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Biogeography of copepods in lakes and ponds of subarctic Québec, Canada

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Abstract

We aimed to determine whether the copepod assemblages in lakes and ponds of northern Québec, Canada, were closer in composition to those found in southern Québec, or to those reported from the subarctic and arctic. Six calanoid and five cyclopoid species were identified from 37 ponds and lakes located in the region between 55° N and 59° N. Species diversity was generally low, ranging from 0 to 4 species per lake. Dominant species were *Leptodiaptomus minutus* and *Acanthocyclops vernalis*. The species assemblages showed high affinity with those found in forested regions of southern Québec. Exceptions were *Leptodiaptomus tyrrelli*, previously only recorded west of Hudson Bay, and *Hesperodiaptomus arcticus*, hitherto recorded north of 58° N. Relationships between the lakes, species, and environmental variables were explored using multivariate analysis. Lakes situated along the coast and on two offshore islands clustered together and were characterised by higher conductivity and pH than those lakes located further inland. *Leptodiaptomus tyrrelli* was common in these coastal lakes. Canonical correspondence analysis revealed statistically significant relationships between copepod distributions and conductivity, dissolved organic carbon and pH. These three variables accounted for 70% of the variation in the species' distribution.

Introduction

Sampling of copepods from lakes for biogeographical and other studies in Québec, Canada, has been restricted in the past to southern parts of the province, up to a maximum latitude of 54° N (e.g. Pinel-Alloul et al., 1979, 1990; Carter et al., 1980). Very little is known about species occurring further north, particularly in the Subarctic. A comprehensive review of Crustacea in Canadian lakes undertaken by Patalas (1990), which encompassed 22 different geographic regions, indicated a dearth of information for lakes found along the eastern shore of Hudson Bay and in the interior of the Ungava Peninsula. This locality is significant both in terms of the lakes present, which probably number in the hundreds of thousands, and the biogeographical link that the region provides between the islands of the Canadian arctic archipelago to the north and temperate North America to the south. Understanding present patterns of species' distributions is necessary to assess future shifts in biodiversity and community structure that might result from climatic changes or increased anthropogenic influences in the region. For example, Patalas (1990) hypothesised that if the mean air temperature were to increase by 3–8 °C as a result of global warming, crustacean species that now have their centres of distribution above 60° N (= 'northern' species) could disappear from the southern portion of their range, and 'southern' species would disperse further north.

We describe the copepod fauna in samples collected from ponds and lakes of subarctic Québec during the summers of 1998 and 1999. The main sampling location (30 lakes) was in the forest-tundra region near the village of Kuujjuarapik (55° 17′ N, 77° 45′ W; Fig. 1). Further samples were collected from a single lake near Rivière l'Eau Claire (56° 13′ N, 75° 29′ W), from three lakes close to the treeline near Rivière Boniface (57° 40′ N, 76° 10′ W), and two lakes well to the north of the treeline (Lac Payne: 59° 25′ N, 74° 20′ W)

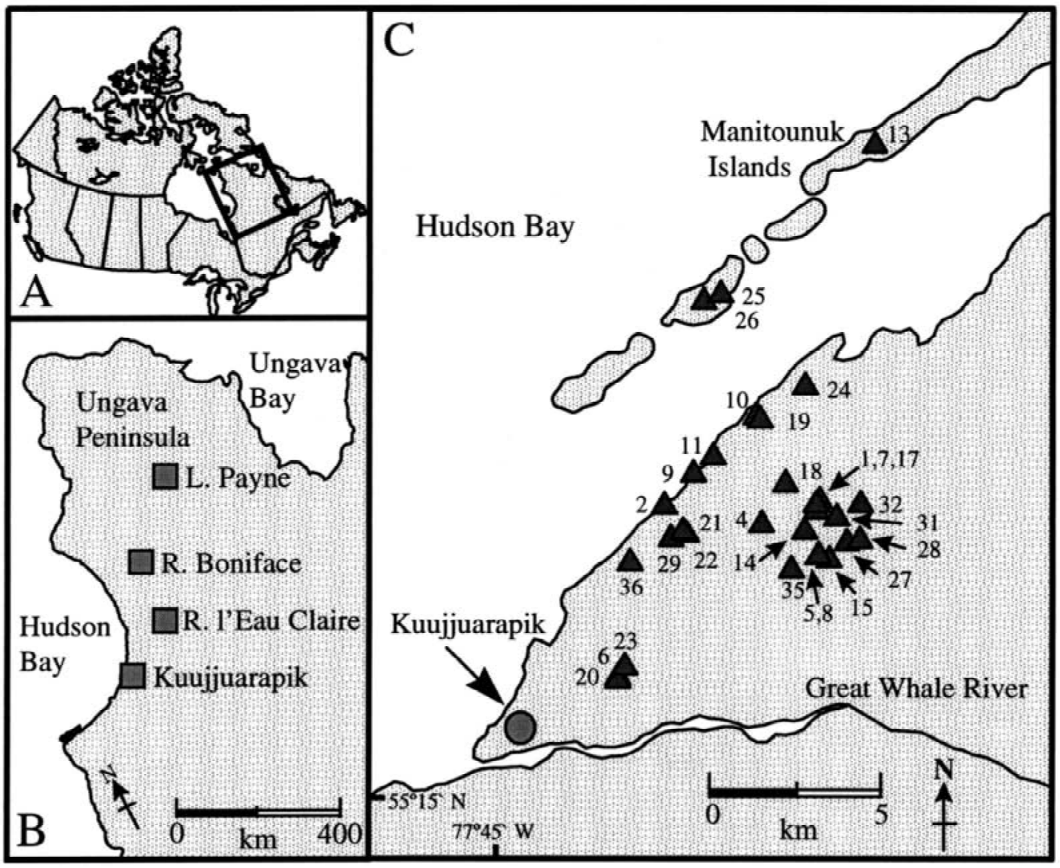

Figure 1. Locations of the lakes from which the samples were collected. Box A shows the position of the sampling area in northern Québec; Box B indicates the locations (squares) of the areas sampled: Kuujjuarapik and the Manitounuk Islands, Rivière l'Eau Claire, Rivière Boniface, and Lac Payne; and Box C the locations (triangles) and numbering system for lakes in the Kuujjuarapik region. The location of the village of Kuujjuarapik is indicated by the circle in Box C.

to assess whether species composition changed across the treeline. During the last glaciation and part of the Holocene, the region was covered by the Laurentide ice-sheet, before being deglaciated approximately 7000 years ago (Dyke & Prest, 1987). Since that time, considerable isostatic rebound (>100 m) has occurred (Allard & Tremblay, 1983); lakes close to the coast at low altitude are, therefore, quite young. We examined the distribution of copepod taxa in northern Québec, to determine whether these species assemblages had a greater affinity with those found in forested regions of southern Québec, or with those in the subarctic and arctic tundra regions to the north.

We also aimed to relate copepod distribution to several environmental variables that were measured in the ponds and lakes at the time of zooplankton sampling. Lakes of northern Québec experienced little anthropogenic influence and airborne pollution and are, therefore, appropriate to investigate fundamental species-environment relationships. Abiotic factors that may be important in structuring copepod assemblages include pH, productivity, lake size and proximity to other lakes (e.g. Dodson, 1992; Shaw & Kelso, 1992; Shurin et al., 2000). Dissolved organic carbon (DOC) was also included as a variable in the present study. DOC decreases significantly with increasing latitude in northern Québec (Fallu & Pienitz, 1999). This trend is related to the location of the treeline, because input of DOC to lakes north of the treeline is low in comparison to lakes further south. Although this variable may not directly influence copepod distribution, as this potential food source is generally not available to the animals, its coloured fraction, referred to as chromophoric dissolved organic matter (CDOM), may influence distributions by providing protection from ultra-violet radiation and changing the availability of light for photosynthesis at the base of aquatic food webs (Laurion et al., 1997; Pienitz & Vincent, 2000). CDOM concentrations also decline markedly as the treeline is crossed.

Description of study sites

No previous limnological data were available for a majority of the lakes studied, and most were unnamed. We numbered the lakes according to the order in which they were sampled. The study region encompassed two major ecoclimatic zones, from the mid-Subarctic to the low Arctic, as defined by the Ecoregions Working Group (1989). At the southern end of the study region the vegetation consists of stands of small spruce trees, predominantly *Picea mariana* (Mill.) B.S.P. and *P. glauca* (Moench) Voss, interspersed with Krummholz (trees that are dwarfed and deformed owing to severe environmental conditions, particularly wind, near the arctic and alpine treeline), and patches of lichens and mosses. The northern limit of the treeline occurred close to Rivière Boniface, and to the north arctic shrub tundra dominated. The topography of northern Québec is characterised by low relief, with a maximum elevation of *circa* 500 m. Along the coast carbonate-derived rock is dominant, while the bedrock geology inland consists of Precambrian granite interspersed with gneiss (Gouvernement du Québec, 1984).

The mean annual air temperature for the period 1959 – 1998 was −4.54 °C, though the average annual temperature for 1998 was −1.56 °C. The average July temperature for 1998 (12.20 °C) was also warmer than the 30-year average (10.20 °C). Ice usually forms on the lakes sometime during late October, and thawing is often not completed until the last weeks of June (Gouvernement du Québec, 1984). The lakes and ponds sampled in this study were small (< 0.3 km^2), irregularly-shaped basins that were between 0.5 and 4 m deep. The exception was Lac Payne, which is a large (500 km^2) and deep lake.

Materials and methods

Sample collection

Zooplankton were sampled from the ponds and lakes during June, July, and August 1998, and July 1999. Specimens were collected with a conical plankton net (mesh size: 63 μm; mouth diameter: 50 cm) that was towed horizontally through the water column from the edge of the water body. The zooplankton was preserved in 4% sugar-buffered formaldehyde (Prepas, 1978). Copepods in the samples were identified to species and counted. Identifications were made with reference to Yeatman (1959), Wilson (1959) and Pennak (1989). The number of individuals counted per sample ranged from 50 to 760. No flow meter was attached to the sampling net, so the volume of lake water filtered by the net could not be determined. Therefore, the numbers of each species of copepod present in a sample are expressed as a proportion (%) of the total sample.

Chemical analysis

Conductivity and pH were recorded *in situ* using a Hydrolab Surveyor 3®. Samples for analysis of dissolved inorganic carbon (DIC) and DOC were stored in brown glass bottles. The analyses were performed using a Shimadzu 5050® TOC analyser. Chromophoric dissolved organic matter fluorescence (F_{CDOM}) was determined by the method of Laurion et al. (1997), in which the height of the fluorescence peak at 450 nm (excitation 348 nm) was divided by the area of the Raman water peak at 400 nm, which was used as an internal standard. Chlorophyll *a* was determined by fluorometry, following the method of Nusch (1980).

Statistical analysis

We measured six chemical variables to examine their influence on the distribution of copepods in ponds and lakes of subarctic Québec. The lakes were also classified according to their maximum dimension (SIZE), where 1 = <10 m, 2 = 10–100 m, 3 = 100–500 m, and 4 = >500 m. SIZE was included as a passive variable in the statistical analysis. Passive variables do not influence the ordination axes, but are added afterwards so that their relationship with the other variables can be determined from the ordination graph. Only lakes which were located near Kuujjuarapik (including the Manitounuk Islands), and for which there was a full data set, were used in the analysis. Twenty-five lakes met these criteria, and relationships between the lakes and the seven environmental variables were examined using Principal Components Analysis (PCA; CANOCO Version 3.12®; Ter Braak, 1988, 1990). Prior to analysis, the variables were tested for skewness and, with the exception of size and pH, were ln

Table 1. Species names and codes for the copepods collected from 37 ponds and lakes in subarctic Québec. *N*: number of lakes in which each species occurred

Species	Code	*N*
Leptodiaptomus minutus	LMIN	22
Leptodiaptomus tyrrelli	LTYR	4
Hesperodiaptomus arcticus	HARC	4
Onychodiaptomus sanguineus	OSAN	1
Epischura lacustris	ELAC	6
Aglaodiaptomus spatulocrenatus	ASPA	1
Acanthocyclops vernalis	AVER	16
Acanthocyclops capillatus	ACAP	1
Diacyclops thomasi	DIAC	6
Eucyclops agilis	EAGI	3
Cyclops scutifer	CSCU	6

(x+1) transformed to approximate a normal distribution.

Canonical Correspondence Analysis (CCA) was performed on the same subset of 25 lakes to assess the influence of the environmental variables on copepod distribution. CCA is a direct gradient analysis technique where the ordination axes are constrained to be linear combinations of environmental variables. The technique remains robust, even when some environmental variables are closely correlated (Palmer, 1993). Species percentages were square-root transformed to remove the effect of the mean on the variance, and rare species were downweighted. 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 variables that could explain statistically significant ($p \leq 0.05$) proportions of variation in the copepod data. The significance of the forward selection 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

Copepods

Eleven species of copepods, comprising six calanoids and five cyclopoids, were identified from the 37 lakes examined in this study. A mean of 1.9 species per lake was recorded, with the range from 0 to 4. Samples from three lakes contained no copepods. The species codes and number of occurrences are presented in Table 1, and relative abundances of each species in Table 2. *Leptodiaptomus minutus* Lilljeborg had the highest frequency of occurrence, being found in 22 of the lakes (59%). It was the dominant species in 15 of those lakes. *Acanthocyclops vernalis* Fischer was also abundant, occurring in 16 lakes (43%). *Diacyclops thomasi* Forbes, *Epischura lacustris* Forbes, and *Cyclops scutifer* Sars were each present in 6 lakes (16%). *Leptodiaptomus tyrrelli* Poppe was common in 4 lakes (11%) along the coast (lakes 2, 10, 13 and 19). Three species were recorded only from a single lake: *Onychodiaptomus sanguineus* Turner (lake 2), *Aglaodiaptomus spatulocrenatus* Pearse (lake 30), and *Acanthocyclops capillatus* Sars (lake 10). *Eucyclops agilis* (Koch) and *Hesperodiaptomus arcticus* Marsh were found in 3 and 4 lakes, respectively.

Environment

The environmental variables recorded for each lake are summarized in Table 3. Sixteen of the lakes were less than 100 m long, with a further fourteen less than 500 m. Only seven of the lakes were greater than 500 m in length. The lakes covered a broad range of pH, from highly acidic (pH = 4.13; lake 6) to alkaline (pH = 9.42; lake 10). DIC concentrations reflected pH, with alkaline lakes generally having greater concentrations of DIC. Conductivity was consistently low, reaching a maximum of only 287 μS cm^{-1} at the coastal sites. DOC and F_{CDOM} both tended to be higher in smaller lakes. Chlorophyll *a* varied considerably, ranging from 0.3 μg l^{-l} in Lac Payne (lake 37) to 15.7 μg l^{-l} in a small pond near Rivière Boniface (lake 3).

A biplot resulting from the PCA is presented in Figure 2. The total percentage variation explained by the first two PCA axes was 80%, with eigenvalues of 0.59 and 0.21 for axis 1 and 2, respectively. The eigenvalues for the third and fourth axes were relatively low (14% and 4%, respectively), and were not considered further. The variables which were significantly correlated ($p \leq 0.05$) with axis 1 included pH, conductivity and DIC on one side of the biplot, and DOC and F_{CDOM} on the other side, whereas chlorophyll *a* was associated with axis 2. In general, similar variables clustered together, as indicated by the small angles between the arrows; e.g. those variables associated with organic carbon (DOC, F_{CDOM}). Lakes close to the coast and on the offshore islands (9, 10, 19, 25, 26) tended to aggregate away from the inland sites, implying that coastal lakes were physically and chem-

Table 2. Percentage composition of the 11 species of copepods recorded from 37 ponds and lakes in subarctic Québec. No copepods were recorded from lakes 3, 11, and 25. Species codes as per Table 1; S: species richness; *N*: number of copepods counted and identified

Lake	Relative abundance (%)											S	*N*
	LMIN	LTYR	HARC	OSAN	ELAC	AGLA	AVER	ACAP	DIAC	EAGI	CSCU		
1	98								1		1	3	83
2		31	14	7			48					4	79
3												0	0
4							100					1	120
5	100											1	237
6	40						60					2	291
7							100					1	75
8	71						29					2	456
9							99			1		2	570
10		99.9						< 0.1				2	233
11												0	0
12	45		15							40		3	614
13		80	20									2	709
14									100			1	325
15	100											1	387
16	99.4		0.1								0.5	3	201
17	99				1							2	532
18	12						88					2	344
19		99					1					2	200
20	70										30	2	131
21							100					1	50
22							100					1	342
23	25						75					2	95
24	67						33					2	112
25												0	0
26	60								40			2	485
27	100											1	103
28	5						95					2	97
29	50						50					2	213
30						100						1	540
31	35				11				50		4	4	434
32	82				3				15			3	760
33	77				8						15	3	216
34	35				11					4	50	4	179
35	60						40					2	87
36					98		2					2	62
37	95								5			2	138

ically different from those inland. These lakes were characterised by higher conductivity and pH.

Copepod-environment relationships

The influence of 7 environmental variables on the distribution of copepods in 25 lakes was assessed using CCA (Fig. 3). It should be noted that *A. spatulocrenatus* occurred only in one lake near Rivière l'Eau Claire, and so was excluded from the analysis. The first two CCA axes, with eigenvalues of 0.61 and 0.27, respectively, accounted for 31% of the variation in the species data. However, CCA axes 1 and 2 explained a high proportion (77%) of the variation

Table 3. Environmental variables measured in 37 ponds and lakes in subarctic Québec. The lakes are grouped according to maximum length: 1 = < 10 m, 2 = 10 – 100 m, 3 = 100 – 500 m, 4 = > 500 m; DIC: dissolved inorganic carbon; DOC: dissolved organic carbon; F_{CDOM}: chromophoric dissolved organic matter fluorescence; -: missing data

Lake No.	Latitude (°N)	Longitude (°W)	Size	Conductivity (μS cm^{-1})	pH	DIC (mg C l^{-1})	DOC (mg C l^{-1})	F_{CDOM} (nm^{-1})	Chl *a* (μg l^{-1})
1	55° 20.13′	77° 37.93′	1	24.6	5.60	0.80	12.50	1.04	0.52
2	55° 20.07′	77° 42.39′	1	79.0	7.35	2.84	8.80	0.50	2.11
3	57° 40.08′	76° 11.31′	1	-	-	8.04	5.78	0.35	15.70
4	55° 19.65′	77° 39.71′	1	37.4	6.57	2.73	6.16	0.77	4.77
5	55° 19.37′	77° 37.78′	1	17.8	4.58	0.59	9.06	1.11	1.86
6	55° 17.25′	77° 43.24′	1	49.0	4.13	2.04	17.70	2.05	0.73
7	55° 20.56′	77° 38.00′	1	31.0	5.79	0.87	17.50	2.19	2.61
8	55° 19.38′	77° 37.77′	1	19.2	4.85	0.57	8.12	0.89	1.97
9	55° 20.60′	77° 41.32′	2	208.0	7.28	16.80	5.37	0.37	2.25
10	55° 21.50′	77° 39.53′	2	153.0	9.42	16.90	14.60	0.15	3.06
11	55° 20.89′	77° 40.80′	2	182.0	9.39	15.80	2.88	0.21	4.28
12	57° 45.20′	76° 11.16′	2	-	-	1.51	12.80	1.05	5.99
13	55° 26.07′	77° 36.78′	2	287.0	9.15	28.70	5.92	0.22	0.83
14	55° 19.76′	77° 38.17′	2	36.7	6.25	2.58	5.02	0.51	0.63
15	55° 19.32′	77° 37.48′	2	36.2	5.90	1.55	8.81	0.71	2.40
16	59° 25.40′	74° 20.89′	2	-	-	1.35	2.75	0.15	2.29
17	55° 20.00′	77° 37.93′	3	31.0	7.50	-	6.85	0.32	2.25
18	55° 20.60′	77° 14.29′	3	56.0	6.71	-	-	0.51	1.29
19	55° 21.55′	77° 39.65′	3	118.0	9.18	12.1	6.38	0.16	2.26
20	55° 17.19′	77° 43.19′	3	34.5	5.20	-	5.40	0.29	1.60
21	55° 19.62′	77° 41.55′	3	106.0	7.84	9.89	3.66	0.28	0.59
22	55° 19.54′	77° 41.48′	3	105.0	7.73	10.10	3.37	0.27	0.64
23	55° 17.38′	77° 43.15′	3	56.1	6.04	3.82	9.75	0.90	1.71
24	55° 22.05′	77° 38.32′	3	205	8.16	23.10	3.91	0.30	0.68
25	55° 23.54′	77° 40.86′	3	104.0	8.80	19.90	3.84	0.06	1.97
26	55° 23.43′	77° 41.26′	3	115.0	8.78	8.24	4.18	0.10	2.00
27	55° 19.60′	77° 37.00′	3	22.0	5.40	0.83	5.28	0.40	5.42
28	55° 19.65′	77° 36.64′	3	33.5	6.35	1.55	9.95	0.90	3.00
29	55° 19.56′	77° 41.87′	3	41.7	8.03	2.74	7.03	0.24	1.33
30	56° 13.66′	75° 29.37′	3	-	-	-	-	-	-
31	55° 20.05′	77° 37.44′	4	37.0	7.00	2.40	4.70	0.24	0.60
32	55° 20.19′	77° 41.26′	4	40.6	7.00	3.00	-	0.16	1.80
33	57° 45.27′	76° 10.25′	4	-	-	-	7.69	0.60	4.70
34	57° 44.06′	76° 08.89′	4	20.0	6.90	1.80	2.50	0.15	1.43
35	55° 19.14′	77° 38.50′	4	21.9	5.60	1.24	5.54	0.42	5.82
36	55° 19.15′	77° 42.98′	4	138.0	8.08	12.50	5.77	0.24	0.96
37	59° 28.00′	74° 20.00′	4	-	-	0.84	1.45	0.02	0.30
Minimum	55° 17.19′	74° 20.00′		17.8	4.13	0.57	2.50	0.02	0.30
Maximum	59° 28.00′	77° 43.24′		287.0	9.42	28.70	17.70	2.19	15.70
Median				41.7	7.00	2.84	5.92	0.33	1.97
Mean				78.9	6.98	7.39	7.31	0.52	2.56

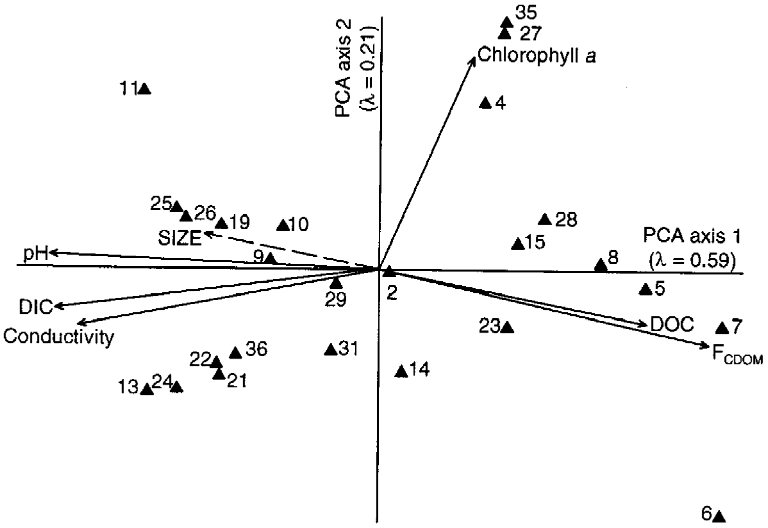

Figure 2. PCA of the 7 environmental variables recorded from 25 lakes in the Kuujjuarapik region, for which complete data sets were available. Lake SIZE was included as a passive variable and is represented by a broken line.

in the species-environment relationship. The species-environment correlations for CCA axis 1 (0.84) and axis 2 (0.63) were high, indicating a reasonably strong relationship between the copepods and the environmental variables. With forward selection and Monte Carlo permutation tests CCA identified a subset of three environmental variables that explained significant ($p \leq 0.05$) proportions of the variation in the species data. These were conductivity, DIC, and pH, which accounted for 70% of the variation in copepod distribution. The positions of the copepod species on the biplot highlights that *L. tyrrelli*, *O. sanguineus* and *H. arcticus* predominated in lakes with higher conductivity.

Discussion

The six species of calanoids and five species of cyclopoids identified from the 37 sites have all been recorded previously in Canadian lakes, and most have a broad distribution (e.g. Pinel-Alloul et al., 1979, 1990; Carter et al., 1980; Taylor et al., 1987; Chengalath & Shih, 1994; Shih & Chengalath, 1994). *Leptodiaptomus minutus* was the dominant calanoid copepod recorded from the lakes (59%), often co-occurring with *A. vernalis* or *D. thomasi*. *Leptodiaptomus minutus* is dispersed widely in eastern North America, including the high Arctic, and its distribution covers a latitudinal range of at least 30°. It is a cold-water species that is widely tolerant of environmental conditions (Carter et al., 1980; Pinel-Alloul et al., 1990). In our study, *L. minutus* occurred in lakes of all sizes and chemical conditions.

Species lists have been compiled for lakes in southern Québec (Pinel-Alloul et al., 1979, 1990), and for ponds near subarctic Churchill, Manitoba (58° 47′ N, 94° 11′ W), on the western side of Hudson Bay (Hebert & Hann, 1986). We compared the copepod assemblages found in northern Québec to those reported from the above localities, in order to determine the extent of species affinity between the regions (Fig. 4). Of the 11 species identified in the present study, two were shared amongst all three regions: *L. minutus* and *A. vernalis*. A further two species, *L. tyrrelli* and *H. arcticus*, were common to western Hudson Bay and northern Québec, but were not recorded in southern Québec. The remaining seven species were found in southern and northern Québec, but not reported from western Hudson Bay. No species were restricted in distribution to the ponds and lakes in our study, whereas several copepods were reported only from western Hudson Bay (4 species) or southern Québec (9 species); no species were common to those two sites alone.

Hudson Bay probably provides an effective geographical barrier to the dispersal of many species. *Leptodiaptomus tyrrelli* has not been recorded from southern Québec (Pinel-Alloul et al., 1979, 1990), or the provinces of Atlantic Canada (Carter et al., 1980), yet is noted briefly by Wilson (1959) as occurring as far east as Labrador. The species is common in

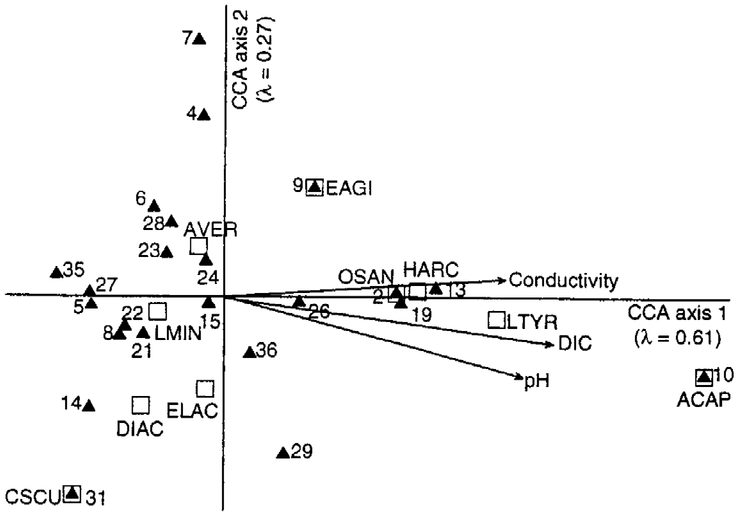

Figure 3. CCA showing the relationship between copepods (open squares), 25 lakes (closed triangles), and the three statistically significant environmental variables (arrows). Species codes as per Table 1. *Aglaodiaptomus spatulocrenatus* was not included in the analysis. Lake scores are plotted as linear combinations of the environmental variables.

Figure 4. Regional distribution of copepods as determined from studies in northern Québec (this study), southern Québec (Pinel-Alloul et al., 1979) and western Hudson Bay (Hebert & Hann, 1986). Species that occur in one data set only are listed at the vertices of the triangle, those shared between two regions are listed on the edge joining them, and those species recorded in all three studies are presented in the centre of the triangle.

western Canada, including British Columbia and Alberta (Chengalath & Shih, 1994; Shih & Chengalath, 1994), and the Yukon Territory (Swadling et al., 2000). The presence of *L. tyrrelli* in coastal lakes of northern Québec might be a result of either vicariance or recent dispersal. Most of the Ungava Peninsula, including the eastern Hudson Bay coast, was glaciated until about 7000 years ago (Lauriol & Gray, 1987). Following retreat of the ice cap there was invasion by marine waters of the Tyrrell Sea. Strong isostatic rebound of the land resulted in isolation of freshwater basins along the coast near Kuujjuarapik that are less than 5000 years old (Saulnier-Talbot & Pienitz, in press). Glacial refuges may have occurred somewhere on the peninsula, but whether this is actually so is unknown. Dispersal of resting stages of copepods via adherence to the feathers, fur, or legs of vertebrates, or via a human agent, is a method whereby freshwater species can colonise new areas (e.g. Reid & Reed, 1994). South-north migrations of birds and mammals are more common than west-east migrations, yet it appears that *L. tyrrelli* has not dispersed from lakes to the north or south of Kuujjuarapik.

Hesperodiaptomus arcticus differed from *L. tyrrelli* in that it was found in many areas to the north of our study region (Hebert & Hann, 1986). Thus, it is more likely to be in the path of south-north migratory routes of birds and mammals, and may have colonised the lakes in our study via passive dispersal. *Hesperodiaptomus arcticus* co-occurred with either *L. tyrrelli* or *L. minutus* in four lakes. In one of those lakes a third diaptomid, *O. sanguineus,* was also present in a sample taken in mid-June (lake 2). Niche separation by size, or temporal and spatial isolation during the life cycles, is common in diaptomids (Pedersen & Litt, 1976). Lake 2 was very small (< 10 m) and shallow (< 0.5 m), and was sampled twice during the sampling season. In the second sample (late August), *O. sanguinensis* was no longer present, although numbers of *H. arcticus* and *L. tyrrelli* remained high. This suggests that there was a temporal separation in the timing of the life cycles, although regular seasonal sampling is needed to confirm this observation.

The CCA revealed that conductivity, DIC and pH explained statistically significant amounts of variation in the data. The strongest relationship was the occurrence of *L. tyrrelli* in coastal lakes that were high in pH and conductivity. High pH and DIC in those lakes probably resulted from dissolution of the carbonate bedrock that formed the basins. Conductivity was increased due to salts carried in seaspray from nearby Hudson Bay. Those variables associated with DOM, specifically DOC and CDOM, did not contribute significantly to the species distributions, as determined by CCA. Similarly, chlorophyll *a* concentration was not significant in this study, although productivity has been shown to be an important factor in some regions (Dodson, 1992).

Only a limited number of environmental variables was measured in this study and it is unlikely that pH, DIC and conductivity alone accounted for the observed distributions. Other determinants, such as lake depth and proximity to nearby lakes, have been shown to be important in structuring zooplankton assemblages (e.g. Dodson, 1992; Shaw & Kelso, 1992). Fish and invertebrate predators can influence both the size of individuals and the species composition of zooplankton in lakes (Brooks & Dodson, 1965; Pinel-Alloul et al., 1995). Fish were observed in several of the larger lakes in this study, and *Chaoborus* sp. was common in many others. We perceived a relationship between the presence of predators and the extent of pigmentation in the copepods, although we did not quantify this. Lakes with visual predators (fish) predominantly contained small copepods that lacked pigmentation. An exception was the presence of *E. lacustris* in five of the seven largest lakes. This large copepod probably preys on smaller species such as *L. minutus* and *D. thomasi*. In lakes where *Chaoborus* sp. (a non-visual predator) was common, the copepods were often big and brightly coloured, and their pigments are believed to provide photo-protection against UV radiation (Hairston, 1979). There was no obvious correspondence between extent of pigmentation and CDOM concentration (a measure of water colour). Thus, we suggest that the type of predators present in a lake had more direct influence on copepod colouration than the degree to which UV penetrated into the lakes.

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