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Diversity of Ephemeroptera and Plecoptera in Norway relative to size and qualities of catchment area

JOHN W. JENSEN

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Based on data from 58 catchment areas, equations expressing the species nnmber of Ephemeroptera and Plecoptera in relation to size of catchment area were calculated for six main regions and for Norway in general. For Plecoptera these relationships were uniform, except for a somewhat lower diversity in Sørlandet, the southernmost part of Norway. Ephemeroptera showed more variation from area to area and between regions, and the diversity was low along the west coast of Norway and especially in Sørlandet.

Significant ($p<0.05$) equations relating the number of ephemeropteran species to the fraction of the catchment area representing woodland, mean specific conductivity, maximum temperatnre, and maximum pH were found. For Plecoptera a significant relationship only existed in relation to pH.

The general number of species to area equations were combined with the equations expressing the relationships between species nnmber and the environmental parameters. The expected numbers of species expressed by these models corresponded better with the recorded numbers than those calculated from size of area alone. Deviation between expected and recorded numbers was especially related to decreasing pH. In catchment areas of 250—700 km^2 in Sørlandet the number of plecopteran species seem to have been reduced by 40—25% and that of Ephemeroptera by 75%.

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INTRODUCTION

The number of species of a taxon (N) in an area may be related to the size of the area (A) by an equation of the form

$$N = CA^z \quad (1)$$

where C and z are parameters of changing values. Such relationships have especially been formulated for various islaud floras and faunas, but also for non-isolated or continental ones (MacArthur & Wilson 1967). Bevanger (1986) presents equations for Norwegian birds, and like Butcher et al. (1981) he discusses their use for the design and management of nature reserves.

Since 1975 about 60 water systems have been surveyed in Norway, mainly in connectiou with conservation plans or hydroelectric development. The standardizing of methods and sampling frequencies make these data comparable. Based on this litterature an aualyses relating the species nnmber of Ephemeroptera and Plecoptera to size of the catchment area of the water systems was performed.

The species numbers relative to the size of the catchment areas were transformed to numbers related to areas of nnit size. Thus, areas of various size may be compared, and relatiouships to environmental characteristics could be evaluated. These relationships were combined with the number of species to area equations into more precise models for the prediction of species numbers. Special attention is given to the effect of acidification.

METHODS AND MATERIAL

In this paper diversity is takeu as the number of Ephemeroptera or Plecoptera found in a catchment area of a certain size. The catchmeut area may be a complete river system, one or more sections of a river system, or an area covering sectious of neighbouring river

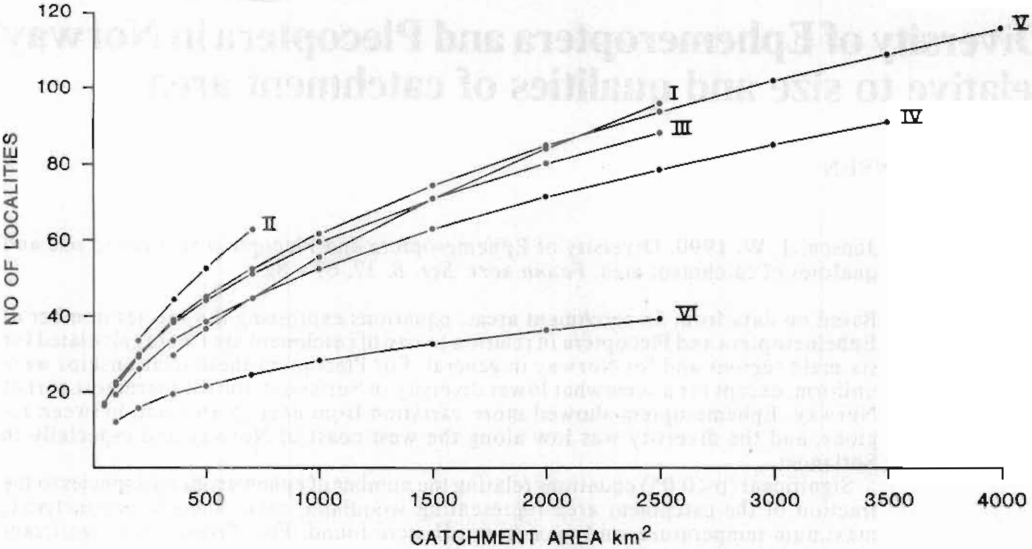

Fig. 1. The number of sampling localities in six regions of Norway in relation to size of catchment areas.

systems. The material incorporates data from 58 such areas and represents 1180 localities from the littoral zone of 415 lakes and ponds aud 1201 stream localities. All areas have been surveyed to record the composition of their freshwater macroinvertebrates. The material has mainly been collected by the kick method (Frost et al. 1971). In all six regions (Fig. 2) the relationship between the nnmber of localities (L) sampled by this method and the size of the catchment area in km² (A) was of the form:

$$L = BA^X \quad (2)$$

These equations were significant ($p<0.05$) for all regions, except region II, and the relationships are shown in Fig. 1. The sampling programme is comparable for all regions, except region VI.

As a qualitative describtion of the areas, the following parameters were chosen: the percentage of the area reprented by woodland (W) measured by planimeter on maps of scale 1:250000 (series 1501), mean range of specific conductivity at 18°C (K), maximum pH, and maximum water temperature in °C (T). All data concerning water quality were taken from stream localities, as most of the recorded species of both orders live in such habitats. References for data on water quality and species nnmbers are presented in Table 1.

The number of species (N) of each taxon was expected to increase with the size of the catchment area in km² (A) according to equation (1). Such equations were calcnlated for the main regions of Norway (Fig. 2) by a curve fitting programme. Based on selected catchment areas, general equations for the Norwegian fauna of Ephemeroptera and Plecoptera were calculated. Using the z values of the general equations, the number of species in catchment areas of nnit size (N_u) were calulated:

$$\lg N_u = \lg N - z \lg A \quad (3)$$

The diversity of catchment areas of different size can be compared by the N_u values.

The relationships between the N_u values and the environmental parameters were tested by several curve fitting programmes, and the equations of best fit were chosen.

The best relationships between N_u and the number of sampling localities (L) for the 36 areas south of 68°N not supposed to be affected by acid precipitation, i.e. the regions I, IV, V, and rivers no. 20—23 in region III, were:

Ephemeroptera: $N_u = 2.72L^{-0.11}$ $r = 0.20$ (4)

Plecoptera: $N_u = 4.06L^{0.04}$ $r = 0.16$ (5)

For region VI they were:

Ephemeroptera: $N_u = 1.5 + 0.004L$ $r = 0.08$ (6)

Plecoptera: $N_u = 4.5 + 0.007L$ $r = 0.10$ (7)

As these relationships are far from significant, even in region VI where the frequency of localities was lowest, the sampling programme seems not to have inflnenced the results.

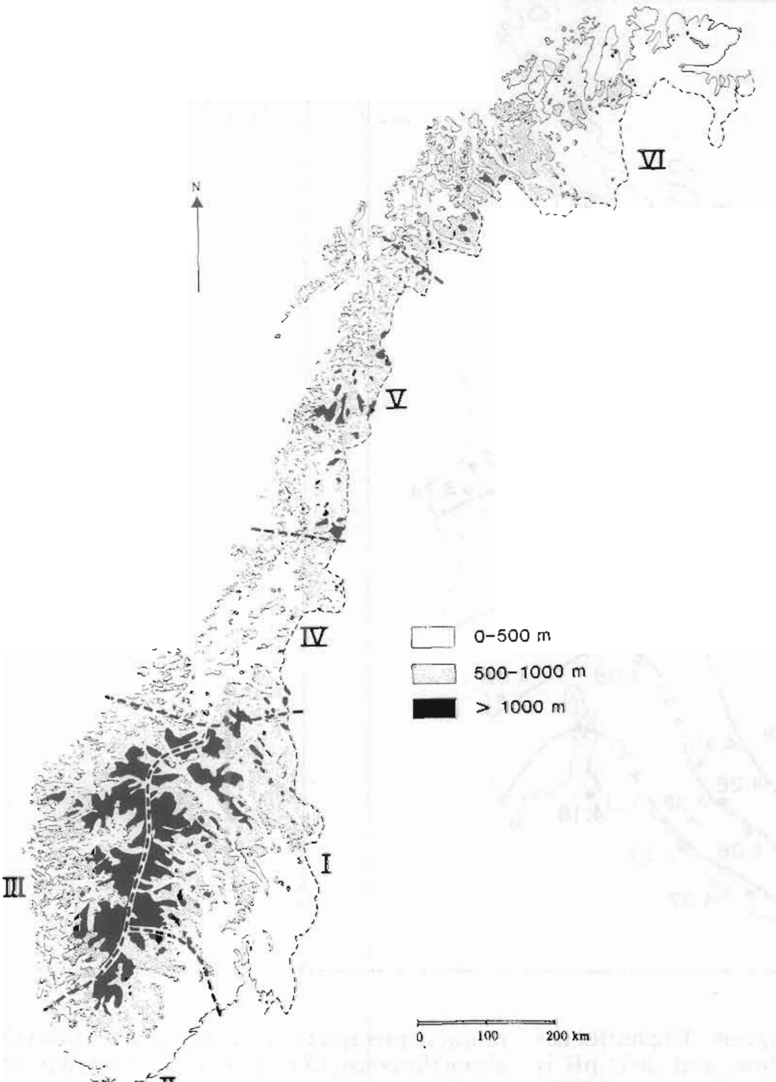

Fig. 2. The six regions of Norway used in this study and elevation in metres after Environmental Statistics (1978)

REGIONAL CHARACTERISTICS

Of the many zoogeographical factors, only altitude (Fig. 2), acid precipitation (Fig. 3), and the parameters presented in Table 1 are considered. Acid precipitation is mainly a problem in the southern parts of Norway, but occasionally it is transported as far north as 70°N (Wright & Dovland 1978).

Region I (Østlandet) represents the eastern slope of the mountain range and the lowlands towards the border with Sweden and the coast (Fig. 2). The region is forested below 1000 m, mainly with conifers. The studied catchment areas are only moderately affected by acid precipitation and some of them have sufficient buffer capacity. All of them represent sections of large river systems, and areas below 220 m are not included.

Region II (Sørlandet) is the most southerly district of Norway. Its geography changes from that of region I towards the qualities of region III. The tree line falls to 500 m in the western parts. This region is most severely

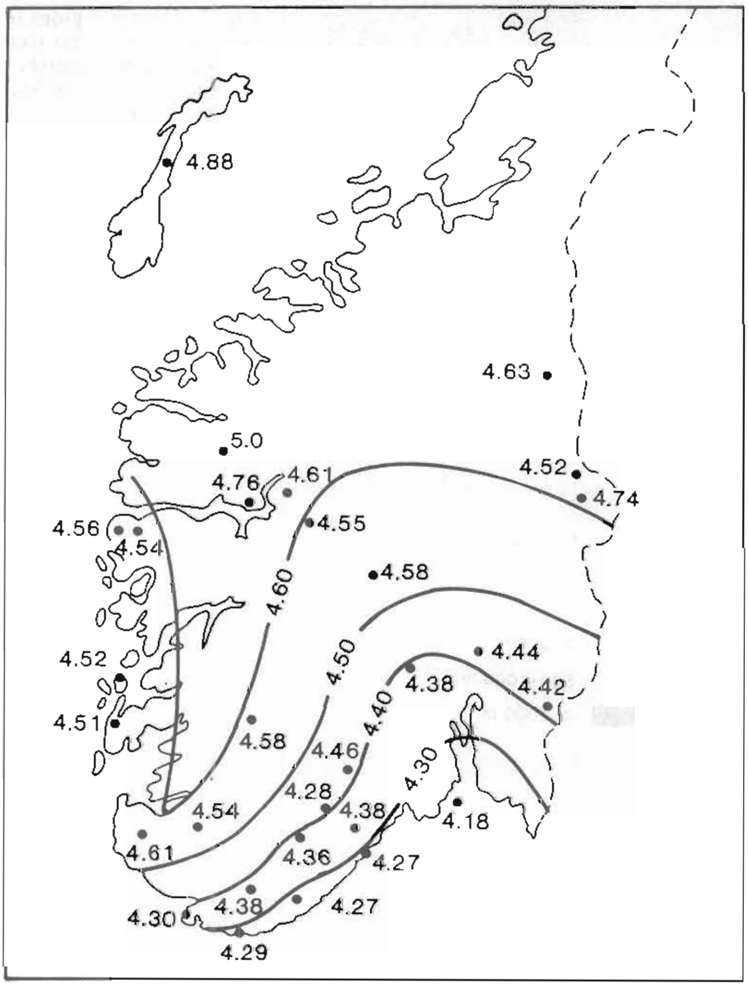

Fig. 3. Mean pH of precipitation over southern Norway based on data from July 1972 to June 1975 (After Dovland et al. 1976).

affected by acid precipitation. The buffer capacity of its waters is low, and their pH is generally below 5.5 (Wright et al. 1977). Fish populations are extinct in about half of the region, and affected in most of the remaining areas (Muniz & Leivestad 1980).

Region III (Vestlandet) is characterized by steep slopes and short rivers between the high mountains and the fjords. Water temperatures are generally low, as many rivers are fed by snow or glaciers all summer. As much as 80—95% of som ecatchment areas is located in th sub-alpine and alpine zoues. The water is soft, in some cases approaching destilled water with K values of 3—4 μScm^{-1} being recorded. The waters of the region have therefore no capacity for resisting the more moderate acid precipitation penetrating northward along the coast. Only two of the studied river systems do not reach the sea.

Region IV (Trøndelag) covers the lowlands of central Norway with only small areas above 1000 m. The tree line is situated at 700—800 m. Normal K values are in the range 20—40 μScm^{-1}. The maximum pH of all river systems was >6.7. Half of them reach the sea.

Region V (Nordland) has a complex topography and geology. Some of the catchment areas are similar to those of region III, but a maximum pH >6.7 was always recorded. Others have a K>50 μScm^{-1}, and two of them (no. 42 aud 44) are forested to a degree comparable to those of region IV.

Table 1. The actual catchment areas of the different regions, their size in km² (A), the percentage representing woodland (W), mean range of specific conductivity as μScm^{-1} at 18°C (K), maximum pH and temperature in °C (T). All water quality data represent lotic stations. The recorded number of species (N), this back-calculated to catchment areas of unit size (N_u), and the expected number of species from equations 9 to 12 (N_e) is also given.

							EPHEMEROPTERA			PLECOPTERA			
No	Catchment area	A	W	K	pH	T	N	N_u	N_e	N	N_u	N_e	References for basic data
	Region I Østlandet												
1	Kynna	341	100	35	6.9	19.1	15	2.3	15	14	4.8	14	Sandlund & Halvorsen 1980
2	Imsa - Trya	580	60	23	7.0	15.5	16	2.1	15	19	5.9	15	Halvorsen 1985
3	Gimsa	535	25	64	7.7	14.7	12	1.6	16	17	5.3	25	Eie 1982a
4	Atna	1300	50	9	6.5	14.8	15	1.5	16	16	4.3	18	Eie 1982b
1-4	Glomma, sections	2756	55	60	7.7	19.1	31	2.4	31	22	5.1	20	The above
6	Josa, Øvre Lågen	492	20	21	7.0	11.4	10	1.4	12	17	5.4	15	Blakar 1982, Halvorsen 1982
7	Rivers in Hemsedal	356	30	10	6.6	11.8	10	1.5	10	16	5.4	14	Bjerke & Halvorsen 1982
	Region II Sørlandet												
8	Sjåvatn-area	240	75	8	5.1	12.4	3	0.5	3	8	2.9	9	Spikkeland 1980a
9	Lifjell-area	725	80	12	5.0	17.3	3	0.3	4	12	3.6	14	Spikkeland 1980b
10	Lyngdalselva	683	90	22	5.2	24.2	5	0.6	4	12	3.6	11	Halvorsen 1981
	Region III Vestlandet												
11	Vikedalselva	118	32	21	5.6	12.0	4	0.9	3	14	5.8	9	Haaland,Fjellheim & Hobæk 1983a
12	Granvinelvi	177	50	19	6.8	14.0	9	1.7	9	14	5.4	12	Haaland,Fjellheim & Hobæk 1983b
13	Flåmsvassdraget	279	14	17	6.8	10.0	4	0.6	9	14	5.0	13	Haaland, Hobæk & Raddum 1981a
14	Utla	330	7	5	6.2	12.0	4	0.6	7	8	2.8	13	Haaland, Hobæk & Raddum 1981b
15	Feiga	49	5	8	6.1	10.0	2	0.6	3	8	3.9	9	NOU 1983
16	Mørkri	277	9	12	6.6	10.0	7	1.1	8	16	5.7	13	NOU 1983
17	Jølstra	712	40	18	6.2	17.0	8	1.0	10	16	4.8	15	NOU 1983
18	Ørstaelva	158	53	23	6.7	12.0	6	1.0	9	14	5.5	12	Haaland, Hobæk & Raddum 1981c
19	Stordalselva	203	34	12	6.5	12.0	5	0.9	8	10	3.8	13	NOU 1983
20	Istra	66	12	13	6.2	12.6	5	1.3	4	12	4.6	10	Nøst 1981a
21	Rauma	1202	15	11	6.9	14.5	11	1.1	15	15	4.1	17	Nøst 1983, 1984a
22	Driva	2482	20	46	7.3	14.7	14	1.1	23	20	4.7	20	Nøst 1981b
23	Todalselva	251	16	10	6.6	15.0	7	1.2	9	16	5.8	13	Nøst 1981c
	Region IV Trøndelag												
24	Gaula	3651	60	66	7.4	15.5	25	1.8	31	21	4.6	21	Koksvik & Nøst 1981
25	Garbergelva	159	60	23	7.0	13.7	18	3.5	10	10	3.9	12	Nøst 1981d
26	Stjørdalselva	2130	70	24	7.3	15.9	29	2.4	25	21	5.1	20	Arnekleiv & Koksvik 1980
27	Ormset-area	87	60	19	6.8	19.7	18	4.3	8	14	6.2	11	Arnekleiv & Koksvik 1983
28	Verdalselva	1464	65	28	7.0	14.2	26	2.5	20	17	4.4	18	Koksvik & Haug 1981
29	Skjækra	252	50	17	6.8	13.0	19	3.2	10	12	4.3	13	Koksvik & Haug 1981
30	Ogna	571	80	44	7.4	20.2	28	3.6	19	12	7.7	15	Nøst & Koksvik 1981a
31	Nesåa	274	35	19	6.9	19.0	14	2.3	12	17	6.0	13	Nøst & Koksvik 1980
32	Høylandsvassdraget	554	75	43	7.2	14.5	24	3.1	16	14	4.4	15	Nøst 1982a
33	Sanddøla - Luru	1592	50	28	7.1	16.2	25	2.3	21	18	4.6	18	Nøst 1982b
34	Sørlivassdraget	1174	60	15	7.0	16.8	22	2.2	19	17	4.6	17	Nøst & Koksvik 1981b
	Region V Nordland												
35	Vefsna	4420	30	68	7.6	16.7	29	1.9	32	21	4.5	22	Koksvik 1976, 1979
36	Eiteråga	272	30	36	7.0	12.9	11	1.8	10	12	4.3	13	Koksvik 1979
37	Lomsdalselva	240	8	19	7.0	13.8	14	2.4	9	18	6.6	13	Arnekleiv 1981
38	Lakselva, Visten	160	30	15	6.8	13.5	9	1.8	8	17	6.7	12	Nøst 1984b
39	Bønnåa	48	14	14	6.8	14.9	4	1.2	5	6	2.9	10	Nøst 1984b
40	Ranaelva, North	749	11	21	7.0	11.7	10	1.2	12	14	4.1	16	Koksvik 1977a

Table 1 continued

No	Catchment area	A	W	K	pH	T	EPHEMEROPTERA N	N_u	N_e	PLECOPTERA N	N_u	N_e	References for basic data
41	Storvasslåga	51	11	32	7.0	9.2	5	1.4	5	8	3.9	10	Koksvik 1978a
42	Valsnesvassdraget	70	65	71	7.5	15.3	12	3.0	9	14	6.4	10	Huru 1982a
43	Beiarelva	869	35	44	7.3	11.5	11	1.2	16	17	4.9	17	Koksvik 1978b
44	Lakselva, Misvær	159	50	65	7.4	15.1	16	3.1	11	14	5.5	12	Koksvik 1978c
45	Saltdalselva	1539	30	60	7.3	14.2	16	1.5	21	17	4.4	18	Koksvik 1977b
46	Sørfjordelva	111	12	14	7.0	9.2	4	0.9	6	8	3.4	11	Koksvik & Dalen 1977
47	Kobbelv	283	17	14	6.9	14.8	4	0.7	10	14	5.0	13	Koksvik & Dalen 1977
48	Hellemo-area	250	6	12	6.8	15.1	7	1.2	8	11	4.0	13	Koksvik & Dalen 1980
Region VI Troms - Finnmark													
49	Elvegårdselva	120	25	50	7.5	16.9	9	1.9	10	9	4.6	11	Huru 1982b
50	Spansdalselva	140	30	89	7.8	15.1	13	2.6	11	11	5.8	12	Huru 1980a
51	Øvre Barduelv	470	50	29	7.3	16.6	15	2.1	15	16	5.8	15	Huru 1981a
52	Nordkjoselva	184	30	66	7.8	13.5	7	1.3	11	12	4.6	12	Huru 1982c
53	Reisavassdraget	2516	15	62	7.6	19.4	19	1.5	26	22	5.2	20	Huru 1980b
54	Snøfjordvassdraget	76	1	33	7.2	14.8	3	0.7	6	10	4.5	10	Huru 1981b
55	Lakselva, Lakselv	1509	45	67	7.5	16.9	23	2.2	23	18	4.7	18	Huru 1982d
56	Julelva	338	15	31	7.1	11.2	6	0.9	10	15	5.1	14	Huru 1981c
57	Vesterelva	466	2	28	7.3	13.9	12	1.6	10	9	2.9	15	Huru 1981d
58	Komagelva	337	5	36	7.4	11.1	7	1.1	9	11	3.8	14	Eie, Brittain & Huru 1982

Region VI (Troms-Finnmark). All of this region is situated north of latitude 68°N. Finnmark, the north-eastern section, is mainly a plateau of 300—400 m in altitude. Troms has a more varied topography. The waters are generally rich in electrolytes, and this region is the only one where a maximum pH >7.0 was recorded in all areas. In the eastern, more continental parts of the region, the water temperature can be as high as in any of the other regions. The last three river systems of Table 1 are located to the Varanger peninsula, the extreme north-eastern tip of Norway. There are almost no forests and the water temperatures are low, similar to those of the coldest rivers in region III.

RESULTS

The number of species recorded in the different regions is presented in Table 1. All number of species to area equations based on these records show an increasing number of species with increasing area (Table 2). For Ephemeroptera different equations were found for the different regions. For Plecoptera they were rather uniform, except for the deviating one of region II. The fit of the equations is $p < 0.05$ or better, except for Ephemeroptera in region II. However, for this region comparable data exist from only three areas.

Region II was extremely poor in ephemeropteran species (Fig. 4). The number in a catchment area of 4000 km² would be only 5, compared to 17 in region III, 21 in region V, and 28—30 in the others. The latter numbers indicate that in a catchment area of 4000 km² in the regions I, IV, and VI one would expect to find 2/3 of the 47 species, which according to Nøst et al. (1986) are recorded in Norway. Region IV is special, as high numbers of species occur in small areas.

The corresponding calculations for Plecoptera give almost identical numbers for all regions, except region II, with 21—23 species in a catchment area of 4000 km² (Table 3). This represents 2/3 of the 35 species which according to Lillehammer (1974) and Nøst et al. (1986) are recorded in Norway. Compared to this the number of species in region II is 40—25% lower within the actual range of catchment area, 240—700 km².

Based on the data from the regions I, IV, V, and catchment areas no. 20—23 in region III,

Table 2. Equations expressing the relationship between number of species (N) and size of catchment area in km² (A) in the different regions.

Region		Equation	r	P
EPHEMEROPTERA				
I	Østlandet	$N = 0.939\ A^{0.420}$	0.82	<0.02
II	Sørlandet	$N = 0.926\ A^{0.217}$	0.46	>0.05
III	Vestlandet	$N = 0.742\ A^{0.372}$	0.79	<0.01
IV	Trøndelag	$N = 8.847\ A^{0.142}$	0.74	<0.01
V	Nordland	$N = 1.593\ A^{0.313}$	0.68	<0.01
VI	Troms - Finmark	$N = 0.829\ A^{0.423}$	0.76	<0.01
PLECOPTERA				
I	Østlandet	$N = 6.972\ A^{0.138}$	0.73	<0.05
II	Sørlandet	$N = 1.019\ A^{0.376}$	1.00	<0.001
III	Vestlandet	$N = 5.171\ A^{0.167}$	0.60	<0.05
IV	Trøndelag	$N = 5.581\ A^{0.157}$	0.77	<0.01
V	Nordland	$N = 4.192\ A^{0.201}$	0.73	<0.01
VI	Troms - Finnmark	$N = 4.441\ A^{0.190}$	0.72	<0.02

what include all areas south of latitude 68°N not supposed to be affacted by acidification, the following general equations were calculated:

Ephemeroptera:

$N = 1.815A^{0.323}$ $r = 0.67$ $p<0.001$ (8)

Plecoptera:

$N = 4.474A^{0.184}$ $r = 0.77$ $p<0.001$ (9)

The corresponding curves appear in Fig. 5. There were generally more species of Plecoptera than of Ephemeroptera in catchment areas <1000 km², and vice versa. However, the river systems of region IV where with one exception always richest in ephemeropteran species.

By back-calculating the number of species to those of catchment areas of unit size (N_u), any area can be compared with the others. Thus, the regional differences within the Ephemeroptera and the uniformity of the Plecoptera fauna are again demonstrated (Table 1). The highest values for Ephemeroptera, $N_u>3.0$, were found in catchment areas <600 km² in region IV and V. Region III is generally poor in Ephemeroptera, and the lowest N_u values approach the level of region II.

Based on the catchment areas selected for the general eqnations, the relationships between N_u and each of the parameters W, K, and T were found. Corresponding relationships for maximum pH were calculated from the data from all catchment areas in regions I—V (Table 4). All equations for Ephemeroptera fit a significance level of $p<0.05$ or better. For Plecoptera only the equation for pH <6.6 was significant. The corresponding curves are presented in Fig. 6. Plecopteran diversity was almost nnaffected by K and W. A temperature decline from 17 to 9°C seem to be of some, but not significant, influence. pH was a definite limiting factor of increasing effect below 6.6. Ephemeroptera were much more sensitive to environmental changes. The parameters could be ranked in the following order of increasing importance: K - W -T -pH. When K declined from 70 to 9 μScm^{-1}, N_u was reduced by 50%. A pH drop from 7.7

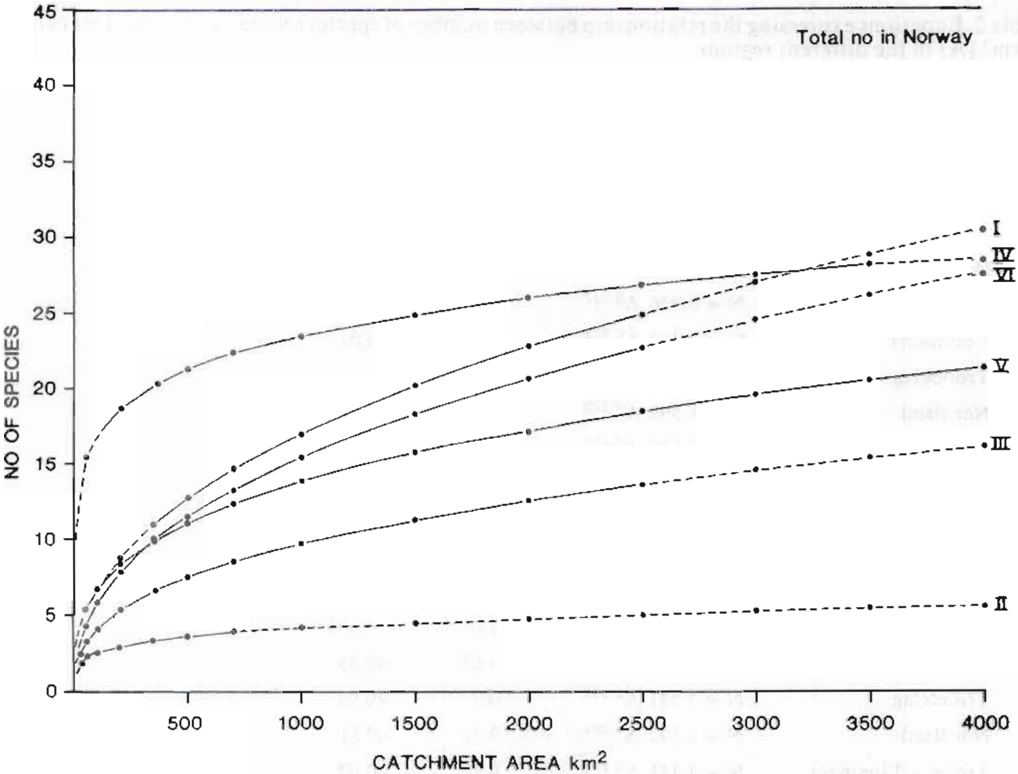

Fig. 4. The number of species of Ephemeroptera in relation to size of catchment area in the different regions, calculated from the equations of Table 2. Solid sections represent range of catchment area from which data exist.

Table 3. The number of species of Plecoptera in relation to size of catchment area in the different regions.

		Catchment area km²											
Region		50	100	200	500	700	1000	1500	2000	2500	3000	3500	4000
I	Østlandet	12.0	13.2	14.5	16.4	17.2	18.1	19.1	19.9	20.5	21.0	21.5	21.9
II	Sørlandet	4.4	5.8	7.5	10.6	12.0	13.7	15.9	17.8	19.2	20.7	21.9	23.1
III	Vestlandet	10.3	11.4	12.6	14.5	15.3	16.1	17.1	17.9	18.5	19.0	19.5	19.9
IV	Trøndelag	10.3	11.5	12.8	14.8	15.5	16.5	17.6	18.4	19.0	19.6	20.0	20.5
V	Nordland	9.2	10.6	12.2	14.6	15.8	16.8	18.3	19.4	20.3	21.0	21.7	22.3
VI	Troms-Finnmark	9.3	10.7	12.2	14.5	15.4	16.5	17.8	18.8	19.6	20.3	20.9	21.5

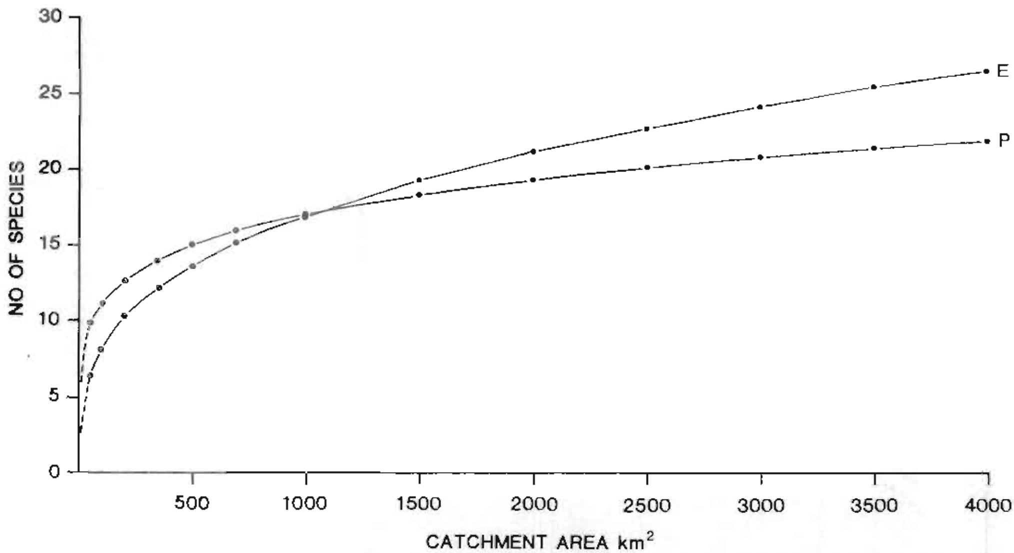

Fig. 5. The number of species of Ephemeroptera (E) and Plecoptera (P) in relation to size of catchment area calculated from the equations valid for Norway in general (8 and 9). Solid sections represent range of catchment from which data exist.

Table 4. Equations expressing the relationships between number of species back-calculated to catchment areas of unit size (N_u) and the following prarameters: mean range of specific conductivity (K), the percentage of catchment area representing woodland (W), maximum water temperature in °C (T), and maximum pH, when all water quality data represent lotic stations. The equation for pH is based on the results from all catchment areas in the regions I—V, the others on all catchment areas in the regions I, IV and V and areas no. 20—23 in region III.

	Equation	r	P
EPHEMEROPTERA			
	$N_u = 0.795\ K^{0.256}$	0.37	<0.05
	$N_u = 0.414\ W^{0.429}$	0.72	<0.001
	$N_u = 0.069\ T^{1.221}$	0.51	<0.01
	$N_u = 5.74\ 10^{-4}\ pH^{4.101}$	0.69	<0.001
PLECOPTERA			
	$N_u = 4.343\ K^{0.028}$	0.09	>0.05
	$N_u = 4.012\ W^{0.049}$	0.19	>0.05
$T \leq 15$	$N_u = 2.164\ T^{0.292}$	0.22	>0.05
$T > 15$	$N_u = 6.543\ T^{-0.094}$	0.06	>0.05
$pH < 6.6$	$N_u = 0.284\ pH^{1.505}$	0.53	<0.05
$pH \geq 6.6$	$N_u = 8.923\ pH^{-0.314}$	-0.07	<0.05

to 5.1 reduced N_u by 80%. A pH of 5.1 seems to be close to the limit for Ephemeroptera, while it affected Plecoptera by reducing their species number by 35%.

For Ephemeroptera the expected number of species (N_e) may be calculated more precisly by correcting the general equation for the influence of the environmental parameters. $N_u{}^4$ as a function of K, W. T, and pH follows from the data of Table 4. Solving for N_u and combining with equation 8 gives:

$$N_e = 0.06K^{0.064}W^{0.107}T^{0.305}pH^{1.025}A^{0.323} \quad (10)$$

This is an adequate for equation pH >6.5. pH <6.5 becomes more limiting and the best approach is:

$$N_e = 5.740\ 10^{-4}pH^{4.101}A^{0.323} \quad (11)$$

The numbers of ephemeropteran species calculated in this way are presented in Table 1. They fit better with the recorded numbers than the values calculated from size of catchment area alone, especially for the cases of regions II and III. The model does not cope with the high records of small areas in region IV, as it limits N_u to a maximum of 2.60. Further it overestimates the species number in river systems in region III where pH >6.5.

For Plecoptera the general equation (9) is as good as any other when pH >6.6. For pH <6.6 the best approach is:

$$N_e = 0.284\ pH^{1.505}A^{0.184} \quad (12)$$

The expected species numbers of Plecoptera are generally in good agreement with the recorded ones.

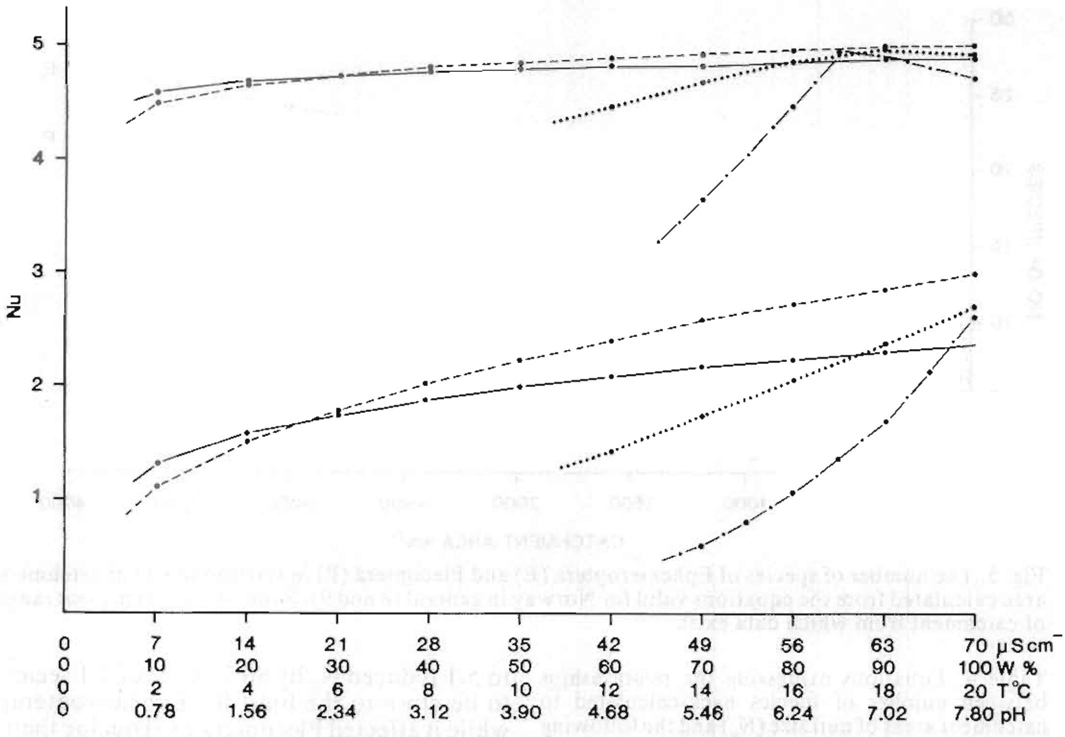

Fig. 6. The relationships between number of species in catchment areas of unit size (N_u) and mean range of specific conductivity (Scm^{-1} — solid lines), the percentage of catchment area covered with woodland (W — broken lines), maximum water temperature (T °C — dotted lines), and maximum pH (mixed lines) for Ephemeroptera above and Plecoptera below.

Expected numbers of ephemeropteran species disregarding the effect of pH were calculated from:

$$N_e = 0.283K^{0.085}W^{0.143}T^{0.407}A^{0.323} \qquad (13)$$

Curves showing such numbers are presented in Fig. 7 for selected cases. For river systems of region V, limited by K <22 μScm^{-1} and in that way comparable to those of the regions II and III, the expected numbers fell just above the recorded ones. The expected numbers of region III are higher than of region V, but the recorded ones lower, and relatively lowest in river systems of pH <6.5. The deviation between expected and recorded nnmbers increased with declining pH. The expected numbers in regiou II are even higher thau in region I, but the slope of the curve is uncertain as it is based on only three cases. However, with reference to the environmental characteristics with the exception of pH, the deversity of the original ephemeropteran fauna of region II could have been close to that of region I.

According to the basic data 6 species of Ephemeroptera were fonnd in region II: *Caenis horaria* (L.), *Leptophlebia marginata* (L.), *L. vespertina* (L.), *Siphlonurus lacustris* Eaton, *Baetis rhodani* (Pictet), and *Heptagenia fuscogrisea* (Retzius). Of these *Leptophlebia* and *Siphlonurus* occurred most regularly. Of 14 species of Plecoptera, the following 6 were recorded in all three catchment areas: *Amphinemura borealis* Morton, *A. standfussi* Ris, *A. sulcicollis* Stephens, *Nemoura cinerea* (Retzius), *Nemurella picteti* Klapálek, and *Leuctra fusca* L. 6 species were fouud in two areas: *Diura nanseni* (Kempny), *Isoperla grammatica* (Poda), *Brachyptera risi* (Morton), *Taeniopteryx nebulosa* (L.), *Leuctra nigra* (Olivier), and *L. hippopus* Kempny. *Siphonoperla burmeisteri* (Pictet) and *Protonemura meyeri* Pictet occurred in one area each. The frequency of the species probably reflects their tolerance to acid water.

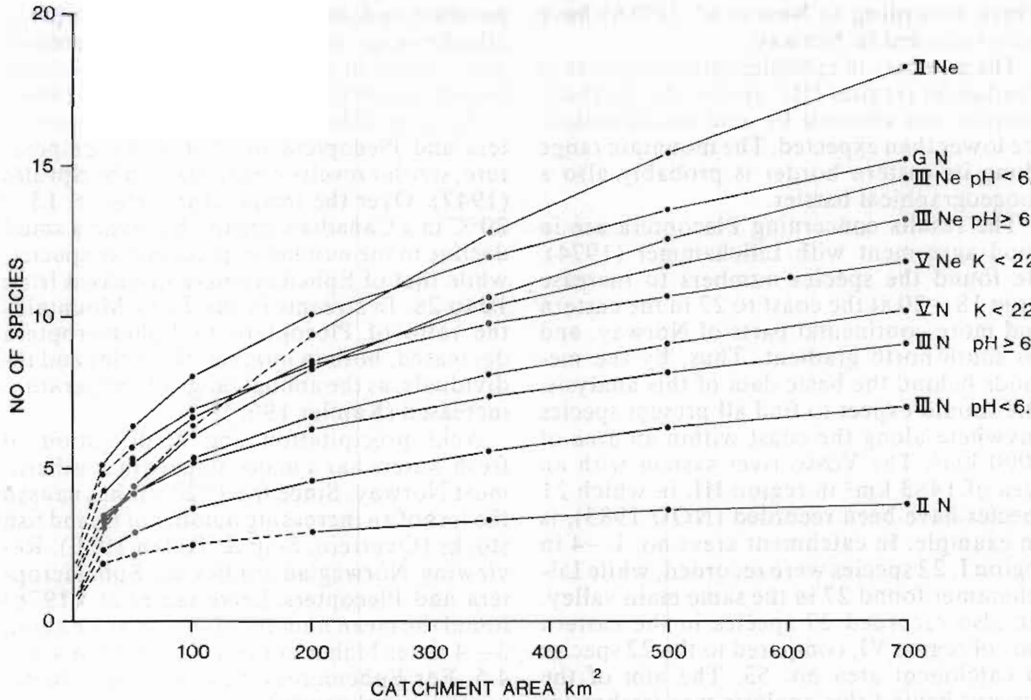

Fig. 7. Number of species of Ephemeroptera (N) based on records and expected numbers (N_e) from equation 13 disregarding pH, in relation to size of catchment area generally (G) and in region II, and for cases in regions III an V selected with references to maximum pH or mean specific conductivity (K). Solid sections represent range of catchment area from which data exist.

DISCUSSION

This analysis gives examples of how the general number of species to area equation (2), developed for terrestrial and especially island faunas, is also valid for freshwater faunas. According to MacArthur & Wilson (1967), the z value for Ephemeroptera (equation 8) is typical for island fauna and that for Plecoptera (equation 9) similar to values obtained for uon-isolated fauna. The difference between the two values is related to the following facts. The plecopterans are relatively insensitive to environmental qualities. Their species numbers are therefore mainly connected to the size of the area and are relatively high in small areas. The ephemeropterans respond more to ecological variation. Their species numbers in small areas are normally lower, but with increasing area and habitat variation they reach higher numbers than the plecopterans. It is discussed whether increase in size of area alone or increased habitat diversity is responible for the increase in species numbers (Gorman 1979). Evidently the species number of an euryoecious taxon like the Norwegian Plecoptera depends mainly on the size of the area, while the habitat diversity is of more importance for more stenoecious animals like the Norwegian Ephemeroptera.

The high numbers of species in the most northern part of Norway, north of latitude 68°N, may be surprising. However, the water quality is better than in the other regious. Waters along the extreme northern coast may be cold. In the more continental districts the temperature is no more limiting than in other parts of Norway, although the summer is short. The recorded species numbers of both Ephemeroptera and Plecoptera are in good agreement with the equations established for southern Norway. This probably holds for the freshwater fauna of the region in general. In the Alta river system Jensen (1985) found for example 34 of the 76 species of Cladocera which according to Nøst et al. (1986) have been recorded in Norway.

The numbers of ephemeropteran species in Vestlandet (region III), also in the northern districts not affected by acid precipitation, are lower than expected. The mountain range along its eastern border is probably also a zoogeographical barrier.

The results concerning Plecoptera are in good agreement with Lillehammer (1974). He found the species numbers to increase from 18—20 at the coast to 27 in the eastern and more continental parts of Norway, and no south-north gradient. Thus, by the methods behind the basic data of this analysis, one should expect to find all present species anywhere along the coast within an area of 4000 km². The Vosso river system with an area of 1483 km² in region III, in which 21 species have been recorded (NOU 1983), is an example. In catchment areas no. 1—4 in region I, 22 species were recorded, while Lillehammer found 27 in the same main valley. He also recorded 27 species in the eastern part of region VI, compared to the 22 species in catchment area no. 53. The aim of the surveys behind this analysis was freshwater invertebrates in general. They were performed by field workers of varying qualifications mainly visiting the localities twice, while the studies of Lillehammer represent those of an experienced specialist. Considering this, the results obtained are satisfactory.

Lillehammer (1985) subdivided region III into a coastal area and lowlands of the inner fjords, recording only 9 species of Plecoptera from the coastal area. In the Yndesdal river system of 120 km² located close to the west coast, Haaland & Raddum (1981) found 12 species, which is equivalent to $N_u = 5.0$ and above the number expressed by the general equation (9). Lillehammer may have sampled an area of inadequate size. According to this analysis, the only districts of Norway holding especially low numbers of plecopteran species are region II and the typical coastal areas of region VI.

The independance of Plecoptera in relation to environmental variation explain their regionally uniform diversity. This is only valid when complete or large sections of river systems are considered. Lillehammer (1974) found a sharp decline in species numbers from the sub-alpine to the middle-alpine zone, both in southern and northern Norway, which was mainly correlated to falling temperature and decreasing amounts of organic allochtonous material. Similar differences with regard to elevation have been found in British streams (Hynes 1961, Minshall 1968).

As to the differences between Ephemeroptera and Plecoptera in relation to temperature, similar results were obtained by Sprules (1947). Over the temperature interval 13—20°C in a Canadian stream, he found a small decline in the number of plecopteran species, while that of Ephemeroptera increased from 10 to 28. In streams in the Tatra Mountains the ratio of Plecoptera to Ephemeroptera decreased, both in number of species and individuals, as the annual range of temperature increased (Kamler 1965).

Acid precipitation and acidification of fresh waters has a major impact in southernmost Norway. Since the 1920's it has caused the loss of an increasing number of inland fish stocks (Overrein, Seip & Tollan 1980). Reviewing Norwegian studies on Ephemeroptera and Plecoptera Leivestad et al. (1976) found the mean number of species to be about 3—4 times higher at pH 6.5—7.0 than 4.0—4.5. For Ephemeroptera this is quite in accordance with the differences between expected and recorded numbers in a catchment area of 200 km² in region II. That this ratio increased to 6 for an area of 4000 km², means that the ephemeropteran fauna of the region is limited to a few species tolerant of acid water. According to Wiederholm (1984) and Økland & Økland (1986) Ephemeroptera are among the most sensitive to acidification. Engblom & Lingdell (1984) showed the number of species in Swedish streams where pH often falls below 5.0 to be only 1/4 to 1/3 of that found in more northern and unaffected streams. According to them, all species found in region II, except *Caenis horaris,* are among the 7 most acid resistant Scandinavia ephemeropterans, tolerating pH as low as 3.5—4.5. *C. horaria* was recorded at a minimum of 5.1 in region II, while Engblom & Lingdell present an experimental limit of 5.4 and an empirical of 5.6.

This analysis definitely demonstrates that plecopterans stand acid water better than the ephemeropterans. In experiments Raddum & Steigen (1981) found three of the species present in region II, *Taeniopteryx nebulosa, Nemoura cinerea,* and *Nemurella picteti,* to be unaffected by pH 4.6—4.7. In 26 watersheds in western Norway, Raddum & Fjellheim (1984) found Plecoptera to tolerate acid water better than Ephemeroptera. Of Ephemeroptera only *Leptophlebia* and *Siphlonurus* occurred at pH <5.0 compared to 12 species of Plecoptera. Comparing two streams 50 km apart in southernmost Sweden, Otto & Svensson (1983) recorded 11 species of Ephemeroptera and 12 of Plecoptera in the one with pH range 5.9—7.3 and none ephemeropteran and 9 of Plecoptera in the other with pH range 4.2—5.9.

The conclusion that the number of species of Ephemeroptera has been reduced by 75% and that of Plecoptera by 40—25% in catchment areas of 250—700 km² in Sørlandet, the southernmost part of Norway, is quite in agreement with what is known about the effects of acidification. So are the assumptions on the impact on the ephemeropteran fauna of Vestlandet.

This work present guidelines for the importance of size when selecting river systems for conservation purposes. In Norway areas <200 km² will in general hold only small numbers of ephemeropteran species. Increasing the area above 1000 km², however, involves only a small gain of plecopteran species and some ephemeropteran. It is further possible to evaluate the species richness of a certain area in any region of Norway. The results are probably also valid for the northern half of Sweden. In catchment areas of about 500 km² Engblom & Lingdell (1984) recorded 25 species of Ephemeroptera in streams east of region IV and 17 east of region V. However, acidification seems to have reach farther north in Sweden than in Norway. In catchment area no. 1 of 341 km², 15 species of Ephemeroptera were recorded and the expected number was 16. In Fulufjäll nature reserve, 80 km to the northeast and just across the border, Engblom & Lingdell found only 6 species, a situation similar to that of region II in southernmost Norway.

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