

# **Ecology of zooplankton in subarctic ponds, with a focus on responses to ultraviolet radiation**

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Academic dissertation

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## Abstract

This thesis focuses on crustacean zooplankton in subarctic ponds across the treeline in the Kilpisjärvi region, of Finnish Lapland, and factors affecting their assemblage structure. The work consists of five separate studies which can be divided into two distinct, yet related, parts: 1) examination of the interrelationships between the zooplankton, habitat structure, and the chemical and physical properties of the water body, 2) the role of ultraviolet radiation in affecting zooplankton survival, behaviour and pigmentation.

The first two studies show that there are clear differences in the chemical and physical properties between ponds across the treeline in northern Fennoscandia, and that these differences are reflected in zooplankton communities. On the basis of their distinct physical and chemical characteristics and zooplankton composition, ponds were divided to four groups: clear and humic mountain birch woodland ponds below the treeline, and tundra ponds and barren ponds above the treeline. Groups differed from each other mainly in temperature, pH, dissolved organic carbon concentration (DOC), bottom type and macrophyte abundance. Below the treeline, where temperature was highest and habitat heterogeneity greatest, zooplankton species number was abundant and mainly characterised by cladocerans living on substratum in comparison to ponds above the treeline. Some copepods were, however, only found in barren ponds (*Mixodiaptomus laciniatus*, *Cyclops scutifer*). Seasonal succession of species was also examined. The succession showed a coherent temperature driven pattern along the studied altitudinal transect from 500 to 1000 m a.s.l. Species seasonal abundance peaked within the temperature range 15–16°C.

The latter three studies examined effects of ultraviolet radiation on zooplankton in subarctic ponds. First, effects of different natural light spectra and UV-absorbing DOC were experimentally examined on the survival of the cladocerans *Daphnia longispina* and *D. pulex*, and a calanoid copepod *Eudiaptomus graciloides*. This study showed that natural levels of UVB and UVA can be lethal to zooplankton located close to the water surface, and that high DOC concentration provides a shelter from UV. Further, two studies were conducted that examined zooplankton responses to UV-radiation in their natural environments. The vertical distribution study showed that *Daphnia longispina* strongly responded to radiation intensity by migrating downward in the water column during brightly lit hours. The last study showed that the amount of UV-protective melanin pigment in the body wall of *Daphnia* is positively correlated with the transparency of waters. This was accompanied by seasonal variability of pigmentation pattern. Pigment synthesis was low during winter and peaked immediately after the ice break-up at the time of the maximum underwater UV intensity. The study also revealed that *Daphnia* are absent from shallow ponds with only negligible amounts of DOC in the water. The findings reported in the last three studies suggest that UV-radiation may impose a considerable environmental stress to subarctic zooplankton.

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## List of papers

The thesis is based on the following studies:

- I** Rautio, M. 1998. Community structure of crustacean zooplankton in subarctic ponds — effects of altitude and physical heterogeneity. *Ecography* 21: 327-335.
- II** Rautio, M. Zooplankton assemblages related to environmental characteristics in treeline ponds in Finnish Lapland. Accepted for publication in *Arctic, Antarctic and Alpine Research*.
- III** Rautio, M. & Korhola, A. Impacts of UV-radiation on the survival of some key subarctic crustaceans. Submitted manuscript.
- IV** Rautio, M. & Zellmer, I.D. Vertical distribution of *Daphnia longispina* (Crustacea, Cladocera) in a shallow subarctic pond: avoidance of UV-radiation? Submitted manuscript.
- V** Rautio, M. & Korhola, A. UV-induced pigmentation in subarctic *Daphnia*. Submitted manuscript.

These are referred to by their Roman numerals in the text.

## Contributions

The following table shows the major contributions of authors and collaborators to the original papers.

	I	II	III	IV	V
Original idea	HS	HS, MR	MR	MR, IZ	MR, AK
Study design and methods	MR, HS	MR	MR, AK	MR, IZ	MR
Empirical data gathering	MR	MR	MR	MR, IZ	MR, ECRU
Manuscript preparation	MR	MR	MR, AK	MR	MR, AK

AK = Atte Korhola

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IZ = Iris Zellmer

## 1. Introduction

The high number of freshwaters and wetlands is a characteristic feature of arctic and subarctic landscapes. Within the circumpolar treeline region, the most abundant type of water body is a shallow pond often formed in glacial depressions or inside ice-wedge polygons. The number of these water bodies is not known but in some places in northern Lapland almost 1500 water bodies greater than 0.05 ha in surface area occur within a 10x10 km square (Raatikainen & Kuusisto 1990). Shallow depth and presence of higher aquatic plants is often related to ponds (Welch 1952). Many of the water bodies in northern Fennoscandia, however, are shallow (Blom *et al.* 1998) yet they are still considered lakes because of their large surface area. In addition, a vast number of small subarctic waters are devoid of higher aquatic vegetation but they are clearly ponds due to their small size. Precise definition is not often essential and thereby in this thesis I consider water bodies smaller than 1 ha ponds but also include larger waters under definition of pond if they are very shallow (< 2 m) and lack fish. These water bodies follow the same general ecological principles as other fresh water bodies, but the extreme climatic conditions and their shallow depth modify these principles. Furthermore, the change in the water body characteristics when crossing the treeline makes subarctic ponds different in a small area and provides a study field for spatial studies.

Some excellent zoological, phycological and limnological studies have been conducted in tundra ponds since the early 20<sup>th</sup> century (e.g. Lundblad 1914, Koli 1956, Kalff 1967, Krogerus 1972, Hobbie 1980, Sheath 1986). Despite these and the long history of zooplankton studies in northern locations (e.g. Reed 1962, Bagge 1968, Anderson 1974, Carter *et al.* 1980, Hebert & Hann 1986, Girdner & Larson 1995), a detailed examination of crustacean zooplankton communities in fishless ponds in northern Fennoscandia has not been undertaken prior

to this study. The study is also among the first ones to concern the effects of natural ultraviolet radiation on zooplankton in Fennoscandia. My aim in this thesis is to make a contribution towards a better understanding of the ecological patterns observable in treeline zooplankton communities.

### 1.1. Environmental conditions in subarctic ponds

Ponds in northern regions are subjected to great fluctuations of temperature and light. Temperatures in the Fennoscandian subarctic belt may range from -35 to +25°C within a year. The mean annual temperature is ca. -2°C (Atlas of Finland 1987). Winter lasts up to nine months and is characterised by limited light. Precipitation largely accumulates during winter as snow, which melts rapidly in early June. As a result, the pH in early summer can be very low when acid compounds are released from the snow; the pH of the spring meltwater may be as low as 4–5 (Sorvari *et al.* 2000). The summer values of pH are influenced by the catchment characteristics; the more barren the catchment the closer the water pH is to the natural pH values of snow and rain (rainwater pH 5.6).

Most subarctic ponds are clear: low temperatures slow the breakdown of organic carbon compounds in soils, terrestrial vegetation is scarce and drainage areas are barren above the treeline. This results in clear oligotrophic waters with low allochthonous nutrient input and organic matter from the catchment (Baron *et al.* 1991). Ponds below treeline have more vegetated catchments and they receive higher loads of nutrients, yet they too are often clear. The few boggy areas that usually exist below the treeline create a few exceptions to the general water colour pattern. Ponds that have mires in their catchment area receive high amounts of humic substances and hence are dark in colour.

Despite the long days of sunlight in summer, primary production in subarctic ponds is low as a result of the low nutrient

concentrations (Stanley & Daley 1976). In subarctic and alpine waters the nitrate ( $\text{NO}_3\text{-N}$ ) concentration is below  $10 \mu\text{g L}^{-1}$ , and phosphate ( $\text{PO}_3\text{-P}$ ) is usually under the detection limit when measured with molybdate-method (unpublished data from > 50 lakes). For Alaskan tundra ponds the representative values for nitrate and phosphate are 1–88 and  $0.6\text{--}2.3 \mu\text{g L}^{-1}$  (Prentki *et al.* 1980). In comparison to subarctic lakes, however, the productivity range in subarctic ponds is slightly greater (Sheath 1986). Due to their shallow depths, ponds heat up more quickly than deeper lakes, which enhances productivity. Light penetration to the bottom of the ponds also favours benthic primary production: most of the primary production in northern ponds is confined to periphyton, i.e. algae growing on different surfaces (Stanley 1976, Niemi 1996). Stanley (1976) measured periphytic production in Alaskan tundra ponds and found that yearly periphytic production ranged from  $4\text{--}10 \text{ g C m}^{-2}$  whereas pond phytoplankton production was only  $1 \text{ g C m}^{-2}$ . Periphyton benefits from the nutrient pool that is stored in the sediment or mineralised within the immediate vicinity of the growing cells as a consequence of high microbial activity in the algal mats (Vincent *et al.* 1993). Thick mats of green algae and cyanobacteria are a typical feature of ponds with soft sediment. Ponds above treeline have usually stoney bottoms covered with a thin film of cyanobacteria or diatom cells (Stanley 1976, Douglas & Smol 1995, Niemi 1996). Macrophytes (angiosperms) are usually present only in ponds below the treeline and in some relatively sheltered ponds on the treeless tundra (Nedler & Pennak 1955, Federley 1972).

Short growing season and the fact that many ponds freeze solid every winter makes them among the most extreme of aquatic habitats. Several physiological adaptations in both flora and fauna are required. Either physiologically resistant cells or cysts (algae) and life forms or eggs (animals) are included in the life-cycle of organisms that are not able to leave the water body before winter. As a

result, there is no inoculum of active phytoplankton cells or zooplankton at ice break as there is in deeper lakes (Stross & Kangas 1969, Sheath 1986). Fish are absent from ponds that freeze solid unless the pond is connected to a deeper lake during the open water period, providing a seasonal dispersal route. Many other species may also be excluded; aquatic insects especially exhibit a strong latitudinal gradient, with decreasing diversity poleward. In North America, the Chironomidae dominate the benthos at high latitudes, with 30 or more species at  $63^\circ\text{N}$  and only six to eight at  $75^\circ\text{N}$  (Welch 1991 and references therein). On the contrary, the microalgal flora of the tundra region is quite diverse and species composition similar with algae of many temperate regions (Sheath & Steinman 1982, Sheath 1986). The green algae, chrysophytes, diatoms and cyanobacteria are the major algal classes, together accounting for 79% of the species (Sheath 1986). Zooplankton taxa that are able to withstand drying and freezing are usually also abundant in subarctic ponds (Anderson 1971). In addition, some northern ponds are occupied by highly opportunistic fauna, such as fairy shrimps (Anostraca), which are absent from more stable environments. Globally fairy shrimps are restricted to ephemeral environments or harsh marginal conditions (Koli 1956, Kerfoot & Lynch 1987). These planktonic crustaceans are slow moving and have no defence against predation by fish (Kerfoot & Lynch 1987). A simplified trophic diagram for subarctic ponds is given in Figure 1.

## 1.2. Regional biogeography of crustacean zooplankton

The high number of ponds in a relatively small area adjacent to the northern treeline offers an interesting research area for zooplankton spatial studies for two reasons: 1) Habitat structure among ponds across the treeline is different, and 2) Zooplankton are abundant including both the truly planktonic species and those living in close association with substratum.

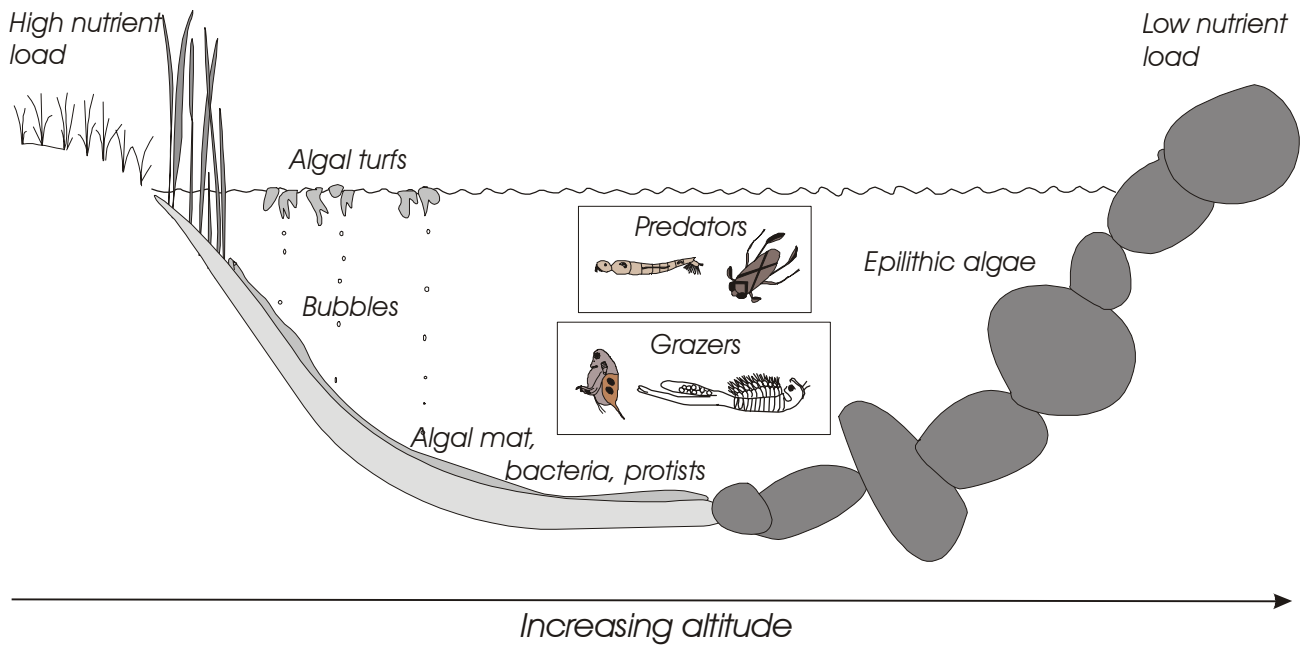


Figure 1. Trophic structure of subarctic ponds. Ponds below treeline receive higher loads of nutrients from the catchment area, and their primary production is mainly conducted to littoral macrophytes and benthic epipelagic algal mats. Oxygen or  $H_2S$  bubbles released from the benthos lift algal turfs onto the surface. Bubbles originate either from high benthic production (Nakamoto 1996) or from subsurface decomposition (Stanley 1976). Primary production in barren ponds is conducted to epilithic algae. Phytoplankton production is scarce in all ponds. The species number of grazers and predators is highest in low altitude ponds and decreases with declining primary production and simpler habitat structure towards the high altitude ponds.

The biogeographical patterns of zooplankton communities arise mainly from two factors: dispersal limitation and the suitability of local environmental conditions. The first includes both the geological history of the area, including the presence or absence of pathways for dispersal such as river networks, lake-systems or dispersal barriers (Carter *et al.* 1980), and capacity of an organism to move or to be easily transported. The second refers to an organism's ability to survive physical, chemical and biological conditions in their new habitat and hence maintain positive population growth in the local environment (Shurin 2000). The relative importance of dispersal and persistence processes in generating differences in species composition among sites varies. If dispersal rates are high, then local processes (abiotic and biotic conditions in the pond) will dominate in shaping species composition within sites. Alternatively, if dispersal is rare,

then species will often be absent from suitable sites and community structure is under strong regional control, i.e. dispersal and extinction shape the species abundance among sites (Shurin 2000).

Zooplankton disperse between separate water bodies most often as resting eggs. Eggs may attach to waterfowl plumage and be transported over vast distances (Maguire 1963). Some eggs have also been noted to pass through bird or fish digestive tracts unharmed (Proctor 1964, Flinkman *et al.* 1994). In general, zooplankton are considered highly effective dispersers over distances on the order of 100 km (Brandlova *et al.* 1972, Pinel-Alloul *et al.* 1995). For instance, Anderson (1971) studied 146 alpine and subalpine waters in western Canada and found that 26 of the 38 discovered species occurred in several sites along the 600 km long subalpine-alpine gradient. However, mountainous areas may restrict regional



dispersal. Dispersal from a suitable habitat on one mountaintop to another is more difficult than colonisation of sites in mountain valleys, which are often connected to each other. Strong dispersal limitation is also evident at very broad scales: mountain ranges and oceans limit the dispersal of zooplankton and hence very few species are considered cosmopolitans with a worldwide distribution (Carter *et al.* 1980).

Despite relatively good regional dispersal abilities, local species richness in northern ponds never equals the number of species in the surrounding area (Patalas 1964, Löffler 1969, Hebert & Hann 1986). As mentioned above, local dispersal barriers explain some variability in species composition between ponds. In addition, the local environment also plays a major role in shaping communities (Shurin *et al.* 2000). Many studies document strong correlations between patterns of zooplankton diversity and e.g. pH (Carter 1971, Sandøy & Nilssen 1986), temperature (Patalas 1990), habitat structure (Whiteside *et al.* 1978), productivity (Tash & Armitage 1967), competition (Rothhaupt 1990) and predator communities (Hebert & Loaring 1980, Schwartz *et al.* 1983). Changes in catchment characteristics cause considerable variation in many of the above mentioned abiotic factors among ponds located close to treeline and these are also reflected in the biotic factors allowing an examination of local processes on a regional scale.

Catchment soils and vegetation types largely define the water chemistry. Strong correlations exist between common physical and chemical variables (e.g., pH, alkalinity, conductivity) and zooplankton composition (Whiteside 1970, Brett 1989). A decrease in faunal diversity for rapidly fluctuating values with all these parameters is expected (Chengalath 1982). For example, decreasing species diversity as a result of a decline in acidification has been reported (reviewed by Brett 1989). However, naturally low pH in many humic waters is not usually a stress factor for the fauna and hence zooplankton can be as abundant as in more neutral sites

(Raddum *et al.* 1980, Sarvala & Halsinaho 1990). Catchment characteristics also define the water colour of the ponds. In clear shallow ponds and lakes, light, including the harmful ultraviolet radiation band, penetrates to the bottom (Sommaruga & Psenner 1997). As early as in 1950's high ultraviolet radiation was suggested to be responsible for the lack or scarcity of plankton in shallow water bodies in northern Patagonia and Swedish Lapland (Thomasson 1956).

Zooplankton distribution is also related to species temperature affinities. In a study on Canadian lakes, Patalas (1990) demonstrated that climate was the most significant factor regulating the zooplankton communities. He found an increase from 8 to 35 species corresponding with an increase of mean July air temperature from 3°C to 15°C. Similarly, Korhola (1999) showed a strong relationship between cladoceran distribution and water temperature in northern Finnish lakes. The effects of temperature on zooplankton distribution arise from e.g. their ability to complete their life-cycle within the period of tolerable physical conditions in the water body. According to Allan (1976), cladocerans complete their life-cycle in 7–8 days at 20°C whereas the corresponding time at 10°C is 20–24 days. Elgmork & Eie (1989) showed a similar temperature effect on copepods in high mountain lakes in Norway. Life-cycle length of *Cyclops scutifer* varied between two and three years. Low temperature may also completely inhibit reproduction (Green 1966, Allan 1976). For instance, *Ceriodaphnia quadrangularis* required a temperature over 8°C to be able to reproduce in a Michigan lake (Allan 1977). Some other cladocerans, on the contrary, are associated to cold environments (Patalas 1990). For instance, *Daphnia middendorffiana* is restricted in its southern limits by a temperature of around 15°C. In addition, calanoid copepod *Mixodiaptomus laciniatus* is only found in cold alpine and northern lakes and ponds (Dussart 1967).

Zooplankton and especially Cladocera are known to be highly responsive to the substrata they inhabit (Flössner 1964,

Whiteside 1978). Within a lake, zooplankton occur in both the pelagic regions, where copepods and the cladoceran families Daphniidae and Bosminidae predominate, as well as in the shallow littoral zone, where the diverse members of the cladoceran family Chydoridae are most abundant (Hann 1989). Whiteside (1978) recognised that the species diversity of chydorids is a function of available habitat (macrophytes, sand, mud) and concluded that the distribution of most chydorid species within a region is determined by habitat diversity. The lack of suitable substratum has resulted in the absence of many chydorids in tundra ponds in both North America and Fennoscandia (Hebert & Hann 1986).

Although water chemistry and habitat structure would allow a species to invade a new pond, interactions with other biota in the pond will determine the final colonisation success. The effects of indirect and direct food web effects and intraspecific competition have been relatively little studied in subarctic ponds. Generally, however, calanoid copepods are considered to be effective at low food densities whereas cladocerans are considered to have higher food requirements (Muck & Lampert 1984). The higher relative abundance of calanoid copepods to cladocerans in many tundra ponds (Hebert & Hann 1986) could therefore partly result from resource competition. However, only few cladocerans are truly planktonic and they seldom encounter calanoids, which are always planktonic. It is therefore more probable that in oligotrophic tundra ponds resource competition occurs between different cladoceran species rather than between higher taxonomic groups. On the other hand, cladocerans living on a substratum may compete for food with other bottom dwellers such as Harpacticoida and Ostracoda.

The invertebrate predator assemblage plays an important role in arctic-alpine pond ecosystems that are devoid of fish (Sprules 1972, Hebert & Loaring 1980, Paul *et al.* 1995). *Chaoborus* larvae and predatory copepods such as *Heterocope* and various cyclopoids are considered most important in

structuring arctic zooplankton communities. Of the studied 135 Canadian arctic ponds *Heterocope* was present in 99 (Hebert & Loaring 1980). Sprules (1972) noticed that despite the proximity of shallow and deep ponds, zooplankton communities remained resistant to invasion from the other pond for years. He concluded that large zooplankton were absent from deep ponds because they were heavily preyed upon by *Chaoborus* and axolotl *Ambystoma*.

Taken together, the above mentioned studies suggest that species richness in zooplankton communities in northern treeline ponds is under strong local control and that dispersal at fairly small regional scales is of lesser importance in generating differences among communities. In mountainous region, however, dispersal may play some role even on a regional scale.

### 1.3. Ultraviolet radiation in high latitude aquatic ecosystems

Ultraviolet radiation is the shortest wavelength spectrum reaching the Earth's surface. It is divided into two wavebands: from 280 to 320 nm are referred as UVB and from 320 to 400 nm, referred to as UVA. In most atmospheric situations the UVB range of the spectrum covers 0.1%, UVA 6% and the visible light (400–700 nm) 50% of global radiation. Despite the low intensity in ground level solar radiation, UV-radiation can cause biological damage due to the great energy content per photon (Frederik *et al.* 1989). DNA's absorption maximum near 260 nm makes UVB biologically the most dangerous spectrum of radiation (Caldwell 1979).

In recent years, ozone loss rates in the arctic region have reached values comparable to those recorded over the Antarctic (Rex *et al.* 1997, Taalas *et al.* 1997). As a result, in the subarctic region, springtime levels of UVB-radiation reaching the surface of the Earth have increased by 10–20% between the late 1970s and 1995 (International Arctic Science Committee, 1995). Although compounds, such as chlorofluorocarbons (CFC) and halons, which break down ozone,

are mainly released from mid-latitudes, the poles are most susceptible to ozone depletion. A combination of extreme cold and stratospheric circulation (the polar vortex) results in conditions that are favourable for ozone destruction (Anderson *et al.* 1991). In addition, ozone depletion over the poles is considered to be of special ecological concern because the biota may have evolved under UV conditions that are substantially lower in intensity than those experienced at lower latitudes (Vincent & Roy 1993).

The penetration of UV wavelengths into water is highly dependent on the concentration of chromophoric dissolved organic matter (CDOM) in the water body. It absorbs a large part of the photochemically active radiation between wavelengths 300–500 nm in fresh and coastal waters (Davis-Colley & Vant 1987). CDOM has a characteristic featureless electronic spectrum decreasing exponentially towards longer wavelength with little signal above 500 nm. In clear fresh waters, the absorption of radiation by phytoplankton may also significantly contribute to the attenuation of UV-radiation (Laurion *et al.* 2000). In general, however, dissolved organic carbon (DOC), which is the most important chromophoric compound, can be used to predict UV transparency (e.g. Laurion *et al.* 1997). With DOC concentration  $< 2 \text{ mg L}^{-1}$ , UVB can penetrate to several meters depth (Schindler *et al.* 1996). Many arctic and subarctic waters are both poor in DOC and shallow; the median measured maximum depth for 98 northern Finnish lakes was 5.1 m (Blom *et al.* 1998) and ponds seldom exceed 1 m. In addition, dissolved organic matter in water bodies above the treeline is usually autochthonous in origin (Baron *et al.* 1991) and less effective than allochthonous DOM at absorbing UV-radiation (McKnight *et al.* 1994). As a consequence, in subarctic ponds all functional groups within the water body, including the benthos, are often exposed to UV-radiation. The intensity of UV-radiation in water is also related to acidification (Schindler *et al.* 1996) since acidification increases transparency as a result of

coagulation and removal of DOC by monomeric aluminium as well as by reduced productivity (Effler *et al.* 1985).

Climate warming may influence underwater UV-intensity in four ways: via changes in atmospheric circulation, ice break-up timing, precipitation, and catchment-induced changes in vegetation. The increases in atmospheric carbon dioxide anticipated over the next 50 years are expected to amplify ozone depletion by cooling the lower stratosphere, which in turn leads to the increased formation of polar stratospheric ice clouds that catalyse CFC-ozone reactions (Austin *et al.* 1992). Increases in  $\text{CO}_2$  also account for the warmer temperatures and shorter period of ice cover (DeStasio *et al.* 1996, Rouse *et al.* 1997, Livingstone 1997). Simulation studies by Huttula *et al.* (1992) and Elo *et al.* (1998) suggest that doubling of  $\text{CO}_2$  will lead to a 1–2 month earlier melting of ice cover in Finnish lakes. Consequently, ice break-up in subarctic lakes would occur in May instead of late June, exposing the lake to the most intensive period of UV-radiation. Climate change driven changes in precipitation varies. In northern Canada, precipitation has fallen by 25% in the past two decades (Pearce 1996), whereas the recent report from IPCC indicate that in northern Fennoscandia precipitation has increased (Watson *et al.* 2001). With decreasing precipitation the runoff and hence the amount of UV-absorbing organic material into the Canadian water bodies has decreased, making the water clearer and hence more exposed to UV (Schindler 1996). Long-term warming in climate may shift the vegetation belts northward, which may significantly affect the DOC-budgets of the waters (Pienitz *et al.* 1997, Blom *et al.* 1998). Thus, both positive and negative feedbacks on the amount of UV-radiation reaching the Earth's surface are expected due to climate warming. UV-radiation itself may also act as a feedback mechanism between DOC and light attenuation. UVB causes photochemical mineralization of DOC (Vähätalo *et al.* 2000), which leads to a deeper penetration of UV-

Table 1. The effects of UV-radiation on freshwater zooplankton.

Reference	Nature and area of study	Main results
Hebert & Emery 1990	Differences in pigmentation, vertical distribution and survival of <i>Daphnia</i> in North America.	Pigmented clones are most typical in clear arctic waters, they stay higher in the water column and have a better tolerance to UV than the non-pigmented clones.
Zagarese <i>et al.</i> 1994	UV induced mortality of <i>Daphnia</i> from lakes with different optical characteristics. Incubations at different depths in Pennsylvanian lakes and mortality measurements in laboratory.	No differences in mortality between clones. Depth dependent mortality strongly related to lake transparency.
Zellmer 1996	The impact of food quality on UVB tolerance in <i>Daphnia pulex</i> , a laboratory experiment.	Survival, percentage of egg bearing females and the number of juveniles produced improved with increasing food concentrations.
Hessen 1996	Distribution of non-melanic and melanic <i>Daphnia</i> in Svalbard. Survival and growth rate measurements in laboratory.	No distinct relation between <i>Daphnia</i> pigmentation, water clarity and depth. In laboratory melanic morph more resistant to UV but had lower growth rates.
Cabrera <i>et al.</i> 1997	A mesocosm study of short- and long-term effects of UV to plankton in Chilean Andes.	Exposure time to UVB and species-specific differences in UV tolerance determine changes in plankton community structure.
Hurtubise <i>et al.</i> 1998	Sensitivity of three cladocerans, an ostracod and an amphipod to solar simulator.	Cladocerans and the amphipod most sensitive to UV, ostracod highly tolerant. No differences in survival between melanized and non-melanized <i>Scapholeberis kingii</i> .
Zagarese <i>et al.</i> 1998	Impact of a vertical movement of a copepod on its UV susceptibility in clear Argentinian lakes.	Vertically moving copepods that were capable of photorecovery had higher survival than individuals in static incubations.
De Lange <i>et al.</i> 1999	Effects of artificial UVB-radiation on the plankton community and food quality of <i>Daphnia</i> . Microcosm experiment.	No responses on community level but irradiated food resulted in slower growth and survival in <i>Daphnia</i> .
Tartarotti <i>et al.</i> 1999	Copepod survival in transparent lakes in Austrian Alps and Chilean Andes.	Differences in UV-induced mortality between species; in their natural environment pigmented, vertically migrating populations relatively well protected from UV damage
Sommaruga & Garcia-Pichel 1999	Composition of mycosporine-like amino acids (MAA pigments) in phytoplankton, benthic algae and a copepod <i>Cyclops abyssorum taticus</i>	Phytoplankton MAA concentration declined with depth, high accumulation of MAAs in <i>Cyclops</i> suggested to be an adaptive strategy for the survival of individuals close to the water column surface.
Hessen & Alstad Rukke 2000	Laboratory study of the effects of water hardness to <i>Daphnia</i> UV susceptibility	Deficiency of Ca, an important element in crustacean body wall, increases the mortality of <i>Daphnia</i> in UV exposures.
Hansson 2000	Copepod pigmentation in arctic and temperate lakes	Arctic populations more heavily pigmented than temperate populations; presence of fish decreases the level of pigmentation.

radiation and again to a greater decomposition of DOC.

Research on the biological effects of ultraviolet radiation has increased exponentially since the mid 1970's. The first studies on the responses of marine and freshwater plankton to UV-radiation mainly dealt with the survival of individual species and changes in photosynthesis (Siebeck 1978, Lorenzen 1979). Initially the concern of UV effects on aquatic ecosystem was especially directed to Antarctic waters. The impact of the spring ozone hole on primary production and food chain processes in the marginal ice zone was predicted to range from negligible to catastrophic (Roberts 1989). During the last decade the focus has shifted from individual species responses to ecosystem responses and changes in food webs and trophic cascades (Williamson *et al.* 1999, Vinebrooke & Leavitt 1998, Wulff *et al.* 2000). Many studies are also combining ultraviolet effects with other global phenomena such as climate warming, acidification and factors driven by them, e.g. changes in dissolved organic carbon concentration (Williamson *et al.* 1999, Sommaruga *et al.* 1999). An overview of the effects of UV-radiation on freshwater zooplankton is given in Table 1.

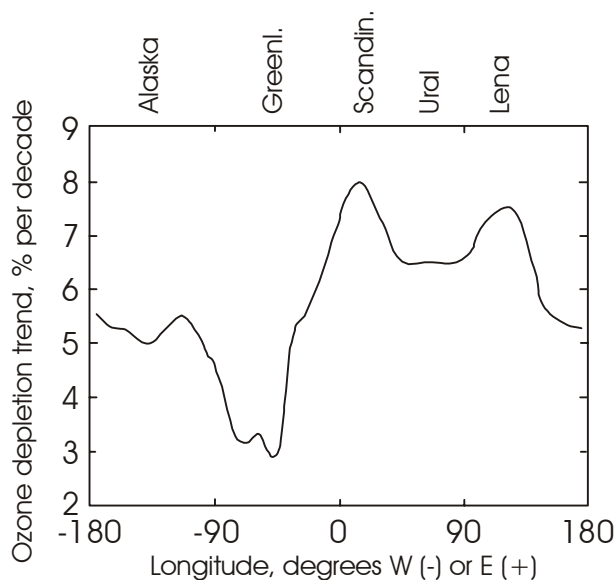


Figure 2. Variation of the ozone depletion trend (yearly average) with longitude at the Arctic Circle. Redrawn from Björn *et al.* (1998).

Ecosystems in northern Europe are especially exposed to increases in UV-radiation. Ozone is being depleted more rapidly over Scandinavia than over most geographical regions at corresponding latitudes (Fig. 2) (Björn *et al.* 1998). Furthermore, as a result of ocean circulation (Gulf stream) the climate in this area is warmer than at corresponding latitudes in North America and Asia resulting in longer open water period and hence longer exposure to radiation. Therefore UV-studies in Lapland gain more thorough understanding the potential impacts of solar radiation on subarctic ecosystem.

## 2. Aims of the study

The main objectives of the thesis were:

- 1) To determine the regional distribution and seasonal changes in the abundance of crustacean zooplankton species among different treeline ponds in the Kilpisjärvi area, and assess the effects of various environmental variables on zooplankton community structure. (I, II).
- 2) To evaluate the effects of ultraviolet light on zooplankton survival, vertical migration behaviour and pigmentation patterns in shallow subarctic water bodies (III, IV, V).

## 3. Introduction to study area

The northernmost areas in Fennoscandia even above the treeline are considered subarctic or subalpine as opposite to arctic (Kalliola 1973). By the phytogeographical definition, the area above the northern treeline is called arctic only when the latitude solely determines the treeline position. In Fennoscandia, however, altitude is responsible for forming the position of the treeline; at sea level even the northernmost areas at 72°N have mountain birch woodland. On the contrary, in the eastern Canada the cold Labrador current cools the climate and

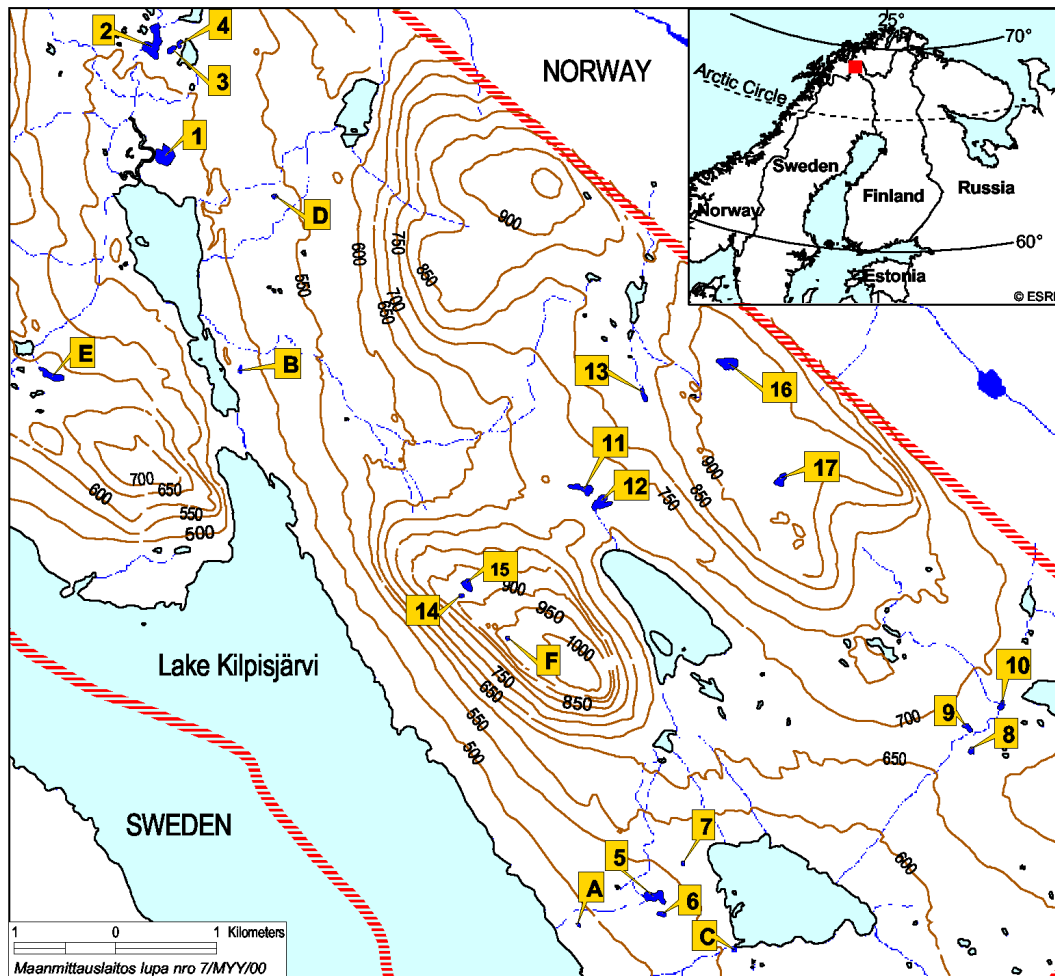


Figure 3. Map showing the locations of the 23 studied ponds in the Kilpisjärvi region. Ponds 1–17 were sampled for zooplankton and physical and chemical characteristics, ponds A–E only for water chemistry and/or the occurrence of *Daphnia*. Treeline of mountain birch follows the 600 m contour.

hence landscape is barren at sea level north of 60°N.

The main part of the study took place in the Kilpisjärvi region (69°02' N, 20°50' E) in the northwest part of Finland (Fig. 3). For paper V some of the samples were collected in the close vicinity outside this area, both in more barren and more forested areas, in order to increase the variability in the optical characteristics among the set of surveyed water bodies.

The Kilpisjärvi region lies in the transition between the North Atlantic oceanic climate and the Eurasian continental climate. The mean annual temperature in the area is –2.6°C, and the growing season is about 100 days (Järvinen 1987). The threshold

temperature +5°C is not reached until early June. Snow usually covers the ground from mid September to mid June. Ice cover may be more than a meter thick in late spring and hence many small water bodies freeze to the bottom. In addition to coldness and ice, winter is characterised by limited light, which affects biological productivity. At a latitude of 70°N (city of Tromsø, Norway) the sun stays below the horizon for 54 days from late November to February. On the other hand, it does not set between mid-June and late July for 62 days.

Altitude in the Kilpisjärvi area ranges from 490 m to 1029 m, the treeline of mountain birch (*Betula pubescens tortuosa*) approximately follows the 600 m contour. The area has been subjected to little human

impact and can be considered natural and undisturbed both in terms of land use and airborne pollution (Rühling 1992). Hikers and reindeer herds are the only large and regular forces affecting the soil structure.

The landscape in Kilpisjärvi is characterised by small lakes and ponds, most of which are of glacial origin and are oligotrophic or ultraoligotrophic. Ponds below the treeline are surrounded by abundant macrophyte (angiosperm) vegetation and the bottom of these low elevation ponds can be covered by thick algal mats, which partly float on the surface, especially among the macrophyte vegetation. The proportion of macrophytes and algae gradually declines above the treeline so that the most barren ponds situated at highest altitudes are completely without macrophytes and thick algal mats. Bryophytes, on the contrary, are present in all ponds (Virtanen 1996). The fauna of the ponds consists, in addition to the studied zooplankton groups, of insect larva such as Odonata, Trichoptera and Ephemeroptera and benthic fauna such as Chironomidae, Nematoda, Ostracoda and Harpacticoida. These groups are most abundant in ponds below the treeline. The Rotifera, Dytiscidae and Corixidae are also present at all altitudes. All the study ponds are fishless according to the present knowledge; for many ponds this assertion is supported by the occurrence of fairy shrimps (*Anostraca*, *Polyartemia forcipata*) which have no defence against fish (Kerfoot & Lynch 1987).

A set of 23 shallow and small ponds in the area was chosen from a bank of approximately 50 ponds to be investigated for the present study (Fig. 3). A detailed description of the crustacean zooplankton fauna and some physical and chemical characteristics was carried out in 17 of these ponds, the six remaining ponds were sampled only for water chemistry and/or the occurrence of daphnids. An additional 15 water bodies in the northwest Finnish Lapland were studied for the purposes of paper V.

## 4. Summary of papers

### 4.1. Distribution of crustacean zooplankton in treeline ponds

Studies I and II contribute to the greater body of work, which describes the zooplankton community structure in subarctic and arctic ponds (Tash & Armitage 1967, Hebert & Hann 1986). In Fennoscandia, however, such work has not taken place prior to this study. In my studies, I attempt to understand the distribution patterns of crustacean zooplankton in treeline ponds by surveying over 20 ponds situated across the treeline. I started from the study of the relationship of individual species and various environmental variables (I). I then proceeded to use these results to determine the similarities and dissimilarities of the zooplankton community structure in different habitat types (I, II). Moving then to the most abundant species occurring in the Kilpisjärvi ponds, I investigated their seasonal dynamics in different types of ponds (II). The descriptive approach was chosen for the first two studies because it is not possible in any ecosystem to construct experiments, which are directed to highly specific problems unless the basic functioning of the system is known.

**Study I** Community structure of crustacean zooplankton in subarctic ponds — effects of altitude and physical heterogeneity

Despite similarities in life-history strategies, many zooplankton species are adapted to highly specific environmental conditions, which determine their distribution (Goulden 1971, Allan 1976, Hebert & Hann 1986, Patalas 1990). The present distribution of crustacean species in the high latitudes is therefore not only determined by dispersal, but is also dependent on the characteristics of the water bodies. The aim of study I was to find out how the various physico-chemical factors determine species distributions across 17 different ponds in a relative small area of subarctic Finland.

The methods used in study I included weekly zooplankton sampling of the 17 ponds

in the summer of 1994 with different environmental characteristics in respect to altitude, temperature, pH and surface area. The relationship between environmental variables and individual species was tested using canonical correspondence analysis (CCA), described by ter Braak (1986). The CCA ordination results indicated that altitude was the most important factor in determining zooplankton communities (Fig. 4 in I). Species numbers declined from 20 to 8 with a 500 m increase in altitude (from 490 m to 940 m). A total of 44 species were identified. Cladocerans were most abundant at low altitudes below the treeline, especially Chydoridae, Daphniidae, Sidae and Macrothricidae. Only two calanoid copepod species were found in the studied ponds and they had very distinct distributions. *Eudiaptomus graciloides* appeared only in low and medium altitude ponds below 700 m a.s.l. whereas *Mixodiaptomus laciniatus* was discovered only at high altitude ponds where it was clearly the dominant species. It is typically highly adapted to cold oligotrophic waters in high altitudes (Dussart 1967).

The increase in altitude did not only affect the water temperature but also the heterogeneity of the pond in terms of habitat diversity. Ponds below the treeline had abundant littoral vegetation and a thick algal

mat on the bottom whereas most barren ponds above the treeline were devoid of angiosperms. Low temperatures and the lack of sediment for rooting exclude macrophytes from most ponds above the treeline. Macrophytes are ecologically significant for a variety of zooplankton and influence the presence or absence of species in the pond. Figure 4 shows the habitat association of some cladoceran genera. The chydorids are especially dependent on macrophytes or epiphytic algae growing on their stipes as a food source (Whiteside 1974, Fryer 1985), and other species may utilise macrophytes as refugia from predators during some stages of their life cycle (e.g. Schwartz *et al.* 1983).

Low pH caused by human activity is a stress factor for most organisms whereas naturally acidic humic waters may have as rich a fauna as in more neutral waters (Raddum *et al.* 1980). Sandøy & Nielssen (1986), however, found that some naturally acidic clear Norwegian waters were avoided by many cladocerans. The ponds surveyed in the study I only included one humic pond with low pH (compare paper II with more ponds surveyed). With this exception, the lowest pH-values were recorded in clear ponds on mountaintops and the number of species declined with declining pH-value. Therefore, altitude may also indirectly

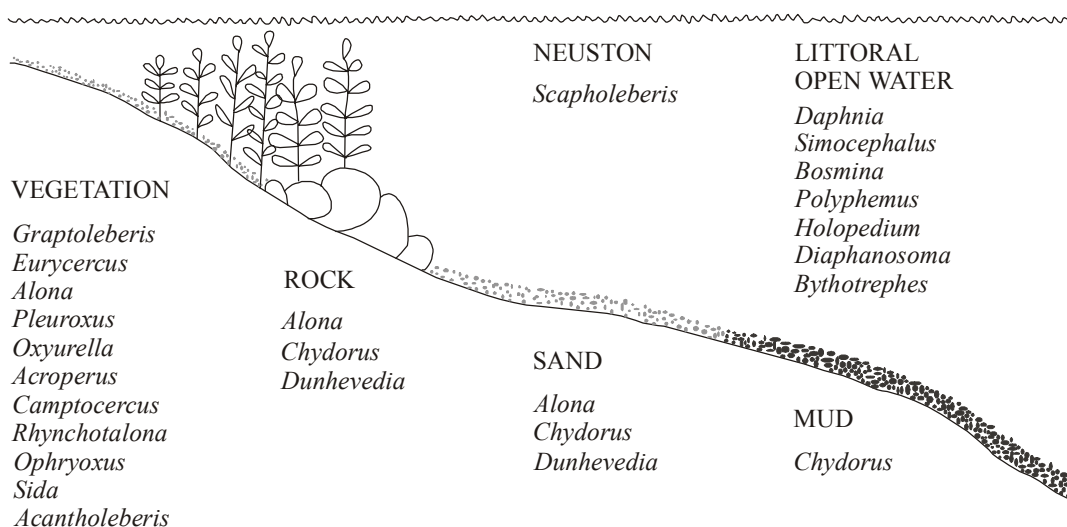


Figure 4. The major ecological niches of cladoceran genera in different microhabitats within a water body. Modified to represent subarctic pond environments from Hann (1989), Korhola & Rautio (2001), and studies I and II.



determine the number of species in this case and hence differences in pH may indicate e.g. differences in productivity more than pH *per se*.

In the Kilpisjärvi ponds, the surface area was least significant in determining species distribution. Several earlier studies have shown the minor influence of surface area on zooplankton (Whiteside 1974, Anderson 1974). Species, like many cladocerans that live close to substratum are more dependent on the microhabitat variability than the water body size. The number of microhabitats is not directly proportional to the size of water body.

In conclusion, the information obtained from paper I was a good starting point for advanced studies. The data clearly showed the importance of altitude to species distribution, but also suggested that the amount of vegetation and production level were probably more important in determining zooplankton distribution.

**Study II** Zooplankton assemblages related to environmental characteristics in treeline ponds in Finnish Lapland

The aim of paper II was to look for distinct quantitative changes in zooplankton abundance in ponds located along a gradient from mountain birch woodland to barren tundra, and to test how well these changes were in accordance with differences in the physical and chemical features of the ponds. The seasonal dynamics of the most common zooplankton taxa in the ponds were also studied. This study used the same material as in I and some additional environmental data. In addition, as opposed to paper I where only presence-absence data was used, this study used quantitative zooplankton abundance data to recognise distinct zooplankton community patterns among the studied ponds. Principal component analysis (PCA) and detrended correspondence analyses (DCA) were used to identify the major gradients in the environmental variable data and zooplankton community compositions, respectively.

Both the PCA and DCA independently emphasised the presence of four distinct pond

groups in terms of their limnological characteristics and zooplankton composition (Figs. 2 and 3 in II). The pond groups were named mountain birch woodland (MBW) clear ponds, MBW humic ponds, tundra ponds and barren ponds, respectively. The change from mountain birch woodland to treeless tundra and from a wider range of environmental conditions to a very narrow range of habitats resulted in clear changes in catchment and habitat types of the ponds, as well as in the species composition and abundance of zooplankton. Pond groups and their features including most common species are summarised in Table 2.

Models describing zooplankton community dynamics do not often include temperature as a factor influencing zooplankton community dynamics. For example, the Plankton Ecology Group (PEG) model, derived from observations of temperate lakes, describes the dynamics of zooplankton communities in the context of seasonal events, such as spring turnover, and biotic interactions, such as competition and predation (Sommer *et al.* 1986). The results presented in paper II suggest that the timing of maximum and minimum abundance for cladocerans is strongly determined by temperature. The peaks and declines of different cladoceran species were associated with a particular range of temperatures. The maximum cladoceran abundance was measured at or right after the seasonal temperature maximum around 15–16°C (Figs. 3 and 6 in II). A cladoceran maximum during the warmest time of a year is also typical in boreal lakes (Kankaala *et al.* 1990, Rask *et al.* 1998). The pattern was strong despite differences in food resources, predator communities and thermal regimes among these water bodies. With temperatures below 10°C the cladoceran abundance was at its minimum; parthenogenetic reproduction of many cladocerans is inhibited if a certain temperature level has not been reached (Allan 1977). This may have caused the low abundance of cladocerans in ponds above the treeline (Fig. 5 in II). The seasonal life-cycle of copepods, which in cold subarctic waters is

Table 2. Characteristics of treeline ponds in northern Finnish Lapland. Values of temperature, pH and conductivity are medians of the measurements during the open water season.

Feature	MBW-clear ponds	MBW-humic ponds	Tundra ponds	Barren ponds
Altitude m	490–600	510–600	600–700	700–1000
Abundance of macrophytes	abundant	common	rare	absent
Bottom type	fine organic	coarse organic	minerogenic	stone
Temperature	12.4	14.1	10.6	9.8
pH	7.2	5.9	7.2	6.3
Conductivity $\mu\text{S cm}^{-2}$	40	16	29	5
$P_{\text{tot(Sept)}} \mu\text{g L}^{-1}$	5	18	4	5
$N_{\text{tot(Sept)}} \mu\text{g L}^{-1}$	310	710	160	190
Species number	16–21	10–21	13–17	9–11
Characteristic species (only occurring in the particular pond group)	<i>Simocephalus vetulus</i> , <i>Lathonura rectirostris</i> , <i>Rhynchotalona falcata</i> , <i>Alona costata</i>	<i>Daphnia longispina</i> , <i>Acantholeberis curvirostris</i>	<i>Holopedium gibberum</i> , <i>Drepanothrix dentata</i> , <i>Bythotrephes longimanus</i> , <i>Megacyclops gigas</i> , <i>Acanthocyclops capillatus</i>	<i>Mixodiptomus laciniatus</i> , <i>Cyclops scutifer</i>

not always completed within one open water period (Elgmork & Eie 1989), is more difficult to discuss on the basis of a three month sampling period. The appearance of some copepods immediately after the thawing of a pond is, however, related to the copepods capacity to store food (Allan 1976). Overwintered specimens take advantage of the energy stores gained during the previous summer and continue development as soon as there is water around them.

In conclusion, the study clearly suggests that zooplankton communities in Kilpisjärvi region reflect the different catchment characteristics and habitat types of the ponds. Habitat characteristics, mainly temperature, also determined the seasonal dynamics of zooplankton.

#### 4.2. The effects of ultraviolet radiation on zooplankton

Results of studies I and II provided knowledge of the basic community characteristics of subarctic ponds in Finnish

Lapland, and were influential in forming my ideas on ultraviolet light effects on zooplankton. These were implemented as a survival experiment (III) and also provided background information for studies of zooplankton UV avoidance (IV) and adaptation (V) response studies.

Damaging effects of UV-radiation expressed by mortality have been reported for different freshwater species (Siebeck & Böhm 1994, Williamson & Zagarese 1994, Zellmer 1998). However, aquatic organisms also have a broad range of adaptive strategies to reduce the deleterious effects of UV-radiation. These strategies include the avoidance of strongly UV-irradiated habitats, the production of UV-screening compounds, and a variety of chemical scavenging mechanisms that detoxify the highly reactive oxidants produced photochemically. Most organisms also show an ability to repair damage caused by UVB. Vincent & Roy (1993) give an excellent review of the different protection and recovery strategies.

### **Study III** Impacts of UV-radiation on the survival of some key subarctic crustaceans

Tundra ponds possess many characteristics that make their biota exposed to ultraviolet radiation; they are shallow, poor in dissolved organic carbon (DOC) and they often lack macrophytes that would provide shelter from radiation. Too high intensity of adverse UV-radiation could influence the distribution of organisms and restrict their occurrence to the most UV-protected sites. This study describes mortality of three subarctic zooplankton species in different underwater light fields.

*Daphnia longispina*, *D. pulex* and *Eudiaptomus graciloides* originating from different water bodies in the Kilpisjärvi area were exposed to natural sunlight and their survival studied. Five filters with different UV absorption properties provided the following light exposures: full sunlight (FS), FS-UVB, FS-(UVB+UVA), 70% reduction of FS, and dark control. Furthermore, in each light exposure (only in *Daphnia* experiments), three different DOC concentrations affected the UV attenuation. To study the UV effects on the same life history stage of each species we conducted the experiment in July-August (daphnids) and in May (*Eudiaptomus*) when populations consisted of adult females.

Mortality of each species was highest in the full sunlight treatment and decreased with declining UV-intensity (Figs. 4 and 5 in **III**). Both UVB (280–320 nm) and UVA (320–400 nm) were damaging to the organisms. The result is in accordance with several other studies. Zellmer (1998) showed that survival was 80% higher in *Daphnia pulex* when both UVB and UVA were excluded as opposed to only UVB exclusion. Similarly, the results from Williamson *et al.* (1999) suggest that the whole UV-spectrum is damaging to *Chaoborus* larvae. DOC enhancements greatly diminished the underwater UV-intensity and hence increased the survival of daphnids. These results support earlier studies by e.g. Vinebrooke & Leavitt (1998) and Hessen & Færøvig (2001) emphasising the importance of the wavelength intensity and also DOC concentration, and moreover the combination

of these two in creating underwater light fields and hence affecting the survival of organisms.

*Eudiaptomus*, which was studied in late spring during the most intensive annual UV-peak, was extremely susceptible to UV-radiation even in cloudy weather. The result probably derives less from species-specific tolerance patterns for UV-radiation between the daphnids and *Eudiaptomus* but more from differences in previous exposure to light, and different protection strategies (pigmentation, vertical migration) between species in their natural environments. *Eudiaptomus* females were taken from under the ice where they had not been exposed to light for seven months (Rautio *et al.* 2000). Migrating *Daphnia* that stay long periods in dark layers of a water column have shown to be more sensitive to UV-radiation than non-migrating *Daphnia* (Siebeck & Böhm 1994). In addition, the *Eudiaptomus* population originated from a 24 m deep lake where it could perform vertical migration and hence avoid the highly irradiated surface. The result may still have an ecological implication. Monitoring records dating back to 17<sup>th</sup> century together with historical time series and recent scenarios predict that the ice-break dates of lakes and rivers in the Northern Hemisphere have shifted earlier and that this development is still continuing (Austin *et al.* 1992, Magnuson *et al.* 2000). With earlier ice-break up and increasing intensities of UV-radiation (Madronich *et al.* 1995), zooplankton may be at risk of injury in spring, especially in shallow water bodies.

### **Study IV** Vertical distribution of *Daphnia longispina* (Crustacea, Cladocera) in a shallow subarctic pond: avoidance of UV-radiation?

Most often, vertical migration (VM) of zooplankton is considered as a defence mechanism against visually hunting predators; the irradiated surface is avoided during the daytime to prevent encounters with fish (Gliwicz 1986, Neill 1990). Recently, however, several studies have suggested that in highly irradiated waters VM could be induced by ultraviolet radiation (Hessen 1993, Tartarotti *et al.* 1999, Leech & Williamson

2001). This study was designed to test whether there is a relation between *Daphnia longispina* vertical migration and UV-radiation. We conducted the study in natural solar radiation at a fishless subarctic pond in Finnish Lapland. Vertical distribution of *D. longispina* was studied during sunny and cloudy weather, and in different times of the day to obtain as much variety in radiation as possible. Predators (*Chaoborus obscuripes* and Corixidae), food (phytoplankton) and temperature were quantified from the same depths as the daphnids as they may also act as possible determinants of zooplankton VM.

Under high irradiance on the sunny days the *Daphnia* avoided the surface whereas during cloudy weather the population was closer to the surface, even during the daytime (Fig. 3a in IV). None of the biological variables explained the observed distribution pattern. In contrast, both UV and photosynthetically available radiation (PAR) were significant in explaining *Daphnia* VM, and moreover, during sunny days the UV-radiation was the only significant explanatory variable (Table 1 in IV). Photoinhibition is well known among phytoplankton and many studies have demonstrated the vulnerability of phytoplankton cells to UV-radiation (Moeller 1994, Hessen *et al.* 1997, Laurion & Vincent 1998). Our data suggest that photoinhibition and hence vertical migration of zooplankton may also be induced by UV-radiation. Similar indications of zooplankton UV-inhibition in their natural habitats have been observed before (Hessen 1993, Tartarotti *et al.* 1999), although some studies indicate that UV, particularly UVB, does not play any role in inducing VM (Bollens & Frost 1990). The results also confirm completely with a recent paper by Leech & Williamson (2001). They showed experimentally that in situ exposure to UV-radiation alters the depth distribution of *Daphnia*.

When studying vertical migration under natural solar radiation it is difficult to distinguish the effects of various wavelengths from the whole spectra in inducing VM. We tried to achieve this by measuring and relating attenuation patterns of different components of

the spectra with *Daphnia* distribution in the water column. The attenuation pattern of UV- and PAR-radiation in the water follows the same trend but varied considerably. All wavelengths diminish in intensity with depth but in the short wavelength side of the spectrum i.e. in the UV-region attenuation is much stronger (Kirk 1994). In the study pond already at 29 cm depth UV-radiation was almost non-existent (Fig. 2 in IV) whereas visible light penetrated to the bottom of the pond. Therefore, daphnids in this study would have needed to avoid only the very surface layer of the water column in order to escape UV-radiation. The observed distribution pattern of *Daphnia longispina* in bright days supports this assumption; the individuals clearly avoided the surface whereas at deeper depths the distribution was more variable.

Although the effects of UV and visible light could not be explicitly separated from each other in this study, visible light should not be the ultimate cause for the observed vertical distribution of *Daphnia longispina* as it is not harmful to zooplankton *per se*. However, despite that, e.g. *Daphnia magna* has been shown to be able to detect UV-radiation (Smith & Macagno 1990), zooplankton may use visible light as the clue for UV-radiation intensity and, thus, higher wavelengths could play an important role in UV protection. Experiments with controlled light spectra would, however, be needed to fully demonstrate the effects of UV- versus PAR-radiation in inducing vertical migration.

#### **Study V** UV-induced pigmentation in subarctic *Daphnia*

An increasing number of naturally occurring compounds in zooplankton has been identified that absorb radiation strongly in the UV-region of the spectrum. These compounds include melanin and mycosporine-like amino acids (Hessen & Sørensen 1990, Sommaruga & Garcia-Pichel 1999, V). The photoprotective properties of carotenoid pigments, however, which are abundant especially in copepods (Hessen & Sørensen 1990) are mainly associated with anti-oxidant mechanisms, such

as inhibition of free radical reactions (Hessen 1994).

In study V, a set of 43 lakes and ponds with different optical characteristics were studied for the occurrence and pigmentation pattern of *Daphnia* sp. In shallow ponds daphnids only occurred in those with sufficient amounts of UV-screening DOC ( $> 5 \text{ mg L}^{-1}$ ). In our study-set, the populations of *Daphnia* sp. in these ponds were heavily pigmented with melanin (Fig. 2 in V) suggesting that, despite the high UV-absorbance by DOC, pigmentation was required to maintain population survival. In deeper lakes, the pigmentation pattern of daphnids was different from that of the ponds. The amount of melanin pigment was negatively correlated with DOC concentration (Fig. 3 in V). Therefore, pigmentation is probably also dependent on the water body depth not just water transparency.

Several authors have suggested that pigmentation is a direct protection mechanism for UV-radiation (Hebert & Emery 1990, Hessen 1993). Attempts to relate pigmentation patterns directly to UV-radiation have, however, been unsuccessful. In addition, very little is known about the inter-annual dynamics of pigmentation. This study showed for the first time a clear relation between melanin pigment concentration in *Daphnia* and the underwater UV environment. Furthermore, the amount of melanin was shown to be correlated with seasonally changing radiation intensity (Fig 5 in V).

Species which possess adaptive mechanisms against UV-radiation, such as *Daphnia* spp., may in high radiation intensities be better competitors than other organisms. On the other hand, pigment induction makes individuals more vulnerable to fish predation (Hairston 1979), and the synthesising of pigments is considered energetically costly (Hebert & McWalter 1983, Hessen 1996). Therefore, in an oligotrophic arctic lake ecosystem, pigment production may lead to a considerable trade-off between producing pigments and higher predation risk and/or energy allocation (Hansson 2000).

## 5. Conclusions

I have attempted to show in this thesis how the distribution and functional response of crustacean zooplankton to ultraviolet radiation are determined by the environment in which they live. A treeline region is a good place for such studies because the changes in the landscape itself and the influence of this on the biota, are sudden and hence result in different water bodies (Pienitz *et al.* 1997, Duff *et al.* 1999).

Results from studies I and II showed that altitude-dependent regulation on zooplankton community structure was strong in the Kilpisjärvi area. Changes in altitude were reflected in most of the studied environmental variables, such as temperature, chlorophyll-a and habitat heterogeneity, which directly influence the distribution of zooplankton populations (Tash & Armitage 1967, Whiteside *et al.* 1978, Patalas 1990). Four major pond types were recognised, which varied from each other by their physical and chemical characteristics. Humic and clear ponds below the treeline formed two groups as well as tundra and barren ponds above the treeline. The latter two differed from each other by their distance from the treeline and catchment area roughness. Community structures of zooplankton were also different in each pond type although differences were not as distinct as in the habitat structure. This supports the assumption that dispersal is not the most important limiting factor for the regional biogeography of zooplankton (Shurin *et al.* 2000). Because altitude determines the position of the treeline and the different vegetation belts in Fennoscandia (Kalliola 1973), and hence the habitat structure of the ponds, its effect is weighted in the studies. Similar results could be obtained from treeline ponds in eastern Canada but without any altitudinal effect because the geographical position of treeline in eastern Canada is determined by latitude as opposite to altitude.

Seasonal succession of the most common species in the Kilpisjärvi ponds revealed that water temperature explained

much of the changes in abundance. Regardless of the altitude or habitat type the maximum cladoceran abundance was measured at or immediately after the seasonal temperature maximum around 15–16°C. Gillooly & Dodson (2000) obtained similar results when studying over 1100 water bodies spanning a latitudinal gradient from 45°S to 80°N: maximum cladoceran abundance was reached at a temperature range of 15–20°C.

I was able to study so few correlations between zooplankton and environmental variables, and only in a descriptive way, that no definite conclusions can be made about the distribution controls of zooplankton in the Kilpisjärvi area. However, there do appear to be limits to distribution and/or colonisation ability within which zooplankton biogeography is determined (**I**, **II**). A more thorough comparison of the community and population structures could greatly advance our understanding of populations inhabiting treeline water bodies. Studies **I** and **II** represent only an indicator of this potential. By experimentally testing factors that control species biogeographical pattern one could infer the ability and limits of species dispersal potential associated with e.g. shifts in vegetation belts. This kind of information is relevant when assessing climate change impacts. In addition to shifts in treeline and vegetation zone positions, climate warming changes soil moisture and chemistry leading to different runoff and hence water chemistry patterns (Boer *et al.* 1990). Species-specific responses of zooplankton can be influenced by these changes.

Organisms living in shallow subarctic water bodies are already now subjected to great intensities in UV-radiation, which is affecting their survival (Zellmer 1998, Hessen *et al.* 1999). Our study on the survival of three zooplankton species in natural solar radiation (**III**) showed that UV-radiation at the surface of the water column can be deleterious, and highlighted the importance of UV-screening DOC in improving survival. This is in accordance with several earlier studies (Vinebrooke & Leavitt 1998, Williamson *et al.* 1999) and suggests that organisms in

shallow aquatic systems are likely to be more sensitive to changes in allochthonous inputs of dissolved organic matter than to thinning of the stratospheric ozone layer and the resulting increase in UV-exposure (Schindler *et al.* 1996).

At least two adaptive mechanisms may explain the occurrence of various groups of zooplankton species in highly irradiated shallow ponds. Species either escape from radiation or tolerate it (Hessen 1993, Hessen & Sørensen 1990, Sommaruga & Garcia-Pichel 1999, Leech & Williamson 2001). Results from study **IV** strongly suggest that *Daphnia longispina* avoids the highly irradiated areas by escaping the brightly-lit surface zone. In addition, *Daphnia* spp. inhabiting water bodies that were exposed to UV to deep depth, were pigmented with UV-absorbing melanin (**V**). Once again, these studies represent just the beginning of the potential impacts of different UV-protection strategies in shaping pond ecosystems in subarctic and arctic regions. A comprehensive research program in comparative UV-radiation responses among different trophic levels would be needed to test the accurate effects of ultraviolet radiation on an ecosystem level.

The last three studies (**III**, **IV**, **V**) indicate that certain populations are at present controlled by UV-radiation to some extent, and that we urgently need to expand our understanding of this factor's ecological importance at present and into the future. Furthermore, the increasing UV-radiation irradiance resulting from a combination of climatic warming (earlier ice-break) and ozone depletion may become lethal for those organisms that are not able to adjust their protection against harmful UV-radiation. This may ultimately result in changes in species composition, dominance patterns and food-web structure in northern waters.

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