# Dispersal limitation and climate-related environmental gradients structure microcrustacean composition in freshwater lakes, Ellesmere Island, Canada

**Angela L. Strecker, Rebecca Milne, and Shelley E. Arnott**

**Abstract:** Dramatic environmental change is expected in the Arctic, yet little is known about the occurrence and community composition of microcrustaceans in Arctic lakes and how this will be influenced by future environmental change. We sampled and calculated relative abundances of microcrustacean species in 54 lakes on Ellesmere Island, Canada. New species records on Ellesmere Island included *Daphnia umbra*, *Tachidius discipes*, and *Artemeopsis stefanssoni*. *Daphnia middendorffiana/tenebrosa* was the most common taxon and often dominated microcrustacean assemblages, likely a result of its pigmentation, which offers resistance to ultraviolet radiation. Species richness was positively associated with nutrients, dissolved organic carbon (DOC), temperature, calcium, and conductivity and negatively affected by elevation. In contrast to most findings in temperate systems, we detected a negative relationship between species richness and surface area. Community composition was influenced by DOC, nutrients, and elevation but was also related to spatial variables, suggesting that spatial gradients in environmental conditions and dispersal are important drivers of differences among sites. Arctic ecosystems are expected to change rapidly in the coming years because of climate change and ozone thinning, and we expect that associated changes in DOC, temperature, and nutrients will affect microcrustacean species richness and distribution throughout the landscape.

**Résumé :** On s'attend à des changements environnementaux spectaculaires dans l'arctique; on connaît, cependant, assez mal la présence et la composition des communauté des microcrustacés des lacs arctiques et comment elles seront influencées par les futurs changements climatiques. Nous avons échantillonné les espèces de microcrustacés dans 54 lacs de l'île d'Ellesmere, Canada, et nous en avons déterminé les abondances relatives. *Daphnia umbra*, *Tachidius discipes* et *Artemeopsis stefanssoni* sont des espèces signalées pour la première fois sur l'île d'Ellesmere. *Daphnia middendorffiana/ tenebrosa* est le taxon le plus commun et il domine souvent les peuplements de microcrustacés, vraisemblablement à cause de sa pigmentation qui lui procure une résistance à la radiation ultraviolette. La richesse spécifique est en corrélation positive avec les nutriments, le carbone organique dissous (DOC), la température, le calcium et la conductivité et en relation négative avec l'altitude. Contrairement à ce qu'on observe la plupart du temps dans les systèmes tempérés, nous détectons une relation négative entre la richesse spécifique et la surface du lac. La composition de la communauté est affectée par le DOC, les nutriments et l'altitude, mais il y a aussi une relation avec les variables spatiales, ce qui fait croire que les gradients spatiaux des conditions du milieu et de la dispersion sont d'importants facteurs explicatifs des différences entre les sites. On croit que les écosystèmes arctiques vont changer rapidement au cours des prochaines années à cause du changement climatique et de l'appauvrissement de la couche d'ozone et nous nous attendons à ce que les changements associés du DOC, de la température et des nutriments affectent la richesse spécifique et la répartition des microcrustacés dans tout le paysage.

[Traduit par la Rédaction]

## Introduction

Relatively little information exists about the aquatic communities of the many hundreds of lakes throughout the High Arctic, with the exception of ongoing research on freshwater diatom assemblages (Douglas et al. 2004). Yet with increas-

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ing climate change, the Arctic is expected to be one of the most severely affected areas (International Arctic Science Committee 2005). Evidence based on paleolimnological studies suggests that biological communities in lakes and ponds in High Arctic regions have already experienced dramatic and unprecedented shifts in composition during the past 150 years, most likely associated with longer ice-free seasons and associated changes in lake productivity (Smol et al. 2005). In addition, recent research has revealed that chemical pollutants, including mercury and brominated flame retardants, are ubiquitous in Arctic lakes and biota (de Wit et al. 2006; Evans et al. 2006). To further our understanding of how these and other stressors will influence the structure and functioning of aquatic ecosystems, it is first necessary to determine what factors control the spa-

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tial distribution and local structure of Arctic aquatic food webs.

Microcrustaceans play a pivotal role in aquatic systems, transferring energy from primary producers to higher trophic levels. They likely have even greater ecological significance in the High Arctic, where food webs are simplified and the majority of lakes are fishless because of their shallow depth (Hershey et al. 2006). In addition, microcrustaceans are sensitive indicators of environmental conditions, as many species have short generation times and widely varying environmental preferences and tolerances. However, little is known about the species composition and distribution of microcrustaceans on Ellesmere Island in the Canadian High Arctic. The studies that have been done in this area have been mostly restricted to the Lake Hazen area. McLaren (1964) sampled microcrustaceans from Lake Hazen, as well as from a nearby pond, finding a total of eight microcrustacean species. A more wide-ranging survey (~38 km$^2$) was conducted by Røen (1981); however, this too was restricted to the Lake Hazen area, although 60 lakes were sampled and 22 species were collected. A more recent study of one lake and a fjord outside of the Lake Hazen basin found only two calanoid copepod species (Van Hove et al. 2001).

Microcrustaceans in temperate regions have been well studied, and a number of factors have been linked to their species richness and composition. These include primary productivity (Dodson 1992; Dodson et al. 2000), nutrient concentrations (Jeppesen et al. 2000; Sweetman and Smol 2006b), lake size (Dodson 1992), pH (Pinel-Alloul et al. 1990; Walseng et al. 2003), calcium, sulphate, and magnesium (Pinel-Alloul et al. 1995), total dissolved solids (Chengalath 1982), and predation (Keller and Conlon 1994). In addition, spatial factors relating to the distribution of lakes across the landscape may also affect microcrustacean community composition by influencing the dispersal of individuals between neighboring sites. Pinel-Alloul et al. (1995) divided variation into that explained by purely environmental variables (e.g., water chemistry), by purely spatial variables (e.g., a latitudinal gradient), and by spatially structured environmental variables (e.g., an environmental gradient across the study area) and found that although microcrustacean community composition depended on both environmental and spatial factors, purely spatial variables did not significantly increase the amount of variation that could be explained. However, Cottenie et al. (2003) detected a significant contribution of purely spatial variation in microcrustacean community composition but found that spatially structured environmental variation was minor, likely because their study area was small (2 km$^2$) compared with that of Pinel-Alloul et al. (1995) ($3 \times 10^5$ km$^2$) and thus did not possess a strong environmental gradient. In addition, Beisner et al. (2006) found that space was a significant driver of microcrustacean community composition when both overland and watercourse distance were considered, suggesting that microcrustaceans may disperse equally well via water and aerial connections.

Although there have been relatively few studies in the Arctic compared with temperate regions, several studies of patterns in microcrustacean community structure have been conducted. Hebert and Hann (1986) surveyed microcrustacean communities across the North American Arctic from Churchill, Manitoba (58°47′N), to Polar Bear Pass, Nunavut (75°42′N), and from Cape Thompson, Alaska (165°46′W), to Frobisher Bay, Nunavut (68°30′W). They found 9–16 microcrustacean species in ponds in glaciated regions of the lower Arctic and 4–10 species in sites on islands in the Canadian High Arctic archipelago (Hebert and Hann 1986). A study of similar scope in the Yukon and western Northwest Territories found a total of 19 crustacean species, where abiotic variables (chloride, silica, and temperature) explained 25% of the variation in species composition (Swadling et al. 2000). A survey of 104 Alaskan Arctic lakes revealed that lake surface area and depth were important drivers of microcrustacean richness, whereas water chemistry and fish composition were insignificant (O'Brien et al. 2004). The Arctic undergoes periods of severe ozone depletion (Bottenheim et al. 2002). This is expected to worsen as atmospheric carbon dioxide levels rise (Austin et al. 1992), cooling the stratosphere and activating ozone-depleting compounds, suggesting that ultraviolet (UV) radiation may play an important role in high latitude locales. However, studies in the Arctic have failed to ascertain whether UV and UV-related factors (e.g., dissolved organic carbon (DOC)) influence microcrustacean community structure. In addition, none of these studies considered spatial variables as predictors in their analyses. Given the high number of lakes and ponds in Arctic regions, we expect that spatial variables (and therefore dispersal) will be important determinants of microcrustacean community structure.

For this study, we had three objectives: (i) to document microcrustacean species found in the northern third of Ellesmere Island; (ii) to determine what potential drivers are associated with species richness and community composition; and (iii) to investigate the relative importance of spatial versus environmental variables in determining species composition using powerful, newly developed statistical techniques, generally referred to as distance-based eigenvector maps (Borcard and Legendre 2002; Dray et al. 2006; Griffith and Peres-Neto 2006). In the past, spatial variables have been incorporated in ecological studies using polynomials of geographic coordinates (trend surfaces) (Borcard et al. 1992). However, this approach is not well suited to sampling in heterogeneous areas or irregular sampling designs and can only generate broad-scale spatial structures (Dray et al. (2006) and references therein). The advantage of distance-based eigenvector map techniques is that they offer flexibility in sampling design and are able to generate structures at a range of spatial scales (Borcard and Legendre 2002), allowing for the description of biological phenomena, such as seed dispersal, that may occur very locally or very broadly. Thus far, there has been little research aimed at understanding the controls on species richness and composition in the Canadian High Arctic and how they may differ from the trends found in temperate zones.

## Materials and methods

### Study site and sampling

Ellesmere Island (Fig. 1) is the northernmost landmass in Canada and is located in the High Arctic. Ellesmere is a region of continuous permafrost, where the winters are long and cold and the summer growing season lasts only 8–

**Fig. 1.** Study location in (*a*) northern Canada, with sampling sites on (*b*) northern Ellesmere Island and (*c*) the Lake Hazen area.
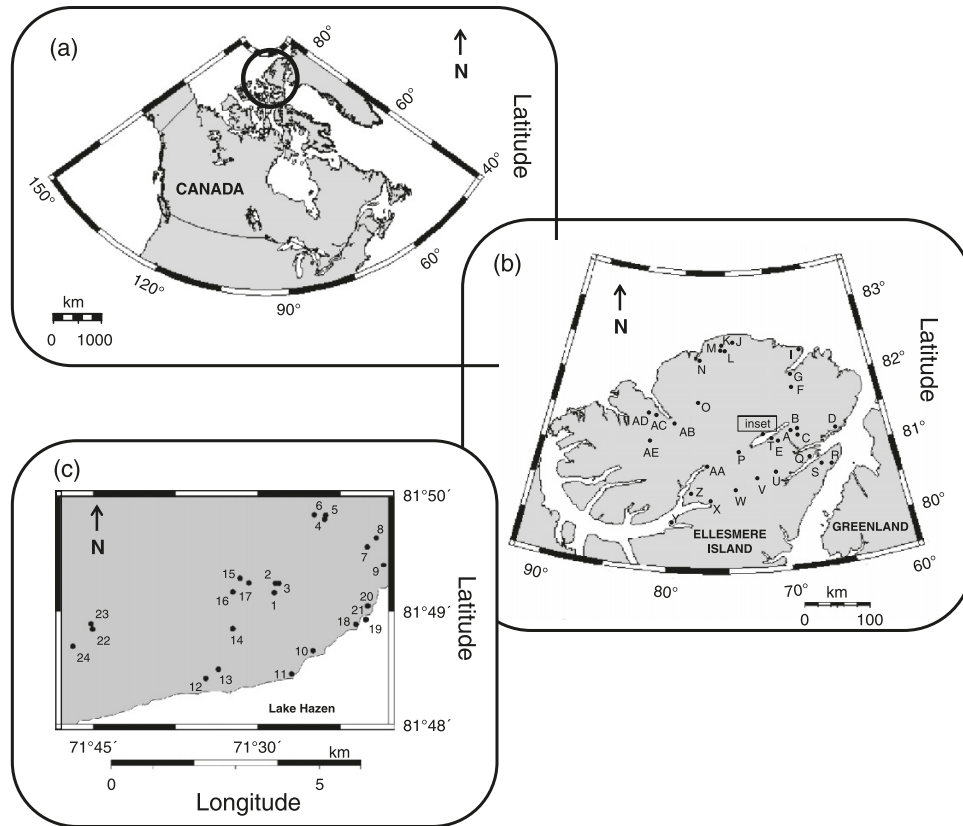


12 weeks (Lévesque et al. 1997). Several glaciers remain, dominating the landscape and affecting the surface materials and climate of Ellesmere Island. Lake Hazen is a large lake north of 80°N latitude, and the area surrounding it is generally warmer and has more lush vegetation cover than other areas of Ellesmere Island (Keatley et al. 2007) because of protection from cold air flows by the surrounding mountain ranges.

Fifty-four lakes or ponds were sampled throughout the northern third of Ellesmere Island; waterbodies were named arbitrarily by the order in which they were sampled, and official lake names, locations, and morphometry are listed in Supplementary Table S1[2]. Samples were taken from 24 lakes in the Lake Hazen basin (81°49′N to 81°51′N), the lowlands immediately surrounding Lake Hazen. The remaining 30 samples were taken from lakes distributed over the northern third of Ellesmere Island (80°36′N to 83°05′N), primarily in the Grant Land Mountains region. A number of sites were located in coastal areas, and elevated calcium and conductivity values in these lakes likely indicate a marine influence (Supplementary Table S1).[2] However, the highest calcium and conductivity concentrations were observed in inland lakes around the polar oasis Lake Hazen, which in some sites may be due to the influence of the local bedrock but in others likely reflects increased evaporation due to warming, resulting in increased concentrations of solutes (Keatley et al. 2007).

Water samples for chemical and chlorophyll *a* analyses were taken by submerging a 1 L Nalgene® bottle below the water surface. Surface water temperature was measured near the shore using a handheld mercury thermometer. Conductivity and pH were measured using a portable Hanna® pHep 3 meter (Hanna Instruments Inc., Woonsocket, R.I., USA) and a YSI 33 conductivity meter (YSI Inc., Yellow Springs, Ohio, USA), respectively. Water samples were sent to Environment Canada's National Laboratory for Environmental Testing for analysis of major ions, nutrients, and metal concentrations (Environment Canada 1994) (Table 1; Supplementary Table S1).[2] A known volume of water was filtered through Whatman® GF/C filters (pore size 1.2 μm), which were then frozen in snow and kept in darkness for chlorophyll *a* analysis (Environment Canada 1994). Where sites were reached by helicopter, elevation was determined by altimeter. In other cases, elevation was estimated with maps from the National Topographic System of Canada (NTS) (Ottawa, Ontario). Length and width of each lake or pond were obtained from measurements using a laser distance finder or from the NTS maps. Lake surface area was estimated from width and length measurements using the formula for an ellipse. We were not able to access lakes by boat, and because of limited information about lakes in this area, mean and maximum lake depths are not available.

Microcrustaceans were collected between 6 and 18 July 2003 using a net (15 cm diameter, 80 μm mesh) fastened to

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**Table 1.** Median, range, and standard deviation (SD) of physical, chemical, and biological characteristics of all study lakes.

|  | Median | Range | SD |
|---|---|---|---|
| Elevation (m) | 221 | 1–1006 | 244 |
| Surface area (ha) | 1.5 | 0.01–54 200 | 7370.9 |
| Surface temp (°C) | 12.5 | 0.5–22.0 | 5.7 |
| Ice cover | 0.0 | 0–1 | 0.4 |
| pH | 8.3 | 7.5–9.0 | 0.3 |
| Conductivity ($\mu S \cdot cm^{-1}$) | 174 | 30–1650 | 379 |
| $SiO_2$ ($mg \cdot L^{-1}$) | 1.64 | 0.13–13.90 | 3.40 |
| Chlorine ($mg \cdot L^{-1}$) | 1.46 | 0.12–32.4 | 7.43 |
| Calcium ($mg \cdot L^{-1}$) | 29.7 | 3.2–451 | 85.3 |
| Chl $a$ ($\mu g \cdot L^{-1}$) | 0.50 | 0.1–1.6 | 0.42 |
| TP ($\mu g \cdot L^{-1}$) | 3.6 | 1.0–10.5 | 2.5 |
| TN ($mg \cdot L^{-1}$) | 0.33 | 0.06–1.99 | 0.56 |
| DOC ($mg \cdot L^{-1}$) | 4.5 | 0.6–40.1 | 11.0 |

**Note:** Abbreviations: chl $a$, chlorophyll $a$; TP, total phosphorus; TN, total nitrogen; DOC, dissolved organic carbon.

the end of a fishing rod. Several qualitative horizontal tows were taken from the surface waters within wading distance from the shore, as the ponds were too shallow to sample quantitatively. All lakes and ponds were sampled for approximately the same amount of time (i.e., similar sampling effort), and microcrustaceans were preserved in a ~4% formalin solution. In a comprehensive study of >2400 lakes in Norway, Walseng et al. (2006) found that there was a high degree of concordance in crustacean species identity in samples taken strictly from each of the littoral and pelagic zones, where all but two species found in pelagic samples were also found in littoral samples. Their study suggests that nearshore sampling can give an accurate assessment of microcrustacean assemblages in lakes and, thus, that our sampling effectively captured the diversity of microcrustacean taxa in lakes on Ellesmere Island. Additionally, both pelagic and littoral taxa are known to respond to environmental gradients (Walseng et al. 2003; Sweetman and Smol 2006*b*) and are therefore useful indicators of changing conditions in Arctic ecosystems.

Microcrustaceans were identified using a Leica MZ16 microscope (for microcrustacean relative abundance in study sites, see Supplementary Table S2)[2] and were generally identified to species, with the exception of juvenile stages, ostracods, and members of the family Chydoridae, the taxonomic affiliation of which is uncertain at northern latitudes in North America (Sweetman and Smol 2006*a*). Although Arctic *Daphnia* have genetic diversity that is comparable with that of temperate zone *Daphnia* (Hobæk and Weider 1999), genetic analysis was beyond the scope of this study, and thus, members of the Arctic *Daphnia pulex* group could not be identified as either *D. middendorffiana* or *D. tenebrosa*, as they showed similar morphological characteristics and are known to hybridize (Weider and Hobæk 2003). Henceforth, they will be referred to as *Daphnia middendorffiana/tenebrosa*. As well, *Bosmina freyi* and *Bosmina liederi* (DeMelo and Hebert 1994) are difficult to distinguish and, thus, will be referred to as *Bosmina freyi/liederi*. Two methods were used for counting the microcrustacean samples: samples with low abundances of microcrustaceans were counted in their entirety, whereas

samples with greater abundances of microcrustaceans were halved multiple times using a Folsom plankton splitter, and fractions were counted in their entirety. The number of fractions counted was determined using species accumulation curves for each lake. Because sampling was not quantitative, microcrustacean relative abundances were calculated for each lake, both with juveniles included and excluded. Species richness, Shannon–Wiener diversity, and Simpson's measure of evenness ($E_{1/D}$) (Magurran 2004) were calculated from relative adult abundance. Higher values of both indices indicate greater diversity and evenness, and the maximum value of $E_{1/D}$ is 1.

## Analyses

Multiple regression using the best subsets procedure in Statistica (version 6; StatSoft Inc. 2001) was used to determine which environmental variables explained patterns in species richness. Many of the environmental variables were significantly correlated, and thus, multicollinearity would have severely affected our results. Instead, we performed a principal components regression, which uses a principal components analysis (PCA) of environmental variables to generate linear combinations of variables, which are then used as explanatory variables in a multiple regression, removing the effects of multicollinearity (Graham 2003). By assessing the loadings of each environmental variable on the principal components axes, we were able to evaluate which variables were important predictors of species richness. Physical and chemical variables thought to be relevant to microcrustacean biology (i.e., calcium, total nitrogen (TN), total phosphorus (TP), DOC, conductivity, elevation, lake surface area, latitude, temperature) were selected for PCA, and the first four principal components were chosen for multiple regression analysis. Dissolved metal concentrations were not considered in the analysis as all were below the ranges found to be toxic in microcrustaceans (Baudouin and Scoppa 1974). Similarly, pH was excluded from analysis, as in all lakes, it was above the pH considered to be harmful to microcrustaceans (pH < 6.0; Marmorek and Korman 1993). Adjusted $R^2$, Mallows' $C_p$, and Akaike's information criterion (AIC) were used to evaluate the strength of the regression models.

Multivariate ordination techniques were used to assess patterns of species abundances using CANOCO (version 4.5; ter Braak and Šmilauer 2002). Similar to our multiple regression analyses, a reduced set of environmental variables thought to be relevant to microcrustaceans was chosen. Spatial variables were created by converting Cartesian coordinates ($x, y$) to a grid using a Lambert conformal conic projection, as UTMs (universal transverse mercator) become distorted in polar regions. Distance-based eigenvector maps were used to transform spatial coordinates to interpret the scale of spatial variation (Borcard and Legendre 2002; Dray et al. 2006; Griffith and Peres-Neto 2006). The transformation of a simple grid into more complex spatial variables at both fine and broader scales allows greater resolution of spatial variability in a sampling area. The program spacemakeR was used to create the eigenvector maps (Dray 2006) using the statistical language R (R Development Core Team 2006). A pairwise Euclidean distance matrix ($d_{ij}$) was computed from the newly created Lambert projection coordi-

nates of sampling sites and was transformed into a truncated connectivity matrix (**W**), defined by the threshold value $t$, where

$$\mathbf{W} = w_{ij} = \begin{cases} 0 & \text{if } i = j \\ 0 & \text{if } d_{ij} > t \\ [1 - (d_{ij}/\max{(d_{ij})}] & \text{if } d_{ij} \leq t \end{cases}$$

Thus, sites that are closer together are given greater weight in the analysis. The value $t$ was determined by testing the neighbourhood connectivity of our sites by performing a Delaunay triangulation, Gabriel graph, relative neighbourhood graph, and sphere of influence (Legendre and Legendre 1998). By testing different neighbourhood connectivity methods, we are able to ascertain at what scale processes such as dispersal are operating, as different methods have differing levels of connectivity. For example, the Delaunay triangulation method had an average of five connections per site in the Lake Hazen area, with a large number of long-distance connections, whereas the relative neighbourhood method had an average of two connections per site, with more localized neighbourhoods and fewer long-distance connections. Fewer, more localized connections might be more important to microcrustaceans, which can disperse via water connections, wind, and waterfowl, all of which may be more important vectors at small spatial scales.

The spatial variables derived from each connectivity matrix were tested with the species abundances in an ordination. We then chose the connectivity method in which the spatial variables generated explained the greatest amount of variation, which was the relative neighbourhood method in all cases. Following this, eigenvectors were computed from the matrix **W**, with those associated with small eigenvalues representing local structures and those associated with large eigenvalues representing regional scales (Dray et al. 2006). As an example, some of the eigenvectors generated for the Lake Hazen sites are illustrated (Fig. 2), where the eigenvector representing the very broadest regional scale has two distinct clusters of sites (Fig. 2a) and each successive eigenvector has progressively more localized clusters of sites, culminating in the most fine-scale local spatial eigenvector (Fig. 2d). It is important to note that although the spatial variables generated have both positive and negative values, this simply separates sites into different clusters and, thus, does not represent positive or negative relationships.

We performed ordinations on a subset of sites (the Lake Hazen region) and on the entire set of lakes from Ellesmere Island. This allowed us to examine the species compositions at small scales (i.e., <10 km), where local factors such as dispersal would be expected to be greater than at larger scales, in contrast with the species compositions at larger scales (>300 km), where environmental gradients may be more important and dispersal would be limiting. Site EPI was excluded from ordinations as there were no organisms recovered in the sampling. All species and juvenile stages were included in our ordinations, as some of the lakes had only juveniles present. In addition, we tested the association of species with differing spatial scales following Brind'Amour et al. (2005), where we classified the spatial variables into scales of very broad, broad, meso, and fine based on

**Fig. 2.** Examples of spatial eigenvectors of the Lake Hazen site at progressively finer scales. Circles are plotted at sampling locations, where larger circles represent larger positive (shaded) or negative (open) values of the eigenvector. (*a*) Variable **very broad1** represents the largest regional-scale variability, (*b*) variable **broad2** represents broad-scale variability, (*c*) variable **meso2** represents intermediate- or meso-scale variability, and (*d*) variable **fine1** represents fine local-scale variability. Notice that at the very broad scale, sites are grouped into two clusters, with increasing numbers of clusters at progressively finer scales.
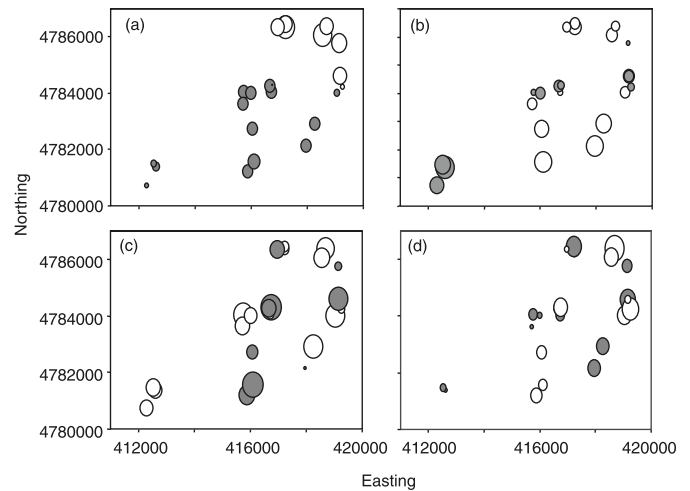


groupings of their eigenvalues (e.g., Fig. 2). We will use this classification scheme throughout, referring to different spatial variables by their scale and number, e.g., **broad1** represents broad spatial scale variable 1. We chose only significant eigenvectors for the spatial submodels, tested each spatial submodel in a redundancy analysis (RDA), and then used the species loadings on the first canonical axis to interpret which species were most influenced by different spatial scales.

A detrended correspondence analysis was conducted on species abundances to assess the length of the environmental gradient, from which it was determined that RDA was appropriate. Species abundances were Hellinger-transformed to reduce the influence of rare species (Legendre and Gallagher 2001). We tested if there was a linear spatial gradient in species abundances, and it was removed from the whole Ellesmere Island set by taking the residuals of the $x, y$ coordinates and species abundances. Forward selection with 499 Monte-Carlo permutations was used to determine which individual environmental and spatial factors had a significant impact on the community composition. Collinearity was detected if the variance inflation factor was >20 (ter Braak and Šmilauer 1998). Environmental variables that were not significant were plotted as supplementary values, which act passively and have no influence on the ordination diagram.

Variation partitioning techniques were used to determine the relative influences of purely environmental (*en*), spatially structured environmental (*sp-en*), and purely spatial (*sp*) variables on species distributions (Borcard et al. 1992). Canonical ordinations are biased by the number of predictor variables and sample size (Peres-Neto et al. 2006), so we employed the estimators of Peres-Neto et al. (2006) to control for this bias and to test the significance of the

**Table 2.** Proportion of lakes and ponds occupied by crustacean taxa found in the Lake Hazen area and northern Ellesmere Island.

| Taxonomic affiliation | Abbreviation | Lake Hazen area, Ellesmere Island | Northern Ellesmere Island |
|---|---|---|---|
| Subphylum Crustacea | | | |
| Class Branchiopoda | | | |
| Order Anostraca | | | |
| *Branchinecta paludosa* (O.F. Müller, 1788) | *B.palud* | 0.63 | 0.20 |
| *Artemiopsis stefanssoni* Johansen, 1921 | *A.stefan* | 0.04 | 0.07 |
| Juvenile Anostraca | juv Anostr | 0.21 | 0.07 |
| Order Cladocera | | | |
| *Daphnia middendorffiana/tenebrosa* | *D.mid/ten* | 1.00 | 0.60 |
| *Daphnia umbra* Taylor et al., 1996 | *D.umbra* | — | 0.03 |
| *Bosmina freyi/liederi* DeMelo and Hebert, 1994 | *B.fr/li* | 0.13 | 0.13 |
| Chydoridae | Chydorid | 0.75 | 0.27 |
| *Holopedium gibberum* Zaddach, 1855 | *H.gibber* | 0.04 | — |
| Order Notostraca | | | |
| *Lepidurus arcticus* (Pallas, 1793) | *L.arct* | 0.04 | 0.03 |
| Juvenile Notostraca | juv Notostr | 0.21 | — |
| Class Maxillopoda | | | |
| Subclass Copepoda | | | |
| Order Calanoida | | | |
| *Limnocalanus macrurus* G.O. Sars, 1863 | *L.macru* | — | 0.03 |
| Calanoid copepodid | cala cpd | 0.08 | 0.23 |
| Nauplii | nauplii | 0.83 | 0.77 |
| Order Cyclopoida | | | |
| *Eucyclops agilis* (Koch, 1838) | *E.agilis* | 0.67 | 0.10 |
| *Megacyclops magnus* (Marsh, 1920) | *M.magnus* | 0.46 | 0.03 |
| *Cyclops scutifer* G.O. Sars, 1863 | *C.scutifer* | 0.33 | 0.57 |
| Cyclopoid copepodid | cycl cpd | 0.96 | 0.63 |
| Order Harpacticoida | | | |
| *Tachidius discipes* Giesbrecht, 1881 | *T.discip* | — | 0.03 |
| *Attheyella nordenskioldi* (Lilljeborg, 1902) | *A.norden* | 0.21 | 0.07 |
| Harpacticoid copepodid | harp cpd | 0.29 | 0.17 |
| Class Ostracoda | Ostracod | 0.46 | 0.17 |

variance fractions, as well as to test for significant differences between fractions.
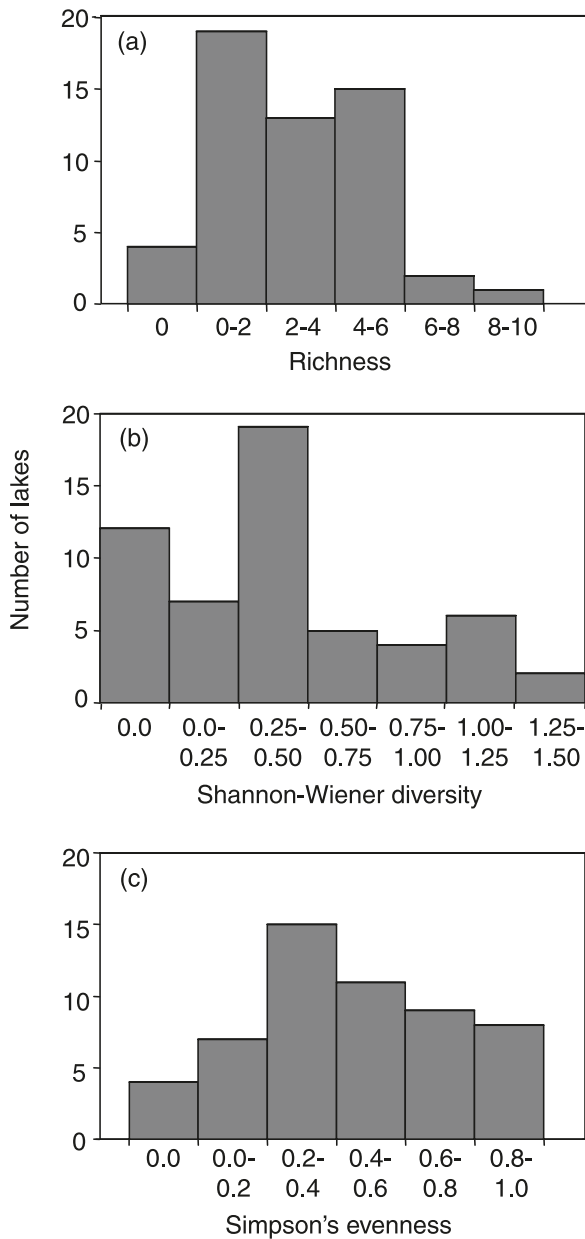
## Results

Fifteen taxa were identified from the lakes and ponds on northern Ellesmere Island (Table 2). The most frequently found microcrustacean taxa were *Daphnia middendorffiana/tenebrosa*, *Cyclops scutifer*, and Chydoridae. Species found in this study that had not previously been noted on Ellesmere Island included *Daphnia umbra* Taylor et al. 1996, *Artemiopsis stefanssonii* Johansen, 1921, and *Tachidius discipes* Giesbrecht, 1881. The frequency of occurrence for the various taxa ranged from 2% to 80% of lakes on Ellesmere, with *D. middendorffiana/tenebrosa* being the most common taxa. In general, most taxa occurred in a low number of lakes; however, taxa in the warmer Lake Hazen region tended to occur with greater frequency (Table 2).

Species richness varied from 0 to 9 taxa per lake, averaging 3.4 taxa per lake (Fig. 3). Species richness in the Lake Hazen area was significantly greater than in lakes in the rest of northern Ellesmere Island ($t = -4.73$, $p < 0.01$, df = 52). Principal component 1 (PC1) explained the majority of variation in species richness, with a small contribution from PC3 (Table 3). PC1 had high positive loadings with temperature, conductivity, calcium, DOC, TN, and TP and negative loadings with surface area, whereas PC3 had a high negative loading with elevation (Table 3). Species diversity, measured by the Shannon–Wiener index, was generally low in most lakes and positively skewed by a large number of small values (mean 0.45; median 0.36) (Fig. 3). Diversity was significantly greater in the Lake Hazen area than in northern Ellesmere ($t = -2.77$, $p < 0.01$, df = 52). Evenness (mean 0.46; median 0.41) (Fig. 3) was significantly greater in northern Ellesmere than in the Lake Hazen region ($t = 2.38$, $p = 0.01$, df = 52).

The overall RDA of all Ellesmere Island sampling sites was significant (trace = 0.39, $F = 4.82$, $p < 0.01$), and we found that the first axis was driven by productivity (TP), ice cover, and broad-scale spatial variation (**broad2**), differentiating between sites in the Lake Hazen region and sites on the rest of the island ($\lambda_1 = 0.28$, $F = 18.15$, $p < 0.01$) (Fig. 4). *Daphnia middendorffiana/tenebrosa* and *Brachinecta paludosa*, an anostracan, were positively associated with TP, whereas juvenile stage copepods were positively related to ice cover. The second axis ($\lambda_2 = 0.04$) was structured by elevation (likely a proxy for temperature and (or) isolation) and different meso-scale (**meso3**, **meso5**) spatial

**Fig. 3.** (*a*) Richness, (*b*) Shannon–Wiener diversity, and (*c*) Simpson's evenness distributions in lakes on Ellesmere Island.



eral cyclopoid and harpacticoid copepod taxa, bosminids, chydorids, and juvenile notostracans. *Holopedium gibberum* and ostracods were positively correlated with meso-scale variable **meso1**. The supplementary environmental variables TN and TP were highly positively correlated with DOC in both the Lake Hazen area and all of Ellesmere, suggesting that DOC and nutrients are likely the most important variables in lakes on Ellesmere Island.

Species that are thought to be effective dispersers, such as the fairy shrimp (*Brachinecta paludosa*; Bohonak and Whiteman 1999) and the pigmented *D. middendorffiana/tenebrosa* (Mellors 1975), were highly correlated with broad spatial scales at the Lake Hazen region (Table 4). As an example, *D. middendorffiana/tenebrosa* was positively associated with the white sampling locations generated by broad-scale spatial variable **broad2** (Fig. 2*b*). In addition, *D. middendorffiana/tenebrosa* was also highly correlated with very broad and broad spatial variables at the larger Ellesmere Island scale. Most cladoceran taxa, juvenile notostracans, ostracods, and nauplii were correlated with very broad and broad spatial structures, suggesting that they have broad distributions. Several cyclopoid and harpacticoid copepod taxa were also highly correlated with very broad and broad spatial scales in both ordinations.

Variation in microcrustacean communities in the Lake Hazen area was mostly explained by purely environmental (*en*) and purely spatial (*sp*) variables, which contributed 29% and 21% of variation, respectively (Fig. 6). In contrast, purely spatial variables contributed very little to overall variation in microcrustacean composition at the larger Ellesmere Island scale (7%), whereas purely environmental variables explained a similar amount of variation at both scales (Ellesmere, 23%; Lake Hazen, 29%) (Fig. 6). Spatially structured environmental (*sp-en*) variables explained little variation at both scales (<4%). Pure spatial and pure environmental variation were significantly different from zero in the Lake Hazen and Ellesmere Island data sets (all variables: $p < 0.01$). As well, there was no difference between environmental and spatial variation at the Lake Hazen scale ($p = 0.60$), but environmental variables explained more variation than spatial variables in Ellesmere Island communities ($p = 0.04$).

## Discussion

Our survey of lakes and ponds on northern Ellesmere Island revealed patterns of species richness and composition that are consistent with climate-induced environmental gradients and spatial structuring. Microcrustacean richness and distribution were correlated with variables that can be influenced by a warmer climate, such as greater nutrient and DOC concentrations resulting from increased terrestrial vegetation and greater conductivity as a result of evaporative concentration of solutes (Keatley et al. 2007). Additionally, microcrustaceans were structured by variables associated with dispersal limitations such as elevation. Although some of the common relationships between environmental variables and microcrustaceans that have been observed in temperate systems were also observed in our study, we found that other variables, such as DOC, can influence Arctic

variables. Cyclopoid and harpacticoid copepods, bosminids, and chydorids were positively associated with elevation and were associated with the meso-scale spatial variables **meso3** and **meso5**.

The Lake Hazen area RDA was also significant (trace = 0.58, $F = 3.84$, $p < 0.01$); however, its first axis was controlled by DOC and elevation (Fig. 5). The variables TN and TP were highly correlated with DOC and were therefore removed as active variables in the analysis. DOC was positively associated with *D. middendorffiana/tenebrosa* and adult *B. paludosa*, whereas elevation was positively correlated with juvenile copepods and juvenile and adult anostracans ($\lambda_1 = 0.34$, $F = 8.91$, $p < 0.01$). The second axis ($\lambda_2 = 0.11$) was driven by spatial variables. Broad regional-scale variables **very broad2** and **very broad3**, as well as meso-scale variable **meso2**, were positively associated with sev-

**Table 3.** (*a*) Multiple regression of principal component variables to predict species richness and (*b*) loading of environmental variables on principal components axes.

*(a)* Multiple regression of principal component variables to predict species richness.

| | Adjusted $R^2$ | $C_p$ | AIC | $F$ ratio | $p$ value | Variable | Coefficient | Partial correlation coefficient | $t$ value | $p$ value |
|---|---|---|---|---|---|---|---|---|---|---|
| Model 1 | 0.39 | 1.28 | 59.55 | 18.23 | <0.01* | PC1 | 0.62 | 0.63 | 5.84 | <0.01* |
| | | | | | | PC3 | –0.16 | –0.21 | –1.53 | 0.13 |
| Model 2 | 0.38 | 1.52 | 57.96 | 33.27 | <0.01* | PC1 | 0.62 | 0.62 | 5.77 | <0.01* |

*(b)* Loading of environmental variables on principal components axes.

| | PC1 | PC2 | PC3 | PC4 |
|---|---|---|---|---|
| Latitude | –0.3104 | **–0.7551** | 0.2853 | –0.4111 |
| Temperature | **0.8458** | 0.0630 | 0.1103 | 0.0717 |
| Conductivity | **0.8773** | 0.2919 | 0.2069 | 0.0448 |
| Calcium | **0.8379** | 0.3512 | 0.1811 | 0.0890 |
| Chl *a* | 0.1707 | **–0.7260** | 0.0127 | 0.5826 |
| DOC | **0.9297** | –0.1951 | –0.0617 | –0.1868 |
| TN | **0.8540** | –0.1626 | –0.1553 | –0.3642 |
| TP | **0.9018** | –0.2657 | –0.0323 | –0.1777 |
| Elevation | 0.0596 | –0.0281 | **–0.9742** | –0.0368 |
| Surface area | *–0.6837* | 0.2232 | 0.0921 | –0.3592 |

**Note:** Smaller values of Mallows' $C_p$ and Akaike's information criterion (AIC) indicate the most parsimonious model. Values in bold type indicate variables with high loadings (>0.7); values in italics indicate moderately high loadings. Abbreviations: chl *a*, chlorophyll *a*; DOC, dissolved organic carbon; TN, total nitrogen; TP, total phosphorus. *p* values followed by an asterisk (*) are significant at *p* < 0.05.
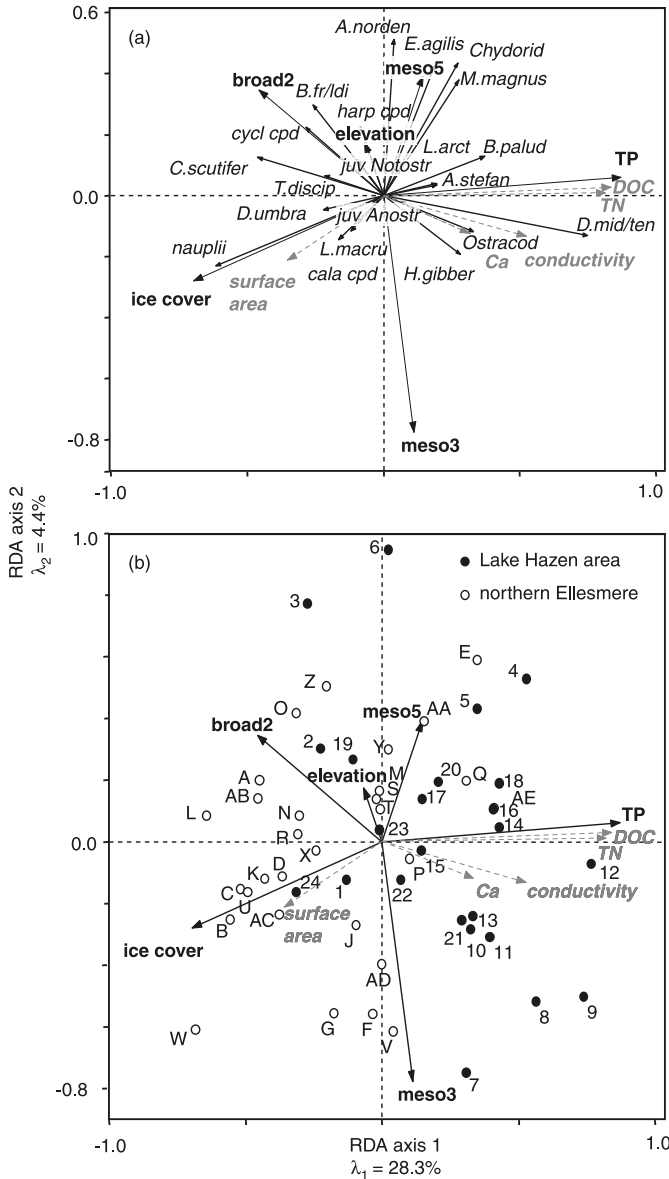
microcrustacean communities. We found evidence of spatial patterns, especially around Lake Hazen, where 21% of variation in species distributions was due to the structuring of communities by spatially related factors, which probably results from dispersal between nearby lakes. However, we also observed low frequencies of microcrustacean taxa and high beta diversity (Lande 1996), both at the Lake Hazen scale (59%) and for all the sites on Ellesmere (73%), suggesting that dispersal is limiting in the harsh landscape of the Arctic.

The main determinants of species richness and composition in our study were nutrients, conductivity (which was highly correlated with calcium), and DOC. Although lake productivity (Dodson et al. 2000; Jeppesen et al. 2000) and calcium (Wærvågen et al. 2002) are well-known predictors of microcrustacean species richness and composition in temperate zones, DOC is rarely a significant driver of microcrustacean community structure (Keller and Pitblado 1984; Hessen et al. 2006; but see Wissel et al. 2003). However, Olson et al. (1995) also found that DOC and colour were important predictors of zooplankton community composition in a chronosequence of lakes in Alaska, where increasing colour in older lakes altered competitive and predator–prey interactions. In Arctic lakes, DOC primarily results from allochthonous input from the surrounding watershed (Hamilton et al. 2001) and the humic content acts to reduce microcrustacean mortality due to UV radiation (Rautio and Korhola 2002*a*). In the Lake Hazen region, lakes have elevated concentrations of DOC and nutrients, probably resulting from the lush vegetation associated with warmer temperatures in the polar oasis (Keatley et al. 2007); however, lakes outside of this polar oasis had significantly lower DOC concentrations (*t* = –4.92, *p* < 0.01, df = 26). In shallow study lakes, we would expect that increased melanization would be the primary way in which microcrustaceans, such as *Daphnia middendorffiana/tenebrosa*, would avoid UV damage in low DOC lakes (Rautio and Korhola 2002*b*). However, we also expect *D. middendorffiana/tenebrosa* to do well in high DOC lakes where they would not produce as much melanin (Rautio and Korhola 2002*b*), and this energy could therefore be redirected towards growth and reproduction, increasing their competitive ability (Hessen 1996). In addition, DOC from terrestrial sources can serve as a food source for microcrustaceans (Carpenter et al. 2005). Indeed, we observed a wide range of *D. middendorffiana/tenebrosa* relative abundances at low DOC (<1%–100% of adults at DOC ≤ 5 mg·L⁻¹, mean = 46%) but higher relative abundances at high DOC (mean = 72%). The role of DOC in structuring microcrustacean communities is likely related to mechanisms of UV avoidance and possibly also food availability and would likely be important in other systems where UV light penetration is high, i.e., high elevation and boreal lakes and ponds. The success of *D. middendorffiana/tenebrosa* may also be due to a lack of fish predation, releasing it from the tradeoffs associated with its larger size and pigmentation. Although we do not have fish data available for our study lakes, many of the ponds probably freeze solid during the winter and, therefore, would not support fish populations.
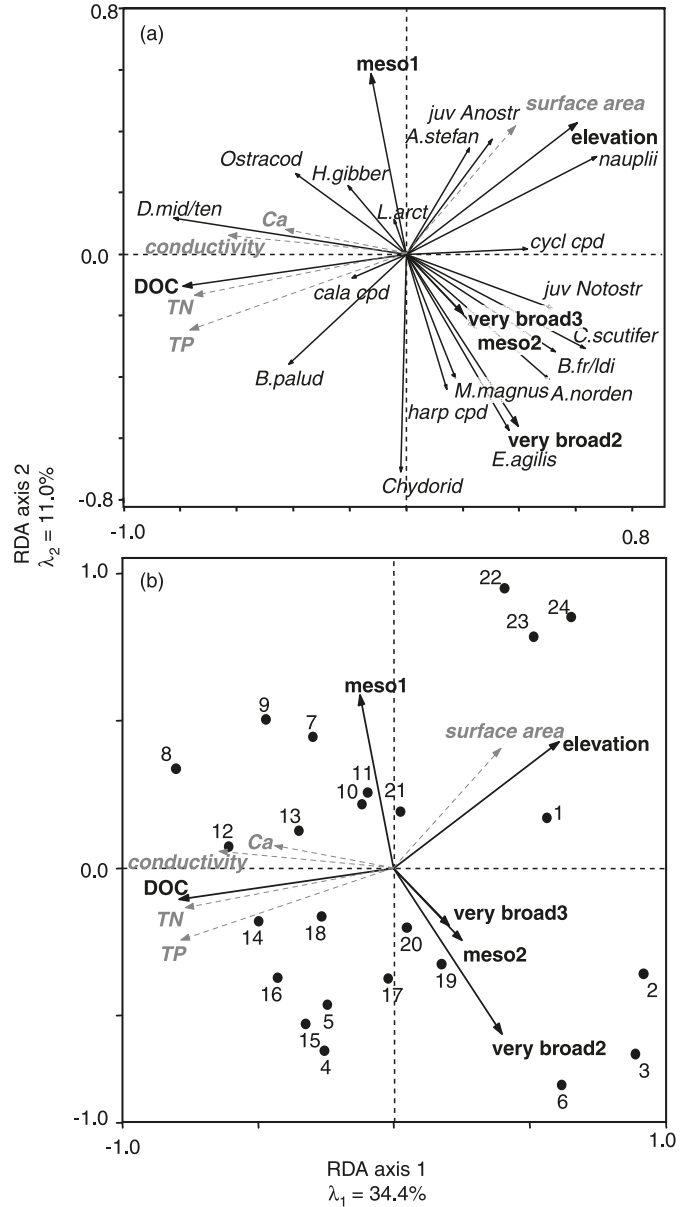
Temperature, temperature-related variables, e.g., surface area, and elevation were secondary determinants of microcrustacean composition and richness. Lakes with large surface areas tend to be colder and take longer to heat than small lakes; thus there is an inverse relationship between temperature and surface area. Elevation is likely a proxy of both temperature and isolation, as its negative influence on

**Fig. 4.** Redundancy analysis of microcrustacean communities from all sample sites on Ellesmere Island. (*a*) Species and (*b*) sample sites (Lake Hazen area, solid circles; northern Ellesmere, open circles) in relation to environmental and spatial variables. Species are represented by thin-line vectors and italic type (see Table 2 for abbreviations), environmental (see Table 1 for abbreviations) and spatial variables are represented by thick-line vectors and bold type, and supplementary environmental variables are shown with shaded, broken-line vectors and bold–italic type. Spatial variables are abbreviated: **broad2**, broad-scale variable 2; **meso3**, meso-scale variable 3; **meso5**, meso-scale variable 5.

**Fig. 5.** Redundancy analysis of microcrustacean communities from sites around Lake Hazen. (*a*) Species and (*b*) sample sites in relation to environmental and spatial variables. Species are represented by thin-line vectors and italic type (see Table 2 for abbreviations), environmental (see Table 1 for abbreviations) and spatial variables are represented by thick-line vectors and bold type, and supplementary environmental variables are shown with shaded, broken-line vectors and bold–italic type. Spatial variables are abbreviated: **very broad2**, very broad-scale variable 2; **very broad3**, very broad-scale variable 3; **meso1**, meso-scale variable 1; **meso2**, meso-scale variable 2.



species richness and positive relationship with juvenile stages probably reflects fewer microcrustacean propagules from upstream sources, colder water temperatures, later ice-off dates, and thus, slower reproduction and development. Hessen et al. (2006) found that high-elevation lakes generally had low species richness, which they attributed to difficulties in colonization. In contrast to the positive relationship that is generally observed between surface area and microcrustacean richness in temperate lakes (Dodson 1992),

we found a negative relationship between surface area and microcrustacean richness. Hessen et al. (2006) and Walseng et al. (2006) also failed to observe a positive relationship between area and crustacean species richness at high latitudes. As larger lakes hold more volume and take longer to heat, this suggests that temperature can override the positive effect of area on microcrustacean richness. We acknowledge that as a result of sampling near the shore, we

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**Table 4.** Species scores on canonical axis 1 for individual spatial submodels (spatial scale followed by spatial variable in parentheses).

| | Lake Hazen, broad (**broad4–5**) | Ellesmere | |
| | | Very broad (**very broad1–2**) | Broad (**broad3–11**) |
| --- | --- | --- | --- |
| *B.palud* | **–0.4856** | 0.1828 | –0.0555 |
| *A.stefan* | **0.3758** | 0.0662 | 0.0791 |
| juv Anostr | **0.5675** | 0.0277 | –0.0435 |
| *D.mid/ten* | **–0.6034** | **0.3698** | **–0.5764** |
| *D.umbra* | | –0.1306 | *0.2609* |
| *B.fr/li* | *0.2266* | 0.0838 | *0.2573* |
| Chydorid | **–0.3283** | *0.2734* | –0.0873 |
| *H.gibber* | –0.0804 | 0.0534 | *–0.2800* |
| *L.arct* | –0.1695 | 0.1023 | –0.1379 |
| juv Notostr | *0.2049* | **0.4294** | **0.3098** |
| *L.macru* | | –0.0196 | 0.0669 |
| cala cpd | *–0.2303* | –0.0487 | 0.1205 |
| nauplii | **0.5117** | *–0.2887* | **0.4337** |
| *C.scutifer* | **0.3115** | –0.1738 | *0.2772* |
| *E.agilis* | –0.0199 | **0.6001** | 0.1106 |
| *M.magnus* | –0.1089 | **0.4795** | –0.0152 |
| cycl cpd | **0.4081** | –0.1202 | 0.0074 |
| *A.norden* | 0.1697 | *0.2070* | 0.1446 |
| *T.discip* | | –0.0935 | 0.0667 |
| harp cpd | 0.0019 | 0.0499 | *0.2233* |
| Ostracod | –0.1154 | 0.0835 | *–0.2009* |

**Note:** Values in bold type indicate species with high loadings (>0.3); values in italics indicate moderately high loadings (0.2–0.3). Only significant spatial submodels are presented. Species abbreviations as in Table 2.

may have missed some hypolimnetic taxa in larger lakes, which would be reflected by lower species richness in larger lakes. However, the hypolimnetic *Cyclops scutifer* was detected in almost 50% of lakes, including several of the largest lakes (Supplementary Tables S1 and S2),[2] suggesting that our sampling was representative of the microcrustacean community in lakes on northern Ellesmere Island. Thus, high-latitude microcrustacean communities appear to be structured by different processes than temperate lake microcrustaceans, as in general, most environmental predictors showed significant variability, suggesting that our results are not an artefact of sampling a restricted range of environmental conditions.

With temperatures in the Arctic expected to rise by 3–5 °C by the end of the 21st century (International Arctic Science Committee 2005), consideration of the effect of warming on microcrustaceans in these lakes is of great importance. Temperature provides both direct, e.g., metabolic, and indirect, e.g., food availability, mechanisms for change in microcrustacean communities. This trade-off between higher production and increased metabolic demands will likely favour smaller species (Moore et al. 1996). This was observed experimentally where daphniid and overall zooplankton biomass declined in high-elevation experimental ponds when the temperature was raised, likely responding to temperature-induced changes in algal composition (Strecker et al. 2004). Although we observed some small-bodied microcrustaceans (e.g., chydorids) in warmer locations, in general, the large-bodied *Daphnia* dominated

**Fig. 6.** Comparison of variation explained in microcrustacean communities in Cottenie et al. (2003), Beisner et al. (2006), Pinel-Alloul et al. (1995), Lake Hazen, and Ellesmere Island. Variation in species abundances is explained by purely environmental (*en*, solid bars), spatially structured environmental (*sp-en*, hatched bars), and purely spatial (*sp*, shaded bars) variables, where the remaining variation is unexplained by the examined variables (open bars). Study areas are listed on right side of the graph.
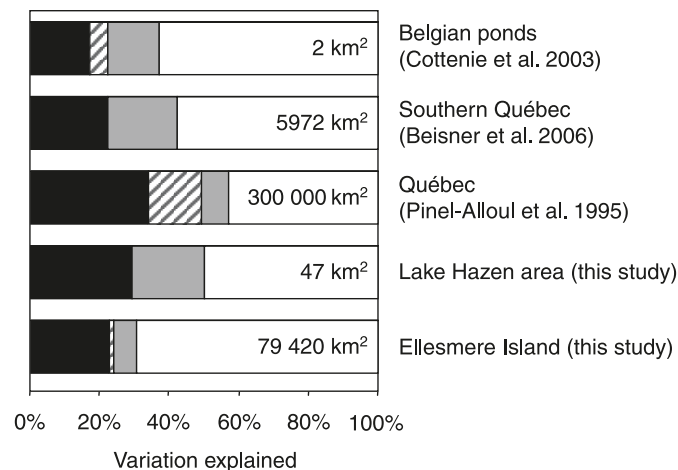


assemblages in lakes with higher temperatures such as those found in the polar oasis Lake Hazen region (15.3 °C ± 4.9 °C in Lake Hazen sites versus 8.5 °C ± 4.7 °C in northern Ellesmere Island sites). This suggests that perhaps the thermal optimum of *Daphnia* has not yet been reached, but with increasing temperature, it will likely be vulnerable to higher metabolic costs.

Temperature also affects reproduction directly by accelerated development (Moore et al. 1996) and indirectly by increasing the length of the growing season. Hebert and Hann (1986) suggested that calanoids are limited in the Arctic by the inability to shorten their life cycle and reproduce within the short growing season. We detected few adult calanoids, and the copepodids tended to be associated with larger lakes, probably because they do not freeze to the bottom and can maintain populations throughout the winter. Thus, a change in the length of the growing season may improve the establishment success and persistence of calanoids and other slow-developing taxa in small Arctic lakes.

Overall, the lakes on Ellesmere Island show low microcrustacean species richness, diversity, and frequency of occurrence. Although the species pools around Lake Hazen and northern Ellesmere Island are similar, average species richness was greater around Lake Hazen. The low frequency of occurrence of species suggests that dispersal limitation is a key factor in structuring these microcrustacean communities. This was also supported by the low fraction of variation explained by spatial variables (7%) in the entire sample set on Ellesmere Island. Dispersal is more likely to be limiting in regions where there are large physical barriers to the movement of microcrustaceans and their vectors. Hessen et al. (2006) found evidence of dispersal limitation to isolated mountainous lakes in a 300+ lake survey in Norway, a landscape similar to that of the Arctic. In temperate systems, there is evidence of dispersal limitation when considering

large geographic regions (Shurin et al. 2000); however, at small geographic and experimental scales, studies have found that dispersal is not limiting (Cottenie et al. 2003; Forrest and Arnott 2006).

Using variation partitioning, we observed large contributions of spatial and environmental variables to patterns in microcrustacean composition, especially in the Lake Hazen region. This is perhaps not surprising, as lakes in close proximity to each other would be more likely to influence species distributions via increased opportunity for short-distance dispersal events. Whiteside et al. (1980) found that recently formed moraine ponds in the Yukon had both calanoid and cyclopoid copepod species, as well as several cladoceran taxa, suggesting that a number of high latitude species can disperse quickly into new locales, in contrast to the view that passive dispersal in invertebrates is extremely limited (Bohonak and Jenkins 2003). Factors explaining microcrustacean community variation at different spatial scales and in different regions are generally consistent: spatial and environmental variables describe roughly equal fractions of variation, with the exception of the two larger scale studies (Québec and Ellesmere) where dispersal is more likely to be limiting at large spatial scales where long-distance dispersal events would be rare. Interestingly, fine-scale spatial variables were not important explanatory variables at either the small Lake Hazen region or the larger Ellesmere Island scale. This suggests that lakes that are very close together generally have similar communities, in agreement with the review of Havel and Shurin (2004), who suggested that dispersal could be rapid at distances <10 km, highlighting the importance of short-distance, frequent dispersal events. However, this may be species-specific: Hebert and Hann (1986) suggest that low dispersal rates have restricted the distribution of certain microcrustacean species, while Sarnelle and Knapp (2004) observed relatively rapid recolonization of lakes by *Daphnia middendorffiana* following removal of fish but failed to detect the copepod *Hesperodiaptomus shoshone*, which they attributed to significant Allee effects.

In contrast, broad and very broad scale spatial variables were important at both the Lake Hazen and Ellesmere Island scale, suggesting that there are likely some large barriers to dispersal that impede species from broadly colonizing the island. In the case of Ellesmere Island, the continuing retreat of the glaciers means that younger lakes, found closer to the glaciers, may show community compositions that exclude some of the slower dispersing species. In addition, younger lakes tend to have lower DOC concentrations and higher UV penetration, which likely will also affect species establishment and composition (Williamson et al. 2001). Finally, although we detected significant contributions of spatial and environmental variables to the total variation explained in microcrustacean community composition, a large portion of variation remained unexplained. This likely reflects our one-time sampling, which may have failed to capture important variation in environmental variables, as well as the entire microcrustacean community, which can be underestimated by 50% by single sampling visits (Arnott et al. 1998).

Local biotic factors are also an important determinant of microcrustacean species composition. We used nutrients as a proxy for phytoplankton productivity, as they represented

a better measure of productivity than chl *a*, which has been shown to be poorly correlated with nutrients in Arctic lakes and ponds, where the predominant contributor is periphytic production (Keatley et al. 2007). Although the lakes in this study are generally fishless, there are other predators that may have an influence on the composition of microcrustaceans. Larger omnivorous copepods may have preyed on small-bodied microcrustaceans; however, these large predators were relatively rare in our study, as most assemblages were dominated by *D. middendorffiana/tenebrosa* or juvenile herbivorous stages of copepods. Other predator groups, such as waterbirds and larval insects, could also have influenced our results. For example, the migratory Red Phalarope waterbird (*Phalaropus fulicarius* (Linnaeus)), can consume *Daphnia*; however, predation rates are low at natural bird densities, suggesting that their impact is minimal (Dodson and Egger 1980). In addition, dipteran larvae were often found in microcrustacean samples, but their abundance was generally low.

Our survey revealed several species that had not been previously detected in lakes on Ellesmere Island. *Artemiopsis stefanssoni*, an anostracan, was identified on Ellesmere Island for the first time in this study. However, it is common throughout the Arctic, including northern Canada and eastern Greenland, and thus, Røen (1981) speculated that *A. stefanssoni* was present on Ellesmere in 1965 but that it was missed in his sampling. *Daphnia umbra* was first identified as a distinct species within the *D. longispina* complex by Taylor and Hebert (1994) and named by Taylor et al. (1996). Although there are records for this species in the lower Arctic, until now there were no records for *D. umbra* or *D. longispina* on Ellesmere Island. Similarly, *Tachidius discipes* has been recorded from other sites in the Arctic (Tash 1971) but not previously from Ellesmere Island. As a result of the scarcity of studies in this area, it is difficult to assess whether these species have recently dispersed to Ellesmere Island or whether they were simply not detected in previous studies. Experimental evidence has found that warming can reduce the invasion resistance of natural zooplankton communities (Holzapfel and Vinebrooke 2005), suggesting that a changing climate may facilitate species colonizations into new habitats. We hope that our study will provide important baseline information about microcrustacean communities against which future changes can be assessed.

Our study has found that the major controls on microcrustacean richness and community composition are factors that are closely related to climate. The Arctic is expected to be subjected to increased temperatures and precipitation in the coming decades (International Arctic Science Committee 2005). Warmer temperatures have altered both the biotic and abiotic characteristics of Arctic lakes. Decreased ice cover has led to longer growing seasons, which have been linked to greater productivity (Smol and Cumming 2000). Nutrients, DOC, and temperature were limiting factors in microcrustacean species distributions in our study, and the release of these constraints with increased warming could allow increased numbers of more southern species to colonize Ellesmere Island. Additionally, we demonstrated that High Arctic microcrustacean communities are structured differently than communities at lower latitudes: dispersal limits

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the ability of microcrustaceans to broadly colonize lakes and ponds on Ellesmere Island, while strong environmental gradients linked to climate change, i.e., high concentrations of DOC and nutrients flushed in from the watershed, are important determinants of survival and long-term persistence in the region.

## Acknowledgements

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