

## WHOLE-LAKE FERTILIZATION EFFECTS ON DISTRIBUTION OF PRIMARY PRODUCTION BETWEEN BENTHIC AND PELAGIC HABITATS

YVONNE VADEBONCOEUR<sup>1,3</sup> DAVID M. LODGE,<sup>1</sup> AND STEPHEN R. CARPENTER<sup>2</sup>

<sup>1</sup>*Department of Biological Sciences, University of Notre Dame, P.O. Box 369, Notre Dame, Indiana 46556 USA*

<sup>2</sup>*Center for Limnology, University of Wisconsin, 680 N. Park Street, Madison, Wisconsin 53706 USA*

**Abstract.** The perception that primary production in lakes is positively related to phosphorus loading is based almost entirely on studies of phytoplankton. This is partly because benthic and pelagic habitats in lakes are often treated as separate ecosystems, the processes of which can be evaluated independently. However, light and nutrients often limit primary producers in both benthic and pelagic habitats. We tested the hypothesis that reductions in light associated with increases in phytoplankton could cause compensatory decreases in benthic algal (periphyton) primary production. We monitored production of periphyton on sediments (epipelon), periphyton on wood (epixylon), and phytoplankton in four lakes in upper Michigan, USA, from 1991 to 1995. During the summers of 1993–1995, we stimulated phytoplankton production in three of the lakes by fertilizing with nitrogen and phosphorus (N:P  $\geq 25$  by atoms) at rates between 0.3 and 2.0 mg P·m<sup>-3</sup>·d<sup>-1</sup>. The response of periphyton to fertilization was substratum specific: epixylon increased with fertilization, but epipelon decreased. However, when area-specific production was extrapolated to the whole-lake scale, epixylon never constituted >4% of benthic primary production. Thus, the decline in epipellic production dominated the benthic response to fertilization. We also estimated whole-lake (epipelon + phytoplankton) primary production. Epipellic algae constituted 50–80% of whole-lake primary production at ambient nutrient levels. However, only 10–40% of primary production was benthic at the highest fertilization rates. The increase in whole-lake primary production caused by water column fertilization was greatly overestimated when we did not include the compensatory decline in epipellic algae as they were shaded by increases in phytoplankton concentrations.

**Key words:** algae; benthic–pelagic links; eutrophication; lakes; light attenuation; nutrients; periphyton; phytoplankton; substratum; whole-lake primary production.

### INTRODUCTION

Total ecosystem primary productivity tends to increase along nutrient gradients and strongly determines productivity of higher trophic levels (Ginsberg and Akçakaya 1992, Power 1992, Gleeson 1994). Lakes, because of their clearly defined boundaries, are systems in which whole-ecosystem primary production can be measured and related to other ecosystem variables. The effect of eutrophication on ecosystem production has been a particular focus of lake ecology. However, primary production in lakes is usually implicitly assumed to be predominantly, or entirely, pelagic, and the contribution of benthic algae (periphyton) to whole-lake primary production is known for only a few lakes (see reviews by Westlake et al. 1980, Wetzel 1983, Sand-Jensen and Borum 1991, Lodge et al. 1998). It has become evident that fish production is highly dependent on benthic secondary production (Hodgson et al. 1993, Vander Zanden and Rasmussen 1996), and that

carbon fixed by benthic primary producers is a main energy source for top predators in “pelagic” food webs (France 1995, Hecky and Hesslein 1995). Therefore, it is likely that exclusion of benthic primary production from estimates of whole-lake primary production skews our understanding of energy and nutrient fluxes in lakes (Strayer and Likens 1986). This is especially true if periphyton and phytoplankton are limited by different factors and if patterns of periphyton production along nutrient gradients do not parallel those of phytoplankton (Borum and Sand-Jensen 1996).

Nutrient availability (especially phosphorus, P) limits phytoplankton production (Vollenweider 1976, Schindler 1978). The effect of water-column nutrients on periphyton production is more complex and substratum specific (Schindler et al. 1973, Fairchild et al. 1985, Cattaneo 1987, Fairchild and Sherman 1993, Turner et al. 1994, Burkholder 1996, Vadeboncoeur and Lodge 2000). Phosphorus sometimes limits periphyton growing on nonnutrient diffusing benthic substrata such as rocks and wood (Ennis 1975, Fairchild et al. 1985, Fairchild and Sherman 1993, Vadeboncoeur and Lodge 2000). In this case, periphyton are inferior competitors to phytoplankton because boundary layers at the mat surface slow nutrient uptake when the water column is the primary nutrient source (Riber and Wetz-

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<sup>3</sup> Present address: Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, Quebec, Canada H3A 1B1. E-mail: yvadeb@po-box.mcgill.ca

TABLE 1. Characteristics of the study lakes.

Lake	Area (ha)	Mean depth (m)	Max. depth (m)	Max. sampling depth (m)	Experimental phosphorus input (mg P·m <sup>-3</sup> ·d <sup>-1</sup> )		
					1993	1994	1995
Paul (piscivore)	1.7	3.7	12	7.0			
Peter (planktivore)	2.7	5.7	19	8.0	1.16	0.67	0.39
West Long (piscivore)	3.4	4.7	18	7.0	1.43	0.86	0.40
East Long (no fish)	2.3	4.9	14	4.0	1.28	0.88	1.99

*Notes:* Dominant fish assemblage (in parentheses) follows the lake name. Paul Lake, the reference lake, was not fertilized. Summer phosphorus input rates are for the fertilization years (1993–1995). Before fertilization, ambient phosphorus input rates were 0.1–0.2 mg P·m<sup>-3</sup>·d<sup>-1</sup> (Carpenter et al. 1996). Maximum sampling depth is the maximum depth at which epipellic samples were collected and corresponded to the last 1 m depth interval at which visibility was adequate for a scuba diver to distinguish the sediment–water interface. Epipellic algal mats always occurred at this depth.

el 1987, Takamura and Iwakuma 1991, Reuter and Axler 1992, Stevenson and Glover 1993, Hwang et al. 1998). However, ground water is often an important nutrient source in lakes (Lodge et al. 1989, Hagerthey and Kerfoot 1998). Even in the absence of ground water influx, nutrient concentrations in the sediment pore-water are consistently higher than those in the water column (Schindler et al. 1987, Hansson 1992). Algae on organic sediments (epipelon) and sand sequester these nutrients and regulate their availability to phytoplankton (Carlton and Wetzel 1988, Hansson 1990, Hagerthey and Kerfoot 1998, Woodruff et al. 1999). Therefore, the impact of water-column fertilization on periphyton primary production may depend on whether groundwater, surface water or atmospheric sources dominate nutrient input pathways. It will also depend on the substratum composition of the lake bottom.

Phytoplankton and periphyton have similar photosynthesis–irradiance response curves (Reynolds 1984, Hill 1996). However, phytoplankton circulate in the mixed layer and can intercept light before it reaches benthic algae. As surface light is attenuated with water column depth, periphyton production per unit habitat area decreases (Round 1961, Björk-Ramberg 1983, Björk-Ramberg and Ånell 1985). Thus, water column fertilization that results in phytoplankton blooms may reduce total benthic algal production by reducing light penetration (Sand-Jensen and Borum 1991, Borum and Sand-Jensen 1996, Havens et al. 1996).

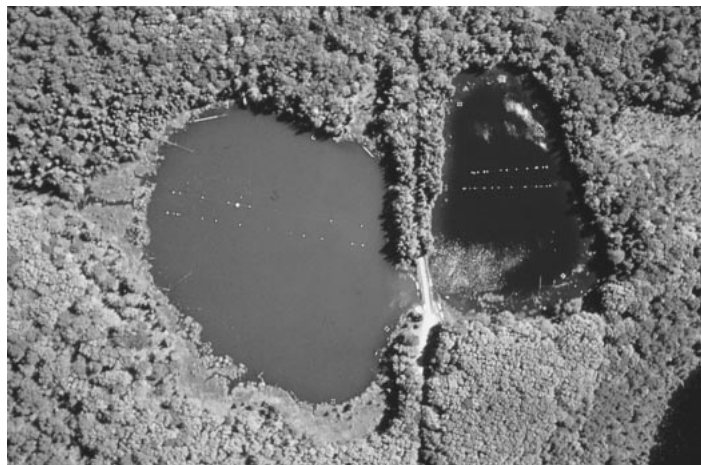
The ability of periphyton to sequester pore-water nutrients, combined with the ability of phytoplankton to intercept light before it reaches the sediments, has led to the hypothesis that primary production in oligotrophic lakes is dominated by periphyton, whereas in eutrophic lakes it is dominated by phytoplankton (Wetzel 1964, 1983, Sand-Jensen and Borum 1991). This hypothesis has not been tested at the whole-lake scale because there are fewer than 30 lakes for which both total periphyton (on natural surfaces) and total phytoplankton biomass have been estimated (Lodge et al. 1998). The best support for the inverse relationship between periphyton and lake trophic status comes from

a comparative study of epipelon in 34 lakes along a total phosphorus (TP) gradient (Hansson 1992). In that study, epipellic biomass was measured at a depth of 0.75 m in all lakes, and the light extinction coefficient, *K* (Kirk 1994), was used as an index of phytoplankton biomass. The distribution of epipellic chlorophyll with respect to *K* was unimodal, and was negatively correlated with *K* in eutrophic lakes (*K* = 1.25–3.5). Thus, the results were consistent with the hypothesized pattern, but the hypothesis was not experimentally tested.

In the current study we measured periphyton and phytoplankton production in four small lakes, three of which were experimentally fertilized. We tested the hypothesis that water-column fertilization can depress periphyton production at the whole-lake scale by reducing light availability to the benthos. We monitored benthic and pelagic algal responses to fertilization, and used these data to model whole-lake algal primary production before and during fertilization.

The purpose of our study was to predict changes in periphyton production due to changes in abiotic resources (nutrients and light) associated with whole-lake fertilization. However, in addition to fertilization, contrasting levels of zooplankton were maintained by fish manipulations (Table 1). Zooplankton herbivory and fertilization both strongly affected phytoplankton, results that are discussed elsewhere (Carpenter et al. 1995, 1996, 1998). Just as zooplankton affect phytoplankton production, benthic grazers can exert strong top-down pressure on periphyton, reducing the response of periphyton to increases in limiting resources (Rosemund 1993, Rosemund et al. 1993). Densities of benthic grazers varied among lakes and years (Blumenshine et al. 2000), and benthic grazers strongly affect periphyton production in the lakes (Y. Vadeboncoeur and D. M. Lodge, *unpublished data*). In the analysis of periphyton responses to fertilization we did not attempt to describe variability due to grazers. Rather, we measured the average effects of changes in nutrients and light on benthic algae, and modeled how this affected the distribution of primary production in the lakes.

PLATE 1. Peter Lake (left) and Paul Lake (right) in August 1993. Peter Lake had been fertilized with N and P daily since May, and the high phytoplankton concentrations seen here occurred throughout the summer. In contrast, phytoplankton production in unmanipulated Paul Lake remained low throughout the study.



We examined the fertilization response of primary producers at three scales. First, we evaluated algal response to fertilization on a habitat-area-specific (periphyton) or volume-specific (phytoplankton) basis that did not consider the relative abundance of each habitat within the lake. In this analysis, we controlled for the confounding effects of light by comparing algal biomass at  $\leq 1$  m water column depth, where light was in excess. At the second scale of analysis, we estimated total periphyton biomass and production based on the relative abundance and productivity of the two benthic substrata, wood and sediments. This allowed us to determine how substratum-specific productivity and distribution affected the overall benthic response to fertilization. Finally, we calculated whole-lake summer averages for benthic and pelagic primary production, and tested whether total periphyton production and the relative contribution of periphyton to whole-lake primary production changed with P addition rate. We used this final analysis to evaluate how the historical focus on the pelagic habitat affects our interpretation of the dynamics of lake primary production along nutrient gradients.

#### METHODS

##### *Study site and whole-lake manipulations*

Paul, Peter, and Long lakes are within 1 km of each other on the University of Notre Dame Environmental Research Center, in the upper peninsula of Michigan, USA ( $89^{\circ}32'$  W,  $46^{\circ}13'$  N). Paul Lake and Peter Lake (see Plate 1) were separated by an earthen dike in 1951 (Carpenter and Kitchell 1993). Long Lake was divided into three basins with plastic curtains in the spring of 1991. Curtain installation altered the hydrology of the lakes and led to increases in dissolved organic carbon (DOC) in East Long Lake and decreases in DOC in West Long Lake (Christensen et al. 1996, Carpenter et al. 1998). This caused dramatic changes in light availability in the lakes, the most marked of which occurred between 1991 and 1992 (Christensen et al. 1996).

Paul Lake was a reference basin throughout the study. During 1993–1995, Peter, West Long, and East Long Lakes were fertilized daily from mid-May to September with  $\text{PO}_4$ ,  $\text{NH}_4$  and  $\text{NO}_3$  at an N:P ratio  $\geq 25$  by atoms (Carpenter et al. 1996, 1998) (Table 1). All data suggest that the primary producers in the lakes were P, not N, limited during fertilization (Carpenter et al. 1998). Therefore, throughout this paper we use P load per cubic meter of epilimnetic volume as a measure of fertilization rate. Before experimental fertilization, P input rates were  $\sim 0.15 \text{ mg P}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$  (Carpenter et al. 1996). Fertilization rates varied among lakes and years (P load =  $0.4\text{--}2 \text{ mg}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$ , Table 1). The study lakes and experimental manipulations are thoroughly described elsewhere (Carpenter and Kitchell 1993, Carpenter et al. 1995, 1996, Christensen et al. 1996, Cottingham et al. 1998).

We monitored three groups of primary producers (epipelton, epixylon, and phytoplankton) in the four lake basins (subsequently referred to as lakes) from 1991 to 1995. Distinct algal taxonomic assemblages typified the three habitats. Before fertilization phytoplankton assemblages were dominated by chrysophytes and dinoflagellates (Cottingham et al. 1998). During fertilization, chlorophytes and cyanobacteria became abundant. Diatoms were rare in the plankton (Cottingham et al. 1998). In contrast, diatoms and filamentous cyanobacteria dominated epipellic assemblages in all years, while colonial cyanobacteria and filamentous chlorophytes were dominant on wood (Y. Vadeboncoeur and D. M. Lodge, *unpublished data*). There was little overlap at the genus level between epipelton and phytoplankton. Thus, dynamics of epipelton were not determined by settling phytoplankton.

We used scuba for benthic sampling. Benthic sampling incorporated a stratified random design in which we divided the shoreline of each lake into 10 sectors of roughly equal length. Each sector was further divided into 5 subsectors. On each sampling date, we selected 4–5 nonadjacent sectors distributed around the

lake for replicate benthic measures within a lake. Within each sector, we randomly chose a subsector to sample.

#### *Monitoring algal biomass and production*

*Epipelton*.—To test whether epipelton responded positively to fertilization in the shallow, high-light epilimnion, we collected epipelton at 1.0 m water depth 3–4 times each summer from 1991 to 1995. On each sampling date, we collected 2 cm deep cores from four sectors using a cutoff 60-cm<sup>3</sup> syringe (25 mm inside diameter). Cores were pooled and preserved with 2% glutaraldehyde. Samples were homogenized, subsampled, and mounted permanently onto 0.45- $\mu$ m filters (Crumpton 1987, Carpenter et al. 1993a). Algae containing cytoplasm were identified to genus and counted. Twenty to thirty cells or colonies were measured to estimate average biovolume of a given taxon.

In 1995, we compared the distribution of benthic chlorophyll and production between the two dominant substrata, sediments and wood. We collected epipellic cores (with the syringe sampler) for chlorophyll analysis along a depth gradient from 0.5 m to the maximum benthic sampling depth in each lake (Table 1). Sampling intervals on the depth transects were 0.5 m until 2.0 m water depth, and at 1.0-m intervals thereafter. Chlorophyll was collected four times from June to August, and on each date we sampled depth transects in four sectors. The top 0.5 cm of each core was frozen, freeze-dried, and extracted in 100% methanol for 24 h (Marker et al. 1980, Hansson 1988). Phaeophyton-corrected chlorophyll *a* was measured fluorometrically (Holm-Hansen 1978).

To estimate whole-lake epipellic production, we measured in situ epipellic <sup>14</sup>C fixation in the upper and lower epilimnion (1.5 m and 2.5 m) and the metalimnion (4.0 m or 4.5 m) two times per year (June/July and July/August) from 1993 to 1995. Intact sediment cores (2 cm sediment + 2 cm overlying water) were collected and incubated in clear acrylic chambers (75 mm high  $\times$  38 mm inside diameter, Vadeboncoeur and Lodge 1998). We collected three light cores, two dark cores, and two cores for dissolved inorganic carbon (DIC) analysis from each depth. The outside of light chambers was covered with opaque plastic tape up to the surface of the sediments to restrict photosynthesis to the surface sediments only. Dark chambers were completely covered in opaque tape. We added 74 kBq <sup>14</sup>C (as NaH<sup>14</sup>CO<sub>3</sub>) to the overlying water of the light and dark chambers. The cores were placed in a tray inside a larger clear acrylic production chamber that was filled with water collected from the sampling depth. The apparatus was then covered with an opaque shield and returned to the sampling depth for 2 h to allow equilibration of <sup>14</sup>C between the overlying and interstitial water (Revsbech et al. 1981, Vadeboncoeur and Lodge 1998). After the equilibration, we removed the opaque shield, and returned the chamber to depth. Immediately

after a 2-h light incubation, cores were processed for scintillation counting (Vadeboncoeur and Lodge 1998). We measured DIC concentrations in the interstitial and overlying water as CO<sub>2</sub> evolved upon acidification using a gas chromatograph (Stainton et al. 1977). <sup>14</sup>Carbon uptake was counted on a Beckman LS 5000 TD (Beckman Coulter, Fullerton, California) with an external quench correction.

*Epixylon*.—Epixylon chlorophyll was measured 3–6 times per summer from 1992 to 1995. In 1992, 10 cm lengths of submerged leatherleaf (*Chamaedaphne calyculata* (L.) Moench) stems were collected in five sectors in each lake. Algae were removed from the stems and filtered onto a glass fiber filter (Fisherbrand G4 [Fisher Scientific, Pittsburgh, Pennsylvania], 1.2  $\mu$ m nominal pore size). Filters were frozen, extracted in 100% methanol for 24 h, and chlorophyll was measured fluorometrically (Holm-Hansen 1978). We assumed each stem was a cylinder and calculated surface area of the stems from the length and diameter (surface area = length  $\times$  diameter  $\times$   $\pi$ ).

In 1993, we permanently marked one log (>25 cm diameter) in each sector in all lakes (except East Long Lake where epixylon was not sampled after 1992). We used a two-syringe periphyton brush sampler (Loeb 1981) to sample periphyton from the logs at ~0.5 m water depth. The same area on a log was never resampled within a year. Processing, filtering, and chlorophyll analysis was as described above for *Chamaedaphne* stems, except that we used Whatman GF/F filters (0.7  $\mu$ m nominal pore size; Whatman Incorporated, Clifton, New Jersey).

*Phytoplankton*.—Phytoplankton chlorophyll was sampled weekly from midlake at depths corresponding to 100, 50, 25, 10, 5, and 1% surface irradiance (Carpenter et al. 1993b). Samples were filtered (Whatman GF/F), frozen, extracted in 100% methanol, and analyzed for chlorophyll fluorometrically (Carpenter et al. 1995, 1996). We measured phytoplankton primary production three times per summer in 1991 and 1992, every two weeks in 1993 and 1994, and every week in 1995. Carbon-14 fixation was measured at the same six depths as chlorophyll (Carpenter et al. 1993b, 1998). Light, temperature, nutrients, and DIC were also measured along the depth profile.

#### *Estimating total benthic and pelagic habitat*

To estimate whole-lake primary production, we had to quantify benthic habitat, which consisted primarily of two substrata, wood and sediment. We measured wood surface area in every second sector of the lakes. Within a sector, we measured length and diameter of all large logs (diameter  $\geq$  10 cm) and the attached branches. For small wood (<10 cm diameter), we placed a 0.25 m<sup>2</sup> quadrat on the sediments at 0.5 m depth intervals between 0.5 m and 4.0 m water depth. We measured length and diameter of all wood within the quadrat and extrapolated depth-specific wood sur-

face area to the whole sector. Each piece of wood was assumed to be a cylinder. Most large wood was anchored on shore and suspended in the water column, allowing epixylon growth over the entire surface. Most small wood rested on the sediments. Therefore, for small wood, half the surface area was assumed to be embedded in the sediments and unavailable for epixylon colonization. Results from the two surveys were summed and multiplied by 2 (because we measured wood in only one-half the sectors) to estimate total surface area of wood in each lake.

Littoral sediments were operationally defined as extending from the lake edge to the last 1 m depth interval at which a scuba diver could still visually distinguish the sediment-water interface (= maximum sampling depth, Table 1). Epipellic algal mats existed at maximum sampling depths. We used a spline interpolation of bathymetric profiles (1 m depth isoclines) to calculate surface area of littoral sediments at 0.1 m depth intervals.

#### *Comparisons of algal responses to fertilization at three different scales*

We calculated summer averages for all response variables, and each lake-year was treated as an independent observation. Correlation of response variables with phosphorus input rate are based on the assumption that each lake-year can be treated as an independent sampling unit, i.e., there is no significant autocorrelation among years for each lake. There was no carryover of nutrients within the water column from autumn to the following spring during the years analyzed here (S. R. Carpenter, *unpublished data*). Nutrient enrichment rates were chosen independently each year and do not follow a simple upward or downward trend (Table 1). Phytoplankton have no significant autocorrelations at time intervals longer than a week (Carpenter et al. 1996, 1998). Thus it appears reasonable to regard each lake-year as a sampling unit for the interpretation of this experiment.

To detect habitat-specific changes in algae at  $\leq 1.0$  m water depth, we regressed biomass of epipellic (cubic millimeters per square centimeter), epixylon (milligrams of chlorophyll per square meter) and phytoplankton (milligrams of chlorophyll per cubic meter) on summer P addition rate and light (procedure GLM, SYSTAT for Windows, version 7.0, SYSTAT Incorporated, Evanston, Illinois). We expressed all biomass relative to the reference lake by subtracting the average summer biomass in the reference lake from the summer average of each treatment lake. This allowed us to control for between-year variation in the reference lake, and changes in epixylon sampling methods between 1992 and 1993.

We estimated whole-lake epipellic production for all five years. We used stepwise multiple regression (SYSTAT, procedure GLM) to determine the best predictor variables for epipellic primary production. We included

light, DOC, temperature, TP, and phytoplankton chlorophyll in the analysis. Only light, DOC, and TP were significant and gave the following regression equation (multiple regression  $R^2 = 0.81$ ,  $P < 0.0001$ ):

$$\begin{aligned} &\text{epipellic primary production} \\ &= 12.7 \times \text{light}^{0.472} \times e^{(-0.024\text{TP} - 0.081\text{DOC})}. \end{aligned} \quad (1)$$

We used Eq. 1 to model epipellic production at 0.1 m depth intervals. Changes in light intensity with depth can be described accurately with the equation (Kirk 1994):

$$I_z = I_0 e^{-Kz}. \quad (2)$$

The light attenuation coefficient ( $K$ ) was measured weekly. We calculated average irradiance at the surface of the lakes ( $I_0$ ) for each week using daily pyroheliometer and day length data. Changes in TP and DOC with depth were most simply described in a two-compartment model in which concentrations were uniform in the epilimnion and changed at the thermocline. We estimated epipellic production from 0.5 m to the maximum sampling depth. We excluded the sediments from 0–0.5 m because algal mats were never observed there, and minimum epipellic chlorophyll concentrations consistently occurred at 0.5 m. Although production between 0 m and 0.5 m was certainly not 0, it was probably much lower than would have been predicted given the high light intensities. Excluding the 0–0.5 m depth interval makes our estimate of whole-lake epipellic production somewhat conservative. Weekly estimates at each depth (milligrams of carbon per square meter per hour) were averaged over the summer and multiplied by sediment surface area at that depth. Depths intervals were summed to get whole-lake epipellic production rates (grams of carbon per hour).

We measured epixylon production only once during the study (Vadeboncoeur and Lodge 2000). We multiplied chlorophyll-specific production rates measured in 1995 by whole-lake epixylon chlorophyll for 1992–1995 to estimate the contribution of epixylon to whole-lake periphyton production. Our estimates allowed us to determine that epixylon was a small component of whole-lake primary production (see *Results*). Therefore, we did not include epixylon in the whole-lake analyses discussed below.

Weekly profiles of phytoplankton production were used in conjunction with chlorophyll, temperature, DIC, total daily incident radiation and water-column light attenuation to estimate daily phytoplankton production (milligrams of carbon per cubic meter) in the photic zone (Carpenter et al. 1993b). For phytoplankton habitat, we calculated pelagic volume based on photic zone depth (depth of 1% light penetration) and lake bathymetry for each week during summer. From these data we calculated average summer whole-lake phytoplankton production (grams of carbon per hour) for 1991–1995.

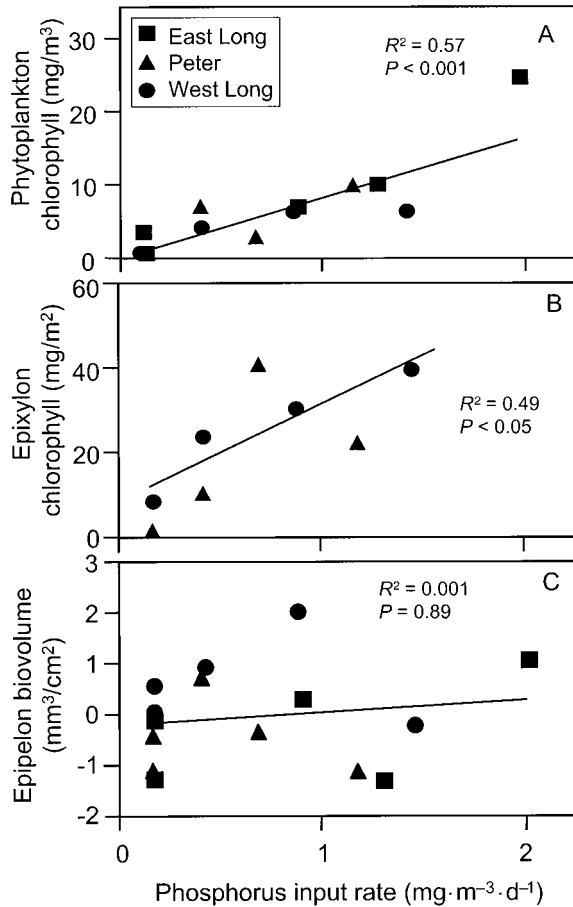


FIG. 1. Algal biomass in the shallow (non-light-limited) littoral zone: (A) phytoplankton chlorophyll (0–1.0 m); (B) epixylon chlorophyll at 0.5 m; (C) epipelton biovolume at 1.0 m. Each point is the summer average and is corrected (treatment – reference) for average biomass in the reference lake. Statistics refer to regression on summer phosphorus addition rate.

We regressed the change in whole-lake epipellic production (relative to prefertilization) on P input rate. We also used linear regression to determine the effect of P input rate on the relative contribution of benthic production to whole-lake (epipelton + phytoplankton) production. We used only 1992 as a prefertilization year to reduce the confounding influence of increasing DOC in East Long and decreasing DOC in West Long. The contribution of periphyton to whole-lake production depends on the ratio of surface area of littoral sediments (benthic habitat) to epilimnetic volume (pelagic habitat), which decreases with increasing lake size (Fee 1979, Carpenter 1983, Lodge et al. 1998). Therefore, we tested for morphometric effects by including surface area to volume ratio as an independent variable. Lastly, we compared changes in phytoplankton production (relative to 1992) with changes in whole-lake primary production for each fertilization year.

## RESULTS

At our first scale of analysis, we compared area-specific changes in algal biomass along the experimental P gradient in a high light environment ( $z \leq 1.0$  m). Periphyton photosaturation usually occurs between 100 and 400  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Hill 1996). Summer light at 0.5 m (averaged across lakes) was 525  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . However, we calculated average summer light intensities at 1.0 m (depth of epipelton sampling) and 0.5 m (depth of phytoplankton and epixylon sampling) and entered it into the regressions to more firmly establish that light was not driving the observed responses. Light did not explain any of the variation in average summer biomass of algae at these shallow depths ( $P > 0.05$  for all three groups).

Both epixylon ( $R^2 = 0.49$ ,  $P < 0.05$ ) and phytoplankton ( $R^2 = 0.57$ ,  $P < 0.001$ ) chlorophyll increased significantly with increasing P load (Fig. 1A, B). Average summer epixylon and phytoplankton chlorophyll concentrations in the treatment lakes were never lower than in the reference lake. When we expressed epipellic biovolume in the treatment lakes relative to the reference lake, there was no relationship to P load ( $R^2 = 0.001$ ,  $P = 0.89$ ). Differences in epipelton biomass relative to the reference lake were as often negative as positive, and the mean change was 0 (Fig. 1C).

Epipellic production data corroborated the absence of a positive response to fertilization seen in the more intensive monitoring of epipellic biomass. Epipellic primary production was a nonlinear function of light (Fig. 2), and log transforming both light and primary production provided the best and simplest fit for the data. Of the other pelagic variables entered into the multiple regression (water-column temperature, phytoplankton chlorophyll, DOC, and water-column TP), only TP ( $P = 0.001$ ) and DOC ( $P = 0.01$ ) were significant. Both TP and DOC had negative regression coefficients (see

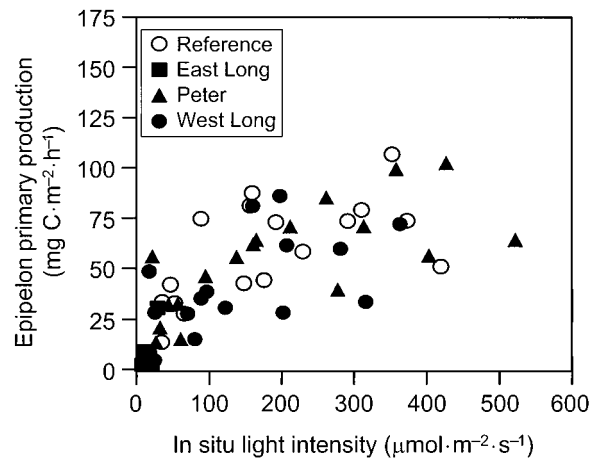


FIG. 2. Epipelton primary production. Each point is the average production at a single depth on a single day. Light intensity is expressed as micromoles of photons per square meter per second.

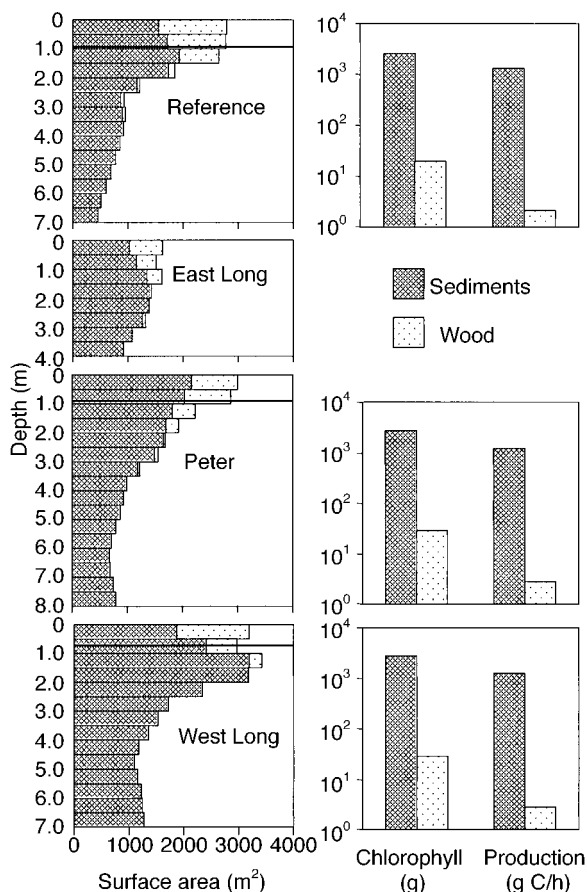


FIG. 3. Distribution of benthic habitat and periphyton. Left column: Surface area of wood and sediments in 0.5 m depth intervals from lake edge to maximum sampling depth (depth at which a scuba diver could still distinguish the sediment-water interface). The line represents the depth of 50% light penetration (i.e., saturating light intensity) averaged over all treatment years. Right column: Total benthic chlorophyll and primary production on sediment and wood in 1995. Epixylon was not measured in East Long Lake in 1995.

Eq. 1). Thus, epipellic production declined with increasing water-column TP (i.e., fertilization) and with increasing organic color.

On a whole-lake basis, wood made up at most 16% (reference lake) of total benthic surface area (Fig. 3). The majority of wood occurred between 0 and 1 m water depth in all lakes (Fig. 3), making our measurements of epixylon production and chlorophyll at 0.5 m reasonable estimates from which to extrapolate to the whole lake. Average area-specific epipellic chlorophyll was up to 10× higher than that of epixylon. Chlorophyll measurements on wood in the reference lake ranged from 1.8 to 130 mg/m<sup>2</sup> (mean = 22 mg/m<sup>2</sup>). Epixylon chlorophyll in the treatment lakes ranged from 0.5 to 55 mg/m<sup>2</sup> (mean = 18 mg/m<sup>2</sup>) before fertilization and from 3 to 560 mg/m<sup>2</sup> (mean = 61 mg/m<sup>2</sup>) during fertilization. Epipellic chlorophyll concentrations in the reference lake in 1995 ranged from 111

to 242 mg/m<sup>2</sup> (mean = 174 mg/m<sup>2</sup>). Epipelon chlorophyll in the treatment lakes ranged from 77 to 389 mg/m<sup>2</sup> (mean = 171 mg/m<sup>2</sup>). This greater biomass on sediments, in combination with the greater surface area of sediments, meant that epixylic chlorophyll in 1995 was only 0.5–1.8% of total benthic chlorophyll (Fig. 3). As with chlorophyll, epixylon production was much lower than that of epipelon. Epipellic production at 1.5 m ranged from 1.5 to 110 mg C·m<sup>-2</sup>·h<sup>-1</sup>, while the range of epixylon was only 1.3–4.2 mg C·m<sup>-2</sup>·h<sup>-1</sup>. Using chlorophyll-specific production rates measured in 1995 (Vadeboncoeur and Lodge 2000), we estimated that epixylon production over all years constituted 0.4–3.6% of total benthic production. Because epixylon chlorophyll and production were such a small fraction of total benthic production, we did not include epixylon when modeling the effects of fertilization on whole-lake distribution of benthic and pelagic algal production.

Before fertilization, epipelon accounted for up to 80% of whole-lake (epipelon + phytoplankton) primary production (Fig. 4A). With increased phosphorus loading, the benthic fraction declined to ~40% in West Long Lake and 10% in East Long Lake, where increased DOC (Christensen et al. 1996) contributed to the decline. The distribution of primary production was not affected by the ratio of littoral surface area to pelagic volume ( $P > 0.05$ ).

Declines in the percentage of benthic production

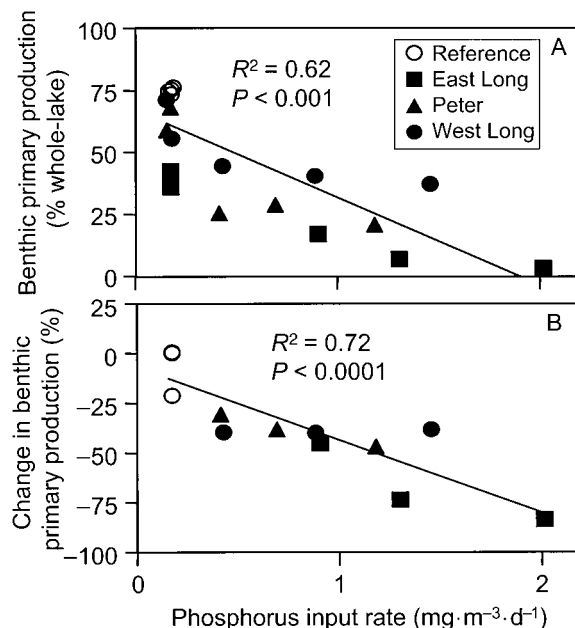


FIG. 4. (A) Relative contribution of algae on sediments to whole-lake (epipelon + phytoplankton) primary production as a function of average summer phosphorus loading to the epilimnion. (B) The percentage change in whole-lake epipellic primary production for each fertilization year (1993–1995) relative to prefertilization values (1992). All points represent summer averages for a single lake-year.

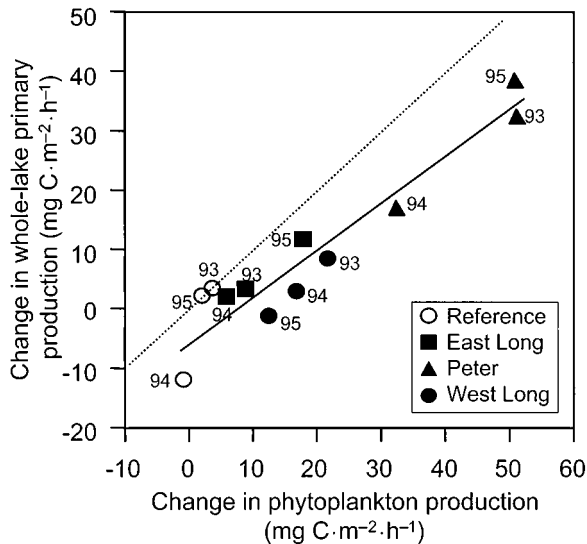


FIG. 5. The change in actual whole-lake primary production (epipelon + phytoplankton) compared to the change perceived when phytoplankton are considered to be the only primary producers. The change in whole-lake primary production =  $0.75 \times$  the change in phytoplankton - 3.88. The changes are relative to 1992 values for whole-lake production. No regression  $P$  value is given because the two variables are autocorrelated, but the slope of the solid line represents the actual change in whole-lake primary production relative to the change in phytoplankton. Each point is labeled for year for comparison to the reference lake during a given year. The dotted line is the 1:1 relationship between changes in phytoplankton production and whole-lake production.

could have resulted from increases in phytoplankton production, decreases in benthic production, or both. Pelagic primary production increased in response to fertilization (Carpenter et al. 1998, Cottingham and Carpenter 1998, Cottingham et al. 1998). A comparison of average summer epipellic production relative to pre-fertilization shows that whole-lake epipellic production decreased markedly with increasing phosphorus load (Fig. 4B). This was especially true in the highly colored East Long Lake. Sometimes in East and West Long Lakes, the increase in phytoplankton production was completely offset by decreases in epipelon production, resulting in no change in whole-lake production relative to the reference basin (Fig. 5). In Peter Lake, where phytoplankton response to nutrients was very strong because of small zooplankton size and low DOC (Carpenter et al. 1998), there was always an overall increase in whole-lake primary production. However, this increase was  $\sim 75\%$  of that indicated by phytoplankton alone.

#### DISCUSSION

##### *Periphyton responses to water column fertilization and changes in light availability*

Epixylon, like phytoplankton, increased as a result of fertilization. About 50% of variation in average sum-

mer epixylon chlorophyll concentration was explained by P input. The few studies on epixylic algae suggest that wood is potentially a C source, but not an N or P source for epixylon (Sinsabaugh et al. 1991, Burkholder 1996, Vadeboncoeur and Lodge 2000). Our results also suggest that epixylon sequester N and P from the water column, and are nutrient limited in these lakes. In their use of water column N and P, epixylon are analogous to periphyton on rocks (epilithon) or artificial substrata such as clay tiles, the two most commonly discussed substrata in periphyton literature. Many studies have demonstrated the importance of P in limiting epilithon in streams (Bothwell 1988, Winterbourn 1990, Stevenson et al. 1991, Peterson et al. 1993, Rosemund et al. 1993), but experiments in lakes are more rare, and the results are equivocal. There was only a weak relationship between epilithic chlorophyll and water column TP in a comparison of Canadian lakes (Cattaneo 1987). Carbon and pH, rather than N or P, sometimes dictate epilithon biomass in soft-water lakes (Fairchild et al. 1989, Fairchild and Sherman 1993, Turner et al. 1994). Although our study lakes are soft-water lakes, they have high rates of  $\text{CO}_2$  flux (Schindler et al. 1997), and the increase in epixylon chlorophyll observed here is similar to increases in epilithon chlorophyll and production in fertilized Canadian Shield and subarctic lakes (Schindler et al. 1973, Shortreed et al. 1984, Björk-Ramberg and Ånell 1985).

In contrast to epixylon and phytoplankton, epipelon showed no positive response to fertilization even at 1.0 m water depth (Fig. 1). Our production data corroborate the biovolume data, suggesting, if anything, a negative correlation with water column fertilization (TP). Epipellic algae from these lakes also showed no response to water column fertilization in laboratory and in situ mesocosm experiments (Blumenshine et al. 1997, Vadeboncoeur and Lodge 2000). Experiments show that epipellic algae sequester nutrients from the sediment pore-water (Carlton and Wetzel 1988, Hanson 1990) and the overlying water (Stanley 1976, Björk-Ramberg 1985, Rueter and Axler 1992). In a comparative study, epipelon were nutrient limited only in very oligotrophic lakes, but biomass was correlated with pore-water, not water column, nutrients (Hansson 1992). Pore-water TP concentrations in West Long and Paul Lake ranged from 100 to 200  $\mu\text{g/L}$  and were  $\sim 10\times$  higher than water column TP (Vadeboncoeur and Lodge 2000). Thus, it is likely that the main nutrient source for epipelon is the sediment pore-water in our study lakes, and that the increase in water-column nutrients with fertilization was negligible when compared to the total pool of nutrients available to epipelon.

Increases in phytoplankton biomass led to a reduction in light penetration in the study lakes (Christensen et al. 1995). As discussed above, we measured epixylon only at 0.5 m, and thus found no relationship with epixylon chlorophyll and light. However, production of



epipelon measured at  $\geq 1.5$  m was strongly light limited. In addition, at any given light intensity, epipellic production was lower when water-column TP or DOC concentrations were high. Various mechanisms may contribute to these relationships. The greatest variations in TP and DOC tended to occur at large scales, i.e., between lakes and years and between the epilimnion and metalimnion, rather than between days within lakes. Thus, the negative relationship with TP and DOC may reflect long-term changes in light quality in fertilized or highly colored lakes. It is inherently difficult to separate the effects of light quality from light quantity, but the differential attenuation of specific wavelengths by phytoplankton and other organic matter may affect epipellic biomass and species composition (Hill 1996, Pillsbury and Lowe 1999). Also, humic compounds reduce phytoplankton P uptake and production (Jackson and Hecky 1980, Francko 1986), and they may have similar effects on periphyton. Finally, we probably systematically underestimated the downwelling component of the light extinction coefficient ( $K_d$ ) in the fertilized lakes by using a spherical sensor for our routine light measurements. Increased scattering of light was a very obvious effect of fertilization, especially in West Long Lake, where blooms of large, flake-like *Anabaena* occurred (Cottingham et al. 1998, Cottingham 1999). Thus, downwelling light, which is important to algae on sediment, may have been overestimated in the fertilized lakes. This negative relationship between epipellic production and TP indicates that effects of fertilization on benthic algae may extend beyond the simple effects of shading by phytoplankton.

Some of the variation in epipellic production could not be related to pelagic variables. In the epilimnion there was often no difference in productivity at 1.5 and 2.5 m sampling depths, suggesting photosaturation. Furthermore, epipellic mats were never well developed at depth  $< 0.5$  m, and algal biomass usually peaked between 1.0 and 3.0 m (data not shown). These patterns suggest that factors such as grazing and disturbance mitigate the relationship between light and epipellic production (Hill 1996).

#### *Whole-benthic response to fertilization*

Benthic primary production declined with increased P loading, but this was only obvious when we examined benthic production at the whole-lake scale. It was necessary to know the distribution of the two benthic substrata with respect to light, and their abundance and productivity in order to estimate the whole-benthic response to fertilization. Most wood consisted of large trees that remained in the shallow littoral zone where they had fallen from the riparian area, and the majority of wood habitat occurred shallower than 50% light penetration (Fig. 3). In contrast, sediments colonized by epipelon extended from the lake edge to well below the presumed compensation depth (1% light). Thus, most benthic surface area was sediment, and the ma-

majority of sediments occurred deeper than 50% light penetration (Fig. 3). Finally, on an areal basis, sediments were  $\sim 5$ –10 times more productive than wood. Average periphyton productivity at high light intensities is  $145 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$  (range:  $0.12$ – $640 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ ) according to a literature survey (Krause-Jensen and Sand-Jensen 1998). Thus, the maximum rate of epipellic production in our lakes ( $\approx 110 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ , Fig. 2) was somewhat below the average literature values. Epixylon production was very low ( $1.3$ – $4.2 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ ), but not atypical of production on hard surfaces in lakes (Schindler et al. 1973, Björk-Ramberg and Ånell 1985).

These differences in productivity and distribution can lead to counterintuitive relationships between the substratum most apparent to the observer and the one that drives overall patterns in total benthic production. For instance, sediments accumulate in the deeper, less disturbed areas of lakes and may be considered unproductive because light is low. However, differences in productivity between substrata can be much greater than within-substratum differences in productivity that are caused by light and nutrients (Vadeboncoeur and Lodge 2000). For example, periphyton production per square meter increased substantially with depth in an oligotrophic arctic lake, due to a change from rocky substratum in the near shore area to organic sediments offshore (Welch and Kalff 1974). In our lakes, epixylon responded positively and very visibly to fertilization with a luxuriant growth of filamentous green algae. However, this increase did little to offset the negative response of epipelon because sediments were more abundant and more productive than wood. Thus, the reductions in light intensity caused by phytoplankton blooms, not the increase in water-column nutrients, dominated the whole-benthic response to fertilization.

Water-column fertilization reduced benthic primary production by reducing light availability to periphyton. This inverse relationship between epipellic algae and phytoplankton along lake productivity gradients has been hypothesized previously (Wetzel 1983, Sand-Jensen and Borum 1991), but this is the first time it has been experimentally tested over a range of fertilization rates. Our results largely support the hypothesized qualitative models. Interestingly, Hansson (1992) found no relationship between epipellic biomass at 0.75 m and TP in lakes where  $K = 0.5$ – $1.75$ . Our lakes are within this range of  $K$  values, and we also saw no relationship between epipellic biomass and P load or light at shallow depths (1.0 m). However, changes in light availability in our study lakes caused marked declines in periphyton production at deeper depths, causing a reduction of epipellic production at the whole-lake scale. Thus, our results support Hansson's (1992) specific finding (no relationship between light and biomass at shallow depths), but suggest that the negative effect of phytoplankton on epipelon extends over a

greater range of lake productivities than indicated by his study.

*Whole-lake primary production and response to fertilization*

Limnologists tend to think of phytoplankton as the main primary producers in lakes. However, in our study lakes the majority of primary production occurred in the benthic habitat in the unmanipulated state, and only shifted to the pelagic habitat when fertilizer was added to the water column. There are relatively few lakes for which comparisons of phytoplankton and benthic algal production are available. However, in about half the lakes found in a literature survey (Lodge et al. 1998) benthic algal production equaled or exceeded phytoplankton production. Thus, our study lakes are not unusual. It is notable that for most lakes in which periphyton dominated algal primary production, high productivity and abundance of epipelagic algae usually drove this pattern (Hargrave 1969, Gruendling 1971, Goldman et al. 1972, Welch and Kalff 1974, Stanley 1976, Björk-Ramberg 1983, Vanriël and Johnson 1995). Lakes with high densities of macrophytes and the associated attached algae are also often dominated by benthic primary production (Wetzel 1964). Conversely, in lakes in which periphyton contribute little to overall production, production of nutrient-limited epilithic algae was estimated (Schindler et al. 1973, Shortreed et al. 1984). This dichotomy probably reflects both differences in lake types (rocky bottomed or soft bottomed) and differences in what appeared to be the most important substratum in these lakes. Both the literature and the results of this study strongly suggest that in shallow lakes in which organic sediments accumulate in the photic zone, epipelagic algae are potentially a large component of whole-lake primary production.

Increases in phytoplankton caused significant declines in epipelagic production by lowering light penetration. In East Long (1993) and West Long (1995) Lakes, the changes in whole-lake primary production relative to pre-fertilization were similar to interannual variation observed in the reference lake (Fig. 5). Thus, at low fertilization rates in the two lakes with heavy grazing and high DOC, the increase in phytoplankton was compensated by an equivalent decrease in epipelagic, and whole-lake primary production did not change. Although whole-lake primary production always increased with fertilization in Peter Lake, the reduction in light penetration meant that the increase over background was ~75% of what was indicated by phytoplankton alone. Thus, the assumption that phytoplankton are the main primary producers in lakes causes both an underestimate of whole-lake primary production in relatively oligotrophic lakes, and an overestimate of the impact of water-column fertilization on total ecosystem primary production (Borum and Sand Jensen 1996).

Our results supported the hypothesis that the redis-

tribution of primary production from benthic to pelagic habitats may be as characteristic of eutrophication as the increase in phytoplankton (Wetzel 1983, Sand-Jensen and Borum 1991). Thus, the assumption that phytoplankton are the only carbon fixers can lead to spurious conclusions concerning the relationship between nutrient loading and ecosystem primary production (Borum and Sand-Jensen 1996). If general, this inverse relationship between benthic and pelagic primary production has broad-scale implications for ecosystem processes. Other perturbations that alter water clarity such as changes in macrophyte density (Scheffer et al. 1993), the establishment of zebra mussels (Strayer et al. 1999, Caraco et al. 2000), and global climate change (Schindler et al. 1996) are also likely to result in shifts between benthic and pelagic primary production. This compensatory relationship will tend to stabilize overall whole-lake primary production, but it is likely to alter pathways of energy flux through lake food webs. Periphyton, like phytoplankton, fix energy and sequester nutrients that subsequently become available to consumers. However, the importance of periphyton carbon in lake food webs is understudied relative to phytoplankton (Hecky and Hesslein 1995, Lowe 1996). It is increasingly understood that benthic invertebrates are a crucial energy source for fish, and therefore, ultimately, so are benthic algae (France 1995, Hecky and Hesslein 1995). Both the magnitude of benthic primary production and its inverse relationship to phytoplankton production suggest that a major component of lake energy budgets is overlooked when benthic algae are not included in estimates of lake primary production (Strayer and Likens 1986). Expanding the whole-lake scale to include benthic habitat will provide a more comprehensive understanding of energy and nutrient pathways in lakes, and refine our ability to predict the effects of anthropogenic perturbations on lakes.

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