

Benthic Macroinvertebrate Communities in Arctic Lakes and Ponds of Central Nunavut, Canada

Authors: Namayandeh, Armin, and Quinlan, Roberto

Source: Arctic, Antarctic, and Alpine Research, 43(3) : 417-428

Published By: Institute of Arctic and Alpine Research (INSTAAR),
University of Colorado

URL: <https://doi.org/10.1657/1938-4246-43.3.417>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Benthic Macroinvertebrate Communities in Arctic Lakes and Ponds of Central Nunavut, Canada

Armin Namayandeh* and

Roberto Quinlan†

*Department of Environmental Science,
Trent University, 1600 West Bank
Drive, Peterborough, Ontario, K9J 7B8,
Canada

†Corresponding author: Department of
Biology, York University, 4700 Keele
Street, Toronto, Ontario, M3J 1P3,
Canada
rquinlan@yorku.ca

Abstract

The diversity and distribution of aquatic benthic invertebrate communities of 17 lakes and 3 shallow ponds near Iqaluit and Rankin Inlet, Nunavut, Canada, were examined to assess patterns with respect to environmental gradients. Macroinvertebrates were collected using 500 µm mesh D-nets, and collected specimens were identified and enumerated; a total of 40 taxa were identified. Multivariate analyses (Redundancy Analysis) of relative abundance (%) data identified habitat (dominant substrate type), water chemistry, nutrients, and food/productivity (total phosphorus, total nitrogen, sulfate, dissolved oxygen, chlorophyll *a*), physical characteristics (maximum depth), catchment-related properties (lake elevation), and climate-related properties as significant environmental gradients influencing community composition. Ecosystem-scale lake characteristics had the greatest influence on benthic communities, followed by substrate type; however, there were substantive amounts of community variation influenced by the interaction between lake characteristics, substrate type, and regional differences. A number of environmental variables may have been significant due to differences in their values when comparing Rankin Inlet region sites versus Iqaluit region sites. The results agree with other studies indicating that benthic invertebrate communities are influenced by environmental gradients acting at different scales ranging from local, within-lake scales to large, regional scales.

DOI: 10.1657/1938-4246-43.3.417

Introduction

Benthic invertebrate studies have been a prominent part of freshwater ecology and biomonitoring research in temperate and boreal regions; however, studies in the Arctic have been scarce. Recent limnological investigations conducted over a large range of the Canadian Arctic suggest that lakes and ponds in the Arctic differ with respect to their physical and chemical characteristics, related to the landscape position of the lakes and ponds, which in turn affects their catchment and limnology (Hamilton et al., 2001; Michelutti et al., 2002; Antoniadis et al., 2003; Lim and Douglas, 2003). These studies, however, focused on analyses of algal (diatom) communities, and as a result there are still few studies that have investigated how the faunal community structure of the lakes and ponds in the Arctic is structured across environmental gradients. Therefore, our understanding of Arctic Canada benthic community composition and ecology remains poor for most regions.

It is well known that limnological characteristics can determine habitat availability for aquatic organisms, and thus influence their distribution, where the limnological characteristics of lakes and ponds are strongly determined by climate conditions and watershed characteristics (e.g. lake productivity and adjacent landscape allochthonous input) (Allan and Johnson, 1997; Kratz et al., 1997; Hawkins et al., 2000). In recent decades synoptic surveys have been used widely to explain the benthic community structure of streams and lakes with respect to multiple environmental variables (e.g. Füreder et al., 2006). These studies are ideal for evaluating whole community structure along multiple envi-

ronmental variables and comparing multiple lakes and rivers of the same region. Using this synoptic method this study attempts to determine what environmental variable(s) strongly influence distribution and diversity of benthic invertebrates in arctic lakes. This may provide insights on future changes in the benthos community composition of these regions' lakes, influenced by climate-mediated changes in catchment limnology and ecosystem processes.

Materials and Methods

STUDY SITES

A total of 5 lakes near Iqaluit (63°47'N, 68°32'W), and 12 lakes and 3 ponds near Rankin Inlet (62°52'N, 92°10'W), Nunavut, Canada, were sampled in July 2006 (Fig. 1). Lakes were selected from 1:50,000 topographic maps (Mapping and Charting Establishment, Department of National Defense, 1967). In order to reduce any potential anthropogenic influence, sampled lakes and ponds were distant from populated areas. For the purpose of this study, the two regions were chosen based on their differences of topography/catchment properties and climate. The study lakes in Iqaluit are characterized by high altitude (mean elevation = 179 m a.s.l.) and smaller catchment area (CA; mean CA = 74.4 ha) than those in the Rankin Inlet region (mean elevation = 21 m a.s.l.; mean CA = 111.6 ha). The dominant substrate is boulder-cobble in the Iqaluit study sites, compared to cobble, gravel, and sand in the Rankin Inlet study sites. The study sites in both regions are located on Precambrian bedrock;

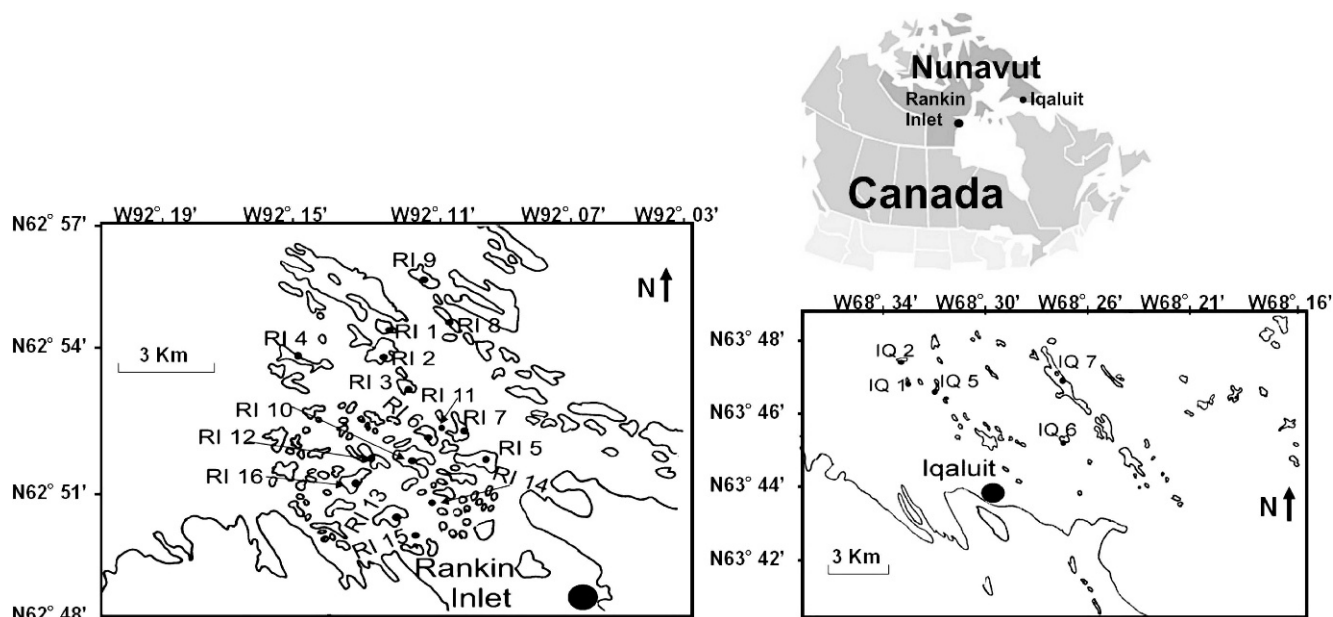


FIGURE 1. Map showing location of 5 study lakes and ponds in the Iqaluit region, and 15 study lakes and ponds in the Rankin Inlet region, Nunavut, Canada, 2006.

however, the lakes and ponds near Rankin Inlet are also located on layers of both sedimentary and volcanic rocks, while the study lakes near Iqaluit are located on intrusive volcanic rocks. Vegetation cover in the catchment of Iqaluit region sites is scarce, while the catchments of Rankin Inlet region sites were nearly 100% covered by vegetation such as grasses, sedges, and lichens.

While the two regions are at a similar latitude, Iqaluit has a lower mean summer (June–August) temperature of 6.3 °C compared to Rankin Inlet mean summer temperature of 8.1 °C (1981–2006, Meteorological Service of Canada; $t = -8.4$, $df = 25$, $P < 0.001$). These climate differences would be expected to have substantive effects on differences in the limnological and ecological dynamics of these two regions that were not explicitly sampled or measured in this study (e.g. thicker ice cover, later date of ice-off, and shorter period of hydrological flow at above-freezing temperatures, shorter growing seasons for both aquatic and catchment vegetation communities).

SAMPLING METHODS

Benthic invertebrates were collected based on Ontario Benthos Biomonitoring Network (OBBN) protocols (Jones et al., 2005). The OBBN protocol was used as an established standard method of sampling benthos, as there are no benthos sampling protocols explicitly designed for arctic lakes and ponds. Using a D-net with 500 μ m mesh, samples were collected by a kick-and-sweep method along three transects selected randomly along the shoreline perimeter, with the transect spanning the shoreline to a depth of 1 m. Initial sampling indicated that there were very low abundances of benthic invertebrate specimens, so kick-and-sweep collection was conducted for an extended period of 10 minutes, or until 100 specimens were collected. In the majority of sampled lakes, smaller insect larvae were collected (first instars). Therefore, the specimens were sorted both at the site using a sorting tray for larger specimens and in the laboratory for smaller instars.

Along with D-net samples, water samples were collected for water chemistry analyses (i.e. major ions, total nitrogen, and total

phosphorus). Samples were collected and subsequently analyzed, following standard methodology, at the National Laboratory for Environmental Testing (NLET) at the National Water Research Institute (NWRI) in Burlington, Ontario (Environment Canada, 1994). Measures of pH, dissolved oxygen, conductivity, and oxidation reduction potential (ORP) were taken using a digital multiparameter sonde (Yellow Stream Instruments model 650). Secchi depth and lake depth were measured for each lake from a canoe at a mid-basin location. Elevation, latitude, and longitude were measured using GPS and compared to topographic maps (1:50,000) for further accuracy. Watershed and lake surface area were determined from topographic maps (1:50,000). Lake-wide visual estimates of the lakes' dominant substrate type (boulder, cobble, gravel, sand, clay), distance of riparian vegetation to the lake shore (i.e. distance from shoreline to vegetation up on the banks), and the catchment's vegetation coverage (i.e. presence or absence scores) were also made in the field (Table 1).

LABORATORY ANALYSES

Macrobenthos collected were keyed to the lowest possible taxonomic level, based on available taxonomic keys and validation of specimen identification by other entomologists and/or taxonomists (Namayandeh, 2008). Many larval Chironomidae were taxonomically distinct such that they could be keyed to species, while other taxa, such as Nematoda, were not keyed beyond a broad taxonomic level due to a lack of diagnostic taxonomic keys. Five major functional feeding groups were delineated: predator, collector-gatherers, shredders, filter feeders, and scrapers (grazers), based on Clark (1973), Cummins (1973), Merritt and Cummins (1996), Larson et al. (1999) and Thorp and Covich (2001).

DATA ANALYSES

The Shannon diversity index (H') was used to determine the benthic invertebrate diversity of the lakes and ponds in the two regions. Pearson correlations were run to determine if any

TABLE 1

Average, minimum, and maximum values of environmental variables in 5 Iqaluit region (IQ) and 15 Rankin Inlet region (RI) ponds and lakes. The column “*t*-test” indicates the *P*-value of an unpaired *t*-test, assuming unequal variances, comparing values in Iqaluit sites versus Rankin Inlet sites: NS = not significant, $P > 0.05$; marg = $0.05 < P < 0.10$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$. “Direction” indicates the pattern of difference in statistically significant *t*-tests. “RDA %” is the amount of species variation (%) explained by the environmental variable in a univariate (singly constrained) RDA, and “*P*-value” is the statistical significance of that environmental variable.

Variable	Code	Units	Mean	Min.	Max.	Transformation	<i>t</i> -test	Direction	Category	RDA %	<i>P</i> -value
total phosphorus— unfiltered	TPU	µg L ⁻¹	6	2	15	sqrt <i>x</i>	***	IQ–, RI+	ecosystem	10.9	**
total nitrogen— unfiltered	TNU	µg L ⁻¹	399	130	827	sqrt <i>x</i>	***	IQ–, RI+	ecosystem	11.8	**
particulate organic carbon	POC	mg L ⁻¹	0.416	0.139	1.080	ln <i>x</i>	*	IQ–, RI+	ecosystem	7.1	NS
chlorophyll- <i>a</i>	CHLA	µg L ⁻¹	1.3	0.4	3.3	ln <i>x</i>	**	IQ–, RI+	ecosystem	10.9	**
chloride	Cl	mg L ⁻¹	18.67	0.79	109.00	ln (<i>x</i> + 1)	***	IQ–, RI+	ecosystem	12.7	**
sulphate	SO4	mg L ⁻¹	4.64	0.83	17.40	ln <i>x</i>	***	IQ–, RI+	ecosystem	11.6	**
calcium	Ca	mg L ⁻¹	10.13	2.45	27.50	ln <i>x</i>	**	IQ–, RI+	ecosystem	8.8	**
magnesium	Mg	mg L ⁻¹	2.15	0.41	9.25	ln <i>x</i>	***	IQ–, RI+	ecosystem	11.9	**
potassium	K	mg L ⁻¹	1.44	0.14	3.51	ln (<i>x</i> + 1)	***	IQ–, RI+	ecosystem	12.0	**
sodium	Na	mg L ⁻¹	10.32	0.56	58.20	ln (<i>x</i> + 1)	***	IQ–, RI+	ecosystem	13.1	**
silica	Si	mg L ⁻¹	0.47	0.04	2.06	ln <i>x</i>	***	IQ+, RI–	ecosystem	7.3	NS
pH	pH	–log[H+]	8.34	7.53	9.09	untransformed	**	IQ–, RI+	ecosystem	7.8	NS
conductivity @ 25 °C	COND	µS cm ⁻¹	131	20	481	ln <i>x</i>	***	IQ–, RI+	ecosystem	12.0	**
oxidation-reduction potential	ORP	mV	65.6	5.9	133.3	sqrt <i>x</i>	***	IQ+, RI–	ecosystem	9.6	*
dissolved inorganic carbon	DIC	mg L ⁻¹	6.4	1.6	16.0	ln <i>x</i>	NS	—	ecosystem	8.3	*
dissolved organic carbon	DOC	mg L ⁻¹	6.0	1.3	17.4	ln <i>x</i>	NS	—	ecosystem	3.7	NS
lake depth	Zmax	m	4.8	1.2	17.2	ln <i>x</i>	NS	—	ecosystem	8.4	*
Secchi depth	Secchi	m	2.8	1.0	7.0	ln <i>x</i>	NS	—	ecosystem	5.0	NS
lake elevation	ELEV	m a.s.l.	61	7	196	ln <i>x</i>	***	IQ+, RI–	catchment+	13.5	**
air temperature	AirT	°C	12.5	8.6	16.1	sqrt <i>x</i>	NS	—	ecosystem	7.0	NS
water temperature	WatT	°C	13.5	8.2	17.8	untransformed	NS	—	ecosystem	4.0	NS
dissolved oxygen	DO	mg [O ₂] L ⁻¹	11.8	7.3	15.7	untransformed	*	IQ+, RI–	ecosystem	12.6	**
Riparian vegetation distance to the shore	Rvdist	m	0.6	0.0	3.0	sqrt <i>x</i>	NS	—	ecosystem	6.0	NS
lake surface area	SA	ha	39.8	0.4	108.0	sqrt <i>x</i>	NS	—	ecosystem	7.5	marg
lake catchment area	CA	ha	102	0.4	361.4	sqrt <i>x</i>	NS	—	catchment+	6.6	NS
latitude (N)	LAT	°	63.1	62.8	63.8	untransformed	***	IQ+, RI–	catchment+	11.7	**
longitude (W)	LONG	°	86.3	68.4	92.3	untransformed	***	IQ–, RI+	catchment+	11.4	**
region ¹	region	— ¹	N/A	N/A	N/A	untransformed	N/A	—	catchment+	11.4	**
substrate ²	sub	— ²	N/A	N/A	N/A	untransformed	N/A	—	habitat	24.3	**

¹ Binary dummy variables, 2 categories: 1 = Iqaluit; 2 = Rankin Inlet.

² Binary dummy variables, 5 categories: 1 = boulder (25–400 cm); 2 = cobble (6.4–25 cm); 3 = gravel (0.2–6.4 cm); 4 = sand (0.006–0.2 cm); 5 = clay (<0.006 cm).

environmental gradients had significant ($P < 0.05$, two-tailed Bonferroni-corrected probabilities) correlations with benthos taxa or functional feeding group composition.

A total of 23 environmental variables along continuous gradients (Table 1) were compared to the benthos composition (% abundance of species/taxa or functional feeding group) of 20 lakes and ponds. Species data were square root transformed prior to analysis, and rare taxa were not excluded, while environmental data were transformed in SPSS for Windows, based on the transformation that minimized the Skewness of the data (Table 1). Based on a Detrended Correspondence Analysis (DCA) axis 1 gradient length of ordinated species data (between 2 and 4 standard deviation [SD] units), it was not clear whether a unimodal or linear response model best fit the species/taxa data, therefore, two separate ordinations were performed, using both linear approaches (Redundancy Analysis; RDA) and unimodal approaches (Canonical Correspondence Analysis; CCA). RDAs of functional feeding group data were performed as a DCA

produced a short (<2 SD) axis 1 species gradient length. All ordinations were performed using CANOCO for Windows v. 4.5 (ter Braak and Šmilauer, 2002). For each set of ordination analyses, environmental variables with significant influence on benthos and functional feeding groups were sequentially removed using a step-wise backwards elimination procedure to remove colinear variables until variance inflation factors (VIFs) were ≤ 10 . As a number of important environmental variables were significantly different between the two regions, additional RDAs were performed including only Rankin Inlet sites, to identify significant habitat-, ecosystem-, and catchment-scale gradients within a single region. Due to the low number of sites in Rankin Inlet-only analyses ($n = 15$), there may be particularly low statistical power associated with $\alpha = 0.05$, therefore alpha was increased to $\alpha = 0.10$ for retaining variables in stepwise elimination multivariate ordination models to improve statistical power. Increasing alpha to 0.10 will increase the type I error rate, which may increase the chance of identifying environmental

variables as significant when they do not have a strong influence on assemblages. However, a low sample size that is typical of data sets from field-based studies in remote areas may produce result outcomes that are dominated by accepting false null hypotheses, which is problematic when vulnerable populations are being studied (*sensu* Taylor and Gerrodette, 1993), which in this case are aquatic ecosystems in a region vulnerable to future climate warming. Analysis of Variance tests (ANOVAs) were performed to determine which specific taxa were significantly influenced by substrate type.

Variance partitioning analyses (*sensu* Borcard et al., 1992) were performed to determine the relative influence of variables operating at different spatial scales *sensu* Johnson and Goedkoop (2002) (Table 1). Dominant substrate type was assigned as a habitat-scale variable, while lake chemistry and physical characteristics (e.g. SO_4 , Z_{max}) were assigned as ecosystem-scale variables. Catchment-, ecoregion-, and geographical-scale variables were amalgamated into one “catchment+” category, including lake catchment area (CA), lake elevation (ELEV), latitude (LAT), longitude (LONG), and ‘region’ (Iqaluit or Rankin Inlet). Latitude and longitude were significantly different when comparing Iqaluit and Rankin Inlet sites (t -tests, $P < 0.05$), and geographical-scale variables were highly colinear if both LAT/LONG and ‘region’ were included in analyses. The categorical variable ‘region’ was retained instead of LAT or LONG, as this variable would better incorporate a number of regional-scale differences amongst the two study locales, including the influence of different climatic conditions, bedrock geology, catchment vegetation type, and biogeographical dynamics due to differences in patterns of dispersion, colonization, and extinction in mainland Rankin Inlet sites compared to Iqaluit sites on Baffin Island. As CANOCO for Windows v. 4.5 produces biased results when conducting VPAs, VPAs were run using the “varpart” command in the “vegan” package of the software program R version 2.12.1 to obtain r^2 -adjusted values of the relative influences of variables influencing benthos community composition (Peres-Neto et al., 2006).

Results

A total of 1071 specimens from 40 benthic macroinvertebrate taxa were collected and identified (Table 2) in 20 sites. As sampling was conducted in July, several weeks after ice-off, and small, early instars were found in the collection nets, it is possible that numbers of collected specimens may have been depressed by the loss of small, early instar specimens through the D-net’s 500 μm mesh. Additionally, it is also possible that numbers of some insect groups may have been underestimated due to rapid emergence of adults in the spring, soon after ice-off in mid- to late June. The most abundant single taxon was *Gammarus lacustris lacustris*. Dominant taxonomic groups included Amphipoda and Diptera (primarily Chironomidae) (Fig. 2, a), while predators and collector-gatherers were the dominant functional feeding groups (Fig. 2, b). Amphipoda were more abundant (%) in Iqaluit sites compared to Rankin Inlet sites ($t = 3.7$, $P = 0.002$, $\text{df} = 18$), while Plecoptera were more abundant in Rankin Inlet sites ($t = 2.1$, $P = 0.05$, $\text{df} = 18$). A number of major taxonomic groups present in Rankin Inlet sites were absent in Iqaluit sites, including Bivalvia, Ceratopogonidae (within Diptera), Collembola, Ephemeroptera, Gastropoda, Nematoda, and Plecoptera, while all taxonomic groups present in Iqaluit were also present in Rankin Inlet. Collector-gatherers were more abundant in Iqaluit ($t = 3.1$, $P = 0.006$, $\text{df} = 18$), while shredders were more abundant in Rankin Inlet ($t = -3.0$, $P = 0.007$, $\text{df} = 18$).

PATTERN OF SPECIES DIVERSITY

There was no difference in species diversity (Shannon H' diversity) when comparing Iqaluit and Rankin Inlet sites ($t = 0.0$, $P = 0.99$, $\text{df} = 18$). There were not significant correlations with any environmental variable ($P > 0.05$), with only modest correlations with some environmental variables (e.g. air temperature, $r = -0.28$; lake surface area, $r = 0.26$). One site (RI 11) had very low species diversity ($H' = 0.55$), and when it was removed from analyses correlations were much stronger, with significant correlations ($P < 0.05$) with a number of environmental variables including major ion concentrations (SO_4 , $r = 0.57$; Ca, $r = 0.50$; Mg, $r = 0.50$; conductivity, $r = 0.50$), air temperature ($r = -0.47$) and lake catchment area ($r = -0.50$). Species diversity was still not different between the two regions with the removal of RI 11 ($t = -0.54$, $P = 0.59$, $\text{df} = 17$). Species diversity was negatively correlated with air temperature in both analyses due to lower species richness in warmer sites, indicating greater dominance by the species that were present.

MULTIVARIATE ORDINATIONS

Linear-based approaches (RDAs) explained greater amounts of species variation compared to unimodal-based approaches (CCAs) (46.3% versus 41.3%, respectively), so RDA results are presented here. Stepwise backwards elimination retained nutrients (TP, TN), productivity/food (CHLA), major ion chemistry (SO_4), dissolved oxygen concentration (DO), lake depth (Z_{max}), and landscape position (lake elevation) as environmental variables that were correlated with benthos community composition. Lake elevation was strongly negatively correlated with all major ions ($r = -0.66$ to -0.87), reinforcing the usefulness of lake elevation as a simple proxy for landscape position in our analyses, as lower elevation sites (presumably with larger inputs of surface water and groundwater inputs compared to high-elevation sites) had higher concentrations of major ions. The first two RDA axes explained 25.1% of total species variation, and 54.2% of species variation was explained by the 7 retained environmental variables (Fig. 3). Based on RDA results, shredders such as *Stictochironomus* species showed a positive correlation with TP, while predators such as *Culicoides* (Ceratopogonidae) were strongly correlated with chlorophyll-*a* (Fig. 3, a). Oligochaetes were more abundant in shallow, productive sites while water mites (Hydracarina) were more abundant in deeper, unproductive sites (Fig. 3, a). There was clear separation of Rankin Inlet versus Iqaluit sites, with the less productive Rankin Inlet sites plotting into the right-hand quadrants of a site-environment RDA biplot (Fig. 3, b). Although calcium was not retained in RDA analyses due to being colinear with other retained variables, passive ordination of Ca indicated that it is highly correlated with RDA axis 1. RDAs consisting of only Rankin Inlet sites retained fewer environmental variables, with greater importance of catchment+ variables (lake elevation, lake catchment area) compared to Iqaluit and Rankin Inlet analyses (Fig. 4, a). The placement of several species in both RDA biplots were similar, with *Gammarus lacustris lacustris* (GamLa-cla) and *Philartus quaeris* (Philaqua) associated with lakes with high dissolved oxygen concentrations (Fig. 4, a). The relative places of several Rankin Inlet sites substantively changed in Rankin Inlet-only analyses; for example, in the full data set RI 01 and RI 02 plotted in the same ordination space (Fig. 3, b), while in the Rankin Inlet-only data set these two sites plotted some distance from each other (Fig. 4, b).

Ordination of functional feeding group data retained four environmental variables, including sodium and silica concentra-

TABLE 2

Benthic invertebrate taxa and their associated functional feeding group, collected and identified from Iqaluit and Rankin Inlet lakes and ponds, July 2006.

Identified taxon	Major taxon	Functional feeding group	Taxon code
<i>Gammarus (lacustris) lacustris</i>	Amphipoda	Collector-gatherers	GamLacla
<i>Sphaerium nitidum</i>	Bivalvia	Filter-feeders	Sphaenit
<i>Culicoides</i> spp.	Ceratopogonidae	Predators	CeratCul
<i>Chironomus crassicaudatus</i>	Chironomidae	Collector-gatherers	Chircras
<i>Cladotanytarsus</i> spp.	Chironomidae	Collector-gatherers	Cladotan
<i>Corynoneura arctica</i>	Chironomidae	Collector-gatherers	Coryarct
<i>Crictopus laricomalis</i>	Chironomidae	Collector-gatherers	Criclari
<i>Cryptochironomus digitatus</i>	Chironomidae	Predators	Crypdiigi
<i>Dicretodipes lobiger</i>	Chironomidae	Collector-gatherers	Dicrlobi
<i>Diplocladius cultriger</i>	Chironomidae	Collector-gatherers	Diplocul
<i>Glyptotendipes baripes</i>	Chironomidae	Shredders	Glypbari
<i>Hydrobaenus fusistylus</i>	Chironomidae	Scrapers	Hydrobfu
<i>Oliveridia tricornis</i>	Chironomidae	Collector-gatherers	Olivtric
<i>Orthocladius doreus</i>	Chironomidae	Collector-gatherers	Orthodor
<i>Paracladius quadrimodosus</i>	Chironomidae	Collector-gatherers	Paracl
<i>Paracricotopus</i> spp.	Chironomidae	Collector-gatherers	Paracric
<i>Paratanytarsus penicillatus</i>	Chironomidae	Collector-gatherers	Parapeni
<i>Procladius (Holotanypus)</i>	Chironomidae	Predators	ProcHolo
<i>Procladius (Psilotanypus)</i>	Chironomidae	Predators	ProcPsil
<i>Psectrocladius sordidellus</i>	Chironomidae	Collector-gatherers	PsectPso
<i>Stictochironomus</i>	Chironomidae	Shredders	Stictoch
<i>Agabus</i> spp.	Coleoptera – Dytiscidae	Predators	Agabussp
<i>Agabus moestus</i>	Coleoptera – Dytiscidae	Predators	Agabmoes
<i>Agabus tristis</i>	Coleoptera – Dytiscidae	Predators	Agabtris
<i>Colymbetis dolobratus</i>	Coleoptera – Dytiscidae	Predators	Colymdol
<i>Hydroporus lapponum</i>	Coleoptera – Dytiscidae	Predators	Hydropla
<i>Oreodytes sanmarkii</i>	Coleoptera – Dytiscidae	Predators	Oreosanm
<i>Stictotarsus gristiotratus</i>	Coleoptera – Dytiscidae	Predators	Sticgris
Collembolla	Collembolla	Collector-gatherers	Collembo
Brachycera	Diptera	Predators	Brachyce
<i>Baetis bundyae</i>	Ephemeroptera	Collector-gatherers	Baetbund
<i>Physa jennessi</i>	Gastropoda	Scrapers	Physajen
<i>Valvata helicoidea</i>	Gastropoda	Scrapers	Valvsinc
Hydracarina	Hydracarina	Predators	Hydracar
Nematoda	Nematoda	Predators	Nematoda
<i>Lepidurus arcticus</i>	Notostraca	Predators	Lepidarc
Oligochaeta	Oligochaeta	Collector-gatherers	Oligoch
<i>Capnia</i> spp.	Plecoptera	Shredders	Capnia
<i>Tipula</i> spp.	Tipulidae	Shredders	Tipula
<i>Philarctus quaeris</i>	Trichoptera	Shredders	Philaqua

tions, lake position (lake elevation) and lake catchment area (Fig. 5, a). Scrapers and collector-gatherers were more abundant in the less productive, more isolated Iqaluit region sites (Fig. 5, b), while filter-feeders, shredders, and predators were more abundant in Rankin Inlet sites, with predators more abundant in sites with small catchments.

HABITAT PREFERENCES

One-factor ANOVAs identified 3 taxa as having different abundances amongst different substrates: *Hydrobaenus fusistylus* ($P = 0.029$), *Physa jennessi* ($P = 0.026$), and *Valvata helicoidea* ($P = 0.026$), with *H. fusistylus* present only on substrate dominated by boulders, and *P. jennessi* and *V. helicoidea* both present only on substrate dominated by sand. Another 4 taxa had marginal differences amongst substrates, including *Gammarus lacustris lacustris* ($P = 0.092$, highest abundances on boulders), *Hydracarina* ($P = 0.056$, highest abundances on cobbles), *Paracladius quadrimodosus* ($P = 0.096$, highest abundances on boulders), and *Capnia* ($P = 0.055$, highest abundances on sand).

VARIANCE PARTITIONING ANALYSES (VPA)

Habitat-, ecosystem-, and catchment-scale environmental gradients explained 64.1% of variation (R^2 values) in benthos communities (Fig. 6); R^2_{adjusted} 's fractions of variation were much lower, likely due to the small sample size of the data set (Peres-Neto et al., 2006). One-fifth of explained variation (12.5%) involved interactions between variables at different scales. For 'pure effects' of variables, ecosystem-scale variables explained the most variation (29.7%), followed by habitat-scale variables (13.2%) and then catchment-scale variables (8.7%). While each category of environmental variables explained significant ($P < 0.05$) amounts of variation in benthos communities when interactions with other categories were included (both for R^2 and R^2_{adjusted} values), no 'pure effect' of any category explained significant amounts of variation (both for R^2 and R^2_{adjusted} values).

For VPAs of Rankin Inlet-only sites, all three categories of environmental gradients explained significant ($P < 0.10$) amounts of variation (for both R^2 and R^2_{adjusted} values), while the

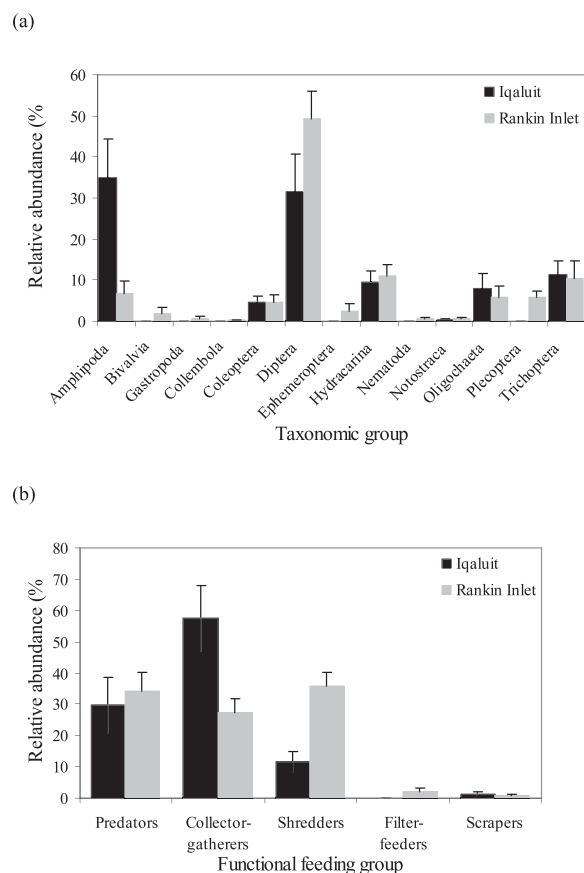


FIGURE 2. Relative abundance (%) of (a) major taxonomic groups and (b) functional feeding groups in Iqaluit region and Rankin Inlet region sites. Error bars represent ± 1 standard error.

catchment category explained significant ($P < 0.10$) amounts of variation for ‘pure effects’ of variables when testing R^2_{adjusted} values. Similar to analyses involving the entire data set of Iqaluit and Rankin Inlet sites, the most variation was explained by ecosystem-scale variables (22.3%), although catchment-scale variables explained similar amounts of variation (17.9%), followed by habitat-scale variables (12.1%), while interactions amongst categories explained 9.1% of variation, for a total amount of explained variation of 61.4% (Fig. 6).

Discussion

PATTERNS OF DIVERSITY AND COMMUNITY COMPOSITION IN CENTRAL NUNAVUT

Gammarus lacustris lacustris, the most abundant taxon collected in this study, is a stenothermal cold-tolerant species with widespread occurrences in cold sites such as high-latitude or high-altitude lakes or cold spring-fed waters at lower latitudes or altitudes (Pennak and Rosine, 1976). Chironomidae usually represent more than one-fifth of the total number of all insects in the arctic region, with an increase of relative abundance in more severe climate conditions (Oliver, 1968). Family Chironomidae accounted for over one-third of specimens collected and enumerated in this study, indicating their relative success in this cold and unproductive arctic region. According to Brundin (1966), chironomids evolved in the cold-water upper reaches of mountain streams that had high dissolved oxygen concentrations and low variation in water temperature. While there is substantial intra-

family variation in temperature preferences of chironomid taxa in the Canadian Arctic (Barley et al., 2006), all subfamilies in this major taxonomic group have cold-adapted species.

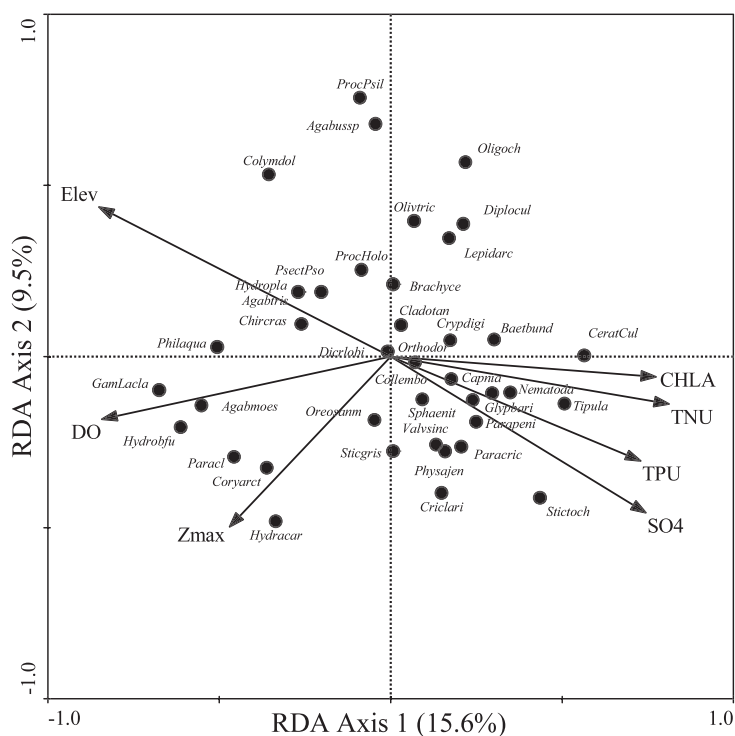
The overall richness of EPT taxa (Ephemeroptera, Plecoptera, and Trichoptera) was very low in both regions, with a total absence of Ephemeroptera and Plecoptera in Iqaluit region lakes. Rankin Inlet region lakes and ponds had only one species of Ephemeroptera present, *Baetis bundyae*. Within the Nearctic, most of the 55 species of mayflies whose range extends north of 60°N are found in the west of the continent, with a steep eastward decline in diversity, likely due to the milder climate and extensive forest cover in Alaska, and the Yukon and western Northwest Territories (Cobb and Flannagan, 1979; Giberson et al., 2007).

Amongst functional feeding groups, the higher abundances of shredders in Rankin Inlet region lakes may be due to the much greater landscape coverage and standing biomass of catchment vegetation observed in this region, compared to Iqaluit region lakes, which is the ultimate source of biomass of coarse particulate organic matter (CPOM) upon which shredders feed. Due to the lower levels of nutrients and algal productivity in Iqaluit region lakes compared to Rankin Inlet region lakes, the higher relative abundance of scraper taxa may be due to a relatively greater proportion of primary productivity being associated with periphyton versus primary productivity occurring in the water column. While lower algal productivity and lack of fine particulate organic matter (FPOM) inputs from sparsely vegetated catchments may limit populations of filter feeders, the low calcium concentrations of Iqaluit region lakes may also explain the absence of filter feeding species, which in this study consisted of *Sphaerium nitidum* (Bivalvia), a molluscan taxa that has high calcium requirements due to producing a calcareous exterior shell. Predator taxa had similar abundances in both regions, and had a strong negative correlation with lake catchment area. As catchment area was most strongly correlated with lake surface area ($r = 0.68$, $P = 0.001$), dissolved organic carbon (DOC) concentration ($r = -0.46$, $P = 0.042$), and depth ($r = 0.45$, $P = 0.050$), this suggests that secondary productivity and the preferred food of predators were relatively more abundant in smaller, shallower, more humic lakes, driven by the higher algal biomass in shallower lakes (Zmax vs. CHLA, $r = -0.47$, $P = 0.037$).

It is surprising how important dissolved oxygen (DO) was as an explanatory variable in RDAs of both the full and Rankin Inlet-only data sets, as the minimum DO measured was $7.3 \text{ mg } [\text{O}_2] \text{ L}^{-1}$. This suggests that the cold-adapted arctic taxa in this region’s lakes and ponds are particularly sensitive to oxygen depletion and other environmental gradients correlated with DO, such as lake productivity (DO vs. TP, $r = -0.67$, $P = 0.001$) and algal biomass (DO vs. CHLA, $r = -0.68$, $P = 0.001$).

The absence of a large number of major taxonomic groups in the Iqaluit region indicate that differences in community composition when comparing benthos communities in Iqaluit sites compared to Rankin Inlet sites may be partially driven by biogeographical influences. Lack of hydrological connectedness to more southerly catchments on the mainland continent may limit the dispersion of taxa into sites near Iqaluit on Baffin Island. It is difficult to tease out the relative influences of climate gradients versus biogeographical isolation, as the more isolated Iqaluit region also has a colder climate. It is worth noting, however, that, on a latitudinal basis, sites from the two regions are within 1° of latitude from each other, so ‘instantaneous’ solar insolation limits on algal productivity should be very similar in the two regions. Although benthos sampling effort was lengthy (~ 10 min per each of three kick-and-sweep transects) at each site, suggesting that we had recorded ‘true’ absences of taxa at sites, it is possible that

(a)



(b)

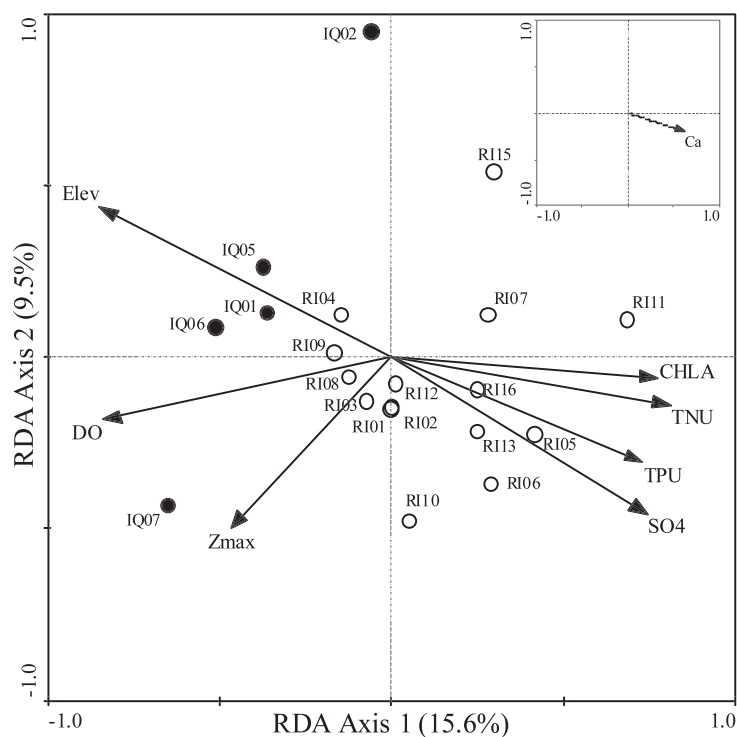
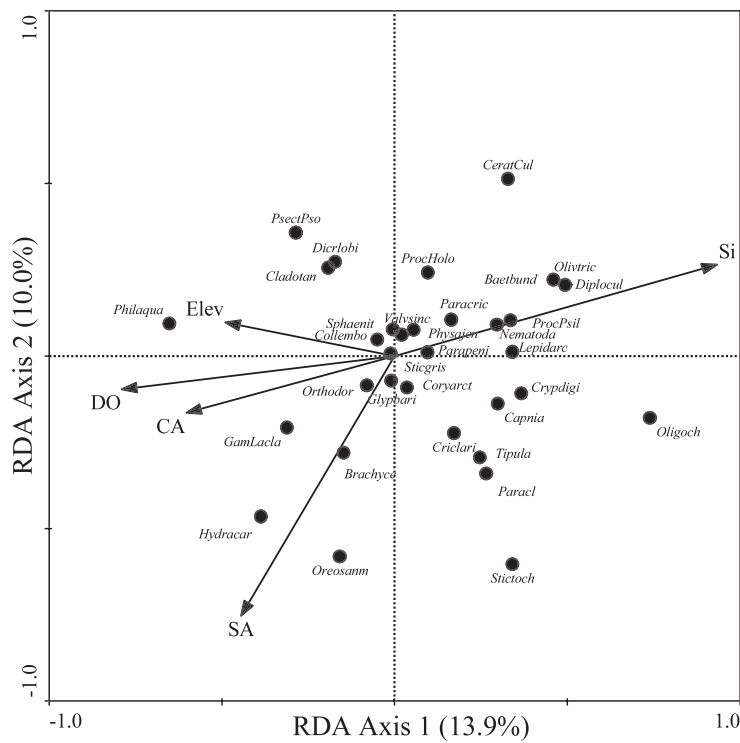


FIGURE 3. Redundancy analyses of benthic invertebrates and significant ($P < 0.05$) environmental variables in 5 lakes near Iqaluit and 15 lakes and ponds near Rankin Inlet, Nunavut. Environmental variable codes are as in Table 1, taxa codes are as in Table 2. (a) taxa-environment biplot; (b) environment-site biplot [inset biplot is passive ordination of calcium (Ca)].

further fieldwork involving benthos sampling at more Iqaluit sites may result in the collection of additional taxonomic groups currently noted as absent in the Iqaluit region. Intensive benthos sampling of stream sites in the Iqaluit region (Medeiros et al.,

2011) similarly recorded the absence of a number of major taxonomic groups, and while there were Ephemeroptera specimens collected in Medeiros et al. (2011), benthos collections of Ephemeroptera were from stream, not lake, sites.

(a)



(b)

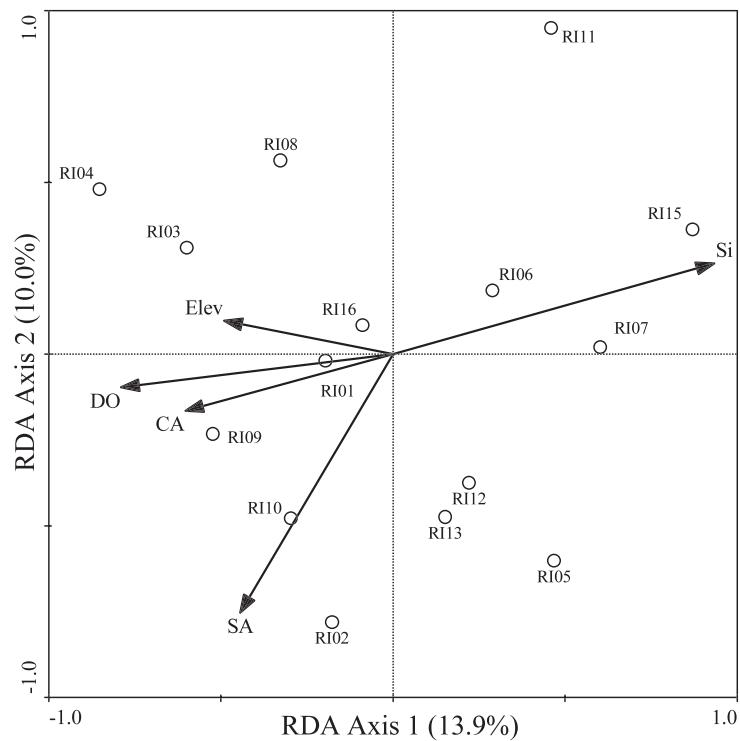
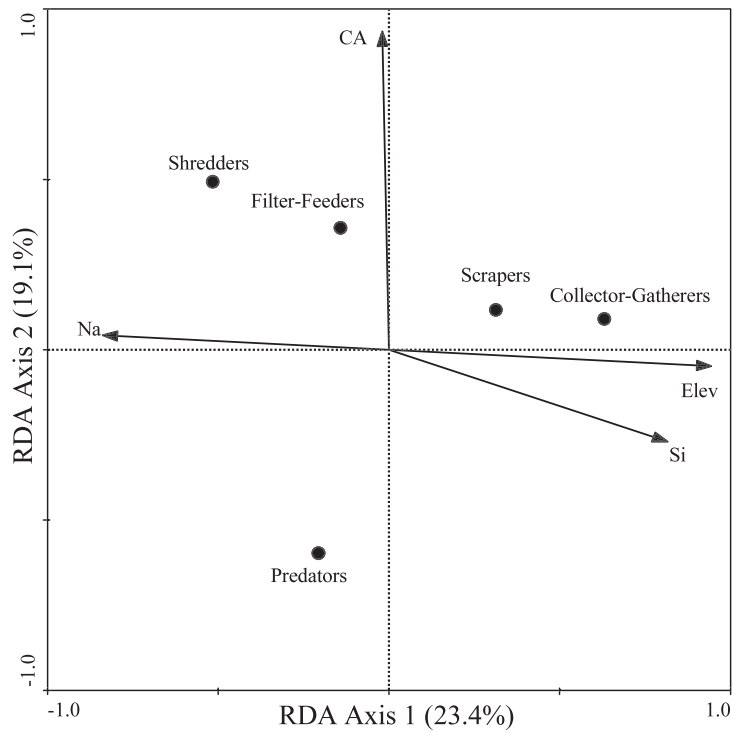


FIGURE 4. Redundancy analyses (taxa-environment biplot) of benthic invertebrates and significant ($P < 0.05$) environmental variables in 15 lakes and ponds near Rankin Inlet, Nunavut. Environmental variable codes are as in Table 1, taxa codes are as in Table 2.

As measured July air and water temperatures during the 2006 field season were not different between Iqaluit and Rankin Inlet sites, the influence of climate on these different benthos communities may act on relatively long time scales, affecting limnological

processes not measured during a summer field season. For example, colder year-round climate in Iqaluit may impose stronger limits on the duration of the summer growing season, due to lag effects such as time of spring melt of accumulated ice- or snowpack. Colder

(a)



(b)

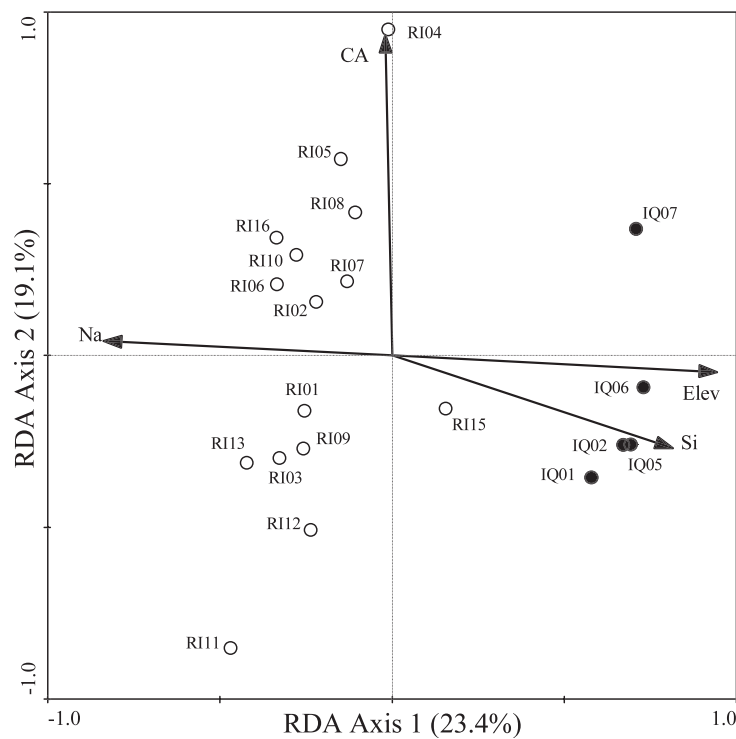


FIGURE 5. Redundancy analyses of 5 functional feeding groups and significant ($P < 0.05$) environmental variables in 5 lakes near Iqaluit and 15 lakes and ponds near Rankin Inlet, Nunavut. Environmental variable codes are as in Table 1. (a) taxa-environment biplot; (b) environment-site biplot.

climate may also decrease overwintering survival of benthos communities, which may be quite long-lived (e.g. up to 7 years per generation) in cold arctic lakes (Butler, 1982), or result in the persistence of taxa with tolerances for much colder winter

temperatures regardless of the relative similarity in summer water temperatures between different regions.

The lack of any difference in species diversity, when comparing Iqaluit and Rankin Inlet sites, despite clear separation

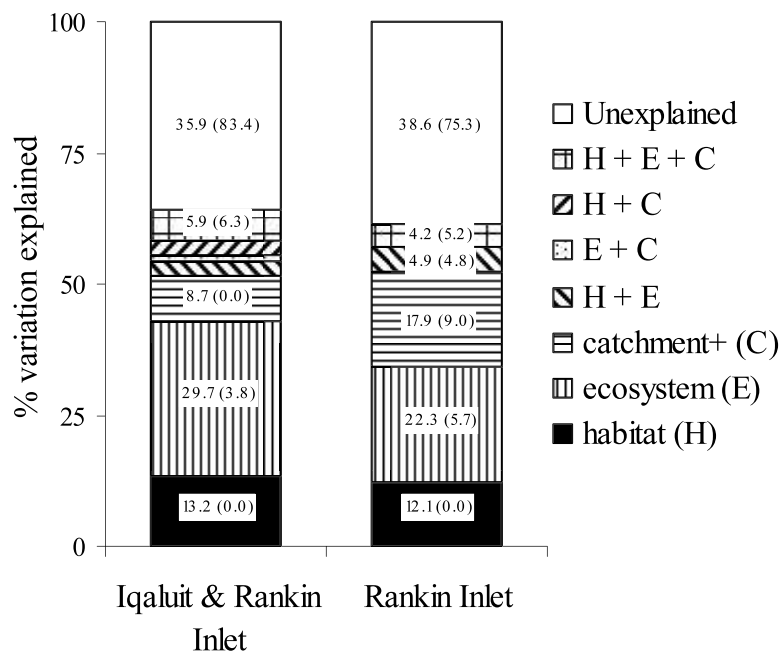


FIGURE 6. Variance partitioning analysis (VPA) results, with significant ($P < 0.05$ or $P < 0.10$ for Rankin Inlet-only analyses) environmental variables partitioned into three categories: habitat (H), ecosystem (E), and catchment+ (C), for both Iqaluit and Rankin Inlet and Rankin Inlet-only analyses. Numbers within bars are percentage of variance explained by each explanatory fraction (R^2); numbers within parentheses are adjusted percentages (R^2_{adj}) of variance explained.

of the two regions' site scores in multivariate ordinations, suggests regional differences in benthos community composition that reflect species replacements according to the ecological preferences of different taxa, as opposed to differences in species richness. Substantive changes in species diversity might not be observed until these environmental gradients are lengthened to include more extreme conditions, such as lakes with more nutrients and productivity beyond this study's TP range of $2\text{--}6\ \mu\text{g L}^{-1}$.

RELATIVE INFLUENCES OF SMALL-SCALE VS. LARGE-SCALE VARIABLES ON BENTHOS

Although latitudinal gradients (e.g. climate-dominated processes) may account for most variation in species richness and community composition in many aquatic systems (e.g. arctic ecosystems) examined at particularly large spatial scales, locally, landscape position and catchment-related gradients have a stronger, more direct impact in structuring aquatic habitats (Johnson and Goedkoop, 2002; Johnson et al., 2004). Variance partitioning analyses at a smaller spatial scale, involving only Rankin Inlet sites, indicated that there was a greater influence of catchment-related gradients, including silica concentration (Si vs. CA, $r = -0.45$, $P = 0.047$), lake elevation, and lake catchment size. Nonetheless, ecosystem-scale variables (e.g. nutrients, major ion chemistry, lake morphometry) had a dominant influence on benthos community composition in both sets of analyses.

While habitat-related variation in benthos communities was more important in full data set analyses versus Rankin Inlet-only analyses (24.3% vs. 19.8% of variation in RDAs), due to a relationship between region and dominant substrate type (e.g. boulder substrate dominated only in the Iqaluit region, sand and clay substrate dominated only in the Rankin Inlet region), the amount of variation associated with the 'pure' effect of habitat remained the same in the two sets of analyses (13.2% vs. 12.1%). The relationship between region and dominant habitat may indicate that there are strong linkages between climate, catchment vegetation, and dominant shoreline substrate type, and hence suitable habitat for particular species of benthos.

CAN REGIONAL DIFFERENCES IN BENTHOS PROVIDE INSIGHT INTO CLIMATE-RELATED CHANGES IN COMMUNITY COMPOSITION?

Comparisons in RDA results for the full data set vs. Rankin Inlet-only analyses emphasize the importance of scale in influencing analysis results. While sample sizes were small in this study, as the study lakes were representative of the water bodies found in each region, increased sample size would likely reduce within-group variability with little change in group means, emphasizing the statistically significant patterns identified in this study. Ecosystem- and catchment-scale variables such as lake surface area and catchment area were retained in Rankin Inlet-only analyses, while nutrient and productivity variables (TP, TN, CHLA) were retained in full data set analyses. This is interesting as the former variables were not different between the two regions, while the latter variables were. As this study's two regions had different year-round climate at similar latitudes, RDA results from full data set analyses may provide insights into how the benthos of arctic lakes and ponds in central Nunavut may change in response to future climate warming of a magnitude similar to the current difference in summer temperature between Rankin Inlet and Iqaluit ($\sim 1\text{--}2\ ^\circ\text{C}$).

If a warmer climate leads to a longer ice-free period in the annual hydrological cycle, increased water flow and permafrost melting may increase in catchment weathering and soil erosion (Rouse et al., 1997). If these climate-related hydrological changes result in an increase in nutrient loading and detrital inputs (Hobbie et al., 1999), there would not only be a change in ecosystem-scale variables (e.g. nutrient, DOC), but also a change in habitat-scale variables, as formerly bare rock along the shoreline may become covered in greater amounts of fine particulate soil matter eroding from the catchment, or detrital remains of catchment vegetation whose growth is enhanced in warmer climates.

Taxa much more strongly associated with Rankin Inlet sites, such as *Culicoides* (Ceratopogonidae) or *Tipula* (Tipulidae), may become more abundant in the Iqaluit region if its climate warms to be more similar to that of Rankin Inlet. However, it may be tenuous to make predictions on specific taxa, as examinations of

individual taxa in this study suggest that a number of mechanisms may be limiting their arctic range, including availability of suitable substrate type or possibly biogeographical limitations on dispersal and colonization. Consequently, it may be more cogent to examine patterns and responses of benthos at the functional feeding group level. For example, experimental manipulations of an arctic pond revealed that artificial fertilization dramatically increased abundances of filter feeders due to increases in primary productivity (Hershey, 1992). Therefore, comparisons of ecosystem productivity and benthos composition between Rankin Inlet and Iqaluit suggest that, if future climate warming results in higher productivity, the importance of filter feeders may increase. Previous limnological studies of arctic lakes and ponds have shown that the main source of carbon inputs is allochthonous, with strong correlations between DOC, adjacent vegetation cover, and productivity in lakes and ponds (Pienitz et al., 1997a, 1997b; Hamilton et al., 2001). While there are currently no differences in DOC concentration between Rankin Inlet and Iqaluit region lakes and ponds, if continued future climate warming results in increases of DOC and allochthonous inputs of detritus from catchment vegetation, there would be future increases in the abundance of shredders. While there are currently no regional differences in ecosystem species diversity, as filter feeders were absent from less productive Iqaluit region lakes, future climate warming may facilitate major ecosystem changes via the colonization of new species, versus more modest changes via shifts in the abundances of already-present benthic species. While biogeographical limits on species dispersal and colonization into the Arctic Archipelago may currently limit the range of a number of Arctic benthic species to the mainland, these limits may decline or disappear as maritime cargo traffic dramatically increases through an ice-free Northwest Passage, providing new opportunities for species invasions into the Arctic (Walther et al., 2009).

Acknowledgments

We would like to thank the staff at Nunavut Arctic College in Iqaluit and Rankin Inlet, and the staff at the Nunavut Research Institute in Iqaluit for their generous support and field assistance. A sincere thanks to our field assistant and guide, Andy Aliyak, in Rankin Inlet, Nunavut. Taxonomic consulting and identification of specimens were provided by Doug Currie (Royal Ontario Museum and University of Toronto), Donna Giberson (University of Prince Edward Island), Rob Roughley (University of Manitoba), and Bohdan Bilij. We would also like to thank Dr. B. L. Madsen (Watercastle Old University, Ministry of Environment, Lemvig, Denmark) and Andrew Donini (Department of Biology, York University) for their consultation on aquatic insect physiology and bionomics. We thank Garry Scrimgeour and two anonymous reviewers who provided comments that improved earlier versions of this manuscript.

References Cited

Allan, J. D., and Johnson, L. B., 1997: Catchment-scale analysis of aquatic ecosystems. *Freshwater Biology*, 37: 107–111.
 Antoniadou, D., Douglas, M. S. V., and Smol, J. P., 2003: The physical and chemical limnology of 24 ponds and one lake from Isachsen, Ellef Ringnes Island, Canadian High Arctic. *International Review of Hydrobiology*, 88: 519–538.
 Barley, E. M., Walker, I. R., Kurek, J., Cwynar, L. C., Mathewes, R. W., Gajewski, K., and Finney, B. P., 2006: A northwest North America training set: distribution of freshwater midges in relation to air temperature and lake depth. *Journal of Paleolimnology*, 36: 295–314.

Borcard, D., Legendre, P., and Drapeau, P., 1992: Partialling out the spatial component of ecological variation. *Ecology*, 73: 1045–1055.
 Brundin, L., 1966: Transantarctic relationships and their significance, as evidenced by chironomid midges with a monograph of the subfamilies Podonominae and Aphroteniinae and Austral Heptagytiae. *Kungliga Svenska Vetenskapsakademien*, 11: 7–472.
 Butler, M. G., 1982: A 7-year life cycle for two *Chironomus* species in arctic Alaskan tundra ponds (Diptera: Chironomidae). *Canadian Journal of Zoology*, 60: 58–70.
 Clark, A. H., 1973: The freshwater mollusks of the Canadian interior basin. *Malacologia*, 13: 1–509.
 Cobb, D. G., and Flannagan, J. F., 1979: The distribution of Ephemeroptera in northern Canada. In Flannagan, J. F., and Marshall, K. E. (eds.), *Advances in Ephemeroptera Biology*. New York: Plenum Press, 155–166.
 Cummins, K. W., 1973: Trophic relations of aquatic insects. *Annual Review of Entomology*, 18: 183–206.
 Environment Canada, 1994: *Manual of Analytical Methods*. Burlington, Canada: National Laboratory for Environmental Testing, Canadian Centre for Inland Waters.
 Füreder, L., Ettinger, R., Boggero, A., Thaler, B., and Thies, H., 2006: Macroinvertebrate diversity in alpine lakes: effects of altitude and catchment properties. *Hydrobiologia*, 562: 123–144.
 Giberson, D. J., Burian, S. K., and Shouldice, M., 2007: Life history of the northern mayfly *Baetis bundyae* in Rankin Inlet, Nunavut, Canada, with updates to the list of mayflies of Nunavut. *Canadian Entomologist*, 139: 628–642.
 Hamilton, P. B., Gajewski, K., Atkinson, D. E., and Lean, D. R. S., 2001: Physical and chemical limnology of 204 lakes from the Canadian Arctic Archipelago. *Hydrobiologia*, 457: 133–148.
 Hawkins, C. P., Norris, R. H., Gerritsen, J., Hughes, R. M., Jackson, S. K., Johnson, R. K., and Stevenson, R. J., 2000: Evaluation of the use of landscape classification for the prediction of freshwater biota: synthesis and recommendation. *Journal of North American Benthological Society*, 19: 541–556.
 Hershey, A. E., 1992: Effects of experimental fertilization on benthic macroinvertebrate community of an arctic lake. *Journal of North American Benthological Society*, 11: 204–217.
 Hobbie, J. E., Peterson, B. J., Bettez, N., Deegan, L., O'Brien, W. J., Kling, G. W., Kipphut, G. W., Bowden, W. B., and Hershey, A. E., 1999: Impact of global change on biogeochemistry and ecology of an arctic freshwater system. *Polar Research*, 18: 207–214.
 Johnson, R. K., and Goedkoop, W., 2002: Littoral macroinvertebrate communities: spatial scale and ecological relationship. *Freshwater Biology*, 47: 1840–1854.
 Johnson, R. K., Goedkoop, W., and Sandin, L., 2004: Spatial scale and ecological relationships between the macroinvertebrate communities of stony habitats of streams and lakes. *Freshwater Biology*, 49: 1179–1194.
 Jones, C., Somers, K. M., Craig, B., and Reynoldson, T. B., 2005: *Ontario Benthos Biomonitoring Network Protocol Manual. Version 1.0*. Toronto: Ontario Ministry of the Environment.
 Kratz, T. K., Webster, K. E., Bowser, C. J., Magnuson, J. J., and Benson, B. J., 1997: The influence of landscape position on lakes in northern Wisconsin. *Freshwater Biology*, 37: 209–217.
 Larson, D. J., Alarie, Y., and Roughley, R. E., 1999: *Predaceous Diving Beetles (Coleoptera: Dytiscidae) of the Nearctic Region with Emphasis on the Fauna of Canada and Alaska*. Ottawa: National Research Council of Canada, 982 pp.
 Lim, D. S. S., and Douglas, M. S. V., 2003: Limnological characteristics of 22 lakes and ponds in the Houghton Crater region of Devon Island, Nunavut, Canadian High Arctic. *Arctic, Antarctic, and Alpine Research*, 35: 509–519.
 Medeiros, A. S., Luszczek, C. E., Shirley, J., and Quinlan, R., 2011: Community-based benthic monitoring in an arctic tundra stream: Iqaluit, Nunavut, Canada. *Arctic*, 64: 59–72.

- Merritt, R. W., and Cummins, K. W., 1996: *An Introduction to the Aquatic Insects of North America*. 3rd ed. Dubuque, Iowa: Kendall/Hunt Publishing Company, 862 pp.
- Michelutti, N., Douglas, M. S. V., Muir, D. C. G., Wang, X., and Smol, J. P., 2002: Limnological characteristics of 38 lakes and ponds on Axel Heiberg Island, High Arctic Canada. *International Review of Hydrobiology*, 87: 385–399.
- Namayandeh, A., 2008: *Diversity and Distribution of Benthic Invertebrates in Lakes and Ponds of Nunavut, Arctic, Canada*. MSc thesis, York University, Toronto, Canada, 104 pp.
- Oliver, D. R., 1968: Adaptation of arctic Chironomidae. *Annales Zoologici Fennici*, 5: 111–118.
- Pennak, R. W., and Rosine, W. N., 1976: Distribution and ecology of Amphipoda (Crustacea) in Colorado. *American Midland Naturalist*, 96: 324–331.
- Peres-Neto, P. R., Legendre, P., Dray, S., and Borcard, D., 2006: Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology*, 87: 2614–2625.
- Pienitz, R., Smol, J. P., and Lean, D. R. S., 1997a: Physical and chemical limnology of 24 lakes located between Yellowknife and Contwoyoto Lake, Northwest Territories (Canada). *Canadian Journal of Fisheries and Aquatic Sciences*, 54: 347–358.
- Pienitz, R., Smol, J. P., and Lean, D. R. S., 1997b: Physical and chemical limnology of 59 lakes located between the southern Yukon and the Tuktoyaktuk Peninsula, Northwest Territories (Canada). *Canadian Journal of Fisheries and Aquatic Sciences*, 54: 330–346.
- Rouse, W. R., Douglas, M. S., Hecky, R. E., Hershey, A. E., Kling, G. W., Lesack, L., Marsh, P., McDonald, M., Nicholson, B. J., Roulet, N. T., and Smol, J. P., 1997: Effects of climate change on the freshwaters of arctic and subarctic North America. *Hydrological Processes*, 11: 873–902.
- Taylor, B. L., and Gerrodette, T., 2002: The uses of statistical power in conservation biology: the Vaquita and Northern Spotted Owl. *Conservation Biology*, 7: 489–500.
- ter Braak, C. J. F., and Šmilauer, P., 2002: *Canoco Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5)*. Ithaca, New York: Microcomputer Power.
- Thorp, J. H., and Covich, A. P., 2001: *Ecology and Classification of North American Freshwater Invertebrates*. 2nd ed. New York: Academic Press, 1056 pp.
- Walther, G.-R., Roques, A., Hulme, P. E., Sykes, M. T., Pyšek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukát, Z., Bugmann, H., Czúcz, B., Dauber, J., Hickler, T., Jarošík, V., Kenis, M., Klotz, S., Minchin, D., Moora, M., Nentwig, W., Ott, J., Panov, V. E., Reineking, B., Robinet, C., Semchenko, V., Solarz, W., Thuiller, W., Vilà, M., Vohland, K., and Settele, J., 2009: Alien species in a warmer world: risks and opportunities. *Trends in Ecology & Evolution*, 24: 686–693.

MS accepted February 2011