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RESEARCH ARTICLE

Low boundary layer response and temperature dependence of nitrogen and phosphorus releases from oxic sediments of an oligotrophic lake

J. L. Anthony · W. M. Lewis Jr.

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Abstract The effects of temperature, diffusive boundary-layer thickness, and sediment composition on fluxes of inorganic N and P were estimated for sediment cores with oxidized surfaces from nearshore waters (2–10 m) of a montane oligotrophic lake. Fluxes of N and P were not affected by diffusive boundary-layer thickness but were strongly affected by temperature. Below 16 °C, sediments sequestered small amounts of P and released small amounts of N. Above 16 °C, the seasonal maximum water temperature, sediments were substantial sources of N (NH_4^+–N = 2–24 mg m^{-2} d^{-1}; $NO_3^- + NO_2^-$–N = 2–5 mg m^{-2} d^{-1}) and P (0.1–0.4 mg m^{-2} d^{-1}), indicating potential responsiveness of sediment–water nutrient exchange, and of corresponding phytoplankton growth, to synoptic warming.

Keywords Climate change · Boundary layer · Nitrogen · Phosphorus · Sediment · Temperature

J. L. Anthony · W. M. Lewis Jr.
Center for Limnology, Cooperative Institute
for Research in Environmental Sciences,
University of Colorado, 216 UCB, Boulder,
CO 80309-0216, USA

J. L. Anthony · W. M. Lewis Jr. (✉)
Department of Ecology and Evolutionary Biology,
University of Colorado, 334 UCB, Boulder,
CO 80309-0334, USA
e-mail: lewis@spot.colorado.edu

Present Address:
J. L. Anthony
Colorado Division of Wildlife, 6060 Broadway,
Denver, CO 80216, USA

Introduction

Net release of nutrients from lake sediments during the growing season could subsidize the growth of epilimnetic autotrophs, while net sequestration could have the opposite effect. Correlation of the ratio of the sediment surface area to epilimnetic water volume (A_e:V_e) with rates of primary production in lakes suggests that an oxidized sediment–water interface (SWI) can provide a significant nutrient subsidy to phytoplankton in at least some lakes (Fee 1979).

Release of nutrients from anoxic hypolimnetic sediments was studied experimentally by Mortimer (1941, 1942, 1971), who proposed control mechanisms, some of which have since been revised to accommodate substantial variation in the role of iron and sulfur as well as gas ebullition (Kalff 2002). Fluxes of nitrogen and phosphorus across an oxidized SWI have been less thoroughly studied. An oxidized SWI may suppress release of nutrients, but a net release from shallow-water sediments may occur nevertheless (Holdren and Armstrong 1980; Liikanen et al. 2002, 2003; Søndergaard 1989). High epilimnetic temperatures may favor release of nutrients by stimulating microbial mineralization of sediment organic matter, which could increase pore-water nutrient concentrations, or could erode the oxidized microzone at the SWI by increasing oxygen demand (Holdren and Armstrong 1980; Jensen and Andersen 1992; Liikanen et al. 2002). Although the documented influence of temperature on rates of nutrient release suggests that epilimnetic sediment–water nutrient exchanges could be responsive to synoptic warming (long-term warming trends), responses of nutrient release to changing temperatures are not well established.

At a given temperature, turbulence influences exchange of soluble nutrients across the SWI. In the diffusive boundary layer (DBL) at the SWI, molecular diffusion leads to solute accumulation within the DBL, but turbulence controls mass transfer across the DBL (Lorke et al. 2003). Strong turbulence reduces the DBL thickness, which enhances solute fluxes from the DBL (Sanford and Crawford 2000; Lorke et al. 2003; Glud et al. 2007). Weak turbulence facilitates development of a thick DBL, which may cause the reactions controlling solute availability at the SWI to be the dominant influence on nutrient release from the DBL (Sanford and Crawford 2000; Lorke et al. 2003; Glud et al. 2007).

Studies of sediment–water nutrient exchange in lakes have incorporated water-column turbulence, but often at turbulence intensities high enough to resuspend sediments (e.g., Reddy et al. 1996; Steinman et al. 2006). In other cases, the effect of turbulence has been studied, but without calibration to measurements in situ (Holdren and Armstrong 1980). Therefore, the influence of weak turbulence on sediment–water nutrient exchanges is poorly known.

We studied oxic sediment–water nutrient exchange in an oligotrophic lake of the Colorado Rocky Mountains, USA. The objective of the study was to quantify the influences of temperature and turbulence (DBL thickness) on sediment–water fluxes of soluble inorganic phosphorus and nitrogen.

Materials and methods

Grand Lake (2.05 km^2; $z_{max} = 81$ m) is an oligotrophic montane lake (2550 m AMSL; 40°N, 105°W; Fig. 1). Benthic landers (cf. Lewis 1975) were used to deploy four gypsum disks (diameter = 5 cm) to the lake bottom at depths of 2, 5, and 10 m. Images from an underwater video camera verified that the disks were placed flush with the sediment surface. After 24 h, the landers were recovered, and the gypsum disks were dried to constant mass at ambient air temperature. DBL thicknesses then were calculated from the mass loss of gypsum (Santschi et al. 1991).

In the laboratory, gypsum disks were placed at the bottom of core tubes (diameter = 5 cm), within which an eccentric drive oscillated a stainless-steel gridded disk (diameter = 5 cm; mesh size = 0.5 cm; oscillation frequency ≈ 1 Hz) in the water overlying each gypsum disk (Fig. 2). Following incubation with grid oscillation, DBL thicknesses were calculated from mass loss of gypsum with correction for ambient Ca^{2+} and $SO_4{}^{2-}$ as given by Santschi et al. (1991); the relationships of DBL thickness to the minimum distance between the oscillating grid and the gypsum disk then were determined for a range of temperatures (Fig. 3). The relationships were used to estimate DBL thicknesses in Grand Lake.

On 31 July 2006, a piston corer was used to collect 11 intact sediment cores (length 30 cm; diameter 5 cm; overlying water column 30 cm) from each of three water-column depths (2, 5, and 10 m; Fig. 1). The estimated depth of the wave base (2.9 m, Håkanson and Jansson 1983) suggests that sediments at 2 m are near the lower depth threshold of influence from surface waves, while

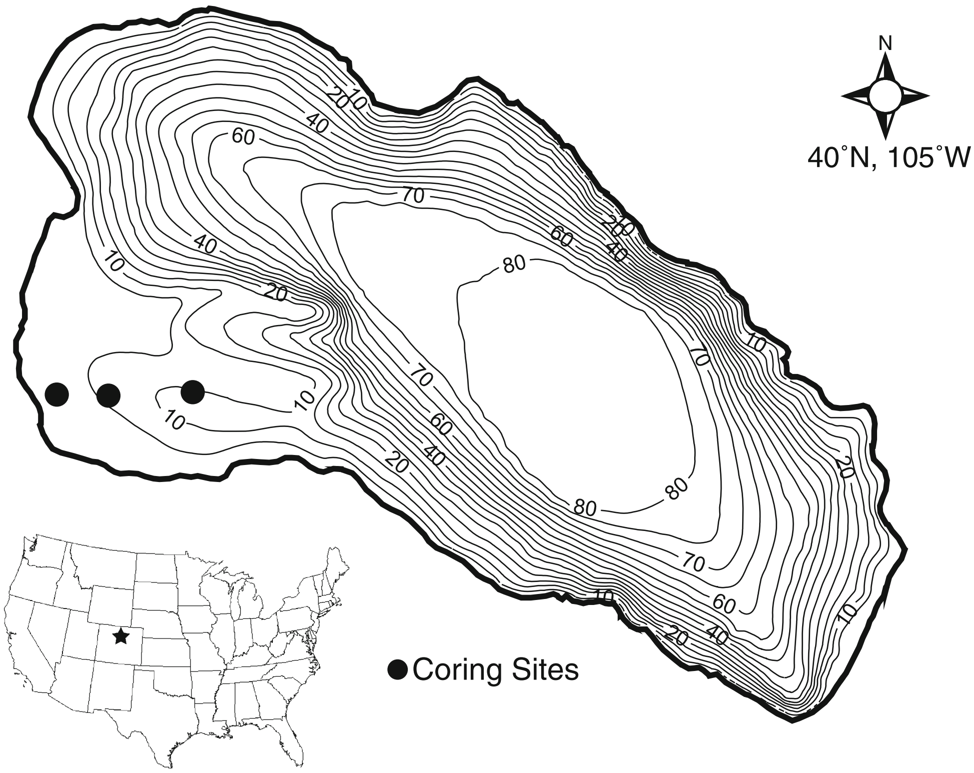

Fig. 1 Grand Lake bathymetry with 5-m isopleths. Sediment cores were taken at depths of 2, 5, and 10 m

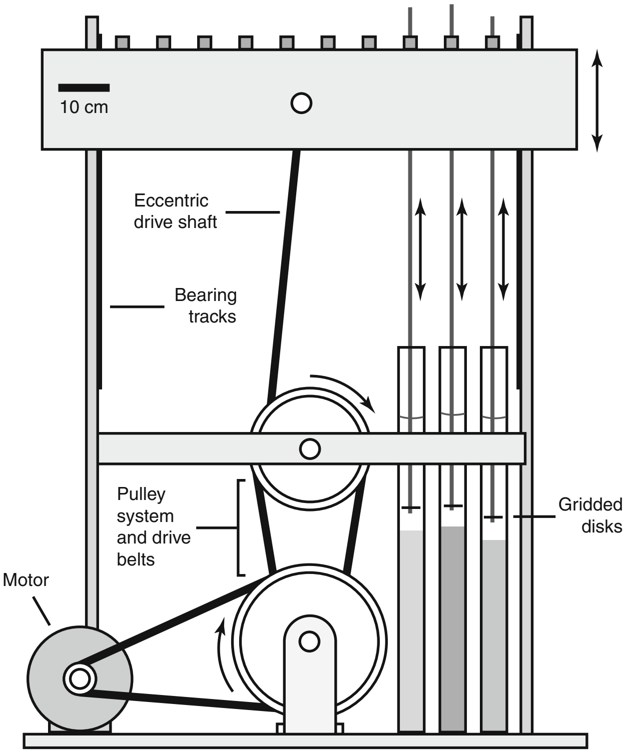

Fig. 2 Diagram of the eccentric-drive apparatus used to generate turbulence by oscillating gridded disks in the water columns over intact sediment cores

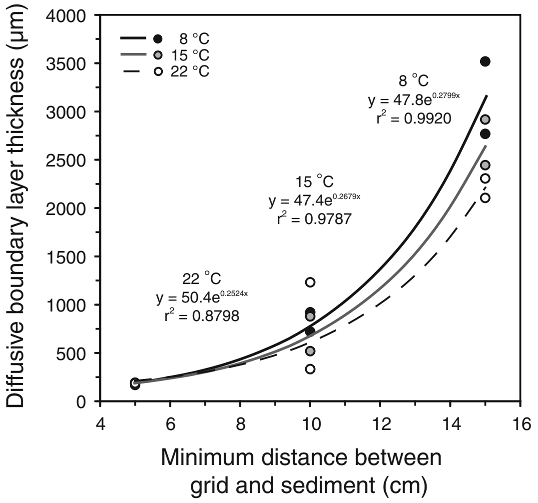

Fig. 3 Calibration of diffusive boundary layer (DBL) thicknesses (calculated from gypsum dissolution) in relation to the minimum distance between the oscillating disks and the sediment water interface (SWI)

sediments at 5 m and 10 m are not. Water was collected in 20-L carboys for experiments. Nine cores from each depth were retained for incubation under conditions of varying turbulence and temperature. The upper 5 cm was taken from the two remaining cores from each depth for determination of water and organic matter content (dried at 106 °C; combusted at 475 °C).

Cores retained for experiments were incubated in a water bath at 8 °C. Prior to incubation experiments, the water overlying each sediment core was purged three times with filtered (0.45 μm pore size) lake water delivered through a porous diffuser that prevented sediment disturbance. Cores then were incubated with three boundary layer conditions induced by varying the minimum distance between the oscillating grids and the SWI (5, 9, and 14 cm). All 27 cores were incubated concurrently. Two empty core tubes, each with 30 cm of filtered lake water, served as controls. Aeration of the water columns was maintained by exposure of the core sample water surface to the atmosphere and circulation of water by grid oscillation.

The cores were incubated for 23 days; incubation temperature of each core was increased progressively from 8–12, 16, 19, and 25 °C by adjusting the water-bath temperature at five-day intervals (3 days at 16 °C). The range of ambient temperatures expected during the growing season in the Grand Lake epilimnion is 8–16 °C; 19 and 25 °C exceed temperatures in situ. At intervals of 24, 72, and 120 h during each temperature treatment, water was removed for sampling and replaced with filtered lake water equilibrated to the incubation temperature. Samples were analyzed for concentrations of soluble reactive phosphorus (SRP; Murphy and Riley 1962), ammonium (APHA 2005), and nitrate + nitrite (ion chromatography, APHA 2005). Mass fluxes of SRP, NH_4^+–N, and $NO_3^- + NO_2^-$–N then were calculated as net change in water column mass per unit area within the test tubes. After incubation, the redox-potential discontinuity (RPD), an approximate visual indicator of the oxidized SWI, was determined as the depth at which oxidized iron was not present (color shift from yellow–orange to gray–black).

Repeated measures ANOVA was used to evaluate the effects of DBL thickness, depth of core collection, and temperature on mean flux rates of SRP, NH_4^+, and $NO_3^- + NO_2^-$. Normalizing square root (SRP and $NO_3^- + NO_2^-$) and log (NH_4^+) transformations include the addition of a constant to allow use of negative fluxes (nutrient uptake by the sediment). Because the ANOVA assumption of sphericity was violated in all cases (Mauchly's Criterion, $p \leq 0.05$), the conservative Greenhouse–Geisser (G–G) *F* adjustment was used to minimize the probability of type-one error in evaluation of the temperature effects. Mean fluxes were compared by testing within each temperature treatment, and sequential Bonferroni adjusted post hoc tests were used to determine the within-subjects effect (temperature).

Results

DBL thickness as measured with gypsum discs averaged 642 μm (range of means across depths, 729–551 μm) in Grand Lake (Table 1); higher thicknesses have been estimated for some Canadian lakes and lower thicknesses are typical of marine sediments (Table 1). Boundary layer thicknesses induced over sediment cores according to equations in Fig. 3 were 200, 600, and 2400 μm at 8 °C. Because oscillation rates were constant across temperature, DBL thicknesses decreased slightly with increasing incubation temperature (Fig. 3), but the influence of temperature cannot be calculated reliably because of the reactivity and biolability of the constituents of interest.

Water content of the upper 5 cm of sediment (mean ± SE) was 87 ± 0.5, 82 ± 0.5, and 81 ± 1% for cores collected at 2, 5, and 10 m, respectively, and organic content was 3.3 ± 0.1, 3.5 ± 0.1, and 4.2 ± 0.1% dry mass. RPD depths of 2.0 ± 0.4, 4.1 ± 0.3, and 6.5 ± 0.4 mm at 2, 5, and 10 m, respectively, at the conclusion of incubations indicate that all cores maintained an oxidized SWI for the duration of incubation.

DBL thickness showed no evidence of affecting fluxes of any of the measured nutrients, nor was there any significant interaction between DBL thickness and depth of core collection or incubation temperature. Depth of core collection was significantly related to fluxes of SRP ($F_{2,17} = 6.9$, $p = 0.006$), NH_4^+ ($F_{2,17} = 13.8$, $p = 0.0003$), and $NO_3^- + NO_2^-$ ($F_{2,17} = 35.8, p < 0.0001$). Fluxes of SRP, NH_4^+, and $NO_3^- + NO_2^-$ varied significantly with temperature (SRP $F_{2.6,44} = 61.1, p < 0.0001$; NH_4^+ $F_{1.4,23.3} = 37.7$, $p < 0.0001$; $NO_3^- + NO_2^-$ $F_{2.2,37} = 22.3$, $p < 0.0001$), and there was a significant interaction between depth of core collection and incubation temperature (SRP $F_{5.2,44} = 6.0, p = 0.0009$; NH_4^+ $F_{2.7,23} = 4.1, p = 0.0212$; $NO_3^- + NO_2^-$ $F_{4.3,37} = 4.4, p = 0.0042$).

SRP at all ambient temperatures (≤16 °C), was either sequestered or released in small amount, but at 19 and 25 °C, the sediments consistently released significant amounts of SRP. When cores were grouped by depth of collection, fluxes of SRP did not differ significantly among groups until the incubation temperature exceeded 16 °C (Fig. 4). SRP effluxes at temperatures above 16 °C were highest in cores collected from 10 m (Fig. 4).

NH_4^+ fluxes also were low or negative at ≤16 °C, and high at 19 and 25 °C. Cores collected from 2 m had the highest NH_4^+ effluxes at all incubation temperatures above 8 °C (Fig. 4). Sediments consistently released $NO_3^- + NO_2^-$, and these effluxes increased with increasing temperature. While NO_3^- dominated these releases at temperatures ≤16 °C, NO_2^- comprised an increasing proportion of the $NO_3^- + NO_2^-$ effluxes during incubations above 16 °C (Fig. 4). $NO_3^- + NO_2^-$ effluxes from cores collected at 2 m generally were significantly lower than those from cores collected at 5 m or 10 m (Fig. 4).

Sequential Bonferroni post hoc multiple comparisons ($\alpha < 0.05$) within depths could not fully resolve differences in fluxes of SRP, NH_4^+, and $NO_3^- + NO_2^-$ across all specific temperature treatments at all depths, but fluxes often were significantly lowest at 8 °C and significantly highest at 25 °C (Table 2). Within the range of temperatures expected in the Grand Lake epilimnion during summer stratification (8–16 °C), mean fluxes of SRP, NH_4^+, and $NO_3^- + NO_2^-$ at each collection depth were significantly lower than those occurring at temperatures above 16 °C (Table 3). Results were the same even with exclusion of the comparatively high fluxes at 25 °C (Fig. 4).

Table 1 Diffusive boundary layer thicknesses (DBL mean ± SE) estimated from gypsum dissolution in situ

Site	Depth (m)	DBL thickness (μm)
Present study		
Grand Lake, Colorado USA	2	729 ± 38
	5	667 ± 63
	10	551 ± 11
Santschi et al. (1991)		
Point Sur, Pacific Ocean	2010	217 ± 32
	3330	199 ± 20
	1185	129 ± 6
	795	153 ± 32
EN 179, Middle Atlantic Bight	133	274 ± 22
	1095	462 ± 54
EN 187, Middle Atlantic Bight	125	245
	925	439 ± 23
Santschi et al. (1986)		
ELA Lake 302, Ontario, Canada	1.2	1165 ± 5
ELA Lake 226 NE, Ontario, Canada	–	1300
ELA Lake 226 SW, Ontario, Canada	–	800
ELA Lake 223, Ontario, Canada	2–2.5	1600
ELA Lake 224, Ontario, Canada	–	1400
ELA Lake 114, Ontario, Canada	1.2	1400

ELA Canadian experimental lakes area

Discussion

Because DBL thickness was not statistically related to fluxes, epilimnetic sediment–water nutrient exchanges in the upper water column of Grand Lake appear to be governed either by pore-water nutrient availability (e.g., as affected by sorption processes or mineralization rates) or

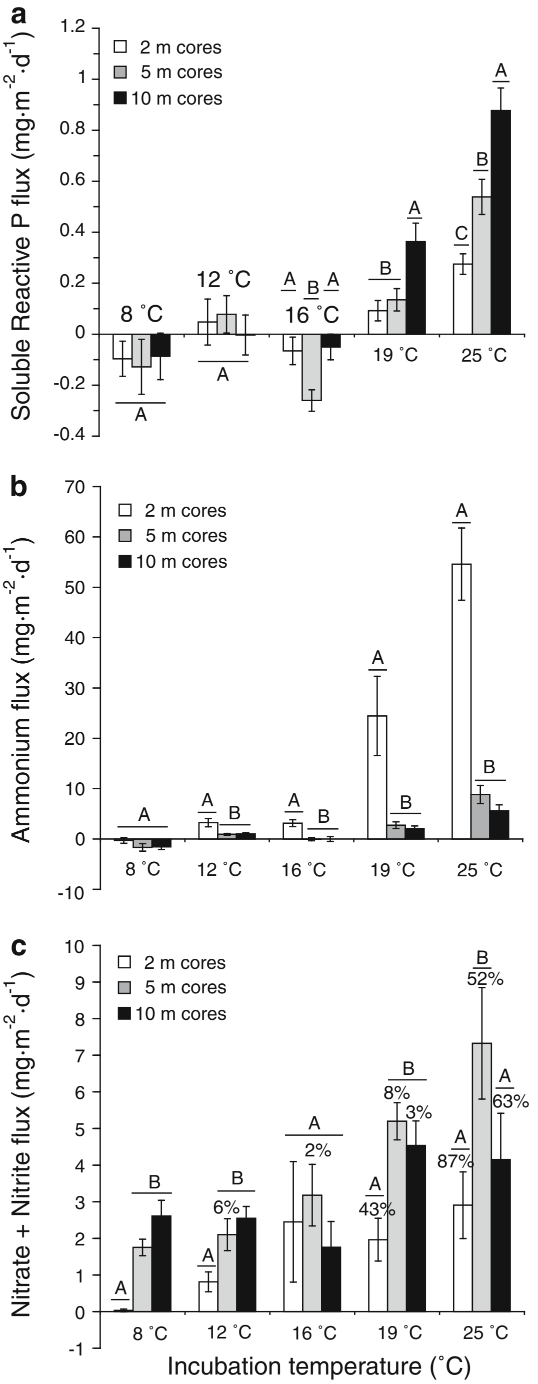

Fig. 4 Mean fluxes ± SE (mg m^{-2} d^{-1}) of (**a**) SRP, (**b**) NH_4^+–N, and (**c**) $NO_3^- + NO_2^-$–N are shown for sediment cores collected at 2, 5, and 10 m and incubated at 8, 12, 16, 19, and 25 °C. Letters (*A–C*) group homogeneous fluxes across depths within temperature treatments, based on the results of *t* tests ($\alpha = 0.05$). When NO_2^- was present, the proportion of the $NO_3^- + NO_2^-$ flux comprised of NO_2^- is displayed as a percentage in (*A*). Fluxes at 2 m were calculated for only eight cores because a grid failure resulted in sediment resuspension in one core

Table 2 Results of post hoc multiple comparisons (sequential Bonferroni-adjusted, $\alpha < 0.05$) within groups (depth of core collection) across the within-subjects repeated measure (incubation temperature)

	Incubation temperature (°C)	Depth (m)		
		2	5	10
SRP	25	C	C	C
	19	B	B	B
	16	A B	A B	A
	12	A B	B	A
	8	A	A	A
NH_4^+	25	D	A C	C
	19	C	A B	B
	16	B	A B	B
	12	B	A B	B
	8	A	A	A
$NO_3^- + NO_2^-$	25	B C	A C	C
	19	B C	B	B
	16	C	A B	B
	12	B	A	B
	8	A	A	A

Letters (A–D) combine fluxes of soluble reactive phosphorus (SRP), ammonium (NH_4^+), and nitrate + nitrite ($NO_3^- + NO_2^-$) into homogeneous groups within depths

by mechanisms of SWI solute mass transfer other than molecular diffusion (Sanford and Crawford 2000). Lower turbulence than observed in situ for Grand Lake would be necessary to maintain a DBL of thickness sufficient to limit sediment–water nutrient fluxes. Lack of influence of the DBL on nutrient flux in Grand Lake is unexpected, given the demonstrated influence of DBL in some other studies (Lorke et al. 2003). Bioirrigation may have masked the effect of DBL thickness by increasing effective surface area for N and P diffusion (Lewandowski et al. 2007).

Depth-dependent differences (2–10 m, Fig. 4) in nutrient fluxes do not correspond to differences in water and organic-matter content, which are small, but larger differences in RPD depth among sediments collected at different depths suggest that fluxes of N may be related to sediment oxygen demand, which could vary with sediment age or lability. Cores with the smallest RPD depths (from 2 m) released the most NH_4^+ and the least $NO_3^- + NO_2^-$ (Fig. 4). Releases of NH_4^+ from more highly oxidized cores likely were suppressed by NH_4^+ oxidation, which favored production of $NO_3^- + NO_2^-$ (Fig. 4), and possibly by sorption processes in the oxidized microzone.

Depth-dependent differences in fluxes of N were consistent with expectations based on RPD depths, but expectations for SRP are not straightforward, as all cores sustained an oxidized SWI. During incubations at temperatures above ambient, the most deeply oxidized cores

Table 3 Mean fluxes (mg m^{-2} d^{-1} ± SE) of soluble reactive phosphorus (SRP), ammonium (NH_4^+), and nitrate + nitrite ($NO_3^- + NO_2^-$) at incubation temperatures within the ambient range (8, 12, and 16 °C) for the Grand Lake epilimnion during stratification, and above the ambient range (19 and 25 °C)

Paired *t* tests compare fluxes at ambient (≤16 °C) and above ambient (> 16 °C) incubation temperatures

	Depth (m)	Flux (mg m^{-2} d^{-1} ± SE)		Pairwise *t* tests (*p*)
		≤16 °C	>16 °C	≤16 versus > 16 °C
SRP	2	−0.04 ± 0.02	0.18 ± 0.03	0.0002
	5	−0.10 ± 0.03	0.34 ± 0.06	<0.0001
	10	−0.05 ± 0.03	0.62 ± 0.70	<0.0001
NH_4^+	2	2.03 ± 0.71	39.52 ± 6.61	<0.0001
	5	0.26 ± 0.21	5.79 ± 1.70	0.0015
	10	−0.19 ± 0.10	3.83 ± 1.12	0.0001
$NO_3^- + NO_2^-$	2	1.10 ± 0.10	2.43 ± 0.43	0.0027
	5	2.34 ± 0.13	6.26 ± 0.55	<0.0001
	10	2.31 ± 0.20	4.34 ± 0.39	0.0022

(10 m, Fig. 4) released the most SRP, but the underlying mechanisms are not clear.

Differences in nutrient fluxes among intermediate temperature treatments generally could not be resolved by sequential Bonferroni post hoc tests (Table 2), but Bonferroni-adjusted critical values can be overly conservative for ecological research (Moran 2003). Even so, significant increases in nutrient fluxes occurred above 16 °C (Table 3). Similar results during incubations of sediment cores with sequentially decreasing, rather than increasing, incubation temperatures (Holdren and Armstrong 1980; Liikanen et al. 2002) showed that nutrient fluxes were responsive to incubation temperature. The mechanism of this response is not clear, but could include one or more of several processes that are thermally sensitive, such as diffusion coefficient or rates of iron oxidation, mineralization, or adsorption.

Liikanen et al. (2002) observed increases in NH_4^+ and SRP fluxes and decreased $NO_3^- + NO_2^-$ fluxes when sediment cores from a eutrophic lake were incubated at temperatures above 16 °C. Although SRP and NH_4^+ fluxes from the eutrophic lake sediments generally were higher than for Grand Lake sediments, the two studies show the potential for temperature-dependent mechanisms to influence sediment–water nutrient exchanges similarly in lakes of markedly different trophic status.

Although the oxidized microzone was not wholly depleted in any sediment cores for Grand Lake, the increasing proportion of NO_2^- in releases of $NO_3^- + NO_2^-$ at high temperature suggests that the cores were approaching redox conditions that might change the release of N and P components. Increased availability of SRP and NH_4^+ in anoxic sediment layers as derived from mineralization and desorption processes could saturate the available sorption sites in a thin surficial oxidized microzone. Substantial nutrient release may occur when the microzone is eroded sufficiently by thermal stimulation of respiration to reduce substantially the inhibition of upward diffusion of SRP and NH_4^+ from anoxic sediment layers.

Another type of phenomenon occurs when sediments warm more rapidly than the overlying water, leading to buoyancy of the sediment pore water. Pore-water convection could cause releases of nutrients at rates substantially higher than those expected by diffusion (Golosov and Ignatieva 1999). This mechanism is unlikely to have occurred during the Grand Lake incubations, however, because circulation of the water overlying the sediment cores would have caused the water column to warm faster than the water in the sediment interstices. If pore water convection were to occur in a lake, the effect likely would be a short-term perturbation followed by a return to lower rates of nutrient exchange across the SWI.

Ebullition of gases from the sediments during high temperature incubations, which was observed in some cores, is a more likely mechanism for the substantial increases in nutrient releases above some specific temperature that can be expected to vary through time and space according to sediment conditions such as organic content and DBL thickness (Andersen and Ring 1999). Ebullition would have favored advection of nutrient-rich pore water from anoxic sediments below the oxidized microzone, resulting in nutrient releases consistent with the substantial increases observed above the temperature threshold and substantial release of SRP and NH_4^+ despite the persistence of an oxidized SWI. Ebullition of gases produced in anoxic sediments below the oxidized microzone also is consistent with the increasing NO_2^- contribution to $NO_3^- + NO_2^-$ (Fig. 4). The same mechanism facilitates release of nutrients from the sediments of eutrophic lakes (Liikanen et al. 2003).

The effect of ebullition might be either temporary or prolonged. If gas production results primarily from temperature-mediated increases in microbial respiration, ebullition may enhance nutrient efflux indefinitely. If ebullition primarily occurs as a result of reduced solubility of gases, however, warming of lakes would likely cause a pulse of nutrients entering the overlying water followed by a return to generally low rates of diffusive exchange.

The present study suggests that, at ambient temperatures, diffusive exchanges of nutrients across an oxic SWI in lakes are limited by the availability of soluble nutrients in the sediment pore water and the capacity of the surficial oxidized microzone to inhibit nutrient release. A controlling influence of the DBL on fluxes of nutrients probably is rare in the relatively turbulent upper water column of lakes. A threshold for substantial nutrient release during incubations at above-ambient temperatures likely occurs when (1) the surficial oxidized microzone is not thick enough to suppress nutrient release or (2) turbulence affects diffusive release of nutrients. Thresholds for substantial nutrient release by either mechanism occurring frequently at temperatures near the seasonal maximum will have implications for the response of lakes to climate change. Whether the influence of temperature on these fluxes reflects steady-state conditions or a short-term perturbation depends on the driving mechanism and has markedly different implications for the response of lakes to seasonal or interannual thermal variation or to synoptic warming. The relevance of any enhanced nutrient releases to phytoplankton in lakes also will depend on the A_e:V_e ratio (Fee 1979) and the consistency of nutrient release over the growing season.

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