Community structure of crustacean zooplankton in subarctic ponds – effects of altitude and physical heterogeneity

Milla Rautio

Rautio, M. 1988. Community structure of crustacean zooplankton in subarctic ponds – effects of altitude and physical heterogeneity. – Ecography 21: 327–335.

Crustacean zooplankton (Cladocera, Copepoda) distribution patterns, community composition and response to altitude, temperature, pH and surface area were studied in 17 fishless subarctic ponds in the Kilpisjärvi area, NW Finnish Lapland. Despite their harshness, the ponds harboured diverse groups of zooplankton. Altogether 50 species were found from ice-out in June–August 1994. There was both a marked decline in the species number and a change in the composition of pond communities with increasing altitude and decreasing temperature as well as decreasing pH. Pond surface area was least significant in determining the species composition. Ponds at low elevations harboured up to 21 species while the fell top ponds usually had <10 species. Chydoridaen cladocerans were the most dominant group even though their number greatly diminished in ponds above the timber line.

M. Rautio (milla.rautio@helsinki.fi), Dept of Ecology and Systematics, Div. of Hydrobiology, FIN-00014 Univ. of Helsinki, Finland.

Ponds in subarctic and arctic regions are subjected to great fluctuations in their physical and chemical conditions because they are shallow and small in size, and located in a harsh climate (Hebert and Hann 1986, Bretchko 1995). During long winters, the ponds are regularly covered by ice, some freezing to the bottom, whereas in summer the water volume often quickly diminishes due to evaporation, and shallow ponds may totally dry out. Ponds at different elevations also experience regional microclimatic variations even within a small spatial scale resulting from the amount of vegetation and the pond's location to the timber line as well as the regional topography (e.g. Pienitz and Smol 1993).

The occurrence of aquatic invertebrates in temporary and semitemporary ponds is largely determined by species' tolerance to the changing environmental conditions or their dispersal and colonization capability in adverse periods (e.g. Carter et al. 1980, Hebert and Hann 1986, Girdner and Larson 1995). Among invertebrates, zooplankton have the widest tolerance in many respects, and therefore they often predominate ponds. As they can reproduce fast (e.g. Allan 1976) and are drought and freezing resistant in certain developmental stages (e.g. Wiggins et al. 1980, Marcus 1990), zooplankton can tolerate a broad range of different waters (e.g. Schmitz 1959, Reed 1962, Tash and Armitage 1967, Anderson 1974). Moreover, the "two-level" structure of the food chain, that is the absence of vertebrate predators, which is typical for small water bodies, favours zooplankton (Hansson et al. 1993) and often results in higher species number in ponds than in nearby lakes with fish (Anderson 1971, Arnott and Vanni 1993).

Although the total number of zooplankton in an area may be high, a single pond seldom contains more than a few species that occur in the region (e.g. Patalas 1964, Anderson 1971, Hebert and Hann 1986, Girdner and Larson 1995). Even small changes in altitude may alter the zooplankton species number. According to Patalas (1964) 5–8 mesozooplankton species are usually found at ponds at 1400–1700 m a.s.1. whereas at 2500–3200

Accepted 2 November 1997 Copyright © ECOGRAPHY 1998 ISSN 0906-7590 Printed in Ireland – all rights reserved

m a.s.l. 2-8 species are found and >3200 m only 1–4. The community composition of a single pond is also affected by the capacity of the pond to hold a certain community, that is the habitat size and diversity (Brown 1981, Fryer 1985), productivity level (Connell and Orias 1964), and niche number which is determined by competition and predation (Hammer and Sawchyn 1968, Sprules 1972, Ranta 1979, Hebert and Loaring 1980).

Subarctic and arctic waters are among the ecosystems that are thought will first react to the global warming (Boer et al. 1990). Arctic and alpine lakes have therefore recently been studied with respect to global change (e.g. Psenner and Schmidt 1992, Douglas et al. 1994, Smol et al. 1996, Weckström et al. 1997). However, there have been few studies because of their remote location, and apparent ecological and economical insignificance as they are fishless. However, these marginal ecosystems, especially in Fennoscandia, are among the most undisturbed ecosystems as far as the atmospheric deposition is concerned (Rühling 1992). Acidification and eutrofication have had no significant effect on these waters yet, making them a valuable reference habitat for polluted waters. Ponds also provide a fascinating field for experimental and theoretical ecology because of their high number and spatial patchiness. The objective of this study is firstly to record the crustacean zooplankton community composition of several subarctic ponds in NW Finland, and secondly to test the effect of altitude, pH, temperature and pond surface area on the species composition. The study will provide ecological and biogeographical information for research projects studying the functioning of arctic and alpine water ecosystems.

Material and methods

Site description and sampling

The Kilpisjärvi region (69°02'N, 20°50'E) in the northwest tip of Finland constitutes the most eastern part of the Scandinavian mountain chain (Fig. 1). As a part of the subarctic region, the maximum summer temperature seldom rises above 15°C. The mean summer (June–August) temperature is 9.0°C whereas the mean annual temperature is only -2.6°C (Järvinen 1987). The timber line (*Betula pubescens tortuosa*) follows the 600 m contour. Lakes and ponds are covered with ice for approximately nine months of the year. The short growing period is, however, compensated by the sun staying continuously above the horizon for 62 days (during winter it does not rise for 54 days). The area encompasses several high altitude ponds, most of glacial origin.

Seventeen ponds were chosen to be studied at altitudes of between 490 and 940 m a.s.l. (Fig. 1). All but one of the ponds are crystal clear, their water originating mainly from melting snow and rain. One pond, however, is located in a *Sphagnum* growing mire and is therefore very stained and humic.

Ponds below the timberline are rounded by an abundant macrophyte vegetation which constitutes mainly *Carex* and *Eriophorum* species. In addition, the bottom of these low elevation ponds is covered by a thick algae carpet which partly floats on the surface, especially among the macrophyte vegetation. The proportion of the macrophytes and algae declines above the timberline so that the ponds on tundra are relatively similar to ponds below the timberline but the ponds situated on fell tops and sides are completely without macrophytes and visible epilithic algae. All the study ponds are fishless to the best of our present knowledge.

Samples from the ponds were collected once a week for three months between June and August in 1994. A 50 µm plankton net was pulled from the surface to the bottom and back to the surface in the same way in each pond in order to take semi-quantative and comparable samples. In order to avoid "unclean" samples with pieces of vegetation and floating algae turfs, the sampling was performed just outside the possible littoral macrophyte zone. Although this technique, especially in low elevation ponds, may not necessarily catch all the individuals that hide near the sediment or among the macrophyte belt, the results show that typical semiplanktonic species were also caught. During the fording through macrophytes towards the centre of the pond, the water column and sediment were also mixed, which results in the samples most likely to represent the

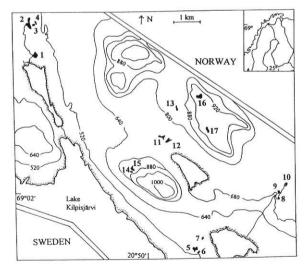


Fig. 1. Location of the study sites by Lake Kilpisjärvi. Ponds are black and numbered. The timber line (*Betula pubescens tortuosa*) follows the 600 m contour line.

Table 1. Locations, environmental characteristics and number of species in the study ponds. Values for depth are estimates except for those marked with a star. Values for pH and temperature outside the parentheses are the averages for the season, in the parentheses the minimum and maximum values. Minimum values for the temperature are measured during the first sampling in June except for those marked with a star.

Zone	Pond number	Area (ha)	Depth (m)	Altitude (m)	рН	Temperature (C°)	Species number	
	1 -	2.6	1.0	490	7.5 [6.5-7.7]	10.4 [1.0-16.0]	18	
	2	2.7	2.0	510	7.4 [6.5-7.8]	12.8 [6.5-16.2]	18	
	3	0.2	1.0	510	6.5 [6.3-6.6]	13.3 [8.2-16-8]	21 14	
Birch forest	4	0.2	1.0	510	7.2 [6.4-7.3]	12.2 [4.2-16.0]	14	
	5	1.4	2.0	530	7.2 7.0-7.4	12.7 [7.5-17.2]	21	
	6	0.3	1.5	520	7.2 7.0-7.3	13.4 7.5-18.0	16	
	7	0.1	0.5	570	5.3 [4.8-6.0]	13.5 [6.0–17.5]	10	
	8	0.1	0.5	680	7.2 [6.2-7.1]	11.0 [4.2-14.1]	13	
	9	0.3	1.5	680	6.8 [6.2-7.1]	12.0 [4.2-15.2]	18	
Tundra	10	0.2	2.0	680	7.2 [6.7-7.4]	10.7 [5.5* - 13.3]	16	
	11	0.8	1.0	710	7.4 [6.5-7.8]	9.3 [2.5-17.2]	14	
	12	1.3	1.0	710	7.5 [6.7-7.8]	9.0 [2.5-16.2]	17	
	. 13	0.3	1.0	770	6.4 [5.8-7.1]	8.2 [1.5-15.8]	9	
	14	0.1	0.5	860	6.2 [5.5-6.5]	10.2 [0.3-16.4]	8	
Fell top or side	15	0.6	7.5*	850	6.3 [6.0-6.7]	9.0 [0.5-14.6]	9	
	16	1.4	3.2*	930	6.4 [6.1-6.9]	8.5 [2.5-14.7]	11	
	17	0.7	1.0	940	5.9 [5.1-6.0]	10.0 [2.2*-16.5]	9	
Mean		0.8	1.7	674	6.8	11.0	14	
Median		0.3	1.0	680	7.2	10.7		
Minimum		0.1	0.5	490	5.3	8.2	14 9	
Maximum		2.7	7.5	940	7.5	13.5	21	

species community in the pond, at least in the smallest ponds.

Temperature and pH measurements were taken from the surface water by using a normal thermometer and a pH pen. Altitude and surface area of each pond were calculated by using a geographical map of the area. Depth was either estimated or in the most difficult cases measured by snorkelling.

Samples were preserved in a 4% formaldehyde solution and later identified and counted in the laboratory under a light microscope. All together 52 crustacean species were found of which all but two were used in data analyses. *Polyartemia forcipata* and *Branchinecta paludosa* (Anostraca) were not quantified because of their large size and net escaping abilities. Five cyclopoid species were not identified but they all clearly represented separate species.

Statistical analyses

The relationship between the number of species in a pond and environmental parameters was tested with a linear regression analysis. For more accurate results of the relative similarities of zooplankton communities between different ponds, DCA (Detrended Correspondence Analyses) was used. DCA computes coordinates for a set of points so that the shorter the distance between points, the more similar are the communities in ponds that the points represent. DCA was run only to illustrate the differences in species occurrence between pond communities; therefore, species relative abundances were not used but only each species' presence or absence during the sampling season. In the study of the relationship between individual species and environmental factors another multiregressional method was used. CCA (Canonical Correspondence Analyses) assumes the species to have bell-shaped response with respect to environmental variables, this is the case if the ranges of the environmental factors are relatively large (Ter Braak 1986). Data for CCA consisted of absolute numbers of each species at each sampling occasion as well as the absolute temperature measurements. Due to the inaccuracy of the pH-pen, only the average pH measurement of each pond throughout the season was used. This has not altered the results significantly since the pH variation was low (Table 1).

Results

The typical characteristics of each pond based on seasonal measurements are shown in Table 1. The lowest pH values were recorded during the thawing period in spring in all but the naturally very acid pond no. 7 as well as in fell top and side ponds which also had relatively low pHs. In these ponds thawing increased pH. After the ice and snow melting period pH varied little in individual ponds. Differences in minimum temperatures are due to the time differences in the ice cover melting process during the first sampling. Some of the ponds at the lowest elevations were already uncovered while most mountain top ponds were still totally covered with ice at the first sampling occasion.

Species number was found to be dependent on the altitude (p = 0.001), the pH (p = 0.017) and the average water temperature during the sampling season (p =

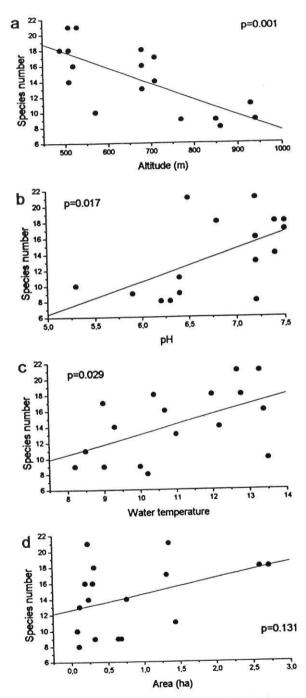


Fig. 2. Linear regression analyses. The relationship between the species number in the study pond and a) altitude, b) pH, c) water temperature and d) surface area.

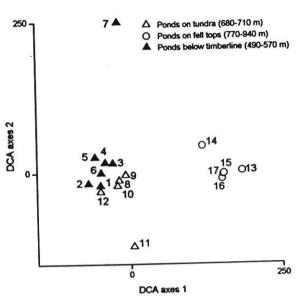


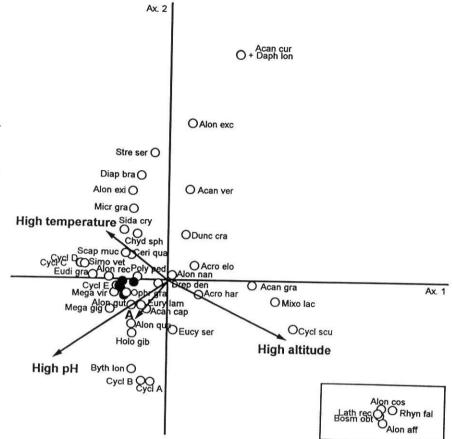
Fig. 3. DCA-plot based on species composition in different ponds during the sampling season.

0.029) (Fig 2). Ponds at lowest elevations had the highest number of species, 21 at most, while mountain top ponds usually had <10 species. Acidic waters contained less species than more alkaline waters as did warm ponds in comparison with cold ponds. Surface area had no significant effect on the number of species (p = 0.174).

DCA divided ponds into two major groups with only two exceptions (Fig. 3). Mountain top ponds formed one group while another group consisted of ponds at lower elevations. Pond no. 7 differed significantly from other pond communities. It was the only humic *Sphagnum*-rounded pond in the study and also the only one that dried out during the season. The reason that pond no. 11 was different from other ponds in the low elevation group is probably due to its large size. Sampling, which was performed in one place, may not have reached all the species in the pond.

The structural dissimilarity between two major pond groups, indicated by DCA, is mainly due to the distribution patterns of certain species. Most cladocerans only occurred in low elevation ponds as did also the calanoid *Eudiaptomus graciloides* while copepods *Mixodiaptomus laciniatus* and *Cyclops scutifer* were only found in mountain top ponds. Individual species preferences for environmental conditions are shown in CCA ordination in Fig. 4.

In the two-dimensional CCA solution the alignment of the pH axes with the first canonical axes indicates that pH was the most important of the four environmental factors considered in determining the structure of the zooplankton community. In the diagram, the points of each species can be perpendicularly projected onto each environmental variable axis. The projection Fig. 4. Ordination diagram of the canonical correspondence analysis (CCA) on the relationship between environmental variables and zooplankton species. Filled circles are redrawn in the lower left box for clarity. Full taxon names are given in Appendix 1. A = Large area,



point of a species corresponds approximately to the weighted average, i.e. the optimum of the species with respect to the environmental variable (Ter Braak 1987–1992). According to the CCA, high elevation ponds with a cold water were occupied by copepods *Cyclops scutifer*, *Mixodiaptomus laciniatus* and *Acanthocyclops crassicaudis* whereas low elevation ponds with relative warm water were occupied by cladocerans *Diaphanosoma brachyurum*, *Alonella exigua*, *Sida crystallina*, *Chydorus sphaericus*, *Ceriodaphnia quadrangula*, *Scapholeberis mucronata*, *Simocephalus vetulus* and *Alona rectangula* as well as by the copepods *Eudiaptomus graciloides*, *Microcyclops gracilis* and unidentified cyclopods C and D.

Low pH determined the occurrence of Acantholeberis currirostris, Daphnia longispina, Alonella excisa, Acanthocyclops vernalis and Dunhevedia crassa. Of these species A. vernalis and D. crassa also occurred mainly in ponds with a small surface area. The point for cladoceran Streplocerus serricaudatus indicated that it occurred in ponds with a relative high temperature, low pH and a small area. Bythotrephes longimanus and the unidentified cyclopods A and B occupied cold water ponds at intermediate elevations and neutral pH. Large surface area determined the occurrence of the species Holopedium gibberum, Alona quadrangularis, A. guttata, A. affinis, Lathonura rectirostris, Bosmina obtusirostris, Eurycercus lamellatus, Eucyclops serrulatus, Acanthocyclops capillatus, Megacyclops gigas, M. viridis and the unidentified cyclopod E.

The cladocerans Alona costata, Rhynchotalona falcata, Polyphemus pediculus, Drepanothrix dentata, Alonella nana, Acroperus elongatus and A. harpae were situated close to the origin. These species occurred in all type of ponds, thus none of the environmental factors studied controlled their distribution.

Discussion

Species number in different ponds

Decreasing maximum species number per pond with increasing altitude is a typical pattern (e.g. Patalas 1964, Hebert and Hann 1986, Raina and Vass 1993). In the Kilpisjärvi region the ponds in birch forests harboured 10-20 species whereas the high altitude ponds harboured 8-12 species (Table 1).

The CCA analysis indicates that altitude, either directly (dispersal and colonization abilities) or indirectly (low temperature leading to short growing period, amount of vegetation), was the main factor in determining zooplankton communities. According to the theory of island biogeography (McArthur and Wilson 1967), the more isolated the habitat (here pond), the smaller the probability for species to colonize it, especially for species like zooplankton that disperse by passive means (Maguire 1963). Therefore, the small number of species in mountain top ponds can be partly explained by the isolation of the water body. Moreover, the abundant littoral vegetation and a thick algae carpet on the bottom of the low elevation ponds indicate the niche diversity to be greater in these ponds than in the stony and coarse high elevation waters without vegetation. An abundant vegetation is usually a sign of relatively high productivity (Wetzel 1983), and therefore of the amount of available food resources for zooplankton. Vegetation also serves as a hiding place for zooplankton from planktivorous predators (Schwartz et al. 1983) such as insect larvae and predatorous zooplankton (Cyclopoids, Polyphemidaes). Although insect predators were not quantified in the study, they were present. Most commonly seen were larvae of the phantom midge (Chaoborus sp.), Corixids, Notonectids and Odonatas. Therefore, zooplankton in low elevation ponds with vegetation must have been able to avoid predators more successfully than in high elevation ponds without vegetation, which in turn may have affected the zooplakton community composition in the altitudinal gradient.

Low pH caused by human activity is a stress factor for most organisms but also naturally acidic waters are avoided by many species (e.g. Schindler et al. 1985, Arvola et al. 1986). In the study ponds, the number of species declined with declining pH value (Fig. 2). With one exception (pond no. 7), lowest pH values were recorded in ponds at high altitude. Therefore, altitude may indirectly determine the number of species also in this case. Also, as the pH values are not particularly low except for pond no. 7, differences in pH may here indicate differences in productivity more than pH per se. Acid lakes are often nutrient-poor compared to more neutral lakes which leads to low primary productivity (e.g. Jansson et al. 1986).

The high content of humic substances indicated by stained colour makes pond no. 7 (pH = 5.3) exceptional in the study area. According to Sarvala and Halsinaho (1990) the influence of acidity is substantially modified by humic matter. Humus may ameliorate the toxic effects of heavy metals such as labile

aluminium. The organic matter of humus is also a significant source of food for zooplankton (Salonen and Hammar 1986).

The larger the surface area and greater the depth, the more species are usually found (e.g. Pennak 1958, Fryer 1985). This pattern is not, however, always true for individual species and the size may not directly determine the number of microhabitats. According to Whiteside's (1974) experiment with chydorids (Cladocera), the number and variability of habitats are more significant than the size of the water body for the abundance of zooplankton. By adding turfs covered with bacteria and algae, the number of chydorids increased from 3-4 to 13. Anderson (1974) obtained similar results. He did not find a relationship between surface area and the mesozooplankton abundance. He speculated that the reason for this is that ponds are more sensitive to the changes in weather than lakes: water temperature follows the air temperature, during dry seasons ponds relatively easily dry out etc. Continuously changing conditions inhibit only some species from dominating the entire community as the duration of environmental optima for an individual species is short. Therefore, more species are usually found in pond ecosystems than in nearby lakes with more constant conditions (Anderson 1971). In the Kilpisjärvi ponds too, the surface area was least significant in determining the species distribution. It is therefore probable that some other environmental factor than surface area would better explain the species distribution. In fact, the amount of macrophytes and algae, including productivity and refuges from predators, would again serve as good factor.

Individual species distribution in relation to environmental factors

Based on the information obtained in the CCAordination, the reasons for certain species distribution among study ponds can be estimated. Temperature and altitude gradients divide species into two separate groups (Fig. 4). The copepods Cyclops scutifer and occupied high eleva-Mixodiaptomus laciniatus tion and cold water ponds. It is strengthened by earlier studies (Reed 1962, Carter 1971) that C. scutifer prefers habitats with relatively deep and cold waters, in Kilpisjärvi it was also most abundant in the two deepest ponds; 3.5 and 6.5 m at 930 m and 850 m a.s.l., respectively. In northern Europe C. scutifer has been found up to 1500 m a.s.l. and in Russia it only occurs in taiga and tundra regions (Rylov 1948). Mixodiaptomus laciniatus is an obligate high altitude species (Dussart 1967) which is found in clear mountain lakes and ponds >500 m a.s.l.

Most cladoceran species are coordinated in the CCA on the left side of the ordination which indicates that they occur in low elevation and relative warm ponds.

Temperature has an effect on the length of the life-cycle of zooplankton. According to Allan (1976), cladocerans complete their life-cycle in 7-8 days at 20°C whereas at 10°C the development from an egg to an adult requires 20-24 days. Therefore, the average water temperature in fell top and side ponds may not have been high enough for cladocerans to successfully complete their life-cycle, resulting in them being scarce in high elevation ponds. This, however, is not indicated by the linear regression analyses (Fig. 2). Low temperature also shortens the growing season which in addition with the total freezing of the pond from surface to the bottom inhibits the occurrence of higher vegetation in high elevation ponds (Nedler and Pennak 1955, Federley 1972). Macrophytes especially affect the distribution of chydoridaes and daphniidaes. All chydorid species live mainly in vegetation (Fryer 1985). Of the daphniid species found in Kilpisjärvi ponds Daphnia longispina was the only species that typically occurs in all kind of waters, whereas all other species are associated with littoral vegetation (Ward and Whipple 1959).

Acroperus harpae was the only cladoceran that was coordinated at the right side of the CCA ordination, indicating that it was abundant in relative high elevation ponds. Acroperus harpae is an exception in the family of Chydoridae since it generally occurs in the pelagic zone and in ponds without higher vegetation (Ward and Whipple 1959).

Only a few species were found at low pH. Cladoceran Acantholeberis curvirostris was only found in pond no. 7 which had the lowest pH-value (5.3). According to Ward and Whipple (1959) it prefers Sphagnum-rounded humid waters. Also, Daphnia longispina was very abundant in pond no. 7 as well as the cyclopod Acanthocyclops vernalis which occurred in acidic waters in general among the study ponds (Appendix 1). According to Rylov (1948), A. vernalis occurs mainly in shallow bogs rounded by Sphagnum. It can, however, be found in waters with pH's >8. Although D. longispina seems to be more acidity-tolerant than other Daphnia species (Arvola et al. 1986, Uimonen-Simola and Tolvanen 1987) the high abundance in pond no. 7 may not be directly determined by low pH. Absence of competition from macrophyte demanding zooplankton may have resulted the distribution of D. longispina in the CCA ordination. The location of the cladocerans Streblocerus serricaudatus and Alonella excisa in several ponds (Appendix 1) as well as their location in the CCA ordination (Fig. 4) indicate that they can tolerate a wide range of pH's.

Despite the four environmental factors (temperature, surface area, pH and altitude) used in CCA do

not explain all the reasons for the species distribution, CCA is still a powerful tool. Although the altitude of the pond and water temperature do not always directly determine the species distribution, their impact on zooplankton species richness is still stronger than other environmental variables', at least via indirect effects. Altitude has an effect on temperature and the temperature has an effect on the amount of vegetation, and through vegetation also on the level of production and niche number. Pond pH sets limits to the species number due to physiological constraints. Surface area, although not significant in this study in determining the species distribution, can in some cases be an indicator of niche diversity. The information obtained from CCA is a good start for advanced studies. Therefore, other more relevant environmental factors may be chosen according to the results in this study. Especially the effect of vegetation requires more studies as well as the productivity level and number and type of predators in each pond. Moreover, as the clear northern waters have been predicted to be the first to respond intensively to climate change (e.g. Pearce 1996, Schindler et al. 1996) it would be reasonable to experimentally compare the effects of temperatures and more intense UVrising radiation in clear water ecosystems. Studies by Hessen and Sørensen (1990) are already suggesting that zooplankton produce more pigments when exposed to intense UV-radiation.

Acknowledgements – I thank Heikki Salemaa for introducing me to the northern waters and his valuable comments on the work and the manuscript, Ilppo Vuorinen for commenting on the manuscript, and Elena Gorokhova, University of Stockholm, for teaching me zooplankton taxonomy. Kilpisjärvi biological station provided facilities for the study during summer 1994.

References

- Allan, J. D. 1976. Life history patterns in zooplankton. Am. Nat. 110: 165–180.
- Anderson, R. S. 1971. Crustacean plankton of 146 alpine and subalpine lakes and ponds in Western Canada. – J. Fish. Res. Bd. Can. 28: 311–321.
- 1974. Crustacean plankton communities of 340 lakes and ponds in and near the national park of the Canadian Rocky Mountains. – J. Fish. Res. Bd. Can. 31: 855–869.
- Arnott, S. E. and Vanni, M. J. 1993. Zooplankton assemblages in fishless bog lakes: influence of biotic and abiotic factors. Ecology 74: 2361–2380.
- Arvola, L. et al. 1986. Effects of experimental acidification on phyto-, bacterio- and zooplankton in enclosures of a highly humic lake. – Int. Rev. Ges. Hydrobiol. 71: 737– 758.
- Boer, M. M., Koster, E. A. and Lundberg, H. 1990. Greenhouse impact in Fennoscandia – preliminary findings of a European workshop on the effects of climatic change. – Ambio 19: 2–10.
- Bretscko, G. 1995. Opportunities for high alpine research, the lake "Vorderer Finstertaler See" as an example (Kühtai, Tirol, 2237 m a.s.l.). – Limnologica 25: 105–108.

- Brown, J. H. 1981. Two decades of homage to Santa Rosalia: toward a general theory of diversity. – Am. Zool. 21: 877–888.
- Carter, J. H. C. 1971. Distribution and abundance of planktonic Crustacea in ponds near Georgian Bay (Ontario, Canada) in relation to hydrography and water chemistry. – Arch. Hydrobiol. 68: 204–231.
- et al. 1980. Distribution and zoogeography of planktonic crustaceans and dipterans in glaciated eastern North America. – Can. J. Zool. 58: 1355–1387.
- Connell, J. H. and Orias, E. 1964. The ecological regulation of species diversity. Am. Nat. 98: 399–414.
- Douglas, M. S. V., Smol, J. P. and Welston, B. Jr. 1994. Marked post-18th century environmental change in high arctic ecosystems. – Science 226: 416–419.
- Dussart, B. 1967. Les Copépodes des eaux continentales, d'Europe occidentale. Part 1. Ed. N. – Boubee and Cie.
- Federley, B. 1972. Introduction: the area, its investigation and the plant cover. – In: Krogerus (ed.), The invertebrate fauna of the Kilpisjärvi area, Finnish Lapland. Acta Soc. Fauna Flora Fenn. 80: 5–36.
- Fryer, G. 1985. Crustacean diversity in relation to the size of water bodies: some facts and problems. – Freshw. Biol. 15: 347–361.
- Girdner, S. F. and Larson, G. L. 1995. Effects of hydrology on zooplankton communities in high-mountain ponds, Mount Rainier National Park, USA. – J. Plank. Res. 17: 1731–1755.
- Hammer, U. T. and Sawchyn, W. W. 1968. Seasonal succession and congeneric association of *Diaptomus* spp. (Copepoda) in some Saskatchewan ponds. Limnol. Oceanogr. 13: 476–484.
- Hansson, L.-A., Lindell, M. and Tranvik, L. J. 1993. Biomass distribution among trophic levels in lakes lacking vertebrate predators. – Oikos 66: 101–106.
- Hebert, P. D. N. and Hann, B. J. 1986. Patterns in the composition of arctic tundra pond microcrustacean communities – Can J. Fish, Aq. Sci. 43: 1416–1425.
- munities. Can. J. Fish. Aq. Sci. 43: 1416–1425. – and Loaring, J. M. 1980. Selective predation and the species composition of arctic ponds. – Can. J. Zool. 58: 422–426.
- Hessen, O. and Sørensen, K. 1990. Photoprotective pigmentation in alpine zooplankton populations. – Aq. Fenn. 20: 165–170.
- Jansson, M., Persson, G. and Broberg, O. 1986. Phosphorus in acidified lakes: The example of Lake Gårdsjön, Sweden. – Hydrobiologia 139: 81–96.
- Järvinen, A. 1987. Basic climatological data on the Kilpisjärvi area, NW Finnish Lapland. – Kilpisjärvi Notes 10: 1–16.
- MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. Princeton Univ. Press.
- Maguire, B. 1963. The passive dispersal of small aquatic organisms and their colonisation of isolated bodies of water. – Ecol. Monogr. 33: 161–185.
- Marcus, N. 1990. Calanoid copepod, cladoceran and rotifer eggs in sea-bottom sediments of northern Californian coastal waters: identification, occurrence and hatching. Mar. Biol. 105: 413–418.
- Nedler, K. H. and Pennak, R. W. 1955. Seasonal faunal variations in a Colorado alpine pond. – Am. Midl. Nat. 53: 419–430.
- Patalas, K. 1964. The crustacean plankton communities in 52 lakes of different altitudinal zones of Northern Colorado. – Verh. Int. Ver. Limnol. 15: 719–726.
- Pearce, F. 1996. Canadian lakes suffer triple blow. New Sci. 2018: 16.
- Pennak, R. W. 1958. Regional lake typology in northern Colorado, U.S.A. – Verh. Int. Ver. Limnol. 13: 264–283.
- Pienitz, R. and Smol, J. P. 1993. Diatom assemblages and their relationship to environmental variables in lakes

from the boreal forest-tundra ecotone near Yellowknife Territories, Canada. – Hydrobiologia 269/270: 391–404.

- Psenner, R. and Schmidt, R. 1992. Climate-driven pH control of remote alpine lakes and effects of acid deposition. – Nature 358: 781–783.
- Raina, H. S. and Vass, K. K. 1993. Distribution and species composition of zooplankton in Himalayan ecosystems. – Int. Revue. Ges. Hydrobiol. 78: 295–307.
- Ranta, E. 1979. Niche of *Daphnia* in rock pools. Arch. Hydrobiol. 87: 205–223.
- Reed, E. B. 1962. Freshwater plankton crustacea of the Conville river area, northern Alaska. – Arctic 15: 27–50.
- Rühling, Å. (ed.) 1992. Atmospheric heavy metal deposition in northern Europe in 1990. – Nord 12. Nordic Council of Ministers, Copenhagen.
- Rylov, V. M. (ed.) 1948. Fauna of U.S.S.R.: freshwater Cyclopoida. – Israel Program Sci. Transl.
- Salonen, K. and Hammar, T. 1986. On the importance of dissolved organic matter in the nutriotion of zooplankton in some lake waters. – Oecologia 68: 246–253.
- Sarvala, J. and Halsinaho, S. 1990. Crustacean zooplankton of Finnish forest lakes in relation to acidity and other environmental factors. – In: Kauppi, P., Anttila, P. and Kenttämies, K. (eds), Acidification in Finland. Springer, pp. 1009–1027.
- Schindler, D. W. et al. 1985. Long-term ecosystem stress: the effects of years of experimental acidification on a small lake. – Science 228: 1395–1401.
- et al. 1996. Consequences of climate warming and lake acidification for UV-B penetration in North American boreal lakes. – Nature 379: 705–708.
- Schmitz, E. H. 1959. Seasonal biotic events in two Colorado alpine tundra ponds. – Am. Midl. Nat. 61: 424–446.
- Schwartz, S. S., Hann, B. J. and Hebert, P. D. N. 1983. The feeding ecology of *Hydra* and possible implications in the structure of pond zooplankton communities. – Biol. Bull. 164: 136–142.
- Smol, J. P. et al. 1996. Inferring past climatic changes in Canada using paleolimnological techniques. – Geosci. Can. 21: 113–117.
- Sprules, W. G. 1972. Effects of size-selective predation and food competition on the high altitude zooplankton communities. – Ecology 53: 375–386.
- Tash, J. C. and Armitage, K. B. 1967. Ecology of zooplankton of the cape Thompson area, Alaska. – Ecology 48: 129–139.
- Ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector tecnique for multivariate direct gradiant analyses. – Ecology 67: 1167–1179.
- 1987–1992. Canoco a Fortran program for Canonical Community Ordination. – Microcomputer Power, New York.
- Uimonen-Simola, P. and Tolonen, K. 1987. Effects of recent acidification on *Cladocera* in small clear-water lakes studied by means of sedimentary remains. – Hydrobiologia 145: 343–351.
- Ward, H. B. and Whipple, G. C. (eds) 1959. Freshwater biology. John Wiley.
- Weckström, J., Korhola, A. and Blom, T. 1997. The relationship between *Diatoms* and water temperature in thirty subarctic Fennoscandian lakes. – Arct. Alp. Res. 29: 75– 92.
- Wetzel, R. 1983. Limnology. Saunders.
- Whiteside, M. C. 1974. *Chydorid* (Cladocera) ecology: seasonal patterns and abundance of populations in Elk Lake, Minnesota. – Ecology 55: 538–550.
- Wiggins, G. B., Mackay, R. J. and Smith, I. M. 1980. Evolutionary and ecological strategies of animals in annual temporary pools. – Arch Hydrobiol. Suppl. 58: 97–206.

Appendix 1. List of species found	during the study and their	presence-absence distribution in	the study ponds.
-----------------------------------	----------------------------	----------------------------------	------------------

Code	Taxon name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	1
	Cladocera											0	0	0	0	0	0	,
Sida cry	Sida crystallina	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	(
	Diaphanosoma brachyurum	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	(
	Holopedium gibberum	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	
	Daphnia longispina	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	
	Simocephalus vetulus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	
	Ceriodaphnia quadrangula	1	0	1	0	1	1	0	0	1	0	1	1	1	1	1	1	
	Scapholeberis mucronata	1	1	1	0	1	1	0	1	1	1	1	1	0	0	0	0	
	Ophryoxus gracilis	1	0	1	1	1	1	0	1	1	1	0	1	0	0	0	0	
	Drepanothrix dentata	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
Acan cur	Acantholeberis curvirostris	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	
Stre ser	Streblocerus serricaudulus	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	
	Lathonura rectirostris	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	Eurycercus lamellatus	1	1	1	0	1	1	0	1	1	1	1	1	0	0	0	0	
	Acroperus elongatus	1	1	1	1	1	1	0	0	1	1	1	1	1	0	0	1	
	A. harpae	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	
	Dunhevedia crassa	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	
	Chydorus sphaericus	1	1	1	1	1	1	0	1	1	1	1	0	1	0	1	0	
	Rhynchotalona falcata	0	1	0	Q	0	0	0	0	0	0	0	0	0	0	0	0	
Alon aff	Alona afinis	1	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	
	A. quadrangularis	0	1	0	0	1	0	0	0	0	0	1	1	0	0	0	0	
Alon gut	A. guttata	1	1	1	0	0	1	0	1	0	1	0	1	0	0	0	0	
Alon cos	A. costata	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	A. rectangula	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	
Alon nan	Alonella nana	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	
Alon exc	A. excisa	1	1	1	1	1	1	1	0	1	0	0	1	0	0	0	0	
Alon exi	A. exigua	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
	Bosmina obtusirostris	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Poly ped	Polyphemus pediculus	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	
Byth lon	Bythotrephes longimanus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
	Calanoida												0	0	0	0	0	
Eudi gra	Eudiaptomus graciloides	0	1	0	1	1	0	0	1	1	1	1	0	0	0	0	0	
Mixo lac	Mixodiaptomus laciniatus	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	
1000	Cyclopoida	0		0	0	0	0	0	0			0	0	0	0	0	1	
Eucy ser	Eucyclops serrulatus	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	
Cycl scu	Cyclops scutifer	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	
Mega vir	Megacyclops viridis	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	
Mega gig	M. gigas	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
Acan ver	Acanthocyclops vernalis	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	
Acan cap		0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	
Acan cra		0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	
Micr gra	Microcyclops gracilis	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	
Cycl A	Unidentified Cyclopoida A	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
Cycl B	Unidentified Cyclopoidia B	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
Cycl C	Unidentified Cyclopoidia C	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	
Cycl D	Unidentified Cyclopoidia D	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	(
Cycl E	Unidentified Cyclopoida E	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	Anostraca	0	0		0	0	0		0		0	1		а	1	,	0	
Poly for	Polyartemia forcipata	0	0	1	0	0	0	1	0	1	0	1	1	1	1	1	0	
Bran pal	Branchinecta paludosa*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

* Branchinecta paludosa was only found in a fell top pond that was not a study site.

This document is a scanned copy of a printed document. No warranty is given about the accuracy of the copy. Users should refer to the original published version of the material.