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The impact of environmental factors on diversity of Ostracoda in freshwater habitats of subarctic and temperate Europe

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In this study, we compared the ostracod species diversity in selected inland-water habitats of Lapland and Poland, and assessed the relationships between ostracod occurrence and abiotic environmental variables. In total, 41 species were collected, of which only 15 species were found in Lapland, as compared with 35 in Poland. Almost all species collected from the Lapland sites were eurybiontic and no clear differences were found between ostracod assemblages inhabiting different habitat types. We hypothesize that this homogeneity might be a consequence of the raised water level during the springtime snow melt, temporarily connecting various waterbodies. The main factors limiting distribution of ostracod species in Lapland appeared to be low pH and low ionic content of water. In Poland, predominantly stenobiontic species were observed. In temporary waters and peat-bogs of this area useful indicator species were identified.

Introduction

Ostracods are tiny ubiquitous arthropods, occurring in all marine and non-marine aquatic habitats, and are even found in some terrestrial habitats such as humid forest soils (Horne *et al*. 2002). Nowadays, there are about 8000 ostracod species globally, of which slightly more than 2000 are freshwater species belonging to three superfamilies: Darwinuloidea, Cypridoidea and Cytheroidea (Martens *et al*. 2008). In the whole Palaearctic, the region with the highest ostracod specific diversity, there are 87 known genera with about 700 freshwater species (Martens *et al*. 2008), but even within Europe there are areas where the ostracod fauna has been less well explored, as e.g. northern Fennoscandia (Iglikowska & Namiotko 2010). The Polish ostracod fauna is faunistically better known, but our knowledge of ecology and relationships with environment is still inadequate, with only a single paper published on this topic to date (by Martins *et al*. 2009).

Ostracods are used as indicators of particular characteristics of aquatic habitats: many species have different, specific tolerance ranges and preferences within the full spectrum of environmental factors (*see* e.g. reviews in Holmes & Chivas

2002, Park & Smith 2003). The development of multivariate methods in ecology in the last decades of the 20th century has helped to reveal species–environment relationships. In Europe, recent papers using such methods have reported on relationships between freshwater ostracods and environmental factors in France (e.g. Marmonier *et al*. 2000), Germany (e.g. Viehberg 2006), Hungary (Kiss 2007), Italy (e.g. Pieri *et al*. 2009), Luxembourg (Gerecke *et al*. 2005), Poland (Martins *et al*. 2009), Portugal (Martins *et al*. 2010), Serbia (Karan-Žnidaršič & Petrov, 2007) and Spain (e.g. Poquet & Mesquita-Joanes 2011). However, data on the assemblages occurring in northern and temperate Europe are still lacking.

The main goals of this study were (1) to conduct faunistic surveys of ostracod assemblages in three types of freshwater habitats: temporary waters, peat-bogs and shallow riparian water of lakes in two geographically and physiographically different regions, northern subarctic Europe (Norwegian and Finnish Lapland) and central temperate Europe (Poland); (2) to compare ostracod species diversity and richness among these habitats and regions; (3) to perform zoocoenological analysis in an attempt to distinguish ostracod assemblage types characteristic and indicative of the studied habitats, (4) to investigate relationships between the occurrence of particular ostracod species and abiotic environmental factors, and (5) to assess usefulness of ostracods as indicators of environmental conditions in freshwater habitats.

Study areas and regional settings

Our studies were focused on two physiographically and climatically different European regions, latitudinally ca. 2000 km apart: one in northern subarctic Europe, namely Lapland (66°28´–69°20´N, 15°24´–27°54´E), and the other in central temperate Europe, Poland (50°28´–54°27´N, 15°36’–23°24´E). In this paper, the term “Lapland” is applied to the regions of Norwegian and Finnish Lapland.

Climatic conditions in Lapland are influenced by two opposing factors. The maritime zone is strongly influenced especially in winter by air masses warmed by the northward flow of the North Atlantic Drift (Gulfstream). This ameliorating influence is countered by the strong cooling effect of arctic and continental air masses from Eurasia. The Scandinavian Mountains play a major role in shaping climate of the Fennoscandia by blocking the warm Atlantic air masses (Tikkanen 2005). Annual air temperature range is about 10 °C along the west coast of Norway, but it is a more extreme (29 °C) in the Finnmark region (to the east of the Scandinavian Mountains) and 26–28 °C in NE Finland. The Scandinavian Mountains are the major factor, so on the western slopes annual precipitation amounts to about 4000 mm near Bodø in Norway, whereas in the rain shadow to the east decreases abruptly to < 400 mm in Finnmark and Finish Lapland. In the east part of Lapland snow cover persists for more than six month (Pulkkinen & Rissanen, 1997, Stebel *et al*. 2007).

In Poland, climatic conditions are shaped predominantly by location, and its continental climate is modified latitudinally by the increase in altitudes from the lowlands of northern Poland to high altitudes of the Carpathian Mountains in the south. The coldest month is usually January, when mean temperatures range from about –1 °C near Szczecin in NW Poland to –8 °C in the Tatra Mountains in the south. The mean temperature in July, the warmest month, is 17 °C along the north coast of Poland but 19 °C in the south and east. The amount of precipitation depends largely on altitude: in the wettest regions of the Carpathian Mountains and the uplands of southern Poland, rainfall ranges from 1000 to 1700 mm per year, but in the lowlands the rain-shadow effect restricts precipitation to < 500 mm per year (Martyn 1995).

Material and methods

Ostracod samples and environmental data were collected at 49 stations: 24 in Lapland (L1–L24) and 25 in Poland (P1–P25) (Fig. 1). Of the 24 sites in Lapland, all sampled in July 2006, 7 were in northern Norway, while the remaining 17 were in four provinces of Finland. In Poland, samples were collected from 25 sites scattered over the whole country (Fig. 1 and Table 1).

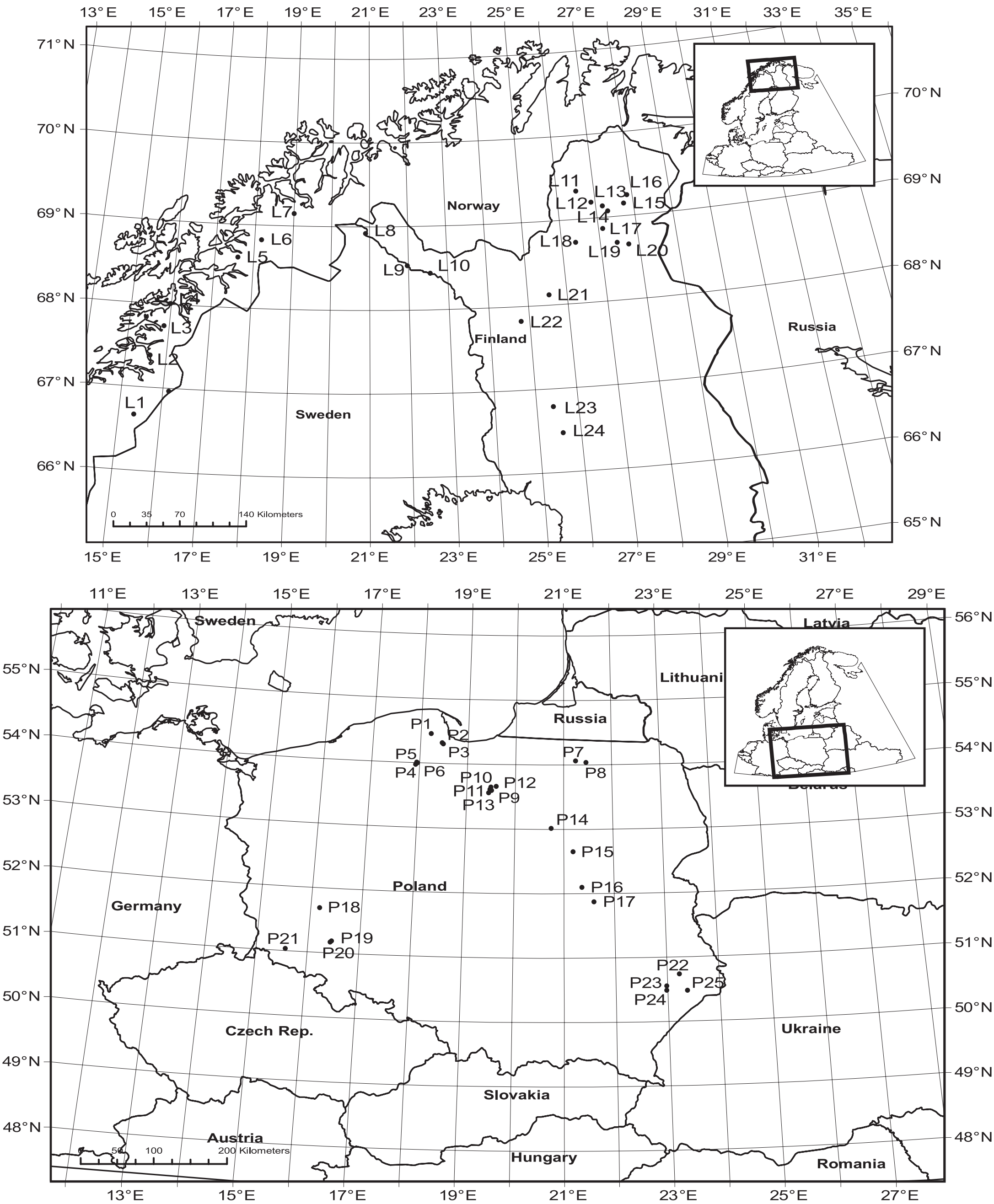

Fig. 1. Location of the studied sampling sites in Lapland and Poland.

Sampling sites were selected to represent three types of freshwater habitat: (1) temporary waters (eight sites in Lapland and eleven sites in Poland), (2) peat-bogs (eight and seven sites, respectively), and (3) shallow riparian water of lakes (eight and seven sites, respectively). Ostracod samples were collected using a hand-net (120 μm mesh size) from the bottom surface of 1 m^2 at depths to max. ~60 cm (i.e. arm's reach). Samples were preserved in the field in 75% ethanol, and later in the laboratory washed with tap water through a 120 μm sieve and preserved in

Table 1. Geographical location and habitat description of the sampling sites in Lapland (L1–L24) and in Poland (P1–P25). Abbreviations of biogeographical provinces in Lapland after Väisänen *et al.* (1992): Le = Lapponia Enontekiö, Li = Lapponia Inari, Lk = Lapponia Kemi, NNØ = Northeastern Nordland, NSI = Inner Southern Nordland, Ob = North Ostrobottnia, TRI = Inner Troms. Numbers of zoogeographical regions in Poland according to Catalogue of the Fauna of Poland: 3 = Pomeranian Lake District, 4 = Masurian Lake District, 6 = Mazovian Lowland, 8 = Lower Silesia, 12 = Lubelska Upland, 13 = Roztocze Upland, 15 = Western Sudeten Mts.).

Code	Site (province/region)	Date of collection	Habitat type	Lat. N	Long. E	Altitude (m a.s.l.)
Lapland						
L1	Semska (NSI)	6 July 2006	temporary	66°40´13´´	15°24´28´´	673
L2	Kvitblik (NNØ)	6 July 2006	temporary	67°23´06´´	15°38´58´´	56
L3	Marsvikbotn (NNØ)	6 July 2006	peat-bog	67°44´50´´	15°54´55´´	326
L4	Innhavet (NNØ)	7 July 2006	peat-bog	68°00´50´´	16°01´29´´	32
L5	Bjerkvik (TRI)	7 July 2006	lake	68°36´31´´	17°37´59´´	271
L6	Setermoen (TRI)	7 July 2006	temporary	68°49´40´´	18°13´18´´	155
L7	Heia (TRI)	8 July 2006	lake	69°09´22´´	19°02´49´´	175
L8	Kilpisjärvi (Le)	8 July 2006	temporary	68°55´24´´	20°56´32´´	566
L9	Luspa (Le)	8 July 2006	temporary	68°32´02´´	22°01´08´´	387
L10	Jatuni (Le)	9 July 2006	peat-bog	68°26´25´´	22°35´54´´	337
L11	Kaamasmukka (Li)	12 July 2006	temporary	69°20´15´´	26°33´57´´	247
L12	Karhujärvi (Li)	12 July 2006	lake	69°11´26´´	26°56´06´´	246
L13	Kaamanen (Li)	12 July 2006	peat-bog	69°08´10´´	27°13´20´´	135
L14	Mukkajärvi (Li)	14 July 2006	peat-bog	69°04´21´´	27°20´42´´	154
L15	Kontionojansuu (Li)	14 July 2006	lake	69°08´46´´	27°47´22´´	129
L16	Pekkala (Li)	14 July 2006	temporary	69°14´35´´	27°54´37´´	142
L17	Sellaniemi (Li)	15 July 2006	peat-bog	68°52´20´´	27°09´27´´	152
L18	Menesjärvi (Li)	15 July 2006	peat-bog	68°43´54´´	26°24´22´´	205
L19	Riistinalompolo (Li)	16 July 2006	peat-bog	68°41´08´´	27°28´55´´	145
L20	Torppar (Li)	16 July 2006	lake	68°39´22´´	27°46´35´´	127
L21	Pokka (Lk)	17 July 2006	temporary	68°07´16´´	25°35´27´´	294
L22	Sirkka (Lk)	9 July 2006	lake	67°49´31´´	24°49´50´´	191
L23	Marrakoski (Ob)	18 July 2006	lake	66°47´17´´	25°26´31´´	94
L24	Rovaniemi Town (Ob)	18 July 2006	lake	66°28´19´´	25°36´58´´	71
Poland						
P1	Kamień (3)	26 Aug. 2006	peat-bog	54°27´44´´	18°15´34´´	200
P2	Otomin Lake (3)	27 June 2008	lake	54°19´11´´	18°29´49´´	132
P3	Otomin Peat-bog (3)	27 June 2008	peat-bog	54°18´48´´	18°30´51´´	103
P4	Wdzydze (3)	28 May 2008	peat-bog	54°00´37´´	17°58´33´´	158
P5	Chądzie (3)	28 May 2008	peat-bog	54°00´03´´	17°59´45´´	138
P6	Krzywe (3)	28 May 2008	peat-bog	53°58´36´´	17°57´45´´	138
P7	Filipówka (4)	12 May 2006	temporary	54°03´52´´	21°17´09´´	124
P8	Pożarki (4)	12 May 2008	temporary	54°02´11´´	21°30´09´´	128
P9	Tynwałdzkie (4)	12 Sep. 2006	lake	53°39´55´´	19°38´42´´	117
P10	Stęgwica (4)	12 Sep. 2006	lake	53°38´56´´	19°32´19´´	74
P11	Silm (4)	16 June 2008	lake	53°36´53´´	19°30´58´´	144
P12	Jeziorak (4)	16 June 2008	lake	53°35´59´´	19°33´16´´	89
P13	Karaś (4)	12 Sep. 2006	lake	53°33´42´´	19°29´40´´	95
P14	Chojnowo (6)	12 May 2006	temporary	53°01´15´´	20°47´02´´	150
P15	Pniewo (6)	12 May 2006	temporary	52°39´21´´	21°13´41´´	100
P16	Ostrów (6)	25 Apr. 2007	temporary	52°06´07´´	21°24´04´´	152
P17	Garwolin (6)	25 Apr. 2007	temporary	51°52´52´´	21°37´50´´	145
P18	Wilków (8)	21 Apr. 2006	temporary	51°41´50´´	16°12´51´´	78
P19	Wilczków (8)	20 Apr. 2006	lake	51°11´05´´	16°29´33´´	123
P20	Kwietno (8)	20 Apr. 2006	temporary	51°10´13´´	16°28´21´´	136
P21	Łupki (15)	19 Apr. 2006	temporary	51°02´14´´	15°36´17´´	290
P22	Zamość (12)	24 Apr. 2007	temporary	50°44´29´´	23°16´32´´	208
P23	Zwierzyniec (13)	18 May 2008	peat-bog	50°33´03´´	23°00´39´´	269
P24	Tarnowola (13)	18 May 2008	peat-bog	50°29´26´´	23°01´06´´	252
P25	Dąbrowa Tomaszowska (13)	24 Apr. 2007	temporary	50°28´39´´	23°24´58´´	281

95% ethanol. Ostracods were identified under a microscope using both valve and soft body characteristics using the keys of Sywula (1974) and Meisch (2000).

A suite of physical and chemical variables (Appendices 1 and 2) were measured at each site. Water temperature, dissolved oxygen content, salinity, conductivity and pH were measured *in situ* using a hand-held multi-parameter instrument (WTW Multi 350i). Phosphate, nitrate, iron and calcium ions in the water were measured using colorimetric tests. A Secchi disc was used to assess water transparency. Sediment properties, like organic matter and water content, were assessed back in the laboratory using the standard procedure of Håkanson and Jansson (2002).

In the faunistic and community analyses, only samples containing > 30 indiv. m^{-2} were considered. Relationships between ostracod site assemblages were examined using UPGMA (Unweighted Pair Group Method with Arithmetic mean) hierarchical clustering based on square-root transformed species abundances per square meter and the Bray-Curtis similarity coefficient. A "similarity profile" (SIMPROF) permutation method (with 999 simulations) was implemented with the UPGMA procedure to test the null hypothesis that samples in a given cluster (representing a group of similar site assemblages) do not differ from each other in their multivariate structure (Clarke & Warwick 2001, Clarke & Gorley 2006). Additionally, after the cluster analysis, individual species contributions to the observed clustering pattern were examined using "similarity percentages" (SIMPER), a procedure that allows assessment of which species are principally responsible for the separation of the sets of samples (assemblage types) (Clarke & Warwick 2001, Clarke & Gorley 2006).

The analysis of similarities (ANOSIM), a non-parametric permutation test (Clarke & Warwick 2001), was used to investigate associations between the site assemblage structure and both the study region, and the type of habitat within the region. For ANOSIM, sampling sites were *a priori* grouped according to two criteria: (1) the region (two groups: Lapland and Poland), and (2) the habitat type within the region (six groups: peat-bogs in Lapland (LP), peat-bogs in Poland (PP), shallow riparian water of lakes in Lapland (LSL), shallow riparian water of lakes in Poland (PSL), temporary waters in Lapland (LTW) and temporary waters in Poland (PTW). Each time 1000 random or actual (if < 1000) number of permutations was used to obtain *r* values and probability levels.

To detect the main patterns and gradients of diversity in particular environmental variables and to assess how the sampling sites differed from each other in abiotic conditions, an unconstrained ordination of the Principal Components Analysis (PCA) was used on the basis of the Euclidean distance matrix, calculated from the standardised values of the studied environmental variables. ANOSIM was also employed in this analysis (Clarke & Warwick 2001).

To explain and describe the relationships between the ostracod species/assemblages and the environmental factors, two methods were employed: Canonical Correspondence Analysis (CCA), a method of constrained ordination detecting main patterns of dependence between two datasets of variables (ter Braak & Šmilauer 2002), and BEST, which analyses every possible combination of variables within the two matrices (environmental and faunal). BEST detects a subset of environmental variables which best explains the samples ordination based on the faunal matrix (for details *see* Clarke & Warwick 2001 and Clarke & Gorley 2006).

Finally, biodiversity of site assemblages was estimated using both the standard measure of the Shannon-Wiener diversity index (H'), and the average taxonomic distinctness (Δ+) which is a measure based on relatedness of species (Clarke & Warwick 1998). To test whether a set of species occurring at a sampled site has the same taxonomic distinctness structure as a so-called "master" list (i.e. an inventory of all species in a given biogeographical region) from which it was drawn, the Taxonomic Distinctness Test (TAXDTEST) was performed (with 1000 random simulations) and the results were presented as a funnel plot (for details *see* Clarke & Warwick 2001 and Clarke & Gorley 2006). The checklist of Silfverberg (1999) as updated by Iglikowska and Namiotko (2010) and supplemented by the records from the Fauna Europaea database (Horne 2004) was adopted as the inventory of non-marine ostracod species for Fennoscandia, whereas for Poland, the updated checklist of non-marine ostracods by Namiotko (2008) served as the master faunal list. The higher classification of the ostracods followed Meisch (2000).

All statistical procedures were run in the PRIMER ver. 6.1.10. programme (Clarke & Gorley 2006), except CCA which was performed using CANOCO ver. 4.56. (ter Braak & Šmilauer 1997–2009) software.

Results

A total of 40 300 ostracods were collected from all study sites (11 157 from Lapland and 29 143 from Poland). At six sites (L5, L10, L23 in Lapland and P1, P18, P21 in Poland), no ostracods were found. The main reasons for the absence was probably either poor environmental conditions: low pH (L10 = 4.3, P1 = 4.2), low calcium content (L5 and L23 = 10 mg dm^3), and low mineralization (conductivity L5 = 60.8, L10 = 56.3, L23 = 57.5, P1 = 44.9, P21 = 64.3 μS cm), or too short time for colonization of a new reservoir, when a temporary pond re-fills after drought (P18 and P21).

The average abundance of ostracods in the remaining samples was 3061 ± 5450 ind. m^{-2} (mean ± SD). A total of 41 ostracod species were identified (Appendices 3 and 4) — 15 in Lapland and 35 in Poland. The average number of species per site (species richness) was 4.3 ± 1.4 in Lapland and 6.3 ± 3.0 in Poland, and this difference was significant (Mann-Whitney test: $U = 114.4$, $p < 0.05$).

Significant differences in the average species richness per sampling site within the habitat types, were found only in Poland: on average 10.1 ± 0.7 species per site in PSL (the riparian shallow lake waters), 4.1 ± 2.5 in PTW (the temporary waters), and 2.6 ± 3.1 in PP (the peatbogs) (Kruskal-Wallis test: $H = 15.2$, $p < 0.001$). In Lapland, the species richness was similar at sites representing all three habitat types: 4.2 ± 1.5 in LSL, 4.4 ± 0.7 in LTW, and 3.7 ± 2.1 in LP (Kruskal-Wallis test: $H = 3.0$, $p = 0.224$).

Also differences between average values of the Shannon-Wiener diversity index for assemblages representing the three habitat types were statistically significant only in Poland (Kruskal-Wallis test: $H = 10.7$, $p < 0.01$; $H' = 1.902$ for PSL, $H' = 1.245$ for PTW and $H' = 0.755$ for PP).

In this study, 56% of the identified species are considered to reproduce sexually, 29% are characterized by the sporadic appearance of males, and 15% are exclusively parthenogenetic.

In Lapland, the most widespread and abundant species were *Candona candida* and *Cyclocypris ovum*, each dominating at nine sites (38% of the Lapland sites: Appendices 3 and 4) with an average relative abundance of 37% and 39%, respectively. A third most numerous species in Lapland was *Pseudocandona rostrata* with an average proportion of 10%. Rare species at the Lapland sites included the crenophilic species *Cryptocandona reducta*, *C. vavrai*, and *Eucypris pigra* as well as *Pseudocandona albicans*. Only one boreal/arctic species — *Fabaeformiscandona lapponica* — was recorded in this area.

In Poland, the dominance structure of the ostracod site assemblages was determined by habitat type. In shallow lakes (PSL), no distinct and common dominant species were found, but those which were the most abundant (average proportion > 5% in PSL) comprise species of the genus *Pseudocandona* (both from the *compressa* and *rostrata* groups, in total ca. 36%) as well as *Cyclocypris laevis* (25%), *Metacypris cordata* (12%), *Candona weltneri* (7%), and *Candonopsis kingsleii* (6%) (Appendices 3 and 4). In temporary waters (PTW), the dominant species included *Bradleystrandesia reticulata* and *Cypris pubera* (both with the average proportion of ca. 30% in PTW), while *Eucypris virens* (13%) and *Pseudocandona pratensis* (8%) contributed smaller proportions. In the majority of the peatbogs in Poland (PP), either no ostracods or only a few individuals were found (Appendices 3 and 4). At the few peat-bog sites at which ostracods occurred, one species was always highly dominant, either *Cyclocypris globosa*, *Cypria ophtalmica* or *Pseudocandona stagnalis*.

In the UPGMA cluster analysis (Fig. 2), four types of ostracod assemblages were identified and subsequently validated by the SIMPROF significance test ($\pi = 3.95$–4.50, $p = 0.01$). The characteristic species (indicated by the SIMPER analysis) of the first assemblage type including all site assemblages from the shallow riparian

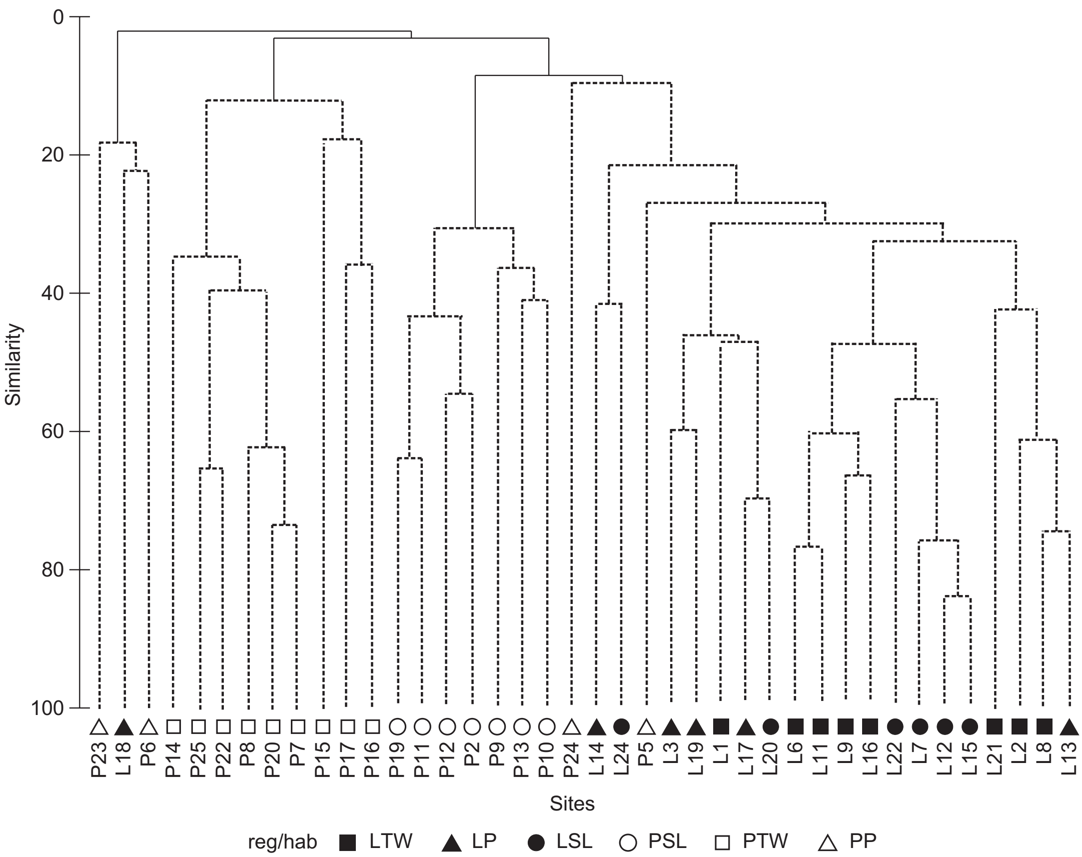

Fig. 2. The UPGMA dendrogram obtained on the basis of Bray-Curtis similarity (%) matrix among ostracod assemblages from the sampling sites in Poland and Lapland. Statistically significant separations of the genuine clusters (i.e. main ostracod assemblage types) demonstrated by the SIMPROF test are marked by solid lines (all other branches dashed lines = no statistical evidence for any sub-separation was found). Abbreviations of the habitat types within the studied regions: LTW = temporary waters in Lapland, PTW = temporary waters in Poland, LSL = shallow riparian water of lakes in Lapland, PSL = shallow riparian water of lakes in Poland, LP = peat-bogs in Lapland, and PP = peat-bogs in Poland. Sampling sites codes as in Table 1.

water of lakes in Poland (PSL) were: *Pseudocandona* spp. (usually represented by juveniles not determined to species level), *Candonopsis kingsleii*, *Cypridopsis vidua*, and *Cypria ophtalmica* as well as *Cyclocypris laevis* and *Metacypris cordata* (Table 2), although the latter two occurred at less than 3/4 of sites. *Darwinula stevensoni* was not abundant but a relatively regular inhabitant of the shallow lakes in Poland. The average mutual Bray-Curtis similarity between the site assemblages representing this assemblage type was 36.8%.

The second slightly less coherent (average faunal similarity between site assemblages of 27.0%) assemblage type, which included all the ostracod site assemblages from temporary waters in Poland (PTW) (Fig. 2) was characterised by four species already mentioned above: *Cypris pubera*, *Bradleystrandesia reticulata*, *Eucypris virens* and *Pseudocandona pratensis* (Table 2).

The third assemblage type linked only two peat-bog sites in Poland (P6 and P23) and one peat-bog site in Lapland (L18) (Fig. 2), and displayed an average faunal similarity of only 19.6%. The main feature of these sites was the 100% frequency of occurrence of *Pseudocandona stagnalis*, as well as a simultaneous presence of *Cyclocypris globosa* and *Bradleystrandesia reticulata* (Table 2 and Appendices 3 and 4).

The last assemblage type was defined by a major cluster and consisted of all but one (*see* above) site assemblages from Lapland and two assemblages from peat-bog sites in Poland (P5 and P24; Fig. 2). The main species indicated by the SIMPER analysis as principally responsible for the separation of this set of samples included *Candona candida* (occurring at 95% of the sites within this assemblage type) as well as *Cyclocypris ovum* and *Pseudocandona rostrata* (each found at 71% sites) (Table 2). The average similarity between all pairs of site assemblages in this cluster was 31.8%.

According to the ANOSIM test carried out using the faunal data, there were statistically significant differences in the site assemblage struc-

Table 2. Frequency of occurrence (%) of ostracod species at the sampling sites representing three habitat types within the two studied regions: LTW = temporary waters in Lapland, LP = peat-bogs in Lapland, LSL = shallow riparian water of lakes in Lapland, PTW = temporary waters in Poland, PP = peat-bogs in Poland, PSL = shallow riparian water of lakes in Poland. Detailed data on the abundance of the identified species at particular sampling sites is given in Appendices 3 and 4.

Species	LTW	LP	LSL	PTW	PP	PSL
Darwinula stevensoni	–	–	–	–	–	86
Candona candida	100	71	83	–	17	71
Candona weltneri	–	–	–	–	–	43
Candonopsis kingsleii	–	–	–	–	17	86
Fabaeformiscandona fabaeformis	–	–	–	11	17	
Fabaeformiscandona hyalina	–	–	–	–	–	57
Fabaeformiscandona lapponica	–	14	–	–	–	
Pseudocandona hartwigi	–	–	–	–	–	43
Pseudocandona marchica	–	–	–	–	17	29
Pseudocandona rostrata	88	57	67	–	–	
Pseudocandona stagnalis	–	14	–	–	67	
Pseudocandona albicans	–	–	17	11	–	
Pseudocandona compressa	–	–	–	–	–	57
Pseudocandona insculpta	–	–	–	–	–	71
Pseudocandona pratensis	–	–	–	56	–	
Pseudocandona sucki	–	–	–	33	–	
Cryptocandona reducta	–	14	–	–	–	
Cryptocandona vavrai	25	–	17	–	–	
Paracandona euplectella	–	–	–	–	17	
Cyclocypris globosa	–	29	–	–	33	
Cyclocypris laevis	–	–	–	22	33	57
Cyclocypris ovum	75	29	83	11	33	43
Cyclocypris serena	25	14	33	–	–	
Cypria exsculpta	–	–	–	–	–	14
Cypria ophtalmica	13	14	17	11	17	86
Ilyocypris decipiens	–	–	–	–	–	14
Ilyocypris gibba	–	–	–	–	–	14
Notodromas monacha	–	–	–	–	–	14
Cyprois marginata	–	–	–	11	–	
Cypris pubera	–	–	–	78	–	
Cypridopsis vidua	38	29	50	11	17	100
Bradleystrandesia fuscata	–	–	–	11	–	
Bradleystrandesia reticulata	50	43	17	56	17	
Eucypris crassa	–	–	–	33	–	
Eucypris pigra	–	14	–	–	–	
Eucypris virens	–	–	–	78	–	
Tonnacypris lutaria	–	–	–	56	–	
Heterocypris incongruens	–	–	–	11	–	
Dolerocypris fasciata	25	14	17	–	–	29
Limnocythere inopinata	–	–	–	–	–	43
Metacypris cordata	–	–	–	–	–	71

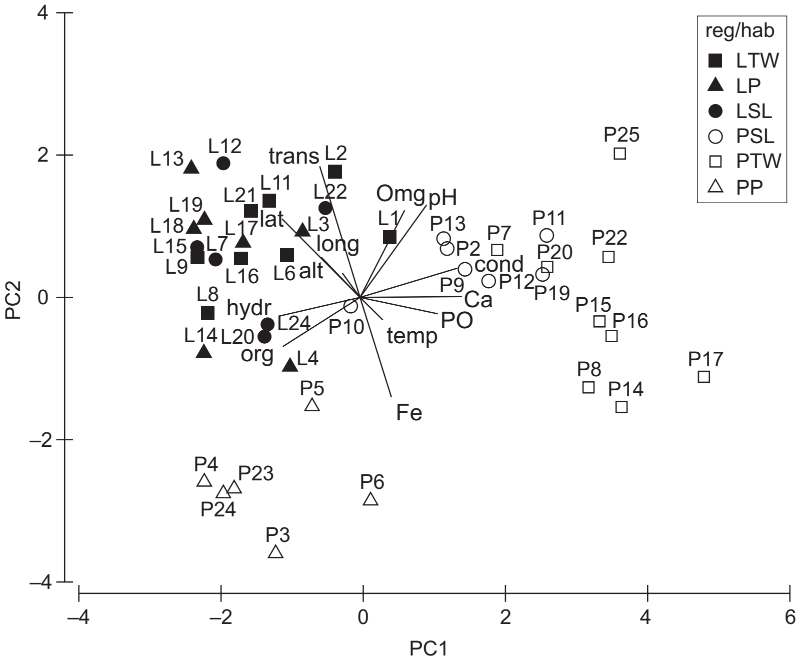

Fig. 3. The biplot displaying PCA ordination of the investigated sites (L1–L24 in Lapland and P2–P25 in Poland, as in Table 1) based on environmental factors. First axis (PC1) explains 34.4% and second axis (PC2) 14.2% of total variability. Abbreviations of habitat types within the studied regions as in Fig. 2. Environmental factors and geographical data: lat = latitude, long = longitude, alt = altitude, temp = water temperature, trans = transparency, Omg = dissolved oxygen content, cond = conductivity, Fe = iron ion content, Ca = calcium ion content, PO = phosphate content, org = organic matter content of bottom sediment, hydr = water content of bottom sediment.

ture between Poland and Lapland (r = 0.363, p < 0.001). However, when the analysis was conducted assuming a grouping by habitat type within the region (six sets of site assemblages), the differences between the habitat types were significant only in Poland ($r \geq 0.599$, $p \leq 0.002$). All the site assemblages in Lapland had a homogeneous species composition regardless of habitat ($r < 0.063$, $p > 0.189$; Table 3).

The PCA ordination of the sampled sites showed that the first three axes explained 59.2% of the total variation (Fig. 3). The factors which determined most of the variance in all sampled sites were conductivity and calcium ion content, as well as organic matter and the water content of the bottom sediments. Four abiotic factors were responsible for separation of the peat-bogs from Poland (PP): (1) high content of organic matter in sediment, (2) high content of dissolved iron in the water, (3) low concentration of dissolved oxygen, and (4) low pH. The temporary waters in Poland (PTW) and the shallow riparian waters of lakes in Poland (PSL) were both defined by: (1) conductivity, (2) pH, (3) dissolved oxygen content, and (4) dissolved phosphate and nitrate content. Moderate values of these factors were typical fo the PSL sites, whereas high (and very high) values typified the PTW sites. The sites in

Table 3. Values of *r* and respective probabilities (in parentheses) of the ANOSIM test carried out using the faunal data for six *a priori* ascertained groups of site assemblages (temporary waters in Lapland LTW, temporary waters in Poland PTW, shallow riparian water of lakes in Lapland LSL, shallow riparian water of lakes in Poland PSL, peat-bogs in Lapland LP and peat-bogs in Poland PP). Values indicating statistically significant differences are set in boldface.

	LTW	LP	PSL	PTW	PP
LSL	0.052 (0.258)	0.063 (0.188)	**0.926** (≤ 0.001)	**0.825** (0.002)	**0.504** (0.002)
LTW		–0.017 (0.483)	**0.948** (≤ 0.001)	**0.842** (≤ 0.001)	**0.566** (≤ 0.001)
LP			**0.618** (≤ 0.001)	**0.671** (≤ 0.001)	**0.214** (0.046)
PSL				**0.874** (≤ 0.001)	**0.599** (0.002)
PTW					**0.714** (≤ 0.001)

Lapland, regardless of habitat, formed a single cluster distinguished by: (1) high transparency of the water, (2) high organic matter content and water content of the bottom sediment (for values of environmental variables measured at particular sites *see* Appendices 1 and 2).

The ANOSIM analysis carried out on the matrix of environmental factors confirmed the division of sites into two regional groups (r = 0.379, p < 0.001). When grouping the sites by habitat type within the region, however, the only statistically significant differences were found in Poland between sites representing three different habitats ($r \geq 0.252$, $p \leq 0.015$; Table 3), reflecting the results obtained from the faunal data (*see* above and Table 4).

After the estimation of the gradient length by Detrended Correspondence Analysis (5.802), the CCA ordination was performed to explore the relationships between independent (environmental) and dependent (species abundance) variables. The first two axes accounted for 60.6% of the total variance of the species–environment relation, and the species–environment correlations were 0.938 for the first axis and 0.791 for the second axis (Table 5). In the analysis, latitude was taken as a covariable and longitude was excluded as a result of forward selection. Five variables appeared significant and most important in explaining the observed ostracod distribution (Fig. 4): Ca (F = 5.71, p = 0.002, λ_A = 0.65), pH (F = 3.27, p = 0.002, λ_A = 0.35), water conductivity (F = 3.17, p = 0.002, λ_A = 0.32), organic matter content of the sediment (F = 2.09, p = 0.004, λ_A = 0.20) as well as dissolved oxygen content (F = 2.04, p = 0.002, λ_A = 0.20). Conductivity and Ca content had the strongest correlations with the first canonical axis, whereas pH and organic matter content of bottom sediment correlated with the second axis. As can be seen in the CCA plot (Fig. 4) there is an interdependence between high values of dissolved oxygen, conductivity and calcium content, and abundances of *Bradleystrandesia fuscata*, *Cypris pubera*, *Cyprois marginata*, *Eucypris crassa*, *E. virens, Heterocypris incongruens*, *Pseudocandona albicans*, *P. pratensis, P. sucki* and *Tonnacypris lutaria*. These species, which are plotted on the right side in Fig. 4, are characteristic of temporary waters. In the bottom-left sector of the plot there are a number of species (*Candona weltneri*, *Candonopsis kingsleii*, *Cypridopsis vidua*, *Darwinula stevensoni*, *Fabaeformiscandona hyalina*, *Limnocythere inopinata*,

Table 4. Values of *r* and respective probabilities (in parentheses) of the ANOSIM test carried out using the environmental variables for six *a priori* ascertained groups of sites (abbreviations as in Tables 2 and 3). Values indicating statistically significant differences are set in boldface.

	LTW	LP	PSL	PTW	PP
LSL	0.010 (0.394)	–0.076 (0.935)	**0.681** (≤ 0.001)	**0.657** (≤ 0.001)	**0.894** (≤ 0.001)
LTW		–0.013 (0.541)	**0.534** (≤ 0.001)	**0.600** (≤ 0.001)	**0.700** (≤ 0.001)
LP			**0.567** (≤ 0.001)	**0.713** (≤ 0.001)	**0.623** (0.002)
PSL				**0.252** (0.015)	**0.710** (≤ 0.001)
PTW					**0.751** (≤ 0.001)

Table 5. Summary of the results of the CCA performed on 43 active samples and 41 active species.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.692	0.350	0.321	0.200	
Species-environment correlations	0.938	0.791	0.870	0.842	5.762
Cumulative percentage variance					
of species data	13.4	20.2	26.4	30.2	
of species–environment relation	40.3	60.6	79.3	90.9	
Sum of all eigenvalues					5.171
Sum of all canonical eigenvalues					1.720

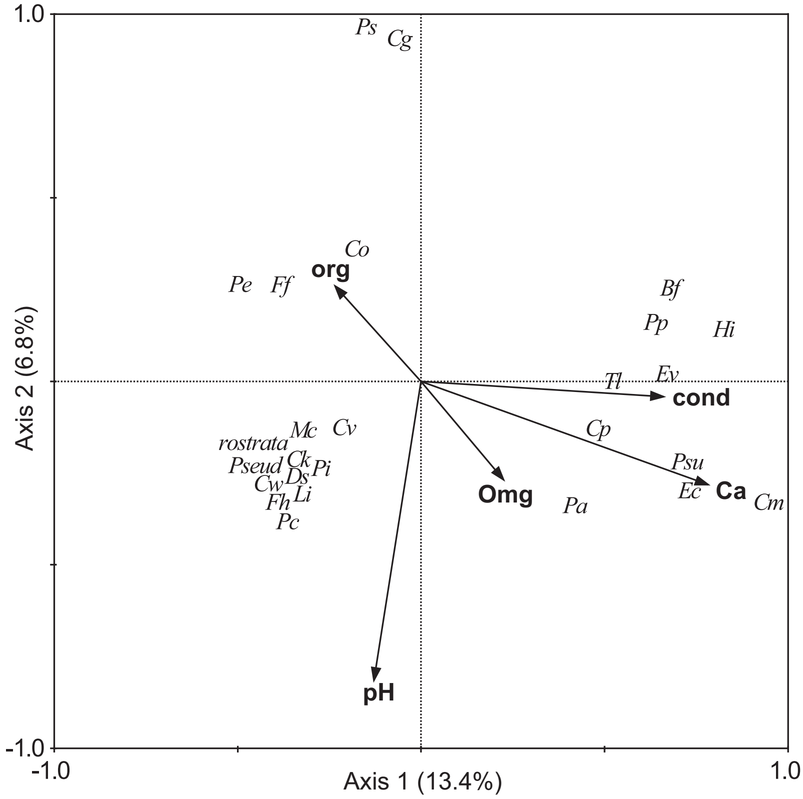

Fig. 4. The CCA ordination of ostracod assemblages and environmental factors in the space defined by the first two canonical axes. Only 26 best fit species were taken into consideration: Bf = *Bradleystrandesia fuscata*, Cw = *Candona weltneri*, Ck = *Candonopsis kingsleii*, Cg = *Cyclocypris globosa,* Co = *Cypria ophtalmica*, Cv = *Cypridopsis vidua*, Cp = *Cypris pubera*, Cm = *Cyprois marginata*, Ds = *Darwinula stevensoni*, Ec = *Eucypris crassa*, Ev = *Eucypris virens*, Ff = *Fabaeformiscandona fabaeformis*, Fh = *Fabaeformiscandona hyalina*, Hi = *Heterocypris incongruens*, Li = *Limnocythere inopinata*, Mc = *Metacypris cordata*, Pe = *Paracandona euplectella*, Pa = *Pseudocandona albicans*, Pc = *Pseudocandona compressa*, Pi = *Pseudocandona insculpta*, Pp = *Pseudocandona pratensis*, Ps = *Pseudocandona stagnalis*, Psu = *Pseudocandona sucki*, *Pseud* = *Pseudocandona* sp., *rostrata* = the species group *rostrata* of the genus *Pseudocandona*, Tl = *Tonnacypris lutaria*. Five environmental factors which appeared statistically significant are indicated (codes as in Fig. 3) and latitude was considered as a covariable.

Metacypris cordata, *Pseudocandona compressa*, *P. insculpta*, *Pseudocandona* sp. and *rostrata* group) the abundances of which are correlated with high oxygen content values and high pH. Furthermore, the abundances of the aforementioned species revealed negative correlation with iron content (e.g. *C. kingsleii* Spearman's correlation: $\rho = -0.42$, $p < 0.01$ and *D. stevensoni* $\rho = -0.44$, $p < 0.01$). In the upper-left sector of the plot, there are species that are characteristic of Polish peat-bogs, namely *Cyclocypris globosa*, *Cypria ophtalmica*, *Fabaeformiscandona fabaeformis*, *Paracandona euplectella* and *Pseudocandona stagnalis*, and their occurrences and abundances proved to be associated with low pH, high organic matter content in the bottom sediment, low values of dissolved oxygen and low calcium content. Finally, it is worth noticing that species characteristic for Lapland are absent from the plot (only the 26 best fitted species were taken into consideration) as a consequence of a lack of any strong relationships between ostracod abundances and environmental factors in Lapland.

The BEST analysis selected six significant and most important environmental factors and geographical variables determining the grouping of the ostracod site assemblages into four main clusters (Fig. 2), i.e. four assemblage types (ρ = 0.503, p = 0.01), these were: latitude, pH, conductivity, dissolved iron content, phosphates and organic content of the bottom sediment. Remarkably four of these (latitude, pH, conductivity and organic matter content) also appeared as significant in the CCA ordination. Latitude naturally separates all ostracod assemblages found in Poland (< 54°27´N) from those found in Lapland (> 66°28´N). Low pH segregates assemblages of acidic sites (pH < 5.3 in peat-bogs in Poland) from all the other assemblages at sites which are characterized by more alkaline conditions with moderate to high pH values. Conductivity subdivides the ostracod assemblages into three groups: (1) assemblages of low conductivity sites (< 180 μS cm^{-1}) in Lapland and the peat-bogs in Poland, (2) assemblages of moderate conductivity sites of shallow lakes in Poland, and (3) assemblages of the highly mineralised (> 800 μS cm^{-1}) temporary waters in Poland. Dissolved iron content is a factor that typifies assemblages of the shallow lakes in Poland where values are close to zero (< 0.05 mg dm^{-3}). Low phosphate content (< 0.25 mg dm^{-3}) characterizes assemblages occurring in Lapland, moderate PO_4^{-3} values characterize assemblages of Polish shallow lakes and peat-bogs, whereas very high PO_4^{-3} values (> 1.00 mg dm^{-3}) are typical from assemblages from temporary waters. Finally, organic matter content in the sediment typifies the assemblages found in Polish peat-bogs.

Funnel plots (Fig. 5) were generated using TAXDTEST to compare the taxonomic diversity (expressed as Δ+) of the ostracod assemblages found in Poland and in Lapland relative to the known non-marine ostracod diversity of the corresponding region. They show that in both regions the ostracod assemblages are representative of the known regional taxonomic diversity. It is noteworthy that in Poland there were statistically significant differences in the average taxonomic distinctness (Δ+) between the habitat types (Kruskal-Wallis test: H = 10.08, p = 0.007), the highest Δ+ values were typical for the assemblages from shallow lakes (PSL), while moderate values were found for those from temporary waters (PTW) and peat-bogs (PP) (mean Δ+ value ± SD for PSL = 75.76 ± 7.13 *versus* that for PTW = 66.71 ± 4.35 and that for PP = 53.25 ± 11.99). However, the power of the performed test was low because most of the assemblages from the peat-bogs (four of seven) had to be excluded from the analysis due to the low abundances (less than 30 ind. m^2) and species richness (less than two species) of the samples.

Discussion

In this study of three types of freshwater habitats (temporary waters, shallow riparian water of lakes and peat-bogs) in Poland, a total of 35 ostracod species was identified, which constitutes 25% of the total number of modern fresh- and brackish-water ostracod species reported from Poland (140, *see* Namiotko 2008). In the Lapland sites representing the same three habitat types, 15 species were found representing 42% of the total number of freshwater ostracod species recorded in this region, i.e. 36 species reported the overall from the Norwegian, Swedish, Finnish and Russian parts of the Fennoscandia north of the Arctic Circle (according to Sars 1890, Ekman 1908, 1914, Alm 1914a, 1914b, 1915, Sars 1925, Akatova & Järvekülg 1965, Vekhov 2001, Iglikowska & Namiotko 2004, 2010). No species new to Norway, Finland or Poland were collected.

In Poland, there were statistically significant differences in average species richness (number of species) of ostracod site assemblages occurring in the three different habitat types. The highest number of species was collected from lake sites and the lowest from peat-bogs. Thus shallow riparian lake habitats seem to provide more suitable and more stable environmental conditions for ostracods as compared with temporary astatic waters and peat-bogs. An important factor resulting in high ostracod species richness in lakes is the presence of emergent vegetation in the riparian zone, which creates a broad range of ecological niches (Cooke *et al*. 2001, Søndegaard *et al*. 2005). In peat-bogs and temporary pools we studied, emergent vegetation was either non-existent or sparse, so the ostracod fauna was relatively poor in species. Habitats provided by temporary waters are highly specific, inhabiting organisms have relatively short life cycles, an ability to survive desiccation, and tolerate high and fluctuating concentrations of dissolved organic and

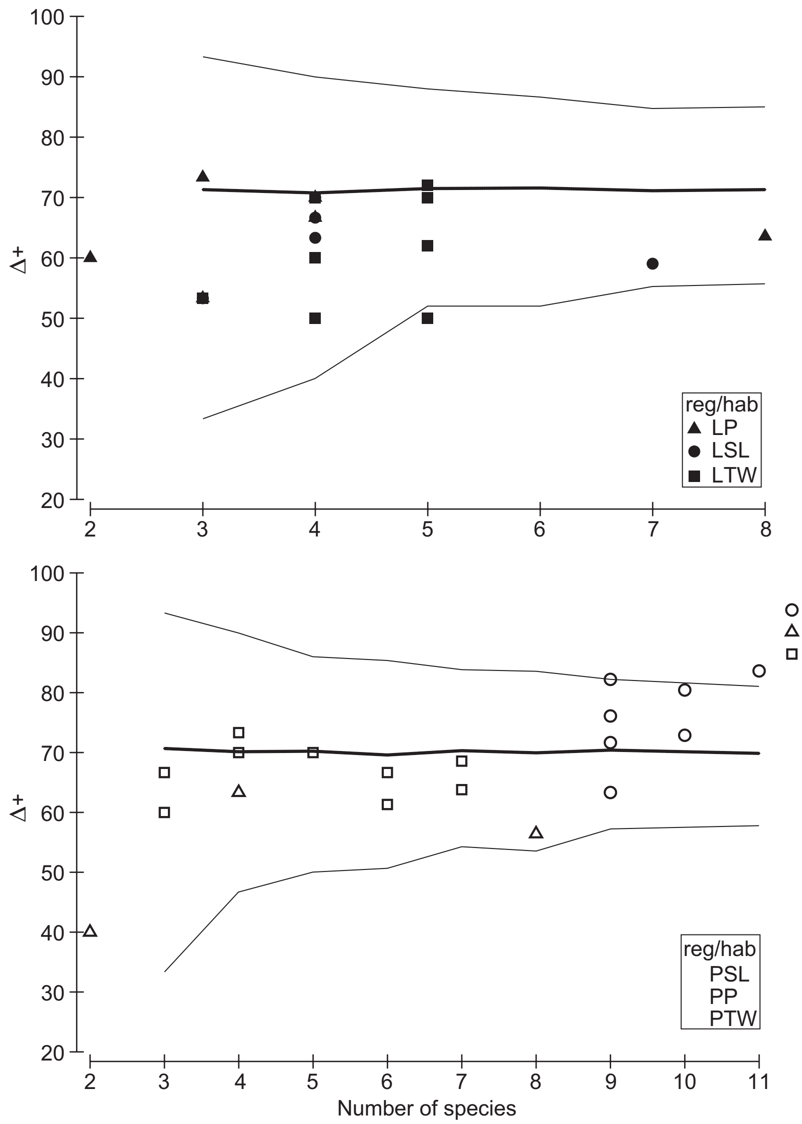

Fig. 5. Funnel plots of Average Taxonomical Distinctness (Δ+) of the ostracod assemblages in Poland (top) and in Lapland (bottom). Thin lines indicate limits within which 95% of the simulated values of the Δ+ coefficient are located, whereas the central thick lines indicate mean Δ+ for the full inventory of freshwater ostracods from Poland and Fennoscandia, respectively. Various symbols as indicated in the legends represent the true values of Δ+ coefficient for the investigated sites of the three habitat types within two regions (codes as in Fig. 2 and Table 2).

inorganic matter (e.g. Williams 2006). Ostracods inhabiting temporary pools are adapted to survive in such variable environments, they have desiccation-resistant stages (resting eggs or juvenile and adult torpidity), short life cycles, photoperiod-dependent egg hatching, parthenogenetic or mixed (where both sexual and asexual lineages occur) reproductive modes or can exhibit a bet-hedging strategy (e.g. Horne 1993, Otero *et al*. 1998, Mezquita *et al*. 2005, Martins *et al*. 2008).

The extremely low diversity and abundance of ostracods observed in peat-bogs was most probably linked to low pH and resulting low availability of dissolved calcium and other ions. Freshwater ostracods have relatively large carapaces, mainly composed of calcium carbonate, therefore it is commonly believed that they require quite high levels of available calcium in the environment to construct their carapace valves. However, we need to know more about complexities of the valve calcification in ostracods (Mezquita *et al*. 1999a, Holmes & Chivas 2002).

The distinction between the three habitat types in Poland was also revealed by the Shannon-Wiener diversity index. There were significant differences in the species diversity between assemblages from the three habitat types (Kruskal-Wallis test: $H = 10.74$, $p < 0.01$). The highest values of the Shannon-Wiener diversity index were found in the assemblages from shallow lakes in Poland, and probably reflected the relative permanence and low variability of these lacustrine environments, relative to temporary waters and peat-bogs. Heino (2000) reported that species diversity increases with the size of a lake, larger water bodies contain more habitats and consequently more potential niches (Søndegaard *et al*. 2005). In this study, the lakes had the highest surface areas and hence the higher values of the Shannon-Wiener diversity index. Heino (2000) reported other factors influencing diversity in lakes such as heterogeneity of water habitat, provenance of bottom sediment (autochthonous remains of *Sphagnum* mosses and humic materials *versus* allochthonous fallen leaves of deciduous trees and shrubs), and amount of riparian vegetation. The results reported herein add pH to Heino's (2000) list of factors influencing diversity. Our results show a statistically significant correlation between pH and observed values of the diversity index (Spearman's correlation: $\rho = 0.46$, $p < 0.01$). Those sites typified by low environmental heterogeneity, with autochthonous bottom sediment and lacking macrophytes were poorest in species richness, conditions that are characteristic of peat-bogs in Poland, where the lowest values of the diversity index were found. In Lapland, the average values of the Shannon-Wiener diversity index were similar in the three types of habitat, and generally lower than in Poland (average H' = 1.074 and 1.377 in Lapland and in Poland, respectively). This is in accord with the generalization that species diversity decreases towards the north (Heino 2002, Willig *et al*. 2003). There were significant differences in species diversity between Poland and Lapland, but such a gradient was not observed within the studied regions. The influence of latitude on the species diversity in the north may be the result of longer persistence of the last glaciation at higher latitudes, so that species had less time to colonize these areas. History, however, does not seem to be the only major determinant of species richness in the northern areas (Heino 2002).

As regards the reproductive mode, 23 of the 41 species identified in the study are considered to reproduce sexually (Meisch 2000). The remaining 18 species probably reproduce parthenogenetically at the sampling sites, although for 11 of these, rare males or sexual populations are reported in the literature (Meisch 2000). In Lapland, nine out of 15 recorded species (60%) are known to be fully parthenogenetic (consisting of female-only populations or with sporadic occurrence of rare males). On the other hand in Poland, 60% of all the the recorded species reproduce sexually. The sex ratio in all studied species was heavily biased in favour of females, with one exception — *Candona weltneri* at P9. In that case, sampling probably took place during the season when males dominated the adult population, since in this species mature males and females are known to appear at different times (Hiller 1972). In Poland, there was a significant relationship between the ratio of parthenogenetic to sexual species and habitat type (Kruskal-Wallis test: $H = 14.08$, $p < 0.001$). The largest proportion of species with asexual reproduction was sampled from temporary waters (mean ± SD = 81.2% ± 29.2%), while significantly lower proportions were observed in peat-bogs (mean ± SD = 6.8% ± 13.4%) and shallow lakes (mean ± SD = 4.5% ± 2.5%). Parthenogenesis enables a population to grow rapidly, so that it can quickly exploit any new reservoir (e.g. when a temporary pond re-fills after drought), thus asexual or mixed reproductive strategies can be an advantageous adaptation in unpredictable habitats (Horne & Martens 1999, Mezquita *et al*. 2005, Martins *et al*. 2008). In lakes and peat-bogs, the environmental conditions are generally more stable, and sexual reproduction appears to be a more favourable mode. Analysis of the assemblages in Lapland showed no statistically significant difference in the ratio of parthenogenetic species between habitat type (Kruskal-Wallis test: $H = 0.105$, $p = 0.949$).

Four types of ostracod assemblages were distinguished using the UPGMA cluster analysis (Fig. 2). The assemblage from temporary waters in Poland was distinguished by four species: *Cypris pubera*, *Eucypris virens*, *Bradleystrandesia reticulata* and *Pseudocandona pratensis*, which are characteristic of temporary pools

(Sywula 1974, Meisch 2000, Gifre *et al*. 2002). Similarly, few species found in the assemblage from Polish peat-bogs (mainly *Cyclocypris globosa* and *Pseudocandona stagnalis*) are typical inhabitants of this habitat (Sywula 1965, 1974, Fryer 1993, Meisch 2000). The assemblage type in shallow riparian water of lakes in Poland, consisted of two sets of species: (1) a group of moderately dominant eurybiontic species (*Cypridopsis vidua*, *Darwinula stevensoni*, *Cypria ophtalmica*, *Cyclocypris laevis*, *Candonopsis kingsleii* and *Candona candida*), and (2) a group of less abundant species typical of central European lakes (*Candona weltneri*, *Pseudocandona insculpta*, *P. marchica*, *P. hartwigi*, *Metacypris cordata* and *Limnocythere inopinata*) (Sywula 1974, Meisch 2000).

In Lapland, we did not find a strong relationships between abundances of the ostracod species and the observed environmental parameters, with one exception. The abundance of *Candona candida* was negatively correlated with organic matter content in bottom sediments ($\rho = -0.06$, $p < 0.01$). In contrast, abundance of this species correlated positively with latitude ($\rho = 0.59$, $p < 0.001$), which implies that it prefers cooler waters of northern Europe. Kiss (2007) found that this species' abundance correlated negatively with water temperature, and Külköylüoğlu *et al*. (2007) reported a negative correlation with air temperature ($\rho = -0.508$, $p < 0.05$). Based on our results and previous papers, *C. candida* is confirmed as an oligothermophilic species, preferring oligotrophic conditions.

Significantly stronger species–environment relationships were found in Poland. The group of species consisting of *Bradleystrandesia fuscata*, *Cypris pubera*, *Eucypris crassa*, *E. virens*, *Pseudocandona albicans*, *P. pratensis* and *P. sucki*, which were placed on the right side of the CCA plot (Fig. 4), appeared to be associated with relatively high values of conductivity, oxygen content and calcium content. High values of environmental factors are characteristic of temporary pools, and *E. virens* almost exclusively inhabits astatic water bodies (Sywula 1974, Mezquita *et al*. 1999b, Meisch 2000, Gifre *et al*. 2002, Külköylüoğlu *et al*. 2007). This species tolerates not only high concentrations of dissolved substances, but also significant fluctuations of salinity, temperature, oxygen and nutrient content (Gifre *et al*. 2002). Külköylüoğlu *et al*. (2007) also reported a positive correlation between *E. virens* abundance and conductivity but a negative one with pH.

The lacustrine species were grouped in the bottom-left sector of the CCA ordination plot (Fig. 4). These species correlate with environmental factors such as high pH, and high content of dissolved oxygen. Phytophilic *Cypridopsis vidua* was recorded in a range of habitats, but it is most often found in lakes (Sywula 1974, Meisch 2000). This species is reported to require high oxygen concentrations (≥ 5 mg dm^{-3}) (Kiss 2007), and its oxyphilic nature was confirmed in the present study. The species was recorded at sites with an average O_2 concentration of 6.2 mg dm^{-3}. *Cypridopsis vidua* tolerates well a broad range environmental factors, even relatively high concentrations of pesticides (Külköylüoğlu *et al*. 2007). However, it is doubtful whether *C. vidua* should be considered a polythermophilic species (Meisch 2000), since it is widespread and abundant in Lapland. An organism with high oxygen requirement is often well adapted to low water temperatures (Mikulski 1982).

The BEST analysis distinguished five environmental factors and one geographical variable which had significant impact on the grouping of the ostracod assemblages: pH, conductivity, Fe and phosphate contents, organic matter content in sediment, as well as latitude. The influence of geographical position is most likely linked to climatic effects. Mezquita *et al*. (2005) and Poquet and Mesquita-Joanes (2011) showed latitude as one of the most important factors determining the distribution of freshwater Ostracoda in Europe. Species living in the north have to tolerate not only low temperatures, but often also low concentrations of dissolved ions and nutrients. In Lapland, waterbodies are frozen for more than half a year, therefore, the species living there must be able to survive such conditions at least during one stage of their life cycle. The Lapland sites were situated either on the western slopes (sites L1–L7) or on the eastern slopes (sites L8–L24) of the Scandinavian Mountains. Although east and west sites experienced significantly different climatic regimes, there were no differences either in their environmental characteristics or in the abundances and species composition of the ostracod assemblages between the two sides of the Mountains.

Many authors have reported that pH significantly affects freshwater invertebrates (e.g. Wickins 1984, Lampert & Sommer 1997, Rossetti *et al*. 2004, Martins *et al*. 2009, Martins *et al*. 2010). Each aquatic organism has its own pH optimum and tolerance range, but if pH exceeds this range, species cannot survive because the regulation of pH within the organism is energetically too costly (Lampert & Sommer 1997).

Ionic content of the medium can have a strong influence on the diversity of freshwater ostracods (e.g. Mezquita *et al*. 2005, Pieri *et al*. 2007, 2009). The *in situ* ionic equilibrium of water can have an effect on both the osmoregulation and the physiological control of an organism's internal ionic balance. In freshwaters, calcium is often the critically limiting ion, and crustaceans such as ostracods require calcium for their carapaces (Lampert & Sommer 1997). Calcium is effective in buffering pH, so in Ca-depleted environments organisms are far more susceptible to extremes of pH (Wickins 1984). The importance of calcium availability in controlling and limiting the post-embryonic development of ostracod individuals, as well as occurrence and diversity of ostracod species and assemblages has been demonstrated in several works (e.g. Mezquita *et al*. 1999a, Holmes & Chivas 2002, Viehberg 2006), although the intensity of the effects depends largely on species.

The analysis of the relationships between the species composition and dominance in the ostracod assemblages indicated that in Lapland, the species diversity was lower than that in temperate Poland and that most of the species recorded in the north appeared to be eurybiontic. No distinct differences in the structure of the ostracod assemblages among the three types of freshwater habitats studied in this subarctic region were found. Freshwater biodiversity in northern Europe is low probably as a result of the short growing season of the aquatic plants, the lack of adequate nutrients and hence the low primary production. Species with long life cycles cannot successfully colonize these habitats, because the season is too short for them to complete their ontogeny (not every species can survive being frozen as mature or juvenile). Development can take much longer in Lapland because of lower water temperatures. Finally, the geological character of the rocks may be important: in Lapland, rocks are mostly acidic which results in natural waters having low pH and being low in calcium (Stebel *et al*. 2007). Both factors limit the diversity of the ostracod populations and in Lapland none of the observed ostracod species have strongly calcified carapaces.

In northern Fennoscandia, numerous ponds and small lakes are a feature of the landscape, in some parts of the region there are 1500 waterbodies per 10 km^2 (Raatikainen & Kuusisto 1990, Rautio *et al*. 2011). We infer that the majority of these waterbodies in Lapland become temporarily connected during springtime, when snowmelt water raises water levels, and hence facilitates the dispersion of aquatic organisms such as ostracods among all water bodies and the colonization of new ones. Consequently, not only do the environmental parameters become uniform throughout but also the ostracod site assemblages are homogenized. This inference is one of several possible hypotheses that may explain our results: it however deserves further, more comprehensive investigation.

In Poland, the temporary pools and the peatbogs are inhabited almost exclusively by sets of ostracod species that are specific to these habitats. These species can be used as indicator species for each of these habitats.

Temporary waters studied in Poland were located in cultivated fields, in the vicinity of villages and towns, or in roadside ditches. The inflow into these temporary water bodies is by rainwater running off fields or roads, potentially enriched with fertilizers, pesticides, manure and pollutants such as oil residues. Therefore, it is not surprising that these temporary waterbodies were found to contain high concentrations of nitrogen, phosphate and mineral compounds. During warm and dry summer, the water gradually dries up, and concentrations of dissolved inorganic and organic substances become progressively higher. The species that inhabit these waterbodies must have the ability to tolerate high nutrients concentration, wide temperature ranges, and hypoxic conditions. Before these waterbodies finally dry up, specialist species lay desiccation-resistant eggs and enter diapause. For many species, the optimal reproductive strategy in temporary waters is parthenogenesis, because even a single egg can be sufficient to ensure recolonisation of a waterbody when it refills (Mezquita *et al*. 2005).

The main interrelated problems facing aquatic organisms inhabiting peat-bogs are low pH and lack of calcium ions (or the difficulty in their uptake). Ubiquitous bog-mosses (*Sphagnum* spp.) not only acidify the water, but also decomposition of a dense mass of decaying moss utilizes much of the dissolved oxygen in the water and all of it in the underlying peat. Only some specially adapted species can tolerate these extreme conditions.

In the lakes in Poland, typical diurnal oscillations in O_2 and CO_2 concentrations and pH shift the balance between photosynthesis (increasing oxygen levels, reducing CO_2 and increasing the alkalinity) and respiration (reducing oxygen levels, increasing carbon dioxide concentrations and hence reducing pH). When pH and oxygen concentrations increase, ionic iron changes from soluble ferrous ions to insoluble ferric ions which tend to precipitate in the form of ferric hydroxide. As a result, iron was not detectable in the water column of the Polish lakes. The littoral zone of a lake supports a high species diversity and while there are specialized lake species, the lakes are also inhabited by eurybiontic species.

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Appendix 1. Physical and chemical properties of water and bottom sediment (organic matter content and hydration) for the studied sites in Lapland (L1–L24).

Site	Temp. (°C)	Oxygen (%)	Oxygen (mg dm^{-3})	Salinity (g dm^{-3})	pH	Conductivity (µS cm^{-1})	Transparency (cm)	Total Fe (mg dm^{-3})	Ca^{2+} (mg dm^{-3})	NO_3^- (mg dm^{-3})	PO_4^{3-} (mg dm^{-3})	Organic matter (%)	Hydration (%)
L1	23.3	108.1	8.65	0.0	7.9	135.5	26.0	1.00	10	0.5	0.125	11.1	50.6
L2	11.5	68.2	7.58	0.0	8.1	282.0	51.0	0.00	40	0.5	0.125	54.5	92.2
L3	19.5	62.8	5.53	0.0	5.9	66.6	42.0	0.05	10	0.5	0.250	6.5	50.5
L4	21.4	80.6	7.42	0.0	5.9	79.5	22.0	0.50	20	0.5	0.250	79.3	86.4
L5	16.0	85.5	7.51	0.0	7.8	60.8	46.0	0.00	10	0.5	0.250	58.6	81.0
L6	20.4	57.1	5.33	0.0	7.0	177.3	39.0	0.05	40	0.5	0.250	85.2	85.0
L7	19.1	54.4	4.85	0.0	6.5	44.9	42.0	0.20	10	0.5	0.250	55.0	88.5
L8	15.1	44.9	4.27	0.0	6.2	53.4	27.0	1.00	10	0.5	0.125	53.2	87.4
L9	15.0	59.7	5.51	0.0	6.2	63.1	36.0	0.30	10	0.5	0.250	70.5	84.0
L10	25.4	70.6	5.72	0.0	4.3	56.3	17.0	0.80	10	0.5	0.500	79.9	88.6
L11	18.3	90.3	8.48	0.0	7.2	95.7	37.0	0.80	10	0.5	0.250	41.3	74.3
L12	16.3	80.2	7.93	0.0	7.6	109.8	43.0	0.00	10	0.5	0.250	73.3	86.7
L13	15.5	68.5	7.13	0.0	6.7	94.2	59.0	0.00	10	0.5	0.250	70.9	92.9
L14	9.6	25.4	3.12	0.0	5.9	104.5	23.0	1.50	10	0.5	0.250	66.0	85.3
L15	12.8	55.0	6.20	0.0	6.6	104.5	28.0	0.05	10	0.5	0.125	81.5	85.3
L16	10.2	53.9	6.38	0.0	7.1	126.7	22.0	0.60	10	0.5	0.250	57.1	85.4
L17	19.0	67.1	6.55	0.0	6.4	106.0	33.0	0.40	10	0.5	0.250	45.6	81.5
L18	16.4	76.2	7.64	0.0	6.2	39.9	33.0	0.00	10	0.5	0.125	59.7	84.1
L19	16.9	51.6	5.26	0.0	6.2	87.7	45.0	0.20	10	0.5	0.125	46.1	85.9
L20	18.0	51.7	5.05	0.0	6.2	115.6	27.0	2.00	10	0.5	0.250	38.3	80.8
L21	17.3	76.3	7.61	0.0	7.6	150.1	27.0	0.00	10	0.5	0.125	68.6	84.1
L22	21.0	73.7	6.18	0.0	7.1	105.8	42.0	0.80	10	0.5	0.250	10.0	50.0
L23	20.1	72.5	6.68	0.0	6.6	57.5	33.0	0.00	10	0.5	0.250	96.1	89.5
L24	18.8	76.1	7.11	0.0	6.9	92.9	26.0	1.50	10	0.5	0.250	68.1	87.7

Appendix 2. Physical and chemical properties of water and bottom sediment (organic matter content and hydration) for the studied sites in Poland (P1–P25).

Site	Temp. (°C)	Oxygen (%)	Oxygen (mg dm^{-3})	Salinity (g dm^{-3})	pH	Conductivity (µS cm^{-1})	Transparency (cm)	Total Fe (mg dm^{-3})	Ca^{2+} (mg dm^{-3})	NO_3^- (mg dm^{-3})	PO_4^{3-} (mg dm^{-3})	Organic matter (%)	Hydration (%)
P1	15.4	52.9	5.02	0.0	4.2	44.9	23.0	1.00	20	0.5	0.125	96.7	88.6
P2	20.2	32.4	2.95	0.0	7.2	196.1	42.5	0.00	40	0.5	0.125	3.8	33.3
P3	17.1	21.7	2.03	0.0	5.0	54.3	14.0	2.00	20	1.0	0.250	86.3	90.7
P4	19.7	54.4	4.92	0.0	4.5	19.1	14.0	0.10	10	0.5	0.250	96.7	94.8
P5	12.8	13.8	1.44	0.0	6.9	264.0	17.5	0.20	20	1.0	0.500	89.2	91.4
P6	17.3	11.9	1.26	0.0	5.3	89.6	14.5	2.00	10	0.5	0.250	14.9	47.1
P7	21.0	101.0	8.50	0.0	8.1	416.0	24.0	0.40	80	0.5	0.125	16.6	54.0
P8	16.8	37.0	3.40	0.2	7.7	801.0	16.5	2.00	160	0.5	1.500	10.5	39.7
P9	22.3	111.6	9.71	0.1	8.9	295.0	16.0	0.00	40	0.5	0.125	38.3	72.9
P10	21.5	69.8	5.90	0.0	7.6	179.4	31.0	0.00	40	1.0	0.125	82.7	87.8
P11	20.2	52.0	4.60	0.0	8.7	384.0	27.0	0.00	80	1.0	0.500	2.0	31.4
P12	18.8	32.3	3.23	0.1	7.8	301.0	25.0	0.00	40	1.0	0.250	2.1	33.9
P13	18.9	72.2	6.81	0.0	8.3	274.0	32.0	0.00	60	1.0	0.250	28.2	69.5
P14	19.0	42.0	3.70	0.6	7.4	1617.0	18.0	2.00	220	0.5	5.000	21.4	56.8
P15	20.3	107.0	9.30	0.2	7.4	863.0	17.5	0.70	120	1.0	5.000	23.6	61.1
P16	18.7	89.2	8.51	2.4	7.7	4500.0	17.0	2.00	140	1.0	0.500	16.2	49.9
P17	22.2	123.2	9.85	0.8	7.9	1658.0	13.0	2.00	140	1.0	10.000	16.2	49.9
P18	14.8	131.5	13.02	0.1	7.6	649.0	34.0	0.05	80	0.5	0.250	10.5	37.3
P19	15.2	131.5	12.84	0.0	8.8	426.0	9.5	0.05	60	2.5	0.000	13.5	61.2
P20	19.2	121.3	11.00	0.0	8.0	288.0	25.0	1.10	40	0.5	0.500	8.7	38.7
P21	12.1	63.2	6.60	0.0	7.0	64.3	23.0	2.00	20	0.5	0.250	22.3	61.6
P22	13.3	127.7	13.30	0.5	7.8	1127.0	24.0	2.00	180	1.0	1.500	16.2	49.9
P23	19.9	63.6	5.87	0.0	4.7	37.0	10.0	0.40	10	1.0	0.125	89.0	93.7
P24	17.6	21.7	1.97	0.0	5.3	40.8	22.0	2.00	10	0.5	0.000	93.2	83.2
P25	10.8	101.7	11.13	1.5	7.9	2920.0	36.0	0.10	160	0.5	5.000	16.2	49.9

Appendix 3. Abundances of particular species/taxa in the samples from the studied sites in Lapland (L1–L24), total sample abundance (*N*), density per m^2 (*D*), percentage of the total sample abundance in the overall number of the collected ostracods from both regions (%), and total absolute abundance of taxa in all samples taken in Lapland (Total) (a = adults, j = juveniles).

Site	*Bradleystrandesia reticulata*	*Candona candida*	*C. candida* (early stages)	*Cryptocandona reducta*	*Cryptocandona vavrai*	*Cyclocypris globosa*	*Cyclocypris ovum*	*C. ovum* + *C. vidua* juv.	*Cyclocypris serena*	*Cypria ophtalmica*	*Cypridopsis vidua*	*Dolerocypris fasciata*	*Eucypris pigra*	*Eucypris* sp.	*Fabaeformiscandona lapponica*	*Pseudocandona albicans*	*Pseudocandona rostrata*	*Pseudocandona stagnalis*	*Pseudocandona* sp. juv.	Cypridinae indet.	*N*	*D*	Percentage
L1		164a 1064j	231j				3a		4a								139a 101j		228j		1934	3868	4.8
L2	39a		2j				1213a				1a	1a 1j									1257	2514	3.1
L3		106a 101j	23j			1a															231	462	0.6
L4			1j									2a									3	6	< 0.1
L6		86j	3j				41a		1a	3a				1j			25a		3 j		163	163	0.4
L7	2	9j					45										7a 1j				64	64	0.2
L8	58a 21j	8a 12j			1a		526a												2j	2j	630	630	1.6
L9	1a	39j			1a												1a		1j		43	86	0.1
L11		19a 68j					17a										1a 1j				106	106	0.3
L12		2j					60a 3j										1a				66	132	0.2
L13		2a 3j					637a 8j										22a 4j			2j	678	678	1.7
L14		13a 1j							1a		82a						11a 2j		4j		114	228	0.3
L15		4a 3j					48a 1j										5a 1j				62	124	0.2
L16	10a	28a 23j									1a						18a 18j		11j		109	109	0.3
L17	103a	27a 287j	26j	4a 6j			112a 64j			3a	7a				11a 2j		9a 18j		17j		696	1392	1.7

L18	28a					2a 25j												7a	4j		66	66	0.2
L19	1a	9a 314j	5j										4a				98a 90j		86j		607	607	1.6
L20		38a 274j			9a		81a 7j		8a	32a 5j	5a						34a 6j		16j		515	1030	1.3
L21		51a 65j					1206a 778j	1352j			140a 4j	17a					12a 17j		15j		3657	7314	9.1
L22		10a 26j					64a		4a		17a 2j										123	246	0.3
L24		1a	1j								19a	10a				1a			1j		33	66	0.1
Total	263	2857	292	10	11	28	4914	1352	18	43	278	31	4	1	13	1	642	7	388	4	11157		

Appendix 4. Abundances of particular species/taxa in the samples from the studied sites in Poland (P2–P25), total sample abundance (*N*), density per m² (*D*), percentages of the total sample abundance in the overall number of the collected ostracods from both regions (%), and total abundance of taxa in all samples taken in Poland (Total) (a = adults, j = juveniles).

Site	*Bradleystrandesia fuscata*	*B. reticulata*	*Candona candida*	*C. weltneri*	*Candona* sp.	*Candonopsis kingsleii*	*Cyclocypris globosa*	*C. laevis*	*C. ovum*	*Cypria exsculpta*	*C. ophtalmica*	*Cypridopsis vidua*	*Cypris pubera*	*Cyprois marginata*
P2			4j		21j	1a		336a/12j		1a	37a	8a		
P4							1a							
P5			7j		39j	22a/14j		1a	44a			1a/1j		
P6		2a					612a/504j	3a						
P7		1931a/4 j										124a	278a/14j	
P8		4a/1191j											5a/1383j	
P9			14a/16j	118a/168j	14j	16a/596j			143a/3j			17a/25j		
P10			2j	2a/80j	55j	21a/6j			24a		9a	11a/9j		
P11						11a		171a/12j			12a	5a		
P12			1a/16j					1584a/102j			11a/1j	89a/2j		
P13				6a/21j	17j	8a			9a/2j		38a	1j		
P14													42a/1614j	52a/69j
P15									154a		1a		29a/4j	
P16	721a/4j							543a						
P19			2j			8a/55j		320a/4j			1a	6a/1j		
P20		293a/1857j											148a/59j	
P22		571a						1a					391j	
P24									219a		5064a/32j			
P25		7a/5j											129a/329j	
Total	725	5865	62	395	146	758	1117	3089	598	1	5206	300	4425	121

Appendix 4. Continued.

Site	*Darwinula stevensoni*	*Dolerocypris fasciata*	*Eucypris crassa*	*E. virens*	*Fabaeformiscandona fabaeformis*	*F. hyalina*	*Fabaeformiscandona* sp. juv.	*Heterocypris incongruens*	*Ilyocypris decipiens*	*I. gibba*	*Limnocythere inopinata*	*Metacypris cordata*	*Notodromas monacha*	*Paracandona euplectella*
P2	1a											206a/5j		
P5					14a		7j							14a/1j
P8			56a	14a/9j										
P9	13a/2j					8a/194j								
P10	1j	2a/1j										18a/410j	93a/35j	
P11	1a										1a	59a/6j		
P12						2a			1a		2a			
P13	5a/3j	1a				18a/21j	13j			1a/1j	3a	1j		
P14			233a	18a										
P15				3a										
P16				215a/9j										
P17				146a/1j										
P19	4a					20j						17a/2j		
P20					18j									
P22				17a				11a/1j						
P23														
P24														
P25			81a	32a										
Total	30	4	370	464	32	263	20	12	1	2	6	724	128	15

Appendix 4. Continued.

Site	*Pseudocandona albicans*	*P. compressa*	*P.* ex gr. *compressa*	*P. hartwigi*	*P. insculpta*	*P. marchica*	*P. pratensis*	*P.* ex gr. *rostrata*	*P. stagnalis*	*P. sucki*	*Pseudocandona* sp. juv.	*Tonnacypris lutaria*	*N*	*D*	Percentage
P2			5j	8a	48a			60j			56j		809	8629	2
P3									1a				1	2	< 0.1
P4													1	1	< 0.1
P5						31a		8j	10a/2j		10j		226	904	0.6
P6									12a		1j		1134	6043	2.8
P7													2351	9404	5.8
P8	3a									3a		10a	2678	21424	6.6
P9		14a	97j		4a	27a		245j			727j		2461	4922	6.1
P10			4j					1j			244j		1028	2056	2.6
P11		152a	17j	15a	59a	10a		4j			19j		554	739	1.4
P12		648a/111j		28a	47a/2j						441j		3088	4117	7.7
P13											32j		201	402	0.5
P14										151a	2j		2181	6543	5.4
P15							117a			17a	42j		367	367	0.9
P16							41a/2j				1j		1536	1536	3.8
P17							12a				4j	2a	165	165	0.4
P19		16a	10j		2a/4j			13j			219j		704	704	1.7
P20												1a	2376	19008	5.9
P22							74a				1j	33a	1100	2200	2.7
P23									199a/7j				206	275	0.5
P24													5315	21260	13.2
P25							72a					6a	661	1322	1.6
Total	3	941	133	51	166	68	318	331	231	171	1799	52	29143		