

Variation in temporal [^{14}C]plankton photosynthesis among warm monomictic lakes of coastal British Columbia

JOHN-MARK DAVIES*, WESTON H. NOWLIN AND ASIT MAZUMDER

WATER AND WATERSHED RESEARCH PROGRAM, DEPARTMENT OF BIOLOGY, UNIVERSITY OF VICTORIA, PO BOX 3020 STN CSC, VICTORIA, BC V8N 3N5, CANADA

*CORRESPONDING AUTHOR: jmdavies@uvic.ca

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*Seasonal patterns of [^{14}C]phytoplankton photosynthesis (PP) were examined in six warm monomictic lakes of coastal British Columbia. Four of our study lakes followed typical lake patterns with maximum PP occurring in the spring and minimal rates occurring during the winter. However, the spring maximum occurred several weeks earlier than lakes in other climatic regions. In addition, maximum rates of daily photosynthesis were observed to occur during the winter months in Maxwell Lake, rather than during the standard growing season. All study lakes except Maxwell Lake had large *Daphnia* in the plankton community. Maxwell was dominated by small crustacean zooplankton implying the importance of trophic structure in mediating seasonal patterns of productivity. The four oligotrophic lakes in our study also exhibited P-deficiency during winter, as indicated by P-debt bioassays and rapid $^{32}\text{PO}_4^{3-}$ turnover rates. Our data suggest that these coastal oligotrophic lakes were co-limited by nutrients and light during winter. The importance of winter (November–March) photosynthetic production to the total annual carbon budget in the six lakes studied here is greater than that typically reported for other temperate zone lakes. If plankton community respiration decreases more than photosynthetic production with wintertime temperatures, then >50% of annual net pelagic carbon fixation could occur in winter in some coastal lakes.*

INTRODUCTION

Factors that limit phytoplankton photosynthesis (PP) commonly include light (photosynthetically available radiation or PAR), temperature (Kirk, 1994) and nutrients (Schindler, 1977). Zooplankton grazing can also influence photosynthetic production (Pace, 1984; Perin *et al.*, 1996). Seasonally these factors vary greatly in north temperate lakes and typically PP is low during winter, increases in the spring, is high in the summer, and declines in autumn (Alvarez-Cobelas and Rojo, 1994; Wetzel, 2001). In ice-covered lakes ~10% of annual areal PP occurs under ice [range 2% to >30% (Alvarez-Cobelas and Rojo, 1994)]. Nutrients and grazing are thought to be the principal factors limiting production during the summer, while PAR and temperature are considered most important during winter months. Quantifying and interpreting seasonal variations of PP rates (Fee *et al.*, 1992) and photosynthetic parameters (Wetzel, 2001; Knoll *et al.*, 2003) are critical for evaluating lake energetics.

There is growing appreciation of the photosynthetic contribution made by phytoplankton growing under low light conditions, especially at the interface between nutrient-replete and nutrient-depleted water (Goldman and McGillicuddy, 2003). Planktonic photosynthesis resulting from imported nutrients has received special attention because it is considered to represent ‘new’ production (Dugdale and Goering, 1967; Eppley and Peterson, 1979). New production occurs in zones of upwelling or mixing and the ratio of ‘new’ versus ‘old’ (recycled nutrient driven) production varies seasonally. For example, Brooks and Edgington (Brooks and Edgington, 1994) found that PP peaked during spring isothermal conditions in Lake Michigan and that this was also an important time of new production.

Coastal lakes of British Columbia (BC) often exhibit elevated chlorophyll *a* (Chl *a*) concentrations during winter (see Results). Despite occurring in several countries (e.g. Canada, Chile, Norway) temperate coastal lakes have been the subject of fewer seasonal PP studies

than have temperate dimictic lakes. The lack of permanent ice cover results from relatively mild air temperatures that typically do not remain below zero during the diurnal cycle. Thus, these lakes are best classified as being warm monomictic lakes (Stockner and Shortreed, 1985). The lack of permanent ice cover means that PAR is not attenuated to the same extent as in ice-covered lakes at a similar latitude. However, similar seasonal changes in both PAR and temperature offer an opportunity to study their relative importance on plankton photosynthesis among lakes, and to examine which factors control photosynthesis during winter months in warm monomictic lakes.

Two physiologically important parameters define the relationship between photosynthesis and light: α^B and P_m^B ; α is the initial slope of the photosynthesis–irradiance (P–E) curve, P_m is the maximum rate of photosynthesis, and the superscript B indicates that each parameter is biomass-corrected for Chl *a* (Fee, 1990; Kirk, 1994). At saturation (P_m^B) the rate of photosynthesis is limited by enzymatic activity (carboxylation enzymes) so, at a physiological level, the same saturating PAR will have a correspondingly smaller P_m^B at lower temperatures (Stemann Nielsen and Jørgensen, 1968). α^B represents the PAR-limited portion of photosynthesis, and in this region of the P–E curve cells have sufficient carboxylation enzymes. Therefore, temperature has much less effect on α^B than it does on P_m^B . Thus, during winter months, lower temperatures ($\sim 4^\circ\text{C}$) should depress P_m^B and limit areal PP. Kirk (Kirk, 1994) hypothesized that low PAR during the winter is less important because it affects a smaller portion of the P–E curve. The ratio of P_m^B to α^B is known as E_k and is a useful parameter for examining seasonal changes of photosynthesis parameters. During winter, P_m^B should decrease, while α^B should increase due to the decrease in available PAR (Kirk, 1994). Under such conditions E_k will be smallest when temperature and light are low, which can make it difficult to differentiate which factor is of greater importance.

Algal physiological studies (i.e. culture studies) are vital to our understanding of organism response to factors that can limit production (e.g. α^B , P_m^B). However, ecological studies (i.e. field studies) offer the opportunity to examine how communities respond to changes in growth conditions and offer insight into how communities compensate for these changes. In temperate lakes, temperature and PAR co-vary and nutrient availability and zooplankton grazing rates change seasonally. The seasonal temperature cycle of coastal BC lakes examined by this study is similar to that of lakes with permanent winter ice cover and therefore offered the opportunity to examine the interaction of variables controlling plankton photosynthesis.

The overall goal of this study was to improve our understanding of seasonal carbon dynamics in coastal BC lakes. Specifically, we examined the relative importance of light and temperature during winter months to test the hypothesis that temperature plays a direct role in limiting ecosystem pelagic photosynthesis (Kirk, 1994). We compare the results with published patterns of PP to determine both how PP seasonal trends in BC coastal lakes compare with other temperate lakes and how PP rates match total phosphorus (TP) models. The objectives were (i) determine the relative importance of annual ^{14}C -fixation during winter, (ii) examine the roles of temperature and light on PP during winter, (iii) examine the seasonal variability of ^{14}C PP and photosynthetic parameters, and (iv) examine other lake processes, including nutrient deficiency and grazer community structure to determine if these influence ^{14}C PP among lakes.

METHOD

Study lakes, field sampling

^{14}C PP was measured on epilimnetic and metalimnetic water samples from six coastal British Columbia lakes. Council Lake (COL), Elk Lake (ELL), Shownigan Lake (SHL) and Sooke Lake Reservoir (SOL) are located near the southern end of Vancouver Island, and Cusheon Lake (CUL) and Maxwell Lake (MXL) are on Saltspring Island (Figure 1). Surface area ranged from 16 to 605 ha and maximum depth from 9.5 to 70 m [Table I (Spafard *et al.*, 2002)]. All the lakes are soft-water, with near-neutral pH and average annual dissolved inorganic carbon (DIC) ranging from 313 to 1057 $\mu\text{mol L}^{-1}$ and average dissolved organic carbon (DOC) $<5.6 \text{ mg L}^{-1}$ (Table I). Flushing rates vary from <1 year to ~ 4.5 years (Table I). Based on Chl *a*, TP and ^{14}C PP the lakes were classified as being oligotrophic to mesoeutrophic (Table I). COL, MXL, SHL and SOL are considered oligotrophic, although MXL has greater temporal change in classification than do the other lakes and might be considered oligo-mesotrophic during winter and spring—up to the onset of stratification. CUL and ELL are best described as being mesotrophic to mesoeutrophic.

Lake water samples were collected at the point of maximum depth in each lake with either a 6 m integrated tube (epilimnion) or a vertically oriented Niskin bottle (metalimnion). Epilimnetic samples were taken from the surface to the depth where temperature changed by $>1^\circ\text{C m}^{-1}$, or if the epilimnion was >5.5 m, then integrated samples were taken to a depth of 5.5 m. Metalimnetic samples were taken near the middle of the metalimnion at the point of maximum temperature change with depth. Water samples were taken in triplicate and immediately

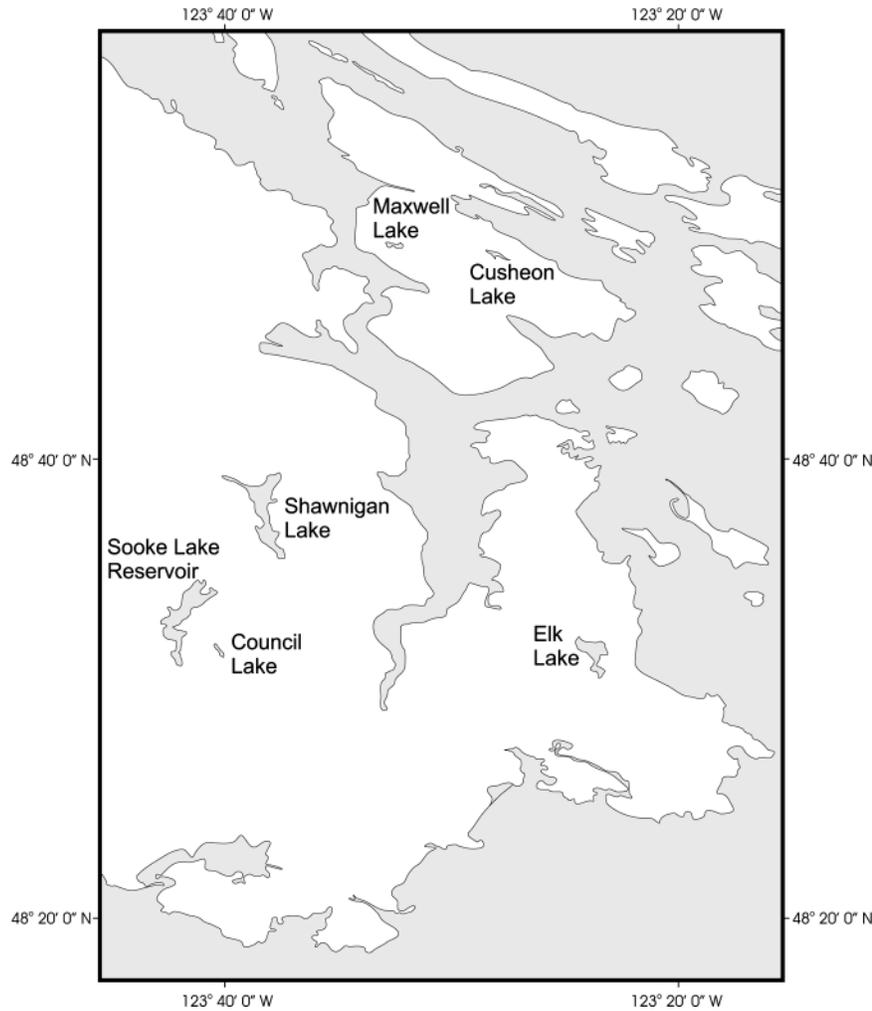


Fig. 1. Location of study lakes on Saltspring Island and southern Vancouver Island, British Columbia, Canada. Council Lake (COL), Cusheon Lake (CUL), Elk Lake (ELL), Maxwell Lake (MXL), Shawnigan Lake (SHL) and Sooke Lake Reservoir (SOL).

Table I: Lake characteristics and trophic classification categories based on Chl a, TP (total phosphorus) and PP (¹⁴C-primary productivity)

Lake	Z _{max} (m)	Z _{mean} (m)	1% Depth May-Oct. (m)	1% depth Jan.–Mar. (m)	DIC	DOC	Flushing rate (years)	Chl a	TP	PP
Council (COL)	17.0	5.2	16.6	9.0	346	2.3	<1	O	UO	O
Cusheon (CUL)	9.5	4.4	6.5	4.8	591	5.4	1.5	O ^a	E	M
Elk (ELL)	19.4	7.7	9.1	7.7	1075	5.6	4.5	M	M-E	M-E ^b
Maxwell (MXL)	17.0	6.5	8.6	7.2	313	4.4	1.5	O ^c	O-M	O ^c
Shawnigan (SHL)	53.0	13.0	11.2	8.4	369	3.1	<1	O	O	O
Sooke (SOL) ^d	70.0	19.5	13.9	11.4	354	2.1	<1	O	UO	O

1% PAR compensation depths (m) are averages from May to October and January to March respectively. Average DIC (dissolved inorganic carbon) is in units of $\mu\text{mol L}^{-1}$, and DOC (dissolved organic carbon) is in units of mg L^{-1} . Average flushing rates are from previous reports (Nordin *et al.*, 1982; McKean, 1992; Holms, 1999; Nowlin *et al.*, 2004). Flushing rate for COL calculated from precipitation and watershed area. For trophic categories: UO = ultraoligotrophic, O = oligotrophic, M = mesotrophic, M-E = meso-eutrophic and E = eutrophic. Noticeable temporal deviations in trophic classification are noted below. Trophic classification follows (Wetzel, 1983). Morphometric data from Spafard *et al.* (Spafard *et al.*, 2002). ^aM in September. ^bE in April. ^c(Chl a) M-E in October–April; (PP) M in February. ^dDue to changes in dam height, SOL depth values are valid from 1989 until winter 2003.

placed in opaque Nalgene containers and stored in coolers until laboratory processing later the same day. A Li-Cor 2π quantum sensor (Li-Cor LI-192SA) was used to measure light extinction (k_d) of PAR ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) on each sampling date. PAR measurements were made at least every meter to a depth of ~7–9 m. To minimize changes in incident light affecting k_d , surface PAR was measured immediately prior to, and after profile measurements to ensure that incident light remained similar. Mean daily epilimnetic PAR values were calculated using the same formula as Guildford *et al.* (Guildford *et al.*, 2000) and were based on a 24 h time period to remove seasonal bias. The epilimnion for calculating mean PAR was defined as the shallower of the depths at which temperature changed by 1°C m^{-1} or the mean depth of the lake. Temperature profiles were obtained using a YSI model 58 temperature/oxygen meter.

Laboratory analyses

Chl *a* was determined in triplicate by filtration through GF/F filters (Whatman) and each sample was frozen until analysis. Chl *a* was extracted in 95% ethanol overnight at 4°C and read on a spectrophotometer using a 10 cm quartz cuvette. Chl *a* calculations were based on Wintermans and Mots (Wintermans and Mots, 1965). TP was measured as phosphate on a Lachat autoanalyzer (Zellweger Analytics, QuickChem 8000) after digesting unfiltered water with potassium persulfate in an autoclave. Alkalinity was determined in at least duplicate for each sampling date using Gran Titrations. DIC was calculated from alkalinity and pH. DOC was determined from water filtrate passed through ashed GF/F filters (Whatman), and measured on a Shimadzu analyser (TOC 5000) using the combustion/infrared technique.

Plankton photosynthesis determination

Methods used for determining [^{14}C]PP follow Fee (Shearer *et al.*, 1985; Fee *et al.*, 1989; Fee, 1990) with slight modifications. In a darkened room water from triplicate samples was pooled. $\text{Na}^{14}\text{CO}_3$ was added to 1.25 L of the pooled sample to a final activity of approximately 0.75 MBq per 1.25 L. The sample was gently mixed with a stirring bar and siphoned into nine (seven light and two dark bottles) 125 mL Pyrex glass bottles with ground glass stoppers. Dark bottles had aluminium foil sandwiched between 4–5 layers of black vinyl (Plasti Dip). Bottles were incubated across a light gradient in a flatbed incubator (Shearer *et al.*, 1985) at *in situ* water temperatures (crushed ice was added, when needed, to maintain constant incubator temperature). The light source was a 150 Watt high-pressure sodium vapor lamp. PAR at each bottle location for all incubations was measured with a 4π sensor (Li-Cor LI-193SA) approximately halfway

through the incubation period. On dates with metalimnetic samples, two incubators were used, one each for epilimnetic and metalimnetic samples. Incubations lasted 3 h. Immediately after incubations, 3 mL of sample was removed from three random bottles and placed in a scintillation vial with 150 μL of 3-methoxypropylamine (Fluka) as a CO_2 trapping agent. The average of these three samples was used to determine the available ^{14}C . From each bottle 30 mL was filtered through 0.45 μm membrane filters (Gelman). Samples were counted for at least 2 min with a precision of 95% in 10 000 disintegrations or for 50 min, whichever came first. Samples were counted on a Beckman LS6000IC scintillation counter. CPMs were converted to DPMs based on a standard curve. Light bottle DPM was corrected for average dark bottle fixation.

Photosynthesis rates were calculated using DIC, ^{14}C available and ^{14}C fixed with an isotopic correction factor of 1.06 (Shearer *et al.*, 1985). P–E parameters (α^B , P_m^B) were calculated using the computer program PSPARMS (Fee, 1990) and P–E curves were fitted using the following equation (Fee, 1990):

$$\text{If } E < \frac{E_k}{20} \text{ then PP} = 0$$

$$\text{If } E \geq 2E_k \text{ then PP} = B P_m^B$$

$$\text{Otherwise PP} = B \alpha^B E' \left[1 - \frac{E'}{4E_k} \right]$$

where E = irradiance (PAR) at a given depth, $E_k = P_m^B / \alpha^B$, $E' = E - E_k/20$ and B = biomass measured as Chl *a*.

Ambient surface PAR at the top of the SOL drinking water intake tower (within 40 km of all study lakes) was logged for the duration of this study (Li-Cor LI-90SZ sensor). Surface PAR for photosynthesis versus depth profiles was calculated using averages of surface PAR for the sampling date, the 3 days prior to and the 3 days after the sampling date. Lake PAR at 0.1 m intervals was calculated based on k_d and these 7-day PAR averages corrected for 6% surface reflectance. Areal [^{14}C]PP was calculated at 0.1 m intervals. Lake-wide annual estimates of areal PP were based on daily PAR measurements. Photosynthetic parameters (α^B , P_m^B), chlorophyll and epilimnetic/metalimnetic depths were linearly interpolated between sampling dates for these calculations. Lake-wide productivity was corrected for lake bathymetry (Spafard *et al.*, 2002). Literature data were digitized using the computer program Grafula 3 (ver. 2.10), and cross-correlation analysis was conducted using SPSS 10.

Nutrient deficiency

P-debt was used to assess the physiological status of phosphorus deficiency in the plankton community. The P-debt bioassay is based on chemostat and lake studies that have demonstrated that P-deficient plankton have a high capacity for phosphate uptake in the dark (Healey and Hendzel, 1979, 1980). Briefly, 100 mL of lake water were placed in an Erlenmeyer flask, Na_2HPO_4 was added to bring the concentration to $\sim 5 \mu\text{mol L}^{-1}$, and was incubated for 24 h in the dark. Immediately after adding phosphate, samples were gently stirred and three subsamples were taken. Using the ascorbic acid/molybdate method, subsamples were analyzed for PO_4^{3-} on a spectrophotometer (Stainton *et al.*, 1977). After the 24 h incubation PO_4^{3-} was again determined on three subsamples. Uptake rates were biomass corrected for Chl *a*. P-deficiency thresholds are assumed to be those given by Healey (Healey, 1975), Healey and Hendzel (Healey and Hendzel, 1979, 1980) and Guildford and Hecky (Guildford and Hecky, 2000).

$^{32}\text{PO}_4^{3-}$ turnover time was measured in a similar manner to Lean and White (Lean and White, 1983) and Mazumder *et al.* (Mazumder *et al.*, 1988). To 100 mL of lake water, carrier-free $^{32}\text{PO}_4^{3-}$ (Sigma-Aldrich) was added to a final activity of 0.9–3.2 kBq mL^{-1} ; 2 mL subsamples were withdrawn and passed through a 0.2 μm Nuclepore filter at 0.5, 1, 2, 4 and 10 min. These filtrates were placed in scintillation vials and counted on a Beckman LS6000IC liquid scintillation counter. The uptake constant was calculated as the slope of the

least-squares regression of the natural log of percentage $^{32}\text{PO}_4^{3-}$ left in the water over time. The reciprocal of the uptake constant is $^{32}\text{PO}_4^{3-}$ turnover time (Lean, 1973).

Zooplankton

Zooplankton were collected in triplicate by vertical tows through the entire water column to a maximum depth of 30 m using a 64- μm mesh 30-cm diameter Wisconsin net. Crustacean zooplankton length measurements were made from at least 150 individuals or all individuals in 10% of the sample. Biomass was calculated from length measurements using published formulae for length–mass relationships (Culver *et al.*, 1985; Yan and Mackie, 1987). The dominant zooplankters numerically and by biomass were nauplii, cyclopoid and calanoid copepods, *Bosmina* spp. and *Daphnia* spp. The more common non-dominant zooplankters included *Diaphanosoma brachyurum*, *Holopedium gibberum*, *Ceriodaphnia* sp. and Chydoridae.

RESULTS

During winter months a thin, temporary layer of ice formed on some of the smaller lakes; however, parts of all the lakes remained open and any ice present was thin (<10 mm). Seasonal surface water temperatures fluctuated in an expected manner for lakes in a north temperate climate, ranging from $<3^\circ\text{C}$ during winter to $>23^\circ\text{C}$ in summer (Figure 2). Likewise, ambient surface PAR changed in a typical seasonal pattern.

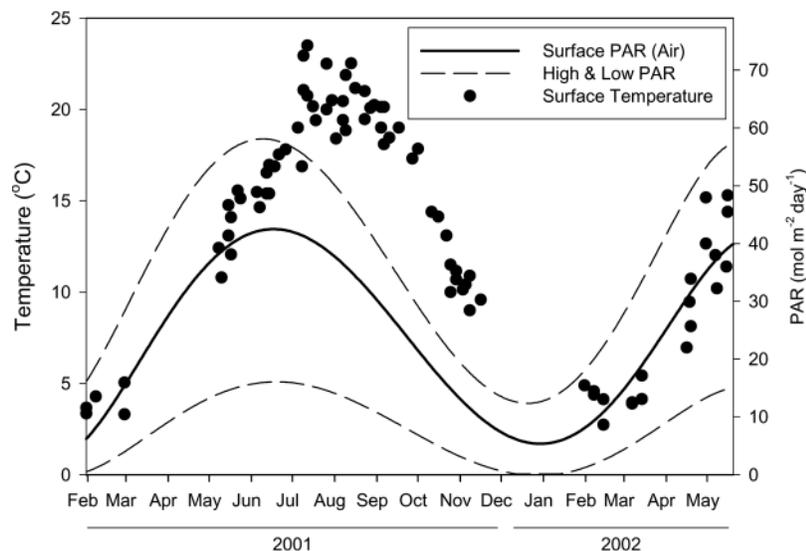


Fig. 2. Seasonal changes in average surface temperature (0–2.0 m) for Council (COL), Cusheon (CUL), Elk (ELL), Maxwell (MXL), Shawnigan (SHL) and Sooke (SOL) lakes. Solid line represents ambient surface PAR measured at SOL drinking water intake tower, dashed lines encompass the PAR range.

Table II: Limnological variables; Chl *a* ($\mu\text{g L}^{-1}$), total phosphorus (*TP*, $\mu\text{g L}^{-1}$) and epilimnetic photosynthesis parameters for COL, CUL, ELL, MXL, SHL and SOL

Date	Chl <i>a</i>	TP	α^B	P_M^B	E_k	PP	Date	Chl <i>a</i>	TP	α^B	P_M^B	E_k	PP
COL							MXL						
14-Jun-01	1.0	4.0	3.7	3.8	285	159	12-Jun-01	1.7	13.1	5.8	3.4	164	247
12-Jul-01	1.1	3.0	2.4	2.8	327	127	9-Jul-01	2.4	7.3	2.3	1.7	204	174
9-Aug-01	0.9	3.6	3.1	2.5	218	96	7-Aug-01	2.9	7.4	2.4	1.9	219	219
6-Sep-01	1.0	3.5	3.4	2.7	221	113	4-Sep-01	3.0	8.3	3.1	2.3	205	236
25-Oct-01	1.3	4.4	4.5	2.0	125	63	29-Oct-01	3.7	10.0	3.1	1.9	169	87
14-Feb-02	1.9	4.8	8.0	2.1	71	104	7-Feb-02	15.5	11.0	7.4	1.2	46	416
14-Mar-02	2.5	NS	5.7	1.3	65	107	7-Mar-02	10.4	NS	5.8	1.0	48	331
19-Apr-02	1.2	3.6	5.6	2.7	133	122	30-Apr-02	2.1	11.9	5.9	3.2	145	223
21-May-02	1.3	4.8 ^b	3.6	3.2	245	179	16-May-02	1.5	11.3 ^b	6.1	4.4	201	180
CUL							ELL						
12-Jun-01	2.7	16.9	3.9	2.32	164	216	14-Jun-01	1.9	15.9	3.9	3.3	238	300
9-Jul-01	2.1	11.8	5.2	4.34	232	288	12-Jul-01	2.2	20.8	9.3	5.5	166	664
7-Aug-01	2.3	13.6	4.7	4.1	239	281	9-Aug-01	5.2	12.8	6.8	4.4	179	936
4-Sep-01	12.8	19.3	3.5	2.3	180	642	6-Sep-01	3.5	13.0	9.6	3.3	96	648
29-Oct-01	2.4	38.7	8.4	1.34	44	73	22-Oct-01	13.0	40.6	1.82	2.8	430	258
7-Feb-02	1.5	14.4	7.8	2.8	99	54	14-Feb-02	10.8	46.0	4.67	1.5	90	388
7-Mar-02	2.6	NS	6.0	2.7	124	95	14-Mar-02	7.5	NS	5.4	1.7	86	426
30-Apr-02	1.1	10.7	6.0	5.40	252	119	19-Apr-02	11.0	20.5	8.5	2.7	90	1549
16-May-02	1.2	9.6 ^b	7.9	4.7	166	151	21-May-02	2.1	22.5 ^b	9.0	5.9	182	474
SHL							SOL^a						
18-Jun-01	1.6	3.9	2.1	3.1	419	244	21-Jun-01	0.4	2.6	3.9	6.7	472	121
3-Jul-01	1.6	3.6	4.1	2.8	192	335	5-Jul-01	0.3	1.6	6.8	4.9	202	114
16-Jul-01	2.0	3.9	2.8	3.3	335	238	18-Jul-01	1.0	1.9	2.9	1.6	155	104
30-Jul-01	1.9	4.5	3.0	2.7	247	263	2-Aug-01	0.8	2.3	3.8	1.7	127	72
13-Aug-01	1.4	3.4	2.5	2.4	269	171	16-Aug-01	0.6	4.8	2.7	2.5	257	75
27-Aug-01	1.5	4.2	5.0	2.8	155	348	30-Aug-01	0.6	2.0	3.9	2.8	198	90
17-Sep-01	1.6	4.2	3.8	2.8	201	131	10-Sep-01	1.0	3.2	2.5	1.8	203	75
1-Oct-01	1.9	3.9	6.1	2.4	111	212	27-Sep-01	1.2	2.8	3.0	1.9	181	63
16-Oct-01	1.6	4.9	6.1	2.1	95	117	11-Oct-01	1.4	4.6	4.8	1.9	110	71
5-Nov-01	1.9	5.0	4.6	1.0	60	82	25-Oct-01	1.5	5.3	4.7	1.6	94	75
28-Jan-02	1.4	6.9	10.4	2.8	76	102	31-Jan-02	0.7	5.5	8.6	2.4	78	52
28-Feb-02	1.1	NS	10.7	2.5	66	112	28-Feb-02	0.6	NS	7.6	1.9	71	63
18-Apr-02	1.0	6.7	23.6	7.3	86	314	16-Apr-02	0.7	5.7	14.8	4.3	81	189
22-May-02	0.9	4.9 ^b	12.4	6.8	153	302	23-May-02	0.8	3.9 ^b	10.7	5.3	138	232

α^B ($\mu\text{gC } \mu\text{gChl}^{-1} \text{ mol quanta}^{-1} \text{ m}^{-2}$), P_M^B ($\mu\text{gC } \mu\text{gChl}^{-1} \text{ h}^{-1}$), E_k (P_M^B/α^B , $\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$) and integrated PP using 7-day average PAR ($^{14}\text{C-PP}$, $\text{mgC m}^{-2} \text{ day}^{-1}$). [^{14}C]PP values represent average pelagic fixation for the entire lake (i.e. calculations account for bathymetry). ^aThis is a drinking water reservoir and it experiences large seasonal changes in water level. ^bMay TP values from samples approximately 1 week prior to other measurements. NS = no sample was analyzed on these dates.

Plankton photosynthesis

Seasonal physiological adaptations reflected by photosynthetic parameters followed expected trends (Table II).

E_k was lowest during winter months (Jan to mid March) in COL, CUL and MXL, while SHL and SOL had low E_k values from autumn until spring (Oct–April). ELL was similar to SHL and SOL, except for October

when E_k was unexpectedly large. During spring, E_k increased rapidly in COL, CUL and MXL because α^B decreased at the same time P_m^B increased. This rate of increase was smaller in SHL and SOL because α^B did not increase until later in the season. The equation between P_m^B and α^B for all lakes when E_k was less than 200 was: $P_m^B = 0.31(\alpha^B) + 0.61$ (Type II regression; $r^2 = 0.50$; $n = 41$). The slope of this relationship is less than 1 indicating that P_m^B varied to a lesser extent than did α^B .

COL and MXL had winter near-surface [^{14}C]PP rates similar to, or higher than, summertime values (Figure 3). The greatest [^{14}C]PP rates in COL occurred in May and June, while rates from February and March were similar to near-surface rates measured in July. MXL had the highest rates during the winter months. Seasonal trends in COL and MXL are in contrast to those observed in the other four lakes. CUL and ELL had highest rates during bloom events in late August to early September (CUL) and April, and to a lesser extent in August, in ELL. Seasonal trends in

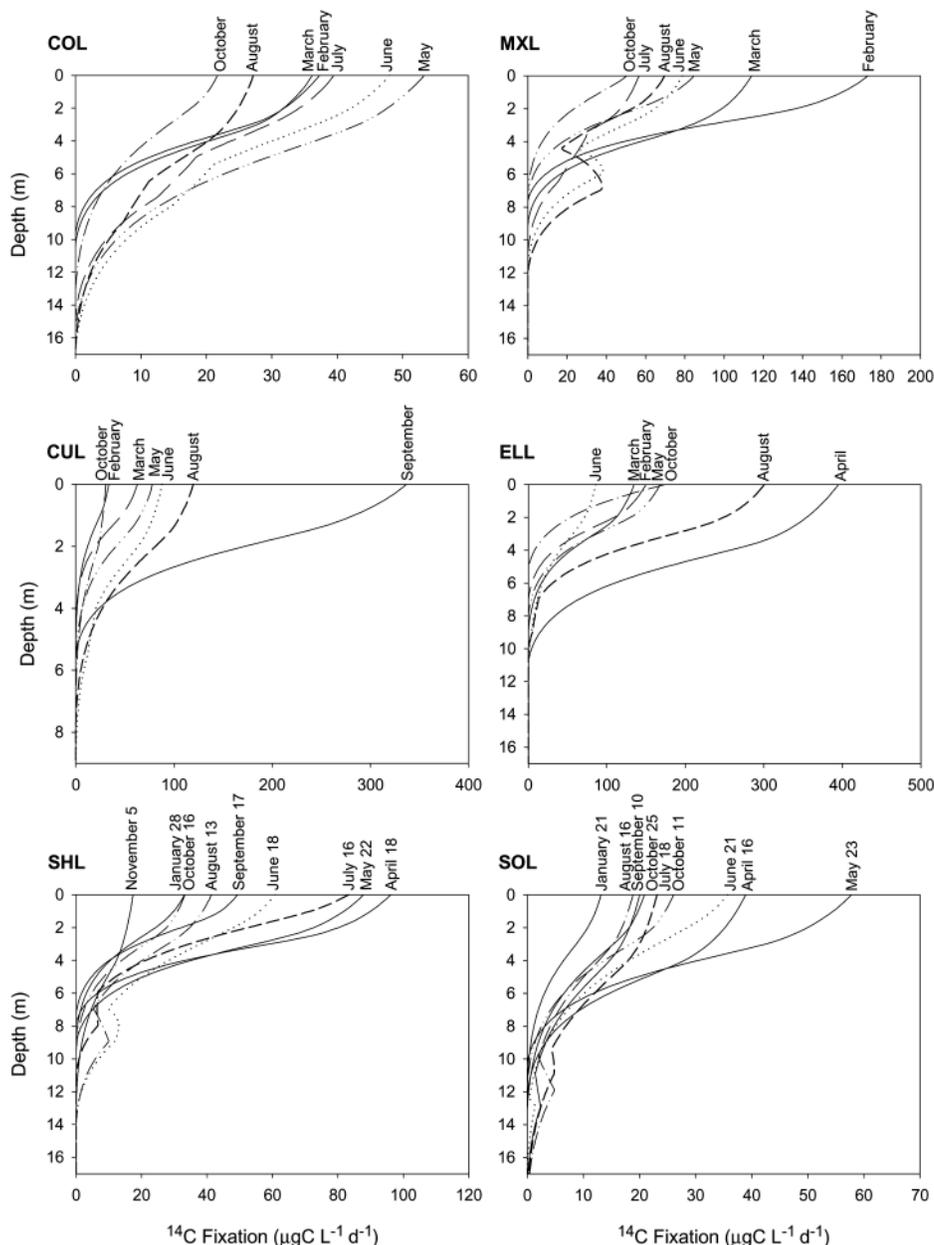


Fig. 3. [^{14}C]PP versus depth for each lake. The corresponding month for each profile is given immediately above the line at depth = 0 m. For clarity, not all months are shown for each lake. Data for months not shown are similar to that of the preceding month.

SHL and SOL were similar to one another with highest near-surface rates occurring in spring, while the lowest rates occurred in late autumn and winter. MXL had the highest rates, after those measured in February and early March, in April, and May. SHL and SOL had relatively deep metalimnia, and although these may be important for other reasons, they did not have a large impact on integral photosynthetic rates. In the oligotrophic to mesotrophic lakes 1% PAR extended into the hypolimnion. Phytoplankton growth in the hypolimnion may be of interest, but is of minor importance for estimating integral photosynthetic rates. MXL had the most pronounced metalimnetic [¹⁴C]PP peak of all the lakes (Figure 3).

There was no apparent seasonal trend in water column transparency as determined by Secchi depth; however, average seasonal compensation depths were lower during winter than in the stratified period (Table I). The average wintertime compensation depths for all lakes, except COL (54%), were between 73 and 85% of the average compensation depth during the stratified period. While decreased transparency during winter may have affected the available PAR to a small extent, the decrease in ambient solar PAR intensity and duration during winter was of greater importance. Seasonal PP depth profiles are strongly influenced by ambient light. Although COL and MXL had high near-surface [¹⁴C]PP in February and March, as expected there was a rapid decrease of this rate with depth compared with summer. This trend can be observed in the other lakes, however, because wintertime rates are lower in these lakes it may be less important to their annual carbon-fixation budgets.

Daily [¹⁴C]PP estimates for our six lakes were summed by month over the year to estimate annual carbon-fixation budgets using daily PAR measurements (Table III). Every month accounted for between 2 and 23% of the annual production. The integral rates follow similar seasonal trends with [¹⁴C]PP versus depth. However, despite similar light saturated near-surface photosynthetic rates in COL during winter and summer, estimates of annual C-fixation demonstrate that COL is similar to SHL and SOL and different from MXL. Our last autumn sampling date in MXL occurred immediately prior to autumn overturn (October 29, 2001). If [¹⁴C]PP rates increased after autumn mixing then carbon budget estimates presented here for November to January are conservative.

Daily estimates were used to calculate average weekly [¹⁴C]PP rates and these were compared with seasonal trends from Alvarez-Cobelas and Rojo (Alvarez-Cobelas and Rojo, 1994). The percentage difference of weekly [¹⁴C]PP was plotted against the annual average, starting from summer solstice (Figure 4). COL, ELL, SHL and SOL closely follow the typical seasonal trend in PP for deep lakes ($\bar{z}_{\text{mean}} > 5$ m). A cross-correlation plot for COL versus a typical deep lake is shown in the bottom lefthand corner of Figure 4a. The other lakes in Figure 4a have similar cross-correlation plots (data not shown). Note that there is approximately a 3 week lag in the correlation. MXL did not follow the typical pattern, and the zero lag correlation is approximately 0 (Figure 4b). With a \bar{z}_{mean} of 4.4 m CUL is classified as a shallow lake by

Table III: Monthly estimates of ¹⁴C-fixation for the six study lakes

Month	Lake [¹⁴ C]PP (kg C lake ⁻¹ month ⁻¹)					
	COL	CUL	ELL	MXL	SHL	SOL
June (2001)	692	2093	20 463	1899	36 582	18 928
July	586	2552	43 159	1590	48 938	21 957
August	445	4352	46 675	1783	36 883	14 411
September	471	4736	43 076	1623	28 051	13 128
October	360	1840	29 570	1055	21 076	13 081
November	250	570	13 352	1011	11 150	8720
December	225	430	11 206	1443	11 051	7427
January (2002)	277	414	13 325	2278	13 456	8177
February	398	559	18 508	2964	14 553	8346
March	550	903	32 453	2978	25 744	15 970
April	600	1003	75 687	2575	47 104	32 663
May	779	1346	48 320	1610	52 106	40 563
Total	5633	20 798	395 794	22 809	346 694	203 371

Rates are based on lake size, so are not comparable between lakes. See text for details on calculations.

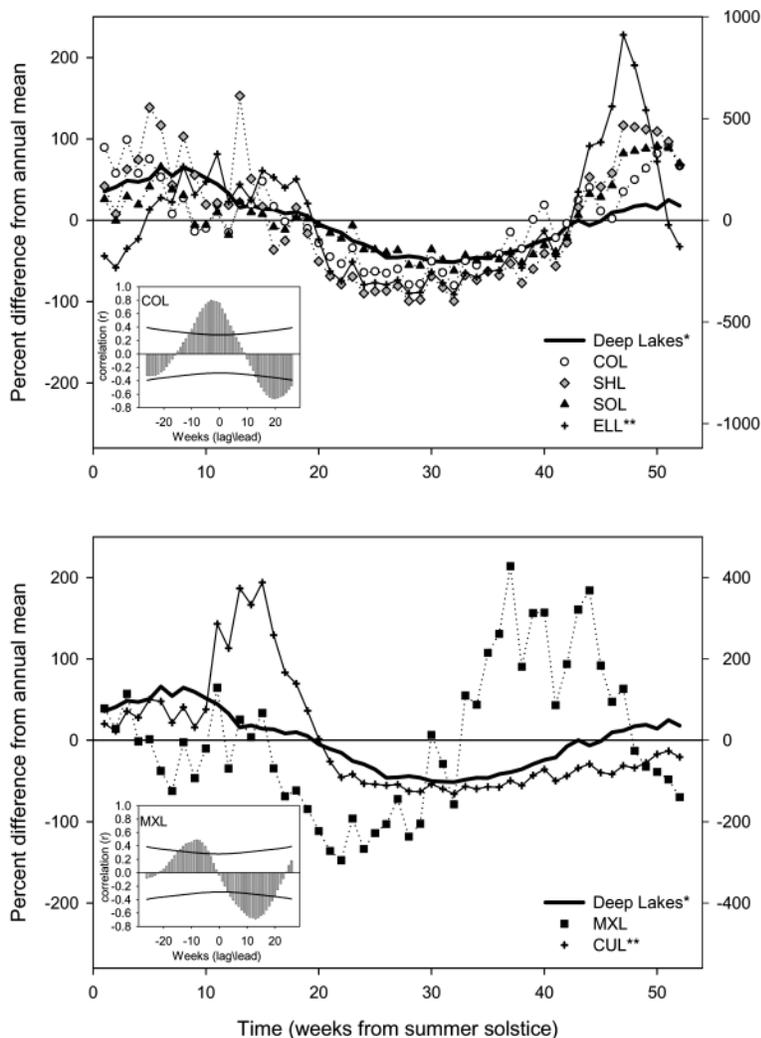


Fig. 4. Weekly production as percentage difference from annual mean compared with the typical seasonal productivity trends of deep lakes (Alvarez-Cobelas and Rojo, 1994). COL, ELL, SHL and SOL follow the seasonal trend (top), whereas CUL and MXL do not (bottom). Inset figures are cross-correlations between the productivity trend of Alvarez-Cobelas and Rojo and COL (top) and MXL (bottom). Lines on inset figures represent significance level ($\alpha = 0.05$). Cross-correlations for ELL, SHL and SOL were similar to COL and the cross-correlation for CUL, like MXL, suggested significantly different seasonal patterns than that of Alvarez-Cobelas and Rojo (Alvarez-Cobelas and Rojo, 1994). *Deep lakes considered to be those with $Z_{\text{mean}} > 5$ m. **ELL and CUL values should be read off the righthand axis, all other lakes are read from the lefthand axis. The units are the same for both axes.

Alvarez-Cobelas and Rojo (Alvarez-Cobelas and Rojo, 1994); however, the pattern of PP in CUL is not similar to either their typical deep or shallow lake.

The relationship between $[^{14}\text{C}]\text{PP}$ and TP for daily measurements was compared with the seasonal predictive model of Smith (Smith, 1979) for 58 north temperate lakes and the model of Stockner and Shortreed (Stockner and Shortreed, 1985) from BC coastal lakes (Figure 5). All data points fell within the 95% confidence limits of Smith (Smith, 1979) except for CUL and ELL winter measurements and the ELL October measurement. On average, Stockner and Shortreed (Stockner and Shortreed, 1985) found greater photosynthetic rates at a given TP than we did; however, their rates over $2 \mu\text{g L}^{-1}$ TP are from

fertilized lakes and may therefore not apply to unmanipulated coastal lakes.

Nutrient and light deficiency

P-debt was used as a physiological assessment of community phosphorus deficiency and compared with culture-modelled thresholds. Greater P-debt values indicate greater P-deficiency (Healey and Hendzel, 1980). COL and MXL were strongly P-deficient during summer and relative to late summer and autumn, COL had greater P-debt during winter (Figure 6). CUL and ELL only showed deficiency during summer months. SHL and SOL were strongly deficient in summer and this level of deficiency decreased during winter months.

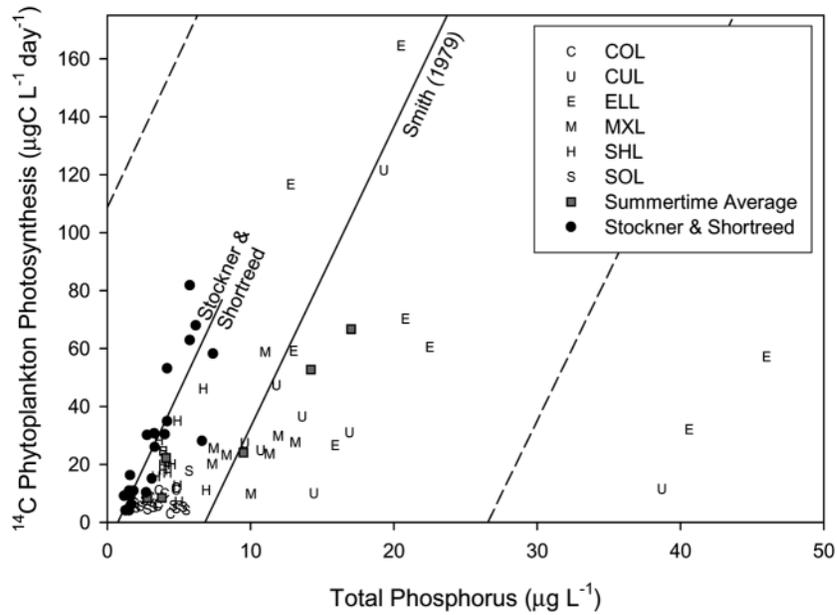


Fig. 5. BC-coastal lake PP determined in this study compared with the linear regressions of Smith (Smith, 1979) and Stockner and Shortreed (Stockner and Shortreed, 1985). Dashed lines represent 95% confidence interval from Smith (Smith, 1979). Smith's study predicted seasonal averages and encompassed a larger range in TP; only that portion of the line corresponding to TP concentrations found in the current study lakes is shown. For more direct comparison, seasonal summertime averages (May–Sept.) have also been plotted for our lakes. Data of Stockner and Shortreed over $2 \mu\text{g L}^{-1}$ TP are from fertilized lakes.

$^{32}\text{PO}_4^{3-}$ turnover time (minutes) was also used as a measure of P-deficiency because it is thought to represent the PO_4^{3-} uptake efficiency of the plankton community and has been found to correspond well with the phosphorus deficiency index (Millard *et al.*, 1996). Turnover times less than 10 min are considered to represent extremely P-deficient systems (Millard *et al.*, 1996; Hudson *et al.*, 2000). In all lakes the majority of summertime PO_4^{3-} turnover times were <10 min (Nowlin, 2003). During February, P-turnover in COL was ~11 min, which was higher than rates in the spring and autumn, but lower than those during July and August. P-turnover in MXL was always <10 min, including the winter (Figure 7). CUL and ELL had the longest wintertime $^{32}\text{PO}_4^{3-}$ turnover times (>35 min), while SHL and SOL had winter turnover times between 18 and 23 min.

Light deficiency was evaluated both with a physical assessment of the light environment measured as mean epilimnetic PAR (\bar{I}_E) and a physiological assessment of epilimnetic phytoplankton (Figure 6). The ratio of \bar{I}_E to the light saturation parameter E_k , or light limiting ratio (LLR), was also used to assess the available light compared with that required for maximal photosynthesis (Millard *et al.*, 1996). In theory, the threshold for determining light deficiency occurs when the average epilimnetic PAR is less than E_k , which corresponds to a ratio of 1. However, Millard *et al.* (Millard *et al.*, 1996) found LLR values of 0.8 or greater to still represent light sufficiency. \bar{I}_E values

during the summer were typically greater than limitation thresholds reported elsewhere (Hecky and Guildford, 1984; Millard *et al.*, 1996). The epilimnion of SHL and SOL are deeper (July and August average, 7.0 m and 9.8 m respectively) than those of COL (5.75 m) CUL, ELL and MXL (all 4.0 m). The greater epilimnetic depth in SHL and SOL is a function of greater fetch and results in a lower \bar{I}_E . Since summertime E_k does not differ vastly between the lakes, LLR was lowest in SHL and SOL during summer.

Zooplankton

Large crustacean zooplankton dominated all the study lakes except MXL. Biomass-weighted mean length was typically greater than 0.8 mm for COL, CUL, ELL, SHL and SOL (Figure 8). *Daphnia* spp. were present in all of these lakes and together with calanoid or cyclopoid copepods constituted the majority of crustacean zooplankton biomass. MXL was distinct from the other lakes in this study with a biomass-weighted mean length of ~0.4 mm. Zooplankton in MXL was dominated by *Bosmina* spp. and cyclopoid copepods.

DISCUSSION

There were distinct differences in the temporal patterns of ^{14}C PP among lakes. Seasonal patterns in COL, ELL,

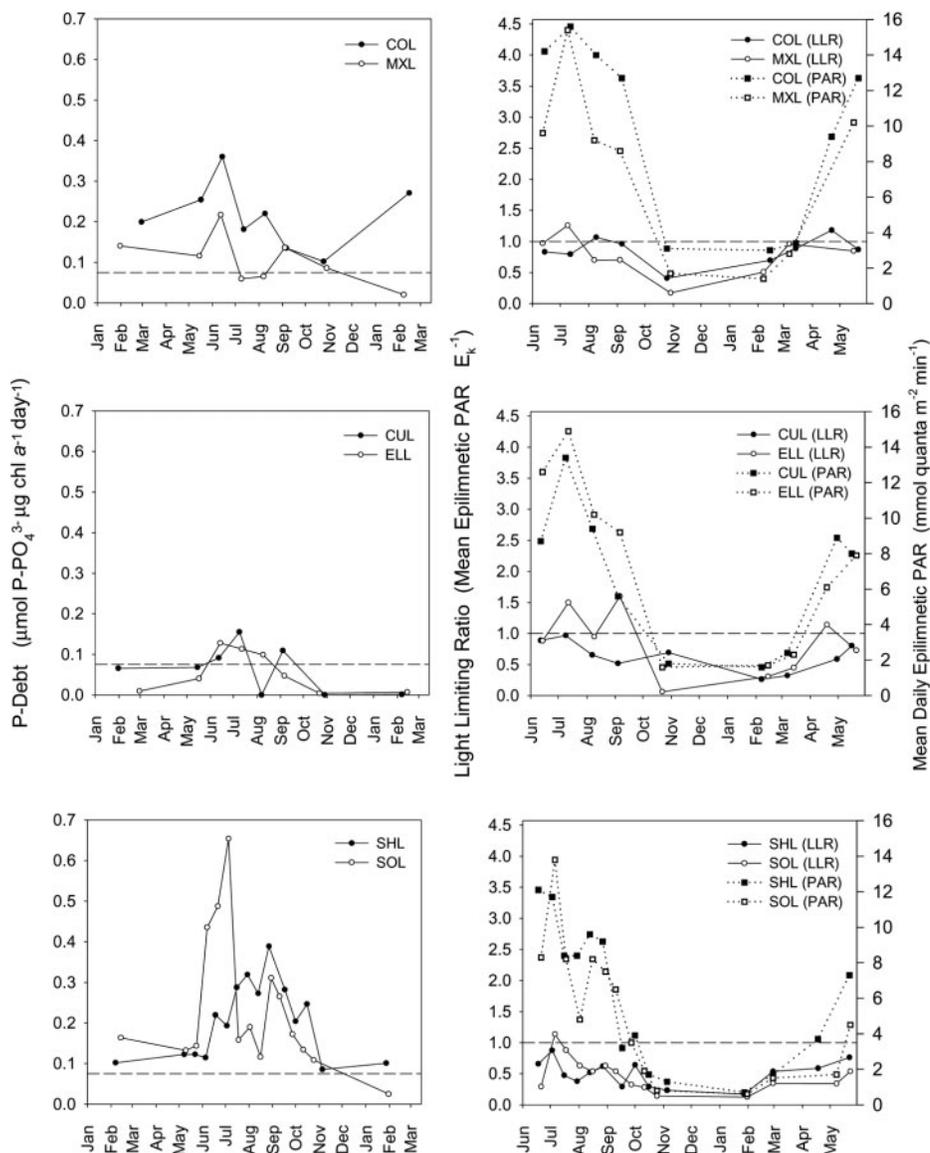


Fig. 6. (Left panel) Whole plankton P-debt from epilimnetic water during the length of this study. Greater P-debt is a measure of greater phosphorus deficiency. Dashed lines represent limitation thresholds (Guildford *et al.*, 2000). (Right panel) \bar{I}_E and the light limiting ratio (LLR). Threshold for \bar{I}_E from Hecky and Guildford (Hecky and Guildford, 1984). The plankton community is not considered to be light deficient when \bar{I}_E is greater than E_k , so the LLR threshold is defined as 1 (Millard *et al.*, 1996). Note that date sequences are different for the left and right panels.

SHL and SOL were typical for deep lakes ($\bar{z}_{\text{mean}} > 5$ m), with the greatest near-surface PP rates in the spring and summer and the lowest rates in autumn and winter. In contrast, MXL had highest rates during winter and early spring. COL had highest near-surface rates in the spring, similar near-surface rates during winter and summer and lowest rates in the autumn. CUL had greatest PP rates in late summer (Figure 3, Table III). The cross-correlation of the four lakes fitting the typical PP seasonal trends of Alvarez-Cobelas and Rojo (Alvarez-Cobelas and Rojo, 1994) was offset by several weeks suggesting that these

coastal lakes reach maximal photosynthesis at an earlier time than other lakes.

High near-surface winter [¹⁴C]PP rates in COL and MXL indicate that neither temperature nor PAR was limiting surface photosynthetic production to a greater extent than that observed during summer. Available light was considered to be limiting during the winter (using both \bar{I}_E and LLR measurements) and is reflected in the physiological parameters. The relatively high wintertime rates are, therefore, primarily a result of increased chlorophyll biomass and light adaptation by the phytoplankton (Table II).

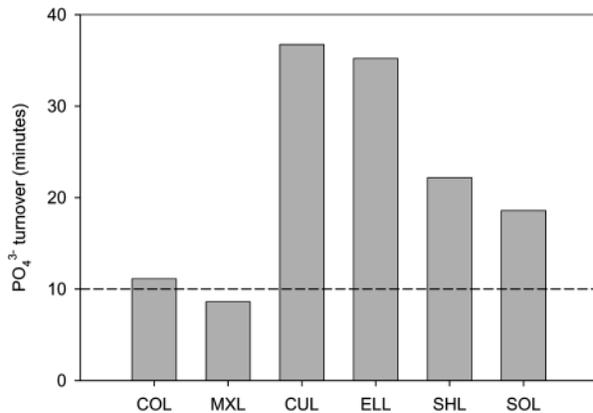


Fig. 7. Winter $^{32}\text{PO}_4^{3-}$ turnover time (minutes). Shorter turnover times represent greater deficiency, the dashed line (10 min) is an approximate threshold for defining severe phosphorus deficiency (Millard *et al.*, 1996; Hudson *et al.*, 2000). Thus, $^{32}\text{PO}_4^{3-}$ turnover times less than 10 min (below the threshold line) are considered to be severely deficient.

Temperature changes elicit algal physiological responses (Raven and Geider, 1988; Falkowski and Raven, 1997) and can affect species composition. Kirk (Kirk, 1994) suggested that low temperature is an important limiting factor of photosynthesis in lakes. However, other research suggests that temperature may not be as important at the ecosystem level (Goldman, 1977; Goldman and McGillicuddy, 2003) except under conditions of light and nutrient sufficiency [cf. (Lomas *et al.*, 2002)]. The concomitant seasonal decrease in ambient PAR and the decrease of maximum depth where C-fixation occurred implicates PAR as a principal factor limiting integral ^{14}C PP during winter. The larger range of α^B compared with P_m^B suggests that PAR (α^B) was more important than temperature (P_m^B) and had more influence on E_k (Jones, 1978). In addition, most C-fixation occurred within the light-limited portion of the P–E curve (Figure 3) where temperature should have a minimal effect on PP.

Besides affecting P_m^B , temperature can also regulate other processes, such as bacterial growth (Pomeroy and Wiebe, 1988; Shiah and Ducklow, 1994) and zooplankton growth and grazing rates (Peters and Downing, 1984; Gillooly, 2000). Low temperatures may therefore affect phosphorus dynamics by changing competitive interactions between algae and bacteria and/or reduced grazing pressure from zooplankton. The extent to which algae increase their competitiveness for nutrient acquisition as a function of temperature was not; however, directly addressed by this study.

The interaction of light, internal loading of phosphorus from sediments, and the extent of mixing influences the size and duration of spring blooms in Lake Michigan (Brooks and Edgington, 1994). In our lakes there was an

increase of TP in the near-surface water during winter (Table II), so our lakes might be considered comparable with such a situation; however, light levels are still relatively low in the winter (February). The hydrologic cycle of southern BC-coastal lakes is different when compared with north temperate lakes that experience winter ice cover. Ice-covered lakes can receive the bulk of runoff and associated allochthonous nutrients during spring runoff, whereas BC-coastal lakes receive the greatest inputs during the winter rainy season (Stockner and Shortreed, 1985; Nowlin *et al.*, 2004). Nutrients from runoff, therefore, enter these lakes in late autumn and early winter. However, the slight increase in nutrients alone cannot explain observed temporal variations in ^{14}C PP because all lakes but MXL had lower integral ^{14}C PP during winter compared with spring or summer. There was also no clear relationship between ^{14}C PP and TP within individual lakes (Figure 5). In MXL, the combination of increased TP together with other variables may help explain the greater wintertime ^{14}C PP rates, and importantly, from an ecosystem perspective, this fixed carbon may represent new production.

P-deficiency indices (P-debt and $^{32}\text{PO}_4^{3-}$ turnover time) suggest that microbial communities in COL and MXL were phosphorus-deficient for most of the year, including winter. This contrasts with other studies that have found severe P-deficiency in summer (when \bar{I}_E is greatest) that declines when ambient PAR is lower, to the point where phytoplankton are light and not nutrient limited (Millard *et al.*, 1996). Despite having lower wintertime PP rates, SHL and SOL were moderately P-deficient during winter ($^{32}\text{PO}_4^{3-}$ turnover time, some P-debt). Even CUL and ELL, which indicated no P-deficiency with P-debt, had $^{32}\text{PO}_4^{3-}$ turnover times lower than the 100–1000 min range measured by Millard *et al.* (Millard *et al.*, 1996) in Lake Ontario during spring and autumn. The coastal lakes in our study therefore maintained a moderate P-deficiency throughout winter, so our data suggest light and nutrients may co-limit [cf. (Healey, 1985)] coastal oligotrophic lakes in winter.

Lake trophic structure has long been known to affect plankton size (Brooks and Dodson, 1965; Pace, 1984) and productivity (Hrbáček *et al.*, 1961). Studies examining the interactions between trophic structure, nutrients, and plankton photosynthesis suggest that small zooplankton-dominated systems will have greater rates of photosynthesis under conditions of nutrient enrichment (Schindler *et al.*, 1997). MXL is populated with threespine sticklebacks (*Gasterosteus aculeatus*), which consequently leads to a zooplankton community characteristic of lakes that experience intense zooplanktivorous fish predation [i.e. dominated by smaller zooplankton taxa such as *Bosmina* sp. and cyclopoid copepods (Brooks and Dodson, 1965)]. In contrast

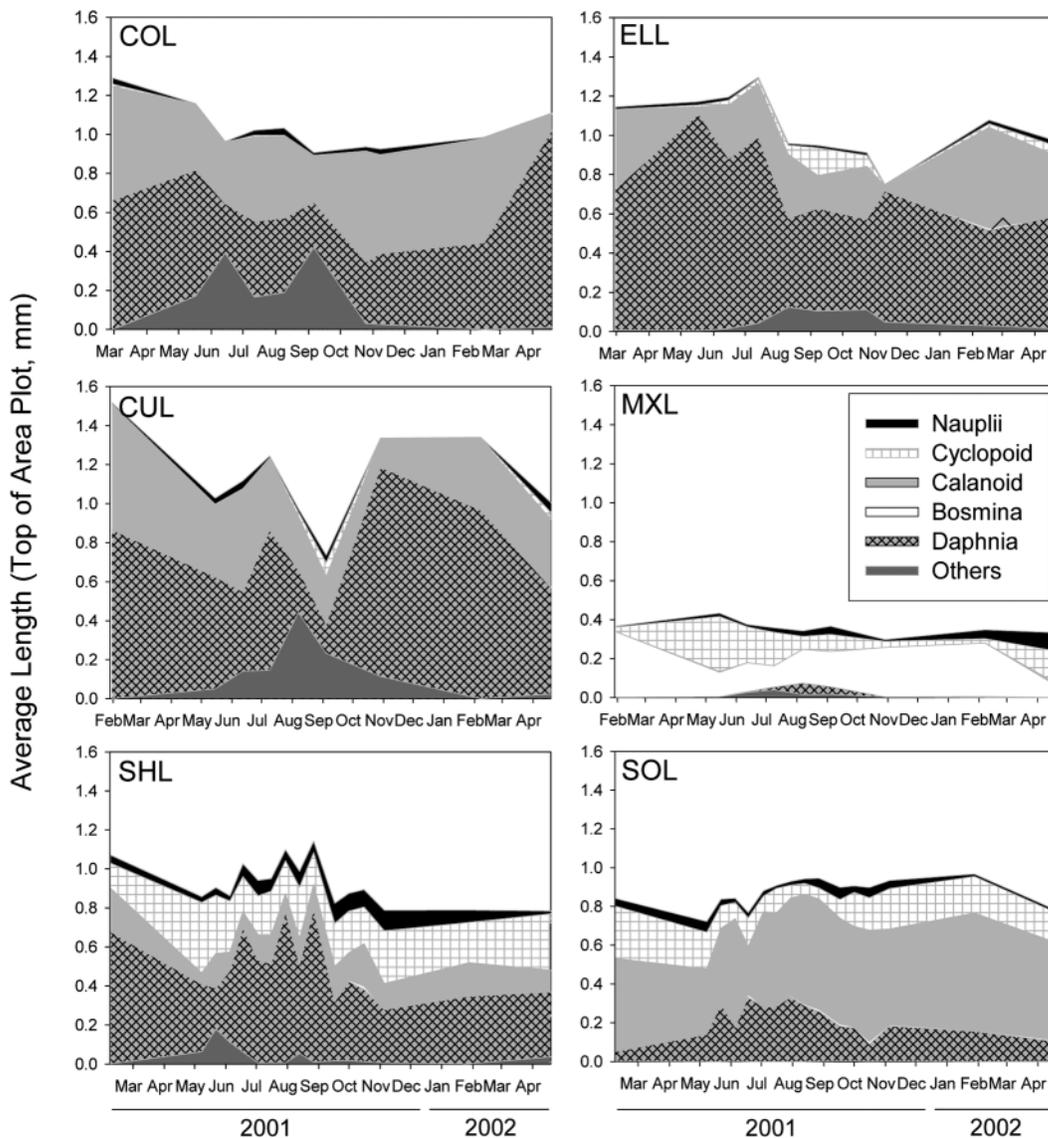


Fig. 8. Average size (length) of the crustacean zooplankton community weighted by zooplankton biomass. The top of all area curves represents the average community length. Taxa-specific areas represent the proportion of biomass that each respective group contributes to the total biomass. For example, in COL on 14 June 2001, the average community length was 0.96 mm and the proportion of biomass contributed by each group was, other = 40.8%, *Daphnia* = 26.1%, *Bosmina* = 0%, Calanoid = 32.5%, Cyclopoid = 0.3% and Nauplii = 0.3%.

to the zooplankton in MXL, large *Daphnia* were present in all the other study lakes. The presence of large *Daphnia* has been demonstrated to reduce or depress algal biomass with increasing TP (Mazumder, 1994). In contrast, odd-linked lakes [*sensu* (Mazumder, 1994)] demonstrate greater responsiveness to changes in potential productivity. Under similar nutrient conditions, or the slightly enriched nutrient conditions during lake mixing, MXL may therefore be expected to show greater increases in production. However, the role of temperature on zooplankton may mitigate direct (i.e. grazing effects) wintertime differences between even- and odd-linked lakes.

Since we did not directly test the respective importance of temperature, light, nutrient dynamics, and zooplankton on [¹⁴C]PP we cannot conclusively identify which factor was most influential at different times of the year within individual lakes. However, we can assess the relative importance of each by comparing seasonal trends within and among lakes. Seasonal changes of light and temperature typically have a strong control of temporal variability in [¹⁴C]PP (Alvarez-Cobelas and Rojo, 1994) but there is also a tight coupling of plankton-structure with these physical variables. Bacterial respiration is more strongly influenced by temperature than is primary productivity (Lefèvre *et al.*,

1994; Lomas *et al.*, 2002) and decreases in bacterial activity may release phytoplankton from nutrient competition. The interaction between light and nutrients (Fahnenstiel *et al.*, 2000) and large zooplankton (Litaker *et al.*, 2002) can also play an important role in the formation of cold-water blooms. Since within-lake TP and productivity were uncorrelated and seasonal temperature and light changes were similar between lakes, we suggest that a major difference in seasonal PP among lakes is based on the composition of the plankton community.

Considering primary production seasonally is important because of demonstrated temporal uncoupling of periods of net photosynthesis and respiration (Blight *et al.*, 1995; Smith and Kemp, 1995, 2001; Serret *et al.*, 1999). Productivity under low light conditions can be seasonally important (Goldman and McGillicuddy, 2003), represent new carbon (Dugdale and Goering, 1967; Eppley and Peterson, 1979) and is necessary for calculating annual photosynthetic budgets (Brooks and Edgington, 1994). Measuring community respiration rates is also vital, especially if respiration of the non-algal component (esp. bacteria) are influenced more by temperature than are phytoplankton. Based on the interpolated seasonal data, we estimated that ^{14}C -fixation from November to March constituted between 22 and 47% of the annual budget for the oligotrophic-oligomesotrophic lakes (i.e. not including CUL and ELL). We have no estimate of the net carbon-fixation over a season since respiration was not measured. However, if community respiration decreases more with decreasing temperature than C-fixation, then the net contribution of wintertime C-fixation would be greater than our current estimates.

This study also challenges definitions of ideal growth conditions for species and/or communities, since 'ideal' or 'optimal' laboratory growth is not necessarily transferable to the field. Whilst low temperature (3–4°C) and low light are not typically considered ideal growth conditions for phytoplankton communities, the interplay of both physical and biological processes (e.g. competition and grazing) presented a niche in one of our study lakes that was quite different from that which would be expected from culture studies. This complicates our ability to develop predictive models, even those that incorporate light, nutrients, temperature, and photosynthetic parameters (Geider *et al.*, 1998) and stresses the importance of studying rate processes and community composition under a spectrum of environmental conditions.

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