Global primary production of lakes: 19th Baldi Memorial Lecture

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Abstract

Global primary production of lakes is controlled by factors that are mainly deterministic (incident irradiance, temperature, ice cover) or mainly stochastic (nonalgal light attenuation, mixing depth, nutrient supply) with respect to latitude. The combined effect of these factors on the global lake population was estimated by Monte Carlo simulation based on lakes sampled randomly from the global lake size and latitudinal abundance density functions. Incident irradiance and temperature have strong and approximately equal effects globally on potential production. Ice cover has an additional effect that is approximately half as great as temperature or irradiance at latitudes where ice cover occurs. Together these 3 variables explain about half of the total constraint on global primary production. Among the stochastic factors, mixed layer thickness has a substantially stronger effect than nonalgal light attenuation. When nutrients and relative light availability in the water column (mixing depth, transparency) are considered together, nutrient limitation is the dominant control on algal biomass and production for about 80% of lake area. Estimated global net primary production per unit area for lakes averages 160 gC/m²/y (gross, 200 gC/m²/y; algal respiration 40 gC/m²/y) under background nutrient conditions, but under current conditions it is 260 gC/m²/y (gross, 360 gC/m²/y; algal respiration 100 gC/m²/y) because of eutrophication. Global totals of net primary production for current conditions are 1.3 PgC/y gross, 1.0 PgC/y net, 0.3 PgC/y algal respiration.

Key words: global production, lake nutrients, lake primary production, lake transparency, photosynthetic efficiency

Introduction

Limnologists have been slow to globalize information on lakes, in part because no widely accepted global inventory of lakes is yet available. Also, remote sensing has not offered a feasible means of collecting diagnostic data for lakes comparable to that available for terrestrial and marine ecosystems. In addition, limnologists until recently accepted the conclusion that only large lakes are globally important because they were assumed to account for most of the global area of lakes (Herdendorf 1990). Finally, the small areal coverage of the Earth’s terrestrial surface by lakes (typically estimated as <2%; Kalff 2002) implies that the functional significance of lakes is not quantitatively as important as that of land or ocean. For these reasons, even after a solid foundation was laid by limnologists working through the International Biological Programme (1964–1974; Brylinsky and Mann 1973, Straskraba 1980), global limnology languished.

Recently, some of the impediments to a global assessment of inland waters have diminished, leading to the emergence of a subdiscipline that could rightly be called global limnology. The wide availability and improving quality of GIS information has facilitated enumeration and measurement of waterbodies over large areas. Limnologists have also begun to question the notion that small waterbodies are functionally insignificant. For example, lakes of moderate to small size are important to the global carbon cycle (Wetzel 1990, Cole et al. 2007, Sobek et al. 2007). The utility of predictive (statistical) limnology, as foreseen especially by Peters (1986) and brought to extensive use by Håkanson (Håkanson and Peters 1995, Håkanson 2004) and to the textbook arena by Kalff (2002), has been particularly important for global limnology.

Physical data of global reach for lakes now provide a platform for functional analysis of lakes (Lehner and Döll 2004). Thus, studies that focus on individual lakes or lake clusters can be supplemented with analyses that
take into account the influences of climate, hydrology, and morphometry of waterbodies across the full global spectrum. Attempts to generalize globally about lakes or other inland waters will strengthen the conceptual basis of limnology and promote a better understanding of the connection of lakes with other ecosystems.

A global analysis of lakes based on existing information can produce a provisional estimate of global primary production of lakes, as shown in this analysis. Global information on lakes and some well established principles for the requirements of photosynthesis also can demonstrate the global influence of factors that determine primary production in lakes. The approach used in this analysis (Lewis 1987, 2010) was to determine potential production of lakes under optimal conditions, then calculate the manner in which potential production is discounted by factors (Fig. 1) that are strongly deterministic (e.g., irradiance, temperature, and ice cover, as related mainly to latitude) or strongly stochastic and must be analyzed through frequency distributions (morphometry, transparency, and nutrient supply). In this way, the components of variance for production across lakes globally can be compared quantitatively.

Abundance and size distribution of lakes

Estimation of the global number and size distribution of lakes is proceeding rapidly now through the development of large canonical datasets (complete global counts extending to a specific lower size limit) and by determination of frequency distributions for lakes in specific regions where an entire lake population can be censused down to a small (0.01 km²) or very small (0.001 km²) size. Frequency distributions may be used in extrapolating from current canonical datasets (lakes > 50 km²) to categories of lakes that are not now included in canonical datasets. The relevant literature is well reviewed by Meybeck (1995), Lehner and Döll (2004), and Downing et al. (2006) and can be summarized briefly for present purposes.

Enumeration of lakes

In the 12th Baldi Lecture, Robert Wetzel (1990) graphically depicted the log-log relationship between lake size and lake abundance as a nearly straight line extending from the largest lakes to lakes of approximately 0.01 km². Wetzel offered this graph as a way of illustrating the very high abundance of small lakes, which, he argued, have exceptionally high metabolic activity per unit area because they are strongly influenced by processes occurring near shore. Wetzel’s graph, although only generalized from his experience with the literature on lakes, is consistent with a subsequent rigorous analysis drawn from composite regional studies by Meybeck (1995) for lakes >0.1 km².

Meybeck showed that decadal (10×) intervals of lake size contain approximately the same lake area per unit land area down to a lake size threshold of about 1 km². He also estimated (as did Tamrazyan 1974) that the average area for lakes between the lower and upper bounds for a decadal lake category corresponds to a fixed value, estimated by Meybeck as 2.6 times the lower bound for any decadal category among lakes >1 km². He emphasized for smaller lakes the need to discount extrapolated lake abundances for the effects of climate in dry regions. With due consideration of aridity, he estimated the global abundance of lakes >0.01 km² (1 ha) as 8 million.

Lehner and Döll (2004) concluded that global

![Efficiency](https://example.com/efficiency.png)

**Fig. 1.** Outline of a method for quantifying factors that control global primary production of lakes. Factors are divided into 2 groups: primarily deterministic in relation to latitude and primarily stochastic in relation to latitude. Primary production is expressed as efficiency in relation to a global upper bound for annual production (10 gC/m²/d, or 3650 gC/m²/y = 100% efficiency).
lakes follow a power law as proposed by Meybeck (1995) and others; they showed for lakes \( \geq 1 \text{ km}^2 \) that 
\[ n = 155791 \times A^{-0.9926} \]
where \( n \) is the number of lakes greater than area \( A \) (km\(^2\)). Their use of this equation to extrapolate to a lower size limit of 0.01 km\(^2\), or a lake area of 3.2 million km\(^2\) equaling 2.4% of global land surface, excluding land with permanent ice cover. They presented a rationale, based on the especially high abundance of small lakes in deglaciated landscapes, for estimating a higher abundance of small lakes than Meybeck (1995) does.

Downing et al. (2006) proposed using the Pareto distribution, which had been used previously for regional or general scale analysis of lake frequency distributions (Hamilton et al. 1992, Vidondo et al. 1997), as a basis for extrapolating the estimates of lake abundances. They calibrated the distribution over the span of the GLWD for lakes \( >10 \text{ km}^2 \) and assumed that the parameters of the distribution thus established would apply to lakes as small as 0.001 km\(^2\). As proof of concept, they demonstrated the applicability of the Pareto distribution to several regional canonical datasets that include small or very small lakes. The probability density function as calibrated with the canonical data for global lakes \( \geq 1 \text{ km}^2 \) is well represented by parameters for Pareto distributions derived from these regional datasets.

The Pareto distribution as applied by Downing et al. (2006) shows, as did Lehner and Döll (2004) by use of the power function, that small lakes are quantitatively more important in accounting for global lake area than previously anticipated, but Downing et al. (2006) showed much larger numbers and areas of very small lakes than earlier studies (total 304 million lakes \( \geq 0.001 \text{ km}^2 \), of which 277 million are 0.001–0.01 km\(^2\)). Fekete et al. (2005) showed that the number of lakes \( >1 \text{ km}^2 \) per unit land area varies as a function of annual runoff for a given size category.

Most recently, Seekell and Pace (2011) asserted that frequency distributions indistinguishable from the Pareto distribution for lakes \( >10 \text{ km}^2 \), over which Downing et al. (2006) calibrated the Pareto distribution, might produce a lower prediction of lake abundance if extrapolated to lake sizes as small as 0.001 km\(^2\).

The global number and area of lakes are still in doubt for lakes \( <1 \text{ km}^2 \). The size frequency distribution from Downing et al. (2006) differs from the distribution incorporating a decline in the rate of increase for numbers of lakes \( <1 \text{ km}^2 \) as approximated by a second-order polynomial that passes through the Pareto estimates for lakes \( >1 \text{ km}^2 \) but bends through Meybeck’s (1995) estimate for lakes 0.01–0.1 km\(^2\) (Fig. 2 and 3),
which gives a total of about 35 million lakes >0.001 km², as compared with the Downing et al. (2006) estimate of 304 million. The Meybeck discount also greatly reduces the estimate of global lake area (from 4.2 to 3.1 × 10⁶ km²).

Similar extrapolation of the Lehner and Döll estimate (~80 million lakes >0.001 km²) would fall between the Meybeck based extrapolation and the Downing et al. (2006) extrapolation. Meybeck’s (1995) estimates for numbers of lakes >10 km² (n = 11 900, as estimated by mode of origin) are lower than the quasicanonical estimate of Lehner and Döll (2004; n = 16 300), but the estimates of area are nearly identical (~2 × 10⁶ km²). Differences in numbers of lakes over this range may be expected because canonical status of the data becomes less secure near the lower size boundary of 10 km².

Lehner and Döll (2004) also documented lake distribution across latitude. Because of small land area and aridity, southern latitudes make only a small contribution to global abundance of lakes (Fig. 4); north and south latitudes are combined throughout the present analysis. The latitudinal distribution pattern is similar across decadal size classes. All classes >0.1 km² show high abundances at 45–70°, which accounts numerically for much of the global lake population. The proportionate abundance in this latitude range is somewhat higher for small lakes than for large lakes. For lakes of intermediate to large size, there is a secondary abundance peak at 35–45° N and a narrow peak near the equator. Lake area peaks at lower latitude than lake abundance.

**Fig. 4.** Abundance of lakes and total area of lakes of one decadal size category (10–100 km²) as a function of latitude (source, Lehner and Döll 2004; percent per 1° latitude). Other size categories show similar distributions. The dashed line is a median.

### Maximum rates of photosynthesis

Maximum photosynthetically active radiation (PAR; 400–700 nm) absorption efficiency for phytoplankton is about 35% expressed as energy (Falkowski and Raven 2007), but maximum photosynthetic efficiency is considerably lower. Talling (1982) estimated the maximum rate of photosynthesis in lakes over an entire day under-optimal conditions as 10 gC/m²/d. Ulhmann (1978) estimated a maximum of 8 gC/m²/d for a mixed layer 1 m thick, and Melack and Kilham (1974) estimated 13 gC/m²/d (assuming a photosynthetic quotient of 1) based on studies of shallow African lakes. Thus, 10 gC/m²/d is a reasonable approximation, but somewhat higher rates may be possible.

Maximum photosynthesis rates occur in thin mixed layers at >200 mg Chl-a/m². Higher abundances of chlorophyll have been documented (Reynolds 2006) but likely do not enhance photosynthetic potential because concentrations >200 mg/m², when confined in a thin mixed layer, take up 95% or more of PAR. Thus, gross photosynthesis of 10 gC/m²/d would require chlorophyll >200 mg/m² as well as warm water with bright sunlight, a long day, nutrient saturation, and a thin mixed layer (Fig 3.19 in Reynolds 2006).

On an energy basis, 10 gC/m²/d gross photosynthesis corresponds to approximately 3% of PAR at 300 cal/cm²/d PAR (145 Watts/m² over 24h, 55 mol/m²/d), which would be typical for clear day solar exposure at low to moderate elevations in the tropics or in midsummer at subtropical or middle latitudes. Thus, the absorption efficiency of 35% is steeply discounted. Explanations include carbon insufficiency at high fixation rates due to low pCO₂ (pH > 8.5) and photorespiration or other inefficiencies derived from photosaturation (Falkowski and Raven 2007). For present purposes, 10 gC/m²/d (3650 gC/m²/y) is taken as the maximum gross photosynthesis and is assigned an ecological efficiency of 100%.

### Morphometric variables

Functional analysis of lakes requires information on morphometry (Håkanson 2004). Frequency distributions for physical variables are essential and must be based on statistical information for large numbers of lakes. Mean depth and maximum depth of lakes are closely related (Straskraba 1980, Håkanson 2004). Regional ratios vary; a globally characteristic ratio is near 0.46 (see numerous estimates compiled by Kalff 2002). The relationship used in this analysis is derived from data of Neumann (1959) for 107 lakes ranging from 4 to 514 m maximum depth (Fig. 5).

Depth is weakly but significantly correlated with area (Fig. 6; Håkanson 2004). Length of shoreline for a lake
of given area can be expressed as shoreline development, which is the ratio of lake perimeter to the perimeter of a circle of identical area. The upper bound of shoreline development increases as lake area increases (Fig. 7). A portion of this increase is related to the increase in precision of shape detection with lake size for maps of a given scale (Håkanson 2004). Physical limits on the attributes of lake basins must also be involved, however. For example, it is not possible to devise a geomorphically stable shape with a shoreline development index of 10 for a lake that has an area of 1 ha. The fine dissection of shape that would be required to create such a high shoreline development index...
for a small basin would be obliterated by physical processes in a short time. The variance underlying the points shown in Fig. 7 can be obtained from a Weibull distribution.

Mixing depth \((z_{\text{mix}})\) has been estimated for a number of lake datasets (Straskraba 1980, Kalff 2002). The value of \(z_{\text{mix}}\) changes in a nonlinear manner up to lakes of about 50 km², beyond which it stabilizes at about 25 m. For lakes of 1–25 km², Ragotskie (1978) showed that thermocline depth (which is somewhat greater than mixed layer depth) \(\approx 4 \times (F)^{0.5}\), where \(F\) (km) is fetch. Coupling, by means of a hyperbolic function, a square root relationship similar to Ragotskie’s, with the assumption that \(z_{\text{mix}}\) approaches an asymptote of 25 m above 50 km² produces the relationship shown in Fig. 8. Fetch must be approximated from area because prevailing wind direction relative to lake axis length is indeterminate; fetch is set to the diameter of a circle equal to the area of the lake.

At low latitudes, the mixed layer can be as much as twice as thick as shown in Fig. 8 because of the weaker density gradient and weaker geostrophic forces that are characteristic of tropical lakes (Lewis 1996, 2010); \(z_{\text{mix}}\) varies episodically in these lakes in response to short term variation in heat flux. Further, lakes with low hydraulic residence times may show thicker mixed layers than other lakes of similar fetch (Straskraba 1980). In small lakes, chromat dissolved organic carbon (DOC) affects mixing depth (e.g., Fee et al. 1996, Persson and Jones 2008) and surface temperature (Tanentzap et al. 2008, Adrian et al. 2009). These phenomena are not taken into account in this analysis.

### Global distribution of surface PAR, water temperature, and ice

A large proportion of the variance among lakes in PAR irradiance and water temperature at the lake surface can be explained by latitude and elevation. For PAR irradiance, elevation causes thinning of the optical atmosphere, which accounts for an increase of about 50% in irradiance at an elevation of 3 km (Barry and Chorley 2003). Variance explained by elevation is not accounted for in this analysis because variance is dominated globally by latitude, even though elevation can be significant regionally. Attenuation coefficients, which are in large part related to moisture, also vary regionally at a given latitude.

The expected total irradiance at any location on the Earth’s surface was calculated by Straskraba (1980, p. 21) from first principles for a specific atmospheric attenuation (0.6) for clear days or 50% cloudiness. For present purposes, Straskraba’s curves were adjusted to be specifically applicable to measured land surface data (Table 1) reported in Lewis (1987) from Landsberg (1961) and with \(\text{PAR} = \text{global irradiance} \times 0.46\) (Talling 1982). Smooth functions corresponding to the annual pattern for any given latitude were used in assigning a characteristic PAR to a given lake on a specific day of the year.

Surface temperature amplitudes for an annual cycle were taken from Straskraba (1980), corrected for low latitudes (0–20°) as proposed by Lewis (1987). Elevation was not considered in this analysis because it has a small effect on the global lake population, even though it can be significant regionally at a given latitude.

### Table 1. Midmonth PAR across latitudes for land surfaces (mol/m²/d).

<table>
<thead>
<tr>
<th>Latitude</th>
<th>0</th>
<th>10</th>
<th>20</th>
<th>30</th>
<th>40</th>
<th>50</th>
<th>60</th>
<th>70</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jan</td>
<td>33.2</td>
<td>36.3</td>
<td>34.7</td>
<td>25.2</td>
<td>15.9</td>
<td>7.2</td>
<td>1.9</td>
<td>0.0</td>
</tr>
<tr>
<td>Feb</td>
<td>35.1</td>
<td>40.1</td>
<td>42.1</td>
<td>31.2</td>
<td>22.2</td>
<td>13.7</td>
<td>6.8</td>
<td>1.1</td>
</tr>
<tr>
<td>Mar</td>
<td>36.4</td>
<td>43.2</td>
<td>47.5</td>
<td>40.8</td>
<td>32.5</td>
<td>22.4</td>
<td>13.6</td>
<td>4.0</td>
</tr>
<tr>
<td>Apr</td>
<td>35.8</td>
<td>44.7</td>
<td>54.0</td>
<td>48.6</td>
<td>42.0</td>
<td>35.3</td>
<td>25.4</td>
<td>11.3</td>
</tr>
<tr>
<td>May</td>
<td>34.5</td>
<td>44.0</td>
<td>54.9</td>
<td>52.9</td>
<td>46.8</td>
<td>41.1</td>
<td>32.2</td>
<td>17.1</td>
</tr>
<tr>
<td>Jun</td>
<td>33.2</td>
<td>44.0</td>
<td>54.9</td>
<td>54.7</td>
<td>49.2</td>
<td>44.7</td>
<td>36.5</td>
<td>20.4</td>
</tr>
<tr>
<td>Jul</td>
<td>33.9</td>
<td>43.2</td>
<td>54.9</td>
<td>53.8</td>
<td>48.4</td>
<td>43.3</td>
<td>35.9</td>
<td>19.3</td>
</tr>
<tr>
<td>Aug</td>
<td>35.1</td>
<td>44.0</td>
<td>54.0</td>
<td>51.2</td>
<td>44.4</td>
<td>37.5</td>
<td>27.2</td>
<td>13.9</td>
</tr>
<tr>
<td>Sep</td>
<td>35.8</td>
<td>44.0</td>
<td>51.2</td>
<td>46.0</td>
<td>37.3</td>
<td>28.1</td>
<td>17.9</td>
<td>6.9</td>
</tr>
<tr>
<td>Oct</td>
<td>36.4</td>
<td>41.7</td>
<td>43.0</td>
<td>36.5</td>
<td>25.4</td>
<td>15.9</td>
<td>5.6</td>
<td>2.6</td>
</tr>
<tr>
<td>Nov</td>
<td>33.9</td>
<td>38.6</td>
<td>36.6</td>
<td>27.8</td>
<td>17.5</td>
<td>9.4</td>
<td>3.1</td>
<td>0.4</td>
</tr>
<tr>
<td>Dec</td>
<td>32.6</td>
<td>35.5</td>
<td>33.8</td>
<td>23.4</td>
<td>13.5</td>
<td>6.5</td>
<td>1.9</td>
<td>0.0</td>
</tr>
<tr>
<td>Mean</td>
<td>34.7</td>
<td>41.6</td>
<td>46.8</td>
<td>41.0</td>
<td>32.9</td>
<td>25.4</td>
<td>17.3</td>
<td>8.1</td>
</tr>
</tbody>
</table>
Latitudinal information on ice cover was taken from a dataset (26,000 records, 417 lakes) posted by the National Snow and Ice Data Center (Benson and Magnuson 2000) and originally derived from Magnuson et al. (2000), who used the dataset to estimate changes in ice cover related to global warming. Elevation and mean or maximum depth are available for a subset of the lakes. The most effective indicators of ice cover are thaw date and the duration of ice cover; date of freezing is more subject to methodological variance. In a stepwise multiple regression analysis, latitude enters the regression first, elevation second, and depth third (Table 2). Components of added variance are smaller at each step; latitude is strongly dominant and is used in this analysis in simulation. The latitudinal effect must be described by a third-order polynomial because of a plateau at 50–60° latitude (Fig. 9). Subsampling from the population (Fig. 9) was done according to probability density at a given latitude, which recognizes variance and the presence of outliers that fall beyond the 95% confidence limits. Even so, the data may contain bias because they are not from random sampling, but rather are the outcome of an uncoordinated data collection effort.

Global growing seasons can be shown as a map of ice cover and stratification by date and latitude separated by a one-month gap between ice on and ice off, or for latitudes with no ice, about 8 weeks of cool season mixing (Fig. 10). Equatorial lakes may mix on a different schedule, however (Talling and Lemoalle 1998); warm monomictic lakes outside the tropics have a somewhat longer mixing period (Fig. 10; Lewis 1983).

**Constraints on production by deterministic factors: incident irradiance, ice, temperature**

Factors affecting primary production that are mainly deterministic because of their strong relationship to latitude can be expressed sequentially in terms of their contribution to the reduction of maximum potential annual production of biomass. Variation of incident irradiance with latitude accounts for a substantial suppression of photosynthesis relative to the maximum (Fig. 11). It may seem counterintuitive that annual potential production increases from the equator to 20° even though it declines at higher latitudes, but the explanation lies in attenuation of PAR irradiance by atmospheric moisture, which reaches its minimum near 20° latitude. Thus, while the highest daily photosynthesis could occur on clear days at any latitude between 0° and 20°, or even at higher latitudes in midsummer, the total annual PAR is affected by atmospheric moisture to such an extent that the peak occurs near 20° rather than near the equator.

Ice has strong potential to suppress primary production, primarily through high albedo, especially with overlying snow; attenuation of irradiance also can occur because of bubbles or other inclusions in the ice (Kalff 2002).

Fig. 8. Relationship between fetch and thickness of the mixed layer for the stratification season (see text). Equation: \( z_{\text{mix}} = \exp(1.87 \times \tanh(0.65 \times \log_e(F) / 1.87) + 1.38) \), \( F = \) fetch, km.

**Table 2.** Results of a stepwise multiple regression for factors explaining variance in ice cover. All variables are significant at \( p < 0.001 \).

<table>
<thead>
<tr>
<th>Dependent Variable</th>
<th>n</th>
<th>Independent Variables, Cumulative Variance, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ice cover duration, days</td>
<td>6390</td>
<td>Latitude 42 Elevation 52 Maximum depth 53</td>
</tr>
<tr>
<td>Day of the year, thaw</td>
<td>7630</td>
<td>Latitude 44 Elevation 57 Maximum depth 57</td>
</tr>
</tbody>
</table>
production under ice often is low or nil, ice is assumed in this analysis to block primary production entirely (Fig. 11). Given better quantitative information on production under ice and the distribution of various kinds of ice globally, it would be possible to make allowance for some production under ice, but more realism in this regard would not likely make much difference in a global view of primary production. PAR corrected annually for seasonal reduction caused by ice cover is symbolized here as $I'_0$.

The third factor in the sequence, potential relative maximum metabolic rate (Fig. 12), is assigned an index value of 1.0 at a temperature $\geq 28$ °C and is discounted at lower temperatures with a $Q_{10}$ of 2.0 (Falkowski and Raven 2007). Because $Q_{10}$ differs across specific ranges of temperature and applies differentially to specific photosynthetic components (Reynolds 2006), a more sophisticated estimate could be made, but would affect global estimates very little.

The 3 mainly deterministic components of potential photosynthesis account for a drastic decline between 20° and 70° latitude, where the effects of declining annual PAR and presence of ice above 35° are compounded by declining mean average temperature (Fig. 11). The effect of the 3 factors also can be expressed in terms of the “conditional” reduction in efficiency, which is efficiency expressed as a proportionate reduction from the efficiency corresponding to all antecedent factors in the reduction sequence (Fig. 11). This approach shows the relative effect of PAR and metabolism to be almost equal above 20° latitude, and ice cover to be about half as important as either of the other 2 factors over the range of 40–70° latitude.

**Stochastic factors: $K_d$, $z_{\text{mix}}$, nutrients**

**The light environment: $K_d$, $z_{\text{mix}}$**

The energy supply for photosynthesis (light environment) within a lake at a given PAR entering the water column ($I'_0$) is determined by the attenuation of irradiance through absorption and scattering and by the thickness of the mixed layer. Factors controlling attenuation are water, chromatic dissolved organic matter (gilvin), phytoplankton, and nonliving particulate matter (tripton).

Attenuation of PAR in a water column can be given as an empirically measured value of $K_d$, the extinction coefficient for downwelling PAR (m$^{-1}$). The coefficient $K_d$ and water surface PAR ($I'_0$) allow a reasonable approximation of scalar irradiance, the total irradiance that reaches a phytoplankton cell at a specific depth (Kirk 1994), except where inorganic turbidity is very high, which is unusual in natural lakes.

Values of $K_d$ can be estimated from relationships between photometer-based measurements of attenuation or
Secchi depth measurements in waters that lack high turbidity (Kirk 1994). This approach would not, however, allow quantitative separation of the 4 factors that influence $K_d$ (Fig. 13). If these 4 factors are known for a given waterbody, they can be combined to generate an estimate of $K_d$ for PAR (Kirk 1994).

The absorbance spectrum for pure water is a constant (Fig. 13). Even so, $K_d$ for pure water ($K_{dw}$) changes with depth as the spectrum of downwelling irradiance changes. Scattering by pure water contributes to PAR extinction (Kirk 1994) but is insignificant relative to $K_{dw}$ in lakes and is not quantified here.

Modeling extinction across the PAR spectrum at 2 cm depth intervals to end points at 1, 3, 5, 10, 15, and 20 m shows changes in $K_{dw}$ over progressively thicker layers of pure water (Fig. 14). For modeling, a constant value of $K_{dw}$ is useful. Because the uppermost portion of the water column is most important for estimating gross production, $K_{dw}$ corresponding to 0–3 m was used (0.13 m$^{-1}$) for present purposes.

The other 3 factors affecting attenuation (gilvin, tripton, and algae) are not strongly related to latitude or to each other. Estimation of $K_d$ for global lakes is therefore possible through the use of frequency distributions for the 2 nonalgal factors (gilvin, tripton) along with the assumption that they are randomly distributed across lakes. The effect of algae on $K_d$ is then calculated from growth potential of algae under constraint of either PAR availability or nutrients (see section on biomass).

Sobek et al. (2007) produced a landmark study of DOC (7514 lakes) concentration with emphasis on lakes above 35° latitude. Their multiple regression analysis showed that 40% of variance among lakes is explained by a combination of soil carbon content, runoff, and elevation, but variance explained by individual factors is low. Elevation was the strongest at 21%; all others were below 10%. For the present analysis, DOC was treated as a random variable distributed as shown in Figure 15. Regional studies have shown relationships of DOC to lake area (Fee et al. 1996, Hanson et al. 2007), but a geographically broader sampling (Fig. 15) does not.
Fig. 13. Examples of attenuation spectra (equated here with downwelling extinction, $K_d$) for water and substances in water. Sources: A and D, Morel and Maritorena 2001; B, DOC entering Grand Lake, CO, 26 August 2009, McCutchan and Lewis, unpublished; C, Iturriaga et al. 1988, Bowers et al. 1996.

Fig. 14. Relationship of $K_{dr}$ for a layer of pure water in relation to layer thickness beginning at 0 m and extending to locations along the curve. Points are values of $K_{dr}$ for layers 0–1, 0–3, 0–5, 0–10, 0–15, 0–20 m. $K_{dr} = 0.158 - 0.0146 \times \log_e(x) - 0.0124 \times (\log_e(x))^2 + 0.00201 \times (\log_e(x))^3$.

Fig. 15. Frequency distribution ($\alpha = 1.218$, $\beta = 5.886$) for DOC from the equation of Sobek et al. 2007: gamma distribution, $y = (x/5.886)^{0.9706} \times 1/(5.886 \times \Gamma(1.218))$, $n = 7514$. Mean = 7.2, median = 5.3 mg/L (Sobek et al. report slightly higher mean and median from the raw data rather than the equation). The inset panel is the frequency distribution of $K_{dg}$ (0–3 m) for global lakes as determined by random sampling of the DOC probability curve and equations shown in Figure 16.
Dissolved organic carbon contains achromatic and chromatic components, the mixture of which varies in lakes. The proportion of humic substances (humic and fulvic acids), which account for most of chromatic component of DOC, averages about 40% in lakes (Thurman 1985); dystrophic lakes have higher percentages, and lakes with high algal biomass have lower percentages. Chromatic DOC (gilvin) can be quantified as color indexed to Pt (mg/L) or to absorbance at 440 nm (m\(^{-1}\)).

The associated absorbance curve is negative exponential (e.g., Fig. 13), but its slope varies. For present purposes, a characteristic slope (S) of 0.017 nm\(^{-1}\) is quantified by the scattering coefficient (K\(_{db}\)), a value for K\(_{db}\) over the PAR range is derived from g\(_{440}\), where g indicates gilvin (Kirk 1994), which is near the maximum absorbance of chlorophyll \(a\) (Chl-\(a\); Cuthbert and del Giorgio 1992). The work of Watanabe et al. (2009) on reservoirs suggests that S is somewhat higher (e.g., 0.019 nm\(^{-1}\)), and that S can be predicted from DOC, but it is not clear whether natural lakes would show the same properties. Because scattering is a negligible concern for the effect of gilvin on K\(_d\) (Kirk 1994), which is near the maximum absorbance of chlorophyll \(a\) (Chl-\(a\); Cuthbert and del Giorgio 1992). The associated absorbance curve is negative exponential (e.g., Fig. 13), but its slope varies. For present purposes, a characteristic slope (S) of 0.017 nm\(^{-1}\), and that S can be predicted from DOC, but it is not clear whether natural lakes would show the same properties. Because scattering is a negligible concern for the effect of gilvin on K\(_d\), a value for K\(_{db}\) over the PAR range is derived from g\(_{440}\) and S = 0.017 nm\(^{-1}\) for the exponential function.

The two measures of gilvin, Pt mg/L and g\(_{440}\) m\(^{-1}\), are closely correlated (Cuthbert and del Giorgio 1992):

\[
Pt \text{ mg/L} = 18.2 \times g_{440} - 0.209, \quad r^2 = 0.99. \tag{1}
\]

Equation 1, when solved for g\(_{440}\) can be used to convert Pt to g\(_{440}\) which is necessary for estimating K\(_{db}\). Large databases that include measurements of both color and DOC over a wide range are scarce, however. Rasmussen et al. (1989) found the data of Juday and Birge (1933) could predict DOC from Pt color at \(r^2 = 0.93\) for 642 lakes of 0–26 mg/L DOC. For present purposes, the reverse relationship was developed from group means reported by Juday and Birge (1933, their Table VIII):

\[
\log_e (Pt \text{ color, mg/L}) = 2.076 \times \log_e (DOC, \text{ mg/L}) - 0.703, \quad r^2 = 0.98. \tag{2}
\]

Values of K\(_{db}\) for specific DOC concentrations were computed at 2 cm intervals over the range 0–3 m from the solar PAR wavelength spectrum, chromatic effects of DOC in water as determined from the relationships of DOC to Pt and of Pt to g\(_{440}\) (equations 1 and 2), and an assumed exponential slope (S) of 0.017 nm\(^{-1}\) for g\(_e\) (Fig. 16).

For analysis of PAR attenuation, particles can be treated as 3 components: phytoplankton, organic detrital particles, and mineral particles. Scattering in each category is quantified by the scattering coefficient \(b\) (m\(^{-1}\)), the beam attenuation attributable to scattering (Kirk 1994). The effect of beam attenuation on K\(_d\) is muted by the decrease in K\(_d\) that occurs when PAR scattered from any nearby beam passes into a beam that is experiencing attenuation caused by scattering.

In an example of the relationship between \(b\) and K\(_{db}\) (Table 3), inorganic solids (mineral solids) show only a 6% translation from \(b\) to K\(_{db}\), and the same is true for organic solids (detritus). These ratios vary from site to site; good examples are scarce, but this example (Table 3) shows why \(b\) has a negligible effect on K\(_d\) up to about \(b = 3\) m\(^{-1}\) (Kirk 1994). Even at values as high as 7 m\(^{-1}\), the effect of \(b\) is modest. Only at high turbidity does \(b\) become a major consideration. Phytoplankton also show low K\(_{db}^*/b\) (Table 3).

The \(b\) for turbid lakes can be quite high (Kirk 1994), but examination of samples collected during phytoplankton counting for lakes that are not visibly turbid typically shows tripton particles to be scarce in relation to phytoplankton cells (pers. observ.). Fine particles (0.5–5 μm), even in small amounts, scatter efficiently but would have a dominant effect on K\(_d\) only in clear lakes with low DOC and low chlorophyll (such as Tahoe; Swift et al. 2006), reservoirs with low hydraulic residence times (Watanabe et al. 2009),

\[
\text{Fig. 16. Empirical relationship between DOC and Pt color (above, equation 2) and a polynomial that fits the relationship for computed values of PAR K}_{db}(0–3 \text{ m}, \text{ m}^{-1}) \text{ for DOC in water (effect of water, K}_{dw}\text{, not included): } \log_e (K_{db}, 0–3 \text{ m}) = -4.44 + 1.80 \times \log_e (DOC, \text{ mg/L}) - 0.149 \times (\log_e (DOC, \text{ mg/L}))^2.
\]
Table 3. Contributions to $K_d$ (attenuation, PAR) by absorbance ($a$), and scattering ($b$) for the 3 main categories of particles in lake water (from equations of Di Toro 1978 and a representative value of $a$ from Reynolds 2006).

<table>
<thead>
<tr>
<th>Optical Feature</th>
<th>Inorganic Solids per mg/L</th>
<th>Organic Solids per mg/L</th>
<th>Algae per μg Chl-a/L</th>
</tr>
</thead>
<tbody>
<tr>
<td>$b$, m$^{-1}$</td>
<td>0.37</td>
<td>0.24</td>
<td>0.010</td>
</tr>
<tr>
<td>$K_{db}$, m$^{-1}$</td>
<td>0.022</td>
<td>0.014</td>
<td>0.001</td>
</tr>
<tr>
<td>$a$, m$^{-1}$</td>
<td>0.031</td>
<td>0.160</td>
<td>0.014</td>
</tr>
<tr>
<td>$K_{da}$, m$^{-1}$</td>
<td>0.030</td>
<td>0.160</td>
<td>0.014</td>
</tr>
<tr>
<td>$K_{db} / b$</td>
<td>0.06</td>
<td>0.06</td>
<td>0.10</td>
</tr>
<tr>
<td>$K_{da} / a$</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

Lakes of low relative depth where resuspension of sediments can occur, or lakes with vigorous bioturbation (Scheffer et al. 1993). The $K_{db}/b$ ratio for inorganic or organic nonliving solids (Table 3), together with a typical tripton concentration of <1 mg/L, suggests that $K_{db}$ for tripton would be most often below 0.02 m$^{-1}$, and therefore not a significant contributor to $K_d$ in natural lakes as a whole, but this matter deserves further study.

Absorbance ($a$) of inorganic particles also must be taken into account as a component of $K_d$. The $K_{da}$ for inorganic solids is low (Table 3), which indicates weak absorbance. For nonliving organic solids (detritus), absorbance is much higher per unit mass but still is minor at concentrations below 0.5 mg/L ($K_{da}$ contribution ≈0.05 m$^{-1}$). For modeling purposes, $K_{dp}$ (all nonliving particles) was considered unimportant in most lakes as compared with other influences on $K_d$ and was set to 0.06 m$^{-1}$.

Scattering is a small proportion (3%) of the total optical effect of algae because of the dominating influence of PAR absorbance by chlorophyll (Scheffer et al. 1993). The contribution of phytoplankton in lakes was based in this analysis on chlorophyll absorbance only. Chlorophyll absorbance varies across taxa and is under the influence of cell size and adaptation to irradiance history (Reynolds 2006). A characteristic value of 0.014 m$^2$ mg$^{-1}$ Chl-a was used in this analysis.

Maximum potential biomass at nutrient saturation: Maximum gross primary productivity ($P_{gmax}$, mg C/mg Chl-a/d), and biomass ($B_g$ mg chlorophyll/m$^3$) can be used to calculate photosynthesis summed vertically and through hours of a given day, $\Sigma B_g P_g$ (mg C/m$^2$/d), given an estimate of $I_0$ and the light response of photosynthesis, as shown by Talling (1957, 1971). For studies across latitude, which involve varied mixed layer temperatures, a metabolic adjustment (M) is also needed. Further, light inhibition of photosynthesis near the surface creates complications that are not explicitly addressed by Talling’s method. An equation for estimating the effect of light inhibition (Jassby and Platt 1976) can be used to estimate column photosynthesis. Reynolds (2006) argued, however, that light inhibition is much less important than would be indicated by data taken from incubations in situ or from samples exposed in a laboratory to the full range of column irradiances. He proposed that calculations of column production be based on $\Sigma B_g P_g$ without any correction for inhibition. This approach may be more defensible for lakes than for oceans, in that rapid attenuation of PAR in most lakes would mean that phytoplankton cells moving even relatively short distances vertically in the water column under the influence of currents typically would be unlikely to experience strong photo-inhibition. According to the simplified approach recommended by Reynolds (2006), column production can be estimated as

$$ \Sigma B_g P_g = B_g P_{gmax} \times z_{0.5k} $$

where $I_0$ is the PAR irradiance at the onset of photosaturation. This equation does not solve the problem of setting $B_g$ and of moving from midday production to daily production for modeling purposes. Both Talling (1957) and Volkenweider (1965) proposed an empirical correction for the latter problem. Reynolds (2006, equation 3.25) used the Volkenweider correction as a means of estimating an upper (nutrient saturated) limit for $B_g$ ($B_{gmax}$, mg Chl-a/m$^3$), which reflects the feedback effect of algal biomass on $K_d$:

$$ B_{gmax} = (1/k_c) \times (0.75 \times (P_{gmax}/R_c)) \times (D/24) \times \ln (0.70 \times (I_{0max} / (0.5 \times I_0))) \times (1/z_{mix}) \times (K_{dw} + K_{dp} + K_{dg}) $$

where $k_c$ is chlorophyll specific extinction of PAR, assumed here to be 0.014 m$^2$/mg Chl-a; $P_{gmax}/R_c$ is the ratio of maximum gross productivity to algal respiration per unit chlorophyll, set to 15 following Reynolds (2006); $I_{0max}$ is maximum site specific PAR as μmol/m$^2$/sec (here based on latitude and day of the year); $z_{mix}$ is mixing depth (m); $K_{dw}$ + $K_{dp}$ + $K_{dg}$ is nonalgal PAR attenuation; D is daylength (hours); and $I_0$ is PAR at the onset of saturation (120 μmol/m$^2$/s, representative from Reynolds 2006). Reynolds (2006) designated chlorophyll per unit volume calculated in this way as “chlorophyll-carrying capacity” ($B_{gmax}$), with the underlying assumption that photosynthesis leading to this biomass accumulation is supported by nutrient saturation. The computation of $B_{gmax}$ which will be referred to here as “maximum potential biomass,” is well suited for present purposes in that it leads to an estimate of maximum production as constrained by factors other than nutrients, assuming the absence of rapid biomass removal by hydraulic factors or grazing.
Proportion of irradiance captured by chlorophyll can be calculated as a ratio, $K_{da}/(K_{da} + K_{dw} + K_{dp} + K_{dg})$, or $K_{da}/K_{d}$. For a given day (summed over depth and hours of the day),

$$\sum B_{cmax}P_{g} = 10 \times M \times I'_{0} / 55 \times (K_{da}/K_{d}),$$

where 10 is maximum possible daily gross photosynthesis (gC/m²/d); $M$ is the metabolic rate as a proportion of maximum ($28^\circ C = 1.0$) with $Q_{10} = 2.0$; and 55 is maximum daily irradiance (mol/m²/d). Summing over days then gives maximum (nutrient saturated) annual gross production, gC/m²/y.

Combining $K_{dp}$, $z_{mix}$: At a given latitude (30° N, for illustration) it is possible to consider $K_{da}$ and $z_{mix}$ as they affect the maximum potential biomass, which in turn determines the maximum daily production (Fig. 17). Two components of $K_{da}$ are fixed, so that $K_{dp}$ and $z_{mix}$ are the sole variables ($K_{dw} = 0.13$, $K_{dg} = 0.06$). Three values of $K_{dp}$ are shown: 0.11 m⁻¹, DOC ≈ 4 mg/L; 0.32 m⁻¹, DOC ≈ 10 mg/L; 0.52 m⁻¹, DOC ≈ 18 mg/L. The constant $(0.13 + 0.06) m^{-1} = 0.19 m^{-1}$ is added to each value of $K_{dp}$ to produce $K_{d}$. From this example (Fig. 17), 3 conclusions are supported:

1. maximum potential biomass per unit volume ($B_{cmax}$) is very sensitive to $z_{mix}$ within the low range of $z_{mix}$ (2–10 m), which would apply to lakes of small to intermediate size;
2. maximum potential biomass per unit volume is greatly suppressed by $z_{mix}$ over the range 10–25 m, the expected mixing depth of lakes of moderate to large size, but the incremental suppression of $B_{cmax}$ between 10–25 m is much smaller than for lower values of $z_{mix}$;
3. the effect of changes in $K_{dp}$ on $B_{cmax}$, even over a relatively wide range of attenuation, is smaller than the effect of $z_{mix}$.

Two additional features of $B_{cmax}$ can be demonstrated (Fig. 18). First, $B_{cmax}$ for the month of peak biomass accumulation (July) is high at all latitudes that have an ice-free season. In addition, decline in $I'_{0}$ and $I_{0max}$ have a powerful suppressing effect on $B_{cmax}$ outside the tropics for months of increasing distance from the month of maximum $B_{cmax}$. The threshold for positive net production rapidly declines as surface irradiance declines seasonally, thus reducing $B_{cmax}$ or even driving it to or below zero for a given $z_{mix}$ that would have been suitable for sustaining a higher $B_{cmax}$ during July. Figures 17 and 18, taken together, indicate that $z_{mix}$ is more important than $K_{da}$ during the interval of peak growth potential, but $K_{d}$ is very important during seasonally declining $I'_{0}$.

For a given latitude, the values of $I'_{0}$, $I_{0max}$, temperature, and day length are obtained deterministically. Given any assumed combination of the stochastic variables nonalgal $K_{d}$ and $z_{mix}$, $B_{cmax}$ for each day of the year according to equation 4 is converted to gross primary production per day.

Fig. 17. Maximum potential biomass ($B_{cmax}$) at 30° N latitude in July as a function of $z_{mix}$ at 3 values of nonalgal $K_{d}$, with constants as listed with equation 4 (arithmetic above, semilogarithmic below).

Fig. 18. Maximum potential biomass at nutrient saturation ($B_{cmax}$) for 3 latitudes with $z_{mix} = 4$ m, nonalgal $K_{d} = 0.3$ m⁻¹ (4 mg/L DOC) from equation 3.
by use of equation 5. The total is then summed over the year (Fig. 19) for the appropriate latitude to give gross phytoplankton production as gC/m²/y. Limitation of algal growth by varied combinations of \( z_{\text{mix}} \) and nonalgal \( K_d \) cover the stochastic efficiency range (Fig. 20), but the probability distribution of gross production within this range can be obtained only by simulation (see section on modeling).

**Nutrients**

Nutrient deficiency may stop the accumulation of biomass before an algal population reaches \( B_{\text{cmax}} \), the maximum biomass associated with nutrient limitation, which can be symbolized by \( B'_{\text{cmax}} \), is determined by the abundance of a limiting nutrient. A large amount of experimental evidence now supports the conclusion that phosphorus (P) and nitrogen (N) deficiency occur with about equal frequency in lakes at all latitudes (Elser et al. 2007). An important secondary conclusion from these experiments is that nitrogen and phosphorus deficiency often are closely balanced in lakes, as shown by the strong tendency of dual enrichment experimental treatments to produce a much stronger biomass response than single enrichment treatments. Single enrichment (N or P) causes biomass responses for the limiting nutrient, but single enrichment often induces growth limitation caused by a second nutrient (N or P).

Because nutrient limitation of biomass development is very common in lakes, it is impossible to produce estimates of gross production in lakes globally without some means of predicting nutrient limitation. Given that nitrogen and phosphorus often are closely balanced in their potential to limit biomass development, it is reasonable for purposes of global simulation to use only one of these nutrients to predict production. Phosphorus offers the best possibility for simulation because its empirical relationships to both production and biomass development have been more thoroughly studied, and because it lacks the large refractory dissolved component that complicates the interpretation of nitrogen availability for phytoplankton (Lewis and Wurtsbaugh 2008). For present purposes, available phosphorus was used as the index of nutrient availability for phytoplankton, and the interpretation of biomass response to nutrients was judged statistically on the basis of empirical relationships between phosphorus concentration and maximum algal biomass.

**Background P concentrations:** Natural (background) P concentrations for lakes can be estimated from P concentrations of streams and rivers in undisturbed watersheds. Flowing waters contain significant amounts of particulate phosphorus in nonliving form (tripton). Because most of this fraction of phosphorus is lost from the mixed layer of a lake through sedimentation, total dissolved phosphorus (TDP) is used here in estimating the lake total P (TP) concentrations derived from P delivered by a stream or river. Frequency distributions of TDP from datasets given by Meybeck (1982) and Lewis et al. (1995) included 32 unpolluted rivers and streams of latitudes ranging from 0 to 70° (Fig. 21). These concentrations are consistent with larger datasets for United States background total P (Smith et al. 2003, Dodds and Oakes 2004), which averages about 50% greater than TDP. The lowest TDP concentrations, which can occur at any latitude, are near 3 μg/L, and the highest concentrations are near 80 μg/L, although a larger database would show a wider range on the upper

---

**Fig. 19.** Global nutrient saturated (light limited) gross production (gC/m²/d) at \( z_{\text{mix}} = 4 \), nonalgal \( K_d = 0.3 \text{ m}^{-1} \).

**Fig. 20.** Zone of potential limitation (grey scale) by PAR via \( z_{\text{mix}} \) and nonalgal \( K_d \) for >95% of global lake area, 0.001 to 10⁵ km².
end corresponding to watersheds with sedimentary rock unusually rich in phosphorus or enrichment by wildlife. The frequency distribution shows a strong skew toward higher concentrations and fits a gamma distribution.

The largest lakes were treated differently from other lakes. Nutrient data indicate that the largest lakes, unless polluted, have a narrower range and lower mean and median background concentrations of total phosphorus than smaller lakes. There are a few exceptions, such as Lake Chad, which reflects natural evaporative concentration of all salts, including nutrients; such lakes were treated individually. Aside from these exceptions, lakes >1200 km$^2$ (n = 89) were divided into two groups: >8000 km$^2$ and 1200–8000 km$^2$. Information on total P for these lakes was collected from the literature. For lakes >8000 km$^2$, with the exclusion of polluted lakes, all had total P concentrations <20 μg/L and were assigned a frequency distribution derived from the shape of the distribution in Fig. 21 but with a maximum P concentration of 20 μg/L rather than 80 μg/L (gamma distribution, median 6 μg/L). Lakes of 1200–8000 km$^2$, after exclusion of polluted lakes and with a few specific exceptions, showed a maximum P concentration near 40 μg/L (gamma distribution, median = 10 μg/L).

P concentrations, current conditions: An approximation of the effect of eutrophication on nutrients in lakes can be reached through a combination of demographic data, estimated nutrient mobilization per capita population, and amount of runoff per unit area. A digital grid map provides estimates of population density for 1° × 1° latitudinal grid cells (Fig. 22) for the entire global surface (Nordhaus and Chen 2009), from which frequency distributions were obtained for population density at all latitudes. Thus, population density can be treated as a random variable with known variance for a given latitude as a component of Monte Carlo simulation. Vollenweider’s (1968) estimate of human phosphorus mobilization (820 g P per capita per year) then was used in estimating phosphorus release above background associated with any given population density. Approximately one-third of this phosphorus is assumed to be particulate (Wetzel 2001). Following the pattern used for estimating phosphorus concentrations under natural conditions, the particulate component was subtracted because of its lower probability of supporting growth of autotrophs in the upper water column of lakes.

Data for specific polluted lakes show that water column P associated with high population densities involves a discount of unknown origin, which may be explained by interception of P on land or loss of TDP to sediments at high concentrations. Population densities higher than 120 indiv/m$^2$, which are commonplace globally (Fig. 22), would be expected to produce lake water concentrations of P progressively >1000 μg/L, but sampling programs that expressly include polluted lakes show only rare instances of concentrations >1000 μg/L. For example, the 115 study lakes for the Organisation for Economic Co-operation and Development (OECD 1982) showed a maximum total P annual mean concentration of 750 μg/L. For this reason, TDP delivery per capita is discounted progressively with increasing population density (Fig. 23) to the degree...
necessary to hold the percentage of lakes with P concentrations >1000 µg/L below 2%. Also, TDP is assumed to be diluted by runoff, as taken from the frequency distribution for a specific latitude (Fig. 24, as obtained from Hong et al. 2007). For a given lake, the sum of anthropogenic and background TDP yields an estimate of TDP from all sources under current conditions (Fig. 25).

**Linkage of nutrients to biomass and background conditions:** The linkage between phosphorus and production is most easily approached in 2 steps: phosphorus in relation to chlorophyll, and chlorophyll in relation to production. Numerous phosphorus-chlorophyll relationships are available (Kalff 2002); that of Pridmore and McBride (1984) is among the most useful for background P concentrations in this analysis in that it incorporates wide geographic breadth (even though it excludes the tropics), shows strong representation from very low to moderately high phosphorus concentrations (95% < 100 µg/L), and excludes highly polluted waters (note that TDP entering a lake is assumed to become mostly TP by the time of maximum biomass):

\[
\log_{10}(B'_{cmax}) = 1.178 \times \log_{10}(TDP) - 0.389, \quad r^2 = 0.83, \quad n = 82.
\]  

The relationship between maximum chlorophyll per unit volume (\(B'_{cmax}, \text{Chl}-\text{a} \text{mg/m}^3\)) and maximum gross primary production, \(\left(B'_c\right)_{gmax}, \text{mg C/m}^3/\text{h}\), can be taken from the extensive dataset developed by Kraus-Jensen and Sand-Jensen (1998) for which empirical measurements show the combined effect of biomass \(B_c\) and productivity \(P_g\) on production:

\[
\log_{10}((B_c P_g)_{gmax}) = 1.06 \times \log_{10}(B'_{cmax}) - 0.4, \quad r^2 = 0.88, \quad n = 140.
\]  

**Linkage of nutrients to biomass under current conditions:** At high nutrient concentrations, the relationship between chlorophyll and nutrient (TDP) concentration shows nonlinearity even on a logarithmic scale because of the phenomenon of nutrient saturation, which decouples nutrient concentration from chlorophyll concentration (McCauley et al. 1989). The relationship between TDP and \(\text{Chl-a}\) that was used for lakes under natural conditions (equation 6) was reconsidered for higher concentrations. McCauley et al. (1989) showed a relationship between P and mean chlorophyll in enriched lakes and also took into account the ratio of total nitrogen (TN) to TP, a cofactor in determining chlorophyll. The predicted chlorophyll from their analysis was adjusted upward by a factor of 2 to account for the ratio (OECD 1982) between mean growing season chlorophyll, as represented by McCauley et al. (1989), and maximum growing season chlorophyll, as used for this analysis in simulation. With this adjustment, the ratio for lakes showing an intermediate TN:TP ratio (15) overlaps strongly with equation 6, but shows an inflection at the highest concentrations of TDP over a range not covered by equation 6. For present purposes, lakes showing TDP <80 µg/L are represented by the curve of Pridmore and McBride (1984), and lakes showing higher TDP are represented by a relationship similar to that of McCauley et al. 1989 for TN:TP = 15. This value was adjusted upward by a factor of 2 to account for the difference between the mean and maximum Chl-a and was constrained with an asymptote of 1000 µg/L Chl-a (Fig. 26).

**Calculation of nutrient limited gross production for background nutrients.** No attempt is made here to relate phosphorus recycling to lake area or morphometry. This is a simplification of reality in that the amount of sediment area subject to resuspension within lakes (“dynamic ratio”); Håkanson 2004) and the vulnerability of some lakes to episodic changes in thickness of the mixed layer (Lewis
2010) affect the resupply of nutrients to the mixed layer during the growing season. In deep lakes the sediment mixing influence often is small, but in shallow lakes it may increase production substantially beyond that expected for a given initial nutrient inventory. Sediment contact, even without sediment mixing, may also be important, as shown empirically by Fee (1979). These sources of variation are inherent in the empirical databases that underlie equations 6 and 7, but a more comprehensive treatment of this issue with special attention to small lakes would strengthen production estimates.

Latitude is important to nutrient-limited production in that it governs irradiance and temperature, and DOC is important in that it governs nonalgal $K_d$. The equation for estimating daily column production, with the Vollenweider convention used as a correction for weaker $I_{\text{mix}}$ before or after the middle of the day, is

$$\Sigma B_{g} = 0.5 \times M \times 0.75 \times (B_{g})_{\text{max}} \times D \times \log\left(\frac{0.7 \times I_{\text{mix}}}{(0.5 \times I_{\theta})}\right) \times 1 / (K_{\text{dp}} + K_{\text{dg}} + K_{\text{dp}}),$$

where the terms are as defined for equation 4. The multiplier 0.5 was used to compensate for overprediction that would otherwise occur because $(B_{g})_{\text{max}}$, as estimated on dates of maximum production (Kraus-Jensen and Sand-Jensen 1998), is not sustained throughout the growing season. The correction factor was developed by comparison of predicted annual gross production with measured annual gross production in lakes across the full range of latitudes.

Temperature and incident irradiance, as influenced by latitude, have a strong suppressing effect on the potential annual production for a given concentration of phosphorus (Fig. 27). The full breadth of variation for fixed values of $z_{\text{mix}}$ and $K_d$ can be shown only by simulation (see section on modeling). Gross production for current nutrient conditions showed a similar pattern but with exaggeration of the more highly productive sectors of the graph.

**Net production**

The phytoplankton growing season is assumed to extend over the ice-free months with a deduction of 2 months (one on either side of the growing season) to allow deep mixing (Fig. 10). At the onset of the growing season, phytoplankton biomass begins to build from a residual inoculum from the previous growing season toward a maximum biomass set either by light or nutrient deficiency (Fig. 28). Size of the inoculum varies greatly, but the final net production estimate is not very sensitive to the size of the inoculum, as shown by sensitivity analysis, because net production is highest during the phase of increasing biomass (phase 1). For present purposes, the inoculum was assumed to be 0.1 mg Chl-$\alpha$/m$^2$, which corresponds to ~5 mg C/m$^2$. Under nutrient saturating conditions with an established mixed layer, the inoculum will grow at the onset of water column stability in a manner that is at first weakly constrained by $K_d$, but slows as biomass accumulation increases $K_{\text{dp}}$ (Fig. 28). Growth can therefore be estimated from a baseline doubling rate (assumed here to be near 1.0 d$^{-1}$ at 28 °C; this value varies with the cell size of phytoplankton) adjusted to water temperature as determined by latitude, $I'_{\theta}$ as determined by latitude, and the effect of biomass on $K_d$.

**Light limitation by $z_{\text{mix}}$ and $K_d$ under nutrient saturation**

For lakes limited by $z_{\text{mix}}$ and $K_d$, biomass will approach $B_{\text{max}}$, an asymptote, in an amount of time determined by the growth rate of the population and maximum potential biomass ($B_{\text{max}}$) for a given latitude in the middle of the growing season; this is the end of phase 1 (Fig. 28). During the last few cell divisions, growth will be suppressed by increase of $K_{\text{dp}}$, leading to the asymptote. Until phase 1 approaches phase 2, net production will be near 80% of gross production (Flynn 2005, Reynolds 2006).

**Fig. 26.** Maximum Chl-$\alpha$ as a function of water column total P in lakes.

**Fig. 27.** Gross production at $z_{\text{mix}} = 4$ m, nonalgal $K_d = 0.3$ m$^{-1}$ with background nutrient concentrations.
the phytoplankton community then enters phase 2, gross production and respiration are balanced (i.e., net production is zero unless biomass is removed). Removal of biomass in lakes generally is far less than gross production (Reynolds 2006). Grazing accounts for approximately 8% as a median across numerous lakes (Kalff 2002) and other losses, including physiological death or sedimentation loss from the mixed layer, may account for another 10%. Thus, an arbitrary but realistic loss rate is set at 20% of gross production per day, which is assumed here for phase 2.

The magnitude of gross and net production under light limiting conditions via \( z_{\text{max}} \) and \( K_d \) for nutrient saturated populations start at an inoculum of 0.1 µg/L Chl-a and \( B_{\text{cmax}} \) corresponding to \( z_{\text{mix}} = 4 \) m with nonphytoplankton \( K_d = 0.3 \) m\(^{-1}\) (Fig. 29). Despite the wide span of biomass separating the initial inoculum and \( B_{\text{cmax}} \), the elapsed time for the population to move through phase 1, approaching \( B_{\text{cmax}} \), is a small fraction of the growing season except at the highest latitudes; above 60% latitude, phase 1 is likely to be incomplete by the time the growing season ends. For most nutrient saturated lakes, gross production is dominated by phase 2. Because the rate of biomass loss is estimated here at 20% d\(^{-1}\), the ratio of net to gross production approaches 20% for the growing season, even though net production is nearer to 80% in phase 1, which is brief except at high latitude.

Phases 1 and 2 can be simulated to produce a full global spectrum of light limited predictions for net production. A preliminary step, however, is to use simulation to determine how often light limitation rather than nutrient limitation controls annual primary production. As shown in the section on modeling, light limitation accounts for a much smaller amount of global variance in annual production than nutrient limitation.

**Nutrient limitation**

Nutrient-limited production is much more efficient in net carbon fixation than light limited production. Phase 2 occurs, but shows lower biomass, as biomass is constrained by nutrient recycling rate rather than light deficiency (Lewis 2010). This constraint on \( B_{\text{cmax}} \) reduces the ratio of respiration to gross production.

Because of self shading, the ratio of net to gross production declines from approximately 80% at low to moderate chlorophyll concentrations to 20% in lakes that show nutrient saturation (see previous explanation). For present purposes, net production was set to 80% of gross for lakes up to Chl-a = 30 µg/L followed by a logarithmically declining percentage from 80 to 20% up to chlorophyll \( \geq 1000 \) µg/L (Fig. 30). The ratio between gross and net production is poorly defined in the literature and requires further refinement for modeling of net production, particularly in nutrient enriched lakes.

---

**Fig. 28.** Basis for modeling net production for algal populations (logarithmic y axis) in a lake under light limiting conditions (upper curve) or nutrient limiting conditions (lower curve). For latitudes below 35 °C, the growing season is extended to displace ice cover and merges the 2 mixing seasons.

**Fig. 29.** Days to reach maximum biomass \( B_{\text{cmax}} \), nutrient saturated, \( z_{\text{mix}} = 4 \) m, nonalgal \( K_d = 0.3 \) m\(^{-1}\), ~4 mg/L DOC as compared with the length of the growing season across latitude.
Phytoplankton, periphyton, and macrophytes

The foregoing analytical framework is based on factors that limit the growth of phytoplankton. Most lakes also show production by periphyton and macrophytes; for shallow lakes, which are abundant among small lakes, and for lakes of high shoreline development (Fig. 7), periphyton and macrophytes can be the main agents of production. The concept of mixing depth does not apply to these organisms because their biomass is fixed spatially within the euphotic zone. Other concepts invoked here for phytoplankton would apply, but any attempt to estimate their contribution based on principles developed for phytoplankton could be greatly in error if their efficiency of photosynthesis were consistently less or greater than that of phytoplankton for any given lake.

In the 12th Baldi Lecture, Wetzel (1990) argued that all metabolic functions are consistently more intense in the littoral area of a lake than in the pelagic area. His arguments were conceptual rather than statistical and applied to all metabolic functions rather than to photosynthesis specifically. Also, Wetzel’s thesis about productivity of the littoral area included the wetland zone surrounding lakes.

Without contradicting Wetzel’s general concept, but focusing specifically on the submerged or floating photoautotrophs rather than emergent or supralittoral plants, the assertion that photosynthesis is consistently more efficient in littoral areas than in pelagic areas of lakes can be generally tested. A valuable explicit comparison is given by Kraus-Jensen and Sand-Jensen (1998), whose analysis showed that the amount of chlorophyll/m² is consistently much higher for periphyton and macrophytes than it is for phytoplankton, as is gross primary production per unit volume of water. Periphyton and macrophytes are not affected by inefficiencies that derive from $z_{	ext{mix}}$ but, like phytoplankton, they may experience self shading at high densities.

From the viewpoint of ecosystem production, a comparison based on surface area rather than volume is more relevant than production per unit volume (Fig. 6 in Kraus-Jensen and Sand-Jensen 1998). The difference between areal photosynthesis of periphyton and phytoplankton, although statistically significant, is small, but macrophytes are much less productive per unit area than phytoplankton among the lakes inventoried by Kraus-Jensen and Sand-Jensen (1998; Fig. 31). These results seem counterintuitive in view of the substantially higher amounts of chlorophyll/m² for periphyton and macrophytes. In part, the biomass contrast is simply an artifact of the volumetric expression of chlorophyll, but it also reflects the lower production per unit chlorophyll for periphyton and macrophytes as compared with phytoplankton (Fig. 31).

![Fig. 30. Change in the ratio of net to gross production with increasing Chl-a in nutrient limited lakes.](image1)

![Fig. 31. Gross production per unit biomass and per unit area for phytoplankton, periphyton, and macrophytes (medians from Kraus-Jensen and Sand-Jensen 1998).](image2)
Kraus-Jensen and Sand-Jensen (1998) concluded that thick tissues of macrophytes explain low photosynthetic output per unit chlorophyll, and that substrate depletion in periphyton mats suppresses periphyton production. In fact when periphyton and macrophytes are combined, their frequency distribution of photosynthesis per unit area is similar to that of phytoplankton. Furthermore, the abundances of phytoplankton as compared with periphyton and macrophytes are complementary (inversely related; Fig. 6 in Kraus-Jensen and Sand-Jensen 1998), presumably because these communities share PAR. Thus, for present purposes there is no reasonable basis for assuming that the littoral photosynthetic cover has a notably higher photosynthetic output per unit PAR or for a given nutrient supply than would be the case for phytoplankton, even though specific circumstances often lead to strong predominance of one type of photosynthetic cover over others (e.g., Scheffer et al. 1993). For present purposes, production per unit surface area in response to specific $I_0$, temperature, and nutrient concentrations in a given lake was assumed to be the same for periphyton plus macrophytes as it is for phytoplankton.

**Monte Carlo simulation of global production**

Monte Carlo simulation of the global population of lakes is accomplished by subdivision of lake area into 11 decadal categories ($10^{-x}$ each), and subdivision of each of these categories into 10 sampling bins equal to $0.1 \log_{10}$ unit of area. The size distribution of lakes in each bin is calculated for each of the 2 density functions for lake abundance (Fig. 2; Pareto and Meybeck). The result in each case is a distribution within a bin that shows a decrease in abundance from smaller to larger lakes in the sampling bin (Fig. 32). Within each bin, 1000 random samples were taken (with replacement). The characteristics of any lake thus sampled are obtained from the flowchart (Fig. 33), leading to

![Flowchart](image.png)

**Fig. 32.** Sampling strategy for Monte Carlo simulations. When values are combined they are weighed by their proportionate contribution to global lake area.
estimates of annual gross and net production. The global contribution of any lake to the frequency distribution for a given bin is weighted according to the relative total area of lakes of that size within the bin. When lakes are combined across bins, they are weighted according to relative areal contributions of the bins across the global distribution.

A second step in the simulation is to choose a latitude for a given lake (Fig. 33). The latitudinal distribution does not fit a formula but can be sampled randomly according to the distribution (Fig. 4).

A lake of known area and latitude also has an estimated fetch, from which $z_{\text{mix}}$ can be determined (Fig. 8). Variances apply at this step, but are not known well enough to simulate; they are probably small in relation to other variances of importance to the simulation. Area also allows estimation of $z$ and $z_{\text{max}}$ with known variance (Fig. 5 and 6).

In lakes for which $z_{\text{mix}} > z_{\text{max}}$, then is set to $z$. Nonalgal $K_d$ then is estimated from DOC (Fig. 15) plus fixed values for $K_{\text{dw}}$ and $K_{\text{dp}}$ (Fig. 34).

The frequency distribution of nutrient saturated (light limited via $z_{\text{mix}}$, $K_d$) gross primary production (Fig. 34, top panel) shows that the Pareto distribution and the Meybeck-derived distribution have similar patterns, but the Pareto distribution has higher total lake area in all categories. The 2 distributions differ most among lakes of low production. This difference is explained by the Pareto distribution’s greater proportion of small lakes, which are concentrated at high latitudes where production is suppressed by low $I_o$ and low M.

The frequency distributions for lakes under nutrient limitation at background and current (enriched) nutrient concentrations are quite different from the distributions

**Fig. 33.** Diagram of the simulation of global primary production in lakes. RS = random sampling.
under nutrient saturation in that they show truncation of high production. The distribution of gross primary production for lakes at background nutrient concentrations as determined by the more restrictive of the 2 possible types of limitation, light (via $z_{\text{mix}}$ and $K_d$) or nutrients, is dominated by the nutrient effect. Only 8% of lake area (5% of lakes) under background nutrient concentrations would be expected to show limitation by light via $z_{\text{mix}}$ and $K_d$ rather than nutrients (Fig. 34, bottom panel, left side). For current conditions (enriched) the distribution of production is less concentrated at low production; nutrient limitation is dominant overall, but light limitation increases to 19% of lake area (12% of lakes).

Simulation allows placement of the distribution of nutrient limitation on the efficiency diagram (Fig. 35). For background nutrients, almost all lakes up to 45° latitude are nutrient limited (Fig. 36). Beyond 45°, light limitation via $z_{\text{mix}}$ and nonalgal $K_d$ becomes more common. Light limitation via $z_{\text{mix}}$ and nonalgal $K_d$ is most likely in lakes with the following features: total

![Graphs showing distribution of nutrient and light limitation](image-url)

**Fig. 34.** Panel 1: frequency distribution of hypothetical gross production of global lake area that is light limited (nutrient saturated) via $z_{\text{mix}}$ and nonalgal $K_d$; Panel 2: same as panel 1 but with nutrient limitation at background (left) and current conditions (right); Panel 3: combined limitation from light and nutrients; Panel 4: ratio of nutrient saturated to nutrient limited production. “Meybeck” refers to lake abundance as derived from Meybeck’s discount for small lakes; “Pareto” refers to estimates made by Downing et al. 2006 (see Figure 2).
P > 20 μg/L (most important), $z_{\text{max}} > 10$ m, and nonalgal $K_d > 0.3$ m$^{-1}$. Lakes above 50° latitude also show latitudinally increasing probability of additional suppression of nutrient based production potential by low $I_0$ and low temperature during the growing season (Fig. 35 and 36).

For current conditions, the global lake populations expands substantially into the higher $P_g$ space, especially below 40° latitude (Fig. 35–37). Light limitation is also more pronounced, especially above 40° latitude (Fig. 36 and 37).

**Global production of lakes**

Gross production of lakes weighted by area across all latitudes averages close to 200 gC/m$^2$/y under background nutrient conditions (Table 4). Current conditions reflecting enrichment caused by anthropogenic mobilization of nutrients seems to have increased gross production globally by about 74% and has moved the global lake population about 40% of the distance from background production toward production with universal nutrient saturation. Net production per unit area also is considerably higher for current nutrient conditions than for background conditions (Table 4), but the percentage increase is lower than for gross production because of the decreasing ratio of $P_n$:$P_g$ at higher nutrient concentrations. Much of the potential increase in net production caused by nutrient enrichment seems to have already occurred; incremental nutrient enrichment is progressively less effective at producing an increase in net production. Algal respiration averages currently about 100 gC/m$^2$/y (gross minus net; Table 4), but total water column respiration, which includes contributions of all heterotrophs and is subsidized by externally derived carbon, will be larger (Pace and Prairie 2005).

![Fig. 35. Distribution of nutrient limitation with latitude (shaded area). The black line within the shaded area is the peak density of nutrient limited lakes. Shading boundaries are as follows, bottom to top, % (1, 10, 25, 50, 75, 90, 99). Above: Nutrient limited production of 92% of lakes as shown in the shaded area; 8% of lakes are light limited. Below: same except percentages are 81 and 19%, respectively.](image-url)
Comparisons of production across ecosystem types typically are based on net production because estimates of gross production are difficult in terrestrial environments. Net production per unit area for lakes is substantially greater than for marine environments (Fig. 38), but not as much as expected given the generally higher concentrations of limiting nutrients available in lakes. The decreasing ratio of net to gross production with increases in nutrient enrichment depresses net production in lakes. Two additional factors explain why net production per unit area in lakes is lower than terrestrial net production.

Table 4. Summary of global production estimates for lakes based on Monte Carlo simulation involving 2 estimates of lake abundance (Pareto and Meybeck; Figure 2). Background conditions are derived from a global frequency distribution for nutrient concentrations in the absence of pollution. Nutrient saturation for all lakes (“potential maximum”) provides a hypothetical contrast with nutrients as currently augmented anthropogenically.

<table>
<thead>
<tr>
<th>Basis</th>
<th>Gross</th>
<th>Net</th>
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<tr>
<td></td>
<td>Background Conditions</td>
<td>Current Conditions</td>
</tr>
<tr>
<td></td>
<td>Background Conditions</td>
<td>Current Conditions</td>
</tr>
<tr>
<td>gC/m²/y</td>
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<tr>
<td>Pareto</td>
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<td>Meybeck</td>
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<td>351</td>
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<tr>
<td>Pg/y</td>
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<tr>
<td>Pareto</td>
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<tr>
<td>Meybeck</td>
<td>0.63</td>
<td>1.05</td>
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</table>

Fig. 36. Ratio of light limitation to nutrient limitation for gross production in global lakes. The scarcity of lakes in the subtropics reflects widespread aridity at latitudes near 25°.

Fig. 37. Median, 25–75 percentile range (boxes) and 2.5–97.5 percentile range (bars) of gross primary production as a function of latitude at background and at current nutrient concentrations, as estimated by simulation.
Producers in lakes do not have full access to incident PAR because they are dispersed within a water column with which they compete for PAR, and the proportion of lake area that is found at low latitudes is modest compared with the proportion of terrestrial photosynthetic cover at low latitudes.

Although mean production per unit area for the 2 lake distributions (Pareto- and Meybeck-derived) is nearly identical, their global totals differ because the Pareto derived lake area (4.2 × 10^6 km^2) exceeds the Meybeck-derived area (3.1 × 10^6 km^2). Terrestrial surfaces account for approximately 53 Pg per year net primary production, and wetlands account for 4 Pg according to Huston and Wolverton (2009); Beer et al. (2010) estimate somewhat higher terrestrial production. For oceans the estimate is 48 Pg/y (Field et al. 1998). Lake production as a percent of net terrestrial production under background conditions would be 1.5% for a Meybeck-based distribution and 2.3% for the Pareto distribution. Estimated net photosynthesis by lakes is close to 1% of all global net photosynthesis.

Acknowledgements

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Symbols

<table>
<thead>
<tr>
<th>Symbol</th>
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<tr>
<td>A</td>
<td>Area, km^2</td>
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<tr>
<td>F</td>
<td>Fetch, m</td>
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<tr>
<td>z</td>
<td>Depth, m</td>
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<tr>
<td>z_{max}</td>
<td>Maximum depth</td>
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<tr>
<td>z_{med}</td>
<td>Mean depth</td>
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<tr>
<td>z_{mix}</td>
<td>Mixing depth</td>
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<td>K_d</td>
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<td>K_{da}</td>
<td>K_d for phytoplankton</td>
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<tr>
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<td>K_d for pure water</td>
</tr>
<tr>
<td>K_{dp}</td>
<td>K_d for tripton (nonliving particles)</td>
</tr>
<tr>
<td>K_{dg}</td>
<td>K_d for gilvin</td>
</tr>
<tr>
<td>b</td>
<td>Scattering coefficient for PAR, m^{-1}</td>
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<td>a</td>
<td>Diffuse absorbance coefficient for PAR, m^{-1}</td>
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<td>I_0 with ice cover assumed to block PAR</td>
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<tr>
<td>I_{max}</td>
<td>Surface PAR irradiance at midday, μmol/m^2/s</td>
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<td>I_k</td>
<td>I as PAR at the onset of saturation for photosynthesis, μmol/m^2/s</td>
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<tr>
<td>k_c</td>
<td>Absorbance of PAR per unit mass of chlorophyll, m^2/mg Chl-a</td>
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<td>B_{c}</td>
<td>Algal biomass as chlorophyll a, mg/m^3</td>
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<tr>
<td>B_{cmax}</td>
<td>Maximum B_{c} for light limiting conditions</td>
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<tr>
<td>B'_{cmax}</td>
<td>Maximum B_{c} for nutrient limiting conditions</td>
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<tr>
<td>P_{g}</td>
<td>Gross photosynthesis per unit biomass (productivity), gC/m^3/h/mg Chl-a</td>
</tr>
<tr>
<td>P_{gmax}</td>
<td>Maximum P_{g}</td>
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<tr>
<td>(B_{c}, P_{g})_{max}</td>
<td>Maximum gross production per unit volume for the growing season, gC/m^3/h</td>
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<td>Σ B_{c} P_{g}</td>
<td>Gross photosynthesis per unit area gC/m^2/hr</td>
</tr>
<tr>
<td>ΣΣ B_{c} P_{g}</td>
<td>Gross photosynthesis per day, gC/m^2/d</td>
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<tr>
<td>D</td>
<td>Daylength, hours</td>
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<tr>
<td>P_n</td>
<td>Net photosynthesis (notation parallel to P_{g})</td>
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<td>P</td>
<td>P with no subscript = phosphorus concentration, μg/L</td>
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<td>R_a</td>
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<tr>
<td>g_{λ}</td>
<td>Attenuation at λ nm caused by gilvin, m^{-1}</td>
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<td>M</td>
<td>Metabolic index, 1.0 = metabolism at ≥28° C, decreasing at Q_{10} = 2 &lt; 28°</td>
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<td>t_{thaw}</td>
<td>Time of thaw (days after 20 Sep) for ice cover</td>
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<td>Duration (days) of ice cover</td>
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<tr>
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<td>Beginning time</td>
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<tr>
<td>t_{2}</td>
<td>Ending time</td>
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Fig. 38. Net primary production per unit area for global components. Terrestrial and wetlands estimates are from Huston and Wolverton (2009) and include their adjustment of tropical moist forest to 700 gC/m^2/y. The ocean estimate is from Field et al. (1998); the lacustrine estimate is from the present study, for current nutrient conditions.

Net Primary Production per Unit Area

<table>
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<tr>
<td>Terrestrial</td>
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<tr>
<td>Lacustrine</td>
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<tr>
<td>Marine</td>
<td>140</td>
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Net Production gC/m^2/y
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