Rotifers in arctic North America with particular reference to their role in microplankton community structure and response to ecosystem perturbations in Alaskan Arctic LTER lakes

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Abstract:
Growing interest in the development of mineral and recreational resources, along with the recognition that arctic ecosystems may be among those most affected by global change, has stimulated the study of arctic systems in recent decades. These have included studies of rotifers. Two approaches have generally been pursued: taxonomic studies to determine the number and species of individuals, and ecological studies that have attempted to determine the trophic relationships between rotifers and other microorganisms in aquatic ecosystems. Results from studies at the Arctic Long Term Ecological Research Site in Alaska, USA are reviewed and the microbial food web is described based on empirical and literature data. Arctic systems are sites of rich opportunity for further studies, especially those which can integrate taxonomic and ecological aspects.
Key words: Rotifera, microplankton, arctic, Alaska

Article:

Introduction

Microplankton, including rotifers, have received considerable attention from aquatic ecologists in recent years because of the pivotal role they play in regulating the transfer of nutrients and energy to higher trophic levels (e.g., Rieman & Christoffersen, 1993). In the classical view, microplankton grazed primary producers and in turn were prey for crustacean zooplankton which are themselves a food resource for larger insects and fish. However, over the last several decades it has become obvious that the classical view is oversimplified and that microplankton act, not only as grazers of primary producers, but also as important consumers of bacterial secondary production (derived from exudates, leaked organic carbon and decomposing organic matter). They may also be consumers of microplankton secondary production, since protozoa and rotifers frequently feed on other protozoans and rotifers.

Another focus of recent research has been the importance of bottom up and top down controls of aquatic ecosystems (Carpenter, 1988). Numerous studies (cf. Carpenter, 1988) have demonstrated that increased nutrient inputs tend to increase biomass at each trophic level, while alteration of higher trophic levels results in a top-down cascade of trophic interactions mediated by the abundance of predators. What has been addressed only marginally is how micro-plankton community structure changes in response to changed controls, and whether the changes modifiy the flow of the bottom-up or top-down regulation.

Given the complexity and varying roles that microplankton play, it is difficult to determine how food webs function at the microbial level and how they respond to perturbations. Arctic ecosystems offer unique opportunities for such studies, because their extreme climate leads to reduced complexity of arctic systems relative to their temperate and tropical counterparts. This paper briefly reviews studies of rotifers in North American arctic systems, especially in relation to the progress and observations made at the Arctic Long Term

Ecological Research Site at Toolik Lake, Alaska.

Previous studies

Taxonomic treatments of Canadian arctic rotifers (Table 1) were recently reviewed by De Smet & Beyens (1995), and will be only briefly mentioned here. De Smet & Beyens (1995) identified 70 taxa of rotifers, bringing to 114 the total number of taxa that had been identified in the Canadian high arctic, but suggested that many more taxa would probably be discovered as the number and intensity of studies increased. They also noted that low species richness and diversity of Canadian high arctic rotifer fauna relative to other regions was probably due to the severe physical environment, short growing season, limited spatial and habitat heterogeneity, the short length of time since the last glaciation of northern Canada, as well as the limited number of studies. De Smet & Beyens (1995) also suggested that the Alaskan arctic might have greater species richness and diversity than the Canadian arctic since large areas of Alaska had escaped glaciation. Chengalath & Koste (1989) collected rotifers from 212 sites in arctic North America and identified 165 species, of which 127 were from arctic sites in Alaska, the Yukon, and the Northwest Territories. This study is one of only two published taxonomic records of Alaskan arctic rotifers, listing 87 species from 38 northern Alaskan sites. The other study (Holmquist, 1975) listed 12 taxa from lakes of northern Alaska. An additional study of rotifers collected from Point Barrow and Nome, Alaska is in progress (De Smet, personal communication). Chengalath & Koste (1989) also cite several older studies that emphasized species descriptions of North American arctic rotifers. Nearly all studies note that most rotifer species found in the arctic are cosmopolitan and that usually only a few species are dominant at any sampling location (De Smet & Beyens, 1995)

Table 1. Recent studies of arctic rotifers in North America

Location	Coordinates	Number of taxa	Reference
Victoria Island, NWT, Canada	69°N, 105°W	112	De Smet (1994), De Smet & Beyens (in press)
Devon Island, NWT, Canada	75°N, 86°W	70	De Smet & Beyens (1995), Minns (1977)
Little Cornwallis Island, NWT, Canada	75°N	51	De Smet & Bafort (1990)
Ellesmere Island, NWT, Canada	81°N	34	McLaren (1964), Nogrady & Smol (1989)
Cornwallis Island, NWT, Canada	75°N	1	Rigler et al. (1974)
Central NWT, Canada	62–66°N	15	Moore (1976)
Northwest Territory & Northern Yukon, Canada & Northern Alaska, USA	above 66°N	127	Chengalath & Koste (1989)
Lakes Peters, Schrader and Wolf, NE Alaska, USA	70°N, 144°W	3	Hobbie et al. (unpublished)
Northern Alaska	above 66°N	12	Holmquist (1975)
Arctic LTER site, Toolik Lake, Alaska	68°N, 149°W	20	Rublee (1992), Rublee & Bette (1995), Rublee & Partusch-Talley (1995) Bettez et al. (in prep.)
Point Barrow and Nome, Alaska	71°N, 156°W		De Smet (personal communication)

Studies of the role of rotifers as components of aquatic ecosystems are also relatively rare in North American arctic ecosystems. Chengalath & Koste (1989) noted 48 publications that included rotifers as members of arctic aquatic communities but gave little detail. Rigler et al. (1974) reported that *Keratella cochlearis* was numerically the second most abundant zooplankter in Char Lake, but that rotifer production was only about 1 % of that of the dominant crustacean zooplankter. Hobbie et al. (unpublished data) found six rotifer species in Lakes Peters, Schrader and Wolf, in northern Alaska, but also noted that they represented less than 2% of the total zooplankton biomass. Rublee & Partusch-Talley (1995) utilized artificial substrates to determine the

response of the microfaunal community to added nitrogen and phosphorus in the Kuparuk River at the Arctic Long Term Ecological Research (LTER) site in northern Alaska. Eight rotifer taxa were found on the substrates, constituting 36% of the microfauna biomass. Microfauna increased in response to nitrogen amendments, but there was no significant increase due to increased phosphorus inputs, although the lack of response may have been due to predation by a high abundance of benthic insects that were the result of a previous fertilization experiment in the river. They also found that the abundance of rotifers and other microfauna on natural rock surfaces in the river was low ($<1 \times 10^3$ rotifers m^{-2}). Fertilization of river reaches stimulated growth of mosses (Bowden et al., 1994), which are ideal substrates for rotifers (De Smet & Beyens,1995), but these were not sampled.

The most extensive studies of the summer seasonal dynamics of rotifer populations and their trophic relationships in the plankton of arctic lakes have been conducted at the arctic LTER site at Toolik Lake in northern Alaska (Bettez et al., in prep; Rublee, 1992; Rublee & Bettez, 1995). The major focus of these studies has been to assess the abundance of micro-plankton (including rotifers) in the water column and to determine their response to perturbations. In unperturbed lakes at the site they reported nine species of rotifers in the plankton, although four dominated: *Keratella cochlearis, Kellicottia longispina, Polyarthra vulgaris* and *Conochilus unicornis*. The abundance of rotifers was low in unfertilized lakes (100–400 individuals l^{-1}), with highest abundance found in late summer (Rublee, 1992). The remainder of this paper will address the response of rotifers to experimental manipulations and feeding studies that have been used to determine trophic interactions of the microplankton community.

Materials and methods

Study site

The Arctic LTER site (68° 38′ N, 149° 43′ W), located in the northern foothills of the Brooks Mountain Range of Alaska, has been under study for over two decades (O'Brien et al., 1997). Climate is extreme: the region is underlain by permafrost with a mean annual temperature of −9°C. Annual precipitation is about 31 cm, with about half falling as rain from late May through September. Ice cover, up to 2 m thick, forms in late September or October and generally thaws in late June. Water temperatures may rise to 12–15°C in the epilimnion by late summer. The combination of cold climate and limited rainfall makes nutrient input a major limiting constraint in the lakes and ponds of the LTER site. As a result, the lakes are highly oligotrophic (Miller et al., 1986) with varying algal, zooplankton and fish populations (Kling et al., 1992; O'Brien et al., 1992).

O'Brien et al. (1997) have described the biotic community of Toolik lake which is typical of the lakes at the LTER site. Algal communities are dominated by small chrysophytes, dinoflagellates, and cryptophytes. Zooplankton include the herbivores *Daphnia middendorfiana* and *Diaptomus pribilofensis*, the carnivore *Cyclops scutifer*, and the larger but much less abundant predator *Heterocope septentrionalis*. Fish, if present, include lake trout, burbot, arctic grayling, and slimy sculpin. At least eight species of chironomids are found in the benthos (Kling et al., 1992). Most data presented here are from Toolik Lake, or from Lake N1, a lake that was fertilized from 1990–1994 by weekly additions of inorganic nitrogen and phosphorus during the summer at rates (3 mM N m^{-2} day^{-1} as $(NH_4)_2SO_4$ and 0.23 mM P m^{-2} day^{-1} as H_3PO_4) which are about four to ten times the normal nutrient loading during the summer. Lake N1 was highly oligotrophic prior to fertilization (Miller et al., 1986).

Rotifers were collected for both enumeration and grazing studies by first concentrating freshly collected water samples by gentle reverse flow filtration through 20-µm mesh net (Dodson & Thomas, 1964). For enumeration, the concentrated samples were preserved with cold glutaraldehyde (1% final concentration), and stored refrigerated until counting following the method of Baldock (1986) which uses rose bengal to stain organisms. In some samples, the dimensions and spine lengths of loricate rotifers were measured.

Rotifer grazing was assessed by directly counting the number of fluorescently labeled food resource analogues that were ingested by individual grazers (Rublee & Gallegos, 1989; Sherr et al., 1987). The food resource analogues included fluorescently labeled bacteria (FLB), fluorescently labeled algae (FLA), fluorescently

labeled yeast (FLY) and fluorescently labeled latex particles (Table 2). Individual microplankters were then hand picked from freshly concentrated samples using glass pasteur pipettes with finely drawn tips, and transferred to filtered lakewater (0.45-µm GFC filters), in blood dilution vials which had been pre-soaked in 10% HCl and rinsed in filtered lakewater. Food resource analogues were then added to the vials and incubated in water baths. Total water volume in the vials was 20 ml, and the number of microplankton generally ranged from 10 to 50 individuals per vial, a range of concentrations that is within the natural ranges found for microplankton in temperate lakes, but does exceed, in some cases, that found for microplankton in arctic lakes. The concentration of food analogues added was either at a level meant to simulate the natural concentration for particles of that size, or spanned a range in order to assess feeding response curves for a particular grazer. Incubation time ranged from several minutes to several hours, and was derived empirically from prior time course sampling to determine optimum balance between enough ingestion to register statistically significant counts, but not so much ingestion that counting ingested particles was difficult.

Table 2. Fluorescently labeled food analogues

Type	Species	Diameter/dimensions (µm)	Source
FLB	*Pseudomonas fluorescens*	1 × 2	Freshwater
FLA	*Nanochloris occulata*	2	Brackish
	Nanochloris sp.	3 × 7	Brackish
	LJ3B (unidentified green)	4–6	Freshwater
	Chlamydomonas rheinhardtii	10	Freshwater
	Chlorella vulgaris	6–8	Freshwater
	Phaeodactylum tricornutum	3 × 20	Marine
	Prorocentrum minimum	15 × 18	Marine
FLY	*Saccharomyces cerevisiae*	4 × 5	Freshwater
	Latex particles	0.49, 2.17, 2.5, 4.3, 5.7, 9.3	

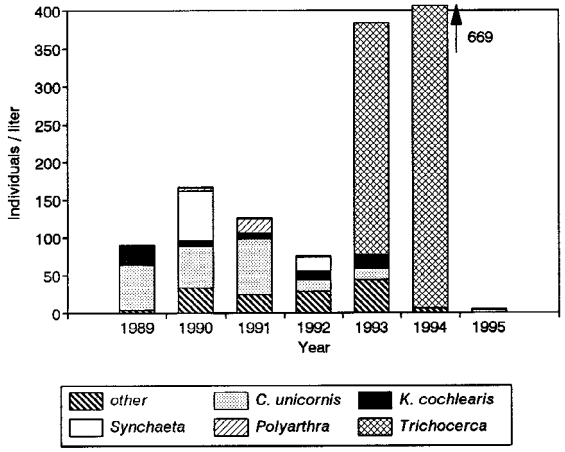

Figure 1. Abundance of rotifers during fertilization experiment of Lake N1 at the Arctic LTER site in Alaska. Lake N1 was fertilized by weekly additions of nitrogen and phosphorus from July to August, 1990–1994.

Following incubation, rotifers were collected on a 20-µm mesh net, washed with filtered lake water to remove excess labeled particles, and then collected on 5.0-µm black polycarbonate filters. Filters were mounted on slides with a 43% sucrose solution and examined by microscopy. Individual microplankters were located on the filter using transmitted light and low magnification (100×–200×) followed by enu meration of ingested particles which were visualized under epifluorescent illumination at higher magnifications (200×–1000×).

A two-step grazing method (Dolan & Coats, 199 1) was also used on one occasion to determine if crustacean zooplankton preyed on the rotifer *Conochilus unicornis*. Briefly, two samples were incubated, both containing fluorescent latex particles and the suspected crustacean predator. One sample also contained the microplankton prey. The method relies on the ingestion of particles by the microplankton, which then appear in the predator if it grazes on the microplankton prey.

Results and discussion

Rotifer species response to fertilization of Lake N1

The response of rotifer species to fertilization in lake N1 was complex. There was a slight increase in rotifer abundance during the first 2 years of fertilization, a decline during the third year, and a dramatic increase in rotifer abundance during the fourth and fifth years (Figure 1). The rotifer abundance dropped to its lowest value after lake fertilization stopped. There was a significant change in rotifer community structure, with a shift from prefertilization dominance by *Conochilus unicornis* and *Keratella cochlearis*, to dominance by a *Synchaeta* sp. during the first year of fertilization, and overwhelming dominance by a *Trichocerca* species during the fourth and fifth years of fertilization (Figure 1). Rotifer abundance declined dramatically during the year following fertilization, which may reflect predatory losses due to increased zooplankton densities as a result of fertilization (Bettez et al., in prep.). Species richness also changed during the fertilization experiment, due to the

appearance of two species, *Conochilus natans* and *Trichocerca* sp., which had not been seen prior to fertilization, and the disappearance of several species during the last year of fertilization.

Rublee (1992) had commented that in general, there tended to be an increase in microplankton biomass with increased trophic status (as estimated by chlorophyll *a* concentrations), although there was no clear relationship between rotifer abundance to trophic status in a suite of nine Arctic LTER lakes over several summers. This lack of relationship between chlorophyll *a* concentration and rotifer abundance remains when data from the fertilization experiment in Lake N1 and from Toolik Lake in 1995 are added to the data set (R = 0.113, 15 d.f., NS). The lack of a clear response suggests that top-down controls on rotifer abundance may be at least as important as food resources in arctic lakes.

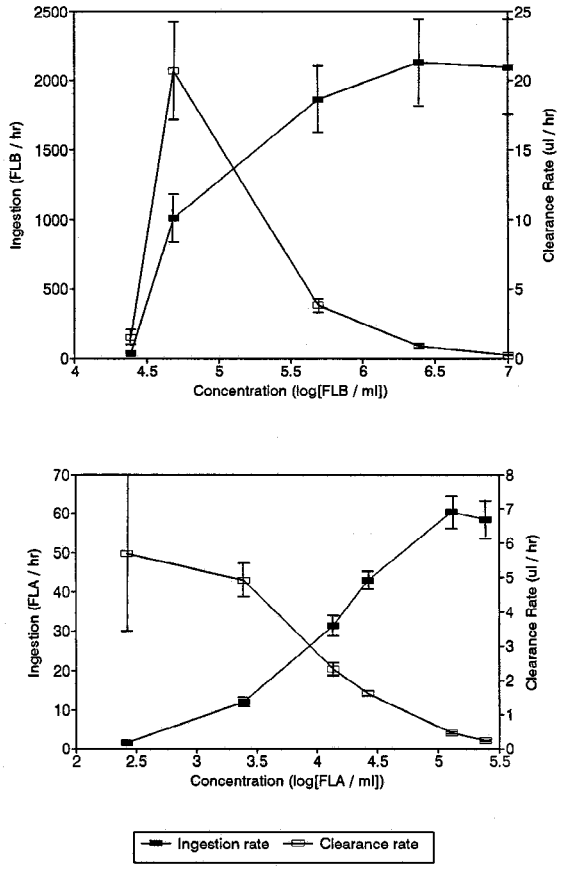

Figure 2. Examples of grazing studies on fluorescent food analogues by arctic rotifers. Upper: *Conochilus unicornis* grazing on 1 × 2-μm fluorescently labeled bacteria (FLB). Lower: *Keratella cochlearis* grazing on 5-μm fluorescently labeled alga (FLA). Error bars, ±1 SE.

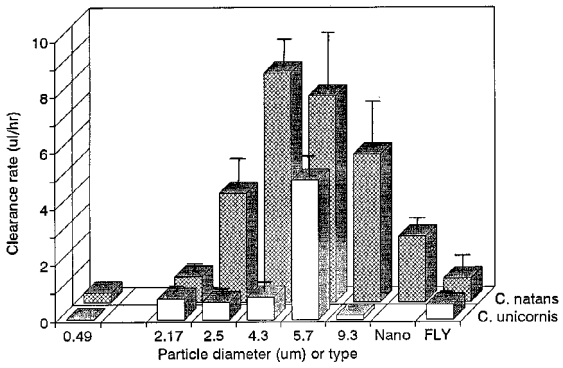

Figure 3. Example of clearance rates of fluorescent latex particles, fluorescently labeled yeast and *Nanochloris* FLA for *Conochilus unicornis* and *Conochilus natans*. Error bars, ±1 SE for *C. unicornis*; *C. natans* data is from a single experiment.

Rotifer grazing

Grazing experiments conducted with various food resources for a variety of rotifer species demonstrated functional response curves, as well as size selectivity. Rotifers displayed Type II/Type III functional responses when presented with FLB or FLA (Figure 2). Clearance rates were variable, ranging from 0 to 20.7 µl ind.$^{-1}$ h^{-1} (Table 3). When presented with fluorescent latex particles, both *C. unicornis* and its congener, the larger *C. natans*, exhibited clearance rates up to 8 µl ind.$^{-1}$ h^{-1}, with highest rates on 5.7- and 4.3-µm diameter particles, respectively (Figure 3). *K. cochlearis* had highest clearance rates on particles of 2.17 µm diameter. *K. quadrata* also selected for small particles, although highest clearance rates were found with 2.5-µm diameter particles. Two other rotifers, *Kellicottia longispina* and *Filinia terminalis*, which are known to be small particle feeders, showed grazing responses on latex particles similar to that of the *Keratella* spp. as expected.

The clearance rates reported here should be considered as low estimates because they were determined using food analogues rather than natural food. However, the results of these grazing studies compare favorably with those reported for rotifers in temperate systems which have generally used other methods to measure grazing

rates (e.g., Gilbert & Bogdan, 1984). Crustacean zooplankton *grazing on* Conochilus unicornis.

Table 3. Experimentally determined clearance rates of rotifers from the Toolik Lake LTER. site

Rotifer	Prey	Clearance rate (μl h^{-1})	Number of experiments
Keratella cochlearis	FLB	0.05–0.46	7
	FLA – *Nanochloris*	0.02–3.7	5
	FLA – LJ3	0.5–5.8	4
	FLA – *Chlamydomonas*	0.25–1.7	6
	FLA – *Chlorella*	0.00–0.56	2
	FLA – *Phaeodactylum*	0.5–15	4
	FLY – *S. cerevisiae*	0.07	1
Keratella quadrata	FLB	0.21	1
	FLA – *Nanochloris*	2.94	1
	FLA – *Chlorella*	0.01	1
Kellicottia longispina	FLB	0.07–0.7	4
	FLA – *Nanochloris*	0.01–0.17	5
	FLA – *Chlamydomonas*	0.28–1.43	5
	FLA – *Chlorella*	0.03–0.29	2
	FLA – *Phaeodactylum*	0.39–1.89	3
	FLY – *S. cerevisiae*	0.05	1
Conochilus unicornis	FLB	0.14–20.7	5
	FLA – *Nanochloris*	0.01–5.5	10
	FLA – *Chlamydomonas*	0.00–0.11	2
	FLA – *Chlorella*	0.10–2.8	3
	FLA – *Phaeodactylum*	4.9–5.5	3
	FLY – *S. cerevisiae*	0.5	1
Conochilus natans	FLA – *Nanochloris*	0.13	1
	FLA – *Chlamydomonas*	0.2	1
	FLA – Phaeodactylum	5.5	1
	FLA – *Prorocentrum*	2.6	1
	FLY – *S. cerevisiae*	0.7	1
Polyarthra vulgaris	FLB and FLA	0	10
Synchaeta sp.	FLB and FLA	0	7
Chromogaster ecaudis	FLB and FLA	0	10
Gastropus stylifer	FLB and FLA	0	8

Crustacean zooplankton ingestion was assayed once with *Conochilus unicornis* serving as a potential food for *Cyclops scutifer* and *Heterocope septentrionalis*. Both crustaceans consumed *C. unicornis*, with the larger *Heterocope* demonstrating that it is a voracious predator when presented with this rotifer as its only food source.

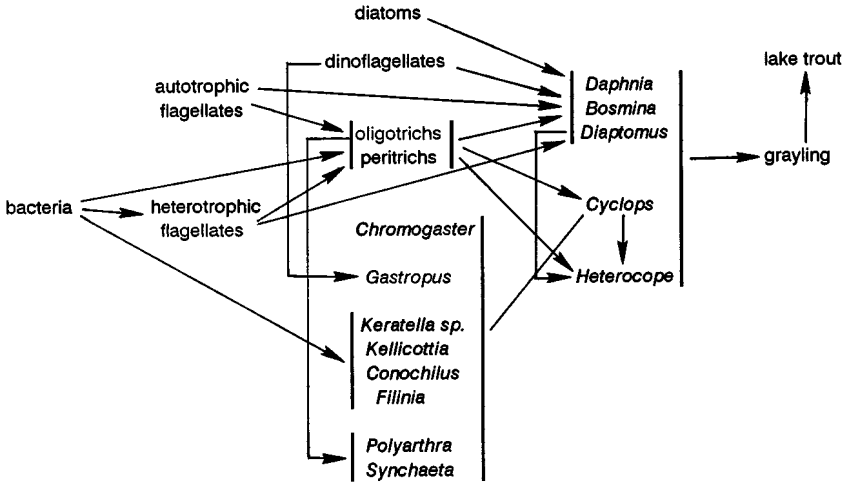

Figure 4. Generalized pelagic microbial food web for arctic LTER lakes.

Microbial food web

The grazing and ecosystem manipulation experiments at the Toolik Lake LTER provide empirical evidence for trophic interactions at a finer level of detail than previously known for these arctic planktonic systems. Insight into nutrition of other rotifer species has been derived from literature studies (e.g., Dumont, 1977; Gilbert & Bogdan, 1984; Pourriot, 1977) and limited additional experimental work at Toolik Lake. For example, *Gastropus stylifer* is known to have a unique feeding habit – it pierces the theca of dinoflagellates and sucks out the cytoplasm. In contrast, *Chromogaster ecaudis* is an autotroph. *Polyarthra vulgaris* and a *Synchaeta* sp. are known to be carnivorous. In numerous experiments with all types of fluorescent food particles, no ingestion was ever observed for any of these species. However, in a single incubation of *Chromogaster ecaudis* with ^{14}C-labeled bicarbonate, significant uptake of isotope occurred over killed controls. Combined, this information allows construction of a more detailed microbial food web for Alaskan arctic lakes, at least to our finest taxonomic level of organism identification (Figure 4).

Conclusions

Although the number of studies of rotifers and their role in arctic aquatic ecosystems is limited, they have provided numerous insights which also present many opportunities for further study. First, taxonomic studies to date suggest that there are many species yet to be identified. Particularly in the Alaskan arctic, which represents a glacial refugium, few taxonomic studies have been conducted, and benthic and littoral habitats as well as riverine habitats have yet to receive attention. Such studies may be especially valuable for comparative studies both to: (1) compare species diversity across landscapes with differing glacial histories as suggested by De Smet & Beyens (1995), and (2) to document existing fauna and the changes which are likely to occur in response to global warming and eutrophication. Integration of genetic characterization into classical taxonomic approaches might also prove extremely valuable since many arctic species are cosmopolitan and thus genetic variability can be compared across latitudinal gradients.

The extreme climate of arctic systems, manifested via limited nutrient input into lakes which keeps them highly oligotrophic also suggests that there are numerous opportunities for ecological studies. Species diversity is limited and food webs are less complex relative to temperate and tropical systems, although the information presented here and from earlier studies suggests that food webs are not simple. Such sites are ideal for studying trophic interactions and regulatory control of aquatic ecosystems, especially at the microbial level, since they represent more tractable food webs in contrast to the much greater complexity of systems at lower latitudes. Again, anticipated global changes which are expected to be most severe in arctic regions present opportunities for studies directed at the response of ecosystems to perturbation.

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