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Littoral-benthic primary production estimates: Sensitivity to simplifications with respect to periphyton productivity and basin morphometry

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Abstract

Periphyton is a critical energy source for consumers in lakes of all sizes, but estimates of average, area-specific littoral zone benthic primary production (LBP) have been hampered by low spatial and temporal resolution of productivity data. We analyzed the sensitivity of estimates of LBP to depth-specific variation in photosynthesis-irradiance (PE) parameters and temporal variation in water clarity using monitoring data from five northern temperate lakes. Maximum photosynthesis rates peaked in the upper epilimnion in all five lakes, and our best daily estimates of LBP ranged from 125 mg C m^{-2} d^{-1} to 425 mg C m^{-2} d^{-1}. Nonlinear variation in maximum photosynthesis (P_{MAX}) with depth caused overestimates in LBP by an average of 10% when mean values of P_{MAX} were applied throughout the euphotic zone. Conversely, applying values of light levels at onset of saturation (E_k) from the upper epilimnion resulted in underestimating LBP by an average of 19% compared with the most data-rich (optimal) calculations. Simplified approximations of bathymetry yielded underestimates or overestimates of LBP, depending on basin shape. Incorporating temporal variation in water clarity and daily solar irradiance did not substantially improve estimates of average summer LBP compared with estimates that incorporated summer average values of K_d, but this result should not be extrapolated to lakes with more variable water clarity. Estimates of average littoral zone benthic primary production can be optimized by incorporating depth-specific variation in maximum periphyton productivity, saturation light intensity, and sediment surface area into calculations.

Lake food webs are sustained by multiple basal energy sources including phytoplankton, attached algae (periphyton) and imported terrestrial carbon (Vadeboncoeur et al. 2003; Karlsson et al. 2009; Vander Zanden et al. 2011). These sources of primary production differ fundamentally both in their accessibility to consumers and in their relative food quality (Brett et al. 2009), which affects the efficiency with which these carbon sources are incorporated into food webs (Vander Zanden et al. 2006). Quantifying the relative role of each of these basal resources in ecosystem metabolism requires an assessment of the total flux of carbon into the lake through each autotrophic functional group (Ask et al. 2009). The contribution of periphyton to ecosystem metabolism remains the least well understood of basal carbon sources in lakes, although alteration of benthic primary production has profound consequences for aquatic food webs (Vadeboncoeur et al. 2003; Higgins and Vander Zanden 2010; Hampton et al. 2011). A growing interest in the functional determinants of the distribution of autochthonous production between benthic and pelagic habitats, or lake autotrophic structure (*sensu* Higgins et al. 2014), calls for a critical assessment of approaches and assumptions that generate estimates of benthic primary production on a whole-lake scale.

Estimates of littoral benthic primary production are still relatively rare, and few estimates are based on spatially and temporally extensive data. Furthermore, quantification of primary productivity in lakes is in transition, with in situ bottle incubations of phytoplankton giving way to open water estimates of whole-lake metabolism using high-frequency oxygen measurements (Hanson et al. 2003). Bottle incubations intentionally isolate phytoplankton from other autotrophs, including periphyton. In contrast, open water oxygen sensor methods can, with intensive deployment of sondes throughout the littoral and pelagic zones, estimate periphyton primary production (Van de Bogert et al. 2007, 2012). Although open water methods can detect the sum of

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phytoplankton and periphyton primary production, their use is problematic for quantifying only periphyton GPP. Periphyton metabolism measurements in small lakes are highly sensitive to the spatial placement of sensors and to wind-induced water movements. Furthermore, calculations of benthic algal contributions to whole-lake metabolism rely on assumptions regarding the proportion of O_2 generated by periphyton that can be detected by a given sensor (Van de Bogert et al. 2007, 2012). The high cost of in situ oxygen sensors combined with the sensitivity of productivity estimates to sensor placement mean that chamber estimates remain a cost effective technique for directly quantifying contributions of benthic algae to whole-lake primary production.

Generalized methods for extrapolating from chamber incubations to estimates of whole-lake phytoplankton production have been available for decades (e.g., Fee 1969, 1979, 1990). Whole-lake phytoplankton production can be derived from mid-day chamber estimates if the light absorption characteristics of the water column are known (Fee 1979). Changes in light with depth are calculated using empirically derived light attenuation coefficients (K_d) and Beers law. Temporal variation in light at depth can be described as a function of the diel cycle in solar radiation or with actual irradiance data and seasonal changes in water clarity (quantified by K_d). The final step in estimating whole-lake phytoplankton production involves accounting for changes in total water volume with depth in the lake, which is a function of morphometry.

Estimates of periphyton contributions to whole-lake primary production and estimates of average littoral periphyton production (LBP) have been executed on a lake-by-lake basis in the absence of any systematic approach (Loeb et al. 1983; Vadeboncoeur and Steinman 2002). Nevertheless, calculations of LBP rely on essentially the same relationships between light and productivity that are used for phytoplankton (Vadeboncoeur et al. 2008). Instead of summing production in a water volume across a series of thin layers stacked on each other, the littoral sediments are divided into a series of concentric rings across the photic zone, and depth-specific productivity estimates are integrated across sediment depth intervals (Loeb et al. 1983; Vadeboncoeur et al. 2008; Malkin et al. 2010). Calculations of LPB are usually based on fewer data than comparable estimates of area-specific whole-lake phytoplankton production. Typically estimates of LBP are based on chamber measurements from 1 to 3 depths and relatively few dates within a lake (reviewed in Wetzel 2001; Vadeboncoeur and Steinman 2002), compared with the >6 depths and weekly or biweekly measurements that are typical of long-term phytoplankton monitoring programs (e.g., Jassby 1998; Carpenter et al. 2001).

We use a previously published method for calculating the distribution of primary production between benthic and planktonic autotrophs (Vadeboncoeur et al. 2008; hereafter the autotrophic structure model) to explore the sensitivity of LBP to extrinsic and intrinsic drivers of periphyton productivity. The purpose of the autotrophic structure model was to quantify littoral contributions to whole-lake production across morphometric and eutrophication gradients, but the method can be adapted to estimate benthic primary production for specific lakes if light and photosynthesis-irradiance data are available. In the current application of the model, we express LBP as average periphyton production per square meter of littoral zone per day, where the littoral zone is the area of the lake where $\geq 1\%$ of incoming solar radiation reaches the sediment. By restricting analysis to the littoral zone only, our computations are not confounded by differences among lakes in the relative abundance of littoral-benthic and euphotic pelagic habitat. We used an extensive field dataset to analyze the sensitivity of estimates of LBP to the sampling resolution of three key input variables: maximum light-saturated periphyton productivity (P_{MAX}), light saturation intensity (an index of photoacclimation quantified by E_k), and water-column light attenuation (K_d). We also compared estimates of LBP generated using bathymetric maps with those generated using simplified models of lake morphometry (Carpenter 1983; Vadeboncoeur et al. 2008).

Materials and procedures

We sampled benthic primary productivity on sediments in five lakes of the North Temperate Lakes Long Term Ecological Research (NTL-LTER) program in Northern Wisconsin from 2005 to 2008 (Table 1). Productivity was measured at 2–4 depths (0.5–8 m) on 3–7 dates (between 22 May and 23 August) in each lake (Devlin et al. 2013; Vadeboncoeur et al. 2014). We used scuba to collect intact sediment cores in acrylic chambers (5 cm diameter, ~10 cm of sediment plus 15 cm of overlying water) from each depth. Each tube was sealed at the bottom with a nylon plug and at the top by a clear plastic lid. Samples were incubated in situ at midday for 2 h. Two chambers from each depth were completely opaque (dark chambers) and the three remaining cores were incubated at light intensities between 200 μmol m^{-2} s^{-1} and 1600 μmol m^{-2} s^{-1} for samples collected from ≤ 5 m and 20–300 μmol m^{-2} s^{-1} for samples collected from 8 m.

Initial oxygen concentrations for the incubations were determined from water sampled with a syringe from directly above the sediments by a scuba diver immediately before collecting the sediment core. For the final measurement, overlying water was siphoned from the incubation chamber into a 60 mL biochemical oxygen demand (BOD) bottle immediately on retrieval from the lake. All water samples were fixed immediately in the field and analyzed for O_2 concentration using the Winkler method (Carignan et al. 1998). Net primary productivity in light chambers and respiration in dark chambers was calculated using the change in O_2 during the incubation period, the volume of the water in the

Table 1. Chemical and physical characteristics of the study lakes. The K_d values represent light attenuation coefficients for the period from 10 May to 15 October for the years in which each lake was studied. The littoral zone is defined as the area of the lake where the sediments receive $\geq 1\%$ surface light.

Lake	Area* (ha)	Mean depth* (m)	Littoral area (%)	Depth ratio	TP* (μg/L)	DOC* (mg/L)	K_d (m^{-1})
Little Rock	8.1	3.1	100	0.47	33.7	5.2	0.33
Crystal	36.7	10.4	91	0.51	8.7	2.4	0.29
Sparkling	64	10.9	68	0.54	7.1	3.3	0.28
Big Muskie	396.3	7.5	83	0.35	17.5	3.8	0.32
Trout	1607	14.6	43	0.41	13.5	2.8	0.34

*Data were obtained from NTL-LTER database (https://lter.limnology.wisc.edu/about/lakes).

chamber, the sediment surface area (m^2), the incubation time in minutes and a photosynthetic quotient of 1.2 for the conversion of mg O_2 to mg C (Williams et al. 1979). Gross primary productivity (GPP) for each light chamber was calculated by adding back the average oxygen consumption rate derived from the two dark chambers. We averaged the GPP from the light cores for each sample date and depth to calculate light-saturated P_{MAX}. We then described P_{MAX} as a continuous function of depth for each date and lake using the LOESS function in R (R Core Team 2014). There were two sample dates for Big Muskie Lake on which the 0.5 m data were lost. We estimated productivity rates for 0.5 m for those dates using the mean of the other two sample dates and chlorophyll-specific productivity. Chlorophyll increased between 0.5 m and 2 m in all lakes (Vadeboncoeur et al. 2014), but chlorophyll-specific productivity was not different between the two upper epilimnion depths. Thus, we are confident that the increase in productivity observed between 0.5 m and 2 m was consistent across dates.

It is necessary to know both P_{MAX} and photosynthetic efficiency (α) at limiting light intensities to accurately compute daily photosynthesis because subsaturating light intensities occur during a substantial portion of the day. The quantity P_{MAX}/α yields the light intensity at onset of photosaturation, E_k (μmol m^{-2} s^{-1}), which is used in conjunction with light dynamics and maximum photosynthesis rates to describe spatio-temporal variation in primary production. We used a Pulse Amplitude Modulated fluorometer (DIVING-PAM, Heinz Walz GmbH, Effeltrich, Germany) to describe variation in E_k with depth in Sparkling and Trout Lakes. The diving PAM uses chlorophyll fluorescence to measure relative electron transport rate (rETR) of photosystem II as a function of light intensity. Photosynthetic irradiance (PE) parameters α and $rETR_{MAX}$ (light saturated electron transport rate) were derived from Rapid Light Curves (RLC) made between 11:00 and 17:00 in late July. Measurements were made along two transects in each lake, at 0.5–1.0 m depth intervals. Each transect was in a different quadrant of the lake and the order of the PE curves was randomized among depths within transect. In this way, we incorporated diel and horizontal variation into estimates of changes in photosynthetic parameters with depth.

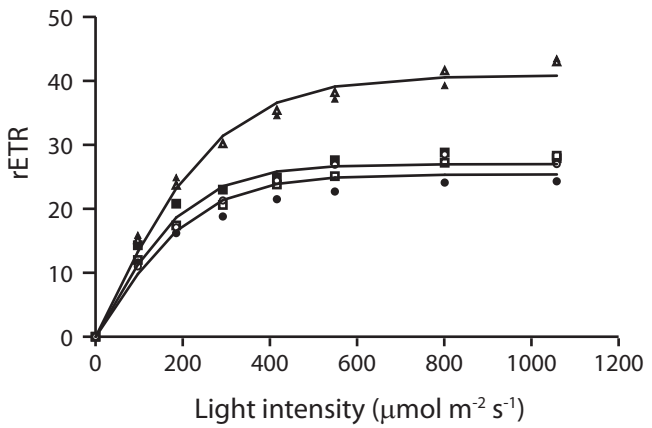

Fig. 1. Trial PE curves testing for the effect of 20 s (open symbols) vs. 3 min (closed symbols) exposure time at each light intensity. Symbols of the same shape represent sequential light curves carried out on the same periphyton community. The light curve with 20 s exposure time per light intensity was done immediately before the curve with a 3 min exposure.

Each RLC consisted of exposing the periphyton to nine progressively increasing light intensities (1–1500 μmol m^{-2} s^{-1}). Exposure times at each light intensity can be between 10 s and 3 min, and the duration of exposure can affect PE parameters (Kühl et al. 2001; Perkins et al. 2011). We tested the effect of exposure time on PE parameters by conducting a series of paired light curves in Sparkling Lake. Each trial consisted of two light curves: first, an RLC was conducted using a 20 s exposure time at each light intensity; this was followed by a light curve in the same location with a 3 min exposure to each sequential light intensity. We ran three sets of paired light curves on sediments in close proximity to each other (Fig. 1). There was no significant effect of exposure time on ETR_{MAX} (paired *t*-test; $p = 0.35$) or α (paired *t*-test; $p = 0.45$). There was a marginally significant ($p = 0.05$) effect of exposure time on E_k, where E_k was up to 15% lower for PE curves with a 3 min exposure time.

Based on this initial test, we used a 20 s exposure time when generating RLC's across depth gradients. For each RLC, the fiberoptic probe of the DIVING PAM was placed in a holder at a distance 3 mm above the sediment-water interface. Sediments were not dark adapted before commencement of the RLC, but the holder excluded ambient light during the light curve. A saturating light pulse was applied after 20 s at each light intensity to determine yield of photosystem II and relative electron transport rate (rETR). Rapid light curves, with no dark adaptation and exposure increments of less than 30 s, are the accepted protocol for biofilms on sediments because they capture the photophysiological state of the biofilm at the time that they are assessed (Perkins et al. 2011). RLC's with short exposure times also minimize the effects of motile algae moving vertically through the sediments in response to the applied light. This is a significant source of variation in intertidal microphytobenthic biofilms (Perkins et al. 2011). Vertical migration is less problematic in lakes, which lack the highly variable daily light cycles imposed by changes in water depth associated with tides.

Measurements of PAM photosynthesis are correlated with results from oxygen exchange and carbon uptake methods (Kromkamp and Forster 2003; Davoult et al. 2009), but PAM fluorometry generates photosynthesis estimates in relative units that are not directly comparable to bulk oxygen exchange methods without intercalibration. We used the RLCs only to assess variation in the light intensity at onset of photosaturation (E_k) with depth. We converted depth to percent surface light, using K_d from each lake. We quantified variation in E_k as a function of % surface light because acclimation to ambient light availability, not depth per se, drives the widely observed decline in E_k with depth (Kühl et al. 2001; Kirk 2011).

When calculating E_k, we restricted our analysis to the non-photoinhibited portion of the RLC (McMinn et al. 2010) because none of the light curves exhibited photoinhibition at in situ light levels (Vadeboncoeur et al. 2014). Periphyton growing at ≤ 5 m did not exhibit photoinhibition at < 1200 μmol m^{-2} s^{-1} while periphyton growing at > 5 m showed no photoinhibition below 800 μmol m^{-2} s^{-1}. We used SAS Proc NLIN to solve for $rETR_{MAX}$ and α using the hyperbolic tangent function of Jassby and Platt (1976):

$$rETR = rETR_{MAX} \tanh \frac{\alpha E}{rETR_{MAX}} \quad (1)$$

where rETR is relative electron transport rate at light intensity E. Proc NLIN converged on a solution in fewer than 15 iterations for all PE curves. All regressions of rETR (observed) on rETR (expected) were highly significant ($p < 0.001$, $R^2 > 0.95$). After solving for the photo-saturation (E_k (μmol m^{-2} s^{-1}) = $rETR_{MAX}/a$), we regressed E_k with % surface light.

The functions describing the variation in P_{MAX} and E_k with depth were used to calculate primary productivity (PPr_{zt}) for specific depths and time. Again, we used the hyperbolic tangent equation from the PE derivation of Jassby and Platt (1976) to conform with our methods of estimating E_k, because different models yield different PE parameters (Frenette et al. 1993):

$$PPr_{zt} = P_{MAXz} \tanh \frac{E_{zt}}{E_{kz}} \quad (2)$$

where P_{MAXz} is the maximum rate of primary productivity at saturating light intensities at depth z, E_{kz} is the light intensity of onset of saturation at depth z, and E_{zt} is the light intensity at depth z and time t (see below). We used lake-specific functions for variation of P_{MAX} with depth. However, we only collected data for variation in E_k with depth for Sparkling and Trout Lakes. We used separate linear regressions to describe the variation in E_k with % surface light in Trout Lake and Sparkling Lake. We pooled PE data from these two lakes to derive an equation that was applied to the other three lakes.

Variation in light availability at depth is used in the above equations to calculate daily or seasonal rates of primary production. Water column light attenuation (K_d) was measured every 2 weeks in three of the lakes and on days that benthic primary productivity was measured in each lake. Daily solar noon light intensities were collected at the University of Wisconsin-Madison, Trout Lake Station weather station. We calculated surface light intensity every 15 min from sunrise to sunset using the following equation (Kirk 2011):

$$E_{0t} = E_{0Noon} \sin\left(\pi \frac{t}{T}\right) \quad (3)$$

Where E_0t is the surface irradiance at time t and is a function of the surface irradiance at solar noon and day length (T in hours) on the day primary productivity was measured in each lake. Light intensity at time t and depth z (E_{zt}) was calculated using Beers law:

$$E_{Zt} = E_{0_t} e^{-zK_d} \quad (4)$$

Combining Eqs. 2–4, we calculated daily benthic primary production for each depth (BP_z) using 15 min time intervals ($\Delta t = 0.25$ h). BP_z (mg C m^{-2} d^{-1}) was computed at 10 cm depth intervals from the lake edge to the depth of 1% surface light for all daylight hours:

$$BP_Z = \Delta t \sum_{\text{sunrise}}^{\text{sunset}} PPr_{zt} \quad (5)$$

We determined average littoral zone periphyton production, LBP (mg C m^{-2} d^{-1}), for each sampling date by multiplying BP_z by sediment surface area at depth (A_z) and dividing the sum by total littoral sediment surface area (A_L):

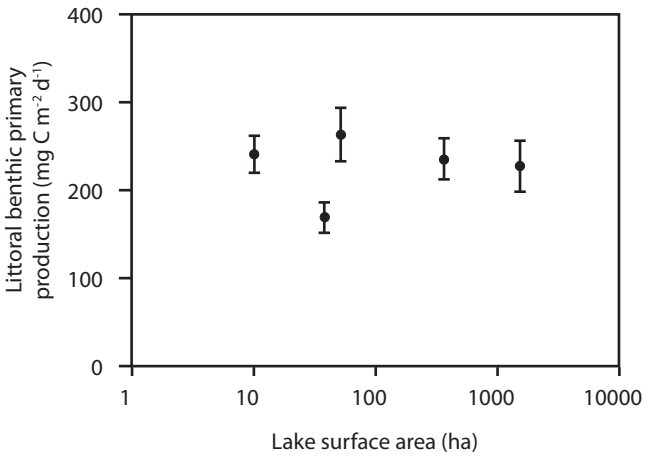

Fig. 2. Area-specific benthic primary production in the littoral zone as a function of lake size. Values are means and standard errors of daily littoral primary production measured on multiple dates within each lake.

$$\mathrm{LBP} = \left(\sum_{0m}^{z\ 1\%} \mathrm{BP}_z \times A_z \right) \div A_\mathrm{L} \tag{6}$$

We used digital geo-referenced bathometric maps of each lake obtained from the NTL LTER (http://lter.limnology.wisc.edu) and divided the area of each bathymetric layer into equal 0.1 m depth intervals.

Sensitivity of LBP to simplifying assumptions

Our most data-rich, or benchmark, estimate of littoral primary production (LBP_{opt}) for each sampling date included the observed variation in P_{MAX} and E_k with depth, used the K_d and solar noon irradiance for the sample date, and used digital elevation maps to determine sediment surface area at depth. We compared this benchmark calculation with calculations that used simplifying assumptions regarding (1) the spatial variation in periphyton photosynthesis; (2) the temporal variation in light availability; and (3) the shape of the lake basin. We used effect size to calculate the percent variation of the simplified model (LBP_s) from the data rich model:

$$\%\ \mathrm{Bias} = \frac{(\mathrm{LBP}_s - \mathrm{LBP}_{opt})}{\mathrm{LBP}_{opt}} \times 100 \tag{7}$$

For all comparisons except between the two methods for estimating morphometry, we calculated effect size for each lake × date combination. We averaged across dates within lakes, such that each lake became a replicate in the analysis. We calculated 95% confidence intervals for % Bias across the five lakes. If the 95% confidence interval crossed 0, then the simplification did not consistently bias estimates of LBP in one direction. The magnitude of the 95% confidence interval was an index of the amount of error generated by the simplified model. We analyzed each lake separately and used dates as replicates for the comparison of morphometric models.

We first tested the sensitivity of daily LBP estimates to observed spatial variation in the PE parameters P_{MAX} and E_k. We compared the optimal daily estimates to calculations that used (1) P_{MAX} from shallowest sample depth; (2) the unweighted average of P_{MAX} from all sample depths; (3) the geometric mean P_{MAX}. To quantify the effects of spatial variation in E_k, we compared LBP_{opt} with estimates that incorporated the observed variation in P_{MAX} with depth but held E_k constant using either (4) the average value of E_k or (5) a literature derived value of E_k (300 μmol m^{-2} s^{-1}; Hill 1996) that is typical of shallow environments. We used incident light and light attenuation (K_d) data from the day of the incubation for all of these comparisons.

We tested the effect of temporal variation in water column light attenuation on estimates LBP by comparing estimates using the optimal model for the days that we measured primary production with estimates for those same days that used an ice free season average of K_d (typically 05 May–12 October) combined with a 2 week average in day length and solar noon irradiance. For both estimates, we used depth-specific values of P_{MAX} and E_k as PE parameters.

The distribution of sediments with depth is a function of lake shape and is rarely uniform. We compared primary production estimates in the study lakes using our best estimates of sediment distribution (derived from digital elevation maps) with those using two simplified morphometric models derived from Vadeboncoeur et al. (2008) and Carpenter (1983). For the simplified model based on Vadeboncoeur et al. (2008), we used mean depth (z_{mean}) and maximum depth (z_{max}) to estimate the depth ratio ($\mathrm{DR} = z_{mean}/z_{max}$) and a lake shape factor γ. There was a typographical error in the placement of γ in Vadeboncoeur et al. (2008). The correct equation is presented here:

$$A_Z = A_0 \left[1 - \left(\frac{z}{z_{MAX}} \right)^{\gamma} \right] \tag{8}$$

$$\gamma = \frac{\mathrm{DR}}{(1 - \mathrm{DR})} \tag{9}$$

where A_0 is lake surface area (derived from the digitized data), and A_Z is area at depth z. The Carpenter (1983) equation treats lake basins as quadratic surfaces and can be used for assessment of littoral sediment distribution (Genkai-Kato et al. 2012):

$$\Delta S = S(z + dz) - S(z) = \left[\frac{6(2\mathrm{DR} - 1)}{z_{mean}^2} z - \frac{2(3\mathrm{DR} - 2)}{z_{mean}} \right] dz \tag{10}$$

where S is the sediment surface area at depth shallower than depth z and dz is an incremental change in depth (0.1 m in our model).

Based on the most data-rich model, summer average LBP was lowest in Crystal Lake (169 mg C m^{-2} d^{-1}) and highest

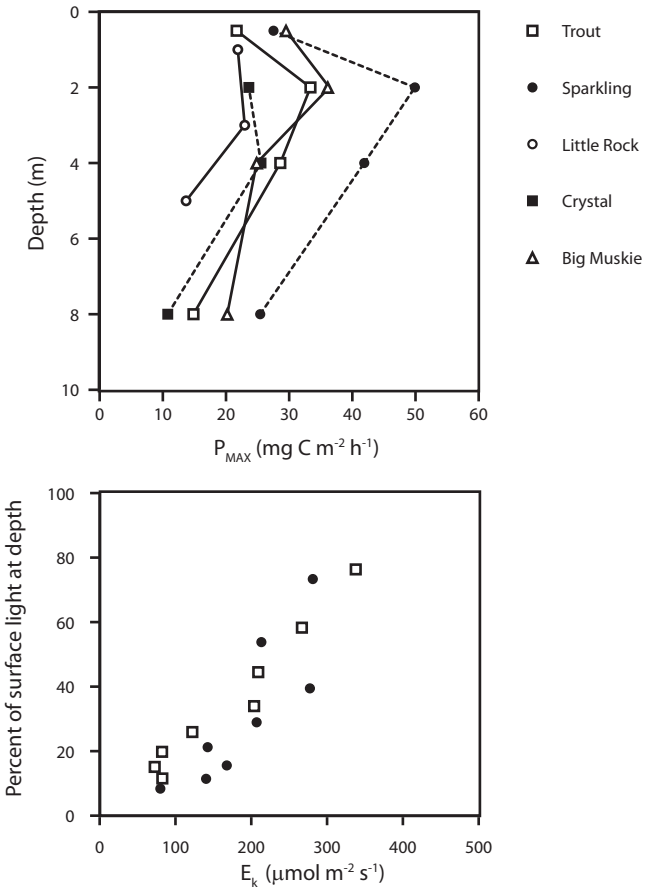

Fig. 3. Light saturated benthic primary production (P_{MAX}) as a function of depth (**a**); and light intensity at the onset of photosaturation (E_k) vs. % surface light at depth in Sparkling and Trout lakes, where $E_k = 3.3\% E_0 + 68$ ($R^2 = 0.69$, $p < 0.0001$) (**b**). E_k data are mean values from two transects in each lake.

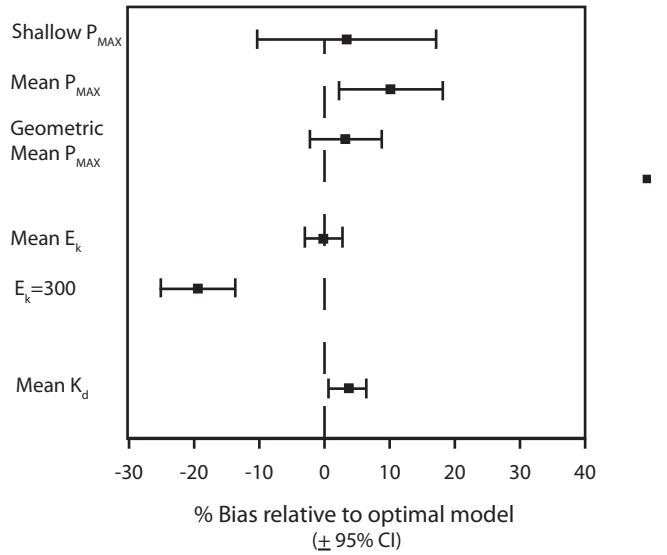

Fig. 4. Average littoral zone benthic primary production (LBP) was sensitive to assumptions regarding variation in photosynthesis-irradiance parameters with depth. The percent deviation from the optimal model depended on whether P_{MAX} at the shallowest depth, the average P_{MAX}, or the geometric mean P_{MAX} was used in LBP calculations. Light intensity of onset of photosaturation model inputs represent scenarios in which E_k is either averaged throughout the littoral zone, or based on a literature-derived constant value of 300 μmol m^{-2} s^{-1}. LBP outcomes using summer average light attenuation coefficients (K_d) were not significantly different than the optimal model that incorporated temporally explicit values of K_d. Values are % deviation from average summer LBP and 95% confidence intervals. Ranges that overlap with the dashed line are not significantly different from the optimal model.

for Sparkling Lake (263 mg C m^{-2} d^{-1}). There was no trend between average littoral zone primary production and either water column P concentration (Table 1) or lake size (Fig. 2).

Assessment and discussion

Effects of spatial variation in photosynthetic parameters

P_{MAX} was highest in the mid epilimnion in in all study lakes (Fig. 3a) and ranged from 4 mg C m^{-2} h^{-1} to 75 mg C m^{-2} h^{-1}. P_{MAX} for any depth × lake combination varied among dates, but no consistent temporal trends were observed in any of the lakes. Photosynthetic maxima occurred between 0.5 m and 5 m (Fig. 3a), which corresponds to between 75% and 25% of surface light (Vadeboncoeur et al. 2014). This mid-epilimnetic productivity maximum likely coincides with a peak in periphyton biomass below the zone of wave disturbance; below this peak, periphyton production is limited by light (Vadeboncoeur et al. 2014). Similar mid-epilimnetic productivity peaks are documented in both marine and freshwater littoral zones (Ask et al. 2009; Forehead and Thompson 2010).

Due to the non-linear distribution of photosynthesis with depth, P_{MAX} parameter selection significantly affected estimates of LBP. Photosynthesis rates might be obtained without using scuba at very shallow depths. Applying P_{MAX} measurements obtained from the shallowest sampling depth (≤1 m) to all depths overestimated LBP by an average of only 3.5%, but the 95% confidence interval was very large because for some day-lake combinations, P_{MAX} exhibited a monotonic decline with depth rather than the typical unimodal pattern (Fig. 3a). Applying the unweighted mean P_{MAX} to all depths overestimated LBP by an average of 10% compared with calculations that used the continuous LOESS function to describe variation in P_{MAX}. Applying the geometric mean productivity to all depths yielded the least variation from the optimal LBP calculation, overestimating LBP by an average of only 3.3% (Fig. 4). All these simplifications tended to yield overestimates relative to the benchmark model because the littoral zone extended below the maximum sampling depth in all lakes except Little Rock Lake.

Light intensity at onset of photosaturation is an index of the degree of photoacclimation of a photoautotrophic

community (Moore et al. 2006). Periphytic algae acclimate to low light by increasing cellular chlorophyll content, which increases light-harvesting efficiency (α). Consequently, algal communities adapted to low light levels (deeper periphyton communities) generally have a higher photosynthetic efficiency and photosaturate at lower light intensities than those adapted to high light intensities (Hill 1996; Falkowski and Raven 2007; Godwin et al. 2014). Combining the data from Trout and Sparkling Lakes, E_k declined with depth ($E_{kz} = 3.3\%\ E_0 + 68\ R^2 = 0.69\ p < 0.0001$, Fig. 3b), indicating increased photosynthetic efficiency at subsaturating light levels (Kühl et al. 2001; Glud et al. 2002). The original autotrophic structure model used a literature-derived value of E_k (300 μmol m^{-2} s^{-1}) that was accurate only for periphyton growing at < 1 m in the study lakes. All but two measured E_k value were < 300 μmol m^{-2} s^{-1}, and applying $E_k = 300$ μmol m^{-2} s^{-1} to all depths underestimated LBP by 19% compared with the optimal model (Fig. 4). Using a single E_k averaged across depths produced an estimate of LBP within ± 2% of the optimal model. This simplification generated the lowest variation from the optimal model of any of the tested parameters. Ideally, the relationship between E_k and depth should be established for any focal lake. However, judicial selection of an average E_k that reflects algal assemblages acclimated to a broad range of light intensities may be sufficient to reduce systematic bias in estimates of LBP.

Variation in P_{MAX} and E_k with depth (Fig. 3) in the study lakes contrasts with the original autotrophic structure model in which P_{MAX} reflected a range of values obtained from lakes around the world, and E_k was representative of epipelic assemblages growing at relatively high light intensities (Vadeboncoeur et al. 2008). Quantifying the form of variation in P_{MAX} with depth in lakes is non-trivial, and the spatial resolution used in this study (3–4 depths) is probably the minimum necessary. The sensitivity of LBP estimates to spatial variation in P_{MAX} and E_k and the relative paucity of benthic primary productivity data make describing photosynthesis-irradiance relationships a high priority when calculating benthic algal contributions to whole-lake metabolism.

Effects of temporal variation in light penetration

The spatial variation in P_{MAX} and E_k demonstrate the strong control exerted by extrinsic determinants of light availability on periphyton production. The light attenuation coefficient (K_d) is temporally variable within and among lakes (Markager and Vincent 2000; Kirk 2011). Importantly, K_d determines both the average light intensity experienced by algae at a given depth and the proportion of the lake bottom that is capable of supporting algal growth. Light attenuation coefficients averaged over the ice-free season were very similar among the lakes during the years that we sampled (0.28–0.34, Table 1), but ranged from 0.21 to 0.36 within individual lakes. Temporal variation in water clarity was not synchronous among the lakes (data not shown). Thus, using a summer average K_d either underestimated or overestimated LBP relative to the optimal model. This variation was within ± 5% of the optimal model (Fig. 4), which is probably acceptable for many current applications of estimating lake autotrophic structure. However, the original autotrophic structure model demonstrated that among-lake variation in K_d, whether generated by DOC or phytoplankton biomass, strongly determines both the total amount of benthic primary production and the relative distribution of primary production between benthic and planktonic habitats (Vadeboncoeur et al. 2008). These general patterns have been strongly supported by subsequent research (Karlsson et al. 2009; Godwin et al. 2014). Although the calculations of LBP were relatively insensitive to temporal variation in K_d in these particular lakes, changes in hydrology associated with climate change may alter the magnitude and timing of DOC loading to lakes (Williamson et al. 1999, 2009). Under these, or similar scenarios, variation in water clarity should be explicitly paired with temporal variation in surface light to most accurately calculate LBP.

Effects of morphometry

Total LBP is determined by both the proportion of lake sediments that are illuminated, and the relative distribution of sediments with respect to depth, which is a function of basin shape. Digital bathymetric maps and the simplified morphometric models were based on the same amount of total sediment surface area within a lake, but the methods yielded different sediment distribution with depth and hence slightly different littoral sediment surface area. The distribution of littoral sediments generated by the Vadeboncoeur et al. (2008) morphometric model corresponded reasonably well with the actual bathymetry of Little Rock, Sparkling and Trout Lakes, but failed to capture irregularities in sediment distribution in Crystal Lake and Big Muskie Lakes (Fig. 5).

The use of the simplified morphometric models in combination with the depth-specific variation in PE parameters significantly affected LBP, leading to substantial over- or underestimates of LBP depending on lake shape (Fig. 6). The Carpenter model yielded LBP values nearly identical to the Vadeboncoeur model for three of the lakes and LBP values similar to the optimal model for the two largest lakes. Simple models of basin shape provide a useful first approximation of the distribution of productivity on littoral sediments, but bathymetric information is increasingly available for lakes and should be temporally stable. Whenever possible, detailed bathymetry should be used to calculate LBP for specific lakes.

Comments and recommendations

Our approach in describing the variation in PE parameters with depth is an unconventional combination of two very

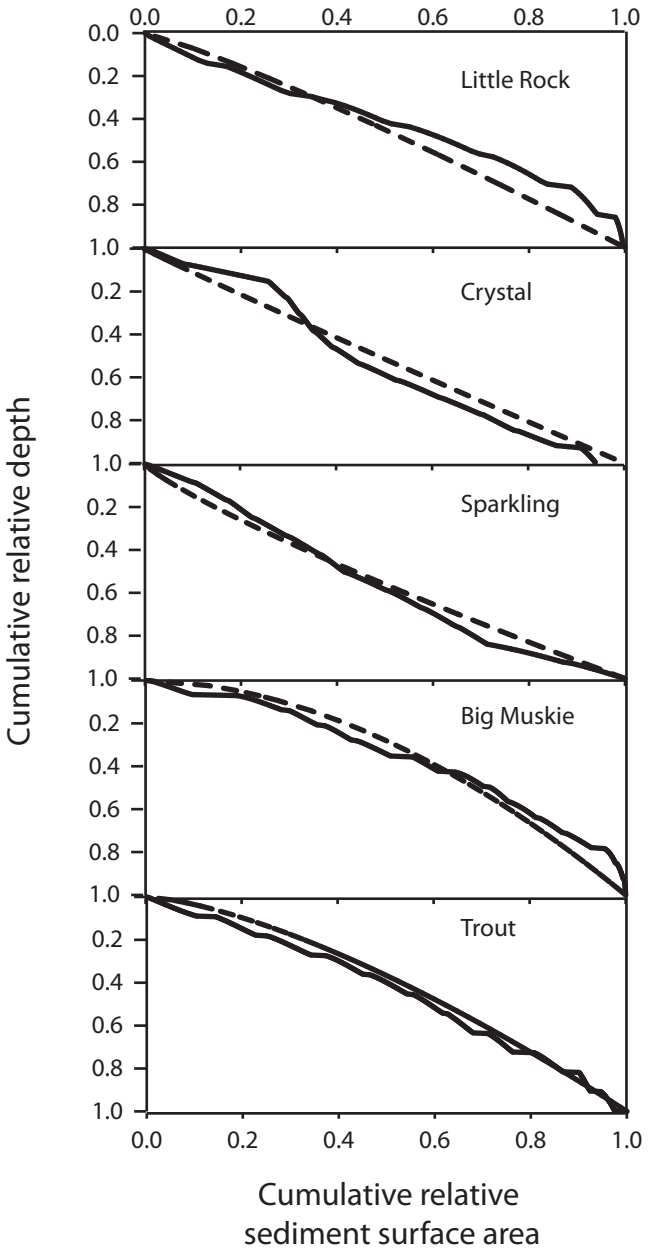

Fig. 5. Distribution of sediments with respect to depth. The *y*-axis is the relative proportion of maximum depth and the *x*-axis is the cumulative fraction of total sediment surface area at that relative depth. The solid line is bathymetry based on bathymetric maps and the dashed line is sediment surface area estimated from the Vadeboncoeur et al. (2008) morphometric model derived from the mean and maximum depth of each lake.

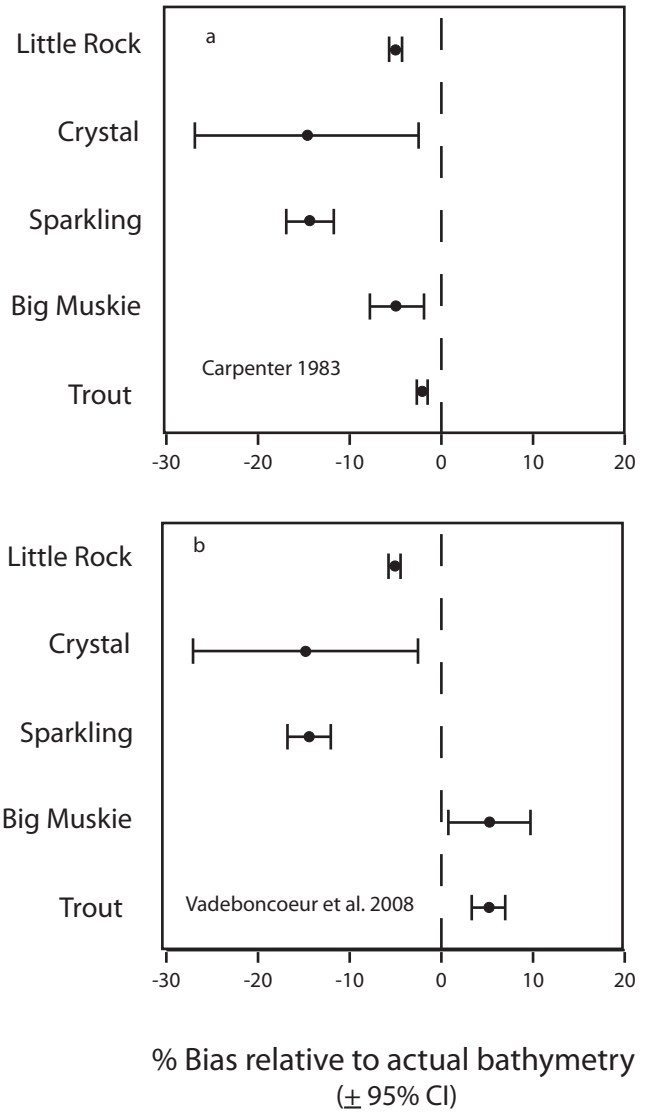

Fig. 6. The influence of using simplified morphometric models of basin shape from Carpenter (1983) (**a**) or Vadeboncoeur et al. (2008) (**b**) rather than actual lake bathymetry on estimates of littoral benthic primary production (LBP). Values are % deviation from optimal estimates of LBP and error bars represent 95% confidence intervals.

different tools in primary production research. Productivity measurements using PAM and oxygen exchange are correlated (Barranguet and Kromkamp 2000; Glud et al. 2002; Perkins et al. 2011), but both methods have associated error and different strengths. Oxygen evolution techniques provide a rapid, relatively inexpensive field method of measuring production that can be converted to carbon fixation rates. Direct production measurements are particularly important for ecosystem-scale research because the chlorophyll-based monitoring techniques developed for phytoplankton translate poorly to periphyton (Baulch et al. 2009; Vadeboncoeur et al. 2014). PAM measurements cannot be directly related to carbon fixation without detailed information about the thickness of the photosynthetically active algal biofilm, which cannot be assessed in situ (Morris et al. 2008; Perkins et al. 2011). However, unlike oxygen exchange methods, PAM fluorometry is an excellent tool for collecting spatially extensive data that characterize photoacclimation of periphyton growing at different depths. E_k derived from

PAM can be higher or lower than those derived from incubation techniques (Barranguet and Kromkamp 2000; Davoult et al. 2008; Hancke et al. 2008), but the overall negative relationship between E_k and ambient light intensity seen in Fig. 3 has been described using a variety of tools including oxygen microelectrodes, carbon uptake, and PAM (Hill et al. 1995; Kühl et al. 2001; Hill and Dimick 2002; Falkowski and Raven 2007). One of our main goals was to assess whether variation in PE parameters with depth affected estimates of littoral zone primary production. Pairing PAM fluorometry with in situ incubations allowed us to address that question.

It is relatively straightforward and inexpensive to use chambers and oxygen exchange methods to measure benthic photosynthesis in lake littoral zones. Subsequent to this study, we have updated our methods to use optical dissolved oxygen probes instead of Winkler titrations to measure O_2. Optical probes do not require sample stirring and fit easily into 60 cc syringes that are used to sample water from chambers. Also, we now use five light and five dark chambers per depth to improve our estimates of P_{MAX}. To get accurate measurements of light saturated photosynthesis (P_{MAX}), incubations need to be made at midday. Photoinhibition of periphyton on sediments is rarely detected at in situ light intensities because of strong photoadaptation to ambient light climates (Vadeboncoeur et al. 2001, 2014). Epilimnetic cores can be incubated at shallow depths to ensure saturating light intensities so long as incubation temperature equals collection temperature.

Either photosynthetic efficiency at limiting light intensities (α) or E_k ($= P_{MAX}/\alpha$) must be known in addition to P_{MAX} to extrapolate to daily production rates. In the absence of access to a PAM fluorometer, E_k can be obtained using a series of screens to reduce light intensity to the chambers. The latter approach greatly increases the number of samples required from each depth. We have found it difficult to get well-defined field PE curves by incubating cores from a single depth at different light intensities for two reasons: first, there is spatial variability in the structure of periphyton on sediments which produces variability in productivity measurements at the scale of centimeters to meters. Second, good resolution is required at low light intensities to accurately describe the light limiting portion of the PE curve. This can be difficult if the changes in O_2 concentrations over the duration of the incubation are small relative to dark chambers. Extending the incubation time for cores at low light intensities and increasing the number of replicates at each light intensity can alleviate these limitations.

The different time scales required for oxygen incubations and PAM fluorometry precluded meaningful comparisons of E_k estimates between the two methods. Intercalibration of RLC's with light curves generated by oxygen methods would involve incubation of a single core at >9 different light intensities. Incubations of 1–4 h (depending on depth) were required to detect a change in oxygen at high light intensities. Constructing a PE curve based on bulk oxygen exchange might require >18 h, a time span over which algae exhibit endogenous photosynthetic rhythms (Perkins et al. 2011). The equation of the line describing the decline in E_k with depth generated by the PAM may differ from any function derived from core incubations, but it is not clear if this difference increases or reduces errors in estimates of LBP. Both methods have associated error, but the PAM is the far superior tool for characterizing spatial variation in photoacclimation of periphyton at the whole-lake scale.

Variation in photosynthetic parameters with depth strongly affected estimates of average littoral primary zone production. Using only P_{MAX} and E_k values obtained from shallow depths for the entire littoral zone introduces bias with opposite signs (Fig. 4). Therefore, the individual bias introduced by each parameter tends to cancel out. However, the unimodal trend in P_{MAX} with depth may not be universal in lakes, and effort invested in determining spatial variation in both PE parameters will yield the most accurate estimates of LBP. This study was conducted during the summer months, and temporal variation in PE parameters was less pronounced than spatial variation. However, annual rates of production would require careful assessment of periphyton productivity during other seasons.

Although temporal variation in light attenuation (K_d) had little effect on estimates of summer LBP (Fig. 4), accurate estimates of K_d are an essential part of the calculation of benthic primary production. We have used the autotrophic structure model to estimate LBP in lakes for which phytoplankton productivity and food web data were available (Vander Zanden et al. 2011). It was surprisingly difficult to find light attenuation data (other than Secchi depth) for those lakes. Routine light meter measurements constitute a critical component of assessing lake autotrophic structure. It would be helpful if K_d measurements for lakes were collected and published more widely. Light attenuation data can be combined with readily available climate data on day length and solar radiation to describe seasonal changes light availability at depth.

Lake basins have non-uniform depth distribution of sediments. The simplified morphometric model of Vadeboncoeur et al. (2008) was derived by fitting a continuous function to a large population of lake basins from throughout the world, while that of Carpenter (1983) was based on fitting lake basins to quadratic surfaces. For these five lakes, the percent bias relative to calculations using actual bathymetry was negatively correlated with depth ratio for both models, which is problematic if it reflects a real bias of these bathymetric models. The Vadeboncoeur et al. (2008) function introduced substantial error into estimates of LBP, in part because it generated large changes in surface area over small depth increments in the shallowest part of the lakes. Although our analysis is not comprehensive, we recommend using the Carpenter (1983) lake morphometry equations, rather than those of Vadeboncoeur

et al. (2008). Ideally, actual bathymetry should be used. Small depth increments (e.g., 0.1 m) are suitable for calculating changes in productivity with depth for highly irregular or turbid basins. Larger depth intervals may be appropriate for deep, clear lakes with extensive littoral zones.

Littoral benthic algae are a critical, but often cryptic, basal resource for lake food webs. Routine inclusion of LBP in whole-lake metabolism and food web studies will enhance our understanding of energy flow in lakes. The data from these five lakes emphasize, once again, the sensitivity of benthic primary producers to the ambient light climate. Eutrophication, invasive species, and variation in DOC loading associated with climate and land use change, all alter the light climate in lakes (Williamson et al. 1999, 2009; Vadeboncoeur et al. 2008, Karlsson et al. 2009; Higgins and Vander Zanden 2010; Hampton et al. 2011; Althouse et al. 2014; Godwin et al. 2014). The effects of these changes in water clarity on benthic algae can be quantified by incorporation of depth-specific variation in periphyton photosynthesis and sediment surface area into models of whole-lake primary production. Benthic algal inputs are the least well constrained portion of trophic basis of production in lakes, and there is a compelling need to better quantify littoral production dynamics in the face of multiple stresses on lake ecosystems.

References

Althouse, B., S. Higgins, and M. J. Vander Zanden. 2014. Benthic and planktonic primary production along a nutrient gradient in Green Bay, Lake Michigan, USA. Freshw. Sci. **33**: 487–498. doi:10.1086/676314

Ask, J., J. Karlsson, L. Persson, P. Ask, P. Bystrom, and M. Jansson. 2009. Whole-lake estimates of carbon flux through algae and bacteria in benthic and pelagic habitats of clear-water lakes. Ecology **90**: 1923–1932. doi:10.1890/07-1855.1

Barranguet, C., and J. Kromkamp. 2000. Estimating primary production rates from photosynthetic electron transport in estuarine microphytobenthos. Mar. Ecol. Prog. Ser. **204**: 39–52. doi:10.3354/meps204039

Baulch, H. M., M. A. Turner, D. L. Findlay, R. D. Vinebrooke, and W. F. Donahue. 2009. Benthic algal biomass—measurement and errors. Can. J. Fish. Aquat. Sci. **66**: 1989–2001. doi:10.1139/F09-122

Brett, M. T., M. J. Kainz, S. J. Taipale, and H. Seshan. 2009. Phytoplankton, not allochthonous carbon, sustains herbivorous zooplankton production. Proc. Natl. Acad. Sci. USA **106**: 21197–21201. doi:10.1073/pnas.0904129106

Carignan, R., A. Blais, and C. Vis. 1998. Measurement of primary production and community respiration in oligotrophic lakes using the Winkler method. Can. J. Fish. Aquat. Sci. **55**: 1078–1084. doi:10.1139/cjfas-55-5-1078

Carpenter, S. R. 1983. Lake geometry: Implications for production and sediment accretion rates. J. Theor. Biol. **105**: 273–286. doi:10.1016/S0022-5193(83)80008-3

Carpenter, S. R., and others. 2001. Trophic cascades, nutrients, and lake productivity: Whole-lake experiments. Ecol. Monogr. **71**: 163–186. doi:10.1890/0012-9615(2001)071[0163:TCNALP]2.0.CO;2

Davoult, D., A. Migné, A. Créach, F. Gévaert, C. Hubas, N. Spilmont, and G. Boucher. 2009. Spatio-temporal variability of intertidal benthic primary production and respiration in the western part of the Mont Saint-Michel Bay (Western English Channel, France). Hydrobiologia **620**: 163–172. doi:10.1007/s10750-008-9626-3

Devlin, S. P., M. J. Vander Zanden, and Y. Vadeboncoeur. 2013. Depth-specific variation in carbon isotopes demonstrates resource partitioning among the littoral zoobenthos. Freshw. Biol. **58**: 2389–2400. doi:10.1111/fwb.12218

Falkowski, P. G., and J. A. Raven 2007. Aquatic photosynthesis, 2nd ed. Princeton Univ. Press.

Fee, E. 1969. A numerical model for estimation of photosynthetic production, integrated over time and depth, in natural waters. Limnol. Oceanogr. **14**: 906–911. doi:10.4319/lo.1969.14.6.0906

Fee, E. 1979. Relation between lake morphometry and primary productivity and its use in interpreting whole-lake eutrophication experiments. Limnol. Oceanogr. **24**: 401–416. doi:10.4319/lo.1979.24.3.0401

Fee, E. 1990. Computer programs for calculating in-situ phytoplankton photosynthesis. Canadian Technical Report of Fisheries and Aquatic Sciences No. 1740. Department of Fisheries and Oceans, Central and Arctic Region, Winnipeg, Manitoba.

Forehead, H. I., and P. A. Thompson. 2010. Microbial communities of subtidal shallow sandy sediments change with depth and wave disturbance, but nutrient exchanges remain similar. Mar. Ecol. Prog. Ser. **414**: 11–26. doi:10.3354/meps08734.

Frenette, J. J., S. Demers, L. Legendre, and J. Dodson. 1993. Lack of agreement among models for estimating the photosynthetic parameters. Limnol. Oceanogr. **38**: 679–687. doi:10.4319/lo.1993.38.3.0679

Genkai-Kato, M., Y. Vadeboncoeur, L. Liboriussen, and E. Jeppesen. 2012. Benthic–planktonic coupling, regime shifts, and whole-lake primary production in shallow lakes. Ecology **93**: 619–631. doi:10.1890/10-2126.1

Glud, R. N., M. Kühl, F. Wenzhöfer, and S. Rysgaard. 2002. Benthic diatoms of a high Arctic fjord (Young Sound, NE Greenland): Importance for ecosystem primary production. Mar. Ecol. Prog. Ser. **238**: 15–29. doi:10.3354/meps238015

Godwin, S. C., S. E. Jones, B. C. Weidel, and C. T. Solomon. 2014. Dissolved organic carbon concentration controls benthic primary production: Results from in situ chambers in north-temperate lakes. Limnol. Oceanogr. **59**: 2112–2120. doi:10.4319/lo.2014.59.6.2112

Hampton, S. E., S. C. Fradkin, P. R. Leavitt, and E. E. Rosenberger. 2011. Disproportionate importance of the nearshore habitat for the food web of a deep oligotrophic lake. Mar. Freshw. Res. **62**: 350–358. doi:10.1071/MF10229

Hancke, T. B., K. Hancke, G. Johnsen, and E. Sakshaug. 2008. Rate of O_2 production derived from Pulse-Amplitude-Modulated fluorescence: Testing three biooptical approaches against measured O_2-production rate. J. Phycol. **44**: 803–813. doi:10.1111/j.1529-8817.2008.00509.x

Hanson, P. C., D. L. Bade, S. R. Carpenter, and T. K. Kratz. 2003. Lake metabolism: Relationships with dissolved organic carbon and phosphorus. Limnol. Oceanogr. **48**: 1112–1119. doi:10.4319/lo.2003.48.3.1112

Higgins, S. N., and M. J. Vander Zanden. 2010. What a difference a species makes: A meta–analysis of dreissenid mussel impacts on freshwater ecosystems. Ecol. Monogr. **80**: 179–196. doi:10.1890/09-1249.1

Higgins, S., B. Althouse, S. Devlin, Y. Vadeboncoeur, and M. J. Vander Zanden. 2014. Potential for large-bodied zooplankton and dreissenids to alter the productivity and autotrophic structure of lakes. Ecology **95**: 2257–2267. doi:10.1890/13-2333.1

Hill, W. R. 1996. Effects of light, p. 121–148. *In* R. Jan Stevenson, M. L. Bothwell and R. L. Lowe [eds.], Algal ecology. Academic Press.

Hill, W. R., M. G. Ryon, and E. M. Schilling. 1995. Light limitation in a stream ecosystem: Responses by primary producers and consumers. Ecology **76**: 1297–1309. doi:10.2307/1940936

Hill, W. R., and S. M. Dimick. 2002. Effects of riparian leaf dynamics on periphyton photosynthesis and light utilisation efficiency. Freshw. Biol. **47**: 1245–1256. doi:10.1046/j.1365-2427.2002.00837.x

Jassby, A. 1998. Interannual variability at three inland water sites: Implications for sentinel ecosystems. Ecol. Appl. **8**: 277–287. doi:10.2307/2641067

Jassby, A., and T. Platt. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol. Oceanogr. **21**: 540–547. doi:10.4319/lo.1976.21.4.0540

Karlsson, J., P. Bystrom, J. Ask, P. Ask, L. Persson, and M. Jansson. 2009. Light limitation of nutrient-poor lake ecosystems. Nature **460**: 506–509. doi:10.1038/nature08179

Kirk, J. T. O. 2011. Light and photosynthesis in aquatic ecosystems, 3rd ed. Cambridge Univ. Press.

Kromkamp, J., and R. Forster. 2003. The use of variable fluorescence measurements in aquatic ecosystems: Differences between multiple and single turnover measuring protocols and suggested terminology. Eur. J. Phycol. **38**: 103–112, doi:10.1080/0967026031000094094

Kühl, M., R. N. Glud, J. Borum, R. Roberts, and S. Rysgaard. 2001. Photosynthetic performance of surface-associated algae below sea ice as measured with a pulse-amplitude-modulated (PAM) fluorometer and O2 microsensors. Mar. Ecol. Prog. Ser. **223**: 1–14. doi:10.3354/meps223001

Loeb, S. L., J. E. Reuter, and C. R. Goldman. 1983. Littoral zone production of oligotrophic lakes, p. 161–167. *In* R. Wetzel [ed.], Periphyton of freshwater ecosystems. Dr. W. Junk Publishers.

Malkin, S. Y., S. A. Bocaniov, R. E. Smith, S. J. Guildford, and R. E. Hecky. 2010. In situ measurements confirm the seasonal dominance of benthic algae over phytoplankton in nearshore primary production of a large lake. Freshw. Biol. **55**: 2468–2483. doi:10.1111/j.1365-2427.2010.02477.x

Markager, S., and W. F. Vincent. 2000. Spectral light attenuation and the absorption of UV and blue light in natural waters. Limnol. Oceanogr. **45**: 642–650. doi:10.4319/lo.2000.45.3.0642

McMinn, A., A. Pankowskii, C. Ashworth, R. Bhagooli, P. Ralph, and K. Ryan. 2010. In situ net primary productivity and photosynthesis of Antarctic sea ice algal, phytoplankton and benthic algal communities. Mar. Biol. **157**: 1345–1356. doi:10.1007/s00227-010-1414-8

Moore, C. M., and others. 2006. Phytoplankton photoacclimation and photoadaptation in response to environmental gradients in a shelf sea. Limnol. Oceanogr. **51**: 936–949. doi:10.4319/lo.2006.51.2.0936

Morris, E. P., R. M. Forster, J. Peene, and J. C. Kromkamp. 2008. Coupling between Photosystem II electron transport and carbon fixation in microphytobenthos. Aquat. Microb. Ecol. **50**: 301–311. doi:10.3354/ame01175

Perkins, R. G., and others. 2011. The application of variable chlorophyll fluorescence to microphytobenthic biofilms. *In* D. J. Suggett, M. Borowitzka and O. Prášil (eds.), Chorophyll a fluorescence in aquatic sciences: Methods and applications, Developments in applied phycology 4. Springer.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R-project.org/

Vadeboncoeur, Y., D. Lodge, and S. Carpenter. 2001. Whole-lake fertilization effects on distribution of primary production between benthic and pelagic habitats. Ecology **82**: 1065–1077. doi:10.1890/0012-9658(2001)082[1065:WLFEOD]2.0.CO;2

Vadeboncoeur, Y., and A. D. Steinman. 2002. Periphyton function in lake ecosystems. Sci. World J. **29**: 1449–1468. doi:10.1100/tsw.2002.294

Vadeboncoeur, Y., E. Jeppesen, M. J. Vander Zanden, H.-H. Schierup, K. Cristoffersen, and D. M. Lodge. 2003. From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. Limnol. Oceanogr. **48**: 1408–1418. doi:10.4319/lo.2003.48.4.1408

Vadeboncoeur, Y., G. Peterson, M. J. Vander Zanden, and J. Kalff. 2008. Benthic algal production across lake size

gradients: Interactions among morphometry, nutrients, and light. Ecology **89**: 2542–2552. doi:10.1890/07-1058.1

Vadeboncoeur, Y., S. P. Devlin, P. B. McIntyre, and M. J. Vander Zanden. 2014. Is there light after depth? Distribution of periphyton chlorophyll and productivity in lake littoral zones. Freshw. Sci. **33**: 524–536. doi:10.1086/676315

Van de Bogert, M. C., S. R. Carpenter, J. J. Cole, and M. L. Pace. 2007. Assessing pelagic and benthic metabolism using free water measurements. Limnol. Oceanogr.: Methods **5**: 145–155. doi:10.4319/lom.2007.5.145

Van de Bogert, M. C., S. R. Carpenter, J. J. Cole, and M. L. Pace. 2012. Spatial heterogeneity strongly affects estimates of ecosystem metabolism in two north temperate lakes. Limnol. Oceanogr. **57**: 1689–1700. doi:10.4319/lo.2012.57.6.1689

Vander Zanden, M. J., S. Chandra, S. Park, Y. Vadeboncoeur, and C. R. Goldman. 2006. Efficiencies of benthic and pelagic trophic pathways in a subalpine lake. Can. J. Fish. Aquat. Sci. **63**: 2608–2620. doi:10.1139/f06-148

Vander Zanden, M. J., Y. Vadeboncoeur, and S. Chandra. 2011. Fish reliance on littoral-benthic resources and the distribution of primary production in lakes. Ecosystems **14**: 894–903. doi:10.1007/s10021-011-9454-6

Wetzel, R. G. 2001. Limnology: Lake and river ecosystems. Academic Press.

Williams, P. J. B., R. C. T. Raine, and J. R. Bryan. 1979. Agreement between the C-14 and oxygen methods of measuring phytoplankton production—reassessment of the photosynthetic quotient. Oceanol. Acta **2**: 411–416.

Williamson, C. E., D. P. Morris, M. L. Pace, A. G. Olson, and O. G. Olson. 1999. Dissovled organic carbon and nutrients as regulators of lake ecosystems: Resurrection of a more integrated paradigm. Limnol. Oceanogr. **44**: 795–803. doi:10.4319/lo.1999.44.3_part_2.0795

Williamson, C. E., J. E. Saros, and D. W. Schindler. 2009. Sentinels of change. Science **323**: 887–888. doi:10.1126/science.1169443

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