

BENTHIC ALGAL PRODUCTION ACROSS LAKE SIZE GRADIENTS: INTERACTIONS AMONG MORPHOMETRY, NUTRIENTS, AND LIGHT

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Abstract. Attached algae play a minor role in conceptual and empirical models of lake ecosystem function but paradoxically form the energetic base of food webs that support a wide variety of fishes. To explore the apparent mismatch between perceived limits on contributions of periphyton to whole-lake primary production and its importance to consumers, we modeled the contribution of periphyton to whole-ecosystem primary production across lake size, shape, and nutrient gradients. The distribution of available benthic habitat for periphyton is influenced by the ratio of mean depth to maximum depth ($DR = \bar{z}/z_{\max}$). We modeled total phytoplankton production from water-column nutrient availability, \bar{z} , and light. Periphyton production was a function of light-saturated photosynthesis (BP_{\max}) and light availability at depth. The model demonstrated that depth ratio (DR) and light attenuation strongly determined the maximum possible contribution of benthic algae to lake production, and the benthic proportion of whole-lake primary production (BP_f) declined with increasing nutrients. Shallow lakes ($\bar{z} \leq 5$ m) were insensitive to DR and were dominated by either benthic or pelagic primary productivity depending on trophic status. Moderately deep oligotrophic lakes had substantial contributions by benthic primary productivity at low depth ratios and when maximum benthic photosynthesis was moderate or high. Extremely large, deep lakes always had low fractional contributions of benthic primary production. An analysis of the world's largest lakes showed that the shapes of natural lakes shift increasingly toward lower depth ratios with increasing depth, maximizing the potential importance of littoral primary production in large-lake food webs. The repeatedly demonstrated importance of periphyton to lake food webs may reflect the combination of low depth ratios and high light penetration characteristic of large, oligotrophic lakes that in turn lead to substantial contributions of periphyton to autochthonous production.

Key words: average lake depth; chlorophyll; DOC; eutrophication; lake productivity; light attenuation; littoral–pelagic links; microphytobenthos; modeling periphyton production; morphometry; periphyton; primary production.

INTRODUCTION

The idea that ecosystem primary production determines the productivity of higher trophic levels is deeply rooted in efforts to measure ecosystem metabolism (Lindeman 1942). Lakes are often categorized based on the magnitude of phytoplankton production in the water column, while contributions of attached algae (periphyton) are rarely measured. Nonetheless, periphyton can make substantial contributions to whole-lake production in small- to moderate-sized lakes (Vadeboncoeur et al. 2003), and stable isotopes show that even in the world's largest lakes, a diversity of fishes rely on littoral energy sources (Hecky and Hesslein 1995, Bootsma et al. 1996, Yoshii 1999). The strong reliance of fish on carbon fixed by periphyton is at odds with the historical

emphasis on phytoplankton-based models of lake food webs. The paucity of estimates of benthic primary production across lake size gradients has led to a dearth of conceptual and empirical models that address the interactive effects of nutrient loading and morphometry on littoral-zone productivity.

The decline in the ratio of littoral surface area to pelagic volume with increasing lake size is at the heart of a perception that periphyton is important only in small or shallow lakes. Available habitat for periphyton depends on illumination of benthic surfaces, and mean depth (\bar{z}) should co-vary with the availability of littoral habitat (Lodge et al. 1998). However, the distribution of benthic surfaces with respect to depth is also a function of basin shape. Basin shape is captured by the depth ratio ($DR = \bar{z}/z_{\max}$), which in natural lakes clusters between 0.3 and 0.7 (Fee 1979, Carpenter 1983). In steep-sided lakes with high DR , the majority of benthic surface occurs in deep areas, while in basins with low

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DR, benthic surface area consists largely of shallow, potentially well-lit littoral plains (Fig. 1).

In addition to total availability of physical habitat, periphyton and phytoplankton are dependent on nutrients and light. Phytoplankton biomass increases with increasing nutrients, (Schindler 1978, Prairie et al. 1989), causing decreased water transparency that negatively affects periphyton (Hansson 1992, Vadeboncoeur et al. 2001). Positive relationships between periphyton biomass (chlorophyll) and lake trophic status are weak or unimodal (Cattaneo 1987, Hansson 1992). Furthermore, periphyton productivity, not biomass, is the variable relevant to an exploration of the potential importance of periphyton in food webs. Periphyton on hard substrata and artificial macrophytes sometimes demonstrate a weak relationship between light-saturated, area-specific photosynthetic rates and nutrients across a eutrophication gradient (DeNicola et al. 2003, Liboriussen and Jeppesen 2006), while periphyton on sediments are negatively impacted by increased shading by phytoplankton (Björk-Ramberg and Ånell 1985, Vadeboncoeur et al. 2003). A predictive understanding of how total littoral primary productivity responds to nutrient enrichment requires both the quantification of light-saturated benthic photosynthesis (BP_{max}), which is rarely measured, and the characterization of the distribution of littoral sediments with light and depth, which is a function of DR.

While the examination of factors driving variation in phytoplankton productivity have engaged the efforts of limnologists for decades, we still have only qualitative models of periphyton productivity (Sand-Jensen and Borum 1991, Wetzel 2001), and those are specifically restricted to small and shallow lakes where macrophytes are abundant. The strong evidence that periphyton and phytoplankton co-dominate the food webs of even the world's largest lakes (Hecky and Hesslein 1995, Bootsma et al. 1996, Yoshii 1999) prompted us to explore the physical and chemical determinants of the relative contributions of periphyton and phytoplankton to whole-lake production across lake size gradients. Our purpose was to explore the effects of basin shape and light attenuation by phytoplankton biomass on potential contributions of periphyton to whole-lake autochthonous production. Rather than attempting to model proximate factors (e.g., grazer density, substrate composition) that determine periphyton productivity within a given lake, we explicitly varied maximum light-saturated periphyton photosynthesis using literature values representing the range of productivity on natural substrata under in situ grazing conditions. The model allows us to explore how morphometry and nutrients interact to determine the relative distribution of algal primary production in benthic and pelagic habitats.

METHODS

We used published relationships to model the distribution of primary production across a lake size

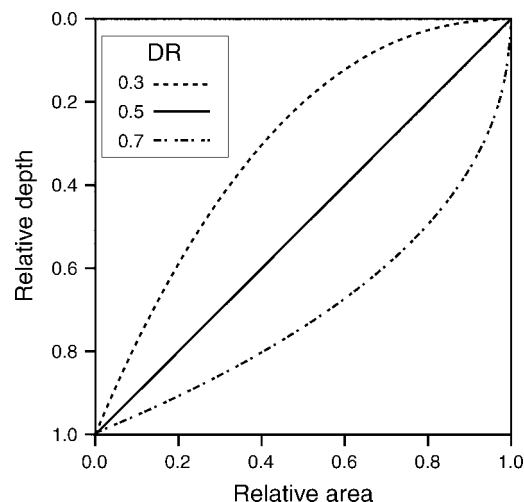


FIG. 1. Distribution of cumulative lake surface area (A/A_0) as a function of relative depth (z/z_{max}) for different depth ratios ($DR = \bar{z}/z_{max}$). The lines denote the proportion of lake sediment surface area occurring at a depth greater than or equal to a given relative depth. The distribution of sediment surface area with depth is described by a shape factor, γ , where $\gamma = DR/(1 - DR)$.

gradient (Tables 1 and 2). Determinants of whole-lake phytoplankton production included inorganic nutrients, light and morphometry. Basin morphometry had two components: size, described by \bar{z} , and a shape factor, $\gamma = DR/(1 - DR)$, derived from the depth ratio ($DR = \bar{z}/z_{max}$). For a given DR, increases in \bar{z} generate concomitant increases in lake surface area (A_0). This simple representation of lake shape was used to generate distributions of sediment area (Fig. 1; Table 1; Eq. 1) similar to those of Carpenter (1983). Model lakes are fully described by DR and \bar{z} , and the model can be run using specific surface areas or volumes. Comparisons were made among lakes with discrete DR and \bar{z} . To inform our evaluation of the influence of DR on primary production in natural lakes, we compiled reliable morphometric data from lakes in the English Lakes District and Canadian shield lakes to calculate DR for lakes across a lake size gradient (Koshinsky 1970, Shannon and Brezonik 1972, Fee 1979, King et al. 2000). We also analyzed morphometric data from the world's largest lakes (surface area $> 500 \text{ km}^2$; Herendorf 1990).

We parameterized phytoplankton productivity (in milligrams of carbon per cubic meter per hour; $\text{mg C} \cdot \text{m}^{-3} \cdot \text{h}^{-1}$) using published ranges and predictive equations for phytoplankton chlorophyll, chlorophyll-specific productivity, light attenuation, and thermocline depth. Total phosphorus (TP) was a proxy for nutrient control of phytoplankton biomass. In the model, midsummer epilimnetic TP concentrations varied between 3 and 1000 mg/m^3 , representing oligotrophic to hypereutrophic lakes. TP determined phytoplankton chlorophyll *a* (Prairie et al. 1989; Table 1; Eq. 3) and

TABLE 1. Equations for the model.

Equation number	Model output	Equation
1	lake surface area, A , at depth z	$A_z = A_0[1 - (z/z_{\max})]^\gamma$
2	lake volume, V , above depth z	$V_z = \gamma z / (\gamma + 1)$
3	phytoplankton chlorophyll a	$\text{Chl} = 0.41 \text{TP}^{0.87}$
4	phytoplankton productivity, PP ($\text{mg C} \cdot \text{m}^{-3} \cdot \text{h}^{-1}$)	$\text{PP}_{\max} = 2.2 \text{Chl}$
5	thermocline depth	$Z_{\text{therm}} = 6.95 A_0^{0.185}$
6	light-attenuation coefficient (m^{-1})	$K_d = K_b + 0.015[\text{Chl}]$
7	light at depth z , time t ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	$I_{zt} = I_{0t} e^{-K_d z}$
8	surface light at time t ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	$I_{0t} = I_{0\max} \sin\left(\pi \frac{t}{\text{daylen}}\right)$
9	daily phytoplankton primary production at depth z (mg C)	$\text{PP}_z = \Delta t \sum_{\text{sunrise}}^{\text{sunset}} \text{PP}_{\max} \tanh(I_{zt}/I_k) (V_z - V_{z-\Delta z})$
10	daily whole-lake phytoplankton production, TPP ($\text{mg C}/\text{m}^2$)	$\text{TPP} = \frac{\sum_{z=0}^{z_{\text{epi}}} \text{PP}_z}{A_0}$
11	daily benthic primary production, BP , at depth z (mg C)	$\text{BP}_z = \Delta t \sum_{\text{sunrise}}^{\text{sunset}} \text{BP}_{\max} \tanh(I_{zt}/I_k) (A_{z-\Delta z} - A_z)$
12	daily whole-lake periphyton production, TBP ($\text{mg C}/\text{m}^2$)	$\text{TBP} = \frac{\sum_{z=0}^{z_{\text{epi}}} \text{BP}_z}{A_0}$

Note: See Table 2 for symbol definitions.

† Sources of equations: Eqs. 1–2, this paper; Eq. 3, Prairie et al. (1989); eq. 4, Guildford et al. (1994); eq. 5, Hanna (1990); Eq. 6, Krause-Jensen and Sand-Jensen (1998); Eqs. 7–10 McBride (1992); Eqs. 11–12, Vadeboncoeur et al. (2001).

chlorophyll a was used to predict phytoplankton carbon fixation (Guildford et al. 1994; Table 1: Eq. 4). Thermocline depth was calculated based on lake area (Hanna 1990; Table 1: Eq. 5). We ran the model both for the epilimnion only and through the thermocline to a depth of 1% surface light. Chlorophyll concentration between the thermocline and 1% light was a function of epilimnetic nutrients, so that metalimnetic chlorophyll concentrations that were up to 5 times greater than epilimnetic chlorophyll in the most oligotrophic lakes (Fee 1976). The attenuation coefficient for downwelling light (K_d) was broken into its components: absorption by phytoplankton (K_{Chl}) and absorption by constituents such as dissolved organic carbon (DOC) and suspended solids (K_b) (Table 1: Eq. 6). We used a background (non-phytoplankton) light attenuation (K_b) of 0.05 m^{-1} for

exceptionally clear lakes, 0.2 for clear oligotrophic lakes, 0.8 for moderately clear lakes, and 2.0 for turbid lakes (Effler et al. 2000, Reinart et al. 2003). For perspective, total K_d ($= K_b + K_{\text{Chl}}$) is 0.08 m^{-1} and 0.18 m^{-1} for Lake Tahoe (USA) and Lake Superior (USA/Canada), respectively, with a range of 0.24 – 1.73 (mean $= 0.73$) in Canada's Experimental Lakes Area (Xenopoulos and Schindler 2001). Light at depth (z) was calculated using Beer's law (Table 1: Eqs. 6–8; see Kirk 1994). Production was calculated at 0.1-m -depth intervals every 15 min of a 15-h day (Table 1: Eq. 9), and summed over all depths to determine whole-lake phytoplankton production (Table 1: Eq. 10).

Models relating benthic algal productivity to water-column nutrients are difficult to develop because only periphyton chlorophyll is typically measured, and

TABLE 2. Definition of model parameters together with units and with input values.

Parameter	Definition	Input values
DR	depth ratio†	0.3, 0.5, 0.7
\bar{z}	mean depth (m)	2, 5, 10, 25, 100
z_{\max}	maximum depth (m)	\bar{z}/DR
Δz	depth interval (m)	0.1
γ	shape factor	$\text{DR}/(1 - \text{DR})$
TP	total phosphorus (mg/m^3)	3, 10, 50, 100, 500, 1000
K_b	non-chlorophyll (i.e., background) light attenuation	0.05, 0.2, 0.8, 2.0
t	hours after sunrise	0.25, 0.5, 0.75, ..., 15
daylen	hours of daylight (day length)	15
$I_{0\max}$	surface light at solar noon ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	1500
Δt	time increment (h)	0.25
BP_{\max}	maximum benthic primary production ($\text{mg C} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$)	5, 50, 120, $28.1 \text{TP}^{0.24}$
I_k	light intensity at onset of saturation ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	$180_{\text{phytoplankton}}, 300_{\text{periphyton}}$

† $\text{DR} = \bar{z}/z_{\max}$.

chlorophyll-specific productivity varies with substratum, grazing intensity, periphyton biomass, and light (Liboriussen and Jeppesen 2006, Vadeboncoeur et al. 2006). Rather than modeling controls on periphyton biomass, we explicitly tested how variation in maximum light-saturated periphyton productivity (BP_{\max}) affected model outcome. We varied BP_{\max} using values representative of the range of substrata and in situ grazing conditions reported in the literature for lakes. The lowest value ($BP_{\max} = 5 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$) is comparable to productivity on rocks and wood in low-alkalinity lakes (Schindler et al. 1973, Björk-Ramberg and Ånell 1985, Turner et al. 1994, Vadeboncoeur et al. 2001). The intermediate value of $50 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ is characteristic of unconsolidated sediments in oligotrophic and mesotrophic lakes. Our highest value ($120 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$) is similar to maximum rates on sediments in a wide range of oligotrophic and moderately productive lakes and of epiphyton production in lakes with moderate to high macrophyte cover (Liboriussen and Jeppesen 2003, Vadeboncoeur et al. 2003, O'Reilly 2006), but it is well below maximum rates reported for lakes and streams (McCormick et al. 1998, Wetzel 2001, Liboriussen and Jeppesen 2003). Given the low contribution of macrophytes to higher trophic levels (James et al. 2000, Kalff 2001), we included macrophytes in our analysis only indirectly as one of many factors that affect areal periphyton productivity.

There are two potential responses of periphyton to nutrient addition for a given lake with a particular shape and substratum composition (captured in the model by varying DR and BP_{\max} , respectively): either periphyton growth is not limited by water-column nutrients and there is a reduction in productivity engendered by shading by phytoplankton biomass, or periphyton is simultaneously positively affected by increased nutrient availability and negatively impacted by reductions in light. We compared littoral contributions to whole-lake primary production when periphyton productivity was a function of light only, and when both light and nutrients limit periphyton productivity. In the light-only model, benthic algal productivity was a function of light at depth (Table 1: Eqs. 6–8 and 11; see McBride 1992), which has been demonstrated for algae on sediments in whole-lake nutrient manipulations (Björk-Ramberg and Ånell 1985, Vadeboncoeur et al. 2001). Our second approach included a stimulatory effect of phosphorus on BP_{\max} , although empirical support for such an effect is inconclusive (Vadeboncoeur et al. 2001, Bonilla et al. 2005, Liboriussen and Jeppesen 2006). DeNicola et al. (2003) found a weak ($R^2 = 0.13$, $P < 0.038$) positive relationship between BP_{\max} and TP on rocks in the shallow littoral zones of a subset of their Irish study lakes. We used this relationship to model an increase in periphyton productivity with TP (Table 1: Eq. 11; Table 2). As in the light only model, realized benthic algal productivity was a function of light and depth (Table 1: Eqs. 6–8 and 11).

Light intensity for onset of saturation (I_k , Eq. 11) for periphyton photosynthesis was set to $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Hill 1996). No photoinhibition parameter was included because the three dimensional structure of periphyton mats precludes any whole-community expression of photoinhibition (Hill and Boston 1991, Dodds et al. 1999). Areal productivity rates were calculated at the temporal and spatial scales described for phytoplankton. Total daily production at each depth was multiplied by the sediment surface area at depth and summed over all depths to determine whole-lake benthic production. The model did not include the equivalent of benthic metalimnetic chlorophyll maxima, which sometimes occur but do not correspond with increases in area-specific productivity (Y. Vadeboncoeur, *unpublished data*).

This model was designed to test the attributes of lakes across eutrophication gradients. It is based on statistical relationships and is not comparable to process models that have been used to explore regime shifts in individual lakes (Scheffer et al. 1993). The output is the average expected distribution of primary production between benthic and pelagic habitats and serves as a heuristic exploration of physical and chemical determinants of periphyton contributions to whole-ecosystem production. The model does not explicitly include top-down effects on productivity for either periphyton or phytoplankton. Rather, variation due to grazing is incorporated in the literature-derived statistical relationships between productivity and resource gradients (Prairie et al. 1989, DeNicola et al. 2003). Below (see *Results*), we discuss specific ranges of nutrients, depth ratios, and rates of primary productivity for clarity of discussion, not because we are attempting to predict primary production in specific natural lakes. We use the model to examine the potential behavior of a range of lake types. Some lakes are unlikely in nature (e.g., highly eutrophic deep lakes), but we include them in our analysis to understand broad patterns in lake ecology.

RESULTS

We used morphometric data from research-lake districts and from the world's largest lakes to assess variation in the depth ratio, DR, in natural lakes. Depth ratios of the world's largest lakes (surface area $> 500 \text{ km}^2$) were distributed between 0 and 1 for shallow lakes ($z \leq 5 \text{ m}$), but the distribution shifted markedly towards lower depth ratios as \bar{z} increased (Fig. 2). Smaller lakes also demonstrated a shift toward lower DR with increasing lake depth (Fig. 2).

In order to generate meaningful estimates of the benthic fraction of whole-lake primary productivity, BP_f , and total benthic primary production, BP, it was essential that the phytoplankton part of the model (1) generate estimates of whole-lake phytoplankton production (in $\text{mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) that are comparable to those found in natural lakes within a given trophic category and (2) produce plausible changes in light with depth. Model estimates of total daily phytoplankton produc-

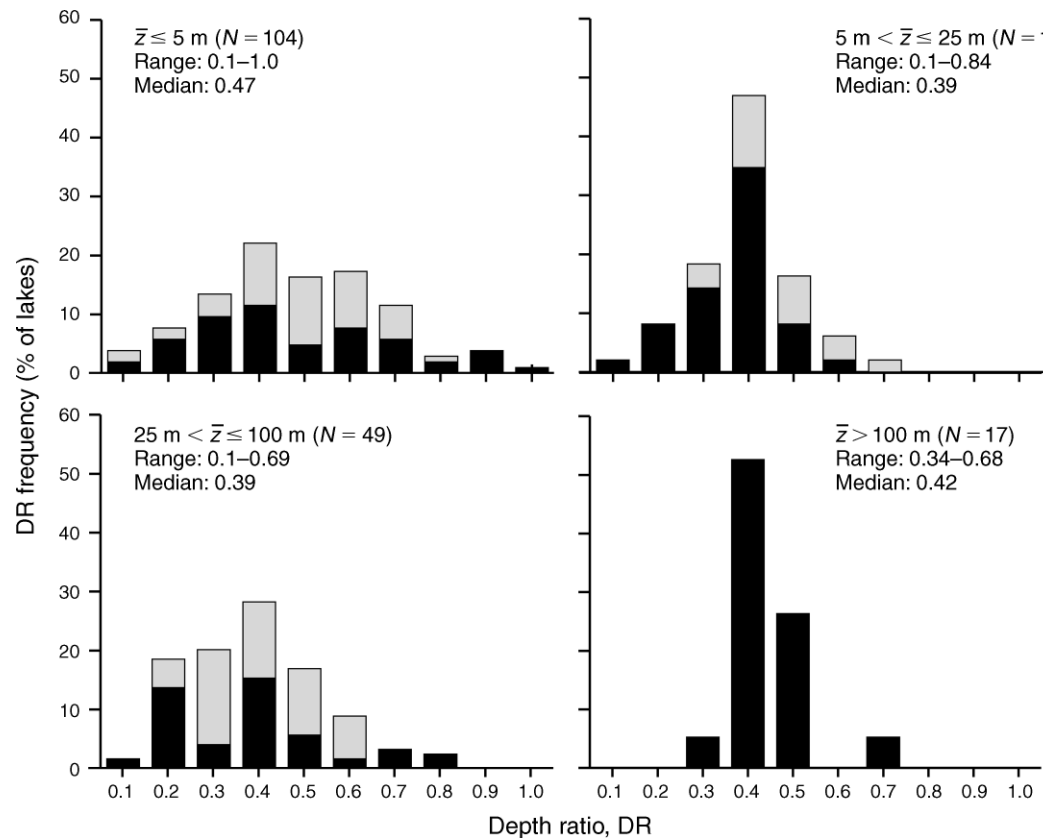


FIG. 2. Frequency distribution of depth ratios (DR) for natural lakes in different depth categories for the world's largest lakes (dark bars) and for several research-lake districts (light gray bars). The x-axis labels represent the midpoint of the DR category. Sources: Koshinsky (1970), Shannon and Brezonik (1972), Fee (1979), Herendorf (1990), and King et al. (2000).

tion were high relative to natural lakes (Kalf 2001, Wetzel 2001), which added a desired conservatism to our arguments concerning the role of periphyton in lakes. However, for oligotrophic lakes, estimates generated by the epilimnion-only model were closer to values reported for natural lakes than when a metalimnetic chlorophyll maximum was included in the model (Table 3) because of very high metalimnetic phytoplankton production in the deepest model lake ($\bar{z} = 100$ m; Appendix). The maximum value generated for phytoplankton produc-

tion in oligotrophic lakes using the epilimnion-only model was comparable to total water-column production in extremely deep oligotrophic lakes (e.g., Lake Tanganyika; Sarvala et al. 1999). The differences between the models are only evident in oligotrophic lakes. In more nutrient-rich lakes, high phytoplankton biomass in the epilimnion prevents sufficient light for photosynthesis from reaching metalimnetic algal communities. Because of the greater similarity of output from the epilimnion-only model to ranges in phyto-

TABLE 3. Comparison of model output with the ranges of area-specific daily phytoplankton primary production observed in natural lakes (from Wetzel 2001).

Trophic category	Phytoplankton primary production, mean (range) ($\text{mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)			Parameterization	
	Wetzel (2001: Tables 15–13)	Model (epilimnion)	Model (1% light)	Parameter	Input values
Oligotrophic	50–300	384 (64–1290)	788 (64–3040)	K_b	[0.05, 0.2]
				TP	[3, 10]
Mesotrophic	250–1000	572 (130–1624)	618 (130–1710)	K_b	[0.2, 0.8]
				TP	[10, 25]
Eutrophic	>1000	1840 (288–4080)	1840 (288–4080)	K_b	[0.8, 2]
				TP	[50, 100, 500, 1000]

Notes: Model scenarios include estimations of phytoplankton production in the epilimnion only, and to a depth of 1% light with a metalimnetic chlorophyll maxima in oligotrophic lakes. We assumed that sources of background light attenuation (K_b) were correlated with phytoplankton biomass for this analysis only. All mean depths (\bar{z}) were included in the models, except that $\bar{z} = 100$ m was excluded from the eutrophic-lake category. Total phosphorus (TP) units are mg/m^3 .

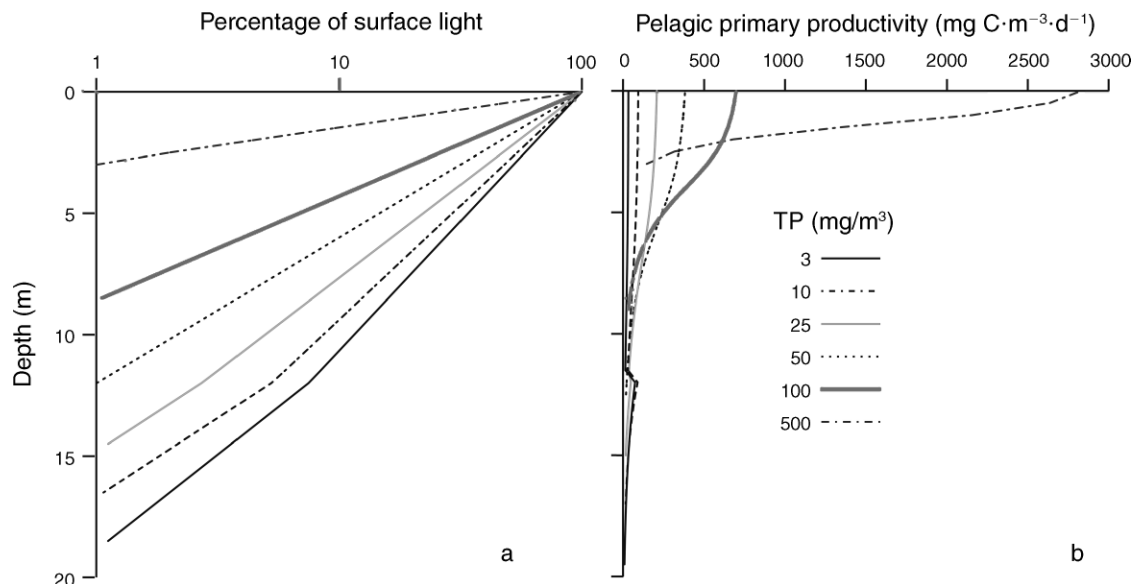


FIG. 3. Modeled (a) light availability and (b) phytoplankton productivity at depth for lakes (mean depth, $\bar{z} = 25$ m; background light attenuation, $K_b = 0.2$) with different phosphorus concentrations. The model did not include a photoinhibition parameter for phytoplankton. Output for this figure included a metalimnetic chlorophyll maximum for oligotrophic lakes.

plankton production reported for natural lakes, we focus on that model in our discussion of BP_f . In general, the model produced variation in phytoplankton productivity and light attenuation with depth that are comparable to those seen in natural lakes. In oligotrophic lakes, light penetrates into the metalimnion, and in the epilimnion there is no decrease in phytoplankton productivity with depth (Fig. 3). At higher nutrient concentrations, light is rapidly attenuated by phytoplankton biomass, and phytoplankton productivity declines with depth (Bowling et al. 1986, Kalff 2001). Thus, the model met the second criterion of producing plausible rates of light attenuation that would cause periphyton productivity to decrease with depth.

For a given depth ratio (DR) the relative contribution of periphyton to whole-lake primary production (BP_f) was always maximum in oligotrophic lakes and was inversely related to mean depth, \bar{z} (Fig. 4). The decrease in relative benthic primary production associated with eutrophication was driven by an increase in light attenuation caused by phytoplankton biomass and occurred even when periphyton productivity was a positive function of nutrients. The effect of DR on patterns of BP_f was negligible in shallow lakes, but when $\bar{z} > 5$ m, the relative contributions of benthic algae to whole-lake primary production were strongly inversely related to DR (Fig. 4). When DR = 0.3, the transition from benthic to pelagic dominance occurred at higher nutrient concentrations than when DR = 0.7. Lakes with low DR experienced a co-dominance of benthic and pelagic metabolism over a broader range of \bar{z} and TP (total phosphorus) than did lakes with high DR (Fig. 4). As expected, when the model was used to predict the distribution of primary production in the epilimnion

only, the relative contribution of benthic algae was higher in deep oligotrophic lakes than when metalimnetic phytoplankton blooms were included in whole-lake production estimates (Appendix).

Maximum BP_f was highly sensitive to the maximum rate of light-saturated benthic photosynthesis (BP_{max} , Fig. 4). When BP_{max} was set to $5 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$, BP_f approached 0.5 only in very shallow lakes ($\bar{z} = 2$ m) and only under low nutrient conditions. In contrast, when light-saturated benthic primary productivity was 50 or $120 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$, periphyton production often dominated ($BP_f \geq 0.5$) whole-lake primary production in oligotrophic and mesotrophic lakes, and $BP_f \geq 0.2$ in deep oligotrophic lakes when DR = 0.3. The relative contribution of periphyton to whole-lake primary production was not strongly affected by setting BP_{max} to a positive function of TP (Fig. 4).

Increases in non-phytoplankton light attenuation (K_b) reduced absolute production of both primary producers, but the effect of K_b on the relative contributions of benthic vs. pelagic primary producers was dependent on DR. Increases in K_b disproportionately affected phytoplankton production in lakes with low DR (Fig. 5). In contrast, in lakes with DR = 0.7, increases in K_b depressed maximum BP_f , and complete dominance by phytoplankton production occurred at lower nutrient concentrations than when DR = 0.3.

DISCUSSION

The shape of the curves in Fig. 4 and the nutrient concentrations and depth ranges over which lakes were dominated by periphyton agree with the limited data on the relative contributions of periphyton to whole-lake primary production observed in natural lakes (Vade-

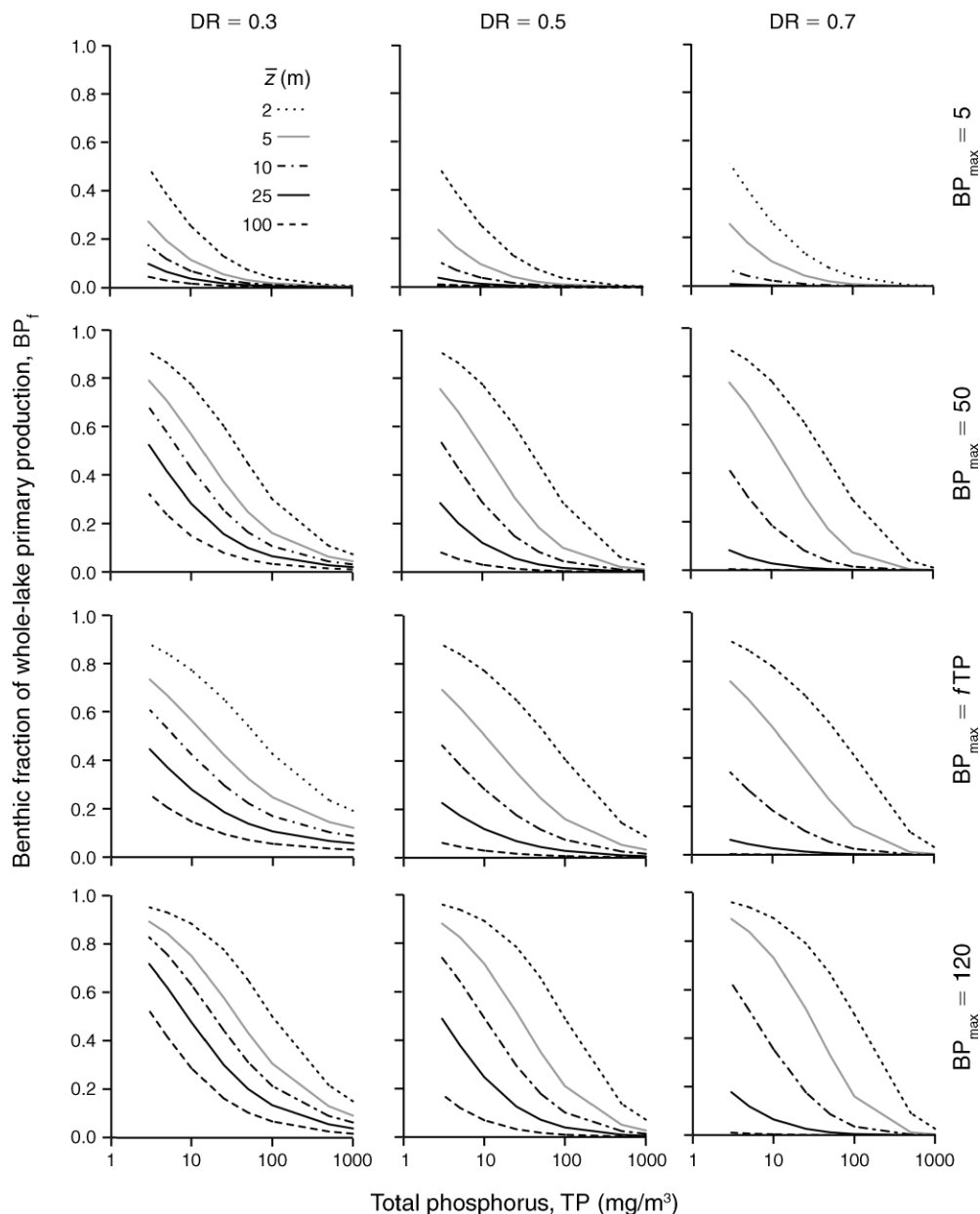


FIG. 4. Periphyton production as a proportion of whole-lake production (BP_f = periphyton + phytoplankton). Rows show model runs for three different values of maximum light-saturated benthic primary productivity (BP_{\max}) and when periphyton productivity is a function of total phosphorus, TP ($BP_{\max} = 28.1 TP^{0.24}$). Columns represent lakes with depth ratios (DR) of 0.3, 0.5, and 0.7; background (non-phytoplankton) light attenuation $K_b = 0.2$.

boncoeur et al. 2003). While this qualitative similarity is promising, the model's sensitivity to the parameterization of benthic primary productivity highlights the compelling need for empirical information on variation in benthic primary productivity in lakes. Maximum light-saturated photosynthetic rate (BP_{\max}) strongly determined the benthic fraction of whole-lake primary productivity, BP_f (Fig. 4). When BP_{\max} was set to 5 $mg\ C\cdot m^{-2}\cdot h^{-1}$, which is typical of periphyton production on rocks in low-alkalinity lakes (Schindler et al. 1973,

Turner et al. 1994, Vadeboncoeur et al. 2001), BP_f decreased rapidly as phytoplankton biomass increased (Fig. 4). Such conditions can lead to the conclusion that periphyton contributions are inconsequential to lake ecosystem function (Schindler et al. 1973). In contrast, a BP_{\max} of 50 or 120 $mg\ C\cdot m^{-2}\cdot h^{-1}$ represents a variety of lake littoral-zone types including littoral zones dominated by unconsolidated sediments, littoral zones with high epiphyton abundance, and the highly productive rocky littoral zones of large lakes (Wetzel 1964,

Vadeboncoeur et al. 2001, Liboriussen and Jeppesen 2003, O'Reilly 2006). At this magnitude of periphyton productivity, deeper oligotrophic and mesotrophic lakes can have high contributions of periphyton to whole-lake autochthonous production. The sensitivity of BP_f to DR and the tendency for deep lakes to be oligotrophic, strongly suggest that moderate or high rates of benthic primary productivity combined with low DR can lead to observed high contributions of periphyton to the food webs of deep lakes.

Although the values of BP_{max} and I_k (light intensity at onset of saturation) used in the model were drawn from the literature, information regarding the forces that drive among-lake variation in photosynthesis–irradiance parameters is scarce. The values of BP_{max} used to parameterize the model were drawn from very oligotrophic lakes and span most of the range of recorded values of benthic photosynthesis in lakes (Schindler et al. 1973, Liboriussen and Jeppesen 2003, Vadeboncoeur et al. 2006). Although experiments demonstrate that periphyton biomass on hard substrata will respond positively to nutrient enrichment (Vadeboncoeur et al. 2001), the few analyses of natural variation in BP_{max} found no significant relationship between BP_{max} and water column P or N concentrations (DeNicola et al. 2003, Liboriussen and Jeppesen 2006). Furthermore, the model demonstrated that even when maximum benthic photosynthesis was a positive function of nutrients, the patterns of variation in BP_f differed only slightly from the outcome when BP_{max} was constant (compare $BP_{max} = f(TP)$ with $BP_{max} = 50$ in Fig. 4). This occurs because whole-lake benthic production responded negatively to the compression of the photic zone. We are not suggesting that nutrients are not important to benthic algae. Rather, water-column nutrient concentrations are poor indices of the total nutrient pool available to benthic algae, which also includes pore-water nutrients and nutrients recycled within the algal mat (Carlton and Wetzel 1988, Hansson 1990, Wetzel 2001). Instead, water-column nutrients are strongly correlated with phytoplankton biomass and thus negatively correlated with the availability of another critical resource, light.

The interactive effects of nutrients (TP, total phosphorus), depth ratio (DR), and non-phytoplankton sources of turbidity (K_b) depended on lake depth. This unexpected outcome was extremely informative when combined with the distributions of DR in natural lakes. In shallow lakes where the mean depth $\bar{z} \leq 5$ m, the effect of increasing nutrients on BP_f was primarily a function of BP_{max} (Fig. 4). The lack of sensitivity of BP_f to K_b and DR in shallow lakes arises because potential thermocline depth and the depth of 1% light occur at depths greater than the maximum depth of the lake. High K_b had a comparable impact on both benthic and pelagic algae in shallow lakes. Thus high K_b acted to depress total lake production, but had little influence on the fractional contribution of each functional group (Fig. 5). Shallow lakes often have high background light

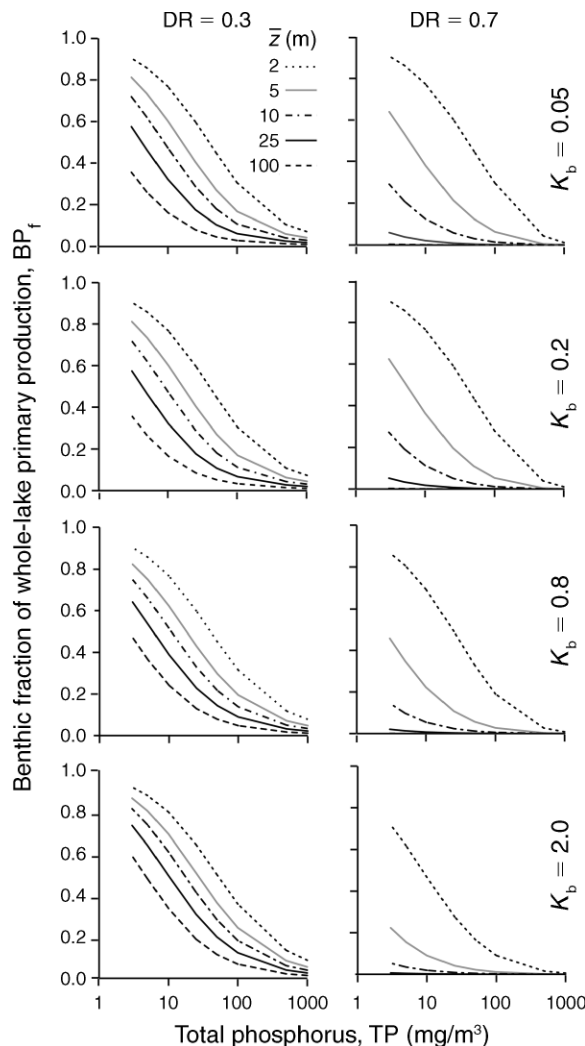


FIG. 5. Effect of depth ratio (DR = 0.3 or 0.7; columns) and non-phytoplankton turbidity (K_b ; rows) on the relative contribution of periphyton to whole-lake primary production ($BP_{max} = 50 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$).

attenuation due to wind generated suspension of sediments or high DOC (dissolved organic carbon) (Reinart et al. 2003), but the model indicates that this will not differentially disfavor either benthic or pelagic primary production in a predictable way. Shallow lakes exhibited both the least sensitivity to DR in model lakes and the widest range ($0 < DR \leq 1$) of depth ratios in natural lakes. A DR approaching 1 promotes dominance by pelagic primary producers. However, this effect is not expected to be evident in the majority of natural lakes with high depth ratios because these lakes are shallow.

There was an increasingly strong effect of DR and K_b on the relative contribution of benthic algae to whole-lake production in lakes as mean depth increased from 5 m to 100 m. Over this range of depths, water column nutrients alone were a poor predictor of BP_f , although

BP_f always decreased with increasing nutrients. At any given TP, z , and K_b , the relative contribution of benthic algae was substantially higher in oligotrophic lakes in which $DR = 0.3$ ($BP_f > 0.2$) relative to oligotrophic lakes in which $DR = 0.7$ (where $BP_f \ll 0.01$). The interactive effects of K_b and DR (Figs. 4 and 5) could lead to substantial differences in the role of littoral algae in lake ecosystem function among lake regions with very different geologic origins, morphometry, and terrestrial DOC loading. Furthermore, our analysis of the world's largest lakes and lake regions for which reliable morphometry data were available showed a clear shift towards low depth ratios with increasing lake depth (Fig. 2). Given that deeper lakes tend to be both oligotrophic and clear, low depth ratios act to maximize the potential contributions of periphyton to the food webs of deeper lakes.

Just as the distribution of primary production in shallow lakes is uninfluenced by DR , DR tells us little about the distribution of benthic habitat with respect to light in extremely deep lakes. If the mean depth is well below the depth of 1% light, the majority of the benthic habitat is not illuminated and the littoral zone makes up only a small fraction of lake surface area regardless of DR . This drives the extremely low fractional contribution of periphyton to whole-lake production observed in the world's deepest lakes (O'Reilly 2006). Nonetheless, many fish species in extremely deep lakes are ultimately dependent on energy fixed by the attached algae that make up a tiny fraction of the total energy budget of these lakes (Hecky and Hesslein 1995, Bootsma et al. 1996, Yoshii 1999, Vander Zanden et al. 2003). This reliance on littoral primary productivity may seem paradoxical except that total littoral production increases with increased lake size and the littoral zones of extremely large deep lakes represent some of the most extensive, structured freshwater habitats in the world.

The model output demonstrates the potential for benthic algae to contribute to whole-ecosystem primary production in a wide variety of lakes. However, only qualitative application of model output to a specific lake is appropriate due to the structure of the model. For instance, the statistical relationship between TP and phytoplankton biomass includes substantial variation due to grazing and N limitation of phytoplankton (Prairie et al. 1989). It is the actual phytoplankton biomass, not the nutrient concentration generating it, that is relevant to realized benthic primary productivity. Furthermore, the BP_{max} values used in the model come from a variety of oligotrophic lakes under ambient grazing conditions. Potential complex interactions between the impact of benthic grazers on BP_{max} and either lake morphometry or trophic status (Hillebrand 2005) were not included in the model due to lack of empirical data. Within these constraints, the model provides information about which types of lakes are most likely to be strongly influenced by periphyton production.

The potential relative importance of periphyton to whole-lake production is highest in shallow oligotrophic lakes. Such lakes are common in high latitudes (e.g., Canada, Northern Europe), and these landscapes are characterized by high densities of lakes and relatively low levels of cultural eutrophication. Periphyton can dominate ecosystem primary production in high-latitude lakes (Björk-Ramberg and Ånell 1985, Vadeboncoeur et al. 2003, Bonilla et al. 2005). In contrast, shallow lakes in agricultural landscapes tend to be eutrophic, and BP_f approaches 0 (Vadeboncoeur et al. 2003). The capacity for deeper oligotrophic/mesotrophic lakes to have moderate periphyton contributions ($0.1 < BP_f < 0.5$) occurs in conjunction with a shifting of the frequency distribution of natural lakes towards morphometries that favor maximum BP_f . Furthermore, deeper lakes are also characterized by low volume-specific phytoplankton biomass, which is correlated with high transparency and high total productive littoral space. These conditions maximize the potential contribution of periphyton to autochthonous production. When combined with known physical-chemical properties of natural lakes, the model outcome challenges the perception that periphyton production is only important in shallow lakes. That both periphyton and phytoplankton drive food webs in lakes worldwide is evidenced by stable-isotope analysis of fishes (Hecky and Hesslein 1995). There is now compelling evidence from whole-lake oxygen-exchange methods, paleolimnological analysis, and direct measurements of benthic primary productivity that attached microalgae are a large proportion of whole-lake primary production in many lakes (Anderson et al. 1995, Vadeboncoeur et al. 2003, Van de Bogart et al. 2007). The model demonstrated that periphyton may simply be a substantial, or at least non-negligible, component of whole-lake primary production in all but the deepest oligotrophic lakes. These results highlight the great need for a more consistent inclusion and greater empirical quantification of littoral processes in the analyses of energy flow in lake ecosystems of all sizes.

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APPENDIX

A figure showing fractional contribution of periphyton to whole-lake primary production (*Ecological Archives* E089-142-A1).