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Zooplankton community composition of lakes in the Yukon and Northwest Territories (Canada): relationship to physical and chemical limnology

Kerrie M. Swadling[1,3,*], Reinhard Pienitz[1] & Thomas Nogrady[2]
[1]*Paleolimnology-Paleoecology Laboratory, Centre d'études nordiques, Université Laval, Québec, QC G1K 7P4, Canada*
[2]*Department of Biology, Queen's University, Kingston, ON K7L 3N6, Canada*
[3]*School of Zoology, University of Tasmania, GPO Box 252-5, Hobart, Tasmania 7001, Australia*
Fax: +61-3-6226 2745. E-mail: k.swadling@utas.edu.au

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Abstract

We analysed associations between zooplankton species composition and local abiotic factors in 30 lakes located along a 900 km south-north transect from Whitehorse (Yukon Territory) to Inuvik (Northwest Territories). The lakes were situated in three broadly defined vegetation zones: (i) Boreal forest (between Whitehorse and Dawson City), (ii) alpine tundra (Ogilvie mountains north of Dawson City) and (iii) subarctic forest-tundra (near Inuvik). Lakes in the alpine tundra were characterised by lower conductivity, temperature, chlorophyll *a* and nutrients than those in the other two zones. Those in the forest-tundra were generally small and shallow, and had higher chlorophyll *a* concentrations than lakes further south. Lakes in forested catchments spanned a larger latitudinal range and exhibited a greater variety of physical and chemical characteristics. However, they were generally deeper, with higher conductivity, temperature and ionic concentrations. Forty-one zooplankton taxa were identified from the 30 lakes, of which the most frequently occurring were the rotifers *Conochilus unicornis*, *Kellicottia longispina*, *Keratella cochlearis* and *Polyarthra vulgaris*, the cladocerans *Daphnia middendorffiana* and *Bosmina longirostris*, and the copepods *Leptodiaptomus pribilofensis*, *Heterocope septentrionalis* and *Cyclops* spp. The lakes contained between two and fifteen species (mean = 6.9). Alpine tundra lakes contained slightly less species (mean = 5.8) than those at lower elevations; in particular the cladoceran fauna was depauperate or absent. Relationships among the lakes, species and environmental factors were examined using canonical correspondence analysis, with forward selection and associated Monte Carlo permutation tests. Chloride, silica and temperature showed statistically significant relationships with species distribution, and together these abiotic factors explained 25% of the variation in zooplankton communities within Yukon and Northwest Territories lakes.

Introduction

Local and regional processes interact to influence the composition of zooplankton communities in lacustrine habitats. At local scales, biotic and abiotic factors shown to correlate with patterns of zooplankton distribution include pH, ionic concentrations, productivity and predator assemblages (e.g. Brooks & Dodson, 1965; Pinel-Alloul et al., 1990, 1995; Dodson, 1992; Shaw & Kelso, 1992; Shurin et al., 2000). Examples of regional scale processes include colonisation history and dispersal mechanisms, which will influence broad-scale trends in distribution. In subarctic and arctic regions, where extended periods of ice cover and extreme seasonality in irradiance restrict primary production to brief summer periods, both dispersal capabilities and environmental conditions could act to limit zooplankton diversity. Species richness might be low in high latitude lakes because few species have the opportunity to colonise them. If this were the case, it

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[*] Author for correspondence.

would be expected that no relationship between species and physical factors would exist. In contrast, if environmental conditions (e.g. low productivity, low temperatures) prevent species from forming viable populations, strong associations between limnology and species distributions would be expected.

In order to examine these predictions, we explored patterns of zooplankton distribution in a series of high latitude lakes in the Yukon (YT) and Northwest Territories (NWT), and used the physical and chemical attributes of these lakes (Pienitz et al., 1997) to investigate the influence that local abiotic factors have on structuring the zooplankton communities. Pienitz et al. (1997) showed that these abiotic factors were strongly related to the bedrock geology and catchment vegetation of the lakes. Lakes in northwestern Canada provide a good opportunity to study fundamental species–environment relationships. Deglaciation of the region occurred within the last 16 000 years (Matthews, 1992), and so species invasions must have taken place relatively recently. Moreover, in comparison with many lakes in southern Canada, northern lakes have experienced little onsite human disturbance.

Approximately 35 species of crustaceans have been recorded in two previous studies of Yukon lakes (Lindsey et al., 1981; Shortreed & Stockner, 1986). The most commonly occurring copepods in both studies were *Cyclops scutifer* and *Diaptomus pribilofensis*, which were distributed over the whole of the regions sampled. *Heterocope septentrionalis* was also distributed widely, and, though never a numerically dominant species, it contributed substantially to biomass. Similarly, cladocerans, including *Daphnia longiremis*, *Daphnia middendorffiana* and *Eubosmina longispina*, were never numerically dominant, but were important contributors to biomass. While copepods and cladocerans were documented quite extensively, less information is available regarding the planktonic rotifer fauna of the lakes. Lindsey et al. (1981) provided abundances of rotifers but, unfortunately, identifications were given only for very common species, such as *Kellicottia longispina*. While rotifers rarely dominate the biomass of a lake they often exceed crustaceans in both abundance and species diversity (Pejler, 1995). Therefore, this group must be included in any efforts to assess factors affecting species richness of lakes.

Materials and methods

Study sites

Two previous papers describe the physical and chemical limnology of 59 lakes located between Whitehorse (YT) and the Tuktoyaktuk Peninsula (NWT) (Pienitz et al., 1995, 1997). The present study examined the zooplankton communities from 29 of those 59 lakes and one additional lake (lake 60). For ease of comparison the labels designated by Pienitz et al. (1995, 1997) were retained, thus this study encompassed lakes 1–25 and 56–60. The 30 lakes were sampled along a south-north transect between Whitehorse, YT (60° 44′ N, 135° 04′ W), and Inuvik, NWT (68° 21′ N, 133° 43′ W), which roughly followed the routes of the Klondike and Dempster Highways (Figure 1). Our set of lakes covers a different and greater latitudinal range than that of previous investigations in the Yukon: between 60° 11′ N, 131° 40′ W and 63° 43′ N, 139° 49′ W (Shortreed & Stockner, 1986), and between 59° 26′ N, 133° 35′ W and 66° 11′ N, 136° 25′ W (Lindsey et al., 1981). The sampling transect traversed three major ecoclimatic provinces (as defined by the Ecoregions Working Group (1989)): (1) Boreal forest, which dominated between Whitehorse and Dawson City; (2) Alpine tundra located in the Ogilvie Mountains north of Dawson City; and (3) Forest-tundra, near Inuvik, which was characterised by dwarf white and black spruce trees (*Picea glauca* and *P. mariana*).

All lakes studied were natural with the exception of lake 4, which is artificially dammed and is used as the water supply for the Whitehorse area. The lakes span large gradients in their physical and chemical limnology. Many of the lakes are rich in HCO_3^-, Ca^{2+} and SO_4^{2-}, with the proportions of these ions reflecting the chemistry of the surrounding soils and bedrock, as well as catchment vegetation type. The duration of ice cover on the lakes ranges from approximately 150 days in the south to 250 days in the north (Pienitz et al., 1997). The lakes were small- to medium-sized (1.1–1260 ha) basins that were circular in shape and greater than 1 m in depth. Although fish are known to inhabit many lakes in the Yukon (Lindsey et al., 1981; Shortreed & Stockner, 1986), we made no observations about the extent of their occurrence in our lakes.

Sample collection

Samples were collected from the lakes between 1 and 24 July 1990. They were obtained from the deepest

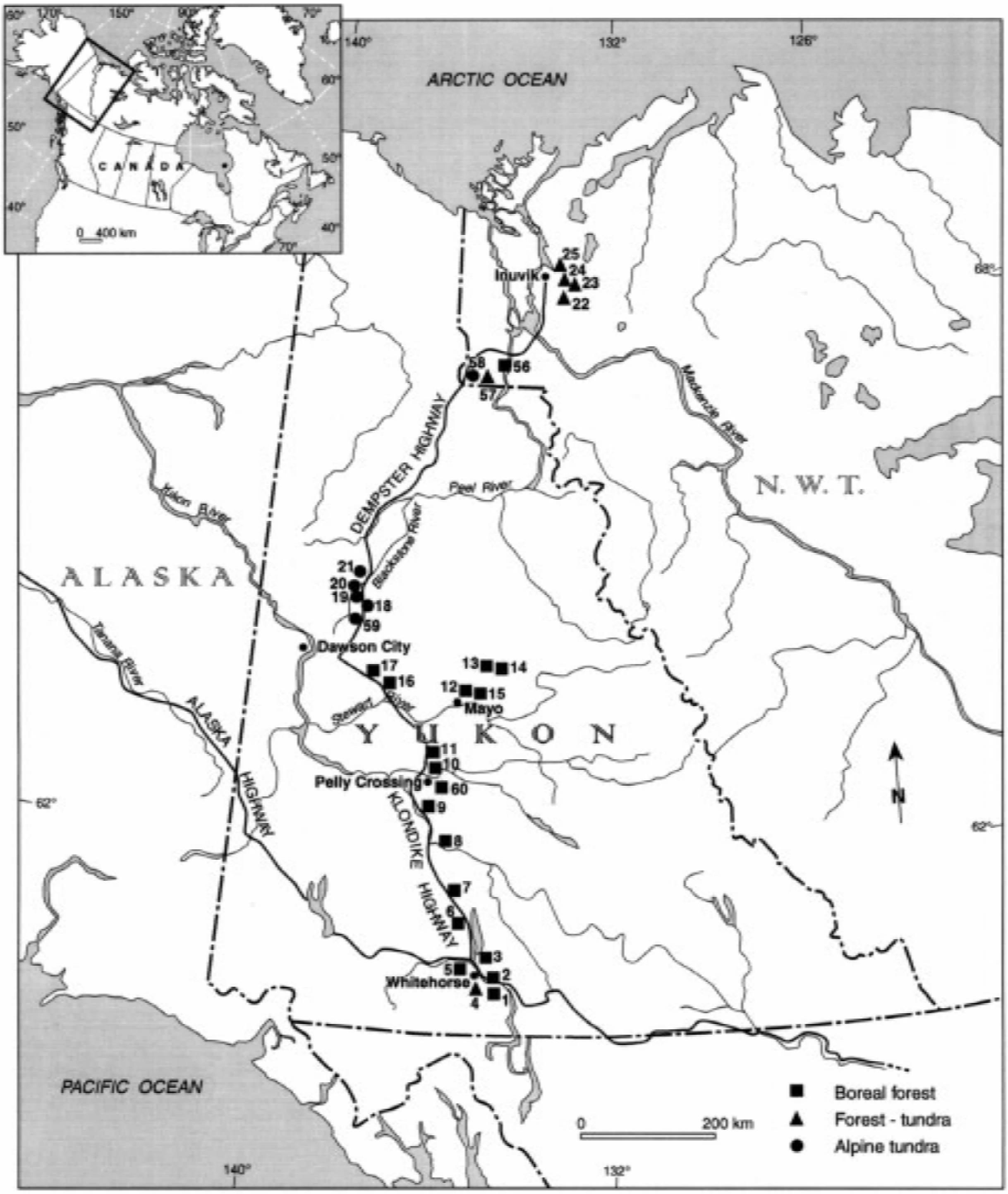

Figure 1. Locations of the 30 lakes sampled in the Yukon and Northwest Territories (N.W.T).

part of the lake, usually near the center. Zooplankton were sampled with a Wisconsin net (mesh size: 50 μm; mouth diameter: 25 cm) that was towed through the water column. Each catch was preserved in 100% ethanol and kept refrigerated until sorted. The zooplankton were identified to the lowest taxon possible, usually to species level. Copepod nauplii could not be identified positively and were pooled. If the number of individuals in a sample was less than 1500 the entire catch was sorted, otherwise it was split so that between 1000 and 1500 organisms were counted. No flow meter was attached to the sampling net, thus the volume filtered could not be determined. Therefore, the numbers of each taxon are expressed as a proportion (%) of the total sample.

Full details of the physical and chemical variables measured are given in Pienitz et al. (1997), and are summarized briefly here. Morphometric and geographical-environmental variables recorded for each site included lake surface area (AREA), altitude (ALT), maximum depth (DEPTH), latitude (LAT) and longitude (LONG). The lakes were further classified as occurring in one of the following vegetation zones: boreal forest (FOREST, including some lakes in peatlands), sub-arctic woodland (WOOD, includes forest-tundra and lichen woodland), and alpine tundra (ALPINE). Field measurements were made of water transparency (TRANS), conductivity (COND), water temperature (TEMP), dissolved oxygen content (DO) and pH. Water samples were collected from approximately 0.5 m water depth using polyethylene sampling bottles. Water chemistry analyses were performed by the National Water Research Institute (Burlington, Ontario). Twenty-one chemical variables were measured: Nitrite (NO_2), nitrate (NO_3), ammonia (NH_3), soluble reactive phosphate-phosphorus (SRP), dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), total Kjeldahl nitrogen (TKN), filtered total ‘dissolved’ phosphorus (TFP), unfiltered total phosphorus (TPU), particulate organic carbon (POC), particulate nitrogen (PN), total chlorophyll, uncorrected (CHLaU) and corrected (CHLaC) for phaeophytin, sodium (Na), potassium (K), calcium (Ca), chloride (Cl), sulphate (SO_4), dissolved silica (SiO_2), iron (Fe) and manganese (Mn).

Statistical analyses

Prior to statistical analysis, the environmental data were screened to reject any variables that had missing values (DO) or values that fell below the minimum detection limit (CHLaC, NO_2, NO_3, NH_3, SRP). Longitude was also excluded. Relationships between the lakes and environmental factors were examined using principal components analysis (PCA; CANOCO Version 3.12; Ter Braak, 1988, 1990). PCA is an ordination technique used to reduce the dimensionality of multivariate data sets and enable graphical presentation of the relationships between factors. Twenty-three variables were included in the analysis, with a further five added as passive variables (ALT, FOREST, WOOD, ALPINE, LAT). Passive variables have no influence on the ordination axes, but are added afterwards so that their relationship with the other factors can be determined from the ordination biplot. The variables were tested for skewness and a ln(x+1) transformation applied to approximate a normal distribution for the following: DEPTH, AREA, COND, TRANS, TPU, TPF, DIC, TKN, TN, SiO_2, SO_4, Ca, Na, K, Cl, CHLaU, POC, PN, Fe and Mn. All lakes were included in the initial analysis, however lake 60 was an extreme outlier that had the effect of compressing the other 29 lakes into a tight cluster on the PCA biplot. The environmental factors were therefore re-analysed with the exclusion of lake 60.

Relationships between the zooplankton taxa and the lakes were analysed with correspondence analysis (CA), an ordination technique that is often used when species’ response curves can be assumed to be unimodal. Taxa were included in the analysis if they were present in two or more lakes and reached a relative abundance of greater than 1% in at least one lake. All species data were square-root transformed to minimize skewness in the data. Twenty-three taxa and 29 lakes were included in the analysis. Rare species were downweighted.

Canonical correspondence analysis (CCA) was performed on the same subset of 23 taxa and 29 lakes to assess the influence of environmental factors on the distribution of zooplankton. CCA is a direct gradient analysis technique where the ordination axes are constrained to be linear combinations of environmental factors. Seven environmental variables had very high ($>$20) variance inflation factors and were removed from the analysis. The 16 remaining variables included in the analysis were PN, Cl, Mn, DEPTH, TRANS, CHLaU, TPF, Ca, DOC, TKN, AREA, pH, SiO_2, Fe, TEMP and COND. The forward selection option of CCA, which is analogous to the technique of stepwise multiple regression, was used to determine the minimum number of explanatory factors that could explain statistically significant ($p\leq0.05$) pro-

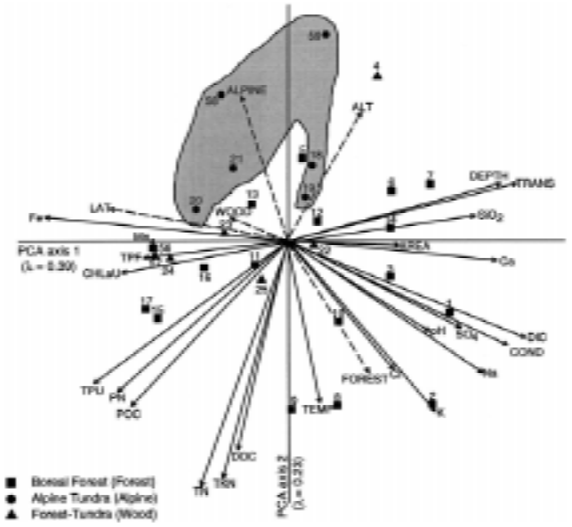

Figure 2. Principal Components Analysis of the 23 physical, chemical and environmental factors measured for 29 lakes (lake 60 excluded). The five passive variables are represented by arrows with broken lines. Shaded region highlights lakes located in the alpine tundra.

portions of variation in the species data. The significance of these variables was assessed using Monte Carlo permutation tests (with 99 unrestricted permutations). The species scores were scaled to be weighted averages of the site scores.

Results

Environment

Table 1 shows the mean and range of the physical, chemical and morphometric variables measured for each lake in the three major vegetation zones. The full data set for 29 of the lakes is presented elsewhere (Pienitz et al., 1997), and so only the data for lake 60 is shown separately here. The lakes within the boreal forest spanned a larger physical and chemical gradient than lakes in the other vegetation zones. They were alkaline (pH), and showed higher mean values for those factors associated with conductivity (COND, Na, Cl, K, Ca, SO_4, DIC). Lakes in the alpine tundra zone were smaller (AREA), and showed lower mean conductivity (COND, Na, Cl, K, Ca, SO_4, DIC), temperature (TEMP), chlorophyll *a* concentration (CHLaU), and nutrient concentrations (SiO_2, TKN, TPU), particularly when compared to boreal forest lakes. Forest-tundra lakes were generally intermediate between the other two zones, though the mean chlorophyll *a* (CHLaU) concentration was higher. PCA of these data showed that alpine tundra lakes tended to group together away from the boreal forest and forest-tundra sites (Figure 2), indicating that these lakes were physically and chemically different, and emphasising the tendencies shown in Table 1. The position of the alpine tundra lakes away from the main spread of the environmental variables suggests they were oligotrophic.

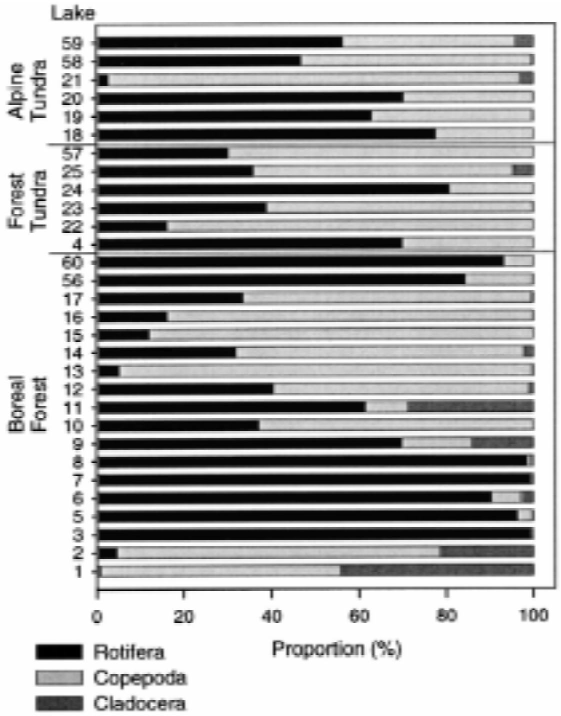

Figure 3. Relative abundance (%) of rotifers, copepods and cladocerans in the 30 lakes of the study.

The conductivity of lake 60 was ten times greater than the maximum of the other 29 lakes (Table 1), so the lake was removed from the PCA (Figure 2). PCA axis 1 explained 39% of the variation in the environmental data, with PCA axis 2 accounting for a further 23%. The variables which were significantly correlated ($p \leq 0.05$) with axis 1 included DEPTH, TRANS, AREA, Fe, Ca, SiO_2 and Mn. Those associated with axis 2 were TEMP, DOC, TKN and TN. In general, similar variables clustered together (as indicated by the small angles between the arrows); for example, those associated with nutrients (TPU, PN, POC and TKN, DOC, TN). Variables related to ionic concentrations (K, Cl, Na, SO_4, COND, DIC) also tended to cluster together, in the bottom right quadrant.

Table 1. Environmental factors measured in 30 lakes of the Yukon and Northwest Territories, showing the mean (SD) and range (minimum, maximum) for lakes in each major vegetation zone. *N* is the number of lakes used for each calculation. Lake 60 is shown separately. Complete data sets for the remaining lakes are found in Pienitz et al. (1997)

Variable	Boreal Forest (*N* = 17)				Alpine Tundra (*N* = 6)			Forest-Tundra (*N* = 6)		
	Mean (SD)	MIN	MAX	Lake 60	Mean (SD)	MIN	MAX	Mean (SD)	MIN	MAX
LAT (°N)	62.5 (1.7)	60.4	67.1	62.8	64.8 (1.1)	64.3	67.1	66.7 (3.1)	60.4	68.2
LONG (°W)	135.7 (0.9)	134.6	138.0	136.6	137.8 (.9)	136.0	138.2	133.9 (1.0)	133.2	135.4
ALT (m)	662 (132)	366	1021	600	1057 (279)	549	1387	305 (417)	30.0	1113
DEPTH (m)	13.0 (12.5)	3.0	49.0	1.1	6.3 (4.9)	1.9	15.5	3.7 (2.2)	1.2	7.0
AREA (ha)	72.4 (84.)	8.6	331	9.5	36.6 (52.9)	4.2	144	217 (512)	1.1	1262
pH	8.2 (0.4)	7.5	8.8	8.6	8.0 (1.2)	5.9	9.3	7.6 (0.5)	6.9	8.1
TEMP (°C)	20.4 (1.8)	17.0	23.0	22.5	15.8 (1.6)	13.5	17.5	17.7 (2.0)	14.0	20.0
COND (μS cm^{-1})	272 (365)	24.0	1500	15000	72.8 (34.5)	32.0	113	105 (47.0)	35.0	153
DO (mg l^{-1})	12.9 (1.0)	11.4	14.4	11.6	12.7 (0.6)	11.7	13.2	12.8 (1.2)	11.1	14.6
TRANS (m)	4.7 (3.3)	1.4	11.5	0.5	4.1 (2.8)	1.9	9.5	2.9 (2.1)	1.0	6.5
TPU (μg l^{-1})	14.3 (8.8)	4.3	35.4	108	11.0 (6.5)	4.0	23.1	22.2 (16.7)	3.7	44.9
TPF (μg l^{-1})	7.4 (4.8)	0.2	14.5	88.4	6.6 (4.0)	2.8	14.1	14.2 (10.8)	2.9	34.1
NO_2 (μg l^{-1})	0.7 (0.7)	0.2	2.9	3.0	0.9 (0.6)	0.2	2.0	1.5 (1.5)	0.2	4.3
NO_3(μg l^{-1})	22.2 (47.9)	10.0	208	10.0	10.0 (0)	10.0	10.0	12.8 (6.9)	10.0	27.0
SRP (μg l^{-1})	1.9 (1.6)	0.5	7.5	20.2	1.2 (0.7)	0.5	2.4	3.1 (3.4)	1.4	10.1
NH_3 (μg l^{-1})	9.0 (8.0)	5.0	31.0	1080	6.0 (2.4)	5.0	11.0	9.0 (6.8)	5.0	22.0
DOC (mg l^{-1})	15.9 (7.2)	7.8	35.1	20.4	7.9 (3.9)	3.1	12.3	13.0 (6.6)	3.8	22.6
DIC (mg l^{-1})	33.0 (35.2)	2.2	134	82.8	9.0 (8.3)	0.3	20.5	8.5 (5.6)	2.1	14.4
TKN (μg l^{-1})	568 (317)	208	1293	13100	263 (163)	72.0	498	493 (223)	121	700
TN (μg l^{-1})	722 (393)	259	1585	14600	343 (175)	123	606	587 (230)	158	803
SiO_2 (mg l^{-1})	4.5 (4.1)	0.2	12.5	6.2	1.4 (0.8)	0.3	2.0	2.6 (2.8)	0.5	7.8
SO_4 (mg l^{-1})	112 (300)	0.5	1242	20500	13.5 (13.4)	1.9	39.0	21.8 (14.3)	5.2	38.9
Ca (mg l^{-1})	23.3 (15.8)	3.5	50.3	265	15.2 (10.0)	5.8	31.6	18.0 (11.6)	6.5	39.2
Na (mg l^{-1})	17.8 (45.1)	0.4	187	827	1.5 (1.6)	0.2	3.7	2.9 (2.7)	0.9	8.3
K (mg l^{-1})	3.9 (7.1)	0.5	29.9	229	0.3 (0.2)	0.1	0.6	1.1 (.5)	0.7	2.1
Cl (mg l^{-1})	6.2 (15.9)	0.4	63.6	659	0.4 (0.1)	0.2	0.6	2.6 (2.2)	0.3	6.1
CHLaU (μg l^{-1})	2.3 (2.6)	0.1	10.5	2.9	0.9 (0.1)	0.8	1.1	2.9 (2.5)	1.1	7.9
CHLaC (μg l^{-1})	1.1 (1.9)	0.1	8.0	5.3	0.5 (0.3)	0.1	0.8	2.0 (2.5)	0.1	6.7
POC (μg l^{-1})	959 (857)	279	3280	3730	474 (177)	252	664	545 (413)	158	1340
PN (μg l^{-1})	131 (115)	40.0	396	596	69.3 (22.9)	40.0	96.0	80.3 (61.1)	26.0	200
Fe (μg l^{-1})	78.2 (146)	5.9	612	15.0	186 (242)	35.2	664	395 (484)	8.6	1280
Mn (μg l^{-1})	12.1 (6.9)	2.0	23.0	11.2	42.7 (58.2)	11.0	160	20.7 (15.0)	5.0	44.0

Zooplankton

Forty-one zooplankton taxa were identified from the lakes, including 22 rotifers, 11 cladocerans and 8 copepods. The relative abundances of each taxon are given in Table 2. Rotifers comprised between 2 and 80% of the total abundance per lake, and cladocerans and copepods accounted for 0–45%, and 0–90%, respectively (Figure 3). The number of taxa present per lake ranged from 2 in lake 60 to 15 in lake 8 (mean = 6.9 per lake) (Table 3). All lakes (except lake 60) contained at least two species of rotifer and one species of copepod. In several lakes no cladocerans were recorded: 4, 15, 18, 19, 21, 59 and 60. Fourteen species were recorded once only. The rotifers encountered most frequently were *Kellicottia longispina* (80% of lakes), *Conochilus unicornis* (60%), *Keratella cochlearis cochlearis* (27%) and *Polyarthra vulgaris* (23%). Cladocerans included *Daphnia middendorffiana* (47%), *Bosmina longirostris* (23%) and *Polyphemus pediculus* (33%). Amongst the copepods *Leptodiaptomus pribilofensis, Heterocope septentrionalis* and *Cyclops* spp. were all recorded from 15 or more lakes.

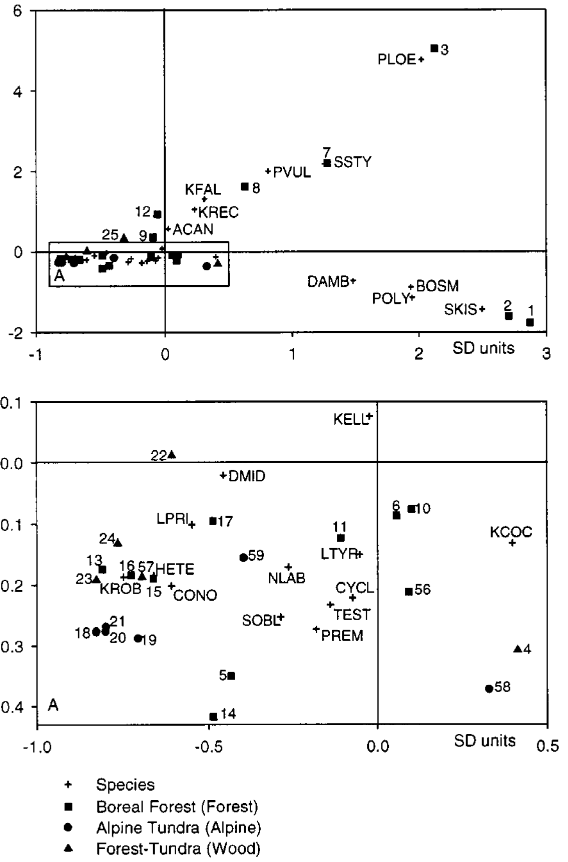

Figure 4. Correspondence Analysis (CA) of 23 zooplankton taxa and 29 lakes (lake 60 excluded). Bottom panel (A) shows portion of CA biplot on an expanded scale. Taxa abbreviations are: *Conochilus unicornis* (CONO), *Kellicottia longispina* (KELL), *Keratella cochlearis cochlearis* (KCOC), *Keratella cochlearis faluta* (KFAL), *Keratella cochlearis recurvispina* (KREC), *Keratella cochlearis robusta* (KROB), *Notholca labis* (NLAB), *Ploesoma truncatum* (PLOE), *Polyarthra remata* (PREM), *Polyarthra vulgaris* (PVUL), *Synchaeta oblonga* (SOBL), *Synchaeta stylata* (SSTY), *Testudinella tridentata* (TEST), *Bosmina longirostris* (BOSM), *Daphnia ambigua* (DAMB), *Daphnia middendorffiana* (DMID), *Polyphemus pediculus* (POLY), *Acanthodiaptomus denticornis* (ACAN), *Cyclops* spp. (CYCL), *Heterocope septentrionalis* (HETE), *Leptodiaptomus pribilofensis* (LPRI), *Leptodiaptomus tyrrelli* (LTYR), *Skistodiaptomus oregonensis* (SKIS).

Figure 4 shows the distribution of 23 zooplankton taxa relative to that of 29 lakes, as determined by CA. The first two axes accounted for 38% of the variance in the data. Lakes 1 and 2 contained very few rotifers (Figure 3), and their distribution was driven largely by the copepod *Skistodiaptomus oregonensis* (SKIS) and the cladocerans *Bosmina longirostris* (BOSM) and *Polyphemus pediculus* (POLY). Lake 3 contained a high proportion of the rotifer *Ploesoma truncatum* (PLOE; 88.5%) and clustered away from the other lakes. Lakes 7 and 8 were the only ones to contain the rotifer *Synchaeta stylata* (SSTY), and the former also had a high abundance of the rotifer *Polyarthra vulgaris* (PVUL; 45.4%). Other lakes in the forested catchments showed less clear patterns in their distribution, although there was some clustering of lakes that were geographically close together. For example, lakes 9–11 all contained high proportions of the rotifer *Kellicottia longispina* (KELL).

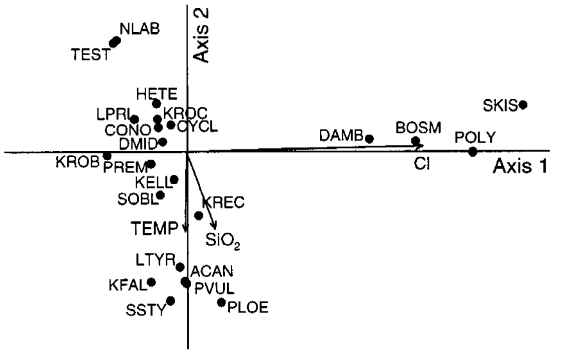

Figure 5. Canonical Correspondence Analysis biplot showing the relationship between zooplankton taxa (closed circles) and the three statistically significant environmental factors (arrows). Species abbreviations as for Figure 4.

The alpine tundra lakes clustered together on the far bottom left of the diagram, suggesting those lakes contained a similar suite of species; e.g. the copepod *Leptodiaptomus pribilofensis* (LPRI) was common to them. However, the paucity of cladocerans in these lakes probably drove their distribution on the biplot. Only two contained cladocerans: Lake 20 had *Daphnia middendorffiana* (DMID; 0.1%) and lake 58 contained *Bosmina longirostris* (BOSM; 2.4%) and *Daphnia ambigua* (DAMB; 2.1%).

Most lakes of the forest-tundra clustered together to the left side of the biplot. The exception being lake 4, which was geographically distant from the others (Figure 1), and was unusual in being an artificially dammed lake. Lakes 22–25 and 57 had *Leptodiaptomus pribilofensis* (LPRI) and *Daphnia middendorffiana* (DMID) in common.

Zooplankton–environment relationships

The influence of 16 environmental variables on the distribution of zooplankton in 29 lakes was assessed using CCA. The results of this analysis are displayed in Figure 5, with the environmental variables represented by arrows and the species depicted by points. CCA axis 1 (30.3%) and axis 2 (16.4%) ex-

Table 2. Percentage composition of the 41 zooplankton taxa recorded from 30 lakes in the Yukon and Northwest Territories. Lakes are grouped according to the vegetation zone in which they occurred

		Boreal Forest											
		1	2	3	5	6	7	8	9	10	11	12	13
	Rotifera												
1.	*Asplanchna priodonta*							0.5	0.1		0.9		
2.	*Brachionus plicatilis*												
3.	*Cephalodella gibba*												
4.	*Conochilus unicornis*	0.2			40.5	6.2			9.3		5.4		3.7
5.	*Gastropus stylifer*			0.9								0.6	
6.	*Kellicottia longispina*	0.6	1.9		5.8	81.2	3.6	36.7	58.1	33.0	55.1	7.9	1.4
7.	*Keratella cochlearis cochlearis*		2.8		0.1		3.8			2.3			
8.	*Keratella cochlearis faluta*							28.0				20.7	
9.	*Keratella cochlearis recurvispina*			0.6		2.2		8.2					
10.	*Keratella cochlearis robusta*												
11.	*Keratella earlinae*							0.2					
12.	*Keratella quadrata frenzeli*							2.4					
13.	*Keratella taurocephala*												
14.	*Notholca labis*												
15.	*Notholca striata*											0.8	
16.	*Ploesoma truncatum*			88.4			0.2	0.2					
17.	*Polyarthra remata*				40.4								
18.	*Polyarthra vulgaris*			9.5			45.4	22.3	2.3			10.3	
19.	*Synchaeta oblonga*				9.6					1.8			
20.	*Synchaeta stylata*							46.4	0.1				
21.	*Testudinella tridentata*												
22.	*Trichocerca* c. *capucina*												
	Cladocera												
23.	*Bosmina longirostris*	9.8	13.9	<0.1									
24.	*Ceriodaphnia quadrangula*							0.1					
25.	*Ceriodaphnia* sp.								2.3				
26.	*Chydorus sphaericus*			0.2			<0.1					0.2	
27.	*Daphnia ambigua*	3.1						0.2		0.1			
28.	*Daphnia galeata mendotae*										27.1		
29.	*Daphnia obtusa*								11.6				
30.	*Daphnia middendorffiana*				<0.1	0.6					1.1	0.7	0.1
31.	*Daphnia pulicaria*												
32.	*Daphnia rosea*												
33.	*Polyphemus pediculus*	31.2	7.4	<0.1	0.2	0.1	0.1	0.1			0.4		
	Copepoda												
34.	*Acanthodiaptomus denticornis*							0.3	7.0				
35.	*Cyclops* spp.	1.0	0.9	<0.1	0.1	1.1		<0.1	3.5	0.1	1.0	0.9	
36.	*Leptodiaptomus connexus*												
37.	*Hesperodiaptomus kenai*										8.2		
38.	*Heterocope septentrionalis*				0.8	<0.1							0.5
39.	*Leptodiaptomus pribilofensis*											42.5	80.1
40.	*Leptodiaptomus tyrrelli*				2.3	5.5				4.1			
41.	*Skistodiaptomus oregonensis*	53.5	64.8	<0.1									
42.	Unidentified nauplii	0.6	8.3	0.3	0.2	0.3		0.6	5.7	58.7	.693	15.4	13.7

Table 2. Continued

	Boreal Forest						Alpine Tundra						Forest-Tundra					
	14	15	16	17	56	60	18	19	20	21	58	59	4	22	23	24	25	57
1.																		
2.						93.3												
3.													7.7					
4.	31.8	5.31	10.1	3.7		69.1	16.1	38.9	78.1			51.5	70.0		1.3	45.6		
5.																		
6.		6.2	4.8	29.8	15.0	0.6		2.4	5.5	11.7	68.0	10.3		2.5	26.0	10.6		
7.					44.0							27.4	9.1		1.3			
8.																		
9.																	19.5	
10.			1.3								0.1							0.2
11.																		
12.																		
13.							0.3							0.5				
14.					0.5								3.9					
15.																		
16.																		
17.					24.2													
18.														1.2	0.1			
19.		0.6			0.5													
20.																		
21.											1.6	5.5						
22.											1.4							
23.											2.4							
24.																		
25.																		
26.																		
27.											2.1							
28.																		
29.																		
30.			<0.1	0.3	0.1		0.1			0.1	<0.1	3.	0.2	3.0				
31.																	0.9	
32.																0.1		
33.	2.1				<0.1													
34.																		
35.	0.7	1.2	0.1	1.5	0.5		2.1	11.7	5.4	1.1	10.4		16.5	0.6	0.5		0.9	1.7
36.						6.7												
37.																		
38.		1.5	0.2	0.1		2.3	0.3	0.6	0.5		1.3		2.9	0.2	1.2		0.1	
39.	55.4	29.2	12.6	19.1	1.6		21.1	24.0	37.7	5.9	21.9	65.1		12.9	11.7	62.9	39.0	28.9
40.																		
41.													4.4					
42.	9.9	55.9	70.8	45.5	13.4		4.6	47.8	17.3	11.8	27.4	3.4	1.5	20.6	17.5	30.2	13.0	9.1

Table 3. Number of zooplankton taxa identified from each lake in each vegetation zone

Lake	Boreal Forest			Total
	Rotifera	Cladocera	Copepoda	
1	2	3	2	7
2	2	2	2	6
3	4	3	2	9
5	5	2	3	10
6	4	3	3	10
7	5	3	0	8
8	9	4	2	15
9	4	2	2	8
10	3	1	2	6
11	3	3	2	8
12	5	2	2	9
13	2	1	2	5
14	1	1	2	4
15	3	0	3	6
16	3	1	3	7
17	2	1	3	6
56	5	2	2	9
60	1	0	1	2

Lake	Alpine Tundra			Total
	Rotifera	Cladocera	Copepoda	
18	3	0	3	6
19	1	0	3	4
20	1	1	3	5
21	3	0	3	6
58	4	2	2	8
59	4	0	2	6

Lake	Forest-Tundra			Total
	Rotifera	Cladocera	Copepoda	
4	4	0	2	6
22	3	1	3	7
23	2	1	3	6
24	2	1	2	5
25	3	2	2	7
57	2	2	3	7

plained a substantial proportion of the variation in the zooplankton–environment relationships. With forward selection and Monte Carlo permutation tests, CCA identified a minimal subset of three environmental variables that explained significant ($p \leq 0.05$) proportions of the variation in the species data. Only these variables are shown on the biplot. In descending order of significance they were chloride (Cl), silica (SiO_2) and temperature (TEMP), and together they accounted for 25% of the total variance explained by the original 16 variables. The relative contribution and significance of these three factors to CCA axes 1 and 2 was assessed by examining the canonical coefficients. Chloride contributed significantly (based on the approximate t-tests) to axis 1, and temperature and silica to axis 2.

Positioning of zooplankton species along the chloride axis highlights that the copepod *Skistodiaptomus oregonensis* (SKIS) and the cladocerans *Daphnia ambigua* (DAMB), *Polyphemus pediculus* (POLY) and *Bosmina longirostris* (BOSM) predominated in lakes with higher ionic concentrations. Along the temperature/silica axis, the copepods *Leptodiaptomus tyrrelli* (LTYR) and *Acanthocyclops denticornis* (ACAN), and the rotifers *Keratella cochlearis faluta* (KFAL), *Polyarthra vulgaris* (PVUL), *Synchaeta stylata* (SSTY), *Keratella cochlearis recurvispina* (KREC) and *Ploesoma truncatum* (PLOE) predominated in warmer lakes with higher silica concentrations.

Discussion

Zooplankton

Forty-one zooplankton taxa were identified from the lakes in the Yukon and Northwest Territories, of which the most commonly occurring (although not necessarily the most abundant) were the rotifers *Conochilus unicornis* and *Kellicottia longispina*, the cladocerans *Daphnia middendorffiana* and *Polyphemus pediculus*, and the copepods *Heterocope septentrionalis*, *Leptodiaptomus pribilofensis* and *Cyclops* spp. Of the species reported in the present study, most have been recorded previously from lakes in the Yukon and Northwest Territories (Whiteside et al., 1980; Shortreed & Stockner, 1986; Chengalath & Koste, 1989), and many have also been reported from northern British Columbia and Alaska (Chengalath & Shih, 1994; O’Brien et al., 1997).

Among the rotifers encountered were a number of widely distributed species, including *Conochilus unicornis*, *Kellicottia longispina* and *Polyarthra vulgaris*.

Less commonly reported species included *Keratella taurocephala*, which was present in lakes 4 and 18. This species has long been recognized as acidophilic (Chengalath & Koste, 1983), yet it occurred in lakes of pH 8.1 and 8.6, respectively. *Keratella cochlearis faluta* and *Keratella cochlearis recurvispina* are generally rare, and their presence in substantial proportions in lake 8 was interesting. One difficulty in assessing the zoogeography of these taxa arises from the fact that many previous papers do not distinguish between the sub-species of the *Keratella cochlearis* species complex. Therefore, the widespread reporting of *Keratella cochlearis* might be misleading, as it is possible that members of the species complex have a relatively restricted distribution compared with the overall range of the complex (Chengalath & Koste, 1983). The presence of *Brachionus plicatilis* in lake 60 was not surprising, as this species is often the dominant (or only) rotifer in lakes of salinities greater than 20 g l^{-1} (Pejler, 1995), and is also typical of alkaline waters. Lake 60 was very shallow (1.1 m) and probably freezes to the bottom in winter. *Brachionus plicatilis* can produce resting eggs (Hagiwara et al., 1995), which would ensure its survival during that time.

The cladoceran assemblage was also composed primarily of commonly occurring species. *Daphnia middendorffiana*, which was present in approximately 50% of the lakes, is reasonably tolerant of a wide chemical gradient, but is particularly susceptible to predation by planktivorous fish (Carter et al., 1980). As the presence or absence of fish was not recorded in our study, we can draw no conclusions about their influence on cladoceran distribution. *Polyphemus pediculus* and *Bosmina longirostris* were found predominantly in lakes of the boreal forest, and were tolerant of wide chemical gradients. However, both species were most common in southern lakes with high conductivity and ionic concentrations. Most of the other cladocerans occurred in low abundances in one to three lakes. Exceptions were *Daphnia galeata mendotae* (27%), which was found in lake 11, and *Daphnia obtusa* in lake 9 (12%).

The compositions of the calanoid copepod assemblages were generally characteristic of those found in high latitudes in North America (e.g. Hebert & Hann, 1986). *Acanthodiaptomus denticornis, Leptodiaptomus tyrrelli, Leptodiaptomus pribilofensis* and *Heterocope septentrionalis* are all typical of high elevations and/or the western subarctic region of Alaska and Canada (Shortreed & Stockner, 1986; Kling et al., 1992). *Acanthodiaptomus denticornis* is thought to be restricted to shallow lakes in unglaciated terrain (Lindsey et al., 1981), but was found to colonize rapidly lakes and ponds on the Klutlan moraines in the Yukon (Whiteside et al., 1980). In the present study it occurred only in lakes 8 and 9, shallow lakes in the southern Yukon. *Skistodiaptomus oregonensis* was found in lakes 1–4, the southernmost sampled in our study. This copepod has been defined as having a centre of distribution south of 60 °N (Patalas, 1990), and it is possible that the most important factor restricting its northern dispersal is an intolerance of the effects of July air temperatures below 15 °C.

The species richness of cyclopoid copepods could not be addressed in our study, as the majority of taxa were early stage copepodids that were not identifiable to species. Cyclopoids occurred in 25 of the 30 lakes, usually accounting for no more than 5% of zooplankton abundance. The exceptions were lakes 4, 19 and 58, where relative cyclopoid abundance reached 16, 12 and 10% respectively. Previous studies have revealed that the cyclopoid fauna of northwestern Canadian lakes is comparatively rich, with 12 species identified from the Yukon and 21 from the Northwest Territories (summarised in Chengalath & Shih, 1994).

Zooplankton–environment relationships

The CCA revealed that the abiotic variables chloride, temperature and silica together explained 25% of the variation in species composition. No other variable tested was statistically significant. This suggests a significant role for other local or regional processes. Local biotic factors which could be important structuring forces include competition, predation, food quality and species behaviour. Other variables, such as lake size, lake location and pH, which have been shown to be important in some other studies (e.g. Shaw & Kelso, 1992), did not explain significant portions of variation in the data. Inclusion of important biotic parameters, such as a measure of the intensity of predation by fish and other planktivorous species, would be expected to result in an explanation of more of the variability. This conclusion was also reached by Pinel-Alloul et al. (1995), who showed, for a series of lakes in southern Québec, Canada, that biotic and abiotic factors considered in concert substantially increased their explanatory power (48%) than when either was considered alone (11–31%).

In this study, a limited number of species was found to be associated with increased chloride concentrations. These included the copepod *Skisto-*

diaptomus oregonensis and the cladocerans *Daphnia ambigua, Polyphemus pediculus* and *Bosmina longirostris*. These species were common in lakes 1 and 2, which had much higher chloride concentrations (63.6 mg l^{-1} and 24.5 mg l^{-1}, respectively) than the average for boreal forest lakes (6.2 mg l^{-1}, excluding lake 60). Lakes 1 (700 μS cm^{-1}) and 2 (1500 μS cm^{-1}) also had higher than average conductivity (mean: 272 μS cm^{-1}), and these lakes contained very few rotifers. Many rotifers do not tolerate conductivities of greater than 400 μS cm^{-1} (Kling et al., 1992).

Along the temperature/silica axis, copepods (*Leptodiaptomus tyrrelli* and *Acanthocyclops denticornis*) and rotifers (*Keratella cochlearis faluta*, *Polyarthra vulgaris*, *Synchaeta stylata*, *Keratella cochlearis recurvispina* and *Ploesoma truncatum*), but no cladocerans, were associated with warmer lake temperatures and higher silica concentrations. In a previous study, the best predictor for a general south to north decline in the number of crustacean species over 22 broad geographic regions of Canada, was mean July air temperatures (Patalas, 1990), which would be correlated with water temperatures. In the northwestern geographical region, which encompassed the areas included in the current study, species richness decreased from the southern to the northern Yukon. However, an increase near the MacKenzie Delta region of the Northwest Territories was counter to the general trend, indicating that factors other than temperature played a major role in structuring these zooplankton communities. The results from the present studies supported this conclusion: even though temperature explained some of the variability observed, the greater majority of the variability was attributable to other processes.

Temperature also decreases with increasing altitude, generally resulting in impoverished lakes in alpine regions. Thus, this variable explained some of the differences between the alpine tundra lakes and those at lower altitudes. In this study, alpine tundra lakes contained a lower mean number of taxa (5.8) than the average for the lakes at lower altitude (7.2).

It is difficult to see how silica would act directly to structure zooplankton communities, and it is more informative to view this factor as it relates to diatoms, which can form a significant dietary component of zooplankton. Silica was an important factor in structuring diatom assemblages in Yukon and Northwest Territories lakes, being found in higher concentrations in boreal forest lakes (Pienitz et al., 1995). Silica concentrations affect the succession and composition of diatom assemblages, which, in turn, will influence the composition and abundance of zooplankton. It is possible that a greater variety and abundance of potential prey items in boreal forest lakes accounted for, in part, the generally greater zooplankton species richness.

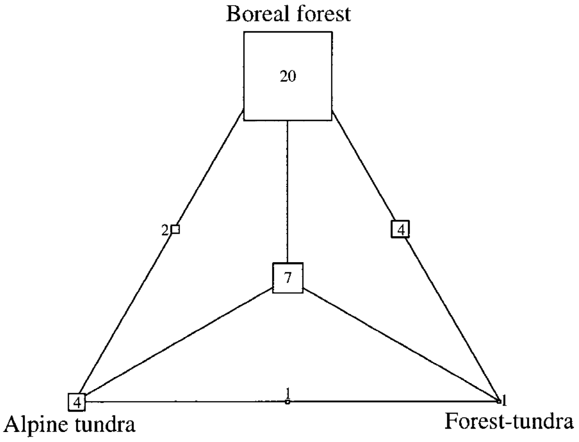

Figure 6. Distribution of zooplankton within and between each major vegetation type. The number of taxa that occur in one vegetation type is represented at the vertices of the triangle, those shared between two types are shown on the edge joining them, and those recorded from all three zones are indicated in the centre of the triangle. The sizes of the squares are scaled to reflect the number of taxa in each category.

In the present study, 25% of the variability was explained by identifiable local, abiotic variables. It is improbable that the remaining 75% of the variation could be explained by other, local variables. It is more than likely that regional factors, including broad botanical ecozones, and dispersal of zooplankton into the region, play a considerable role as well. In Figure 6 we compare the number of taxa found in the three major vegetation zones, to examine similarities between the zones. The two species from lake 60, the copepod *Leptodiaptomus connexus* and the rotifer *Brachionus plicatilis* are excluded due to the unusual chemistry and biology of this lake. Of the remaining thirty-nine species, seven (17%) were found in lakes of all three zones, four (10%) were common to the boreal forest and forest-tundra, two (5%) to the boreal forest and alpine tundra, and only one (3%) to the forest-tundra and alpine tundra. Twenty (51%) species were found only in lakes of the boreal forest, four (10%) in the alpine tundra and one (3%) in the forest-tundra. The majority of lakes sampled was in the boreal forest zone, which might account for why the greatest number of taxa was found there. Alternatively, the more favourable conditions experienced by these lakes (e.g. higher temperatures, greater volume, high chlorophyll *a* concentrations; Pienitz et al., 1997) might be responsible for the higher diversity.

Decreased species richness is common at higher latitudes, as the lakes tend to be isolated from biogeographic pools of potentially colonizing species (Starkweather, 1990). However, in the present study, latitude was not a statistically significant factor in explaining variation in the species distribution. Dispersal by zooplankton is facilitated by the production of resting stages that might become attached to the feathers and fur of birds and mammals during their south–north migratory routes (Reid & Reed, 1994). Evidence for the importance of such migrations was obtained by Patalas (1990), who analysed the patterns of zooplankton distribution in western Canada. Similarities in the fauna between the Yukon and British Columbia indicated that dispersal between these regions was likely. In contrast, faunal communities in lakes from the MacKenzie Delta region were more similar to those in northern Manitoba, linked together by migratory routes, than to those in the northern Yukon. Such processes possibly explain the poor relationship between latitude and zooplankton diversity observed in the present study.

Following an opportunity for dispersal, successful colonization depends on a species' ability to avoid predators while competing for resources such as food and space. The length of the growing season in lakes at high latitudes is curtailed by short periods of sunlight and an extended ice cover. Low temperatures and short growing seasons are believed to decrease the diversity and limit the distribution of cladocerans in the Arctic (Kling et al., 1992). To be successful colonisers at high latitudes, zooplankton must also display physiological and life history traits which are conducive to survival in the polar environment, including completion of the life cycles within a limited period and the ability to form resting stages during unfavourable conditions (Hebert & Hann, 1986). The lakes near Inuvik contained a similar suite of species, with *Daphnia middendorffiana*, *Cyclops* spp. and *Leptodiaptomus pribilofensis* being the common crustaceans. Although these lakes are ice-covered for a longer period than the southern lakes, higher productivity in the summer might enable these taxa to complete crucial parts of their life cycles in reduced time.

In conclusion, local abiotic factors were important in structuring the zooplankton communities of Yukon and Northwest Territories lakes. However, from our analysis, it appears that a range of variables not measured in this study must also have been important. For example, the interactions of zooplankton with fish and phytoplankton might act to influence species distributions, and the harshness of subarctic and arctic habitats probably contributes significantly to species composition. Those species with good dispersal capabilities, and the ability to withstand extremes in temperature, day-length and productivity, will be successful colonizers of lakes at high latitudes.

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