

Chlorophyll *a* seasonality in four shallow eutrophic lakes (northern British Columbia, Canada) and the critical roles of internal phosphorus loading and temperature

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Abstract Chlorophyll *a* (Chl *a*) seasonality was investigated in four shallow eutrophic lakes located in north-central British Columbia (western Canada). Chlorophyll *a* concentration maxima in all four lakes occurred during the late summer/early autumn when near-surface total phosphorus ([Tot-P]) and total dissolved P concentrations, pH, and water temperature were highest. Mass balance and inferential analyses showed that bloom-triggering P loads came mostly from within-lake sources, but that mechanisms controlling internal loading in Charlie and Tabor (lakes having hypolimnetic oxygen deficits during summer) were fundamentally different than those in Nulki and Tachick (isothermal, well oxygenated lakes). Although the timing and intensity of

major blooms were associated with late summer/early autumn P loads, average summer [Chl *a*] were predicted well by previously developed models based solely on spring overturn [Tot-P]. Instantaneous within-lake [Chl *a*] were best predicted by models incorporating both surface [Tot-P] and temperature ($r^2 = 0.57\text{--}0.70$). Moreover, [Tot-P] and temperature combined accounted for 57% of among-lake variations in instantaneous [Chl *a*]: $\log [\text{Chl } a] = 0.038 (\text{°C}) + 0.006 ([\text{Tot-P}]) + 0.203$ ($P < 0.001$), where [Chl *a*] and [Tot-P] are in $\mu\text{g l}^{-1}$. Positive associations between instantaneous [Chl *a*] and temperature support climate change models that forecast changes in phytoplankton productivity even if nutrient loading rates remain constant.

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Introduction

Phytoplankton are important components of lake ecosystems in that they are primary sources of organic carbon; however, excessive growth resulting from anthropogenic nutrient loads can lead to extreme water fouling (Kenefick et al., 1992; Kotak et al., 1993), trophic-level failures such as fish kills (Nguyen & Wood, 1979; Glibert

et al., 2002; Perkins & Underwood, 2002), and shifts in species composition, diversity, and health at multiple trophic levels (Schindler & Scheuerell, 2002; Vadeboncoeur et al., 2003; Johnson & Chase, 2004). Several cultural factors have contributed to the eutrophication of lakes in the northern interior of British Columbia (B.C., western Canada), including: (1) agricultural- and forestry-related deforestation, (2) nutrient-rich municipal and industrial wastes, (3) residential and recreational developments in riparian areas with ineffectively managed septic systems, and (4) nutrient-rich runoffs from fertilized crop lands and livestock holding areas. Despite concerns that human activities are accelerating eutrophication rates in northern B.C., there is little basic information regarding phytoplankton seasonality and factors controlling blooms in this region of North America.

The objective of this study was to use multi-year datasets to evaluate annual cycles of chlorophyll *a* concentration ([Chl *a*], an indicator phytoplankton biomass) in four shallow lakes located in the northern interior of B.C., and to assess the factors associated with seasonal blooms. Charlie and Tabor lakes develop hypolimnetic oxygen (O₂) deficits during summer and winter stratified periods, while Nulki and Tachick are well-mixed lakes that do not develop summer O₂ deficits. Chlorophyll *a* seasonality was assessed in relation to variations in total phosphorus ([Tot-P]) and total dissolved phosphorus ([Tot-P_{diss}]) concentrations, and to shifts in surface to bottom [O₂], temperature, and pH profiles. Also, regression-based models were developed that predict instantaneous within- and among-lake [Chl *a*] from [Tot-P] and temperature alone, and from the two variables combined.

Study lakes

Morphometric characteristics of the study lakes are given in Table 1. Nulki and Tachick lakes (Pacific drainage) lie parallel to one another, and are connected by a 3-km long channel (Fig. 1a, b). They support one fishing lodge each, sparsely distributed shoreline homes and cabins, and 500–800 people live scattered

Table 1 Location, morphometry, and basic hydrology of the four B.C. study lakes

Lake (elevation)	Coordinates	Max. length (km)	Shoreline length (km)	Max. depth (m)	Avg. depth (m)	Surface area (ha)	Watershed area (km ²)	Volume (m ³ × 10 ⁶)	Relative depth (%)	Flushing rate (volumes yr ⁻¹)
Charlie lake (691 m)	56°21'24" N, 121°01'00" W	14.6	38	15.0	7.0	2,776	298	139.6	0.25	0.14–0.20
Tabor lake (704 m)	53°55'28" N, 122°32'03" W	3.4	9	9.2	4.6	408	44	22.0	0.40	Approx. 0.43 ^a
Nulki lake (762 m)	53°54'24" N, 124°09'00" W	8.0	25	7.6	4.5	1,657	440 (combined)	72.1	0.17	Approx. 0.8
Tachick lake (762 m)	53°57'20" N, 124°11'49" W	9.9	30	7.6	4.5	2,202		96.4	0.14	Approx. 1.0

Flushing rate is the proportion of lake volume replaced per unit time, calculated by: $\text{Outlet}_{\text{disch}}/V$, where $\text{Outlet}_{\text{disch}}$ is discharge via lake outlet and V is lake volume. Relative depth is maximum depth as a percentage of the mean diameter, calculated by: $50 \times Z_m \times \sqrt{\pi}/\sqrt{A_o}$, where Z_m is maximum depth and A_o is surface area (Wetzel & Likens, 1990). Resistance to mixing increases with increasing relative depth, such that deep lakes with small surface areas (high relative depth) are more resistant to mixing than shallow lakes with large surface areas (low relative depth). Differences in relative depth might explain why Charlie and Tabor lakes are periodically stratified during summer months while Nulki and Tachick lakes do not stratify in summer (see text)

^a Skaret Creek was diverted away from Tabor Lake from the mid-1970s to 1997 (Fig. 1c). In 1997, it was directed back into Tabor Lake at the natural point of entry. The flushing rate was 0.24 volumes yr⁻¹ over the diversion period

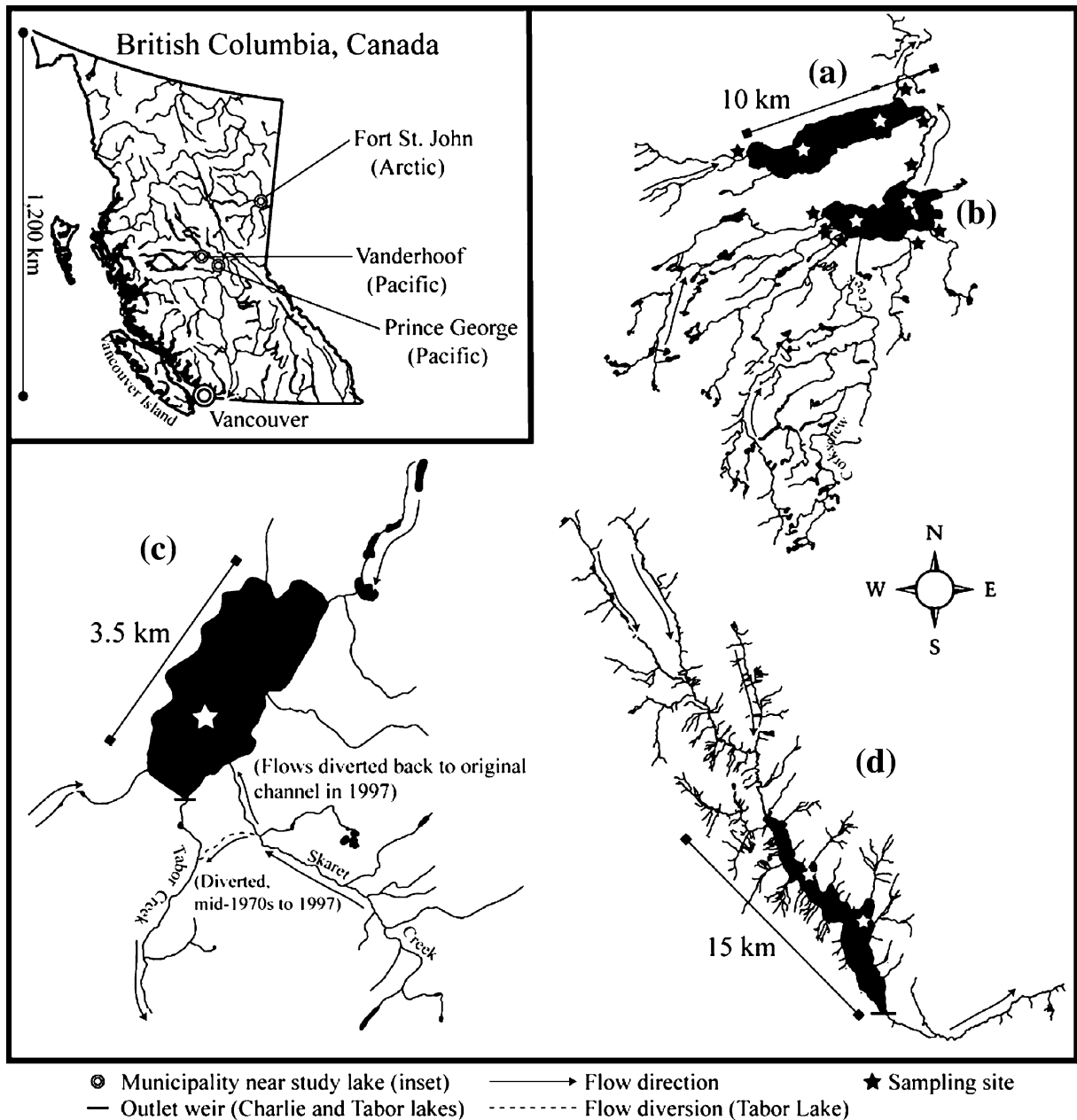


Fig. 1 Location of the four study lakes in the province of B.C. (western Canada): (a) Tachick Lake (Pacific Ocean drainage, near Vanderhoof [inset]), (b) Nulki Lake (Pacific Ocean drainage, near Vanderhoof [inset]), (c) Tabor Lake

(Pacific Ocean drainage, near Prince George [inset]), and (d) Charlie Lake (Arctic Ocean drainage, near Fort St. John [inset]). See Table 1 for morphometry and geographic coordinates

throughout the watershed. The southern margin of the Nulki–Tachick watershed is hilly to mountainous, but most of the watershed is gently sloped. Soils are dominated by moderate- to well-drained clayey, sandy and gravelly textures (Farstad & Laird, 1954). Thirty-five to

50% of the watershed's forests (mostly white spruce [*Picea glauca*], subalpine fir [*Abies lasiocarpa*], lodgepole pine [*Pinus contorta*], with intermixed patches of trembling aspen [*Populus tremuloides*]) were cleared between the late 1940s and the present.

Tabor Lake (Pacific drainage) is the drinking water supply for a subdivision of 200 people located along the western shoreline, with the eastern shoreline being mostly forested. The watershed is mostly forested (species similar to Nulki–Tachick watershed) with scattered farms and ranches, and has soil textures similar to the Nulki–Tachick watershed. The western portion of the watershed is gently sloped to hilly, with the eastern portion being steeply sloped to mountainous. Skaret Creek, Tabor Lake's primary tributary, was diverted away from the lake and into the outlet (Tabor Creek) sometime prior to the mid-1970s (Fig. 1c). The flushing rate of Tabor Lake was reduced from 0.43 to 0.24 volumes yr^{-1} by this diversion (Table 1). Flows were diverted back to the lake in 1997 to set the flushing rate back to natural conditions and to restore fish habitat.

Charlie Lake (Arctic drainage) is the most-northern study lake (Fig. 1d). Two thousand people live along the shoreline, with most living near the southern east and west shorelines. Most homes along the south-western shoreline are presently connected to a system that transfers domestic wastes, including sewage, out of the watershed. However, these homes were serviced by septic fields up until the early 1990s, many of which had nutrient-rich seepages to the lake. Except for the north-eastern shoreline which is steeply faced, the relief of the watershed is gently sloped. Soils are dominated by highly erodable clays and silts, and > 50% of the forest cover (mostly trembling aspen) has been cleared. Water levels have been controlled by a weir since 1981, and data show that the weir increased summer maximum levels by 1.2 m.

Methods

Lake sampling and analysis

Nulki and Tachick lakes were sampled bi-weekly at the two deepest locations (6–7 m) from spring through late autumn 1997, and once during the winter of 1998 when they were ice covered (Fig. 1). Tabor Lake was sampled weekly at its deepest location (9.2 m) during the spring through autumn of 1994, 1996–1997, and 2000–2001, and periodically during the winters of 1997

and 2000–2001 when it was frozen over. Charlie Lake was sampled monthly at the two deepest locations (15 m each) during the spring through autumn of 1990–1994, and at least twice during each winter when it was frozen over.

Water samples were collected from surface (1-m depth) and bottom (1 m above sediments) strata in Nulki and Tachick lakes, and from surface, mid-depth, and bottom strata in Tabor and Charlie lakes. They were analysed for [Tot-P] and [Tot-P_{diss}] with the ascorbic acid reduction-molybdate blue colourimetric method (H_2SO_4 hydrolysis, detection limit [DL] = $2 \mu\text{g l}^{-1}$; Greenburg et al., 1992). Samples for [Tot-P_{diss}] from Nulki and Tachick lakes were filtered through a syringe-fitted Nalgene® cellulose-acetate membrane ($0.45 \mu\text{m}$) in the field immediately after collection, with samples from Tabor and Charlie lakes being filtered in the lab within 24 h of collection. Samples (250-ml at 1-m depth) for Chl *a* analysis were collected from Nulki and Tachick lakes at the two deep sites, and at six open-water sites (outside of littoral zones) randomly selected on each sampling trip. The samples were mixed together, then two 500-ml sub-samples were taken from the composite. Sub-samples were filtered through a 47-mm diameter Whatman® glass-fibre filter ($1.2 \mu\text{m}$) and Chl *a* residues preserved with MgCO_3 , freeze-dried, and stored in the dark until analysis. Chlorophyll *a* was extracted with MgCO_3 /acetone and concentrations measured by colourimetry (DL = $0.1 \mu\text{g l}^{-1}$; Greenburg et al., 1992). Samples for Chl *a* analysis taken from Tabor and Charlie lakes were collected and processed using a similar approach; however, samples were collected only at the deep sites.

Surface to bottom [O_2] and temperature profiles (0.5-m intervals for Nulki, Tachick, and Tabor/1-m for Charlie) were taken at each site with a calibrated YSI O_2 -temperature meter. In Nulki and Tachick lakes, the pH of surface and bottom waters was measured in the field with an Accumet AP10 meter calibrated to pHs 4, 7, and 10. The pH of surface, mid-depth and bottom samples from Charlie Lake was measured in the lab when P analyses were performed. pH was measured irregularly in Tabor Lake, but reasonably consistently in the lab on surface and bottom samples collected in 1996–1997.

Tributary sampling and P loading

Nulki–Tachick tributaries (at mouths) and outlets (immediately downstream of lakes) were sampled for [Tot-P] and [Tot-P_{diss}] every 3–5 days between April 18 and May 7 (five freshet samples) and once every 2 weeks between May 7 and November 12 1997 (13 summer through autumn samples). Flows were measured continuously in Corkscrew Creek (Nulki Lake's primary tributary; Fig. 1b) with a stage-calibrated pressure transducer. Flows in smaller tributaries and outlets were estimated with the velocity–area method (Gordon et al., 1992) when water samples were collected. To facilitate P-loading estimates, [Tot-P] were converted to lake P mass (total mass of P in water column) for each sampling date by multiplying average [Tot-P] by lake volume. Average [Tot-P] was estimated by taking the average of concentrations observed at the two sampling sites (Fig. 1a, b). Average concentration was an appropriate value from which to estimate P mass in the lakes because horizontal and vertical concentration gradients were negligible during open-water seasons. Tributary P loads to Nulki and Tachick lakes were estimated for the 1997 open-water season (May 7–November 12) by multiplying [Tot-P] by flow. For days between sampling trips, [Tot-P] and flows were estimated by linear interpolation (regression-based data filling between measured values), with P exports being similarly estimated. Rainwater volumes deposited on the lake surfaces were estimated daily by multiplying rain quantities (mm) by lake surface area (Table 1). Rain quantities were measured with an MSC rain gauge (35-mm opening) positioned near Vanderhoof (15 km north of the lakes). Daily rainwater P loads to the lakes were estimated by multiplying rainwater volumes (m³) by an assumed [Tot-P] of 30 mg m⁻³ (Shaw et al., 1989). P loading rates from dry deposition were assumed to approximate 0.07 mg Tot-P m⁻² per day (Shaw et al., 1989).

Chl *a* correlates

From surveys of 19 lakes in southern Ontario and 11 lakes in the north-eastern United States (USA), Dillon & Rigler (1974) showed that

average summer (spring overturn to September) [Chl *a*] are positively correlated ($r = 0.93$) with spring overturn [Tot-P] (spring [Tot-P] or sp. [Tot-P]). Using similar approaches, Prepas & Trew (1983) and Ostrofsky & Rigler (1987) showed that the spring Tot-P-Chl *a* association is also strong for lakes in Alberta ($n = 25$, $r^2 = 0.67$) and subarctic Northwest Territories (N.W.T.; $n = 49$, $r^2 = 0.42$), respectively. To determine whether these associations held for the B.C. study lakes, tabulated datasets from Dillon & Rigler (1974), Prepas & Trew (1983), and Ostrofsky & Rigler (1987) were combined. Then, the 95% confidence intervals (C.I.) of summer average log [Chl *a*] versus spring log [Tot-P] least-squares regression line were computed. Available spring [Tot-P] versus average summer [Chl *a*] pairs for the B.C. lakes were then overlaid on this regression line \pm 95% C.I. It was inferred that the data from the four B.C. lakes fit previously published spring Tot-P-Chl *a* models if they fell within or near the 95% C.I. of the regression.

Results

General seasonality

Chlorophyll *a* concentrations ranged from 1 to 112 $\mu\text{g l}^{-1}$ ($35 \pm 36 \mu\text{g l}^{-1}$ [avg. \pm 1 SD]) in Nulki Lake, and from < 1 to 101 $\mu\text{g l}^{-1}$ ($29 \pm 30 \mu\text{g l}^{-1}$) in Tachick Lake from May 1997 to February 1998 (Fig. 2a). In Nulki Lake, [Chl *a*] were low from May to mid-July (6–27 $\mu\text{g l}^{-1}$) and from late October to February (1–11 $\mu\text{g l}^{-1}$). Maxima in Nulki Lake (71–112 $\mu\text{g l}^{-1}$) occurred between late July and early October with brief minima occurring in mid-August (35 $\mu\text{g l}^{-1}$) and mid-September (19 $\mu\text{g l}^{-1}$; Fig. 2a). Similarly, [Chl *a*] in Tachick Lake were low in May and June (5–14 $\mu\text{g l}^{-1}$) and from late October to February (< 1–14 $\mu\text{g l}^{-1}$), with maxima (83–101 $\mu\text{g l}^{-1}$) occurring between mid-July and mid-September (Fig. 2a). Distinct minima also occurred in Tachick Lake in mid-August and mid-September (Fig. 2a).

Chlorophyll *a* concentrations in Tabor Lake were also consistently highest during the late summer and early autumn, and lowest during the late autumn (mid-November) through winter

(December–March) when the lake was frozen over (Fig. 3a). While [Chl *a*] in Tabor Lake were generally low in May through mid-July, a minor bloom sometimes occurred in early May shortly after ice off (Fig. 3a). Late summer/early autumn blooms in Tabor Lake were considerably less intense than those in Nulki and Tachick lakes, with [Chl *a*] ranging from $11 \pm 7 \mu\text{g l}^{-1}$ in 2000 to $25 \pm 20 \mu\text{g l}^{-1}$ in 1994.

Chlorophyll *a* seasonality in Charlie Lake was similar to that in the more southern lakes. Maxima ($93 \pm 70 \mu\text{g l}^{-1}$) consistently occurred during the late summer and early autumn, with [Chl *a*] being lowest from January to April ($4 \pm 3 \mu\text{g l}^{-1}$) and from October to December ($23 \pm 17 \mu\text{g l}^{-1}$; Fig. 3a). As in Tabor Lake, minor blooms sometimes occurred in Charlie Lake shortly after ice off (Fig. 3a). The highest [Chl *a*] observed in Charlie Lake ($235 \mu\text{g l}^{-1}$) was considerably higher than that observed in Nulki ($112 \mu\text{g l}^{-1}$), Tachick ($101 \mu\text{g l}^{-1}$), and Tabor ($67 \mu\text{g l}^{-1}$) lakes.

Chlorophyll *a* seasonality in the four B.C. study lakes coincided, in general, with the seasonality of [Tot-P], [Tot-P_{diss}], water temperature, and pH (Figs. 2, 3). Surface [Tot-P] and [Tot-P_{diss}] were consistently lowest during the early summer, late autumn, and winter, with concentration maxima occurring during the late summer and early autumn (Figs. 2b, 3b). Less pronounced surface [Tot-P] and [Tot-P_{diss}] maxima often occurred in Tabor and Charlie lakes in early May following ice off, with the timing of these maxima coinciding with the minor spring blooms described above (Fig. 3b). Surface temperatures were about 0°C during winter months, with spring warming beginning in May following ice off (Figs. 2c, 3c). Temperatures were highest (about 20°C) in July and August with autumn cooling starting in early September. Minor spring blooms in Tabor and Charlie lakes coincided with warming spring temperatures, with major late summer/autumn blooms in all four lakes occurring when summer

Fig. 2 Seasonal trends (at surface and bottom) in Nulki (left panels) and Tachick (right panels) lakes from May 1997 to March 1998: (a) [Chl *a*], (b) [Tot-P], (c) temperature, and (d) pH. Data are averages of measures taken at the east and west sampling sites (Fig. 1a, b). [Tot-P_{diss}] data are not shown

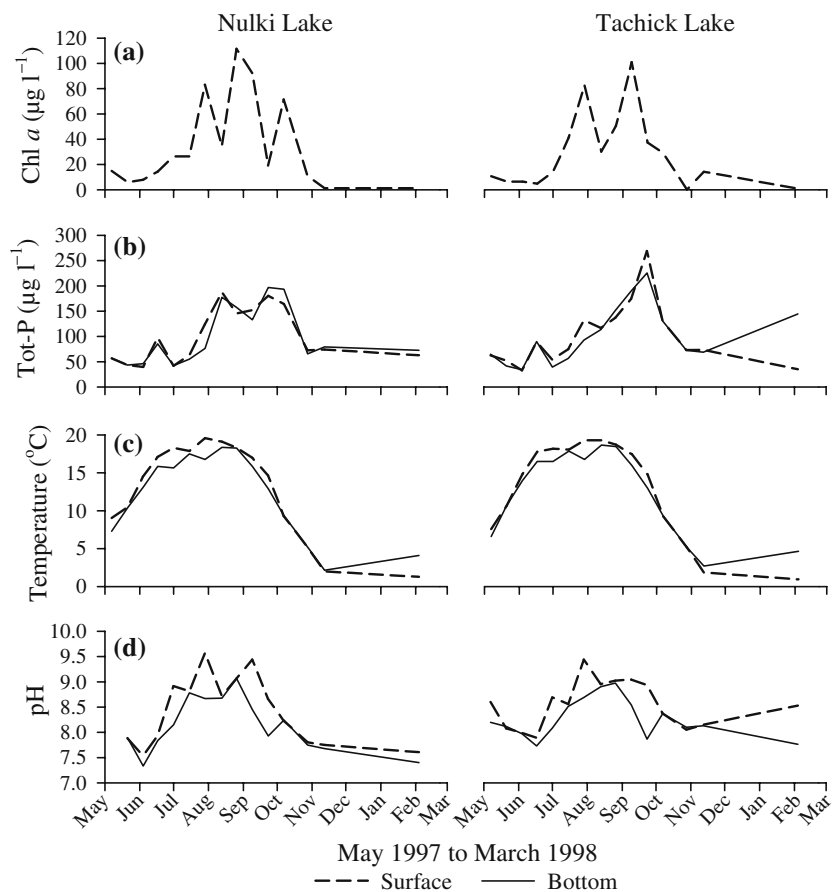
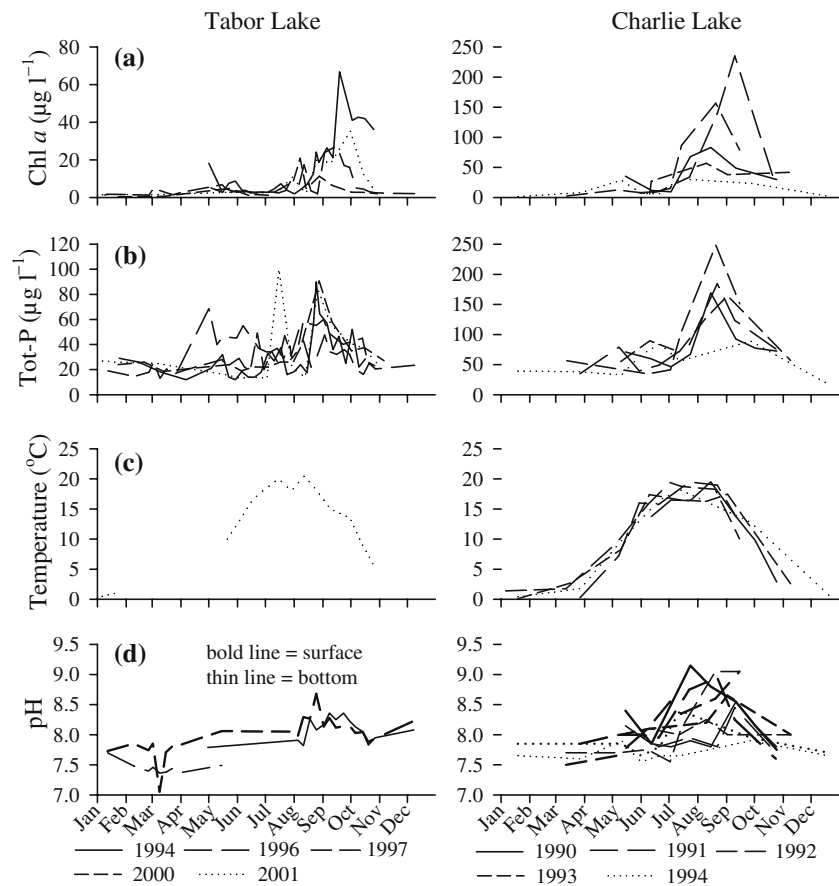


Fig. 3 Seasonal trends (at surface) in Tabor (left panels) and Charlie (right panels) lakes over 5-year periods: **(a)** [Chl *a*], **(b)** [Tot-P], **(c)** temperature, and **(d)** pH. Data for Charlie Lake are averages observed at the north and south sampling sites (Fig. 1d). [Tot-P_{diss}] data are not shown



temperatures were highest (Figs. 2a,c, 3a,c). Surface pH was 7.5–8.5 during the late autumn, winter, and spring when [Chl *a*] were low, and up to 9.5 during late summer/early autumn blooms (Figs. 2d, 3d).

Chl *a* correlates

Regression analysis of combined data from Dillon & Rigler (1974), Prepas & Trew (1983), and Ostrofsky & Rigler (1987) confirmed that spring [Tot-P] is a strong predictor of average summer [Chl *a*] in temperate North American lakes over a large geographic range, such that (Fig. 4):

$$\text{Avg. summer [Chl } a] = 1.31 [\text{sp. Tot-P}] - 1.03, \quad (r^2 = 0.78, P < 0.001) \quad (1)$$

where [Chl *a*] and [sp. Tot-P] are $\log \mu\text{g l}^{-1}$. Nine spring [Tot-P] versus average summer [Chl *a*] pairs were available for the B.C. lakes. Of these,

six [Chl *a*] estimates fell within the 95% C.I. of the model (Eq. 1), with one falling on and two immediately above the upper C.I. (Fig. 4). Therefore, the best-fit model combining data from the B.C. lakes with those from the other lake groups was almost identical to Eq. 1:

$$\text{Avg. summer [Chl } a] = 1.35 [\text{sp. Tot-P}] - 1.06, \quad (r^2 = 0.77, P < 0.001). \quad (2)$$

Although spring [Tot-P] is a strong predictor average summer [Chl *a*] in temperate North American lakes, [Chl *a*] in the B.C. lakes at any given time (instantaneous) were not strongly correlated with [Tot-P]. Regressions of $\log [\text{Chl } a]$ versus $\log [\text{Tot-P}]$ showed that [Tot-P] accounted for 36–49% of within-lake variations in [Chl *a*], with [Tot-P_{diss}] accounting for less of the variation (4–17%). Surface temperature alone was also a good predictor of instantaneous within-lake

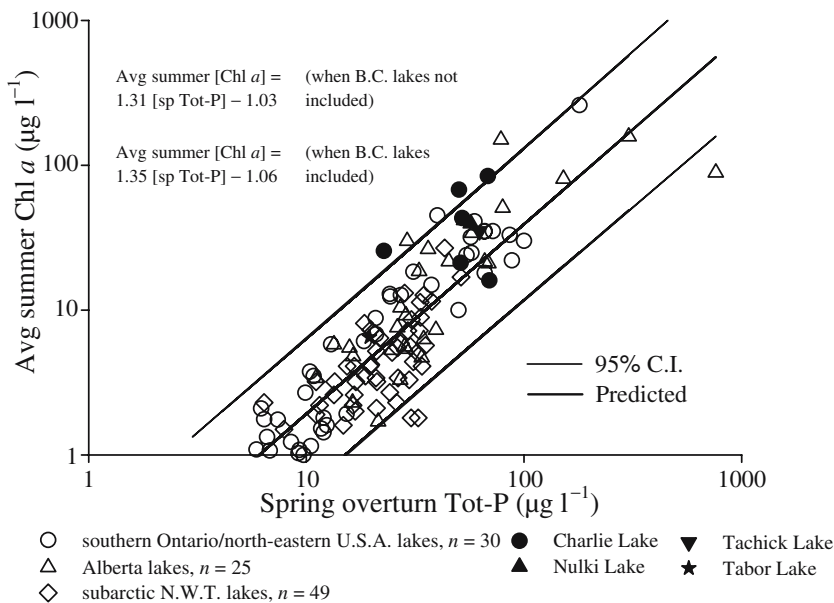


Fig. 4 Average summer [Chl *a*] (at surface) in relation to spring overturn [Tot-P] across four regions of temperate North America: (1) north-central B.C. (i.e., lakes from the present study—Nulki, Tachick, Tabor, and Charlie lakes), (2) southern Ontario/north-eastern USA (Dillon & Rigler,

1974), (3) Alberta (Prepas & Trew, 1983), and (4) subarctic N.W.T. (Ostrofsky & Rigler, 1987). Prediction and 95% C.I. lines do not incorporate data from the B.C. lakes. See Eqs. 1, 2 in text for statistical significance

[Chl *a*], accounting for 22–57% of within-lake variations. Combined data for the four B.C. lakes yielded the following univariate models based on instantaneous surface [Tot-P] and temperature (Fig. 5a, b):

$$\text{Log [Chl } a] = 1.30 (\text{log [Tot-P]} - 1.22) \quad (3)$$

$(r^2 = 0.45, P < 0.001)$

$$\text{Log [Chl } a] = 0.056 (^\circ\text{C}) + 0.438 \quad (4)$$

$(r^2 = 0.35, P < 0.001)$

where measures of [Chl *a*], [Tot-P], and temperature are taken concurrently at any time of the year, including winter. Substituting [Tot-P] in Eq. 3 with [Tot-P_{diss}] resulted in a model accounting for only 18% of among-lake variations in [Chl *a*]. Multivariate regression models incorporating both surface [Tot-P] and temperature accounted for a higher proportion (57–70%) of within-lake variations in [Chl *a*] ($P < 0.008$) on an instantaneous basis. Combining data for the four study lakes yielded the following model based on surface [Tot-P] and temperature combined (Fig. 6):

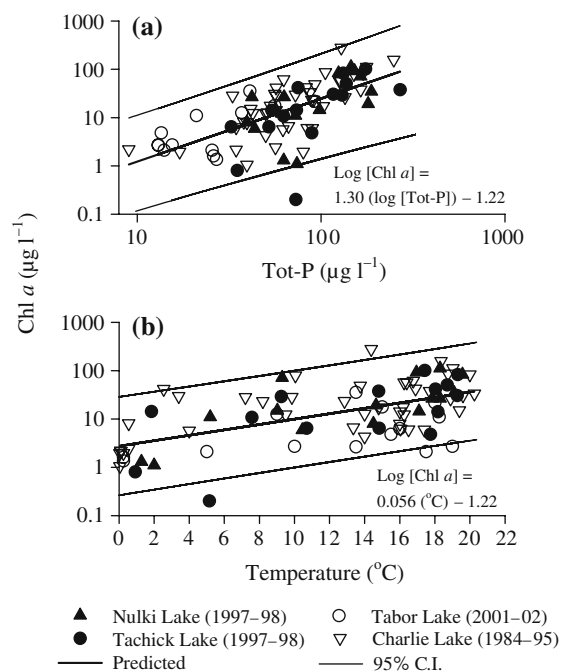


Fig. 5 Instantaneous [Chl *a*] (at surface) in the four B.C. study lakes in relation to concurrent measures of (a) [Tot-P] and (b) water temperature. All seasons, including winter, are represented by the data points. See Eqs. 3, 4 in text for statistical significance

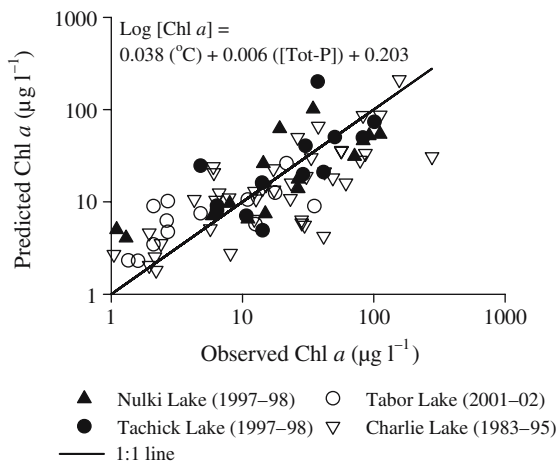


Fig. 6 1:1 line for model predicting instantaneous [Chl *a*] (at surface) in the four B.C. study lakes from [Tot-P] and water temperature combined. All seasons, including winter, are represented by the data points. See Eq. 5 in text for statistical significance

$$\text{Log [Chl } a] = 0.038 (^\circ\text{C}) + 0.006 ([\text{Tot-P}]) + 0.203$$

$$(r^2 = 0.57, P < 0.001). \quad (5)$$

Thus, while average summer [Chl *a*] in North American temperate lakes can be predicted reasonably well from spring [Tot-P] alone (Eqs. 1, 2), Eqs. 3–5 indicate that both [Tot-P] and temper-

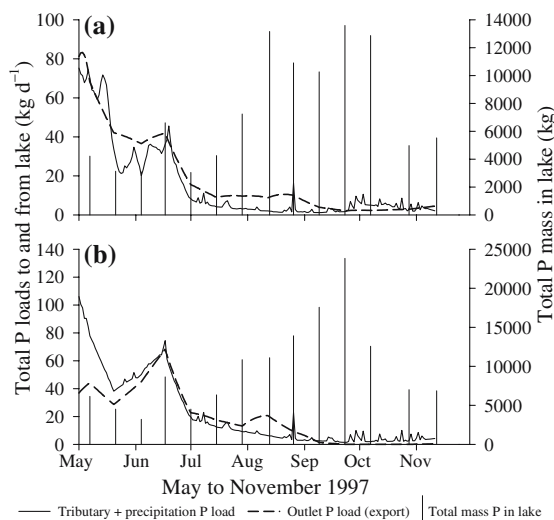


Fig. 7 External P loading (tributary + atmospheric) and P export (outlets) rates in relation to total P mass in the lakes over the period May 1997 to November 1997: (a) Nulki Lake and (b) Tachick Lake

ature are important determinants of [Chl *a*] on an instantaneous basis.

P loading and vertical gradients

Phosphorus concentrations in Nulki and Tachick lakes were highest several weeks after the period of maximum external loading (Figs. 2b, 7), indicating that loads associated with summer and autumn [Chl *a*] maxima came mostly from within-lake sources. In agreement, computations based on differences between external P loads to the lakes and export via outlets indicated that 97% of the P entering Nulki (12,382 kg P) and Tachick (17,694 kg P) lakes during late summer/early autumn blooms came from within-lake sources (Fig. 7). Nulki and Tachick lakes were isothermal throughout the May–November ice-free period (Fig. 2c). Reflecting this, [Tot-P] and [Tot-P_{diss}] were uniform from surface to bottom in both lakes during ice-free seasons, including the period between mid-July and early October when internal loading rates were highest (Figs. 2b, 7). Similarly, [O₂] showed little surface to bottom variation during ice-free seasons and were typically > 7 mg l⁻¹ in all strata. pH in Nulki and Tachick lakes was constant from surface to bottom during open-water periods when [Chl *a*] were low; however, surface pH was typically 0.5–1.0 units higher than bottom pH during [Chl *a*] maxima (Fig. 2d). Nulki and Tachick lakes were inversely stratified and anoxic below 5-m depth during the winter when they were frozen over. During winter, [Tot-P] and [Tot-P_{diss}] in Tachick Lake were about 3-fold higher in the anoxic strata (140 and 80 µg l⁻¹, respectively) than at the surface (40 and 30 µg l⁻¹); however, vertical concentration gradients in Nulki Lake were negligible (Fig. 2b).

The high surface [Tot-P] and [Tot-P_{diss}] associated with late summer/early autumn blooms in Tabor Lake also occurred when little water was entering the lake via surface runoff, with this similarly suggesting that bloom-triggering loads originated from within-lake sources. Like Nulki and Tachick lakes, Tabor Lake was inversely stratified during the winter months, with [O₂] declining rapidly with increasing depth below 5-m (Fig. 8a). During winter, [Tot-P] and [Tot-P_{diss}]

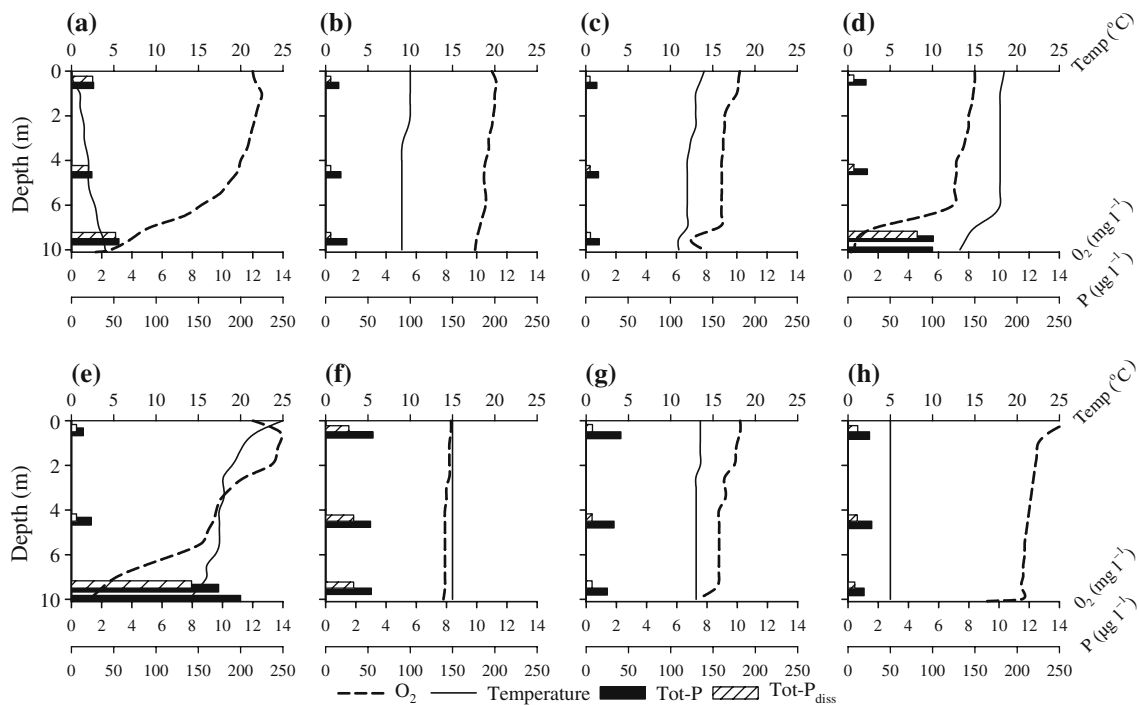


Fig. 8 Seasonality of temperature, $[O_2]$, $[Tot-P]$, and $[Tot-P_{diss}]$ profiles in Tabor Lake from January 2001 to October 2001: (a) winter (January 21), (b) spring (May 21), (c) early

summer (June 3), (d) summer (July 29), (e) summer (August 12), (f) early autumn (September 9), (g) mid-autumn (September 30), and (h) late autumn (October 28)

were typically 2-fold higher at the bottom than at the surface and mid-depth (Fig. 8a). Spring turnover in Tabor Lake typically occurred in early to mid-May, with mixing creating isothermal conditions (Fig. 8b). Presumably, spring turnover would have mixed P-enriched bottom waters with relatively dilute surface waters; however, spring mixing only resulted in a slight increase in surface concentrations (Fig. 8c). Unlike Nulki and Tachick lakes that were isothermal and well oxygenated through open-water seasons, Tabor Lake typically started to develop a thermocline in early June (Fig. 8). During summer stratification, Tabor Lake was often anoxic below 8-m depth, with $[Tot-P]$ and $[Tot-P_{diss}]$ in these strata being several-fold greater than those in mid-depth and surface strata (Fig. 8d,e). With autumn cooling, thermal stratification in Tabor Lake was lost in late August or early September (Fig. 8f). Late summer/early autumn thermocline breakdowns mixed P-enriched deep strata with more-dilute surface strata and this, unlike the result observed

during spring overturn, resulted in substantial P enrichment of the photic zone (Fig. 8f, g). As in Nulki and Tachick lakes, surface pH in Tabor Lake was elevated (> 8.2) during the late summer/early autumn when $[Chl a]$ were highest, and lowest (< 7.8) during the remainder of the year when $[Chl a]$ were low (Fig. 3d). pH was also slightly elevated in bottom strata during late summer/early autumn blooms (Fig. 3d).

Vertical gradients in Charlie Lake were similar to those in Tabor Lake, such that anoxic conditions developed in deep strata during winter and summer stratified periods with Tot-P and Tot-P_{diss} accumulating in these strata (Fig. 9). The main difference between Charlie and Tabor lakes was that stratification in Charlie Lake was unstable during summer with summer mixing sometimes resulting in isothermal conditions. As in the other lakes, surface pH in Charlie Lake was highest when $[Chl a]$ were highest, with pH in bottom strata also being slightly elevated during late summer/early autumn blooms (Fig. 3d).

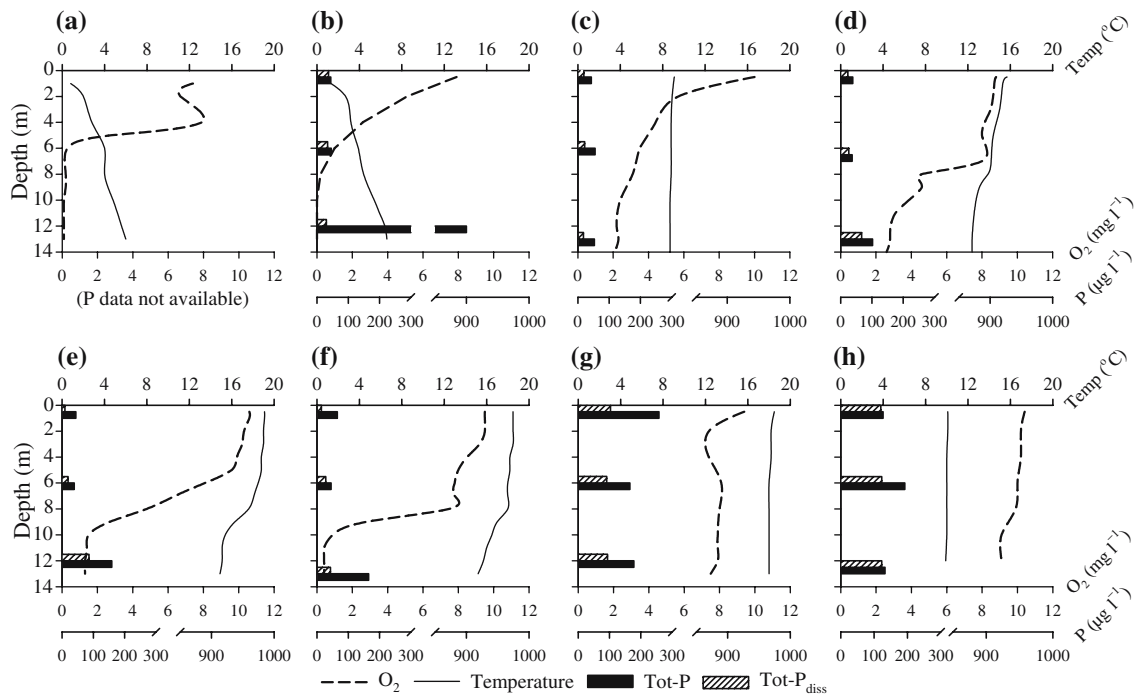


Fig. 9 Seasonality of temperature, $[O_2]$, $[Tot-P]$, and $[Tot-P_{diss}]$ profiles in Charlie Lake from January 1992 to September 1992: (a) winter (January 6), (b) late winter (March 12), (c) spring (May 6), (d) early summer (June 8),

(e) mid-summer (July 2), (f) mid-summer (July 14), (g) late summer (August 20), and (h) early autumn (September 15). Data shown are from the north deep site (Fig. 1d)

Discussion

Models predicting average summer $[Chl a]$ from spring $[Tot-P]$ (e.g., Dillon & Rigler, 1974; Prepas & Trew, 1983; Ostrofsky & Rigler, 1987) are often used by lake and watershed managers to develop lake-specific P loading objectives, to monitor long-term water quality trends, and to evaluate actions taken to control cultural eutrophication. The models are particularly useful because they are simple yet reliable, cost effective (i.e., based on only two parameters), and applicable over a large geographic range (Fig. 4; Eqs. 1, 2). In theory, they apply to temperate lakes in which bloom dynamics during open-water seasons are controlled by P that enters the water column during spring. Although bloom dynamics in the B.C. lakes were controlled by P internally loaded during summer and autumn (Figs. 7–9), average summer $[Chl a]$ in the lakes were predicted reasonably well by a spring- $[Tot-P]$ model based on three lake groups (Fig. 4; Eq. 1).

Total phosphorus concentration was not an exceptionally strong predictor ($r^2 = 0.45$) of $[Chl a]$ in the B.C. lakes on an instantaneous basis (Fig. 5a; Eq. 3). However, models incorporating both $[Tot-P]$ and temperature accounted for 57–70% of within-lake variations in $[Chl a]$ on an instantaneous basis. This correlation was also significant when data for the four lakes were pooled, such that surface $[Tot-P]$ and temperature combined accounted for nearly 60% of $[Chl a]$ variations in the lakes as a group (Fig. 6; Eq. 5). Phosphorus is an important determinant of $[Chl a]$ in temperate lakes because it is a growth-limiting essential nutrient (Schindler, 1977), and the positive association between temperature and $[Chl a]$ was likely due to increased growth-associated enzyme activity at warmer temperatures (Markager et al., 1999). Collos et al. (2005) similarly found that phytoplankton growth rates in a Mediterranean coastal lagoon increased with increasing temperature over the range 6–26°C, but that zooplankton grazing rates decreased over

this range. Thus, the positive association between [Chl *a*] and temperature could be partly due to decreases in grazing-related Chl *a* losses at warmer temperatures.

The importance of water temperature as a determinant of [Chl *a*] has also been shown over large latitudinal scales, such that Flanagan et al. (2003) observed that average concentrations during ice-free seasons decreased with increasing latitude in a survey of 269 lakes ranging from 41°N (temperate) to 79°N (Arctic). They concluded that these latitudinal differences were more strongly associated with differences in temperature than with spatial differences in nutrient availability and trophic structure. Positive associations between instantaneous [Chl *a*] and water temperature in the B.C. lakes (Fig. 5b) support climate change models that forecast changes in phytoplankton productivity even if nutrient loading rates remain constant. Thus, the incorporation of temperature as a variable in regional climate models for lakes in the United Kingdom (UK) resulted in predictions of increased spring [Chl *a*] under projected climate warming scenarios; conversely, such models have forecasted reduced [Chl *a*] during autumn because elevated spring productivity could reduce nutrient availability in autumn (Elliott et al., 2005).

Despite differences in O₂ and P dynamics in Nulki and Tachick lakes (well oxygenated, vertical [P] gradients negligible), and Tabor and Charlie lakes (hypolimnetic O₂ deficits/P accumulations) during open-water seasons, Chl *a* seasonality was similar in the four lakes (Figs. 2, 3). Differences in vertical [O₂] and [P] gradients among the lakes were reflective of differences in thermal stability, with Nulki and Tachick lakes being isothermal through much of the open-water season, Charlie Lake being intermittently stratified, and Tabor Lake being almost always stratified. Differences in thermal stability during open-water seasons are probably reflective of morphometric differences, such that the relative depths of Nulki (0.17%) and Tachick (0.14%) lakes provide little resistance to mixing, with those of Charlie (0.25%) and Tabor (0.40%) lakes providing some and moderate, respectively, resistance to mixing (see Table 1 for definition

of relative depth). The east–west orientations of Nulki and Tachick lakes and flat watershed topography makes them particularly susceptible to wind-induced mixing.

Chlorophyll *a* concentrations in the B.C. lakes were consistently highest during the late summer/early autumn, and lowest during the late autumn, winter and early summer (Figs. 2a, 3a). Data from Tabor and Charlie lakes also indicate that lakes in the region can have comparatively minor blooms during the spring following ice off (Fig. 3a). Seasonality in the four B.C. lakes was similar to that described for other temperate lakes having very different morphometric characteristics, watershed geologies/soils, trophic structures, and land uses. For example, Munawar & Munawar (1986) showed that spring and late-summer [Chl *a*] maxima regularly occur in the Laurentian Great Lakes (Ontario), which are orders of magnitude larger and deeper than the B.C. lakes and considerably different with respect to trophic structure and watershed development. Hecky et al. (1986) described a similar bloom periodicity in two very large, but shallow, multi-basin lakes in Manitoba (Lake Winnipeg and southern Indian Lake). Chlorophyll *a* maxima in Shagawa Lake (Minnesota), a lake being similar in length to Nulki and Tachick lakes but considerably deeper, consistently occur in late August/early September with concentrations typically declining sharply shortly following blooms (Megard & Smith, 1974) as observed in our study lakes (Fig. 2a). Schindler (1977) showed that *Aphanizomenon* blooms typically occur during the late summer/early autumn in Canadian Shield lakes which are much less productive than interior B.C. lakes, and Lund (1955) showed that diatom blooms typically occur during spring in the UK.

Late summer/autumn blooms in the four B.C. lakes were triggered by internally loaded P, but profile data suggest that internal loading mechanisms were variable among the lakes. Deep strata in Tabor and Charlie lakes were anoxic during winter and summer stratified periods (Figs. 8, 9). The accumulation of P in anoxic strata during stratified periods was likely the result of redox-mediated P dissolution from profundal sediments (Mortimer, 1971; Larsen et al., 1981; Nürnberg, 1984; Carignan & Lean, 1991). Supporting this,

Petticrew & Arocena (2001) used Tabor Lake bottom water and sediment geochemistry to model redox processes and determined that iron phosphate dissolution during anoxia generated high concentrations of dissolved P. Phosphorus-rich bottom waters in Tabor and Charlie lakes mixed through the water column during the late summer/early autumn when thermal stratification was disrupted (Figs. 8, 9), and this enrichment at the surface was consistently associated with major blooms. The ecological significance of internal P-loading has also been demonstrated for Chesapeake Bay (Virginia/Maryland) where up to 74% of phytoplankton P demands are supplied by sediments (Cowan & Boynton, 1996), in the relatively small and shallow Halfmoon and Nakamun lakes (Alberta) where sediments were shown to contribute nearly 1,500 and 150 kg Tot-P, respectively, to the water column during anoxic periods (Riley & Prepas, 1984), in Shagawa Lake (Minnesota) where half of the annual P supply (2,000–3,000 kg) to the water column is from bottom sediments (Larsen et al., 1981), and in Lake Washington (Washington) where up to 95% of phytoplankton P demands are provided by within-lake sources (Lehman, 1980).

In comparison, Nulki and Tachick lakes were isothermal during open-water seasons, with vertical $[O_2]$ gradients being negligible; thus, conditions in the lakes should not have supported high rates of redox-mediated P dissolution from bottom sediments. In situ and laboratory experiments by Jacoby et al. (1982), Jensen & Andersen (1992), Olila & Reddy (1995), Koski-Vähälä et al. (2001), and Macedo et al. (2001) demonstrated that P is released from sediments under aerobic conditions when pH is > 9 and when water overlying sediments is warmer than about 15°C. Hydroxyl ions in alkaline waters compete with $H_2PO_4^-$ for exchange sites on sediments, and warm temperatures hasten the decomposition of P-containing organics (Andersen, 1975; Kamp-Nielsen, 1975; Jacoby et al., 1982; Jensen & Andersen, 1992; Koski-Vähälä et al., 2001). Thus, the warm temperatures (up to 20°C) and high pHs (> 9) observed from surface to bottom in Nulki and Tachick lakes during the summer (Fig. 2c, d) could have promoted P release from bottom sediment despite the oxidising conditions. Elevated

pHs in the B.C. lakes during the late summer/autumn (Figs. 2d, 3d) were presumably the result of intense photosynthesis (Andersen, 1974; Jacoby et al., 1982; Søndergaard, 1988). The production of OH^- during photosynthesis probably accelerates P dissolution from bottom sediments and this would, in turn, promote more phytoplankton growth—i.e., a “feed back” loop linking phytoplankton P demands to P dissolution from bottom sediments.

Although we suspect that bottom sediments are a major source of P in the B.C. lakes during summer and autumn, rooted macrophyte decomposition and translocation might contribute to seasonal P loads. Nulki, Tachick, and Tabor lakes have extensive macrophyte beds that grow to the surface and often extend > 100 m from shore (T. French, unpubl. observation). Jacoby et al. (1982) showed that macrophyte decomposition in Long Lake (Washington) contributes 200–400 kg P to the water column during winter months, with this equating to 25–50% of the total external load. Simmons (1997) reported that macrophyte decomposition in Tabor Lake contributed 1,958 kg P to the water column (44% of total load) during the spring through early autumn 1995, with up to 52% of the P load being contributed by bottom sediments. Although macrophyte decomposition/translocation in Nulki and Tachick lakes might also contribute significant P loads, macrophyte-associated loads to Charlie Lake would be minimal because the lake’s macrophyte community is very sparse (T. French, unpubl. observation). Given the number of alternate P releasing processes, it is likely that periods of rapid internal P loading in Nulki, Tachick, and Tabor lakes would occur even if their extensive macrophyte beds did not exist.

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