

## Freshwater Ostracoda (Crustacea) of Inari Lapland in northern Finland

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Received 5 February 2010; Accepted 4 May 2010

**Abstract** – Collections of ostracods from various habitats in and around Lake Inari, Finnish Lapland, provide the first record of these crustaceans from Finland north of the Arctic Circle. From a total of 35 sites visited, 14 species were collected, out of which four appeared to be new to Finland: *Fabaeformiscandona lapponica*, *Pseudocandona pratensis*, *Eucypris pigra* and *Paralimnocythere relictata*. Two major assemblage groups were recognised by clustering classification and multi-dimensional scaling ordination, one dominated by *Cyclocypris ovum*, the second by *Candona candida*. Taxonomic diversity of the most assemblages was of expected range based on the inventory of 53 freshwater species of Finland.

**Key words:** Subarctic Ostracoda / freshwater / Finland / faunal similarity / taxonomic diversity

### Introduction

The knowledge of recent freshwater ostracod fauna of Finland is relatively poor when compared with that of other Fennoscandian countries (Ekman, 1914; Alm, 1915; Sars, 1923, 1925; Silfverberg, 1999; Horne, 2004) or with that of other Finnish microcrustaceans (Silfverberg, 1999). There are only a few detailed regional (e.g. Särkkä *et al.*, 1997, on spring meiofauna of Western Finland around Jyväskylä) or local (e.g. Holopainen and Passivirta, 1977, on meiobenthos of lake Pääjärvi ca. 100 km north from Helsinki) faunistic surveys including freshwater ostracods, however all these have been carried out in southern Finland. There was no faunistic synopsis or checklist available for Finnish freshwater ostracods until 1999 when Silfverberg (1999) published a provisional list of Finnish Crustacea. In this distributional list a total of 64 ostracod species are included, of which (after exclusion of marine and brackish-water species, and omission of synonymy and nomina nuda) 49 true freshwater inland species may be retained as valid records. Out of 19 Finnish biogeographical provinces (regionalisation according to Silfverberg, 1999), the highest species richness is recorded definitely in Nylandia in southern Finland (33 freshwater species), where several studies have focused on coastal assemblages of the Gulf of Finland (e.g. Hirschmann, 1909 or Hagerman, 1967). However, so far 12 of these 19 provinces have been completely neglected, having no records

of freshwater ostracods available, particularly the most northerly situated provinces (latitude higher than ca. 67°00' N), including Lapponia inarensis (Inari Lapland) (Silfverberg, 1999).

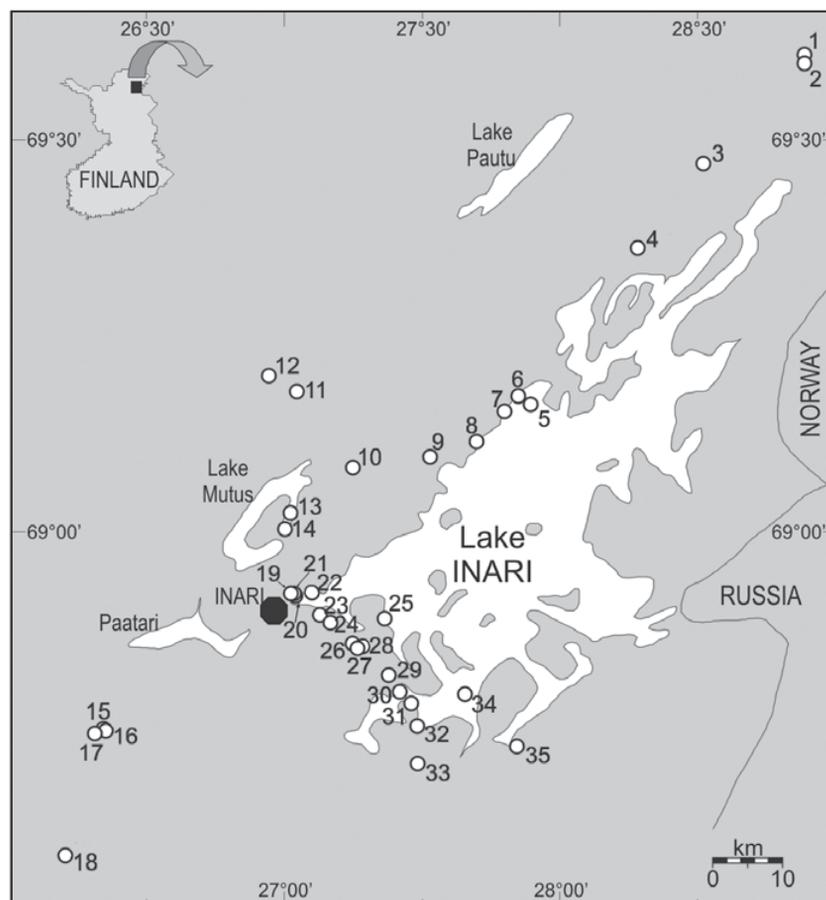
On the basis of collections from a single north-boreal/sub-arctic hydrological catchment of Lake Inari, the present study aims to fill this zoogeographical gap in the knowledge of Finnish freshwater ostracods and to contribute to acquisition of comprehensive distributional data which is recently considered one of the main key topics for future research on climate change effects on freshwater biodiversity in northern regions (Heino *et al.*, 2009).

### Regional setting and study sites

The study sites (Fig. 1, Table 1) are located within the Inari Lapland (Lapponia inarensis), the northernmost of 19 Finnish biogeographical provinces (Silfverberg, 1999), which administratively belongs to the Province of Finnish Lapland, and is bordered to the east by Russia, and to the northeast, north and west by Norway. It is situated within the northern part of the watershed of central Lapland, where the rivers drain to the Barents and White Seas (Pulkkinen and Rissanen, 1997).

Lake Inari (Inarijärvi) situated about 300 km far to the north of the Arctic Circle at 119 m a.s.l., is an oligotrophic and dimictic lake with very minor anthropogenic alterations. Originated as an ice-dammed lake (Lunkka *et al.*, 2004), it has at present an area of 1040 km<sup>2</sup> (the third

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**Figure 1.** Location map of lake Inari area and the sampling sites.

largest lake in Finland: [Stebel \*et al.\*, 2007](#)), a maximum depth of 95 m and a mean depth of 15 m ([Hyvärinen and Kajander, 2005](#)). The water is transparent to the depth of 4 to 10 m and exhibits low contents of nutrients ( $150 \mu\text{g total N}\cdot\text{dm}^{-3}$ ,  $4 \mu\text{g total P}\cdot\text{dm}^{-3}$ ), neutral pH of 7.2 and low total phytoplankton biomass ( $0.15 \text{ mg}\cdot\text{dm}^{-3}$ ) and chlorophyll a content ( $1.3 \mu\text{g}\cdot\text{dm}^{-3}$ ) ([Lepistö \*et al.\*, 2004](#)).

The climate in the area is continental, influenced by the Gulf Stream, with cool winters and relatively warm summers. The mean long-term (1971–2000) annual temperature is  $-1^\circ\text{C}$  to  $0^\circ\text{C}$ , while the mean January and July temperatures are between  $-14^\circ\text{C}$  and  $-12^\circ\text{C}$  and between  $12^\circ\text{C}$  and  $16^\circ\text{C}$ , respectively. Precipitation is relatively low, with a long-term annual average of 350–450 mm, and with the highest values (60 mm per month) in July and August. A permanent snow cover usually occurs from mid-November to late May ([Stebel \*et al.\*, 2007](#)).

Botanically, the area belongs to the north boreal and low-alpine regions ([Stebel \*et al.\*, 2007](#)), bordering the subarctic vegetation zone and laying just near the northern limits of both, the continuous pine forest and the northern Aapa mire complex ([Luoto and Seppälä, 2000](#); [Paiunen, 2005](#)). The waterlogged areas (approx. 10% of the surface) are covered by bogs and nutrient-poor fens dominated mainly by peat mosses ([Stebel \*et al.\*, 2007](#)).

Until late 1980's, the Inari area was considered pristine but recent studies on environmental contamination have revealed remarkable high level of airborne contamination due to emission from the Cu and Ni smelters of the mining area in the Russian Kola Peninsula ([Pulkkinen and Rissanen, 1997](#)).

## Material and methods

Ostracod samples were collected from 16 sites in Lake Inari and 19 sites adjacent to the lake ([Fig. 1](#)) during three field visits in snow-free periods (July and August of 2002, 2003 and 2004) by the first author. Each sampling site was fixed with a hand-held Geographical Positioning System and coordinates are given in [Table 1](#). All 35 sampling sites are situated in the catchment area of Lake Inari, however, due to a variety of the sampled waterbodies ([Table 1](#)), different sampling methods were necessary to obtain representative samples, and thus the samples had only qualitative value. Shallow habitats of lake littoral, bogs, peat-bogs, ditches, rivers, springs and ox-bow lakes were sampled using a hand-net (120  $\mu\text{m}$  mesh size), whereas lake sublittoral with a dredge (120  $\mu\text{m}$  mesh size). The samples were preserved in the field

**Table 1.** Coordinates and habitat description of the sampling sites in the Inari Lapland. Site numbers match those in Figures 1, 2 and 3.

Site	Coordinates		Depth (m)	Habitat description
	N	E		
1	69°35'50"	28°52'39"	0.15	Road-side ditch
2	69°35'11"	28°52'39"	0.15	Lake littoral with sandy and muddy bottom
3	69°27'36"	28°30'42"	0.15	Peat-bog
4	69°21'13"	28°16'23"	0.15	Oxbow lake
5	69°09'13"	27°53'03"	7.00	Lake sublittoral with sandy and muddy bottom
6	69°09'51"	27°50'24"	0.10	Lake littoral with muddy bottom
7	69°08'42"	27°47'22"	0.20	Peat-bog connected with sandy bottom littoral
8	69°06'22"	27°41'19"	0.15	Ditch on a border of a private property
9	69°05'12"	27°31'14"	0.20	Inflow of a small river to lake Inari
10	69°04'22"	27°14'21"	0.15	Road-side ditch
11	69°10'13"	27°02'10"	0.15	Peat-bog
12	69°11'26"	26°56'06"	0.20	Peat-bog connected with lake
13	69°00'51"	27°00'46"	0.15	Temporary pool within stones and marshland
14	68°59'37"	26°59'34"	0.10	Small temporary pool within a marshland
15	68°44'02"	26°20'08"	0.15	Small temporary pool within marshland
16	68°43'54"	26°20'34"	0.15	Temporary pool within stones and marshland
17	68°43'42"	26°18'10"	0.10	Helocrene spring
18	68°34'06"	26°11'50"	0.20	Helocrene spring
19	68°54'36"	27°00'53"	0.10	Lake littoral with muddy bottom
20	68°54'37"	27°01'38"	0.15	Lake littoral with stony and muddy bottom
21	68°54'26"	27°01'54"	0.50	Lake littoral with sandy bottom
22	68°54'41"	27°05'31"	18.00	Lake sublittoral with muddy bottom
23	68°52'57"	27°07'11"	0.15	Peat-bog
24	68°52'20"	27°09'28"	0.10	Peat-bog
25	68°52'40"	27°21'19"	0.10	Littoral with stony bottom
26	68°50'42"	27°14'19"	0.20	Littoral with muddy bottom
27	68°50'20"	27°15'26"	0.15	Road-side ditch
28	68°50'30"	27°16'30"	1.00	Lake littoral with muddy bottom
29	68°48'15"	27°22'11"	0.20	Lake littoral with stony and muddy bottom
30	68°46'58"	27°24'33"	0.20	Lake littoral with stony and muddy bottom
31	68°46'03"	27°27'05"	0.30	Lake littoral with stony and muddy bottom
32	68°44'16"	27°28'25"	0.15	Lake littoral with stony bottom
33	68°41'19"	27°28'29"	0.10	Small temporary pool with marshland
34	68°46'47"	27°38'46"	0.10	Lake littoral with stony bottom
35	68°42'41"	27°50'04"	0.10	Lake littoral with sandy bottom

in 75% ethanol, then in the laboratory washed with tap water through a 120 µm sieve and preserved in 96% ethanol. Ostracods were hand-picked and identified using keys of Sywula (1974) and Meisch (2000), with taxonomy and nomenclature following the latter. The study material is housed in the Laboratory of Limnology of the University of Gdańsk.

Relationships between site assemblages (samples with absolute abundances > 30) were examined using UPGMA (unweighted pair group mean average) hierarchical clustering based on species relative abundances (percentages) and Bray-Curtis similarity coefficient. Additionally to UPGMA clustering, MDS (non-metric multi-dimensional scaling) ordination was employed.

To investigate associations between site assemblage structure and habitat types, every sampling site was initially classified as representing one of the four habitat classes (lake littoral, temporary pools, springs or peat-bogs) and further the statistical differences between groups

of sites were tested with analysis of similarity (ANOSIM), a non-parametric permutation procedure (Clarke and Warwick, 2001).

Biodiversity of the site assemblages was assessed using two binary (presence/absence) measures based on taxonomic relatedness of species: 1) average taxonomic distinctness (Delta+) and 2) variation in taxonomic distinctness (Lambda+). Using the Lambda+ index in addition to that of Delta+ allows one to distinguish between assemblages having the same Delta+ value but substantially differing in the diversity of higher taxa to which the assemblage species belong (consistent intermediate taxonomic distances *versus* very diverse, low and high, distances between pairs of species) (for details see Clarke and Warwick, 2001). Both these indices have a particular virtue of being largely independent of sample size and can be tested against an expectation based on the species list for the region (Clarke and Warwick, 2001). Thus, the null hypothesis that observed subsets of species

from the sampled sites in the Inari Lapland (species richness  $\geq 3$ ) are representative (*i.e.* have the same taxonomic distinctness structure) of the biodiversity expressed in the full species inventory of Finland was tested by the TAXDTEST algorithm. Six-level classification (species, genus, subfamily, family, superfamily, order) was used according to Meisch (2000).

Finally, faunal similarity between the Inari Lapland and two adjacent areas for which data on regional ostracod distribution are available was computed by Sørensen similarity coefficient which is Bray-Curris calculated on presence/absence data. All procedures were run on PRIMER ver. 6.1.10 software (Clarke and Gorley, 2006).

## Results and discussion

The studied material consists of 7031 individuals. Of the total of 38 samples from the 35 sites, only two samples (from sites nos. 20 and 33) did not yield any ostracods. Samples from the other sites differ in the total absolute abundances of collected individuals varying between just 1 (site no. 5) and 951 (site 8), with the mean number equalling 195. A total of 14 species were identified (Table 2): *Candona candida* (Müller, 1776), *Cryptocandona reducta* (Alm, 1914), *Cryptocandona vavrai* Kaufmann, 1900, *Fabaeformiscandona lapponica* (Ekman, 1908), *Pseudocandona pratensis* (Hartwig, 1901), *Pseudocandona rostrata* (Brady and Norman, 1889), *Pseudocandona stagnalis* (Sars, 1890), *Cyclocypris globosa* (Sars, 1863), *Cyclocypris ovum* (Jurine, 1920), *Cyclocypris serena* (Koch, 1838), *Bradleystrandesia reticulata* (Zaddach, 1844), *Eucypris pigra* (Fischer, 1851), *Cypridopsis vidua* (Müller, 1776) and *Paralimnocythere relictata* (Lilljeborg, 1863). Further two taxa represented by juveniles were identified to the genus level: *Pseudocandona* sp. and *Cyclocypris* sp. but most probably these represent *P. rostrata* and *C. ovum*, respectively.

Four of the collected species have not previously been recorded in Finland: *Fabaeformiscandona lapponica*, *Pseudocandona pratensis*, *Eucypris pigra* and *Paralimnocythere relictata*. Occurrence of *F. lapponica* in north Finland was not unexpected, as this species (including its variety *F. l. var. arctica* (Alm, 1914)) has been formerly reported from Sweden, Norway, Greenland, Novaya Zemlya, and Western and Eastern Siberia (Ekman, 1914; Alm, 1915; Sars, 1925; Meisch, 2000; Semenova, 2007), and it is considered by some authors as an arctic species with unknown ecology (Semenova, 2003, 2007). The southernmost record of *F. lapponica* from south-western Germany (Löffler, 1961) needs to be verified (see discussion in Meisch, 2000). *Pseudocandona pratensis*, although reasonably common in Europe in a variety of habitats (Meisch, 2000) and reported from Western Siberia and Caucasus (Semenova, 2007), it is known only from scattered records and it is rare in the north (Meisch, 2000). Relying on the distribution map presented in Fauna Europaea (Horne, 2004), our finding of *P. pratensis* in the Inari Lapland should be considered the northernmost

record of this species in Europe and the first record in Fennoscandia. *Eucypris pigra* is a typical crenophile and as reported formerly from Sweden and Norway (Alm, 1915; Sars, 1925), its occurrence in the study area was not surprising. Finally, discovery of *P. relictata*, the fourth species new to Finland, in an oxbow-lake seems to be also an interesting record of this uncommon European species. To summarise, the present collection brings the total number of recent freshwater ostracod species recorded in Finland to 53 and places Lapponia Inarenensis after Nylandia (33 freshwater species) and Tavastia borealis (15 species) as the third Finnish biogeographical province having the highest species record (out of seven provinces for which data on freshwater ostracods are available, see above in Introduction). Except for the four species that appeared new to Finland, all the other species from the Inari Lapland are known from southern Fennoscandia (Alm, 1914; Sars, 1923, 1925; Silfverberg, 1999), but only three of these have been found further north in Europe, such as in archipelagos of Svalbard (*Candona candida* and *Cyclocypris ovum*) or Franz Josef Land (*Cyclocypris globosa*), where they have been recorded along with the species restricted to the Arctic Circle (compare *e.g.* Olofsson, 1918).

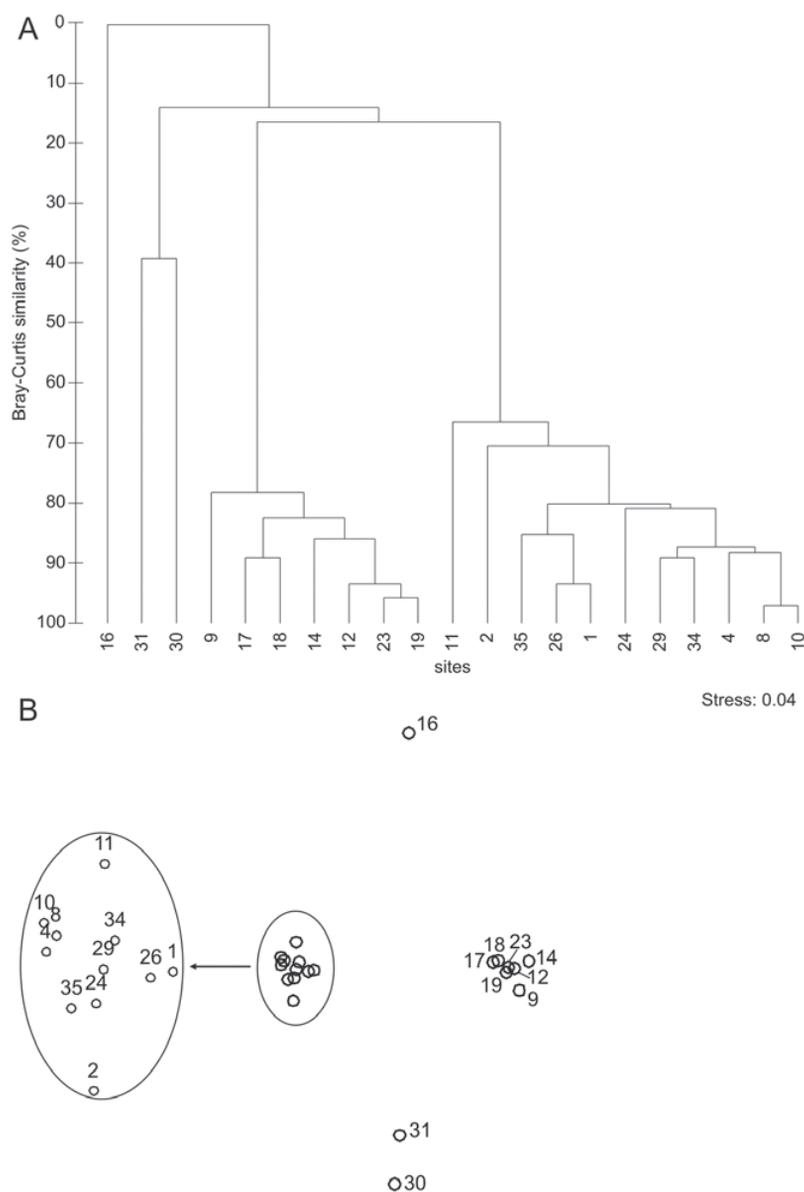
The most numerous and common species in the studied area were the eurytopic *Candona candida* (25 sites, 58.6% of the total abundance) and *Cyclocypris ovum* (24 sites, 29.7%) (Table 2). It is worth a note here the finding of one adult male of *C. candida* (site no. 17), a species which is generally represented by parthenogenetic populations, in some of which rare males occur with no identifiable geographical pattern (Meisch, 2000). *Pseudocandona rostrata* considered very rare species in the central and western Europe, ranked the third common and abundant species in the Inari Lapland (22 sites, 5.3%). All other species occurred at  $\leq 8$  sites, the least common being *Pseudocandona pratensis*, *Cyclocypris serena* and *Paralimnocythere relictata* found only at one site each. Overall, species richness at the individual sampling sites was low and ranged from one (five sites) to seven (site no. 24) with the mean value of 3.6 (Table 2).

Because UPGMA clusters were reasonably sharp and MDS stress was low (0.04), an agreement of the classification with the ordination methods was nearly excellent (Fig. 2). In both, the UPGMA dendrogram and the MDS plot two major clusters of the sampling site assemblages are shown (Fig. 2). Additionally, the monospecific assemblage (*Cyclocypris globosa*) from the site no. 16 and a pair of the clustering together sites 30 and 31 are clearly separated from the two major groups.

The first major cluster consisted of samples taken at sites 9, 12, 14, 17, 18, 19 and 23. They displayed high average mutual Bray-Curtis similarity of 83.8% since all were clearly dominated by *C. ovum* (mean relative abundance = 82%), whereas *C. candida* and *P. rostrata* had low abundances (mean 10% and 4%, respectively) (Table 2). These sites represented a variety of habitat types (lake littoral with adjacent waterbodies, temporary marshy ponds, peat-bogs and helocrene springs, see

**Table 2.** Species relative abundances (percentages) at the sampling sites in the Inari Lapland.

Site	<i>Bradley-strandesia reticulata</i>	<i>Candona candida</i>	<i>Cryptocandona reducta</i>	<i>Cryptocandona vavrai</i>	<i>Cyclocypris globosa</i>	<i>Cyclocypris ovum</i>	<i>Cyclocypris serena</i>	<i>Cypriodopsis vidua</i>	<i>Eucypris pigra</i>	<i>Fabaeformiscandona lapponica</i>	<i>Paralimnocythere relictata</i>	<i>Pseudocandona pratensis</i>	<i>Pseudocandona rostrata</i>	<i>Pseudocandona stagnalis</i>
1		71.43		0.95	0.95	15.24		6.67					4.76	
2		65.31						30.61					4.08	
3	6.25					87.50							6.25	
4		87.68				0.97	3.14				7.97		0.24	
5		100.00												
6						87.50								12.50
7		9.09		36.36		9.09							45.46	
8		96.99				1.23			0.11	1.67				
9		0.99		0.50		75.74				0.50			16.82	5.45
10		100.00												
11	1.33	62.67		22.67	5.33								8.00	
12		7.63				89.95							2.42	
13		100.00												
14	1.01	0.34			2.02	96.63								
15										100.00				
16					100.00									
17	0.46	21.76	1.39	0.46		75.93								
18		17.14		0.95		71.43			7.62	0.95			1.91	
19		12.20				81.30		0.27					5.15	1.08
21	6.67					26.67							46.66	20.00
22		22.22	11.11										66.67	
23		12.10				85.48							2.42	
24	2.46	78.00	1.48	0.49		1.31				0.33			15.93	
25						50.00							50.00	
26		76.39				12.50		8.33					2.78	
27	7.69	23.08				69.23								
28		33.33				8.33							58.34	
29	0.39	84.38				4.69			0.78	1.56			8.20	
30						0.99		4.95	1.98			1.98	90.10	
31		7.69				12.82		46.16					33.33	
32				29.00		42.00							29.00	
34		88.40				11.60								
35		82.00						12.00					6.00	



**Figure 2.** Dendrogram for hierarchical clustering using group-average linking (A) and multi-dimensional scaling ordination (B) of 21 studied sites (of total absolute abundances > 30) based on Bray-Curtis similarities on relative species abundances.

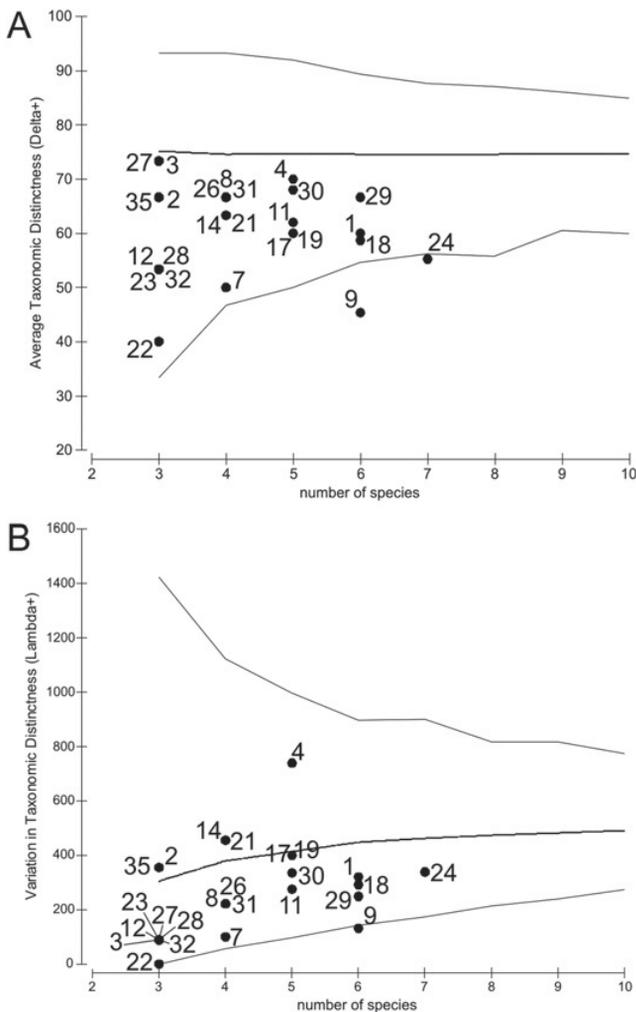
Table 1) but their joint feature was a presence of extremely abundant sedge spreads on their shores. Although clear preferences of *C. ovum*, the dominant species at these sites, to vegetated habitats have not been yet demonstrated, observations from Lapland (in the study area as well as in northern Sweden and Norway) suggest that this widely tolerant active swimmer may be phytophilic at least in shallow waterbodies of northern regions (pers. observ.).

The second major cluster, including also a variety of waterbodies, comprised assemblages from the following sites 1, 2, 4, 8, 10, 11, 24, 26, 29, 34 and 35. These assemblages had also high average faunal similarity (78.1%), and were most notable for apparent predominance of *C. candida* (mean relative abundance = 81%),

while the relative abundance of *P. rostrata*, *C. vidua* and *C. ovum* was  $\leq 5\%$  (Table 2).

The main species responsible for loose clustering of two remaining assemblages from the sites 30 and 31, both from lake littoral, were *P. rostrata* (mean relative abundance 62%) and *C. vidua* (26%).

The ANOSIM test for ostracod assemblage disparities between groups of the sampling sites representing four main habitat types (lake littoral, temporary pools, springs and peat-bogs) showed no statistically significant differences ( $R = 0.013$ ,  $P = 0.441$ , 1000 random permutations). Thus, it remains unclear at present, which environmental factors are responsible for the observed faunistic differences between the major clusters of the sampling sites



**Figure 3.** Funnel plot for simulated average taxonomic distinctness Delta+ (A) and for variation in taxonomic distinctness Lambda+ (B). Thin lines indicate limits within which 95% of simulated values of Delta+ and Lambda+ indices lie, whereas central thick lines indicate mean Delta+ and Lambda+ for the full inventory of Finnish freshwater ostracod species. Dots represent the true values of Delta+ and Lambda+ indices for the studied sites with species richness  $\geq 3$ .

distinguished by both, the UPGMA classification and MDS ordination.

Biodiversity of the site assemblages was measured using two Clarke and Warwick's (2001) measures based on taxonomic relatedness of species. Sampling site Delta+ values ranged in the study area from 40 to 73 (mean  $\pm$  standard deviation =  $60.6 \pm 8.0$ ), while those of Lambda+ from 0 to 740 ( $228.8 \pm 177$ ). As these taxonomic biodiversity indices are relatively recent, there is so far only one example of their application in freshwater ostracod studies to be compared with the present data (Danielopol *et al.*, 2007). Although these authors (Danielopol *et al.*, 2007) examined fossil Miocene assemblages from the Vienna Basin, geographically and stratigraphically totally distinct from those of the present study,

they found average taxonomic distinctness of 16 assemblages to be in the range between 48 and 73 (mean  $\pm$  standard deviation =  $59.7 \pm 7.1$ ), being fully comparable and statistically not different with the values obtained in the Inari Lapland (t test = 0.340,  $P = 0.735$ ).

The null hypothesis that the taxonomic diversity of the studied site assemblages of species richness  $\geq 3$  is not significantly different from that based on the inventory of 53 species known from Finland was tested by Clarke and Warwick's (2001) approach and the results are presented in Figure 3 as the funnel plots. Although all Delta+ values for the studied sites demonstrate generally reduced average distinctness lying below the mean value drawn from the inventory of the Finnish freshwater ostracods (Fig. 3A), only one site (no. 9) lies far outside the lower 95% of the mean Delta+ value ( $P = 0.014$ ). This is because all six species in the sample from this site belong to only one family Candonidae (Table 2), which results also in the significantly reduced Lambda+ value ( $P = 0.022$ ) (Fig. 3B). The other sample with marginally significant reduction of the average distinctness ( $P = 0.044$ ) but of the expected value of Lambda+ (Fig. 3) is that of the peat-bog site 24 where out of a total seven species recorded only one belonged to other family than Candonidae (Table 2). Although it is difficult to explain, it is also worth mentioning that the mean value of Delta+ of the seven site assemblages clustered by the dominance of *Cyclocypris ovum* is significantly lower than that of the cluster dominated by *Candona candida* (mean Delta+ value  $\pm$  standard deviation for the former cluster =  $56.3 \pm 4.5$  versus that for the latter one  $64.1 \pm 6.1$ ; t test = 3.037,  $P = 0.008$ ). However, we did not find any significant differences of the average distinctness between samples collected from lacustrine littoral habitats and those from peat-bogs ( $62.4 \pm 5.1$  versus  $57.9 \pm 8.6$ , t test = 1.457,  $P = 0.163$ ).

The closest areas for which data on regional ostracod distribution are available are situated in Swedish Lapland (Ekman, 1908) and in Norwegian Finnmark and Russian Kola Peninsula, the latter two considered one region (Alm, 1914). The species richness of the Inari Lapland (14 species) is fairly similar to those of Swedish Lapland (12 species) and Norwegian Finnmark including Kola Peninsula (10 species), but only two species are common for the three areas (*C. candida* and *C. globosa*), and in total 26 species are known from the whole region comprising these three areas. Faunal similarities among the areas are rather low, ranging between 18% and 50% (mean = 33%). The Inari Lapland, having the central location, shows the highest similarity with two other area considered, *i.e.* 50% with Norwegian Finnmark and Kola Peninsula (sharing six species), and 31% with Swedish Lapland (sharing only four species). However, the available data for thorough zoogeographical and ecological interpretations are far from complete, exemplifying how little attention has been paid to these crustaceans in northern Fennoscandia. Efforts should be made in future to advance our knowledge on the distribution for most freshwater taxonomic groups, particularly at higher latitudes, as the current lack

of sufficient data hampers any attempts to predict the consequences of the anthropogenic stress and climate change on the freshwater biodiversity. Since the freshwater organisms are highly vulnerable to the above factors and their extinction rates exceed or at least equal those of the better known terrestrial animals, that issue requires urgent attention (Heino *et al.*, 2009).

*Acknowledgements.* We acknowledge the pertinent comments of two anonymous reviewers which helped to clarify several issues in the draft version of the manuscript. This contribution was partly supported by funds from the University of Gdańsk project no. BW-1411–5-0337–6 (2006).

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