

Shallow freshwater ecosystems of the circumpolar Arctic¹

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Abstract: This review provides a synthesis of limnological data and conclusions from studies on ponds and small lakes at our research sites in Subarctic and Arctic Canada, Alaska, northern Scandinavia, and Greenland. Many of these water bodies contain large standing stocks of benthic microbial mats that grow in relatively nutrient-rich conditions, while the overlying water column is nutrient-poor and supports only low concentrations of phytoplankton. Zooplankton biomass can, however, be substantial and is supported by grazing on the microbial mats as well as detrital inputs, algae, and other plankton. In addition to large annual temperature fluctuations, a short growing season, and freeze-up and desiccation stress in winter, these ecosystems are strongly regulated by the supply of organic matter and its optical and biogeochemical properties. Dissolved organic carbon affects bacterial diversity and production, the ratio between pelagic and benthic primary productivity via light attenuation, and the exposure and photoprotection responses of organisms to solar ultraviolet radiation. Climate warming is likely to result in reduced duration of ice-cover, warmer water temperatures, and increased nutrient supplies from the more biogeochemically active catchments, which in turn may cause greater planktonic production. Predicted changes in the amount and origin of dissolved organic matter may favour increased microbial activity in the water column and decreased light availability for the phytobenthos, with effects on biodiversity at all trophic levels, and increased channelling of terrestrial carbon to the atmosphere in the form of greenhouse gases.

Keywords: Arctic ponds, bacteria, climate change, primary producers, zooplankton.

Résumé : Cette revue fait la synthèse des données limnologiques et des conclusions d'études réalisées sur des étangs et des petits lacs de nos sites de recherche dans les régions arctiques et subarctiques du Canada, en Alaska, au nord de la Scandinavie et au Groenland. Plusieurs des plans d'eau étudiés contiennent d'épais tapis microbiens benthiques qui croissent dans des conditions relativement riches en nutriments, alors que la colonne d'eau sus-jacente est pauvre en nutriments et ne peut supporter que de faibles biomasses phytoplanctoniques. Cependant, la biomasse de zooplancton peut être substantielle, étant supportée par le broutement des tapis microbiens, les apports de débris, les algues et les autres organismes planctoniques. En plus des grandes fluctuations annuelles de la température, d'une courte saison de croissance et des stress hivernaux liés au gel et à la dessiccation, ces écosystèmes sont régulés en bonne partie par l'apport de matière organique et les propriétés optiques et biogéochimiques de celle-ci. Le carbone organique dissous a des effets sur la diversité et la production bactérienne, sur le rapport entre la productivité primaire pélagique et benthique via l'atténuation de la lumière, et sur l'exposition et les réponses photoprotectrices des organismes au rayonnement solaire ultraviolet. Le réchauffement climatique va probablement entraîner une réduction de la durée du couvert de glace, un réchauffement des températures de l'eau et une augmentation des apports en nutriments provenant des bassins versants dont les processus biogéochimiques seront plus actifs. Ces impacts peuvent à leur tour faire augmenter la production planctonique. Les changements prévus dans la quantité et l'origine de la matière organique dissous peuvent favoriser une plus grande activité microbienne dans la colonne d'eau et une réduction de la disponibilité de la lumière pour le phytobenthos, incluant des effets sur la biodiversité à tous les niveaux trophiques, ainsi qu'un transfert plus important du carbone terrestre vers l'atmosphère par l'émission de gaz à effet de serre.

Mots-clés : bactéries, changements climatiques, étangs arctiques, producteurs primaires, zooplancton.

Introduction

A major feature of Arctic landscapes is their large number of lakes and ponds, which in some regions can cover up to 90% of the total surface area (Raatikainen & Kuusisto,

1990; Pienitz, Doran & Lamoureux, 2008). For example, the Mackenzie Delta contains about 45 000 shallow lakes within an area of 13 000 km² (Emmerton, Lesack & Marsh, 2007), and the Yukon Delta has about 200 000 lakes and ponds (Maciolek, 1989). In its entirety, the Arctic has been referred to as "the world's largest wetland" (Kling, 2009). These numerous small lakes and ponds contribute significantly to Arctic biodiversity and can be

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viewed as oases in the tundra. They provide feeding, drinking, and nesting grounds for migrating birds and other wildlife, and many Arctic plants flourish in and around these aquatic and semi-aquatic habitats.

Many Arctic freshwater ecosystems were formed following the last glacial period when depressions that were left behind by the retreating ice masses filled with meltwater to become shallow rock basin lakes and ponds (Pienitz, Doran & Lamoureux, 2008) (Figure 1a). When organic matter accumulated in these rock ponds, tundra ponds were formed. They are likely the dominant category of ponds in the circumpolar Arctic (Figures 1b–d). Other ponds have been formed by the thermal erosion of permafrost soils, and are abundant throughout the circumpolar Arctic. These so-called thaw (or thermokarst) lakes and ponds can have substantial terrigenous inputs, resulting in high turbidity and large concentrations of dissolved organic carbon (DOC) (Figures 1e–f). Another class of circumpolar ponds is formed in depressions on Arctic ice. These range from small cryoconite holes on glaciers to large supraglacial lakes on the Greenland Ice Sheet and on Arctic ice shelves (Pienitz, Doran & Lamoureux, 2008). The lifespan of these ice-bound water bodies can be quite short if sudden drainage occurs through rifts in the ice or when the ice is lost by calving events; however, they can also last for many decades or longer if continuously fed by meltwater each summer (Mueller, Vincent & Jeffries, 2006). There is increasing interest in the biogeochemical activity of these glacial ecosystems in the north and south polar regions (Hodson *et al.*, 2008).

There has been a resurgence of interest in the global limnology of small lakes and ponds, with the recognition that these waters account for a much greater total surface area than previously thought. Downing *et al.* (2006) developed a global model for lakes based on the Pareto distribution and concluded that the total surface area of the world's natural freshwaters (estimated as 4.2 million km²) is dominated by lakes less than 1 km² in area. The lower bound for their analysis was lakes of 0.001 km², given that this was the limit for accurate GIS determinations. The most abundant ponds in the Arctic (and perhaps elsewhere) are of a length scale of tens of metres or less, and thus an areal scale of 0.0001 km² or less, implying that the Downing *et al.* (2006) estimate of the global importance of small water bodies is highly conservative. Furthermore, the density of Arctic lakes and ponds may be much greater than that implied by calculations based on annual runoff (Figure 3 in Downing *et al.*, 2006) because of the abundance of water-filled depressions in deglaciated terrain and the impermeable nature of permafrost, which favours surface water accumulation. Ponds also have high biogeochemical reactivities (Downing, 2008) and larger sediment/water, land/water, and water/air contact zones per unit volume by comparison with larger lakes. These shallow waters on the tundra are thus likely to be biogeochemical hotspots, and collectively may play an important role in global carbon fluxes (Sobek *et al.*, 2003; Walter *et al.*, 2006; Tranvik *et al.*, 2009; Laurion *et al.*, 2010).

Shallow depth and extensive coverage by aquatic macrophytes are often considered to be defining features

of ponds. Many shallow water bodies in the Arctic are considered lakes rather than ponds despite their depth because of their large surface area. An extreme example is Lake Taymyr in Siberia (latitude 75° N), which extends over 4560 km² with an average depth as shallow as 2.8 m (but depth estimates vary among reports; Robarts *et al.*, 1999). In addition, a vast number of small Arctic waters are devoid of higher aquatic vegetation, especially on the treeless rocky tundra. These are classified as ponds due to their small size; however, the separation between lakes and ponds is arbitrary. In this review we consider “ponds” to be fishless water bodies that typically are smaller than 1 ha, but we have also included larger waters under the definition if they are shallower than 3 m and are without fish.

The extreme northern climate and the shallow depths of Arctic ponds exert strong overriding influences on their ecosystem structure and dynamics. For instance, most of them have much lower hydrological connectivity and freeze solid during winter, which prevents the occurrence of fish but allows extensive crustacean communities to inhabit the systems during the open water period (*e.g.*, Rautio, 2001). Substantial light reaching the bottom also means that primary production is possible both in the water column and the benthos. The benthos often contributes a large fraction of the total autotrophic productivity of these ecosystems, with increasing dominance towards the North (Vadeboncoeur *et al.*, 2003). Benthic communities also play a major role in greenhouse gas production. Carbon dioxide (CO₂) and methane (CH₄) emissions from ponds have been shown to come mainly from sediment respiration (in boreal ponds: Kortelainen *et al.*, 2006), and the CH₄ produced by sediments in shallow waters may have little chance to be oxidized by methanotrophs before reaching the atmosphere. The small size of ponds also means that they are closely connected to terrestrial processes (Pienitz, Smol & Lean, 1997). For example, spring bacterial communities can have a terrestrial origin (Roiha *et al.*, forthcoming), and bacterial growth is highly influenced by allochthonous carbon inputs from the surrounding catchment (Crump *et al.*, 2003). The functioning of Arctic ponds is therefore strongly interconnected with terrestrial ecosystems and the atmosphere through a dynamic where ponds act as sinks for organic allochthonous material (Hamilton *et al.*, 2001) and as sources of greenhouse gases (Walter *et al.*, 2006; Laurion *et al.*, 2010).

Intensive studies on Subarctic and Arctic ponds began in Barrow, northern Alaska, in the 1970s, and included a description of pond water chemistry, estimates of biomass stocks for organisms from bacteria to plankton and benthos, and measurements of biological productivity (Hobbie, 1980). From the 1980s onwards, there has been less emphasis on this type of ecosystem, although detailed paleolimnological surveys have been undertaken at many locations and have provided valuable chemical and related survey data (*e.g.*, Duff, Douglas & Smol, 1992; Douglas & Smol, 1994; Keatley, Douglas & Smol, 2008). In this review we place emphasis on our limnological observations at diverse sites in the circumpolar Arctic (Figure 2, Table I). We review results that have been obtained from ponds sampled across a temperature gradient from forest–tundra



FIGURE 1. Photos of ponds studied. a) Resolute rock ponds, b) Kilpisjärvi tundra ponds, c) Zackenberg tundra pond, d) polar desert pond in the Ward Hunt Island region, e) Mackenzie thaw ponds, and f) BGR site thaw ponds.

in Subarctic Quebec (see Bhiry *et al.*, 2011 for background information about this site) to High Arctic polar desert in the north of Canada and Greenland, spanning a DOC gradient from greater than 50 to less than 2 mg·L⁻¹. In these habitats, the biota is subject to extreme forcing by the physical environment, and global change effects are also

likely to be pronounced in the future. Our results comprise observations on shallow water bodies at the Toolik Lake Long Term Ecological Research site, Alaska (8 ponds), the Mackenzie Delta (8), Resolute Bay (5), Ellesmere and Ward Hunt Islands (6), Bylot Island (62), northern Quebec (135), Greenland (41), and northern Scandinavia (30) (Figure 2).

These ponds fall into the thaw, tundra, and rock basin pond categories (Table I) according to their origin and catchment type. Tundra pond data from the classic studies at Barrow, Alaska, are included here for comparison, and are from Hobbie (1980); see Lougheed *et al.* (2011) for recent changes at this site. Data from Svalbard, Norway (Ellis-Evans *et al.*, 2001; Laybourn-Parry & Marshall, 2003; Van Geest *et al.*, 2007) are also presented. All ponds in this review are referred to as Arctic ponds unless we are specifically comparing the Subarctic and Arctic systems. More general limnological reviews of lakes, ponds, and rivers from throughout the Arctic include Prowse *et al.* (2006) and Vincent and Laybourn-Parry (2008), and reviews of climate-related studies of Arctic aquatic ecosystems include Schindler and Smol (2006), Wrona *et al.* (2006), and Prowse *et al.* (forthcoming).

Physical and chemical characteristics of circumpolar ponds

Arctic ponds are subject to large seasonal fluctuations of temperature and light. Air temperatures in the circumpolar belt may range from -40 to $+30$ °C within a year and are closely reflected in the water temperatures (Rautio, Korhola & Zellmer, 2003; Laurion *et al.*, 2010), although the latter are highly influenced by radiative transfer and heat storage, and the water can be warmer than the overlying air. Most ponds freeze solid in winter (*e.g.*, 255 frozen days in Bylot Island thaw ponds during winter 2008-2009; I. Laurion, unpubl. data) and can have warm and rapidly changing temperatures in summer (Figure 3a). Due to their shallow depth, most ponds do not establish a stable stratification in summer, but can stratify for a few hours depending

on wind and cloud conditions (or for several days if they are DOC-rich), with the exception of turbid and/or DOC-rich thaw ponds that are stratified both in summer and winter and that only show brief mixing periods in autumn

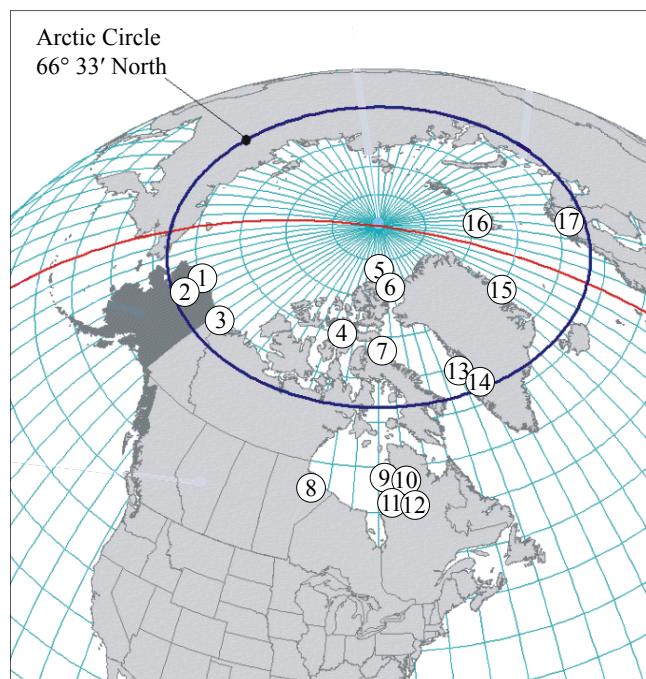


FIGURE 2. More than 200 ponds were sampled from 16 different Subarctic and Arctic regions during the last 15 y. 1 = Barrow, 2 = Toolik, 3 = Mackenzie Delta, 4 = Resolute, 5 = Ward Hunt, 6 = Hazen, 7 = Bylot, 8 = Churchill, 9 = Boniface, 10 = BGR site, 11 = Kuujjuarapik, 12 = KWK site, 13 = Disko, 14 = Kangerlussuaq, 15 = Zackenberg, 16 = Svalbard, and 17 = Kilpisjärvi.

TABLE I. Climatic characteristics among the studied circumpolar regions. Precipitation, annual and July air temperatures are a mean for 2001-2010 for Toolik (Source: Toolik LTER site), Bylot, Boniface, BGR, Kuujjuarapik (Centre d'études nordiques SILA stations) and Kilpisjärvi (Kilpisjärvi biological station). Data for Ward Hunt are a mean for 2005-2009 (SILA station). Data for Disko, Kangerlussuaq and Zackenberg are means for 2001-2009 (Sources: Arctic Station, ASIAQ, Greenland Ecological Monitoring program, respectively). Svalbard data are means for 1961-1990 (Norwegian Meteorological Institute). Meteorological information for other regions is from Environment Canada for an unspecified time span. July water temperature is from year specified for each region. na = not available.

Region	Ponds studied	Pond type	Coordinates	Altitude (m)	Annual precipitation (mm)	Mean annual air temperature (°C)	Mean July air temperature (°C)	Mean July water temperature (°C)
Barrow	25	thaw	71° 15' N 156° 40' W	<100	106	-12.1	4.7	7.1 (1971) ¹
Toolik	8	tundra	68° 38' N 149° 36' W	720	203	-7.7	12.2	14.2 (2004)
Mackenzie	8	thaw	69° 42' N 134° 28' W	<100	168 ²	-10.6 ²	11.0 ²	11.5 (2004)
Resolute	5	rock	74° 41' N 94° 49' W	<100	110	-16.4	7.0	4.9 (2002)
Ward Hunt	2	rock	83° 04' N 75° 08' W	<100	154	-18.3	1.6	3.1 (2003)
Hazen	4	tundra	81° 50' N 70° 25' W	150-250	25	-19.7	7.1	9.7 (2003)
Bylot	62	thaw	73° 09' N 79° 59' W	<100	193 ³	-13.4 ³	7.4 ³	11.0 (2008) 13.0 (2009)
Churchill	30	tundra	58° 45' N 93° 49' W	<100	265	-6.9	12.0	12.9 (2005)
Boniface	6	thaw	57° 44' N 76° 14' W	120	na	-4.9	12.5	na
BRG site	14	thaw	56.37° N 76° 13' W	188	na	-3.1	12.2	16.3 (2005) 15.7 (2006)
Kuujjuarapik	8	tundra	55° 16' N 77° 44' W	<100	670	-2.5	12.2	16.5 (2002)
KWK site	39	thaw	55° 20' N 77° 30' W	105	na ⁴	na ⁴	na ⁴	14.1 (2008) 18.1 (2010)
Disko	11	tundra/thaw	69° 20' N 53° 50' W	0-81	400	-6.2	7.5 ⁵	10.4 (2004)
Kangerlussuaq	14	tundra	66° 50' N 50° 25' W	120-520	151	-5.6	9.6	12.5 (1999)
Zackenberg	16	tundra	74° 30' N 20° 40' W	1-150	209	-8.7	7.7 ¹	8.8 (1997) ¹
Svalbard	6	thaw	78° 56' N 11° 48' W	<50	385	-8.3	4.9	~10
Kilpisjärvi	30	tundra/rock	69° 02' N 20° 50' E	480-1000	459	-2.3	10.9	12.0 (1994)

¹July-August, ²Tukttoyaktuk, ³Pond Inlet, ⁴information is not available but the site is situated only 16 km from Kuujjuarapik, ⁵Illulisat.

and spring (Figure 3b). Studies on the bottom waters of this latter category of ponds at the Kwakwatanikapistikw site (hereafter KWK) in northern Quebec showed that temperatures remained above 2.5 °C during winter (2009-2010), while at a site *ca* 100 km further north (the Bundesanstalt für Geowissenschaften und Rohstoffe Hannover site, hereafter BGR) winter water temperatures dropped to 0.5 °C (2005-2006; Breton, Vallières & Laurion, 2009). The very small volume of water that is left unfrozen in that type of thaw ponds during winter likely has a high conductivity due to freeze-concentration of solutes (as described by Schmidt *et al.* [1991] for Antarctic ponds) and may allow ongoing microbial activity, although this has yet to be evaluated.

Arctic ponds are often well oxygenated in summer, but the sediments can be anoxic and accompanied by anaerobic decomposition and CH₄ production, especially in the most productive ponds. Thermally stratified thaw ponds, such as the KWK and BGR ecosystems, often show hypoxic bottom waters or anoxic hypolimnia. Winter ice cover persists for up to 9 months, and ponds are also subject to continuous winter darkness. Thus, these ecosystems are limited by solar energy supply for all but a few weeks to months of the year. Precipitation largely accumulates during winter as snow, which melts rapidly in May-June. As a result, the pH of pond water in early summer can decrease to low values when acid materials from the atmosphere that have accumulated over winter are released from the melting snow; the pH of the spring meltwater may be as low as 4–5 (Sorvari, Rautio & Korhola, 2000; Roiha *et al.*, forthcoming). Summer pH values are influenced by the catchment bedrock and soil and vegetation characteristics and vary considerably among different Arctic regions (Table II). Small ponds surrounded by peat and *Sphagnum* spp. mosses are humic and can have pH values below 5 in the summer (Kilpisjärvi pond 7 in Rautio, 1998 and subarctic pond BON9 in Breton, Vallières & Laurion, 2009), but for most ponds the pH is more typically close to neutral or slightly alkaline (Table II).

Northern ponds span a wide range of optical conditions in their water column since their dissolved organic matter content, which strongly controls the attenuation of short-visible and ultraviolet (UV) radiation, varies greatly in terms of quantity and optical characteristics (Laurion, Vincent & Lean, 1997; Gareis, Lesack & Bothwell, 2010; Watanabe *et al.*, 2011). Given their low nutrient status (see below), conditions are generally not favourable for algal blooms, and phytoplankton rarely contribute significantly to light attenuation in these waters (Watanabe *et al.*, 2011). Therefore, excluding the turbid and/or humic thaw ponds, visible light (PAR) most often reaches the bottom sediments of the predominantly very shallow Arctic ponds and is rarely limiting to photosynthesis during open water conditions in summer. When concentrations of coloured dissolved organic matter (CDOM), and its correlate DOC concentrations, are low enough, substantial UV radiation also penetrates to the bottom of ponds (Figure 4), exposing both pelagic and benthic communities to continuous UV radiation during summer.

In most cases, Arctic ponds are oligotrophic in terms of nutrient concentrations in the water column. However, the interstitial water within the benthic microbial mats may contain up to 2 orders of magnitude higher concentrations of nutrients (Villeneuve, Vincent & Komárek, 2001; Rautio & Vincent, 2006). Chemical data for the overlying water are therefore a misleading guide to the nutrient conditions experienced by the cyanobacteria, diatoms, and other organisms growing in the phytobenthos (Bonilla, Villeneuve & Vincent, 2005). Soluble reactive phosphorus (SRP) and nitrate (NO₃⁻) concentrations in interstitial waters of Kuujjuarapik and Resolute ponds were 60 to 170 times higher than in the lake water (Rautio & Vincent, 2006). Similarly, in the shallows of Ward Hunt Lake, SRP and NO₃⁻ were 2.5 to 43 times higher in the interstitial mat water (Villeneuve, Vincent & Komárek, 2001). Although SRP concentration in the water column is often below 1 µg·L⁻¹ and NO₃⁻ below 10 µg N·L⁻¹ in circumpolar ponds (Table II), higher concentrations are also reported, for example up to 2.3 µg SRP·L⁻¹ and 88 µg NO₃⁻·L⁻¹ in Alaska tundra ponds (Prentki *et al.*, 1980). Higher concentrations of SRP and nitrate have been measured in the surface waters of thaw ponds (up to 19 µg SRP·L⁻¹

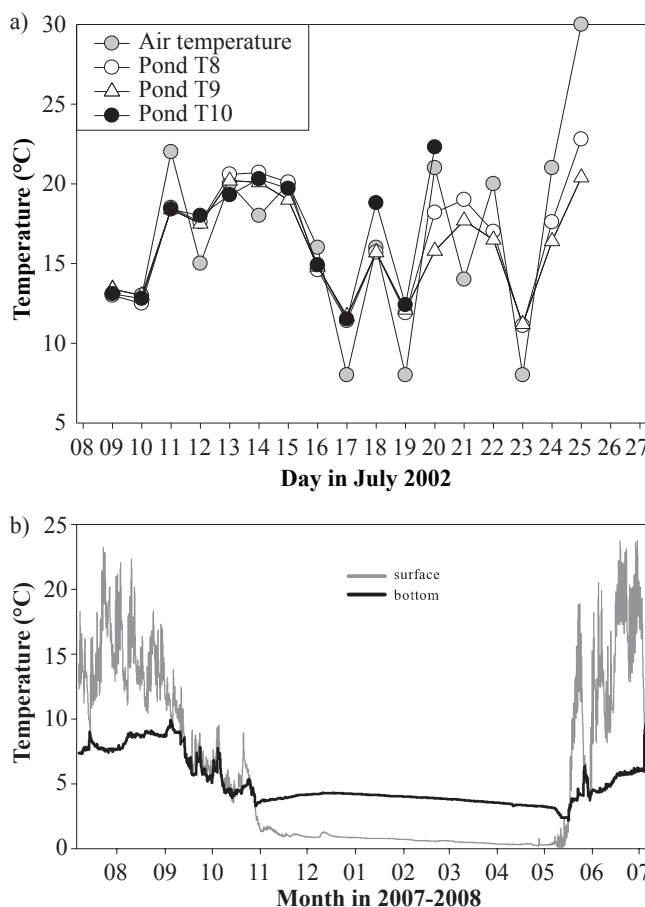


FIGURE 3. Seasonal temperature changes in northern Quebec ponds. a) Water temperature follows the shifts in air temperature (T10 dried out on July 20). Ponds as in Rautio and Vincent (2006). b) Temperature at the surface (0.15 m) and bottom (2.0 m) of pond KWK16 (maximal depth ~2.2 m) followed over 1 complete year from 6 July 2007 to 11 July 2008. Data from Laurion *et al.* (2010).

TABLE II. Some chemical and biological characteristics of circumpolar ponds (surface water averages \pm SD are given). Data for each region are from 2-62 ponds and from 1-13 measures per variable (replicated years or dates within a year). Productivity (PP = primary productivity as P_{max} and BP = bacterial productivity) are often from only few ponds per region while other measurements are from most if not all ponds. Data from Svalbard are from Ny Ålesund. Data sources: Hobbie (1980), Ellis-Evans *et al.* (2001), Rautio (2001), Villeneuve, Vincent & Komárek (2001), Laybourn-Parry and Marshall (2003), Bonilla, Villeneuve & Vincent (2005), Rautio & Vincent (2006), Van Geest *et al.* (2007), Christoffersen *et al.* (2008b), Breton, Vallières & Laurion (2009), Rautio, Bonilla & Vincent (2009), Laurion *et al.* (2010), Roiha *et al.* (2011) and unpublished data from the authors. na = not available.

Region	Water										Benthos	
	pH	Cond. $\mu\text{S}\cdot\text{cm}^{-1}$	DOC $\text{mg}\cdot\text{L}^{-1}$	TP $\mu\text{g}\cdot\text{L}^{-1}$	TN $\mu\text{g}\cdot\text{L}^{-1}$	SRP $\mu\text{g}\cdot\text{L}^{-1}$	NO_3^- $\mu\text{g}\cdot\text{N}\cdot\text{L}^{-1}$	Chl- <i>a</i> $\mu\text{g}\cdot\text{L}^{-1}$	PP (P_{max}) $\mu\text{g}\cdot\text{C}\cdot\text{L}^{-1}\cdot\text{h}^{-1}$	BP $\mu\text{g}\cdot\text{C}\cdot\text{L}^{-1}\cdot\text{h}^{-1}$	Chl- <i>a</i> $\text{mg}\cdot\text{m}^{-2}$	PP (P_{max}) $\text{mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$
Barrow	7.3	160	12.5	13	800	1.2	6.5	0.4	0.6	na	na	13
Toolik	7.8 \pm 0.8	124 \pm 105	9.2 \pm 2.6	8 \pm 6	225 \pm 189	2.8 \pm 2.2	4.0 \pm 0.8	0.8 \pm 0.4	3.2 \pm 1.1	0.7 \pm 0.3	105 \pm 105	60 \pm 28
Mackenzie	8.4 \pm 0.3	691 \pm 560	29.4 \pm 5.9	14 \pm 2	< 100 \pm 0	2.0 \pm 0.2	< 2 \pm 0	1.3 \pm 0.8	8.3 \pm 5.1	0.3 \pm 0.1	na	151 \pm 37
Resolute	8.5 \pm 0.1	323 \pm 176	2.1 \pm 0.5	5 \pm 0.5	185 \pm 34	1.3 \pm 0.5	1.3 \pm 10.5	1.2 \pm 1.1	0.6 \pm 0.3	na	85 \pm 46	9 \pm 8
Ward Hunt	8.5	100	4.4	3 \pm 2	120	< 2 \pm 0	30.0	0.3 \pm 0.3	na	na	88 \pm 24	9
Hazen	8.3 \pm 0.5	440 \pm 400	15.7 \pm 15.1	35 \pm 14	1110 \pm 1350	1.6 \pm 0.1	na	1.4 \pm 1.5	na	na	121 \pm 88	na
Bylot	8.4 \pm 1.0	83 \pm 42	12.1 \pm 6.5	35 \pm 46	191 \pm 352	2.0 \pm 2.1	102 \pm 154	2.7 \pm 3.7	na	18 \pm 12	na	na
Churchill	8.1 \pm 0.1	582 \pm 93	12.0 \pm 1.0	12 \pm 1.0	600 \pm 50	4.0 \pm 0.5	54.4 \pm 5.0	na	na	na	na	na
Boniface	5.4 \pm 0.6	18 \pm 3	13.4 \pm 4.7	28 \pm 21	na	4.1 \pm 0.5	na	3.2 \pm 3.4	na	na	na	na
BRG site	7.0 \pm 0.6	65 \pm 76	4.9 \pm 3.0	97 \pm 94	375	2.3 \pm 0.6	51.1 \pm 42.6	2.2 \pm 2.3	na	1.4 \pm 1.2	na	na
Kuujuarapik	7.0 \pm 0.7	84 \pm 71	10.0 \pm 4.0	14 \pm 11	550 \pm 215	1.2 \pm 0.5	3.4 \pm 0.9	2.9 \pm 1.9	5.8 \pm 5.1	na	229 \pm 157	23 \pm 19
KWAK site	6.8 \pm 0.5	361 \pm 556	7.9 \pm 2.2	60 \pm 24	282 \pm 62	4.8 \pm 5.6	51.9 \pm 33.6	5.6 \pm 4.7	32.9 \pm 10.3	0.89 \pm 0.34	na	na
Disko	7.7 \pm 1.0	135 \pm 156	na	32 \pm 59	na	na	na	1.4 \pm 1.0	na	na	na	na
Kangerlussuaq	8.2 \pm 0.5	298 \pm 165	na	15 \pm 6	858 \pm 269	10.0 \pm 3	< 5	1.4 \pm 1	na	na	na	na
Zackenbergl	6.8 \pm 0.4	23 \pm 17	9.4 \pm 4.6	10 \pm 7	363 \pm 219	na	na	1.7 \pm 1.3	2.3 \pm 1.3	na	11.3 \pm 8.5	19 \pm 16
Svalbard	7.7 \pm 0.5	257 \pm 100	1.2 \pm 0.7	33 \pm 38	760 \pm 594	19 \pm 16	na	2.7 \pm 1.2	13 \pm 9	14 \pm 6	na	na
Kilpisjärvi	6.8 \pm 0.9	22 \pm 18	4.7 \pm 5.3	8 \pm 6	295 \pm 218	na	na	1.4 \pm 0.9	3.0 \pm 2.9	0.1 \pm 0	10 \pm 12	22 \pm 19

and 959 $\mu\text{g}\cdot\text{NO}_3^- \cdot \text{N}\cdot\text{L}^{-1}$), with even greater values in their bottom waters. Thaw ponds therefore tend to have elevated concentrations of total phosphorus, and the highest values have been measured in the most turbid ponds (up to 320 $\mu\text{g}\cdot\text{TP}\cdot\text{L}^{-1}$; Breton, Vallières & Laurion, 2009; Laurion *et al.*, 2010).

DOC is highly influenced by soil properties of the surrounding catchment. Ponds above tree line and with low amounts of vegetation in drainage areas are transparent, with DOC concentrations usually < 2 $\text{mg}\cdot\text{L}^{-1}$ (Rautio, 2001; Rautio & Vincent, 2006). Ponds in areas with organic soils, especially when surrounded by wetlands or peaty soils, may receive high inputs of allochthonous nutrients and organic

matter. In such ponds, DOC can exceed 20 $\text{mg}\cdot\text{L}^{-1}$ (Breton, Vallières & Laurion, 2009; Laurion *et al.*, 2010; up to a maximum of 60 $\text{mg}\cdot\text{L}^{-1}$ in a newly formed thaw pond on Bylot Island). The catchment characteristics also largely control the type of DOC in water bodies. Terrestrial-derived (allochthonous) material differs substantially from organic matter of lake-derived (autochthonous) carbon in its chemical and optical properties, and likely influences the whole pond ecosystem structure. Autochthonous dissolved organic carbon has been shown to be less effective than the same concentration of allochthonous DOC at absorbing UV radiation (McKnight *et al.*, 1994), and the benthic and planktonic communities in autochthonous carbon-dominated lakes will be exposed to high levels of UV radiation during the open water period. Thaw ponds are dominated by allochthonous carbon (Breton, Vallières & Laurion, 2009), while ponds with rocky catchments are influenced more by autochthonous carbon (Rautio & Vincent, 2007; Roiha *et al.*, forthcoming). In addition to controlling underwater UV radiation, the DOC influences the availability of light for photosynthesis (Karlsson *et al.*, 2009), and microbial food web and mineralization processes (Vincent, 2009). DOC thereby strongly affects a broad range of other limnological properties, including the relative balance between benthic and pelagic primary productivity (Karlsson *et al.*, 2009), resource availability to organisms higher in the food web (Salonen & Hammar, 1986; De Lange, Morris & Williamson, 2003), and zooplankton species composition and pigmentation (Rautio & Korhola, 2002). DOC also influences the ratio between autotrophy and heterotrophy in aquatic systems (Hope, Kratz & Riera, 1996). Higher DOC concentrations favour bacterioplankton and result in stronger heterotrophy (Sobek *et al.*, 2003). In oligotrophic water bodies, there may be a threshold shift from net autotrophy to net heterotrophy at DOC concentrations around

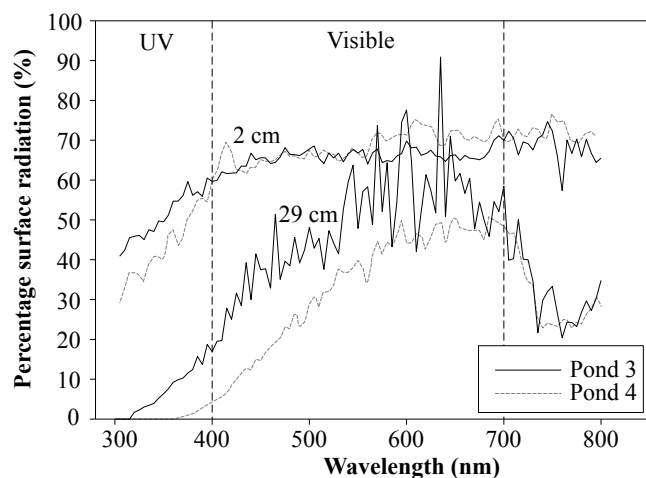


FIGURE 4. The spectral attenuation of irradiance on 28 July 1998 for Pond 3 (DOC = 4.7 $\text{mg}\cdot\text{C}\cdot\text{L}^{-1}$) and Pond 4 (DOC = 9.7 $\text{mg}\cdot\text{C}\cdot\text{L}^{-1}$) in Kilpisjärvi. Percentage surface radiation is shown for 2 and 29 cm depths. Ponds as in Rautio (2001).

5 mg·L⁻¹ (Jansson *et al.*, 2000). Circumpolar ponds span both sides of this threshold and may therefore function very differently from each other in terms of carbon balance; however, there have been no studies to date on this aspect.

Bacteria

Bacterial activity (here including all heterotrophic prokaryotes, Bacteria plus Archaea) has a large influence on the carbon dynamics of ponds (*e.g.*, Torgersen & Branco, 2008). Bacteria are responsible for recycling inorganic nutrients and producing most greenhouse gases from both allochthonous and autochthonous carbon. Bacteria also represent an important food web link between allochthonous organic carbon and higher trophic levels (Jansson *et al.*, 2007). This allows ponds to be at the same time large sinks of carbon through sedimentation yet also net sources of carbon to the atmosphere through greenhouse gas emissions. Shallow aquatic systems have been shown to play a major role in organic carbon decomposition and have been identified as biogeochemical “hot spots” on the tundra for carbon cycling (McClain *et al.*, 2003; Cole *et al.*, 2007). Permafrost thaw ponds especially have been identified as potentially major players in global climate dynamics (Walter, Smith & Chapin, 2007; Schuur *et al.*, 2009). Climate predictions require a better understanding of all feedback mechanisms, and bacterial activity and its controlling factors in polar ecosystems require ongoing attention.

Bacterial production (BP) data, especially from the benthos, are scarce in the polar regions (but see Ask *et al.*, 2009; Adams, Crump & Kling, 2010; Roiha *et al.*, forthcoming; and Table II). Furthermore, most BP estimations to date have been obtained with the ³H-leucine incorporation method (Kirchman, 1993), and this requires the use of assumed conversion factors to convert BP to carbon units. These factors are highly uncertain since the ratio of leucine incorporation to bacterial production can range from < 1 to 20 kg C·mol⁻¹ leucine (del Giorgio & Williams, 2005). In the circumpolar pond data series presented here, bacterial carbon production was estimated using a conversion factor of 3.1 kg C·mol⁻¹ leucine, within the range for oligotrophic waters (Simon & Azam, 1989).

Temperature, oxygen, and biological productivity (affecting the nature and quantity of available organic carbon) are likely to be the most important factors influencing bacterial activity. The low temperatures of circumpolar ponds may lead to lower production rates, but respiration should also be lower (and bacterial growth efficiency higher). Nevertheless, bacteria are adapted to their environment, and likely sensitive to any increase in temperature (higher Q₁₀ at lower temperature range was shown for benthic bacteria by den Heyer & Kalff, 1998; Pace & Prairie, 2005). However, closer inspection of the Kilpisjärvi data (Roiha *et al.*, forthcoming) shows that BP changes seasonally, peaking in July at the time of maximum water temperature. A strong temperature control has also been observed on shallow lake bacterial production at Toolik Lake, Alaska (Adams, Crump & Kling, 2010).

Being highly dependent on organic matter quantity and lability, bacterial activity varies greatly in circumpolar

ponds (Table II). Our combined pond data (Table II) show no close relationship between averaged BP and averaged Chl-*a* ($r = 0.859$, $P = 0.062$), nor between BP and DOC, although such relationships have been reported elsewhere (Jansson *et al.*, 1996; Granéli, Bertilsson & Philibert, 2004; Sawström *et al.*, 2007). At individual sites, however, there may be significant relationships: *e.g.*, BP, abundance, and biomass were each positively correlated with DOC in 16 ponds at Kilpisjärvi (Roiha *et al.*, forthcoming).

The highest BP values in our data set were obtained in Bylot Island thaw ponds (varying from 116 to 1052 µg C·L⁻¹·d⁻¹), where organic matter is abundant (constantly supplied by eroding thawing peat) and apparently labile (low humification index, Breton, Vallières & Laurion, 2009; high CDOM spectral slope). DOC coming from the Arctic terrestrial environment has been shown to be relatively labile (Holmes *et al.*, 2008). Moreover, DOC in these ponds is likely to be highly photolyzed, given that the ponds are shallow and exposed to 24-h daylight in summer; sunlight exposure and photolysis has been shown to increase DOC lability (Zhang *et al.*, 2009). At other sites, BP was in the same range as the maximum rate of primary production (P_{max}), and closer to the ranges reported in temperate lakes (6–91 µg C·L⁻¹·d⁻¹; del Giorgio, Prairie & Bird, 1997) or in the freshwater portion of the Mackenzie River in the Arctic (2.9–9.4 µg C·L⁻¹·d⁻¹; Vallières *et al.*, 2008). However, time- and depth-integrated values of primary production (PP) are largely influenced by light attenuation, and the most turbid and/or humic ponds will likely have lower pelagic PP compared to BP, leading to net heterotrophy. Few data are available on benthic BP of circumpolar ponds. For example, in shallow (2.8–4.6 m) Swedish subarctic lakes, benthic BP was shown to be lower than benthic PP (respectively 55 and 80 mg C·m⁻²·d⁻¹, Ask *et al.*, 2009). Typically, the benthic BP is 2–3 orders of magnitude greater than in the water column, a phenomenon already recognized half a century ago (Kuznetsov, 1958). This is likely caused by the orders-of-magnitude higher level of nutrients and organic carbon recycled within the sediments and benthos and found in the interstitial waters of the microbial mats, which enhances primary productivity (Villeneuve, Vincent & Komárek, 2001; Rautio & Vincent, 2006; Varin *et al.*, 2010) and hence BP. The large increases in CO₂ and CH₄ concentrations at the very bottom of the water column during calm conditions are indicative of this high decomposition activity occurring in the sediments. Turbid thaw ponds of the Subarctic region (BGR and KWK) are a special case relative to this balance between autotrophy and heterotrophy. Light is attenuated very rapidly in most of these ponds (Watanabe *et al.*, 2011), which limits the planktonic and benthic PP but favours BP, leading to net heterotrophy and large emissions of greenhouse gases (GHG).

Primary producers

Many factors affect the composition, pigment structure, and biomass of primary producers in circumpolar ponds, including the low nutrient inputs, persistent low temperatures, freeze-up and desiccation stress during the long winters, high PAR and UV radiation during the short

summers, and zooplankton grazing pressure. Moreover, dissolved organic carbon, particularly the chromophoric fraction (CDOM), significantly affects the light regime and consequently the photosynthetic potential of the water body (Bonilla, Rautio & Vincent, 2009; Karlsson *et al.*, 2009).

In Arctic ponds and shallow lakes, primary producers are represented by 2 different microbial communities: phytoplankton and benthic mats. These communities differ greatly in their biomass, species composition, and overall structure. The dilute phytoplankton often represent less than 2% of total photosynthetic biomass in these ecosystems (Bonilla, Villeneuve & Vincent, 2005). For instance, benthic chlorophyll *a* concentrations (8–261 mg·m⁻²) were orders of magnitude higher than those of the phytoplankton (0.008–1.4 mg·m⁻²) in 17 ponds of Alaska and Canada (Bonilla, Villeneuve & Vincent, 2005; Bonilla, Rautio & Vincent, 2009). The phytoplankton flora is diverse, and the community composition is generally similar to that in temperate regions (Sheath & Steinman, 1982; Sheath, 1986). Green algae, chrysophytes, diatoms, and cyanobacteria are the major algal classes, together accounting for 79% of the species composition (Sheath, 1986). The nanophytoplankton biomass of Arctic lakes is often dominated by chrysophytes (Charvet, Vincent & Lovejoy, forthcoming) and cryptophytes (Sheath, 1986). Flagellates, including Chrysophyta, Cryptophyta, and Dinophyta, dominate the phytoplankton communities of northern Finland (Forsström, Sorvari & Korhola, 2009 for lakes), similar to communities of Svalbard, Alaska, and Canada (Laybourn-Parry & Marshall, 2003; Bonilla, Rautio & Vincent, 2009; Charvet, Vincent & Lovejoy, forthcoming). In a recent survey of thaw pond flora, Subarctic ponds (*n* = 23) were mostly dominated by Chlorophyceae and Chrysophyceae, and Arctic thaw ponds (*n* = 14) were dominated by cyanobacteria, along with Chlorophyceae (Dupont, 2009).

In the benthos, the phototrophic community is often dominated by cyanobacteria. Thick, colourful cyanobacterial mats are a typical feature of ponds with soft sediments (Vézina & Vincent, 1997), while ponds above tree line usually have rocky bottoms covered with a thin to thick film of cyanobacteria and diatoms (Stanley, 1976; Douglas & Smol, 1995; Niemi, 1996; Vincent, 2000; Michelutti *et al.*, 2003). For example, benthic mats in Kilpisjärvi ponds, in Finnish Lapland, are known to be composed primarily of cyanobacteria, and in lower densities, of Chlorophyta and diatoms (L. Forsström, pers. comm.). Similar species composition is also frequently found in benthic mats of other Subarctic and Arctic regions (Bonilla, Rautio & Vincent, 2009). Species diversity is affected by growing conditions; for example, in a series of shallow lakes of the Canadian Arctic, periphytic diatom species diversity was inversely correlated with latitude, implying an effect of duration of growing season (Michelutti *et al.*, 2003).

Ponds from a given region generally have higher nutrient concentrations than lakes, and their primary production (PP) is also slightly greater. In 4 Barrow ponds, the daily phytoplankton productivity was 21 mg C·m⁻²·d⁻¹, while in a nearby lake (mean depth 2 m) it never rose above 3 mg C·m⁻²·d⁻¹ (Stanley, 1976). The same range of values

was recently measured on Bylot Island, with averages of 14.5 mg C·m⁻²·d⁻¹ in ponds compared to 2.3 mg C·m⁻²·d⁻¹ in nearby oligotrophic lakes. Phytoplankton primary production peaks in Arctic ponds varied between 45 and 260 mg C·m⁻²·d⁻¹, being lower than in temperate oligotrophic lakes (Sheath, 1986). Due to their shallow depths, ponds also heat up more quickly than deeper lakes, which enhances productivity. Higher nutrient stocks in the benthos (Vincent *et al.*, 1993; Villeneuve, Vincent & Komárek, 2001; Bonilla, Villeneuve & Vincent, 2005) and high light levels reaching the bottom of the ponds favour benthic PP, and thus most of the PP in northern ponds is confined to the phytobenthos (Stanley, 1976; Niemi, 1996; Vincent, 2000; Rautio & Vincent, 2006; Squires *et al.*, 2009; P_{max} values are given in Table II).

Phytoplankton also experience strong photoinhibition in clear ponds, whereas benthic algae, often located only a few tens of centimetres below the surface, use all of the available radiation (Figure 5). In Kuujuarapik, Resolute, and Kilpisjärvi ponds, benthic algae contributed 39–99% of the total PP per unit area (*i.e.*, planktonic plus benthic; plankton 0.2–8.7 mg C·m⁻²·h⁻¹ and benthos 1.8–191.8 mg C·m⁻²·h⁻¹; Rautio & Vincent, 2006; Mariash *et al.*, 2011). The difference between planktonic and benthic PP is consistent with the phototrophic biomass difference between these habitats, although an increase in PP results in a smaller increase in the algal biomass in phytoplankton than in benthic algae (Figure 6). The most probable reason for this is zooplankton grazing on phytoplankton production (Rautio & Vincent, 2006; Mariash *et al.*, 2011), while the benthic mats are relatively unimpacted by grazing. The contribution of benthic algal mats to total primary production is also inversely related to the depth of the pond. In a comparative survey performed during summer seasons in a series of Alaskan shallow lakes (< 2.5 to > 4.5 m depth), the relative contribution of benthic production was maximal in the shallowest sites (total PP ranging from 78 to 184 mg C·m⁻²·d⁻¹; Whalen, Chalfant & Fischer, 2008). However, DOC concentration influences this relationship in highly humic ponds where

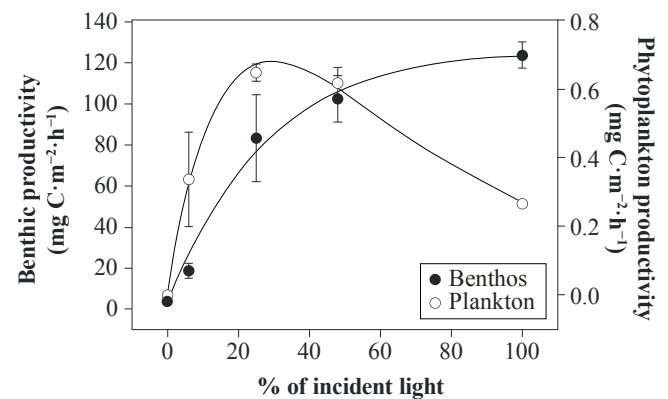


FIGURE 5. Photosynthesis versus irradiance for phytoplankton and benthic algae in a Mackenzie pond (69.42° N, 134.28° W). 100% light equals 1130 μmol photons·m⁻²·s⁻¹. Phytoplankton exhibit strong photoinhibition with maximum photosynthesis at only 30% light, while benthic algae maximize their production at full sunlight. More information of the pond in Rautio *et al.* (2009).

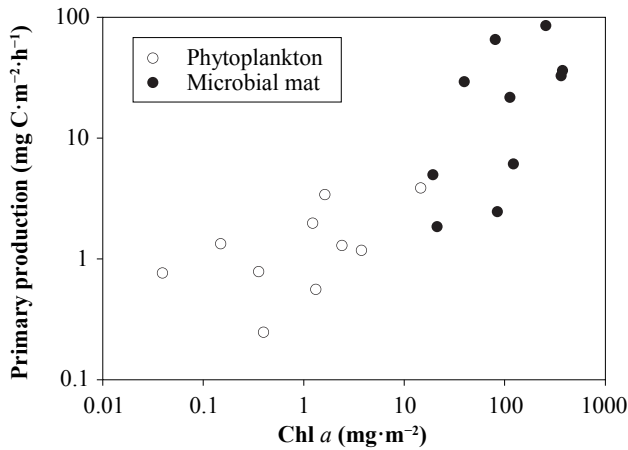


FIGURE 6. Relationship between chlorophyll and primary productivity for water column and benthic algae in 10 Subarctic and Arctic ponds (3 Kuujjuarapik, 4 Resolute, and 3 Toolik ponds). Kuujjuarapik and Resolute data as in Rautio and Vincent (2006).

light attenuates rapidly within the first few centimetres. Hence, high inputs of allochthonous carbon can switch lake primary productivity from benthic to pelagic dominance (Karlsson *et al.*, 2009). However, our data suggest (Table II) that even high DOC (up to 30 mg C·L⁻¹) is not enough to attenuate light sufficiently to alter the dominance of benthic primary productivity in Arctic ponds.

Due to their shallow depth, in most ponds both phytoplankton and benthic algae are also exposed to UV radiation, even at relatively high DOC sites (Schindler *et al.*, 1996; Figure 4), and photoprotective compounds are commonly found in Arctic primary producers. There was a positive correlation between photoprotective pigments and UV-penetration in ponds at Toolik, Resolute, Hazen, Ward Hunt, and Kuujjuarapik (Bonilla, Rautio & Vincent, 2009). The highest photoprotection was found in planktonic communities located in highly transparent Resolute and Ward Hunt ponds with low CDOM and high UV penetration (Bonilla, Rautio & Vincent, 2009).

As at other latitudes, anthropogenic eutrophication can significantly affect PP and the trophic structure of shallow Arctic aquatic ecosystems. For example, a paleolimnological study showed that the activities of Thule Inuit whalers affected the production of a pond on Ellesmere Island ca 800 to 340 y ago (Hadley *et al.*, 2010). More recently, Meretta Lake received untreated sewage from Resolute Bay for 4 decades (1949 to 1998), leading to the pronounced growth of photosynthetic sulfur bacteria, and later to an increment in phytoplankton biomass (Antoniades *et al.*, 2011). However, nutrient enrichment has significantly different effects on the benthos and the plankton of Arctic freshwater ecosystems. The phytoplankton are much more sensitive than benthic mats to changes in the trophic status of the water since they are strongly limited by low nutrient concentrations in the water column, while the benthic mats have nutrient-rich interstitial waters (Bonilla, Villeneuve & Vincent, 2005) and diverse nutrient recycling and scavenging mechanisms (Varin *et al.*, 2010). However, the short summer seasons in the Arctic significantly limit PP of these shallow lakes relative to those in temperate regions. As a consequence of climate warming, the combined effect of ice

cover reduction, warmer temperatures, and increased nutrient supplies from the more biogeochemically active catchments will likely enhance phytoplankton standing stocks and productivity (Bonilla, Villeneuve & Vincent, 2005; Bonilla, Rautio & Vincent, 2009; Antoniadis *et al.*, 2011) in the future, and may reduce the extent of benthic dominance of overall ecosystem productivity.

Zooplankton and zoobenthic communities

Subarctic and Arctic freshwater zooplankton communities have been profoundly impacted by Pleistocene glaciations (Weider & Hobaek, 2000). Species surveys have revealed that the richness of microcrustaceans in Arctic ponds is higher in areas that were unglaciated 10 000 y ago such as the Arctic Slope of Alaska and Peary Land in North Greenland by comparison with largely glaciated areas such as most of Greenland, the Canadian Arctic Archipelago, the Russian Arctic Archipelago, and Svalbard (Hebert & Hann, 1986; Samchyshyna, Hansson & Christoffersen, 2008). For instance, the maximum zooplankton species richness in the Arctic occurs in Alaska, with 54 reported crustacean zooplankton species (Rautio *et al.*, 2008; Figure 7). This unusually high diversity derives mainly from the history of glaciations but also from the higher temperatures in Alaska (Table I). The high species number in northern Scandinavia is likely the result of efficient dispersal from the south and from a more Subarctic than Arctic-like climate.

Calanoid copepods seem to be the most sensitive zooplankton to low temperatures or to environmental factors related to low temperatures, with only 3 species, *Limnocalanus macrurus*, *Drepanopus bungei*, and *Eurytemora* sp. recorded at sites in Canadian Arctic islands with less than 350 degree-days (Hebert & Hann,

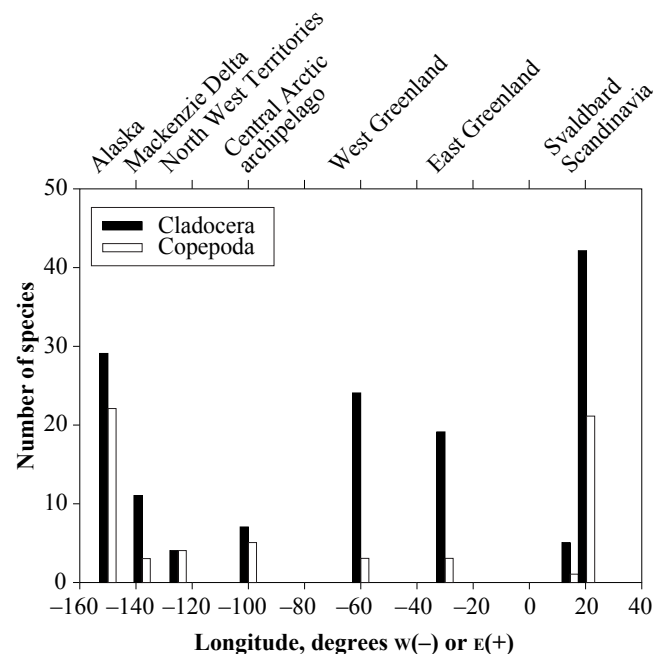


FIGURE 7. Species number of Cladocera and Copepoda along latitude gradient 68°–78° N. Redrawn from Rautio *et al.* (2008) with updates from Samchyshyna, Hansson, and Christoffersen (2008).

1986; Van Hove *et al.*, 2001). Of these only *D. bungei* is found in ponds, while the 2 other species do not tolerate winter freezing in ponds. The low number of zooplankton on Arctic islands derives also from limited dispersal between islands. Larger numbers of copepods are recorded further south, for example 6 calanoid and 5 cyclopoid species in the shallow lakes and ponds of the Whapmagoostui-Kuujuarapik region of Subarctic Quebec (Swadling *et al.*, 2001).

Despite the differences in species number among regions, Arctic ponds in general are species-poor when it comes to zooplankton and zoobenthos. Their short growing season, their high exposure to ultraviolet radiation, and the fact that many ponds freeze solid every winter and may also dry out (at least partly) makes them among the most extreme of aquatic habitats. Several physiological adaptations in both flora and fauna are required. Either physiologically resistant cells or cysts (protists) and life forms or eggs (crustaceans) are included in the life-cycle of organisms that are not able to leave the water body before winter, and organisms also need to be able to protect themselves from high UV radiation (reviewed by Rautio & Tartarotti, 2010). For example, cladocerans become pigmented with photoprotective melanin as a response to UV radiation, and the synthesis of melanin is especially common among Arctic *Daphnia* species (*e.g.*, Hebert & Emery, 1990; Hessen, 1996; Hansson, Hylander & Sommaruga, 2007). Melanin acts by absorbing UV radiation before it enters the body tissues (Figure 8).

Fish are absent from ponds that freeze solid unless the pond is connected to a deeper lake during the open water period, providing a seasonal dispersal route. Zooplankton

communities benefit from the absence of fish, allowing them to be bigger in size and 2 to 5 times more abundant than communities in Arctic lakes (Rautio & Vincent, 2006). Fairy shrimps (Anostraca) are especially adapted to ephemeral environments or harsh marginal conditions (Kerfoot & Lynch, 1987), and 5 species are found in circumpolar ponds (Samchyshyna, Hansson & Christoffersen, 2008), of which 4 are dominant (Table III). Glacial history, dispersal rates, and variable environmental conditions are among the main factors explaining the large regional differences in zooplankton species composition and number in the Arctic. Patalas (1990) demonstrated that climate was the most significant factor regulating

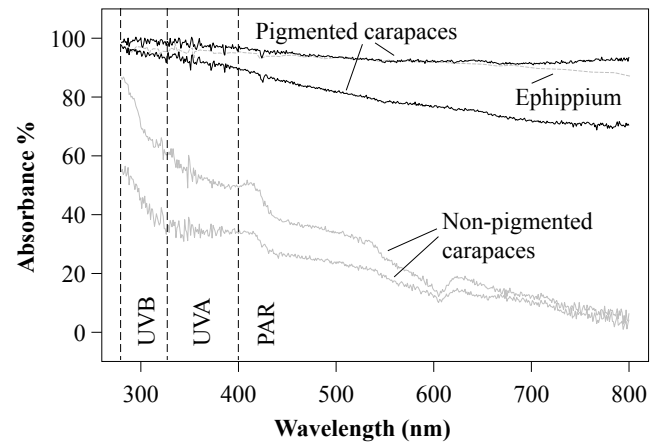


FIGURE 8. UV radiation (UVB = 280–320 nm, UVA = 320–400 nm) and PAR (visible light 400–700 nm) absorbance through non-pigmented and pigmented (with melanin) *Daphnia* sp. carapaces and ephippia. Pigmented *Daphnia* and ephippia are from Resolute pond A1 and non-pigmented *Daphnia* from Kuujuarapik pond S8, as in Rautio and Vincent (2006).

TABLE III. Dominant macrozooplankton species in the studied circumpolar ponds. Alaska = Toolik ponds, High Arctic archipelago = Resolute and Ellesmere Island ponds, Northern Quebec = Kuujuarapik ponds, Greenland = Disko, Kangerlussuaq and Zackenberg, Scandinavia = Kilpisjärvi ponds. na = not available.

Alaska	High Arctic Archipelago	Churchill	Northern Quebec	Greenland	Scandinavia
<i>Cladocera</i>	<i>Cladocera</i>	<i>Cladocera</i>	<i>Cladocera</i>	<i>Cladocera</i>	<i>Cladocera</i>
<i>Daphnia pulex</i>	<i>Daphnia middendorffiana</i>	<i>Daphnia middendorffiana</i>	<i>Daphnia pulex</i>	<i>Daphnia pulex</i>	<i>Daphnia longispina</i>
<i>Daphnia middendorffiana</i>	<i>Eurycerus</i> sp.	<i>Daphnia pulex</i>	<i>Daphnia pulicaria</i>	<i>Daphnia middendorffiana</i>	<i>Daphnia umbra</i>
<i>Eurycerus</i> sp.		<i>Daphnia pulicaria</i>	<i>Ceriodaphnia quadrangula</i>		<i>Bosmina</i> sp.
<i>Polyphemus pediculus</i>		<i>Daphnia tenebrosa</i>			<i>Polyphemus pediculus</i>
<i>Copepoda</i>	<i>Copepoda</i>	<i>Copepoda</i>	<i>Copepoda</i>	<i>Copepoda</i>	<i>Copepoda</i>
<i>Heterocope septentrionalis</i>	<i>Drepanopus bungei</i>	na	<i>Leptodiaptomus minutus</i>	<i>Cyclops abyssorum</i>	<i>Eudiaptomus graciloides</i>
<i>Diaptomus pribolofensis</i>			<i>Hesperodiaptomus arcticus</i>	<i>Leptodiaptomus minutus</i>	<i>Mixodiaptomus lacinitaus</i>
<i>Anostraca</i>	<i>Anostraca</i>	<i>Anostraca</i>	<i>Anostraca</i>	<i>Anostraca</i>	<i>Anostraca</i>
<i>Polyartemiella hazeni</i>	<i>Artemiopsis steffansoni</i>			<i>Branchinecta paludosa</i>	<i>Polyartemiella forcipata</i>
<i>Branchinecta paludosa</i>	<i>Branchinecta paludosa</i>				<i>Branchinecta paludosa</i>
<i>Notostraca</i>	<i>Notostraca</i>	<i>Notostraca</i>	<i>Notostraca</i>	<i>Notostraca</i>	<i>Notostraca</i>
	<i>Lepidurus arcticus</i>			<i>Lepidurus arcticus</i>	

the distribution of present-day zooplankton communities. He found an increase from 8 to 35 species corresponding with an increase of mean July air temperature from 3 °C to 15 °C. Similarly, Korhola (1999) showed a strong relationship between cladoceran distribution and water temperature in northern Finland. A survey of 40 ponds in the Kuujuarapik area revealed that chydorids, ostracods, and insect larvae were positively associated with higher water temperatures, whereas calanoid copepods were negatively associated with temperature (Jose, 2009).

The effects of temperature on zooplankton and zoobenthos distribution arise mainly from their ability to complete their life-cycle within the period of tolerable physical conditions in the water body. Cladocerans complete their life-cycle in 7–8 d at 20 °C, whereas the corresponding time at 10 °C is 20–24 d (Stross & Kangas, 1969; Allan, 1976). Copepods in circumpolar ponds are univoltine, that is, they have 1 brood per year (Figure 9). Low temperature may also completely inhibit their reproduction. For example, *Ceriodaphnia quadrangularis* required a temperature over 8 °C to be able to reproduce (Allan, 1977). Some other cladocerans, by contrast, are acclimated to cold environments (Patalas, 1990). For instance, *Daphnia tenebrosa* is restricted in its southern limits by a temperature of around 15 °C (Yurista, 1999). In addition, the calanoid copepod *Mixodiaptomus laciniatus* is only found in cold lakes and ponds (Dussart, 1967).

Some taxonomic groups of Cladocera are also known to be highly responsive to the substrata they inhabit. The species diversity of chydorids is a function of available habitat (macrophytes, sand, mud), and the distribution of most chydorid species within a region is determined by habitat diversity (Whiteside, Williams & White, 1978). The lack of a suitable substratum has resulted in the absence of many chydorids from High Arctic ponds (Hebert & Hann, 1986).

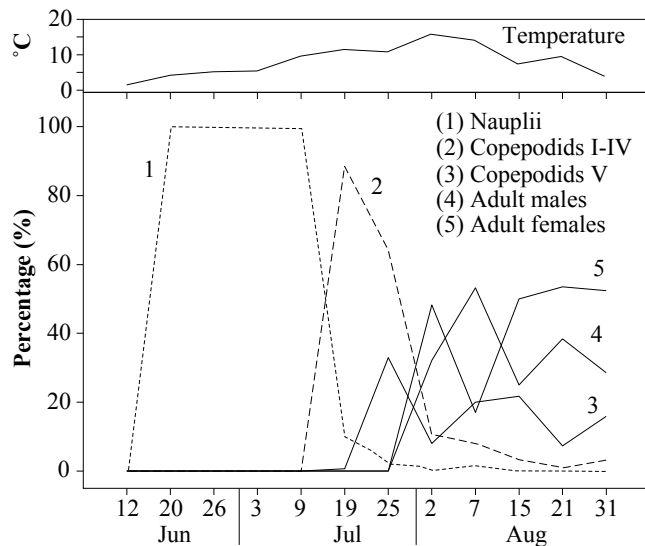


FIGURE 9. Life-cycle of a calanoid copepod, *Mixodiaptomus laciniatus*, in Pond 13 in Kilpisjärvi. The pond became ice free on June 27. Pond as in Rautio (2001).

Aquatic insects exhibit a strong latitudinal gradient, with decreasing diversity poleward. In North America, the Chironomidae dominate the benthos at high latitudes, with 30 or more species at 63° N and only 6 to 8 at 75° N (Welch, 1991 and references therein). Chironomidae genera *Chironomus*, *Corynoneura*, *Cricotopus*, *Orthocladius*, *Procladius*, *Sergentia*, and *Tanytarsini* are often abundant in ponds (Walker & Mathewes, 1989). Abiotic conditions largely define the species distribution, while competitive exclusion does not occur among Arctic insects because their densities are usually very low. High Arctic islands in the Canadian Arctic Archipelago, including Devon and Cornwallis Island, have the most severe environment for aquatic insect survival and as a consequence the lowest diversity. Ostracods, amphipods, molluscs, turbellarians, and oligochaetes also contribute to the high-latitude benthic invertebrate community, but the number of species present is smaller than in more southern latitudes. For example, only a few species of freshwater bivalves and gastropods occur in the Arctic. The largest and most abundant benthic invertebrate species in many High Arctic ponds is the notostracan *Lepidurus arcticus* (Christoffersen, 2001). It inhabits numerous localities in Arctic and Subarctic circumpolar areas from approximately 60° N to 80° N, and is recorded in all Arctic regions.

The zoobenthos obtains its energy from the benthic PP and associated microbial activity (Peterson, 1999), and this may also be the case for zooplankton in the water column. There is evidence from some Arctic ponds that bottom-growing algae and cyanobacteria, despite their poorer quality in terms of essential fatty acids (Mariash *et al.*, 2011), are a food source for zooplankton (Hecky & Hesslein, 1995; Rautio & Vincent, 2006; 2007; Cazzanelli *et al.*, forthcoming). For example, the planktonic primary production in some Greenland ponds has been calculated to support only 60% of the total carbon consumption by zooplankton (Cazzanelli *et al.*, forthcoming). Similarly, in High Arctic ponds at Resolute Bay, the densities and production rates of phytoplankton were too small to sustain zooplankton, with up to a 70% shortfall relative to the zooplankton carbon demand (M. Rautio, unpubl. data). To compensate for this, zooplankton obtained additional food sources from the biomass-rich benthos, where the reserves of organic matter are potentially available for even obligate planktonic feeders by resuspension (Rautio & Vincent, 2007). The detection of scytonemin in the body of 2 crustaceans (*Daphnia middendorffiana* and the fairy shrimp *Branchinecta paludosa*) suggests that these species can graze on benthic cyanobacteria rich in this photoprotective pigment (Rautio, Bonilla & Vincent, 2009). In Arctic ponds the heterotrophic microbial food web, which includes bacteria, heterotrophic nanoflagellates, and ciliates, also becomes a food source for zooplankton, especially to *Daphnia* sp. (Christoffersen *et al.*, 2008b).

Recently it has become evident that aquatic food webs may also rely on external (allochthonous) carbon (Karlsson, Jansson & Jonsson, 2002; Solomon *et al.*, 2008), and the high catchment to lake area ratios potentially influence the functioning of Arctic ponds. Allochthonous organic carbon (in particulate and dissolved forms) may affect the

recipient food webs (Cole *et al.*, 2006; Rautio, Mariash & Forsström, 2011). This material can potentially subsidize heterotrophic organisms in ponds, and may be directly available or may require transformation by microorganisms prior to supporting animal consumers. However, there have been no studies to our knowledge on the importance of allochthonous carbon in Subarctic or Arctic pond food webs, apart from research at the bacteria level (Roiha *et al.*, forthcoming).

Patterns of genetic diversity in Arctic freshwater communities

Genetic diversity is important for maintenance of the viability and the evolutionary or adaptive potential of populations and species (Ellstrand & Elam, 1993). Studies on genetic diversity in Arctic invertebrates have been scant and mostly focused on the cladoceran *Daphnia*. As observed for the species richness of zooplankton (see above), the clonal richness of zooplankton (*Daphnia* sp.) has been found to decline with distance from the edge of the Beringian region that remained ice free during the last glacial period (Weider & Hobaek, 2003). Other studies on passively dispersed zooplankton taxa have revealed the presence of genetically distinct phylogroups (corresponding to major refugia) with substructure within some refugia, indicating resistance to extinction in these groups (Cox & Hebert, 2001). Production of diapausing eggs that can survive unfavourable conditions for centuries and the parthenogenetic mode of reproduction, which allows the refounding of populations from a single individual, may have reduced genetic bottlenecks during recolonization (Hebert, 1987). There is increasing evidence that the Arctic has served as an important contact zone for different refugial races and has been instrumental for the origin of hybrid polyploid species (Dufresne & Hebert, 1997; Little *et al.*, 1997; Brochmann *et al.*, 2003). The cladoceran *Daphnia* sp. is one of the best studied species inhabiting Subarctic and Arctic ponds (*e.g.*, Hessen, 1996; Chételat & Amyot, 2009). Members of the *Daphnia pulex* complex are keystone herbivore species in these habitats and include 6 morphologically cryptic species. *Daphnia pulex* and *Daphnia pulicaria* are widely distributed in temperate North America. *D. pulex* shows little divergence in mtDNA haplotypes, whereas *D. pulicaria* can be subdivided into eastern, western, and polar lineages according to mtDNA divergence (Dufresne & Hebert, 1997). Hybridization between *D. pulex* and *D. pulicaria* has led to the origin of numerous polyploid clones endemic to Subarctic and Arctic ponds and collectively known as *Daphnia middendorffiana* (Dufresne & Hebert, 1994), a species commonly occurring in many regions of the Arctic (Table III). Many temperate zone populations of the *D. pulex* complex reproduce by cyclic parthenogenesis (an asexual phase followed by a sexual phase), but Subarctic and Arctic lineages reproduce predominantly by obligate parthenogenesis (strictly asexual reproduction) (Beaton & Hebert, 1988).

Daphnia tenebrosa is the other Arctic endemic species of the *D. pulex* complex and includes both diploid and polyploid clones (Dufresne & Hebert, 1995). It is

found predominantly in lakes and is often associated with the copepod *Heterocope septentrionalis* (Dzialowski & O'Brien, 2004). Clonal diversity in Subarctic and Arctic *Daphnia* sp. is often low, with an average of 1.5–1.7 clones per pond in Churchill (Weider & Hebert, 1987), although the regional clonal diversity can amount to 50 different clones. Past studies in Churchill have shown that conductivity and invertebrate predation have an important impact on clonal distribution of *D. pulex* (Weider & Hebert, 1987; Wilson & Hebert, 1992). A recent study in Kuujjuarapik (135 ponds) has shown that clonal diversity is also low (1.86 clones per pond) (Jose, 2009). Clones belonging to the different lineages of *D. pulex* complex were associated with different pond characteristics. *D. pulex* clones were found in ponds with high conductivities, eastern *D. pulicaria* clones were positively associated with transparent waters with low pH, and western *D. pulicaria* clones were associated with *Chaoborus larvae* (an important predator of *Daphnia* first instars) (Jose, 2009). Considerable interclonal variation in tolerance to temperature, conductivity, and pH has been found in the Kuujjuarapik clones (Jose & Dufresne, 2010).

Tundra ponds and climate change

It is predicted that global warming will cause major changes in permafrost cover, soil stability, and vegetation throughout the Arctic region (ACIA, 2005; Prowse *et al.* forthcoming; Vincent *et al.*, forthcoming). Permafrost thawing, soil erosion, and enhanced plant growth in the catchment all increase the transfer of organic matter from terrestrial to aquatic systems (Schoor *et al.*, 2008). The liberation of a large organic carbon pool that has accumulated over many thousands of years in tundra soils may be particularly important for global carbon cycling and the global climate (Walter, Smith & Chapin, 2007), but this is still controversial (Van Huissteden *et al.*, 2011). Increased availability of carbon and warmer water temperatures stimulate microbial growth and respiration in ponds, and the greenhouse gases (GHG) thereby liberated represent a biotic positive feedback to climate warming. This mechanism is not yet considered in global climate models (IPCC, 2007). Climate impacts on temperature, light regimes, carbon availability, and oxygen levels will all influence the microbial production of GHG in ponds (Vincent, 2009). Studies on circumpolar ponds have shown that these systems are acting as significant sources of GHG to the atmosphere, but that emissions are highly variable within a specific site and between sites of different geomorphologies and latitudes (*e.g.*, Tank *et al.*, 2009; Laurion *et al.*, 2010, and references therein). For example, using the average surface flux values from Subarctic and Arctic ponds (excluding the polygon ponds with cyanobacterial mats), Laurion *et al.* (2010) calculated an annual diffusive flux from Canadian thaw ponds of 95 Tg CO₂ and 1.0 Tg CH₄. For comparison, global emissions from lakes were estimated to be 1.9 Pg CO₂·y⁻¹ (Tranvik *et al.*, 2009). This estimate of the annual CH₄ flux from Canadian thaw ponds may be low (ebullition was not considered), but it is comparable to the global annual evasion of 3.8 Tg CH₄ calculated

for Northern Siberian thaw lakes and significant in comparison to the 6–40 Tg CH₄ emitted annually by northern wetlands (Walter *et al.*, 2006). Methane emissions can be especially high under anoxic conditions in lakes underlain by organic-rich soils such as in Siberia (Yedomo soils). Climate change is likely to increase the contribution by lakes in permafrost regions. Permafrost thawing will also mean that high concentrations of nutrients will be transported into ponds and lakes, especially in the early phase of permafrost thawing. Higher nutrient concentrations enhance primary and secondary production as is illustrated by an example from North-East Greenland (Figure 10). Based on 9 y of data, it was found that warmer and nutrient-richer years generally led to a higher abundance of phytoplankton and crustaceans as well as altered species composition (Christoffersen *et al.*, 2008a).

Higher air temperatures not only alter organic matter transport from land to the water, but also lead to earlier ice melting in spring, which exposes ponds to intense UV radiation (Prowse *et al.*, forthcoming and references therein). This is likely to be lethal for those organisms that are not able to adjust their protection against harmful UV radiation. As early as the 1950s, high UVR was suggested

to be responsible for the lack or scarcity of plankton in shallow water bodies in northern Patagonia and Swedish Lapland (Thomasson, 1956), and more recently Rautio and Korhola (2002) showed that the absence of *Daphnia* sp. in most DOC-poor ponds in Finnish Lapland is also related to high UV. On the other hand, increased snowfall in winter (predicted by climate models; ACIA, 2005) can lead to longer melting times in spring and may compensate for the temperature-induced earlier ice melting. Permafrost degradation also involves erosion and increased turbidity of the water column, which will decrease exposure to UVR (Watanabe *et al.*, 2011), especially if the thawing soils are organic and release humic compounds. Possible evidence of such effects is the observation that non-melanic *D. pulex* clones have shown nearly a threefold increase in abundance in Churchill ponds since 1985, leading to the displacement of melanic clones in 30% of the ponds. Air temperature has increased 4–5 °C in Churchill over the past 25 y, and mean conductivity of the water has also increased, from 453 μS·cm⁻¹ to 1252 μS·cm⁻¹ (Weider, Frisch & Hebert, 2010). Further studies examining differences in tolerance to temperature and conductivity between melanic and non-melanic clones are needed to further understand the environmental factors associated with these clonal changes.

Pond biota are also affected by the risk of habitat loss. Run-off from icecaps, glaciers, and accumulated snow may lead to land slumping (Burn & Kokelj, 2009; Pokrovsky *et al.*, 2011) and/or drainage and subsequent drying up of water bodies. Melting of ice in the permafrost and the resultant erosion and drainage are also changing aquatic habitats and their biogeochemical functioning (Van Huissteden *et al.*, 2011). Increased evaporation-precipitation ratios have likely been the main cause of the extensive recent disappearance of small lakes and ponds, witnessed both in Siberia (Smith *et al.*, 2005) and Arctic Canada (Smol & Douglas, 2007). Complete desiccation and the loss of aquatic habitat is a severe final threshold (*sensu* Smol & Douglas, 2007), but even a small reduction in the duration of the growth period may have strong effects on species that need several weeks to complete one life-cycle.

Perhaps one of the most difficult changes to predict is how higher temperatures will influence the dispersal of new species towards the North and the survival of native Arctic species. Because native species of the Arctic cannot redistribute themselves to higher latitudes (at least the northernmost species), it is expected that competition will increase with new species coming from the South. As a consequence, the species richness in the Arctic is predicted to increase with climate warming (*e.g.*, Patalas, 1990 for zooplankton). This greater total species number will be gained through compression and loss of optimal habitat for native Arctic species. A recent study at the Churchill site has already reported a striking change in clonal composition that may have been mediated by temperature and related changes (Weider, Frisch & Hebert, 2010).

Conclusion

Freshwater ecosystems cover a vast area of the circum-polar Arctic, and the most common water body types are

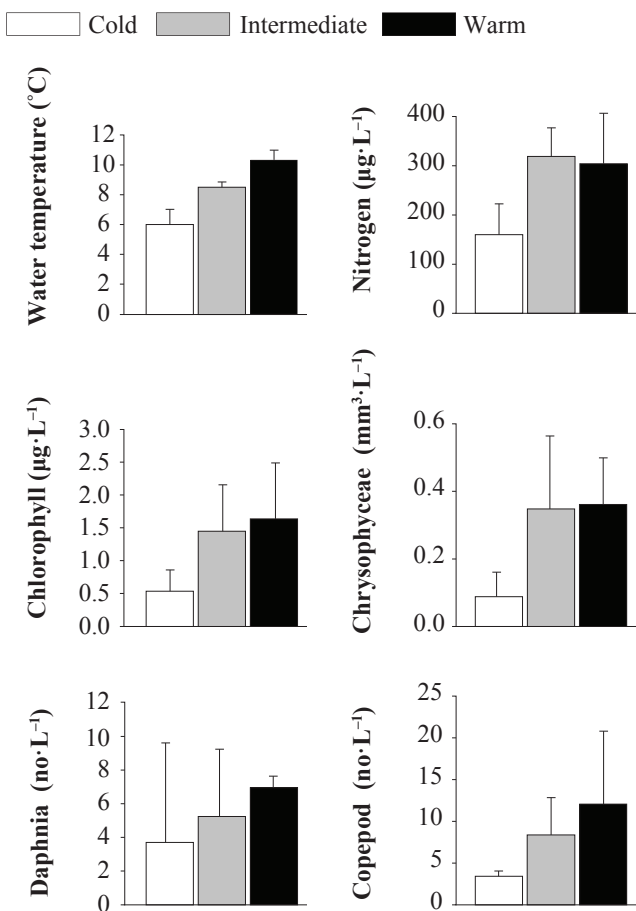


FIGURE 10. Calculated mean values of chlorophyll, biomass of two phytoplankton (as biovolume) and abundance of three zooplankton genera during 3 warm, 3 intermediate, and 3 cold years, equivalent to average water temperatures of 6, 8, and 10 °C during July–August. Data from Christoffersen *et al.* (2008b).

small ponds and shallow lakes. Many of the ponds dry out during the course of the short polar summer, or freeze solid during winter, limiting the duration of biological productivity and the presence of active organisms to a few months a year. Only the deepest of these waters have a liquid phase throughout the year, although the quantity of water is often very small. The small size of ponds and the resultant strong connectivity with the atmosphere, land, and benthos compensate for the short duration of the summer. Ponds heat up rapidly, which enhances production. They receive relatively more nutrients from the catchment per unit area than larger lakes (smaller lake: catchment area), and the constantly mixing water column is in contact with benthos and the nutrient and carbon reserves stored in it. As a result of this connectivity, the primary, bacterial, and secondary productivity in Arctic ponds is greater than in Arctic lakes.

In comparison to Arctic lakes, the productivity and biomass in most Arctic ponds is dominated by their rich microbial benthic communities (Figure 11). The availability of light and nutrients allows the benthic primary production to dominate, while the water column remains oligotrophic and low in biological productivity. The large influence of allochthonous carbon on ponds means that they are more DOC-rich and less transparent than deeper lakes, but solar radiation still reaches the bottom due to the shallow depth of the ponds, and only in most turbid thaw ponds is light attenuated substantially by the water column.

The secondary production of zooplankton in Arctic ponds is partly based on carbon sources other than phytoplankton. A variety of coupling processes between the water column and benthos operate, providing additional food sources to the zooplankton and other higher trophic levels. Thus, one of the most distinctive characteristics of Arctic ponds compared to lakes is the importance of benthic relative to planktonic processes for the functioning of these ecosystems.

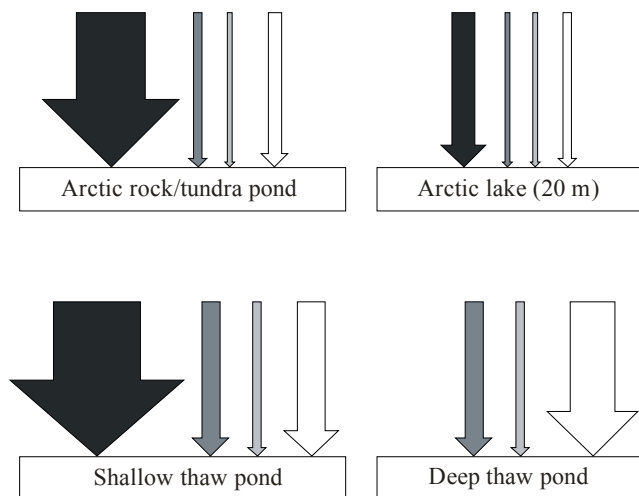


FIGURE 11. Schematic presentation of the relative importance of benthic and pelagic primary producers, bacterial production, and allochthonous humic compounds as contributors of biogenic energy in different types of Arctic ponds and a lake. The weighting of arrows is based on the data presented in the paper. Deep thaw pond refers to ponds that are deep enough (2–3 m) for extinction of light before it reaches the bottom. Black = benthic algae, dark grey = phytoplankton, light grey = bacterioplankton, and white = allochthonous carbon.

Future temperature increases combined with permafrost thawing and higher allochthonous carbon and nutrient loads to the ponds may severely affect the fine balance that is currently observed in high-latitude freshwater ecosystems between benthic and upper water column processes. Ponds, because of their small size and shallow depth, are especially sensitive to changes in temperature and the precipitation/evaporation balance. Permafrost thawing can also have significant consequences for the effect of circumpolar ponds on GHG emissions, but there are large differences among Arctic regions: at some sites the ponds are expanding and receiving increased organic carbon inputs from the tundra, while at other sites landscape erosion is resulting in pond drainage and loss. Long-term monitoring at multiple sites throughout the circumpolar Arctic is urgently needed to capture this large regional variability and to track the effects of climate change on these abundant freshwater ecosystems.

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