Norwegian water bugs. Distribution and ecology (Hemiptera–Heteroptera: Gerromorpha and Nepomorpha)

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Coulianos, C.-C., Økland, J. & Økland, K.A. 2008. Norwegian water bugs. Distribution and ecology (Hemiptera–Heteroptera: Gerromorpha and Nepomorpha). Norw. J. Entomol. 55, 179–222.

The distribution of the 53 species of water bugs in Norway is shown by 50-km square maps. A total of 8,832 specimens from various collections were identified and inspected. Species records from 139 squares included the northernmost sites on the European continent for eight species and at the highest altitude in Northern Europe for one species. More than one half of the species (28) had a southern type of distribution, occurring in the southernmost part of Norway, south of Trøndelag. This is well in line with a general decrease in European biodiversity going northwards from Central Europe. Most tolerant to climate were six all-Norwegian species. Three hypothetical late- and postglacial immigration routes for water bugs into Norway were suggested.

Material on hibernation, life cycles and wing morphology are presented and discussed. New material on habitat preferences and avoidances was based on 602 sites (476 lakes) investigated from 1960-1978. Water bugs were searched for (but not always found) and environment variables registered or measured (type of surface water like lake, pond etc., elevation above sea level, water temperature, aquatic vegetation, sediment, wave action, content of Ca and Mg, pH, and water colour). A statistical method based on deviations from a hypothetical random distribution was employed and significant environmental preferences, absences and/or avoidances could be shown for the 12 most frequent species. Most species preferred lakes or ponds and were significantly absent from smaller water bodies. Some of the significant preferences for a particular environmental variable were probably of indirect nature due to correlation with other factors.

Key words: distribution, ecology, freshwater, Hemiptera, Heteroptera, Gerromorpha, Nepomorpha, Norway.

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INTRODUCTION

The water bugs are true bugs (Hemiptera-Heteroptera) and comprise semiaquatic (Gerromorpha) and aquatic members (Nepomorpha). The present paper gives updated information on the distribution of the Norwegian water bugs. It also uses statistical methods for elucidating habitat preferences. In this paper "Norway" refers to the shaded area in Figure 1.

Recent contributions to the knowledge of the distribution of water bugs in Norway are Jastrey (1981) who listed 44 species from Norway with information on their distribution and habitat preferences, and Dolmen (1996) who listed

50 species with their distribution in the 18 Norwegian counties and with red-list status for 12 species. Since that time new material of water bugs in museums and private collections has been studied by Coulianos (1998) who listed 52 species and noted their distribution in the 37 Norwegian faunistic districts. Ødegaard & Coulianos (1998) gave a proposal to red-list status for 10 species. Aagaard et al. (2002) listed 52 species with their distribution and frequency in the five Norwegian regions with red-list status for 10 species. New district records were given by Grendstad et al. (2000), Dolmen (2004), Hågvar & Hatlen (2004) and Hågvar (2006, 2007). Dolmen (2004) also added *Corixa panzeri* Fieber, 1848, to the Norwegian list of species. In the 2006 Norwegian Red List, nine of the 53 species of water bugs known from Norway were listed (Ødegaard et al. 2006). Olsen (2008) reports new localities for 34 species of water bugs.

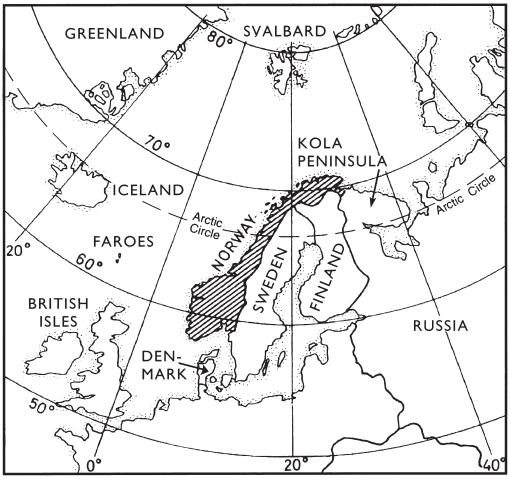

Figure 1. In this contribution the term "Norway" refers to the Norwegian mainland (shaded).

MATERIAL & METHODS

Three groups of material have been studied and are shown by the following symbols used on the distribution maps in Figure 2 and 3. ● = Group A. Material collected after 1950 leg. Økland. ◗ = Group B. Material from 1950 and later collected by others. ○ = Group C. Material from before 1950 collected by others.

The following collections have been studied: Zoological Museum, University of Oslo (ZMO) (including the Group A material); Zoological Museum, University of Bergen (ZMB); Stavanger Museum; Zoological Department, Tromsø Museum; Plantevernet, Planteforsk, Ås; Zoological Museum, University of Lund and Swedish Museum of Natural History, Stockholm (NRM). The private collections of C-.C. Coulianos, S. Hågvar and B. Sagvolden were also studied. In all 8,838 specimens have been examined.

Published records were checked against material in collections. Non-verifiable records have been omitted. Publications with records of water bugs in Norway are listed by Coulianos (1998). For later publications see the Introduction.

Determination of species was made by the first author. Exceptions are records of *Nepa cinerea* L. and *Ranatra linearis* L. in the Group A material determined by J. Ø., including a few controlled records reported to J. Ø. and K.A. Ø. by others.

The distribution maps of Norway in Figures 2-3 are according to the system with 50-km squares of European Invertebrate Survey (EIS). Endrestøl (2005) describes a new version of the system for Norway, based on the datum EUREF89 (WGS84). He also compares this version with an older system based on the datum ED50 which is used in the present paper. The difference between the two systems is about 150-200 m in the terrain. This does not influence geographical aspects on the national level. The revised "Strand system" (K.A. Økland 1981) is used for names of geographical regions.

Notes on the Group A material

This material is based on 602 sites where water bugs were searched for (but not always found) and where environmental variables were registered. Included in the distribution maps of the species and in Table 1 are a few 50-km squares where a given species was collected although environmental variables were not registered. The material was collected 1960-1978 during the summer (1 June–30 September).

Samples were taken by wading. The major collecting device for each person was a rod sieve with upper diameter 22 cm and mesh width 1 mm. They were used for sweeping through the aquatic vegetation with a scything motion. The uppermost water layer down to a depth of one meter was particularly studied, with stray samples down to about 1.5 m. In lakes, about 200 m of the shore line was investigated, usually including the outlet. On each site other aquatic groups such as Gastropoda, Bivalvia, Porifera, Bryozoa, Hirudinea and some Crustacea were also seached for and samples collected. Most of the sites were investigated once. Collecting time for lake sites was about one hour. Five lakes named in Table 4 were especially well investigated. The collected specimens were placed in 70 % ethanol.

Environmental variables in the Group A data

Seven surface water types were recognised: *lakes, ponds, ditches, puddles, mires, slow-flowing rivers* and *rapid-flowing rivers*. Lake: surface area usually more than 2,500 m^2 (about 50x50 m). Pond: surface area usually less than that of a lake. Ponds are generally so shallow that rooted plants can grow all over the bottom, and changes in water level are moderate; they rarely if ever dry out or freeze to the bottom. Ditches, mires and puddles are in the present study treated as "smaller water bodies". In these sites changes in water level may be large. Many are dry for parts of the year, and they often freeze to the bottom during winter. Most of the rivers were slow-flowing (23 of the 27 river sites). Here the water velocity was low enough to allow the sedimentation of various particles.

The presence or absence of the species in lakes was related to 11 environmental variables: elevation above sea level, water temperature measured 10 cm below the water surface, specific conductivity (µS cm^{-1} at 18 ºC), total hardness (German degrees, ºdH, 1 ºdH = 10 mg ´CaO´l^{-1}), Ca, Mg, pH and water colour (Pt mg l^{-1}).Three qualitative variables were used to describe the shore of the lake, each divided into four categories. For aquatic macrovegetation: 1) *Sphagnum* bog: the zone between dry land and the lake water is dominated by *Sphagnum* moss in which typical bog plants grow (e.g. *Eriophorum* spp., *Drosera* spp., *Pinguicula vulgaris* L.); 2) Poor vegetation: the shore has no or only sparse stands of helophytes; 3) Rich vegetation (quantitatively): the shore has a dense bed of helophytes; 4) Rich vegetation (quantitatively and qualitatively): in addition to a dense bed of helophytes, plant species typical of eutrophic habitats are present (e.g. *Iris pseudacorus* L., *Sagittaria sagittifolia* L., *Lemna* spp., *Ceratophyllum demersum* L.). Sediment in shallow water characterizes the site or the littoral zone as such: 1) Dy; 2) Stones and sand, meaning small amounts of organic sediments; 3) Dygyttja: a sediment intermediate between dy and gyttja; 4) Clay and gyttja. These two types of sediment were merged into one since they usually represent eutrophic habitats and also because of the low number of lakes investigated in the two groups. Wave exposure: 1) Small; 2) Small and medium; 3) Medium; 4) Heavy wave action.

Statistical analysis

Statistical treatment was based on Group A data that was collected using the same field technique. This treatment was made by K.A.Ø. using Excel.

Frequency deviations

For each environmental variable, several categories or intervals (for quantitative variables) were defined. The frequency of occurrence of a given species in each category or interval of a variable was calculated as the deviation from the value expected if the distribution was assumed to be random (cf. J. Økland 1969, 1990: 278, formula 1):

$$F_i = \frac{\dfrac{N_i}{N} - \dfrac{n_i}{n}}{\dfrac{n_i}{n}} \cdot 100$$

where F_i = frequency deviation for interval i, n_i = number of localities investigated in interval i, $n = \sum n_i$ = total number of localities investigated, N_i = number of localities where the species was found in interval i, and $N= \sum N_i$ = total number of localities where the species was found. The levels of significance of the frequency deviations were calculated by the chi square method (cf. K.A. Økland & J. Økland 1996). Probability levels are marked as follows: *** = 0.001, **= 0.01, *= 0.05, + = 0.1.

Four concepts will be used in the discussion of frequency deviations for a given species within an interval or in a category of a variable:

● *Absence*: the species is not present, and this is significantly different from the expected result.

● *Avoidance*: the frequency of occurrence is significantly lower than expected.

● *Presence*: the species occurs within an interval or in a category at a frequency that does not deviate significantly from the expected value.

● *Preference or favouring*: the frequency of occurrence is significantly higher than expected.

False negative records are assumed not to influence the extent to which the species prefers or avoids a certain environmental category. Since so many lakes were investigated, it is reasonable to assume that the proportion of false negative records was the same in all four categories into which each environmental variable was grouped or divided.

Frequency deviations were calculated only for the 12 species which were represented by more than 15 records in lakes (cf. Table 3). For elevation above sea level, frequency deviations were only calculated for lakes in South Norway north to (and including) Sør-Trøndelag where the vertical climatic gradient may be especially steep.

Pearson correlations

For calculating Pearson correlations coefficients, categories of the qualitative variables (aquatic macrovegetation, sediment and wave action in lakes) were numbered according to a logical scheme representing a series of steps which usually reflect decreasing favourability for benthic communities in fresh water (J. Økland 1990:123). Four variables were log-transformed (specific conductivity, total hardness, calcium and magnesium).

RESULTS

Survey of main results

A survey of the 53 species of water bugs in Norway is given in Table 1. For each species are shown the number of 50-km EIS squares for the three different groups of material, number of localities, number of records and key words for the distribution in Norway. Figure 2, Map 3 shows areas with collected specimens, comprising 139 of the 189 50-km EIS squares in Norway. Squares without records exist especially along the borders to Sweden and Finland where often only a smaller part of a square belongs to Norway. Also along the coast there are empty squares, here often because of small land areas. Maps of the distribution in Norway of the 53 species are presented in Figure 3.

Table 2 shows the number of species with a given distribution type within the various families of water bugs and the total number of species belonging to each distribution type. The most frequent type of distribution is southern (28 species). This covers a smaller or greater area of Norway south of Trøndelag. 23 other species also inhabit these southern parts but extend to areas further north. 11 of them have been recorded in Trøndelag as well; four also in Nordland, two also in Troms, and six species have an all-Norwegian distribution. Of the remaining two species one has a northern range with a single record in Finnmark, and one has an eastern distribution.

The following results pertain to the Group A material. The number of records of each species in different types of surface waters appears from Table 3. Table 4 shows the number of species in a given surface water type, and the mean number of species in each type. Maximum 15 species were recorded from lakes, with an average of 1.0. Ponds had maximum four species (average 1.5), and smaller water bodies maximum two (average 0.1). In the small group of river habitats up to five species (average 0.8) were recorded. The lakes marked and named in Table 4 were more closely studied both in terms of collection time and number of habitats investigated (in connection

Table 1. Survey of the 53 species of aquatic Heteroptera in Norway. For each species is indicated the number of 50-km squares in which a species is represented in the three groups of material (A-C) corresponding to symbols on its distribution map, the total number of squares represented by the species, the number of localities and the number of records. A record is defined as the occurrence of a particular species at a particular locality on a particular date. Key words for the type of distribution are included. For author names and years, see the chapter on "Survey of the species".

Species recorded from Norway	**No of 50-km squares**				**No of localities**	**No of records**	**Type of distribution in Norway**
	Material			Total			
	A	**B**	**C**				
Mesoveliidae							
1. *Mesovelia furcata*	4	9	1	14	25	34	Southern
Hebridae							
2. *Hebrus pusillus*	-	1	4	5	6	17	Southern
3. *Hebrus ruficeps*	-	5	15	20	30	37	Northwards into Trøndelag
Hydrometridae							
4. *Hydrometra gracilenta*	-	8	1	9	41	53	Southern
5. *Hydrometra stagnorum*	2	6	2	10	19	20	Southern
Veliidae							
6. *Microvelia reticulata*	3	5	5	13	26	31	Southern
7. *Velia caprai*	3	7	3	13	38	45	Northwards into Trøndelag
8. *Velia saulii*	7	2	4	13	18	18	Northwards into Trøndelag
Gerridae							
9. *Aquarius najas*	2	1	4	7	10	13	Southern
10. *Aquarius paludum*	2	2	1	5	8	11	Southern
11. *Gerris argentatus*	2	5	1	8	20	33	Southern
12. *Gerris lacustris*	50	12	7	69	291	331	Northwards into Troms
13. *Gerris lateralis*	22	21	21	64	123	127	All-Norwegian
14. *Gerris odontogaster*	21	15	5	41	111	120	All-Norwegian
15. *Gerris thoracicus*	-	4	3	7	10	11	Southern
16. *Limnoporus rufoscutellatus*	7	4	6	17	34	37	Eastern
Nepidae							
17. *Nepa cinerea*	20	5	-	25	123	139	Southern
18. *Ranatra linearis*	2	6	-	8	24	29	Southern
Corixidae							
19. *Micronecta minutissima*	2	-	-	2	5	7	Southern
20. *Micronecta poweri*	8	7	1	16	21	27	Northwards into Trøndelag
21. *Cymatia bonsdorffii*	12	16	3	31	71	85	Northwards into Troms
22. *Cymatia coleoptrata*	-	-	1	1	1	1	Southern
23. *Glaenocorisa cavifrons*	3	30	4	37	76	91	All-Norwegian
24. *Glaenocorisa propinqua*	-	1	-	1	1	1	Southern

Table 1. *Continued*

Species recorded from Norway	**No of 50-km squares**				**No of localities**	**No of records**	**Type of distribution in Norway**
	Material			Total			
	A	**B**	**C**				
25. *Arctocorisa carinata*	7	33	16	56	99	117	All-Norwegian
26. *Arctocorisa germari*	3	26	4	33	79	81	Northwards into Nordland
27. *Callicorixa praeusta*	2	8	3	12	20	23	Northwards into Trøndelag
28. *Callicorixa producta*	26	36	19	81	129	155	All-Norwegian
29. *Callicorixa wollastoni*	10	24	9	43	73	78	All-Norwegian
30. *Corixa dentipes*	1	11	4	16	35	45	Southern
31. *Corixa panzeri*	-	1	-	1	2	3	Southern
32. *Corixa punctata*	-	5	2	7	9	13	Southern
33. *Hesperocorixa castanea*	1	11	3	15	24	33	Southern
34. *Hesperocorixa linnaei*	11	6	1	18	51	57	Southern
35. *Hesperocorixa sahlbergi*	21	12	5	38	111	116	Northwards into Nordland
36. *Paracorixa concinna*	-	6	-	6	14	14	Southern
37. *Sigara distincta*	14	19	5	38	165	179	Northwards into Nordland
38. *Sigara dorsalis*	32	8	3	43	202	204	Northwards into Troms
39. *Sigara falleni*	6	2	2	10	32	32	Southern
40. *Sigara fallenoidea*	1	-	-	1	1	1	Northern
41. *Sigara fossarum*	5	6	2	13	35	35	Northwards into Trøndel
42. *Sigara hellensii*	-	1	1	2	3	3	Southern
43. *Sigara lateralis*	-	2	-	2	8	8	Southern
44. *Sigara limitata*	-	3	2	5	8	8	Southern
45. *Sigara longipalis*	-	1	-	1	2	2	Southern
46. *Sigara nigrolineata*	3	5	11	19	38	38	Northwards into Trøndelag
47. *Sigara scotti*	14	9	1	24	103	103	Northwards into Trøndelag
48. *Sigara semistriata*	8	25	2	35	79	80	Northwards into Trøndelag
49. *Sigara striata*	2	3	2	7	17	17	Southern
Aphelocheiridae							
50. *Aphelocheirus aestivalis*	-	1	-	1	2	3	Southern
Notonectidae							
51. *Notonecta glauca*	6	13	7	26	80	88	Northwards into Trøndelag
52. *Notonecta lutea*	2	13	5	20	130	136	Northwards into Trøndelag
53. *Notonecta reuteri*	-	4	1	5	15	15	Southern

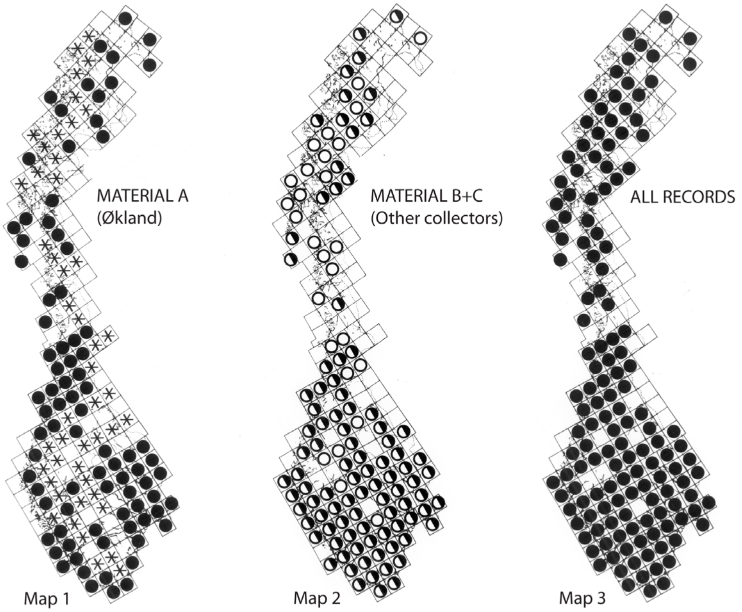

Figure 2. Maps of Norway showing 50-km squares according to the European Invertebrate Survey (EIS). The grid lines run south–north and west–east. **Map 1**. Squares represented by investigations after 1950, by J. & K.A. Økland (Group A material). ●= water bugs collected. ✱ = investigated, no water bugs observed or collected, but also here environmental variables were registered. **Map 2**. Other collectors (Group B and C material), ◗ = data from 1950 or later, ○= data only from before 1950. Such data are also present in some of the squares marked by the former symbol. **Map 3**. All records.

Table 2. Survey of the number of species with given distribution type within the families of aquatic Heteroptera in Norway. The counties Trøndelag (meaning Sør-Trøndelag and Nord-Trøndelag), Nordland and Troms are named from south to north. Species also inhabiting the northernmost county Finnmark are regarded as All-Norwegian.

		Also in					
	Southern, south of Sør-Trøndelag	**Trøndelag**	**Nordland**	**Troms**	**All-Norwegian**	**Northern**	**Eastern**
Mesoveliidae	1	-	-	-	-	-	-
Hebridae	1	1	-	-	-	-	-
Hydrometridae	2	-	-	-	-	-	-
Veliidae	1	2	-	-	-	-	-
Gerridae	4	-	-	1	2	-	1
Nepidae	2	-	-	-	-	-	-
Corixidae	15	6	4	1	4	1	-
Aphelocheiridae	1	-	-	-	-	-	-
Notonectidae	1	2	-	-	-	-	-
Total	28	11	4	2	6	1	1

Table 3. Number of localities investigated within categories of surface water type, and the number of records of the given species of Heteroptera. For the 38 species in the Group A material.

	Lakes	Ponds	Smaller water bodies	Rivers	Total
Localities investigated	476	49	50	27	602
Species					
1. *Mesovelia furcata*	7	0	0	0	7
5. *Hydrometra stagnorum*	1	0	0	0	1
6. *Microvelia reticulata*	4	0	0	0	4
7. *Velia caprai*	4	0	0	0	4
8. *V. saulii*	4	0	1	0	5
9. *Aquarius najas*	2	0	0	0	2
10. *A. paludum*	2	0	0	0	2
11. *Gerris argentatus*	9	0	0	0	9
12. *G. lacustris*	94	8	0	5	107
13. *G. lateralis*	16	7	3	0	26
14. *G. odontogaster*	28	6	0	1	35
16. *Limnoporus rufoscutellatus*	8	2	0	0	10
17. *Nepa cinerea*	24	1	-	4	29
18. *Ranatra linearis*	2	-	-	-	2
19. *Micronecta minutissima*	2	-	-	-	2
20. *M. poweri*	7	-	-	-	7
21. *Cymatia bonsdorffii*	17	-	-	-	17
23. *Glaenocorisa cavifrons*	2	1	-	-	3
25. *Arctocorisa carinata*	3	9	-	1	13
26. *A. germari*	2	1	-	-	3
27. *Callicorixa praeusta*	1	1	-	-	2
28. *C. producta*	22	15	-	2	39
29. *C. wollastoni*	6	1	1	-	8
30. *Corixa dentipes*	3	-	-	-	3
33. *Hesperocorixa castanea*	1	-	-	-	1
34. *H. linnaei*	19	1	-	-	20
35. *H. sahlbergi*	27	9	-	2	38
37. *Sigara distincta*	23	-	-	-	23
38. *S. dorsalis*	69	4	1	4	78
39. *S. falleni*	8	1	-	1	10
40. *S. fallenoidea*	1	-	-	-	1
41. *S. fossarum*	7	1	-	-	8
46. *S. nigrolineata*	4	-	-	-	4
47. *S. scotti*	27	1	-	-	28
48. *S. semistriata*	10	1	-	-	11
49. *S. striata*	4	-	-	-	4
51. *Notonecta glauca*	20	2	-	1	23
52. *N. lutea*	4	-	-	-	4
Total number of records	494	72	6	21	593

with other projects). They had from eight to 15 species each, this number being higher than the maximum number of seven for the remaining 471 lakes. Table 5 shows the ranges of environmental variables for the investigated localities and for the different species.

For the 12 most frequent species in Group A lakes, Figures 4-15 show their occurrence in relation to 10 environmental variables. These occurrences are illustrated in relation to the zero value expected on the basis of random distribution. Significant environmental preferences for these species appear from Table 6 using nine of the variables (omitting magnesium) and Table 7 summarizes in the same way significant absences or avoidances.

Table 4. Number of species of aquatic Heteroptera present in four types of water bodies. Group A material. [1]Lake Sukkevann, [2]Lake Rønnebergdammen, [3]Lake Østensjøvann, [4]Lake Borrevann, [5]Lake Grennesvann

Type of water body	Number of species 0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Total	Mean
Lake	253	113	52	26	11	3	8	5	1[1]	1[2]	-	-	1[3]	1[4]	-	1[5]	476	1.0
Pond	17	4	17	10	1	-	-	-	-	-	-	-	-	-	-	-	49	1.5
Smaller water body	46	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	50	0.1
River	14	8	4	-	-	1	-	-	-	-	-	-	-	-	-	-	27	0.8
Total	330	127	75	36	12	4	8	5	1	1	-	-	1	1	-	1	602	-

The latter reactions implies a significant decreased occurrence in relation to that expected on the bases of random distribution.

Survey of the species

In the following survey of the Norwegian water bugs the information on general distribution is according to Jansson (1986), Aukema & Rieger (1995) and Wachmann et al. (2006). For the distribution in Norway see Figure 3. The information on life cycles comes from evaluating the dates of collecting for the species and in some cases from the dissection of females.

Family Mesoveliidae

1. *Mesovelia furcata* Mulsant & Rey, 1852
General distribution: Europe, North Africa and a large part of Asia. Rather common in SE Norway, with 34 records from 25 localities, all from lakes including those surrounded by *Sphagnum* bogs. The lakes had poor as well as rich mesotrophic or eutrophic vegetation. Mostly the species lives on floating leaves of macrophytes. Jastrey (1981) found it mainly in oligotrophic lakes with fairly rich vegetation. It hibernates as egg, larvae has been found from late June and the new generation of adults from beginning of July. In Norway the species is univoltine but partially bivoltine in Denmark (Damgaard 1997) and S Sweden (Coulianos pers.obs.). Norwegian records are of the apterous form, the only record of the macropterous form is from AK: Drøbak (EIS 28) 18 July 1917, 1♂ leg. H. Warloe coll. ZMO.

Family Hebridae

2. *Hebrus pusillus* (Fallén, 1807)
General distribution: Europe, North Africa and from Asia Minor to Kirgizia. In Norway not common, with 17 records from six localities in SE Norway. First reported from Norway by Warloe (1925) (as *Microvelia schneideri* f. macroptera) and by Holgersen (1942). An additional record is from VE Tjøme (EIS 19) 9 August 1968 leg. A. Fjellberg coll. ZMB. There is no information of the habitat of the species in Norway. In Denmark, England, Germany and Sweden it is univoltine and is known from small lakes, heath and fen ponds and is found on the surface at the shore amongst dense vegetation, sometimes amongst *Sphagnum* (Damgaard 1997, Huxley 2003, Wachmann et al. 2006, Coulianos pers.obs.). Most probably this applies also to the habitats of the species in Norway, where it is univoltine, hibernates as adult.

3. *Hebrus ruficeps* Thomson, 1871
General distribution: Most of Europe (except in the south) eastwards to Siberia and Central Asia. In Norway not uncommon northwards into Trøndelag and found at 30 localities with 37 records. It lives in peat pools, fens, bogs and mires and is mostly found in *Sphagnum* vegetation. Mostly micropterous, in Norway with only three records of the macropterous form. Univoltine,

Table 5. Ranges of environmental variables for the 602 localities investigated, and for localities where the given species were found. N=number of localities with the species. Group A material.

	N	Elevation above sea level m	Water temp. °C	Specific conductivity µS cm $^{-1}$	Total hardness °dH	Ca mg l^{-1}	Mg mg l^{-1}	pH	Water colour Pt mg l^{-1}
Localities investigated		0–1835	6–24	4.7–761.4	0.10–16.40	0.7–105.8	0–20.3	4.4-9.9	0-400
1. *Mesovelia furcata*	7	2–129	14–22	30.4–90.4	0.80–2.20	5.0–10.5	0.4–3.2	6.3–8.1	23–85
5. *Hydrometra stagnorum*	1	15	18	55.3	0.75	3.9	0.8	6.4	18
6. *Microvelia reticulata*	4	50–129	17–22	45.8–90.4	0.95–2.20	4.6–10.5	1.3–3.2	6.3–7.0	18–65
7. *Velia caprai*	4	2-18	16-22	42.1-104.4	0.60-1.65	2.5-6.7	1.1-3.0	6.4-8.1	15-150
8. *V. saulii*	5	10–338	12–19	19.9–103.5	0.25–1.95	1.4–8.5	0.2–3.7	5.1–7.1	10–100
9. *Aquarius najas*	2	37–96	16–19	24.7–42.3	0.50–0.55	2.1–2.5	0.7–1.1	5.9–6.8	10–40
10. *A. paludum*	2	9–144	16–18	41.9–181.6	0.90–3.30	4.6–17.0	0.8–4.1	6.2–7.6	10
11. *Gerris argentatus*	9	9–169	13–22	30.4–181.6	0.80–3.30	4.3–17.0	0.4–4.1	6.3–7.6	18–85
12. *G. lacustris*	107	1–697	9–22	11.7–430.0	0.15–11.05	1.1–54.0	0–16.6	4.7–9.3	3–150
13. *G. lateralis*	26	1–886	10–22	12.5–430.1	0.30–13.30	1.1–80.9	0.2–8.2	5.1–9.0	4–250
14. *G. odontogaster*	35	2–635	10–22	13.9–270.1	0.45–8.25	1.1–49.0	0.4–7.3	5.2–9.5	5–150
16. *Limnoporus rufoscutellatus*	10	9–144	15–22	23.4–181.6	0.45–3.70	1.1–21.0	0.4–4.1	6.1–8.8	5–40
17. *Nepa cinerea*	29	0–307	13–22	26.8–259.2	0.45–7.10	2.1–41.9	0.4–6.5	5.7–8.8	5–150
18. *Ranatra linearis*	2	64–85	14–20	30.5–48.6	0.50–1.15	2.5–5.7	0.7–1.5	5.9–6.3	45–50
19. *Micronecta minutissima*	2	9–129	16–17	90.4–181.6	2.20–3.30	10.3–17.0	3.2–4.1	6.8–7.6	65
20. *M. poweri*	7	3–358	13–18	32.4–166.3	0.70–5.30	3.2–32.7	0.7–3.0	6.7–8.7	10–32
21. *Cymatia bonsdorffii*	17	10–188	13–22	17.1–162.5	0.20–3.80	1.1–21.0	0.2–4.5	4.7–8.8	20–150
23. *Glaenacorisa cavifrons*	3	5–93	13–17	80.0–244.9	0.55–2.10	1.1–8.5	1.7–6.2	5.2–7.0	10–80
25. *Arctocorisa carinata*	13	1–371	11–22	28.5–401.4	0.75–7.00	2.1–38.3	0.8–7.3	5.1–9.1	15–200
26. *A. germari*	3	3–10	13–18	94.4–376.0	1.70–6.40	8.5–34.8	2.2–6.5	7.0–9.4	40–70
27. *Callicorixa praeusta*	2	5–103	14–22	162.5–430.0	3.70–11.05	21–51.1	3.0–16.6	7.4–8.8	50
28. *C. producta*	39	1–1,020*	10–23	12.9–276.5	0.20–7.30	1.1–39.8	0–8.6	5.1–9.6	4–250
29. *C. wollastoni*	8	10–245	11–17	22.3–129.7	0.30–4.15	2.1–24.9	0–5.6	5.8–7.7	10–150
30. *Corixa dentipes*	3	14–21	16	79.8–94.0	1.40–1.65	7.1–10.7	0.7–1.7	6.5–6.8	40–125
33. *Hesperocorixa castanea*	1	60	21	26.3	0.25	1.1	0.4	4.7	60
34. *H. linnaei*	20	1–164	13–22	30.4–259.2	0.80–3.70	4.6-21.0	0.4–4.5	6.0–8.8	23–125
35. *H. sahlbergi*	38	1–1,010*	11–22	20.1–430.0	0.30–11.05	1.4–51.1	0.4–16.6	5.8–8.9	5–160
37. *Sigara distincta*	23	1–245	12–20	18.1–228.3	0.20–2.80	1.1–14.9	0–4.3	4.7–9.2	5–125
38. *S. dorsalis*	78	0–153	11–21	19.8–376.0	0.25–8.25	1.1–49.0	0.4–8.6	5.4–9.4	4–150
39. *S. falleni*	10	9–133	13–22	30.4–181.6	0.80–3.30	3.9–17.0	0.4–4.5	6.1–7.6	5–150
40. *S. fallenoidea*	1	21	21	60.5	1.55	9.2	1.1	9.5	80
41. *S. fossarum*	8	37–133	13–22	30.4–88.3	0.55–2.05	2.1–9.9	0.4–4.5	5.9–7.0	23–150
46. *S. nigrolineata*	4	9–528	10–16	19.5–181.6	0.55–3.30	2.8–17.0	0.7–4.1	6.3–7.6	40–125

Table 5. *Continued*

	N	Elevation above sea level m	Water temp. °C	Specific conductivity µS cm $^{-1}$	Total hardness °dH	Ca mg l^{-1}	Mg mg l^{-1}	pH	Water colour Pt mg l^{-1}
47. *S. scotti*	28	1–85	13–21	24.7–228.3	0.30–3.00	1.4–15.6	0–4.3	5.9–9.2	5–125
48. *S. semistriata*	11	9–635	9–22	13.9–162.5	0.20–4.15	1.1–24.9	0.2–4.5	4.7–8.8	4–150
49. *S. striata*	4	9–103	14–22	30.4–181.6	0.80–3.70	5.0–21.0	0.4–4.1	6.4–8.8	23–85
51. *Notonecta glauca*	23	1–129	13–22	39.1–181.6	0.95–3.70	4.3–21.3	0.7–4.1	6.1–8.8	10–125
52. *N. lutea*	4	51–68	14–21	30.4–151.4	0.80–3.00	5.0–13.5	0.4–4.7	6.3–7.0	23–160

* not Group A material, but from internal database

hibernates as adult.

Family Hydrometridae

4. *Hydrometra gracilenta* (Horváth, 1899)
General distribution: Most parts of Europe (not in the Mediterranean area) and Asia to the Far East and China. In Norway found at 41 localities with 53 records from the SE part where it is rather common. In Denmark, England, Germany and Sweden it lives at the margin of smaller lakes and ponds with rich vegetation and is also found in *Sphagnum* bogs. Univoltine, hibernates as adult (Damgaard 1997, Huxley 2003, Wachmann et al. 2006, Coulianos pers.obs.). Most certainly this applies also to the habitats of the species in Norway.

5. *Hydrometra stagnorum* (Linnaeus, 1758)
General distribution: North Africa, Middle Asia and almost all Europe with the exception of N Scandinavia and N Russia. In Norway found in coastal localities from the SE to the SW at 19 localities with 20 records. Information of its habitats in Norway is sparse, but it seems to live in the same type of habitats as the preceding species including slow-flowing waters. In Denmark and Sweden it is often found in waters with very sparse or no vegetation like rock pools where it can be very abundant (Damgaard 1997, Coulianos pers.obs.). Jastrey (1981) found the species in localities with sparse vegetation in secluded areas in shallow water. Univoltine, hibernates as adult.

Family Veliidae

6. *Microvelia reticulata* (Burmeister, 1835)
General distribution: Europe (not in the South) eastwards to Siberia, China and Japan. In Norway found in the SE, not uncommon and found at 26 localities with 31 records. It lives on the water surface at the margins of lakes and ponds with rich macrophyte vegetation. In Denmark and Britain it is partially bivoltine (Damgaard 1997), and in warmer areas in Germany with even three generations per year. All Norwegian specimens seen by us are apterous. The records of macropterous specimens in Warloe (1925) refer to *Hebrus pusillus* according to specimens in ZMO. In Norway univoltine, hibernates as adult.

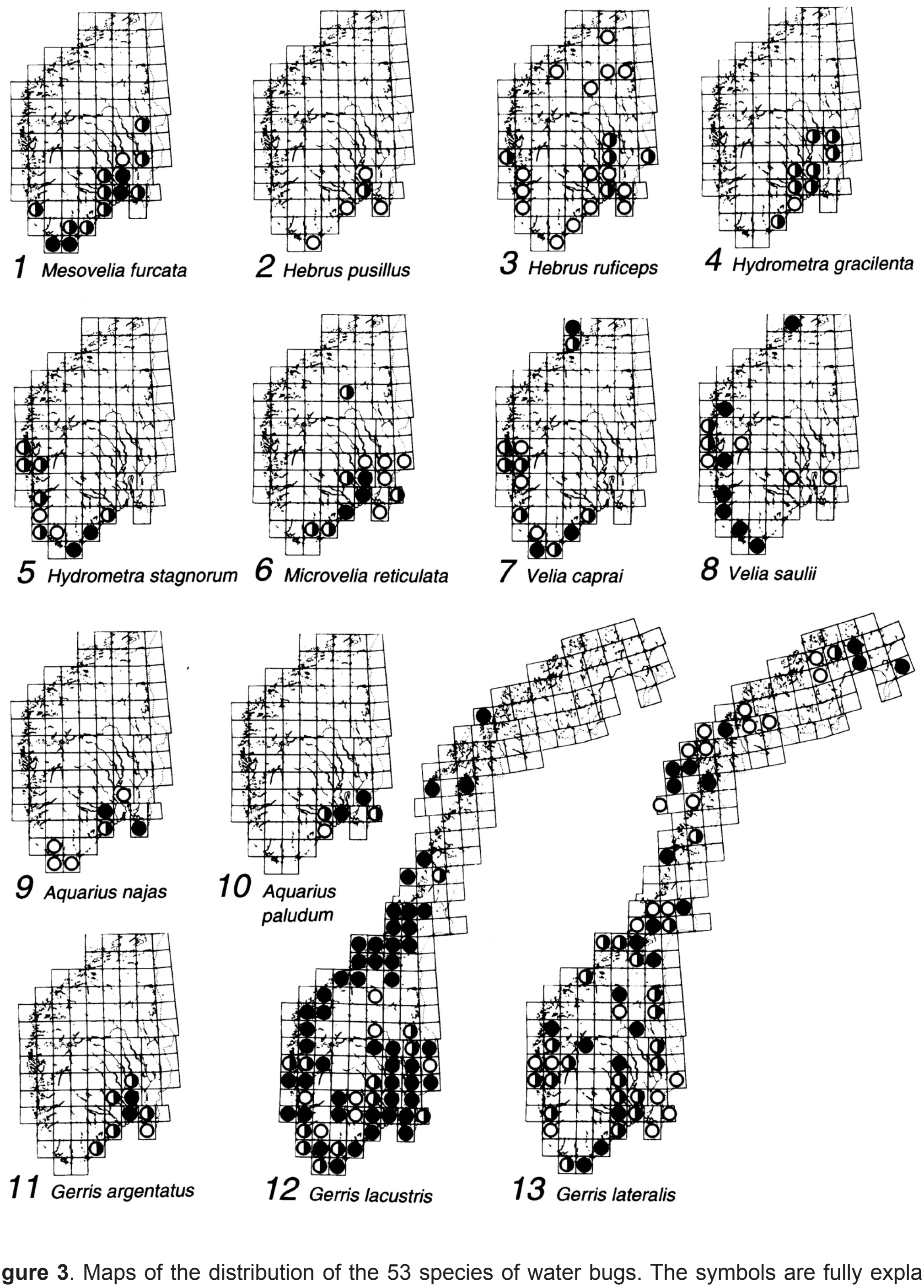

Figure 3. Maps of the distribution of the 53 species of water bugs. The symbols are fully explained in the text; cf. also the short description in the legend to Figure 2. ● = Data after 1950, coll. Økland. Environmental variables registered. ◗= Data from 1950 and later, other collectors. ○= Data from before 1950, various collectors. Species numbers 1-13.

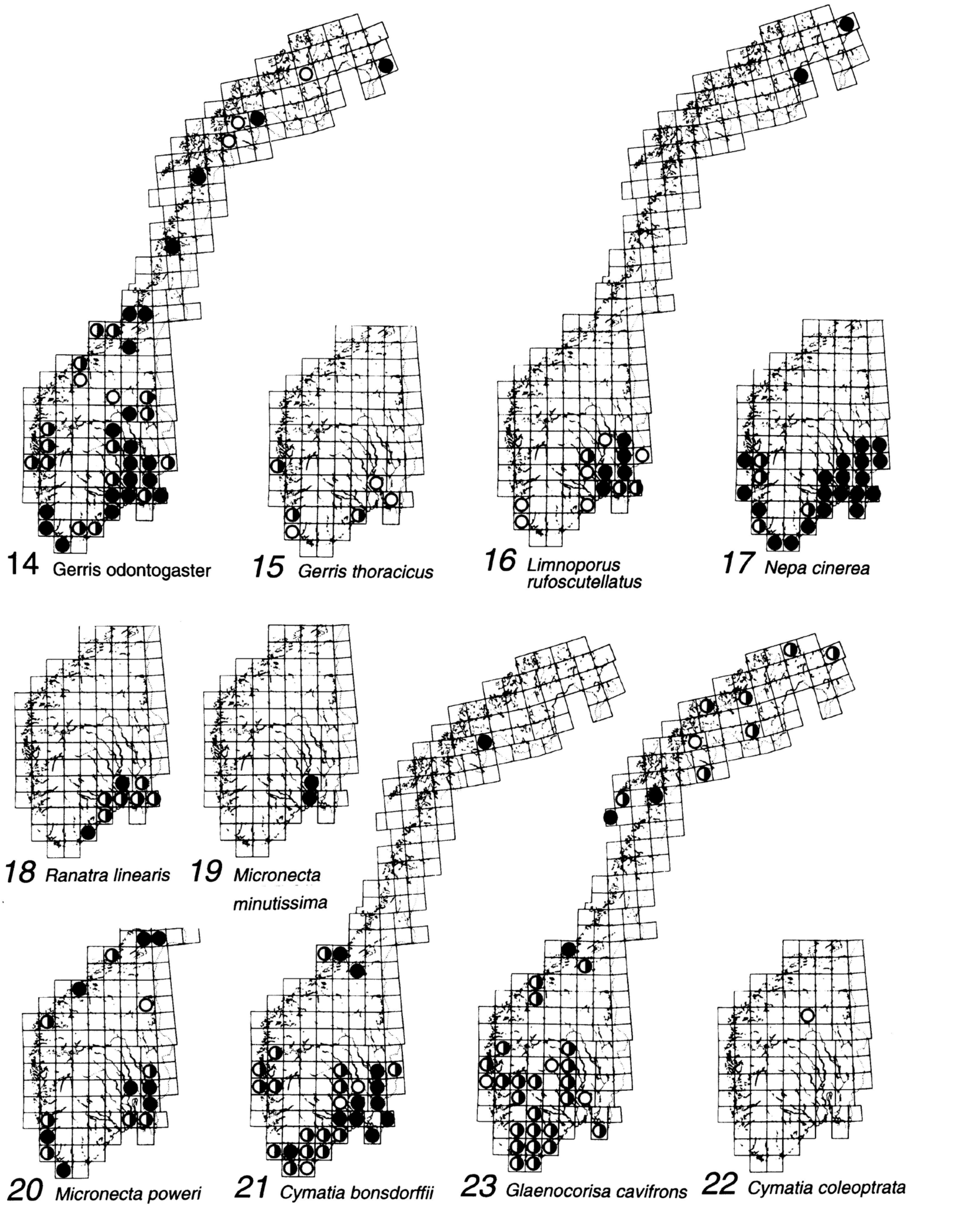

Figure 3 continued. Maps of the distribution of the 53 species of water bugs. The symbols are fully explained in the text; cf. also the short description in the legend to Figure 2. ●= Data after 1950, coll. Økland. Environmental variables registered. ◗= Data from 1950 and later, other collectors. ○ = Data from before 1950, various collectors. Species numbers 14 -23.

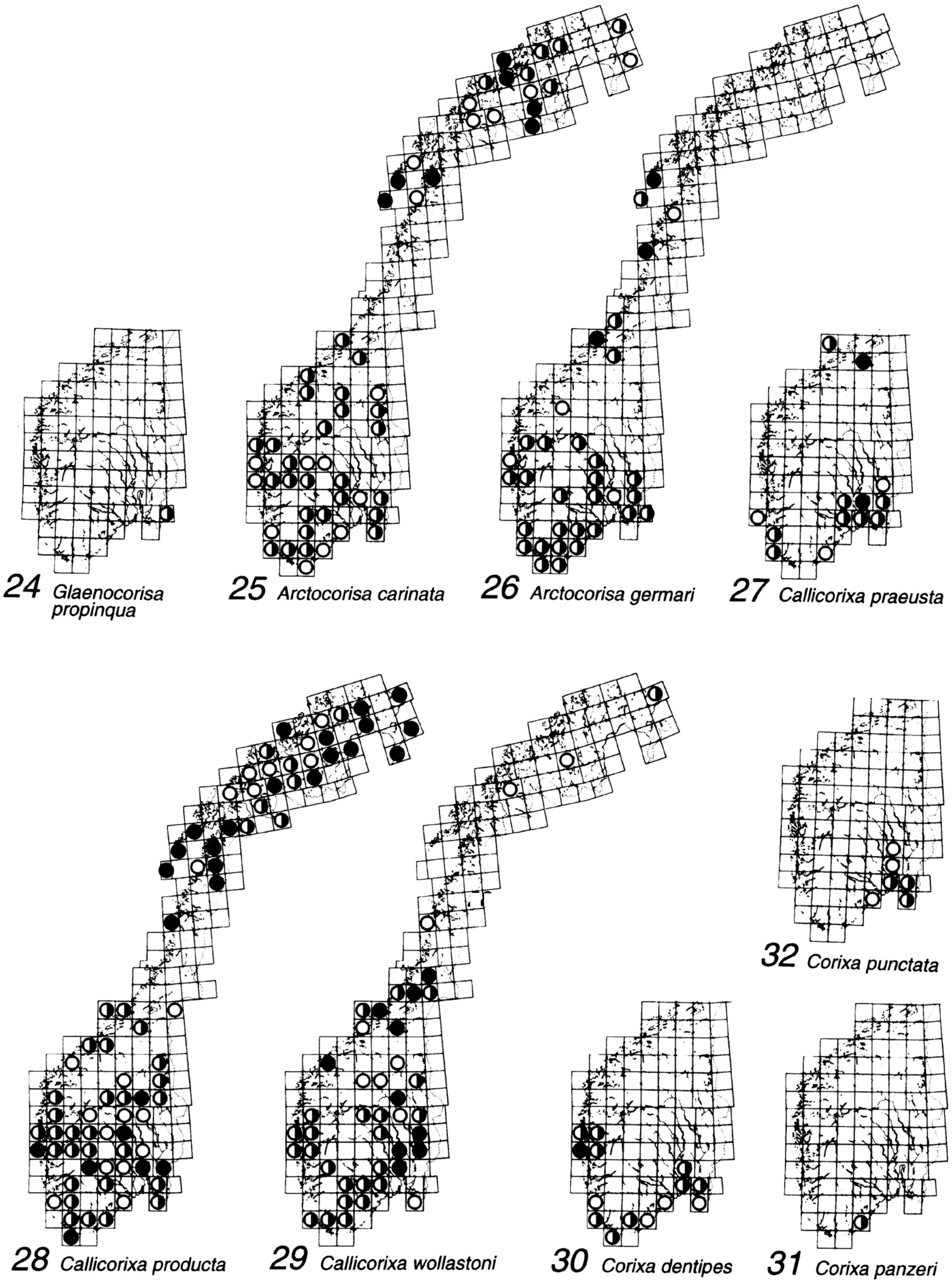

Figure 3 continued. Maps of the distribution of the 53 species of water bugs. The symbols are fully explained in the text; cf. also the short description in the legend to Figure 2. ●= Data after 1950, coll. Økland. Environmental variables registered. ◗ = Data from 1950 and later, other collectors. ○ = Data from before 1950, various collectors. Species numbers 24-32.

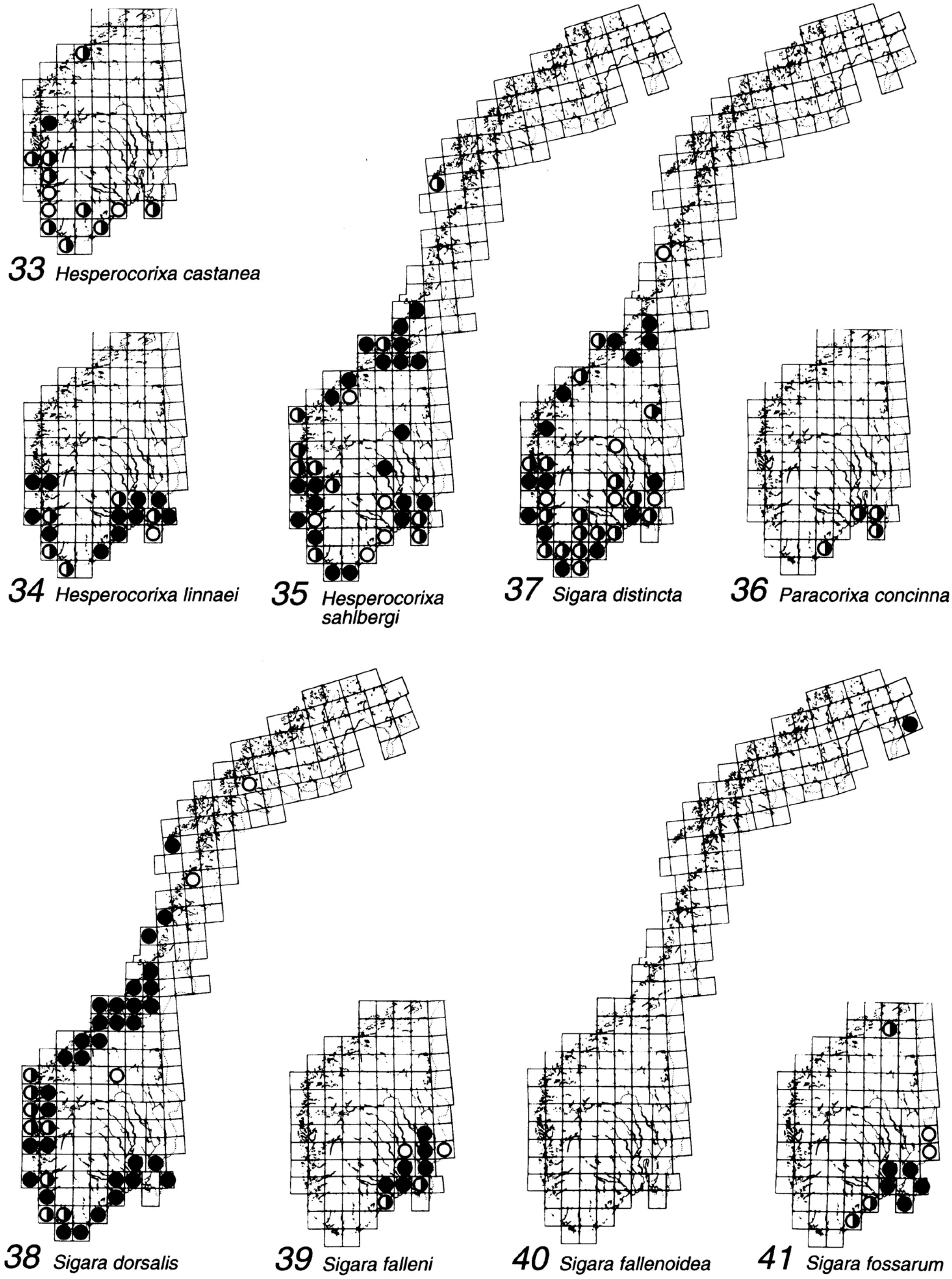

Figure 3 continued. Maps of the distribution of the 53 species of water bugs. The symbols are fully explained in the text; cf. also the short description in the legend to Figure 2. ● = Data after 1950, coll. Økland. Environmental variables registered. ◗ = Data from 1950 and later, other collectors. ○ = Data from before 1950, various collectors. Species numbers 33-41.

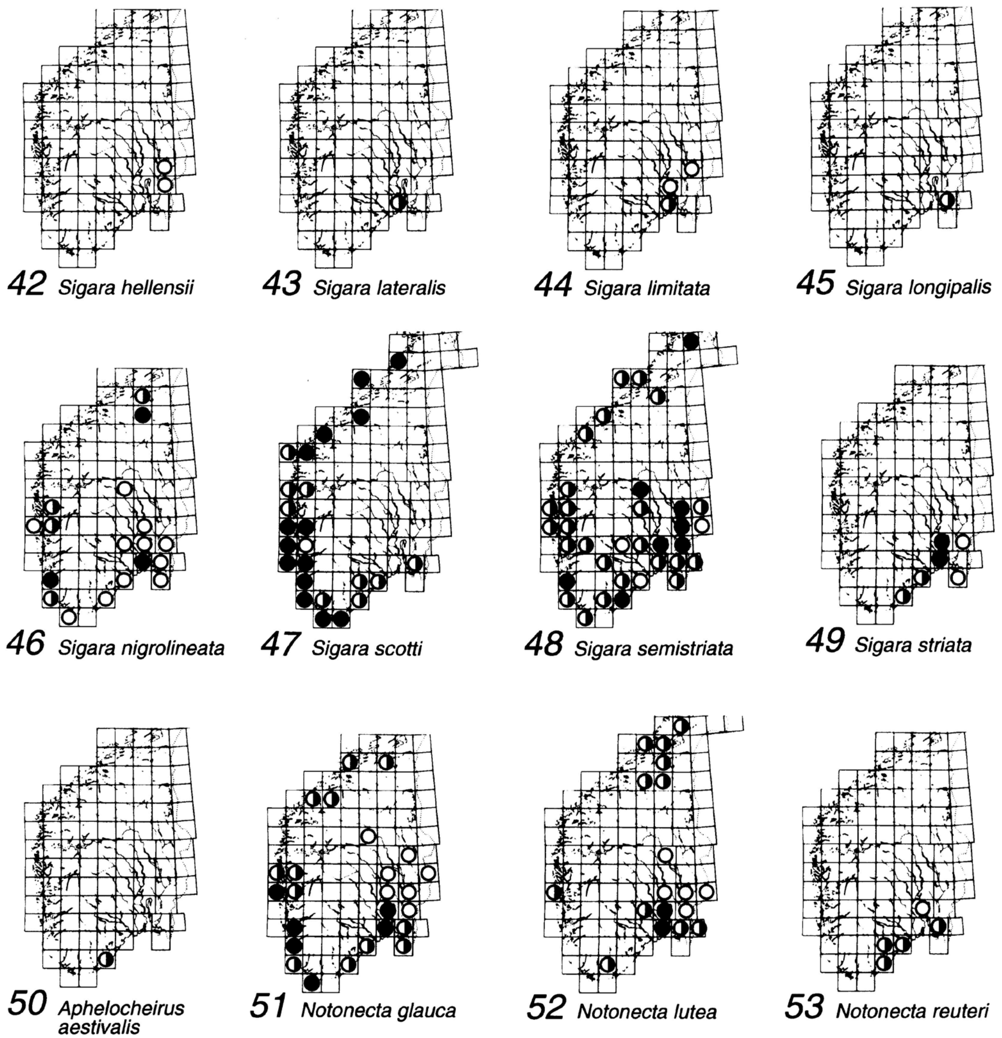

Figure 3 continued. Maps of the distribution of the 53 species of water bugs. The symbols are fully explained in the text; cf. also the short description in the legend to Figure 2. ●= Data after 1950, coll. Økland. Environmental variables registered. ◗ = Data from 1950 and later, other collectors. ○ = Data from before 1950, various collectors. Species numbers 42-53.

7. *Velia caprai* Tamanini, 1947
General distribution: All Europe except the northeastern part. In Norway found in coastal areas in the S and SW northwards into Trøndelag in 38 localities with 45 records. The records from SE Norway in Warloe (1925) and Jastrey (1981) refer to *V. saulii* according to specimens in ZMO. It is found in lotic habitats, mainly in small streams and creeks, often in colonies and at shady places of the shore. It has seldom been found in lakes. Univoltine, hibernates as adult.

8. *Velia saulii* Tamanini, 1947
General distribution: Europe, eastwards to

Western Russia. The distribution in Fennoscandia is very restricted. In Sweden it is only found on the island of Gotland, in Denmark from northernmost Jutland and in Finland, only in the southeast. In Norway (with the exception of two old records from the SE) found in coastal localities northwards into Trøndelag. 18 localities and records. There is very little information of its habitats in Norway. It seems to prefer larger, more open and not so shady, slow-flowing waters. In Britain it is mostly found on still water especially such with stony margins (Huxley 2003). According to Andersen & Kaiser (1964) it is night-active and is during the day hiding among vegetation and under stones. Univoltine, hibernates as adult.

Family Gerridae

9. *Aquarius najas* (DeGeer, 1773)
General distribution: Most of Europe with the exception of the northernmost part. Also in North Africa. In Norway rare, found in the S and SE in 10 localities with 13 records. It is rheophilous and occurs usually gregarious in great numbers – in moderately-flowing rivers and especially at shady parts in woodland or near bridges. It is seldom found on lakes. Jastrey (1981) found it on a small creek outlet in the sea with periodically brackish water. All Norwegian records are of the apterous form. Univoltine, hibernates as adult.

10. *Aquarius paludum* (Fabricius, 1794)
General distribution: Most of Europe with the exception of the northwestern part and most of Spain and Portugal. Also in most of Asia and in Burma, India, Thailand and Vietnam. In Norway a rare species with 11 records from eight localities in the SE part. It is found in lakes where it prefers open areas free from vegetation and away from the shore. It is usually gregarious but does not appear in such masses as *A. najas*. Hibernates as adult. In Denmark and S Sweden the species is partially bivoltine (Damgaard 1997, Coulianos pers.obs.), and in Germany it is bivoltine or partially bivoltine (Wachmann et al. 2006). The data are too sparse to draw any conclusions of its life cycle in Norway.

11. *Gerris argentatus* Schummel, 1832
General distribution: The whole of Europe, western North Africa and eastwards to Central Asia and the Far East. In Norway found in the SE at 20 localities with 33 records. According to our data it is found at the shore of lakes with rich vegetation. It has also been found in lakes surrounded by *Sphagnum* bogs. It is partially bivoltine and hibernates as adult.

12. *Gerris lacustris* (Linnaeus, 1758)
General distribution: The whole of Europe. Also in North Africa and in Asia eastwards to China and Korea. In Norway found northwards into Troms as a common species with 331 records from 291 localities. It preferred lakes and was significantly absent from water bodies smaller than ponds. However, it is known to inhabit also small or very small water bodies (Vepsäläinen 1973, Wachmann et al. 2006, Coulianos pers. obs.). The species showed preference for lowland areas up to 400 m altitude and avoidance for higher regions (Figure 4, variables 1-2). For the lake habitats in Figure 4 it appears that *G. lacustris* preferred high water temperature, aquatic vegetation of *Sphagnum* bog or of a rich growth of other helophytes, including stands where eutrophic species are represented, sediments of dy (a signal of dystrophic conditions) or dygyttja or clay/gyttja (the latter indicating eutrophic environments), small wave action, high concentrations of calcium and magnesium in the water and high water colour. *G. lacustris* avoided low water temperature, shores with poor aquatic vegetation and where stones dominate the shoreline, medium wave action, low concentrations of calcium and magnesium and low water colour. The species showed no response to pH. These habitat requirements are in agreement with what is known of the ecology of the species from other parts of Fennoscandia. Hibernates as adult. According to an analysis of phenological data *G. lacustris* is bivoltine in Norway as is the case in other parts of Fennoscandia and Germany (Andersen 1973, Wachmann et al. 2006).

13. *Gerris lateralis* Schummel, 1832
General distribution: The whole of Europe (except the SE part) and in Asia eastwards to the

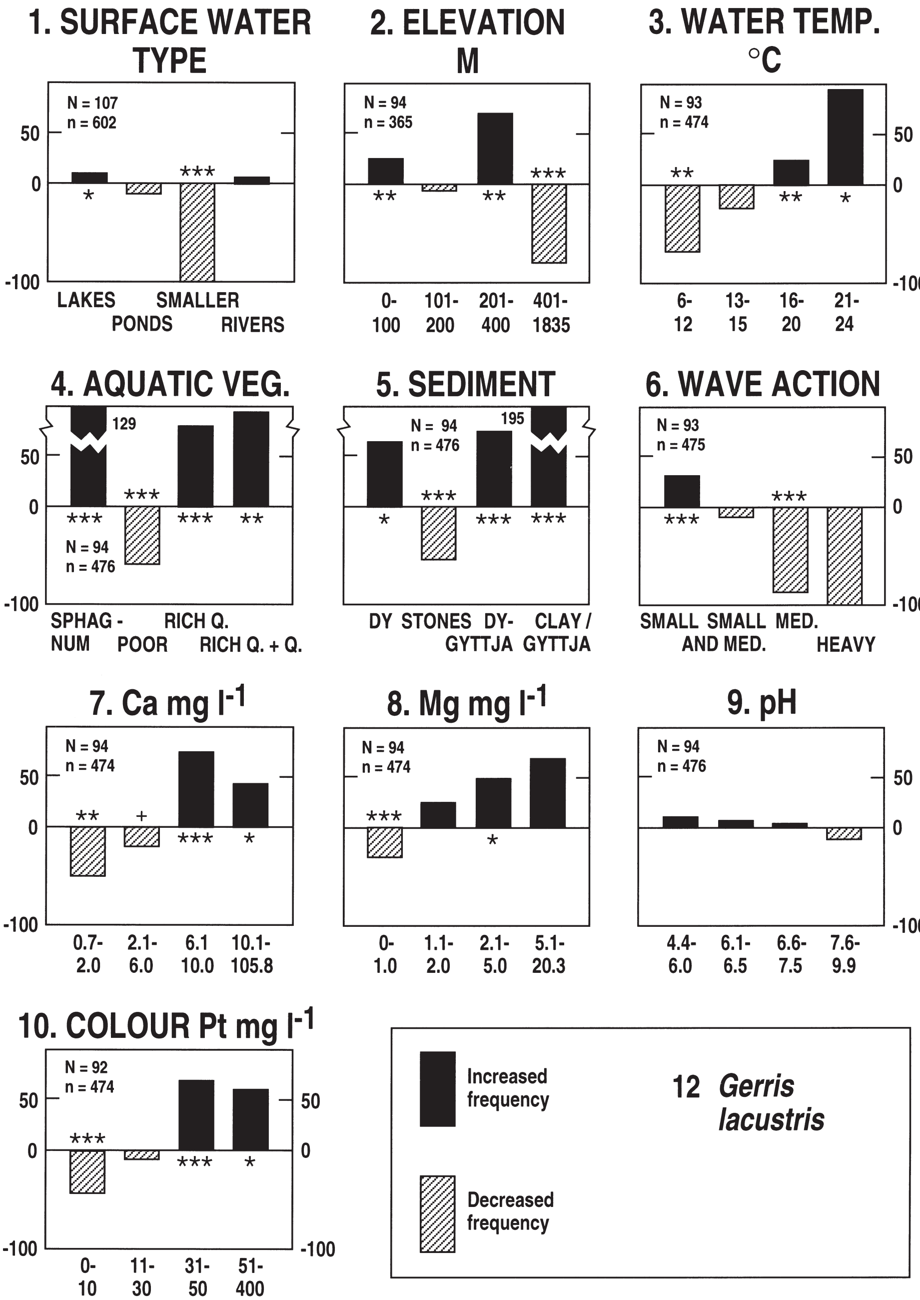

Figure 4. Occurrence of *Gerris lacustris* in relation to 10 environmental variables. The frequency of occurrence is expressed as deviations from the zero value expected on the basis of random distribution. Black bars: higher frequency, shaded bars: lower frequency. Probability levels for significant deviation: *** = 0.001, ** = 0.01, * = 0.05, + = 0.10. All types of surface waters were used for Variables 1 and 2; lakes only were used for Variables 3–10; localities in South Norway were used for Variable 2; for Variables 1 and 3–10 lakes throughout Norway were used.

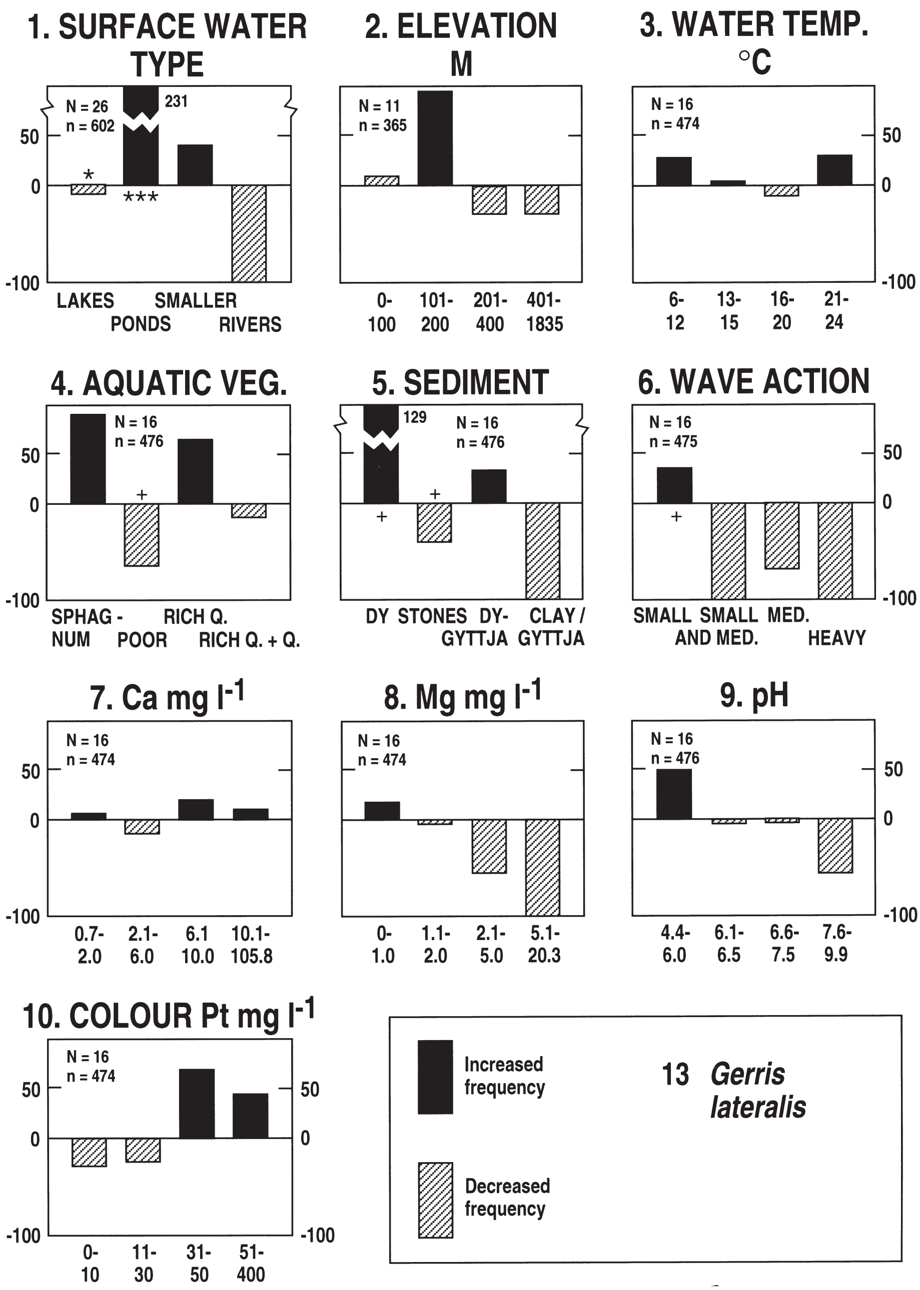

Figure 5. Occurrence of *Gerris lateralis* in relation to 10 environmental variables. For more information cf. the legend to Figure 4.

Far East. Common and distributed throughout Norway. Found in 123 localities with 127 records, including the northernmost in Europe. This species had few significant responses to the environmental variables analysed in Figure 5. The strongest response was for the type of surface water (variable 1): a preference for ponds and avoidance of lakes. There was no response to elevation above sea level (variable 2). For the 16 records from lakes there was a preference for those of small wave action (which also characterizes ponds) and avoidance of sites with poor aquatic vegetation where stones dominate the shoreline. The remaining lake variables gave no significant responses (water temperature, calcium, magnesium, pH, water colour). This is an indication of wide ecological amplitude and well in line with its wide distribution range. The preference for ponds and other small waters with rich vegetation which creates shaded hiding places is known also from Denmark, Germany and Sweden (Damgaard 1997, Wachmann et al. 2006, Coulianos pers.obs.). Univoltine and hibernates as adult.

14. *Gerris odontogaster* (Zetterstedt, 1828)
General distribution: The whole of Europe with the exception of the Iberian Peninsula and the Mediterranean, most of Asia eastwards to the Far East. Common and distributed throughout Norway and found in 111 localities with 120 records, including the northernmost in Europe. This species preferred ponds and was significantly absent from smaller water bodies (Figure 6, variable 1). However, it is also recorded from small and very small waters (Huxley 2003, Wachmann et al. 2006, Coulianos pers. obs.). It showed a preference for lowland areas and avoidance of those above 400 m altitude (variable 2). For the lake habitats we note that *G. odontogaster* preferred aquatic vegetation of *Sphagnum* bog, or of rich stands of helophytes including eutrophic species, sediments of dygyttja or clay/gyttja, small wave action, high concentrations of calcium and magnesium in the water and high water colour. *G. odontogaster* avoided poor vegetation, shorelines dominated by stones, low concentrations of calcium and magnesium and low water colour. The species was significantly absent from lakes of low water temperature. This is well in line with its avoidance of areas of high elevation. It showed no response to the pH level. Jastrey (1981) recorded it also from mountain areas and by the sea in slightly brackish waters. Hibernates as adult, and analysed phenological data indicate that it is partially bivoltine in Norway up to Trøndelag. The data from localities further north are too scanty to permit any conclusions of the life cycle of the species in these areas.

15. *Gerris thoracicus* Schummel, 1832
General distribution: The whole of Europe, North Africa and South Asia eastwards to Afghanistan. Also in N India and Kashmir. In Norway rare and found in the SE and SW parts with 11 records from 10 localities. Records in Warloe (1925) from the faunistic districts ON and BØ refer to *G. lateralis* according to specimens in ZMO. The species typically inhabits shallow pools and small puddles, often with a muddy bottom, ditches and slow-flowing waters. In Fennoscandia it is almost exclusively found in coastal areas, including rock pools. In Finland it is only found in rock pools at the Baltic coast (Vepsäläinen 1973). This is also a common habitat for the species in Sweden. In other parts of its distribution area it is also found in inland localities. The localities in Norway are all at the coast. Univoltine, hibernates as adult.

16. *Limnoporus rufoscutellatus* (Latreille, 1807)
General distribution: A Holarctic species distributed in the whole of Europe with the exception of the Iberian Peninsula and the Mediterranean. In Asia eastwards to the Far East, China and Japan. Also in Alaska and Canada. In Norway found at 34 localities with 37 records, common in the SE and with isolated records in the SW and NE, including the northernmost in Europe. The species prefers small water bodies with still or slow-flowing water and with dense shore-vegetation. It has a strong migratory behaviour and most individuals are macropterous. Univoltine, hibernates as adult.

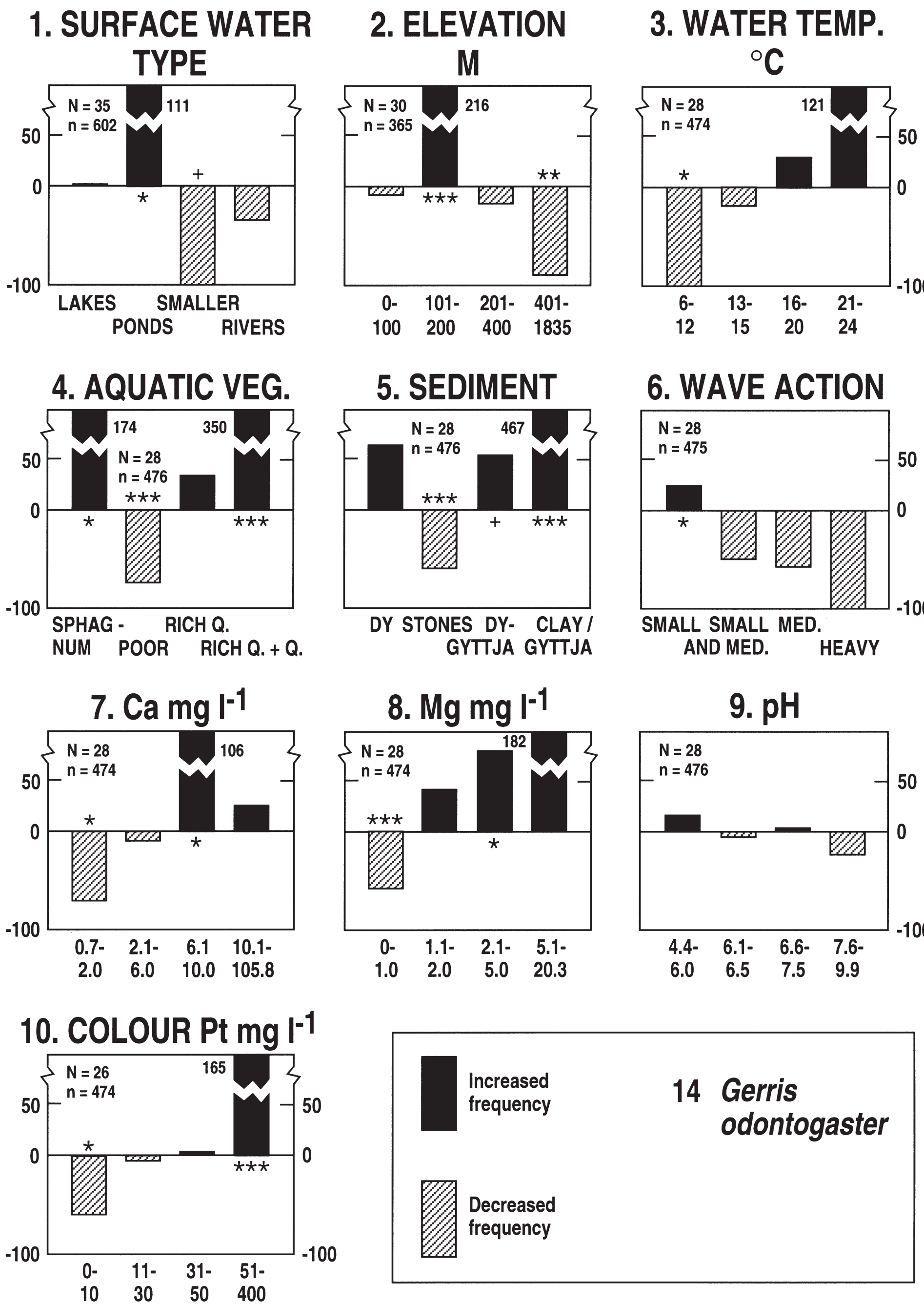

Figure 6. Occurrence of *Gerris odontogaster* in relation to 10 environmental variables. For more information cf. the legend to Figure 4.

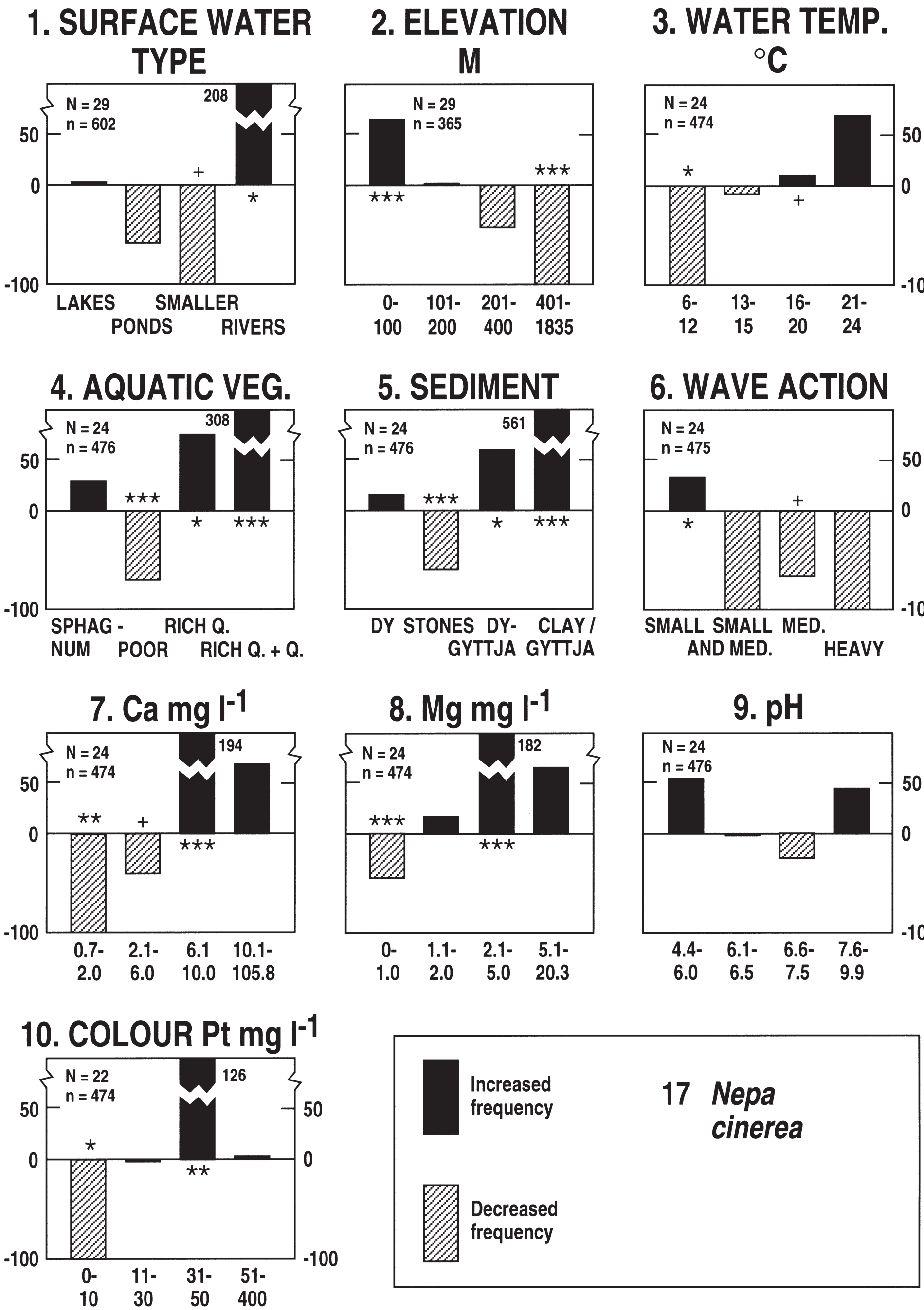

Figure 7. Occurrence of *Nepa cinerea* in relation to 10 environmental variables. For more information cf. the legend to Figure 4.

Family Nepidae

17. *Nepa cinerea* Linnaeus, 1758

General distribution: Widely distributed in the Palaearctic with the exception of the S and SE parts. In Norway common in the southern part with 139 records from 123 localities. Our records show that it occurred in lakes and ponds but preferred rivers, and was significantly absent from the smaller water bodies (Figure 7, variable 1). Variable 2 shows preference for lowland habitats up to 100 m altitude. This is connected to its coastal distribution in many areas (Figure 3) and significant absence from sites above 400 m. In the lake habitats in Figure 7 (variables 3-10), *N. cinerea* preferred rather high water temperature, rich vegetation, also where eutrophic plant species were represented, sediments of dygyttja or clay/gyttja, small wave action, high concentrations of calcium and magnesium in the water and high water colour. *N. cinerea* avoided sites with poor aquatic vegetation and stony shore, medium wave action, fairly low concentrations of calcium and low concentrations of magnesium. The species was significantly absent at low water temperature, low concentrations of calcium and low water colour. *N. cinerea* showed no response to the pH level in the water. Univoltine, hibernates as adult.

18. *Ranatra linearis* (Linnaeus, 1758)

General distribution: Most of the Palaearctic region with the exception of the most southern and eastern parts. In Norway not common, found in the SE part in 24 localities with 29 records. The typical habitat is not too shallow lakes and ponds with emergent vegetation. The insects sit among the plants near the water surface waiting for suitable prey. The species is a good flyer and can be found in new ponds and gravel pits, often within a year or two of excavation. This has been recorded in Britain (Huxley 2003) and Sweden (Coulianos pers.obs.) Univoltine, hibernates as adult in the water. It can be active under the ice and often appears at the surface when holes are drilled in the ice for fishing.

Family Corixidae

19. *Micronecta minutissima* (Linnaeus, 1758)

General distribution: Europe from SE England to Poland, and from S Norway to S Finland and lowland Russia. Not recorded from S Europe. In Norway rare and found in the SE from five localities with seven records listed by J. Økland (1964) and Coulianos (1998). First recorded from Norway by J. Økland (1964), earlier published records refer to *Micronecta poweri* according to specimens in ZMO. This was also suspected by Jastrey (1981). Red-listed as Endangered (EN). The species is found in still or slow-flowing water especially at shallow depth at the shore, and it prefers stony bottom with sand or clay. It avoids rich vegetation and accumulation of organic matter (Jansson 1977). However, the Norwegian localities had rich vegetation, and the sediment was gyttja or dygyttja. Under optimal conditions the species can be extremely abundant. In Norway univoltine, hibernating as IV (rarely III) larva.

20. *Micronecta poweri* (Douglas & Scott, 1869)

General distribution: Europe from N Spain, British Isles, Fennoscandia to Russia. In Norway not common and found northwards into Trøndelag in 21 localities with 27 records. The habitat is similar to that of the preceding species. It prefers oligotrophic waters but can be found also in moderately eutrophic sites (Jansson 1977). The Norwegian records are from these two types of waters. Univoltine, hibernates as IV stage larva.

21. *Cymatia bonsdorffii* (C. R. Sahlberg, 1819)

General distribution: Northern part of Europe, Asia to NE China and the Far East. In Norway common and found throughout the country, evenly distributed in the south, isolated records from Trøndelag and Troms. Found in 71 localities with 85 records. In material A the species was only collected in lakes and had a significant preference for this type of surface water (Figure 8, variable 1). We also note that *C. bonsdorffii* preferred lowland sites at 101-200 m altitude and was significantly absent from those above 400 m (Figure 8, variable 2). For the remaining variables in Figure 8 it may be noted that the species preferred high water temperature, rich aquatic vegetation where eutrophic plants occurred, sediments of dygyttja or clay/gyttja, small wave action, relatively high concentrations of calcium and magnesium in the

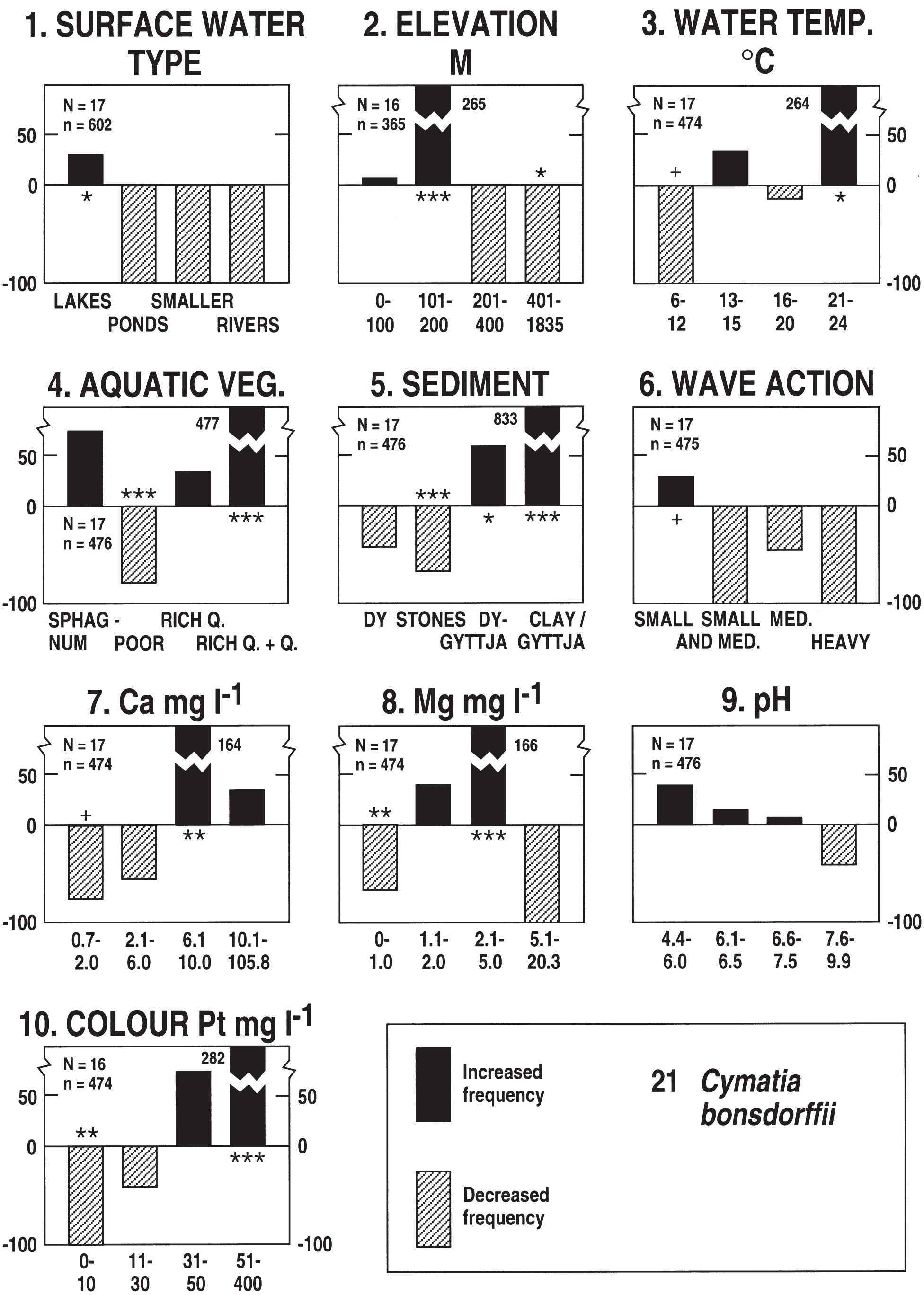

Figure 8. Occurrence of *Cymatia bonsdorffii* in relation to 10 environmental variables. For more information cf. the legend to Figure 4.

water and high water colour. The species avoided poor aquatic vegetation, stony shores and low concentrations of calcium and magnesium. *C. bonsdorffii* was significantly absent from lakes with low water temperature and low water colour. It showed no response to the pH level of the water. Even if it has a wide tolerance to the pH level, it has been reported to prefer acid water (Huxley 2003, Wachmann et al. 2006). It also seems to have a wide tolerance to types of aquatic vegetation. Jastrey (1981) said that in Norway the species often had been found in oligotrophic lakes with sparse vegetation. On the other hand Henrikson & Oscarson (1985) reported it from Sweden in lakes with rich vegetation. In Norway univoltine, hibernates as adult.

22. *Cymatia coleoptrata* (Fabricius, 1777)
General distribution: North and Central Europe, Asia to E Siberia. Not in N Fennoscandia. From Norway there is only an old record from ON Dovre leg. Boheman probably in 1832, according to a specimen in coll. NRM. Concerning the extensive collecting of water bugs in Norway in recent years with no records of this species, its status in Norway seems uncertain. Red-listed as Data Deficient (DD) in Norway. In S Sweden the species is widely distributed, common and often very abundant in smaller lakes, ponds and ditches with rich aquatic vegetation; mostly brachypterous, macropterous individuals capable of flight are very rare. Univoltine, hibernates as adult.

23. *Glaenocorisa cavifrons* Thomson, 1869
Often regarded as a subspecies of *G. propinqua* (see below) but we follow Jansson (2000) who considered it to be a distinct species. General distribution: A Holarctic species known from Ireland, Great Britain (Wales, Scotland, Shetland Is), Norway, Sweden, Finland, Estonia, Russia to the Far East, Alaska and Canada. In Norway common and widely distributed, found in 76 localities with 91 records, including the northernmost in Europe. Norwegian records published before 1998 mostly as *G. propinqua*. It inhabits oligotrophic lakes and smaller waters of some depth, mostly with sparse vegetation. By Raddum et al. (1979) characterized as a pelagic predator often eaten by fish. In acidified waters with pH 4.5-4.9 where the fish population was depleted or extinct it could be very abundant. *G. cavifrons* was rare in waters with pH ≥ 5.0. In Group A material three records with pH 5.2-7.0 (Table 5). Univoltine, hibernates as adult.

24. *Glaenocorisa propinqua* (Fieber, 1860)
General distribution: Europe from S England, Central Europe, Denmark, S Fennoscandia to Central Russia. In Norway only one record (Coulianos 1998). All Norwegian records published before 1998 refers to *G. cavifrons*. Red-listed as Data Deficient (DD) There is no information of its habitat requirements in Norway. In Sweden it lives in oligotrophic lakes and deeper ponds with sparse vegetation. It is a pelagic predator which can be found at considerable depths, down to 14 m (Henrikson & Oscarson 1985). In SW Sweden it has spread northwards in acidified waters where the fish population has diminished or been extinct. In such waters it can be extremely abundant. In Denmark and Sweden univoltine or partially bivoltine, hibernates as adult (Damgaard 1997, Coulianos pers.obs.).

25. *Arctocorisa carinata* (C. R. Sahlberg, 1819)
General distribution: Europe with a boreo-alpine type of distribution. Isolated populations on Iceland, the Faeroe Is, in N Britain and Fennoscandia, and in the Alps and Balkan mountains. Also in W Siberia. The distributional history of the species has been studied by Jansson (1980). See also J. Økland & K.A. Økland (1999). In Norway common, widely distributed and found in 99 localities with 117 records, including the northernmost in Europe. Typical habitats in Norway are large or medium sized lakes with sparse vegetation and often acidic water. Raddum et al. (1979) found it frequent and abundant in acid lakes with pH 4.5-4.9. Jastrey (1981) reports it from larger and deep lakes and in brackish pools at the coast. In Sweden and Finland common in rock pools. Univoltine, hibernates as adult.

26. *Arctocorisa germari* (Fieber, 1848)
General distribution: British Isles, Fennoscandia,

northern part of Central Europe, the Alps, Balkan mountains, Russia, Mongolia and Siberia. In Norway common and found northwards into Nordland in 79 localities with 81 records. It occurs at places with a wide range of ecological conditions. A common habitat is rather large and deep lakes with sparse or very little vegetation. It tolerates a wide span of pH. Jastrey (1981) found evidence for two generations per year in SW Norway. Hibernates as adult.

27. *Callicorixa praeusta* (Fieber, 1848)
General distribution: Europe except the Mediterranean, Asia to the Far East, Mongolia, Kamtsjatka and China. In Norway not common, found northwards into Trøndelag in 20 localities with 23 records. In many types of still and slow-flowing waters with rich vegetation and high level of nutrients. Jastrey (1981) found it in polluted waters. Partially bivoltine in Norway. Hibernates as adult.

28. *Callicorixa producta* (Reuter, 1880)
General distribution: Fennoscandia, Denmark, Germany, N Russia, Kazakhstan, Mongolia, Siberia, Far East. In Norway common, widely distributed throughout the country and found in 129 localities with 155 records, including the northernmost in Europe. Our data showed preference for ponds, and it avoided, but tolerated lakes. The species was significantly absent from the smallest water bodies (Figure 9, variable 1). Records were too few in S Norway for a calculation of response to elevation above sea level. For the lake habitats in Figure 9 (variables 3-10) we note that *C. producta* preferred sites with high water temperature, rich aquatic vegetation with eutrophic species, sediment of dygyttja, high concentrations of calcium and magnesium in the water and high pH values. The species avoided stony shores, fairly low calcium concentrations and pH levels of 6.6-7.5. *C. producta* was significantly absent from lakes with low water temperature, and showed no response to wave action and water colour. Jastrey (1981) found it in fairly rich lakes and ponds and in oligotrophic lakes on the coast of W Norway as well as in smaller waters in mountain districts. In Finland, Sweden and on Bornholm it is common in rock pools. Jastrey (1981) reported two generations per year in SW Norway. Our data indicate that it is partially bivoltine in S Norway but univoltine north of Trøndelag.

29. *Callicorixa wollastoni* (Douglas & Scott, 1865)
General distribution: Faroe Is, N Britain, Ireland, N Scandinavia, Russia, Siberia and NE China. In Norway common and widely distributed especially in the S. Found in 73 localities with 78 records, including the northernmost in Europe. It inhabits oligotrophic lakes, ponds and mires. According to Jastrey (1981) the species shows a preference for mountain districts, but is also found in small lakes and ponds in the lowlands. In N Britain the typical habitat is acid moor land and upland tarns and lochs (Huxley 2003). Univoltine, hibernates as adult.

30. *Corixa dentipes* Thomson, 1869
General distribution: British Is, Central Europe, Denmark, S Fennoscandia, Russia, Siberia. In Norway rather common and found in 35 localities with 45 records. Lives in a wide range of still and (more rarely) slow-flowing waters. Jastrey (1981) found it in both small ponds with rich vegetation and in larger, oligotrophic lakes. It occurs often together with other species of Corixidae such as *C. punctata*. Univoltine, hibernates as adult.

31. *Corixa panzeri* Fieber, 1848
General distribution: Europe except the NE part. In N Europe including S Scandinavia mainly in coastal areas. In Norway found in one coastal locality with two records in a deep, meromictic brackish-water lake where the salinity in the surface layer was 1.2-2.3 ‰ (Dolmen 2004). A new record from the same area is reported by Olsen (2008). These habitats are of the same type as reported from Denmark and Sweden where the species in most cases is found in coastal areas in dammed fjords, and in smaller lakes and ponds with slightly saline water. Hibernates as adult. Life cycle in Scandinavia not known. In Norway red-listed as Vulnerable (VU).

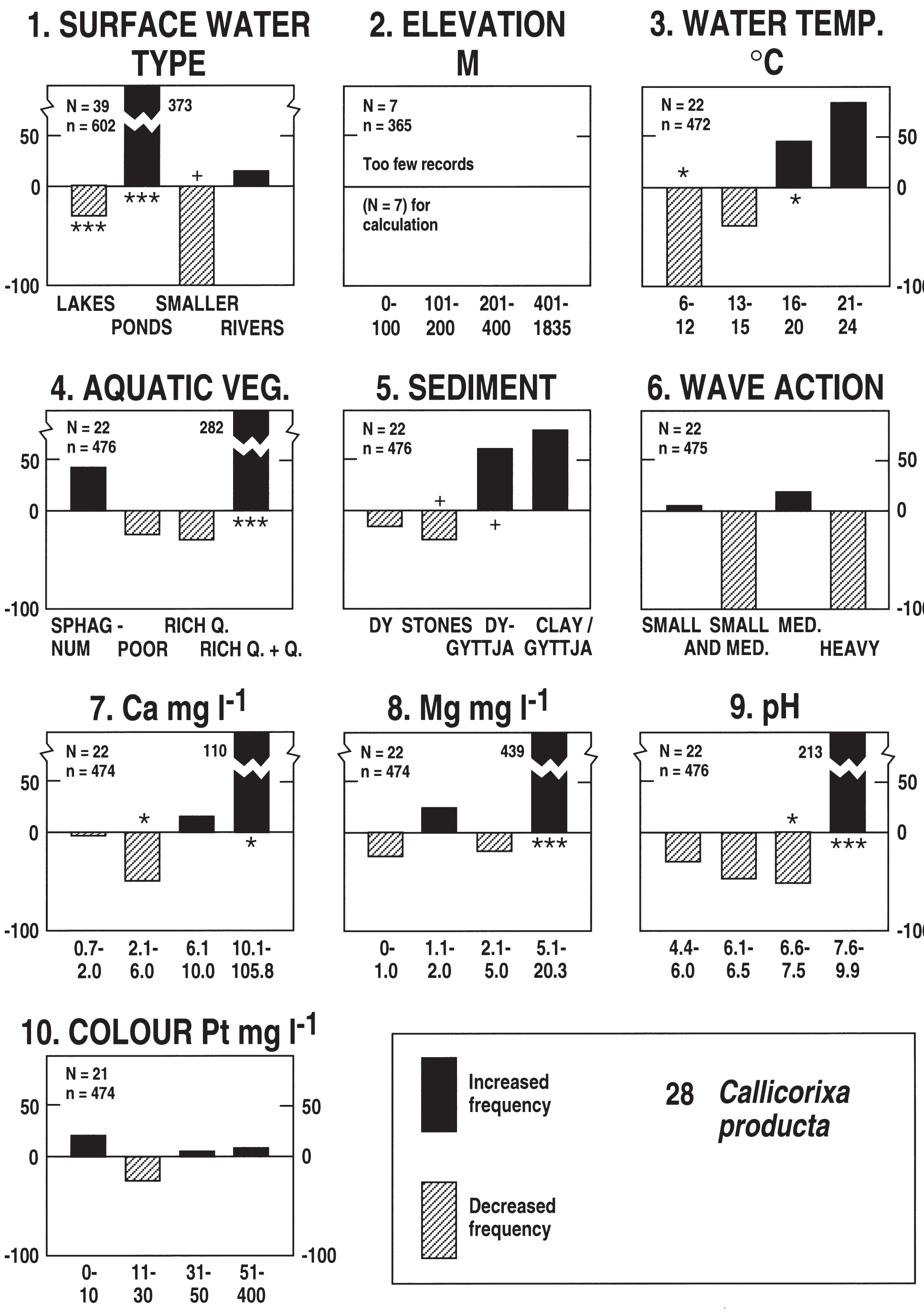

Figure 9. Occurrence of *Callicorixa producta* in relation to 9 environmental variables. For more information cf. the legend to Figure 4.

32. *Corixa punctata* (Illiger, 1807)
General distribution: Europe from S Scandinavia to N Africa, Asia Minor, Caucasian region to China and India. In Norway rare, found in the SE in nine localities with 13 records. Usual habitats are ponds or slow-flowing waters with rich vegetation. Norwegian habitats are eutrophic and mesotrophic ponds. It seems to avoid larger lakes. Univoltine, hibernates as adult.

33. *Hesperocorixa castanea* (Thomson, 1869)
General distribution: Europe except the SE part. From S Scandinavia, Great Britain to Spain, Portugal and Poland. In Norway rather common and found in 24 localities with 33 records. Habitats outside Norway are dystrophic and oligotrophic ponds, tarns and other small, often acidic waters with thick vegetation. In the Group A material only in one water body, surrounded by *Sphagnum* bog and pH 4.7. Univoltine, hibernates as adult.

34. *Hesperocorixa linnaei* (Fieber, 1848)
General distribution: Europe except the northernmost part, east to Siberia, N Africa. In Norway rather common and found in 51 localities with 57 records. This species preferred lakes and was also present in ponds (Figure 10, variable 1). It has a preference for lowland areas and a significant absence from sites above 200 m altitude (variable 2). This is connected to its tendency for coastal sites. The only inland record is from HES: Hamar (EIS 46) (Olsen 2008). For the lake habitats in Figure 10 (variables 3-10) it showed preference for high water temperature, rich aquatic vegetation including eutrophic plants, sediments of dygyttja or clay/gyttja, small wave action, high concentrations of calcium and magnesium in the water and high water colour. *H. linnaei* avoided sites with fairly low concentrations of calcium and low concentrations of magnesium and fairly low water colour. It was significantly absent from sites with low water temperature, poor aquatic vegetation and a shore dominated by stones, medium wave action, and low concentrations of calcium and low water colour. It showed no response to the pH level. Life cycle not known, hibernates as adult.

35. *Hesperocorixa sahlbergi* (Fieber, 1848)
General distribution: Europe south of 65° N latitude east to E Siberia. In Norway common northwards into Nordland, found in 111 localities with 116 records. It preferred ponds and was significantly absent from smaller water bodies (Figure 11, variable 1). It preferred lowland areas up to 100 m altitude, avoided those above 200 m, and was significantly absent from those above 400 m (variable 2). The lake habitats in Figure 11 (variables 3-10) showed preference for high water temperature, rich aquatic vegetation, also stands with eutrophic plants, sediments of dygyttja and clay/gyttja, small wave action, high concentrations of calcium and magnesium in the water, slightly acidic water (pH 6.1-6.5) and high water colour. Its affinity to slightly acidic water should be pointed out since this water type is rare in eutrophic environments with high concentrations of calcium. *H. sahlbergi* avoided lakes with fairly low water temperature, poor aquatic vegetation and stony shores, medium wave action, low concentrations of calcium and magnesium, pH level of 6.6-7.5 and low water colour. It was significantly absent from sites with the lowest temperature range (6-12 °C). Probably univoltine, hibernates as adult.

36. *Paracorixa concinna* (Fieber, 1848).
General distribution: From British Is, Denmark, S Fennoscandia, Central and SE Europe to E Siberia and China. In Norway rare and found in 14 localities with 14 records, all in coastal sites of S Norway, in small eutrophic ponds (Dolmen & Simonsen 1989, Olsen 2008). Also in a brackish-water lake with salinity 1.2-2.3 ‰ (Dolmen 2004). This is in agreement with its known habitats, usually ponds, gravel pits and small lakes. It prefers slightly saline brackish water (Savage 1994). Its life cycle in Norway is not known, in England it is partially bivoltine (Savage 1971). Hibernates as adult. In Norway red-listed as Near Threatened (NT).

37. *Sigara distincta* (Fieber, 1848)
General distribution: N and Central Europe eastwards to E Siberia and Mongolia. In Norway common northwards into Nordland and found in

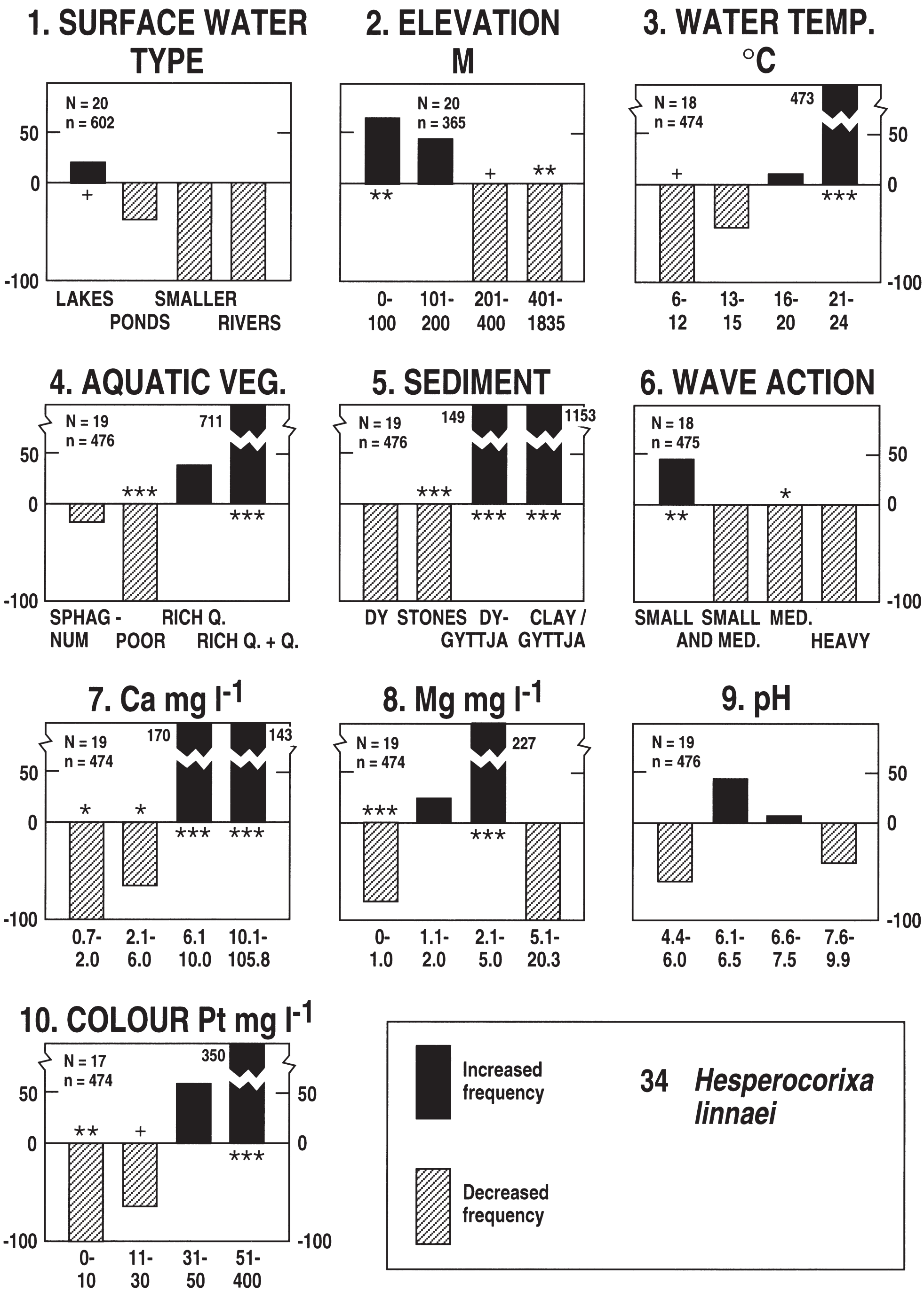

Figure 10. Occurrence of *Hesperocorixa linnaei* in relation to 10 environmental variables. For more information cf. the legend to Figure 4.

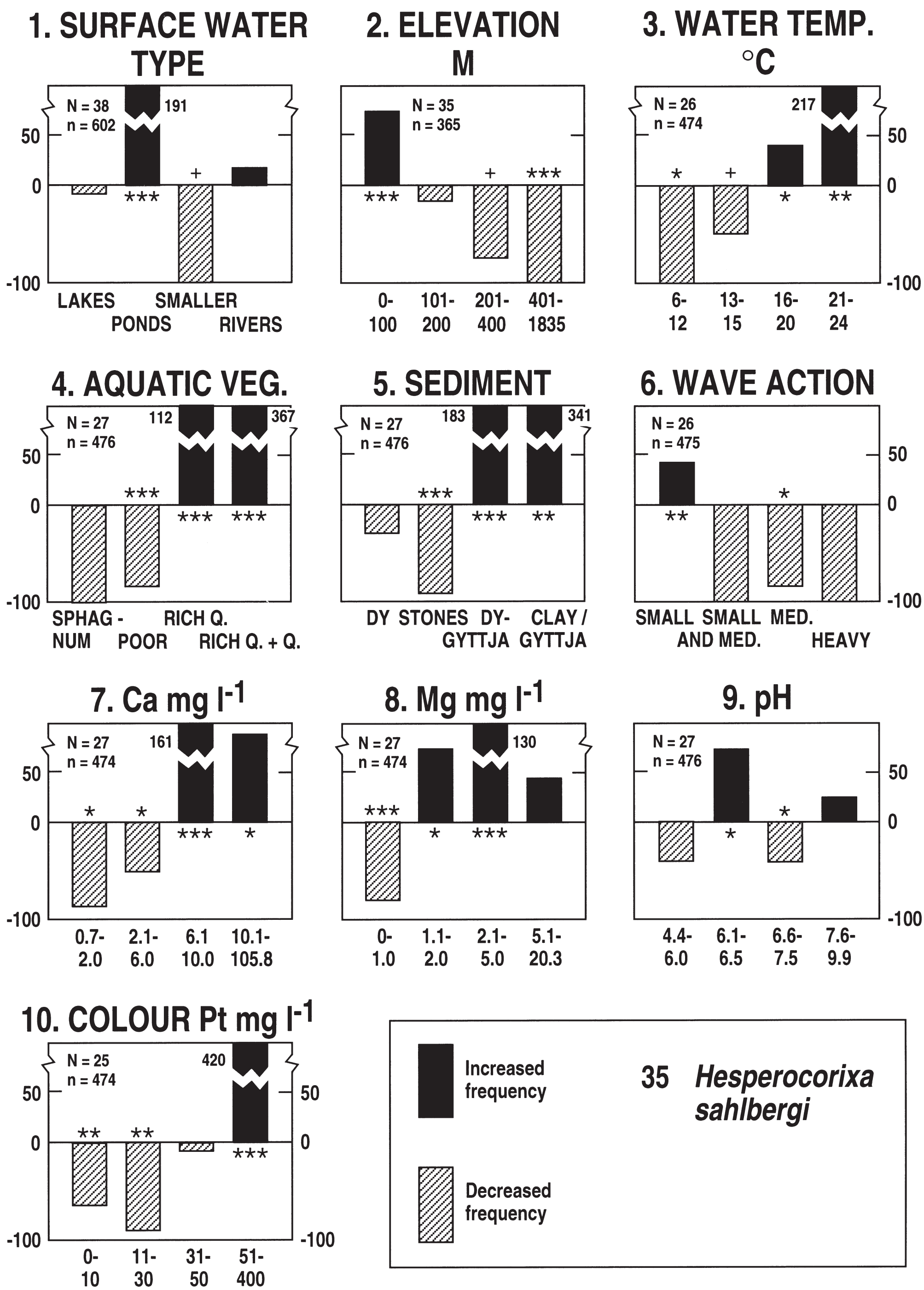

Figure 11. Occurrence of *Hesperocorixa sahlbergi* in relation to 10 environmental variables. For more information cf. the legend to Figure 4.

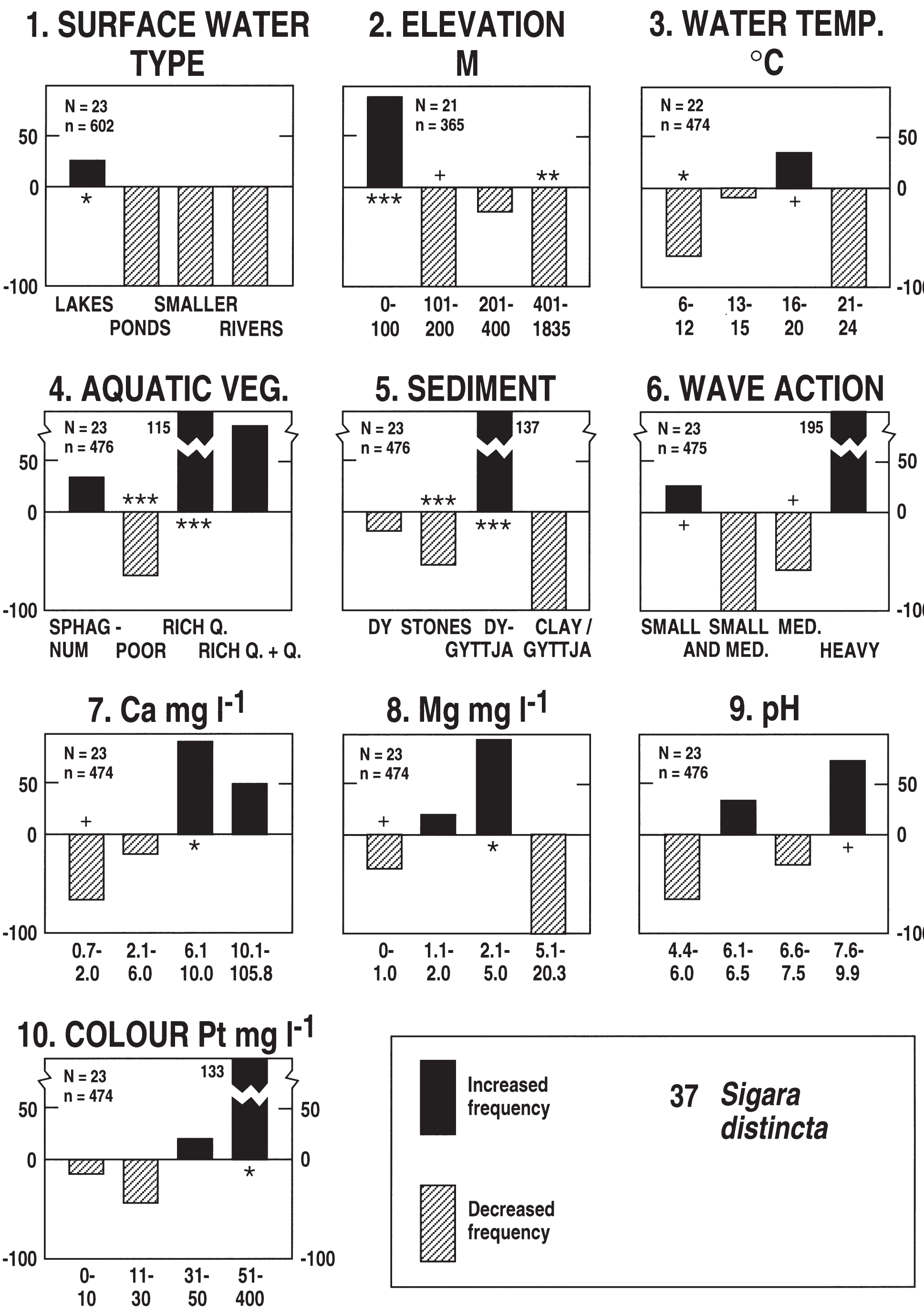

Figure 12. Occurrence of *Sigara distincta* in relation to 10 environmental variables. For more information cf. the legend to Figure 4.

165 localities with 179 records. In our data it was only collected in lakes and preferred lowland sites up to 100 m altitude and had a significant absence above 400 m (Figure 12, variables 1-2). It had a preference for relatively high water temperature, rich aquatic vegetation, sediments of dygyttja, small wave action, relatively high levels of calcium and magnesium in the water, high pH values and high water colour. *S. distincta* avoided sites with low water temperature, poor aquatic vegetation and stony shores, medium wave action and low concentrations of calcium and magnesium. Jastrey (1981) found it in small temporary ponds and in oligotrophic and eutrophic lakes, noting absence in the mountain districts. Our data indicate that it is bivoltine in Norway. Hibernates as adult.

38. *Sigara dorsalis* (Leach, 1817)
General distribution: Scandinavia, British Is, Belgium, France, Italy, Greece. In Norway common, found northwards into Troms in 202 localities with 204 records. This species preferred lakes and avoided water bodies smaller than ponds (Figure 13, variable 1). The coastal affinities of this widely distributed species is mirrored in a preference for extreme lowland areas up to 100 m altitude, avoidance of those of 101-200 m, and significant absence from those above 200 m. For the lake habitats in Figure 13 it appears that *S. dorsalis* preferred rather high water temperature, rich aquatic vegetation, also stands where eutrophic plant species occurred, sediments of dygyttja, small wave action, rather high contents of calcium and magnesium in the water and high water colour. It avoided sites with poor aquatic vegetation and stony shores, medium wave action, low concentrations of calcium and magnesium and low water colour. *S. dorsalis* was significantly absent from lakes with low water temperature and showed no response to the pH level. Nilssen (1980) found it in a small acidified watershed. Jastrey (1981) reported occurrence in larger lakes with little organic matter in the bottom substrate and sparse vegetation, and also found it to have two generations per year. Hibernates as adult.

39. *Sigara falleni* (Fieber, 1848)
General distribution: The whole of Europe eastwards to Siberia and China. In Norway rather common, found in the SE in 32 localities with 32 records. It prefers waters rich in calcium and avoids rich vegetation. It lives in lakes, ponds and small slow flowing waters with clear, non-acidic, non-saline waters (Huxley 2003). Hibernates as adult. Life cycle in Norway not known. In Britain and Germany it is bivoltine (Southwood & Leston 1959, Wachmann et al. 2006).

40. *Sigara fallenoidea* (Hungerford, 1926)
General distribution: A Holarctic species found on Ireland, in N Fennoscandia, Russia to Far East, Mongolia, Alaska and Canada. In Norway only one record, from Finnmark (Coulianos 1998), the northernmost in Europe. The locality was a eutrophic lake-bay with rich vegetation and pH 9.5 (K.A. Økland 1970). In N Sweden it has been found in a very shallow tarn with dy-bottom and sparse vegetation (Persson 1966) and abundantly in a bay of Rånelven river with rich vegetation and gyttja-bottom (Nilsson & Bondestad 1987). In Ireland it is found amongst water vegetation in calcareous lakes (Southwood & Leston 1959). The life cycle is not known. In Norway red-listed as Near Threatened (NT).

41. *Sigara fossarum* (Leach, 1817)
General distribution: Most of Europe, eastwards to E Siberia. In Norway northwards into Trøndelag, rather common in the SE and found in 35 localities with 35 records. Some older records refer to other species (Coulianos 1998). We have found it in lakes or ponds with rich to poor vegetation and pH 5.9-7.0. It has been recorded from ponds with scanty vegetation (Dolmen & Simonsen 1989) and in a deep brackish-water lake with low salinity (Dolmen 2004). Life cycle in Norway not known. In Britain and C Europe it is bivoltine (Southwood & Leston 1959, Wachmann et al. 2006). Hibernates as adult.

42. *Sigara hellensi* (C. R. Sahlberg, 1819)
General distribution: S Fennoscandia, Denmark, C Europe to Russia and Ukraine. In Norway rare with two old records from two localities and recently rediscovered in an eddy by the outlet of river Jøndalsåa in still water (Olsen 2008). Red-

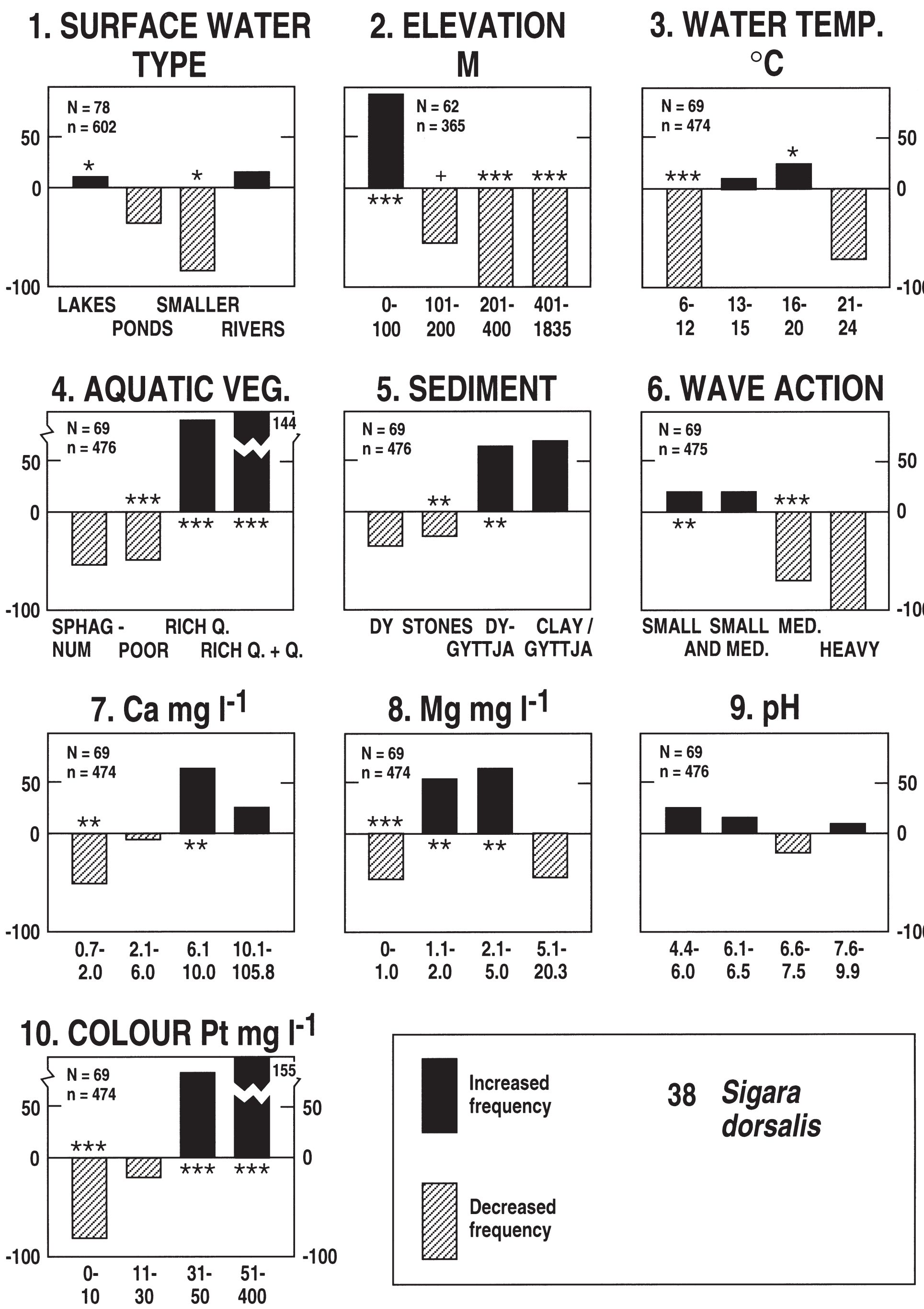

Figure 13. Occurrence of *Sigara dorsalis* in relation to 10 environmental variables. For more information cf. the legend to Figure 4.

listed as Endangered (EN). It lives in small, slow-flowing waters like ditches and small streams, often in agricultural districts. In Sweden it is univoltine and hibernates as adult (Coulianos pers.obs.)

43. *Sigara lateralis* (Leach, 1817)
General distribution: British Is, S Fennoscandia, C and S Europe, N Africa, C and S Asia to China, India, Africa. In Norway rare, found in the S in eight localities with eight records. Some of the records in Jastrey (1981) refer to other species (Coulianos 1998). It has been found in eutrophic ponds (Dolmen & Simonsen 1989) and often occurs in ponds polluted by cattle and in slightly saline or brackish waters (Coulianos pers.obs.). In Britain and Germany it is bivoltine (Southwood & Leston 1959, Wachmann et al. 2006). Hibernates as adult.

44. *Sigara limitata* (Fieber, 1848)
General distribution: British Is, S Fennoscandia, C and S Europe eastwards to W Siberia. In Norway rare, found in the SE in eight localities with eight records. First reported from Norway by Dolmen & Simonsen (1989) from a pond with clay bottom and very scanty vegetation. It is recorded from different kinds of ponds, often shallow with moderate vegetation, moorland ponds, ponds with alkaline water or cattle ponds (Huxley 2003, Southwood & Leston 1959, Wachmann et al. 2006). In C Europe bivoltine, in Britain probably so (Southwood & Leston 1959, Wachmann et al. 2006).

45. *Sigara longipalis* (J. Sahlberg, 1878)
General distribution: Fennoscandia, Denmark, C Europe, Russia eastwards to E Siberia. In Norway only recorded from two localities approximately 30 km apart: an artificial mesotrophic pond with sparse vegetation and in some ponds rich in lime (Spikkeland et al. 1998). Red-listed as Vulnerable (VU). In Sweden it has been found in newly excavated ponds with very sparse vegetation and ponds and small lakes with eutrophic conditions and rich vegetation (Coulianos pers.obs.). Life cycle not known. Hibernates as adult.

46. *Sigara nigrolineata* (Fieber, 1848)
General distribution: Europe, N Africa, SW Asia. In Norway rather common, found northwards into Trøndelag in 38 localities with 38 records. Very little is known of its habitats in Norway. Jastrey (1981) found it mostly in ponds, including temporary ones. It is known from a great variety of ponds, rarely from slow-flowing waters and shows different habitat preferences in upland and lowland districts, respectively (Huxley 2003, Wachmann et al. 2006, Coulianos pers. obs.). Hibernates as adult. Bivoltine in Britain, C Europe and S Sweden (Southwood & Leston 1959, Wachmann et al. 2006, Coulianos pers. obs.).

47. *Sigara scotti* (Douglas & Scott, 1868)
General distribution: SW Scandinavia, British Is, C and W Europe. In Norway common in coastal areas northwards into Trøndelag and found in 103 localities with 103 records. It preferred lakes, in lowland areas up to 100 m altitude (Figure 14, variables 1-2) connected to its coastal distribution. For the lake habitats in Figure 14 (variables 3-10) we note preference for high water temperature, rich aquatic vegetation, sediment of dygyttja, a fair amount of calcium in the water and high water colour. *S. scotti* avoided sites with relatively low water temperature, poor aquatic vegetation, stony shores and low concentrations of calcium. It was significantly absent from sites with the lowest temperature (below 13^{o} C) and showed no response to wave action, magnesium, and the pH level. In S Norway bivoltine, north of Hordaland univoltine. Hibernates as adult.

48. *Sigara semistriata* (Fieber, 1848)
General distribution: N and C Europe, eastwards to Mongolia and E Siberia. In Norway common, found northwards into Trøndelag in 79 localities with 80 records. We have found it in lakes with poor or rich vegetation, bottom with gyttja, dy or dygyttja and in localities surrounded by *Sphagnum* bog. Jastrey (1981) found it mainly in temporary or semi-permanent ponds, often in swamps with a peat bottom. This is also a preferred habitat in Sweden (Coulianos pers.obs.). Univoltine, hibernates as adult.

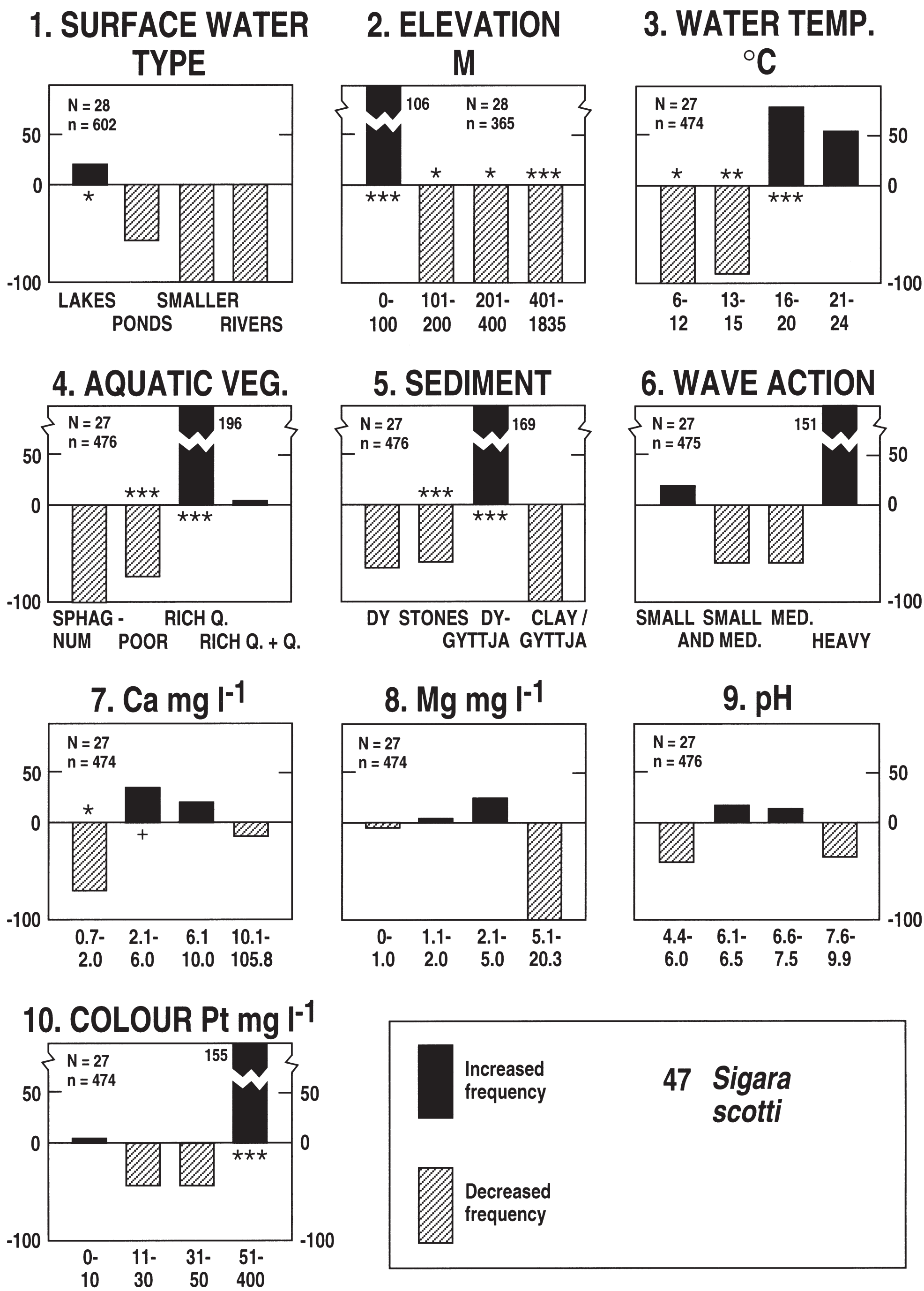

Figure 14. Occurrence of *Sigara scotti* in relation to 10 environmental variables. For more information cf. the legend to Figure 4.

49. *Sigara striata* (Linnaeus, 1758)
General distribution: Europe except the Iberian Peninsula, eastwards to E Siberia and NW China. In Norway not common, found in SE in 17 localities with 17 records. The records from the districts ON, RY and NTI in Warloe (1925) refer to *S. dorsalis* according to specimens in ZMO. Found in a variety of habitats, usually in eutrophic lakes and slow-flowing waters. Life cycle in Norway not known. In Britain and Germany it is bivoltine (Southwood & Leston 1959, Wachmann et al. 2006). Hibernates as adult.

Family Aphelocheiridae
50. *Aphelocheirus aestivalis* (Fabricius, 1794)
General distribution: Europe south to the N Mediterranean, Turkey, Georgia. In Norway rare, found in the S in two localities with three records. Recently rediscovered at one of the localities (Olsen 2008). Red-listed as Near Threatened (NT). It lives in flowing waters rich in oxygen. One of the Norwegian localities was in AAY Froland: Nidelva, a river with a maximum depth of 5 m, water current speed 0.5-1 m/s, and a bottom substrate of gravel and stones with sparse vegetation. Here it was very abundant (Sættem 1986). Univoltine, hibernates as adult.

Family Notonectidae
51. *Notonecta glauca* Linnaeus, 1758
General distribution: The whole of Europe, Egypt, eastwards to E Siberia and N China. In Norway common and found northwards into Trøndelag in 80 localities with 88 records. It was not found in the smallest water bodies and had no significant response to the other topographical types of surface water (Figure 15, variable 1). A preference for lowland areas up to 100 m altitude and significant absence from sites above 200 m are notable from variable 2 in the same figure. This is connected to the coastal location of the areas where the statistical material was collected. However, there are several older records from sites more inland. Jastrey (1981) did not find it in the mountain districts. From the lake habitats in Figure 15 (variables 3-10) it appears that *N. glauca* preferred high water temperature, rich aquatic vegetation, including places with eutrophic plants, sediments of dygyttja or clay/gyttja, small wave action, high concentrations of calcium and magnesium in the water and high water colour. It avoided sites with poor aquatic vegetation and stony shores, fairly low concentrations of calcium and low concentrations of magnesium, and low water colour. *N. glauca* was significantly absent from lakes with low water temperature, medium wave action, low concentrations of calcium and a low level of pH. Univoltine, hibernates as adult.

52. *Notonecta lutea* Müller, 1776
General distribution: Fennoscandia, C Europe, the Alps and SE European mountains, eastwards to E Siberia. Not in W and S Europe. In Norway common, found northwards into Trøndelag in 130 localities with 136 records. Norwegian records are mostly from dystrophic, moderately acid ponds, tarns and *Sphagnum* localities in coniferous woodland, but also in eutrophic ponds or small lakes in agricultural land (Dolmen & Aaagaard 1973, Jastrey 1981, Olsvik 1981, also our data). Such varied habitats have been recorded also in Denmark, Germany and Sweden (Damgaard 1997, Lundblad 1936, Wachmann et al. 2006, Coulianos pers.obs.). Univoltine, hibernates as egg.

53. *Notonecta reuteri* Hungerford, 1928
General distribution: N, C and E Europe eastwards to Far East, China and Japan. In Norway rare, found in SE in 15 localities with 15 records. Norwegian records are from bog- or forest ponds and tarns with scanty vegetation, apart from *Sphagnum* mosses, situated in 110-460 m altitude and with pH 4.4-5.0 (Dolmen 1989). In such types of habitats it has also often been found in Sweden but here also in more eutrophic ponds and small lakes (Coulianos pers.obs.). Univoltine, hibernates as egg.

DISCUSSION

Geographical distribution
All major parts of Norway are covered by the 50-km squares where water bugs have been collected (Figure 2, map 3). Consequently, we have a firm basis for a discussion of geographical distribution patterns.

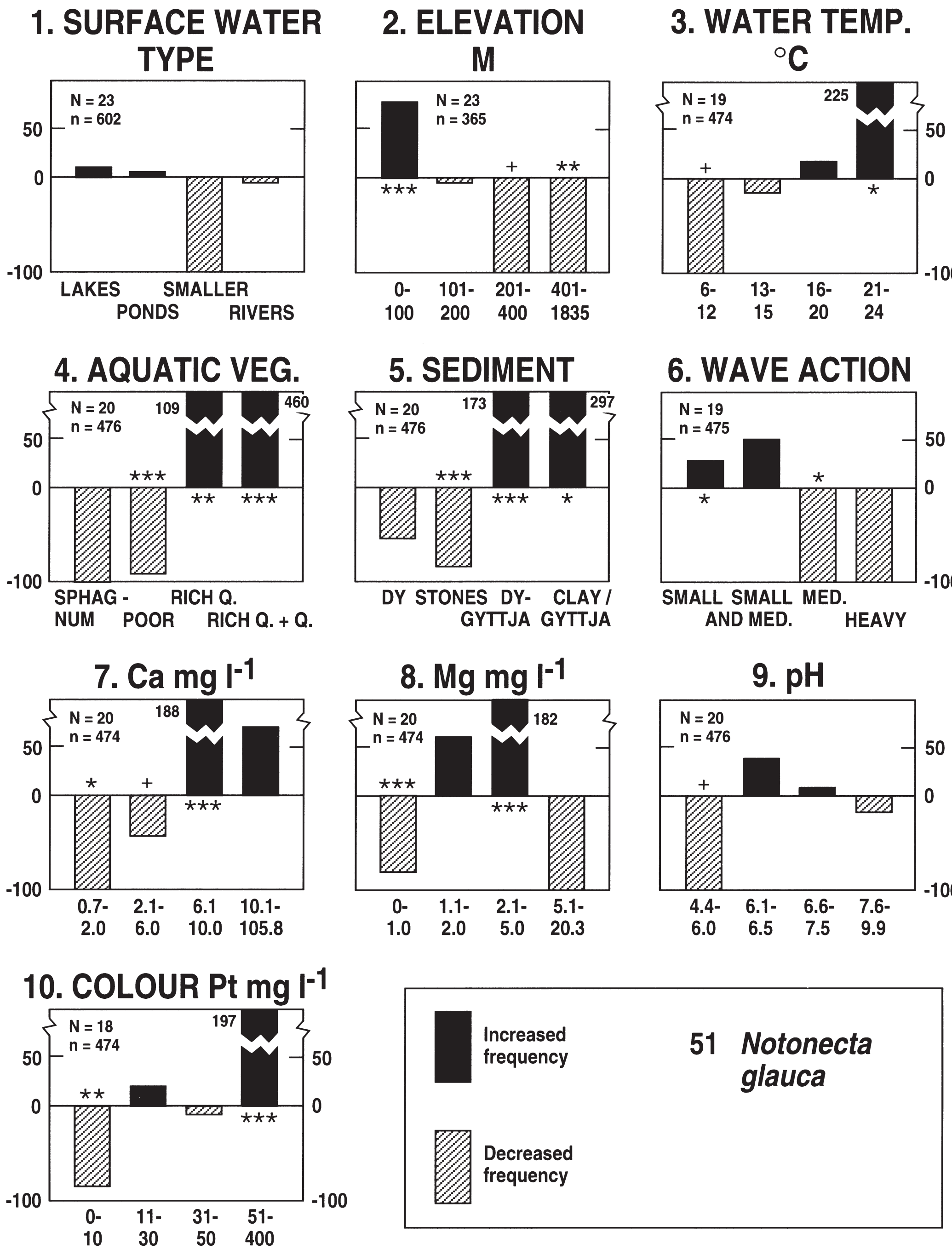

Figure 15. Occurrence of *Notonecta glauca* in relation to 10 environmental variables. For more information cf. the legend to Figure 4.

In a global perspective the distribution of the Norwegian water bugs belong to the following categories of distribution: 1) Holarctic: three species, 2) Palaearctic: eight species, 3) West-Palaearctic: five species, 4) Euro-Siberian: 26 species, 5) European: 11 species. More details may be found in the chapter on Results (Survey of the species).

Hypothetical late- and postglacial immigration routes for water bugs to Norway are 1) from the southeast from Sweden and Finland, 2) from the northeast from Russia, and 3) from the south and the southwest from Denmark, the "Dogger land" in the North Sea, and the British Isles. For general aspects of such immigration routes see J. Økland (1990: 425), Solem & Alm (1994), J. Økland & K.A. Økland (1999: 61), and for *Arctocorisa carinata* see Jansson (1980).

The wide latitudinal and vertical gradients in Norway are reasons for the considerable variations in the length of summer, the duration of ice-cover on lakes, and for other environmental variables influenced by temperature. These gradients make Norway particularly suitable for biogeographical studies. The 243 000 lakes (J. Økland & K.A. Økland 2006: 26) include the northernmost ones on the European continent, north of 70° N (Figure 1). This area comprises the 20 northernmost 50-km squares of North Norway (Figure 3). Figure 3 also shows that a total of seven species of water bugs named in the chapter on Results (Survey of the species) are represented in this northernmost area. The only habitat in Norway with *Sigara fallenoidea*, south of 70 ° N, is also the northernmost record in Europe.

In Norway we also find the habitats with the highest altitudes in Northern Europe. One species (*Callocorixa producta*), found up to 1,020 m above sea level, represents these highlands.

In Norway some southern species are only found south of the solid line in Figure 16. The dashed line past Bergen in this figure reflects a narrow area with a favourable coastal climate inhabited by several southern species. But between the

Figure 16. In Norway, Sweden and Finland many species are restricted to areas southeast of the solid line. The continuation of the boundary of this zone in western South Norway is roughly marked by a dashed line northwards past Bergen. From J. Økland & K.A. Økland (2005) with kind permission of Springer Science and Business Media.

dashed line in the west and the Norwegian part of the solid line further east in Figure 16 colder mountain areas dominate. Here water bugs are scarcer – there are several examples in Figure 3.

In many groups of freshwater plants and invertebrates there is a clear tendency for southern species to penetrate further north in Sweden and Finland than in Norway. In Sweden this northern limit (shown as the solid line in Figure 16) is termed 'limes norrlandicus' since it runs through the area of Norrland (Moen 1999: 100). The following 10 species of Norwegian water bugs inhabit such more northern areas in Sweden and/or Finland: *Mesovelia furcata, Hydrometra gracilenta, Aquarius najas, Aquarius paludum, Gerris argentatus, Nepa cinerea, Ranatra linearis, Hesperocorixa linnaei, Sigara falleni* and *Notonecta glauca.*

Ecological aspects

Within Norway the southern lowlands have a fairly long summer (Sund 1968: 241). Here abundant marine deposits and cultivated fields often supply nutrients to the limnic habitats. In addition to their climatic advantages, these habitats therefore provide suitable localities for species which prefer or demand eutrophic or productive places to live.

The discussion of ecological aspects mostly includes results from the Group A material. Here the number of records in lakes was large enough for statistical treatments for 12 species. These species often have significant common reactions. This appears from many of the nine environmental variables tabulated in the vertical columns in Table 6 showing tendencies for environmental **preferences**, and in Table 7 comprising **absences and/or avoidances**. Statements on preference, avoidance and absence, as well as different probability levels for the statistical corroborations of these concepts, are treated in the chapter on Material and methods. Tables 6-7 are constructed from the frequency deviation diagrams for the 12 species, previously shown in Figures 4-15. More details may be found in these figures. The discussion mainly comprises the reaction of the species named in Tables 6-7.

One species listed at the bottom of Table 6 (*Notonecta glauca*) had no significant reactions to variable 1, surface water type. Of the remaining 11 species **six preferred lakes, four preferred ponds, and one preferred rivers**. The preference which about one half of the species showed for lakes may be related to several variables which differ from those in smaller water bodies. Lakes have higher environmental stability, number of niches, and higher probability of immigration of new species. The extinction rate is also lower in lakes. The smallest water bodies (ditches, puddles and mires) are shallow, and their small water volumes make them unstable environments, liable to dry out in summer and freeze to the bottom in winter. Drying and freezing are disadvantages for wingless species and stages. In small water bodies also the chemical and physical properties of the water generally change more rapidly than in larger habitats. In addition, small habitats have a low number of niches, and mortality and extinction rates may be high. In Norway the short summer is generally the main growth season, but it is also the season when drought most often occurs. Of the seven species which had significant absences or avoidances for type of surface water in Table 7, six had a significant absence in small water bodies or avoided them.

For variable 2 in Table 6, elevation above sea level, the many crosses are accompanied by "Low", meaning preference for lowlands. In Table 7, the corresponding column is dominated by the word "High", meaning that the species avoided highlands or were significantly absent in such regions.

One effect of variation in elevation is through temperature. This is a principal factor in biogeography and ecology, with many effects. For this variable 3 in Table 6 we note that 10 species preferred high temperature. In Table 7 the corresponding column is dominated by the word "Low", meaning that the species avoided sites with low water temperature in summer or are significantly absent from such places. Water temperature is negatively correlated with elevation above sea level (K.A. Økland & J. Økland 2000: Table 2). Both elevation above sea level and water temperature vary on a geographical level and have been considered in the former section on Geographical distribution.

In his survey of the Norwegian water bugs, Jastrey (1981) collected mainly in "areas on the shoreline with some vegetation. Few species are generally found outside this area". In the present study the importance of aquatic vegetation has been confirmed by the material shown in Tables 6-7 for variable 4, with statistical corroboration.

For both aquatic vegetation and variable 5, sediment, the presence of organic materials are key words linking some of the categories to effects on water bugs. Seven species with bullets in the left hand row of Table 6 all preferred gyttja found in eutrophic lakes, while two species with bullets on the right side preferred dy sediments associated with the dystrophic lake type. The difficult category dygyttja may include many eutrophic lakes. Table 7 shows that all species avoided "Stones" – such habitats with small amounts of organic matter were avoided. We accordingly note a positive reaction for eutrophic

Table 6. Significant environmental **preferences** for the 12 species of Norwegian water bugs whose occurrence was tested statistically by the frequency deviation method. Group A material. Results are shown for 9 environmental variables. Variable No. 8 (Magnesium) is omitted. For continuous variables, low values are indicated by **x**, high values by ●. For non-continous variables, the two medium categories are treated as either low or high if one of them is preferred by the species. No significant preference or (for sediment) ecologically difficult category (dygyttja) is shown by a dash (–). For aquatic vegetation "quant." indicates quantitatively, and "eutro." eutrophic. For sediment "dystro." indicates dystrophic, and "eutro." eutrophic. Preference for these categories are also marked by●. For variables 2-7 and 9-10 only lakes are considered, and for variable 2, only lakes in South Norway.

Environmental variables	**1. Surface water type**	**2. Elevation above sea level**	**3. Water temp.**	**4. Aquatic vegetation**	**5. Sediment**	**6. Wave action**	**7. Calcium**	**9. pH**	**10. Water colour Pt**
12. *Gerris lacustris*	Lakes	✖ Low 0-400 m	● High 16-24 °C	*Sphagnum* ● ● Rich quant. ● Rich eutro.	Dy dystro. ● ● Gyttja eutro.	✖ Small	● High 6.1-106 mg l^{-1}	–	● High 31-400 mg l^{-1}
13. *Gerris lateralis*	Ponds	–	–	–	Dy dystro. ●	✖ Small	–	–	–
14. *Gerris odontogaster*	Ponds	✖ Low 101-200 m	–	*Sphagnum* ● ● Rich eutro.	● Gyttja eutro.	✖ Small	● High 6.1-10 mg l^{-1}	–	● High 51-400 mg l^{-1}
17. *Nepa cinerea*	Rivers	✖ Low 0-100 m	● High 16-20 °C	● Rich quant. ● Rich eutro.	● Gyttja eutro.	✖ Small	● High 6.1-10 mg l^{-1}	–	● High 31-50 mg l^{-1}
21. *Cymatia bonsdorffii*	Lakes	✖ Low 101-200 m	● High 21-24 °C	● Rich eutro.	● Gyttja eutro.	✖ Small	● High 6.1-10 mg l^{-1}	–	● High 51-400 mg l^{-1}
28. *Callicorixa producta*	Ponds	–	● High 16-20 °C	● Rich eutro.	–	–	● High 10.1-106 mg l^{-1}	● High 7.6-9.9	–
34. *Hesperocorixa linnaeii*	Lakes	✖ Low 0-100 m	● High 21-24 °C	● Rich eutro.	● Gyttja eutro.	✖ Small	● High 6.1-106 mg l^{-1}	–	● High 51-400 mg l^{-1}
35. *Hesperocorixa sahlbergi*	Ponds	✖ Low 0-100 m	● High 16-24 °C	● Rich quant. ● Rich eutro.	● Gyttja eutro.	✖ Small	● High 6.1-106 mg l^{-1}	✖ Low 6.1-6.5	● High 51-400 mg l^{-1}
37. *Sigara distincta*	Lakes	✖ Low 0-100 m	● High 16-20 °C	● Rich quant.	–	✖ Small	● High 6.1-10 mg l^{-1}	● High 7.6-9.9	● High 51-400 mg l^{-1}
38. *Sigara dorsalis*	Lakes	✖ Low 0-100 m	● High 16-20 °C	● Rich quant. ● Rich eutro.	–	✖ Small	● High 6.1-10 mg l^{-1}	–	● High 31-400 mg l^{-1}
47. *Sigara scotti*	Lakes	✖ Low 0-100 m	● High 16-20 °C	● Rich quant.	–	–	✖ Low 2.1-6 mg l^{-1}	–	● High 51-400 mg l^{-1}
51. *Notonecta glauca*	–	✖ Low 0-100 m	● High 21-24 °C	● Rich quant. ● Rich eutro.	● Gyttja eutro.	✖ Small	● High 6.1-10 mg l^{-1}	–	● High 51-400 mg l^{-1}

Table 7. Significant environmental **absences and/or avoidances** for the same species of water bugs as treated in Table 6. Absence is marked in *italics*, avoidance in corpus. For further explanation see the legend to Table 6, but note that the symbols (crosses and bullets) are not used below.

Environmental variables	1. Surface water type	2. Elevation above sea level	3. Water temp.	4. Aquatic vege-tation	5. Sediment	6. Wave action	7. Calcium	9. pH	10. Water colour Pt
12. *Gerris lacustris*	*Absent smaller water bodies*	High 401-1835 m	Low 6-12 °C	Poor	Stones	Medium	Low 0.7-6 mg l^{-1}	–	Low 0-10 mg l^{-1}
13. *Gerris lateralis*	Lakes	–	–	Poor	Stones	–	–	–	–
14. *Gerris odontogaster*	*Absent smaller water bodies*	High 401-1835 m	*Absent low 6-12 °C*	Poor	Stones	–	Low 0.7-2 mg l^{-1}	–	Low 0-10 mg l^{-1}
17. *Nepa cinerea*	*Absent smaller water bodies*	*Absent high 401-1835 m*	*Absent low 6-12 °C*	Poor	Stones	Medium	*Absent low 0.7-2 mg* l^{-1}	–	*Absent low 0-10 mg* l^{-1}
21. *Cymatia bonsdorffii*	–	*Absent high 401-1835 m*	*Absent low 6-12 °C*	Poor	Stones	–	Low 0.7-2 mg l^{-1}	–	*Absent low 0-10 mg* l^{-1}
28. *Callicorixa producta*	Lakes *Absent smaller water bodies*	–	*Absent low 6-12 °C*	–	Stones	–	Low 2.1-6 mg l^{-1}	High 6.6-7.5	–
34. *Hesperocorixa linnaeii*	–	*Absent high 201-1835 m*	*Absent low 6-12 °C*	*Absent poor*	*Absent stones*	*Absent medium*	*Absent low 0.7-2 mg* l^{-1} Low 2.1-6 mg l^{-1}	–	*Absent low 0-10 mg* l^{-1} Low 11-30 mg l^{-1}
35. *Hesperocorixa sahlbergi*	*Absent smaller water bodies*	*Absent high 401-1835 m* High 201-400	*Absent low 6-12 °C* Low 13-15 °C	Poor	Stones	Medium	Low 0.7-6 mg l^{-1}	High 6.6-7.5	Low 0-30 mg l^{-1}
37. *Sigara distincta*	–	*Absent high 401-1835 m* and *101-200 m*	Low 6-12 °C	Poor	Stones	Medium	Low 0.7-2 mg l^{-1}	–	–
38. *Sigara dorsalis*	Smaller water bodies	*Absent high 201-1835 m* Medium 101-200 m	*Absent low 6-12 °C*	Poor	Stones	Medium	Low 0.7-2 mg l^{-1}	–	Low 0-10 mg l^{-1}
47. *Sigara scotti*	–	*Absent high 101-1835 m*	*Absent low 6-12 °C* Low 13-15 °C	Poor	Stones	–	Low 0.7-2 mg l^{-1}	–	–
51. *Notonecta glauca*	–	*Absent high 201-1835 m*	*Absent low 6-12 °C*	Poor	Stones	*Absent medium*	*Absent low 0.7-2 mg* l^{-1} Low 2.1-6 mg l^{-1}	*Absent low 4.4-6.0*	Low 0-10 mg l^{-1}

or dystrophic sites with presence of much organic matter.

It is not surprising that the mechanical beating of waves may influence the well-being of water bugs both directly and through indirect channels like preventing presence of aquatic vegetation. This may explain that for variable 6, wave action, small wave action was preferred by 10 species in Table 6, and Table 7 shows avoidance or significant absence at sites with "Medium" wave action.

Norwegian lakes range from ultraoligotrophic low-productive systems to hypertrophic sites. In some of them the water quality approaches that of distilled water. This is mirrored in a median value of 1.1 mg Ca l^{-1} in one thousand lakes from all over Norway (Skjelkvåle et al. 1997). Because productivity is low in many Norwegian water bodies, the amount of food available for water bugs is often small.

Only *Sigara scotti* shows preference for a low calcium concentration in the water (2.1-6 mg Ca l^{-1}). The remaining species with significant reactions preferred higher levels (Table 6). Even *S. scotti* seems to demand sites that have at least some calcium since it avoided lakes with the lowest concentration, 0.7-2 mg l^{-1} (Table 7). Also the remaining species with reactions avoided or were significantly absent from sites with low concentration (cf. Table 7).

The significant positive reaction for high calcium concentration in the water for 10 species (variable 7 in Table 6) is most likely of indirect nature, connected for instance to a tendency for increasing amounts of plant nutrients when calcium concentration increases. In Norway calcium concentration in many water courses increases downstream, cf. also the negative correlation between elevation and calcium shown in K.A. Økland & J. Økland (2000: Table 2).

Most of the species did not react significantly on pH (Tables 6-7, variable 9). This variable, representing the H^+-concentration in the water, has been in focus especially in relation to acidification of lakes. Two species preferred waters of high pH (above 7.6), and one species a low range (6.1-6.5), marked with a cross. The latter species avoided sites with higher pH (6.6-7.5), cf. Table 7. One species was significantly absent from sites in the lowest pH category (4.4-6.0). Several physiological functions are influenced by changes in the pH value, such as the regulation of Ca^{++} and Na^+, respiration, and the internal acid/base balance. There are also interactions with fish. If predation from fish decreases or stops in acidified lakes, this favours several species of water bugs, especially those with pelagic habits like *Glaenocorisa propinqua* (see the chapter on Results, Survey of the species).

The 10 species with reactions to variable 10, water colour, showed preference for high colour (cf. the bullets in Table 6). Eight of them avoided or were significantly absent from sites with low colour (Table 7). Reactions on water colour are most likely of indirect nature. Table 6 indicates that the species reacting on water colour prefer rich aquatic vegetation, or sites with *Sphagnun* vegetation (variable 4). The presence of much organic matter associated with the latter lake types probably explains the positive reactions of the species on high water colour.

Acknowledgements. We are indebted to the directors and the officials in the entomological departments of the institutions mentioned in the chapter on Material and methods. Thanks also to Sigmund Hågvar and Bjørn Sagvolden for permitting us to study their private collections. We also extend our thanks to The Norwegian Research Council for Science and the Humanities (NAVF) which provided financial support for field work throughout Norway from 1960 to 1973. Field work in the 37 lakes of the Eikeren watercourse was supported by the Eikeren committee, representing the counties of Buskerud and Vestfold. The University Office for Drawing and Photography in Oslo, and Anders Endrestøl, provided technical assistance. The editor of Hydrobiologia gave permission to reprint Figure 16. We also thank an unknown referee for valuable comments to the manuscript.

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Received: 30 June 2008
Accepted: 1 October 2008