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Benthic and pelagic food resources for zooplankton in shallow high-latitude lakes and ponds

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SUMMARY

1. Shallow lakes and ponds are a major component of the northern landscape and often contain a high zooplankton biomass despite clear waters that are poor in phytoplankton.
2. In this study we quantified zooplankton food sources and feeding rates in the shallow waters of two contrasting high-latitude biomes: subarctic forest tundra (Kuujjuarapik, Quebec) and high arctic polar desert (Resolute, Nunavut). Five substrate types were tested (beads, bacteria, picophytoplankton, filamentous plankton and microbial mats). Special attention was given to the role of benthos, a component that is usually poorly integrated into models of aquatic foodwebs.
3. Consistent with observations elsewhere in the circumpolar region, high concentrations of adult macrozooplankton occurred in all sites (up to 17 100 crustaceans m^{-3}) while phytoplankton concentrations and primary productivity were low. The communities were composed of multiple species, including *Daphnia middendorfiana*, *Hesperodiaptomus arcticus*, *Leptodiaptomus minutus*, *Artemiopsis stefanssoni* and *Branchinecta paludosa*.
4. Detritus made 89–98% of the planktonic resource pool and bacteria contributed the highest biomass (up to 29 mg C m^{-3}) of the planktonic food particles available to zooplankton. Benthic resources were dominated by microbial mats that grew in nutrient-rich conditions at the base of the ponds and which dominated overall ecosystem biomass and productivity.
5. All species were flexible in their feeding but there were large, order of magnitude differences in clearance rates among taxa. These differences likely resulted from different grazing strategies among cladocerans, copepods and fairy shrimps, and possibly also from adaptation to specific food types and size ranges that occur locally in these waters.
6. The subarctic cladocerans *Ceriodaphnia quadrangula* and *D. middendorfiana*, and the arctic fairy shrimp *B. paludosa* were observed to graze directly on the microbial mats and the feeding experiments confirmed their assimilation of benthic substrates. The other zooplankton species showed a more pelagic feeding mode but were capable of using microbial mat filaments, thus may be indirectly linked to benthic processes via resuspension.
7. Our study indicates that the classical aquatic food web in which phytoplankton provide the sole production base for grazers does not apply to northern shallow lakes and ponds. Instead, microbial mats increase the physical complexity of these high latitude ecosystems and likely play a role in sustaining their high zooplankton biomass.

Keywords: arctic, benthic-pelagic coupling, feeding patterns, microbial mats, zooplankton

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Introduction

Shallow, clear-water lakes and ponds are a major feature of high latitude landscapes and an important class of freshwater ecosystems. Phytoplankton biomass and productivity are low in these waters as a result of nutrient limitation (Kalff, 1971; Alexander *et al*., 1980) and grazing by zooplankton, which often form the top of the food chain (Hansson, Lindell & Tranvik, 1993; Rautio, 2001). Federle *et al.* (1979) showed a fivefold increase in primary production and substantial increase in algal biomass in a small tundra pond only 16 days after the removal of zooplankton. Despite the limited abundance of water column resources that can be easily grazed, zooplankton biomass and abundance in northern ponds are often substantial and higher than in deeper lakes with similarly low chlorophyll *a* (Chl *a*) levels (O'Brien, Buchanan & Haney, 1979; Rautio, 2001; Swadling *et al*., 2001). This apparent inconsistency between resource-poor water columns and biomass-rich zooplankton stocks led to the early suggestion that zooplankton must have access to additional resources beyond the water column food (McLaren, 1958). Similar imbalances in carbon budgets between pelagic algae and zooplankton are known for other freshwaters (Nauwerk, 1963; Salonen, Arvola & Kononen, 1983). More recently it has been shown that zooplankton are capable of feeding on carbon sources other than phytoplankton, including dissolved organic matter, allochthonous materials and bacteria (Salonen & Hammar, 1986; Wylie & Currie, 1991; Hessen, 1992; Tranvik, 1992; Grey, Jones & Sleep, 2001).

Several potential sources of carbon must be considered for shallow water ecosystems, in addition to phytoplankton. One of the most striking features of high latitude lakes and ponds is the well-developed benthic community of microbial mats (Vézina & Vincent, 1997; Villeneuve, Vincent & Komarek, 2001; Vadeboncoeur *et al*., 2003). The small size and shallow depth of the ponds connect them closely to benthic processes. The substantial reserves of organic matter stored in the microbial mats on the bottom of all high-latitude ponds are potentially available for even obligate planktonic feeders by the resuspension of mats (both living and dead) or via food web utilisation of dissolved organic carbon released from the mats. Additionally allochthonous organic matter from surrounding wetlands may enter the water column (Hessen, Andersen & Lyche, 1990). These benthic algal and detrital sources have been traditionally ignored in foodweb studies, but their potential role has been given increasing attention in high latitude studies (Hecky & Hesslein, 1995; Hansson & Tranvik, 2003; Sierszen, McDonald & Jensen, 2003).

The harsh northern pond environment freezes solid for most of the year and should likely select for fast colonising species and generalists of broad tolerance. Yet these ecosystems typically contain only few rotifers (Stross, Miller & Daley, 1980) that are usually thought of as pioneer species responding rapidly to changing environmental conditions. Instead, the zooplankton communities are dominated by stable and abundant macrozooplankton communities (O'Brien *et al*., 2004). In fact, these high-latitude waterbodies are as species-rich as alpine lakes at mid-latitudes (A. Brancelj *et al*., unpublished data) indicating that the dense and variable grazer communities should be able to utilise a wide spectrum of planktonic (Kling, Fry & O'Brien, 1992) as well as other resources in order to maintain their high biomass.

In the present study, we evaluated macrozooplankton feeding in grazer communities of the high latitude ponds of northern Canada with the aim of estimating the ability of dominant subarctic and arctic populations of freshwater zooplankton to graze on different prey, ranging in size from bacteria to large benthic filaments. We hypothesised that phytoplankton, bacteria, benthic mats and resuspended benthic algae provide distinct food sources for pond zooplankton that in turn lead to the observed high abundances of macrozooplankton. We evaluated the zooplankton feeding patterns by quantifying potential pelagic and benthic food sources in the ponds and by way of multiple types of feeding assays: fluorescent beads, radiolabelled cultures and radiolabelled natural substrates. We conducted these assays at two sites that spanned the range of high latitude conditions: subarctic ponds in the forest-tundra region of subarctic Quebec and high arctic ponds in the polar desert catchments of the Canadian Arctic Archipelago.

Methods

Sample collection and food inventory

The subarctic forest-tundra sampling site was located near the village of Kuujjuarapik, on the coast of

eastern Hudson Bay (55–56°N, 77–78°W). The high arctic polar desert site was on Cornwallis Island in the vicinity of Resolute Bay, in the Queen Elizabeth Islands (74–75°N, 94–95°W). The subarctic sites had vegetated watersheds with shrub tundra and patches of black spruce whereas the high arctic sites had barren desert catchments that were largely devoid of vegetation. Five ponds were sampled in the Subarctic between 7 and 25 July, and four ponds and a deeper waterbody were sampled in the High Arctic between 18 and 26 August, 2002. All subarctic ponds were small in surface area (<0.1 ha) and shallow (<1.0 m). The four high arctic ponds spanned a range of sizes (0.0005–6 ha) but all were <1.5 m deep. On Cornwallis Island we also sampled the inshore waters of Meretta Lake, a larger waterbody that has a maximum depth of 9 m. Temperature, conductivity and pH were measured with an Oakton water analyser probe. During our sampling period none of the High Arctic sites were ice-covered and all had low mean water temperatures (3.6–6.3 °C; Table 1).

Samples for nitrate nitrogen (NO_3-N), soluble reactive phosphorus (SRP), unfiltered total phosphorus (TP) and unfiltered total nitrogen (TN) were taken from the mixed water column with acid-washed sampling bottles. To determine the nutrient resource conditions experienced by the phytobenthos, additional samples were taken from the interstitial water of the mats using a 10 mL syringe that was inserted into surface stratum of the benthic mats and emptied into a sampling bottle. Dissolved and particulate organic carbon (DOC and POC) samples were also taken from the water column. All samples were treated according to sampling procedures outlined in the Analytical Methods Manual of Environment Canada (1979). Aliquots of water (250–1000 mL) for Chl *a* were collected on average six times per site during the study period. The samples were GF/F filtered and frozen until analysis following Nusch (1980). Microbial mat chlorophyll was sampled with a 10 mm diameter plastic syringe that had been cut and sharpened. The top 1 mm was frozen until extraction and analysis as in Vézina & Vincent (1997). Additional cores were taken to determine the organic carbon content of the mats by weighing before and after combustion for 2 h at 400 °C.

Table 1 Background limnological data for the five subarctic and five high arctic waterbodies

Site	Area (m^2)	Depth (m)	T (°C)	pH	Cond. ($\mu S\ cm^{-1}$)	DOC ($mg\ L^{-1}$)
S6	320	0.3	14.9	6.0	39.5	4.6
S7	15	0.3	23.5	6.6	210.0	8.8
S8	14	0.3	16.6	7.3	56.2	13.2
S9	24	0.4	16.1	7.4	54.0	10.3
S10	100	0.5	16.8	7.6	60.9	12.6
A1	40 000	1.5	3.6	8.5	244.4	2.8
A2	2 62 000	9.0	4.7	8.5	151.0	1.7
A3	5	0.2	6.3	9.6	622.0	3.0
A4	60 000	0.3	4.5	8.4	385.0	2.0
A5	20 000	1.0	4.1	8.4	623.7	1.8

The values for temperature, conductivity (Cond.) and pH are mean values for 12–17 midday measurements in July for subarctic S8–S10 ponds, and 4–5 measurements in late August for arctic A1–A5 sites. A2 = Meretta Lake. Dissolved organic carbon (DOC) values are from single measurements.

Water samples for bacterial enumeration were preserved in 2% (final concentration) formaldehyde. Sample preparation for microscopy involved staining of 3 mL of sample with 0.05 $\mu g\ mL^{-1}$ of the nucleic acid-staining fluorochrome 4′,6-diamidino-2-phenylindole (DAPI) for 1 h, followed by filtration through a 0.2 μm black Nucleopore membrane. Filters were mounted on slides with Aqua-Poly Mount and frozen until examination at 1000× magnification. Picophytoplankton samples were prepared for microscopy by filtering 10–15 mL through a 0.2 μm Anodisc membrane. Slides were frozen until examination at 1000× using a Zeiss fluorescence microscope with green and blue excitation. Samples for protists (phytoplankton and protozoa) were preserved in the field with 1% glutaraldehyde and 0.1% paraformaldehyde and stored at 4 °C. Utermöhl sedimentation, DAPI fluorescence and Nomarski optics (inverted fluorescence microscopy as in Lovejoy *et al.*, 1993) were used to locate, measure and enumerate protists >2 μm in size.

To establish an inventory of food items potentially available for zooplankton in the water column we calculated the abundance of bacteria, picoplankton, phytoplankton and ciliates. Because size and shape of algae are important for zooplankton food selection and ingestibility we measured the length of each algal taxon and classified them in either nanoplankton (2–20 μm) or microplankton (20–200 μm) categories. For genera such as *Dinobryon* and chain-forming diatoms we used the average colony size as a discriminator of length because this is how the zooplankton encounter algae in the water column. Phytoplankton biomass was calculated as wet weight

from measured algal volumes and converted to carbon biomass according to Rocha & Duncan (1985). For picophytoplankton, an average cell volume of 1.8 μm^3 was calculated followed by conversion to carbon as for phytoplankton. Bacterial carbon biomass was calculated by using an average cell volume 0.03 μm^3 and volume-biomass conversion factor of 0.308 pg C μm^{-3} (Fry, 1988). Because we did not have information of algal volumes in the microbial mats, we estimated the benthic algae carbon concentration by assuming a C : Chl *a* value of 35 : 1, a value near the lower range for phytoplankton (Sládecek & Sládeckova, 1964; Vincent, Bertrand & Frenette, 1996). Higher conversion factors would likely overestimate the active algal carbon in microbial mats where photosynthesis is concentrated at the very top of the community. The carbon values were further used to calculate the percentage of living cells in total POC (Table 2).

As an overall analysis of zooplankton abundance in high-latitude waterbodies, we collected samples from 32 sites, including lakes with fish ($n = 17$, mean depth = 8.9 m), lakes without fish ($n = 7$, mean depth = 7.3 m) and shallow ponds without fish ($n = 8$, mean depth = 0.7 m. Lake samples were collected from northern Finland (68–70°N, 20–22°E) between 14 and 22 September 2000. The samples were taken from the deepest point of the lake using a 200 μm mesh size net which was lowered near the bottom and gently pulled back to the surface to obtain a quantitative sample. Depending on the zooplankton abundance, this was carried out one to five times per lake. Pond zooplankton were additionally sampled in eastern subarctic and arctic Canada in 2002, together with the limnological data presented in this paper. These samples were collected from an undisturbed water column for the estimation of population densities. A 4 L sampling container was filled six to 10 times (24–40 L) and the sample passed through a 50 μm mesh. The zooplankton were washed from the filter into a bottle. All samples were preserved in the field with formaldehyde (final concentration 4%). Only adult zooplankton were taken into account when counting population densities.

Zooplankton grazers for the feeding experiments and dry weight (DW) measurements were collected by horizontal trawls using a 50 μm mesh plankton net with a 25 cm diameter. As trawling most likely affected the zooplankton community density in these small ponds, no time series of samples were collected. The live animals were transported into the laboratory in 1 L bottles and all experiments were started within few hours from the collection of zooplankton. On average, 50 individuals per species were frozen in preweighed 2.5 mL plastic vials for later DW measurements (12 h in 60 °C).

Primary production

Photosynthetic rates were measured *in situ* using the ^{14}C-bicarbonate protocol as in Vincent *et al.* (1993).

Table 2 Nutrient concentrations in the water column and in the interstitial water from microbial mats, and different fractions of particulate organic carbon (POC) in seston and in microbial mats at the Kuujjuarapik (S6–S10) and Resolute (A1–A5) sites. Per cent live cells refers to the percentage of algae and bacteria cells in POC_{total}.

	NO_3-N (μg L^{-1})		SRP (μg L^{-1})		TN (μg L^{-1})		TP (μg L^{-1})		POC_{total} (mg m^{-2})		POC_{cells} (mg m^{-2})		POC (% live cells)	
Site	Water	Mat	Water	Mat	Water	Mat	Water	Mat	Water	Mat	Water*	Mat**	Water	Mat
S6	3.0	–	0.5	–	193	–	4	–	160	73 700	4.2	9200	2.6	12.5
S7	2.0	–	1.7	–	602	–	12	–	440	48 800	9.3	5000	2.1	8.4
S8	4.0	60.0	1.2	208.0	774	1 40 200	9	3420	105	77 900	6.5	13 400	6.2	17.2
S9	4.0	40.0	1.0	92.0	612	16 220	33	940	180	75 400	6.1	13 000	3.5	17.2
S10	4.0	40.0	1.4	88.0	568	35 800	13	1290	230	19 600	24.1	800	10.7	3.9
A1	2.0	20.0	1.5	60.0	226	1620	5	60	400	31 700	11.4	3000	2.9	9.5
A2	1.0	20.0	1.0	118.0	146	8080	5	570	260	42 000	12.7	4000	4.9	9.5
A3	1.0	37.5	2.3	101.3	412	1 15 250	21	10 700	130	31 200	7.9	2700	6.1	8.6
A4	1.0	20.0	1.2	60.0	172	4980	5	520	40	56 800	2.7	4300	6.2	7.6
A5	1.0	20.0	1.3	94.0	194	1540	4	150	430	11 600	5.8	700	1.4	6.0

*From measured biovolumes of algae and bacteria converted to carbon.

**From Chl *a*, converted to carbon with a C : Chl *a* conversion factor of 35:1.

SRP, soluble reactive phosphorus; TN, unfiltered total nitrogen; TP, unfiltered total phosphorus.

Three light bottles and one dark bottle were filled with 50 mL of mixed pondwater for water column primary production, and with 50 mL of GF/F filtered pond water and a 10 mm diameter pellet of microbial mat (thickness 1 mm) to measure microbial mat photosynthesis. All bottles were inoculated with 0.2 μCi mL^{-1} of ^{14}C-bicarbonate. Incubations were at 10 cm depth and the measurements were extrapolated to the total water column on the assumption that depth-related changes *in situ* PAR do not affect primary production in shallow tundra ponds (Stanley & Daley, 1976), and phytoplankton are likely to be photosynthesing at maximum rates throughout the water column. The bottles were incubated for 2–4 h simultaneously for all ponds in one region, transported into the lab in the dark and the contents of each bottle were then filtered through a 25 mm diameter GF/F filter. The filters were placed in 7 mL scintillation vials with 0.25 mL 0.5 N HCl to remove inorganic carbon and stored at 4 °C. Aliquots of 200 μL with 200 μL ethanolamine were stored for total activity. Filters with microbial mats were subsequently ground with a Teflon tissue grinder (Fisher Scientific Company, Ottawa, Canada), 5 mL scintillation cocktail (Beckman Ready Safe, Beckman Coulter Canada Inc., Mississauga, Canada) was added to all samples and they were counted in a Beckman 6500 scintillation counter (Beckman Coulter Canada Inc., Mississauga, Canada). Dark uptake rates were subtracted from the light uptake to obtain the photosynthetic carbon uptake. Dissolved inorganic carbon samples were taken from each pond, GF/F filtered and analysed by the National Laboratory for Environmental Testing using methods given in Environment Canada (1979).

Grazing experiments

Grazing rates of the dominant zooplankton species were measured by four types of feeding assay: fluorescent polymer beads (Duke Scientific Corporation, California, CA, U.S.A.), ^{14}C-labelled picophytoplankton, ^{14}C-labelled filamentous cyanobacteria, and ^{3}H-labelled bacteria from the water column and microbial mats originating from the study ponds.

All fluorescent beads were incubated in GF/F-filtered pond water for 24–48 h before the commencement of the experiment for the beads to be coated with natural proteins to improve palatability (DeMott, 1986). The beads were offered to zooplankton as a mixture of 0.5, 1.0, 5.0 and 10. μm size beads with maximum concentrations of respectively 800, 250, 70 and 10 beads mL^{-1}. These were within the natural range of similar size of food in water column for the 5.0 and 10. μm beads but were reduced for the 0.5 and 1.0 μm beads to facilitate microscopy. Depending on species, 10–20 individuals were sorted to beakers (250 mL for fairy shrimps, 120 mL for all others) containing a bead feeding solution. After mixing with a glass-rod, the incubation lasted for 10–20 min for cladocerans, 15–30 min for copepods and 45 min for fairy shrimps. Differences in times were based on the size of animals and were shorter than the gut passage time according to the observation that only few beads were found in the hindgut during the microscopy. The incubations times were too short for any settling of the beads on the bottom of the beakers. The experiment was terminated by pouring carbonated water (Alka-Seltzer, Bayer Inc., Toronto, Canada) into the experimental beakers to narcotise the animals, after which the animals were rinsed using a 50–200 μm sieve to remove excess beads, and preserved with formaldehyde. Prior to microscopic analysis, the formalin was washed off and the zooplankton were incubated for 3–24 h in a proteinase-K (Sigma-Aldrich Canada Ltd., Oakville, Canada) cell digestion solution (final concentration 0.1 μg μL^{-1}). This bleached the carapace pigmentation and dissolved the tissue of the organisms allowing the gut of the animal to be clearly visualised. The animals were placed between a slide and cover slip and the number of beads was counted within each individual with a fluorescence microscope under 400× magnification.

Cultures of picophytoplankton (size 1.5 μm) originating from a pond in Kuujjuarapik and filamentous *Oscillatoria* sp. (strain E7) from a benthic mat in a Resolute pond, were brought into unialgal culture in BG11 medium as in Vézina & Vincent (1997). The Oscillatorian has a cell length of 7.2 μm and filaments were composed of a minimum of two cells, but up to >100 cells. In their natural environment, the filaments are intertwined in cohesive mats, but vary greatly in length. Here the cultures were not continuously shaken which would lead to shorter filaments. Subcultures of these materials were labelled with ^{14}C and offered to the zooplankton using a method modified from Kankaala (1988). One millilitre of dense cell suspension was added to 100 mL of GF/F filtered water from the specific pond where the animals originated. The algae

were inoculated with 0.2 μCi mL^{-1} of ^{14}C-bicarbonate for 1–4 days under natural light. The zooplankton was collected up to 12 h before the experiment, 10–50 individuals, depending on the species, were gently sorted into beakers containing filtered pond water (250 mL for fairy shrimps, 120 mL for all others) and given 0.5 mL of the non-labelled thick algae suspension for acclimation to the food (30 min). Two millilitres of labelled cells were injected into the beakers, gently stirred with a glass rod and left to be grazed between 10 and 45 min. Each species was studied separately for picophytoplankton and filamentous algae and in three replicates. Blanks were made with formalin-killed animals. To determine the ^{14}C-activity of labelled algae, 30 mL of suspension was filtered through GF/F filters. The samples were subsequently dissolved with 0.5 mL 0.1 M KOH at 37 °C for 20 h after which 2 mL of scintillation cocktail were added and the samples then ground with a Teflon tissue grinder. A further 3 mL of scintillation cocktail were added, and the samples then homogenised, and subsequently counted in a scintillation counter.

Natural water column bacteria were labelled with [^3H-methyl] thymidine. Pond water was filtered through a 20 μm net into a sterile 100 mL glass bottle and inoculated with 0.2 μCi mL^{-1} ^3H-thymidine 1 day prior to the experiments. Labelling occurred over 12–18 h at room temperature after which the suspension was filtered through a 2 μm Nuclepore filter. A 5–10 mL of the filtrate with labelled bacteria were added to 120 or 250 mL of pond water containing zooplankton and incubated for 15–45 min depending on the species. The experiment was terminated by bicarbonate treatment (Alka-Seltzer) after which the beaker contents were poured onto a 100 or 600 μm mesh and rinsed. The animals were then rinsed onto 0.2 μm cellulose nitrate filters (diameter 25 mm) and washed three times with ice-cold trichloroacetic acid (TCA) and ethanol. Samples for total bacteria activity were taken and blanks estimated with formalin-killed animals.

Cohesive pieces of mats or mats attached to stones were placed in beakers to study grazing on microbial mats and were covered with GF/F filtered water, spiked with ^3H-thymidine at 0.2 μCi mL^{-1} activity and allowed to incubate for 1–3 days. Before the experiment, sections of mat of known surface area were placed in new beakers and covered carefully with GF/F filtered water. This was carried out with a help of a funnel to minimise resuspension. Zooplankton were added to beakers and incubated 60 min after which they were removed from the beakers with a pipette into a Petri dish containing Alka-Seltzer, rinsed onto a 100–600 μm mesh to remove excess label and then rinsed onto cellulose nitrate filters in a similar fashion to the bacteria grazing experiment. Several 8 mm diameter cores were taken from the mats and treated with TCA and ethanol to determine the ^3H activity in the mats. All filters with the ^3H-labelled samples were stored in 7 mL scintillation vials in a freezer until analysis. The filters were dried overnight at 60 °C before 0.5 mL ethylacetate was added to dissolve them. They were then ground and counted as for the ^{14}C samples.

Results

Resource pools

All of the subarctic and arctic sites were oligo-mesotrophic in terms of inorganic nitrogen and phosphorus concentrations in the water column and also had low Chl *a* concentrations (Tables 2 and 3). However, the interstitial water within the mat contained up to two orders of magnitude higher concentrations of these nutrients. Consistent with these high nutrient concentrations, both Chl *a* concentration and

Table 3 Chlorophyll *a* concentrations (mg m^{-2}) and primary productivity values (mg C m^{-2} h^{-1}) in the water column and microbial mats at the subarctic Kuujjuarapik (S6–S10) and arctic Resolute (A1–A5) sites

	Chl *a* (mg m^{-2})			Primary productivity (mg C m^{-2} h^{-1})		
Site	Water	Mat	% Mat	Water	Mat	% Mat
S6	0.3	298.8	99.9	–	–	–
S7	0.3	115.7	99.7	–	–	–
S8	1.6	378.7	99.6	3.4	35.4	91.3
S9	1.2	366.1	99.7	2.0	32.4	94.3
S10	3.8	21.6	85.1	1.2	1.8	60.8
A1	2.4	84.9	97.2	1.3	2.4	65.6
A2	1.6	112.7	98.6	0.4	21.5	98.1
A3	0.4	75.5	98.8	–	–	–
A4	3.1	122.4	99.7	0.2	6.0	96.1
A5	1.3	19.5	93.6	0.6	4.9	89.9

Per cent mat refers to the percentage of total Chl *a* or production per unit area. Note that the calculation for Meretta Lake (A2) is for inshore waters of 1 m depth. Chl *a* values are means of six measurements per site on average for the water column and one measurement for mats. Primary productivity values are means of triplicates.

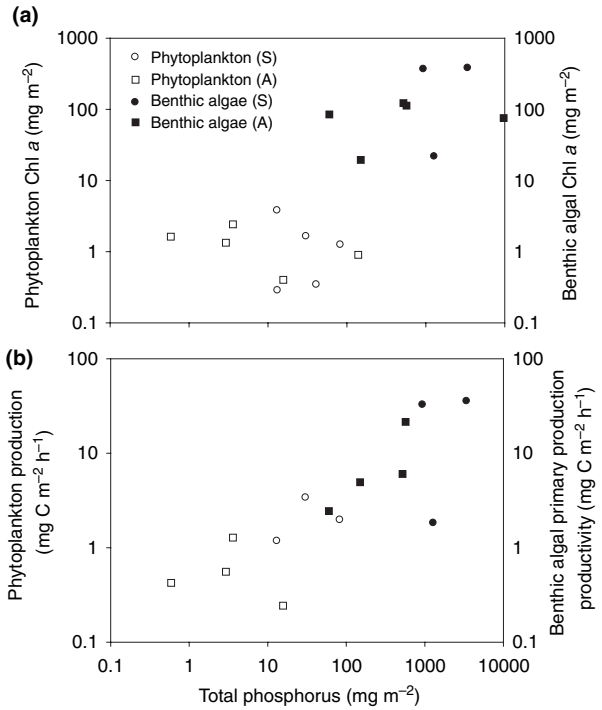

Fig. 1 (a) Chlorophyll *a* and (b) primary productivity as a function of total phosphorus (TP) for subarctic (S) and arctic (A) water column and microbial mats. TP values are habitat-specific: the values for the phytoplankton are measured from water column and values for the benthos are for the sediment interstitial water.

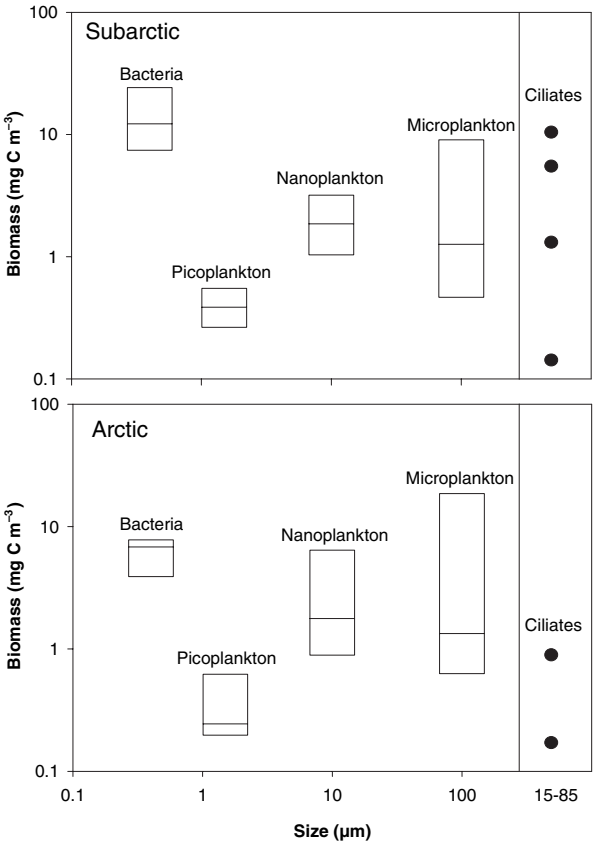

Fig. 2 Box plot of biomass of different size classes of potential zooplankton food in the water column of the studied ponds. Median, 25th and 75th percentiles are shown, each box is based on five samples. For ciliates, all values are shown (one zero value for the subarctic and three zero values for the arctic are not shown because of the log-scale). Bacteria: 0.4 μm, picoplankton: 1.5 μm, nanoprotists: 2–20 μm, microprotists: 20–200 μm, and ciliates (average size was 46 μm for subarctic ponds and 42 μm for arctic ponds).

primary production were higher in the benthic mat communities than in the plankton of the overlying water and were positively correlated with habitat-specific TP (Fig. 1). The benthic community at Kuujjuarapik averaged 236 mg Chl *a* m^{-2}. This represented more than 99% of the total autotrophic biomass (water column and mats) per unit area for all but one pond (S10) where the biomass on the sandy bottom contributed 85% of the total biomass. The mats and plankton in Resolute had lower chlorophyll biomass in comparison with sites in Kuujjuarapik. These high arctic mats averaged 83 mg Chl *a* m^{-2} and represented over 93% of the total autotrophic biomass. At both sites the mats were dominated by filamentous cyanobacteria (mostly Oscillatorians, notably *Leptolyngbya* spp. and *Oscillatoria* spp.) but also contained protists and bacteria. The relative primary production in mats versus plankton was consistent with the biomass ratios, although more variable (Fig. 1b). Subarctic mats contributed 60–95% and arctic mats 65–96% of the total (i.e. planktonic plus benthic) primary production per unit area. In both regions there were benthic algal mats in some ponds that were several mm thick and generated oxygen bubbles that lifted parts of the mats to the surface. Typically, however, the mats were 1–2 mm in thickness.

The biomass distribution of bacteria, pico-, nano- and microplankton and ciliates in the water column, which we used as an estimate of the food resources available to grazing zooplankton, was similar between the two regions (Fig. 2). Bacteria had the highest biomass and picophytoplankton the lowest. Ciliates varied greatly in biomass among ponds and were not detected at some sites. According to median values, nanoplankton contributed more to the biomass than did the microplankton but there was variability among sites. Seventy per cent of the total phytoplankton biomass was associated with taxa that were

<30 μm (data not shown). According to Burns' (1968) linear relationship between carapace length and the maximum-sized polystyrene beads ingested by zooplankton, 30 μm is close to the maximum size of a food particle that many of the zooplankton species studied are able to ingest. However, more recent studies have shown that when fed on algae, zooplankton can ingest larger size cells (DeMott, 1995) suggesting that microplanktonic algae were at least partly available to zooplankton as food.

Zooplankton communities

Our overall analysis of zooplankton abundances in high-latitude waterbodies from several sites in the circumpolar region showed that shallow ponds harboured more abundant populations than the lakes (Fig. 3). Fishless ponds had on average more than 50 times higher abundance of zooplankton than fishless lakes despite the similar nature of the sites in terms of their trophic status; e.g. water column Chl *a* concentrations. Zooplankton density was higher in lakes containing fish and was mainly because of the higher density of small sized *Bosmina* and *Cyclops* species (data not shown) that likely escape grazing from high-latitude fish species such as arctic char. The primary finding of this analysis, however, is that high-latitude ponds typically contain high zooplankton densities.

Detailed examination of the pond zooplankton at the Kuujjuarapik sites showed that *Daphnia*

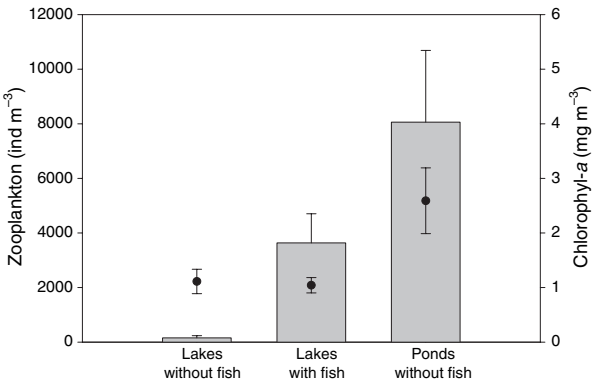

Fig. 3 Adult crustacean zooplankton abundance (bars) in oligotrophic (Chl *a* <5 μg/L) high-latitude waterbodies above the treeline in northern Canada and Finnish Lapland. The Chl *a* values are given as filled circles. Error bars are SE. Lakes without fish: $n = 7$, mean depth = 7.3 m; lakes with fish: $n = 17$, mean depth = 8.9 m; ponds: $n = 8$, mean depth = 0.7 m.

middendorfiana occurred in all subarctic ponds and was accompanied by *Leptodiaptomus minutus* (S8, S9, S10), *Hesperodiaptomus arcticus* (S10), *Ceriodaphia quadrangula* (S8) and *Scapholeberis mucronata* (S6). The arctic sites at Resolute were inhabited by *D. middendorfiana* (A1, A2), calanoid copepods (A2, A3), cyclopoid copepods (A1, A4, A5), and the two fairy shrimp crustaceans (Anostraca) *Branchinecta paludosa* and *Artemiopsis stefanssoni* (A1, A4, A5). Rotifers occurred in all ponds, notably the genera *Keratella*, *Synchaeta*, *Polyarthra* and *Notholca* with an average community abundance of 7200 individuals m^{-3}. Concentrations of cladocerans reached up to 12 900 individuals m^{-3} (304 g DW m^{-3}) in the subarctic and 1200 individuals m^{-3} (67 g DW m^{-3}) in the arctic ponds. Adult calanoid copepods occurred in both regions with concentrations up to 3000 individuals m^{-3} (17 g DW m^{-3}) whereas adult cyclopoid copepods were less abundant with only 200 individuals m^{-3} (2 g DW m^{-3}). The fairy shrimp *A. stefanssoni* had a maximum abundance of 3300 (170 g DW m^{-3}) and *B. paludosa* 1180 individuals m^{-3} (323 g DW m^{-3}).

Feeding rates

The feeding characteristics of 12 crustacean zooplankton populations were assayed with beads, bacteria, picophytoplankton and/or benthic filamentous algae suspended in the water. All species of Cladocera and Anostraca ingested beads whereas, of the copepods studied, only *H. arcticus* fed on the beads and none of the rotifers ingested the beads. This is a commonly observed pattern in which copepods are able to discriminate beads from natural food despite their protein coating (DeMott, 1986). The clearance rates showed that all crustacean species that fed on the beads were able to ingest even the smallest size beads that were within the bacterial size range, and represented the resource pool that was most abundant in the ponds studied. All natural food items were ingested by all species studied, indicating broad feeding capabilities.

Subarctic and arctic zooplankton differed in their feeding rates and food selectivity. Subarctic species fed on the three largest bead sizes with equal clearance rates (Table 4) and often showed increased feeding rates on filamentous algae in comparison with bacteria and picophytoplankton (Table 5). On

Table 4 Size-selective feeding by zooplankton on mixtures of 0.5, 1.0, 5.0 and 10 μm beads (1000 ml^{-1} total). Values are means ± SE for *n* individuals. Multiple comparison test: line below the numbers (characterizing the clearance groups) indicates there is no significant difference between clearance rates. Data not shown for species that did not ingest any of the beads (*L. minutes* and rotifers).

Species	Site	*n*	Clearance rate [L (mg dry weight grazer)$^{-1}$ d^{-1}] 0.5 μm (1)	1.0 μm (2)	5.0 μm (3)	10 μm (4)	Multiple comparison test*	P-value
H. arcticus	S10	15	0.01 ± 0.002	0.02 ± 0.005	0.01 ± 0.003	0.1 ± 0.1	4 2 3 1	<0.0001
C. quadrangula	S8	40	1.8 ± 0.2	3.9 ± 0.4	3.7 ± 1.4	4.2 ± 0.8	2 4 3 1	<0.0001
D. middendorfiana	S8	4	0.1 ± 0.04	0.2 ± 0.01	0.2 ± 0.1	1.7 ± 0.2	4 3 2 1	<0.0001
D. middendorfiana	S10	10	0.4 ± 0.1	0.7 ± 0.2	0.2 ± 0.04	0.9 ± 0.2	4 2 1 3	0.0137
D. middendorfiana	A1	15	1.8 ± 0.4	3.2 ± 0.7	5.3 ± 1.0	5.7 ± 0.8	4 3 2 1	0.0030
A. steffansoni	A5	10	0.4 ± 0.1	0.3 ± 0.7	4.6 ± 1.0	3.2 ± 0.7	3 4 1 2	<0.0001
B. paludosa	A1	10	0.1 ± 0.02	0.2 ± 0.03	2.2 ± 1.0	3.5 ± 0.6	4 3 2 1	<0.0001

*ANOVA followed by Bonferrom/Dum test with adjusted alpha (0.0083).

Table 5 Clearance rates of zooplankton on bacteria (0.4 μm), picophytoplankton (1.5 μm) and filamentous algae (14 μm, minimum length of one filament) derived from subarctic and arctic ponds

Species	Site	*n*	Clearance rate [L (mg dry weight grazer)$^{-1}$ day^{-1}] Bacteria 0.4 μm	Picoplankton 1.5 μm	Filaments ≥14 μm	Multiple comparison test*	*P*-value
L. minutus	S8	50	0.3 ± 0.1	0.1 ± 0.0	5.1 ± 0.6	F B P	<0.0001
L. minutus	S9	30	0.5 ± 0.1	0.6 ± 0.1	38.3 ± 13.7	F P B	0.0229
H. arcticus	S10	30	–	0.02 ± 0.0	2.5 ± 2.4	F P	0.3462†
C. quadrangula	S8	50	3.0 ± 0.2	4.3 ± 0.9	28.1 ± 13.9	F P B	0.1188
D. middendorfiana	S9	15	0.5 ± 0.1	1.9 ± 0.4	11.8 ± 10.4	F P B	0.3877
D. middendorfiana	S10	10	–	0.5 ± 0.1	57.4 ± 18.9	F P	0.0064†
D. middendorfiana	A1	12	0.4 ± 0.1	1.5 ± 0.1	2.0 ± 1.5	F P B	0.3659
D. middendorfiana	A2	20	0.1‡	5.3 ± 0.8	3.1 ± 2.8	P F	0.5275†
Cyclopoida	A4	12	0.1 ± 0.03	2.3 ± 1.0	2.1 ± 2.1	P F B	0.4937
A. steffansoni	A5	25	0.4 ± 0.01	9.5 ± 1.2	2.1 ± 0.5	P F B	0.0004
B. paludosa	A1	15	0.01 ± 0.001	0.2 ± 0.0	0.7 ± 0.1	F P B	0.0022

Values are mean ± SE for three replicate experiments with *n* number of individuals in each replicate. Multiple comparison test: line below the letters (B, bacteria; P, picoplankton; F, filaments) indicates there is no significant difference between the clearance rates.
*ANOVA followed by Bonferroni/Dunn test with adjusted alpha (0.0167).
†From *t*-test.
‡Single sample.

average, filaments were foraged 10–100 times more than the smallest natural food particles. For arctic zooplankton the maximum clearance rates on beads were observed for the two largest sizes, 5 and 10 μm, but these differences were statistically significant only for *B. paludosa*. Such an increase in clearance rates with larger food particles was not observed for natural planktonic food particles; on the contrary, the long filaments were often foraged to a lesser extent than 1.5 μm picophytoplankton. The cladocerans *D. middendorfiana* and *C. quadrangula* had highest mean clearance rate values among the subarctic species. In the Arctic, the clearance rates varied little among species, except for food items <5 μm (Fig. 4). Smaller size food particles were grazed least by the large size fairy shrimp *B. paludosa*.

The results from feeding on ^{3}H-labelled microbial mats revealed that all of the seven studied species were able to feed on the cohesive microbial mats but that the ingestion rates varied greatly among species, from 0.1 to 22.8 μg C $individuals^{-1}$ day^{-1} (Table 6). In general, most species remained in the water column during the feeding experiment and their ingestion rates on the mat were low, <1 μg C $individuals^{-1}$ day^{-1}. However, three species, subarctic *C. quadrangula* and *D. middendorfiana* and arctic *B. paludosa* were observed to swim down to the mats to graze and this was reflected in their much higher

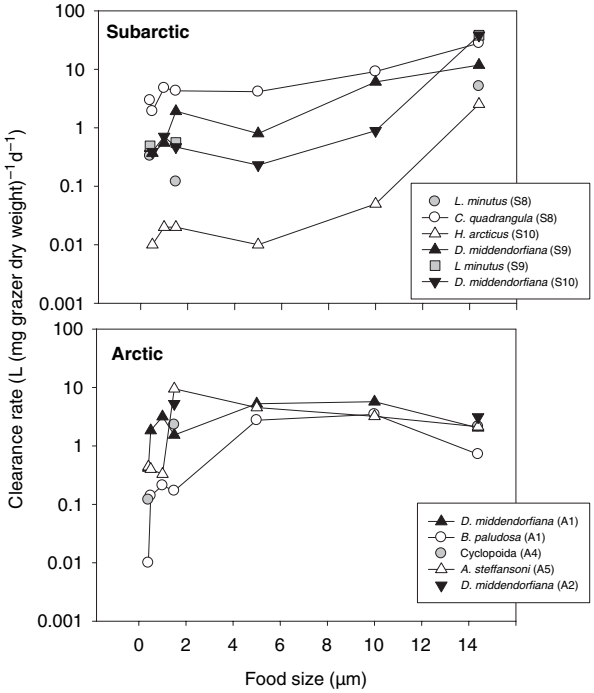

Fig. 4 Mean clearance rates for 11 subarctic and arctic zooplankton populations. The food particles tested included bacteria (0.4 μm), small beads (0.5 and 1.0 μm), picoplankton (1.5 μm), larger beads (5.0 and 10.1 μm), and filamentous algae (minimum length of one filament = 14 μm). The subarctic zooplankton include the cladocerans *Ceriodaphnia quadrangula* and *D. middendorfiana* and the copepods *L. minutus* and *H. arcticus*. The arctic zooplankton include the cladoceran *D. middendorfiana*, the fairy shrimps *Branchinecta padulosa* and *A. stefanssoni* and one species of Cyclopoida. Each point is a mean of three replicates. Note the log scale.

rates of ^{3}H-labelling from the mats. When taking the animal biomass in consideration, the copepod *L. minutus* also proved to be an efficient microbial mat consumer, with a measured ingestion rate equivalent to 38% of its body weight per day.

Discussion

In all of the studied ponds, particulate organic carbon of both seston and microbial mats was mainly composed of detritus. Subarctic water columns contained on average 5% and the arctic water columns 4% of living cells which are in accordance to the 5–13% range of living seston material (algae and bacteria) reported in arctic Barrow ponds (Stross *et al.*, 1980). In a detritus-dominated water column, the bacterial community would be expected to be productive and form a large part of the pelagic food resource for zooplankton. Indeed, bacterial biomass in the ponds was similar to the total phytoplankton biomass and clearly higher than the biomass of picophytoplankton alone. Drakare (2002) and Drakare *et al.* (2003) have shown that when bacteria have access to non-algal organic carbon they dominate the picoplankton because of their superior competition for inorganic nutrients. Humic DOC may additionally favour bacteria as it contains both energy and nutrients and may be broken down into utilisable forms by UV-photodegradation in these clear, shallow waters. This may account for the observation that in humic-rich subarctic ponds the biomass difference between bacteria and picophytoplankton was more pronounced than in the arctic polar desert ponds. Higher bacterial biomass may also reflect the increased release of dissolved organic matter from the benthic microbial mats at warmer temperatures.

Bacteria have been shown to form a substantial part of zooplankton diets in temperate latitudes (Kankaala, 1988; Wylie & Currie, 1991). In this study, our assays showed that although zooplankton ingested bacterioplankton, they had higher clearance rates for other food items. Zooplankton have been shown to control

Table 6 Species ingestion on microbial mat material (μg C individuals^{-1} day^{-1}) and its contribution to animal's body weight (% carbon weight)

Site	Species	*n*	Weight* (μg C individuals^{-1})	Ingestion (μg C individuals^{-1} day^{-1})	% Body weight
S8	*Ceriodaphnia quadrangula*	45	0.8	1.9 ± 0.7	232.8
S9	*Daphnia middendorfiana*	20	11.8	4.9 ± 0.7	41.5
S9	*Leptodiaptomus minutus*	40	2.1	0.8 ± 0.3	38.0
A1	*Daphnia middendorfiana*	50	28.0	0.5 ± 0.2	1.8
A1	*Branchinecta paludosa*	12	137.0	22.8 ± 11.2	16.7
A4	Cyclopoida	30	25.0	0.4 ± 0.4	1.5
A5	*Artemiopsis steffansoni*	50	25.8	0.1 ± 0.1	0.3

Ingestion values are mean ± SE for three experiments with *n* individuals in each experiment.
*Carbon weight was estimated as 50% dry weight.

the abundance of bacterivorous flagellates in subantarctic ponds (Tranvik & Hansson, 1997). This reduced grazing pressure on bacteria, in addition to favourable growing conditions may contribute to the high bacterial biomass in northern ponds. The measured 10–100 times higher clearance rates for phytoplankton suggest that the low phytoplankton biomass in the waterbodies studied was at least partly a result of herbivorous grazing. Chrisholm, Stross & Nobbs (1975) have earlier shown that *Daphnia*, which commonly occurs in tundra ponds is capable of filtering the entire pond volume within only 2 days.

The minimum food particle size for a given filter-feeding zooplankton species is determined by the setae distance of its filtering apparatus (Hessen, 1985) whereas the maximum size of particles ingested can be estimated from the body length (Burns, 1968). We were unable to determine a maximum food particle size for any of the species studied although species lengths varied between 0.7 mm (*Ceriodaphnia quadrangula*) and 10.2 mm (*B. paludosa*). It is likely that the small size range of food in this study prevented us from seeing the upper size limits of food for zooplankton as for most pelagic species of cladocerans and copepods food that is <30 μm is the preferred particle size (Monakov, 2003). However, the similarities observed in size-dependent feeding for cladocerans, copepods and anostracans were striking and unexpected. Cladocerans usually feed most efficiently on bacteria and picophytoplankton and show reduced feeding rates for longer filaments, while copepods tend to increase their ingestion with larger food particles (Fulton, 1988; DeMott, 1990). In our study, all cladocerans filtered effectively on beads ≥1 μm and on picophytoplankton but the highest clearance rates among subarctic cladocerans were measured for filamentous algae. Although other work has also shown that *Daphnia* can feed on Oscillatorian filaments >1 mm in length (Haney, 1987), the limitations of our experimental setup need to be considered. The length of filaments in the suspended feeding solution could not be controlled and may have varied between 14 μm (short filaments) to several millimetres, providing possibly food sources of varied accessibility to different species. In addition, as crustaceans are known to be able to regulate their filtering rate depending on the food concentration (O'Brien, 1974; Mourelatos & Lacroix, 1990), the measured clearance rates may simply reflect the feeding rate response to food concentration; already moderate concentrations of filaments may saturate copepod feeding whereas the concentrations of larger beads may have been too low for estimating accurate feeding by smaller grazers. Within these limitations, however, these results provide an indication of the sizes and types of particles that zooplankton can exploit in high-latitude waters.

The high deviations in clearance rates between the same species from different sites may also partly result from the limitations of our experimental setup. However, this may also reflect differences in feeding history, or behavioural and genetic differences between populations. It has also been shown that individuals of the same population can differ in their responses to different tasting food (DeMott 1988). Similar adaptation to taste or simply to a presence of certain size or type of food may explain the different size-dependent tendencies in clearance rates between subarctic and arctic zooplankton. Such seasonal adaptation to changes in natural seston and resultant differences in ingestion are known for marine copepods (Skiver, 1980) and could result from the adjustment of the filtering area and mesh size of the filter-comb to a certain size of food in their natural habitat (Voigt & Benndorf, 2000).

Our analysis of resources showed that the benthos made up 65–98% of the total primary productivity in the sites studied, including the littoral zone of the 9 m deep arctic Meretta Lake. These results are in accordance with earlier studies that have emphasised the importance of periphyton production in high latitude and other highly transparent lakes (Welch & Kalff, 1974; Vadeboncoeur *et al*., 2003). Periphyton especially on soft sediments have access to high concentrations of nutrients diffusing up from the sediments and from their interstitial waters (Hansson, 1992; Hillebrand & Kahlert, 2001) which as shown in the present study, can be orders of magnitude higher than nutrient concentrations in the overlying water column. Periphyton also benefit from the favourable light milieu in shallow and low turbid waters. Despite both the large biomass and high production rate the benthic microbial mats are rarely considered a trophic component of zooplankton foodwebs, although it is known that when algal concentration in the benthos is particularly high, *Daphnia magna* and *D. pulex* can collect them at the bottom (Fryer, 1987). Overall, there are few reports in the literature that consider benthic

algae as a direct food source to zooplankton (Heywood, 1972; Hansson *et al.*, 1993; Hecky & Hesslein, 1995). More recently, Hansson & Tranvik (2003) showed using stable isotopes that it is likely that some zooplankton species feed directly on benthic algae at the sediment surface in sub-antarctic and arctic lakes.

The microbial mat organic carbon content in the subarctic ponds was on average 12% algae and 88% detritus including bacteria and other heterotrophic organisms. In arctic ponds the equivalent values were 8% and 92%. This algal content is much higher than the reported value 0.06% sediment organic carbon in arctic Barrow ponds (Alexander *et al.*, 1980) but the benthic Chl *a* concentrations in our ponds were also 10- to 100-fold higher than in Barrow ponds. Despite the relatively high algal abundance in the microbial mats, detritus still contributed most of the benthic organic matter, therefore sequestering the nutritionally best-quality algal food in a mass of non-living material. Alexander *et al.* (1980) invoked this dilution effect to argue that epipelic algae could not make a significant contribution to zooplankton food resources. However, other research has shown that detritus can contribute significantly to zooplankton food. According to the studies reviewed by Monakov (2003) crustaceans grow particularly fast when feeding on fresh and decaying detritus. Also bacteria can utilise detritus of any age and origin and subsequently play a role as food for many cladocerans.

All of zooplankton species studied here incorporated the radiolabel from microbial mats indicating that they are able to feed on the benthic communities. However, the ingestion rate of zooplankton on this mat material and its contribution as per cent of body weight per day varied greatly among species. Species that were observed to swim down to the mats during the experiment (subarctic *C. quadrangula* and *D. middendorfiana* and arctic *B. paludosa*) ingested mats at rates equivalent to 16–230% of their body weight per date. Values >100% are common in the literature (reviewed by Monakov, 2003) and often result from the short incubation time that may overestimate the ingestion over a longer time period. Species that stayed in the water column during the experiment ingesting only resuspended material incorporated mats at a body weight equivalent of 0.3–38% per day. These values imply that microbial mats are likely to be accessible even to planktonic species and that this trophic link between mats and zooplankton varies greatly among species. Cladocerans and anostracans may feed directly on benthic mats including algae, bacteria, other heterotophic organisms and detritus, by sucking lose particles into their feeding chamber, while copepods are able to bite off parts of filaments and bigger particles (DeMott, 1982; DeMott & Moxter, 1991). All species may also ingest mat material indirectly via the DOC-bacteria pathway and via suspended particles and detritus derived from the mats. In this study the mats were labelled with ^{3}H-thymidine which is incorporated by bacteria. Therefore measured ingestion resulted from bacteria and from organisms that had ingested nanoflagellates, ciliates and mixotrophic algae. It is also likely that there was non-specific binding of the ^{3}H-thymidine to cyanobacterial filaments and so part of the transfer of label to the zooplankton may reflect direct feeding on the mat Oscillatorians. In addition, all zooplankton species in the plankton grazing experiments were able to ingest resuspended filamentous algae that originated from microbial mat, suggesting that autotrophic benthic algae may also contribute to the zooplankton diet.

In the windswept open tundra, resuspension from the mats to the seston is likely to be common. Shallow waterbodies are well mixed, and bacteria, cyanobacterial trichomes, associated protists and larger pieces of mat material are regularly mixed up into the water column. Such resuspension from the sediments has also been reported to be a constant phenomenon during the summer months in Alaskan tundra ponds (Miller, Prentki & Barsdate, 1980). This physical coupling between the water column and the underlying benthic environment creates heterogeneity in ponds and provides opportunities for additional food sources for zooplankton. However, the high biomass of microbial mats in high-latitude ponds implies that they are not heavily controlled by grazing or by resuspension losses. Vadeboncoeur *et al.* (2003) have also reported that grazing did not decrease benthic primary production in Greenland; on the contrary, the periphyton productivity was highest in these oligotrophic lakes where the densities of large benthic grazers were also highest. Our relatively high ingestion values on microbial mats may therefore be overestimated in comparison with grazing in natural environments because of the absence of alternative food in seston during the experiment. Zooplankton in

ponds may rely more on easily digestible suspended seston food than particles that need to be torn apart from cohesive mats. On the other hand, direct grazing on mats or on suspended mat aggregates may be energetically efficient and allow zooplankton to allocate more energy to other vital activities such as growth and reproduction, more so than the harvesting of a dilute phytoplankton diet would allow (Hecky & Hesslein, 1995). Our results point to the importance of benthic resources but additional work is required to quantify the degree of coupling between benthic mats and zooplankton and to thereby develop a more accurate picture of high-latitude foodwebs.

In conclusion, our observations from subarctic and arctic lakes and ponds indicate commonalities in ecosystem structure and trophic relationships. Primary production in these systems is dominated by the nutrient-rich benthos and the water column contains multiple species of zooplankton at high abundance. Our feeding experiments show that there is much variability in food selection and assimilation rates among species and also among populations of the same species consistent with earlier observations. Zooplankton feed on and may control algal biomass in the water column. Several zooplankton species are also capable of feeding directly on the benthic mats, with high assimilation rates. Certain other species can ingest particles from mats that are brought up into suspension. We suggest that benthic-pelagic coupling, already well recognised for fish feeding in deeper arctic waterbodies (Hobson & Welch, 1995; Hershey *et al*., 1999; Sierszen *et al*., 2003), is important for the multidimensional food web structure and functioning in subarctic and arctic ponds. The interactions between the benthos and water column are likely to play a major role in the productivity, nutrient transfer, species richness and resource partitioning of zooplankton in the ubiquitous ponds of the north circumpolar environment.

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