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ORIGINAL PAPER

# Crustacean zooplankton in lakes of the far north of Ontario, Canada

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**Abstract**

The far north of Ontario, Canada, is a region that is very vulnerable to future change due to climate warming and resource extraction. Despite its vast size (~ 450,000 $km^2$) and large numbers of lakes (> 700,000), there has been very little study of aquatic ecosystems in this remote area. To address this lack of limnological data, forty-one northern Ontario lakes spanning two physiographic regions, the Hudson Bay Lowlands and the Canadian Shield, were sampled during 2012 for crustacean zooplankton and water chemistry. These sub-Arctic lakes support diverse crustacean plankton communities with species richness similar to the richness of lakes in central and northeastern Ontario. While some of the species collected appear to be at the northern limit of their distributions, most relatively common Ontario species occurred throughout the 2012 study area. The physico-chemical characteristics showing relationships with species richness and relative abundances were variables associated with lake morphometry, ionic strength and nutrient status. There were differences in community richness and composition between Lowlands and Shield lakes; however, these differences do not seem attributable to biogeographical influences on species occurrences. Rather, the lower species richness and differences in community composition in Lowlands lakes relative to Shield lakes appear to be largely related to lake morphometry. The shallower and generally smaller Lowlands lakes provide much less habitat diversity, i.e. niche space, than the larger, deeper Shield lakes, leading to simpler communities.

**Keywords** Crustacean zooplankton · Lakes · Hudson Bay Lowlands · Canadian Shield

## Introduction

The far north of Ontario, Canada (> 50°N latitude) contains over 700,000 lakes and is one of the largest relatively undisturbed areas on earth. However, change is coming to this vast (~ 450,000 $km^2$) region. The discovery of massive metal deposits in the "Ring of Fire" (ROF) area of the far north has stimulated great interest for future large-scale mining development (Hjartarson et al. 2014). As well, the most northerly portions of Ontario are expected to show the greatest warming due to climate change (Colombo et al. 2007). Some aquatic ecosystems in northern Ontario are already showing biological responses to a warming climate, as demonstrated by paleolimnological studies using diatoms (Rühland et al. 2013) and cladocerans (Jeziorski et al. 2015).

Basic ecological research to develop our scientific understanding of the nature and sensitivity of aquatic ecosystems is critically needed for the ROF region and more broadly throughout the north. Here, we provide an assessment of crustacean zooplankton communities in northern lakes spanning two physiographic regions (Hudson Bay Lowlands, Canadian Shield) that encompass two ecozones (Hudson Plains and Boreal Shield, respectively). These physiographic regions (and ecozones) differ greatly in their overall characteristics. The Shield is a glacially scoured landscape defined by its hard, weathering resistant Precambrian bedrock, typically with thin soil cover. Relief is often high and lakes are often deep. The Lowlands are underlain by much softer Paleozoic and Proterozoic sedimentary bedrock, often covered by substantial deposits of glacial till and peat. The low-relief Lowlands slope very gradually to the coasts of Hudson and James bays, and the flat terrain and poor drainage have resulted in the largest

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wetland complex in North America. Lakes are typically shallow and small, but may sometimes be quite large.

Given the dramatic landscape differences between these regions, it is likely that lake zooplankton communities also show differences; however, the nature of crustacean zooplankton communities in lakes of the far north of Ontario is largely unknown. To date, only two studies have examined patterns of zooplankton distribution and abundance in this vast, remote region. Keller and Pitblado (1989) examined zooplankton communities in 39 lakes distributed across the Arctic watershed of Ontario as part of their large-scale Ontario surveys. Paterson et al. (2014) sampled 17 lakes in the Hawley Lake/Sutton River region of the Hudson Bay Lowlands near the Hudson Bay coast. In order to advance our understanding of northern lakes, the present analysis builds on previous work by examining zooplankton communities in 41 remote lakes of the far north of Ontario, and comparing these to zooplankton communities in other areas of the province.

Zooplankton are a very valuable component of aquatic ecosystems because they occupy central positions in aquatic food webs. They play multiple roles within the energy flow system of a lake (i.e. predators as well as phytoplankton grazers; Thorp and Covich 1991), transferring energy to higher level organisms. Also, the relationships between many zooplankton species and lake characteristics have been relatively well studied (e.g. Keller and Pitblado 1984; Pinel-Alloul et al. 1990; Thorp and Covich 1991; Pinel-Alloul et al. 2013; Palmer and Yan 2013), which makes them valuable as indicator organisms for assessing environmental change (Valois et al. 2010; Jeppesen et al. 2011). Zooplankton species occurrence depends on four general factors: (1) zoogeographical region (2) physical and chemical requirements of the species (3) availability of compatible food and (4) presence of predators and competitors (Leavitt et al. 1989; Thorp and Covich 1991; Hessen et al. 2006).

Examining patterns in communities generally provides a more robust means to characterize a habitat than do assessments of single species or univariate metrics (Sprules 1977; Yan et al. 1996). Thus, we employed multivariate analyses to examine relationships between zooplankton assemblages, water chemistry and lake physical characteristics across our 41 study lakes. We addressed the following questions: (1) what relationships exist between zooplankton species richness, zooplankton community composition, and lake physico-chemical characteristics in the far north of Ontario? (2) Are there differences in the crustacean zooplankton communities of lakes in the Hudson Bay Lowlands and the Canadian Shield? (3) Are zooplankton communities in the far north of Ontario different than communities in other areas of the province?

## Study sites

In July 2012, Laurentian and Queen's Universities collaborated to sample 29 lakes across a broad, very remote section of northern Ontario including the ROF area (Fig. 1). Within the study area, the boundary between the Hudson Bay Lowlands and the Canadian Shield physiographic regions was nominally defined using the existing Ontario Ministry of Natural Resources and Forestry (MNRF) map boundary, such that there were 14 Shield lakes and 15 lakes on the Lowlands. Also in the summer of 2012, the MNRF Broad Scale Monitoring Program (BSM) sampled zooplankton from 12 lakes (8 Shield, 4 Lowlands) located throughout a broad region of northern Ontario, which were added to the data set (Fig. 1). In total, 41 lakes were sampled, 22 on the Shield and 19 on the Lowlands. These included a wide range of lake sizes and depths and water chemistry characteristics (Table 1). Consistent with a previous study of these lakes (MacLeod et al. 2017), Shield lakes generally had greater area, depth, and ionic strength, but lower dissolved organic carbon (DOC) and total phosphorus (TP) concentrations than Lowlands lakes ($p < 0.01$; Mann–Whitney $U$ test, Table 1).

## Methods

### Sampling

The Laurentian/Queen's survey and the MNRF-BSM survey used the same sampling techniques. At a central location on each lake, depth and transparency (Secchi depth) were determined using a sonar depth sounder and Secchi disc, respectively. A water sample was obtained from each lake using a large, weighted plastic bottle (4-L) with a restricted inlet that allowed water to enter the sampler at a slow rate. The device was rinsed with lake water before being lowered to the Secchi depth or 1 m off bottom (which ever was shallower) and then slowly retrieved allowing the bottle to fill with water evenly across all depths. Chemistry samples were forwarded to the Dorset Environmental Science Centre of the Ontario Ministry of the Environment and Climate Change for analysis using methods described in MOEE (1983).

A single zooplankton haul at a central location was collected using a standard protocol for all lakes. Where depths exceeded 5 m, a vertical haul was performed from 1 m off bottom to the surface, while in shallower lakes a 4 m long horizontal haul was performed with the net completely submerged, but not contacting the bottom. Nets were non-metered and composed of 80 µm polyester mesh

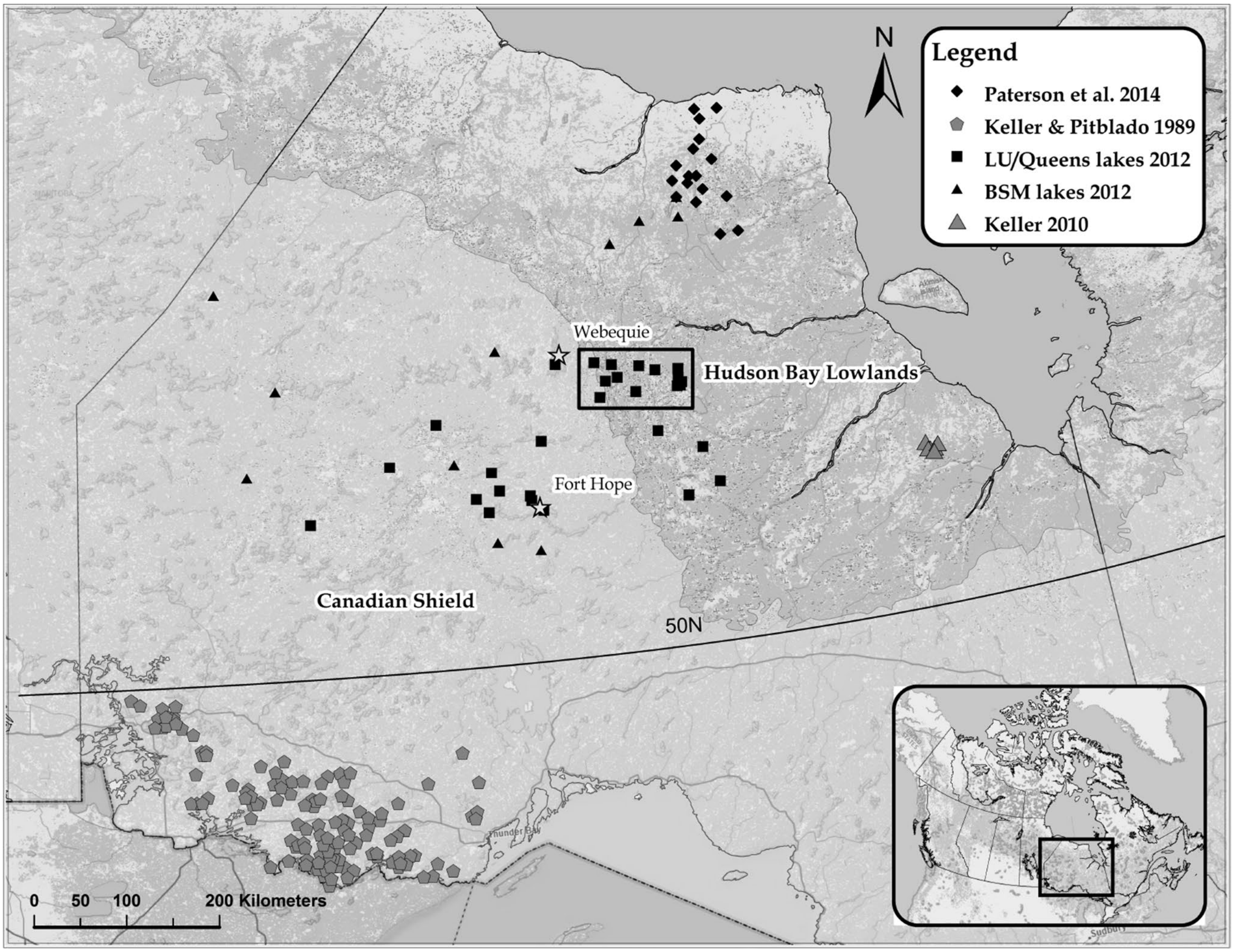


**Fig. 1** Lakes sampled in 2012 by Laurentian and Queen's Universities (LU/Queen's lakes 2012) and the MNRF BSM survey (BSM lakes 2012). The central rectangle (with inset) includes lakes in the 'Ring of Fire' area. Locations of other northern Ontario lake surveys used for comparison (Shield lakes south of 50°N latitude from the broad Ontario surveys of Keller and Pitblado (1989); Lowlands lakes north of 54°N from Paterson et al. (2014) and south of 52°N from Keller (2010), unpublished data) are also shown

(62 µm for the BSM survey) with a 30 cm diameter mouth. Both these mesh sizes retain all the species considered here. Samples from the Laurentian/Queen's survey were preserved in the field with 15% formalin solution while the BSM survey used 85% ethanol as a field preservative. Because of the differential shrinkage caused by these different preservatives, length–weight ratios could not be used to generate comparable biomass estimates. Therefore, only species counts were used.

## Zooplankton counting and identification

Crustacean zooplankton were counted using the methods outlined in Paterson et al. (2014). Briefly, samples were split using a Folsom plankton splitter. Individual species target counts of 45–60 for adults and 15–35 for juvenile copepods (calanoid or cyclopoid nauplii or copepodids) were obtained, with a minimum total count of 240 individual zooplankton to ensure that no one species comprised more than 20% of the total count. The major keys used for identification were Brooks (1957, 1959), Wilson (1959), Yeatman (1959), Smith and Fernando (1978), DeMelo and Hebert (1994), Hebert (1995), and Taylor et al. (2002).

When zooplankton data were compared to other surveys some taxa had to be combined to account for differences in taxonomy over the period covered by the surveys. Changes in taxonomy have occurred for some daphnids (Dodson 1981; Colbourne and Hebert 1996; Hebert and Finston 1997), bosminids (DeMelo and Hebert 1994; Korinek et al. 1997; Taylor et al. 2002), cyclopoids (Dussart and Fernando 1990), *Diaphanosoma* (Korinek 1981), and *Holopedium* (Rowe 2000). Accordingly, *Daphnia catawba* and *Daphnia pulicaria* were combined with

**Table 1** Descriptive statistics for lake chemistry and morphometry for the 2012 survey lakes ($n = 41$, 19 Lowlands and 22 Shield)

| Variable | Region | Mean | Median | Max | Min | SD | Coefficient of variation |
|---|---|---|---|---|---|---|---|
| Lake depth (m)* | Lowland | 3.56 | 1.90 | 16.00 | 1.20 | 4.32 | 1.21 |
| | Shield | 8.09 | 6.10 | 30.10 | 1.90 | 6.52 | 0.81 |
| Lake area (ha)* | Lowland | 1047.77 | 498.78 | 5061.70 | 35.78 | 1198.72 | 1.14 |
| | Shield | 4990.10 | 1678.35 | 28100.00 | 309.00 | 6886.05 | 1.38 |
| Alkalinity (mg $L^{-1}$ $CaCO_3$)* | Lowland | 28.01 | 23.20 | 68.00 | 0.95 | 17.93 | 0.64 |
| | Shield | 46.16 | 41.35 | 110.00 | 18.30 | 22.51 | 0.49 |
| pH | Lowland | 7.42 | 7.43 | 7.93 | 6.94 | – | – |
| | Shield | 7.82 | 7.79 | 8.25 | 7.41 | – | – |
| Conductivity (μs $cm^{-1}$)* | Lowland | 61.73 | 51.00 | 137.00 | 21.20 | 34.02 | 0.55 |
| | Shield | 99.45 | 86.60 | 232.00 | 44.00 | 46.09 | 0.46 |
| Ca (mg $L^{-1}$)* | Lowland | 10.14 | 7.80 | 28.30 | 3.14 | 6.59 | 0.65 |
| | Shield | 14.65 | 12.65 | 34.90 | 5.44 | 7.29 | 0.50 |
| DOC (mg $L^{-1}$)* | Lowland | 13.50 | 13.30 | 18.60 | 7.80 | 2.83 | 0.21 |
| | Shield | 10.68 | 11.45 | 15.40 | 4.90 | 2.70 | 0.25 |
| Cl (mg $L^{-1}$) | Lowland | 0.56 | 0.22 | 2.45 | 0.11 | 0.70 | 1.25 |
| | Shield | 0.29 | 0.24 | 1.11 | 0.10 | 0.20 | 0.71 |
| Mg (mg $L^{-1}$)* | Lowland | 1.44 | 1.27 | 2.81 | 0.48 | 0.72 | 0.50 |
| | Shield | 3.07 | 2.63 | 7.92 | 1.16 | 1.63 | 0.53 |
| K (mg $L^{-1}$)* | Lowland | 0.16 | 0.15 | 0.26 | 0.09 | 0.04 | 0.26 |
| | Shield | 0.48 | 0.40 | 1.04 | 0.18 | 0.20 | 0.42 |
| Si (mg $L^{-1}$)* | Lowland | 0.33 | 0.26 | 1.46 | 0.02 | 0.34 | 1.03 |
| | Shield | 1.02 | 0.92 | 2.00 | 0.12 | 0.49 | 0.48 |
| Na (mg $L^{-1}$) | Lowland | 0.78 | 0.53 | 2.37 | 0.32 | 0.56 | 0.72 |
| | Shield | 0.60 | 0.52 | 1.45 | 0.41 | 0.23 | 0.38 |
| $SO_4$ (mg $L^{-1}$)* | Lowland | 0.17 | 0.15 | 0.35 | 0.05 | 0.08 | 0.45 |
| | Shield | 0.54 | 0.43 | 1.65 | 0.10 | 0.36 | 0.67 |
| Fe (μg $L^{-1}$)* | Lowland | 199.47 | 140.00 | 510.00 | 60.00 | 145.51 | 0.73 |
| | Shield | 91.64 | 72.00 | 330.00 | 10.00 | 73.95 | 0.81 |
| True colour (TCU)* | Lowland | 86.02 | 83.00 | 155.00 | 31.00 | 33.25 | 0.39 |
| | Shield | 45.01 | 45.70 | 93.20 | 5.20 | 23.87 | 0.53 |
| Total N (μg $L^{-1}$) | Lowland | 391.05 | 384.00 | 513.00 | 297.00 | 61.78 | 0.16 |
| | Shield | 353.45 | 370.50 | 472.00 | 163.00 | 71.17 | 0.20 |
| Inorganic N (μg $L^{-1}$) | Lowland | 17.89 | 18.00 | 28.00 | 4.00 | 6.54 | 0.37 |
| | Shield | 22.09 | 20.00 | 68.00 | 12.00 | 11.73 | 0.53 |
| Total P (μg $L^{-1}$)* | Lowland | 15.36 | 15.60 | 25.20 | 8.00 | 5.18 | 0.34 |
| | Shield | 9.95 | 9.50 | 18.20 | 3.60 | 3.19 | 0.32 |

*significant ($p < 0.01$) difference based on a Mann–Whitney $U$ test

*Daphnia pulex* as *D. pulex* (complex), *Daphnia* sp. were divided among the other *Daphnia* species proportionally according to their abundance, *Bosmina freyi* and *Bosmina longirostris* were combined with *Bosmina liederi* as *Bosmina* sp., *Diaphanosoma brachyurum* and *Diaphanosoma birgei* were combined as *D. birgei*, *Tropocyclops prasinus mexicanus* and *Tropocyclops extensus* were combined as *T. extensus, Eucyclops speratus* was relabelled as *E. elegans,* and *Holopedium gibberum* and *Holopedium glacialis* were combined as *H. glacialis*.

## Statistical analyses

R version 3.0.2 was used as the primary software for statistical analyses. Zooplankton abundance data for 2012 were first thinned by removing juvenile life stages and rare species (species which did not make up a minimum of 1% of the overall sample in at least one lake). Twenty-one species remained to be included in the ordination analysis. The data were then converted to percentages and square root transformed to reduce the effects of very abundant taxa.

Detrended Correspondence Analysis (DCA) was run using the Vegan add-on package for R. Axis lengths of DCA1 and DCA2 were 2.1 and 2.0, respectively, i.e. both < 3.0, indicating that linear ordination techniques (rather than unimodal) were suitable (Lepš and Šmilauer 2003). Redundancy analysis (RDA) was chosen for its ability to explore relationships between the species composition of lakes while including environmental variables as constraints to the ordination axes. The following physical and chemistry variables were included in the RDA: lake depth, lake area, lake length, dissolved inorganic carbon (DIC), DOC, Ca, Cl, Mg, K, Si, Na, $SO_4$, Fe, alkalinity, pH, true colour, total nitrogen (TN), inorganic nitrogen (IN), TP, and conductivity. Variables were $\log^{10}$ transformed prior to analysis in order to achieve a near-normal distribution. A forward selection step was used with the RDA to reduce the number of co-linear constraining variables. Monte Carlo permutation tests (1000 permutations) were run to determine the significance of each forward selected variable and to test the significance of each ordination axis defined by the forward selected constraining variables. Vectors of variables which were not included in the forward selection step were added to the plots post-analysis using permutational fitting to provide a visual reference of their relationship to the other data (i.e. they were included as passive samples).

Analysis of similarities (ANOSIM) is also a useful technique for examining spatial differences (Oliver and Beattie 1996; Chapman and Underwood 1999). It was used here to test for statistical differences in zooplankton assemblage composition between Shield and Lowlands lakes in the 2012 survey. Mann–Whitney *U* tests were used to identify where differences existed for the relative abundances of individual species between the Shield and Lowlands lake groups.

## Results

Thirty-four species of crustacean zooplankton were identified in the 41 lakes from the 2012 survey. The most common species were *B. freyi, Chydorus sphaericus, Epischura lacustris, Daphnia mendotae, H. glacialis, Diacyclops bicuspidatus thomasi, D. birgei, Leptodiaptomus minutus* and *Skistodiaptomus oregonensis*, all of which occurred in more than 50% of the surveyed lakes. Species occurrence (%) by physiographic region is listed in Table 2, and occurrence is compared to other Ontario lake surveys in Table 3.

Species richness in individual lakes ranged from 6 to 16 and was significantly (positively) correlated (Spearman rank correlation $p < 0.01$) with lake depth ($r = 0.427$), lake area ($r = 0.356$), lake length ($r = 0.545$), Ca ($r = 0.493$), DIC ($r = 0.480$), Mg ($r = 0.472$), Si ($r = 0.550$) and conductivity ($r = 0.489$). Average species richness in the Lowlands lakes was 9.1, which was lower than the average richness (11.6) in the Shield lakes (Mann–Whitney *U* test $p < 0.01$).

RDA ordination characterized general patterns and identified the primary sources of environmental and biological variation among the 41 lakes (% of variation explained: RDA1 = 8.4%, RDA2 = 5.8%, RDA3 = 4.7%). Figures 2 and 3 show the first two axes from the forward selection RDAs for species scores and lake scores, respectively. The species with the strongest positive loadings on RDA1 were *D.b.thomasi* (0.656), *Daphnia longiremis* (0.518), *D. mendotae* (0.500), and *Eubosmina longispina* (0.488). The species with the strongest negative loadings on RDA1 were *C. sphaericus* (− 0.715) and *T. extensus* (− 0.457). The only species with a strong positive loading on RDA2 was *C. sphaericus* (0.689), while the only species with a strong negative loading on RDA2 was *Ceriodaphnia* sp. (− 0.476). The only species with a strong positive loading on RDA3 was *Alona* sp. (0.495), while the only species with a strong negative loading on RDA3 was *D. longiremis* (− 0.543).

Considering lake scores (Fig. 3), lakes in the upper left quadrant were generally Lowlands lakes from the ROF area. They were characterized by higher nutrients (TN, TP), DOC, and colour, lower ionic strength, shorter lake length, smaller area and lower depth. *C. sphaericus* had the highest relative abundance among species in these lakes (Fig. 2). Lakes in the bottom right quadrant were Shield lakes from the center of the study area (Fig. 3). They were associated with comparatively high ionic strength (Ca, Mg, K), conductivity, alkalinity, pH and greater lake area/depth. *D. longiremis, Daphnia retrocurva* and *Mesocyclops edax* had the highest relative abundance among species in these lakes (Fig. 2). Lakes in the top right quadrant were scattered, but included most lakes closest to Hudson Bay. They were characterized by comparatively high Cl concentrations. *E. longispina, D. mendotae* and *D.b. thomasi* had the highest relative abundances in these lakes (Fig. 2). The lakes in the bottom left quadrant were also scattered geographically. They had higher Fe and IN, with lower Cl concentrations. *T. extensus, B. freyi,* and *Ceriodaphnia* sp. were important species in lakes from this quadrant (Fig. 2).

ANOSIM showed a significant ($p < 0.01$) overall difference in species assemblage composition at a regional scale between Shield and Lowlands lakes. On average, Shield lakes had higher relative abundances of *D. longiremis*, *S. oregonensis*, *M. edax*, and *T. extensus*, and lower relative abundances of *C. sphaericus* than Lowlands lakes ($p < 0.05$).

## Discussion

The study lakes supported a diverse assemblage of crustacean zooplankton species. Species richness in our survey lakes (6–16 species per lake, 34 total) was similar to that

**Table 2** Relative occurrence of crustacean zooplankton species in the 2012 survey lakes ($n = 41$, 22 Shield, 19 Lowlands)

| Species | Abbreviation | % of all lakes | % of Shield lakes | % of Lowlands lakes |
|---|---|---|---|---|
| *Bosmina freyi* | B frey | 100.0 | 100.0 | 100.0 |
| *Chydorus sphaericus* | Ch sphaer | 92.7 | 86.4 | 100.0 |
| *Epischura lacustris* | Ep lac cp | 85.4 | 77.3 | 94.7 |
| *Daphnia mendotae* | Da m | 78.0 | 90.9 | 63.2 |
| *Holopedium glacialis* | Hol glac | 78.0 | 86.4 | 68.4 |
| *Diacyclops bicuspidatus thomasi* | Cy bi thom | 78.0 | 90.9 | 63.2 |
| *Diaphanosoma birgei* | Dia birg | 73.2 | 81.8 | 63.2 |
| *Leptodiaptomus minutus* | Lepto minu | 61.0 | 45.5 | 78.9 |
| *Skistodiaptomus oregonensis* | Skis oreg | 56.1 | 77.3 | 31.6 |
| *Ceriodaphnia* sp. | Cerio sp | 36.6 | 45.5 | 26.3 |
| *Tropocyclops extensus* | Trop ext | 36.6 | 50.0 | 21.1 |
| *Daphnia longiremis* | Da long | 31.7 | 59.1 | 0.0 |
| *Daphnia retrocurva* | Da retr | 22.0 | 31.8 | 10.5 |
| *Leptodora kindtii* | Lep kind | 22.0 | 22.7 | 21.1 |
| *Alona* sp. | Alona sp | 19.5 | 18.2 | 21.1 |
| *Acanthocyclops vernalis* | Cyc vern | 19.5 | 22.7 | 15.8 |
| *Mesocyclops edax* | Meso edax | 19.5 | 36.4 | 0.0 |
| *Sida crystallina* | Sida crys | 14.6 | 13.6 | 15.8 |
| *Eubosmina longispina* | E long | 14.6 | 18.2 | 10.5 |
| *Daphnia catawba* | Da cat | 12.2 | 9.1 | 15.8 |
| *Bosmina liederi* | B lied | 9.8 | 9.1 | 10.5 |
| *Eubosmina* sp. | Eub sp | 9.8 | 18.2 | 0.0 |
| *Polyphemus pediculus* | Pol pedic | 7.3 | 9.1 | 5.3 |
| *Acroperus harpae* | Ac harp | 4.9 | 4.5 | 5.3 |
| *Daphnia pulicaria* | Da pul | 4.9 | 4.5 | 5.3 |
| *Leptodiaptomus siciloides* | Lep sicilo | 4.9 | 9.1 | 0.0 |
| *Eucyclops agilis* | Eucy agil | 4.9 | 4.5 | 5.3 |
| *Eurycercus lamellatus* | Eury lam | 2.4 | 0.0 | 5.3 |
| *Latona setifera* | Lat setif | 2.4 | 4.5 | 0.0 |
| *Daphnia* sp. | Dap sp | 2.4 | 4.5 | 0.0 |
| *Graptoleberis testudinaria* | Grap tes | 2.4 | 0.0 | 5.3 |
| *Leptodiaptomus ashlandi* | Lepto ashl | 2.4 | 4.5 | 0.0 |
| *Leptodiaptomus sicilis* | Lepto sicil | 2.4 | 4.5 | 0.0 |
| *Macrocyclops albidus* | Mac albid | 2.4 | 0.0 | 5.3 |

reported by Keller and Conlon (1994) (5–15 species per lake, 28 total) and Keller and Pitblado (1989) (6–17 species per lake, 37 total) for Shield lakes, and by Paterson et al. (2014) (6–12 species per lake, 30 total) for Lowlands lakes.

Positive correlations of species richness with morphometry (lake size, lake depth) indicated that larger, deeper lakes support more diverse communities of zooplankton, consistent with the theory of island biogeography which links increased habitat size with higher species richness (MacArthur and Wilson 1967). While many internal (e.g. lake shape) and external (e.g. inflow characteristics) factors may affect habitat diversity and niche space, deeper, larger lakes directly provide a more variable habitat, which increases the niche space and promotes greater biodiversity. A direct example of this is the distribution of hypolimnetic species such as *D. longiremis*, which are not likely to successfully colonize shallower waters (Keller and Conlon 1994) and were only found in the deeper Shield lakes in our survey (Table 2). Ca, Mg and conductivity were also correlated with richness, because these variables were all higher in the larger, deeper Shield lakes, which on average had higher zooplankton richness (11.6) than the Lowlands lakes (9.1). However, it is not likely that ionic strength directly affects zooplankton community structure over the range observed in our lakes. For example, all Ca levels were above 2.5 mg $L^{-1}$, and are thus unlikely to have negatively affected distributions of Ca-sensitive *Daphnia* species (Tessier and Horwitz 1990; Jeziorski et al. 2008).

**Table 3** Comparison of species occurrence in lakes of the 2012 survey to other Ontario zooplankton studies

| Species | % of 2012 lakes ($n$=41) | % of N lakes from Paterson et al. (2014) and Keller, W. (unpublished data) ($n$ = 23) | % of NW lakes from Keller and Pitblado (1989) ($n$ = 137) | % of NE lakes from Keller and Pitblado (1989) ($n$ = 161) | % of Algoma lakes from Keller and Conlon (1994) ($n$ = 60) |
|---|---|---|---|---|---|
| *Bosmina* sp. | 100 | 100 | 96 | 95 | 92 |
| *Chydorus sphaericus* | 93 | 80 | 79 | 27 | 7 |
| *Epischura lacustris* | 85 | 80 | 52 | 64 | 42 |
| *Daphnia mendotae* | 78 | 60 | 93 | 80 | 40 |
| *Holopedium glacialis* | 78 | 45 | 77 | 90 | 68 |
| *Diacyclops bicuspidatus thomasi* | 78 | 80 | 96 | 89 | 27 |
| *Diaphanosoma birgei* | 73 | 20 | 79 | 85 | 50 |
| *Leptodiaptomus minutus* | 61 | 85 | 95 | 94 | 92 |
| *Skistodiaptomus oregonensis* | 56 | 55 | 63 | 71 | 42 |
| *Ceriodaphnia* sp. | 37 | 5 | 20 | 21 | 3 |
| *Tropocyclops extensus* | 37 | 10 | 75 | 71 | 88 |
| *Daphnia longiremis* | 31 | 20 | 24 | 67 | 17 |
| *Daphnia retrocurva* | 22 | 0 | 62 | 66 | 15 |
| *Leptodora kindtii* | 22 | 10 | 7 | 24 | 8 |
| *Alona* sp. | 20 | 15 | 3 | 0 | 0 |
| *Acanthocyclops vernalis* | 20 | 10 | 39 | 18 | 0 |
| *Mesocyclops edax* | 20 | 10 | 73 | 87 | 88 |
| *Daphnia pulex* group | 15 | 35 | 12 | 26 | 52 |
| *Sida crystallina* | 15 | 10 | 2 | 9 | 3 |
| *Eubosmina longispina* | 15 | 5 | 0 | 32 | 17 |
| *Eubosmina* sp. | 10 | 35 | 0 | 0 | 0 |
| *Polyphemus pediculus* | 7 | 15 | 8 | 0 | 8 |
| *Eucyclops agilis* | 5 | 10 | 1 | 0 | 0 |
| *Eurycercus lamellatus* | 2 | 5 | 0 | 0 | 0 |
| *Latona setifera* | 2 | 5 | 0 | 0 | 0 |
| *Leptodiaptomus sicilis* | 2 | 0 | 30 | 15 | 3 |
| *Daphnia tenebrosa* | 0 | 10 | 0 | 0 | 0 |
| *Acantholeberis curvirostris* | 0 | 5 | 0 | 0 | 0 |
| *Limnocalanus macrurus* | 0 | 0 | 14 | 3 | 0 |
| *Cyclops scutifer* | 0 | 0 | 8 | 65 | 5 |
| *Onychodiaptomus sanguineus* | 0 | 0 | 4 | 0 | 5 |
| *Daphnia dubia* | 0 | 0 | 4 | 22 | 30 |
| *Daphnia ambigua* | 0 | 0 | 2 | 21 | 0 |
| *Senecella calanoides* | 0 | 0 | 2 | 0 | 7 |
| *Orthocyclops modestus* | 0 | 0 | 2 | 0 | 15 |
| *Eubosmina coregoni* | 0 | 0 | 1 | 0 | 8 |
| *Eubosmina tubicen* | 0 | 0 | 0 | 27 | 0 |
| *Aglaodiaptomus leptopus* | 0 | 0 | 0 | 0 | 27 |

Only species occurring in at least 5% of the lakes in one or more surveys are included. N lakes are northern Ontario lakes above 54°N. NW lakes are in northwestern Ontario below 50°N. NE lakes are in northeastern Ontario below 48°N. Algoma lakes are below 47°N near Lake Superior

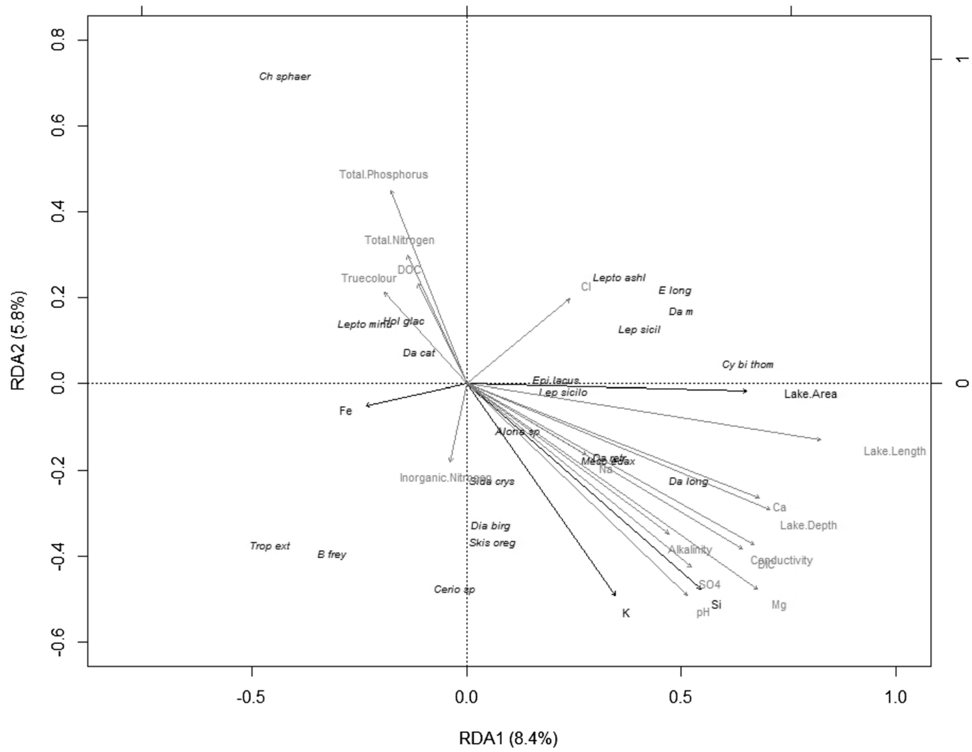


**Fig. 2** RDA species ordination of 2012 survey lakes ($n = 41$): species in italics. Passive chemical variables are shown in grey, active variables in regular black font

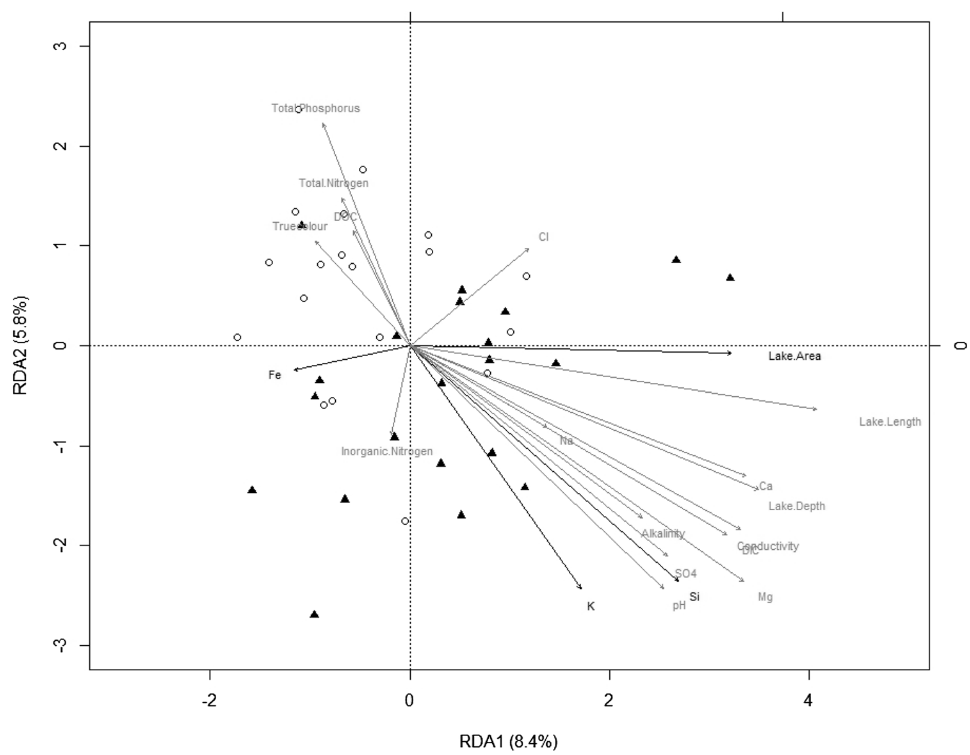


**Fig. 3** RDA lake ordination of 2012 survey lakes with lakes labelled by region; Shield (triangles) and Lowlands (circles) ($n = 41$; 22 Shield, 19 Lowlands). Passive chemistry variables are shown in grey, active variables in regular black font

Since most of the observed correlations between species relative abundances were positive, species generally appeared to respond to environmental gradients in a similar fashion. There were few instances of negative species correlations that might indicate competitive or predatory interactions. A particular exception was the very common *B. freyi* which had a significant ($p < 0.01$) negative correlation with *D. mendotae* suggesting a competitive interaction (DeMott and Kerfoot 1982). *B. freyi* was also negatively ($p < 0.01$) correlated with *D.b. thomasi* suggesting a possible predator/prey interaction.

Species present in over 50% of the 2012 study lakes (*B. freyi, C. sphaericus, E. lacustris, D. mendotae, H. glacialis, D. b. thomasi, D. birgei, L. minutus*, *and S. oregonensis*) were also common in other surveys of Ontario lakes that generally have been conducted in more southern areas of the province, on the Canadian Shield (Table 3). Many of the species common in the 2012 study lakes, including *Bosmina* sp.*, C. sphaericus, H. glacialis, D. b. thomasi, L. minutus, E. lacustris,* and *Acanthocyclops vernalis,* have also been commonly reported from Arctic and sub-Arctic lakes (Hebert and Hann 1986; Swadling et al. 2001; Symons et al. 2014). However, species characteristics of Arctic/sub-Arctic lakes futher north, such as *Leptodiaptomus tyrrelli*, and *Daphnia middendorfiana/tenebrosa* (Hebert and Hann 1986; Swadling et al. 2001; Symons et al. 2014), were not found in the 2012 survey lakes, indicating that these lakes are all south of the distribution of these species.

Although they are located in different ecozones, Lowlands (Hudson Plains Ecozone) and Shield (Boreal Shield Ecozone) lakes in the 2012 survey had generally similar species composition. However, ANOSIM did indicate some differences, Shield and Lowlands lakes did separate in ordination space (Fig. 3), and some species showed apparent differences in the extent of occurrence between regions (Table 2).

In more southern lakes in Ontario, *S. oregonensis* tends to be most important in the zooplankton communities of shallower, more productive lakes, while *L. minutus* is most prominent in the communities of deeper oligotrophic lakes (Keller and Pitblado 1984). In complete contrast, in lakes of the far north of Ontario *S. oregonensis* was most common in the deeper, less productive Shield lakes (77%) while *L. minutus* was most common in the shallower, more nutrient-rich Lowlands lakes (79%). Similar to *S. oregonensis,* other species which are generally favoured by shallow, productive conditions in other Ontario lakes, including *D. retrocurva* and *T. extensus* (Keller and Pitblado 1984) were also less common in Lowlands lakes than Shield lakes. Reasons for these apparent differences in distribution patterns between northern and more southern lakes are not clear but perhaps differing thermal conditions in sub-Arctic lakes may play a role, since *L. minutus,* a species apparently favoured in Lowlands lakes, is a cold stenotherm.

Overall, of the species that had a > 20% difference in occurrence between Shield and Lowlands lakes, most were still reasonably common in both sets of lakes (> 20% occurrence in each lake set, Table 2). Exceptions were *D. longiremis* and *M. edax* which were absent from the Lowlands lakes collections. As indicated earlier, the absence of *D. longiremis*, a hypolimnetic species, from the shallow Lowlands lakes is not surprising given the thermal habitat limitations in these shallow lakes that lack hypolimnia. The reason for the absence of *M. edax* from the Lowlands lakes is not clear; however, in agreement with results from this survey, the species does seem to be generally restricted to more southerly lakes. *M. edax* was very rare in sub-Arctic lakes further north in Ontario (Paterson et al. 2014) and was not reported from surveys of sub-Arctic and Arctic lakes further north in Canada (Hebert and Hann 1986; Swadling et al. 2001; Symons et al. 2014). It appears that this survey may have been conducted near the northern limit of the range of *M. edax*. This may also be the case for *T. extensus* and possibly *D. mendotae*, which were common in this survey but were rare or absent in surveys further north (Hebert and Hann 1986; Swadling et al. 2001; Paterson et al. 2014; Symons et al. 2014). The absence of *Cyclops scutifer* from the 2012 survey lakes agrees with previous observations of its scarcity in northwestern Ontario (Keller and Pitblado 1989).

The defining physico-chemical characteristics of our Shield lakes compared with the Lowlands lakes in the 2012 survey were greater lake size and depth, greater ionic strength (pH, Ca, Mg and conductivity) and lower DOC and TP. Because of its influence on habitat diversity and niche space, morphometry is likely a strong driver of differences in communities between these lakes. This finding is consistent with prior surveys of Ontario lakes that have identified lake morphometry as a major correlate with zooplankton community composition (Keller and Pitblado 1984; Keller and Conlon 1994), and have demonstrated strong links between depth, lake chemistry and zooplankton community structure (Keller and Conlon 1994; Keller et al. 2002; Yan et al. 2008). Since crustacean zooplankton communities in the far north of Ontario are generally similar to communities in more southern lakes and exhibit many similar relationships to physico-chemical conditions, much of the knowledge on zooplankton responses to environmental stressors that is developed in more southern regions of Ontario can likely be extended north to help predict the effects of future anthropogenic disturbances on lakes in this vast, understudied landscape.

Although relationships between crustacean zooplankton communities and lake physico-chemical characteristics emerged from our analysis, much of the variation in community structure remained unexplained. This may largely reflect the fact that our analysis could not include evaluation of the possible effects of biological controls on species assemblages, which can be very important (Keller et al. 1992; Keller and Yan 1998; Keller et al. 2002). Planktivorous fish (Valois et al. 2010; Webster et al. 2013) and in their absence macroinvertebrate predators (Yan et al. 1991; MacPhee et al. 2011) can have strong effects on zooplankton prey communities. Biological controls on zooplankton assemblages may be particularly intense in very shallow lakes (Keller and Conlon 1994), such as most of the lakes in the Hudson Bay

Lowlands, which may offer little habitat separation between species. An important future research direction would be the evaluation of the roles of vertebrate and invertebrate predators in structuring northern zooplankton communities.

## Conclusions

Lakes in the far north of Ontario supported diverse crustacean plankton communities with species richness similar to lakes previously surveyed in other parts of northern Ontario. The species most common in these lakes were also commonly found in other Ontario surveys. While some of the species collected, including *M. edax*, *T. extensus*, and *D. mendotae*, appear to be at or near the northern limit of their Ontario distributions, the most relatively common Ontario species occurred throughout the 2012 study area.

The important lake characteristics related to species relative abundances and richness included variables associated with lake morphometry (lake depth and size). This suggests that while there were differences in community richness and composition between Lowlands and Shield lakes, these differences do not seem attributable to biogeographic influences on species distributions. Rather, the lower species richness and different community composition in Lowlands lakes relative to Shield lakes appears to be related to lake morphometry. The smaller, shallower Lowlands lakes provide much less habitat diversity, i.e. niche space, than the deeper Shield lakes, leading to simpler communities.

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### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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