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Microphytobenthos in Shallow Arctic Lakes: Fine-Scale Depth Distribution of Chlorophyll *a*, Radiocarbon Assimilation, Irradiance, and Dissolved O_2

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Abstract

We compared in three shallow Alaskan Arctic lakes physical properties of bulk sediment and the fine-scale (1 mm increments to 20 mm sediment depth) vertical distribution of dissolved O_2, scalar irradiance, chlorophyll *a*, and radiocarbon assimilation by microphytobenthos to better understand the structural and functional significance of this community. Sediments showed water contents of 86–98%, and dry bulk densities of 0.012–0.146 g cm^{-3}, depending on depth. Chlorophyll *a* displayed no clear vertical pattern, suggesting mixing of surface layers and showed lakewise averages of 5.1–23.7 $\mu g\ cm^{-3}$. Sediments were oxic to 1.5–5.5 mm and showed attenuation coefficients of 1.17–2.07 mm^{-1} for photon scalar irradiance. Photosynthetic activity was localized near the sediment surface, as 57–81% of $H^{14}CO_3^-$ added to intact cores was recovered in the 0–2 mm zone. Only 26–44% of the chlorophyll *a* in vertical profiles was sited in the euphotic zone, but microphytobenthos in underlying, aphotic sediments immediately photosynthesized at or near rates for the surface sediment when artificially irradiated. Area-based chlorophyll *a* in the euphotic plus photosynthetically capable aphotic microphytobenthos was 62–105 times higher than that of the phytoplankton, pointing to the potential importance of benthic autotrophs to Arctic lake food webs.

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Introduction

Microphytobenthos, the microscopic photosynthetic organisms living in and on sediment surface, is recognized as an important component of shallow marine and freshwater environments. Multiple ecosystem functions have been attributed to freshwater microphytobenthos. These communities often contribute significantly to whole lake primary productivity (Vadeboncoeur and Steinman, 2002) and energy supply to food webs (Hecky and Hesslein, 1995). Benthic microalgae can biostabilize sediment thorough mat formation (Dodds, 2003) or release of extracellular polymers (Spears et al., 2007). Microphytobenthos may directly modulate nutrient fluxes at the sediment-water interface through assimilation and mineralization (Van Luijn et al., 1995; Spears et al., 2008). Moreover, photosynthetic O_2 production by benthic microflora indirectly impacts nutrient mobility by altering the spatial distribution of microbial activities (Lorenzen et al., 1998) and speciation of redox-sensitive metals (Gerhardt et al., 2005).

The productivity, abundance, species distribution, and heterogeneity of the microphytobenthos have been described spatially in the horizontal on scales ranging from submeter to whole lake, while the relationship between environmental factors affecting abundance and activity of the benthic phototrophs at the ecosystem level (irradiance, temperature, substratum, nutrients, resuspension) has been frequently characterized (reviewed by Stevenson et al., 1996; Poulí ková et al., 2008). Microphytobenthos is active in the upper few millimeters of sediment, a region of strong gradients in physical, chemical, and biological properties (Davis and McIntire, 1983). Although considerable insight has been gained regarding the function of the microphytobenthos by evaluating benthic exchange rates of dissolved gases and solutes in chambers and intact cores, or activity in homogenized samples, these approaches provide integrated or averaged information and do not reflect the micrometer to millimeter scale in the vertical at which benthic algae are sorted and photon scalar irradiance is rapidly attenuated (Glud et al., 2009).

Extensive investigations have provided microscale details in the vertical dimension of the light climate as well as patterns of biomass distribution, migration, production, and photophysiology of benthic algae in euphotic marine sediments and have further explored the photosynthetic capability of metabolically inactive cells in upper aphotic sediments (reviewed by MacIntyre et al., 1996; Underwood and Kromkamp, 1999; Kromkamp and Forster, 2006). Comparable reports are sparse for freshwater ecosystems, and most frequently give depth distributions for only one or two variables. Fine-scale profiles of photosynthesis have been given for a temperate acidic lake (Koschorreck and Tittel, 2002) and a microbial mat in an Antarctic lake (Vopel and Hawes, 2006). High-resolution measurements of photosynthesis-irradiance (P-I) responses in benthic algal assemblages have been documented in lentic (Dodds, 1992) and lotic environments (Dodds et al., 1999), while microscale vertical profiles of N_2 fixation, gross photosynthesis, chlorophyll *a*, and radiant energy have been described for a cyanobacterial assemblage in a stream (Dodds, 1989).

Global surveys indicate that inland waters are overwhelmingly small (<10 ha surface area) and shallow (<10 m mean depth, $\bar{z}$),

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with a high ratio of littoral surface to pelagic volume (Wetzel, 1990; Downing et al., 2006). Thus, most lakes should show both a high contribution of the benthic component to whole lake primary production and strong coupling between benthic and pelagic habitats (Schindler and Scheuerell, 2002). Over the last decade, syntheses and directed studies in efforts to view lakes holistically with respect to trophic dynamics and energy flow have spurred interest in refining our understanding of factors driving variations in the distribution and production of benthic algae on whole-lake scales (e.g. Vadeboncouer et al., 2002, 2008; Vander Zanden et al., 2006). Despite these contemporary advances, aspects of the microenvironment in which benthic photosynthetic activity occurs remain largely unexplored in lakes.

The abundance of shallow lakes and ponds is a characteristic feature of the Arctic (Hobbie, 1984), where generally high optical clarity and low levels of water column nutrients suggest that benthic algae should be especially important in whole-lake primary productivity, and linkages between benthic and pelagic habitats should be particularly strong. We recently showed that microphytobenthos account for as much as 77% of total primary production in lakes located in the Arctic Foothills province of Alaska (Whalen et al., 2008), where the importance of benthic phototrophs as a food resource to multiple levels of limnetic and benthic consumers has been previously demonstrated (Sierszen et al., 2003). A specific aim of this study was to expand our earlier effort to understand the role of benthic microalgae in shallow Arctic lake productivity by providing insight into physicochemical gradients and structural and functional aspects of the benthic algal assemblage at vertical scales relevant to community function. Secondary, broader goals in detailing fine-scale benthic algal activity and associated environmental influences were to: (a) give the first detailed comparison of the vertical structure of the microenvironment of lacustrine benthic photoautotrophs with similar, more common observations for shallow marine systems; and (b) begin to fill an informational gap regarding our conceptual and empirical understanding of the role of benthic photoautotrophs in contemporary efforts to holistically assess trophic dynamics and energy flow in lake ecosystems (e.g. Vadeboncoeur et al., 2002; Vander Zanden et al., 2005, 2006). To these ends we made highly resolved vertical determinations of dissolved O_2, the sediment light field, and $H^{14}CO_3^-$ assimilation in intact sediment cores and supplemented these with millimeter scale analyses of chlorophyll *a* concentration and photosynthetic capability in three Arctic Foothills lakes showing different sediment properties.

Materials and Methods

SITE DESCRIPTION

This study was conducted on three lakes (S-3, E-4, and Island Lake), located at about 68°N and 149°W (Table 1), 20 km north of the Phillip Smith Mountains in the Arctic Foothills province of Alaska. Detailed descriptions of regional physiography and vegetation physiognomy are given by Wahrhaftig (1965) and Walker et al. (1994). Briefly, the landscape is a mosaic of tussock tundra, wet sedge tundra, and dwarf shrub communities, all underlain by continuous permafrost. Snow cover persists for 7–9 months. The mean annual air temperature is −6°C, while precipitation averages 20 cm annually, with about 40% as snow (Ping et al., 1998).

The study lakes are regionally representative with respect to size, mixing regimes, and physicochemical and biological properties. The mean ($\bar{z}$) and maximum (z_{max}) depths and surface areas of S-3 and E-4 are similar at about 1.4 m, 4.7 m, and 4 ha (Table 1). In contrast, the respective values for Island Lake are greater at 4.7 m, 13.5 m, and 65 ha. Lakes E-4 and S-3 fully circulate on an intermittent basis during the mid-June through mid-September ice-free period, while Island Lake is thermally stratified for most of the brief Arctic summer. All three lakes show concentrations of NO_3^--N, NH_4^+-N, and soluble reactive phosphorus at <0.2 μM throughout the water column during the summer months. Rooted aquatic plants are sparse, and soft sediment dominates the bottom substrate.

SAMPLE COLLECTION

All lakes were sampled on one date each between 27 June and 4 July 2009. A vertical profile of field irradiance was determined at 0.5 m increments in the deepest part of each lake with a Li-Cor LI-250 Quantum Radiometer fitted with an LI-192SA underwater quantum sensor. The attenuation coefficient, K_d (m^{-1}), was calculated from the Lambert-Beer law (Kirk, 1994). A Van Dorn sampler was used to fill duplicate opaque, polyethylene bottles of one liter volume with water from the depth of penetration of 25% surface irradiance (2.8 m in S-3 and Island Lake; 1.5 m in E-4). A location in each lake where the sediment surface corresponded with the 25% light depth was randomly identified and multiple sediment cores were then collected in clear polycarbonate sleeves (4.7 cm inside diameter × 50 cm length) with a KB gravity corer. Cores and overlying water were sealed on each end with clear plugs, eliminating air from the headspace. Additional one liter samples of water were collected as previously described near the sediment-

TABLE 1

Location and physical and biological characteristics of the study lakes. Values of the attenuation coefficient are for the water column.

Lake	Location	Surface area (ha)	Depth mean $\bar{z}$ (m)	 maximum z_{max} (m)	Phytoplankton chlorophyll *a* (μg L^{-1})	Attenuation coefficient K_d (m^{-1})
S-3	68°37.796′N, 149°37.466′W	4.2	1.4	4.8	0.58	0.47
E-4	68°37.194′N, 149°29.656′W	4.0	1.4	4.7	2.26	0.92
Island Lake	68°31.700′N, 149°28.530′W	65.4	4.7	13.5	1.11	0.49

water interface (bottom water). All sediment and water samples were transported in the dark to the Toolik Lake Field Station.

On return to the lab, cores were carefully extruded into clear, 4.7 cm inside diameter × 12 cm long polycarbonate cylinders leaving a 2–4 cm layer of overlying bottom water. Only cores maintaining clear overlying water from the time of collection to the point of experimentation (within 24 h of collection) were used in this study. A sodium metal halide lamp (Hydrofarm Radiant Systems; 1000 W) and neutral shade cloth vertically positioned above the surface of the core or circulating water bath provided light in an otherwise darkened room for manipulations that required constant irradiance. In the case of intact cores, tubes were wrapped with black tape from the sediment-water interface to a sediment depth of 30 mm to prevent stray light from influencing results.

PHYSICAL AND CHEMICAL PROPERTIES

Cores were assayed in 0.5 cm increments from the sediment surface to 1.5 cm for selected physical and chemical properties. Water content was calculated as the mass of pore water as a percent of total water-saturated sediment, dry bulk density was determined as the mass of dry matter (105 °C for 24 h) per volume of total water-saturated sediment, and percent organic content was computed from the mass loss on ignition (550 °C for 4 h) of oven-dried samples (Percival and Lindsay, 1997). The carbon:nitrogen ratio of dried sediment was determined on a Thermo Electron Corporation Delta Plus XP mass spectrometer.

Sediment O_2 distributions were determined with a Unisense microprofiling system, which employs a Clark-type microelectrode with an internal reference and guard cathode. The electrode had a sensing tip of 50 μm and a linear O_2 response from 0 to 100% air saturation. Stirring sensitivity of the electrode was $<2\%$ and the 90% response time was <5 s. Calibration was conducted for each O_2 profile by recording sensor response in air-saturated and anoxic samples. The position of the sediment-water interface was estimated by simultaneously observing the sediment surface and electrode tip under a magnifying lamp, and the microelectrode was advanced downward vertically through the sediment in 25–100 μm increments with a manually operated micromanipulator. Sensor current was measured using a picoammeter.

We constructed a fiber-optic microprobe to measure high resolution light distribution in surficial sediment incorporating design characteristics of previous efforts (Jørgensen and Des Marais, 1986; Dodds, 1992; Kühl et al., 1997). A scalar sensor of approximately 50 μm diameter was formed on the tapered tip of a 100 μm diameter fiber (Ocean Optics) that was stripped of cladding at the distal end, threaded through a hypodermic needle and sealed with black epoxy to prevent exposure to stray light. The fiber optic probe was connected to an Ocean Optics USB4000 spectrometer and showed a response that was independent of wavelength from 400 to 1000 nm and isotropic (10%) for light at angles from $-155°$ to $+155°$.

The vertical distribution of photon scalar irradiance below the sediment surface was measured by lowering the fiber probe into the sediment from above at an angle of 45° to the vertical while the sediment surface was constantly exposed to about 250 μmol photons m^{-2} s^{-1}. The sediment surface was defined as the point where half of the diffusing sphere remained visible (Lassen et al., 1992). The fiber probe was manually advanced through the sediment by a micrometer in steps of 18–35 μm vertical distance, and the spectra from 400 to 700 nm were integrated. The attenuation coefficient, K_d, (mm^{-1}) was calculated.

BIOLOGICAL PROPERTIES

Depth profiles of chlorophyll *a* (chl *a*) and photosynthetic capability of the microphytobenthos were determined for sediments in 1 mm sections from the sediment surface to 10 mm depth and from 14 to 15 and 19 to 20 mm depth. Sediment was extruded with a micrometer-driven piston, and slices were rinsed into receiving vessels.

Chl *a* determinations were made fluorometrically with a Turner Designs Model TD-70 fluorometer on filter-trapped (Whatman GF/F) particulate matter in water (250 mL) from the 25% light depth and sediment in each 1 mm section following a 24 h dark extraction at -5 °C in a buffered 90% acetone solution. Midway through the extraction filters were pulverized. This protocol gave a chl *a* yield not significantly different from grinding after a 24 h extraction. When measuring fluorescence, we followed the methodology of Welschmeyer (1994) that does not involve acidification, but maintains a desensitized response to phaeopigments and chlorophyll *b*.

The depth distribution of photosynthetic capability was evaluated for 1 mm core sections transferred to clear 43 mL vials that were then filled with filtered (Whatman GF/F followed by Millipore 0.22 μm) bottom water. Tests indicated that $>99\%$ of planktonic photosynthesis was eliminated from bottom water by filtration. Vials were amended with 53 kBq $NaH^{14}CO_3$ (specific activity 2.07 GBq $mmol^{-1}$) and placed in the horizontal on a vertically oriented rotating carousel (6 rpm) in a water bath at 12 °C, the approximate surface sediment temperature at the time of sample collection. All vials were exposed to a nominal photon scalar irradiance of 70 μmol photons m^{-2} s^{-1} except those from the 6 to 7 and 8 to 9 mm depth intervals, which were wrapped in foil to exclude light. After 4 h, the contents of each vial were homogenized by shaking, and a 3 mL subsample was filtered (Whatman GF/F), rinsed, and acid fumed for 6 h. Filter-trapped particulate material in Aquasol-2 liquid scintillation cocktail was assayed for radiocarbon incorporation with a Packard Model 1900TR Liquid Scintillation Analyzer. Net photosynthetic $H^{14}CO_3^-$ uptake was estimated by subtracting the mean disintegrations per minute in the two dark-incubated vials from values in light-incubated vials.

The depth distribution of *in vitro* photosynthetic activity was assessed for intact sediments. Cores were sealed with clear acrylic plugs, and radiocarbon (265 kBq $NaH^{14}CO_3$) was injected into the overlying 1–1.5 cm deep water through a septum on the surface plug. Mixing of the radiocarbon in the overlying and interstitial water was accomplished by gently rotating the syringe held at 45° from the vertical during slow label addition followed by pre-incubation in the dark for 4 h. We previously showed (Whalen et al., 2006) that this method of $H^{14}CO_3$ addition evenly distributed the radiocarbon into the superficial sediment. Duplicate cores were then incubated statically in a 12 °C water bath where the surface of the sediment core was exposed to a field irradiance of about 250 μmol photons m^{-2} s^{-1}. A third core was dark-incubated in the water bath with a foil wrap. Experiments were terminated after 4 h by vacuuming the overlying water and rapidly removing 1 mm sections into glass vials precharged with 0.5 mL of 1 *N* HCl.

TABLE 2

Physical and chemical properties of sediments in the study lakes. Values are the mean for duplicate cores except the molar C:N ratio where a single core was analyzed.

Lake	Depth interval (mm)	Dry bulk density (g cm^{-3})	Water content (%)	Organic content (% dry wt)	C:N (moles)
S-3	0–5	0.012	98	55	13.7
	5–10	0.023	97	61	13.4
	10–15	0.038	96	63	14.1
E-4	0–5	0.026	97	57	11.4
	5–10	0.045	95	60	10.6
	10–15	0.068	94	60	11.6
Island Lake	0–5	0.075	93	77	11.9
	5–10	0.102	90	79	ND*
	10–15	0.146	86	81	11.7

*ND = no data

Uncapped vials were loaded onto a rotary shaker (100 rpm) overnight under a fume hood to purge unassimilated radiocarbon. Sediment was dried (60 °C) and homogenized, and the entire sample was subjected to high temperature (900 °C) combustion in an O_2 atmosphere using a Harvey Instrument Corporation Model OX 600 Biological Material Oxidizer. The evolved $^{14}CO_2$ was trapped at >92% efficiency (determined by combusting mannitol standards of known radioactivity) in a scintillation cocktail containing phenethylamine (Harvey OX-161) and radioassayed. Radioactivity in the dark-incubated core was subtracted from values in light-incubated cores at each depth increment to estimate net photosynthetic radiocarbon uptake.

Results

All three lakes had low volume-based concentrations of phytoplankton chl *a*, with values varying from 0.58 to 2.26 μg L^{-1} (Table 1). Shallow mean depths and low K_d values for field irradiance in the water column (0.47–0.92 m^{-1}) ensured the euphotic zone (depth of penetration of 1% surface irradiance) extended to the entire sediment surface of lakes S-3 and E-4 and to 89% of the sediment surface in Island Lake. All sediments were flocculent with a high water content to 1.5 cm depth (Table 2). The two shallower lakes (S-3 and E-4) were most similar, showing sediment water contents of 94–98% and dry bulk densities of 0.012–0.068 g cm^{-3}, in contrast to values of 86–93% and 0.075–0.146 g cm^{-3} for Island Lake. Organic content was universally high, consistent with low dry bulk densities. Values varied from 55 to 81%. Molar C/N values of 10.6–14.1 indicated that organic matter in the surficial sediment was largely autochthonous in origin.

Sediment chl *a* concentrations varied by more than an order of magnitude when the entire data (72 core sections) were considered, with values ranging from 2.6 to 37.0 μg cm^{-3} (Fig. 1). However, within each lake, chl *a* concentrations were reasonably consistent between core sections at comparable depths below the sediment surface. Between-section variability expressed as the standard error of the mean averaged 17–20%, depending on lake. Depth-integrated (0–20 mm) chl *a* concentrations showed somewhat less variability between duplicate cores for each lake, showing standard errors of 13% for S-3 and 19% for both Island Lake and E-4. Five of six cores showed a decrease in chl *a* between the 0–1 and 1–2 mm depth intervals. Otherwise, there was no clear and consistent vertical pattern of change in chl *a* to a depth of 20 mm in any lake. Chl *a* concentrations at 10 mm represented 56–237% ($\bar{x}$ = 113%) of surface values, while concentrations at 20 mm were 69–263% ($\bar{x}$ = 123%) of surface values. On the whole, chl *a* values were lowest in S-3 and highest in Island Lake, with respective means of 5.1 μg cm^{-3} and 23.7 μg cm^{-3}. Lake E-4 showed an average of 11.5 μg chl *a* cm^{-3}.

Dissolved O_2 profiles for duplicate cores within each lake were markedly similar (Fig. 2). Oxygen concentrations decreased steadily with increasing depth below the sediment surface in all cases, but there were distinct differences among lakes. Sediments were more highly consolidated in Island Lake than in S-3 or E-4 (Table 2), and the rate of O_2 decline with increasing depth below the sediment surface was therefore correspondingly greater. Thus, dissolved O_2 was depleted at about 1.5 mm below the sediment

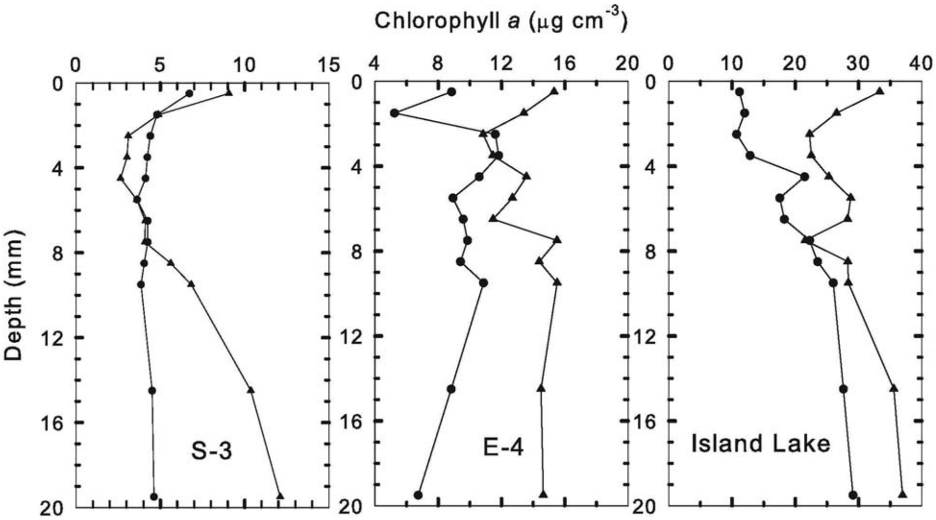

FIGURE 1. Depth distribution of chlorophyll *a* in surficial sediments of duplicate cores from each study lake. Concentrations are plotted at the midpoint of each 1 mm depth increment.

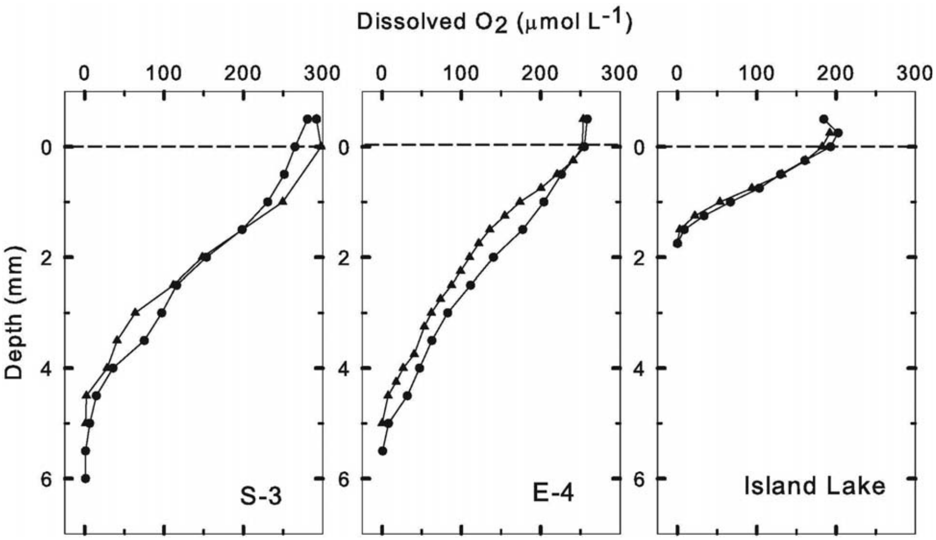

FIGURE 2. Depth distribution of dissolved O_2 in surficial sediments of duplicate cores from each study lake. Each profile represents the mean of three series of measurements. The dashed line marks the sediment-water boundary.

surface in Island Lake, while oxic sediment persisted to a depth of about 5–5.5 mm in the other two lakes.

Similar to sediment profiles for dissolved O_2, the pattern of attenuation of photon scalar irradiance in the sediment of duplicate cores from each study lake was highly reproducible (Fig. 3). Photon scalar irradiance was attenuated rapidly with increasing depth below the sediment surface. Attenuation coefficients averaged 1.17, 1.70, and 2.07 mm^{-1} for S-3, E-4, and Island Lake, respectively, with values increasing with increasing dry bulk density and decreasing water content of sediments (Table 2). Calculated euphotic depths for the respective lakes were 3.9, 2.7, and 2.2 mm. These values were somewhat shallower than the observed depth of O_2 penetration in S-3 and E-4, but deeper than the depth of O_2 penetration in Island Lake.

Depth profiles for *in vitro* photosynthetic activity of the microphytobenthos indicated that most of the net photosynthesis was confined to the 0–2 mm depth interval (Fig. 4). On average, this zone accounted for 57, 63, and 81% of the total disintegrations per minute (dpms) of radiocarbon recovered in particulate material in S-3, E-4, and Island Lake, respectively. Below 2 mm, the percent of total recovered radiocarbon declined gradually to the 5–6 mm increment in S-3 and E-4. The 0–4 mm and 0–3 mm zones in these two lakes showed similar percent recovery of total dpms (74% and 79%, respectively) as the 0–2 mm zone in Island Lake. Measureable radiocarbon was incorporated into particulate material below the calculated depth of penetration of 1% of sediment surface irradiance in all lakes. For instance, 3% of total assimilated dpms was recovered in the 5–6 mm increment in S-3 and in the 4–5 mm increment in E-4, while 2% was found in the 3–4 mm zone in Island Lake.

Although both *in vitro* photosynthetic activity and photon scalar irradiance were largely confined to the upper 4 mm or less of sediment in intact cores, microphytobenthos in deeper sediments of all lakes maintained the ability to immediately photosynthesize when artificially irradiated (Fig. 5). Photosynthetic capability in subsurface sediment slurries was generally at or in excess of the surface value to a depth of 15 mm in S-3. Similarly, rates of $H^{14}CO_3^-$ assimilation did not decline clearly relative to surface values until sediment depth exceeded 10 mm in E-4 and 6 mm in Island Lake. Radiocarbon assimilation in the 19–20 mm depth

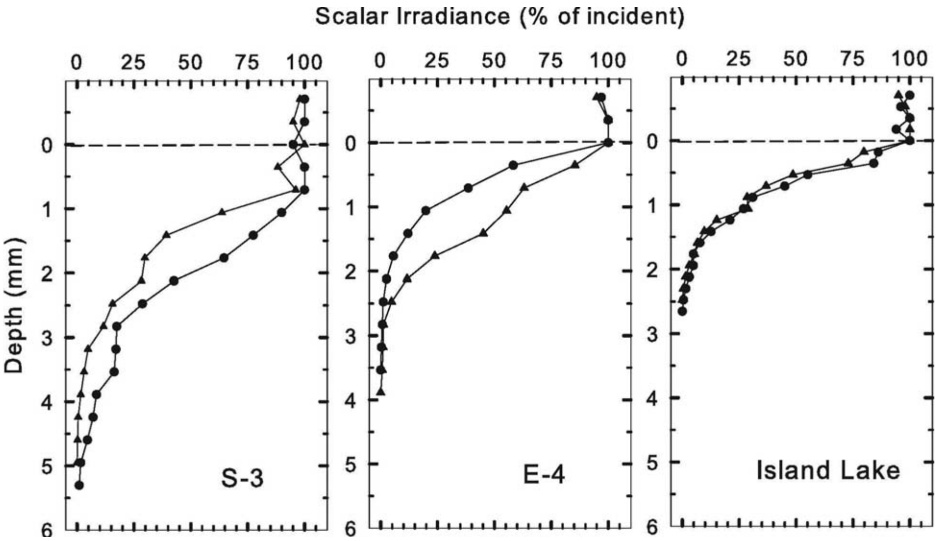

FIGURE 3. Depth profiles for photon scalar irradiance in surficial sediments of duplicate cores from each study lake. Data are normalized to photon scalar irradiance at the sediment surface and each profile represents the mean of three series of measurements. The dashed line marks the sediment-water boundary.

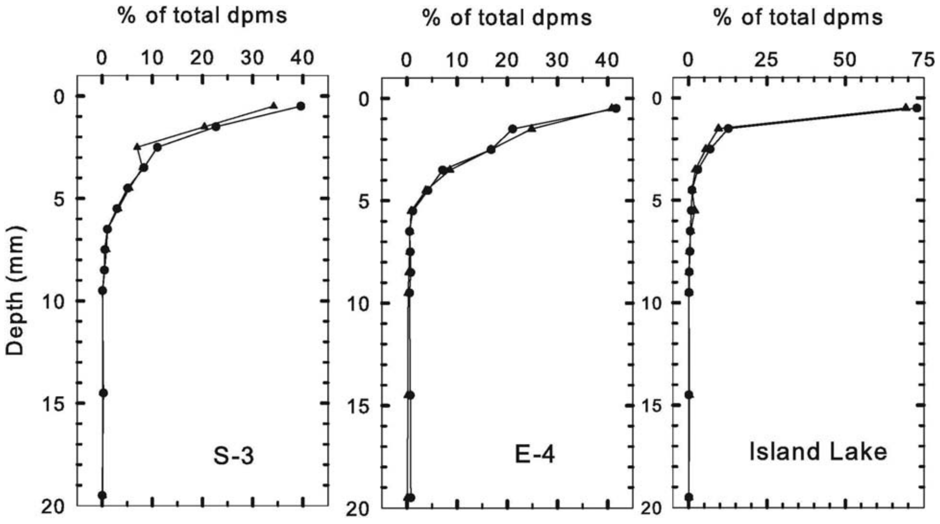

FIGURE 4. Depth profiles for *in vitro* photosynthetic activity in sediments of the study lakes as determined by $H^{14}CO_3^-$ assimilation in intact sediment cores incubated in the light. Data are given as disintegrations per minute (dpms) incorporated into microphytobenthos in 1 mm depth increments as a percentage of total dpms assimilated by the entire core. Data for duplicate light-incubated cores for each lake are plotted as at the midpoint of each 1 mm depth increment and are corrected for dpms assimilated by that depth increment in a single, dark-incubated core.

interval averaged 72, 10, and 8% of values recorded at the sediment surface for S-3, E-4, and Island Lake, respectively.

Discussion

Previous lacustrine studies have described selected fine-scale physicochemical or biological aspects of the environment inhabited by microphytobenthos (e.g. Sweerts et al., 1989; Koschorreck and Tittel, 2002). Our study aimed for the first time to fully characterize the microstructure, activity, and physical environment of the microphytobenthos by simultaneously using multiple descriptors in shallow lakes where benthic microalgae comprise a significant fraction of whole lake primary production. Using this approach we see structural and functional characteristics and qualitative patterns that cannot be identified in less detailed vertical analyses or homogenized samples, but have important implications for whole lake primary production and energy transfer.

The study lakes appear to be regionally representative with respect to water column and sediment concentrations of chl *a*. Our volumetric phytoplankton chl *a* concentrations of 0.6–2.3 μg L^{-1} are similar to earlier reports from surveys in Arctic Foothills lakes (Kling et al., 1992; Levine and Whalen, 2001; LaPerriere et al., 2003; Whalen et al., 2008) and other regions of the Arctic (Pienitz et al., 1997a, 1997b; Hamilton et al., 2001; Lim et al., 2001; Michelutti et al., 2002), which often show values around 1–2 μg L^{-1}. In contrast to the phytoplankton, comparatively few studies have focused on the benthic pigments in high-latitude lakes, and cross-site comparison is confounded by differences in the depth of sediment sampled. Our average concentrations of 5–24 μg chl *a* cm^{-2} for the surficial 1 cm of sediment are roughly half or less of previously reported values of 8–69 μg cm^{-2} for the 2 cm depth increment (Whalen et al., 2006, 2008; Gettel et al., 2007) in other Arctic Foothills lakes and are similar to concentrations of 8–38 μg cm^{-2} given for the surface 1 cm of sediment in subarctic lakes (Björk-Ramberg, 1983; Björk-Ramberg and Ånell, 1985; Hansson, 1992).

Spatial heterogeneity in the distribution of microphytobenthos is manifested by between-core variability in chl *a* concentration at comparable 1 mm depth increments (Fig. 1). Our data showed average between-core standard errors of 17–20% for comparable depth increments, depending on lake, and are consistent with other reports for cores of roughly similar diameter (4.7 cm) to those used here. Kromkamp and Forster (2006) found that standard errors for

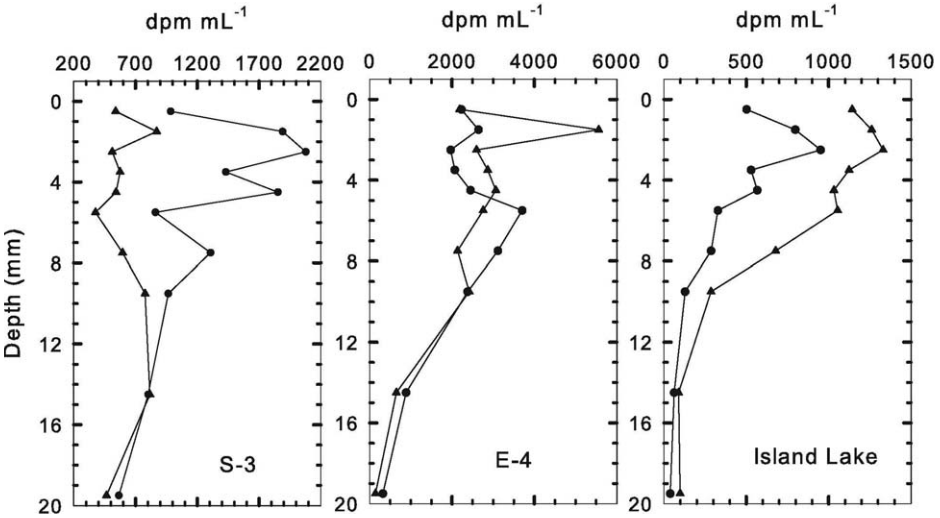

FIGURE 5. Depth profiles for photosynthetic capability ($H^{14}CO_3^-$ assimilation) by microphytobenthos in sediments of the study lakes. Data are given as disintegrations per minute mL^{-1}(dpm mL^{-1}) of slurried sediment for each 1 mm depth increment continuously exposed to a photon scalar irradiance of 70 μmol photons m^{-2} s^{-1} for 4 h. Data are plotted at the midpoint of each depth increment and are corrected for dpms assimilated by dark incubated samples.

chl *a* ranged from 6 to 22%, 6 to 53%, and 6 to 145% in estuarine sediment at intersample distances of 20, 100, and 500 cm, respectively. Similarly, Varela and Penas (1985) demonstrated that at least five cores were needed from a 50 cm × 50 cm area to reduce the coefficient of variation for chl *a* concentration to 45% in an intertidal sand flat.

Extant vertical profiles of sediment chl *a* in lakes are at ≤ 0.5 cm resolution and show highest concentrations in the surface increment with measurable chl *a* several centimeters below the sediment surface (Hickman and Round, 1970; Nienhuis and De Bree, 1984; Wasmund, 1984; Khondker and Dokulil, 1988; Cyr, 1998). However, these profiles lack detail with respect to the vertical zonation of photosynthetically active or capable biomass. Our fine-scale analysis of the vertical distribution of sediment chl *a* (Fig. 1) is in qualitative agreement with similar high resolution measurements from coastal marine environments that show a maximum chl *a* concentration in the surface 1 mm of sediment with continuously decreasing or reduced but constant chl *a* concentrations with increasing sediment depth below 1 mm to 5 or 10 mm (MacIntyre and Cullen, 1995; Herlory et al., 2004; Cartaxana et al., 2006). A chl *a* maximum in surficial marine sediment may be attributed to settling of suspended material from overlying water prior to core processing (MacIntyre and Cullen, 1995). Using average water column chl *a* concentrations (Table 1) and an assumed 25 cm of overlying core water, we calculate that settled chl *a* represents only 1–4% of the chl *a* measured in the 0–1 mm depth increment (Fig. 1), and we therefore exclude this bias as a causative factor. Most frequently, a chl *a* maximum in surficial marine sediment is ascribed to migration in response to irradiance and tidal cycles (Pinckney and Zingmark, 1993). Phototactic activity has likewise been demonstrated for freshwater microphytobenthos (e.g. Round and Eaton, 1966) and we cannot discount that possibility. However, the somewhat elevated surficial chl *a* generally observed here is most likely a methodological artifact attributable to subcore-scale topographic heterogeneity in the height of the sediment surface. We defined the zero depth as that point where sediment contacted the entire circumference of the rim of the core sleeve on extrusion, which visibly resulted in a generous assignment of the extent of the 0–1 mm depth increment.

Penetration depths and gradients for dissolved O_2 beneath the sediment surface of a lake bottom depend on the dynamic balance between oxygenic photosynthesis and heterotrophic activity, bioturbation, and a diffusive boundary layer (DBL) at the sediment-water interface where turbulence is replaced by molecular diffusion as the dominant mode of mass transport (Revsbech and Jørgensen, 1986; Reimers, 2007). Determinations of O_2 penetration depths in lakes are few, with the reported values of 0.4–14 mm spanning a factor of 35 for lakes of small to moderate size (Sweerts et al., 1986, 1991; Carlton and Wetzel, 1988; Frenzel et al., 1990; Sass et al., 1997; Gerhardt et al., 2005). Our values of 1.5 mm (Island Lake) and about 5 mm (S-3 and E-4) fall midway among those in previous reports. As with our investigation, most studies involve limited observations on a single lake, rendering difficult identification of the underlying reasons for high variability. Nonetheless, weather-related differences have been observed (Sass et al., 1997) and changes related to season or bathymetry have been linked to the settling of organic matter in coastal marine (Rasmussen and Jørgensen, 1992) and lacustrine environments (Martin et al., 1998).

The degree to which core-determined sediment O_2 distributions in these studies are representative of *in situ* profiles is unclear, and experimental protocols likely contribute to lake-wise differences in sediment O_2 gradients. Overlying water in sediment cores is often stirred to mimic the DBL, but faithful reproduction requires previous determination of the *in situ* DBL by direct measurement (Sweerts et al., 1989) or knowledge of the current speed of water overlying the sediment surface (Frenzel et al., 1990). In part, because these conditions can be expected to vary spatially and are difficult to determine, Martin et al. (1993) elected not to stir the overlying water as a standardization procedure in a systematic transect of sediment O_2 distributions in Lake Baikal. Similarly, to facilitate cross-lake comparison, we measured sediment O_2 profiles in unstirred cores and acknowledge that the resultant increase in transfer resistance for O_2 flux across the sediment water interface could influence both the O_2 concentration and penetration depth (e.g. Sweerts et al., 1989). Nonetheless, the bias was likely minimal. Our profiles for S-3 and E-4 corroborate well the penetration depths of 5–7 mm given by Sweerts et al., (1986) for a similarly flocculent (85% water content), highly organic sediment with stirred overlying water. The effect of an increased DBL from stagnant overlying water is minimized in oligotrophic conditions when O_2 uptake rates are low (Martin et al., 1993) and the sediment O_2 demand of about 7 mmol m^{-2} d^{-1} for lakes in this region (Cornwell and Kipphut, 1992) is among the lowest recorded.

Microscale assessment of the distribution of diffuse light in reconstituted and intact marine sediments shows attenuation coefficients most frequently varying from ~1 to 4 mm^{-1} (reviewed by MacIntyre et al., 1996; Underwood and Kromkamp, 1999), while Dodds (1992) reported a K_d value of 3.25 mm^{-1} for a sedimentary diatom mat in a freshwater drainage ditch. Lower and higher K_d values are associated with sandy and cohesive sediments, respectively (Kühl et al., 1994). Strong scattering in the former can result in both a peak light intensity at the surface of up to 200% of incident values and deeper light penetration in sediment, while a dominance by absorption in organic sediments leads to a peak irradiance at the sediment surface and more rapid down-core light attenuation (Gerbersdorf et al., 2005). Our K_d values of 1.2–2.1 mm^{-1} compare most favorably with those for sandy sediments, but shapes of profiles of photon scalar irradiance more closely resemble those for cohesive sediments. High water content of the flocculent organic sediment at our sites (Table 2) is likely responsible for both low K_d values and the monotonic decrease in irradiance with increasing depth below the sediment surface.

Measurements of gross photosynthesis in cohesive marine sediments using O_2 microelectrodes indicate that the majority of the photosynthesis occurs in the surface 0.4 mm (Underwood and Kromkamp, 1999), while photosynthetic activity may extend to 2 mm in sandy sediment (Gerbersdorf et al., 2005). Although $H^{14}CO_3^-$-derived productivity estimates for intact cores must be cautiously interpreted due to vertical gradients of the radiocarbon label (Revsbech et al., 1981), our experiments are in qualitative agreement with these electrochemical marine observations that show a rapid decline in photosynthesis with increasing sediment depth. However, deeper light penetration in our flocculent sediments supports a more extensive euphotic zone than even sandy marine sediments. Some 20–40% of the total radiocarbon recovery in particulate material occurred below 2 mm depth, and extremely low but measurable assimilation was recorded as deep as the 5–6 mm depth interval in S-3. Low but measurable radiocarbon uptake consistently observed in sediments at depths just below the 1% light level of about 2.5 μmol photons $m^{-2} s^{-1}$ may represent shade adaptation of the fraction of the population deeper beneath the sediment surface. Compensation light intensities of around 2–4 μmol photons $m^{-2} s^{-1}$ have been observed in fine-scale analysis of benthic algal production using O_2 microelectrodes (e.g. Ploug et al., 1993), and in shade-adapted diatom cultures (Geider et al., 1985). Finally, close tracking between down-core decreases in radiocarbon assimilation and spectral irradiance in all lakes suggests that spatial variations in the specific activity of $H^{14}CO_3^-$ in the vertical dimension did not seriously compromise the observed profiles of photosynthesis in intact cores.

The presence of viable algae several centimeters deep in aphotic sediment has long been known in both marine (Wasmund, 1989) and freshwater (Hickman and Round, 1970) environments, but the photophysiological status of microphytobenthos in near-surface (2–10 mm) aphotic sediment has been extensively studied only in marine habitats. Here we provide for the first time on a millimeter scale comparative analysis of the photosynthetic response of the microphytobenthos of euphotic and upper aphotic lake sediments (Fig. 5). Both down-core and between-core variability in radiocarbon assimilation likely reflects microscale differences in phytomass as well as errors introduced in subsampling suspended particulates in incubation vessels. Further, it is unclear whether the photosynthetic photon flux density of 70 μmol photons m^{-2} s^{-1} elicited subsaturated or saturated photosynthesis, as values of I_k (irradiance representing the onset of photosaturation) for resuspended microphytobenthos as low as 30 μmol photons m^{-2} s^{-1} have been reported (MacIntyre et al., 1996). Nonetheless, a consistent pattern of relatively constant algal biomass and radiocarbon uptake to 10 mm in S-3 and E-4 and to 5 mm in Island Lake (cf. Figs. 1 and 5) points to aphotic populations as photosynthetically capable as their active (euphotic) counterparts in all study lakes.

Physical disturbance from waves and water currents is widely considered responsible for homogeneous vertical distribution of chl *a* in the upper few centimeters of lake sediment (Wasmund, 1984; Cyr, 1998), and, by extension, is the likely cause for the presence of photosynthetically capable microphytobenthos in near-surface aphotic sediment here. Resuspension has been inferred from sediment trap studies in shallow lakes in the Arctic Foothills region, including E-4 (Fortino et al., 2009). Sediment resuspension and redistribution processes are rarely studied directly with respect to the microphytobenthos (Cyr, 1998), but are a function of fetch, wind speed and duration, and sediment properties such as grain size, and water and organic content (Hilton, 1985; Bloesch, 1995). Following Bachmann et al. (2000), we calculate that wind-driven waves are not likely to directly influence the sediment surface at the site of sampling in any of these relatively small lakes (maximum fetch <1400 m) at maximum sustained wind speeds ($\leq$6 m s^{-1}; http://toolik.alaska.edu/edc/abiotic_monitoring/data_query.php). However, resuspended materials from extensive, shallower zones can be deposited at the sampling sites, and shear stresses from circulatory currents (Hamilton and Mitchell, 1997) can effect sediment flux. Turnover events (Hilton, 1985) and ice scour (Quesada et al., 2008) present additional possible avenues of vertical and horizontal sediment redistribution and homogenization in these lakes.

The photosynthetically capable biomass was dominated by inactive cells, as only 26–44% of the chl *a* in vertical profiles was sited in the euphotic zone, and therefore was photosynthetically active. It is noteworthy that aphotic microphytobenthos (photosynthetically inactive biomass) exposed to light immediately resumed photosynthesis at rates comparable to the euphotic component of the assemblage. Similar observations for shallow marine sites have been interpreted to indicate that the rate of vertical mixing is compatible with the persistence of the photosynthetic response of the aphotic layer, as benthic microalgae show a progressive reduction in P-I parameters when maintained in the dark for prolonged (days to weeks) periods (Blanchard and Cariou-Le Gall, 1994; MacIntyre and Cullen, 1995). Despite uncertainty regarding the factors responsible for sediment mixing here, a sizeable pool of photosynthetically inactive biomass is apparently mixed with a frequency that is adequate to maintain high rates of benthic productivity in communities potentially exposed to frequent substrate disturbance during a short ice-free season. Alternatively, Arctic microphytobenthos may be better adapted than temperate assemblages to extensive darkness, as Antarctic diatom isolates immediately resumed high levels of photosynthesis when exposed to light after several months of dark incubation (Peters and Thomas, 1996). In either case, diminished photosynthetic capability in deeper sediments (e.g. 20 mm, Island Lake; Fig. 5) relative to surface values could reflect an excessive duration of burial.

Area-based evaluations of the pigment content of sediment and the overlying water emphasize the potential importance of benthic phototrophs in lake productivity and energy transfer to higher trophic levels (e.g. Brunberg et al., 2002), but these assessments are heavily influenced by the vertical extent of the sediment layer considered. Use of the actively photosynthesizing component of the microphytobenthos may provide the most meaningful comparison. Here, area-based chl *a* in the euphotic microphytobenthos was 18–27 times higher than that of the phytoplankton, and these factors increase to 62–105 if the aphotic, but photosynthetically capable, component of the communities is considered. However, sediments experience reduced incident irradiance relative to the overlying water and show attenuation coefficients higher by over three orders of magnitude. Decreased irradiance at the sediment surface and a vertically narrow euphotic zone may be compensated by the increased abundance of algae in the sediment and a horizontally expansive region of sediment surface exposed to light (89–100% in the study lakes) in shallow Arctic lakes and ponds, as whole lake primary production in this region is often dominated by the microphytobenthos (Ramlal et al., 1994; Stanley, 1976; Whalen et al., 2008).

In accord with comparable marine studies, our labor intensive investigation involved detailed analysis of multiple variables for a limited number of cores collected one time from a single location. The experimental design of sampling sediments from three lakes at a comparable light environment (25% penetration of incident irradiance to the sediment surface) provides information on among-lake variability for measured variables. However, the overall approach also has limitations. Our study gives no information on within-lake spatial or temporal (seasonal) variability for assessed properties. Subcore-scale topographic heterogeneity and difficulty in assigning the zero depth can cause vertical offsets that result in misalignment of profiles for interdependent variables (e.g. Tankéré et al., 2002) such as light, O_2 concentration, and photosynthesis as occasionally noted above. The need to dedicate cores to a single analysis during destructive sampling introduces additional uncertainty in the fine-scale depth distribution of properties that show steep vertical gradients.

The comprehensive suite of descriptors simultaneously measured here at meaningful vertical scales for the first time in a lacustrine environment can be broadly interpreted to give initial insight into the structural and functional characteristics of the microphytobenthic community, which have been largely undocumented but are important to whole-lake primary production in shallow freshwater systems. Qualitatively, we observe a decline in the O_2 penetration depth, increase in K_d, and decrease in the zone of active photosynthesis as the water content decreases and dry bulk density and organic content increase from S-3 to E-4 to Island Lake. Further, we demonstrate that photosynthesis is confined to a <5 mm surficial zone even in these flocculent Arctic lake sediments, and cells clearly sited in aphotic sediments are photosynthetically capable when exposed to light, similar to their marine counterparts. Although generalizations concerning the structural and functional aspects of marine microphytobenthos have emerged from multiple investigations, details are location specific (MacIntyre et al., 1996), and this will likely apply to freshwater environments as well. Accordingly, studies of this type should be extended to lakes in other regions as well as to other sediment types and lake morphometries to develop a broad conceptual understanding of the microenvironment inhabited by the freshwater microphytobenthos.

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