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Abundance of Philaenus spumarius in relation to types of plant community in the Tvärminne archipelago, southern Finland[1]

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Eight main types of plant community capable of supporting populations of the meadow spittlebug (*Philaenus spumarius* (L.), Homoptera), were distinguished on the islands of the Tvärminne archipelago, off the south coast of Finland. The area is subject to land upheaval amounting to about 42 cm in 100 years. The flora and vegetation of the island meadows develop through successive stages determined by edaphic, climatic and biotic factors which themselves are changed by land upheaval. The meadows are mostly very small. The secular succession of the vegetation is rendered irregular by yearly and longer-term fluctuations in climate. Changes in the vegetation affect the choice of food-plants available and so cause fluctuations in the size of the spittlebug populations. The amplitude of these fluctuations, depends on the type and constancy of the various plant communities.

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I. Introduction

The present study forms part of a series of investigations into the ecology and genetics of *Philaenus spumarius* (L.) (Homoptera). The work has been in progress since 1960 and has resulted in about 30 publications (see, e.g. HALKKA *et al.* 1967, 1970, 1971, 1974, 1975, 1976).

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[1]Report no. 540 from Tvärminne Zoological Station, University of Helsinki

The present paper concentrates on (1) those plant communities in which *Philaenus* lives and (2) on the abundance, fluctuations in populations size, and causes of mortality of *Philaenus* in such communities. Few studies have been made on plant communities in the tiny meadows, "miniature meadows" on the small rocky islands of the archipelago (HÄYRÉN 1914, LUTHER 1961). From 1898 to 1960, the flora and vegetation of the Tvärminne archipelago have changed considerably (LUTHER 1961). In view of this inconstancy of the plant communities, some of the miniature meadows described in previous papers were reanalysed. But the analysis is not intended primarily as a contribution to plant sociology. Emphasis has been placed on the factors, biotic and abiotic, determining the success of *Philaenus* populations.

II Study area

The study area comprises the part of the archipelago of the south coast of Finland that lies between 60°N in the north, 23°10'E in the west, and 23°40'E in the east. Most of the islands are included in nature conservation areas and belong either to the Tvärminne Zoological Station or to the Jussarö Strict Nature Reserve. When land and water are taken together, the area comprises about 200 km^2.

Philaenus spumarius was present on 101 of the 337 islands examined. The vegetation of the meadows was analysed in July 1971 on 56 islands, with altogether 110 meadows (Fig. 1). Many other meadows were investigated in all or some of the years 1969 - 1975, and notes were made on short-term changes in the development of the plant associations.

Tvärminne has an annual mean temperature of about +5.1°C, February averaging -6.0°C and July 16.2°C. Annual precipitation amounts to about 556 mm, about one-fourth of which falls in the form of snow. In early summer, droughts are frequent and may cause withering and death of many plants, or at least of their aerial shoots. The islands consist largely of bare rock, and the miniature meadows often entirely on rock pools and other accumulations of rain-water for their water supply. Spray from the sea (salinity about 0.6 %) is of little significance.

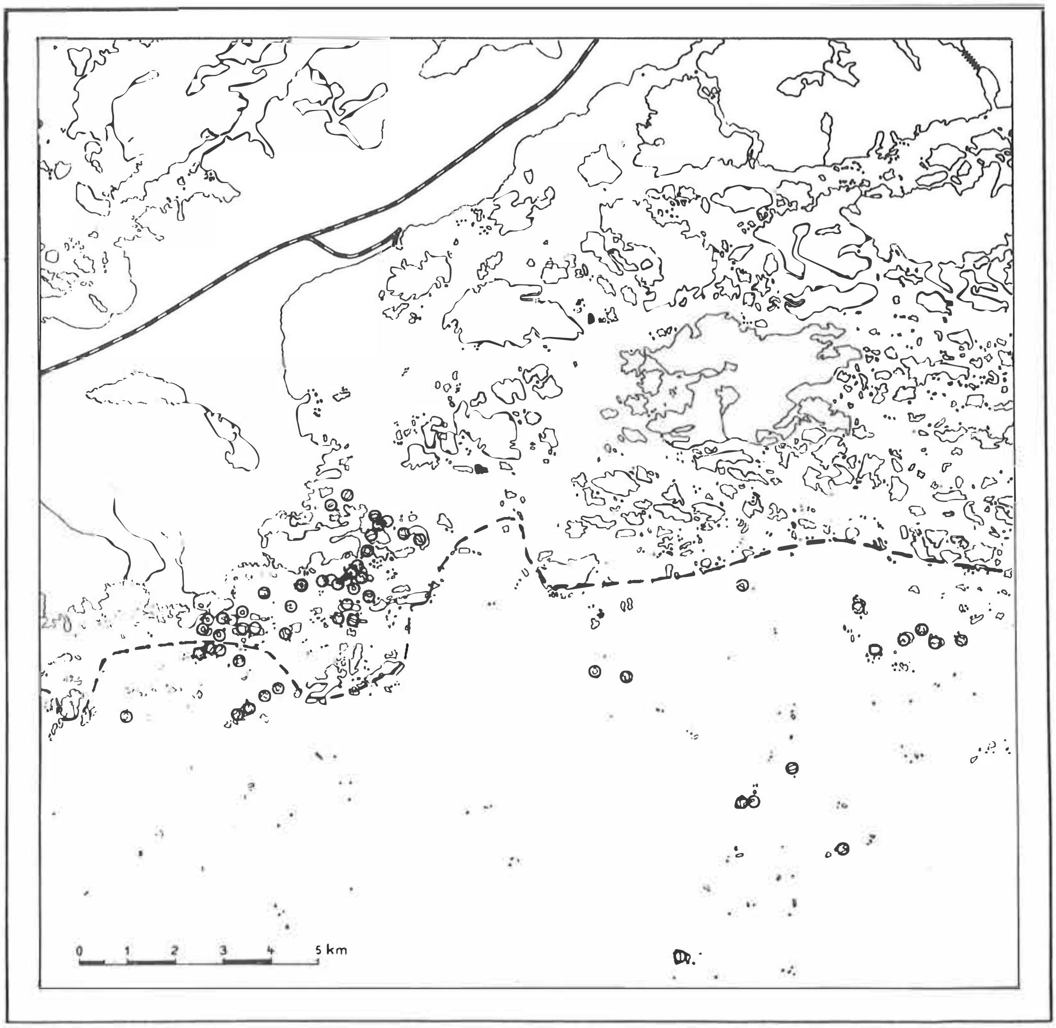

Fig. 1. The islands investigated. The borderline between outer archipelago zone and the sea zone, as determined by LUTHER (1961), is indicated by a broken line.

Tides are negligible in the Baltic, but variable air pressure and winds from varying directions cause the sea level to fluctuate with a maximal amplitude of about -80 cm and +110 cm from the mean level. The fluctuation is greatest in winter and smallest in summer, but only about 2 - 3 % of the changes exceed ± 50 cm (see STENIJ and HELA, 1947). The univoltine *Philaenus* overwinters in the egg, and so the species meets the greatest changes in water level at this stage of the life cycle.

The islands investigated are all rather small, many of them being less than 100 m in length. With few exceptions, they are less than 10 m high. Meadows cover only a small fraction of the surface, which consists predominantly of bare granite. The surface of the rock is often partly covered by lichens, algae and, occasionally, mosses.

The meadows most measure less than 10 m in maximal diameter and generally have sharp edges. Practically all the plant communities described in the present study exist in such very small meadows. As the soil on the rock is generally very shallow, these "miniature meadows" (cf. HALKKA *et al.*, 1970) or "mini-meadows" are as apt to dry out as large flowerpots.

III Methods

1. Analyses of vegetation

Each meadow complex inhabited by *Philaenus spumarius* was divided into communities and the communities which appeared to harbour constant *Philaenus* populations (subpopulations) were then examined in detail. The following features were measured, estimated or recorded:

1. Total area of the meadow complex.
2. Area of the community investigated.
3. Herbs in a 4 m^2 plot. Coverages of all the plant species were estimated on the following scale: +, 1, 2, 3, ... 10, 20, 30, ... 100 %. The most prevalent plants outside the plot were also recorded both from the community concerned and from the whole meadow complex. The community and the meadow complex were photographed. In the most important communities of meadows the sequence of changes was recorded by taking photographs with the same field of view every year from 1969 to 1975.

4. Height above sea level.
5. Lie of the ground: level, sloping, steeply sloping.
6. Aspect: N, E, S, W.
7. Exposure to winds: open, somewhat sheltered, well protected.
8. Thickness of soil and litter sediment.
9. Coverage of stones, %.
10. Coverage of drift material, %.
11. Coverage of moss stands, %.
12. Wetness of soil and litter: dry, medium, wet.
13. Bird density: low, moderate, high.
14. Density of vole burrows: low, moderate, high.
15. From a 0.6 litre sample of soil:
    a) type
    b) pH
    c) specific conductivity 10 x millimho/cm (S/m)
    d) Ca (mg/l)
    e) K
    f) P
    g) Mg.

    The soil samples were investigated in the Soil Research Laboratory of the Agricultural Research Centre (Tikkurila). The sample was dried at 45°C in the 0.6 l cardboard box in which it was placed in the field. For determining pH and specific conductivity, 2.5 times the volume of water was added to the soil sample. The contents of exchangeable Ca, K and Mg and the readity soluble P were measured from samples of the filtrate of a 1:10 mixture of soil: ammonium acetate (pH 4.65) with a flame photometer (Ca and K), a colorimeter (P) and an atomic absorption spectrophotometer (Mg) (see VUORINEN and MÄKITIE 1955, KURKI *et al.* 1965).

For describing the plant associations, the index of species association (IA) (see MUELLER-DOMBOIS and ELLENBERG 1974, p. 229) and the coefficient of correlation (r) between the species were determined from coverage estimates. Constancy (C) was calculated as C = 100 B/N, where B is the number of plots in which the species in question was found, and N the total number of plots. Dominance (D) was calculated as $D = \sum A/N$, where A is the coverage of a given species in a plot and N the number of plots in which the species was found. Autecological analysis was made by regression analysis (DRAPER and SMITH 1966) and least squares analysis (HARVEY 1966).

Diversity was determined from coverages by SHANNON's index of general diversity formula $-\sum P_i \ln P_i$.

2. Analysis of Philaenus populations

The sizes of the *Philaenus spumarius* populations were determined by the miniature cage method (see HALKKA *et al.* 1967, 1970). At first, we tried to isolate all the nymphs at the 4th or 5th instar. But as this method is tedious, it was used on only 32 plant stands. Each meadow was visited at least three times, and we tried to find all the spittle masses every time. As the third search usually added well below 10 % of the total number of masses, the method may be considered semiquantitative. This means that, taking the year 1969 as the first generation, fluctuations in number were followed with a high degree of precision for seven successive generations.

Isolation of nymphs in small cages without doubt increases net nymph mortality. If the food-plant begins to wither, the nymph is unable to migrate to a fresh plant. But even uncaged nymphs often die on plants that are withering, and in fact many of the nymphs isolated during drought periods were already moribund. Moreover, during droughts nymphs often die during vain attempts to find a fresh plant. For these reasons, the miniature cage method probably gives a fairly realistic picture of variability of nymph mortality in different generations (years). In the populations investigated, drought was the chief cause of nymph mortality.

The inter-year variation in population size (C) was calculated from the formula $C = 100\ s/\bar{x}$, where s = standard deviation and $\bar{x}$ mean

In addition to the miniature cage method, two less accurate methods were used for estimating population size: sweep net sampling and single counts of the total number of the spittle masses. In sweep net sampling, work was usually continued to the point at which 50 sweeps produced fewer than 10 individuals. The use of this same criterion in successive years may give a rough estimate of variability in population size.

IV Results

1. The plant species and the variability in their abundance

Together, the 110 miniature meadows investigated had a flora comprising 144 herbaceous species. Tables 1 and 2 list some data on the autecology of the common species. The nomenclature used in these Tables and elsewhere in this study follows EHRENDORFER (1973) with some minor exceptions. The plants have been determined at species level, with the exception of *Agrostis canina*, *Poa pratensis* and *Rumex acetosella*, all of which were recorded at the *s.lat.* level. Many of the species are represented exclusively or mainly by seashore ecotypes, the commonest of these being *Plantago major*, *Potentilla anserina*, *Sonchus arvensis* and *Tripleurospermum maritimum*.

For a long time after an island emerges from the sea it remains entirely within the reach of wave action and so no soil collects on the surface of the rock. In the outer archipelago, the splash zone on exposed shores may be several metres high. In protected coves and in fissures and depressions above the splash zone, gravel and sand may accumulate. The first plants on an emerging island are usually found in crevices, for these hold soil formed from various drift materials (HÄYRÉN 1931). The first species able to gain a foothold on a new island are *Puccinellia capillaris, Festuca rubra, Allium schoenoprasum, Tripleurospermum maritimum* and *Sedum acre.* (see LUTHER 1961). In addition to crevices, rock pools gather windborne materials along their rims and so accumulate organic debris that forms another nucleus for the development of vascular plant stands.

Decaying plants, animal debris, and heaps of organic and inorganic drift together form a substrate for plant communities large enough to be called "miniature meadows". The species composition of such meadows depends largely on the ratio of mineral soil to humus. This ratio is highest in the shore meadows and lowest in the bogs formed on the site of former rock pools.

Grouped according to the type of soil, the common species in the archipelago fall into three groups:

1. Plants on mineral soil: *Tanacetum vulgare, Rumex crispus, Sedum telephium* and *Vicia cracca.*

2. Plants on both mineral and organic soil: *Filipendula ulmaria* and *Solidago virgaurea.*

3. Plant on organic soil: *Carex canescens, Peucedanum palustre* and *Potentilla palustris.*

With little relation to its other qualities, the water content of the soil is highly variable both spacially and temporally. Early summer is generally the period when the water content of the soil is lowest. On the basis of soil moisture, the plants can be grouped as follows:

1. Species of dry ground: *Allium schoenoprasum, Rubus idaeus, Rumex acetosella, Sedum acre, Sedum telephium* and *Solidago virgaurea.*

2. Indifferent species: *Achillea millefolium* and *Epilobium angustifolium.*

3. Species of wet ground: *Carex canescens, Cornus suecica, Epilobium palustre, Peucedanum palustre* and *Potentilla palustris.*

Some of the plants are sensitive to drought, and often all that survives is the parts buried deep in the soil. These plants

Table 1. The common plant species of the island meadows. For each species, the following data are given: soil pH, specific conductivity, Ca, K, P and Mg content.

		pH			Specific conductivity 10xmmho/cm, 20°C			Ca mg/l			K mg/l			P mg/l			Mg mg/l		
	n	$\bar{x}$	min.	max.	$\bar{x}$	min.	max.	$\bar{x}$	min.	max.	$\bar{x}$	min.	max.	$\bar{x}$	min.	max.	$\bar{x}$	min.	max.
Achillea millefolium	18	5.9	5.0	6.3	3.5	1.1	8.7	1 028	525	1 750	179	50	420	10	3	24	634	155	1 390
Agrostis stolonifera	37	5.7	4.4	7.1	6.2	1.1	24.3	2 923	350	63 000	161	50	420	18	3	129	643	100	1 430
Agrostis tenuis	32	5.5	4.3	6.4	3.8	1.1	24.3	948	350	1 775	175	70	310	12	2	44	548	97	1 430
Allium schoenoprasum	18	5.4	4.3	6.3	2.0	1.1	3.7	1 208	525	5 250	156	85	290	46	3	580	400	97	1 170
Alnus glutinosa	19	5.5	4.4	6.3	4.7	1.6	13.1	979	350	2 400	165	70	350	7	2	17	628	178	1 700
Angelica archangelica	29	5.9	5.2	6.8	5.2	1.0	15.5	1 538	350	9 400	194	80	420	17	2	129	809	213	1 900
Angelica sylvestris	32	5.9	4.7	6.8	3.9	1.0	14.8	1 269	350	9 400	171	70	420	13	2	129	610	175	1 390
Avenella flexuosa	12	5.1	4.4	6.4	1.7	1.1	3.5	752	350	1 400	122	85	190	16	3	102	270	97	511
Barbarea stricta	7	6.0	5.5	6.3	3.1	1.4	7.1	1 593	675	3 700	184	95	310	22	9	56	827	240	1 900
Carex canescens	10	4.9	4.4	5.9	2.4	1.1	4.4	800	275	2 150	99	30	220	11	2	36	303	100	608
Carex nigra	33	5.4	4.4	6.4	3.5	1.1	12.0	917	275	3 350	162	30	300	14	2	102	532	137	1 700
Cornus suecica	11	5.1	4.7	6.2	3.0	1.1	12.0	584	275	1 075	136	30	290	17	2	102	348	137	624
Epilobium angustifolium	7	5.5	4.8	6.3	3.4	0.9	7.1	1 375	150	3 700	201	55	420	19	5	56	725	72	1 900
Epilobium palustre	7	5.2	4.7	5.9	3.5	1.8	8.3	900	525	1 600	97	50	195	27	7	102	496	155	1 170
Festuca arundinacea	7	5.8	5.0	6.6	8.0	3.1	15.5	1 157	550	1 975	156	75	260	10	6	15	740	377	1 710
Festuca rubra	67	5.6	4.3	6.8	4.4	1.1	24.3	1 234	350	9 400	168	55	420	24	2	580	594	97	1 900
Filipendula ulmaria	43	5.7	4.6	6.6	4.4	1.1	15.5	1 051	350	2 400	180	80	420	9	2	24	702	209	1 710
Galeopsis bifida	7	5.5	4.7	6.2	2.3	1.7	3.4	1 221	700	1 800	121	80	195	39	12	102	480	135	961
Galium palustre	41	5.7	4.7	6.8	5.3	1.1	23.5	1 329	400	9 400	177	55	420	18	2	129	704	235	1 700
Hypericum perforatum	7	5.7	5.0	6.1	2.0	1.1	3.4	968	700	1 300	140	70	250	10	3	27	488	190	961
Juncus gerardii	11	6.1	5.2	7.1	10.0	1.9	23.9	6 407	450	63 000	164	75	260	13	4	46	563	220	1 210
Leontodon autumnalis	17	6.1	5.3	6.7	6.6	1.2	24.3	1 071	350	1 775	192	85	380	13	3	44	707	209	1 430
Lysimachia vulgaris	43	5.6	4.4	6.8	4.3	1.1	14.8	1 006	350	2 400	165	55	300	9	2	24	638	178	1 810
Lythrum salicaria	39	5.5	4.4	6.8	4.1	1.1	23.5	1 287	350	9 400	152	55	300	20	2	129	610	100	1 810

	n	pH $\bar{x}$	min.	max.	Specific conductivity 10xmmho/cm, 20°C $\bar{x}$	min.	max.	Ca mg/l $\bar{x}$	min.	max.	K mg/l $\bar{x}$	min.	max.	P mg/l $\bar{x}$	min.	max.	Mg mg/l $\bar{x}$	min.	max.
Ophioglossum vulgatum	8	5.8	5.2	6.2	6.4	1.0	14.8	1 047	600	1 575	185	80	250	7	3	14	793	213	1 210
Peucedanum palustre	15	5.0	4.4	5.9	3.2	1.2	11.4	713	275	1 600	132	30	290	18	2	102	373	137	1 170
Phalaris arundinacea	41	5.7	4.4	6.8	4.3	0.9	15.5	1 048	150	3 350	162	55	420	11	2	56	612	72	1 710
Plantago major	22	6.1	5.2	7.1	8.8	1.1	24.3	3 914	350	63 000	192	70	380	14	3	46	782	190	1 430
Plantago maritima	10	6.1	5.7	7.1	13.4	2.9	24.3	7 220	550	63 000	230	90	380	16	4	46	793	377	1 430
Poa pratensis	16	5.8	4.7	6.4	3.5	1.1	5.8	1 250	400	3 350	182	80	300	16	2	56	733	211	1 700
Potentilla anserina	19	6.2	5.7	7.1	8.1	1.0	24.3	1 459	450	63 000	188	70	380	12	2	46	699	190	1 430
Potentilla palustris	14	5.0	4.4	5.5	2.7	1.1	8.3	679	275	1 475	89	30	220	9	2	18	288	100	593
Rhinanthus minor	8	5.7	4.6	6.8	2.7	1.2	5.7	1 840	350	9 400	133	75	175	25	5	129	464	178	985
Rubus idaeus	23	5.5	4.4	6.7	2.8	0.9	15.5	1 046	150	2 400	147	55	350	11	3	33	540	72	1 710
Rumex acetosa	18	5.5	4.7	6.3	2.7	1.1	8.7	914	350	1 800	166	55	290	20	3	102	485	177	1 210
Rumex acetosella	10	5.0	4.3	6.8	1.6	1.1	2.5	845	450	1 325	112	55	190	13	4	24	255	97	412
Rumex crispus	25	6.0	5.0	6.8	3.9	1.2	10.5	1 665	350	9 400	152	70	300	24	6	129	662	175	1 700
Sagina procumbens	16	5.7	4.8	6.8	4.8	1.6	13.1	1 533	350	9 400	152	75	420	19	3	129	618	253	1 370
Scutellaria galericulata	17	5.7	4.6	6.8	4.4	1.9	15.5	1 788	500	9 400	148	55	300	22	5	129	799	178	1 810
Sedum acre	22	5.8	4.3	6.8	3.2	1.1	12.6	1 369	350	9 400	172	80	380	19	6	129	507	97	1 510
Sedum telephium	20	5.8	4.6	6.4	3.2	1.0	14.8	1 153	350	5 250	167	80	350	38	3	580	532	177	1 510
Silene vulgaris	7	5.9	5.4	6.3	3.0	1.4	7.1	1 750	925	3 700	194	125	310	33	8	86	924	385	1 900
Solidago virgaurea	23	5.3	4.3	6.3	1.8	1.0	3.4	947	500	2 050	144	55	350	17	3	86	372	97	1 510
Sonchus arvensis	26	6.1	5.2	7.1	8.1	1.0	24.3	3 434	350	63 000	193	70	380	13	3	46	729	190	1 430
Sorbus aucuparia	8	5.6	4.6	6.3	4.2	1.3	12.6	831	500	1 275	175	80	380	8	3	14	497	178	1 200
Stellaria graminea	15	5.7	4.6	6.4	2.7	1.2	9.6	1 017	600	1 600	164	80	290	14	4	26	569	210	1 210
Tanacetum vulgare	40	5.8	4.7	6.8	2.7	1.0	12.6	1 259	350	5 250	186	70	380	31	3	580	648	190	1 900
Taraxacum spp.	10	6.2	5.7	6.8	5.0	1.0	24.3	1 930	475	9 400	172	50	310	29	5	129	659	175	1 430
Trifolium repens	6	5.8	5.2	6.3	5.1	1.1	9.5	867	525	1 175	145	80	260	10	6	15	478	301	686
Tripleurospermum maritimum	29	5.6	4.3	7.1	5.5	1.1	24.3	3 653	475	63 000	152	75	310	27	3	129	643	97	1 700
Valeriana salina	34	5.9	5.2	6.6	3.8	1.0	14.8	1 138	350	3 700	190	70	420	12	2	56	723	190	1 900
Veronica longifolia	44	5.8	4.6	6.4	2.8	1.0	8.7	1 203	350	5 250	187	70	420	26	3	580	661	177	1 810
Vicia cracca	40	5.9	4.7	6.8	4.3	1.0	24.3	1 306	350	9 400	175	70	380	16	2	129	652	177	1 700

Table 2. Stepwise regression and least-squares analysis of the effects of some independent variables on the percent biomass of a species. – ^{x} = $P < 0.05$, ^{xx} = $P < 0.01$, ^{xxx} = $P < 0.001$.

	r	T	R^2 %
Achillea millefolium			
Vascular plant species per meadow	.816	3.56^{xxx}	66.7
Agrostis stolonifera			
Vole burrows	.281	3.03^{xx}	7.9
Agrostis tenuis			
Vascular plant species/4 m^2	.570	6.94^{xxx}	32.5
Coverage of vascular plants	.241	2.12^{x}	5.8
Total explanation			35.2
Allium schoenoprasum			
P	.934	31.58^{xxx}	87.4
Ca	.357	-7.31^{xxx}	12.8
Total explanation			91.6
Alnus glutinosa			
Soil humidity	.220	2.33^{x}	4.8
Angelica archangelica			
Vascular plant species/4 m^2	.724	10.81^{xxx}	52.5
Height of meadow above sea level	-.222	-2.33^{xx}	4.9
Total explanation			54.8
Angelica sylvestris			
pH	.259	1.97^{x}	6.7
Vascular plant species per meadow	.325	2.91^{x}	10.5
Total explanation			91.6
Avenella flexuosa			
Coverage of vascular plants	-.256	-3.66^{xxx}	6.6
pH	-.230	-3.87	5.3
Total explanation			35.2
Carex canescens			
Coverage of mosses	.319	2.47^{x}	10.2
pH	-.302	-2.20^{x}	9.2
Total explanation			14.1
Carex nigra			
Soil humidity	2.48	3.52^{xxx}	8.1
Height of meadow above sea level	.216	2.86^{xx}	4.7
Total explanation			14.7
Cornus suecica			
Maximal height of island above sea level	.337	4.14^{xxx}	11.4
pH	-.225	-2.99^{xx}	5.1
Total explanation			18.3
Epilobium angustifolium			
Area of meadow	.395	4.46^{xxx}	15.7

	r	T	R^2 %
Festuca rubra			
Area of island	-.270	-2.90^{xx}	7.3
Filipendula ulmaria			
Coverage of vascular plants	.303	3.57^{xx}	9.2
Height of meadow above sea level	-.261	-3.51^{xx}	6.8
Protectedness of meadow	.273	2.82^{xx}	7.5
Total explanation			23.7
Galium palustre			
Coverage of plants	.359	2.85^{xx}	12.9
Soil humidity	.325	2.27^{x}	10.6
Total explanation			16.9
Leontodon autumnalis			
Specific conductivity of soil	.389	3.97^{xxx}	15.2
pH	.290	2.97^{xx}	8.4
Protectedness of meadow	-.248	-2.93^{xx}	6.2
Total explanation			26.6
Lysimachia vulgaris			
Regression variables:			
Vascular plant species per meadow	.510	6.19^{xxx}	26.0
Amount of drift materials	.255	3.81^{xxx}	6.5
Coverage of vascular plants	.189	3.08^{xx}	3.6
Total explanation			37.1
Class variable		F	
Aspect faced by meadow		4.05^{x}	8.6
Total explanation			45.7
Lythrum salicaria			
Slope of meadow	-.235	-2.15^{x}	5.5
Height of meadow above sea level	.191	2.64^{xx}	3.7
Soil humidity	.210	2.36^{x}	4.4
Vole burrows	.221	2.07^{x}	4.9
Total explanation			18.1
Peucedanum palustre			
Coverage of mosses	.292	2.35^{x}	8.5
Soil humidity	.282	3.32^{xx}	8.0
Height of meadow above sea level	.214	2.01^{x}	4.6
Total explanation			18.8
Plantago major			
Specific conductivity of soil	.480	5.52^{xxx}	23.1
Vole burrows	.254	2.49^{x}	6.5
Total explanation			27.4
Plantago maritima			
Specific conductivity of soil	.550	6.11^{xxx}	30.3
Protectedness of meadow	-.188	-1.97^{x}	3.5
K	.306	2.27^{x}	9.4
Total explanation			38.0
Potentilla anserina			
Specific conductivity of soil	.507	6.09^{xxx}	25.7
Tanacetum vulgare			
Soil humidity	-.364	-4.05^{xxx}	13.3

	r	T	R^2 %
Philaenus spumarius			
Filipendula ulmaria	.526	6.87^{xxx}	27.7
Galium palustre	.310	5.14^{xxx}	9.6
Lysimachia vulgaris	.269	3.73^{xxx}	7.3
Epilobium angustifolium	.201	2.92^{xx}	4.6
Total explanation			48.3

include *Allium schoenoprasum, Tripleurospermum maritimum, Rumex acetosa, R. acetosella, Solidago virgaurea* and *Filipendula ulmaria*. Some of these are important food plants of *Philaenus* and their fate is thus a significant factor in the variable mortality of the spittlebug.

The pH of the soil varies between 4.3 and 7.1 in the study area. On the basis of soil pH, the plant species may be grouped as follows:

1. Plants preferring a relatively low pH: *Avenella flexuosa, Carex canescens, Cornus suecica, Peucedanum palustre* and *Potentilla palustris*.

2. Indifferent species: *Festuca rubra, Lysimachia vulgaris, Lythrum salicaria* and *Tripleurospermum maritimum*.

3. Plants preferring a relatively high pH: *Angelica sylvestris, Leontodon autumnalis, Plantago major, Achillea millefolium, Angelica archangelica, Juncus gerardii, Plantago maritima, Potentilla anserina, Rumex crispus, Silene vulgaris, Sonchus arvensis* and *Valeriana salina*.

The specific conductivity of the soil ranges between 0.9 and 24.3 10 xmillimho/cm. The highest conductivity values are found in shore meadows with plenty of decayed *Fucus vesiculosus* and other drift material. On the basis of the specific conductivity (S/m) of the soil, the plant species may be grouped as follows:

1. Preferring low S/m: *Allium schoenoprasum, Avenella flexuosa, Carex canescens, Rumex acetosella* and *Solidago virgaurea*.

2. Indifferent to S/m: *Agrostis stolonifera, A. tenuis, Festuca rubra, Leontodon autumnalis, Taraxacum* spp., *Tripleurospermum maritimum* and *Vicia cracca*.

3. Preferring high S/m: *Plantago major, P. maritima, Potentilla anserina, Juncus gerardii* and *Sonchus arvensis*.

The species growing on soil of low specific conductivity usually live well above the splash zone on dry mineral soil or in peat bogs.

The species in the "high S/m" group usually live nearer the shore.

The Ca content of the soil varies between 150 and 63 000 mg/l. A high Ca content is typical of shore meadows with plenty of drift material, particularly heaps of bivalve shells or *Fucus*. On the basis of soil Ca, the plant species can be grouped as follows:

1. Low Ca: *Avenella flexuosa*, *Carex canescens*, *Cornus suecica*, *Peucedanum palustre* and *Potentilla palustris*.

2. Variable Ca: *Agrostis stolonifera*, *Plantago major* and *Sonchus arvensis*.

3. High but variable Ca: *Allium schoenoprasum*, *Silene vulgaris*, and *Barbarea stricta*.

In most of the bogs and meadows on dry mineral soil, the Ca content is low. In the meadows near the shore Ca values are higher, although very variable.

The potassium content of the soil varies between 30 and 420 mg/l. In many of the meadows, the K content is high, especially in shore meadows with plenty of drift heaps. On the basis of soil K the plants may be grouped as follows:

1. Low K: *Carex canescens*, *Epilobium palustre*, *Potentilla palustris* and *Rumex acetosella*.

2. Variable K: *Achillea millefolium*, *Agrostis stolonifera*, *Festuca rubra* and *Phalaris arundinacea*.

3. High K: *Angelica archangelica*, *Leontodon autumnalis*, *Plantago major*, *P. maritima*, *Silene vulgaris*, *Sonchus arvensis* and *Valeriana salina*.

Again, the K content was low in the bogs above the splash zone and high in the shore meadows, in particular in soil affected by heaps of *Fucus* or bivalve shells.

The phosphorus content of the soil varied between 2 and 580 mg/l, and was mostly much higher than in inland meadows. The P contents are highest in meadows with soil enriched by gull and waterfowl guano. On the basis of soil P, the plants can be grouped as follows:

1. Low P: *Alnus glutinosa*, *Filipendula ulmaria*, *Lysimachia vulgaris*, *Ophioglossum vulgatum*, *Potentilla palustris* and *Sorbus aucuparia*.

2. Variable, sometimes very high P: *Allium schoenoprasum, Tanacetum vulgare, Galeopsis bifida, Sedum telephium, Taraxacum* spp., *Tripleurospermum maritimum* and *Veronica longifolia.*

As expected, plants growing close to the nesting sites of gulls and other birds tended to be of this second group.

The magnesium content of the soil varies between 72 and 1900 mg/l. The values measured are higher than those for island meadows, and tend to be especially high in the drift zone with heaps of *Fucus* and other products of the sea. On the basis of soil Mg, the plants fall into the following groups:

1. Low Mg: *Avenella flexuosa, Carex canescens, Cornus suecica, Potentilla palustris* and *Rumex acetosella.*

2. Variable Mg: *Epilobium angustifolium, Festuca rubra, Lythrum salicaria, Rubus idaeus* and *Tripleurospermum maritimum.*

3. High Mg: *Angelica archangelica, Ophioglossum vulgatum, Plantago major, P. maritima, Scutellaria galericulata* and *Silene vulgaris.*

The coverages of the common plant species seem to correlate with height above sea level. For instance, the coverages of *Carex nigra, Lythrum salicaria* and *Peucedanum palustre* tend to be high in meadows well above the splash zone. On other hand, *Angelica archangelica* and *Filipendula ulmaria* seem to favour sites close to sea level.

Among biotic factors, the density of the residend bird populations greatly influences the composition of the plant associations. Birds eat parts of plants and enrich the soil with their excrements and pellets. The bird populations fluctuate in size from year to year, and may reach very high densities on some of the islands in some years. In 14 % of the meadows birds had strong effects on the vegetation, and in an additional 18 % they had minor effects. For example, high concentrations of excrement hampered the growth of some plants, whereas others were resistant. The latter group included *Allium schoenoprasum, Sedum acre, Tanacetum vulgare, Galeopsis bifida, Taraxacum* spp., *Tripleurospermum maritimum* and *Veronica longifolia.*

Periodically, small mammals, in particular voles, do noticeable damage to the vegetation. The field vole, *Microtus agrestis,* may reach densities high enough to set back succession in the plant communities. Subsequent recovery is slow. For example, in 1968 and 1969 field voles destroyed parts of some of the meadow complexes; in 1971, although the number of voles was greatly reduced, the impact on the vegetation was still strong in 11 % of all the plant stands investigated and a little less apparent in another 6 %.

In some of the islands only barren ground remained on the site of a previously densely vegetated minimeadow. The disappearance of most of the perennial plants left the site free for colonizing annuals. A good example of a succession starting after depredation by voles is afforded by the "B" meadow on Östra Mellanspiken (Table 3; see also HALKKA *et al.* 1975b).

Two physical factors, droughts and floods, are particularly harmful to parts of meadow complexes and may destroy them completely. Droughts were common in May and June during the latter part of the study period.

Floods occur in two forms: accumulation of rain water in depressions and flooding of shore meadows by an occasional rise in the sea level. After two stormy periods in January and November 1975 the water rose to about 110 cm above the mean level and parts of the meadows on Allgrundet and Östra Mellanspiken were completely destroyed. On the site of previously dense vegetation nothing remained but gravel.

2. Correlation between species. Grouping of species.

Correlations between species were calculated on the presence or absence principle, from the index of association (IA; Fig. 2). The coefficient of correlation, r, was calculated from the coverages of the different species (Fig. 3).

In delineating the communities, IA values are more useful than r, but r gives some valuable information not afforded by IA. Calculations of IA gave the following groups:

1. Open meadows in the geolittoral zone: *Juncus gerardii* and *Plantago maritima* (at lower levels); *Sonchus arvensis*, *Plantago major*, *Potentilla anserina* and *Leontodon autumnalis* (at slightly higher levels).

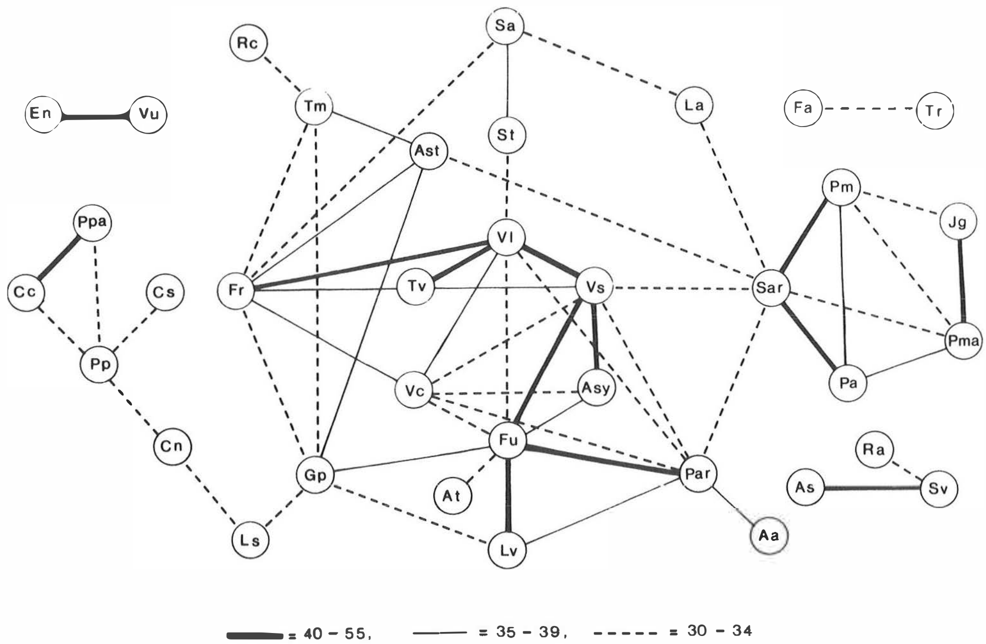

Fig. 2. The index of species association based on coexistence. Symbols: Aa = *Angelica archangelica* Af = *Avenella flexuosa*, Am = *Achillea millefolium*, As = *Allium schoenoprasum*, Ast = *Agrostis stolonifera*, Asy = *Angelica sylvestris*, At = *Agrostis tenuis*, Bs = *Barbarea stricta*, Cc = *Carex canescens*, Cn = *Carex nigra*, Cs = *Cornus suecica*, En = *Empetrum nigrum & E. hermaphroditum*, Ep = *Epilobium palustre*, Fa = *Festuca arundinacea*, Fr = *Festuca rubra*, Fu = *Filipendula ulmaria*, Gb = *Galeopsis bifida*, Gp = *Galium palustre*, Hp = *Hypericum perforatum*, Jg = *Juncus gerardii*, La = *Leontodon autumnalis*, Ls = *Lythrum salicaria*, Lv = *Lysimachia vulgaris*, Ov = *Ophioglossum vulgatum*, Par = *Phalaris arundinacea*, Pm = *Plantago major*, Pma = *Plantago maritima*, Pp = *Peucedanum palustre*, Ppa = *Potentilla palustris*, Ppr = *Poa pratensis*, Ra = *Rumex acetosella*, Rac = *Rumex acetosa*, Rc = *Rumex crispus*, Ri = *Rubus idaeus*, Rm = *Rhinanthus minor*, Sa = *Sedum acre*, Sar = *Sonchus arvensis*, Sg = *Scutellaria galericulata*, Sgr = *Stellaria graminea*, Sp = *Sagina procumbens*, St = *Sedum telephium*, Sv = *Solidago virgaurea*, Svu = *Silene vulgaris*, T = *Taraxacum* spp., Tm = *Tripleurospermum maritimum*, Tr = *Trifolium repens*, Tv = *Tanacetum vulgare*, Vu = *Vaccinium uliginosum*, Vc = *Vicia cracca*, Vl = *Veronica longifolia*, Vs = *Valeriana salina*.

2. Seashore rocks and crevices: *Solidago virgaurea*, *Allium schoenoprasum* and *Rumex acetosella*.

3. Ombrotrophic peat-moor bogs: *Vaccinium uliginosum*, *Empetrum nigrum* and *Empetrum hermaphroditum*.

Table 3. Succession of plant species in a meadow on Östra Mellanspiken destroyed by field voles (*Microtus agrestis*) in 1968 - 1969; the voles practically disappeared in 1969. Plot size 2 m x 2 m, coverages given as biomass percentages.

	1969	1971	1972	1973	1974	1975
Epilobium rubescens	2	1	-	-	-	-
Sagina procumbens	+	4	+	-	-	-
Rumex acetosella	-	+	+	-	-	-
Peucedanum palustre	-	+	1	-	-	-
Veronica longifolia	-	+	1	-	-	-
Galeopsis bifida	+	+	+	-	-	+
Tripleurospermum maritimum	+	5	2	-	-	+
Rumex crispus	+	+	+	-	+	1
Potentilla palustris	20	4	3	5	1	2
Galium palustre	+	10	10	3	1	1
Agrostis spp.	+	10	5	10	3	+
Filipendula ulmaria	4	5	10	30	30	20
Lythrum salicaria	+	9	20	20	20	60
Hierochloe odorata	+	1	20	20	40	6
Lycopus europaeus	+	6	15	30	50	30
Athyrium filix-femina	+	1	1	4	5	7
Festuca rubra	-	20	2	1	+	-
Scutellaria galericulata	-	4	5	2	1	+
Vicia cracca	-	2	10	5	2	2
Lysimachia vulgaris	-	+	+	+	3	3
Luzula multiflora	-	-	-	+	-	-
Trifolium repens	-	-	-	+	-	-
Stellaria graminea	-	-	-	+	-	+
Carex canescens	-	-	-	+	2	+
Typha latifolia	-	-	-	-	+	1
Poa trivialis	-	-	-	-	-	+
Juncus bufonius	-	-	-	-	-	+
Coverage %	30	80	95	99	100	100
Sum of partial coverages	31	86	106	131	154	135

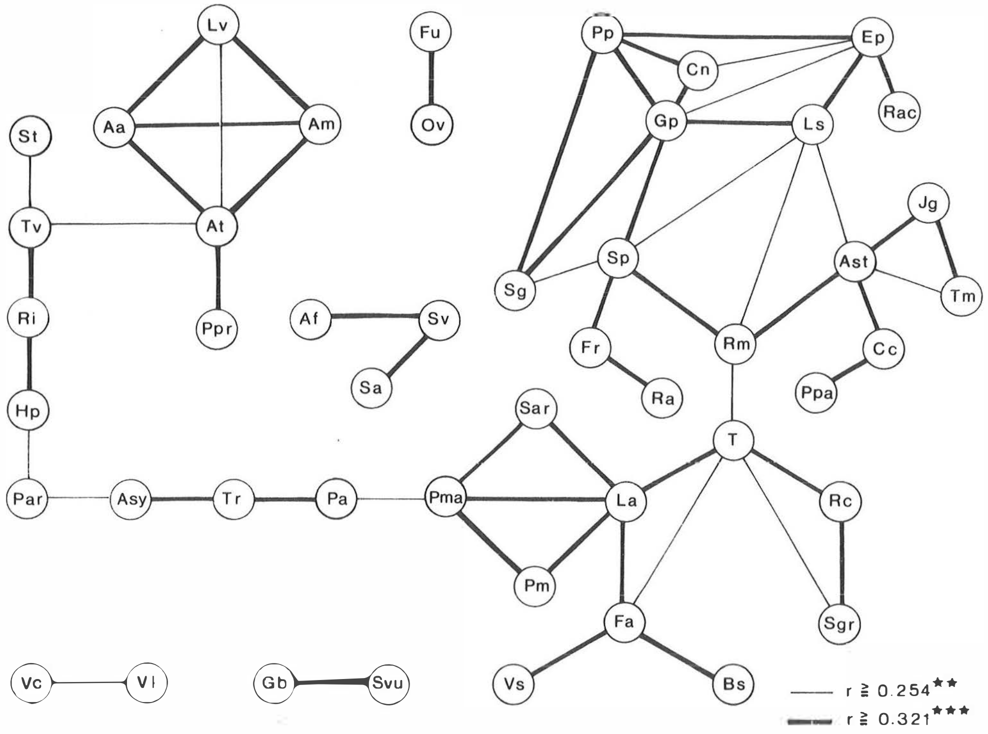

Fig. 3. Significant and highly significant correlation coefficients between coverages of plant species. Symbols as in Fig. 2.

4. Water bogs: *Carex canescens, Potentilla palustris,* often also *Peucedanum palustre, Carex nigra, Cornus suecica, Lythrum salicaria* and *Galium palustre.*

5. Shore meadows with a few alders and tall forbs and grasses: *Filipendula ulmaria, Lysimachia vulgaris* and *Phalaris arundinacea.*

6. Stone-strewn meadows with soil rich in minerals: *Veronica longifolia, Tanacetum vulgare, Festuca rubra* and *Valeriana salina,* often also *Vicia cracca, Sedum acre, S. telephium* and *Angelica sylvestris.*

7. Seaside meadows with soil rich in humus: *Rumex crispus, Tripleurospermum maritimum,* and *Agrostis stolonifera,* often also *Festuca rubra, Galium palustre* and *Vicia cracca.*

A comparison of the groupings indicated by IA and by r produced the following results:

1. The same groups occur in Figs. 2 (for IA) and 3 (for r), with the exception of the ombrotrophic peat-moor species group, which is present only in Fig. 2.

2. Some of the groups in Figs. 2 and 3 are identical. This is especially true of those in meadows that are periodically flooded, such as open meadows in the geolittoral zone and water bogs.

3. Certain of the species groups based on IA split up when tested by the coefficient of correlation method. These are communities in which several species are robust herbs. In such communities, interspecific competition may lead to greater variability. Examples of possibly competing species pairs include *Filipendula ulmaria* vs. *Lysimachia vulgaris* and *Empetrum* spp. vs. *Vaccinium uliginosum*. On the basis of coverages of such dominant plant species, the communities can be divided into smaller units. These units may differ from each other as food sources of *Philaenus*, especially if important food-plants are used in delimiting the units.

4. Certain groups based on r contain species not included in the corresponding groups based on IA. These additional species may be useful for dividing the associations into smaller units.

3. Plant communities

The 110 meadows investigated were grouped into plant communities of 8 types (Table 4). Some of these could be further divided into subtypes on the basis of differences in species composition or of the most dominant species.

1. *Juncus gerardii - Sonchus arvensis* meadows. Only the meadows from the higher part of the *J.gerardii* zone are of interest in this context, as *Philaenus* is absent or rare in the parts near the shore. The characteristic species are *Juncus gerardii, Sonchus arvensis, Plantago major, P. maritima, Potentilla anserina* and *Leontodon autumnalis*. The number of herbs averages 13 species/4 m^2 and diversity is moderate. Herb coverage is generally small, stones and drift material usually covering more than 40 % of the total area. Moss coverage is insignificant. Floods, ice, or

Table 4. Per cent constancy (C) and per cent biomass value (B) among community types (meadow types).

	Juncus gerardii – *Sonchus arvensis* (1)		*Festuca rubra* – *Rumex crispus* (2)		*Tanacetum vulgare* – *Veronica longifolia* (3)		*Filipendula ulmaria* – *Alnus glutinosa* (4)		*Allium schoenoprasum* – *Solidago virgaurea* (5)		*Cornus suecica* – *Peucedanum palustre* (6)		*Carex canescens* – *Potentilla palustris* (7)		*Empetrum* – *Vaccinium uliginosum* (8)	
	C	B	C	B	C	B	C	B	C	B	C	B	C	B	C	B
(1) *Plantago maritima*	82	2	-	-	3	+	-	-	-	-	-	-	-	-	-	-
Juncus gerardii	64	1	18	2	3	+	5	+	-	-	-	-	-	-	-	-
Sonchus arvensis	100	9	-	-	30	2	14	+	-	-	-	-	-	-	-	-
Leontodon autumnalis	55	1	18	+	20	+	5	+	-	-	-	-	-	-	-	-
Plantago major	82	7	27	+	18	1	14	+	-	-	-	-	-	-	-	-
Potentilla anserina	64	13	9	+	18	+	19	1	-	-	-	-	-	-	-	-
Glaux maritima	27	+	-	-	-	-	5	+	-	-	-	-	-	-	-	-
Triglochin maritimum	18	+	9	+	-	-	-	-	-	-	-	-	-	-	-	-
Achillea ptarmica	18	3	-	-	8	1	-	-	-	-	-	-	-	-	-	-
Trifolium repens	18	2	9	+	8	+	-	-	-	-	-	-	-	-	-	-
Angelica archangelica	45	6	27	1	35	1	29	3	-	-	-	-	-	-	-	-
Festuca arundinacea	27	+	-	-	5	1	10	+	-	-	-	-	20	1	-	-
Hieracium spp.	100	13	100	13	13	1	100	10	20	+	-	-	-	-	-	-
(2) *Rumex crispus*	18	+	73	2	20	+	14	+	10	+	29	+	20	+	-	-
Sagina procumbens	18	+	55	1	13	+	10	+	-	-	-	-	20	+	-	-
Centaurium littorale	9	+	27	+	-	-	-	-	-	-	-	-	-	-	-	-
Cochlearia danica	-	-	18	+	-	-	5	+	-	-	-	-	-	-	-	-
Elymus arenarius	-	-	9	+	5	+	-	-	-	-	-	-	-	-	-	-
Taraxacum spp.	9	+	36	+	10	+	5	+	-	-	-	-	-	-	-	-
Tripleurospermum maritimum	55	3	91	2	10	+	-	-	50	2	43	+	20	+	-	-
Festuca rubra	82	2	82	6	73	3	24	1	90	5	29	2	40	1	40	3
Vicia cracca	36	1	55	3	45	2	33	+	20	+	29	+	-	-	20	+
Poa pratensis	9	+	27	+	20	+	10	+	-	-	29	+	-	-	-	-
Galeopsis bifida	-	-	18	+	8	+	-	-	10	2	14	+	-	-	-	-
Scutellaria galericulata	9	+	36	1	13	+	19	+	-	-	14	+	40	+	-	-
Rhinanthus minor	-	-	27	+	5	+	5	+	-	-	14	+	20	+	-	-
Cerastium holosteoides	-	-	9	+	3	+	5	+	-	-	-	-	-	-	-	-
Cirsium vulgare	-	-	9	+	5	+	5	+	-	-	-	-	-	-	-	-
(3) *Veronica longifolia*	-	-	9	+	83	3	14	+	40	1	29	1	-	-	20	1
Valeriana salina	18	+	-	-	60	3	38	2	-	-	-	-	-	-	-	-
Tanacetum vulgare	9	+	9	+	78	12	10	+	30	4	29	+	-	-	-	-
Myrica gale	-	-	-	-	8	1	-	-	-	-	-	-	-	-	-	-
Hypericum perforatum	-	-	-	-	15	+	5	+	-	-	-	-	-	-	-	-
Anthriscus sylvestris	-	-	-	-	8	+	-	-	-	-	-	-	-	-	-	-
Barbarea stricta	-	-	-	-	15	+	-	-	-	-	14	+	-	-	-	-
Viola riviniana	9	+	-	-	10	+	-	-	-	-	-	-	-	-	-	-

	Juncus gerardii – Sonchus arvensis (1)		*Festuca rubra – Rumex crispus* (2)		*Tanacetum vulgare – Veronica longifolia* (3)		*Filipendula ulmaria – Alnus glutinosa* (4)		*Allium schoenoprasum – Solidago virgaurea* (5)		*Cornus suecica – Peucedanum palustre* (6)		*Carex canescens – Potentilla palustris* (7)		*Empetrum – Vaccinium uliginosum* (8)	
	C	B	C	B	C	B	C	B	C	B	C	B	C	B	C	B
Agrostis tenuis	27	3	9	1	38	3	29	3	30	1	14	+	–	–	40	–
Sedum telephium	18	+	–	–	38	+	5	+	20	+	–	–	–	–	–	–
Achillea millefolium	–	–	–	–	30	1	10	1	20	1	–	–	20	+	–	–
Silene vulgaris	–	–	9	+	10	+	5	+	10	1	–	–	–	–	–	–
(4) *Phalaris arundinacea*	36	1	18	1	48	1	62	2	10	+	14	1	–	–	–	–
Alnus glutinosa	18	6	–	–	15	3	48	14	–	–	–	–	20	6	–	–
Filipendula ulmaria	9	1	36	3	48	9	81	37	–	–	14	+	–	–	20	1
Lysimachia vulgaris	18	3	18	+	43	3	81	19	–	–	29	3	40	1	20	2
Ophioglossum vulgatum	9	+	–	–	8	+	19	+	–	–	–	–	–	–	–	–
Agropyron repens	–	–	–	–	–	–	14	+	–	–	–	–	–	–	–	–
Scophularia nodosa	–	–	–	–	5	+	10	+	–	–	–	–	–	–	–	–
Angelica sylvestris	18	1	27	1	43	1	48	2	–	–	–	–	–	–	–	–
Calamagrostis epigejos	9	+	–	–	5	+	14	+	–	–	–	–	–	–	–	–
(5) *Solidago virgaurea*	–	–	9	+	20	+	–	–	100	15	29	+	–	–	40	1
Allium schoenoprasum	–	–	18	+	13	1	10	+	80	1	14	+	–	–	20	+
Rumex acetosella	–	–	9	+	3	+	5	+	60	2	–	–	–	–	20	+
Sedum acre	27	+	9	+	30	+	–	–	60	1	–	–	–	–	–	–
Rubus idaeus	–	–	9	+	30	3	24	+	50	1	–	–	–	–	–	–
Avenella flexuosa	–	–	–	–	10	+	5	+	40	2	14	+	20	+	20	+
Rumex acetosa	–	–	–	–	30	+	5	+	30	2	29	7	–	–	–	–
Stellaria graminea	9	+	18	1	20	+	5	+	30	+	–	–	–	–	–	–
Crepis tectorum	–	–	18	+	3	+	–	–	20	+	–	–	–	–	–	–
(6) *Cornus suecica*	–	–	–	–	5	+	10	4	–	–	57	15	20	+	40	5
Peucedanum palustre	–	–	18	+	–	–	14	+	–	–	71	2	40	1	60	1
Galium palustre	55	1	64	8	28	+	43	1	10	+	86	6	20	+	–	–
Lythrum salicaria	27	1	100	20	13	+	33	1	10	+	100	21	40	1	60	1
Carex nigra	9	+	27	1	23	1	33	2	–	–	100	12	40	1	80	1
Fragaria vesca	–	–	–	–	8	+	5	+	–	–	14	+	–	–	–	–
Epilobium palustre	–	–	27	+	–	–	–	–	–	–	43	+	20	+	–	–
(7) *Potentilla palustris*	–	–	18	1	–	–	5	+	–	–	14	+	100	46	80	10
Carex canescens	–	–	9	+	–	–	–	–	–	–	14	+	80	2	80	1
Agrostis canina	–	–	–	–	–	–	5	+	10	2	–	–	20	+	–	–
Eriophorum angustifolium	–	–	–	–	–	–	–	–	–	–	14	+	40	+	20	+
Agrostis stolonifera	73	3	73	10	28	+	14	+	10	1	29	1	80	11	20	+
Sorbus aucuparia	18	+	–	–	13	+	–	–	–	–	–	–	20	+	–	–
Lycopus europaeus	–	–	18	3	–	–	5	+	–	–	–	–	20	1	–	–
(8) *Vaccinium uliginosum*	–	–	–	–	–	–	–	–	–	–	–	–	20	1	80	20
Empetrum nigrum	–	–	9	+	–	–	–	–	–	–	–	–	20	+	60	16
E. hermaphroditum	–	–	–	–	3	+	–	–	–	–	14	+	–	–	40	22
Rubus chamaemorus	–	–	–	–	–	–	–	–	–	–	–	–	20	+	40	1
Dryopteris carthusiana	–	–	–	–	–	–	5	+	–	–	14	+	–	–	20	+
Epilobium angustifolium	–	–	–	–	13	3	5	2	–	–	–	–	–	–	20	4
Juniperus communis	–	–	–	–	5	+	–	–	–	–	14	+	20	+	20	2
Number of sample areas	11		11		40		21		10		7		5		5	

dense vole populations sometimes cause considerable changes in total biomass. This meadow type has the highest values for specific conductivity and content of minerals (Ca, K and Mg). The soil is slightly acid. The high Ca content is partly caused by broken mussel shells.

Meadows of this type appear in the outer archipelago zone, mostly on islands rising to more than 8 m above sea level. The soil is generally rich in minerals and its humus content is increased by decaying *Fucus* and other algae washed ashore.

2. *Festuca rubra - Rumex crispus* meadows. These meadows are situated further from the shore than type 1 meadows. Consequently, some of them are splashed with sea water only during storms. The characteristic herbs include *Festuca rubra, Rumex crispus, Tripleurospermum maritimum, Vicia cracca, Agrostis stolonifera, Lythrum salicaria, Galium palustre* and *Sagina procumbens*. The number of herbs averages 13 species/4 m^2, and diversity is moderate. The coverage of stones and drift material is lower and that of herbs higher than in type 1. The coverage of mosses is low. Great changes in biomass are sometimes caused by voles. The soil is slightly acid, the K and Mg contents and the specific conductivity being clearly lower than in type 1. The contents of Ca and P are very high, especially the latter, which originates from bird excrements and pellets.

Meadows of this type are typically situated in the sea zone in depressions on rocky treeless islets about 5-6 m high. As the vegetation has a large underground biomass, the soil is rich in humus.

3. *Tanacetum vulgare - Veronica longifolia* meadows. These meadows are generally situated in the upper geolittoral or epi-littoral zone. The characteristic herbs include *Tanacetum vulgare, Veronica longifolia, Festuca rubra* and *Valeriana salina*. The number of herbs averages 13 species/4 m^2, and diversity is great. The high coverage of stones and/or drift material reduces the coverage of herbs to 57 %. The coverage of mosses is low, about the same as in meadows belonging to type 2. Voles cause only minor changes. The soil is mildly acid, specific conductivity being low, but the Ca, K and P contents high. Bivalve shells, remains of bird eggs, bird excrement, and decayed *Fucus* add to the quantity of Ca, K and P ions in the soil.

Type 3 is the commonest type of miniature meadow on rocky islands in the Tvärminne archipelago and is present both in the outer zone and in the sea zone. The *Tanacetum - Veronica* type is divisible into four subtypes. The (a) *Epilobium angustifolium - Rubus idaeus* subtype is not uncommon in the sea zone, particularly in the eastern part of the study area (the Jussarö archipelago). The other three subtypes, (b) *Sedum telephium - Agrostis tenuis*, (c) *Lysimachia vulgaris - Phalaris arundinacea - Angelica sylvestris* and (d) *Filipendula ulmaria - Agrostis stolonifera*, were all found in the outer archipelago zone, and (b) also in the sea zone.

4. *Filipendula ulmaria - Alnus glutinosa* community. The densest vegetation of this type consists in fact of small patches of the alder belt. These meadows are found in the upper geolittoral and epilittoral zones. The characteristic plant species include *Filipendula ulmaria*, *Alnus glutinosa*, *Lysimachia vulgaris*, *Phalaris arundinacea* and *Angelica sylvestris*. The number of vascular plants averages 14 species/4 m^2, and diversity is great. Owing to the tallness of the dominant herbs, the biomass of these meadows is large, despite in general moderate coverages of individual species. Annual variation in biomass is not great, although in some of the meadows the biomass of *Filipendula* and *Alnus* decreases drastically after prolonged droughts. The soil is slightly acid and enriched with nutrients originating from remains of *Fucus*, bivalve shells, etc. Ground water was found in some of the meadows.

The meadows of the *Filipendula - Alnus* type are situated in the outer archipelago zone, and occasionally in the sea zone in sites protected from heavy wind and wave action. In the sea zone the alder does not occur and in the outer archipelago zone it is often bushy. This rather common type is divisible into two subtypes, the *Filipendula ulmaria - Angelica sylvestris - Valeriana salina* subtype being commoner close to the open sea than the subtype characterized by the presence of *Lysimachia vulgaris*.

5. *Allium schoenoprasum - Solidago virgaurea* meadows. Meadows of this type are found in depressions and crevices in the rock a bit removed from the seashore. The characteristic herbs include

Allium schoenoprasum, Solidago virgaurea, Festuca rubra, Rumex acetosella, Sedum acre and *Tripleurospermum maritimum.* The number of herbs averages not more than 9 species/4 m^2, but even so diversity is moderate. The coverage of herbs is low and the coverage of mosses higher than in types 1-4. *Allium - Solidago* meadows are sensitive to drought, and for this reason the green biomass, if measured late in the summer, depends largely on whether the early summer was dry or wet. The specific conductivity is low, and so are the K and Mg contents. The soil is relatively rich in Ca and P, probably because many birds favour these meadows or their surroundings as nesting sites. There is no ground water.

Allium - Solidago meadows are found both in the zone of the outer islands and in the sea zone, on soils of varied humus or mineral content.

6. *Cornus suecica - Peucedanum palustre* meadows. This meadow type occurs above the geolittoral zone. The characteristic herbs are *Cornus suecica, Peucedanum palustre, Lythrum salicaria, Carex nigra* and *Galium palustre.* The number of herbs averages 11 species/4 m^2, and diversity is moderate. The coverage of herbs is large, that of mosses 19 %. Voles occasionally cause wide fluctuations of biomass in this meadow type. The specific conductivity is low, but the Ca, K, P and Mg contents are relatively high. The high consentration of ions is partly due to the frequent presence of dense bird populations. There is no ground water.

These meadows are all in the sea zone. The soil, 10-50 cm thick, consists of either peat or soil mixed with small amounts of gravel or sand.

7. *Carex canescens - Potentilla palustris* community. This bog-like community occurs above the geolittoral zone. The characteristic plant species include *Carex canescens, Potentilla palustris* and *Agrostis stolonifera.* The number of herbs averages only 10 species/4 m^2, and diversity is low. The coverage of herbs is high and the mean coverage of mosses as high as 39 %. The soil is distinctly acid and specific conductivity low. The Ca, K , Mg and P contents are low, but

clearly higher than in corresponding communities on the mainland far from the sea. The communities are periodically molested by voles. There is no ground water.

The communities occur both in the outer archipelago zone and in the sea zone on peat soil usually about 20-30 cm thick.

8. *Empetrum* spp. - *Vaccinium uliginosum* community. These communities are always situated well above the geolittoral zone. The characteristic herbs include *Empetrum hermaphroditum, E. nigrum, Vaccinium uliginosum, Potentilla palustris, Carex canescens* and *C. nigra*. The number of herbs averages only 10 species/4 m^2, and diversity is small. Both herbs and mosses have high coverages. The changes caused by voles in the biomass of these peat-moors are much larger than in wet pine peat-moors on the mainland. The soil is fairly acid and has a low specific conductivity. The Ca, K, P and Mg contents were the lowest found in any of the communities, but distinctly higher than on the mainland. This is due to the nutrients provided by the sea and by birds. There is no ground water.

This type occurs in the outer archipelago zone and in the sea zone on peat soil about 15-50 cm thick.

4. The meadow complexes as microclimatic mosaics

Meadow complexes consisting of more than one meadow type are common even on very small islets. Allgrundet is only 70 m long and at most 50 m broad. Yet the meadow complex on this practically treeless islet (there are a few bushy alders and rowan trees) comprises several meadow types. On Allgrundet, temperature was recorded in 1971 and 1972 at five sites, each representing a different type of community. The five sensors were placed in the litter layer just above the soil, with the sixth or "control" measuring point in the open air at about 50 cm height. The thermometer was a "Wallac" automatic self-recording device.

An outline of the results is presented in Fig. 4. The measuring points, situated in different, partially isolated minimeadows of a meadow complex, belong to community types "*Filipendula - Alnus*" (point 1), "*Allium - Solidago*" (point 3) and "*Carex - Potentilla*" (point 5). The distances between

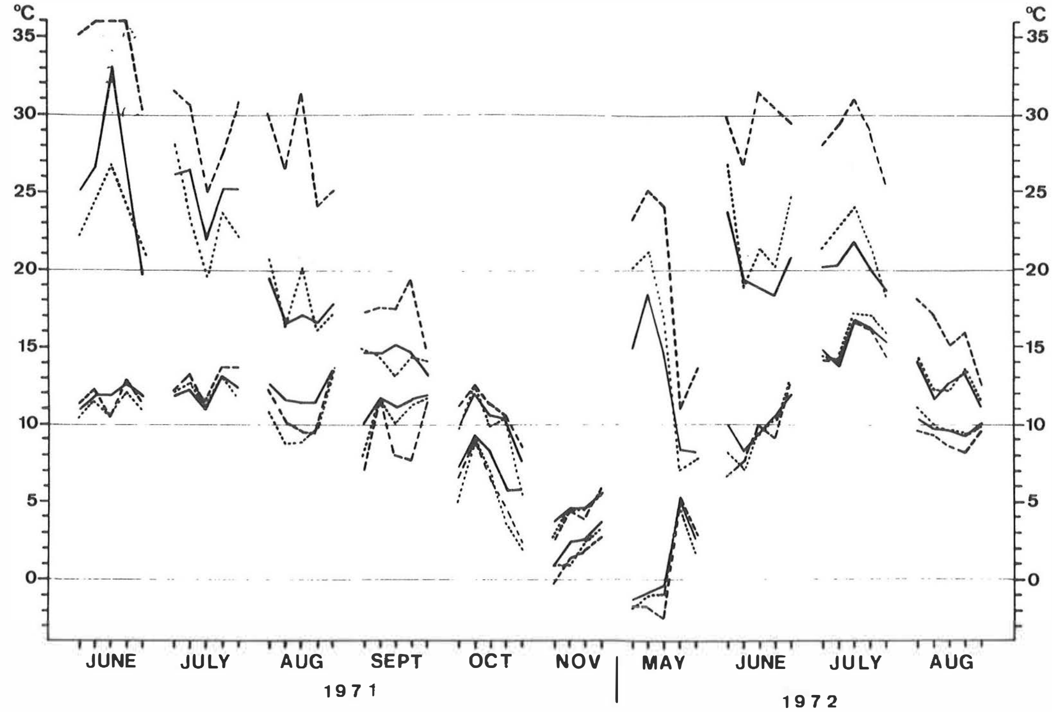

Fig. 4. Amplitude of the daily temperature in three different minimeadows on the island of Allgrundet. Solid line: meadow 1 (*Filipendula - Alnus*), dashed line: meadow 3 (*Allium - Solidago*), dotted line: meadow 5 (*Carex - Potentilla*). The 4- or 5-day periods were chosen from the 3rd week of each month with some exceptions caused by malfunctioning of the automatic temperature records.

the measuring points were 12 m (1-3), 9 m (3-5) and 18 m (1-5). The pairs of diagrams show the minimum and maximum daily temperatures during 5- or 4-day periods in a minimeadow.

The daily temperature fluctuation is greatest at point 3, the *Allium schoenoprasum - Solidago virgaurea* community, and during the summer months, the daily maximum is at all times highest in this minimeadow. In contrast, the daily maxima for meadow 1 (*Filipendula ulmaria - Alnus glutinosa)* and meadow 5 (*Carex canescens - Potentilla palustris)* intersect during each of the measuring periods.

The daily minimum temperatures vary from minimeadow to another much less than the maxima; the diagrams for all three measuring points tend to overlap. From late October to early May minima may be below the freezing point.

The great differences in the maxima between the three types of minimeadows indicate that even in adjacent sites on a small island the conditions of life for the food-plants of *Philaenus*, and for the spittlebug itself, are ecophysiologically quite different. As pointed out in the next section, the microclimatic differences between the meadow types appear to have distinct influence on between-site variability in the mortality of *Philaenus* nymphs.

5. Size and density variation in *Philaenus* populations

Many of the *Philaenus* populations live in minimeadows flanked on all sides by barren rock. In such tiny habitats, populations that vary in size must inevitably vary in density. On larger islands and in large meadow complexes, the population may expand or diminish its area according to the number of individuals present each year.

The factors regulating the establishment and maintenance of *Philaenus* populations in the Tvärminne archipelago include 1. the degree of isolation (distance from the nearest source population), 2. the topography of the island, especially whether the shore is of a type on which spittlebugs washed ashore can find vegetation and 3. the total area of meadows on an island. These three factors explain 78 % of the variability in population size (HALKKA *et al.* 1971).

The results of the latest investigations corroborate the earlier results, but show, in addition, that the different meadow types are not all equally favourable as habitats of *Philaenus*. In protected sites with a good or moderate water supply, minimeadows of the *Filipendula* - *Alnus* type, even though very small, may be able to maintain large *Philaenus* populations. At the other extreme, meadows of the *Festuca* - *Rümex* type, even though large, can support only sparse populations.

The most significant single factor regulating the size and density of *Philaenus* populations is, in fact, the food-plant composition of a meadow. The four most important food-plants explain 48 % of the variability in population size (Table 2).

In the Tvärminne archipelago, the distribution of *Filipendula ulmaria* is the prime ecological factor linked with variations in the density and/or size of *Philaenus* populations.

The temporal variability of population density was investigated in 7 successive years, 1969-75, in 25 meadows. These meadows represent 7 of the 8 community types described above (Table 5). In addition, observations on fluctuations in population density were made over shorter periods in about 30 other meadows. Averaged over the study period, densities were highest in the *Filipendula - Alnus* meadows. These densities differed highly significantly from those of both *Allium - Solidago* and *Festuca - Rumex* meadows.

The high maintenance capacity of the *Filipendula - Alnus* meadows is due to the presence of *Filipendula ulmaria* and *Lysimachia vulgaris* as abundant and constant components of the vegetation. These two herbs are the favourite food-plants of the spittlebug (Table 6). In addition to *Filipendula* and *Lysimachia*, a number of other herbs favoured as food-plants by *Philaenus* grow in *Filipendula - Alnus* meadows (Tables 4 and 6).

The relatively high densities of spittlebug populations in *Carex - Potentilla* meadows are probably due to the low mortality percentages typical of these meadows. Although *Potentilla palustris* is highly favoured as a food-plant, it is not common enough in the Tvärminne archipelago to rank higher than 7th in the food-plant list (Table 6).

In *Allium - Solidago* meadows the density of the *Philaenus* population depends on the ratio of *Solidago* to *Allium* in the plant community. The higher the ratio, the higher, potentially, is the density of the spittlebug populations. During droughts, the nymph populations of these meadows suffer great losses, and consequently the density of the adults fluctuates strongly.

In meadow complexes there is less fluctuation in population size than there is in the component minimeadows (Table 5). Usually, one of the minimeadows is suitable for *Philaenus* in a dry year, and another in a wet year, and in the complex as a whole the population size remains relatively constant.

Table 5. Density of *Philaenus spumarius* populations and coefficient of variation in different community types.

Community	Meadows studied	Individuals/m^2 Nymphs	Individuals/m^2 Adults	Coefficient of variation, % Nymphs	Coefficient of variation, % Adults
Sonchus - Juncus	1	0.1	0.1	266	266
Festuca - Rumex	6	0.5	0.4	194	192
Tanacetum - Veronica	2	7.6	4.2	102	101
Filipendula - Alnus	5	34.2	26.7	83	88
Allium - Solidago	7	8.0	4.6	143	149
Carex - Pontentilla	3	9.3	6.4	90	90
Empetrum - Vaccinium	1	0.4	0.4	263	264

None of the meadow types is completely resistant to the adverse effects of prolonged drought. The limits between which the numbers fluctuate are narrowest for the *Filipendula - Alnus* meadows and widest for the *Sonchus - Juncus*, *Empetrum - Vaccinium*, *Festuca - Rumex*, and *Allium - Solidago* meadows. The great diversity of the *Filipendula - Alnus* meadows, the generally adequate water supply, and, consequently, the relatively high stability of the vegetation all contribute to the success of

Table 6. Survival percentages of 3rd to 5th instar nymphs in the years 1969 - 1975 on 12 important food plants of *Philaenus spumarius*.

	1969		1970		1971		1972		1973		1974		1975	
	total	% live	total	% live	total	% live	total	% live	total	% live	total	% live	total	% live
Achillea millefolium	5	100	44	80	41	85	601	91	125	15	63	75	42	62
Solidago virgaurea	447	97	255	63	537	63	2 180	96	2 341	8	438	74	164	56
Lysimachia vulgaris	1 284	98	1 149	94	1 749	75	534	87	1 297	54	589	73	181	71
Filipendula ulmaria	1 402	95	550	70	913	62	2 705	88	2 115	20	1 544	68	632	54
Lythrum salicaria	405	99	322	85	382	47	957	88	1 619	51	1 027	83	411	67
Tripleurospermum maritimum	96	99	101	82	165	65	479	85	144	11	164	79	139	30
Potentilla palustris	116	97	109	81	128	63	141	88	566	73	384	72	361	63
Tanacetum vulgare	152	100	212	92	485	61	323	78	132	26	139	81	145	61
Rumex acetosella	1	100	0	0	11	9	19	79	2	50	6	0	4	50
Rumex acetosa	40	80	61	43	140	34	222	59	150	7	49	27	28	32
Rubus idaeus	0	0	4	25	2	0	35	46	42	0	2	0	5	20
Vaccinium uliginosum	0	0	9	56	0	0	24	25	31	100	0	0	18	11

the *Philaenus* populations. The relatively small daily fluctuation in temperature is largely due to protection from very intense solar radiation by the shade of the alders and the taller herbs (Fig. 4). This, in turn, probably means that the relative humidity of the air close to the ground is fairly constant. In very bad years, mortality rates are high in some *Filipendula - Alnus* meadows, too: in 1973 mortality of 3rd - 5th stage nymphs was 96.3 % on *Filipendula ulmaria* (N = 1357) and 38.3 % on *Lysimachia vulgaris* (N = 149) on Allgrundet (cf. Fig. 5), where there was no ground water.

In *Carex - Potentilla* meadows, floods rather than droughts appear to be the main cause of mortality. But as floods are much less frequent than droughts in the archipelago, *Potentilla palustris* is a favourable food-plant for *Philaenus* (Fig. 5).

The *Allium - Solidago* meadows are very sensitive to drought, owing to the high temperatures reached at ground level on sunny days (Fig. 4). *Philaenus* nymphs do not tolerate low humidity for long periods, and in 1973 the nymphs on *Solidago* in the *Allium - Solidago* meadow on Allgrundet had a mortality rate of 98.4 % (N = 493) (cf. Fig. 5, survival percentages on *Solidago* and *Tripleurospermum*).

The shore meadows, especially in the sea zone, are subject to catastrophes caused by varying sea level and consequent variability in other physical as well as edaphic and biotic factors. This explains the great variability in the size of *Philaenus* populations in the *Festuca - Rumex* meadows and *Juncus - Sonchus* meadows. In winter, the movements of the ice may detach herbs and *Philaenus* eggs from the islands, and in spring and early summer floods may wash nymphs into the sea.

V Discussion

Philaenus spumarius is a polyphagous insect, and at all stages of its life cycle is highly dependent on the plant species available as food or as sites for ovipositing. Hence a good knowledge of the ecology of the habitat meadows is needed as a basis for investigations on its ecological genetics. The vegetation of the island meadows in the Tvärminne area undergoes drastic changes in as little as 50 years as seen from a

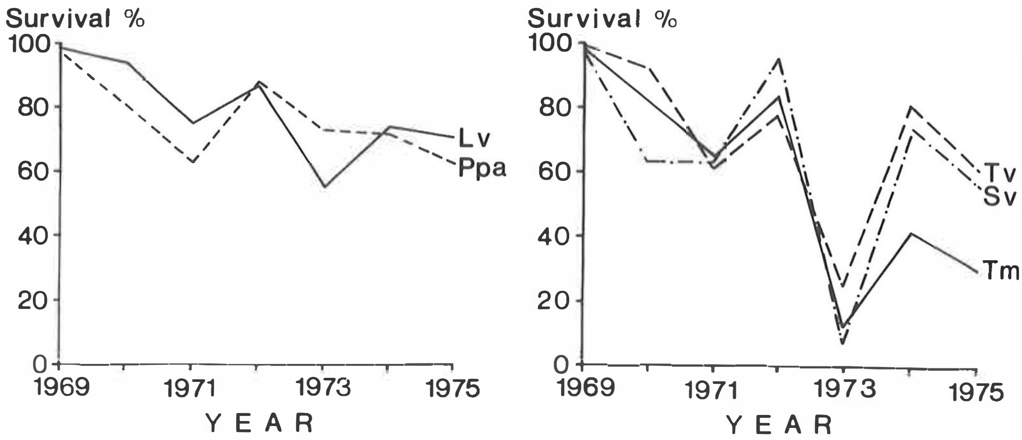

Fig. 5. Survival percentages of 3rd to 5th instar *Philaenus* nymphs on five food plant species in 1969 - 1975.
Lv = *Lysimachia vulgaris*, Ppa = *Potentilla palustris*,
Sv = *Solidago virgaurea*, Tm = *Tripleurospermum maritimum*,
Tv = *Tanacetum vulgare*.

comparison of the papers by HÄYRÉN (1914) and LUTHER (1961). The data gathered for the present study, when compared with the results of LUTHER (1961), show that within a period of about 10 years the vegetation changes profoundly. Even during the study period the common plant species changed in some of the meadows we investigated. In a minimeadow on the island of Kummelgrundet, *Lysimachia vulgaris* was almost completely replaced by *Lythrum salicaria* and some other plants in 1973 - 74. In two minimeadows on different islands (Allgrundet and Östra Mellanspiken) *Filipendula ulmaria* practically disappeared and was replaced by plants better able to tolerate wave action and/or drought.

The plant associations have been described in the present study as a starting point for investigations into the ecological genetics of *Philaenus*. This has naturally meant that the descriptions are incomplete from the point of view of plant sociology. Little attention has been paid to meadow types not favoured by *Philaenus*, and some types have been omitted altogether from the study. The meadow types described here occur over a wide area in the central part of the archipelago. fringing the coasts of the gulf of Finland and the northcentral part of the Baltic Sea (see HÄYRÉN 1902, 1914; BRENNER 1916, 1921;

LUOTOLA 1931; PALMGREN 1961; REBASSOO 1975). In the central and southern Baltic (STERNER 1933) comparable meadows have a somewhat dissimilar species composition. The islands at the eastern end of the Gulf of Finland (see ULVINEN 1937) and in the Gulf of Bothnia (see LEIVISKÄ 1908, BRENNER 1931, VALOVIRTA 1937, SIIRA 1970) likewise have their own meadow types.

The stage of development reached by the shore meadows in the different archipelagoes of the Baltic Sea depends ultimately on the rate of land upheaval, which is almost zero at the eastern end of the Gulf of Finland, and more than 100 cm in 100 years in the northern half of the Gulf of Bothnia. In the Tvärminne archipelago, land upheaval amounts to about 42 cm in 100 years.

In response to this land upheaval, the vegetation of the Baltic Sea islands undergoes long-term changes in the form of a characteristic secular succession. In the sea zone, the waves effectively remove material from some of the coves and deposit it in others. In sites where the sea deposits decaying algae, broken shells of bivalves and other organic material, sturdy plant colonizers soon establish expanding populations. During the earliest stages of meadow formation, owing to the harsh conditions of the sea zone, the number of plant species able to maintain a continuous population is very small. Under such conditions, *Philaenus* populations usually become extinct and are re-established several times before the food-plants gain a permanent foothold (see HALKKA *et al.* 1970, 1971).

On the other islands, i.e., at later stages of land upheaval, the meadows in protected sites have relatively stable composition, and the *Philaenus* populations which they support fluctuate less in size than the populations of the younger islands. The original *Festuca* - *Rumex* meadows are transformed into *Filipendula* - *Alnus* meadows.

In shallow depressions on rocky islands situated several metres above sea level, *Festuca* - *Rumex* meadows may be transformed into *Cornus* - *Peucedanum* meadows.

The *Allium* - *Solidago* meadows are established in rock crevices at a relatively early stage of land upheaval. They tend to retain their species composition almost unchanged at later stages of land upheaval. In cuplike depressions in the rock, *Festuca* -

Rumex meadows change into *Carex* - *Potentilla* bogs and later into *Empetrum* - *Vaccinium* bogs, which occur in the outer archipelago zone, also.

In the more protected islands of the outer archipelago zone, the secular succession differs somewhat from that seen in the sea zone. In shore meadows frequently flooded by the slightly saline (0.6 %) sea water, *Scirpus uniglumis* - *Triglochin maritimum* meadows change into *Juncus* - *Sonchus* meadows. Further succession may lead to either *Tanacetum* - *Veronica* or *Filipendula* - *Alnus* meadows. The *Allium* - *Solidago* meadows are present in rock crevices in this zone, too. (see HÄYRÉN 1914).

The success of a *Philaenus* population at the stage of establishment depends largely on the type of shore meadow colonized. (cf. HALKKA *et al.* 1971). In the *Festuca* - *Rumex* stage, the meadow often can maintain a population only for year or so. Where such a *Festuca* - *Rumex* meadow forms part of a meadow complex with other, more luxurient meadow types, the prospects for the *Philaenus* population will be better. Transformation of a *Festuca* - *Rumex* meadow into a *Filipendula* - *Alnus* or a *Carex* - *Potentilla* meadow usually means that the *Philaenus* population is no longer in danger of extinction.

Many physical and biotic variables may temporarily divert the secular succession from its normal course. The effects of field voles (*Microtus agrestis)* have been discussed in a previous paper (HALKKA *et al.* 1975b). Mainly by destroying the food-plants, voles may wipe out small *Philaenus* populations and markedly reduce the size of larger populations. Obviously, the same herbs serve as food-plants for voles and spittlebugs, and *Microtus* sometimes destroys both the aerial shoots and the underground parts of the food-plants of *Philaenus* in a miniature meadow.

In the island populations of *Philaenus* no other biotic factor is such a threat as field voles. Among the physical factors, the two extremes, droughts and floods, are the most important regulators of population size in *Philaenus*. The need of spittlebug nymphs for an adequate xylem supply means that, especially in dry summers, the success of a population depends on the number of "right" or "wrong" food-plant choices. Table 6 shows that *Solidago virgaurea* is a hazardous choice: in a wet year (e.g. 1969) survival may be as high as 97 %, but in a dry year (1973) as low as 8 % (cf. HALKKA and MIKKOLA, in press). On the other hand, *Lysimachia vulgaris* and *Potentilla palustris* are relatively safe food-plants: survival varies between 98 and 54 on *Lysimachia* and between 97 and 63 on *Potentilla* (Table 6).

Solidago, Lysimachia and *Potentilla* are dominants of different types of meadow, each characterized by some peculiar microclimatic features. On Allgrundet, *Solidago* is the dominant plant species in meadow 3, *Lysimachia* is common in meadow 1, and *Potentilla* is dominant in meadow 5. The microclimatic differences between these meadows, 3 being much less stable than 1 or 5, probably account for the differences observed in the capacity of the food-plants to support *Philaenus* nymphs.

Neither the microclimate nor the plant community of a mini-meadow remain constant from year to year. But in each the meadow type the changes tend to remain within certain limits. The variability of population size in *Philaenus* reflects extent of physical and biotic variability (Table 5). For populations of adult spittlebugs, the coefficient of population size fluctuation in *Filipendula - Alnus* meadows is only 88 % and in *Carex - Potentilla* meadows 90 %, but in *Allium - Solidago* meadows it is 149 %.

Fluctuation is most extreme in meadow types in which the *Philaenus* populations are always very sparse. The plant species typical of such meadows (*Juncus - Sonchus, Festuca - Rumex,* and *Empetrum - Vaccinium*) are unable to support large numbers of spittlebug nymphs. In addition, these meadow types may be wiped out by flood or drought (see Table 5). What types of meadow develop on an emerging island in the course of land upheaval largely depends on the topography of the rock surface. The fitness of *Philaenus* populations, in turn, depends on the meadow types available for colonization and maintenance of a population. This means that the topography of an emerging but still meadowless island can be used for predicting the approximate size of the *Philaenus* population living on the island after a given time interval (say, 500 years). A necessary proviso for such predictions is, of course, that the macroclimate remains stable during that time.

The peculiar and meadow-specific conditions prevailing in the minimeadows also dictate the genetic composition of the

Philaenus populations (HALKKA, RAATIKAINEN and HALKKA 1974).

The emerging islands finally become large enough to support spittlebug populations that are comparable in size and habitat area to populations living on the mainland. At this stage the populations are also similar in genetic composition to the mainland populations (HALKKA *et al.* 1974).

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