularis at lower altitudes. In only one locality, Damtjern, are all three species present. Therefore, owing to the difficult conditions in Vassfaret, there may be interspecific competition between *N. avicularis* and *N. picteti* in the forest region, restricting the latter species to the montane areas. In other areas *N. avicularis* is not found above the subalpine region (c.f. Heimdalen), but *N. picteti* occurs in lowland localities when conditions are more favourable. The relationships between these three Nemourids deserve further attention.

Oslo region

The data from the lakes in the Oslo region are given in Table IV. They are ice free longer than localities in the other three areas. Setten and Borrevann are free of ice for nearly 8 months, Setten because of its large size and Borrevann because of its low altitude and proximity to the Oslo Fjord. Complete ice cover is rare on these lakes before December/January. Water temperatures in the Oslo region are correspondingly higher during the summer months.

Røytjern, Setten, and Nøklevann, lying on hard acid rocks and surrounded by coniferous forest, have lower electrolyte values. The catchment areas of Bogstadvann and Burudvann are largely composed of slow weathering eruptive rocks, so that their electrolyte content is not as high as Semsvann, which lies

										Plecoptera		
<i>C. moesta</i>	<i>Siphonurus linneanus</i>	<i>S. aestivalis</i>	<i>Ephemera vulgata</i>	<i>Cloëon dipterum</i>	<i>C. simile</i>	<i>Heptagenia fuscogrisea</i>	<i>Nemoura cinerea</i>	<i>Nemoura avicularis</i>	<i>Leuctra fusca</i>			
+++			+	+	++							++
I			+	+		++	+					
	+		+	+	++	+++		++				+
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partly on basic Cambro-Silurian sediments. In addition, more farming is carried on around Sems vann.

Borrevann is situated below the post-glacial marine boundary, which has resulted in the deposition of large amounts of marine clay in the area. This, together with the high level of farming practised around the lake, has produced a lake which is among the most eutrophic in Norway. The levels of KMnO_4 consumption in the localities from the Oslo region are remarkably similar, with values ranging from 12.7 to 22.8 mg/l O_2 . However, the origin and nature of the organic substances probably vary considerably.

The Ephemeropteran fauna is rich in both species and numbers. It includes a number of species more or less restricted to lowland localities, such as *Cloëon dipterum* and *Caenis horaria*. The restriction of such species to lowland habitats is likely to be a combination of temperature, substratum and the availability of food. However, the most abundant species is the widespread *Leptophlebia vespertina*.

The regulation of Nøklevann, in connection with its use as a source of drinking water for the city of Oslo, seems to have had little effect on the mayfly and stonefly fauna. However, the increased use of the water from Borrevann for drinking purposes has been a contributory factor to its increasing eutrophication. In Borrevann conditions are obviously not suitable for some mayfly species, such

as *L. vespertina* and *Heptagenia fuscogrisea*, which are either absent, or present in very small numbers.

The following additional species were recorded by Økland (1964) from Borrevann: the Ephemeroptera, *Ephemera vulgata*, *Siphonurus aestivalis* and *Caenis nocturna*, and the Plecoptera *N. cinerea* and *N. picteti*. Both stoneflies and *S. aestivalis* were extremely rare and only isolated specimens were taken during the whole period of Økland's intensive study. *Ephemera vulgata* and *C. nocturna* were also uncommon and were more usual on substrata types other than those investigated in this study, namely mud and sand especially at greater depths than sampled. There is also the possibility that the composition of the littoral community has changed in the last 10 years in response to the accelerating rate of eutrophication (Morgan 1970).

The Plecopteran fauna of the lentic localities in the Oslo region is poor, suggesting that few species are successful in the more productive lowland habitats except where they are large in size.

LIFE CYCLES

Owing to their small numbers in samples the following species recorded in this study are not discussed in respect to their life cycles: *Siphonurus aestivalis*, *S. linneanus*, *Ephemera vulgata* and *Isoptera obscura*.

EPHEMEROPTERA

Ameletus inopinatus Eaton

This species is present in small numbers in the lower lentic habitats in Heimdalen. Previous investigations (Gledhill 1959, Larsen 1968, and Ulfstrand 1968) concluded that the species is univoltine with a long emergence period. The present results do not diverge from this, emergence reaching a peak in Øvre Heimdalsvatn in the first week in July, but mature nymphs are still found as late as September. Growth appears to take place under the ice as most nymphs are almost fully grown shortly after ice break.

Siphonurus lacustris Eaton

In a Welsh stream (Hynes 1961) nymphs of *S. lacustris* were small throughout the winter, grew rapidly during March, April, and May and emerged in June. Small nymphs appeared again a month later, but hatching was spread over several months, some overwintering in the egg stage. A wide variation in incubation period was also found experimentally by Degrange (1960). In Heimdalen and around Finse the life cycle is essentially similar, but the timing is different. By ice break in June most nymphs are only 2-4 mm in length. Growth is then rapid, and emergence reaches a peak in Heimdalen at the beginning of August, and at Finse 3-4 weeks later, no

doubt owing to later ice break and lower temperatures. In Swedish Lappland the emergence period extends from mid-July to early September, with a peak at the end of July (Ulfstrand 1969). More detailed studies on the life cycle of *S. lacustris* in Øvre Heimdalsvatn will appear in a future paper.

Baëtis macani Kimmins

The life cycle of *B. macani* will form the subject of a separate publication. Briefly, its life cycle is one of extremely rapid growth during the first half of the ice-free period followed by emergence during the second half. Thus at Finse, emergence reaches a peak in September, whereas in Heimdalen it occurs in August.

Centroptilum luteolum (Müller)

The life cycle of *C. luteolum* has been the subject of some discussion in respect of whether it is multivoltine or just a case of an extended emergence period (Bretschko 1965, Macan & Maudsley 1968 and Lavandier & Dumas 1971). The general consensus is that there are two generations per year, a slow growing winter one and a rapidly growing summer one. The data from Semsvann (Fig. 6) suggest that there are two generations per year, a winter generation emerging in June and a summer generation which emerges in August. In June most of the population is ma-

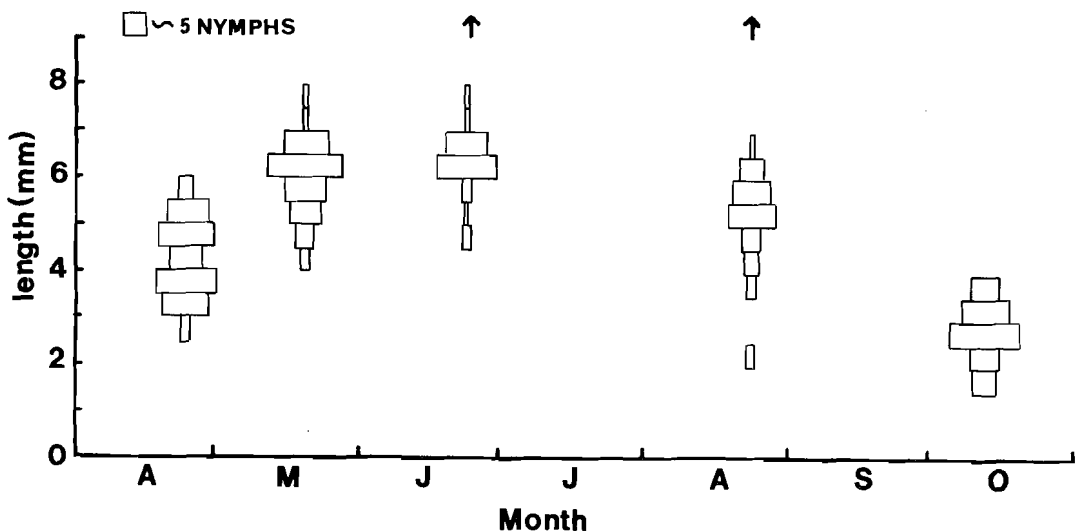


Fig. 6. Life cycle of *Centroptilum luteolum* in Semsvann (loc. 32). ↑ indicates adults were taken.

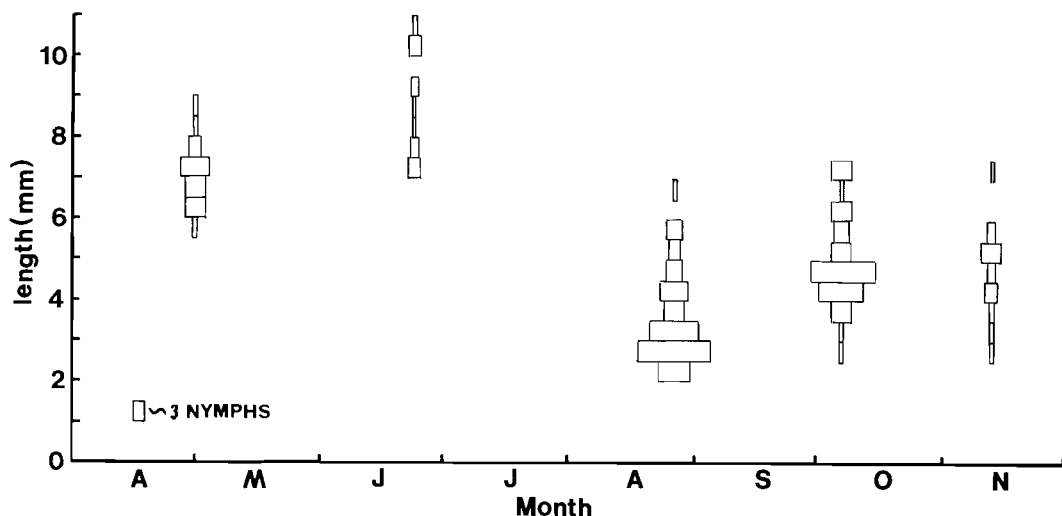


Fig. 7. Life cycle of *Cloëon dipterum* in Bogstadvann (loc. 33).

ture and none are less than 4.5 mm, while in August more than half the population is below 5.5 mm, thus indicating that a new generation has hatched during July. Data from Setten and Borrevann are compatible with the species being multivoltine. Grimeland (1966a) records the flight period of *C. luteolum* in South Trøndelag as from mid-June to the end of August, without any major break. Therefore, even if multivoltine, there is probably a great deal of overlap between the two generations.

Cloëon dipterum (L.)

Previous studies on the life cycle of *C. dipterum* (Brown 1961, Macan 1961, Kjellberg 1973) have shown it to be predominantly univoltine, although in some summers a second rapidly growing generation occurs. In both Bogstadvann and Borrevann *C. dipterum* is univoltine, the nymphs reaching maximum size and emerging during July (Fig. 7). Growth of the next generation is fairly rapid during August and September, reaching 4–5 mm by early October. Growth continues during the period of ice cover, and by the end of April a length of 6–8 mm is attained.

Cloëon simile Eaton

In Britain, *C. simile* has two generations per year, one emerging in May and June and the other during September (Macan 1961). Grime-

land (1966a) gave two flight periods for this species in South Trøndelag, June/July and August. In Bogstadvann only one generation is apparent, emerging in August after *C. dipterum*, but sample numbers are low so the species may well be multivoltine in Bogstadvann.

Heptagenia fuscogrisea (Retzius)

The growth and life cycle of *H. fuscogrisea* has been studied by Bengtsson (1968) in northern Sweden, where it was univoltine and emerged during June and July. Most growth occurred during the autumn and early spring. In the Vindelälven area of northern Sweden Ulfstrand (1969) captured adults during July and early August. In both Setten and Røytjern, for which most data are available, emergence occurs in June (Fig. 8). By the end of July small nymphs of the next generation are already present in collections. After hatching, growth is more rapid in Røytjern than in Setten, possibly owing to the higher average temperatures in the smaller Røytjern. Scattered results from Vassfaret and Bogstadvann differ little from the situation in Setten and Røytjern.

Leptophlebia marginata (L.) and *L. vespertina* (L.)

The life cycle of these two species, which are best treated together, has been well docu-

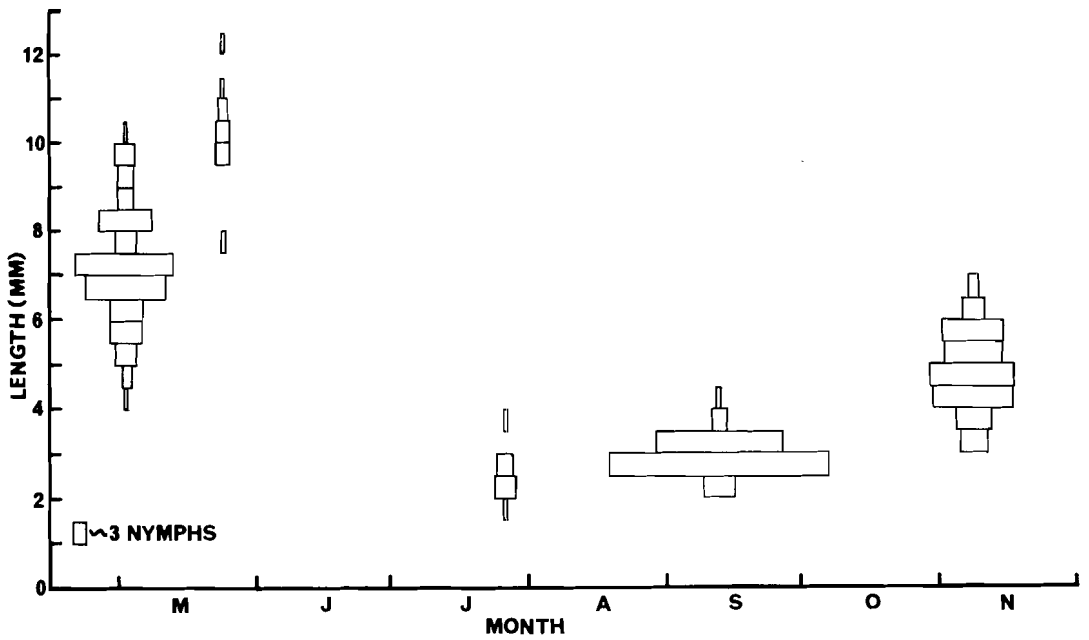


Fig. 8. Life cycle of *Heptagenia fuscogrisea* in Setten (loc. 30).

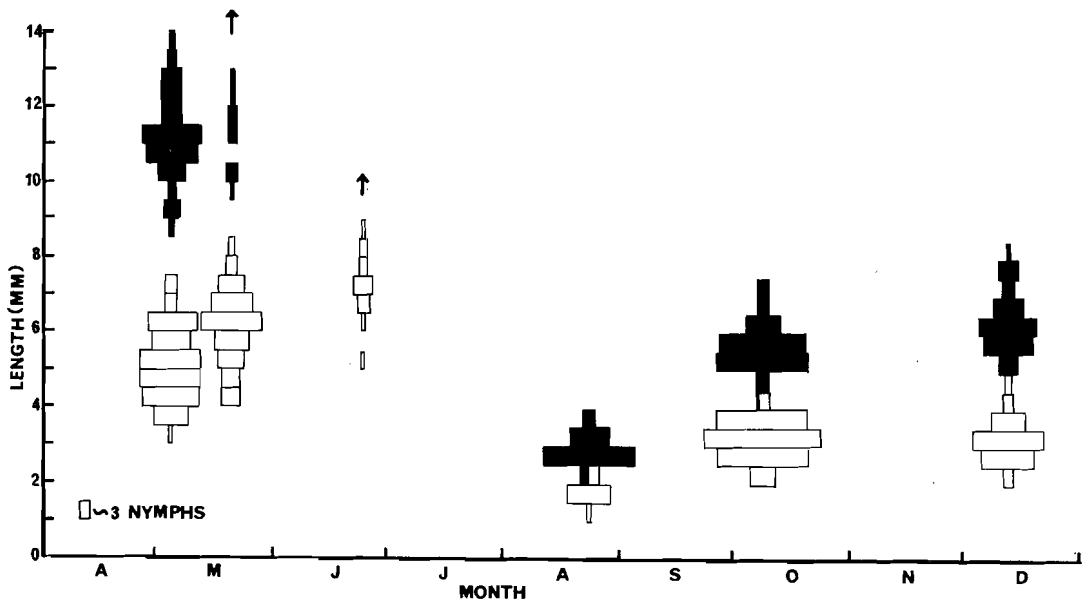


Fig. 9. Life cycles of *Leptophlebia marginata* (shaded) and *L. vespertina* (unshaded) in Burudvann (loc. 29). Arrows indicate the presence of adults of the respective species.

mented in Britain (Moon 1938, Macan 1961, 1965, and Brittain 1972b). In Sweden, *L. vespertina* has been studied by Kjellberg (1972, 1973) and *L. marginata* by Bengtsson (1968). Both species are univoltine, with the possible exception of the Swedish mountains

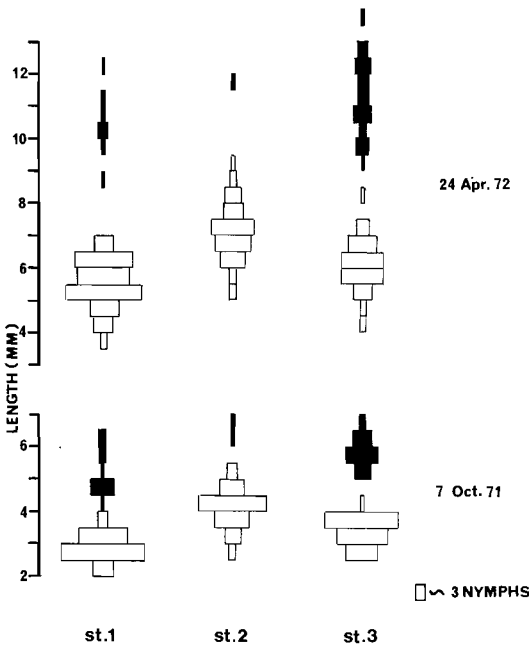


Fig. 10. Size difference between *Leptophlebia marginata* (shaded) and *L. vespertina* (unshaded) at 3 sampling stations around Bogstadvann (loc. 33).

(Kjellberg 1973), *L. marginata* being larger at a given time and emerging earlier than *L. vespertina*. Emergence of both species takes place later in Scandinavia than in Britain because of lower water temperatures and the presence of a cover of ice until May/June. In the present study the limits recorded for the flight period of *L. marginata* were 24

April to 15 July and for *L. vespertina* from 24 May to 9 September. Generally the peak emergence of *L. marginata* varied from May in lowland localities to June/July in the higher regions, while that of *L. vespertina* was in most cases approximately one month later. A major factor determining the time of emergence of these two species is temperature (Macan & Maudsley 1966, Brittain, in press) so it is to be expected that emergence will take place later at higher altitudes. Nymphal growth in a lowland locality, Burudvann, is shown in Fig. 9.

The absolute size of each species at a given time can also vary within the same lake. For example, in Bogstadvann size differences are apparent between the three sampling stations (Fig. 10). Stations 1 and 3 are stony shores, while station 2 is a shallow bay with emergent vegetation where both temperature and primary production are generally higher. In addition, station 2 has a smaller population of *L. marginata* which would reduce any possible interspecific competition.

Caenis horaria (L.)

In a study of what was at the time thought to be a population composed solely of *C. horaria*, but may have been a composite population of *C. horaria* and *C. moesta* (Moon 1938), it was found that no growth occurred during the winter months. The species was univoltine, emerging in June and July and small nymphs appearing again by the end of July.

Essentially the same situation as Moon (1938) found in the English Lake District was

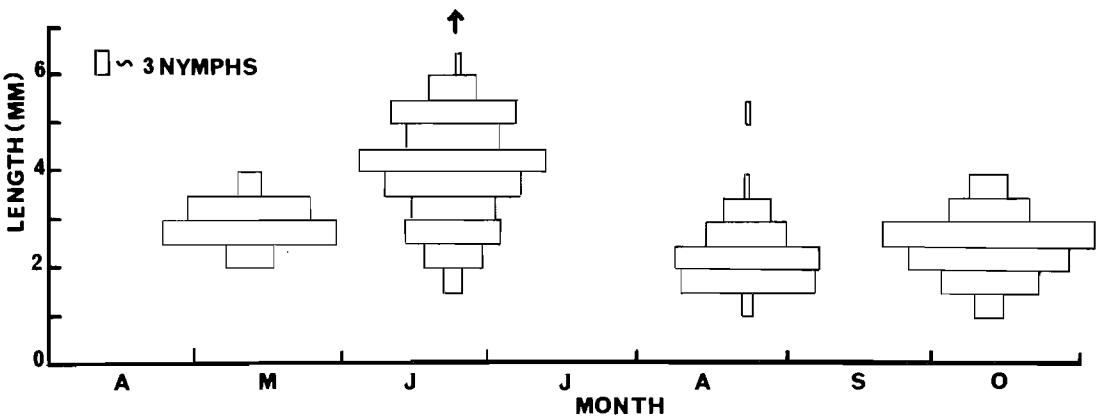


Fig. 11. Life cycle of *Caenis horaria* in Semsvann (loc. 32). ↑ indicates adults present.

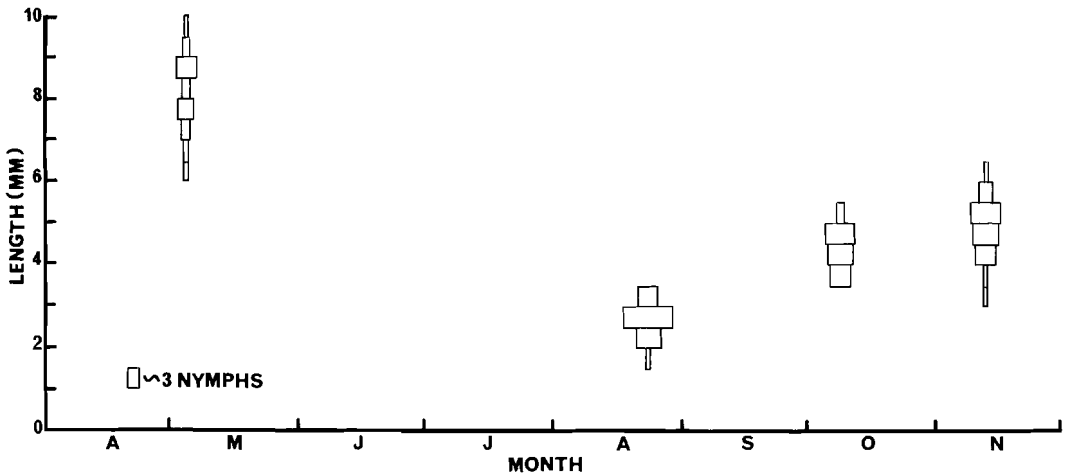


Fig. 12. Life cycle of *Nemoura avicularis* in Burudvann (loc. 29).

found in the Oslo region (Fig. 11). Small nymphs appeared in August and had reached a length of 2.5–3.0 mm by October. From October until May there was virtually no growth, the second period of growth taking place in the month or so before their emergence during June and July.

Caenis moesta Bengtsson

From the data available the life cycle of *C. moesta* is very similar to that of *C. horaria*. There are only small differences in mean size and size distribution of the two species. This may be a reason for the absence of bimodality in Moon's (1938) results for '*C. horaria*'.

PLECOPTERA

Amphinemura standfussi Ris

Amphinemura standfussi is a univoltine species which emerges later than many other lentic stoneflies. In Heimdalen emergence is concentrated in the month of August and most growth takes place in the two months prior to emergence.

Brinck (1949) and Benedetto (1973) record a similar situation from the mountainous and northern parts of Sweden, while in southern Sweden (Brinck 1949) the species is more hiemal. From northern Norway Tobias & Tobias (1971) registered adults during August.

Nemoura avicularis Morton

This species has a one-year life cycle in a wide range of localities. Its life cycle has

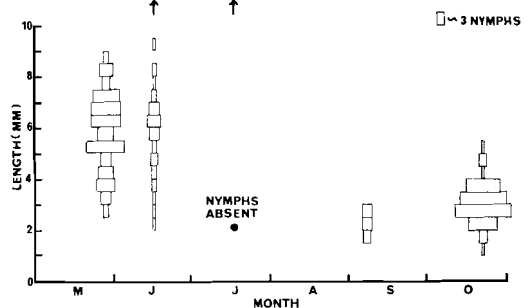


Fig. 13. Life cycle of *Nemoura cinerea* in Dam-tjern (loc. 22). ↑ indicates adults taken.

been studied in a number of countries and reviewed by Brittain (1973). In the lentic habitats investigated emergence took place soon after ice break, during May and June. The nymphs of the next generation are first found in collections during August and growth is then fairly rapid during the autumn, a length of 5–6 mm being attained by the beginning of November (Fig. 12).

Nemoura cinerea (Retzius)

Field studies of *N. cinerea* (Brinck 1949, Hynes 1961, Svensson 1966, and Benedetto 1973) have reported this species to be univoltine with a long emergence period and often a large spread in nymphal size. However, from laboratory studies, Khoo (1964) concluded that *N. cinerea* was semivoltine and demonstrated the presence of extended egg hatching and nymphal dormancy.

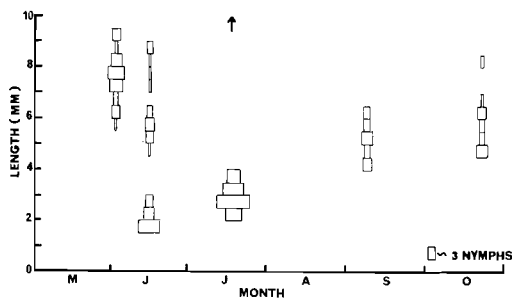


Fig. 14. Life cycle of *Nemoura cinerea* in Lake 1205 (loc. 18). ↑ indicates adults taken.

In lentic localities around Oslo emergence began by the end of May. At 850 m in Vassfaret adults were common at the end of June, whereas in the mountain localities adults were most abundant during July. In the lowland localities up to and including Damtjern in Vassfaret, *N. cinerea* showed a clear univoltine life cycle. For example, in Damtjern (Fig. 13) emergence began 2–3 weeks after ice break and continued well into July. Small nymphs appeared in September and reached an average length of 3 mm by the middle of October. By the spring there was considerable spread in population size, resulting in a relatively long emergence period. Above the tree line, however, the pattern became rather different. Emergence did not commence until the end of June, reached a peak during July, and continued as late as September. Small nymphs were already present in June, at the same time as mature nymphs. This bimodality was especially noticeable in Lake 1205 (Fig. 14).

Eggs of *N. cinerea* from Lake 1205 were incubated in the laboratory at 10° C where they hatched after 25–26 days. The earliest emergence which could have physically taken place in Lake 1205 was, owing to the cover of ice, the beginning of June. Even at a temperature of 10° C, which is higher than present in the field at that time, small nymphs would not appear in collections until early July. However, by this time the average length of the nymphs in the field was nearly 3 mm (Fig. 14), having been present in collections since mid-June. The obvious conclusion is therefore that *N. cinerea* takes at least two years to complete its life cycle in such habitats. Thus little growth takes place

during the first 9–10 months after oviposition. Most growth occurs during the following summer, from approximately 2 to 6 mm in length.

If the species were univoltine in all localities it would be difficult to explain the larger mean size of populations during September and October in the higher situated localities where temperatures and also probably available food are lower. It is unlikely that temperatures in a habitat such as Damtjern reach values that are inhibitive to growth for any significant period. In fact, maximum–minimum thermometers were located in Damtjern and Lake 1205 during the period 17 July to 8 September 1971. For this period the maximum and minimum temperatures were for Damtjern, 17.2° C and 9.8° C, and for Lake 1205, 15.1° C and 5.5° C. A median temperature more than 3° C higher in Damtjern would explain the shorter incubation period and the more rapid initial growth, enabling it to complete its life cycle within a year.

The nymphs, originating from the eggs hatched in the laboratory from Lake 1205, were kept at 10° C for a period. By the middle of November their mean length was 3.3 mm, a length which corresponds well with the length in Damtjern, rather than that in Lake 1205. Therefore it appears that the two life cycle types are determined primarily by environmental factors, of which temperature is of major importance. Nutritional factors are also probably of importance.

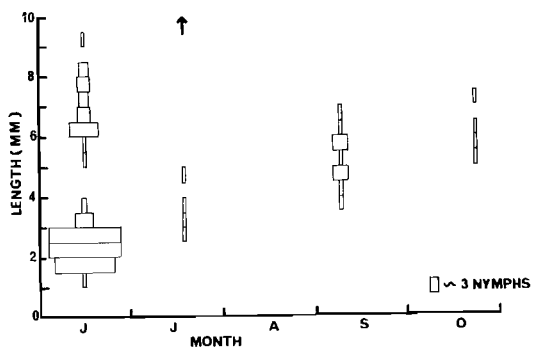


Fig. 15. Life cycle of *Nemurella picteti* compiled from the summation of results from Lakes 1171, 1205 and 1220 (locs. 19, 18 and 16, respectively). ↑ indicates adults taken.

Nemurella picteti Klapalek

In common with *N. cinerea*, *N. picteti* is recorded as having a long flight period and being univoltine (Hynes 1941, Brinck 1949, Khoo 1964, Ulfstrand 1969 and Lavandier & Dumas 1971). However, as was the case with *N. cinerea*, there is evidence that the species takes two years to complete its life cycle in the mountain localities in Vassfaret and at Finse. As numbers were small, results from Lakes 1171, 1205 and 1220 were combined in Fig. 15. In addition the results of hatching eggs and rearing the nymphs from Lake 1220 at a temperature of 10° C showed that even at 10° C the nymphs did not attain the size of the field population during the autumn, indicating that the field population probably hatched before ice break. In a Pyrenean stream, Lavandier & Dumas (1971) found that the population of *N. picteti* was bimodal prior to emergence in February, but they postulated that the smaller nymphs emerged the same year, in October and November. Such a long emergence period is impossible above the tree line in Norway owing to the long duration of ice cover. Also water temperatures are lower in the Norwegian mountains.

The presence of a life cycle taking more than one year is a fairly common feature in the Setipalpia, but previous studies of the Filipalpia have shown them to be almost solely univoltine. Only three species, *Nemoura cinerea* (Khoo 1964), *Leuctra nigra* (Khoo 1964), and *L. ferruginea* (Harper 1973) have been reported as being semivoltine. However, if a longer life cycle were to exist in the European Filipalpia, *N. picteti* and *N. cinerea*, both widespread species with long emergence periods and often with considerable size variation within a single population, would be obvious candidates.

Leuctra fusca L.

Previous investigations (Hynes 1941, Brinck 1949, and Ulfstrand 1968) have shown that in *L. fusca* most growth is accomplished during the summer months, and it is therefore a typical aestival species (Brinck 1949). Data from Setten fit in well with these earlier studies, mature nymphs occurring at the end of July, whereas no nymphs were found in May or September.

Capnia atra Morton

As small nymphs are present during the autumn and emergence takes place at or immediately prior to ice break, considerable growth must occur under the ice. There is, however, according to previous investigations (Brinck 1949, Svensson 1966 and Benedetto 1973) a pause in growth during the middle of the winter.

Around Finse, imagines and mature nymphs occurred during June and the first half of July. By the end of August small nymphs, 2–3 mm long, were present in Sandaavatn, Lake 1430, and Flakavatn, but it was not until the end of September that nymphs of similar size were present in the other Finse localities, by which time nymphs from the three former localities were nearly 5 mm long. This difference in nymphal growth rate and/or egg incubation period may be a function of temperature and the length of the ice-free period, but this point needs further investigation before a definite judgement can be made. Even in the most extreme habitats, *C. atra* was univoltine. A female from Lake 1430 laid eggs which hatched over a period of 7–13 days at 4° C (Lillehammer, personal communication). Imagines were present in the field long after emergence had taken place, up to 6 weeks in some cases.

Diura bicaudata (L.)

Early investigations suggested that *D. bicaudata* was univoltine with a very short egg incubation period (Hynes 1941, Brinck 1949), but later investigations combining laboratory and field studies (Khoo 1968, Schwarz 1970) have shown that it may have both one and two-year life cycles, depending on the presence or absence of diapause in the egg stage. In the localities investigated in the present study a two-year life cycle is the most likely, small nymphs being present in collections at the same time as or shortly after emergence of the adults.

GENERAL DISCUSSION

Within each area and also generally there was a correlation between the concentrations of calcium and magnesium. The correlation coefficient (r) for all the localities taken to-

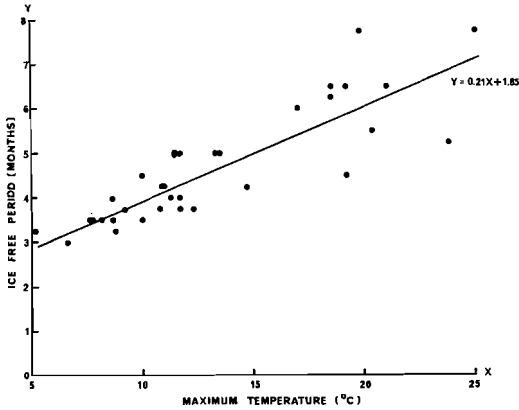


Fig. 16. The relationship between the length of the ice-free period and the maximum temperature recorded in the locality during sampling.

gether was 0.86. As may be expected the correlation was stronger within the three smaller, more geologically homogeneous areas, than in the larger and more varied Oslo region. Calcium concentrations and conductivity were also correlated ($r = 0.93$), although as with calcium and magnesium the regression coefficients for each area had somewhat different values as a result of variations in the proportion of the various chemical components. Therefore in future investigations of this nature, especially within a particular area, it may be necessary to measure only one of the three factors, calcium magnesium and conductivity, rather than all three. The calcium and pH values show a similar relationship to that found for total hardness and pH by Økland (1969) from a survey of several hundred lakes over the whole of Norway.

The length of the ice-free period plays an important role in the temperature regime of a freshwater habitat. In the present investigation there was a strong correlation between the length of the ice-free period and the maximum temperature recorded in the locality ($r = 0.86$) (Fig. 16). The temperature values are, however, the maximum of several spot readings, but the placement of maximum-minimum thermometers in eight localities during the summer of 1971 showed that as the maximum spot temperature increased, so the absolute maximum rose. The relationship between them was good ($r = 0.96$). The length

of the ice-free period varied from as little as three months at Finse to nearly eight months in some lowland localities. The actual period is determined by a combination of factors, of which size, altitude, and winter precipitation are important.

The number of species and their abundance varies for both Ephemeroptera and Plecoptera with changes in vegetation. That the sub-alpine region is especially important in this respect is well seen in the Heimdalen area (Table II). The mean number of Ephemeropteran species in the different vegetation regions of the four study areas was as follows: high alpine zero, mid-alpine 0.2, low alpine 0.7, subalpine 3.3 and boreal 4.8 species. Thus the limit for lentic Ephemeroptera was in the mid-alpine region and even in the mid-alpine and low alpine regions there were very few species capable of colonising lentic localities. These are principally summer growing species, such as *Baëtis macani* and *Siphonurus lacustris*. However, once in the subalpine there was a considerable increase both in species and abundance. For example, in the same water course in Heimdalen there was a fourfold increase in the number of species and approximately a hundredfold increase in the number of Ephemeropteran nymphs from the low alpine to the subalpine. There was a further increase in the boreal zone, especially in the more lowland localities where 8 or 9 species were often present. The dramatic change in the subalpine region is no doubt a result of a combination of biotic and abiotic factors, of which tempera-

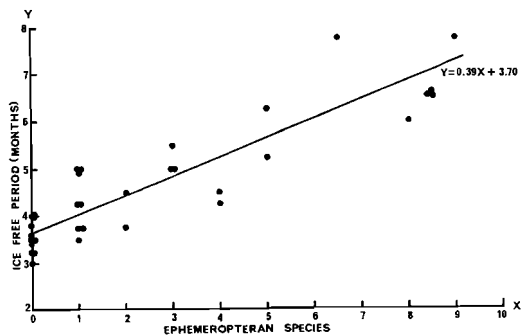


Fig. 17. The relationship between the length of the ice-free period and the number of Ephemeropteran species recorded from the locality.

ture and the increased supply of allochthonous matter are clearly important. There is a good correlation between the number of Ephemeropteran species and the duration of the ice-free period ($r = 0.88$) (Fig. 17), indicating the importance of temperature and possibly also the length of the period of autochthonous primary production.

The number of Plecopteran species also showed changes with different vegetation regions. Lentic Plecoptera were found as far up as the high alpine region, but again there was an increase in the number of species as the supply of allochthonous matter increased. Leaves, especially those of *Salix* spp, form a major food source for many Plecoptera in subalpine and alpine areas (Lillehammer, personal communication). Plecoptera appear to be less successful in lowland lentic habitats; both species number and abundance have low values. There are few characteristically lowland lentic Plecopteran species like *Cloëon dipterum* and *Ephemerula vulgata* among the Ephemeroptera. The Plecopteran species most commonly encountered in lowland lentic habitats are more widespread species such as *Nemoura cinerea*, *N. avicularis* and *Nemurella picteti*. However, Plecoptera are more abundant in lotic habitats and around the outflows of large lakes (Lillehammer, personal communication). Possibly temperature, substratum, and interspecific competition play a role here.

Increased eutrophication can also lead to the disappearance of some species of Ephemeroptera (Morgan 1970). Such a situation may occur or may indeed have occurred in Borrevann and a number of other Norwegian lakes artificially enriched by agricultural, domestic, and industrial products. Lowland Plecoptera may be equally or even more threatened by such changes.

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Anaerobiosis in some alpine Coleoptera

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Sømme, L. 1974. Anaerobiosis in some alpine Coleoptera. *Norsk ent. Tidsskr.* 21, 155–158.

Anaerobiosis was studied in adult Coleoptera overwintering in the mountains at Finse, South Norway. No mortality occurred in *Lepyrus arcticus* Payk. after 50 to 60 days in nitrogen at 0° C, or in *Byrrhus pilula* L. and *Otiorrhynchus dubius* Strøm kept up to 120 days under these conditions. About 80 % of *Pelophila borealis* Payk. survived 156 days. During anoxia considerable amounts of lactate accumulated in the haemolymph of all species.

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At Finse, on the mountainous plateau of Hardangervidda in South Norway, several species of Coleoptera are found in a sedimentation flat at 1200 m a.s.l. (Østbye 1969). Some species, like the carabid beetle *Pelophila borealis* Payk., overwinter in the soil of this flat (Østbye & Sømme 1972). The flat has been deposited by the adjacent river, which partly originates from the glacier Hardangerjøkulen. The vegetation of the flat has been described by Lien et al. (1974). Due to flooding of the river, the overwintering sites of the beetles may be covered by water, and the beetles subsequently enclosed by ice. The survival of *P. borealis* under these conditions depends on their anaerobic metabolism. As described by Conradi-Larsen & Sømme (1973a, b) almost all adults of this species survived 8 to 127 days in nitrogen at 0° C. During anaerobiosis large amounts of lactate accumulated in their haemolymph.

Several other species of Coleoptera overwinter in the sedimentation flat. Like *P. borealis* they may experience serious oxygen deficiencies when the flat is covered by ice. Thus anaerobic metabolism may be of vital importance to other beetles as well. The purpose of the present investigation was to study

the effect of anaerobic conditions on various species of adult beetles from this particular habitat.

METHODS

Adult beetles were collected in September 1973. While *P. borealis* appeared in large numbers, other species were less common. The beetles were put in plastic boxes filled with soil and placed in the ground at the overwintering sites (Conradi-Larsen & Sømme 1973b). In December 1973 and January 1974 the boxes were removed and the beetles placed in glass tubes filled with nitrogen as described by Conradi-Larsen & Sømme (1973b). The tubes were stored at 0° C, which approximately corresponds to the soil temperature at the overwintering sites of the beetles. After various time intervals the tubes were broken and the survival rates of the beetles recorded. Apparently normal beetles were counted as alive, beetles moving but unable to walk as moribund, and those without movements as dead.

The content of lactate in the haemolymph was measured in some beetles after removal

from anoxia. Drops of haemolymph were collected from a puncture in the neck, or by cutting off one of the legs. Analysis of lactate was carried out according to Ström (1949).

RESULTS AND DISCUSSION

The survival of beetles stored in nitrogen at 0° C for various time intervals is shown in Table I. Although the material is limited, it appears that all species have a high capacity for survival under anaerobic conditions. Most of the adults of *P. borealis* survived 156 days in nitrogen, which is a longer period than previously recorded (Conradi-Larsen & Sømme 1973b). Both *Byrrhus pilula* L. (Byrrhidae) and *Otiorrhynchus dubius* Ström (Curculionidae) survived 120 days of anoxia. Only one specimen of *Amara alpina* (Carabidae) and a few specimens of *Lepyrus arcticus* (Curculionidae) were available, but the results

Table I. Survival of adult beetles stored in nitrogen at 0° C.

Species	Days in N ₂ /0°	No. of beetles	
		Alive	Dead or moribund
<i>Pelophila borealis</i>	117	3	1
	156	14	4
<i>Amara alpina</i>	51	1	0
<i>Byrrhus pilula</i>	30	2	0
	48	4	0
	58	2	0
	120	2	0
<i>Lepyrus arcticus</i>	48	1	0
	58	2	0
<i>Otiorrhynchus dubius</i>	30	2	0
	58	1	0
	120	3	0

Table II. Content of lactate in the haemolymph of adult beetles stored in nitrogen at 0° C.

Species	n	Days in N ₂ /0°	Conc. of
			lactate (mM) x ± SE
<i>Pelophila borealis</i>	4	117	37.1 ± 0.65
<i>Amara alpina</i>	1	51	13.3
<i>Byrrhus pilula</i>	4	48	20.2 ± 1.44
<i>Lepyrus arcticus</i>	2	48	18.3
<i>Otiorrhynchus dubius</i>	1	51	46.7

indicate a high capacity to survive under anoxia in these species as well.

During anoxia lactate was accumulated in the haemolymph of all species (Table II). The concentration varied from species to species, but appeared to be exceptionally high in *O. dubius*. Further investigations are necessary to see if other end products of anaerobic metabolism are formed.

It is concluded that all of the species studied can survive extended periods of anoxia. Anaerobic metabolism during anoxia is demonstrated by the presence of lactate in their haemolymph. Since oxygen deficiencies are likely to occur in the natural habitats of the beetles, anaerobic metabolism appears to be an important part of winter survival in all species.

As demonstrated by Påsche & Zachariassen (1973), adults of the longicorn beetle *Rhagium inquisitor*, which overwinters under the bark of dead coniferous trees, can survive long periods of low oxygen tension. In general it may be expected that anaerobiosis in insects is more common than previously recognized. A large number of insect species overwinter in moist habitats of various kinds, and may experience periods of anoxia during the winter. Further studies should be carried out on overwintering and anaerobic metabolism in species from different habitats.

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Notes on little known spiders in Norway

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Hauge, E. 1974. Notes on little known spiders in Norway. *Norsk ent. Tidsskr.* 21, 159–160.

Six species of spiders are reported for the first time in Norway: *Clubiona terrestris* Westr., *Scotina gracilipes* (Blw.), *Hahnia helveola* Sim., *H. nava* (Blw.), *Cornicularia kochi* (Cambr.) and *Diplocentria replicata* Holm. In addition records are given for six little known species in Norway.

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Recently I examined two collections of spiders, one from student training courses during 1969–1971 in Hardanger, Western Norway, and a smaller one from the saltfjellet area in Nordland. The material comprises 12 species, of which 6 are new to Norway, and 6 very little known in our country, so I have found it justified to present these species in the list below.

Clubiona compta C. L. Koch

The species is hitherto known only from three localities in Eastern Norway (Tamb-Lyche 1942). New localities are: One ♀ 29 May 1969 at the island of Storsøy, HOy: Tysnes; 1 ♂ + 1 ♀ 22 May 1970 at Lio, HOi: Kvinnherad; 1 ♀ 21 May 1971 at the island of Ånuglo, HOy: Tysnes.

Clubiona terrestris Westr.

Tamb-Lyche (1942) proved that the specimen of Strand (1898) was not *C. terrestris*, and the following records are probably the first in Norway: One ♂ + 1 ♀ was found at Lio, HOi: Kvinnherad 22 May 1969, and at the same locality: 1 ♂ + 2 ♀♀ 30 May 1969,

1 ♀ 13 May 1971, and 1 ♀ 23 May 1971. This habitat is a rich mixed deciduous forest. In addition 1 ♂ was found 11 May 1971 at Dalen, HOi: Varaldsøy and 1 ♀ 23 May 1971 from a spruce forest at the island of Ånulo, HOy: Tysnes.

Clubiona subsultans Thor.

First record from Western Norway: One ♀ in a mixed forest of deciduous trees and evergreens at Ånuglo, HOy: Tysnes, 13 May 1970.

Zora spinimana (Sundev.)

The species is hitherto known only from Oslo (Strand 1904a), and from Son, Ak (Waalder, pers. comm.). New record: One ♂ 11 May 1970 near Rosendal, HOi: Kvinnherad.

Scotina gracilipes (Blw.)

One ♀ 25 August at Ljosmyr, HOi: Kvinnherad. The species is new to Norway.

Hahnia helveola Sim.

From Ånuglo, HOy: Tysnes we have 1 ♀ 21 May 1969 and 2 ♀♀ 21 May 1971. There is

also 1 ♀ from HOi: Strandebarm, 600 m NE Breievne, Nord Oma, 7 July 1967 (T. Solhøy leg.). The species is new to Norway.

Hahnia nava (Blw.)

Four records from the same locality, namely Ljosmyr, HOi: Kvinnherad: One ♀ 12 May 1970, 4 ♀♀ 25 August 1970, 3 ♀♀ 23 May 1971, 2 ♀♀ + 3 ♂♂ 13 May 1971. These are the first records from Norway.

Oreonetides abnormis (Blw.)

One ♀ 28 May 1969 near Jemtelandsvatn, HOi: Kvinnherad and 1 ♀ 13 May 1970 from a mixed forest at the island of Ånuglo, HOy: Tysnes. I also found 1 ♂ under a stone 23 August 1969 at Fløien, HOy: Bergen. Further, 1 ♀ from HOi: Varaldsøy 30 June 1969 (T. Solhøy leg.). The only previous record in Norway is from Bergen (Strand 1904b).

Microneta viaria (Blw.)

Previously known from Hallingdal (Strand 1899), from Ringsaker (Waalder 1972), and from Røros (Cooke 1967). New records: One ♀ 30 May HOi: Kvinnherad; 1 ♀ 13 May 1970 at Ånuglo, HOy: Tysnes; 1 ♀ at Ljosmyr, HOi: Kvinnherad 23 May 1971. Further, 2 ♀♀ from a birch forest 8 July 1971, TRy: Harstad.

Lepthyphantes cristatus (Menge)

We know this species from Trøndelag and from Østlandet. New records: One ♀ + 1 ♂ at Lio, HOi: Kvinnherad 30 May 1969. From the island of Ånuglo there are two records: One ♀ 13 May 1970 and 1 ♀ 23 May 1970, both in a spruce forest.

Diplocentria replicata Holm.

One ♂ was captured in pitfall traps at Saltfjellet in the period of 13–18 July 1973. The

habitat is a broken birch forest with mainly *Uaccinium myrtillus*, in a west-faced slope of a valley approx. 550 m above sea level. UTM coordinates: 33 W WP 016958. The species is new to Norway.

Cornicularia kochi (Cambr.)

One ♀ at the same time and place as *Diplocentria replicata*. The species is new to Norway.

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Symphyla and Pauropoda from two coniferous forests in South Norway

HANS PETTER LEINAAS

Leinaas, H. P. 1974. Symphyla and Pauropoda from two coniferous forests in South Norway. *Norsk ent. Tidsskr.* 21, 161-166.

Two species of Symphyla, *Scolopendrellopsis subnuda* (Hansen) and *Symphyllella vulgaris* (Hansen), and two species of Pauropoda, *Allopaupopus verticillatus* Scheller and *Pauropus lanceolatus* Remy, are reported from two coniferous forests in South Norway. These animal groups were previously not known from coniferous forests in Norway. The Symphyla appeared to be restricted to the mineral soil. Of the Pauropoda, *A. verticillatus* was also only found in the mineral soil, while *P. lanceolatus* preferred raw humus and even living moss. The latter species was found in densities of several hundred per m² in one locality. Specimens from the first instar of *P. lanceolatus* were found throughout the year, indicating an extended reproduction period.

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The Symphyla and Pauropoda both belong to the soil fauna. They are quite common, but appear in small numbers. For this reason they play a minor role in the detritus food chain to which they belong. Very little is known about these animals in Norway. Scattered reports on one species of Symphyla exist (von Porat 1887, Ellingsen 1891 and 1903, and Lie-Pettersen 1898). Børset (1969) mentioned some finds of Symphyla in the Oslo area, and Scheller (pers. comm.) found some 10 species of Pauropoda and about 5 species of Symphyla. During a study on Collembola and Protura in two coniferous forests, both symphyls and pauropods were found.

STUDY AREAS

The investigation was carried out in two different areas of South Norway, both in Eu-Piceetum Myrtillus sub-association. The first locality was at Nordmoen in Nannestad (UTM:32V PM 169 819), and the other at Slørstad in Ås (UTM:32V PM 014 178). At

Nordmoen there was an element of pine amongst the spruce.

The soil has a typical podzol profile with a sharp distinction between the raw humus (A₀) and the underlying A₂ and B horizons. The raw humus is 2.5-4 cm thick at Nordmoen, and 6-9 cm at Slørstad. The mineral soil at Nordmoen consists of loamy sand only, with no stones at all. At Slørstad, however, there are many rather large stones, which make the conditions in the soil, which is also loamy sand, more heterogenous.

The climate is basically continental at Nordmoen, but more oceanic at Slørstad. During the past few years there has been very little or no snow at Slørstad. When soil samples were taken during the winter of 1973, the soil was never frozen on the sampling days. At Nordmoen there was snow, and the soil was frozen for 4 to 5 months.

MATERIAL AND METHODS

The aim of this investigation was to study Collembola and Protura, which occur in high

Table I. Number of symphyls (s) and pauropods (p) recorded at the Nordmoen locality. Number of soil samples in brackets.

	Depth of samples in cm							
	0-3		3-6		6-9		9-12	
1972:								
8 May	—	(60)	—	(60)				
10 June	—	(60)	—	(60)				
11 July	—	(60)	3s	(60)				
14 Aug.	—	(60)	3s	(60)	—	(15)	—	(15)
14 Sept	—	(60)	3s	(60)	1s	(15)	3s	(15)
21 Oct.	—	(60)	2s	(60)	—	(15)	—	(15)
13 Nov.	—	(60)	—	(60)	—	(15)	—	(15)
19 Dec.	—	(20)	—	(20)	1s	(20)	—	(5)
1973:								
23 Jan.	—	(20)	—	(20)	1s	(20)	3s	(8)
8 Mar.	—	(20)	—	(20)	—	(20)	—	(14)
13 Apr.	—	(20)	—	(20)	2s	(20)	—	(14)
21 May	—	(60)	—	(60)	7s	(15)	2s	(15)
							1p	

numbers. Consequently the chosen size of the soil samples was small – 10 cm². Soil cores, which were taken down to 6–12 cm depth, were subdivided into slices of 3 cm thickness. Random squares were laid out at both study areas. During each sampling day, one soil sample was removed from each square. From May 1972, monthly soil samples were taken at Nordmoen for one year, with the exception of Feb. 1973. The numbers and depth of the soil samples are shown in Table I. At Slørstad, soil samples were taken 9 times during one year, beginning on 21 Sept. 1972. The numbers and depth of the soil samples are shown in Table III.

In addition to the regular sampling schedule, some additional samples from Nordmoen

are included: on 25 June and 15 Oct. 1971 some soil samples of 33.2 cm² were taken and subdivided into 2 cm and 3 cm thick slices respectively. On 9 Aug. 1972, 20 soil samples of 10 cm² × 6 cm were taken.

The extraction method used was a Macfadyen (1962) high gradient canister extractor.

RESULTS

Nordmoen

The results from the monthly samples are shown in Table I. All the symphyls from these samples are *Scolopendrellopsis subnuda* (Hansen), and the only pauropod was a *Pauropus lanceolatus* Remy.

From one of the 4 soil cores taken on 25 June 1971, 14 symphyls and 7 pauropods were extracted. Table II shows the vertical distribution of the animals. The following species were found: Symphyla: 1 *Symphylella vulgaris* (Hansen) and 13 *Scolopendrellopsis subnuda*. Pauropoda: 7 *Allopauropus verticillatus* Scheller.

In 7 soil cores taken 15 Oct. 1971 (4 cores 21 cm deep and 3 cores 12 cm deep), one pauropod – *A. verticillatus* – was found between 12 and 15 cm depth.

Five of the samples from 9 Aug. 1972 contained one *A. verticillatus* each. All were found in the mineral soil at 3–6 cm depth.

Table II. The vertical distribution of the symphyls (s) and pauropods (p) in a soil core taken at Nordmoen 25 June 1971. The humus horizon was about 2 cm thick.

Depth of the soil slices in cm	Number of symphyls (s) and pauropods (p)	
0-2	—	—
2-4	7s	—
4-6	3s	—
6-8	1s	—
8-10	—	2p
10-12	2s	4p
12-14	—	—
14-16	1s	1p

Table III. Number of symphyls (s) and pauropods (p) recorded at the Slørstad locality. Number of soil samples in brackets.

	Depth of samples in cm							
	0—3		3—6		6—9		9—12	
1972:								
21 Sept.	—	(10)	—	(10)	1s	(10)	2s	(10)
	—		—		—		—	
25 Oct.	—	(10)	—	(10)	—	(10)	—	(8)
	5p		1p		—		—	
6 Dec.	—	(10)	—	(10)	—	(10)	2s	(6)
	—		—		1p		—	
1973:								
9 Feb.	—	(10)	—	(10)	—	(9)	—	(3)
	3p		7p		4p		2p	
22 Mar.	—	(10)	—	(10)	3s	(10)	—	(4)
	—		2p		1p		—	
10 May	—	(20)	—	(20)				
	—		2p					
17 June	—	(20)	2s	(20)				
	28p		4p					
4 Aug.	—	(20)	—	(20)	—	(10)		
	1p		7p		1p			
4 Sept.	—	(20)	—	(20)	2s	(9)		
	9p		3p		2p			

Slørstad

Many pauropods but no symphyls were found in soil samples from the uppermost 3 cm of the humus. Pauropods were also extracted from the moss layer. All belonged to *P. lanceolatus*.

The results of Symphyla and Pauropoda from the regular samples are seen in Table III. The only species found were *S. subnuda* and *P. lanceolatus*. The fraction of soil cores with pauropods from each sampling day varied from 0 to 30 %, with a 17.2 % average for the whole sampling period. The highest number of pauropods in one soil core was 30. The proportions of adults and the different instars of *P. lanceolatus* from each sampling day are seen in Table IV. Third instar to adult stages of symphyls were found throughout the year in both areas.

DISCUSSION

Symphyla

According to Michelbacher (1949) the symphyls are found in all soil types, but they prefer soils with an open texture as they are

not capable of burrowing their own runways in the soil.

In the present survey, the symphyls were not found in the uppermost part of the soil profile (Tables I and III). In those instances where they were found between 6 and 9 cm depth at Slørstad, the raw humus layer was not more than 6 cm thick. At Nordmoen the humus horizon is much thinner, and here the symphyls are often found between 3 and 6 cm depth. It appears therefore that the transition between the mineral soil and the humus is an upper border for the vertical migration of the symphyls. The only possible exceptions to this are the two symphyls found between 3 and 6 cm depth at Slørstad 17 June 1973. However, it should be pointed out that the mineral soil rose a few mm in this soil slice.

It is well known that symphyls are found in the deeper soil (Salt et al. 1948, Michelbacher 1949, Edwards 1958). Nevertheless, the conditions which these animals encounter in the mineral soil are quite different from soils which are usually considered to be optimum for symphyls. Edwards (1958) found that sand was the least favourable of symphyls. From these observations one would expect that the symphyls, like most of the

Table IV. The composition of adults and the different instars of *P. lanceolatus* from 7 sampling days at Slørstad.

	1972 6 Dec.	9 Febr.	22 March	1973 10 May	17 June	4 Aug.	4 Oct.
Adult		2	1	1	2		2
Subad.	1	1			3		
3. instar		1	1	1	7		3
2. instar		2			17	1	3
1. instar		10	1		2	4	6

other soil-dwelling microarthropods, would prefer the humus horizon as being most suitable. It is very porous and is rich in fungal mycelia and decaying organic matter, which are considered to be the diet of both symphyl genera from this investigation. It is difficult to understand why a large soil animal like *S. subnuda* (2.5 cm) prefers to live in the dense mineral soil. The other animals found here are much smaller (the collembols 0.2–0.5 mm and the mites 0.1–0.2 mm).

It might be possible that the symphyls specialize in living on decaying roots, and the hollows after these do serve as runways for the animals. However, most of the roots are found in the humus horizon.

The acidity possibly prevents the animals from migrating up into the raw humus. This horizon is far more acid than the mineral soil. Edwards (1958) mentioned that he never found dense symphyl populations in too acid soils.

Most of the year the raw humus has a high humidity. At Nordmoen the soil moisture was measured each sampling day as long as the soil was unfrozen. Except for one day, the soil moisture was found to vary between 30 and 40 % of the water-holding capacity at pF 0.5. Consequently this factor would not explain the vertical distribution of the symphyls.

Edwards (1959 and 1961) found that there are notable vertical migrations during the season. He also found that egg-laying took place in the deeper soil. During this survey no specimens from the first two instars were found. Reproduction probably takes place at a deeper level in the soil, which was not included in my sample.

Pauropoda

Concerning the pauropods in Scandinavia, Brinck (1964 and Meidell (1971) state that

they are restricted to the soil in deciduous forests which are relatively undisturbed by human manipulation. The pauropods are known to be quite common in coniferous forests in the more southern areas of USA and Europe (Starling 1944, Price 1973, Scheller pers. comm.). For this reason one could expect them to be found in this kind of forest in Norway too. However, the conditions for soil animals are often quite different in these areas. In southern coniferous forests it is not uncommon to find a distinct organo-mineral layer (A_1) (H. Høydahl pers. comm.). This layer shows favourable conditions for many soil-dwelling animals. Starling (1944) mentions an A_1 -layer of ~6 cm thickness where most of the myriapods were found.

Thirteen of the 14 pauropods found at Nordmoen were *A. verticillatus*. The size of these were about 0.5 mm. Scheller (1971) mentions that this species was not found above the 25 cm depth. In the present survey it was found as high up as the 3–6 cm depth, but it was never seen in samples from the humus horizon. The finds of Scheller (1971) were made in deciduous forests. It looks as though the vertical distribution of this species is somewhat different in these two soil types, and that the humus content in the soil is the major factor.

All pauropods from Slørstad and one from Nordmoen were *P. lanceolatus*. This species is considerably larger than *A. verticillatus*, about 1.5 mm, and its biology is quite different. Table III shows that it is mainly found in the humus horizon and even in living moss. But some finds also show that it might migrate down into the mineral soil. This species was much more numerous than *A. verticillatus*. However, the number of animals per soil core from each sampling day varied from 0 to 1.6, with an average for the whole sampling period of 0.6. From the re-

sults it is clear that the animals are highly aggregated, but this material is too small to state anything about the seasonal variation of the population density. Nevertheless, it is clear that throughout the year average population is a few hundred per m². To study this population, one should probably have used a sampling device 10 times larger than the one used here.

In a pine forest in North Carolina, Starling (1944) found an average population density of 538 Pauropoda per m². Salt et al. (1948) from a one month sampling obtained a density estimate of 629 per m². Both these figures are close to the corresponding value of the present survey (600 per m²). However, all these densities are far exceeded by the finds of Price (1973) in a ponderosa pine forest in California (17,883 pauropods per m²). This indicates that in very favourable conditions the Pauropoda might be one of the most numerous microarthropods in the soil.

Starling (1944) found June and July to be the main period of reproductive activity. From Table IV it is seen that specimens of the first instar were found during almost every season. The duration of this instar is known to be about 2 weeks, but is obviously much longer during the cold season. This indicates that some reproduction takes place throughout the season of the year when the animals may be active.

A. Fjellberg (pers. comm.) has recently found pauropods in some other habitats. In a sheep pasture he found *Allopauropus vulgaris* and *A. gracilis*, and under the rotten bark on a standing dead pine about 1.5 m above the ground he found *A. gracilis* in large numbers.

It is obvious that both symphylls and pauropods have a much wider distribution in Norway than previously known. Further research is needed to determine their distribution pattern and their ecological importance in the microarthropod community in the coniferous forest soil.

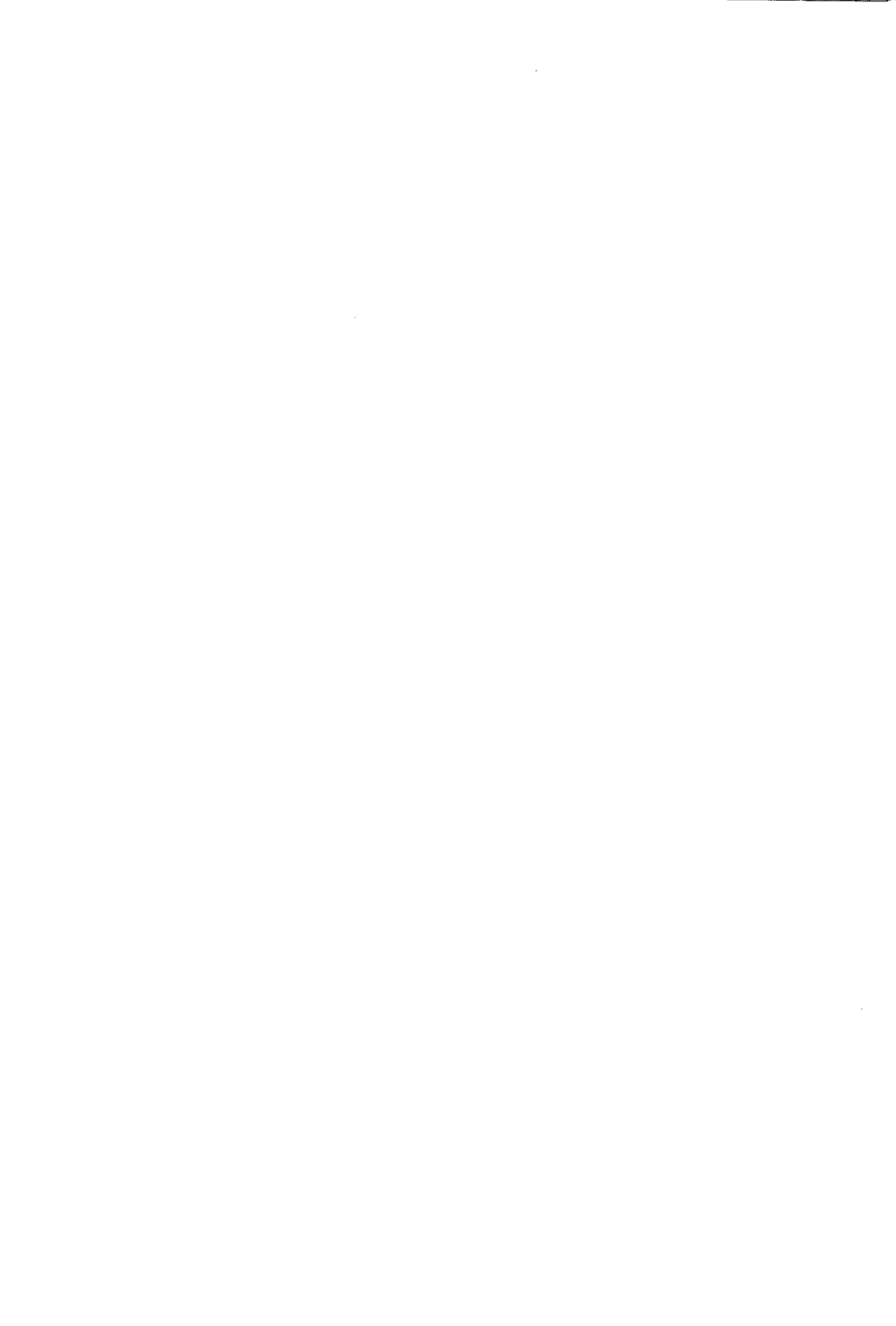
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Notes on two northern species of the genus *Platycheirus* St.-Farg. et Serv. (Dipt., Syrphidae)

TORE RANDULFF NIELSEN

Nielsen, T. R. 1974. Notes on two northern species of the genus *Platycheirus* St.-Farg. et Serv. (Dipt., Syrphidae). *Norsk ent. Tidsskr.* 21, 167-172.

Platycheirus fjellbergi nov. sp. is described from material collected in Norway and Sweden. The species is compared with the nearly allied *P. ambiguus* Fall. and *P. hirtipes* Kan., and differing characters are given. In addition, *P. angustitarsis* Kan. is reported from Norway.

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PLATYCHEIRUS FJELLBERGI NOV. SP.

The material of this species was collected in Abisko, northern Sweden, and in Finnmark and Jotunheimen in Norway. In Abisko (68°32'N, 18°48'E) it was found rather frequently on low-alpine slopes at altitudes of 700-950 m a.s.l., in Finnmark, at Fiskevann (69°05'N, 18°28'E) it was caught at the border of a taiga lake, less than 100 m a.s.l., and in Jotunheimen (ca. 61°30'N, 8°30'E) on alpine slopes at 1100 m a.s.l. In most cases the species seemed to be attracted to catkins of *Salix*. The finds probably indicate a boreal and alpine distribution.

Platycheirus fjellbergi nov. sp. bears a great resemblance to *P. ambiguus* Fall. in having the same greyish abdominal spots, the narrow front metatarsus, and the curled bristle at the tip of front femora.

Male

Head. Eyes touching for a distance about equal to length of vertical triangle. The angle of approximation of eyes 100-110°. Frons and face with bluish to yellowish lustre;

frons slightly shining, face more so. Frontal and facial dusting whitish to yellowish, the hairs mainly blackish. Profile of face rather flat, and central prominence and upper mouth-edge about equally protruding. Jowls and occiput lightly dusted except for upper part of occiput; this part with blackish hairs, occiput and jowls otherwise with whitish-yellow hairs. Antennae normally black (in 2 ♂♂ a faint yellowish spot at base of third joint). Third joint roundish, only slightly longer than deep. Arista black, almost quite bare.

Thorax. Mesonotum and scutellum black with slight metallic lustre, the hairs whitish-yellow. Pleurae shining with faint whitish or yellowish dusting; the hairs equally coloured. Wings lightly greyish tinged, stigma greyish-yellow. Legs predominantly black; femorae yellow at tip, tibiae yellow at base (t_1 with apical ca. $\frac{1}{3}$ yellow), tarsi black with the underside of p_1 dark greyish-yellow. t_1 and t_2 with a few rather long black lateral bristles towards tip. f_1 with some long dark and a few whitish hairs on basal half, and with a row of black bristles on apical half. These bristles

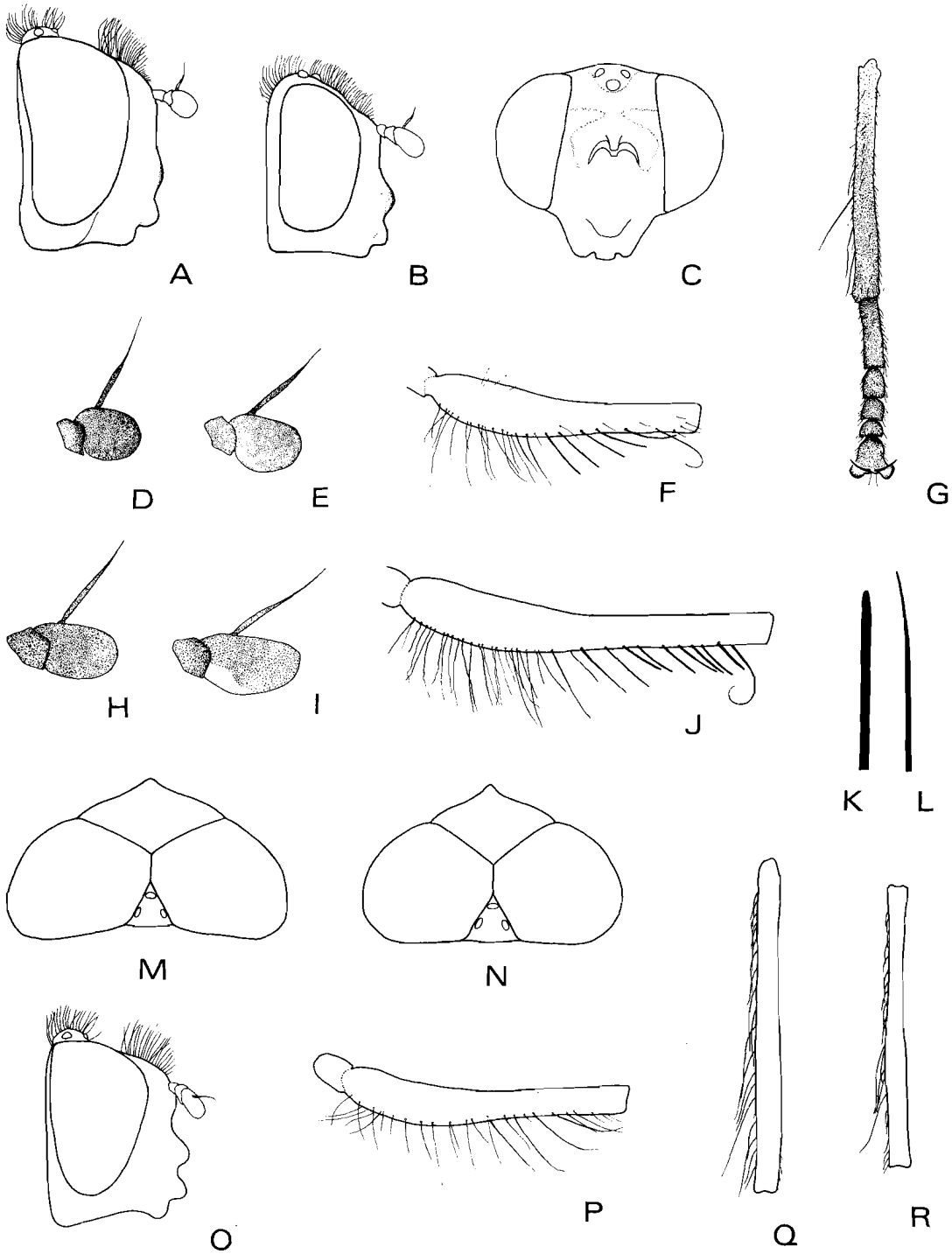


Fig. 1. *Platycheirus fjellbergi* nov. sp. A) Head in profile, male. B) Head in profile, female. C) Head in frontal view, female. D) Antenna, male. E) Antenna, female. F) Front femora, male. G) Right frontal leg of male. H) Antenna, male. I) Antenna, female. J) Front femora, male. K) Bristle of male front femora. L) Hair from anterior half of front femora. M) Male, head seen from above. N) Male, head seen from above. R) Tibia of p_2 , male. *P. ambiguus* Fall. H) Antenna, male. I) Antenna, female. J) Front femora, male. K) Bristle of male front femora. M) Male, head seen from above. *P. hirpites* Kan., male. L) Hair from anterior half of front femora. O) Head in profile. P) Front femora. Q) Tibia of p_2 .

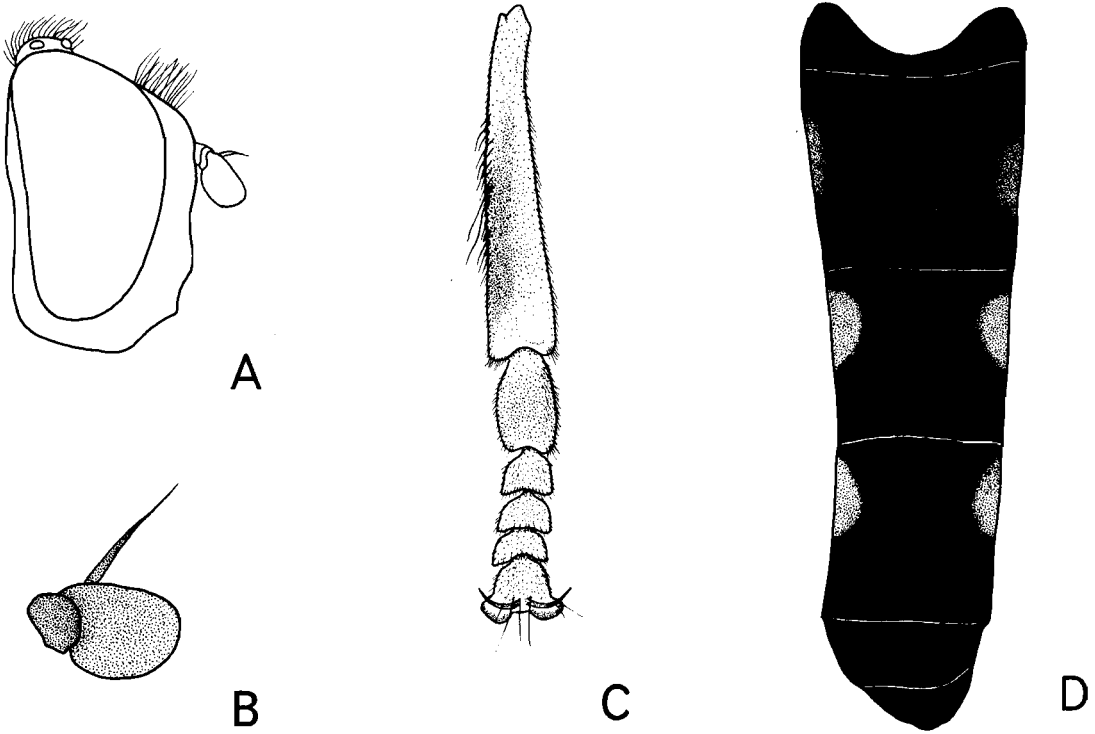


Fig. 2. *Platycheirus angustitarsis* Kan., male. A) Head in profile. B) Antenna. C) Right frontal leg. D) Abdomen.

are decreasing in length towards tip of f_1 . f_1 also with a long curled hair before apex. Squamulae greyish to yellowish-white with posterior rim dark greyish-brown. Halteres greyish-brown with the knob darkened.

Abdomen. Tergites black, slightly shining. The triangular spots of tergite 2-4 bronzy brown with greyish-white dusting. Tergite 5 shining metallic black. The hairs mainly follow the ground-colour of the tergites, lateral hairs rather long and whitish. Sternites pellucid brownish-black with faint whitish dusting, the hairs whitish-yellow.

Female

Head. Vertical triangle and frons glittering black, frons with whitish dusting narrowly along eye-margins and then on the triangular spots in the middle of frons. The hairs black on anterior part of vertical triangle and on upper part of frons, lower part of frons mainly with yellowish hairs. Antennae somewhat larger than in the male, black and with third joint a little longer than deep. Arista

black and almost bare. Face a little more protruding and 'nosy' than in the male, whitish or whitish-yellow dusted except for the facial tubercle, upper mouth-edge, and jowls; the hairs are whitish-yellow. Occiput whitish to whitish-yellow dusted, more yellowish dusted on upper parts; the hair colour mainly follows the colour of the dusting.

Thorax. Mainly as in the male, but mesonotal hairs a little shorter. Wings and legs as in the male, except for the characteristic hairs and bristles of p_1 and p_2 . Squamulae and halteres as in the male.

Abdomen. Tergites shining black with the triangular spots of tergite 2-4 metallic grey, and with much of the same purple and greenish-yellow lustre as in female of *P. ambiguus*. Sternites and abdominal pubescence as in the male.

MATERIAL

The material totals 17 ♂♂ and 15 ♀♀. Holotype: male specimen dated Norway, Spiter-

Table I. A comparison between the sexes of *Platycheirus fjellbergi* nov. sp., *P. ambiguus* Fall. and *P. hirtipes* Kan.

<i>P. fjellbergi</i> nov. sp.	<i>P. ambiguus</i> Fall.	<i>P. hirtipes</i> Kan
♂	♂	♂
Frons not especially broad. Angle at approximation of eyes 100–110°. Fig. 1N.	Frons broad. Angle at approximation of eyes ca. 130°. Fig. 1M.	Frons not especially broad. Angle at approximation of eyes ca. 110°.
Third antennal joint normally black, short and roundish; 1.2 times as long as broad. Fig. 1D.	Third antennal joint brownish-black, often with a yellow spot below at base; 1.6 times as long as broad. Fig. 1H.	Third antennal joint black, short and roundish; 1.2 times as long as broad.
Face and frons rather flat, not much protruding. Fig. 1A.	Face and frons rather flat, profile much resembling that of <i>P. fjellbergi</i> .	Face and frons more protruding, face rather 'nosy'. Fig. 1O.
Mesonotal pubescence whitish-yellow.	Mesonotal pubescence whitish-yellow.	Mesonotal pubescence blackish.
Front tarsi including the last joint black.	Front tarsi greyish-yellow, the last joint often yellow.	Front tarsi including last joint black.
f ₁ black (except tip yellow); apical half with strong, black bristles that decrease in length toward tip of femora. The bristles rounded at their tips. Fig. 1F and 1K. f ₁ also with a long curled bristle just before apex.	f ₁ yellowish, often brownish posterolaterally; apical half with strong, black bristles of about same length. The bristles rounded at their tips. Fig. 1J and 1K. f ₁ also with a long, curled bristle just before apex.	f ₁ black (except tip yellow); apical half with black hairs that are not especially thick. The hairs decrease in thickness towards their tips. Fig. 1P and 1L. f ₁ without any especially curled bristle at apex.
t ₁ laterally with only a few long, black hairs at the middle of tibia. Fig. 1G.	t ₁ laterally with only a few long, yellowish hairs at the middle of tibia.	t ₁ laterally with a long row of isolated black, bristly hairs in practically entire length of tibia.
t ₂ with the lateral hairs just at apex short, the hairs black. Fig. 1R.	t ₂ with the lateral hairs just at apex short, the hairs yellow.	t ₂ with the lateral hairs just at apex long. Fig. 1Q.
Squamulae light greyish, posterior rim greyish-brown.	Squamulae whitish, posterior rim yellow.	Squamulae as in <i>P. fjellbergi</i> .
♀	♀	♀
Antennae black. Third joint short and roundish, 1.4 times as long as deep.	Antennae black, third joint with a yellow spot below at base. It is 1.7 times as long as deep.	Antennae black. Third joint short and roundish, 1.3 times as long as deep.
f ₁ and f ₂ black except for the yellow tip. f ₃ all black.	f ₁ and f ₂ mainly yellow. f ₃ broadly yellow at base.	f ₁ and f ₂ as in <i>P. fjellbergi</i> . f ₃ yellow at tip.
Squamulae greyish-white with posterior rim darker.	Squamulae purely white, posterior rim whitish.	Squamulae with posterior rim whitish-yellow.
Tergites black with the spots rather greyish dusted.	Tergites black with the spots glittering metallic bluish.	Tergites shining metallic black.
Rather small species.	Medium-sized species.	Rather small species.

stulen 1100 m, On: Lom 6 July 1974, Tore Nielsen leg. Allotype: female specimen with the same data. Paratypes: specimens dated Fiskevann, Fø: Sør-Varanger 17 July 1969 (1 ♀), I. & T. Nielsen leg.; Sverige, T. Lpm: Abisko 25 June 1972 (1 ♂), 19 June 1973 (1 ♂, 4 ♀♀), 20 June 1973 (7 ♂♂, 2 ♀♀), 22 June 1973 (3 ♂♂, 2 ♀♀), 27 June 1973 (1 ♂, 1 ♀), Arne Fjellberg leg.; Norway, Valdresflya, On: Ø. Slidre 13 July 1973 (1 ♀) and Spiterstulen, On: Lom 6 July 1974 (3 ♂♂, 3 ♀♀), Tore Nielsen leg.

Holotype, allotype and a number of paratypes are deposited in the collection of the author, and a number of paratypes in the collections of Zoological Museum, University of Bergen, and of A. Fjellberg.

COMPARISON WITH RELATED SPECIES

Platycheirus fjellbergi nov. sp. has been compared with two species it much resembles, the larger *P. ambiguus* Fall., with which it might have been confused, and *P. hirtipes* Kan., which has been found in a neighbouring area of northern Finland and which may show a similar distribution and occurrence (Table I).

PLATYCHEIRUS ANGUSTITARSIS KAN.

This small but characteristic species was described by Kanervo (1934) from material collected in the Petsamo area of the western part of Kola peninsula. It has also been reported from Vajgatsj in northern Siberia (Stackelberg 1970), and finds until now have indicated a distribution on the tundra of the far north.

A find of this species in Jotunheimen (southern Norway) in 1973 was surprising, and shows a quite far extension towards south and west. The specimen, a male, was caught in the upper part of the Leir-

dalen valley (61°36'N, 8°10'E) on 14 July. The locality was a dry alpine slope at 1200 m a.s.l. between mountains rising up to 2000 m or more. The vegetation was dominated by *Cyperaceae*, *Salix*, *Ranunculus acris*, and *Aconitum septentrionale*, and so the locality has probably many of the same conditions as those of the tundra.

The specimen has been found identical with Finnish material, and shows the following characters: face rather flat; t_1 slightly dilated towards tip, front metatarsus scarcely dilated, yellowish, but t_1 with a blackish stripe laterally. Abdomen black, the spots brassy black with slight greyish dusting, those on tergite 2 indistinct (Fig. 2).

Superficially, *P. angustitarsis* looks like a tiny *P. albimanus* Fall. or a dark, rapidly flying *Melanostoma*. In the field it may therefore easily be overlooked or confused with the species mentioned.

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Abundance and diversity in the fauna of nocturnal moths at two sites in South Norway

ALF BAKKE

Bakke, A. 1974. Abundance and diversity in the fauna of nocturnal moths at two sites in South Norway. *Norsk ent. Tidsskr.* 21, 173-184.

From 1969 to 1971, light-trap catches were made every night from early spring until late autumn at Grimstad, 2 km from the coast, and at Åmli, 44 km further north in the inland of South Norway. More than 29 thousand specimens from the families Notodontidae, Saturniidae, Endromididae, Lasiocampidae, Lymantriidae, Drepanidae, Polyplocidae, Noctuidae, Hylophilidae, and Plusiidae, comprising 230 species, were trapped. Numbers of each species caught at the two sites every year are listed. The flight periods of the various species in 1971 are indicated. Comparisons are made with records from the same area about a hundred years ago, between the records from the two sites, and between the records from the various years. An attempt is made to estimate the percentage of the total number of species collected in a year which is likely to be trapped in periods of ten days during the season.

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Human influence on nature has considerably changed the distribution and abundance of plant and animal life during the last century. This has been recorded in many vertebrates. Changes in the composition of the invertebrate fauna are more difficult to notice because very few reports are available on the fauna of earlier times which might have made a comparison possible. This demonstrates the necessity of carrying out faunistic inventory work which can provide a basis for ecological studies of future generations.

Some families of Lepidoptera belong to the groups of insects which faunistically and systematically were studied in Norway during the 19th century. From a few areas faunistic data were published. The southern part of the county of Aust-Agder, on the south coast of Norway, is one of these areas (Schneider 1882).

At two sites in the same area, light-trap catches were made from 1969 to 1971, as part of a bio-climatological programme supported by the Agricultural Research Council of Norway. The objects of the study were to analyse the composition of the fauna based

on a precisely described method, to collect information on the flight periods of the species and on the abundance and diversity of species during the season, to compare the present fauna with the records of earlier periods, especially those of Schneider (1882), to compare the fauna of two sites within the same area, but with different distance from the coast, and to study changes in the abundance of the various species during the three-year period.

MATERIAL AND METHODS

Areas of investigation

The light-traps were situated at two sites in the county of Aust-Agder AAy (Strand 1943) in southern Norway (Fig. 1): one at Dømmesmoen horticultural school, Grimstad, altitude 30 m, approximately 2 km from the coast; the other at Åmli, altitude 150 m, 1 km south of the commercial centre of the community, approximately 37 km from the coast and 44 km north of Grimstad. Both

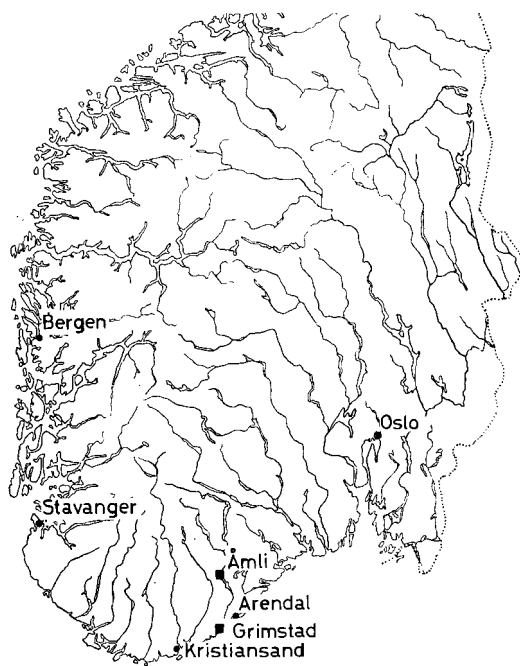


Fig. 1. Map of South Norway indicating the geographical position of the sites, Grimstad and Amli.

sites are surrounded by agricultural fields and forests.

Around the Grimstad site, oak trees, *Quercus robur*, constitute an important part of the forest, but Scots pine, *Pinus sylvestris* and Norway spruce, *Picea abies*, are present in the neighbourhood together with most of the deciduous trees growing in southern Norway. Around the horticultural school is a park area with numerous foreign trees, bushes, and other plants of various kinds. The landscape is rather flat, broken by bedrocks. The trap was sited on a hillock with tall oak trees close by.

At Amli there are only a few oak trees. Spruce and especially pine dominate, but birches, *Betula pubescens*, willows, *Salix* sp., and poplars, *Populus tremula*, are scattered mostly at the edges of the coniferous forests. The site was at the bottom of a valley, 400 m from a river, and surrounded by mountains up to an elevation of 400–500 m. The trap was sited at a south-west facing edge of the forest.

The light-trap

The light-traps were built after the model of Robinson (Robinson & Robinson 1950) with

baffles and a HPL 125 W mercury-vapour bulb. The traps were sited with the bulb at a level of 1 m above the ground.

The catches took place at both sites every night in the following periods: 1969, from 15 April to 30 September; 1970, from 15 April to 30 October; and 1971, from 10 April to 8 November.

The moths were anaesthetized and killed by acetyltetrachloride when they entered the trap.

The catches

The material from each night was collected in paper bags. The following identifications were made: all specimens of the families Notodontidae, Saturniidae, Endromiidae, Lasiocampidae, Lymantriidae, Drepanidae, Ploceidae, grouped under the name Bombyces, and Noctuidae, Hylophilidae, Plusiidae grouped under the name Noctuoidea. The nomenclature follows Opheim (1958, 1962). A total number of 29,128 specimens comprising 230 species is included in the material, 15,405 specimens from Grimstad and 13,626 from Amli.

RESULTS

The total number of moths of each species collected every year at the two sites is presented in Table I. Thirty-eight species of Bombyces were recorded. The number of species was 32 on both sites, but only 26 were found on both sites. Twelve species were recorded only on one of the sites, six on each. Two were recorded for the first time in Norway; *Selenephra lunigera* Esp., 5 specimens, Amli 1970 (Bakke 1971), and *Drymonia trimacula* Esp., 9 specimens, Grimstad 1971. *Parmelina ridens* F., recorded for the first time in Norway in 1969 (Bakke 1970) at a locality close to Grimstad, was found at Grimstad 1970 (7 specimens) and 1971 (2 specimens).

A total species number of 192 Noctuoidea was recorded, 175 species at Grimstad and 157 at Amli. Sixteen species were found at Amli, but not at Grimstad, and 34 at Grimstad, but not at Amli. *Erastria trabealis* Sc. was new to the Norwegian fauna (Bakke 1970), and 20 species were recorded in Aust-Agder for the first time.

Table I. Number of moths trapped at Grimstad and Åmli

	Grimstad			Åmli		
	1969	1970	1971	1969	1970	1971
Bombyces						
Notodontidae						
<i>Cerura furcula</i> L.					1	
<i>C. hermelina</i> Goeze				2	3	
<i>C. vinula</i> L.			1	1		
<i>Staurophus fagi</i> L.		1	1			
<i>Drymonia ruficornis</i> Hufn.	1	3	6			
<i>D. trimacula</i> Esp.			9			
<i>Pheosia tremula</i> Cl.	1	4	27	3	3	4
<i>P. gnoma</i> F.	16	11	28	2	4	11
<i>Notodonta ziczac</i> L.		1	1	2	1	
<i>N. dromedarius</i> L.	2	3	1	3		2
<i>N. anceps</i> Goeze	8	2	14	1	1	
<i>Odontosia carmelita</i> Esp.			1	1	4	4
<i>O. sieversi</i> Mén.					1	1
<i>Lophopteryx capucina</i> L.	3	1		1	1	1
<i>Pterostoma palpinum</i> L.	1	1	2	11	10	5
<i>Ptilophora plumigera</i> Esp.			3		1	9
<i>Phalera bucephala</i> L.		2	1			
<i>Pygaera curtula</i> L.	6	5	1	13	12	20
<i>P. pigra</i> Hufn.	1					9
Saturniidae						
<i>Saturnia pavonia</i> L.		1				1
Endromididae						
<i>Endromis versicolora</i> L.				2		2
Lasiocampidae						
<i>Trichiura crataegi</i> L.	3	1	2	39	15	8
<i>Poecilocampa populi</i> L.		45	57		1	66
<i>Lasiocampa quercus</i> L.			1	9		2
<i>L. trifolii</i> Esp.		1				
<i>Macrothylacia rubi</i> L.	1	1	3	3	4	6
<i>Selenephera lunigera</i> Esp.					5	
<i>Epicnaptera ilicifolia</i> L.			3	5	9	7
<i>Dendrolimus pini</i> L.	1	2		4	1	
Lymantriidae						
<i>Leucoma salicis</i> L.	3	1		2	7	1
<i>Lymantria monacha</i> L.	1					
Drepanidae						
<i>Drepana lacertinaria</i> L.	1			9	1	2
<i>D. falcataria</i> L.	4		1	11	4	1
Polyplocidae						
<i>Tethea</i> or Schiff.	7		1	31	12	5
<i>T. fluctuosa</i> Hb.	1	1	2			
<i>T. duplaris</i> L.				1		
<i>Achlya flavicornis</i> L.	2	9	1	13	55	26
<i>Parmelina ridens</i> F.		7	2			
Noctuoidea						
Noctuidae						
<i>Colocasia coryli</i> L.				1	4	6
<i>Episema caeruleocephala</i> L.			1			
<i>Apatele leporina</i> L.				3	1	
<i>A. megacephala</i> Schiff.	3			1		3
<i>A. psi</i> L.	5			1		1
<i>A. menyanthidis</i> View.	1				5	
<i>A. auricoma</i> F.		1	3			1
<i>A. rumicis</i> L.	39	8	9	40	29	15
<i>Cranioophora ligustri</i> Schiff.	18	2				
<i>Cryphia divisa</i> Esp.	4		2	1		1
<i>Euxoa recussa</i> Hb.					1	

	Grimstad			Åmli		
	1969	1970	1971	1969	1970	1971
<i>E. obelisca</i> Schiff.			39			
<i>E. cursoria</i> Hufn.	} 92	48	2	} 6	9	19
<i>E. nigricans</i> L.			16			
<i>E. tritici</i> L.			34			
<i>Agrotis ypsilon</i> Rott.			3			
<i>A. segetum</i> Schiff.	9	21	15		3	1
<i>A. clavis</i> Hufn.	26	18	17	1		1
<i>A. vestigialis</i> Rott.	4	2	3	1	1	
<i>A. exclamationis</i> L.	952	410	173	1127	621	92
<i>Lycophotia varia</i> Vill.	17	9	3	14	11	8
<i>Actebia praecox</i> L.	1					
<i>Epipsilia grisescens</i> F.			1			
<i>Chersotis cuprea</i> Schiff.	1	1	3	69	103	145
<i>Spaerlotis ravidata</i> Schiff.			2			
<i>Coenophila subrosea</i> Steph.			2	14	51	11
<i>Graphiphora augur</i> F.	28	12	30	14	32	24
<i>Diarsia brunnea</i> Schiff.	13	30	79	12	31	29
<i>D. festiva</i> Schiff.	7	6	12	7	1	10
<i>D. rubi</i> View.	27	15	4	26	28	16
<i>Ochropleura plecta</i> L.	48	8	7	80	28	15
<i>Amathes glareosa</i> Esp.	17	5	18			
<i>A. baja</i> Schiff.	128	38	230	75	83	104
<i>A. c-nigrum</i> L.	31	31	34	11	13	4
<i>A. triangulum</i> Hufn.	187	16	151	14	6	1
<i>A. sexstrigata</i> Haw.	17	1	39	8	7	25
<i>A. xanthographa</i> Schiff.	39	2	48	3	9	
<i>Anomogyna speciosa</i> Hb.				5		1
<i>Axylia putris</i> L.	59	41	47			
<i>Anaplectoides prasina</i> Schiff.	5	4	11		4	3
<i>Eurois occulta</i> L.	12	19	11	17	27	5
<i>Cerastis rubricosa</i> Schiff.	6	15	8	3	49	23
<i>C. sobrina</i> B.	2			1	4	15
<i>Ammocomia caecimacula</i> Schiff.	2		2	4		
<i>Noctua orbona</i> Hufn.	2		1			
<i>N. pronuba</i> L.	251	164	869	29	18	32
<i>N. fimbriata</i> Schreb.	5		2			
<i>Actinotia polyodon</i> Cl.	9		8	25	17	9
<i>Scotogramma trifolii</i> Rott.	12	17	80	10		
<i>Mamestra brassicae</i> L.	10	8	3		2	
<i>M. contigua</i> Schiff.				2	3	5
<i>M. thalassina</i> Hufn.	21	18	17	45	37	32
<i>M. suasa</i> Schiff.	98	36	16	134	191	110
<i>M. oleracea</i> L.	314	58	105	25	13	10
<i>M. pisi</i> L.	5	7	4	20	6	4
<i>M. nana</i> Hufn.	1	2		174	144	26
<i>M. glauca</i> Hb.	5			14	4	
<i>M. bicolorata</i> Hufn.		1			3	3
<i>Hadena rivularis</i> F.				28	14	20
<i>H. lepida</i> Esp.	1	1	1	72	43	30
<i>H. bicrusis</i> Hufn.	8	3		15		
<i>H. conspersa</i> Schiff.	11		1	50	13	3
<i>Polia nitens</i> Haw.	16	30	33	38	84	19
<i>P. hepatica</i> Cl.	1	1		23	30	5
<i>P. nebulosa</i> Hufn.	32	12	5	4	1	1
<i>Heliophobus reticulata</i> Vill.	22	4	3	220	93	76
<i>Tholera popularis</i> F.	4	2	2	6	8	2
<i>T. cespitis</i> Schiff.	21	31	49	48	65	95
<i>Cerapteryx graminis</i> L.	302	107	165	280	220	465
<i>Lasionycta proxima</i> Hb.				4	12	1
<i>Orthosia gothica</i> L.	48	87	62	228	475	192
<i>O. populi</i> Strøm	2	12	1	13	1	1
<i>O. miniosa</i> Schiff.	1	2	1			
<i>O. stabilis</i> Schiff.	27	80	38	3	8	
<i>O. cruda</i> Schiff.	30	176	387		2	2

	Grimstad			Ämli		
	1969	1970	1971	1969	1970	1971
<i>O. incerta</i> Hufn.	4	14	11	41	67	34
<i>O. advena</i> Schiff.		2	2	8	38	14
<i>O. gracilis</i> Schiff.	2	3	5		1	
<i>Panolis flammea</i> Schiff.			2	1	11	5
<i>Leucania lithargyria</i> Esp.	22	3	13	4		5
<i>L. conigera</i> Schiff.	259	114	142	75	88	40
<i>L. comma</i> L.	28	9	2	138	40	26
<i>L. impura</i> Hb.	125	47	57	60	54	43
<i>L. pallens</i> L.	69	39	27	23	23	26
<i>L. obsoleta</i> Hb.			1			
<i>Cucullia umbratica</i> L.	2			4		
<i>Calophasia lunula</i> Hufn.		3	2		7	
<i>Brachionycha nubeculosa</i> Esp.				1	9	1
<i>Dasytoplia templi</i> Thnbg.		1	5	4	1	4
<i>Bombycia viminalis</i> F.	91	14	27	119	40	21
<i>Lithomoia solidaginis</i> Hb.	8	1	1	17	5	10
<i>Lithophane socia</i> Hufn.		1	3			2
<i>L. lamda</i> F.		1		1	3	4
<i>L. furcifera</i> Hufn.			1		1	
<i>L. ingrica</i> H.-S.	1	1	6		7	5
<i>Xylina vetusta</i> Hb.	13	10	7	16	27	21
<i>Xylocampa areola</i> Esp.	5	5	3			
<i>Allophyes oxyacanthae</i> L.	4	5	9	89	7	19
<i>Calotaenia celsia</i> L.	10	11	11	14	7	10
<i>Eumichtis satura</i> Schiff.	53	28	58	7	1	3
<i>E. adusta</i> Esp.	16		1	73	1	4
<i>Griposia aprilina</i> L.	3	12	16	2		4
<i>Dryobotodes eremita</i> F.			2	1	1	5
<i>Antitype gemmea</i> Tr.	15	9	8	36	53	38
<i>A. chi</i> L.		9	1		1	1
<i>Eupsilia transversa</i> Hufn.	18	34	18	4	26	10
<i>Conistra vau-punctata</i> Esp.	1	3	15			
<i>C. vaccinii</i> L.	25	60	38	26	166	87
<i>C. rubiginea</i> Schiff.						1
<i>Agrochola lota</i> Cl.		1	7	1	1	7
<i>A. macilenta</i> Hb.		2	15		2	10
<i>A. circellaris</i> Hufn.	1	1		1		6
<i>A. helvola</i> L.	24	24	54	25	5	27
<i>A. litura</i> L.	17	15	39	36	5	39
<i>Parastichtis suspecta</i> Hb.	2	1	1	14	24	10
<i>Cirrhia aurago</i> Schiff.			1			1
<i>C. lutea</i> Ström.	2	5	22	20	10	59
<i>C. icteritia</i> Hufn.	4	5	10	18	19	30
<i>C. citrigo</i> L.		1				
<i>Amphipyra perflua</i> F.	8	5	27	2	15	12
<i>A. tragopogonis</i> L.	14	8	18	22	6	6
<i>Rusina tenebrosa</i> Hb.	40	9	18	82	48	60
<i>Dipterygia scabriuscula</i> L.	28	6	5		1	2
<i>Apamea sublustris</i> Esp.	1	1		1	1	1
<i>A. monoglypha</i> Hufn.	22	28	28	29	15	4
<i>A. crenata</i> Hufn.	18	12	2	33	21	
<i>A. lateritia</i> Hufn.	73	20	25	43	31	24
<i>A. remissa</i> Hb.	23	12	10	12	10	5
<i>A. illyria</i> Frr.		2	1	1	4	1
<i>A. unaminis</i> Hb.					1	1
<i>A. sordens</i> Hufn.	1					
<i>A. ophiogramma</i> Esp.	2				1	
<i>A. secalis</i> L.	95	25	37	27	32	3
<i>A. furva</i> Schiff.		6	5			
<i>A. rubirena</i> Tr.				6	6	
<i>Procus strigilis</i> L.	39	26	8	91	17	13
<i>P. latrunculus</i> Schiff.	9	3				
<i>P. fasciunculus</i> Haw.	10	3	1	62	23	2
<i>P. literosus</i> Haw.				5		

	Grimstad			Åmli		
	1969	1970	1971	1969	1970	1971
<i>Luperina testacea</i> Schiff.	31	38	114		1	
<i>Trachea atriplicis</i> L.	15	19	16			
<i>Euplexia lucipara</i> L.	27	6	11	27	12	8
<i>Phlogophora meticulosa</i> L.			1			
<i>Thalpophila matura</i> Hufn.	3		5			
<i>Hyppa rectilinea</i> Esp.					1	1
<i>Caradrina morpheus</i> Hufn.	} 534	348	521	} 8	14	6
<i>C. alsines</i> Brahm			22			
<i>C. superstes</i> O.			40			
<i>C. cinerascens</i> Tngstr.	8	5	3	56	14	21
<i>C. selini</i> B.					1	
<i>C. clavipalpis</i> Scop.	3		1			
<i>Petilampa minima</i> Haw.	8	17	2			
<i>Celaena haworthii</i> Curt.			1	1	3	3
<i>C. leucostigma</i> Hb.		2	3			2
<i>Hydraecia oculea</i> L.						
<i>H. fucosa</i> Frr.	} 469	408	421	19	7	22
<i>H. lucens</i> Frr.						
<i>H. crinanensis</i> Burr.						
<i>Gortyna micacea</i> Esp.	285	95	159	430	182	180
<i>Zenobia subtusa</i> F.		1		2	1	1
<i>Cosmia trapezina</i> L.	181	47	210	76	35	10
<i>Enargia paleacea</i> Esp.	6	5	11	25	27	33
<i>Rhizedra lutosa</i> Hb.		2	1			
<i>Arenostola phragmitidis</i> Hb.	1		1			
<i>A. fluxa</i> Hb.			6			
<i>A. pygmina</i> Haw.	5	3	5	18	8	5
<i>Pyrrhia umbra</i> Hufn.					1	1
Hylophilidae						
<i>Bena prasinana</i> L.	11	1	2	2		
<i>Pseudoips bicolorana</i> Fuessl.			2			
<i>Nycteola degenerana</i> Hb.				1	1	9
Plusiidae						
<i>Erastria trabealis</i> Se.	1					
<i>Catocala fraxini</i> L.	2	6	4	5	1	13
<i>Plusia interrogationis</i> L.			1	8	20	3
<i>P. festucae</i> L.	3			8	1	1
<i>P. bractea</i> Schiff.	36	7	6	27	12	8
<i>P. chrysitis</i> L.	128	20	41	129	52	35
<i>P. iota</i> L.	1	1		2		
<i>P. pulchrina</i> Haw.	100	29	18	220	43	24
<i>P. gamma</i> L.	97	71	43	72	27	9
<i>P. confusa</i> Steph.	1	2		1		1
<i>Polychrysis moneta</i> F.	9		1	4		
<i>Unca triplasia</i> L.	2				1	
<i>U. tripartita</i> Hufn.	1			3	2	3
<i>Scoliopteryx libatrix</i> L.			1	2	1	
<i>Lygephila cracca</i> Schiff.				1		
<i>Laspeyria flexula</i> Schiff.	2	4	1	1	2	
<i>Rivula sericealis</i> Scop.	15	3	1			
<i>Zanclognatha tarsipennalis</i> Tr.	1	7	9		2	
<i>Z. nemoralis</i> F.	1	1	1			
<i>Herminia derivalis</i> Hb.	10	1	1			
<i>Bomolocha fontis</i> Thnbg.	1	1		1	2	
<i>Hyppa proboscidalis</i> L.	12	8	3	16	4	4

Not all moths of the genus *Hydraecia* are identified to species because of the difficulties in giving correct identification (Knaben 1956). But all four species given in the list are

identified in the material from both localities. The *Euxoa* species and *Caradrina morpheus*, *C. alsines* and *C. superstes* were probably not correctly identified in 1969 and 1970. Only

Åmli, Norway 1971.

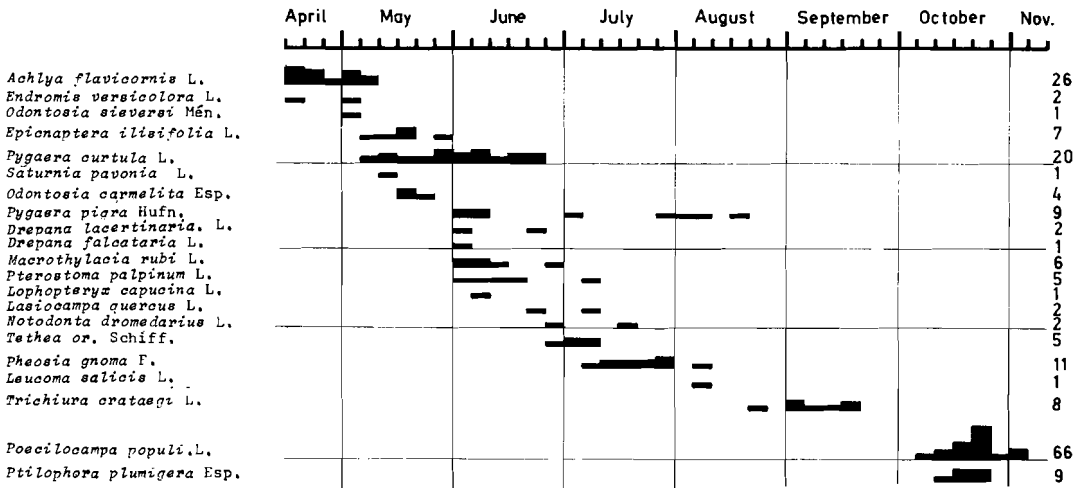


Fig. 2. The flight periods of Bombyces at Åmli in 1971. The columns are based on a logarithmic scale, $y = 1 + 3 \log n$. Figures to the right indicate the total number of individuals caught during the season.

the number of specimens of the genera is therefore presented in Table I.

The light-trap catches of Bombyces at Åmli in 1971, and of Noctuoidea at Grimstad in 1971 are given in Figs. 2 and 3. The numbers of individuals of each species caught in the course of the year are summarized. Each month is divided in six periods of five days starting from 15 April. The last periods of May, July, August, and October have six days. To obtain comparable units, the total amount of the six-day periods is reduced by the number equal to one daily average.

DISCUSSION

The fauna of the area

The southern part of Aust-Agder county (AAy) is estimated to be one of the districts of Norway with the most diverse lepidopterous fauna (Opheim 1958, 1962). The reason for this may be the mild climate and the great variety of plants (Murdock et al. 1972).

Opheim (1958) listed 57 species of Bombyces from Norway. The present investigation adds three new species giving a total of 60 species. In AAy 52 species were recorded, and 38 species were found in the light-trap catches. By 1973, 305 species of Noctuoidea

had been recorded from Norway. Opheim (1962) listed 289 species and 15 have been added in recent years, one as a result of the present study. In AAy 235 species were recorded, and 192 of those (82%) were caught in the light-traps at Grimstad and Åmli. Pulliainen (1965) studied the noctuid fauna at Varkaus in South Finland (1960-63) and listed 107 species.

The lepidopterous fauna is influenced by species with a southern continental distribution. Species with their main range in central Europe, like *Drymonia ruficornis* Hufn., *D. trimacula* Esp., *Notodonta anceps* Goeze, *Parmelina ridens* F., *Orthosia miniosa* Schiff., *Xylocampa areola* Esp., *Conistra vau-punctatum* Esp., *Luperina testacea* Schiff., *Thalophila matura* Hufn. and *Griposia aprilina* L. clearly indicate this. Nevertheless, some more northern species are part of the fauna, e.g. *Selenophera lunigera* Esp., *Anomogyne speciosa* Hb., *Chersotis cuprea* Schiff. and *Apamea rubrivena* Tr. (Nordstrøm et al. 1961, 1969).

Flight periods

The flight periods of the various species are indicated in Figs. 2 and 3.

Some species had two flight periods during 1971. This indication of two generations

Grimstad, Norway 1971

	April	May	June	July	August	September	October	November	
<i>Orthosia cruda</i> Schiff.	■	■	■	■					387
<i>Orthosia gotica</i> L.	■	■	■	■					62
<i>Orthosia incerta</i> Hufn.	■	■	■	■					11
<i>Ceraestia rubricosa</i> Schiff.	■	■	■	■					8
<i>Eupsilia transversa</i> Hufn.	■	■	■	■					18
<i>Conistra vaccinii</i> L.	■	■	■	■					38
<i>Lithophane inopica</i> H.-S.	■	■	■	■					6
<i>Lithophane socia</i> Hufn.	■	■	■	■					3
<i>Xylina vetusta</i> Hb.	■	■	■	■					7
<i>Orthosia stabilis</i> Schiff.	■	■	■	■					38
<i>Conistra vau-punctatum</i> Esp.	■	■	■	■					15
<i>Orthosia miniosa</i> Schiff.	■	■	■	■					1
<i>Lithophane furcifera</i> Hufn.	■	■	■	■					1
<i>Orthosia advena</i> Schiff.	■	■	■	■					2
<i>Orthosia gracilis</i> Schiff.	■	■	■	■					5
<i>Xylocampa areola</i> Esp.	■	■	■	■					3
<i>Orthosia populi</i> Ström	■	■	■	■					1
<i>Panolis flammea</i> Schiff.	■	■	■	■					2
<i>Scolecoperyx libatrix</i> L.	■	■	■	■					1
<i>Actinotia polydon</i> Ci.	■	■	■	■					8
<i>Hadena lepida</i> Esp.	■	■	■	■					1
<i>Manestra thalassina</i> Hufn.	■	■	■	■					17
<i>Agrotis exclamationis</i> L.	■	■	■	■					173
<i>Anaplectoides prasinana</i> L.	■	■	■	■					2
<i>Apatele ruficosta</i> L.	■	■	■	■					9
<i>Caradrina morphoea</i> Hufn.	■	■	■	■					521
<i>Euplexia lucipara</i> L.	■	■	■	■					11
<i>Calophasia lunula</i> Hufn.	■	■	■	■					2
<i>Trachea atriplicis</i> L.	■	■	■	■					16
<i>Manestra oleraceae</i> L.	■	■	■	■					105
<i>Manestra euasa</i> Schiff.	■	■	■	■					16
<i>Manestra brassicae</i> L.	■	■	■	■					3
<i>Dipterygia scabriuscula</i> L.	■	■	■	■					5
<i>Amathes c-nigrum</i> L.	■	■	■	■					34
<i>Rusina tenebrosa</i> Hb.	■	■	■	■					18
<i>Plusia pulchrina</i> Haw.	■	■	■	■					18
<i>Agrotis segetum</i> Schiff.	■	■	■	■					16
<i>Apatele auricoma</i> F.	■	■	■	■					3
<i>Leucania oomma</i> L.	■	■	■	■					2
<i>Apamea crenata</i> Hufn.	■	■	■	■					2
<i>Amathes triangulum</i> Hufn.	■	■	■	■					159
<i>Manestra pisi</i> L.	■	■	■	■					4
<i>Leucania obsoleta</i> Hb.	■	■	■	■					1
<i>Zanclognatha nemoralis</i> F.	■	■	■	■					1
<i>Azylia putris</i> L.	■	■	■	■					47
<i>Heliothobus reticulata</i> Vill.	■	■	■	■					3
<i>Plusia chryseitis</i> L.	■	■	■	■					41
<i>Hadena conspersa</i> Schiff.	■	■	■	■					1
<i>Caradrina seleni</i> B.	■	■	■	■					3
<i>Diarzia brunnea</i> Schiff.	■	■	■	■					79
<i>Agrotis clavus</i> Hufn.	■	■	■	■					17
<i>Caradrina alsinea</i> Brakm.	■	■	■	■					22
<i>Diarzia rubi</i> View.	■	■	■	■					4
<i>Polia nebulosa</i> Hufn.	■	■	■	■					5
<i>Apamea illyria</i> Frr.	■	■	■	■					1
<i>Polia nitens</i> Haw.	■	■	■	■					33
<i>Apamea remissa</i> Hb.	■	■	■	■					10
<i>Cerapteryx graminis</i> L.	■	■	■	■					165
<i>Plusia gamma</i> L.	■	■	■	■					43
<i>Euxoa tritici</i> L.	■	■	■	■					34
<i>Leucania conipera</i> Schiff.	■	■	■	■					142
<i>Apamea secalis</i> L.	■	■	■	■					37
<i>Amathes baja</i> Schiff.	■	■	■	■					230
<i>Noctua pronuba</i> L.	■	■	■	■					869
<i>Apamea lateritia</i> Hufn.	■	■	■	■					25
<i>Apamea monophylla</i> Hufn.	■	■	■	■					28
<i>Ochropleura plecta</i> L.	■	■	■	■					7
<i>Lycophobia varia</i> Vill.	■	■	■	■					3
<i>Leucania pallens</i> L.	■	■	■	■					27

Grimstad, Norway 1971. cont.

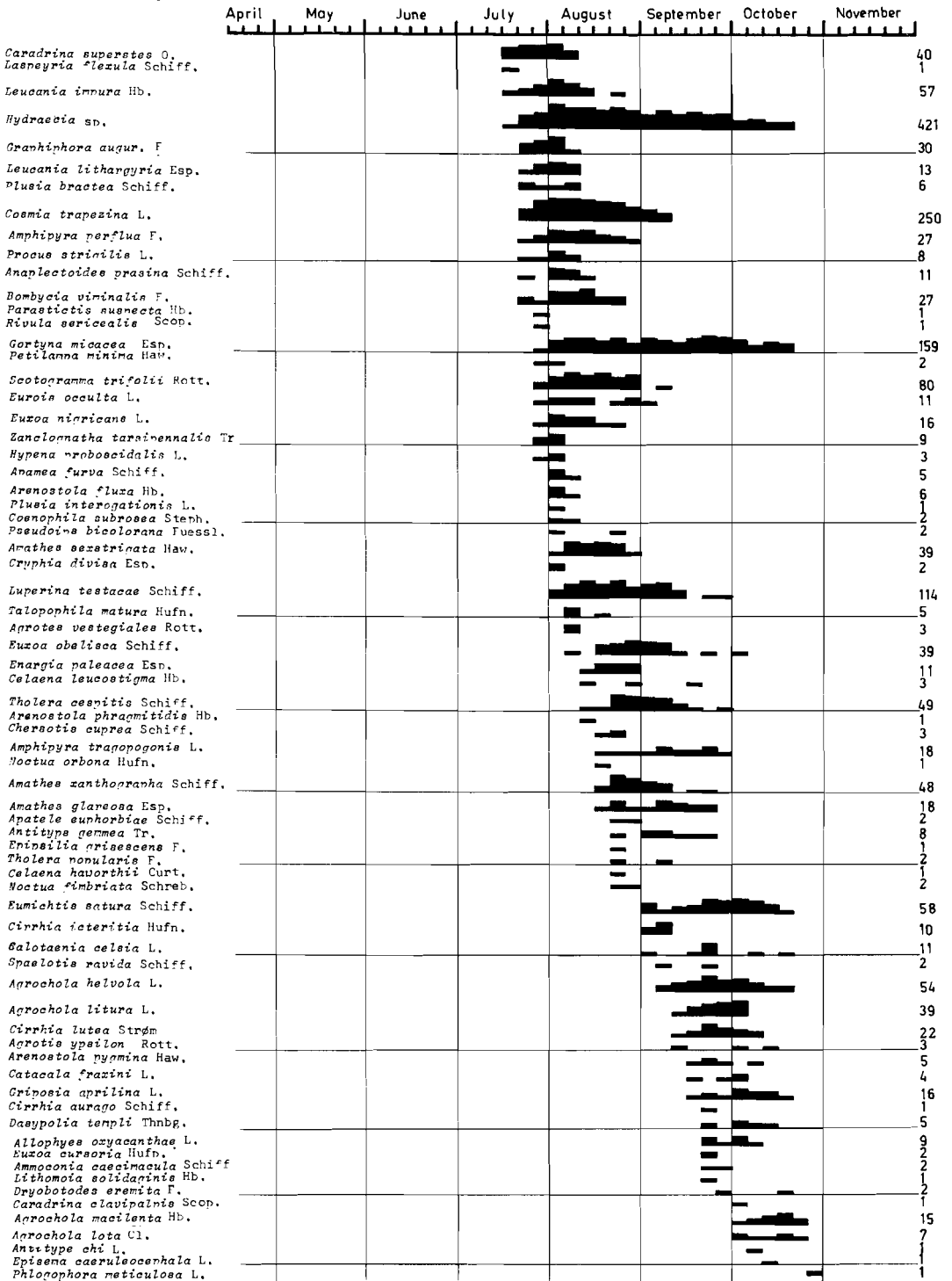


Fig. 3. The flight periods of Noctuoidea at Grimstad in 1971. The columns are based on a logarithmic scale, $y = 1 + 3 \log n$. Figures to the right indicate the total number of individuals caught during the season.

every year can be registered for *Pygaera pigra* Hufn., *Agrotis segetum* Schiff., *Amathes c-nigrum* L., *Mamestra oleraceae* L., *Diarsia rubi* View, and *Plusia gamma* L.

A late autumn flight and early spring flight, indicating hibernation at the adult stage, are demonstrated for *Eupsilia transversa* Hufn., *Conistra vaccini* L., *C. vaupunctatum* Esp., *Litophane ingraca* H.-S., and *Xylina vetusta* Hb. Records from Åmli 1971 indicate that *Dasypolia templi* Thunbg. and *Litophane lamda* F. belong to this group as well.

The flight periods are spread over the season from April until October. Most species are flying in July and August, but there are also species flying only in early spring or late autumn. To describe the fauna in an area therefore requires trapping several times during the year. An analysis of the species diversity in the caught material at various times during the seasons is important for planning faunistic investigation. An attempt was therefore made to find how high a percentage of the total number of species which were found during the season could be trapped in periods of ten days. Figs. 4 and 5 demonstrate the results when Bombyces species and Noctuid-species are separated. The figures give the average catches at Grimstad and Åmli of all three years. The highest percentage of Noctuids (40 %) was trapped in the last period of July, while the middle part of June produced most species of Bombyces (26 %). The number of species caught during a limited period depends on the size of the material in the catches (Fisher et al. 1943) – the more individuals the higher the number of species. Light-trap efficiency therefore influences the number of species which are caught in a limited period. It was not intended that the project should study the efficiency of catching lepidoptera by means of light-trapping. Many objections can therefore be made against the methods and material when used for that purpose. However, based on the Noctuid material from the light-trap model used in this study it is possible to draw some conclusions which at least may have validity for the coast region of southern Scandinavia. If we have to choose one period, the best one is undoubtedly the last part of July. About 40 % of the species can be expected to be in the catches at this

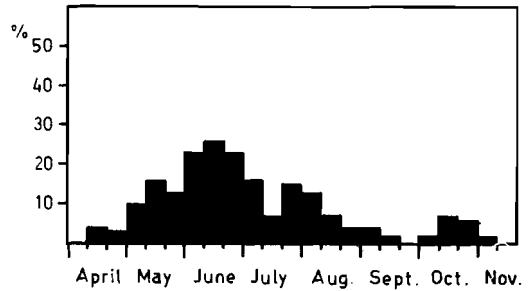


Fig. 4. Percentage of species of the population of Bombyces likely to be trapped in 10-day periods during the season.

time. If two catching periods are possible, the first one should be chosen in late June and the other one in early August – this would give approximately 60 %. Four periods are necessary to cover the early spring species, the early and late summer species, and the late autumn species. Trapping periods in the first part of May, last part of June, first part of August, and first part of October should give approximately 80 % of the population in the area.

The number of Bombyces which were caught in the same four periods amounted to only about 46 % of the species (Fig. 4). The best four periods for catching Bombyces are the middle of May, the middle of June, first part of August, and middle of October, which should give approximately 64 % of the species. This estimation is based on the assumption that different species are flying in the four periods, which may not always be true. A minor reduction of the figures may therefore be necessary.

Comparison with records from the same area 100 years ago

The lepidopterous fauna of the southern part of Aust-Agder was relatively well studied during the second part of the 19th century. Mr. Nicolai Aall, who lived at Nes Jernverk in Holt, collected insects of various groups and made a considerable collection (Natvig 1943). One of the best lepidopterologists in Norway at that time, J. Sparre Schneider, spent four seasons together with him (1872, 1873, 1875, 1876), collecting butterflies and moths in the surroundings. His collecting

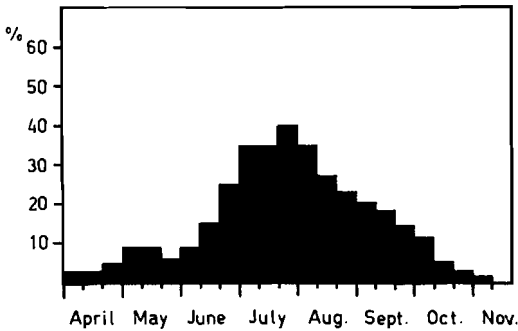


Fig. 5. Percentage of species of the population of Noctuoidea likely to be trapped in 10-day periods during the season.

activity covered the period from 22 June until 5 September. The result of his investigations, also including material from Aall's collection, was published (Schneider 1882). The publication gives one of the most comprehensive registers of lepidoptera from any part of Norway in this century. The registration of Schneider and Aall was mainly based on catching with net and rearing larvae. Their methods were hardly as effective for most nocturnal species as the light-trap catches of today. On the other hand, the diurnal species and the nocturnal species which are not attracted to light, are included in their material, but not in light-trap catches. Schneider (1882) gave no exact data for the abundance of the species. He only mentioned if the species were common or rare.

Therefore, a comparison of the fauna based on different methods cannot be made without many reservations. However, some simple conclusions can be made. Schneider (1882) mentions 28 species of Bombyces. Of these, *Aglia tau* L. and *Orgia antiqua* L. were not recorded in the light-trapped material because they are diurnal species. *Thyatria batis* L. was found in light-traps at Bjelland, Tromøy July 1968 and at Flageborg, Øyestad July 1969. This is less than 30 km from Grimstad as well as from Nes Verk, where Schneider collected most of this material. *Eriogaster lanestris* L. is the only Bombyces species which has not been recorded in the area in recent years. The light-trap catches gave 38 species, of which 14 were not mentioned by Schneider (1882). This is a 50% increase in number of species compared to what he found.

Schneider (1882) mentioned 112 Noctuid species, of which 12 were not caught in the light-traps. Five of these are diurnal species. They have all been recorded in the area in recent years. Five were recorded by the author in light-traps at other sites in the area. Only one species, *Catocola nupta* L., has not been seen in the area during the last 30 years. The light-trap catches gave 12 Noctuid species, of which 93 were not mentioned by Schneider. This is a 91% increase in the number of species compared to Schneider's records.

Comparison between the two sites

Great similarities can be seen in the fauna composition of the two sites. This was expected because of the short distance (44 km) between the sites. But some differences are easy to find in the material. Some species are more abundant at Grimstad, the southernmost site, e.g. *Agrotis segetum* Schiff., *Amathes glareosa* Esp., *Axyليا putris* L., *Luperina testacea* Schiff. and *Orthosia cruda* Schiff. These are all species with southern distribution in Fennoscandia (Nordstrøm et al. 1969). The higher number of species at Grimstad is due to the influence of these southern species.

The first group of species more abundant at Åmli, are *Mamestra nana* Hufn., *Hadena rivularis* F., *H. lepida* Esp., and *Polia hepatica* Cl., which are widely distributed in Fennoscandia and Denmark (Nordstrøm et al. 1969). Local variation must be the reason why they are more common at Åmli than at Grimstad, because both sites are within their main range. The other groups are species like *Cersotis cuprea* Schiff., *Coenophila subrosea* Schiff., *Brachionycha nubeculosa* Esp. and *Lasionycta proxima* Hb. which are northern and high altitude species whose southern limit is the coastal area of Southern Norway.

Changes in the population levels of some species

The population level of some species changed during the three-year period. Some species declined. This is distinctly pronounced in *Agrotis exclamationis* L., *Heliophobus reticulata* Vill., *Ochropleura plecta* L. and *Apantele rumicis* L. in both sites. Other species increased in number, for instance *Orthosia cruda* Schiff. and *Luperina testacea* Schiff.

In some species it is also possible to see either the bottom level or the top level of a fluctuation curve in the second year. However, the period is too short to demonstrate reliable fluctuation trends.

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Spinosellina forms of *Sminthurides schoetti* (Axelson) and *S. parvulus* (Krausbauer) (Collembola) in Norway

ARNE FJELLBERG

Fjellberg, A. 1974. *Spinosellina* forms of *Sminthurides schoetti* (Axelson) and *S. parvulus* (Krausbauer) (Collembola) in Norway. *Norsk ent. Tidsskr.* 21, 185–186.

An examination of specimens of *Sminthurides schoetti* and *S. parvulus* killed just before moulting has proved that the thorn-like setae in the basal part of dens is a juvenile trait of the genus *Sminthurides*.

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Palissa (1961) described the new species *Sminthurides dento-spinalis* from Germany for which he created the new subgenus *Spinosellina* Palissa, 1965 (syn. *Spinosella* Palissa, 1961 nec Vosmaer, 1885) characterized by two strong basoventral thorns on dens. Murphy (1960) had published observations of similar juvenile *Sminthurides* from Wales, and Lawrence (1963) presented additional material from England and Ireland. As all these specimens were juvenile he supposed that they might be immature *S. malmgreni* (Tullberg), whose adults occurred associated with the *Spinosellina* forms. The assumption that *Spinosellina* is juvenile *Sminthurides* was supported by Hüther (1967) with material from Germany, Spain, and Sudan.

From the Stigstuv area (1200 m a.s.l.), on the high mountain plateau of Hardangervidda in SW Norway, I collected several juvenile *Sminthurides* that possess the basal thorns of *Spinosellina*. Fortunately some of the specimens were killed just before moulting, so the cuticula of the present and the coming instar can be studied on the same individual. It was found that the coming in-

star has normal, slender setae just beneath the thick basal thorns of dens. This fact proves that the *Spinosellina* character is a juvenile trait of *Sminthurides* (Fig. 1).

A careful examination of the moulting specimens shows that both *S. schoetti* and *S. parvulus* have juvenile *Spinosellina* forms. *S. schoetti* has 2 basal thorns on dens while *S. parvulus* has 3. The juveniles of both species lack the 3 + 3 long trichobothria on Abd. I–IV, while the 2 + 2 trichobothria of Abd. V–VI are well developed. The mucro of both species is simple without basolateral seta, quite different from the strongly differentiated mucro of the adults.

In a sample from Ireland (Muckish Mountain, Co. Donegal) sent to me by Macfadyen, there was one juvenile *Spinosellina* form of *S. schoetti* identical with the Norwegian specimens.

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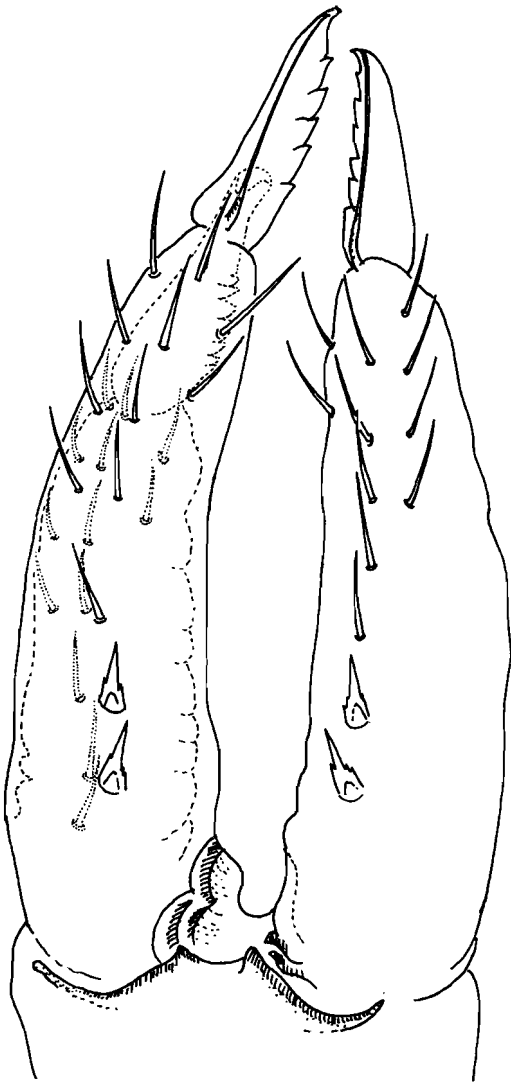


Fig. 1. *Spinosellina* form of *Sminthurides schoetti* showing transformation to the adult phenotypé. Ventral view of dens of a specimen from Ireland.

Received 16 April 1974

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A constant pressure microrespirometer for measurements of O₂-consumption in Collembola

ELSE-MARGRETE CONRADI-LARSEN

Conradi-Larsen, E.-M. 1974. A constant pressure microrespirometer for measurements of O₂-consumption in Collembola. *Norsk ent. Tidsskr.* 21, 187-190.

In order to determine O₂-consumption in individual collemboles, a modified constant pressure respirometer was constructed. The respirometer consists of 0.1 mm and 2 mm glass capillaries, glued together. The 2 mm capillary is the respiration chamber and is sealed with a Vaseline coated cover slip. The small capillary and a part of the respiration chamber is filled with KOH, so that a pressure reduction in the chamber will draw the KOH column downwards.

Measurements of O₂-consumption were carried out on *Isotoma violacea* Tullberg and *Tetrachantella wahlgreni* Linnaniemi collected at Finse, 1200 m a.s.l. in the winter. In *T. wahlgreni* the increase of the O₂-consumption was linear for the temperatures 10°, 20°, and 25° C. At 10° C the O₂-consumption in both species was 0.3 mm³O₂/mg/h. The present results seem to be in agreement with O₂-consumption measurements carried out on collemboles by use of Cartesian diver and Warburg respirometers.

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The Engelmann constant pressure respirometer (Engelmann 1963) can be used to measure O₂-consumption in small insects (Dixon 1971). An Engelmann respirometer with a 0.3 mm capillary makes it possible to measure O₂-consumption in insects of about 1 mg fresh weight. The respirometer did not function sufficiently accurately when smaller capillaries than 0.3 mm were used. To measure O₂-consumption in high mountain species of collemboles, 10-20 animals have to be used in one respirometer. In order to determine the O₂-uptake of single collemboles, it is necessary to use capillaries of 0.1 mm or smaller. For this reason attempts were made to construct a modified respirometer. This was based partly on the Engelmann method and partly on a respirometer according to Cunningham and Kirk (Kirk 1959).

THE APPARATUS

The design of the respirometer shown in Fig. 1 is very simple. It consists of two glass capillaries fastened together with epoxy glue.

The respiration chamber is a 2 cm long piece of a 2 mm capillary. To this is fastened a 0.1 mm capillary of about 5 cm length. The ends of the capillaries are ground so that they fit together and no glue is allowed to penetrate into the small capillary. Constant temperature is obtained in a water bath with a Braun thermomixer. For temperatures below 20° C a Colora immersion cooler is used.

PROCEDURE

The respirometer is cleaned by drawing a mixture of soap (Deconex 11) and water through it, followed by distilled water and acetone. Dry air is then drawn through the respirometer until it is completely dry. 0.3 M KOH is drawn up through the small capillary and about 4 mm into the respiration chamber. A small piece of dry cotton wool is introduced into the respiration chamber so that no fibre will come in contact with the KOH meniscus. The animal is now introduced and then another small piece of cotton wool which has been slightly moistened with water.

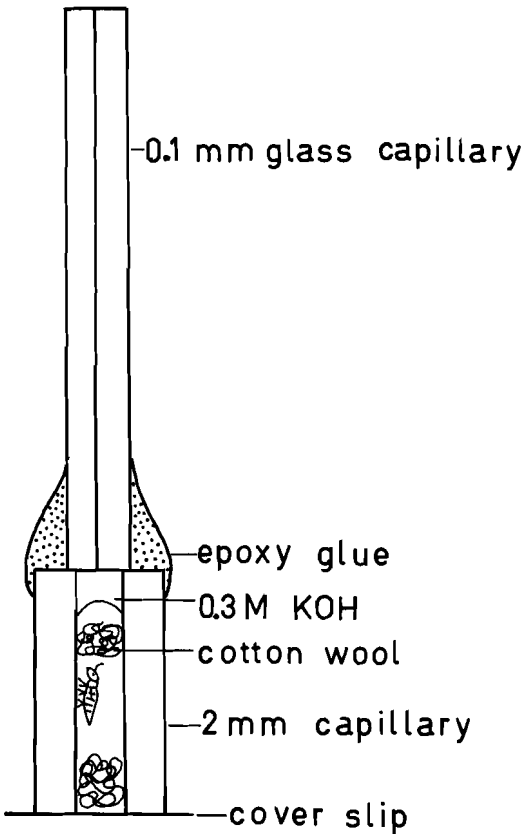


Fig.1. Constant pressure microrespirometer.

Finally, the respiration chamber is sealed with a piece of cover glass coated with Vaseline.

The respirometer is placed in a constant temperature water bath with about 4 cm of the small capillary above the water surface. As the respirometer is placed in the water bath, a droplet of KOH is placed on the top of the small capillary. For the following 30 min., care is taken that the top of the capillary is kept wet with KOH so that no air will penetrate into the small capillary. Then the top of the capillary is dried. As the animal in the respiration chamber is taking up O₂, and CO₂ is absorbed in the KOH, the KOH column in the small capillary is drawn downwards according to the pressure reduction in the respiration chamber. The rate of the fall of the meniscus is measured by calipers with an accuracy of 0.1 mm.

For correction of changes in the environmental pressure and temperature a control

respirometer without animal is used. The eventual movement of the KOH meniscus in the small capillary of the control respirometer is measured for the same time intervals as for those containing animals. The values are corrected according to the changes in the control respirometer.

RESULTS AND DISCUSSION

The respirometer was used for O₂-consumption measurements on two collembole species, *Isotoma violacea* Tullberg and *Tetrachantella wahlgreni* Linnaniemi, collected at Finse, about 1200 m a.s.l. during the period December 1973 to April 1974.

Before the measurements the animals were acclimatized to 0° C for 1-3 days. For *I. violacea* the measurements were carried out at 10°, 20°, and 30° C. The results are shown in Fig. 2. The O₂-consumption increased with increasing temperature, but the values for 30° C were too low to give a linear diagram. Most of the animals used for the 30° measurements died within a few hours at this temperature, and it is suggested that 30° C is too warm for these low temperature acclimatized collemboles. As 30° C seems to be lethal for *I. violacea* in winter, the measurements for *T. wahlgreni* were carried out at 10°, 20°, and 25° C. The animals survived 25° C and a more linear relationship was found (Fig. 2).

Compared to other methods used for de-

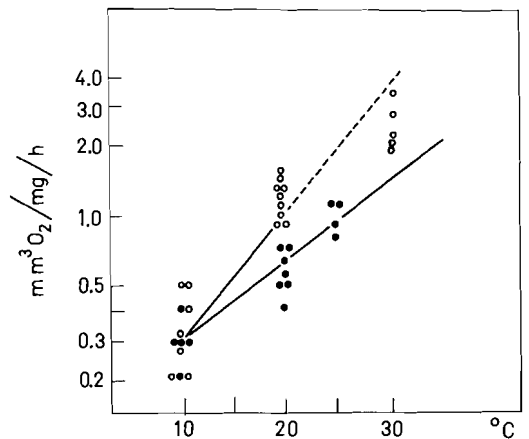


Fig. 2. O₂-consumption in *Isotoma violacea* and *Tetrachantella wahlgreni*. O single values for *I. violacea*, ● single values for *T. wahlgreni*.

termination of O₂-consumption in individual collemboles, the present method appears to give satisfactory results. A number of respiration measurements was carried out by Zinkler (1966), who used a Warburg apparatus of increased sensitivity. At 18° C the O₂-consumption in the different species varied from 0.4–0.6 mm³ O₂/mg/h. The weight of the animals varied from 0.7–2.9 mg. According to Zeuthen (1947), the rate of the O₂-uptake in the small species used for the present study should be higher than in the larger species used by Zinkler.

Tilbrook & Block (1972) determined the O₂-consumption with Cartesian diver micro-respirometer of an Antarctic collembole, *Cryptopygus antarcticus*. In specimens weighing about 0.05 mg, the O₂-consumption was found to be 0.25 mm³ O₂/mg/h at 10° C. For the present measurements, collemboles weighing from 0.04–0.09 mg were used. The average O₂-consumption for these specimens was found to be 0.3 mm³ O₂/mg/h.

The present results for O₂-consumption in collemboles attained by use of the constant pressure micro-respirometer seem to be in agreement with results of measurements carried out by Cartesian diver and Warburg respirometer.

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Spiders new to Norway

FINN ERIK KLAUSEN

Klausen, F. E. 1974. Spiders new to Norway. *Norsk ent. Tidsskr.* 21, 191-194.

Seven species of spiders new to Norway are recorded: *Argenna subnigra* (O. P.-Cambr.), *Zelotes electus* (C. L. Koch), *Clubiona similis* L. Koch, *Scotina celans* (Blw.), *Attulus cinereus* (Westr.), *Attulus saltator* (Sim.) and *Tetrilus macrophthalmus* (Kulcz.). A short description of locality is given for each species.

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During collecting in South and West Norway in 1972 and 1973 I captured seven species of spiders which are new to the fauna.

At least two of the species, *Clubiona similis* L. Koch and *Attulus cinereus* (Westring), are probably widespread and common in the coastal sand dunes of the southern and south-western districts of Norway. As knowledge of the Norwegian spider fauna is still poor, little can be said of the remaining five species. Three of them, though, are decidedly rare, *Zelotes electus* (C. L. Koch), *Scotina celans* (Blackwall) and *Tetrilus macrophthalmus* (Kulczynski). For these I have given a description of characters.

All measures are given in mm. Measurements between eyes are taken between the most distant point of opposite margins. Diameter of an eye means the greatest diameter. AM, AL, PM, PL: antero median, antero lateral, postero median and postero lateral, respectively.

Argenna subnigra (O. P. Cambridge 1861)

V: Moutmarka, Tjøme (UTM: 32V NL 800490), 9 July 1973, 1 ♀.

The specimen was taken on a shore in the upper littoral zone, composed of pebbles and

stones up to 15 cm in diam. Vegetation was sparse, mostly *Angelica archangelica* and short grass tussocks.

Zelotes electus (C. L. Koch 1839)

VAY: Hanangermona, Farsund (UTM: 32V LK 662393), 1 July 1973, 1 ♀.

The specimen was caught on a heath near several thickets of young *Pinus silvestris*. The heath had a sparse covering of *Calluna vulgaris* and *Empetrum nigrum*. The underlying sandy soil lay fully exposed to the air, however in some places covered by small patches of *Rhacomitrium* sp.

Total length 4.3. Carapace: Length 1.70, width 1.35. Yellow brown with a tint of red, bordered with black and with some radiating black or dark grey streaks. Blackened around eyes. Chelicerae: Yellow brown, inner margins with two teeth, outer with three. Sternum: Yellow brown, faintly suffused with grey, covered with black hairs. Abdomen: Dark sooty grey or black covered with black hairs. Legs: Femora yellow, blackened distally. Patellae black, dorsal sides brown, tibiae black with two brown parallel streaks running along the dorsal side. Metatarsi and tarsi yellow brown suffused with black. Tibiae

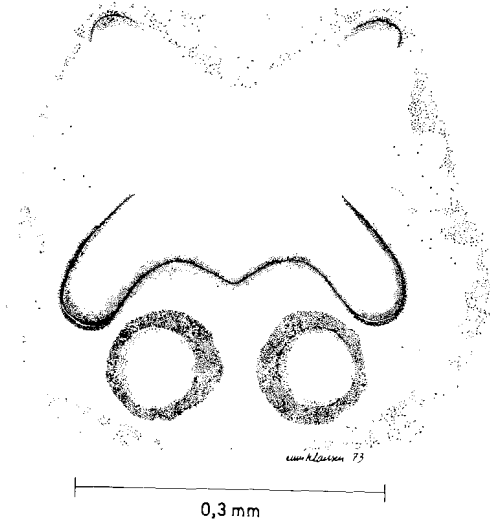


Fig. 1. *Zelotes electus* (C. L. Koch) ♀, epigyne.

I and II with no spines, metatarsi I with one pair of ventral spines, metatarsi II with two spines. Epigyne: See Fig. 1.

Clubiona similis L. Koch 1866.

VAY: Nordhasselbukta, Farsund (UTM: 32V LK 599409), 1 July 1973, 1 ♀, 2 ♂♂.

The specimens were taken on sand dunes covered by *Ammophila arenaria*, about 50 m from the sea. The area is similar to the high beach and fore dunes as described by Ardö (Ardö 1957).

Scotina celans (Blackwall 1841)

HOY: Bjørnåsen, Os (UTM: 32V LM 025722), 17 Sept. 1972, 1 ♂.

The specimen was taken by sieving ground material in a pine forest. The field layer consisted of *Calluna vulgaris*, *Erica tetralix* and *Vaccinium* spp., with *Pleurozium schreberi*, *Hylocomium splendens*, some *Polytrichum* sp. and *Sphagnum* sp. in the ground layer.

Total length 2.75. Carapace: Length 1.58, width 1.20.

Attulus cinereus (Westring 1861)

VAY: Hanangermona, Farsund (UTM: 32V LK 662393), 1 July 1973, 4 ♀♀, 4 ♂♂ and (UTM: 32V LK 661385), 2 July 1973, 2 juv. Nordhasselbukta, Farsund (UTM: 32V LK 599409), 1 July 1973, 1 ♀.

The specimens from Hanangermona (UTM: 32V LK 662393) were taken on the heath identical with that described under *Zelotes electus*. Specimens from Hanangermona (UTM: 32V LK 661385) and Nordhasselbukta (UTM: 32V LK 599409) were taken on sand dunes covered by *Ammophila arenaria*, similar to that described under *Clubiona similis*.

Attulus saltator (Simon 1868)

Ø: Mærrapanna, Onsøy (UTM: 32V PL 024631), 28 July 1972, 1 ♂.

The specimen was caught on a small grass field about 100 m from the sea and 3–4 m a.s.l. The field consisted of mostly short grasses overlying deposits of shell fragments of *Mytilus edulis*. A few small windswept shrubs of *Crataegus monogyna* and *Rosa* sp. were scattered in the field.

Tetrilus macrophthalmus (Kulczynski 1897)

HOY: Sandviksfjellet, Bergen (UTM: 32V KN 981028), 23 Sept. 1973, 2 juv., 30 Sept. 1973, 4 ♀♀, 1 ♂, 2 juv.

The specimens were taken in an ant hill of *Formica rufa* lying on a steep west bent slope, about 150 m a.s.l. The ant hill, about 0.5 m high, was made up of needles from artificially introduced spruces, *Picea abies* and *Picea sitchensis*, growing in the area. The slope is an old overgrown rockslide. This, together with steep elevation, gives good drainage of the ground, which is dominated by *Deschampsia flexuosa*. A few *Sorbus aucuparia*, *Acer platanoides* and *Fraxinus excelsior* are scattered among the prevailing spruces.

Female

Total length 3.25. Carapace: Length 1.45, width 1.10. Clypeus width 0.142. Measure

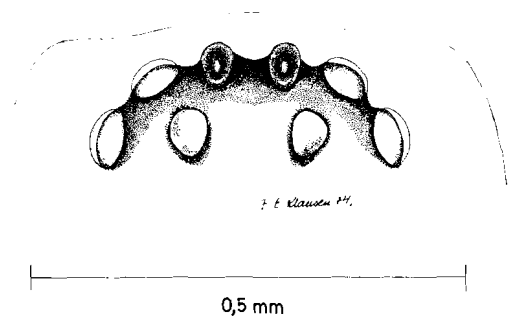


Fig. 2. *Tetrilus macrophthalmus* (Kulczynski) ♀, dorsal side of cephalic region.

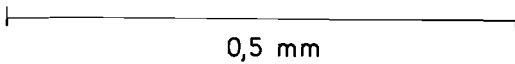
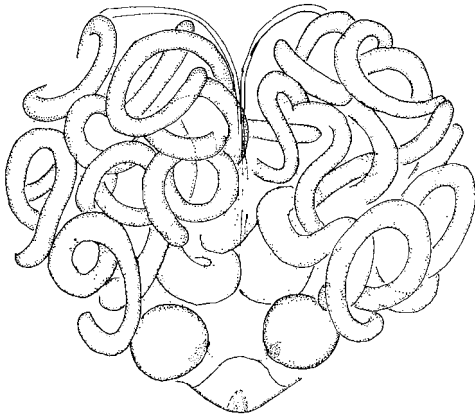


Fig. 3. *Tetrilus macrophthalmus* (Kulczynski) ♀, ventral side of vulva.

between PM eyes 0.200, PL eyes 0.388, AL eyes 0.300, AM eyes 0.150, between AM and PM eye 0.213. Diameter of PM eyes 0.063, AL eyes 0.075, PL eyes 0.075. See also Fig. 2. Colours yellow brown, blackened around eyes, a few black spines mainly in the cephalic region. Chelicerae: Yellow brown. Outer

margins with 3 teeth, inner with 4. Sternum: Whitish yellow with dark grey hairs. Abdomen: Whitish yellow suffused with sooty grey. Covered with dark grey hairs. A longitudinal faint grey line divides an irregular whitish area on the frontal part, hind part dark grey broken up by 3-4 whitish transverse bars. Legs: Yellow brown somewhat suffused with grey. Tibia I and II with a line of 6 proventral and 5 retroventral spines, metatars I and II with 4 and 3, respectively. Vulva: See Fig. 3.

Male

Colours and markings same as for female. Total length 3.40. Carapace: Length 1.75, width 1.23. Clypeus width 0.133. Measure between PM eyes 0.213, PL eyes 0.438, AL eyes 0.313, AM eyes 0.150, between AM and PM eye 0.200. Diameter of PM eyes 0.075, AL eyes 0.875, PL eyes 0.875. Chelicerae: Number of teeth at margins same as for female. Legs: Number of spines on tibiae and metatarsi as for female. Male palp: See Fig. 4.

For identification of the species, I consulted the description and drawing given by Locket & Millidge (1953) and the drawing given by Bristowe (1939). However, the specimens in my collection stand close to *Tetrilus arietinus* (Thorell 1871), as the arrangement and size of the eyes seem to be almost intermediate between the two species. Further, two female specimens from an unpublished material from Vassfaret, province of Oppland (coll. E. Hauge), display the same eye pattern. Lehtinen (1964) also noted these irregularities in *Tetrilus arietinus* taken in Finland.

In identifying the species as *Tetrilus macrophthalmus* I consider the following characters decisive: The relative size and distance of the PM and PL eyes together with their relative position forming a straight or nearly procurved line. The length of the outer lamella of the male palpal organ has also been paid some importance (Locket & Millidge 1953, p. 25).

ACKNOWLEDGEMENT

I am indebted to Professor Hans Kauri, head of the Zoological Museum, Bergen, for his help and criticism of the manuscript.

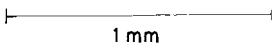
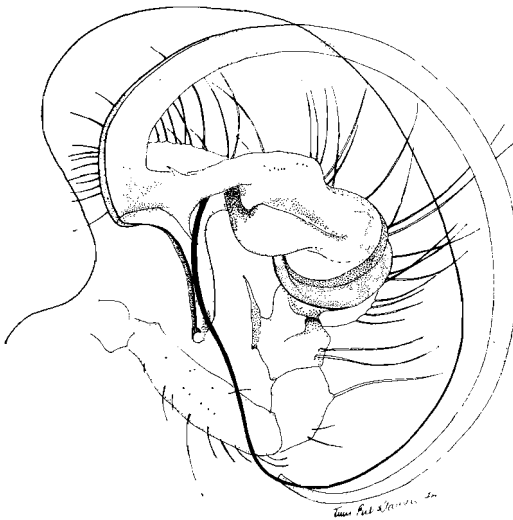


Fig. 4. *Tetrilus macrophthalmus* (Kulczynski) ♂, right palp, seen from inner side.

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Norwegian stoneflies. II. Distribution and relationship to the environment

A. LILLEHAMMER

Lillehammer, A. 1974. Norwegian stoneflies. II. Distribution and relationship to the environment. *Norsk ent. Tidsskr.* 21, 195-250.

Distribution of the Norwegian stoneflies is discussed, and the species and their dependence on certain ecological factors in different parts of the country are investigated and compared. Considerable differences are present between the stonefly associations in the various areas, especially between low and high altitudes and between southern and northern Norway. There is a reduction in species in the Sub-Alpine and Low-Alpine vegetation belts, paralleled by the reduction in deciduous trees and bushes, mainly *Salix*. This trend is apparent in both southern and northern Norway. Thirty-one species were taken in northern Norway, while in southern Norway 29 species were recorded. In both northern and southern Norway the inland areas contained the highest number of species. In the south there was a clear reduction in species towards the coast. The investigations have demonstrated that faunistic differences between the various areas of Norway are so great that previous attempts to generalize about the classification of streams are to a large extent rendered invalid.

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INTRODUCTION

When the present studies on Norwegian stoneflies were started in 1965, one aim was to find the distribution of the stonefly species

present in Norway. Another was to determine the main environmental factors decisive to the distributions. Earlier knowledge of the Norwegian stonefly fauna was insufficient to give any idea of which areas were central and which were periferal for each species. Therefore recording had to be carried out together with the evaluation of environmental factors important for the distribution of the species.

The distribution of stoneflies has been examined by several authors, including Illies (1952b, 1953b, 1955, 1961, 1965 and 1967), Rauser (1962, 1968 and 1971) and Ricker (1964). The known world distribution of the various species is given by Illies (1966) and Zwick (1973).

Detailed descriptions of the stonefly fauna from different areas of Europe have been given by authors such as Wojtas (1964) for Poland, Kaiser (1972) for Denmark, Mendl (1969) for the Hamburg area, and Zwick (1967) for Schleswig-Holstein in Germany, Hynes (1967) for England, Zhiltsova (1964) for the European parts of the USSR, (Meinander (1965) for Finland, and Brinck (1949, 1958) for Sweden and Novaya Zemlja.

In North America, which has faunal connections with northern Europe, distributional studies have been made by among others Ricker (1964), Ross & Ricker (1971), Baumann & Gaufin (1970), and Baumann (1970).

The above-mentioned authors discussed distribution from a zoogeographical viewpoint. Authors like Brinck (1949) and Rauser (1968, 1971) also used association diagrams, which show a close resemblance in the distribution of some species, but a loose or complete absence of a relationship between the distribution of other species. They also classified stonefly habitats. Ulfstrand (1968b) also made an attempt to group the fauna according to origin and immigration into Fennoscandia.

In the present work the intention is to present the stonefly fauna recorded from different parts of Norway and from selected representative areas so as to determine the central and periferal areas of distribution of the species, both in terms of altitude, longitude and latitude, and zoogeography. In addition, more detailed investigations on the distribution in relation to remaining factors such as temperature and quality and quantity of vegetation were undertaken for the purpose

of discussing the influence on the distributional patterns obtained, and the classifications of stonefly habitats.

MATERIAL AND METHODS

Distribution records were based on both nymphs and imagos. Imagos were collected by hand under stones and by sweep netting in the vegetation along rivers, streams, and lake shores.

Authors such as Hynes (1961) and Minshall & Kuehne (1969) collected nymphs by a kicking technique which was used in streams and rivers where stony substrata occurred. The method has been improved by Kershaw et al. (1968) and tested by Frost et al. (1971).

The method is effective, but influenced by net mesh, the duration of sampling, kicking intensity, stream flow, the behaviour of the fauna, and other environmental parameters (Allen 1959, Maitland & Penney 1967). According to Frost et al. (1971) about 60% of the specimens are taken by the first kick. With three kicks almost 90% of the organisms are obtained.

In the present study three or four kicks were taken in each locality on each occasion. In lentic localities the kicking technique was modified from its use in running-water studies, whereby for a period of 3 minutes the substratum was disturbed by kicking while a net was passed forwards and backwards over the disturbed area.

Different species have different life cycles, and as young nymphs are difficult to collect, this made it necessary to sample in the same locality at different times of the year to be sure that all the species present were recorded. The number of specimens used in the distribution studies totalled about 45,000.

About 500 localities were examined and if possible they were visited several times, up to once a month in the period February to October.

In addition, the following collections from institutions and persons were examined and used in the distribution maps, Figs. 25-58: The Royal Norwegian Society of Science and Letters Museum, Trondheim; Tromsø Museum, Tromsø; Zoological Museum, University of Bergen; Zoological Museum, Oslo, and that of Mr. Dahlby, Ørlandet. In both



northern and southern Norway supplementary sampling was carried out by several persons mentioned in the acknowledgements.

Physical and chemical data from the streams are based on the following, usually determined on each sampling occasion: laboratory measurements of total, calcium, and magnesium hardness by the EDTA method, pH readings in the field using a Radiometer 29 pH meter, and water temperature measurements carried out at the time of sampling.

DISTRIBUTION OF THE NORWEGIAN SPECIES

Previous records and present collecting routes

The first list of Norwegian stoneflies based on the collections of Siebke, Esmark, Schøyen, Collett, and Sommerfeldt was given by Schøyen (1887). Later Morton (1901), Kempney (1900 and 1901), Klapalek (1912) and Esben-Petersen (1902, 1910) published the results of investigations in Norway. Brekke (1941) published a revision of the Norwegian plecopteran fauna with a list of 34 Norwegian species. Brinck (1949) revised the plecopteran species recorded from Finland, Norway and Sweden, and concluded that 29 valid species had been found in Norway. This was also mentioned by Brekke (1965).

These earlier registrations of the stonefly fauna in Norway, summarized by Brekke (1965), were not carried out as systematically planned investigations of the country. This unrepresentative material could only serve as a guide in the work on the species' distribution in Norway. Therefore a planned investigation in different parts of Norway, mainly executed in the period 1965–1970, was carried out. The sampling routes are shown in Fig. 1. The routes were chosen through knowledge acquired about distribution and ecology of the stoneflies, taking the assumed immigration routes and factors such as geology, climate and vegetation into account.

Information about the Norwegian stoneflies has also been published by Lillehammer (1965, 1966, 1968), Tobias & Tobias (1971), Tobias 1973, 1974) and Brittain (1974).

Fig. 1. The investigated areas (shaded).

Results

The number of species taken in Norway by the present author was 34. Of these, 5 were

Table 1. The main distribution of Norwegian stoneflies

Species	Present in southern Norway	Present in northern Norway	In all parts of Norway	Southern distribution	Only in the eastern parts of southern Norway	Northern distribution
<i>Arcynopteryx compacta</i>	X	X	X			
<i>Diura bicaudata</i>	X	X	X			
<i>Diura nanseni</i>	X	X	X			
<i>Isogenus nubecula</i>	X			X	X	
<i>Perlodes dispar</i>	X			X	X	
<i>Isoperla difformis</i>	X	X	X			
<i>Isoperla grammatica</i>	X	X	X			
<i>Isoperla obscura</i>	X	X	X			
<i>Dinocras cephalotes</i>	X	X	X			
<i>Siphonoperla burmeister</i>	X	X	X			
<i>Xanthoperla apicalis</i>	X	X			X	
<i>Taeniopteryx nebulosa</i>	X	X	X			
<i>Brachyptera risi</i>	X	X	X			
<i>Amphinemura borealis</i>	X	X	X			
<i>Amphinemura standfussi</i>	X	X	X			
<i>Amphinemura sulcicollis</i>	X	X	X			
<i>Nemoura arctica</i>		X				X
<i>Nemoura avicularis</i>	X	X			X	
<i>Nemoura cinerea</i>	X	X	X			
<i>Nemoura flexuosa</i>	X	X			X	
<i>Nemoura sahlbergi</i>		X				X
<i>Nemoura viki</i>		X				X
<i>Nemurella picteti</i>	X	X	X			
<i>Protonemura intricata</i>		X				X
<i>Protonemura meyeri</i>	X	X	X			
<i>Capnia atra</i>	X	X	X			
<i>Capnia bifrons</i>	X	X			X	
<i>Capnia pygmaea</i>	X	X	X			
<i>Capnia vidua</i>	X	X				X
<i>Capnopsis schilleri</i>	X	X			X	
<i>Leuctra digitata</i>	X	X	X			
<i>Leuctra fusca</i>	X	X				
<i>Leuctra hippopus</i>	X	X	X			
<i>Leuctra nigra</i>	X	X	X			

recorded as new to Norway (Lillehammer 1968, 1972a, b and c), one of them as a new species, *Nemoura viki* Lillehammer, 1972.

However, the total number of species taken in Norway seems to be 35, as *Amphinemura norwegica* is described from the Pasvik area in Finnmark by Tobias (1973). This species has not been examined by the present author. The distribution of the Norwegian species is plotted in Figs. 25–58.

Of the 29 species taken in Norway south of the Dovre mountains, seven were not taken west of the central mountain chain (Langfjellene). As a result the northern areas of Norway have more species than the southern

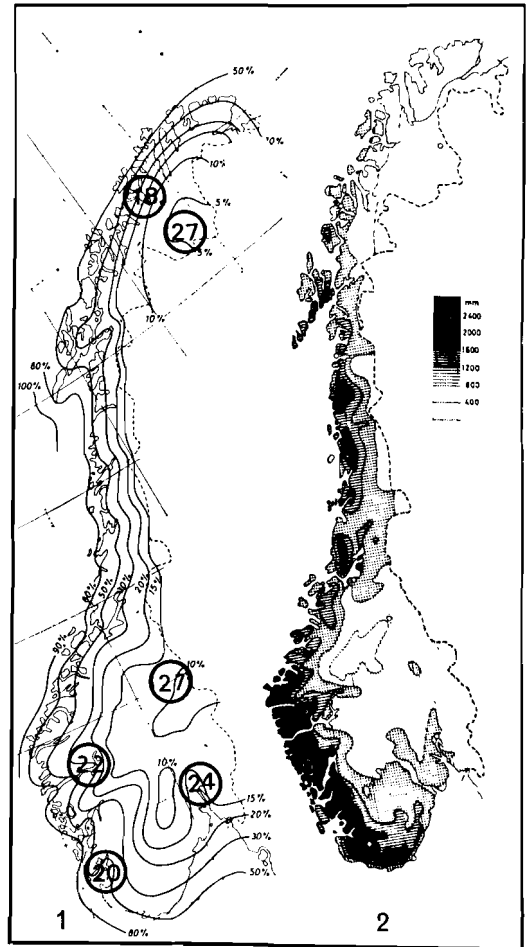


Fig. 2. (1) The oceanicity factor (K) in % in different parts of Norway, and the number of Plecoptera species in different parts of the country. (2) Mean annual precipitation in mm (from Johannessen 1963). ○ Number of species in the area.

parts (Table I). In Norway south of Dovre, the greatest number of species (27) is found in North Østerdal and the surrounding areas. The number of species decreases towards the west, south-west and south (Fig. 2).

In Finnmark the number of species found in the Kautokeino area is 27, whilst the Alta area has only 18 species. Most of the species (21) were collected in all parts of Norway, but five were not found in southern Norway and two not in northern Norway.

The records show that there are marked differences in the distribution of the various species. There are species with a strict northern distribution, only taken in Finnmark, Troms and Nordland. In southern Norway there are species which have a southern or an eastern distribution (Table I).

Discussion

In both Finnmark and southern Norway the highest number of species seems to occur in the inland areas where also the lowest oceanity factor (K) is found (Fig. 2). The oceanity

$$\text{factor } K = \frac{d_1 \cdot d_2}{60 \cdot A \cdot \sin(\varphi + 10)}$$

is based on d_1 = days with more than 0.1 mm precipitation per year, d_2 = days with daily mean between 0° and 10° C per year, A = the difference between the warmest and coldest month in the year, φ = latitude.

The counties of Trøndelag and Nordland, however, do not reflect the same clear trends since *Nemoura avicularis*, *Capnia bifrons* and *Capnopsis schilleri*, the species with a clearly eastern distribution in southern Norway, occur in localities with a high oceanity factor.

These differences might be connected with factors such as climate, vegetation, altitude, latitude and immigration routes. This will be discussed subsequently in this part and in later works.

In Fennoscandia 40 species of Plecoptera are recorded (Table II), five of which are not recorded in Norway. Two of these, *Brachyptera braueri* and *Capnia nigra*, have only been found in the southernmost parts of Sweden, while *Rhabdiopteryx acuminata* has only been taken in Finland. The other two species, *Nemoura dubitans* and *Isopterna serricornis*, have both been collected in Finland and Sweden. However, all five are rare species and many of the observations are old. *Nemoura viki* and *Amphinemura norwegica*

Table II. The Fennoscandian species of Plecoptera

Species	Sweden	Norway	Finland
<i>Arcynopteryx compacta</i>			
(Mc. Lachland)	X	X	X
<i>Diura bicaudata</i>			
(Linnaeus)	X	X	X
<i>D. nanseni</i> (Kempny)	X	X	X
<i>Isopterna nubecula</i>			
Newman	X	X	X
<i>Perlodes dispar</i>			
(Rambur)	X	X	X
<i>Isopterna difformis</i>			
(Klapálek)	X	X	X
<i>I. grammatica</i> (Poda)	X	X	X
<i>I. obscura</i> (Zetterstedt)	X	X	X
<i>Dinocras cephalotes</i>			
Curtis	X	X	-
<i>Xanthoperla apicalis</i>			
(Newman)	X	X	X
<i>Siphonoperla</i>			
<i>burmeisteri</i> (Pictet)	X	X	X
<i>Isopterna serricornis</i>			
(Pictet)	X	-	X
<i>Brachyptera braueri</i>			
(Klapálek)	X	-	-
<i>B. risi</i> (Morton)	X	X	-
<i>Rhabdiopteryx</i>			
<i>acuminata</i> Klapálek	-	-	X
<i>Taeniopteryx nebulosa</i>			
(Linnaeus)	X	X	X
<i>Amphinemura borealis</i>			
Morton	X	X	X
<i>A. norvegica</i> Tobias	-	X	-
<i>A. standfussi</i> Ris	X	X	X
<i>A. sulcicollis</i> Stephens	X	X	X
<i>Nemoura arctica</i>			
Esben - Petersen	X	X	X
<i>N. avicularis</i> Morton	X	X	X
<i>N. flexuosa</i> Aubert	X	X	X
<i>N. cinerea</i> (Retzius)	X	X	X
<i>N. dubitans</i> Morton	X	-	X
<i>N. sahlbergi</i> Morton	X	X	X
<i>N. viki</i> Lillehammer	-	X	-
<i>Nemurella picteti</i>			
Klapálek	X	X	X
<i>Protonemura meyeri</i>			
Pictet	X	X	X
<i>P. intricata</i> (Ris)	-	X	X
<i>Capnia atra</i> Morton	X	X	X
<i>C. bifrons</i> (Newman)	X	X	-
<i>C. nigra</i> (Pictet)	X	-	-
<i>C. pygmaea</i>			
(Zetterstedt)	X	X	X
<i>C. vidua</i> Klapálek	X	X	X
<i>Capnopsis schilleri</i>			
(Rostock)	X	X	X
<i>Leutra digitata</i>			
Kempny	X	X	X
<i>L. fusca</i> Linnaeus	X	X	X
<i>L. hippopus</i> Kempny	X	X	X
<i>L. nigra</i> (Olivier)	X	X	X

are so far known only from Norway. The number of species present in each of the

Fennoscandian countries is very similar, with 36 in Sweden (Brinck 1949, Illies 1952c, and Müller & Thomas 1972), 35 in Norway and 33 in Finland (Meinander 1965). The Fennoscandian plecopteran fauna is therefore well represented in Norway.

DISTRIBUTION IN SELECTED AREAS

The results of the distributional studies discussed above made it necessary to carry out detailed faunal studies in different parts of Norway, chosen to represent different faunal

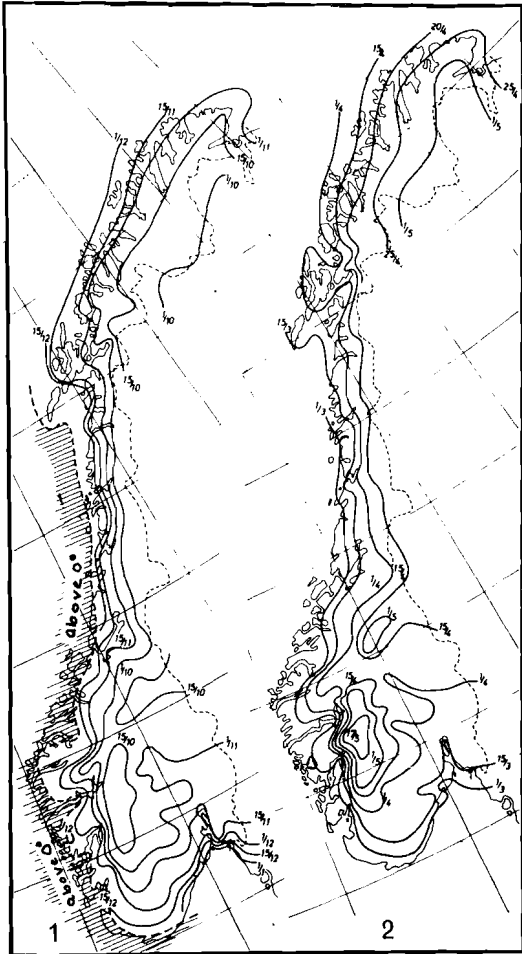
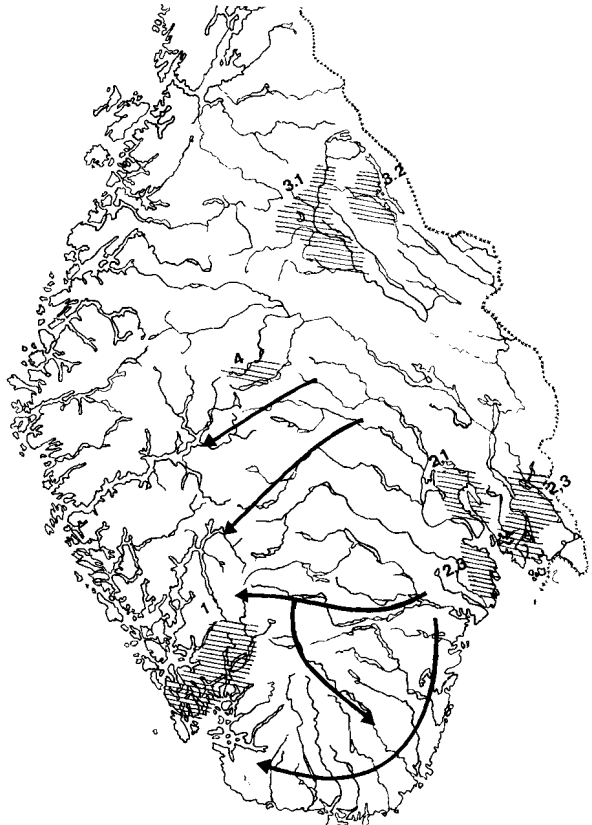
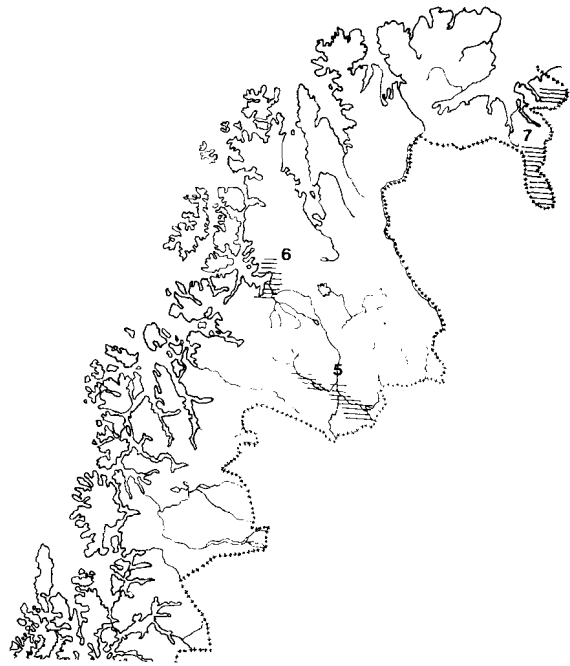


Fig. 3. (1) Mean date for the beginning of winter (daily mean temperature falls below 0° C). The shaded areas always have a daily mean temperature above 0°. (2) Mean date for the beginning of spring (daily mean temperature rises above 0° C) (from Johannessen 1963).



areas (Table I) where geographical, geological, climatological (Figs. 2 and 3) and botanical aspects could be studied separately.

The location of the study areas is shown in Fig. 4. The arrows indicate more detailed special investigations along the most probable invasion routes to western Norway.

The areas chosen were: 1. The area north of Boknafjord, Rogaland and the southernmost areas of Hordaland. 2. The area around Oslofjord. 3. North Østerdal and the surrounding areas. 4. The Øvre Heimdal area. 5. The area around Kautokeino. 6. The Alta area. 7. South Varanger including Pasvik and Korp fjell.

To categorize the main vegetation zones, the system of Sjörs (1963, 1967) was used. According to this system, area 1 ranges from the North Atlantic Pine-Birch Woodland and heath region through the Sub-Alpine Birch Woodland belt to the Alpine belts. Area 2 is situated in the Boreo-nemoral zone, area 3 in the Sub-Arctic and Boreo-montane sub-zone and area 4 in the upper part of the Sub-Alpine Birch Woodland and the Alpine belts. Area 5 (Kautokeino) also lies in the Sub-Alpine and Alpine belts. In area 6 (Alta) there are pine woods in the lowest parts, while most of the area lies in the Sub-Alpine Birch Woodland belt and the Alpine belts. In area 7, Pasvik is situated in the Sub-Arctic and Boreo-montane sub-zone while the Korp fjell area lies in the Sub-Alpine and Alpine belts.

The major part of the study was undertaken in area 1 where there are very marked climatic and botanic gradients, and considerable difference in the altitude within a relatively small area, making it possible to investigate an extremely large range at nearly the same time.

SOUTHERN NORWAY

Area 1. North Rogaland and South Hordaland

After a preliminary investigation of the plecopteran fauna of 64 localities, covering

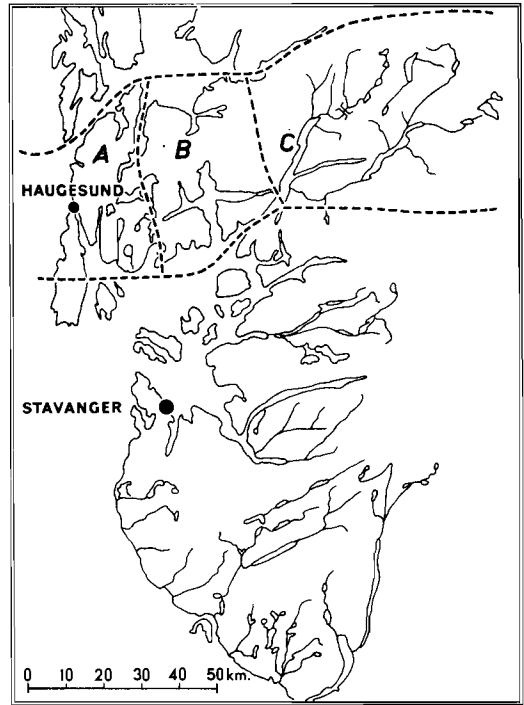


Fig. 5. The investigated parts of area 1. A = coastal areas, B = central areas, C = inner fjords.

the whole of Rogaland and the southern parts of Hordaland, the area between Boknafjorden and Bømlafjorden-Åkrafjorden was chosen as the most representative for this investigation. There are clear climatic and vegetation gradients which make the area suitable for examining the gradient of the decrease in species which seems to occur towards the coasts of Norway, especially the western seaboard.

Area description

The area is shown in Fig. 5, and studies were carried out in 41 localities.

Pre-Eocambrian rock complexes occur in the lower sections of the valleys, phyllites higher up the valley sides, and acidic igneous rocks on the top. Drift material consisting of stones, gravel and sand occurs in the river valleys of the inner area. In the lower areas along the fjords, marine clay deposits occur which become larger towards the coast (Holdedal 1960).

The coastal climate dominates over large

Fig. 4. The investigated areas (shaded) and the presumed immigration routes towards the west (arrows).

parts of the area (Figs. 2 and 3), and it is only in the inner areas that the mean January temperature falls below 0° C. In the outermost areas the mean January temperature is more than +2° C (Fig. 3.1). The whole area experiences heavy precipitation between 1200 mm and 2000 mm in the outer areas, and more than 2000 mm in the inner areas.

On the coastal area of the Haugesund peninsula, west of Skjoldefjorden and Ålfjorden, heights of more than 100 m a.s.l. are rare. In the central areas, east of Ålfjorden and Skjoldefjorden, the mountains are higher, between 500 and 700 m a.s.l. in the outer parts and up to 1000 m a.s.l. in the inner parts (the area of Sandeid and Vikedal). In this area there are prominent valleys. In the inner areas, east of Vikedal, the mountains are even higher (up to 1600 m a.s.l. in the north-eastern parts) and the fjords cut deeply into the mountain massif.

The vegetation of the area of the Hauge-sund peninsula consists mainly of bog and heath vegetation. Wooded areas total about 8%. In the central area the wooded areas on average constitute about 24% of the area.

In the inner area, which is mainly mountainous, the wooded area totals about 8%.

River and stream descriptions

In the inner areas, streams and rivers are abundant and the deep valleys contain some of the longest and largest rivers in Rogaland. The streams alternate between fast flowing and more slow flowing reaches. The stone size is very variable at all altitudes and the streams are generally fringed by dwarf willow up to about 7–800 m a.s.l.

In the lowland areas there is often a dense fringe of alder, willow and birch along the rivers and streams, in which the substrate consists of different gravels and stones. Pollution is minimal and only occurs for a short distance near the fjords.

In the central areas, the streams are of the same type as in the lowland inner areas. The vegetation is rich along the streams. The streams are seldom polluted to any noticeable degree, and if they are, they flow only a short distance before reaching the sea.

The outer areas have very little wooded vegetation except in the shallow valleys. There is often a dense fringe of alder and

other deciduous trees along the streams which on the whole are smaller and shorter than in the central and inner areas.

Calcium hardness varied to some extent in the lowlands. Values up to 1.7 mg Ca⁺⁺/l were found in the coastal and central areas and up to 0.9 in the inland regions. Usually the values were much lower and below 1.0 mg Ca⁺⁺/l. In the highest areas up to 0.4 mg Ca⁺⁺/l was measured. Usually the values were much lower. The pH is around 6.0 in the lowlands of the whole area, but on average it is a little higher at the coast than in the inner areas where the lowest pH value measured was 5.3.

Stonefly fauna

In this area 19 species were collected (Table III). *Diura bicaudata* were taken in lakes and their outlets at higher altitudes, and *Dinocras cephalotes* was taken in a stream at Suldal. The total number of species in the southern part of West Norway is 20, since *Isoperla difformis* was taken at Oltedal, Jæren, to the south of study area 1.

The lowland region of the inner fjords supports the highest number of species (18), and the number of species decreases towards the coastal areas where only 9 species were collected. The number of species also decreases with altitude. In the alpine areas of 900–1000 m a.s.l., only 3 species, two in lakes and one in streams, were taken.

The results are compiled from investigations of 41 streams throughout the whole area. Table III shows the stonefly fauna of selected streams which are representative of coastal areas, the central areas, the inner fjord lowland and the higher areas of the inner areas. The following discussion is based mainly on these streams.

One of the 9 species taken in the coastal area, *Amphinemura standfussi*, was only taken by one small stream, Tosketjønnbekken, 70–80 m a.s.l. and above the existing tree line in this area. The other rare species, *Isoperla grammatica*, was collected at two localities.

The species from Byrkjelandselv (stream), Sveio, were all taken in high numbers except *Nemoura cinerea*. The association was dominated by *Amphinemura sulciollis* and *Protonemura meyeri* and there were no strictly

Table III. Species distribution in selected water courses and the number of specimens taken in the whole of area 1 (North Rogaland and south Hordaland)

	<i>Leuctra fusca</i>	<i>Amphinemura sulcipectus</i>	<i>Brachyptera risi</i>	<i>Siphonoperla burmeisteri</i>	<i>Isoperla grammatica</i>	<i>Leuctra hippopus</i>	<i>Nemoura cinerea</i>	<i>Protonemura meyeri</i>	<i>Amphinemura standfussi</i>	<i>Diura nanseni</i>	<i>Leuctra nigra</i>	<i>Nemurella picteti</i>	<i>Amphinemura borealis</i>	<i>Leuctra digitata</i>	<i>Isoperla obscura</i>	<i>Capnia pygmaea</i>	<i>Taeniopteryx nebulosa</i>	<i>Diura bicaudata</i>	<i>Dinocras cephalotes</i>
<i>Coastal area</i>																			
Stream Byrkjelandsbekken	X	X	X	X		X	X	X											
Stream Torskjetjønnbekken	X	X	X		X	X	X	X	X										
<i>Central area</i>																			
Stream Sandeidelva	X	X	X	X	X	X	X	X	X	X	X	X	X				X		
<i>Inner area lowland</i>																			
Stream Hogganviksbekken		X	X	X		X	X	X	X	X	X	X	X	X					
Stream Nordelva	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
Stream Storelva	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X		
Stream Suldalslågen	X	X	X	X	X	X	X	X		X		X	X	X	X	X	X		X
<i>Inner area, high altitudes</i>																			
Stream Botnavatnbekken						X	X	X	X	X	X	X			X				
Stream Svartavatnelv							X		X	X	X	X		X					
Lake Halvfjordingsvatn												X						X	
Number of specimens taken in																			
coastal areas	99	136	121	45	29	320	39	175	36	0	0	0	0	0	0	0	0	0	0
central areas	125	83	40	6	1	188	3	27	5	19	51	5	25	0	0	0	1	0	0
inner areas, lowland	170	69	247	11	11	209	83	21	38	48	29	7	155	63	9	174	49	0	2
inner areas, high altitude	26	118	63	1	9	506	45	21	128	40	171	123	0	84	9	0	1	81	0

carnivorous species present, since *Siphonoperla burmeisteri* was said by Brinck (1949) to be omnivorous.

The faunal elements of Tosketjønnbekken were also taken in relatively high numbers. The only rare species was the omnivore *Isoperla grammatica*. The association was, however, dominated by other species than Byrkjelandselv, namely by *Leuctra hippopus* and to a certain extent by *Brachyptera risi*. The two streams are very different. Byrkjelandselven (stream) has by far the greater water volume and along the banks of the stream there is a dense fringe of deciduous trees. The banks of Tosketjønnbekken support only isolated willow bushes among vegetation dominated by heather.

In the central area 14 species were found. In one of the streams, Sandeidelven, all of them were represented. In this stream *Leuctra hippopus* was the most common species, followed by *Brachyptera risi*. The carnivore *Diura nanseni*, which was absent in the coastal area, was present in the central area, as are the herbivores *Amphinemura borealis*, *Leuctra nigra* and *Nemurella picteti*.

In the inner lowland areas, Hogganvikbekken (stream) is the same size as Tosketjønnbekken, while Nordelva and Storelva are larger.

In Hogganviksbekken 12 species were taken, while in Storelva there were 16 species, and in Nordelva 17 species. Among the species of the area not present in Hogganviksbekken, *Taeniopteryx nebulosa*, *Capnia pygmaea*, *Leuctra fusca*, *Isoperla grammatica* and *Isoperla obscura*, only *I. obscura* seems to be restricted to larger streams, as all the other species were also taken in small streams in the area. Of the total fauna in the lowland area it seems to be only this species whose presence depends on stream size. The differences between the outer and inner areas in species composition, such as the absence of *Amphinemura borealis*, *Diura nanseni*, *Leuctra nigra* and *Nemurella picteti* from the coastal area, must be attributed to other factors, such as climatic, vegetation and substratum. In the inner area, lowland *Leuctra hippopus*, *Leuctra fusca* and *Brachyptera risi* are the most common species. The great differences in altitude in the inner parts produce considerable differences in the faunal associations. There are 17 species at altitudes from

0–50 m (Storelva and Nordelva). At a height of about 700 m above sea level there are only 8 species. At higher altitudes the reduction continues, with fewer individuals of the few species still present.

To determine zonation trends, investigation of vertical distribution was carried out and compared with the floristic zonation described by Sjörs (1963) and Gjærevoll (1973). The results will be presented and discussed later.

Area 2. The surroundings of the Oslofjord

This is a lowland area consisting of inner fjord and coastal areas chosen for comparison with the lowlands of area 1. The vegetation is that of the Boreo-Nemoral zone, which is the same as most of southern Sweden.

Area Description

The area (Fig. 4) consists of 3 parts: 2.1, the area around the inner Oslofjord; 2.2, the area around the lower parts of the river Glåma. The localities in these two areas are situated in the counties of Østfold and Akershus; 2.3, the western coastal areas which are situated in the county of Vestfold. In these areas 34 streams were investigated. The bedrock in the region to the north and west of the Oslofjord consists of slightly altered calcareous Cambro-Silurian rocks interspersed by areas of igneous rocks. On the east side gneiss predominates. Near the fjord on both sides there are significant deposits of marine clay (Holtedal 1960).

The coastal areas (2.3) have a mean January temperature which is slightly above 0° C, while in the inner area (2.1) the mean January temperature lies around -5° C. In area 2.2 the mean January temperature ranges from a little above 0° C in the southern parts to below -5° C in the northern parts. The whole area lies within the July isotherm of 15° C.

In the area to the west of the Oslofjord, precipitation is 800–1200 mm a year. In the area to the east of the Oslofjord the precipitation is lower, between 400 and 800 mm a year.

Most of the region is lowland with extensive areas of drift material except for a number of cliffs on both sides of the Oslo-

fjord. In the coastal parts the cliffs seldom reach over 200 m a.s.l.

Nearer Oslo the hills are somewhat higher, from 300–400 m a.s.l. North of Oslo elevations between 500 and 700 m a.s.l. are reached. The flatter parts of all three areas are intensively cultivated. This is most pronounced in the central regions of Vestfold and Østfold. Nearer the coast there are small areas rich in deciduous trees; otherwise spruce-dominated coniferous forests predominate above the cultivated areas.

Stream descriptions

The streams in the area around the inner Oslofjord (2.1) rise in hills where spruce and pine are dominant. Where the streams flow through cultivated areas there is often a dense fringe of deciduous trees, usually alder, along their banks. Streams where pollution is relatively mild are still to be found. The streams in the eastern parts of 2.2 rise largely from boggy, spruce forest areas. The streams in the central parts run through cultivated areas and are usually markedly polluted.

The streams of area 2.3 are usually smaller than in the other areas and there is a dense band of deciduous trees along the streams. The pollution is relatively mild.

In all three areas the stream substratum varies from sand and gravel to larger stones.

Calcium hardness and pH vary considerably. At low water levels prior to snow melting, calcium hardness values over 1 mg Ca⁺⁺/l are common in the inner area (2.1). The highest value recorded was 12.2 mg Ca⁺⁺/l. In the coastal areas the values were even higher, ranging from 3.1 to 16.1 mg Ca⁺⁺/l. In the eastern area the values were markedly lower, from 0.4 to 1.7 mg Ca⁺⁺/l. In this area pH varied between 5.0 and 7.0, the higher values being recorded in streams on marine deposits. On average pH was somewhat lower than in the other two areas. Measurements of pH in Vestfold (2.3) lay between 6.4 and 7.1 and in area 2.1 between 5.5 and 7.6.

Stonefly fauna

Area 2 contains 24 species of Plecoptera (Table IV). There are marked differences

between the three parts of the area. In areas 2.1 and 2.2 there are nearly the same number of species, 22 and 21 respectively. The differences in this case are that *Nemoura flexuosa*, *Amphinemura standfussi* and *Capnia bifrons* have been taken in area 2.1, but not in area 2.2. The opposite is true of *Isogenus nubecula* and *Isoperla obscura*.

The most striking difference between areas 2.1 and 2.2 is the dominating position of the Capniids in the former area. In area 2.1 *Capnia atra*, *C. bifrons* and *Capnopsis schilleri* are to be found in nearly every stream investigated, with some dominated by *Capnia bifrons* and *Capnopsis schilleri* such as Sæterbekken, while others such as Lomma are dominated by *Capnia atra*.

In area 2.3 only 7 species were taken. Streams in the central parts of this area are heavily polluted and much of the original fauna must certainly have disappeared; thus only the small streams along the coast which are not markedly polluted can support a stonefly fauna. The dominating faunal elements here are *Nemoura cinerea*, *Brachyptera risi*, *Capnia bifrons* and *Isoperla grammatica*.

Among the carnivorous species *Diura nanseni* dominates in area 2.1, where also the omnivorous species *Isoperla grammatica* and *Isoperla difformis* are common. In areas 2.2 and 2.3 only *Isoperla grammatica* is common. *Diura nanseni* is found in area 2.2, but not in 2.3.

The streams in the extremely variable terrain of area 2.1 are on average richer in species than the eastern streams of area 2.2. This is also true of the comparison between streams in areas 2.1 and 2.3. The most common species in the streams of area 2 as a whole are *Nemoura cinerea*, *Nemoura avicularis*, *Brachyptera risi*, *Isoperla grammatica*, *Capnia bifrons*, and *Amphinemura sulciollis*.

In the lakes of area 2, *Amphinemura sulciollis*, *Nemoura avicularis*, *Nemoura cinerea*, *Nemurella picteti*, *Leuctra fusca*, *Isoperla obscura* and *Siphonoperla burmeisteri* were collected.

Distributional tendencies in area 2 are the same as in area 1 (Rogaland–Hordaland), as the highest number of species were taken in the inner areas (2.1) and there is a marked reduction in species towards the coastal area. However, the results are not as conclusive as

Table IV. Species distribution, in selected water courses, and the number of specimens taken in the whole of area 2 (the area around the Oslofjord)

	<i>Arcynopteryx compacta</i>	<i>Diura bicaudata</i>	<i>Diura nanseni</i>	<i>Isognenus nubecula</i>	<i>Perlodes dispar</i>	<i>Isoperla difformis</i>	<i>Isoperla obscura</i>	<i>Isoperla grammatica</i>	<i>Dinocras cephalotes</i>	<i>Siphonoperla burmeisteri</i>	<i>Taeniopteryx nebulosa</i>	<i>Brachyptera risi</i>	<i>Amphinemura borealis</i>	<i>Amphinemura standfussi</i>	<i>Amphinemura sulcicollis</i>	<i>Nemoura avicularis</i>	<i>Nemoura cinerea</i>	<i>Nemoura flexuosa</i>	<i>Nemurella picteti</i>	<i>Protonemura meyeri</i>	<i>Capnia atra</i>	<i>Capnia bifrons</i>	<i>Capnia pygmaea</i>	<i>Capnopsis schilleri</i>	<i>Leuctra digitata</i>	<i>Leuctra fusca</i>	<i>Leuctra hippopus</i>	<i>Leuctra nigra</i>		
Area 2.1																														
Stream Sæterbekken			X			X				X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	
Stream Østernbekken		X				X		X		X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	
Stream Sørkedalselv		X		X	X	X		X		X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	
Stream Lomma		X				X		X		X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	
Stream at Semsvann		X						X				X	X	X	X	X	X	X		X	X		X	X	X	X	X	X	X	
Area 2.2																														
Stream Glåma			X	X				X			X		X				X								X	X	X	X	X	
Stream at Tangen			X			X		X		X	X	X	X							X				X	X	X	X	X	X	
Stream at Tunnsjø								X		X	X				X	X	X		X						X	X	X	X	X	
Stream at Øgderen					X	X					X	X			X	X	X							X	X	X	X	X	X	
Area 2.3																														
Stream at Tjøme								X				X			X	X														
Stream at Freberg								X				X	X			X	X													
Stream at Melsvik								X					X			X	X													
Stream at Tjølling												X				X	X													
Lakes:																														
Semsvann Area 2.1																X	X		X											
Holsfjorden Area 2.1										X					X	X	X		X											
Øyeren Area 2.2							X																			X				
No. of specimens taken in																														
2.1	0	0	97	0	3	44	0	5	0	118	59	226	44	23	261	84	55	31	26	24	205	322	0	443	135	93	754	142		
2.2	0	0	36	3	1	9	6	74	0	12	43	122	26	0	187	18	243	0	17	11	1	0	0	21	19	17	162	15		
2.3	0	0	0	0	0	0	0	57	0	0	0	57	24	0	1	6	120	0	0	0	0	227	0	0	0	0	0	0		

those of area 1 as pollution may have excluded some species from area 2.3.

Area 3. North Østerdalen and its surroundings

This area is the most continental in southern Norway and is situated within the Sub-Arctic and Boreo-Montane sub-zones.

Area description

In this area (Fig. 4), 37 streams and rivers and 3 lakes were investigated. The area has two main parts which are markedly different: 1. The valley of the River Glåma and its tributary valleys, 2. The Femund-Istern area. The bedrock consists of Cambro-Silurian sediments in the north and west and Eocambrian sandstone in the south and north-east. Drift material, lain down by lakes dammed up by ice in the late glacial period, is abundant.

The area is situated in a part of Norway which has little precipitation, generally between 400 and 600 mm a year, although parts of the area have less than 400 mm.

The western part, the Glåma valley (area 3.1), has heights ranging from about 300 m a.s.l. at Atna, via Tynset at 482 m a.s.l., to Røros at 600 m a.s.l. West of the Glåma valley the landscape is usually higher, as is also the case in the eastern part of area 3.2, where the lake Femunden situated at an altitude of about 600 m a.s.l. is surrounded by land mainly between 600 and 700 m a.s.l. The whole of area 3 is dominated by coniferous woodland with the tree line at about 900 m a.s.l. In the Glåma valley itself and in the tributary valleys there is much rich soil and the lower parts are cultivated. In the damper areas *Alnus* and *Salix* are often common. At about 600–700 m the forest is often open and dry, and the soil is poor. This is typical of the area around Femunden, which differs markedly as regards vegetation from the westerly river valleys. Around Femunden, *Salix* predominates and the area is sparsely cultivated. The forest floor is dominated by moss, lichen and heather.

Stream descriptions

The valley of North Østerdal is dominated by the River Glåma, the largest river of



Fig. 6. The stream, Storbekken, at Tynset in the Glåma valley.

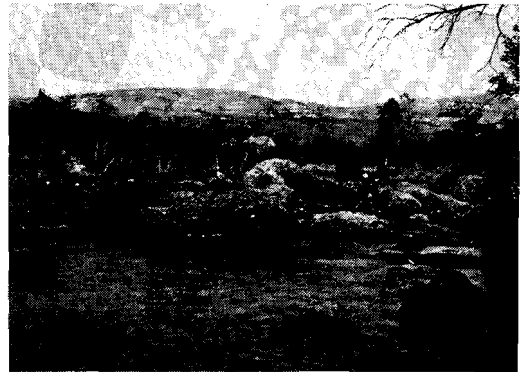


Fig. 7. The stream, Tufsinga, in the Femunden area.

southern Norway. The river alternates between riffles and slow-flowing sections, and long stretches are densely fringed by deciduous trees. The part of the river which is inside this area lies between Atna and Røros, a section which receives tributaries from numerous smaller and larger streams, the largest one coming from the west. Where the streams run through cultivated areas, there is often a dense fringe of *Alnus* and *Salix* (Fig. 6).

The Femunden-Istern area is dominated by large lakes and in this work the tributary streams at the western side of Femunden were investigated from Tufsinga in the north to Rendalen in the south. Along the streams there is often a great deal of *Salix* vegetation (Fig. 7). In this area there is little cultivated land and stream pollution is negligible.

In the Glåma area local pollution is marked where the streams run through a populated area. The pollution of the Glåma may be

Table V. Species distribution in selected water courses and the number of specimens taken in the whole of area 3 (North Østerdalen and its surroundings)

	<i>Arcynopteryx compacta</i>	<i>Diura bicaudata</i>	<i>Diura nanseni</i>	<i>Isogetus nubecula</i>	<i>Perlodes dispar</i>	<i>Isoperla difformis</i>	<i>Isoperla obscura</i>	<i>Isoperla grammatica</i>	<i>Dimocras cephalotes</i>	<i>Siphonoperla burmeisteri</i>	<i>Taeniopteryx nebulosa</i>	<i>Brachyptera risi</i>	<i>Amphinemura borealis</i>	<i>Amphinemura stadfussi</i>	<i>Amphinemura sulciollis</i>	<i>Nemoura avicularis</i>	<i>Nemoura cinerea</i>	<i>Nemoura flexuosa</i>	<i>Nemurella picteti</i>	<i>Protonemura meyeri</i>	<i>Capnia atra</i>	<i>Capnia bifrons</i>	<i>Capnia pygmaea</i>	<i>Capnopsis schilleri</i>	<i>Leuctra digitata</i>	<i>Leuctra fusca</i>	<i>Leuctra hippopus</i>	<i>Leuctra nigra</i>		
Area 3.1																														
Stream Storbekken		X					X	X		X	X	X	X	X	X	X	X		X		X	X		X	X	X	X	X	X	
Stream Kvendalsbekken		X					X	X	X	X	X	X	X	X	X	X	X	X		X	X	X		X	X	X	X	X	X	
Stream at Fåsett		X					X	X	X	X	X	X	X	X	X	X	X	X		X	X	X		X	X	X	X	X	X	
Stream Auma		X					X	X	X	X	X	X	X	X	X	X	X	X		X	X	X		X	X	X	X	X	X	
Stream Stortela		X					X	X	X	X	X	X	X	X	X	X	X	X		X	X	X		X	X	X	X	X	X	
Stream Glåma		X					X	X	X	X	X	X	X	X	X		X	X		X	X	X		X	X	X	X	X	X	
Area 3.2																														
Stream Tufsinga			X	X	X	X	X	X	X		X				X				X	X	X				X	X	X	X	X	
Stream at Buvika		X			X			X		X	X				X	X			X	X	X		X		X	X	X	X	X	
Stream at Gjota										X	X	X	X	X	X	X	X	X	X	X	X		X		X	X	X	X	X	
Stream at Tørråsen			X					X		X	X	X				X	X	X	X	X	X				X	X	X	X	X	
Lakes:																														
Narsjøen Area 3.2		X												X	X	X														
Storsjøen Area 3.2		X								X																				
Savalen Area 3.1		X													X	X														
No. of specimens taken in																														
3.1	17	21	97	0	0	0	6	18	11	308	65	61	33	11	81	2	14	6	2	6	146	203	13	202	18	67	88	31		
3.2	0	25	7	2	0	2	55	100	13	30	26	19	0	2	71	7	11	0	6	11	88	0	0	24	6	6	250	40		

significant in some reaches, such as below Tynset.

Hardness and pH were measured in 1967, 1968 and 1970. The highest values were recorded in streams in the Glåma valley. In the smaller streams pH varied from 7.0 to 7.6 and in the rivers from 7.0 to 7.8. The Ca^{++} content ranged from 4.3 to 18.3 mg/l in the small streams and from 4.7 mg/l to 13.1 mg/l in the rivers.

In the Femund area pH lay between 5.6 and 6.0 and the Ca^{++} content between 0.3 mg/l and 2.0 mg/l.

Stonefly fauna

The area is rich in species and supports 27 of the 29 species which have been taken in Norway south of the Dovre Mountains (Table V). The only species not present here are the rare *Perlodes dispar* and *Xanthoperla apicalis*.

Faunistically the area divides itself into two parts. 1. The western area with the valleys of the Glåma and its tributaries, which contains the higher number of species (25). In this area *Capnia atra*, *Capnia bifrons* and *Capnopsis schilleri* are common and can be taken in great numbers in most streams. *Amphinemura borealis* and *Amphinemura sulci-collis* are also common and numerous. *Arcynopteryx compacta* was only taken once, in the Atna valley.

2. The eastern area consisting of the western side of Femunden contains 22 species. Of these *Isogenus nubecula* and *Isoperla difformis* are not present in the Glåma area, while conversely *Capnia bifrons*, *Capnia pygmaea*, *Nemoura flexuosa*, *Amphinemura borealis* and *Arcynopteryx compacta* have not been taken in the eastern area.

The most marked difference is the weak position of the Capniids in the eastern area compared to the strong position of *Capnia bifrons*, *Capnia atra* and *Capnopsis schilleri* in the western areas. This is the same trend as found in area 2, the Oslofjord.

In the lakes of area 3, five species were taken, *Nemoura avicularis*, *Nemoura cinerea*, *Amphinemura sulci-collis*, *Siphonoperla burmeisteri* and *Diura bicaudata*.

Among the carnivorous species *Diura nanseni* dominates in streams and rivers. The rare *Isogenus nubecula* was only taken in the stream Tufsinga in the northern part of the

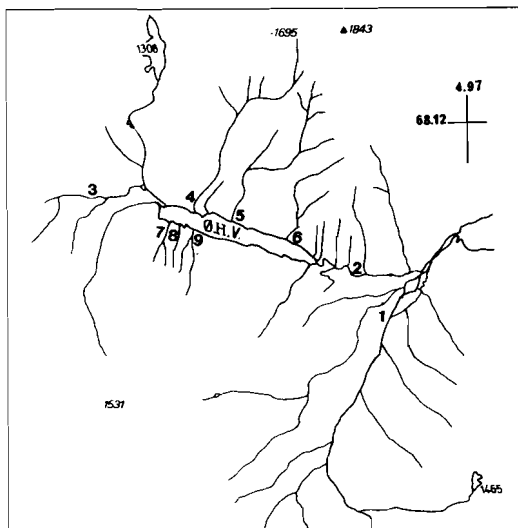


Fig. 8. Sketch of the lake, Øvre Heimdalsvatn, and the streams investigated (1–9). Map coordinates refers to UTM system.

area. *Dinocras cephalotes* is present in certain sections of some rivers while *Diura nanseni* occurs nearly everywhere. *Diura bicaudata* is common in lakes.

Area 4. Øvre Heimdalen

This is a smaller area than the others. It was chosen because it was suitable for a study of both the stream and lake Plecopteran faunas and enabled comparisons to be made with the species association of the lake outlets where there is a mixing of both lotic and lentic elements. The area is also situated in a part of Norway where the tree line is highest and where the alpine areas can be easily reached.

Area description

The valley Øvre Heimdalen is situated on the eastern side of the Jotunheim Mountains. In this area (Fig. 8) 11 streams and 3 lakes were investigated, ranging in altitude from 1060 m to 1500 m a.s.l. Some of the surrounding mountains, however, reach heights of 1700–1800 m a.s.l.

The bedrock on the northside of the valley is largely gabbro, while on the southside syenite predominates. The area is covered by a thick layer of glacial drift. Lying in the rain shadow of the western mountains, precipitation is between 600 and 800 mm a year.

The bottom of the valley lies in the upper part of the Sub-Alpine birch belt and the tree line is somewhat higher on the northern side of the valley than on the southern side. The bottom of the valley and the wooded sides are often thickly covered by dwarf willow and dwarf birch.

Stream descriptions

The main river follows the valley in a west-east direction. The tributary streams run more or less at right angles to this. Most of the streams rise at heights above 1400 m, some from springs while others have melting snow as their main source.

In the bottom of the valley the streams often have a more or less dense fringe of *Salix*. This diminishes with altitude, and above 1200 m it is only present in especially sheltered places. At and above 1300 m there are only sporadic bushes, the main vegetation being grass.

Around Øvre Heimdalsvann stream temperatures lie at about 0° C during the winter, while in the summer they may reach temperatures of 15–18° C, although the mean is markedly lower (Kloster, personal communication). The pH varies from 6.1 to 7.4, but the most common values are from 6.5 to 6.8. The Ca⁺⁺ content was from 0.5–2.0 mg/l and Mg⁺⁺ about 0.5 mg/l.

Øvre Heimdalsvatn

This lake has recently been the subject of intensive study under the auspices of IBP. It is 3 km long, has an area of 0.78 km² and a catchment area of 24.4 km². The lake is shallow – its greatest depth is 13 m. Near the shore the substratum is mainly stony, the stone band being most extensive in the outlet area. Around the inlet there is only a thin band of stones below which sand predominates.

Øvre Heimdalsvatn is usually ice-covered from October to the beginning of June. From January to June surface temperatures lie between 0° and 1° C. In the latter part of June, July, August and most of September, temperatures generally lie between 7° and 14° C, while from October to December they are below 2° C. The pH usually varies between 6.5 and 7.0. The Ca⁺⁺ content varied between 1.5 and 4.5 mg/l, the Mg⁺⁺ between 0.5 and 1.0 mg/l.

Stonefly fauna

In this area, 21 species have been taken. Among the 29 species in southern Norway, the rare *Perlodes dispar*, *Xanthoperla apicalis* and *Isogenus nubecula* are absent. *Amphinemura borealis* and *Capnia pygmaea*, which have not been taken above the boreal coniferous zone in southern Norway, are also absent. In addition *Siphonoperla burmeisteri*, *Nemoura flexuosa* and *Isoperla difformis* have not been recorded.

Twenty species have been taken in streams (Table VI). Among the herbivorous species the most common were *Amphinemura standfussi*, *A. sulcicollis*, *Nemoura cinerea*, *Capnia atra* and *Leuctra nigra*. *Capnia bifrons* was also common both in the Sub-Alpine belt and in the Low-Alpine belt where willow is abundant along the streams. The dominating carnivorous species of the whole area was *Diura nanseni*, although the omnivore *Isoperla obscura* was equally common. There are large differences in the stonefly fauna of the various vegetation belts. This will be discussed later.

There are also considerable differences in the fauna of streams which flow throughout the year (streams 1–6) and the three small streams (7–9) which are more or less temporary. In the latter only *Nemoura cinerea*, *Nemurella picteti* and *Isoperla grammatica* were taken.

In Øvre Heimdalsvatn 10 species were taken (Table VI). The most common herbivore species were *Nemoura avicularis*, *Nemoura cinerea*, *Nemurella picteti* and *Capnia atra*. The carnivore *Diura bicaudata* was very common and seems to be the main invertebrate predator in the littoral fauna of the lake.

In Brurskardstjønn (about 1300 m a.s.l.) 6 species were taken in the lake, 5 of them herbivores. In Blåtjønn (1465 m a.s.l.) 4 species were taken, 3 of them herbivores. The plecopteran fauna of Blåtjønn was dominated by *Capnia atra* and *Diura bicaudata*.

The outlets of Øvre Heimdalsvatn and Blåtjønn were richer in species than the lakes. The outlet of Øvre Heimdalsvatn supported 12 species and the outlet of Blåtjønn 5 species. The stonefly fauna of the outlet of Øvre Heimdalsvatn consists of the lake species and in addition *Isoperla grammatica* and *Taeniopteryx compacta*. In the outlet of

Blåtjønn *Diura bicaudata*, *Arcynopteryx compacta*, *Capnia atra*, *Amphinemura standfussi* and *Isoperla obscura* were taken. As in the case of streams and lakes, there was a reduction of species from the Sub-Alpine belt to the Middle Alpine belt. The most common carnivore was again *Diura bicaudata*.

Distribution westwards along presumed emigration routes

Seven species are restricted to eastern parts of southern Norway where most of them occur widely (Table I). Among these are *Nemoura avicularis*, *Capnia bifrons*, *Capnopsis schilleri* and *Nemoura flexuosa*. Even *Capnia atra* does not extend too far west. Therefore three of the most likely entry routes into western Norway were investigated in detail.

The lowest (ca. 900 m a.s.l.), and probably the most suitable since there is almost continuous birch woodland over the pass, is via Valdres over to Lærdal, Sogn. The other two possibilities – up Hallingdal and over to Eidfjord, and from Telemark over Haukeli to Hordaland and Rogaland – are somewhat higher and go above the tree line.

Collecting in these areas showed that *Capnopsis schilleri*, *Capnia bifrons*, *Nemoura avicularis*, *Capnia atra* and *Nemoura flexuosa* had somewhat different distributions. *Nemoura flexuosa* had the most eastern distribution of the species and was not taken during the present investigations. *Capnia bifrons* and *Capnopsis schilleri* had the next most easterly distribution. In Valdres *Capnia bifrons* went furthest up (Tyinkrysset) while *Capnopsis schilleri* has so far only been found in Østre Slidre. Neither species was taken in Hallingdal, while in Telemark both were taken more or less the same distance west, *Capnia bifrons* in Hjartdal and *Capnopsis schilleri* in Seljord.

Nemoura avicularis was collected in Østre Slidre, Svenkerud in Hallingdal, and Seljord in Telemark. In the southern part of the country they occurred as far west as at the Byglandsfjord.

Capnia atra goes furthest west of the species discussed here, although absent in the south-west of the country. Further north the species occurs in Lærdal and at Eidfjord, right down to the fjord. In the south, the

most westerly locality is Grungedal in Telemark.

Discussion: southern Norway

Area 1, Rogaland and South Hordaland, which contains a considerable range of environmental factors, shows very great differences in faunal associations. The coastal areas are poor in species, but those present are numerous. In area 2 the same tendency is apparent, the inner area (2.1) having the most species. This gradient from inner areas towards the coast seems to indicate an important distributional trend.

Within areas 2 and 3 there are pronounced differences in the fauna. In the area of the inner Oslofjord (2.1), where there is a rich cover of deciduous trees along the streams, the Capniids dominate. The same is true of area 3.1, the Glåma valley, where deciduous trees are also common along the streams. In the eastern parts of both areas 2.2 and 3.2, the Capniids are poorly represented. Therefore the Capniids as a group seem to prefer streams on rich soils with deciduous trees along the streams.

The Capniids also have their main distribution area in the eastern part of south Norway. Two of them, *Capnia bifrons* and *Capnopsis schilleri*, have not been taken in western Norway, and the distribution of the other two species, *Capnia atra* and *Capnia pygmaea*, is very restricted in the west. This may be connected with the factors mentioned above. South-west Norway and the southern part (Sørlandet) differ from the rest of the country in that *Capnia atra* seems to be absent both in high altitude lakes and streams, and in streams in lower altitudes. In the high altitude lakes, the common herbivores are *Nemoura cinerea* and *Nemurella picteti*. They also occur in streams. *Capnia pygmaea* may be common, but the species has only been taken below the alpine belts. There also seems to be a trend of a decreasing number of species as the deciduous trees and willow bushes along the streams become absent at higher altitudes. This is most pronounced among the herbivorous species. The above trends will be compared as far as possible with those in northern Norway, and some of the trends themselves will be examined further in the zonation studies.

NORTHERN NORWAY

The northern areas of Norway support a special fauna (Table I). Studies making it possible to compare the fauna of these areas with those of southern Norway were preferable, but the long travelling distance presented problems. Therefore, the research could not be of the same intensity as in the south, and the areas were investigated only once a year. The area around Kautokeino and the coastal areas were visited both in 1968 and 1972, while the Pasvik area was visited only in 1966. The comparisons may, therefore, not be so valid as in the south. Nevertheless, the studies were carried out in the latter part of June and July, the best months for Plecopteran investigations in these areas, where the snow and ice disappears during the first part of June.

Area 5. Kautokeino

This area was chosen because it lies within the most continental area of Norway.

Area description

The area (Fig. 4) is part of the large Kautokeino rural district which covers much of inner Finnmark. It consists mostly of a plateau cut into by river valleys. In this area, 16 streams and 8 lakes were investigated.

The bedrock is Pre-Eocambrian which in the far north changes to Eocambrian sediments. The whole area is covered by a thick layer of drift material, notably along the Kautokeino river (Sollid et al. 1973).

Precipitation is less than 400 mm a year. In Kautokeino village the valley floor lies at 3–400 m a.s.l. and the surroundings seldom reach over 600 m a.s.l. In the north-western areas the landscape is somewhat higher with heights of 700 m a.s.l. and above. The area is situated in the Sub-Alpine birch belt and the Alpine belts.

In the valleys there is often very dense growth of birch and willow, above which there is a belt of willow, which may be very dense in the lower parts.

Stream descriptions

The landscape is rich in lakes and streams, most of them running into the Kautokeino

River, a part of the Alta watercourse. Both small and large streams were investigated.

The pH was fairly constant at the time of measurement, from 6.6 to 7.0. The Ca^{++} content varied quite a lot, from 0.83 to 28.7 mg/l. The highest values were recorded in small streams coming from shallow lakes with slow renewal.

Stonefly fauna

During this investigation 26 species were taken (Table VII). However, the total number is 27, as *Dinocras cephalotes* was taken in the Anojokka area in 1969. The five species taken solely in northern Norway are *Capnia vidua*, *Nemoura arctica*, *Nemoura sahlbergi*, *Nemoura viki* and *Protonemura intricata*. The last mentioned is the only one which has not been taken in this area, there being only two records of this species, both further north.

All the 27 species were taken in streams, while in lakes and lakes outlets there were 10 species in each. In this area *Diura bicaudata* was common both in streams and lakes and dominated among the carnivorous stoneflies. *Diura nanseni* was widespread in both lakes and streams, but was never as numerous as *Diura bicaudata*. The third of the large carnivores, *Arcynopteryx compacta*, was only found in lake outlets and streams. All three occurred together in the outlet of Stuurajavrrre and in Masijokka.

The most common omnivorous species was *Isoperla obscura*, which was taken in lakes, outlets and streams.

Among the herbivorous species *Leuctra hippopus* and *Capnia atra* were the most widespread species, followed by *Nemoura avicularis* and *Nemoura cinerea*.

In the streams the most common were *Leuctra hippopus*, *Capnopsis schilleri*, *Capnia atra*, *Leuctra nigra* and *Nemoura cinerea*. In certain streams *Nemoura arctica*, *Nemoura sahlbergi* and *Nemoura viki* were very numerous. All the Norwegian *Nemoura* species have in fact been taken in streams in this area. In lakes, four of them, *Nemoura avicularis*, *Nemoura arctica*, *Nemoura cinerea* and *Nemoura viki*, were taken.

Area 6. Alta and its surroundings

This area (Fig. 4) represents the fjord areas

Table VII. Species distribution in selected water courses and the number of specimens taken in the whole of area 5 (Kautokeino)

	<i>Arcynopteryx compacta</i>	<i>Diura bicaudata</i>	<i>Diura nanseni</i>	<i>Isoperla difformis</i>	<i>Isoperla obscura</i>	<i>Isoperla grammatica</i>	<i>Dinocras cephalotes</i>	<i>Siphonoperla burmeisteri</i>	<i>Taeniopteryx nebulosa</i>	<i>Brachyptera risi</i>	<i>Amphinemura borealis</i>	<i>Amphinemura standfussi</i>	<i>Amphinemura sulcicollis</i>	<i>Nemoura arctica</i>	<i>Nemoura avicularis</i>	<i>Nemoura cinerea</i>	<i>Nemoura flexuosa</i>	<i>Nemoura sahlbergi</i>	<i>Nemoura viki</i>	<i>Nemurella picteti</i>	<i>Protonemura intricata</i>	<i>Protonemura meyeri</i>	<i>Capnia atra</i>	<i>Capnia pygmaea</i>	<i>Capnia vidua</i>	<i>Capniopsis schilleri</i>	<i>Leuctra digitata</i>	<i>Leuctra fusca</i>	<i>Leuctra hippopus</i>	<i>Leuctra nigra</i>				
Streams:																																		
Ravnatjokka	X														X	X						X			X			X	X	X	X			
Stream at Masi	X	X	X												X	X	X					X			X		X	X	X	X	X			
Masi jokka	X	X	X														X	X					X			X		X	X	X	X			
Suopatjokka		X	X	X	X						X												X			X		X	X	X	X			
Stream at Suopatjavrre			X												X	X						X			X		X	X	X	X	X			
Hannujokka		X										X			X	X		X			X		X		X	X	X	X	X	X	X			
Fidnatjokka		X	X	X	X	X		X	X				X		X	X	X				X	X	X	X		X	X	X	X	X	X	X		
Stream at Aiddejavrre		X	X	X	X				X				X		X	X	X				X	X	X	X		X	X	X	X	X	X	X		
Stream at Caskijas 1			X		X								X									X	X			X		X	X	X	X	X		
Stream from Ellijavrret								X						X	X					X			X			X		X	X	X	X	X		
Stream from Emmejavrre				X											X	X				X						X		X	X	X	X	X		
Stream at Caskijas 2														X	X	X							X											
Outlets:																																		
Stuorajavrre	X	X	X		X									X	X								X	X	X									
Lake at Caskijas	X	X			X									X	X	X				X	X		X		X									
Lakes:																																		
Suopatjavrre		X	X		X							X		X	X	X							X									X		
Stuorajavrre		X	X		X								X	X	X					X														
Gædgejavrre		X											X	X																				
Lake at Caskijas		X														X							X											
No. of specimens	38	312	47	91	265	15	1	1	4	0	3	5	23	186	75	206	12	190	79	14	0	15	50	5	13	34	11	0	250	165				

of Finnmark, northern Norway and can in this sense be compared with the inner areas of Rogaland (area 1). The main differences are in latitude, vegetation belts and in the fact that the oceanity factor is much lower.

Area description

Ten streams and 2 lakes were investigated in the area. The central parts consist largely of sandstone and greenstone, while the peripheral parts consist of little altered Eocambrian sediments. Drift material is present, especially in the stream valleys.

The climate has a pronounced continental character. Precipitation generally lies between 400 and 600 mm a year, although the southern parts can have below 400 mm. The June isotherm is similar to the inner fjords of area 1 (western Norway). The July temperature is lower and can be compared to the western coastal areas or the mountain areas of southern Norway.

In the Alta area there are deep valleys which converge on the fjord at Alta. In the southern and eastern parts of the area, mountains between 800 and 700 m a.s.l. are common, while in the western parts the landscape is generally higher, with mountains of 1100 m a.s.l. and above. Around the village of Alta and the lower parts of the valleys there are pine woods, mixed with willow, alder and other deciduous trees. Above this, in the Sub-Alpine belt, there is largely birch and willow.

Stream descriptions

The main river in this area is the River Alta. In addition, there are numerous small and large streams. In places there is a dense fringe of deciduous trees along the streams which consists mainly of willow, alder and birch. In the Sub-Alpine belt willow dominates alongside the streams and may be very dense and high in the lower sections. Higher up the bushes are lower, but growth may still be dense. In the Alpine belts the willow gradually disappears (Figs. 9, 10).

Calcium hardness was measured both during 1968 and 1972 in several places, and values varied between 0.9 and 2.7 mg Ca⁺⁺/l. Values of pH lay generally between



Fig. 9. Stream by Leirbotnvann in the Sub-Alpine belt.

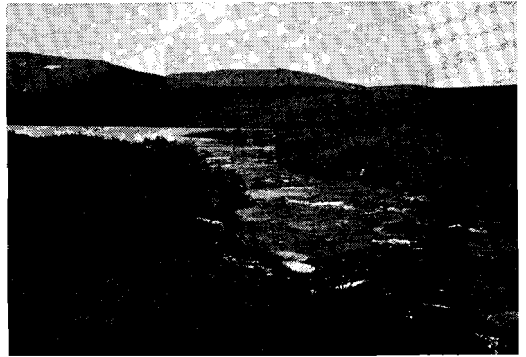


Fig. 10. Stream in Stokkedalen in the Low-Alpine belt.

6.0 and 6.8, although somewhat lower in the higher areas.

Stonefly fauna

In this area 18 species of stoneflies were taken (Table VIII). Of the five species which are restricted to northern Norway, only two were represented, *Nemoura arctica* and *Nemoura sahlbergi*.

The dominant carnivore was *Arcynopteryx compacta*, which occurred in lakes, lake outlets, and in streams. *Diura bicaudata* was also common and was taken in streams, lakes and lake outlets. *Diura nanseni* was taken in streams and lake outlets and all three species were taken together in the outlet of a lake (Fig. 10). The most common herbivores were *Capnia atra*, *Leuctra hippopus*, and *Nemoura cinerea*. In this area 16 species were taken in streams, 7 in lake outlets, and 5 in lakes.

Area 7. South Varanger

In South Varanger, studies were carried out in two widely separated areas (Fig. 4): the Pasvik area and the Korp fjell area. The Pasvik area is situated in the northern part of the Sub-Alpine and Boreo-Montane sub-zone, while the Korp fjell area lies in the upper part of the Sub-Alpine belts, where it is close to the arctic vegetation zone (Sjors 1963).

Area description

Ten streams and five lakes in the Pasvik area, and three streams and two lakes in the Korp fjell area were investigated.

The whole area belongs to the Precambrian 'Baltic shield', but there are differences in the Pasvik area. Around Spurvvann in the north-west, there are younger formations with intrusions of basic rocks. The Quarternary deposits are mainly moraine material (Boyum 1970).

The climate is less continental than the Kautokeino area, but precipitation is low (below 400 mm a year). The Korp fjell area has the highest oceanity factor.

The south-eastern parts of Pasvik consist mostly of boggy areas at an altitude of between 50 and 100 m a.s.l. In the west, the landscape is somewhat higher, with heights of about 200 m a.s.l. In the north-west it is even higher (about 300 m). The area investigated on Korp fjell lies between 200 and 260 m a.s.l.

Most of the Pasvik area is covered by coniferous forest. Along the streams and rivers there is often a dense fringe of willow. In the north-west there are areas which lie on the border of the Sub-Alpine belt. There is also here a great deal of willow along the streams, especially in the lower parts. The flora is also described by Kalheber & Tobias (1971).

On Korp fjell, birch woodland predominates around Korp vann, while above this and along the streams willow dominates.

Stream descriptions

The Pasvik area is dominated by the River Pasvik, which forms the border between Norway and the USSR. The river comes from lake Enare in Finland and is mainly slow-flowing, with sand and gravel substrata.



Fig. 11. Stream at Ivargammevann in Pasvik.

Riffles, with substrata of larger stones, occur occasionally. Most of the streams in this area drain into the River Pasvik. The substratum of these is mostly large stones (Fig. 11), but there are also some streams with finer substrata of gravel and sand such as Gjokbekken (stream 4) and Skjellbekken (stream 7).

In the Korp fjell area only three streams were investigated. They all had a mixed substratum of stones, gravel and sand. Measurements of hardness and pH were made on several occasions. Values of pH around 7.0 were common in the Pasvik area (see also Boyum 1970), and the lowest recorded was 6.6. Calcium hardness varied generally between 1 and 2 mg Ca⁺⁺/l. The highest values were recorded in Storkilden, pH 7.4 and 3.0 mg Ca⁺⁺/l and a stream flowing from Spurvvann, pH 7.1 and 3.4 mg Ca⁺⁺/l.

On Korp fjell, Oterbekken had pH 6.5 and 1.7 mg Ca⁺⁺/l and Bannebekken pH 6.7 and 2.2 mg Ca⁺⁺/l.

Stonefly fauna

In South-Varanger 24 species were recorded, 23 in Pasvik and 15 at Korp fjell, Table IX.

At Korp fjell two of the 15 species were taken in lakes and 13 in streams. The total number of species taken in lakes in area 7 was 13, the highest in Norway.

The dominating carnivorous species in the Pasvik area is *Diura bicaudata*, which was taken in great numbers in lakes, lake outlets and streams. Next to *Diura bicaudata* in abundance was the omnivore *Isoperla obscura*

Table IX. Species distribution in selected water courses and the number of specimens taken in the whole of area 7 (South Varanger)

	<i>Arcynopteryx compacta</i>	<i>Diura bicaudata</i>	<i>Diura nanseni</i>	<i>Isoperla difformis</i>	<i>Isoperla obscura</i>	<i>Isoperla grammatica</i>	<i>Dinocras cephalotes</i>	<i>Siphonoperla burmeisteri</i>	<i>Taeniopteryx nebulosa</i>	<i>Brachyptera risi</i>	<i>Amphinemura borealis</i>	<i>Amphinemura standfussi</i>	<i>Amphinemura sulcicollis</i>	<i>Nemoura arctica</i>	<i>Nemoura avicularis</i>	<i>Nemoura cinerea</i>	<i>Nemoura flexuosa</i>	<i>Nemoura sahlbergi</i>	<i>Nemoura viki</i>	<i>Nemurella picteti</i>	<i>Protonemura intricata</i>	<i>Protonemura meyeri</i>	<i>Capnia atra</i>	<i>Capnia pygmaea</i>	<i>Capnia vidua</i>	<i>Leuctra digitata</i>	<i>Leuctra fusca</i>	<i>Leuctra hippopus</i>	<i>Leuctra nigra</i>	<i>Capnopsis schilleri</i>				
PASVIK																																		
Streams:																																		
From Elenvann		X	X					X			X		X			X	X														X			
From Vinterfiskevann		X			X	X					X		X			X		X									X			X				
From Ivargammevann		X			X	X					X		X			X		X												X				
Gaukbekken, Lower		X			X	X					X		X			X		X			X						X			X				
Ødevannsbekken					X	X		X			X																							
from Storkilden					X														X	X						X					X			
Skjellbekken						X											X		X							X								
Pasvikelven	X	X			X			X	X		X		X		X	X																		
from Svartbrysttjern					X						X		X																					
Steinbekken											X					X											X							
Lakes:																																		
Elenvann		X	X		X						X		X	X																				
Vinterfiskevann		X			X						X		X			X								X			X							
Ivargammevann		X			X						X		X			X																		
Langevann	X	X	X																															
Svartbrysttjern					X						X		X									X												
KORPFJELLET																																		
Stream at Korp fjellet	X				X	X		X			X	X	X	X							X	X		X		X		X	X	X	X	X		
Lake at Korp fjellet								X			X									X	X		X			X								
No. of specimens from South Varanger	10	425	4	0	353	70	0	147	1	0	359	67	322	1	7	189	14	6	7	293	1	1	18	0	0	3	9	0	49	18				

which was also taken in the same habitats. *Diura nanseni* and *Arcynopteryx compacta* were also present. The most common herbivorous species were *Nemoura cinerea* and *Amphinemura borealis*, which also occurred in large numbers. Four of the five northern species were taken in this area, *Nemoura arctica*, *Nemoura sahlbergi*, *Nemoura viki* and *Protonemura intricata*.

The total number of species in area 7 is 28, as *Amphinemura norwegica*, *Leuctra fusca*, *Capnia vidua* and *Isoperla difformis* were registered by Tobias (1973, 1974).

Discussion: northern Norway

Of the areas investigated, Kautokeino and Pasvik contained the richest fauna with 27 and 28 species, Alta and Korp fjell the poorest with 18 and 15 species, respectively.

There are marked differences between the areas. The three carnivorous species occupy quite different positions. In Pasvik *Diura bicaudata* completely dominated and was numerous both in lakes, outlets and streams while *Diura nanseni* and *Arcynopteryx compacta* were rare. Around Kautokeino *Diura bicaudata* still dominated, but *Diura nanseni* and *Arcynopteryx compacta* were more common and were taken in greater numbers. Around Alta *Arcynopteryx compacta* was more common than either *Diura bicaudata* or *Diura nanseni*. In all three areas *Arcynopteryx compacta*, *Diura bicaudata* and *Diura nanseni* were taken at least once together in lakes or outlets. Among the omnivores, *Isoperla obscura* was common in Pasvik and Kautokeino but not around Alta.

Among the herbivores, *Leuctra hippopus*, *Nemoura cinerea* and *Capnia atra* were most common in Alta. In Pasvik *Amphinemura borealis* and *Nemoura cinerea* were the most common while in the Kautokeino area *Nemoura avicularis*, *Nemoura cinerea*, *Leuctra hippopus* and *Capnia atra* were the most common herbivorous species. Most marked was the absence of the *Amphinemura* species in the Alta area.

COMPARISON OF SOUTHERN AND NORTHERN NORWAY

There were considerable differences in the fauna distribution in the 7 areas investigated.

For the most part they hold different species. Even the species which they have in common vary in occurrence from area to area. The differences between the north and south in the distribution of the carnivore species *Diura nanseni*, *Diura bicaudata* and *Arcynopteryx compacta* are marked. In the north the three species are very common and occur in small and large streams, lakes and outlets, sometimes occurring together. In the south, however, they have a quite different distribution. *Diura bicaudata* is found solely in lakes and outlets and *Diura nanseni* is nearly always taken in streams, both lowland and high altitude. In the Low-Alpine belt and above, *Arcynopteryx compacta* takes over as the most common carnivorous species. The three species were never taken together in the south.

The wider ecological preference of these species in northern Norway indicates that environmental conditions are nearer the optimal.

Two other species, the herbivore *Amphinemura borealis* and the omnivore *Isoperla obscura*, also have a wider distribution in the north and therefore also seem to be in or near their optimal environment.

Both in the east and west of southern Norway there is a reduction in the number of species from inner fjords towards coastal areas. In southern Norway the species of the family Capniidae are mainly found in the parts where there are rich soils with deciduous trees along the streams. This is documented both in areas 2 and 3.

Common for northern, southern and western areas is the decrease in species where the deciduous trees and willow bushes disappear from along the streams at higher altitudes.

The fauna of the Sub-Alpine birch wood areas is richer in the continental areas in northern Norway and poorest in the western areas in southern Norway. The differences shown in the present work were so marked that it seems natural to compare the results with the results of other investigations made in northern Fennoscandia by Brinck (1949), Brinck & Wingstrand (1949), Brinck & Froehlich (1960), Bagge (1965, 1968), Ulfstrand (1967, 1968a & b, 1969), Ulfstrand et al. (1971), Meinander (1972). They are all shown to be different from the Norwegian areas and from each other. The Kilpisjärvi area in Finland (Meinander 1972) is situated at the

same latitude as Kautokeino, but further west. The registered fauna consisted of 25 species, of which *Diura nanseni*, *Diura bicaudata*, *Leuctra hippopus* and *Capnia atra*, *Amphinemura sulcicollis* and *Nemoura cinerea* were widespread and numerous. *Leuctra fusca* was rare and *Brachyptera risi* was absent.

In the upper Vindelølv area (Ulfstrand 1969) the fauna also consisted of 25 species, but there was not the same association of species. The dominating species was *Leuctra fusca*, followed by *Diura nanseni*, *Isoperla grammatica* and *Amphinemura standfussi*.

The Messaure area had 27 species (Müller & Thomas 1972), the same as the Kautokeino area, but differing in the absence of *Nemoura viki*.

HORIZONTAL AND VERTICAL DISTRIBUTION

During the investigation of the study areas, certain distribution zones, both horizontal and vertical, became apparent. They have been examined further and the results are discussed in this chapter.

Zonation in the distribution of freshwater animals has been discussed by several authors (Thieneman 1926, Ricker 1934, Illies 1952a, 1953a, Müller 1955). The zones have been mainly named after fish species, but some authors (Smitsaert 1959, Pawlowski 1959) have characterized zones according to environmental factors such as substratum and stream velocity. Illies & Botosaneanu (1963) gave a revised classification where they used the divisions Potamon, Rhithron and Crenon and a sub-division of each of them.

Zonation in the distribution of Plecoptera has been documented by many authors (Dodds & Hisaw 1925, Hynes 1941, Brinck 1949, Berthélemy 1966, Minshall 1968, Elgmork & Sæther 1970, Hynes 1971, Kownacka 1971, Woodall & Wallace 1972 and Ikonomov 1973) and studies have been made along the length of rivers by, e.g., Percival & Whitehead 1929, 1930, Berg 1948, Brinck & Wingstrand 1949, 1951, Illies 1952a, 1958, Badoc 1953, Müller 1954, Albrecht & Bursche 1957, Hynes 1961 and Maitland 1966.

The generalization in the subdivision of rhithron made by Illies & Botosaneanu (1963) has been subject to criticism from many authors. Hynes (1970) discusses this and con-

cludes that it is difficult to use the described zones in general, and Maitland (1966) says: 'Some species are limited by temperature, others by substrate, amount of suspended matter, calcium etc.'

This seems to fit in well with what was observed by the present author in different areas of Norway. The author therefore carried out zonation investigations to test the influence of certain factors on distribution.

The investigation in all studied areas indicated some distributional trends. Firstly, the decreasing number of species from areas rich in deciduous trees to areas poor in deciduous trees. Secondly, the decrease in deciduous trees with altitude and the associated decrease in species. Thirdly, the decrease in species towards the coastal areas.

The stonefly association at different stations in a stream

This investigation was carried out during the period 1967–1971 in Sæterbekken, Bærum, near Oslo and in area 2.1.

Stream description

Sæterbekken is about 3 km long and alternates between riffles and pools along its whole length. Three stations were chosen, the lowest station (1) about 150 m a.s.l. and the highest (3) at about 400 m a.s.l.

Station 1 (Fig. 12) lies in a cultivated area with extensive marine sediments. The substratum varies from large stones, embedded tightly in the bottom via unstable, rounded stones of different sizes, to gravel and sand. There is a dense fringe of deciduous trees along the stream dominated by *Alnus*. Al-



Fig. 12. Sæterbekken, station 1.



Fig. 13. Sæterbekken, station 3.

lochthonous matter, abundant at this station, largely originating from leaves, is richest where stones trap the leaves and in pools where they sink to the bottom.

Station 2 lies among conifers in the upper part of the marine sediments at about 300 m a.s.l. There are scattered groups of deciduous trees along the stream still dominated by *Alnus*. A small farm is situated on one side of the stream. The substratum is not as diverse as station 1, but there are pools and riffles. In the riffles the bottom is largely stable with tightly embedded, rounded stones. There is less allochthonous matter than at station 1.

Station 3 (Fig. 13) is situated above the marine sediments and in the coniferous forest where there only are a few deciduous trees,

which are mainly birch. The soil is boggy with moss, heather and grass. Ferns also occur along the streams. The substratum consists mainly of jagged stones. Allochthonous matter is poor, consisting mainly of coniferous needles.

There are marked differences in water temperature between stations 1 and 3 (Fig. 14). This is especially marked in April and May. The melting of snow and the rise in temperature begin three weeks earlier at station 1. During the winter, temperatures are about 0° C at all stations, although in the lower section of station 3 there is a spring which holds a winter temperature of 2–3° C. Water chemistry data are given in Tables X and XI.

Stonefly fauna

There was a decrease in the number of species present from 20 to 14 from station 1 to station 3 (Table XII). At station 3 two species dominated, *Leuctra nigra* and *Leuctra hippopus*, with *Brachyptera risi* subdominant. The only Capniid taken was *Capnopsis schilleri*, but the species was rare at that station.

Table X. The total hardness at different stations of Sæterbekken in 1969 and in 1970. n = number of measurements

	Maximum	Minimum	Mean	n
<i>1969</i>				
Station 1	5.20	1.68	3.26	13
Station 2	5.94	1.17	3.03	13
Station 3	2.20	0.70	1.46	11
<i>1970</i>				
Station 1	4.54	2.14	3.37	11
Station 2	5.00	1.58	2.62	9
Station 3	2.44	1.18	1.71	11

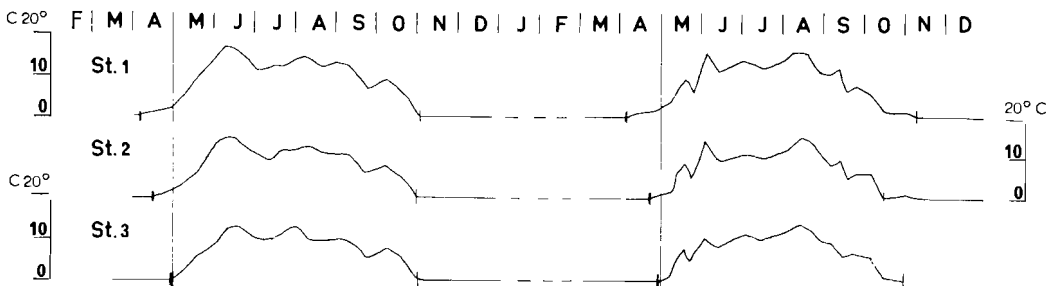


Fig. 14. Water temperatures at three stations in Sæterbekken during 1969 and 1970.

Table XI. The pH at different stations of Sæterbekken in 1969 and in 1970. n = number of measurements

	Maximum	Minimum	Mean	n
<i>1969</i>				
Station 1	7.0	6.4	6.75	16
Station 2	7.0	6.1	6.57	14
Station 3	6.3	5.8	6.16	13
<i>1970</i>				
Station 1	7.2	5.5	6.63	8
Station 2	6.6	5.4	6.01	5
Station 3	6.6	5.8	6.01	6

At station 2, 17 species were taken, *Leuctra hippopus* and *Leuctra digitata* dominating with *Amphinemura sulcicollis* and *Capnopsis schilleri* subdominant. *Capnia bifrons* was also taken.

At station 1 the dominant species were *Capnia bifrons* and *Capnopsis schilleri*, followed by *Brachyptera risi* and *Leuctra hippopus*.

At station 3, two species dominated together, constituting about 66 % of the specimens. At station 2, two species also dominated, constituting about 50 % of the specimens. At station 1 two species also dominated, making up about 45 % of the specimens. This study showed a strong dominance at station 3 where there are less species, less allochthonous matter and less varied substratum and a much weaker dominance where there are most species, most allochthonous matter and the most varied substratum. The zonation study also showed a decrease in species and numbers of Capniids from areas rich in deciduous trees to areas poor in deciduous trees. The reduction in species and differences in dominance from station 1 to 3 seem therefore to be due to factors such as: the decrease of varied substratum in the biotope; the decrease in allochthonous organic matter.

The stonefly association in Boreal-coniferous, Sub-Alpine, Low and Middle-Alpine belts

These studies were carried out in three different faunistic areas: the inner fjords of the western area (1), the Øvre Heimdal area (4), on the eastern slopes of the central

Table XII. The stonefly association at three stations in Sæterbekken. – Signifies less than one percent.

Station	1	2	3
	Frequency %	Frequency %	Frequency %
<i>Leuctra digitata</i>	1.0	18.4	4.0
<i>Leuctra hippopus</i>	12.5	32.5	26.0
<i>Leuctra nigra</i>	1.8	2.5	40.4
<i>Protonemura meyeri</i>	–	3.9	–
<i>Amphinemura sulcicollis</i>	3.4	10.2	4.8
<i>Amphinemura standfussi</i>	–	–	3.6
<i>Brachyptera risi</i>	12.7	3.4	9.6
<i>Taeniopteryx nebulosa</i>	2.9	–	–
<i>Nemurella picteti</i>	–	2.5	4.8
<i>Nemoura cinerea</i>	–	–	3.2
<i>Capnopsis schilleri</i>	27.6	6.3	–
<i>Diura nanseni</i>	3.8	1.5	1.6
<i>Leuctra fusca</i>	1.8	–	–
<i>Capnia bifrons</i>	17.3	–	–
<i>Amphinemura borealis</i>	–	–	–
<i>Nemoura avicularis</i>	3.8	1.5	–
<i>Isoperla difformis</i>	2.5	–	–
<i>Nemoura flexuosa</i>	–	–	–
<i>Siphonoperla burmeisteri</i>	4.5	–	–
<i>Capnia atra</i>	1.3	–	–
Number of species	20	17	13
Number of specimens	1129	206	250

mountains of southern Norway and the Kautokeino area (5) in Finnmark, northern Norway.

The western area

The studies were carried out in Sauda and Røldal (Figs. 15, 16, 17, 24), where altitudes varied from 10 to about 1000 m a.s.l. Coniferous woodland occurs up to 500 m, the Sub-Alpine belt up to about 700 m, the Low-Alpine up to about 850 m a.s.l. and finally the Middle-Alpine belt above this.

Station descriptions

Station 1 in Nordelva (Fig. 24) lies at about 10 m a.s.l., station 2, Elgjuvet, at about 500 m a.s.l. Station 3 was in Botnavatn (Fig. 16) about 700 m a.s.l. and at the border between the Sub-Alpine and the Low-Alpine belts. Station 4 at 850 m and in the upper part of the *Salix* vegetation area. Station 5



Fig. 15. Inner fjord area, Sauda, station 2. The Sub-Alpine belt.

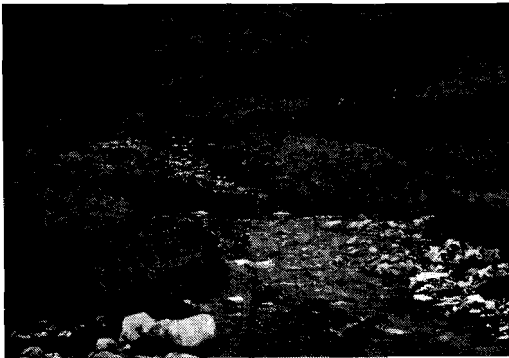


Fig. 16. Inner fjord area, Sauda, station 3. Stream in the Low-Alpine belt.

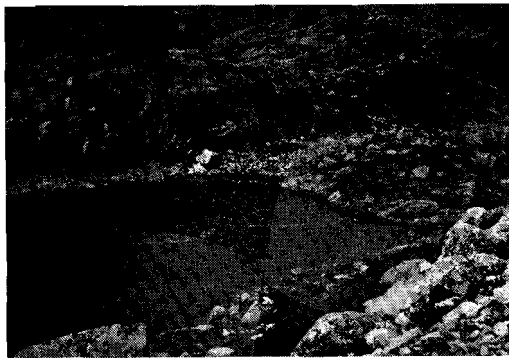


Fig. 17. Inner fjord area, Sauda, Lake in the Middle-Alpine belt.

(Fig. 17) at 900 m and above the area with *Salix* along the streams.

The substratum was mixed at all stations, both riffles and pools being present. At the lowest stations, however, the stones are more rounded than at the upper stations.

The temperature was measured each time the localities were sampled, but the temperatures shown in Table XIII only refer to days where the temperature was taken at nearly the same time. The stream at Botnavatn sometimes had a thick ice covering, making the measurements impossible. Hardness and pH were measured several times (Table XIV).

At station 1 there is a dense fringe of deciduous trees, *Alnus* being the most common. At station 2, *Alnus* is still present but *Salix* is more common. At station 3 there are only scattered *Salix* bushes and grass vegetation dominates. Allochthonous matter is less than in Sæterbekken, with most at stations 1 and 2, less at station 3, and very little at stations 4 and 5.

Stonefly fauna

The number of species decreases from 17 at station 1, to 2 at station 5 (Table XV).

Two species, *Amphinemura borealis* and *Capnia pygmaea*, were found only below the birch belt. Only one specimen of *Siphonoperla burmeisteri* was taken at station 2 during the years 1965–70.

Table XIII. Water temperatures (°C) at three stations in the vertical zonation investigation carried out in the western area.

Date	Station		
	1	2	3
28 Apr. 66	2.0	1.5	–
15 June 66	7.0	5.0	3.0
28 May 67	4.0	1.0	–
10 July 67	6.0	6.5	3.0
3 Sept. 67	9.0	7.0	6.0
28 May 70	4.5	3.5	1.0
4–5 Apr. 71	4.0	0.7	–
Mean	6.4	5.8	3.3

Table XIV. Maximum and minimum measurements of pH, Ca⁺⁺ hardness and Mg⁺⁺ hardness at three stations in the vertical zonation investigation in area 1

Stations	pH			Mg ⁺⁺ mg/l		
	Max	Min	Min	Max	Min	Max
1	6.0	5.6	0.1	0.9	0.1	0.2
2	6.7	6.3	0.2	1.7	0.1	0.2
3	6.0	5.5	0.1	0.4	0.1	–

These species seem to be restricted to the zones below the Sub-Alpine belt. Eight species disappeared from an altitude of 500 to 700 m a.s.l. By 850 m a.s.l. one more species disappeared at the same time as the rest of the *Salix*. At 950 m only 2 species were present. There was therefore a gradual decrease in species number with the decrease in deciduous trees and bushes. The most marked decrease occurred from 500 to 700 m a.s.l. where the main decrease in the amount of *Salix* along the stream took place. The species which disappeared were *Amphinemura sulcicollis*, *Nemurella picteti*, *Isoperla grammatica*, *Leuctra digitata*, *Leuctra fusca*, *Taeniopteryx nebulosa* and *Brachyptera risi*. Between 700 to 850 m a.s.l. *Protonemura meyeri* disappeared and between 850 and 900 m *Leuctra hippopus*, *Leuctra nigra*, *Diura nanseni* and *Isoperla obscura* also disappeared. The only stoneflies in streams at 900 m and above were *Nemoura cinerea* and *Amphinemura stand-*

fussi. In the lakes of the area *Diura bicaudata* and *Nemurella picteti* were present.

At station 1, the dominating species were *Leuctra hippopus*, *Leuctra fusca* and *Brachyptera risi* which constituted 25%, 20% and 16% respectively. The next most common was *Capnia pygmaea* with 9%. At station 2 the dominating species were *Amphinemura sulcicollis*, *Leuctra digitata* and *Leuctra hippopus* with respectively 23%, 17% and 18%. *Amphinemura standfussi* was also numerous with about 12%. At station 3, *Leuctra hippopus* dominated completely with 73.5%. *Leuctra nigra* dominated with 59% at station 4 and *Nemoura cinerea* with about 94% at station 5.

The associations at the various stations show clear differences. The clear dominance of one species at stations 3, 4 and 5 can be contrasted with stations 1 and 2 where three species are codominant. This is nearly the same as found in Sæterbekken, where the

Table XV. The frequency of the stonefly association at different attitudes and vegetation belts in area 1, North Rogaland and South Hordaland - signifies less than one percent.

Vegetation zones	Boreal	Sub-Alpine	Low-Alpine	Middle-Alpine	
Vegetation along the stream	<i>Salix, Betula Alnus</i>	<i>Salix, Betula</i>	<i>Salix</i>	<i>Only Grass</i>	
m a.s.l.	10	500	700	850	950
Stations	1	2	3	4	5
<i>Capnia pygmaea</i>	9.0				
<i>Amphinemura borealis</i>	5.2				
<i>Siphonoperla burmeisteri</i>	-	-			
<i>Amphinemura sulcicollis</i>	7.4	23.4			
<i>Isoperla grammatica</i>	-	1.8			
<i>Leuctra digitata</i>	1.3	17.0			
<i>Leuctra fusca</i>	20.1	1.4			
<i>Taeniopteryx nebulosa</i>	-	-			
<i>Brachyptera risi</i>	16.0	9.0			
<i>Protonemura meyeri</i>	-	3.5			
<i>Leuctra hippopus</i>	25.3	18.6	73.5		
<i>Leuctra nigra</i>	2.9	1.6	18.1	59.0	
<i>Diura nanseni</i>	1.1	3.5	4.4	11.7	
<i>Isoperla obscura</i>	-	-	-	5.9	
<i>Amphinemura standfussi</i>	3.8	11.9	1.5	11.7	6.1
<i>Nemoura cinerea</i>	3.1	1.6	1.5	11.7	93.9
<i>Nemurella picteti</i>	-	1.4			
Number of species	17	15	7	6	3
Number of specimens	442	487	407	16	15

poorest biotopes had clear dominance over two species. The decrease in the number of specimens between stations 3 and 4 where *Salix* showed a marked decrease, was also clear.

In conclusion it can be stated that there is a reduction in stonefly species and numbers when there is a reduction in the amount of allochthonous matter from deciduous trees, mainly *Salix*, and a fall in temperature.

Eastern area

This area embraced the Sub-Alpine, Low-Alpine and Middle-Alpine belts of central Norway.

The results of zonation investigations in area 1 indicated that the main reduction in species was correlated with the reduction in *Salix* vegetation along the streams.

To obtain further information concerning this trend, studies had to be carried out in different faunal areas, such as eastern Norway and northern Norway. One of the most convenient areas for such a study was Øvre Heimdal. Six streams in Øvre Heimdalen were chosen and the work was carried out during the period 1969 to 1972.

Stream descriptions

The lowest parts of the streams are situated in the upper part of the Sub-Alpine belt (at about 1060 m a.s.l. where there is a very dense fringe of dwarf willow mixed with birch along the stream (Fig. 18)).

The substratum is unstable, and there is a mixture of stones of various sizes and gravels. There is a fair amount of organic allochthonous matter.

The upper edge of the *Salix* belt is at an altitude of 12–1300 m a.s.l. where there is no continuous fringe, but scattered low bushes at especially sheltered places. The main vegetation is grass. The substratum is more stable, the stones are usually larger and there is less allochthonous organic matter in the streams.

At an altitude of about 1300 to 1400 m a.s.l. the only vegetation is grass (Fig. 19). The substratum is a mixture of large stones, gravel and small stones, and it is unstable. There are only small amounts of allochthonous matter.

At altitudes above 1400 m even the grass cover becomes patchy. The substratum is

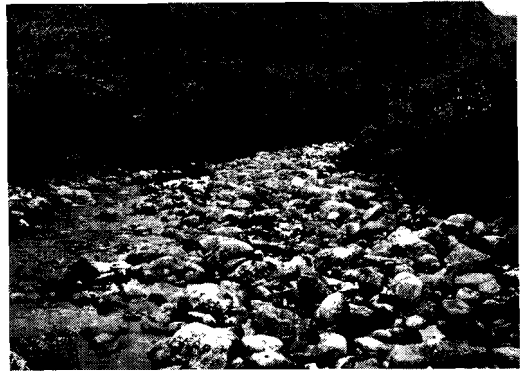


Fig. 18. Øvre Heimdal, Stream Flybekkin in the Sub-Alpine belt.

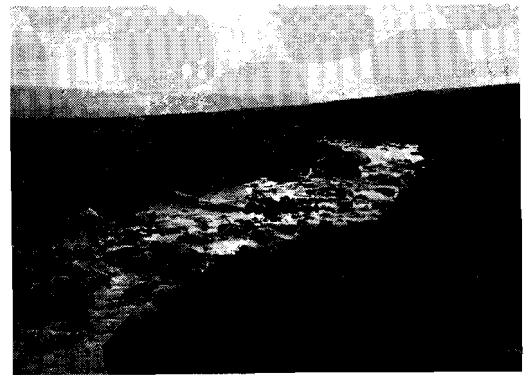


Fig. 19. Øvre Heimdal, Stream Flybekkin in the Middle-Alpine belt.

similar to lower altitudes and only small amounts of allochthonous matter were present.

Stonefly fauna

As in the west (area 1), the main decrease in species took place in the same area as the main reduction in *Salix* vegetation along streams, where the number of species dropped from 20 to 11. Above this the reduction continued, and at about 1400 m only *Arcynopteryx compacta*, *Isoperla obscura*, *Amphinemura standfussi* and *Capnia atra* were present. The only species numerous at this height was *Arcynopteryx compacta* (Table XVI).

A comparison of herbivores, carnivores and omnivores, according to Brinck's (1949) classification, showed that the reduction in species was largely among the herbivores. The fauna above 1400 m consisted of one carni-

Table XVI. The stonefly association at different altitudes and vegetation belts in area 4, Øvre Heimdal

Vegetation belts	Sub-Alpine	Low-Alpine	Middle-Alpine
Heights in m. a. s. l.	1000 – 1100	1200 – 1300	1400 – 1450
<i>Isoperla grammatica</i>	X		
<i>Dinocras cephalotes</i>	X		
<i>Taeniopteryx nebulosa</i>	X		
<i>Amphinemura sulcipectus</i>	X		
<i>Nemoura avicularis</i>	X		
<i>Capnopsis schilleri</i>	X		
<i>Leuctra digitata</i>	X		
<i>Leuctra fusca</i>	X		
<i>Leuctra hippopus</i>	X		
<i>Diura nanseni</i>	X	X	
<i>Brachyptera risi</i>	X	X	
<i>Nemoura cinerea</i>	X	X	
<i>Nemurella picteti</i>	X	X	
<i>Protonemura meyeri</i>	X	X	
<i>Capnia bifrons</i>	X	X	
<i>Leuctra nigra</i>	X	X	
<i>Arcynopteryx compacta</i>	X	X	X
<i>Isoperla obscura</i>	X	X	X
<i>Amphinemura standfussi</i>	X	X	X
<i>Capnia atra</i>	X	X	X
Number of species	20	11	4

vore, one omnivore and two herbivores, the latter three only being taken in small numbers.

Northern area

Vertical zonation in Sub-Alpine and the Alpine belts.

The third area which was examined for zonation in species was the Kautokeino area, where a high percentage of arctic faunal elements is present.

The comparison of the stonefly fauna was made between the area around the Kautokeino river (Fig. 20) and the following streams in the Caskias area: a stream in the upper part of the *Salix* belt, a stream just above the *Salix* belt and a stream at a height of about 700 m a.s.l. where there are polygons.

Kautokeino is situated at about 300 m a.s.l. and in the Sub-Alpine vegetation belt, while the stream in the upper part of the *Salix* belt and the stream just above were situated in the Low-Alpine belt. The uppermost streams were situated in the Middle-Alpine belt.

Stonefly fauna

From the Sub-Alpine to the upper part of the Low-Alpine belt there was a reduction



Fig. 20. Kautokeino, Stream Raavatjokka in the Sub-Alpine belt.



Fig. 21. Kautokeino, stream in the Middle-Alpine belt at Caskijas.

Table XVII. The stonefly association at different altitudes and vegetation belts in area 5, Kautokeino

Vegetation belts	Sub-Alpine	Lower Low-Alpine	Higher Low-Alpine	Middle-Alpine
<i>Siphonoperla burmeisteri</i>	X			
<i>Isoperla difformis</i>	X			
<i>Isoperla grammatica</i>	X			
<i>Diura nanseni</i>	X			
<i>Taeniopteryx nebulosa</i>	X			
<i>Amphinemura borealis</i>	X			
<i>Amphinemura standfussi</i>	X			
<i>Amphinemura sulcicollis</i>	X			
<i>Leuctra digitata</i>	X			
<i>Nemoura cinerea</i>	X			
<i>Nemoura flexuosa</i>	X			
<i>Nemoura sahlbergi</i>	X			
<i>Nemoura viki</i>	X			
<i>Capnia pygmaea</i>	X			
<i>Capnia-vidua</i>	X			
<i>Nemoura avicularis</i>	X	X		
<i>Nemurella picteti</i>	X	X		
<i>Protonemura meyeri</i>	X	X		
<i>Leuctra hippopus</i>	X	X		
<i>Leuctra nigra</i>	X	X		
<i>Capnopsis schilleri</i>	X	X		
<i>Isoperla obscura</i>	X	X		
<i>Diura bicaudata</i>	X	X	X	
<i>Arcynopteryx compacta</i>	X	X	X	
<i>Capnia atra</i>	X	X	X	
<i>Nemoura arctica</i>	X	X	X	X
Number of species	26	11	4	1

from 26 to 11 species; above the *Salix* belt the fauna were reduced to 4 species (Table XVII). Three of these were the same species taken in the corresponding vegetation belt in south-eastern Norway, *Diura bicaudata*, *Arcynopteryx compacta* and *Capnia atra*. The fourth, *Nemoura arctica*, is confined to northern Norway.

Discussion of vertical zonations

In all three zonations there was a reduction in species, generally paralleled by the reduction in *Salix* vegetation along the streams with increasing altitude and by the reduction in organic allochthonous matter in the streams. In all three areas there was a reduction to one or two herbivorous species in streams someway into the Middle-Alpine belt. These were *Nemoura cinerea* and *Amphinemura standfussi* in south-western Norway, *Amphinemura standfussi* and *Capnia atra* in Øvre Heimdal and *Nemoura arctica* around Kautokeino.

The zonation in area 1 showed that *Capnia*

pygmaea and *Amphinemura borealis* were not present above the coniferous forest and that *Siphonoperla burmeisteri* also seems to belong to the same vegetation belt. These species were not taken in the Sub-Alpine belt of Øvre Heimdal, although they are all taken in the coniferous forests in the surrounding areas and in the rest of eastern Norway. However, around Kautokeino all four species were taken in the Sub-Alpine belt, but not higher.

Horizontal distribution of species

The decrease in species from inner fjords of Rogaland to the coastal areas which was documented above was examined further from 1966 to 1971.

The intention was to choose streams where all factors were as constant as possible, although temperature varied greatly. The temperature differences are shown in general terms in Table XVIII.

Stream descriptions

The streams chosen were: Byrkjelandselva



Fig. 22. Stream Byrkjeldselva at Sveio in the coastal area (A).

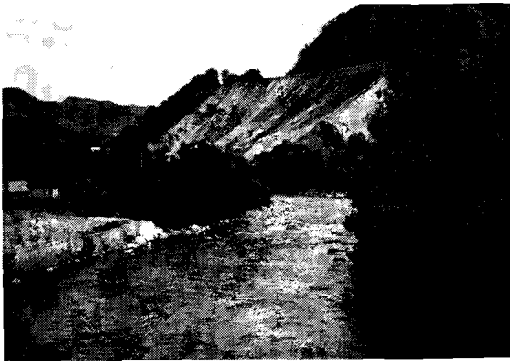


Fig. 23. Stream Sandeidelva at Sandeid in the central area (B).



Fig. 24. Stream Nordelva at Sauda in the inner fjord area (C). Station (1), in the vertical zonation, and station (3) in the horizontal zonation.

in Sveio, Hordaland (Fig. 22); Sandeidelva in Vindafjord (Fig. 23) and Nordelva in Sauda (Fig. 24), both in Rogaland. They represented the range from coastal areas with an atlantic climate to inner fjord areas with a more continental climate. All the stations were

nearly the same height above sea level (from 5 to 10 m). The streams were chosen to be as similar as possible regarding size of substratum and amount of vegetation along the streams. In an attempt to eliminate differences in results arising from differences in stream size, small and large streams both in coastal areas and in the fjord areas were examined for comparison. In all streams, areas with riffles and pools and with different substrata were investigated. The amount of allochthonous matter was similar, although somewhat less in Nordelva than in the other two streams. The dominant deciduous trees were *Alnus*, but *Salix* and other trees were also present. All three streams were surrounded by cultivated land.

Physical and chemical data from the streams are given in Table XIX.

Stonefly fauna

The same trends were found as during the investigation of the total area (Table XX).

Leuctra digitata, *Capnia pygmaea* and *Isoperlina obscura* were only taken in Nordelva and in fact have not been taken west of the inner fjords.

Table XVIII. Temperatures (°C) at three stations in the horizontal distribution investigation

Date	Station		
	1	2	3
28 Apr. 66	11	3	2
15 June 66	15	14	7
22 March 67	5	1	1
28 May 67	12	—	4
10 July 67	16	12	6
3 Sept. 67	12.5	10.5	9
28 May 70	16	12	4.5
8 Apr. 71	7	3	4
Mean	11.7	7.9	4.9

Table XIX. Maximum and minimum measurements of pH, Ca⁺⁺ hardness and Mg⁺⁺ hardness at three stations in the horizontal zonation in area 1

Stations	pH		Ca ⁺⁺ Min	mg/l Max	Mg ⁺⁺ mg/l	
	Max	Min			Min	Max
1	6.7	6.4	0.4	1.7	0.3	0.4
2	6.4	5.3	0.2	1.7	0.1	0.2
3	6.0	5.6	0.1	0.9	0.1	0.2

Table XX. The stonefly association at a horizontal gradient in area 1. North Rogaland and South Hordaland – signifies less than one percent.

Stations	Coastal area 1 Frequency %/0	Middler area 2 Frequency %/0	Inner fjords 3 Frequency %/0
<i>Siphonoperla burmeisteri</i>	9.3	1.2	–
<i>Amphinemura sulciollis</i>	22.4	16.5	7.4
<i>Protonemura meyeri</i>	29.1	3.8	–
<i>Leuctra hippopus</i>	13.5	36.6	25.3
<i>Leuctra fusca</i>	14.7	25.2	20.2
<i>Brachyptera risi</i>	10.6	7.4	16.0
<i>Nemoura cinerea</i>	–	–	3.1
<i>Isoperla grammatica</i>	–	–	–
<i>Taeniopteryx nebulosa</i>	–	–	–
<i>Amphinemura borealis</i>	–	5.0	5.2
<i>Diura nanseni</i>	–	3.4	1.2
<i>Nemurella picteti</i>	–	–	–
<i>Leuctra nigra</i>	–	–	2.9
<i>Amphinemura standfussi</i>	–	–	3.8
<i>Leuctra digitata</i>	–	–	1.3
<i>Isoperla obscura</i>	–	–	–
<i>Capnia pygmaea</i>	–	–	9.0
Number of species	7	14	17
Number of specimens	483	497	442

These species seem to be 'continental' in Norway and associated with mountains and their surroundings. Seven more species have not been taken in Byrkjelandsbekken, and five of them are absent west of Sandeid-elven. Two of the species, *Isoperla grammatica* and *Amphinemura standfussi*, are absent from Byrkjelandsbekken, but have been taken in other streams in the area, although both are rare.

Discussion of zonations

All the vertical zonation studies showed a reduction in numbers and species which was correlated with a decrease in deciduous trees and the amount of organic allochthonous matter. This is in agreement with the results of the studies carried out by Hynes (1961) and Minshall (1968) who investigated streams at different altitudes in Britain. They found differences which they associated with differences in food and temperature.

Certain species seem to be restricted to certain vegetation zones and belts in southern Norway but to different ones in the north. This demonstrates the difficulty in making generalizations valid for widely separated areas with different faunal associations.

The horizontal zonation studies demonstrated a decrease in species towards the coast which in some cases could be connected with temperature. Since, however, the reduction was so marked and involved widely distributed southern species, other factors or combination of factors not considered in this investigation could be involved.

DISTRIBUTION AND HABITAT PREFERENCE

During the investigation of the faunal associations of the seven areas and the zonation studies it was seen that the species had somewhat different distributions and habitat preferences in different parts of Norway.

In certain of the investigated areas some species seemed to exhibit a preference for streams of different size. Brinck (1949) gave habitat preferences for the Swedish species together with notes on their European distribution. Ulfstrand (1967, 1968a, b) and Ulfstrand et al. (1971) gave further information about some of the Swedish species. There were some differences in habitat preference of certain species between Sweden and areas on the continent. Some of the Norwegian

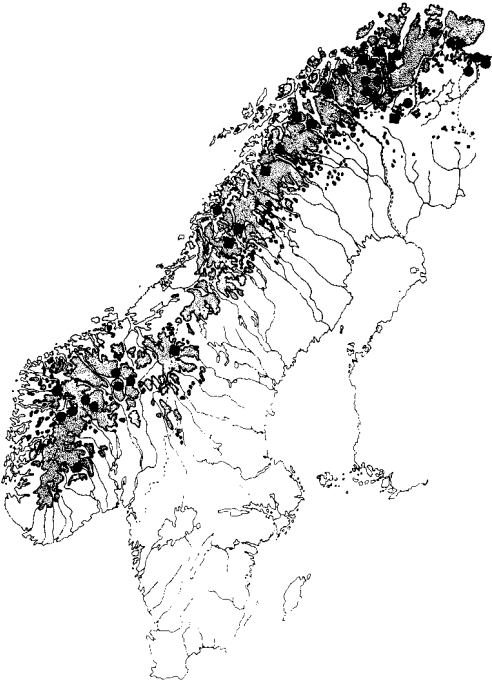


Fig. 25. Distribution of *Arcynopteryx compacta* (Mc Lachland). ■ Records from Sweden and Finland. The Alpine areas are dotted.

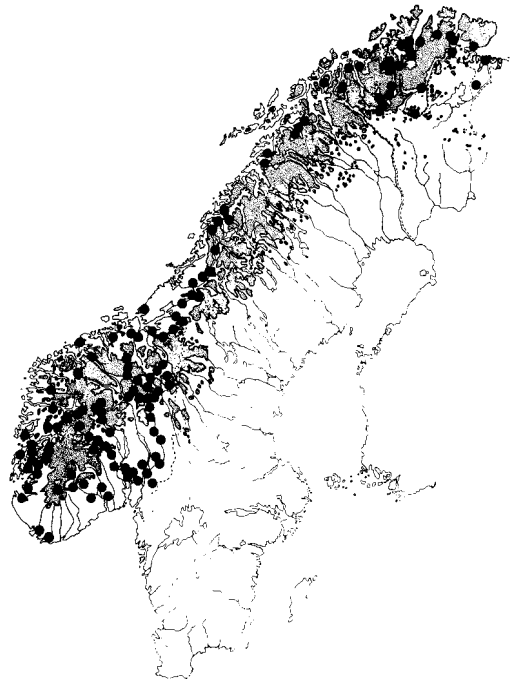


Fig. 27. Distribution of *Diura nanseni* (Kempney).

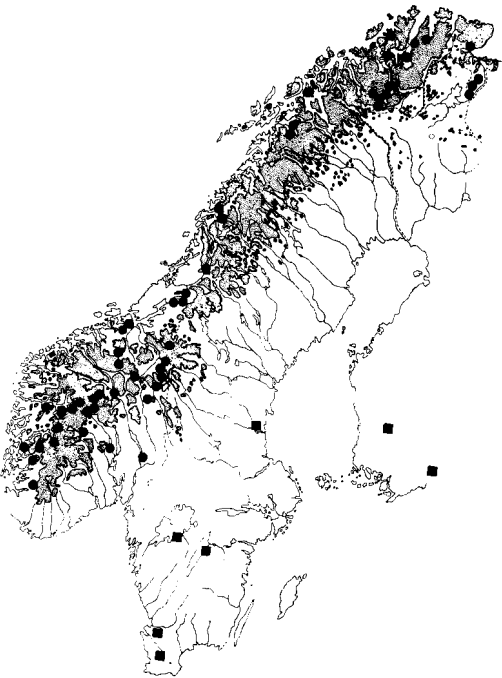


Fig. 26. Distribution of *Diura bicaudata* (Linne). ■ The southernmost records in Sweden and Finland.



Fig. 28. Distribution of *Perlodes dispar* (Rambur). ■ The northernmost records in Sweden.

species also seem to differ in habitat preference from area to area in Norway and from that indicated by Brinck and Ulfstrand.

Brinck (1949) mentioned *Leuctra hippopus*, *Leuctra nigra*, *Capnia bifrons* and *Nemoura flexuosa* as eucoenic in small streams. Ulfstrand (1968) found that *Amphinemura sulci-collis*, *Leuctra hippopus*, *Leuctra digitata* and *Dinocras cephalotes* were more abundant in or even restricted to smaller watercourses, while *Amphinemura borealis*, *Leuctra fusca* and *Isoperla obscura* tended to avoid or be sparse in small streams. However, *Isoperla obscura* has also been reported from large rivers in the Netherlands, Switzerland and in the Tyrol (Brinck 1949).

In the following the distribution and observed habitat preference of the various species will be presented.

Fam. Perlodidae

Arcynopteryx compacta occurs in all parts of the country (Fig. 25). The species was mainly taken in Alpine areas. In southern Norway the lowest locality was 700 m a.s.l. at Haldagsenøyri, Atna. In the north *Arcynopteryx compacta* occurs at all altitudes and in lakes, outlets and in streams of different sizes. The species occurs in the same types of habitats as the *Diura* species. In the south it has only been taken in running waters at higher altitudes where it is the most common carnivorous species. Localities in which it has been taken range from about 700 to 1465 m a.s.l. In Fig. 33 localities are plotted which indicate the distribution trend in Fennoscandia.

Diura bicaudata occurs all over the country (Fig. 26), in the north in small and large streams, lakes and lake outlets. The species is most numerous and is the dominant carnivore in all the investigated biotopes in the Pasvik area which lie within the Sub-Arctic and Boreo-montane sub-zones. This area seems to contain the environmental factors nearest to the optimum for this species. In southern Norway it only occurs in lakes, mostly in high altitude lakes in the Sub-Alpine and Low-Alpine belts, but it may also be numerous in large lowland lakes such as Mjøsa and Sperillen. The highest locality was about 1500 m a.s.l. Finnmark seems to be the central

area for this species. In Sweden the species is a relict in some southern lakes (Brinck 1949).

Diura nanseni (Fig. 27) is the most widespread carnivorous species in Norway. The species has been taken in the same habitats as *Diura bicaudata* in the north, but it is not as common as *Diura bicaudata* in Pasvik and Kautokeino. In the south *Diura nanseni* is the dominant carnivorous stonefly of all types of running water below the Low-Alpine vegetation belt. The species is absent from the low coastal areas of south-western Norway, although in the inner fjords it has been taken from sea level to 900 m a.s.l. in the Low-Alpine vegetation belt. The highest record is 1300 m a.s.l. at Øvre Heimdal. Generally *Diura nanseni* is most common within the coniferous forest areas and in the Sub-Alpine belt. According to Brinck (1949) this species has not been taken south of lake Vättern in Sweden.

Perlodes dispar (Fig. 28) has only been found in three localities, all in the south-eastern part of Norway. The northernmost find is from Sørkedalselven, Oslo, where the nymphs were taken from unstable substratum. In Sweden the species is mainly distributed in the southern parts (Brinck 1949).

Isogenus nubecula (Fig. 29) has a wider distribution and has been taken as far north as in Tufsinga (700 m a.s.l.), North Hedmark. The only locality where the species is numerous is on stony substratum in the river Glåma south of Kongsvinger. In Fennoscandia this species seems to have an eastern distribution and has been taken in northern Finland (Meinander 1965). The species is absent in the southern parts of Sweden (Brinck 1949).

Isoperla difformis (Fig. 30) occurs sporadically in both northern and southern Norway. It is only in the inner fjord area of the Oslofjord that the species seems to be common, and it seems to prefer places where there is some silting or fine substrata beneath the stones. It has only once been taken in western Norway. The highest situated stream where the species was taken was at about 700 m a.s.l. In southern Norway it was taken only in running water within the Boreal pine



Fig. 29. Distribution of *Isogenus nubecula* Newmann. ■ The northernmost records in Sweden and Finland.

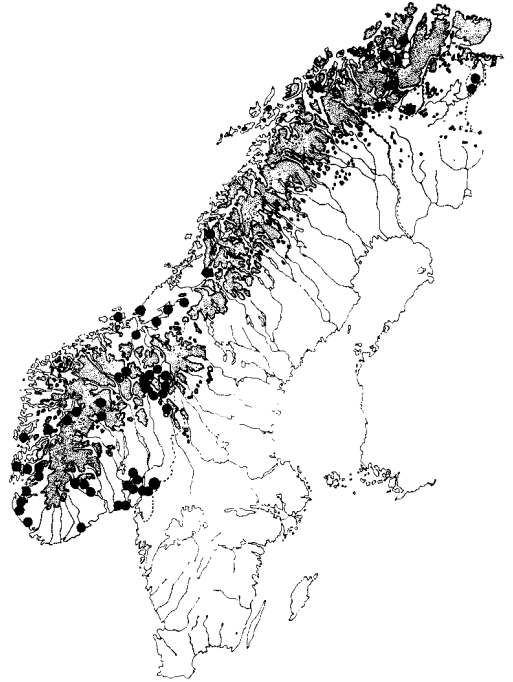


Fig. 31. Distribution of *Isoperla grammatica* (Poda).



Fig. 30. Distribution of *Isoperla difformis* (Klapálek).

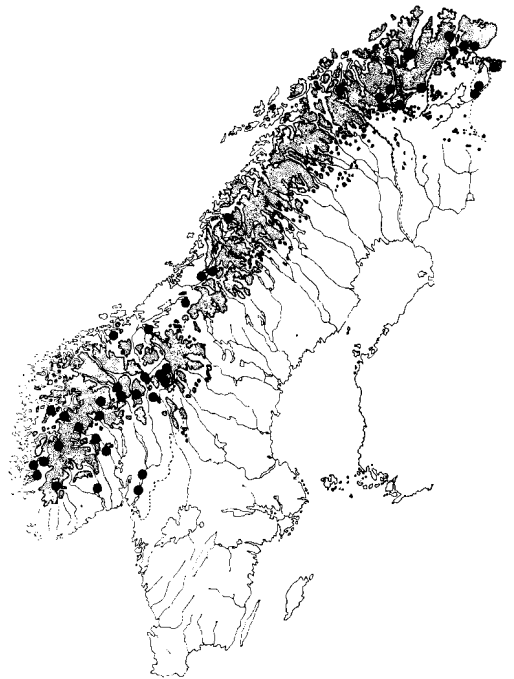


Fig. 32. Distribution of *Isoperla obscura* (Zetterstedt).

forest areas, and in northern Norway it occurred also in the Sub-Alpine vegetation belt. In Sweden the species was taken both in the southern and northern parts, but mainly in southern streams (Brinck 1949).

Isoperla grammatica (Fig. 31) is the most common of the *Isoperla* species. In the south it was taken both in coastal areas and at high altitudes (1100 m a.s.l.). It inhabits small streams, temporary or permanent, large streams and rivers. The species has not been taken in lakes. It does not occur above the Sub-Alpine belt, being common in the Boreal coniferous forest areas. In Sweden it was taken in all parts of the country (Brinck 1949).

Isoperla obscura (Fig. 32) was taken in all parts of the country. In northern Norway the species has been found in small and large streams, rivers, lakes and lake outlets. In the coastal areas the species is rare. In southern Norway the species occurs in all types of freshwater in the central mountain areas where it was taken up to 1465 m a.s.l. It was seldom found in the lowlands where it is restricted to large streams and rivers, but it has been taken as far south as below Øyeren in the Glåma watercourse, Akershus. In the west it is most common in the mountains, only occurring in large streams in the lowlands and then only in inner fjord areas.

In some areas *Isoperla obscura* seems to occupy a wider spectra of habitats than elsewhere. These are the North Østerdalen area, the mountain areas of Øvre Heimdal and the areas of Kautokeino and Pasvik. *Isoperla obscura* was taken both in northern and southern Sweden, but according to Brinck (1949) the species is eucoenic in northern rivers.

Fam. Perlidae

The carnivore *Dinocras cephalotes* (Fig. 33) was found in scattered localities from Telemark in the south to Finnmark in the north. Most of the records are from the central mountain areas of southern Norway where it was taken in small and medium-sized streams, largely in the Boreal pine forest zone, although it has also been taken in the Sub-Alpine belt (1090 m a.s.l. in Øvre Heimdal). In the west the species has been taken twice in Rogaland. In the north nymphs have

been taken in Anajokka near Kautokeino. This is the northernmost record of this species. In Sweden *Dinocras cephalotes* was not taken in the northernmost parts and it has not hitherto been recorded from Finland.

Fam. Chloroperlidae

In this family there are only two species, both omnivorous. *Xanthoperla apicalis* (Fig. 34) has been taken at scattered localities in the boreal forest areas in southern Norway, once in northern Norway and not at all in western Norway.

Siphonoperla burmeisteri (Fig. 35) occurs in all types of freshwaters in southern Norway in the boreal coniferous forest area up to the Sub-Alpine. In Sauda it was once found in the lowest part of the Sub-Alpine belt. The highest locality is at Mellsen in Øystre Slidre at about 1000 m a.s.l. in the upper part of the coniferous forest belt. It is common in the west, including the coastal areas. In the north it has been taken in small and large streams, rivers and lakes in the pine forest area of Pasvik, where it is common. Outside this area it is more scarce. The species was taken both in northern and southern Sweden and is, according to Brinck (1949), eucoenic in northern streams.

Fam. Taeniopterygidae

In this family there are two species, both herbivorous. *Taeniopteryx nebulosa* (Fig. 36) has been taken in all parts of Norway, but is absent in the coastal lowland areas of North Rogaland and Vestfold. It occurs at all heights up to about 1200 m a.s.l. in the Low-Alpine belt. The species may be common and numerous both on stable stone substrata covered by moss and algae and in streams with a sand bottom and silting. It is found in all types of biotopes, except lakes, although it may be very common in outlets. The species has been taken both in northern and southern Sweden (Brinck 1949).

Brachyptera risi (Fig. 37) has also been taken in all parts of Norway, but in Troms and Finnmark only in the fjord and coastal areas. In southern Norway it was taken in the outermost coastal areas of both North

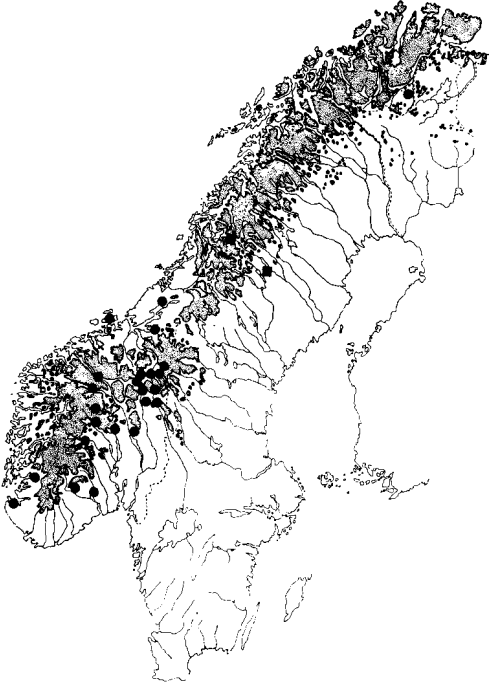


Fig. 33. Distribution of *Dinocras cephalotes* (Curtis). ■ The northernmost records in Sweden.

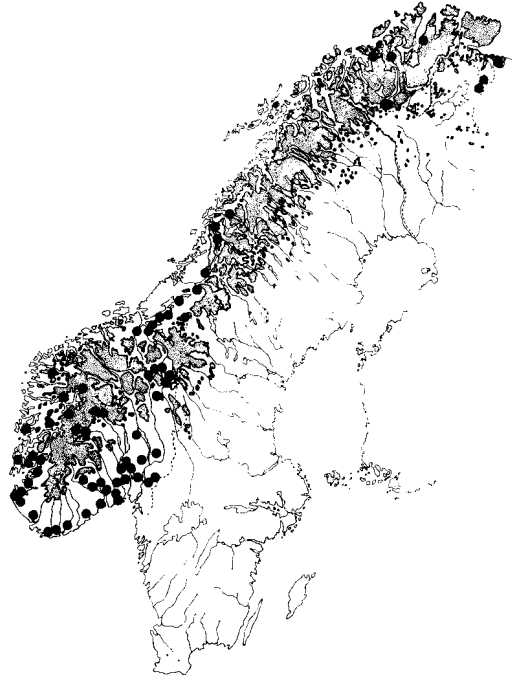


Fig. 35. Distribution of *Siphonoperla burmeisteri* (Pictet).



Fig. 34. Distribution of *Xanthoperla apicales* (Newman).

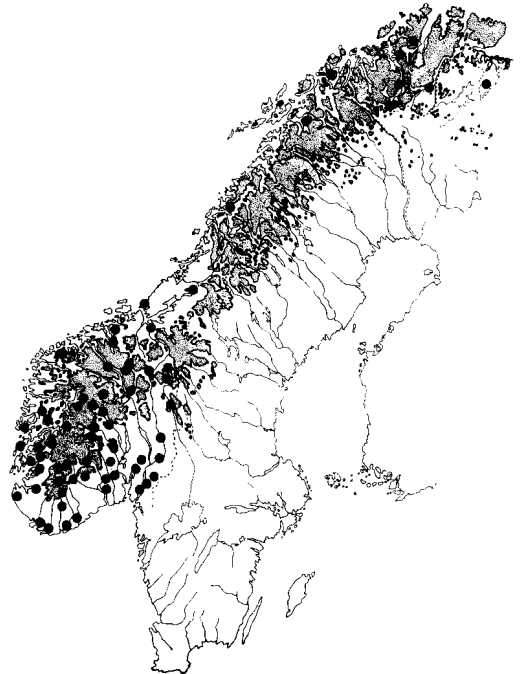


Fig. 36. Distribution of *Taeniopteryx nebulosa* (Linnaeus).

Rogaland and Vestfold. In mountainous areas it was taken at 1100 m a.s.l. in the Low-Alpine belt. The species is one of the most common stoneflies in the lower parts of southern Norway and may be one of the species dominating the stonefly fauna of small streams. However, it seems to be rare in stream sections where there is much silting. *Brachyptera risi* was taken both in northern and southern Sweden, and according to Brinck (1949) the species is eucoenic in southern rivers. It is not recorded from Finland.

Fam. Nemouridae

In this family the three *Amphinemura*, six *Nemoura* and the two *Protonemura* species are all herbivore, but they show great differences in distribution and dependence on environmental factors.

Amphinemura borealis (Fig. 38) has been taken in both southern and northern Norway. It is recorded over most of southern Norway in both small and large streams, although most numerous in large rivers such as the Glåma and the Suldalslågen where silting occurs with fine substrata among the stones. It has not been taken above the coniferous tree line. In the north the species has also been taken in the Sub-Alpine belt, but it is only common in the coniferous forest area of Pasvik, where it is numerous in both small streams and large rivers. It is also found in lakes in this area. The species seems to prefer certain substrata at least outside the area which seems to be optimal, the Pasvik area. The species is found both in southern and northern Sweden, but is according to Brinck (1949) eucoenic in northern rivers.

Amphinemura standfussi (Fig. 39) also occurs in both southern and northern Norway, although absent in some coastal areas. It is often numerous and is one of the highest occurring species. At high altitudes it is numerous in the outlets of lakes. The highest locality was in the Middle-Alpine belt at 1465 m a.s.l. in Øvre Heimdal. The species occurs on stony substrata in small and large streams, rivers and, at higher altitudes, in lakes and their outlets. In Sweden (Fig. 40) the species has been taken both in the southern and northern parts of the country.

Amphinemura sulcicollis (Fig. 40) is the commonest species in this genus, and has been taken all over Norway. It is also common and numerous in the coastal areas. This species may also be common in the Sub-Alpine belt and it has been taken up to 1100 m a.s.l., in Øvre Heimdalen. The species is common in small and large streams and in rivers. *Amphinemura sulcicollis* also occurs in lakes both in southern and northern Norway. In the south it has been recorded from lowland lakes such as Tyrifjorden and from high altitude lakes such as Øvre Heimdalsvatn. In Sweden it occurs in all parts of the country (Brinck 1949).

Nemoura arctica in Norway seems restricted to Troms and Finnmark (Fig. 41). The species occurs in small and large streams, in lakes and outlets, both in places with stable stone substrata and places with much fine sand and an unstable bottom. At higher altitudes (Middle-Alpine belt) the species may be the sole plecopteran species and in such localities can be very numerous. In Sweden it has been taken as far south as the River Vindelälven, Swedish Lapland (Ulfstrand 1969).

Nemoura avicularis (Fig. 42) has been collected in northern and southern Norway, but not in western Norway. In eastern Norway it occurs both in the coastal areas and in the mountains. In Øvre Heimdalen it has been taken in the Low-Alpine belt at heights of 1300 m a.s.l. In both the north and south it has been found in small and large streams, rivers and lakes in the lowlands and at higher altitudes. In streams it seems to prefer a slow current and an unstable substratum with silting, and has been collected in streams with fine sand as substratum. The species is recorded from both southern and northern Sweden (Brinck 1949).

Nemoura cinerea (Fig. 43) is widespread in Norway, both in the south and the north, and is common in the coastal areas and in the mountains. In Øvre Heimdal it was taken in the Middle-Alpine belt at a height of 1465 m. In streams where there is a rich stonefly fauna, the species is scarce, but where there only are a few species present *Nemoura cinerea* may be numerous, as is the case in

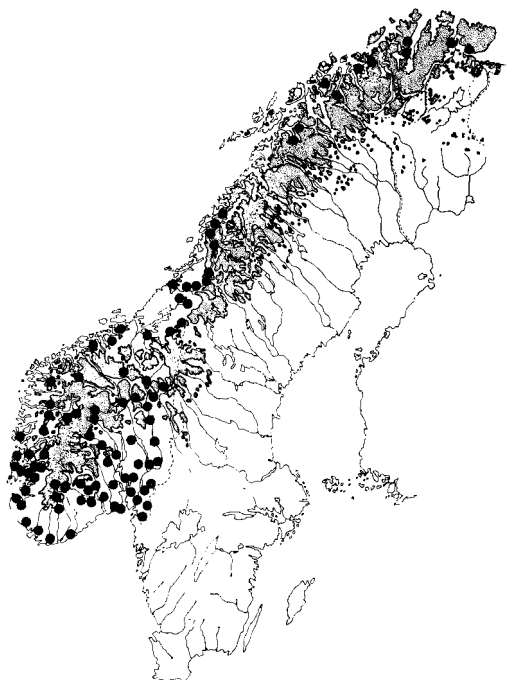


Fig. 37. Distribution of *Brachyptera risi* (Morton).

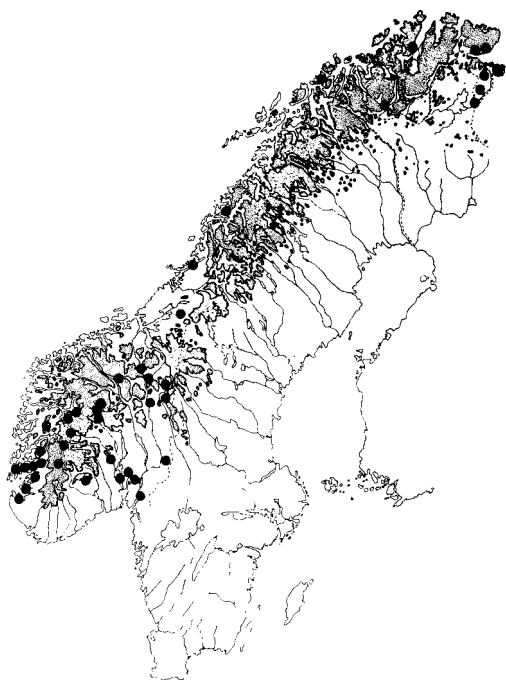


Fig. 39. Distribution of *Amphinemura standfussi* (Ris).

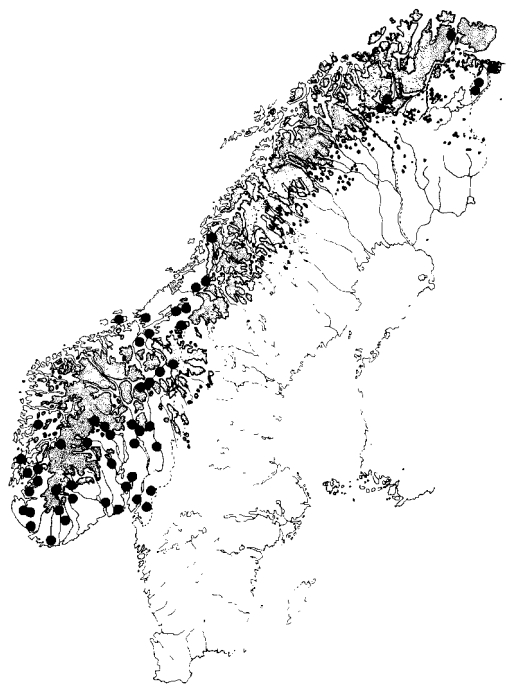


Fig. 38. Distribution of *Amphinemura borealis* (Morton).

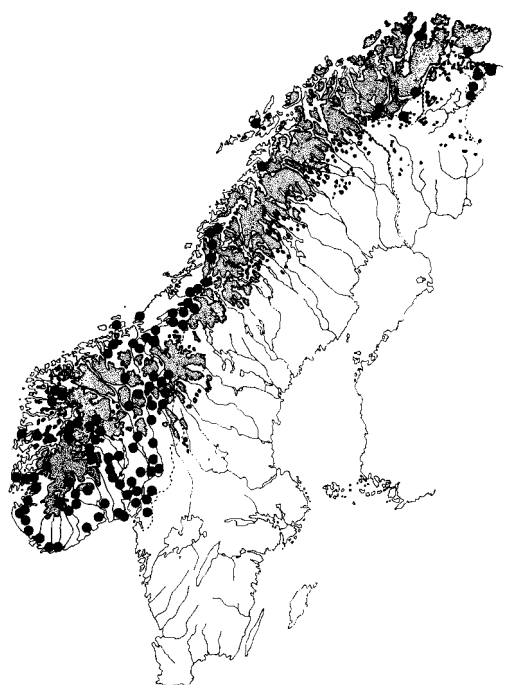


Fig. 40. Distribution of *Amphinemura sulcicollis* (Stephens).



Fig. 41. Distribution of *Nemoura arctica* Esben-Petersen. ■ The southernmost records in Sweden and Finland.

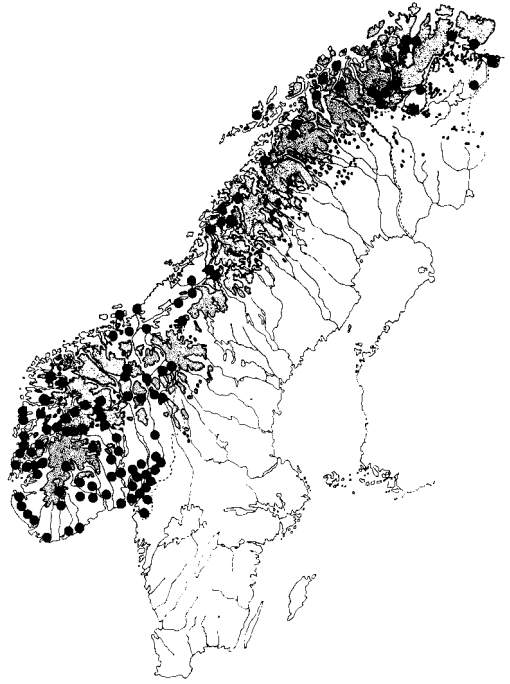


Fig. 43. Distribution of *Nemoura cinerea* (Retzius).



Fig. 42. Distribution of *Nemoura avicularis* Morton.

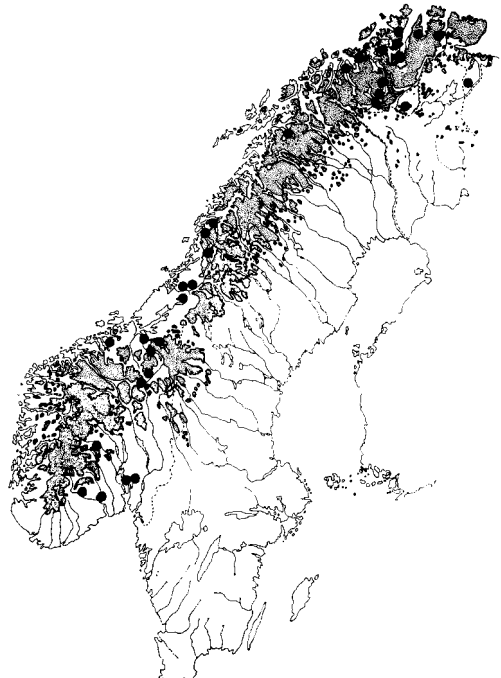


Fig. 44. Distribution of *Nemoura flexuosa* Aubert.

high altitude lakes and streams both with stony stable substrata and with sand and unstable substrata. The species occurs in all parts of Sweden (Brinck 1949).

Nemoura flexuosa (Fig. 44) has been taken both in southern and northern Norway, but seems to be more common in the north. The species is absent from western Norway, the coastal areas of eastern Norway, and Setesdal in the south. In southern Norway the species has only been taken within the coniferous forest areas. It seems to be most common in small forest streams in the areas west of Oslo and around Tynset, Hedmark. In northern Norway it is most common in the Sub-Alpine belt of the fjord areas of Finnmark. In Sweden the species is rare towards north (Brinck 1949).

Nemoura sahlbergi (Fig. 45) has only been taken in the counties of Finnmark, Troms and in Nordland at Narvik, although it has been taken further south in Sweden. The species is common in the fjord areas of Finnmark and has been taken mainly in the Sub-Alpine belt. In Pasvik the species occurs in the Sub-Arctic and Boreo-montane Sub-zone. *Nemoura sahlbergi* seems to be most common in small streams. In Sweden the species has been taken as far south as Messaure (Müller & Thomas 1972).

Nemoura viki (Fig. 46) has only been found in Finnmark where it may be numerous in slow-flowing small streams; it has also been collected in lakes and outlets. The species has been taken in the Sub-Arctic and Boreo-montane Sub-zone, and in the Sub-Alpine and Low-Alpine belts where *Salix* occurs along the watercourse.

Nemurella picteti (Fig. 47), although present in both southern and northern Norway, has not been found in the coastal areas of North Rogaland and Vestfold. The species occurs in small and large streams, rivers and lakes, both in the lowlands and in the mountains. *Nemurella picteti* is among the highest altitude species in the mountains, and it may be the sole herbivorous species in lakes of the Low-Alpine belt. It is also sometimes collected together with *Capnia atra* in such habitats. The highest locality is at about 1400

m a.s.l. in Øvre Heimdalen. The species occurs on both stable stone substrata and in substrata composed of sand and mud. The species is taken in all parts of Sweden (Brinck 1949).

Protonemura intricata (Fig. 48). I have only taken it twice in Norway in small streams in the Sub-Alpine zone of the northern part of Finnmark. The species is not recorded from Sweden but has been collected in both the northern and southern parts of eastern Finno-scandia (Meinander 1965).

Protonemura meyeri (Fig. 49) occurs in both southern and northern Norway, but is rare in the fjord areas of northern Norway. In the coastal areas in the west and south it is common and often numerous.

In south Norway *Protonemura meyeri* has been taken in the Low-Alpine vegetation belt up to altitudes of 1300 m a.s.l. It occurs in small and large streams and in rivers, but is most numerous in small streams. The species is found in all parts of Sweden (Brinck 1949).

Fam. Capniidae

In this family there are five Norwegian species, all herbivores.

Capnia atra (Fig. 50) was taken in both the north and the south, but not in the southern parts of western Norway. In Hardanger and Sogn the species was taken in the inner fjord areas. Further northwest the species may be more common than indicated in Fig. 50. In eastern Norway the species has not been collected south of Oslo and Hjartdal in Telemark. In southern Norway the species is most common in the mountains, where it is numerous in streams and lakes. The highest record is from a stream at about 1500 m a.s.l. in Øvre Heimdal, located in the Middle-Alpine vegetation belt. In the central lowlands of eastern Norway the species occurs on stony substratum in small and large streams, rivers and large lakes such as Mjøsa. However, the main distributional area in southern Norway is Sub- and Low-Alpine belts of the central mountain areas. In northern Norway, *Capnia atra* is common in lakes, outlets, small streams and large rivers.

Both in North-Norway and in the central mountain areas of South-Norway the species



Fig. 45. Distribution of *Nemoura sahlbergi* Morton. ■ Finds from Sweden and Finland.

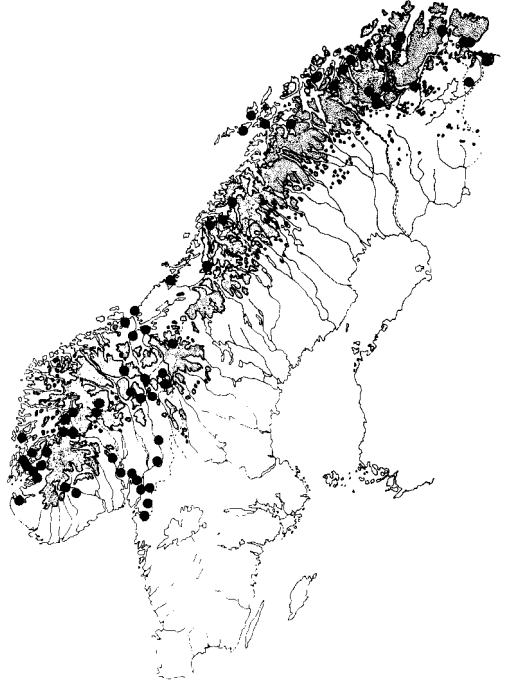


Fig. 47. Distribution of *Nemurella picteti* Klappäck.



Fig. 46. Distribution of *Nemoura viki* Lillehammer.

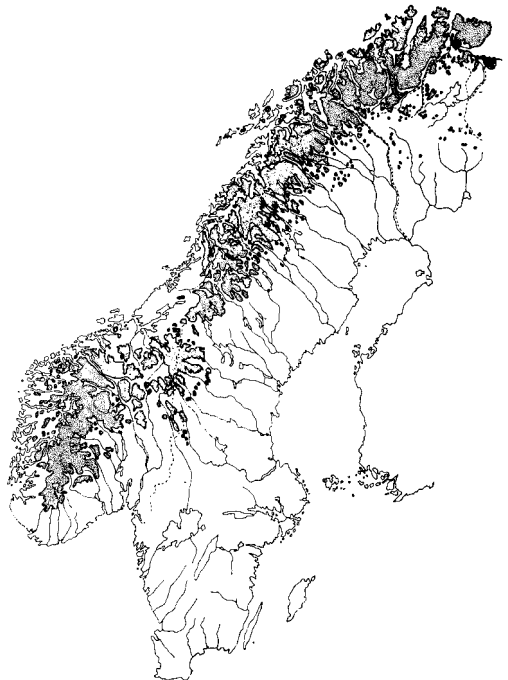


Fig. 48. Distribution of *Protonemura intricata* (Ris).

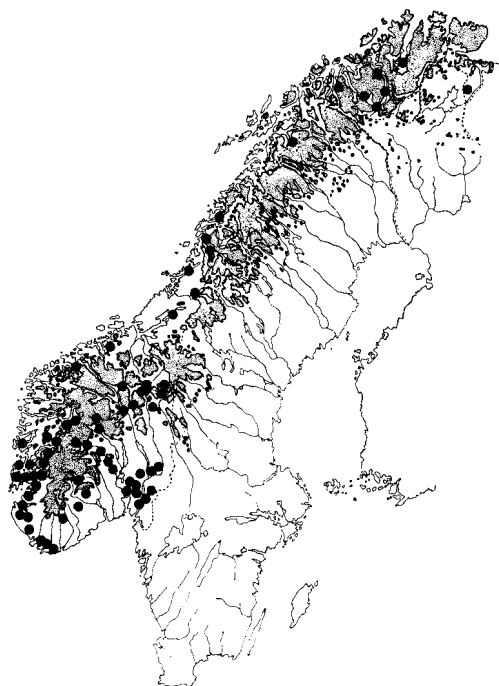


Fig. 49. Distribution of *Protonemura meyeri* (Pictet).

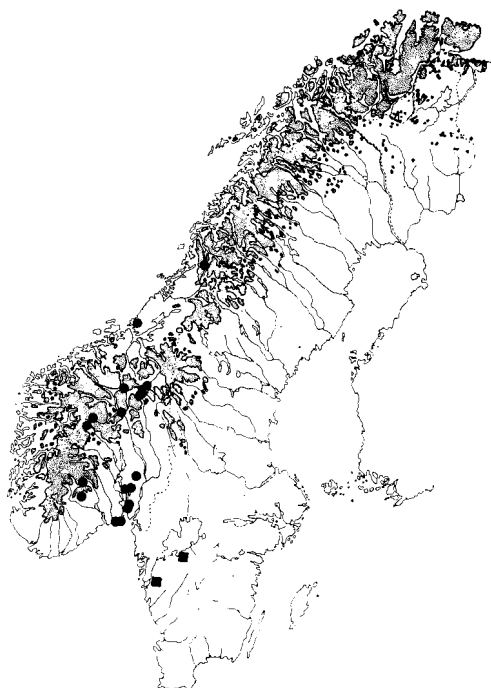


Fig. 51. Distribution of *Capnia bifrons* (Newman).
■ The northernmost records in Sweden.

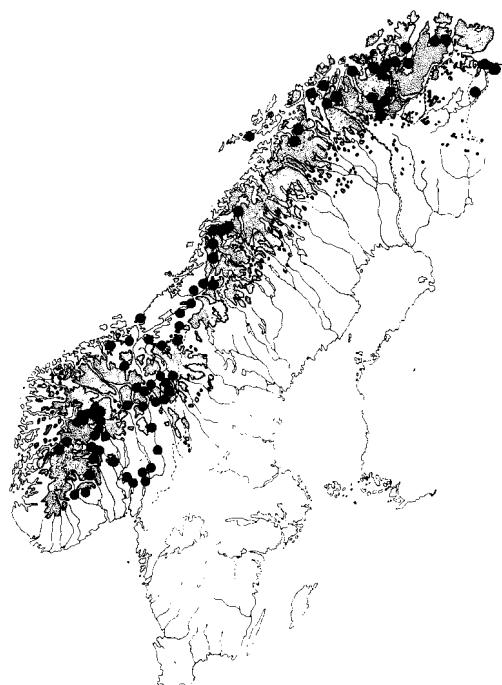


Fig. 50. Distribution of *Capnia atra* (Morton).

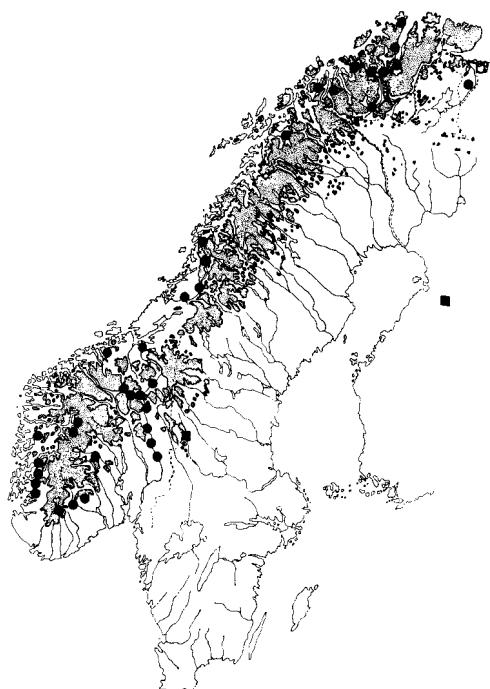


Fig. 52. Distribution of *Capnia pygmaea* (Zetterstedt).
■ The southernmost records in Sweden and Finland.

seems to be more commonly distributed and present in a wider range of habitats than elsewhere. In Sweden not taken in the southernmost parts (Brinck 1949).

Capnia bifrons has its northernmost distribution in Fennoscandia in Norway (Fig. 51). It has been taken in widely separated localities. The species is common and numerous in small streams largely in the western parts of the Oslofjord and Tynset areas. The species is numerous in some streams in Telemark, common in small streams in Øvre Heimdal, where it occurs in the Low-Alpine vegetation belt at heights of about 1200 m. It has also been taken in the Sub-Alpine belt in other parts of East Norway. The northernmost find is to the south of Mosjøen, Nordland. In the south the species is very numerous in some small coastal streams such as on the island of Nøtterøy, Vestfold. The species is most abundant in streams where the bottom is unstable and composed of small stones and gravel. In Sweden, it has not been taken north of lake Vänern (Brinck 1949). The species has not been recorded from Finland.

Capnia pygmaea (Fig. 52) is also found in both southern and northern Norway, but has a distribution which is different from *Capnia atra* and *Capnia bifrons*. It is the only Capniid species in the inner fjord areas of southwestern Norway, and goes further west than *Capnia atra*. In the east, the species is most common in the Glåma valley from Røros in the north to Elverum in the south. Around Tynset, the species occurs in small and large streams and in rivers such as the Glåma. In the southern section it is restricted to the River Glåma, where it is very numerous. In northern Norway it has been taken in both large and small streams. *Capnia pygmaea* seems to prefer stream sections where the bottom is unstable and fine sand occurs between the stones, that is, in places where some silting occurs. In southern Norway the species has not been taken above the coniferous tree line, but in northern Norway it occurs in the Sub-Alpine belt. It has been found as far south as Sætedalen, Vest Agder, which is the southernmost locality in Europe. In Sweden only taken in the northern parts (Brinck 1949).

Capnia vidua (Fig. 53). I have only taken it in six localities in the counties of Finnmark, Troms and Nordland, where it occurs in small streams with unstable substrata. It has been taken in both the coastal areas and inland, but not above the Sub-Alpine vegetation belt. In Sweden taken as far south as Messaure (Müller & Thomas 1972).

Capnopsis schilleri (Fig. 54) has been recorded from both northern and southern Norway, but not in western Norway, its distribution being easterly. It is common and numerous in both the Oslofjord area and North Østerdalen. The species has been taken in small and large streams, but is most numerous in small streams with unstable substrata in which fine sand forms a part. *Capnopsis schilleri* also occurs in large rivers such as the Namsen near Grong, North Trøndelag, where silting takes place. Its main distribution area in southern Norway is within the coniferous forest areas, but it has also been taken in the Sub-Alpine vegetation belt. In the north the species is mainly found in the Sub-Alpine vegetation belt. The highest locality is at about 1100 m a.s.l. in Øvre Heimdalen. In Sweden the species is taken both in south and north.

Fam. Leuctridae

In this family there are four herbivorous species. *Leuctra digitata*, which was taken over most of Norway, seems to be associated with mountainous areas in southern Norway (Fig. 55). It has only been taken in the inner fjord areas in the south-west and the eastern mountains. Its distribution is nearly the same as *Capnia pygmaea*, but *Leuctra digitata* goes further south in eastern Norway and it is common in the streams around Oslo which are not too heavily polluted. *Leuctra digitata* is most numerous in small streams, but it also occurs in large streams. In the mountains the species is common in the Sub-Alpine vegetation belt in Øvre Heimdalen at about 1200 m a.s.l. According to Brinck (1949) this species is ecoenic in northern streams and has not been taken in the southernmost parts of Sweden.

Leuctra fusca is found mainly in southern Norway (Fig. 56). The northernmost find is from Bodø, Nordland and Pasvik, Finnmark,

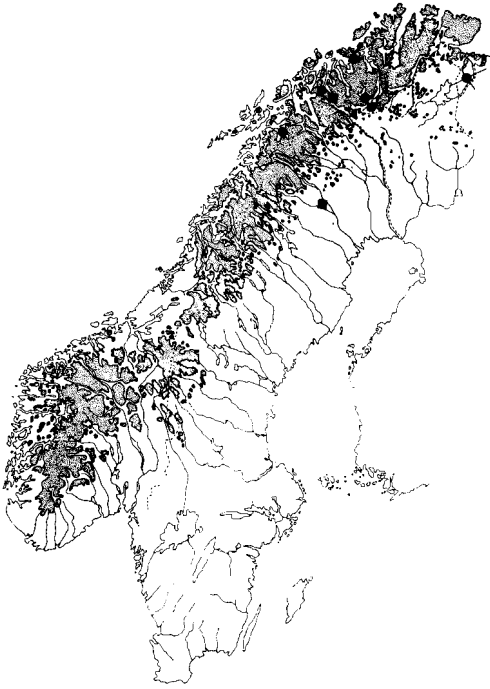


Fig. 53. Distribution of *Capnia vidua* Klapálek.
■ Records from Sweden and Finland.



Fig. 55. Distribution of *Leuctra digitata* Kempny.

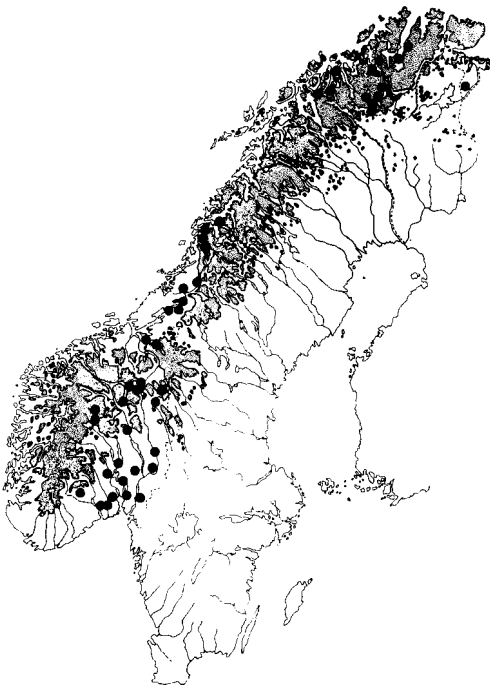


Fig. 54. Distribution of *Capnopsis schilleri* (Rostock)

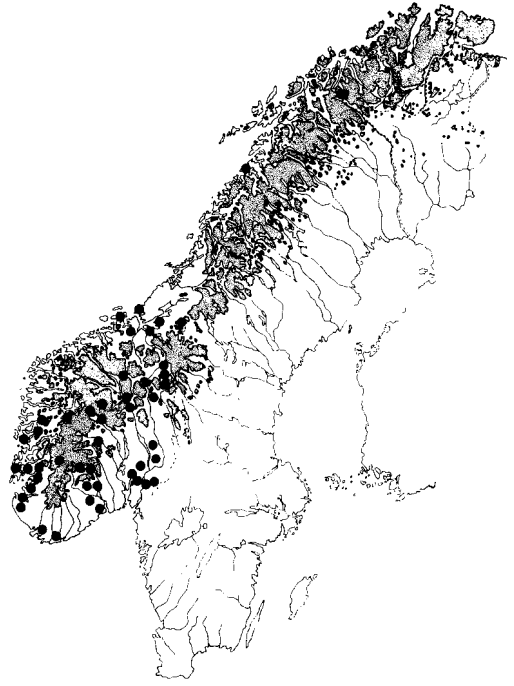


Fig. 56. Distribution of *Leuctra fusca* (Linnaeus).
■ The northernmost record in Finland.

Tobias (1974). In southern Norway the species is common and numerous both in the coastal areas in the west and in the Sub-Alpine belts in the mountains. It has been taken in small and large streams, in rivers and lakes. *Leuctra fusca* may be one of the dominating species both in rivers such as Suldalslågen and in small streams such as Leir-elva. The highest locality is at 1100 m a.s.l. in Øvre Heimdalen. The species has been taken both in southern and northern Sweden (Brinck 1949).

Leuctra hippopus is probably the most common Norwegian stonefly species, and occurs all over Norway (Fig. 57). It often dominates the stonefly fauna, especially where Capniids are absent. It has been taken in the coastal areas of the south-west and the south and it is also common in the Sub-Alpine vegetation belt in the mountains. The Low-Alpine belt at heights of 1100 m a.s.l. is its limit. The species is common and numerous in small and large streams and rivers and has been taken on different substrata. It also occurs in lakes. It is as common in northern Norway as in the south. The species has been taken both

in northern and southern Sweden (Brinck 1949).

Leuctra nigra is found in both southern and northern Norway (Fig. 58), but not in the coastal areas of the south-west. The species is most common in small streams, but also occurs in large streams. *Leuctra nigra* is the species in the genus *Leuctra* which usually goes highest up the mountains. It is common in the Sub-Alpine vegetation belt and the highest locality is at about 1200 m and in the Low-Alpine belt of Øvre Heimdal. The species has been taken both in northern and southern Sweden and is, according to Brinck (1949), a characteristic inhabitant of small stony streams.

Discussion

Several species have shown great differences in habitat preference and some of the most pronounced differences will be discussed below.

Leuctra fusca has been said to prefer large rivers (Ulfstrand 1968), but in southern Norway this is not the case and *Leuctra fusca* is a common inhabitant of both small and large

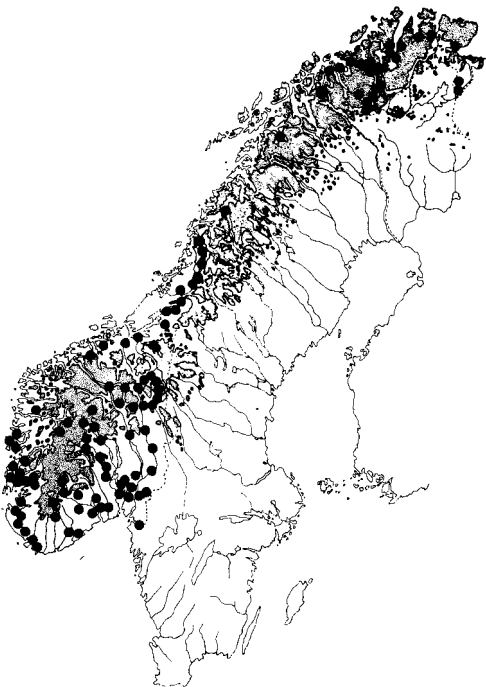


Fig. 57. Distribution of *Leuctra hippopus* Kempny.

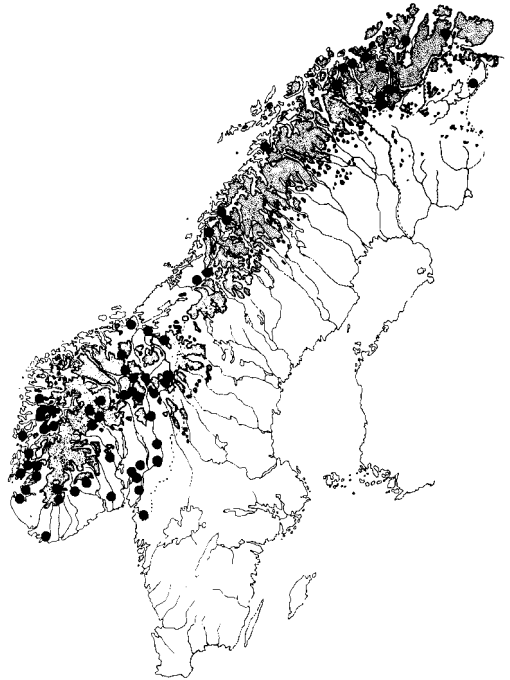


Fig. 58. Distribution of *Leuctra nigra* (Olivier).

streams and rivers. It is one of the dominant stonefly species in the River Suldalslågen as well as the small stream, Leirelva near Fagernes, Oppland. The species is often taken together with *Leuctra digitata* and they alternate in dominating parts of the stream, as at three stations at different altitudes in Leirelva, where *Leuctra hippopus*, *Leuctra digitata* and *Leuctra fusca* constituted 68 % of the stonefly fauna. The species may be a dominant species in small streams in the Sub-Alpine belt of western Norway such as in Elgjuvet, Sauda and also in the small coastal streams of western Norway such as Torsketjønnbekken, Haugesund. Thus, there are great differences within southern Norway and between these areas and the northern areas investigated by Ulfstrand (1968).

In the northern areas of Norway, *Leuctra fusca* was rare. The species was rare in the Kilpisjärvi area (Meinander 1972), but was common further south in the area of the upper Vindelv (Ulfstrand 1969). Thus, *Leuctra fusca* is common in small and large streams and rivers in southern Norway, most common in large streams in the upper Vindelv area, and rare further north.

Ulfstrand (1969) also found that *Leuctra hippopus* was more abundant in or restricted to small streams, which is not the case in Norway, where *Leuctra hippopus* is one of the most common and widespread species. It is common in rivers, large and small streams over nearly the whole country. Thus the species seems to have a wider ecological valence in Norway than in the Lapland streams investigated by Ulfstrand.

The differences in occurrence of the species in north and south Norway are also marked for *Isoperla obscura*, *Amphinemura borealis* and *Capnia atra*. This is mentioned above. Still more marked are the differences in the occurrence of the three most common carnivore stoneflies in Norway, *Arcynopteryx compacta*, *Diura bicaudata* and *Diura nanseni*. In North Norway all three species might occur together, both in outlets and streams and in different vegetation belts. In South Norway *Arcynopteryx compacta* has been taken mainly in streams in the Sub-Alpine belt and above. *Diura nanseni* mainly in streams in Sub-Alpine belt and below. *Diura bicaudata* in lakes both in the Boreal coniferous zones in the Sub-Alpine belt and above.

STONEFLY HABITATS

The results of the present work naturally pose the question whether one can generalize about a classification of stonefly habitats. Classification of watercourses into stoneflies' habitats has been made by several authors (Hynes 1941, Brinck 1949, Illies 1952, 1967, Berthélemy 1964, 1966 and Rauser 1971). Detailed classifications of watercourses based on ecological factors important for the distribution of Plecoptera have been given by Hynes (1941), Brinck (1949) and Rauser (1971). The first two restrict their classification to the faunas of England and Sweden respectively. Rauser (1971), however, makes an attempt to fit the total European Plecopteran fauna into a classification system. His divisions into lentic streams, mountain streams, etc. of the Arctic- and Boreal zones seems to be based on invalid generalization at least of the Norwegian streams. Most streams run through very different areas, there often being a repeated change in both substratum and stream velocity both at high altitudes and in the lowlands. A geographical zonation based on substratum and stream current is therefore not workable. It is only in restricted areas, mainly in the cultivated areas of south-eastern Norway, that rivers and streams may have a dominant substratum for long stretches. However, these streams are often so polluted that they cannot be used in such a comparison.

However, if one follows his classification of streams in the boreal and arctic areas of Fennoscandia, the characteristic species of the streams are still invalid to a high degree. The main reason for this seems to be that Rauser's classification is based upon incomplete records of the Scandinavian Plecopteran fauna, especially from Norway. In addition, he applied Brinck's (1949) results too widely.

According to Rauser (1971) the Arctic zone mountain currents and lakes are dominated by *Capnia atra* – *Diura nanseni*. The present investigation has shown that *Capnia atra* may be a dominant species in the high mountains, but not *Diura nanseni*. There are, however, such great differences between southern and northern Norway, environmentally and faunistically, that all such generalizations are rendered invalid. In southern Norway *Capnia atra* and *Arcynopteryx*

compacta often dominate high-altitude streams, sometimes together with *Amphine-mura standfussi*. In lakes *Capnia atra* and *Diura bicaudata* usually dominate, although sometimes with *Nemurella picteti*, *Nemoura cinerea*, or *Nemoura avicularis*. In the southern areas *Capnia atra* is absent and there *Diura bicaudata* and *Nemurella picteti* are often most numerous. In northern Norway *Capnia atra* and *Diura bicaudata* may dominate the fauna of both lakes and streams.

According to Rauser (1971), the *Taeniopteryx nebulosa* and *Isoptera obscura* are characteristic for lentic currents of the boreal zone. In the streams west of Oslo which Rauser says belong to this type, *Isoptera obscura* has not been recorded at all. If the species is present there, it is rare, and not characteristic. Even *Taeniopteryx nebulosa* is not characteristic for this stream type, as the species is just as common in stony streams with moss vegetation in the mountain areas.

Finally *Diura nanseni* should be the characteristic carnivore stonefly species of the hilly-land and piedmont currents of the boreal zone, and not the *Dinocras cephalotes* mentioned by Rauser. *Dinocras cephalotes* is only found in isolated localities. Thus the above examples serve to show that Rauser's (1971) system for the northern areas is invalid.

Attempts to use the systems presented by Hynes (1941) and Brinck (1949) for the Norwegian fauna have also had little success. Brinck (1949) divided habitats into spring, trickles, small eutrophic forest streams, southern streams, northern streams, southern rivers, northern rivers, jokks, ponds, southern lakes and northern lakes. He also stated that the classification based on different perceptible environmental conditions only serves as long as there is a true correlation between the species and the habitats, i.e. a habitat which does not correspond to a specific zoön has no authorization in the classification. Most of the Norwegian landscape is quite different from the Swedish, and this certainly makes the environmental factors act differently in Norway and in Sweden by producing another faunal association out of the total environmental impact on each species. Not all the habitats listed by Brinck (1949) fit well into

the Norwegian landscape. This is illustrated by reference to western Norway, where high mountains provide cold water from melting snow for most of the summer. The water flows down into the lowlands which have a more or less atlantic climate. According to Brinck's (1949) classification, most of the larger streams have temperatures which fit well into the jokk type. Along much of their length they would also be of the jokk type regarding substratum and stream velocity, but between these parts there are still flowing silting sections at all attitudes. Faunistically, however, they do not belong to either the jokks or the northern streams. Typical inhabitants of the jokks, *Capnia atra* and *Arctopteryx compacta*, are absent in the southern parts and the streams do not have the same association of species which are typical for the northern streams of Brinck (1949).

Variation along the length of a single watercourse is most pronounced in western Norway, but also occurs in most other areas of the country. Therefore no attempt will be made in this study to classify streams.

Ulfstrand (1968) discussed the classification of lotic biotopes and their animal communities and made the following classification: 1. The biotope classification, where he concluded that a substratum classification was the most suitable. 2. The community classification. He mentioned the attempt made by Berthélemy (1966) to adopt faunistic criteria in his studies. These were largely unsuccessful and he concludes 'Community classification, based on characteristic species or species constellations (f. Berg 1948) will generally have only regional applicability'. In the present work Ulfstrand's (1968) conclusion is reinforced by the faunistic differences observed in the seven investigated areas of Norway and the considerable differences in the biotope preferences of the species in northern and southern Norway indicate that generalizations should be avoided where possible.

THE STONEFLY FAUNAS OF DIFFERENT AREAS GROUPED ZOOGEOGRAPHICALLY

The zoogeography of stoneflies has been discussed by authors such as Brinck (1949),

Illies (1953, 1955, 1965), Rauser (1962, 1971), Ricker (1964), Ulfstrand (1968) and Udvardy (1969). The different species of northern Europe have been grouped according to origin and as immigrants into Fennoscandia from the south or the north-east. Such a grouping has been carried out on the fauna of the seven areas investigated in this work (Tables III-IX) following Ulfstrand's (1968) model.

Group 1 consists of the species which are distinctly north-eastern and absent from western Europe: *Capnia pygmaea*, *Diura nanseni*, *Nemoura arctica* and *N. sahlbergi*.

Group 2 consists of basically north-easterly species which have a smaller or larger number of outposts in central and/or western Europe: *Amphinemura borealis*, *Leuctra digitata*, *Capnia atra*, *Capnopsis schilleri*, *Arcynopteryx compacta*, *Diura bicaudata* and *Siphonoperla burmeisteri*.

Group 3 encompasses the species which are widespread in western Europe and are often predominantly southerly: *Amphinemura standfussi*, *A. sulcicollis*, *Brachyptera risi*, *Capnia bifrons*, *Dinocras cephalotes*, *Isoperla difformis*, *Isoperla grammatica*, *Isoperla obscura*, *Leuctra fusca*, *Leuctra hippopus*, *Leuctra nigra*, *Nemoura avicularis*, *Nemoura cinerea*, *Nemoura flexuosa*, *Nemurella picteti*, *Perlodes dispar*, *Protonemura meyra* and *Taeniopteryx nebulosa*.

In addition to the species in the groups given by Ulfstrand (1968), the present author has added *Nemoura viki* to group 1.

Xanthoperla apicalis and *Isogenus nubecula* are added to group 2. According to Brinck

(1949), they are north-eastern species which came from Central Europe. Also *Protonemura intricata* is placed in the same group by the present author. In Fennoscandia the species has a north-eastern distribution, but is mainly distributed in Central Europe. *Capnia vidua* is placed in group 3 because the species has a wide distribution in western Europe.

The number of species from the three groups represented in different areas are listed in Table XXI. The northern areas Kautokeino, Pasvik and Alta contain the highest number of north-eastern species and the lowland areas of Oslofjord and Rogaland the lowest. In both southern and northern Norway the areas which are most continental contain the highest number of north-eastern species (groups 1 and 2).

A comparison between the faunas of the Sub-Alpine and Low-Alpine belts of Rogaland and Øvre Heimdal shows that Ø. Heimdal has the higher number of north-eastern species.

There are also differences within the main areas. In Rogaland the coastal area has only one species of north-eastern origin, the central area three, and the inner five. The coastal area has a higher percentage of southern species than both the central and inner areas. The same is true of the coastal and inner areas of the Oslofjord. Neither of the coastal areas have a distinctly north-eastern (group 1) species, and only one of them a basically north-eastern species (group

Table XXI. The presence of zoogeographical groups in the investigated areas of Norway

Areas	Total No. of species	Zoogeographical groups		
		1	2	3
1. Rogaland area	17	2	3	12
2. Rogaland Coastal area	9	0	1	8
3. Rogaland Middler area	14	1	2	11
4. Rogaland Inner area, lowland	17	2	3	12
5. Rogaland Inner area, high altitudes	15	1	3	11
6. Oslofjord area	24	1	5	18
7. Oslofjord Inner area (2.1)	22	1	6	15
8. Oslofjord Coastal area (2.3)	7	0	1	6
9. North-Østerdal	27	2	8	17
10. Ø. Heimdal	21	1	5	15
11. Kautokeino	27	5	7	15
12. Alta	18	3	6	9
13. South-Varanger	28	5	9	14

2). There are differences between Rogaland and the Oslofjord in the inner lowland areas as there are two distinctly north-eastern species in Rogaland while there is only one in the Oslo area.

Finally, the areas in northern Norway which are near the immigration routes of the north-eastern species support the highest number of species. In southern Norway, the areas with the most continental climate have the highest number of such species, while the areas with the most pronounced atlantic climate have very few north-eastern species.

CONCLUSION

In general the distribution of Norwegian stoneflies seems to be connected with major factors such as differences in climate, vegetation region and historical immigration. However, the more local distribution seems to be associated with several other factors, of which the amount of deciduous vegetation in the vicinity of the watercourse, the amount of allochthonous organic matter, substratum and temperature are among those shown to be of importance in the present study. Such factors clearly interact differently to produce different faunal associations in the various areas. In part III: Field studies on ecological factors influencing distribution, and in part IV: Laboratory tests on ecological factors influencing distribution, these factors will be documented and discussed individually in more detail.

SUMMARY

In the present work about 500 streams and lakes from all parts of Norway were investigated. The material consists of about 45,000 specimens.

The distribution of the Norwegian species is plotted in Figs. 25-58.

Thirty-four of the 35 Norwegian species have been collected by the author, twenty-nine of these 35 species in southern Norway and 32 in northern Norway. Seven of the species present in southern Norway have not been

recorded west of the central mountain chain (Langfjellene).

The most continental areas in southern Norway, North Østerdalen and its surroundings, support the highest number of species.

In the south there is a decrease in number of species towards west, south-west and south. There is also a reduction in species towards the coastal areas. This trend was examined in southern Norway and in the north there also seems to be a similar trend.

There are differences between southern and northern Norway in the presence of different species in various vegetation belts. While *Capnia pygmaea*, *Amphinemura borealis* and *Isoperla difformis* only occur in the Boreal coniferous areas in southern Norway, they all occur in the Sub-Alpine belt in northern Norway.

A reduction in species paralleled by the reduction in deciduous vegetation and the amount of organic allochthonous matter in the streams was observed in all parts of Norway. This trend was investigated in different vegetation belts in three study areas. The trend is mainly connected with the reduction in *Salix* vegetation along the streams. Above the *Salix* belt only a few species are common, *Diura bicaudata*, *Arcynopteryx compacta*, *Capnia atra*, *Amphinemura standfussi*, *Nemoura cinerea*, *Nemurella picteti* and in northern Norway *Nemoura arctica*. Only two or three of them are usually taken together in each area.

The Capniids are mainly distributed in the eastern parts of southern Norway and they are most common where there is a rich soil and deciduous trees along the streams.

Seventeen of the Norwegian species were taken in lakes at least once. The highest number of species was taken in the high altitude lake, Øvre Heimdalsvann, and in the lakes in northern Norway.

Some species seemed to be restricted to certain substrata and streams of certain size in some areas of Norway, but had a wider distribution in other areas. There were great differences in this respect between southern and northern Norway and between low and high altitudes.

The investigations have shown that there are such great faunistic differences between the different areas of Norway that previous generalizations about the classification of

streams are to a large extent rendered invalid.

The northern areas Kautokeino, Pasvik and Alta support the highest number of north-eastern species, and the lowland areas in southern Norway the lowest. The most continental areas in southern Norway contain the highest number of north-eastern species, and the coastal areas of Rogaland and Oslofjord the lowest.

Generally, distribution of Norwegian stoneflies seems to be connected with major factors such as differences in climate, vegetation region and historical immigration. More locally, distribution seems to be associated with factors such as the amount of deciduous vegetation in the vicinity of the watercourse, the amount of allochthonous organic matter, and substratum and temperature.

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Bokanmeldelser

Günther, Kurt K. 1974. Staubläuse, Psocoptera. *Tierwelt Deutschlands, Teil 61*. 314 pp., 437 ill. VEB Gustav Fischer, Jena. Pris 69.- M.

Psocoptera er en relativt lite undersøkt insektgruppe. Det skyldes ikke bare at de lett kan bli oversett fordi de er små, men også at de kan være vanskelige å oppbevare. Eksemplarer på nål skrumper inn til det ugjenkjennelige, og andre former for oppbevaring kan også by på problemer. Dette er årsakene til at de fleste museer har få støvlus i sine samlinger, skriver Günther. Heller ikke støvlusenes biologi og økologi er tilstrekkelig kjent. Generelt er de fleste arter knyttet til vegetasjonen, hvor mange av dem lever av sopp- og algebelegg. Andre arter lever under sten, i huler eller i fuglereder, og en ikke liten gruppe forekommer ofte i hus. Deres forekomst innendørs er tegn på høy fuktighet og muggdannelse. Støvlusene kan ikke gjøre direkte skade i hus, men er sjenerende ved at de sprer seg til matvarer.

K. K. Günthers bok om støvlus har bl. a. sin store betydning ved at den vil stimulere til videre arbeid med denne gruppen. Her samles og henvises til det meste av det man vet om Psocoptera innen det angitte geografiske område. Boken innledes med en generell del, som har en detaljert beskrivelse om støvlusenes morfologi. Denne delen inneholder bl. a. også kapitler om biologi, utbredelse og fylogeni, samt metoder til innsamling og preparering.

Den største og viktigste delen av boken er den systematiske. Denne er bygget opp med en serie av bestemmelsestabeller, som fører til underorden, familie, slekt og art. Hver art har fått en detaljert omtale, og forfatteren har bestrebet seg på å gjøre denne så grundig og nøyaktig som mulig. For de fleste arter foreligger flere tydelige illustrasjoner. Artsbestemmelser vil ofte være avhengig av karakteristiske kjennetegn ved genitalorganer, både hos hunner og hanner, eller egen-skaper ved analregionen. For hver art gis en oversikt om det man vet om dens levevis, forekomst og utbredelse.

Tierwelt Deutschlands omfatter etterhvert en rekke bind om insekter, og det siste om støvlus er et verdifullt bidrag til bestemmelseslitteraturen. Den norske støvlusfauna er dårlig undersøkt, men denne boken vil iallfall være et utgangspunkt for den som vil studere disse insektene.

Lauritz Sømme

Barbosa, P. & Peters, T. M. (eds.) 1972. *Readings in Entomology*, 450 pp. W. B. Saunders Co., Philadelphia, London, Toronto. Pris £ 2.80.

Dette er en samling utvalgte artikler over entomologiske emner. Artiklene er hentet fra forskjel-

lige tidsskrifter, og gjengitt i sin helhet som avtrykk av originalen. Stoffet er redigert i syv hovedavsnitt, som bl. a. spenner over taksonomi, økologi, fysiologi og etologi. Et stort avsnitt under tittelen «Man and insect» er viet den anvendte entomologi.

Boken er beregnet som tilleggslesning for studenter i entomologi, men vil også være av interesse for mange andre. Med det utvalget av artikler som er gjort, blir man kjent med mange av de viktigste landevinninger innen faget i den siste 10-års periode. Artiklene er for en stor del oversiktsartikler, men noen av dem er rene originalavhandlinger.

I det hele inneholder boken et rikt utvalg av entomologisk lesestoff, og blir på en måte en historisk dokumentasjon av viktige begivenheter innen fagets senere periode. Gjennom dette opplegget blir leseren mer fortrolig med det arbeid og den teknikk som ligger bak resultatene, enn man blir gjennom en vanlig lærebok.

Selv om alle artikler belyser viktige prinsipielle sider av entomologien, kunne det i noen tilfelle vært valgt artikler av litt nyere dato. En artikkel om ferromoner fra 1963 er et eksempel på dette. Men alt blir foreldet etter hvert, og den beste måten å rette på det, er å lage en ny utgave. Det ville være å ønske at den gode idé fra «Readings in entomology» ble fulgt opp med flere bind, både for å ta opp andre områder, og for å supplere de som allerede er behandlet.

Lauritz Sømme

Slåma, K., Romanuk, M. & Sorm, F. 1974 *Insect Hormones and Bioanalogs*. 477 pp. Springer Verlag, Wien, New York. Pris \$ 45.90.

Insektenes hormoner har vært gjenstand for stor oppmerksomhet i de senere år, ikke minst etter det ble oppdaget en rekke syntetiske stoffer med tilsvarende effekter. Den store forskningsinnsats innen området skyldes tildels muligheten av å benytte insekthormoner til insektbekjempelse. Blant de mange stoffer med juvenil hormon aktivitet ligger muligheter for å utvikle selektive insektmidler, og insektmidler som insektene ikke kan bli resistente mot.

Fagområdet har etterhvert blitt så omfattende, og nye arbeider kommer så raskt at man lett mister oversikten. Av den grunn er det av stor betydning at vi her får en bok med en bred fremstilling, skrevet av tre av de fremste forskerne på området. Både Slåma, Romanuk og Sorm har gjennom sin forskning gitt vesentlige bidrag; den første gjennom en rekke insektfysiologiske arbeider, de to andre særlig ved kjemisk syntese av stoffer med juvenil hormon effekt.

Boken innledes med et avsnitt om hormon-

produserende, endokrine organer hos insekter. I dette avsnittet er inkludert en kort omtale av hjernehormonet eller «aktiveringshormonet», som stimulerer prothoraxkjertelens produksjon av hudskiftehormon. Den kjemiske sammensetning av aktiveringshormonet er fremdeles uklar, men det dreier seg antagelig om et protein med mol.vekt mellom 10 000 og 50 000.

Den største delen av boken omhandler de syntetiske juvenile hormoners kjemi og fysiologiske effekter. I stedet for det vanlige uttrykk juvenil hormon analoger innfører forfatterne «juvenoider» som betegnelse på slike stoffer. Disse omfatter i dag et stort antall forbindelser. Selv om man ut fra deres kjemiske bygning og egenskaper kan forutsi noe om deres biologiske effekt, kan denne bare avgjøres med sikkerhet gjennom forsøk med levende insekter. I boken legges derfor stor vekt på gjennomgåelsen av de biologiske testmetoder som etterhvert har blitt utviklet. For å få sammenlignbare resultater i forskjellige laboratorier, er det viktig at disse metodene standardiseres. Boken gir en bred oversikt over testmetoder med forskjellige insektarter, og det legges vekt på å vise hvorledes resultatene bør vurderes.

Hovedtrekkene ved de viktigste juvenoiders kjemiske sammensetning og syntese gjennomgås i et eget kapittel. Videre gis en detaljert omtale av juvenoidenes fysiologiske og biokjemiske virkninger. Selv om hele fagområdet er av nyere dato, har det samlet seg en anseelig mengde kunnskaper om juvenoidenes fysiologiske effekter på forskjellige utviklingsstadier, inkludert embryonale stadier og voksne insekter. Videre foreligger en rekke undersøkelser over deres effekt på metabolisme, enzymsyntese og andre biokjemiske funksjoner.

Bruk av juvenoider som insekticider er forbundet med mange praktiske vanskeligheter, som f. eks. stoffenes stabilitet i felten. Det er mulig at tidlige arbeider spente forventningene for høyt. Fremdeles er det en lang vei å gå før vi får anvendbare insekticider basert på juvenoider. De potensielle muligheter til å utvikle selektive midler, samt liten fare for uønskede sidevirkninger, gjør at man i høyeste grad bør satse videre på dette området. I dag er man allerede langt på vei med metoder til bekjempelse av mygg og insekter i lagrete matvarer.

Avsnittet om hudskiftehormonet, ecdyson, og stoffer med ecdyson effekt er også interessant. Fra forskjellige planter kjenner man i dag et meget stort antall naturlig forekommende steroider med ecdyson effekt. Selv om noen av disse kan ekstraheres i forholdsvis store mengder, kan disse stoffene foreløpig vanskelig anvendes som insekticider.

Bakerst i boken finner man en liste over ca. 350 juvenoider. Listen viser et representativt utvalg av forbindelser med forskjellig kjemisk sammensetning. For hvert stoff er angitt dets biologiske effekt på de mest benyttede forsøksinsekter. Den samlede oversikt denne listen gir over juvenoidenes kjemi og biologiske virkninger vil være til stor nytte for forskere på området.

Boken er antagelig den mest omfattende fremstilling av insektenes hormoner og tilsvarende syntetiske forbindelser, som hittil er skrevet. Den kan anbefales som en grundig håndbok for alle som er interessert i området.

Lauritz Sømme

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