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Zooplankton Assemblages Related to Environmental Characteristics in Treeline Ponds in Finnish Lapland

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Abstract

Zooplankton communities of 17 subarctic ponds with differing catchment areas and habitat types in northern Finland were surveyed during the open water season from June to August. Ponds were located along a gradient that changes from a mountain birch woodland to a treeless tundra. In all sites, cladoceran abundance dominated that of copepods although there was a consistent pattern of increasing relative abundance of copepods toward the most barren ponds. Species richness declined with increasing altitude but diversity remained constant. Zooplankton communities within the same habitat type were similar. Temporal variation in species abundance showed a coherent temperature driven pattern along the whole altitudinal transect.

Introduction

Lakes and ponds in northern Finland are situated along a natural, 100-km-long south-north gradient from spruce and pine forest to mountain birch woodland and finally to barren tundra. This change in the catchment vegetation characteristics is strongly reflected in the chemical and physical conditions of the respective water bodies (Weckström et al., 1997; Blom et al., 2000). The lakes can be divided into two distinct groups according to their environmental characteristics. Forest lakes are small, warm, acidic, and highly colored polyhumic waters with high concentrations of total organic carbon (TOC) and iron (Fe). Arctic lakes are large, cold and clear water bodies with higher alkalinity, pH and calcium (Ca) values.

The chemical and physical environment in the water bodies affects the community status of these lakes and ponds. There are significant correlations between several plankton taxa and certain chemical (pH, NO₃-N) and catchment (altitude, bedrock) characteristics in northern Sweden lakes (Nauwerck, 1994). Distinct changes in diatom, chironomid, and cladoceran species composition and diversity have also been noted in lakes in Finnish Lapland when moving from coniferous forest zone to barren tundra (Weckström et al., 1997; Korhola, 1999; Olander et al., 1999).

Small ponds are the most numerous aquatic ecosystems in northern Fennoscandia. The division of ponds into two groups according to the forest type or the presence or absence of forest in the catchment area only partly explains the environmental variability among ponds. Ponds are shallow, which makes them more homogeneous than larger lakes because water column is seldom stratified; however, smaller catchment areas allow more variability in water chemistry between nearby ponds than within lakes.

The biota in ponds is also different from the lake biota. Due to their shallowness, some ponds may totally dry out in summer or freeze to the bottom during winter, which greatly affects the organisms and may control the species composition more than variability in water chemistry (Williams, 1987). Several studies have provided evidence that the number of cladoceran species, for example, in ephemeral ponds decreases as the duration of the wet phase shortens (Mahoney et al., 1990; Girdner and Lar-

son, 1995). As a consequence of freezing, ponds without seasonal dispersal routes, such as inlets or outlets, also lack vertebrate predators, mainly fish. In general, species assemblages may differ substantially between nearby waters despite the large-scale similarities in regional physical and chemical environments (Patalas, 1964; Hebert and Hann, 1986); thus, a single pond usually contains only a few species of the total zooplankton assemblage that occur in the region.

In the absence of vertebrate predators, invertebrates and especially plankton can be abundant in ponds. Zooplankton community structure and seasonal patterns in the absence of fish are thought to be mainly controlled by food abundance (Lair and Ayadi, 1989), competition (Sprules, 1972; Rothhaupt, 1990), habitat heterogeneity (Fryer, 1985), and temperature and hydrography (Moore, 1996; Girdner and Larson, 1995). Zooplankton species number is also clearly connected with altitude (Pennak, 1958; Reed, 1962; Hebert and Hann, 1986; Sandøy and Nilssen, 1986; Raina and Vass, 1993; Rautio, 1998) that influences biota either indirectly via changes in forest and vegetation zones or directly through physical parameters such as temperature. The critical altitude seems usually to be the treeline, above which the number of species greatly declines and the species composition changes. According to Patalas (1964) the number of mesozooplankton species declined from eight to one when moving from the altitude of 1400 to 3200 m above sea level.

The aims of this paper are (1) to provide data on natural physicochemical variability of treeline ponds in northern Finnish Lapland, (2) to determine crustacean zooplankton species composition and abundance in relation to environmental characteristics, and (3) to describe the seasonal succession of the most common zooplankton taxa. The paper is a continuum to the earlier study where preliminary analysis of the zooplankton distribution among different ponds was made based on the species presence-absence data (Rautio, 1998).

Material and Methods

STUDY AREA AND SAMPLING

A total of 17 shallow, small (mean area = 0.8 ha, range 0.1–2.7 ha) ponds were randomly chosen from a bank of approximately 50 ponds in the Kilpisjärvi area in northwest Fin-

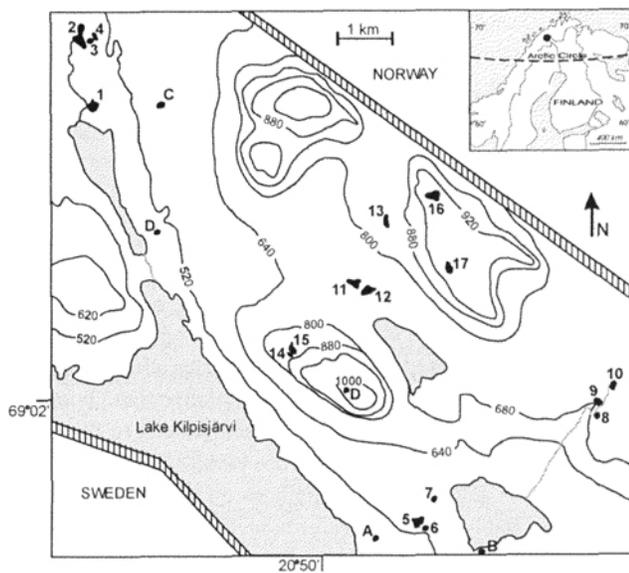


FIGURE 1. Location of study ponds and their identification numbers in Kilpisjärvi, northwest Finland. Ponds labeled with letters (A–D) were sampled only for water chemistry and chlorophyll-*a*.

land that are studied for their environmental characteristics and crustacean zooplankton communities (Fig. 1). The environment is described by Rautio (1998). Pond numbering followed Rautio (1998); pond 1 was located at the lowest (490 m) and pond 17 at the highest (940 m) altitude. Six ponds were in the mountain birch woodland (MBW) and 11 above the treeline of birch (*Betula pubescens tortuosa*) that follows the 600-m contour. Though several ponds are connected by inlets to larger lakes and may harbor summer populations of fish, current knowledge suggests all ponds are fishless. For ponds 3, 7, 9–15, and 17 this was also indirectly supported by the occurrence of fairy shrimps (*Polyartemia forcipata*, Anostraca) which elsewhere are effectively preyed upon by fish (Kerfoot and Lynch, 1987).

Invertebrate predators were not quantified in this study. Previous literature published from the study area (Bagge, 1968; Krogerus, 1972) as well as our personal observation, however, give some information of the occurrence of various taxa in the ponds. The most common predatory insect groups in the area include beetles (Coleoptera) and water bugs (Heteroptera) which occurred in all studied ponds. Dragon flies (Odonata) and caddis flies (Trichoptera) were more restricted to ponds that were surrounded by macrophytes, and phantom midge larvae (Diptera: Chaoboridae) to humic waters (Bagge, 1968; Krogerus, 1972).

Temperature and pH were measured weekly during the summer 1994 from the surface water by a mercury thermometer and a Hanna Instruments pH-meter. Altitude above sea level and surface area of each pond were calculated by using a geographical map of the area. Maximum depth was either estimated visually or measured accurately by snorkelling and with a help of a plumb line. Most ponds were less than 2 m deep and freeze to bottom in winter. Only the ponds 15 and 16 were deeper, 6 m and 3 m, respectively.

Conductivity and the concentration of dissolved organic carbon (DOC), total nitrogen, total phosphorus, and planktonic and epilithic chlorophyll-*a* were measured one to five times during open water period between 1996 and 1999. In addition to ponds in which zooplankton was sampled, the above mentioned variables were studied in some other ponds in the area (ponds A–E in Fig. 1). Conductivity was measured in situ with a Hanna

Instruments sensor. Samples for nutrients were analyzed by Lapland Regional Environmental Centre within 48 h of the sampling using standard methods of the National Boards of Waters in Finland. The chlorophyll-*a* samples were filtered through Whatman GF/C glass fiber filters and calculated spectrometrically after Jeffrey and Humphrey (1975). Epilithic chlorophyll was determined from 7.5 × 2.5-cm slides that were left in the ponds at 30-cm depth for 1 mo (July 1996). Slides were carefully washed with distilled water. The solution was then filtered (GF/C) and the chlorophyll-*a* was measured as the planktonic samples.

Zooplankton samples were taken weekly during the day time from early June until late August 1994. Sampling was performed with a 50- μ m plankton net just outside the littoral vegetation if present and always at the same sampling location. The net was gently pulled horizontally 4 times through a 1-m-course at each sampling site. For the consistent sampling performance the samples were treated as quantitative. Plankton samples were preserved in a 4% formalin solution in the field and later identified and counted under a binocular or an inverted microscope, using magnifications of 25× to 400×. Naupliar stages of copepods were not included in the study. Identification of the species was based mainly on the following sources: Rylov (1948), Enckell (1980), Lilljeborg (1982), and Amoros (1984).

STATISTICAL ANALYSES

The environmental data available for all ponds consist of eight catchment, habitat, water chemistry, and biological variables. These data include altitude, surface area, maximum depth, surface-water temperature, pH, DOC, bottom type (stone, coarse brown, soft light, thick algae mats) and presence/absence of angiosperm vegetation. Principal component analysis (PCA) was used to summarize the major patterns of variation within these data. PCA is an indirect ordination technique where data may be examined visually and any structure identified (Everitt, 1978).

Detrended correspondence analysis (DCA) was used to identify major patterns of the zooplankton community compositions. This analysis was chosen because of the gradient length of 2.9 SD units and the strong arch effect gained in PCA. Gradient lengths can be used to ascertain whether linear or non-linear ordination methods are more appropriate in statistical analyses. Gradients longer than 2 standards deviation (SD) units indicate that the data are nonlinear, whereas gradient lengths <1.5 SD refer to linear responses (ter Braak and Prentice, 1988). DCA is an indirect gradient method that summarizes directions of variation in a given data set and reveals relationships between ecological assemblages (Hill and Gauch, 1980). Prior to the analyses, absolute species abundances were $\ln(x + 1)$ -transformed to reduce skewed distributions. Both ordination analyses were performed using the computer program CANOCO, version 4.0 (ter Braak and Smilauer, 1998).

Results

Axes 1 and 2 of the PCA had eigenvalues of 0.47 and 0.26, respectively, and accounted for 46.7% of the total variance in the environmental data. The first PCA axis is mainly an altitude-bottom type/temperature axis and separates high-altitude ponds, plotted in the right of the diagram, from the low-altitude and soft bottom ponds with littoral vegetation, plotted on the left. axis 2 is related more clearly to pH and surface area. The position of ponds along the PCA ordination allowed their division into four distinct groups (Fig. 2). Four of the MBW ponds (A, B, 3, 7), which were boggy with coarse sediment bottom and

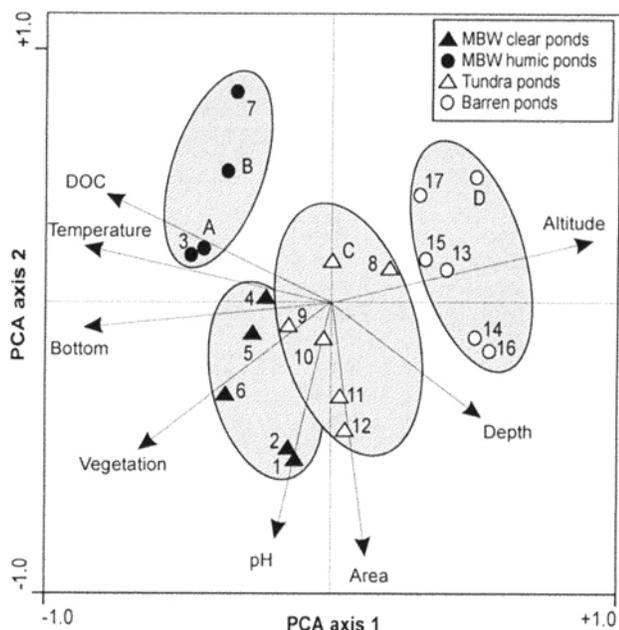


FIGURE 2. Principal component analysis (PCA) ordination of the environmental variables in the 17 ponds.

had *Sphagnum* mosses in the catchment, were separated from the rest of the ponds in the ordination. These are referred as MBW humic ponds. The five MBW clear ponds 1–2 and 4–6 had clear water and were surrounded by dense littoral vegetation. Their bottom type varied from light sediment to thick algal mats. The ponds just above the treeline had relatively abundant littoral vegetation and formed a tundra pond group. Ponds in higher altitudes, at mountainsides or tops, were without emerged vegetation and had stone bottoms and were called barren ponds (Fig. 2).

Depending on the habitat type the ponds varied from each other in seasonal water temperature patterns and water chemistry. Barren ponds were covered with ice early in the sampling season in June, whereas the mean temperature for MBW ponds at that time was already over 5°C (Fig. 3). The maximum temperature, which was below 18°C for the entire open water period in all pond groups was found in early August. Temperature was highest throughout season in the MBW ponds and lowest in the barren sites, except for the last sampling occasion when tundra

ponds were colder than some of the barren ponds. This was probably caused by the large depth:area ratio in ponds 15 and 16, which prevented them from cooling down as rapidly as the more shallow ponds. All tundra ponds were shallow and exposed to wind; thus their temperature declined more rapidly than that of deep barren ponds. In late August the temperature in MBW ponds was still over 10°C.

All ponds had low nutrient and chl-*a* concentration (Table 1). The slightly higher total nutrient values in MBW-humic ponds were probably related to the nutrients that were bound to humic substances (Münster et al., 1999). Values of pH were circumneutral in MBW-clear and tundra ponds. In MBW-humic ponds the water was more acidic, which is typical of humic waters. Barren ponds also had lower pH values (mean 6.3) because in the rocky catchment the runoff, which originates mostly from melting snow and naturally acid rain (pH 5.6), is not buffered by the soils or vegetation.

The DCA analysis, which was chosen to test whether catchment and habitat differences were reflected in the zooplankton, indicated that communities differed between ponds (Fig. 4). The eigenvalues of the first two axes were 0.41 and 0.18, and together the two axes accounted for 29% of the cumulative variance. Small value of percentage of variance explained is typical to species data and is due to large number of taxa and many zero values (ter Braak, 1994). Assemblages from the same catchment and habitat type were scattered close to each other along the DCA ordination space. The most compact group was formed of the barren pond communities, whereas MBW and tundra communities were scattered in the ordination with more variation in their locations. The scattering pattern could also be seen as a continuum along the altitude gradient from MBW to tundra and to barren.

The number of species per pond varied between 7 and 20 (Fig. 5). Although the declining trend in total species number from MBW to barren ponds was clearly detectable, it resulted only from the change in the number of Cladocera (linear regression $r^2 = 0.6$, $P = 0.001$). The total number of Copepoda did not change significantly with the altitude ($r^2 = 0.02$, $P = 0.87$). Although the total species number greatly diminished with increasing altitude, the Simpson's index of species diversity did not change significantly (linear regression $r^2 = 0.36$, $P = 0.59$), thus the diversity differences between ponds were not connected to altitude or pond habitat type.

Although the species number and composition varied be-

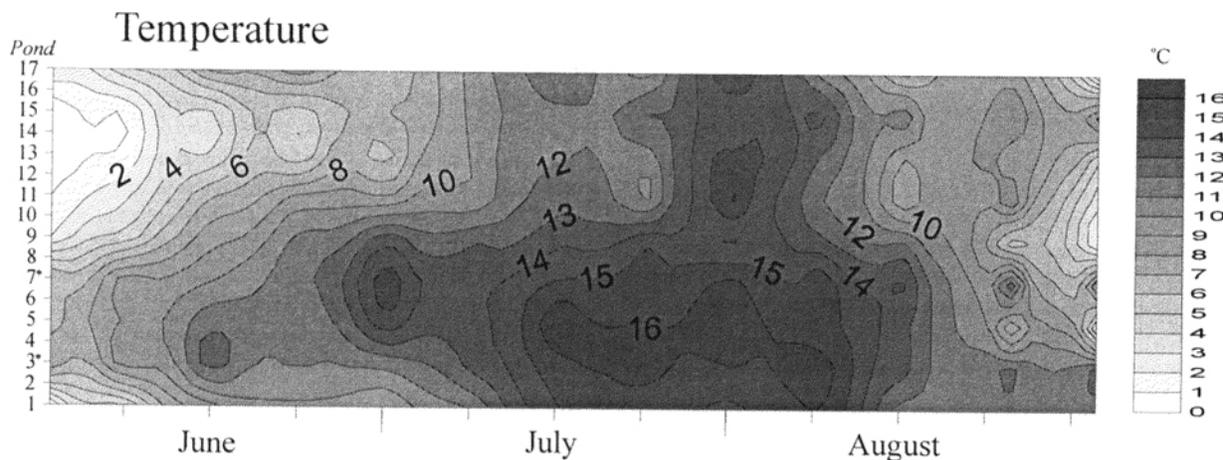


FIGURE 3. Seasonal development of water temperature in ponds at 10 cm depth. * denotes MBW-humic ponds.

TABLE 1

Characteristics of the study ponds. Data from ponds that lack zooplankton information are also included.

	MBW-clear	MBW-humic	Tundra	Barren
Altitude (m)	490–600	510–600	600–700	700–1000
Number of ponds	5	4	6	6
Mean pH	7.2	5.9	7.2	6.3
Mean conductivity ($\mu\text{S cm}^{-1}$)	40	16	29	5
Mean DOC ($\mu\text{g L}^{-1}$)	4.2	11.0	3.6	1.2
$P_{\text{tot(June)}}$ ($\mu\text{g L}^{-1}$)	4	13	4	5
$P_{\text{tot(Sept)}}$ ($\mu\text{g L}^{-1}$)	5	18	4	5
$P_{\text{tot(Sept)}}$ ($\mu\text{g L}^{-1}$)	220	340	160	130
$N_{\text{tot(June)}}$ ($\mu\text{g L}^{-1}$)	310	710	160	190
$N_{\text{tot(Sept)}}$ ($\mu\text{g L}^{-1}$)	0.6	0.9	—	0.4
Epilithon chl- <i>a</i> _{July} ($\mu\text{g L}^{-1} \text{cm}^{-2}$)	8.6	10.8	1.4	0.4

tween the pond groups, only one third of the species (13/39) were restricted to one habitat type (Table 2). Still only five species were present in all pond categories, which indicated that most species had affinity preferences to certain environmental characteristics. *Simocephalus vetulus*, *Lathonura rectirostris*, *Rhynchotalona falcata*, and *Alona costata* were only found in clear MBW ponds. They all occurred in very low numbers, however, and contributed less than 1% of the total species abundance found in that pond group. Equally rare was *Acantholeberis curvirostris*, that was only found in humic ponds, and *Holopedium gibberum*, *Drepanothrix dentata*, *Bythotrephes longimanus*, *Megacyclops gigas*, and *Acanthocyclops vernalis* which were only found in the tundra ponds. *Cyclops scutifer*, which only occurred in barren ponds represented 3% of the barren zooplankton abundance, whereas *Mixodiaptomus laciniatus*, found only in barren ponds, and *Daphnia longispina*, occurring only in humic MBW ponds formed 30 and 76%, of the zooplankton abundance in these ponds, respectively.

The species that were found in all pond groups and could therefore be considered most cosmopolitan were *Ceriodaphnia*

quadrangula, *Chydorus sphaericus*, *Alonella nana*, *Bosmina obtusirostris*, and *Polyphemus pediculus*. Of these *C. sphaericus*, *A. nana*, and *B. obtusirostris* were also the most abundant species in the surface-sediment data of the 53 lakes in the same area (Korhola, 1999).

The copepods *Mixodiaptomus laciniatus* and *Microcyclops gracilis* and the cladocerans *Polyphemus pediculus*, *Bosmina obtusirostris*, *Chydorus sphaericus*, *Acroperus elongatus*, *Scapholeberis mucronata*, and *Daphnia longispina* each had an abundance of more than 5% of the zooplankton community in one of the studied pond groups (Table 2). These were further studied in detail for their distribution and seasonal succession patterns among ponds.

Mixodiaptomus laciniatus occurred only in barren ponds where it was very abundant and formed over 75% of the whole

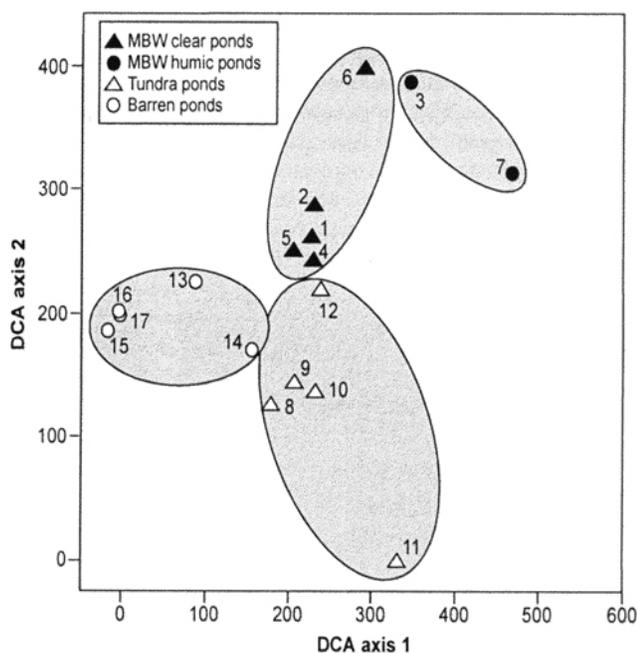


FIGURE 4. Detrended correspondence analysis (DCA) ordination of the crustacean zooplankton communities in the 17 studied ponds. Ponds from the same catchment type are grouped.

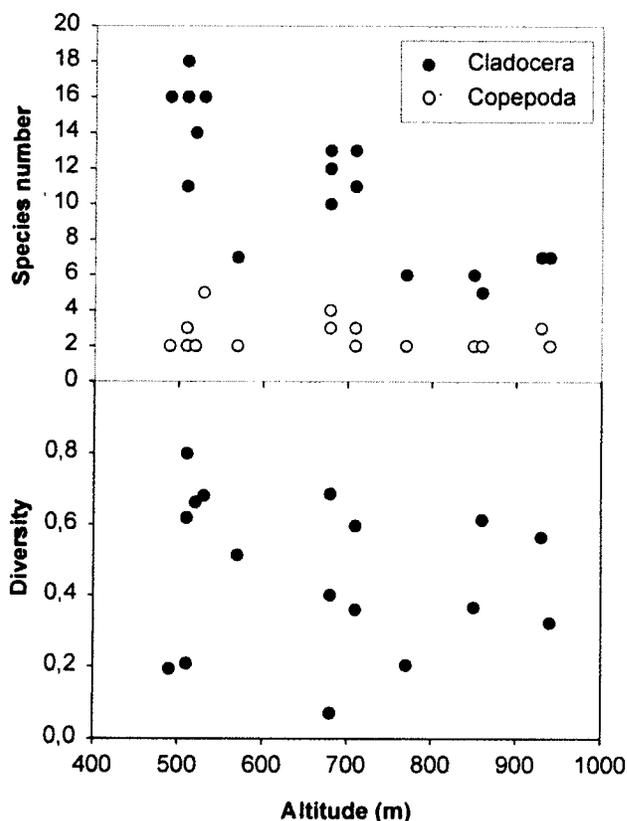


FIGURE 5. Dependence of species number and Simpson's index of diversity on altitude.

TABLE 2

Species occurrence and representation (%) in different catchment type ponds. Values over 5%, in bold, represent species that were studied for their seasonal succession.

Taxon name	MBW _{clear}	MBW _{humic}	Tundra	Barren
Cladocera				
<i>Sida crystallina</i>	>0.00	0.03	0.00	0.00
<i>Diaphanosoma brachyurum</i>	>0.00	0.12	0.00	0.00
<i>Holopedium gibberum</i>	0.00	0.00	0.01	0.00
<i>Daphnia longispina</i>	0.00	30.18	0.00	0.00
<i>Simocephalus vetulus</i>	0.22	0.00	0.00	0.00
<i>Ceriodaphnia quadrangula</i>	0.73	2.01	0.21	0.95
<i>Scapholeberis mucronata</i>	1.16	5.18	1.27	0.00
<i>Ophryoxus gracilis</i>	0.07	0.02	0.08	0.00
<i>Drepanothrix dentata</i>	0.00	0.00	0.01	0.00
<i>Acantholeberis curvirostris</i>	0.00	0.03	0.00	0.00
<i>Streblocerus serricaudatus</i>	1.16	2.18	1.27	0.00
<i>Lathonura rectirostris</i>	>0.00	0.00	0.00	0.00
<i>Eurycercus lamellatus</i>	0.05	0.07	0.32	0.00
<i>Acroperus elongatus</i>	0.97	5.46	1.08	5.71
<i>A. harpae</i>	0.29	0.21	0.57	2.58
<i>Dunhevedia crassa</i>	0.00	0.05	0.00	0.04
<i>Chydorus sphaericus</i>	2.18	5.79	0.32	1.16
<i>Rynchotalona falcata</i>	>0.00	0.00	0.00	0.00
<i>Alona affinis</i>	0.21	0.00	0.04	0.00
<i>A. quadragularis</i>	0.07	0.00	0.05	0.00
<i>A. guttata</i>	0.13	0.05	0.08	0.00
<i>A. costata</i>	0.06	0.00	0.00	0.00
<i>A. rectangula</i>	0.07	0.00	0.01	0.00
<i>Alonella nana</i>	1.50	0.76	0.38	1.86
<i>A. excisa</i>	0.28	4.36	0.02	0.00
<i>A. exigua</i>	0.02	0.10	0.00	0.00
<i>Bosmina obtusirostris</i>	60.37	2.18	65.82	7.20
<i>Polyphemus pediculus</i>	29.03	33.38	28.37	1.15
<i>Bythotrephes longimanus</i>	0.00	0.00	0.01	0.00
Calanoida				
<i>Eudiaptomus graciloides</i>	1.91	0.00	0.31	0.00
<i>Mixodiaptomus laciniatus</i>	0.00	0.00	0.00	75.96
Cyclopoida				
<i>Eucyclops serrulatus</i>	0.00	0.00	0.01	0.02
<i>Cyclops scutifer</i>	0.00	0.00	0.00	3.01
<i>Megacyclops viridis</i>	0.05	0.02	0.01	0.00
<i>M. gigas</i>	0.00	0.00	0.06	0.00
<i>Acanthocyclops vernalis</i>	0.00	0.28	0.19	0.00
<i>A. capillatus</i>	0.00	0.00	0.14	0.00
<i>A. crassicaudis</i>	0.00	0.02	0.01	0.36
<i>Microcyclops gracilis</i>	0.46	7.50	0.00	0.00
Total species number	26	24	26	12

community. As naupliar stages were not included in the study *M. laciniatus* was recorded only from mid-July onward after copepodite stages appeared. In addition to *M. laciniatus*, *A. elongatus* preferred barren ponds where it occurred in relatively high numbers, but also habited lower altitude ponds. Also Korhola (1999) found this species typical of cold lakes with minerogenic bottoms. *Daphnia longispina* but also *C. sphaericus*, *S. mucronata*, *A. elongatus*, and *Microcyclops gracilis* were associated with the two humic ponds in mountain birch woodland. *Polyphemus pediculus* and *B. obtusirostris* were the most common species occurring in nearly all the studied ponds.

The seasonal succession of most of the studied species, especially cladocerans seemed to follow quite closely water temperature (Fig. 6). The peak numbers were recorded at the time or shortly after the seasonal maximum temperature. Most species

were also completely absent from the water column in early June when some of the ponds were still partly ice-covered. The only exceptions to this pattern were *Microcyclops gracilis* which reached maximum in early summer and *Bosmina obtusirostris* and *Daphnia longispina*, which were present in the water column from the ice-break onward. MBW-humic pond 7 dried out in early August, which caused a peculiar seasonal pattern in *D. longispina*.

Discussion

Extreme environments with steep environmental gradients are ecologically interesting because sudden changes in species composition can occur within relatively small areas (Cwynar and Spear, 1991; MacDonald et al., 1993). Catchment characteristics are the main factors creating large-scale environmental gradients. One of the most significant ecotones in Finland is the northern treeline, which is the boundary between the boreal coniferous forest taiga zone and the treeless tundra. In a smaller scale, however, several other, more local transitions in the environmental range can be recognized. These can be products of changes in the soil type, vegetation or disturbances in the landscape. To what extent aquatic ecosystems are influenced by different gradients in the environmental range depends largely on the size of their catchment area. Large lowland lakes usually have large catchments and thus reflect the overall soil and bedrock features in the region. Small headwaters, on the contrary, have relatively small catchments and therefore even small-scale changes in catchment characteristics may affect the functioning of the water body.

The present study indicates that physical and chemical features as well as the crustacean species composition in the Kilpisjärvi region varied widely among the ponds with different catchment and habitat types. This is ecologically significant because it supports the hypothesis (e.g., Korhola et al., 1998) that the relationship between organisms and environmental factors determining their distribution is clearest at boundaries between different environmental ranges. At a regional scale, timing of ice breakup, length of the ice-free period, and the general heat content are defined by the location (shelter, altitude) and morphometry of the water body. The amount of macrophyte vegetation, chemical weathering in the catchment area, and the distribution of predators are related to the various catchment or habitat characteristics.

Temperature has been shown to be critical to the survival and reproduction of zooplankton (Allan and Goulden, 1980; Goss and Bunting, 1983; Moore et al., 1996). Many cladocerans are unable to reproduce until the water has reached a certain temperature level, e.g., *Ceriodaphnia quadrangula* demands temperature over 8°C for reproduction (Allan, 1977), and the egg production of *Simocephalus vetulus* is restricted when temperature is below 7°C (Green, 1966). In cold habitats such as subarctic ponds where temperature may rise above this level only temporarily and for a short period (1–2 wk) the occurrence of such species is limited. This was also seen in this study; the number of cladoceran species declined with declining temperature. Growth rates of individuals are also strongly affected by temperature (Allan, 1976; Nauwerck, 1978; Hanazato and Yasuno, 1985; Lonsdale and Levinton, 1985). In general, growth rates decrease with decreasing temperature. The development of a cladoceran from an egg to an egg lasts 7 to 8 d at 20°C but 20 to 24 d when temperature declines 10°C (Allan, 1976).

Changes in temperature also correspond with species succession (Green, 1966; Sommer et al., 1986). During winter, crus-

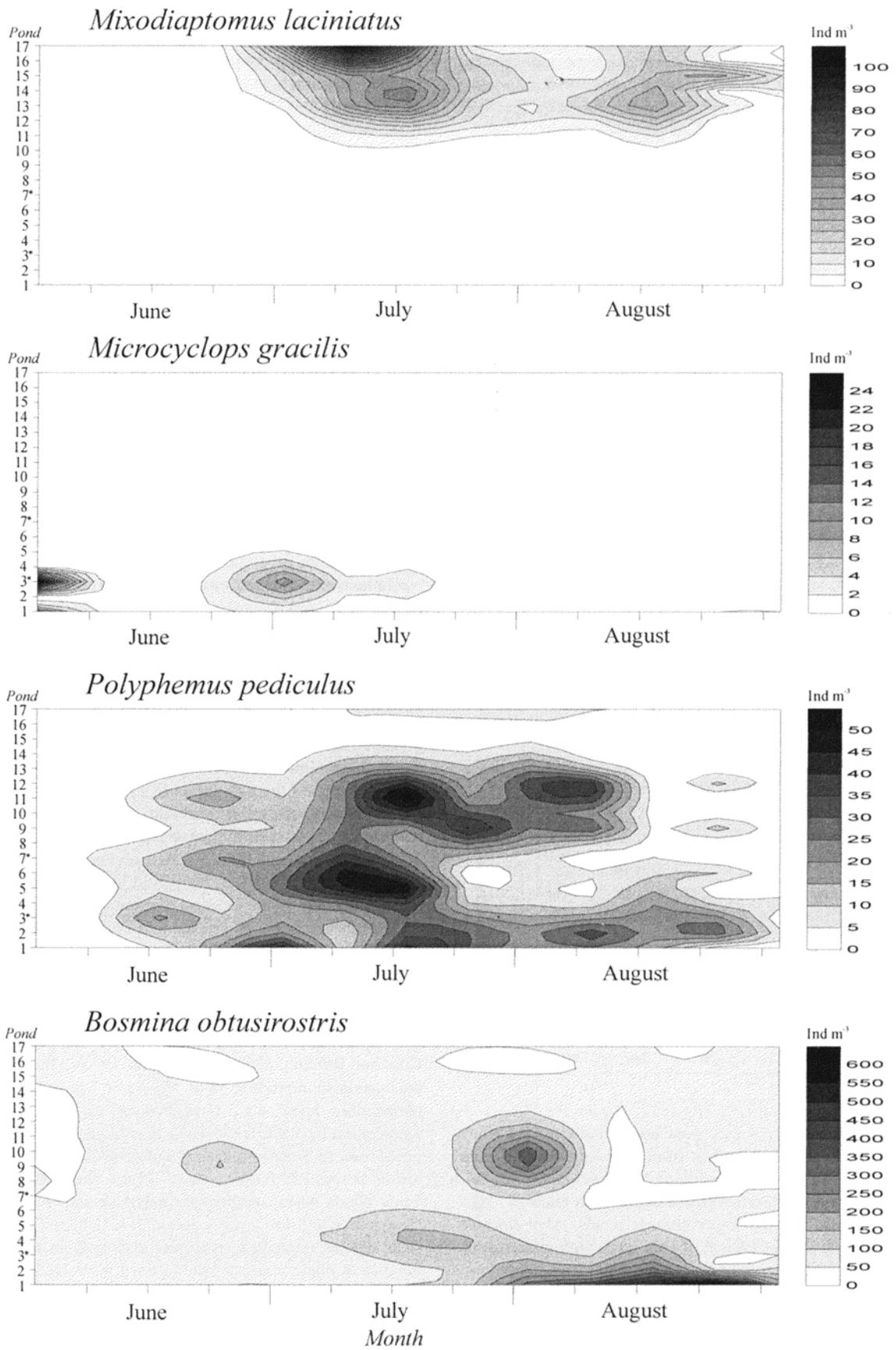


FIGURE 6. Seasonal succession pattern of the most abundant crustacean zooplankton species in the ponds. * denotes MBW-humic ponds. Note the difference in scales.

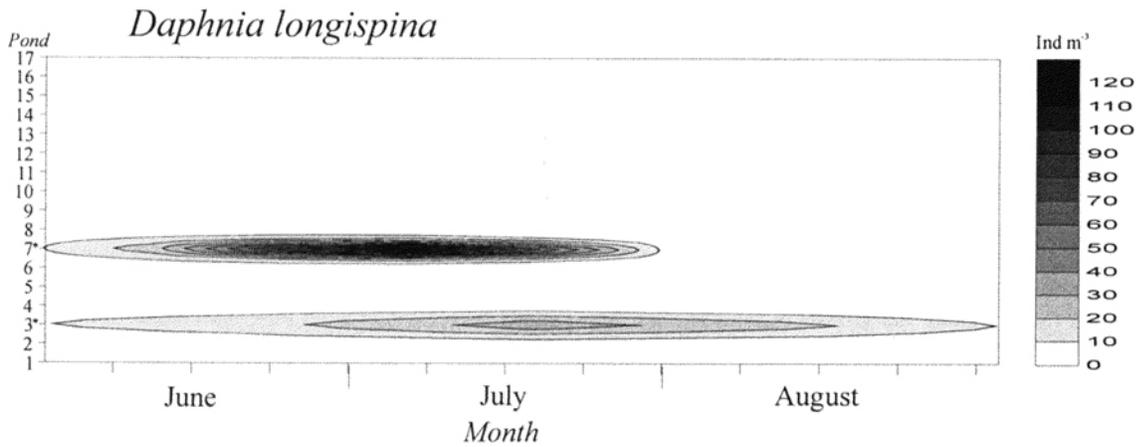
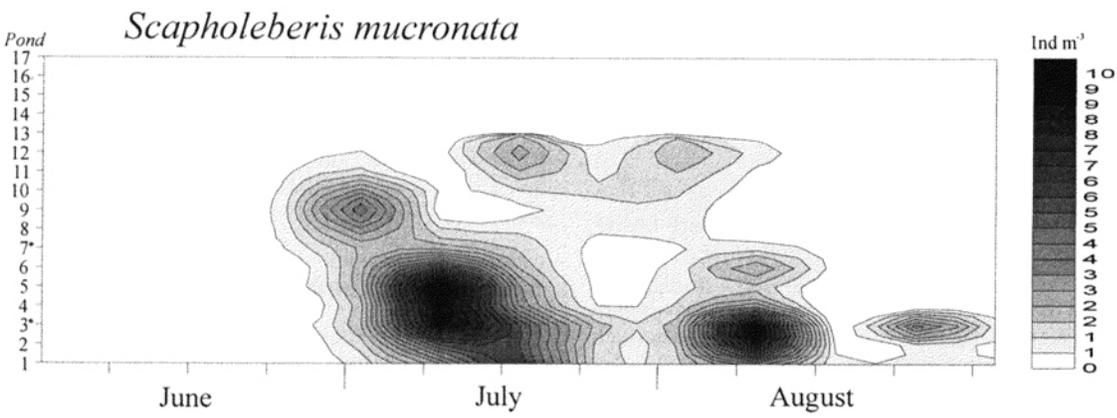
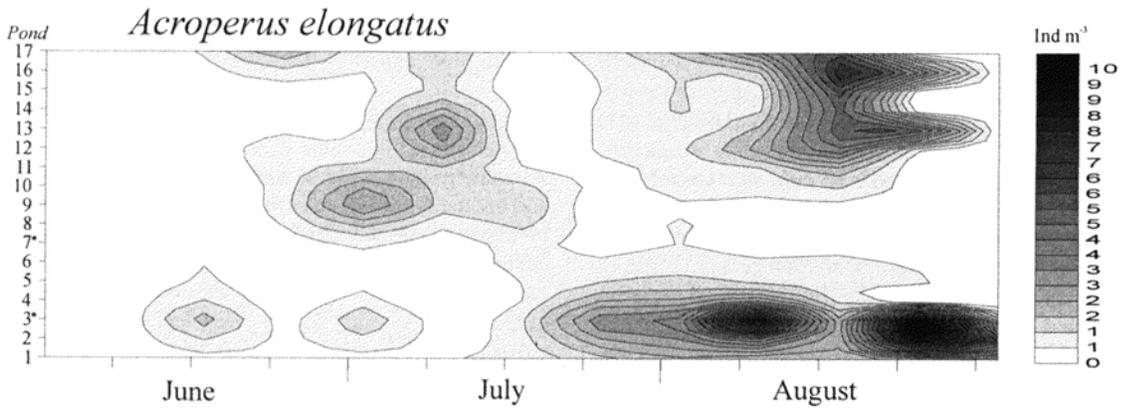
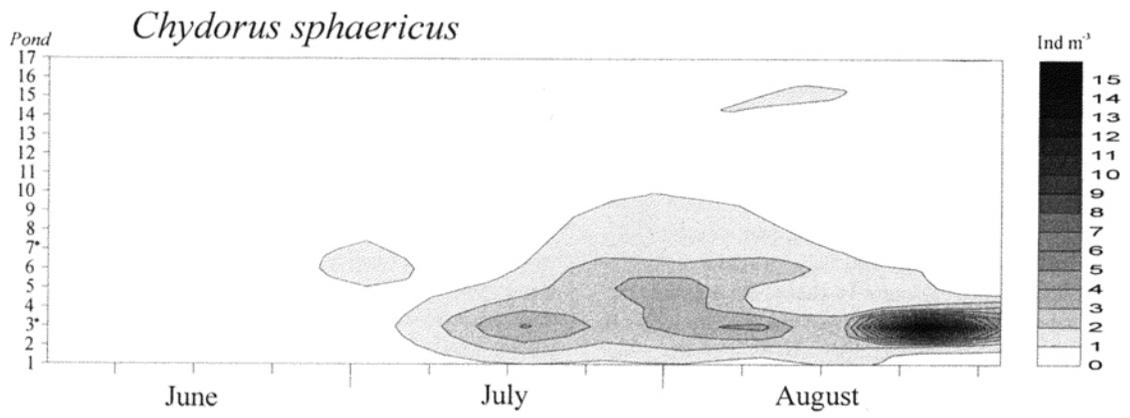


FIGURE 6. Continued.

tacean zooplankton population density and species diversity are minimal due to low temperature and low food concentration. Cladocera overwinter as resting eggs, and Copepoda as late copepodite stages and adults or as resting eggs (Allan, 1976). All overwintering stages must be able to tolerate dissipation and complete freezing in shallow subarctic ponds that freeze solidly. At the time of ice breakup zooplankton densities begin to increase. According to previous studies (Lair and Ayadi, 1989; Romo, 1990), copepod nauplii as well as overwintered Cyclopoida adults are the first ones found in the water column, followed by the Cladocera which hatch from the resting eggs. In this study, the cyclopod *M. gracilis* appeared first in the water column in spring whereas cladoceran occurrence was restricted to mid and late summer (Fig. 6). Naupliar stages were not included in this study which accounts for the absence of *M. laciniatus* early in the sampling season (Fig. 6).

A recent study by Gillooly and Dodson (2000) clearly demonstrates how cladocerans peak within the same narrow temperature range 15 to 20°C regardless of the region. This was also found in the ponds studied here where maximum cladoceran abundances were regularly measured at or right after the seasonal temperature maximum around 15 to 16°C (Fig. 3). Similar temperature defined patterns were not so clear in copepods because they have longer generation times than cladocerans (Elgmork and Eie, 1989), and their habit of overwintering as hatched individuals (Allan, 1976), which makes the interpretation of the results more difficult in samples taken during one summer period. Copepods, however, tolerate low food concentration and temperature better than cladocerans (Lampert and Muck, 1985), and are able to continue development and dominate in harsh times and unfavorable habitats. In addition to survival, development, and reproduction, temperature also indirectly influences food supply (algal biomass) and soil and sediment properties (habitat availability) as well as the predator assemblage.

The richer topsoil in MBW pond catchments was most probably the reason for higher nutrient concentrations and thus algal biomass measured in these ponds (Table 1). These factors most likely allowed the higher number of zooplankton species, namely Cladocera, in MBW ponds via higher food levels (phytoplankton) and richer habitat heterogeneity (abundant higher vascular plants, bottom characteristics). Many cladocerans, such as *Sida crystallina*, *Eurycercus lamellatus*, *Rhynchotalona falcata*, *Ophryoxus gracilis*, and *Acantholeberis curvirostris* are strongly associated with vegetation (Hann, 1980; Korhola, 1999). This association, together with the unfavorable temperature conditions, possibly explains their absence from barren ponds. Some zooplankton species such as *Acantholeberis curvirostris* and *Acanthocyclops vernalis* are typically found in acidic, humic waters (Rylov, 1949; Ward and Whipple, 1959) but several other species also tolerate low pH if humus content is high (Sarvala et al., 1999). Therefore the rather high number of species found in humic MBW ponds despite their low pH is typical. DOC is a potential energy source for zooplankton (Salonen and Hammer, 1986), and may also indirectly increase food for zooplankton by promoting the growth of phytoplankton by altering nutrient availability (Vinebrooke and Leavitt, 1998). Additionally DOC acts as a protective shield against short wave solar radiation (ultraviolet radiation, UV). This is a significant advantage in polar areas where the high altitude, long daily solar hours, and ozone depletion increase the ground level UV-radiation. Although there is variation in species response to elevated UV irradiances (Siebeck, 1978; Williamson et al., 1994; Zagarese et al., 1997), *Daphnia* seems to be highly sensitive to high UV concentration (Van Donk and Hessen, 1995; Zellmer, 1998).

Therefore the limited distribution of *Daphnia longispina* in this study to only humic ponds may be a result of its incapability to withstand high radiation present in clear ponds. On the other hand, *D. longispina* is a high efficiency bacterial feeder and probably utilizes allochthonous carbon sources in humic ponds (Kankaala, 1988).

Invertebrate predators acted as top predators in the sampled ponds. In the absence of fish predation the length of the growing season and the quality of the substratum and vegetation largely determines distribution of aquatic insects (Bagge, 1968). Therefore, the water bodies above the treeline rank as the least favorable habitats for aquatic insects; they, like zooplankton, were most abundant below the treeline. The impact of invertebrate predators on zooplankton species number could not be estimated. However, it is clear that there are interactions between predatory insects and zooplankton in these ponds. Quantifying this would require more experimental work.

Conclusions

The present study of the relationship between the catchment and habitat types and the crustacean abundance in treeline ponds in subarctic Fennoscandia show that crustacean zooplankton community composition is related to specific environmental gradients, and closely reflect the various physical and biological gradients in the study region. Seasonal succession of most studied species was related to water temperature. Peak abundance was reached during the time of maximum temperature. Since altitude influences temperature development, therefore maximum temperature was reached in barren ponds later than in MBW ponds. The timing of zooplankton maximum was also respectively off set between the ponds; maximum abundances occurred later in high altitude ponds. As one of the first zooplankton community analyses of small bodies of water performed in northern Fennoscandia, the study serves as a starting point for further investigations of geographical constraints in the development of zooplankton populations.

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