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Nitrification contributes to winter oxygen depletion in seasonally frozen forested lakes

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Abstract In lakes that experience seasonal ice cover, understanding of nitrogen–oxygen coupling and nitrification has been dominated by observations during open water, ice-free conditions. To address knowledge gaps about nitrogen–oxygen linkages under ice, we examined long-term winter data (30 + years, 2–3 sample events per winter) in 7 temperate lakes of forested northern Wisconsin, USA. Across lakes and depths, there were strong negative relationships between dissolved oxygen (DO) and the number of days since ice-on, reflecting consistent DO consumption rates under ice. In two bog lakes that routinely experience prolonged winter DO concentrations below 1.0 mg L^{-1}, nitrate accumulated near the ice surface mainly in late winter, suggesting nitrification may depend on biogenic oxygen from photosynthesis. In contrast, within five oligotrophic-mesotrophic lakes, nitrate accumulated more consistently over winter and often throughout the water column, especially at intermediate depths. Exogenous inputs of nitrate to these lakes were minimal compared to rates of nitrate accumulation. To produce the nitrate via in-lake nitrification, substantial oxygen consumption by ammonium oxidizing microbes would be required. Among lakes and depths that had significant DO depletion over winter, the stoichiometric nitrifier oxygen demand ranged from 1 to 25% of the DO depletion rate. These estimates of nitrifier-driven DO decline are likely conservative because we did not account for nitrate consumed by algal uptake or denitrification. Our results provide an example of nitrification at temperatures < 5 degrees C having a substantial influence on ecosystem-level nitrogen and oxygen availability in seasonally-frozen, northern forested lakes. Consequently, models of under-ice dissolved oxygen dynamics may be advanced through consideration of nitrification, and more broadly, coupled nitrogen and oxygen cycling.

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Introduction

Most naturally formed freshwater lakes are located
above 45° North (Verpoorter et al. 2014) and typically
freeze during winter. Following from work by Striegl
et al. (2001), a surge of recent research has confirmed
that biogenic gases often accumulate over winter in
seasonally frozen lakes (Ducharme-Riel et al. 2015;
Denfeld et al. 2016) along with oxidized solutes
including nitrate, sulfate, and carbonate/bicarbonate
from methane oxidation (Gammons et al. 2014;
Hanson et al. 2006; Powers et al. 2017). These
findings point to active benthic and planktonic com-
munities (Bertilsson et al. 2013; Hampton et al. 2017)
that affect whole-lake chemistry through sustained
aerobic and anaerobic biological processes under
ice—which may not be surprising given similar
observations from permanently frozen lakes (Mor-
gan-Kiss et al. 2016; Powers and Hampton 2016).

Though not often addressed in oxygen-based stud-
ies in aquatic ecosystems, nitrification directly
accounts for a portion of oxygen consumption (Hall
and Jeffries 1984; Clevinger et al. 2014). Microbial
oxygen consumption may be particularly influential
when ice and snow cover a lake's surface, because air–
water gas exchange is essentially cut off while oxygen
production from aquatic photoautotrophs can be low
due to darkness (Kirillin et al. 2012; McKnight et al.
2000). In extreme cases of oxygen depletion, "win-
terkill" of fish can occur (Magnuson et al. 1985).
However, surprisingly little is known about the rates of
nitrification under ice in seasonally frozen lakes, and
how this nitrogen (N) transformation is related to a
lake's winter oxygen budget (but see Knowles and
Lean 1987).

Understanding about nitrification beneath lake ice
and its resulting effects on oxygen dynamics could
guide future applications and interpretations of oxy-
gen-based ecosystem metabolism models. One con-
sideration is that ecosystem respiration rates derived
from fitted nighttime oxygen data reflect integrated
oxygen consumption rates, including autotrophic
processes such as nitrification, and thus may overes-
timate aerobic respiration. A second consideration is

that photoinhibition of nitrification during the day
(French et al. 2012) might introduce a diel cycle,
especially when clear ice forms (Katz et al. 2015),
potentially influencing the validity of the assumption
that daytime and nighttime ecosystem respiration rates
are equal (Winslow et al. 2016). These examples
reflect upper limits to the amount of biological
information that can be extracted from oxygen-based
models alone, especially in systems where dissolved
oxygen and inorganic carbon are not perfectly cou-
pled, as would be expected when processes such as
nitrification contribute substantially to the oxygen
dynamics.

Recently Powers et al. (2017) found that nitrate
accumulated overwinter, using > 30 years of under-
ice measurements in five northern oligotrophic and
mesotrophic lakes. The results suggested strong sea-
sonal forcing by the number of ice covered days.
Exogenous inputs of nitrate from stream water and
groundwater to these lakes accounted for only 0 to
13% of the nitrate accumulation. Thus, in-lake nitri-
fication, which consumes oxygen, was likely respon-
sible for generating the majority of the nitrate.
However, the influence of nitrification on winter
oxygen dynamics has not yet been quantified in these
lakes, and has rarely been addressed in lakes overall
(but see Knowles and Lean 1987; Liao and Lean
1978).

Here, we examine the stoichiometric oxygen
requirements of nitrification, and potential influences
of nitrification on winter dissolved oxygen (DO)
dynamics, through comparison of winter DO depletion
and NO_3–N accumulation rates. This research builds
on findings of winter nitrate accumulation in Powers
et al. (2017), again using the number of days since ice-
on to account for seasonal forcing, with the addition of
new oxygen data. We also include new data sets for
two bog lakes that routinely experience winter DO
concentrations below 1.0 mg L^{-1}, enabling compar-
isons between lakes that vary in trophic status. In total,
more than 30 years of winter data for nitrate, DO, and
supporting physico-chemical dynamics were explored
in seven seasonally frozen north temperate lakes.

Methods

We used 30 + years of winter limnological data from
seven study lakes of the North Temperate Lakes Long-

Term Ecological Research (NTL-LTER) project (Allequash, Big Muskellunge (hereon Big Musky), Crystal, Sparkling, and Trout Lakes, as well as Crystal and Trout Bogs; https://lter.limnology.wisc.edu), located in northern WI, USA. Maximum lake depth ranged from 2.5 to 35 m. Lake depth, ice duration, winter data availability, and mean winter conditions are summarized in Table 1. Each lake was sampled 2–3 times each winter and water chemistry was determined using consistent field and laboratory methodologies. Under-ice water samples were taken over the deepest point of each lake at three depths through a 20 cm bore hole: surface (0–5 cm below the bottom of the ice), deep (1 m above lake bottom), and midpoint of the water column for water chemistry. Temperature and DO profiles were measured at 1-m intervals. Our analysis focuses on nitrate + nitrite–nitrogen (hereafter NO_3–N, $\mu g\ L^{-1}$), and DO ($mg\ L^{-1}$), with supporting physico-chemistry for ammonium (NH_4–N, $mg\ L^{-1}$) and dissolved inorganic carbon (DIC, $mg\ L^{-1}$). For each sampling date, we also calculated depth-integrated, whole water column DO concentration using vertical profiles. Expanded methods are in the SI.

Relationships between concentration and days since ice-on

With days since ice-on as our time variable, we used linear mixed effects models (Bates et al. 2015) to estimate lake-specific and depth-specific rates of change in NO_3–N and DO over winter (random intercepts for each lake, depth, and variable; SI). In model fitting for DO declines and NO_3–N accumulation, we focused on the linear portion over the first 100 days since ice-on, prior to ice thinning, which included the majority of data. To avoid interpolation across a sampling gap during early winter, which applied to bog lakes only, we used a fitting window that excluded the first 7 days after ice-on. All available winter data were used to guide interpretations. Analyses and figures were produced using R (R Core Team 2016). Loess fits were used for visualization.

Potential oxygen consumption by nitrifiers

We calculated the potential DO consumption required to produce the fitted winter NO_3–N accumulation rates via nitrification. This estimation was made using the N:O stoichiometry for autotrophic nitrification reactions. The overall reaction of nitrification is:

$$NH_4^+ + 2O_2 \rightarrow NO_3^- + 2H^+ + H_2O \tag{1}$$
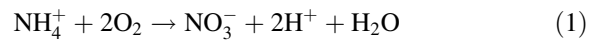
and requires consumption of 2 mol O_2 per mole of NO_3–N produced. In the underlying steps, ammonium is oxidized first to nitrite (NO_2^-), then to NO_3^-, by microbes. Using the 2:1 molar ratio, molar NO_3–N accumulation rates were converted into units of potential DO consumption, then compared to the observed DO depletion in open water. These calculations were first performed depth-specifically, by comparing the potential DO consumption rates by nitrifiers to DO depletion rates from the same depth.

Ecosystem-level quantification of NO_3–N accumulation and DO depletion rates

To produce estimates of the ecosystem-level nitrate accumulation and oxygen depletion rates, we require assumptions about the height of water represented by each sampling depth. These representative water heights are not known, reflecting complications from highly dynamic and depth-penetrating mixing patterns that have been revealed in recent winter research (Pernica et al. 2017; Bruesewitz et al. 2014). Because nitrification is thought to be a benthic-dominated process in these lakes (Powers et al. 2017), estimates of ecosystem-level oxygen consumption by nitrification may be obtained through knowledge of the sediment surface area associated with a given depth. In Big Musky, Crystal, Sparkling, Trout, > 70% of the benthic surface area occurs closer to the middle sampling depth than the deep or surface sampling depths (SI), while Allequash had 49% of benthic surface area closer to middle depth.

To address the above complexities, we considered five alternative approaches to ecosystem-level flux estimation using chemical data combined with hypsometry data at 0.5 m intervals, which explains the proportion of surface area represented by a given depth interval. Similar approaches have been employed relatively recently to calculate whole-system fluxes (Beaulieu et al. 2014; Deemer et al. 2011; Grantz et al. 2012). Each approach incorporates different assumptions about the weighting of surface, middle, and deep samples in ecosystem-level quantification. The five approaches are described below.

Table 1 Summary of lake features and data availability

Lake name	Max depth (m)	Mean depth (m)	Lake area (km²)	Catchment area (km²)	Mean ice duration (days)	Sample group	NO₃N data availability			Mean under ice condition						
							# of obs.	# of years	Mean # obs per year	NO_3N (µg L⁻¹)	NH_4N (µg L⁻¹)	O_2 (mg L⁻¹)	DIC (mg L⁻¹)	TDP (µg L⁻¹)	Water temp (°C)	pH
Allequash, north basin	8	2.9	1.12	21.5	146	Surf (0 m)	51	30	1.7	38	66	9.8	12	6.3	0.46	7.2
						Mid (4 m)	54	30	1.8	99	78	7.3	13	8.8	2.9	7.1
						Deep (6 m)	51	31	1.6	58	320	2.8	16	31	3.9	7
Big Musky	21.3	7.5	3.96	4.0	140	Surf (0 m)	59	30	2	27	70	14	6.3	5.9	0.49	7.4
						Mid (10 m)	63	32	2	59	83	9.8	6.4	10	3	7
						Deep (17 m)	60	31	1.9	13	530	3	9.9	130	3.8	6.7
Crystal Lake	20.4	10.4	0.367	0.86	138	Surf (0 m)	58	30	1.9	12	42	15	0.78	4.2	0.57	6.5
						Mid (10 m)	63	32	2	17	51	11	1.1	3.9	3.5	6
						Deep (17 M)	62	32	1.9	59	240	6.3	2.9	9.1	4.1	5.8
Sparkling	20	10.9	0.64	1.4	136	Surf (0 m)	62	30	2.1	22	42	14	9	4.3	0.53	7.7
						Mid (10 m)	65	32	2	62	33	10	8.9	3.7	3.3	7.2
						Deep (17 m)	65	32	2	43	810	4.1	13	38	3.8	6.9
Trout Lake, south basin	35.7	14.6	10.9	47	133	Surf (0 m)	64	30	2.1	62	24	13	11	3.2	0.69	7.7
						Mid (15 m)	70	31	2.3	59	14	12	11	4.1	1.6	7.6
						Deep (28 m)	70	32	2.2	160	170	7.2	13	10	2.3	6.9
Crystal Bog	2.5	1.7	0.05	151	183	Surf (0 m)	46	27	1.7	37	300	6.2	2.4	8.4	1	5.1
						Deep (2 m)	46	28	1.6	7.7	430	1.2	4	8.2	3.9	5.4
Trout Bog	7.9	5.6	0.14	153	183	Surf (0 m)	50	31	1.6	14	210	3.1	3	18	0.76	4.8
						Mid (3 m)	54	31	1.7	6.3	230	1.1	4.1	17	3.5	4.9
						Deep (6 m)	53	31	1.7	7.2	500	0.39	4.5	46	3.9	5.1

Adapted from Powers et al. (2017) to include bog lakes, with data restricted to early and middle winter (< 100 days since ice-on)

(1) Depth-ignorant fit: No depth weights used. For each solute, a single coefficient describing the rate of change was fit across depths. (2) Simple hypsometrically-weighted approach: Surface height $= 0.5 \times$ middle depth, *excluding* surface-middle boundary depth; deep height $=$ lake max depth $- 0.5 \times$ (deep depth $+$ middle depth), *excluding* middle-deep boundary depth; rest of water height goes to middle; water heights converted to hypsometric weights using hypsometry data. (3) Hypsometrically-weighted with a conservative surface zone: Surface height $= 0.5$ m; deep height $=$ lake max depth $- 0.5 \times$ (deep depth $+$ middle depth), *excluding* middle-deep boundary depth; rest of water height goes to middle; water heights converted to hypsometric weights using hypsometry data. (4) Hypsometrically-weighted with a conservative surface zone and a conservative deep zone: Surface height $= 0.5$ m; deep water height bounded by the lake bottom and 1 m above the deep sampling depth; rest of water height goes to middle; water heights converted to hypsometric weights using hypsometry data. (5) Simple middle depth rate as an indicator of the ecosystem-level rate: This approach does not require further assumptions about the height of water that each sample represents; depth weights are surface $= 0$, middle $= 1$, deep $= 0$.

The degree of "middle-weightedness" for these approaches is as follows: 5 (most middle-weighted), 4, 3, 2, 1 (least middle-weighted). In the reported results, we emphasize the minimum and maximum estimates obtained from these five approaches.

Results

Oxygen declined over winter at middle and deep sampling depths in all seven lakes (Fig. 1). Among the five oligotrophic-mesotrophic lakes, fitted DO depletion rates were highest in deep water, ranging from 50 µg L^{-1} days^{-1} (5.0 mg L^{-1} per 100 days) in Big Musky Lake to 71 µg L^{-1} days^{-1} in Allequash Lake (1.55–2.23 µM days^{-1}, Table S1), and lowest at the surface, ranging from 7.2 µg L^{-1} days^{-1} in Allequash to 21 µg L^{-1} days^{-1} in Big Musky (0.23–0.66 µM days^{-1}). Hypoxia developed in some years in the deep layer of Allequash and Big Musky, after about 50 days since ice-on. Deep waters of Trout remained relatively oxygenated (DO > 2.5 mg L^{-1}) and colder (mean < 3 °C) than the other lakes. The two bog lakes (Trout Bog and Crystal Bog) typically became nearly anoxic (< 0.5 mg L^{-1} DO) or hypoxic (< 3 mg L^{-1} DO) over the majority of the water column by 60 days since ice-on, although surface water typically remained oxygenated (3–10 mg L^{-1}) during winter.

All lakes began the ice-on period with similar and relatively low NO_3–N concentrations across all depths. In all lakes, deep water was more DO-depleted, DIC-rich, and NH_4–N-rich relative to middle and surface depths. In oligotrophic-mesotrophic lakes, there was a progressive shift from NH_4–N dominance to NO_3–N dominance of the DIN pool over the course of winter, with NO_3–N concentrations > 100 µg L^{-1} at middle depth by late winter (~ 100 days since ice-on) (Fig. 2). In Allequash, Big Musky, and Sparkling Lakes, model-fitted NO_3–N accumulation rates between 0 and 100 days since ice-on were highest at middle depth (Fig. 3). Trout Lake and Crystal Lake had higher NO_3–N accumulation rates in deep water (Trout $= 3.0$ µg L^{-1} days^{-1}; Crystal $= 1.1$ µg L^{-1} days^{-1}) than at middle or surface depths. Trout Lake was unique in having a pronounced decline in deep water NO_3–N after 100 days since ice-on. In the two bog lakes, NO_3–N accumulation was restricted to late winter, near the ice surface.

Based on the co-occurring rates of NO_3–N accumulation and DO depletion at a given depth, potential oxygen use by nitrifiers ranged from 1 to 25% of the DO depletion rate (Fig. 4). Among oligotrophic-mesotrophic lakes that had non-negligible DO declines ($n = 14$, excludes surface of Allequash Lake), the mean potential oxygen use by nitrifiers was 9%. In deep water, potential oxygen use by nitrifiers represented 5–19% of DO depletion in Allequash, Crystal, Sparkling, and Trout (Fig. 4), but < 1% in Big Musky. At surface and middle depths of Sparkling and Trout, nitrifier oxygen demand represented 10–18% of the fitted oxygen depletion rate, as did the middle depth of Allequash and Big Musky.

Across the five different approaches to ecosystem-level quantification (Table S2), nitrifier oxygen demand in Allequash Lake represented 8–10% of the DO depletion, and corresponding estimates were 7–14% in Sparkling, 5–13% in Big Musky, 9–15% in Trout, 4–7% in Crystal, 2–3% in Trout Bog, and < 2% in shallower Crystal Bog based on the two available sampling depths (surface and 2 m). In both bog lakes, much DO depletion occurred during unsampled periods of early winter, and the nitrogen dynamics during this time are not yet known.

Fig. 1 Winter oxygen depletion expressed using the number of days since ice-on. Data are from deep, middle, and surface of the lake. Integrated water column concentrations from complete oxygen profiles (1-m intervals) are also shown. Lines are loess fits to aid visualization of winter trends. Lakes are generally not sampled during the first few weeks of ice-on, except the two bog lakes during years with early ice arrival
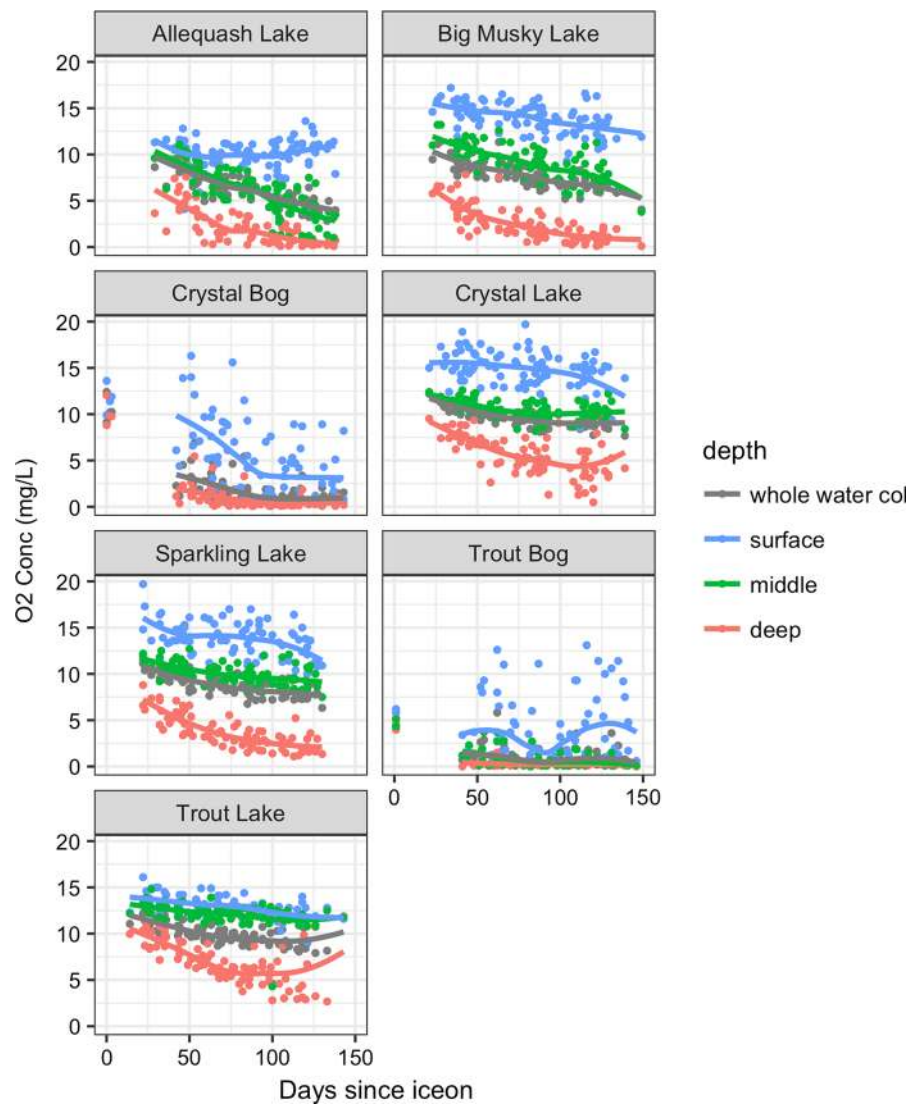
Discussion

Winter is a critical period of anoxia risk in lakes, and nitrification can hasten the transition between aerobic and anaerobic conditions (Clevinger et al. 2014; Hall and Jeffries 1984), with broad ecological and biogeochemical consequences (Gu 2012). Our results indicate that nitrification occurs in seasonally-frozen forested lakes at temperatures < 5 °C, at ecosystem-relevant rates that influence not only water column N speciation, but also oxygen supply. A study of winter conditions in more eutrophic lakes by Knowles and Lean (1987) provides one of the few other examples in which oxygen loss via nitrification has been examined beneath seasonal ice cover. Such observations during seasonal ice cover provide a unique window on oxygen and nitrogen cycles of lakes, when exogenous inputs from the atmosphere, precipitation, and the surrounding landscape are minimal. Because an unknown amount of NO_3–N was consumed by algal uptake and denitrification, these apparent NO_3–N accumulation rates represent net nitrification and are likely conservative estimates for gross nitrification and gross oxygen consumption by nitrifiers. Our results raise the possibility that oxygen-based studies and models of aerobic respiration and primary production under ice
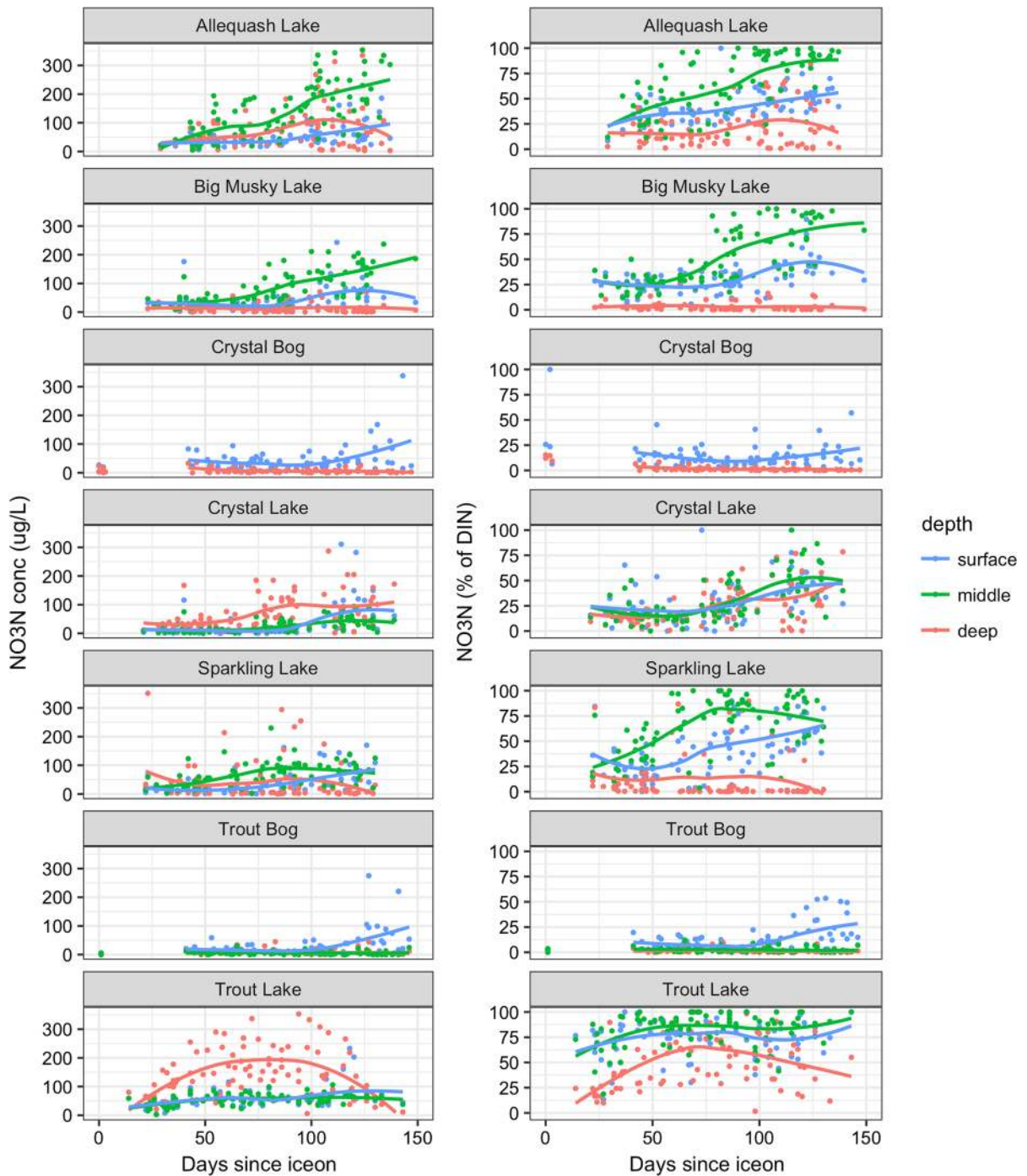
Fig. 2 Nitrate (NO₃–N) observations in deep, middle, and surface water expressed as a function of the number of days since ice-on. Adapted from Powers et al. (2017). In the right column, nitrate is plotted as the % of DIN (NO₃–N + NH₄–N). Lines are loess fits to aid visualization of winter trends. A few high values exceed the plotted scale

may be advanced by incorporating nitrifier effects. The lack of air–water gas exchange during ice cover offers useful opportunities to test the biological components

of oxygen-based ecosystem metabolism models, inclusive to nitrification and aerobic or anaerobic processes (Hanson et al. 2006).
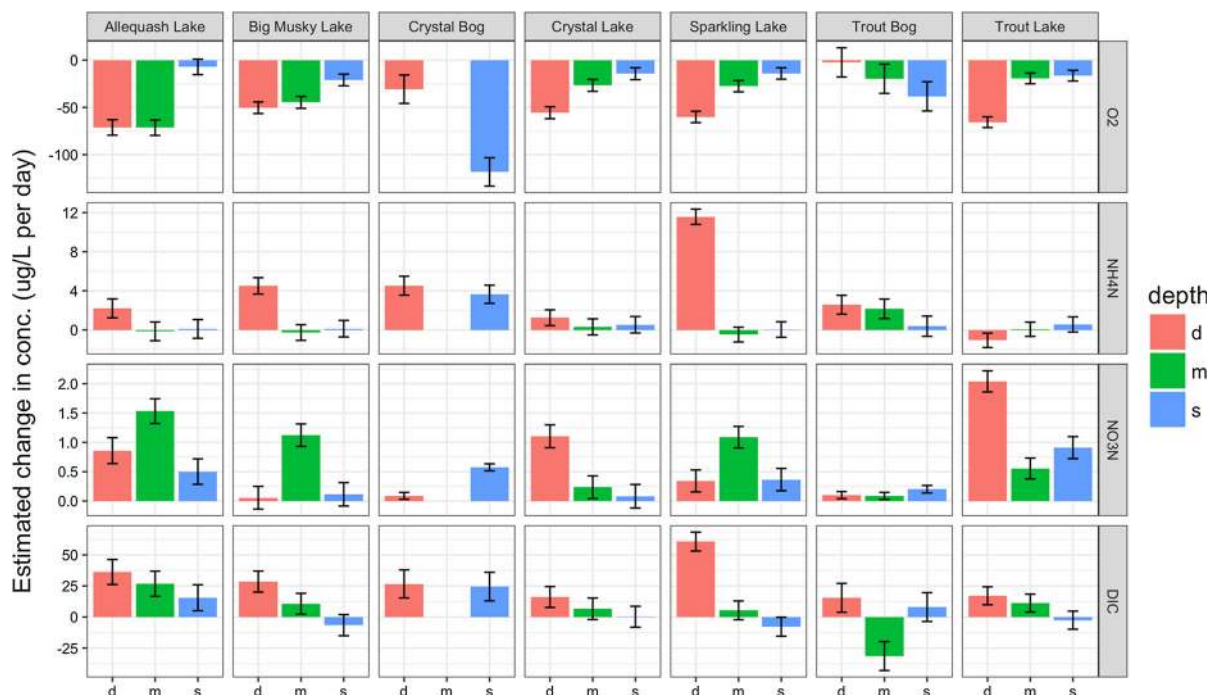
Fig. 3 Fitted winter changes in dissolved O_2, NH_4–N, NO_3–N, and DIC under ice in the seven lakes over the first 100 days since ice-on. Estimates are from linear mixed effects models. Whole (gray) indicates fitted values are from data at all 3 depths. Note different y-axis for each row. Key: d = deep, m = middle, s = surface

In oligotrophic-mesotrophic lakes during early and middle winter (0 to 100 days since ice-on), the oxygen requirement to support observed nitrate accumulation (Fig. 4) ranged from 1 to 25% of the DO depletion rates at those depths (mean of 9%). These calculations were based on observations showing that nitrate often accumulated over winter, especially in shallower oligotrophic-mesotrophic lakes (Allequash and Big Musky), and near the bottom of two deeper oligotrophic lakes (Crystal Lake and Trout Lake). Simultaneously there were pronounced winter DO declines across multiple lakes and depths, especially for middle and deep samples. Given the potential for interannual variability, these negative relationships between DO and days since iceon were relatively strong. The observed patterns of oxygen depletion reflect aerobic respiration of organic carbon combined with autotrophic, oxygen-consumptive processes such as nitrification and methane oxidation. Autotrophic oxygen consumption has not been frequently addressed in oxygen-based ecosystem metabolism models but could apply to other lakes during ice cover. A remaining question is: Why do nitrifier contributions to oxygen depletion vary among lakes? Possibilities are that nitrification is lower in lakes with low surface:volume ratios such as Trout Lake, or lakes with high water clarity such as Crystal Lake, where ammonium oxidizers can be inhibited by light.

Nitrate accumulation and DO declines were more pronounced in middle and deep water compared to the surface, likely because nitrification and respiration occur predominantly in the benthos, as has been widely reported in other aquatic environments (e.g., Pauer and Auer 2000). Photosynthesis and algal uptake of nitrate in surface waters could be masking the nitrification signal. However, surface water samples represented a relatively thin layer of the water column according to temp-DO profiles (Powers et al. 2017). Denitrification may also co-occur in deep water through coupled nitrification–denitrification, although the observed NO_3–N accumulation implies that nitrification exceeds denitrification under ice in these forested lakes. Net nitrification can occur if nitrification and denitrification are decoupled, as might be expected when N mineralization occurs in an aerobic matrix. Functional dominance by intermediate depths is further supported by the correspondence between middle and depth-integrated DO dynamics in Fig. 1.
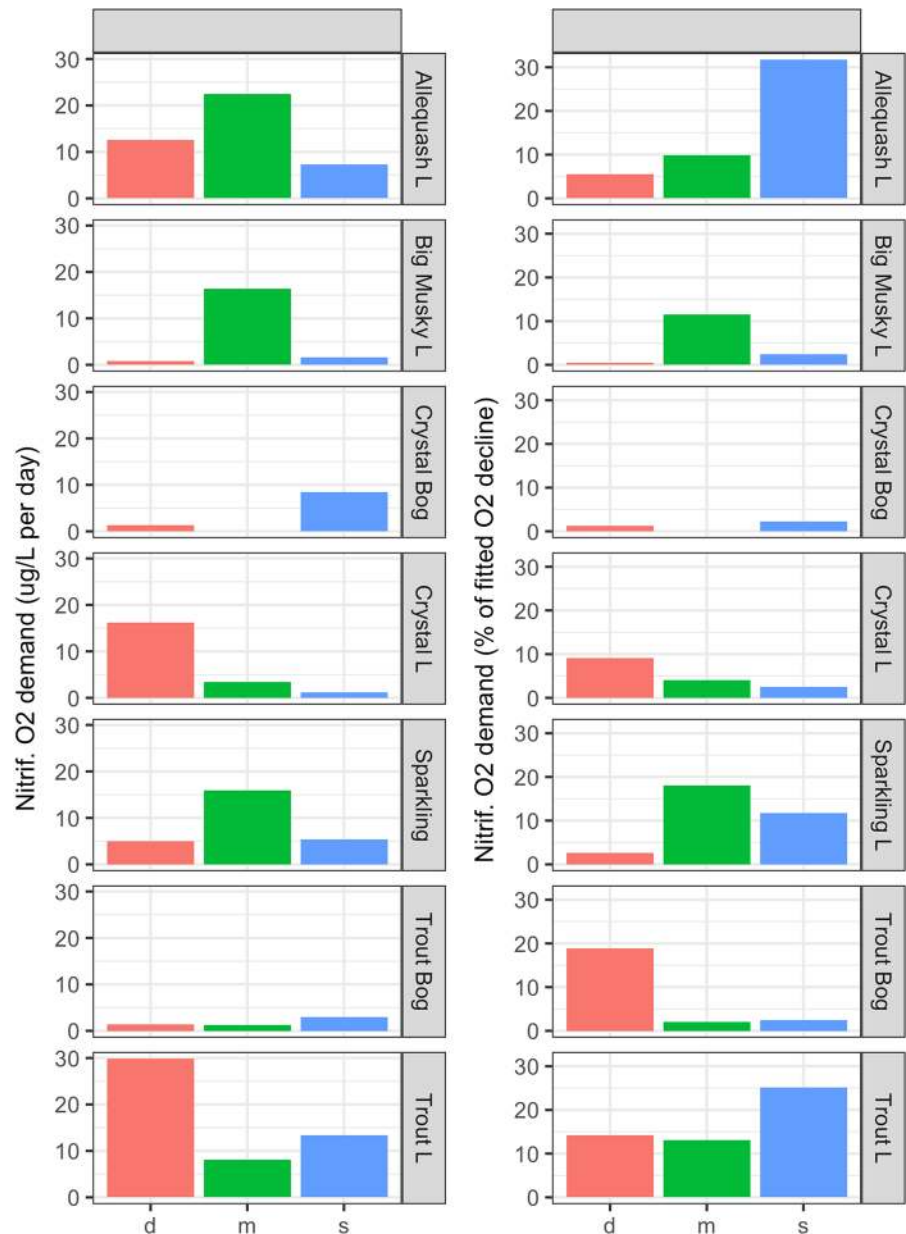
The variation in water chemistry between depths implies at least some degree of stratification, and thus the presence of NO_3–N may reflect depth-specific nitrification. However, in three lakes, surface and middle NO_3–N coincided with NH_4–N accumulation in deep waters (Allequash, Big Musky, Sparkling, Powers et al. 2017), suggesting some vertical transfer of N and/or DO, especially during late winter. Below 4.0°°C, water density increases as it warms (Wetzel 2001), and relatively small density gradients under ice

may promote circulation (Bruesewitz et al. 2014), perhaps delivering oxygenated water to benthic nitrifiers; this provides a possible explanation for the maintenance of DO concentrations above 2.5 mg L^{-1} in deep water of Crystal and Trout, the two deepest lakes (> 20 m), which in turn had the highest deep-water NO_3–N accumulation rates.

Compared to the oligotrophic-mesotrophic lakes, winter oxygen depletion in two smaller bog lakes (Crystal Bog and Trout Bog) proceeded more rapidly.

The lack of NO_3–N accumulation during early and midwinter in these bog lakes may reflect an absence of nitrification, or coupled nitrification–denitrification. However, NO_3–N did sometimes accumulate in bog lakes during late winter, suggesting nitrification may be supported by biogenic oxygen during enhanced photosynthesis under thinning ice or clear ice (Katz et al. 2015; Kerfoot et al. 2008), which has not been commonly demonstrated in bog lakes. In the oligotrophic-mesotrophic lakes, oxic conditions were typically maintained throughout winter. The lack of pronounced winter oxygen declines in surface samples of Allequash Lake, Crystal Lake, and Trout Bog could be explained by a combination of winter photosynthesis and low aerobic respiration. A more integrated understanding of winter oxygen dynamics across diverse lakes combined with ice phenology trends (Jensen et al. 2007; Magnuson et al. 2000) may increase understanding about the biogeochemical consequences of a changing winter.

Author contributions SMP led the manuscript effort. SMP and EHS generated the research questions and designed the study approach. SMP, SEH, and SGL contributed to statistical analyses. SMP and SGL contributed figures. EHS and NRL contributed data. SMP, EHS, HMB, NRL, and SEH interpreted results. All authors contributed to writing of the paper.

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