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PRIMARY RESEARCH PAPER

Epipelic and pelagic primary production in Alaskan Arctic lakes of varying depth

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Abstract We compared on eight dates during the ice-free period physicochemical properties and rates of phytoplankton and epipelic primary production in six arctic lakes dominated by soft bottom substrate. Lakes were classified as shallow ($\bar{z} < 2.5$ m), intermediate in depth ($2.5 \text{ m} < \bar{z} < 4.5$ m), and deep ($\bar{z} > 4.5$ m), with each depth category represented by two lakes. Although shallow lakes circulated freely and intermediate and deep lakes stratified thermally for the entire summer, dissolved oxygen concentrations were always >70% of saturation values. Soluble reactive phosphorus and dissolved inorganic nitrogen (DIN = NO_3^-–N + NH_4^+–N) were consistently below the detection limit (0.05 μmol l^{-1}) in five lakes. However, one lake shallow lake (GTH 99) periodically showed elevated values of DIN (17 μmol l^{-1}), total-P (0.29 μmol l^{-1}), and total-N (33 μmol l^{-1}), suggesting wind-generated sediment resuspension. Due to increased nutrient availability or entrainment of microphytobenthos, GTH 99 showed the highest average volume-based values of phytoplankton chlorophyll *a* (chl *a*) and primary production, which for the six lakes ranged from 1.0 to 2.9 μg l^{-1} and 0.7–3.8 μmol C l^{-1} day^{-1}. Overall, however, increased $\bar{z}$ resulted in increased area-based values of phytoplankton chl *a* and primary production, with mean values for the three lake classes ranging from 3.6 to 6.1 mg chl *a* m^{-2} and 3.2–5.8 mmol C m^{-2} day^{-1}. Average values of epipelic chl *a* ranged from 131 to 549 mg m^{-2} for the three depth classes, but levels were not significantly different due to high spatial variability. However, average epipelic primary production was significantly higher in shallow lakes (12.2 mmol C m^{-2} day^{-1}) than in intermediate and deep lakes (3.4 and 2.4 mmol C m^{-2} day^{-1}). Total primary production (6.7–15.4 mmol C m^{-2} day^{-1}) and percent contribution of the epipelon (31–66%) were inversely related to mean depth, such that values for both variables were significantly higher in shallow lakes than in intermediate or deep lakes.

Keywords Primary production · Phytoplankton · Epipelic · Arctic

Introduction

A pelagic-based paradigm has historically dominated lacustrine research (Vadeboncoeur et al., 2003). Due to spatial segregation, benthic habitats have often been considered functionally independent from pelagic environments (Carpenter et al., 1996) with

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parallel communities of microbes, primary producers and consumers (Vadeboncoeur et al., 2002). However, many recent food web analyses indicate that both benthic and planktonic phytomass contribute directly or indirectly to the energetic requirements of multiple zooplankton (Rautio & Vincent, 2007) and fish taxa (Bootsma et al., 1996; Vander Zanden & Vadeboncoeur, 2002), and there are some indications that benthic primary production may be more efficiently transferred to higher trophic levels than pelagic phytomass (Heckey & Hesslein, 1995).

If littoral-pelagic linkages are crucial to lake ecosystem function (Palmer et al., 2000; Schindler & Scheuerell, 2002), any detailed food web analysis must necessarily begin with an evaluation of both pelagic and benthic primary production. Global surveys indicate that inland waters are dominated by small (<10 ha surface area), shallow (<10 m mean depth, $\bar{z}$) lakes that have a high ratio of littoral surface to pelagic volume (Downing et al., 2006). Accordingly, most lakes should show both a high contribution of the benthic component to total primary production and strong coupling between benthic and pelagic habitats (Schindler & Scheuerell, 2002). Despite the acknowledgement that a holistic view of lake dynamics must integrate benthic and pelagic processes and that morphometric considerations generally favor high rates of benthic autotrophy, only about 30 studies worldwide have partitioned lentic primary production between benthic and pelagic components (Vadeboncoeur & Steinman, 2002).

Along a trophic gradient, benthic primary production can be especially important in oligotrophic systems where nutrient limitation of the phytoplankton can favor benthic production by enhancing light penetration to epipelic algae associated with nutrient-rich sediments (Vadeboncoeur et al., 2001). Shallow lakes and ponds are a characteristic feature of arctic environments (Hobbie, 1984), where high optical clarity and low levels of pelagic nutrients suggest that the benthos should be important in whole lake primary productivity. Although estimates of phytoplankton primary production for this region are sparse, the contribution of the benthos to total primary production is virtually unquantified. Benthic and pelagic primary production have been simultaneously assessed in only a single deep ($\bar{z} = 10.2$ m) lake (Welch & Kalff, 1974) and a few shallower ($\bar{z} < 3$ m) arctic lakes (Stanley, 1976; Ramlal et al., 1994; Bonilla et al., 2005; Rautio & Vincent, 2007; Whalen et al., 2006). Others (Vézina & Vincent, 1997; Bonilla et al., 2005) have compared total community biomass (chlorophyll *a* (chl *a*)) between the phytoplankton and benthic mats in ponds of the Canadian High Arctic.

Omission of the benthic component leads not only to a serious underestimate of total primary production in arctic lakes, but also prohibits a full understanding of food web dynamics. Logistic and financial constraints attendant to investigations at remote field locations are frequently cited as reasons for our imperfect knowledge of all aspects of arctic lake dynamics. These arguments are especially applicable to investigations of the biomass and activity of the phytobenthos, which may require diver assistance or timely transport and manipulation of undisturbed substrates.

Logistics aside, analysis of the functional significance of linkages and feedbacks between benthic and pelagic environments, beginning with an evaluation of the distribution of whole lake primary production between habitat types, is a regional scientific imperative. Models of global climate change predict an amplified annual surface air temperature increase for the arctic relative to the global mean (Prowse et al., 2006). Regionally, the observed or predicted impacts of increased surface air temperature include a reduction in annual snow cover, thawing of permafrost and drainage of permafrost-based lakes, warming of lake waters, earlier ice-out and longer growing seasons, enhanced nutrient delivery to lakes, and shifts in terrestrial vegetation that alter patterns of organic carbon loading to lakes, which can in turn affect the underwater light climate (Serrese et al., 2000; Overland et al., 2004; Hinzman et al., 2005; Prowse et al., 2006; Schindler & Smol, 2006). The influence of altered hydrologic budgets and perturbations to physical and chemical cycles of arctic lakes on lake productivity and decomposition processes is uncertain. However, low energy flow and simple food web structure suggest a high sensitivity of high latitude ecosystems to global environmental change (Roots, 1989). The present contribution of benthic habitats to total primary production in arctic lakes is an informational gap that must be addressed as a reference to assess lacustrine response to climate change.

Our study in the Arctic Foothills region of Alaska was a component of a larger effort to relate landscape-scale characteristics to lake productivity and food web structure, while simultaneously compiling baseline information for future identification of climate-mediated changes in limnological conditions in this region. Within the framework of the overall research objectives, we evaluated chl *a* levels, determined rates of total primary production, partitioned these biological variables between benthic and pelagic habitats, and assessed the relationship of these variables to physicochemical properties in regionally representative lakes. To better understand ecosystem function, we endeavored to capture the regional variability in lake morphometric properties and lake-catchment relationships, as well as the spatial and temporal heterogeneity of target measurements. Therefore, within five catchments we sampled on eight occasions six lakes that varied widely in mean depth and surface area. We hypothesized that mean depth would be the master variable determining the relative distribution of primary production between benthic and pelagic habitats, but that total primary production would remain constant across lakes.

Methods

Site description

This study involved 6 lakes located at about 68°N, 149°W, some 20 km north of the Brooks Range in Alaska, USA (Fig. 1). The regional physiography and vegetation physiognomy of the study site typify the 95,000 km^2 Arctic Foothills region of Alaska and are

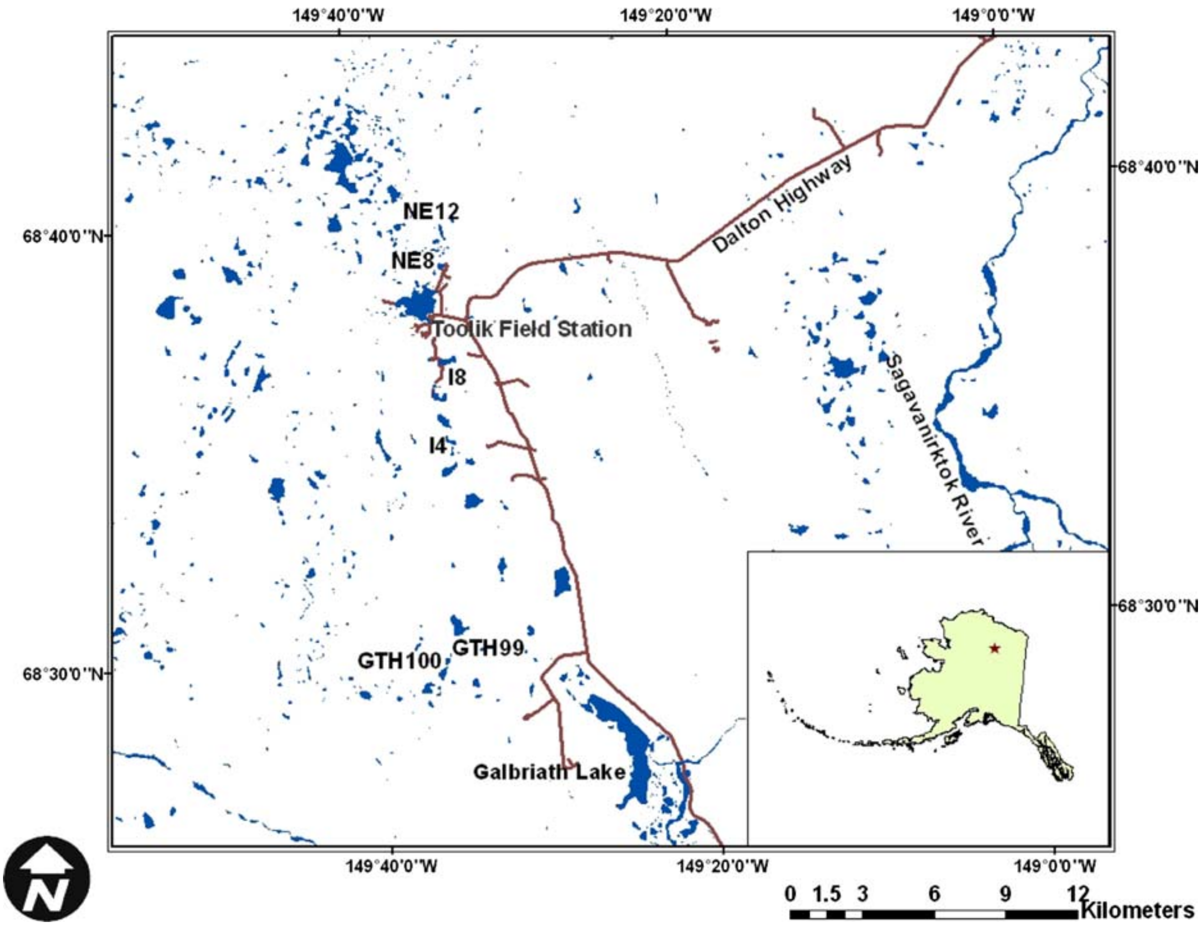

Fig. 1 Location of the study lakes

described in detail by Wahrhaftig (1965) and Walker et al. (1994). Briefly, permafrost is continuous on the landscape of low, rolling hills. Snow cover persists for 7–9 months, and rivers cease to flow during winter. Lakes and ponds are ice-covered for about 9 months and are surrounded by tussock tundra, wet sedge tundra, or dwarf shrub communities. Well-drained ridge tops are occupied by drier heath tundra. The mean annual air temperature is −6°C, while precipitation averages 20 cm per year, with roughly 40% occurring as snow (Ping et al., 1998).

Study lakes were generally accessed by helicopter (less frequently by foot) and were sampled from an inflatable raft. All lakes were located between 690 and 950 m a.s.l. and were selected to encompass a range of mean depths (1–8 m) expected for the majority of Arctic Foothill lakes. We classified our lakes as shallow ($\bar{z} < 2.5$ m; GTH99 and NE8), intermediate in depth (2.5 m $< \bar{z} <$ 4.5 m; I4 and I8), and deep ($\bar{z} > 4.5$ m; GTH 100 and NE 12) when qualitatively and quantitatively comparing values for physicochemical and biological properties (Table 1).

The study lakes varied widely with respect to many morphometric and catchment characteristics (Table 1). Lake surface area ranged from 0.7 to 18.3 ha and volume ranged from 14 to 642 × 10^3 m^3. Watershed area ranged from 13 to 3,010 ha, while the catchment:lake area ratio ranged from 6 to 165. Maximum and mean depths ranged from 2.8 to 17.5 m and from 1.3 to 7.6 m, respectively. Other morphometric characteristics showed more uniformity. Shoreline development factors ranged from 1.09 to 1.43, while depth ratios ranged from 0.37 to 0.51.

Six lakes were chosen in three pairs (GTH 99 and GTH 100; I4 and I8; NE 8 and NE 12) where each member of a pair (Fig. 1) could be accessed by foot and sampled on the same day following a single helicopter drop-off. Distances between lake pairs varied from 0.1 km (GTH 99 and GTH 100) to 3.2 km (I4 and I8). GTH 99 flows into GTH 100. Otherwise, only I4 and I8 have clearly defined surface inlets. All lakes have a single outlet stream and a bottom substrate dominated by soft sediment with few, if any, rooted macrophytes. The six lakes span five catchments. Each member of lake pairs I4-I8 and NE 8–NE 12 are in separate catchments, while GTH 99 and GTH 100 share a common catchment.

Sample collection

Lake pairs were sampled on eight occasions over a 3-year period, during late June through mid-August of the ice-free season. Sampling of individual lake pairs was conducted on three dates in 2001 and 2002 and on two dates in 2003.

Mid-lake profiles of water temperature and dissolved oxygen were obtained with a YSI Model 85 multiparameter water quality meter (YSI Incorporated, Yellowsprings, OH, U.S.A.). Profiles of photosynthetic photon flux density (PPFD) were determined with a LiCor LI-250 Quantum Meter (LiCor Biosciences, Lincoln, NE, U.S.A.) interfaced with an LI-192SA underwater quantum sensor. Incident irradiance was continuously recorded during June through August with a LiCor LI-1400 data logger and LI-192 terrestrial quantum sensor.

Opaque polyethylene bottles (1-l volume) were filled in duplicate from a 2.2-l Van Dorn sampler (Wildlife Supply Company, Buffalo, NY, U.S.A.) at

Table 1 Morphometric characteristics for six Arctic Foothill lakes

Lake	Depth classification	Surface area (ha)	Volume (×10^3 m^3)	Maximum depth (m)	Average depth (m)	Depth ratio	SDF[a]	Catchment area (ha)	C:L area ratio[b]
GTH 99	Shallow	0.7	14	4.1	2.1	0.51	1.09	13	18
NE8	Shallow	5.0	63	2.8	1.3	0.45	1.39	28	6
I4	Intermediate	8.2	263	8.0	3.2	0.40	1.41	422	51
I8	Intermediate	18.3	642	9.5	3.5	0.37	1.43	3010	165
GTH 100	Deep	5.4	350	15.7	6.5	0.41	1.09	93	17
NE12	Deep	7.1	566	17.5	7.6	0.43	1.43	125	17

[a] Shoreline development factor

[b] Catchment:Lake area ratio

depths corresponding to 50%, 22%, 10%, and 1% of surface PPFD (depths determined from the underwater profile), while duplicate surface samples (100% light depth) were collected into similar bottles by hand immersion. One or two additional water samples were collected at approximately equally spaced intervals between the bottom of the euphotic zone (depth of penetration of 1% surface PPFD) and the sediment surface if the euphotic zone did not extend to the sediment surface.

Five sediment cores were collected from a depth of about 0.25 m (defined here as the 100% light depth for sediments) by hand-inserting from shore clear polycarbonate cylinders (4.7 cm inside diameter × 50 cm length; 17.3 cm^2 surface area) into the sediment. Replicated (5) cores of similar dimension were taken with a KB gravity corer (Wildlife Supply Company, Buffalo, NY, U.S.A.) from locations in the lake where the sediment surface corresponded with the 50%, 22%, 10%, and 1% PPFD depths. Cores (with overlying water) were capped on each end with clear plugs and immediately covered with opaque bags. Samples of water and sediment plus overlying water were returned to the Toolik Lake Field Station, located within a 30 km radius of the sampling sites (Fig. 1).

Biological measurements

Phytoplankton chl *a* and primary production (^{14}C technique) determinations were made on water samples from the euphotic zone of each lake. Duplicate chl *a* measurements were made fluorometrically with a Turner Designs Model TD-70 fluorometer (Turner Designs Inc., Sunnyvale, CA, U.S.A.) on filter-trapped (Whatman GF/F) particulates following a 24 h extraction in a buffered 90% acetone solution. Midway through the extraction filters were pulverized, which gave a chl *a* yield not significantly different from grinding after a 24 h extraction. The methodology we used (Welschmeyer, 1994) does not involve acidification, but maintains a desensitized response to phaeopigments. Replicated (3), clear 73-ml polystyrene bottles and a single opaque bottle of similar size were filled with water from each depth for primary productivity determinations. Each bottle was amended with 39 kBq $NaH^{14}CO_3$ (specific activity 2.0 GBq $mmol^{-1}$) and clear bottles were suspended at a central station in Toolik Lake at the PPFD-specific depths corresponding to 100%, 50%, 22%, 10%, and 1% of the surface value (determined as described above). Toolik Lake is optically similar to all study lakes except GTH 99, which shows the highest attenuation coefficient for radiant energy (Table 2). Opaque bottles were secured in a shoreside incubator. Logistic constraints precluded sample incubation in the collection lakes. Incubations were terminated after 24 h by filtration (Gelman Metricel GN-6 filters; 0.45 μm pore diameter). Rinsed (5-ml deionized water), air-dried filters were assayed for radiocarbon incorporation into the particulate fraction by liquid scintillation spectrometry with a Packard Model 1900TR Liquid Scintillation Analyzer (Packard Instrument Company, Downers Grove, IL, U.S.A.).

Chlorophyll *a* and productivity measurements were also made for the epipelon in the euphotic zone. Determination of the sediment depth of the actively photosynthesizing zone is problematic. Although studies often indicate rapid attenuation of light in the upper few mm, photosynthesis has been reported to a depth of 1 cm in flocculent sediments (e.g., Vadeboncoeur & Lodge, 1998). Sediments here were frequently (depending on sampling depth) very flocculent (porosity 84–98% v/v) and highly organic (40–87%), making it difficult to consistently remove a superficial layer of <2 cm in depth and suggesting that the zone of photosynthesis likely extends to 1 cm or more. Thus, we focused on the 0–2 cm layer (defined as surface sediment) in chl *a* and epipelic productivity determinations. Surface sediment from duplicate cores was resuspended in 100 ml of deionized water. A subsample of the suspension was filtered (Whatman GF/F) and analyzed for chl *a* as described above. The remaining three cores from each PPFD level were extruded undisturbed into clear polycarbonate cylinders (12 cm length) similar in diameter to the sample collection cores leaving a 2 cm layer of overlying lake bottom water. Radiocarbon (39 kBq $NaH^{14}CO_3$) was injected into the overlying water while cores were gently rotated. We (Whalen et al., 2006) previously showed that this method of $H^{14}CO_3$ addition immediately and evenly distributed the radiocarbon into the superficial sediment.

Two cores from each depth were placed in wire frames within acrylic chambers covered with neutral density screens to simulate the light environment at the depths of sample collection. The remaining core

Table 2 Mean values (±1 SD) for selected variables in six Arctic Foothill lakes

	Shallow		Intermediate		Deep	
	GTH 99	NE8	I4	I8	GTH 100	NE12
Attenuation coefficient, k_d (m^{-1})	1.1 (0.4)	0.5 (0.1)	0.8 (0.1)	0.9 (0.2)	0.7 (0.1)	0.5 (0.1)
Percent lake volume in euphotic zone	98 (4)	100 (0)	95 (2)	88 (7)	81 (12)	83 (8)
Percent sediment surface in euphotic zone	94 (13)	100 (0)	85 (5)	72 (7)	50 (8)	59 (8)
Phytoplankton chlorophyll *a*						
Volume-based (μg l^{-1})	2.9 (1.7)	1.3 (0.7)	1.5 (0.8)	1.4 (0.7)	1.3 (0.6)	1.0 (0.6)
Whole lake, area-based (mg m^{-2})	5.7 (3.3)	1.6 (0.8)	4.3 (1.2)	4.1 (1.8)	6.2 (1.4)	6.0 (2.0)
Epipelic chlorophyll *a*						
Area-based (mg m^{-2})	458 (316)	235 (202)	544 (1094)	699 (1125)	422 (218)	258 (198)
Whole lake, area based (mg m^{-2})	474 (236)	430 (220)	581 (1037)	517 (622)	122 (56)	139 (28)
Phytoplankton primary production						
Volume-based (μmol C l^{-1} day^{-1})	3.8 (2.7)	2.1 (1.0)	1.8 (1.7)	1.9 (2.3)	1.2 (1.1)	0.7 (0.4)
Whole lake, area-based (mmol C m^{-2} day^{-1})	3.6 (1.5)	2.8 (1.2)	5.9 (2.9)	5.6 (3.7)	4.8 (2.3)	3.8 (1.1)
Epipelic primary production						
Area-based (mmol C m^{-2} day^{-1})	7.5 (6.5)	4.8 (5.0)	3.8 (6.7)	4.9 (5.5)	15.9 (18.0)	5.4 (6.0)
Whole lake, area based (mmol C m^{-2} day^{-1})	6.3 (5.5)	18.1 (16.8)	3.5 (5.1)	3.3 (3.0)	2.0 (1.1)	2.8 (2.3)
Total primary production (mmol C m^{-2} day^{-1})	10.0 (5.1)	21.0 (16.8)	9.4 (7.1)	8.9 (5.7)	6.8 (2.7)	6.6 (1.5)
Percent total primary production by epipelon	55 (23)	77 (17)	28 (18)	35 (21)	30 (14)	39 (24)

Lakes are classified as shallow, intermediate, or deep based on mean depth. See text for details

from each depth was inserted into an opaque chamber. Chambers were placed in the shallows (25 cm depth) of a local pond for 24 h. Incubation temperatures in epipelic and planktonic productivity determinations differed by ≤3°C from the temperature of sample collection. Following incubation, the 0–2 cm layer of superficial sediment was rinsed into a 125-ml polyethylene bottle and immediately frozen. Samples were later thawed, acidified to pH 3, and purged with high purity N_2 for 1 h to remove the remaining $DI^{14}C$. Dried (60°C), homogenized samples were weighed and subsamples were subjected to high temperature (900°C) catalytic combustion in a Harvey Model OX 600 Biological Material Analyzer (R.J. Harvey Instrument Corporation, Hillsdale, NJ, U.S.A.). The evolved CO_2 was trapped in a scintillation cocktail containing phenethylamine (Harvey OX-161) and assayed for β-activity.

Chemical measurements

Alkalinity was determined potentiometrically. Freshly collected sediment porewater at 1 cm below the sediment surface was analyzed for dissolved inorganic-C (DIC) by thermal conductivity gas chromatography (Shimadzu GC8A Thermal Conductivity Gas Chromatograph; Shimadzu Scientific Instruments, Columbia, MD, U.S.A.) using a gas stripping technique (Stainton, 1973). Syringe-filtered (0.45 μm pore diameter) water was stored frozen and later analyzed for NO_3^-–N + NO_2^-–N (hereafter referred to as NO_3^-–N), NH_4^+–N, and soluble reactive phosphorus (SRP) using the Cu–Cd reduction, phenol hypochlorite, antimony-phospho-molybdate complexation methods, respectively (Parsons et al., 1984). Detection limits for NO_3^-–N, NH_4^+–N, and SRP were 0.05 μM, while the precision for repeated analyses ($n = 10$) at 0.2 μM N or P was <10%. Unfiltered water was stored frozen and later analyzed for total nitrogen (TN) and total phosphorus (TP) by persulfate oxidation (Sólorzano & Sharp, 1980a, b). All nutrient determinations were performed by automated flow injection analysis using a Lachat QC 8000 Ion Analyzer (Lachat Instruments, Loveland, CO, U.S.A.).

Calculations and data analysis

Attenuation coefficients for radiant energy, k_d (m^{-1}), were calculated following Kirk (1994). Volume-based rates of phytoplankton primary production and area-based rates of epipelic primary production were calculated according to Wetzel & Likens (2000) from available $DI^{12}C$ and the fraction of added radiocarbon recovered from the filter (phytoplankton) or combusted sediment (epipelon). Available $DI^{12}C$ in the water column was determined from alkalinity and pH determinations and temperature-corrected acidity constants (Stumm & Morgan, 1996). Available porewater $DI^{12}C$ was calculated from the CO_2 concentration measured in the headspace of porewater samples (1 cm depth) equilibrated in He-filled serum vials and temperature-corrected values of Henry's constant (Weiss, 1974). An isotope discrimination factor of 1.06 was assumed in all primary productivity calculations (Wetzel & Likens, 2000). Following Miller et al. (1986), our 24 h incubations were used to give day-rate estimates of phytoplankton and epipelic primary production. The arctic summer is characterized by continuous daylight such that single 24 h incubation for phytoplankton production gives an estimate only 13% lower than that provided by summing the results of multiple consecutive incubations over a similar time period (Whalen & Alexander, 1984). High respiratory activity in sediment and a long incubation could potentially dilute the radiocarbon label through photosynthetic withdrawal of $DI^{14}C$ and production of $DI^{12}C$, leading to an underestimate of epipelic primary production. This is not likely here for three reasons. First, the incubation did not include a period of darkness that would facilitate net accumulation of $DI^{12}C$. Second, total CO_2 in the flocculent superficial sediment was most frequently <50% higher than values calculated for bottom water from alkalinity determinations, suggesting low rates of respiration in superficial sediment in this unproductive, cold environment. Third, we recovered as photosynthate a maximum of 1.1% of the added radiolabel in midsummer experiments.

Detailed bathymetric maps were prepared for each lake from sonar-based depth assessment along multiple GPS-mapped lake transects. The total biomass of phytoplankton in the euphotic zone was estimated by multiplying the mean volumetric chl *a* concentration between consecutive sampling depths with the total volume of water in that stratum and summing the products. Likewise, the total biomass of epipelic algae in the euphotic zone was estimated by multiplying the mean area-based chl *a* concentration between consecutive sampling depths with the total area of sediment surface within that stratum and summing the products. Whole lake rates of phytoplankton and epipelic primary production were estimated in a similar manner. These summed biomass and productivity values were divided by the lake surface area to give whole lake, area-based (per m^2 lake surface) estimates for these variables.

Comparisons of means for physicochemical and biological variables were made by *t*-tests or single factor Analysis of Variance coupled with Tukey's Honestly Significant Difference procedure (JMP software; SAS Institute, Cary, NC, U.S.A.). Variables expressed as percentages were arcsine square root-transformed prior to analysis. All other data met assumptions of normality and homoscedasticity. Statistical analyses were conducted at a significance level of $\alpha = 0.05$.

Results

Physicochemical variables

Lakes classified as deep or intermediate in depth showed thermal stratification, while shallow lakes circulated freely (Fig. 2A). Dissolved oxygen concentrations showed little vertical variability irrespective of mean depth and remained at >70% saturation throughout the summer (data not shown).

Attenuation coefficients (k_d) for radiant energy showed no relationship with $\bar{z}$, as the highest and lowest mean values were associated with the two shallow lakes, GTH 99 and NE8 (Table 2). Although the distance between lakes was <100 m, the mean k_d value for GTH 99 was significantly greater than that for GTH 100. Average (±1 SD) euphotic depths for the six lakes ranged from 4.8 ± 1.3 m in GTH 99 to 9.6 ± 1.4 m in NE12. Essentially 100% of the lake volume and sediment surface was contained in the euphotic zone for shallow lakes (Table 2). Values decreased to about 90% of the lake volume and 80% of the sediment surface for lakes of intermediate mean depth, and further declined to roughly 80% of the volume and 55% of the sediment surface for deep lakes. The decreases in percent lake volume and percent sediment surface area in the euphotic zone with increasing mean depth were statistically significant (Table 3). Arctic Foothill lakes begin to stratify thermally within days of ice-out such

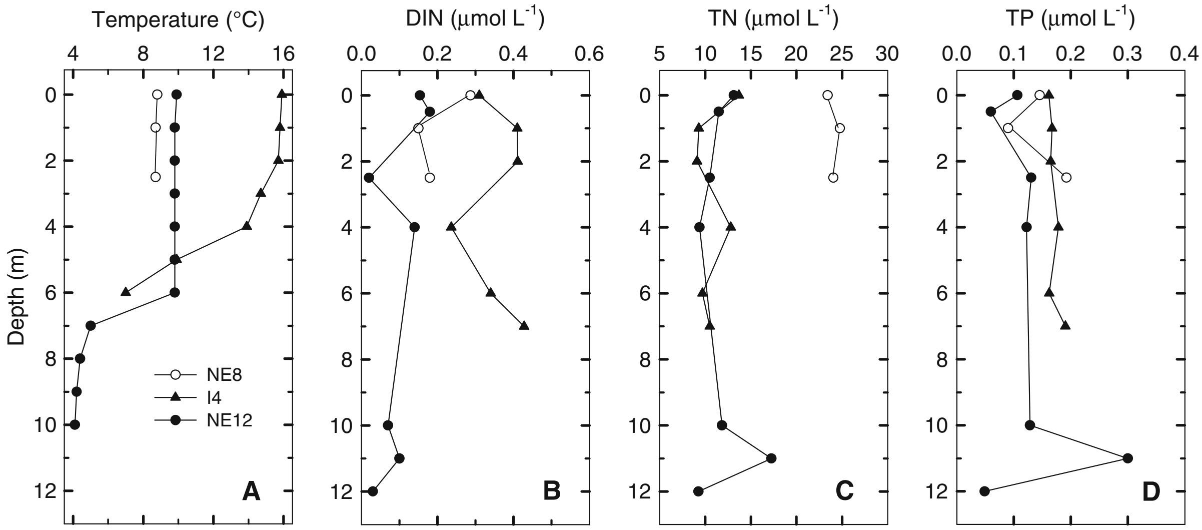

Fig. 2 Representative depth profiles for (**A**) temperature; (**B**) dissolved inorganic nitrogen, DIN; (**C**) total nitrogen, TN; and (**D**) total phosphorus, TP in Arctic Foothill lakes categorized with respect to mean depth as shallow (NE8), intermediate in depth (I4), or deep (NE12). Sampling dates were August 7, 2001 (NE8 and NE12) and July 19, 2001 (I4)

Table 3 Multiple comparison of means for physical and biological variables in Arctic Foothill lakes by Tukey's honestly significant difference procedure

Variable	Depth category		
	Shallow	Intermediate	Deep
Percent sediment surface in euphotic zone	97^{a}	78^{b}	54^{c}
Percent lake volume in euphotic zone	99^{a}	91^{b}	82^{c}
Phytoplankton chlorophyll *a*			
Volume-based (μg l^{-1})	2.1^{a}	1.4^{ab}	1.2^{b}
Whole lake, area-based (mg m^{-2})	3.6^{a}	4.2^{ab}	6.1^{b}
Epipelic chlorophyll *a*			
Whole lake, area-based (mg m^{-2})	452^{a}	549^{a}	131^{a}
Phytoplankton primary production			
Volume-based (μmol C l^{-1} day^{-1})	3.0^{a}	1.9^{b}	0.9^{c}
Whole lake, area-based (mmol C m^{-2} day^{-1})	3.2^{a}	5.8^{b}	4.3^{ab}
Epipelic primary production			
Whole lake, area-based (mmol C m^{-2} day^{-1})	12.2^{a}	3.4^{b}	2.4^{b}
Total whole lake primary production (mmol C m^{-2} day^{-1})	15.4^{a}	9.1^{ab}	6.7^{b}
Percent of total primary production by epipelon	66^{a}	31^{b}	34^{b}

Mean values for each variable are given for lakes categorized as shallow, intermediate, or deep with respect to mean depth. Within each row, different letter superscripts denote significant *a posteriori* differences between means ($n = 16$)

that the euphotic depth exceeded the mixing depth for all lakes on all sampling occasions except for one date for lake I4.

Nutrient concentrations showed little or no vertical structure despite development of a hypolimnion in intermediate and deep lakes. Dissolved inorganic-N ($DIN = NO_3^{-}\text{–}N + NH_4^{+}\text{–}N$) concentrations (Fig. 2B) were consistently low (<0.5 μM) in all lakes except GTH 99, where averages for the water column varied from undetectable to 17 μM. In all lakes, however, NO_3^{-}–N contributed little to DIN. Nitrate concentrations were consistently near or below the detection limit of 0.05 μM, except in GTH 99 where concentrations sometimes averaged 0.8 μM. In contrast to DIN, soluble reactive-P concentrations were at or below the detection limit (0.05 μM) in all lakes (data not shown). Total nitrogen (Fig. 2C) and TP (Fig. 2D) varied little across lakes, with mean values ranging from 11 to 33 μM and from 0.19 to 0.29 μM, respectively. Consistent with the data for DIN, mean concentrations of TN and TP were highest in GTH 99, but were only slightly elevated (0.5 to 2-fold) relative to the other five lakes.

Biological variables

Profiles of phytoplankton chl *a* consistently showed homogeneous concentrations throughout the euphotic zone in shallow lakes, but frequently showed elevated levels at the base of the euphotic zone in intermediate and deep lakes (Fig. 3A). As with nutrients, the highest mean volume-based phytoplankton chl *a* concentration was observed in GTH 99 (2.9 μg l^{-1}), while comparable means for the other five lakes ranged from 1.0 to 1.5 μg l^{-1} (Table 2). Overall, the mean volume-based phytoplankton chl *a* concentration in shallow lakes was significantly higher than in deep lakes due to the influence of persistently high values in GTH 99 (Table 3).

Mean whole lake, area-based phytoplankton chl *a* ranged from 1.6 to 6.2 mg m^{-2} with highest values recorded in the deep lakes due to a more vertically extensive euphotic zone (Table 2). Nonetheless, the mean of 5.7 mg chl *a* m^{-2} for the shallow lake GTH 99 ranked midway among the study lakes due to the influence of high mean volume-based chl *a* concentration. Overall, the rank order of lake categories for whole lake, area-based phytoplankton chl *a* was reversed relative to the volume-based values, and shallow lakes showed a significantly lower mean than deep lakes, but the value for lakes of intermediate depth did not differ significantly from either of these averages (Table 3).

Epipelic chl *a* showed no pattern with depth and demonstrated considerably more variability between replicates taken at the same depth than volume-based phytoplankton chl *a* (cf. Fig. 3A and B). Mean values for whole lake, area-based epipelic chl *a* ranged over a factor of about 5 when all lakes were considered, 122–581 mg m^{-2} (Table 2). However, epipelic chl *a* concentrations did not differ among depth categories (Table 3).

Despite periodically high phytoplankton chl *a* values at the base of the euphotic zone in intermediate and deep lakes (Fig. 3A), volume-based rates of phytoplankton primary production declined with increasing depth in all lakes (Fig. 4A). Means ranged

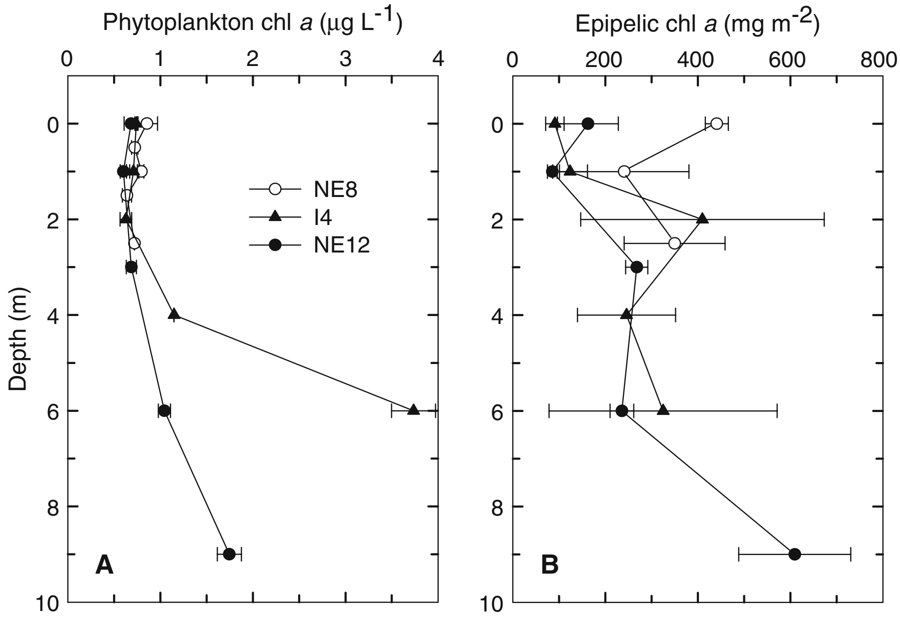

Fig. 3 Representative depth profiles of: (**A**) phytoplankton chlorophyll *a* (chl *a*); and (**B**) epipelic chl *a* in the euphotic zone in Arctic Foothill lakes categorized with respect to mean depth as shallow (NE8), intermediate in depth (I4), or deep (NE12). Error bars represent one standard deviation of triplicate (phytoplankton) or duplicate (epipelon) determinations and sometimes lie within the symbols. Sampling dates were August 7, 2001 (NE8 and NE12) and July 19, 2001 (I4)

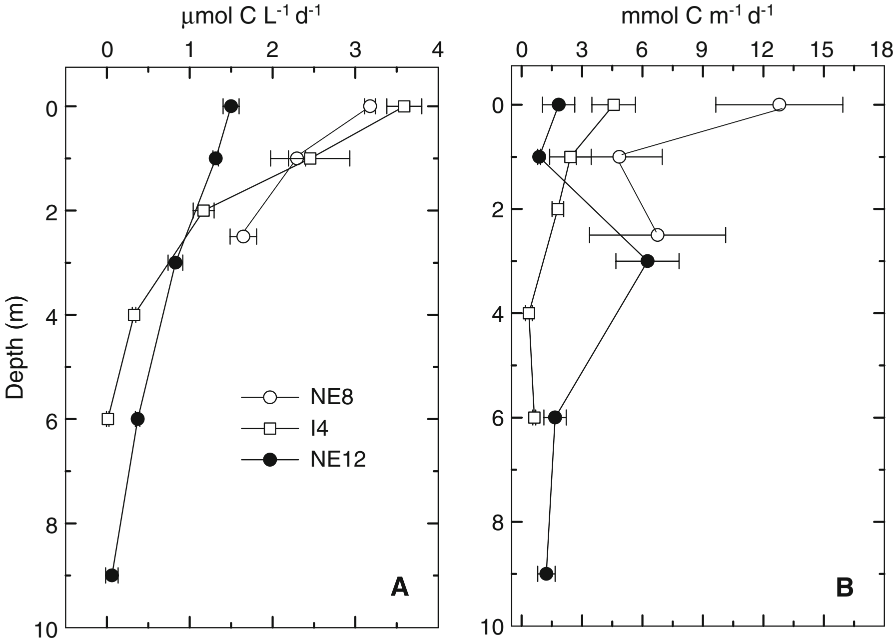

Fig. 4 Representative depth profiles of: (**A**) phytoplankton primary production (µmol C l^{-1} day^{-1}); and (**B**) epipelic primary production (mmol C m^{-2} day^{-1}); in Arctic Foothill lakes categorized with respect to mean depth as shallow (NE8), intermediate in depth (I4), or deep (NE12). Error bars represent one standard deviation of triplicate (phytoplankton) or duplicate (epipelon) determinations and sometimes lie within the symbols. Sampling dates were August 7, 2001 (NE8 and NE12) and July 19, 2001 (I4)

from 0.7 to 3.8 µmol C l^{-1} day^{-1} (Table 2). In accord with the chl *a* and nutrient data, GTH 99 showed the highest mean value. Evaluation of the data by depth category showed a significant increase in volume-based phytoplankton primary production as mean depth declined (Table 3).

Whole lake, area-based phytoplankton primary production ranged over a factor only slightly in excess of two, 2.8–5.9 mmol C m^{-2} day^{-1} (Table 2). Consistent with phytoplankton chl *a*, expression of primary productivity on a whole lake, areal versus volumetric basis reversed the position of shallow lakes when means were rank-ordered according to depth categories. Shallow lakes showed significantly lower rates than lakes of intermediate depth, while deep lakes were not statistically distinguishable from the other two depth categories (Table 3).

In agreement with epipelic chl *a* (Fig. 3B), epipelic primary production showed no pattern with depth and high variability between replicate determinations at each depth (Fig. 4B). Mean values for whole lake, area-based epipelic primary production ranged over a factor of about 9, from 2.0 to 18.1 mmol C m^{-2} day^{-1} (Table 2). Ranked data indicated a generalized increase in epipelic primary production with decreasing mean depth. Shallow lakes showed significantly higher rates of epipelic primary production than intermediate or deep lakes, which did not differ from each other with respect to productivity by the epipelon (Table 3).

Total primary production ranged over a factor of 3, from 6.6 to 21.0 mmol C m^{-2} day^{-1} (Table 2). In contrast, mean depth ranged over a factor of 6 (Table 1). Shallow lakes showed significantly higher rates of total primary production than deep lakes, due to high rates of productivity by the epipelon (Table 3). Higher rates of production were accompanied by an increased importance of the epipelon in overall lake productivity. The epipelon accounted for roughly 33% of total primary production in intermediate and deep lakes, but up to 77% in shallow lakes (Table 2). The relative contribution of the epipelon to total primary production was significantly higher in shallow lakes than in lakes classified as intermediate or deep, while the importance of the epipelon was not significantly different for these latter two depth categories (Table 3).

Discussion

Although the study lakes were distributed across five watersheds and varied widely in size, catchment:lake area ratio, and thermal regime, five of the six lakes were remarkably similar with respect to concentrations of nutrients and values of k_d. However, the average attenuation coefficient for the eight sampling dates was higher in the shallow GTH 99 than in the other lakes, and elevated nutrient concentrations, particularly NH_4^+–N, were episodically observed. Ammonium has been demonstrated to desorb from resuspended lake sediment (Reddy et al., 1996; Ogilvie & Mitchell, 1998), while high levels of TN and TP in the water column are frequently associated with resuspension of lacustrine sediments (Søndergaard et al., 1992; Schelske et al., 1995; Reddy et al., 1996; Hamilton & Mitchell, 1997). It is likely that wind-generated mixing of superficial sediment is responsible for periodically elevated nutrient levels in GTH 99 rather than a difference in catchment properties or catchment-lake relationships, as the deep GTH 100 is located within 100 m of GTH 99 but shows physicochemical characteristics similar to the other four lakes. Nutrient concentrations and values of k_d in NE8, which is shallower than GTH 99, were consistent with those of intermediate and deep lakes. Resuspension is related to the nonlinear and interactive influences of fetch, wind velocity, and depth (Scheffer, 1998). Low, rolling hills afford lakes in this region varying degrees of protection from the influence of wind, suggesting that not all shallow lakes are subject to resuspension.

Exclusive of GTH 99, inorganic nutrient levels in the study lakes agree well with surveys of lentic systems from other regions of the circumpolar arctic, where concentrations of NO_3^-–N, NH_4^+–N, and SRP are generally below 0.5, 1.0, and 0.2 μM (Pienitz et al., 1997a, b; Rühland & Smol, 1998; Duff et al., 1999; Hamilton et al., 2001; Levine & Whalen, 2001; Lim et al., 2001; Michelutti et al., 2002). Lake surveys in the Arctic Foothill region (Kling et al., 1992; Levine & Whalen, 2001) show similarly low inorganic nutrient levels with occasional outliers that may reflect sediment resuspension by wind.

In accord with nutrient and k_d values, volume-based mean chl *a* concentrations were remarkably similar and independent of $\bar{z}$ for five of the study lakes, but were elevated more than twofold in GTH 99. Overall, our volume-based phytoplankton chl *a* concentrations compare favorably with previous reports from surveys in Arctic Foothill lakes (Kling et al., 1992; Levine & Whalen, 2001; LaPerriere et al., 2003) and other regions of the arctic (Pienitz et al., 1997a, b; Hamilton et al., 2001; Lim et al., 2001; Michelutti et al., 2002), which most frequently center around 1.5 μg l^{-1}.

Volume-based rates of phytoplankton primary production showed a significant inverse relationship with $\bar{z}$ due to a calculated euphotic depth well in excess of $\bar{z}$ for shallow lakes and progressively deeper euphotic zones over which rates are integrated in intermediate and deep lakes. As with chl *a*, the average volume-based rate of phytoplankton primary production in GTH 99 exceeded values for other lakes. Although NE8 was shallower, the volume-based rate of phytoplankton primary production was only 55% of the value for GTH 99. Elevated chl *a* and volume-based phytoplankton primary production in GTH 99 relative to NE8 likely represent the effects of wind, which can in shallow lakes both resuspend meroplankton (Carrick et al., 1993; Schelske et al., 1995; Hansson, 1996; Schallenberg & Burns, 2004) and stimulate the phytoplankton by nutrient release (Ogilvie & Mitchell, 1998; Schallenberg & Burns, 2004). Increases in phytoplankton chl *a* or primary production upon nutrient addition in bottle bioassays (Whalen & Alexander, 1983; Levine & Whalen, 2001), limnocorrals (O'Brien et al., 1992), and whole-lake experiments (O'Brien et al., 2005) in Arctic Foothill lakes point to a likely positive response of the phytoplankton to wind-aided increases in water column nutrients. However, comparison of the composition and biomass of the phytoplankton and benthic algae (Carrick et al., 1993) or the depth of entrainment of superficial sediments by wind-induced resuspension (Schallenberg & Burns, 2004) is necessary to determine algal recruitment from lake sediments.

Although high volume-based rates of phytoplankton primary production were favored by an entirely illuminated water mass and possibly elevated nutrients in some shallow lakes, the low mean depth ensured that average whole lake, area-based rate of phytoplankton production was significantly lower than the value for intermediate lakes and at least qualitatively less than that for deep lakes. Values of incident irradiance during our 24 h incubations fell evenly within the second and third quartiles for all daily irradiance data continuously recorded from June through August of each year, indicating that incubations were performed on representative days with respect to insolation. Thus, we used the average daily rates of area-based phytoplankton primary production and a 100 day growing season (Miller et al., 1986) to roughly estimate annual phytoplankton production rates of about 280–590 mmol C m^{-2}. These rates fall toward the low end of other reports for Arctic Foothill lakes. A similar extrapolation produced estimates of 640 and 860 mmol C m^{-2} for GTH 112 and GTH 114 (Whalen et al., 2006), while Whalen & Alexander (1986) and Miller et al. (1986) give values ranging from 620 to 1,040 mmol C m^{-2} year^{-1} for intensive, multi-year observations in Toolik Lake. Other reports for the North American arctic (Hobbie, 1964; Kalff, 1967; Kalff & Welch, 1974; Welch et al., 1989) vary from about 75–1,250 mmol C m^{-2} year^{-1}, easily encompassing our estimated rates.

Few studies have assessed epipelic chl *a* concentrations in high latitude lakes. Our data qualitatively show lower concentrations in deep lakes than in intermediate and shallow lakes. However, high spatiotemporal variability and limited sampling reduced our ability to detect any statistically significant differences among lake classes. Our mean values of epipelic chl *a* are similar to previously reported concentrations of 332–575 mg m^{-2} in Arctic Foothill lakes (Whalen et al., 2006; Gettel et al., 2007). However, they are generally higher than the 19–409 mg chl *a* m^{-2} reported for subarctic epipelon (Sorsa, 1976; Björk-Ramberg, 1983; Björk-Ramberg & Ånell, 1985; Hansson, 1992; Liboriussen & Jeppesen, 2003) and the 20–379 mg chl *a* m^{-2} observed in algal mats of ponds in the high arctic (Bonilla et al., 2005; Rautio & Vincent, 2007). High epipelic chl *a* concentrations here and in other Arctic Foothill lakes relate at least in part to sampling methodology, as the 2 cm sediment sample depth in Arctic Foothill studies by Whalen et al. (2006) and Gettel et al. (2007) exceeds the ≤1 cm common to many prior reports. Viable pigments and live algae have frequently been reported to several cm below the sediment surface (Stanley, 1976; Cariou-LeGall & Blanchard, 1995), including sediments below the zone of active photosynthesis (Sand-Jensen & Borum, 1991). Thus, variability among studies in the depth of sediment sampled renders difficult both cross-site comparisons of epipelic chl *a* values and correlation of photosynthetic rates to pigment concentrations.

Rates of epipelic primary production in our study lakes are in accord with other, highly variable, arctic data. Moreover, in contrast to chl *a* data, values are less likely to be influenced by the depth of sediment processed. Using assumptions analogous to those for phytoplankton productivity, we calculate that 200–1,810 mmol C m^{-2} year^{-1} was fixed in our lakes by the epipelon. Somewhat lower lake-wise variability and rates were reported by Stanley (1976) for six shallow ($\bar{z} = 0.2$ m) tundra ponds, 330–830 mmol C m^{-2} year^{-1}. Other rates for a shallow coastal lake and two other Arctic Foothill lakes (all at $\bar{z} = 2$–2.2 m) vary from 190 to 370 mmol C m^{-2} year^{-1} (Stanley, 1976; Whalen et al., 2006) and are somewhat lower than the value of 630 mmol C m^{-2} year^{-1} that we calculate for GTH 99, which is of comparable mean depth. An additional report (Ramlal et al., 1994) for shallow ($\bar{z} = 1.5$ m) Lake 118 in the Northwest Territories (Canada) gives a much higher value of 2,810 mmol C m^{-2} year^{-1}.

The relative contribution of epipelic algae to total primary production was constant at about 32% for intermediate and deep lakes, but was significantly higher at 66% for shallow lakes. Collectively, these and observations for other arctic lakes with mud bottoms suggest the relative importance of epipelic primary production remains reasonably level with decreasing $\bar{z}$ to a break point of about 2 m (Fig. 5A). Below this point, the epipelon increasingly contributes to total area-based primary production with decreasing depth, as irradiance at the sediment surface increases while the euphotic water volume declines. The availability of nutrients constrains phytoplankton productivity, while light is generally considered to limit epipelic productivity (Liboriussen & Jeppesen, 2003). Even cyanobacterial mats in ultraoligotrophic ponds of the Canadian High Arctic have been demonstrated to be nutrient sufficient (Bonilla et al., 2005). Experimental fertilizations at subarctic and temperate latitudes (Björk-Ramberg & Ånell, 1985; Vadeboncoeur et al., 2001; Liboriussen & Jeppesen, 2003) have been demonstrated to alter light-nutrient relationships to effect a redistribution of primary productivity from benthic to pelagic compartments without changing total primary production. Likewise, a lake survey along a eutrophication gradient (Vadeboncoeur et al., 2003) showed a narrow range of total production but a decline in the benthic fraction with increasing water column nutrient content. Low water column nutrient concentrations (Levine & Whalen, 2001; Michelutti et al., 2002) as well as relatively restricted ranges of values for k_d (Chalfant, 2004) and possibly depth ratios (Table 1; also Whalen et al., 2006) may

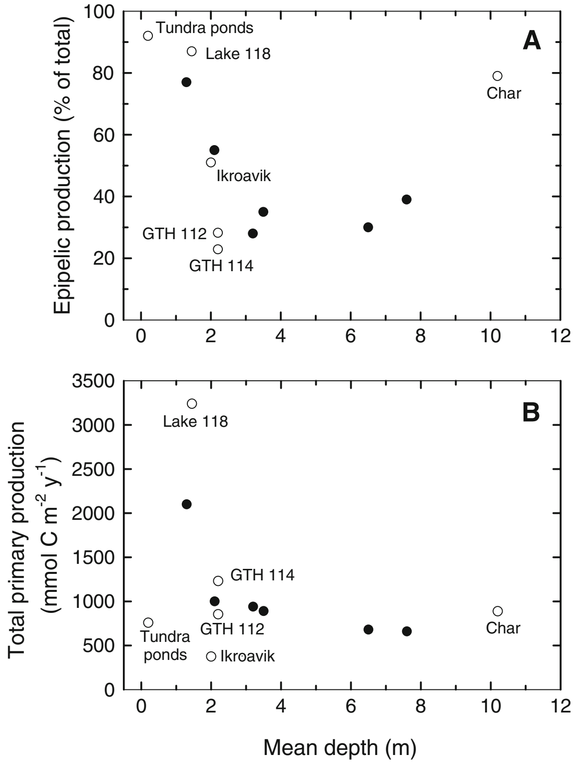

Fig. 5 The relationship between mean depth and (**A**) percent contribution of the epipelon to total primary production in arctic lakes; and (**B**) total (phytoplankton plus epipelic) primary production in these lakes. Values for our six study lakes in (**A**) and (**B**) are indicated by solid circles, while those from previous studies are identified by open circles. Sources: Lake 118, Ramlal et al. (1994); Ikroavik and tundra ponds, (Stanley, 1976); Char, (Welch & Kalff, 1974); GTH 112 and GTH 114, Whalen et al. (2006)

ensure that with some exceptions $\bar{z}$ serves as a master variable determining the distribution of a relatively narrow range of rates of total production (Fig. 5B) between the epipelon and phytoplankton in unpolluted arctic lakes dominated by soft substrate (Fig. 5A).

The relationship in Fig. 5A for the epipelon in geographically diverse arctic lakes conforms to a conceptual biphasic model advanced by Vadeboncoeur & Steinman (2002) relating $\bar{z}$ to the importance of benthic productivity in lacustrine systems. The dominance of mud bottoms in Arctic Foothill lakes guided our epipelic emphasis. Additional, more spatially extensive observations are needed to firmly establish the linkage between depth and the distribution of lacustrine primary production in arctic regions, and these should include other benthic substrata which may show different rates of productivity (e.g., Welch & Kalff, 1974; Vadeboncoeur & Lodge, 2000). Nonetheless, our analysis of the rates and distribution of primary production between benthic and pelagic habitats provides for the first time the underpinning for a comprehensive analysis of food web structure in Arctic Foothill lakes along a gradient of mean depths. Further, our study establishes a necessary and valuable baseline for identifying photoautotrophic responses to regional, climate-mediated changes in lacustrine physicochemical conditions.

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