

Factors regulating phytoplankton production and standing crop in the world's freshwaters

D. W. Schindler

Department of Fisheries and the Environment, Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba R3T 2N6

Abstract

A regression analysis of global data for freshwater phytoplankton production, chlorophyll, and various nutrient parameters revealed the following: A high proportion of the variance in both annual phytoplankton production and mean annual chlorophyll could be explained by annual phosphorus input (loading), once a simple correction for water renewal time was applied. Good relationships were also found between phosphorus loading and mean total phosphorus concentration, and between total phosphorus concentration and chlorophyll. The slope of the regression of total phosphorus on phosphorus loading for stratified lakes was not significantly different from that for unstratified lakes, suggesting that the effect of stratification on phosphorus concentration is insignificant compared to external sources of the element. Nutrient input, which was unavailable in previous analyses, appears to be an important factor in controlling freshwater production. There is some evidence for a correlation between latitude and nutrient input, and it is possible that this may explain the good correlation between latitude and production observed by earlier investigators.

In an earlier synthesis of IBP freshwater primary production results, Brylinsky and Mann (1973) and Brylinsky (in press) concluded that variables related to energy availability had a greater influence on phytoplankton production than those related to nutrient availability. They found that 57% of the variability in global primary production could be explained by latitude alone. Brylinsky and Mann, however, recognized the scarcity of good data for nutrient input to lakes in the IBP data set. They suggested (p. 12) that some of the influence attributed to energy might be due to its driving of circulation systems, so that nutrient availability might be affected directly. Recently, more data on nutrients, including input and output dynamics, have accumulated, chiefly as the result of investigations of the eutrophication of lakes. These data, plus our own experimental studies in lakes, suggested that nutrients played a preeminent role in controlling phytoplankton production and standing crop. Of all the variables which may control aquatic production and standing crop, only nutrients are amenable to control by humans. It therefore seemed worthwhile to repeat Brylinsky and Mann's analysis, including this new information (Schindler and Fee 1974).

The following analysis is highly biased toward glacial lakes in north temperate and subarctic regions, where most limnological activity has been concentrated. More complete data are sorely needed for water bodies in tropical and arctic regions, in the southern hemisphere, and in unglaciated areas before a definitive global analysis of production and factors affecting it can be made.

Increases in the annual input of nutrients (phosphorus in particular) have been found to cause corresponding increases in phytoplankton production and standing crop, regardless of latitude (Vollenweider 1968, 1975, 1976; Vollenweider et al. 1974; Kalff and Welch 1974; Dillon 1975; Dillon and Rigler 1974; Schindler 1976; Schindler et al. 1974). Indeed, the literature on eutrophication includes many high values for phytoplankton production and standing crop at northern latitudes (Mathiesen 1971; Bindloss 1974; Ahlgren 1970; Wetzel 1966; Schindler and Comita 1972; Sakamoto 1966; Barica 1975). The relationship between nutrient supply and algal standing crop and production has also been firmly established by experimental studies in whole lakes, at different latitudes (Schindler 1976; Schindler and Fee 1973; Persson et al. 1975).

Table 1. Comparison of maximum ranges of sites treated by Brylinsky and Mann (1973), Brylinsky (in press), and this study. Data in columns 1 and 2 not given in above papers were supplied by Brylinsky (pers. comm.).

	(1) Brylinsky and Mann (1973)	(2) Brylinsky (in press)	(3) Present Study
Latitude	0-75°N	10°N-71°N	38°S-75°N
Area, km ²	0.5-31,500	0.04-30,000	0.002-83,300
Mean depth, m	1.2-730	0.6-325	1.1-313
Production, kcal·m ⁻² ·yr ⁻¹	30-13,320	8-13,000	28-5,600
Water renewal time, year	0.01-130	0.1-118	0.09-247

E. Fee provided many discussions of this topic. M. Brylinsky and K. H. Mann provided data from IBP lakes, as well as a rigorous critique of the manuscript. K. Patalas also pointed out many flaws in the analysis, some of which could be corrected. R. V. Schmidt and T. Rusczyński carried out the data analysis. Many scientific friends from around the world provided unpublished data on their studies, for which I am grateful.

Methods

Data were gathered from several sources, including the published literature, manuscript reports, and personal communications from scientists involved in the IBP, OECD-eutrophication, and other projects, and our own files. The following data were tabulated: annual production per unit area by the ¹⁴C or light bottle oxygen methods, annual mean concentrations of chlorophyll and total phosphorus, annual input of phosphorus and nitrogen, mean depth, and water residence times. Oxygen data were converted to carbon by multiplying by 0.312. When data from such a variety of sources, collected by different methods and investigators, are compared, large discrepancies are to be expected. Because all of the parameters studied spanned nearly three orders of magnitude in total range, it was expected that even occasional large errors would not obscure relationships on the scale sought here. Net production was used rather than gross, because this is the value available for consumption at higher trophic levels, and because results of the ¹⁴C method appear

to be closer to net than to gross production. This seemed a more logical way of combining ¹⁴C and O₂ light bottle results than by using an unknown "fiddle factor" for relating respiration to ¹⁴C results. Recent analyses have shown that respiration in highly productive lakes is usually a high proportion of gross production because the ratio mixing depth:depth of euphotic zone is typically high in such lakes. In many cases, respiration may be 50% or more of gross production (e.g. Ganf and Horne 1975). The proportion appears to vary greatly from lake to lake, probably as a result of differences in morphometry, drainage basin characteristics, and types of consumer organisms, as well as productivity differences, and there seems to be no constant which could be used with validity to correct ¹⁴C data from all sites. Relationships were tested by regression analysis, as in Brylinsky and Mann's studies.

Site description

The characteristics of sites analyzed in different IBP treatments are shown in Table 1. Our sites range from 38°S to 75°N latitude, from 0.002 to 8.3×10^4 km² in area, from 1.1 to 313 m in mean depth, and from 28 to 5,600 kcal·m⁻²·yr⁻¹ in net production. At first glance, the data analyzed in the different studies appear to be similar. There are, however, several important differences. I was unable to obtain nutrient data for most of the very productive tropical sites treated by Brylinsky, so that it was impossible to include them. Only one tropical site, Lake George, Uganda, had sufficient data

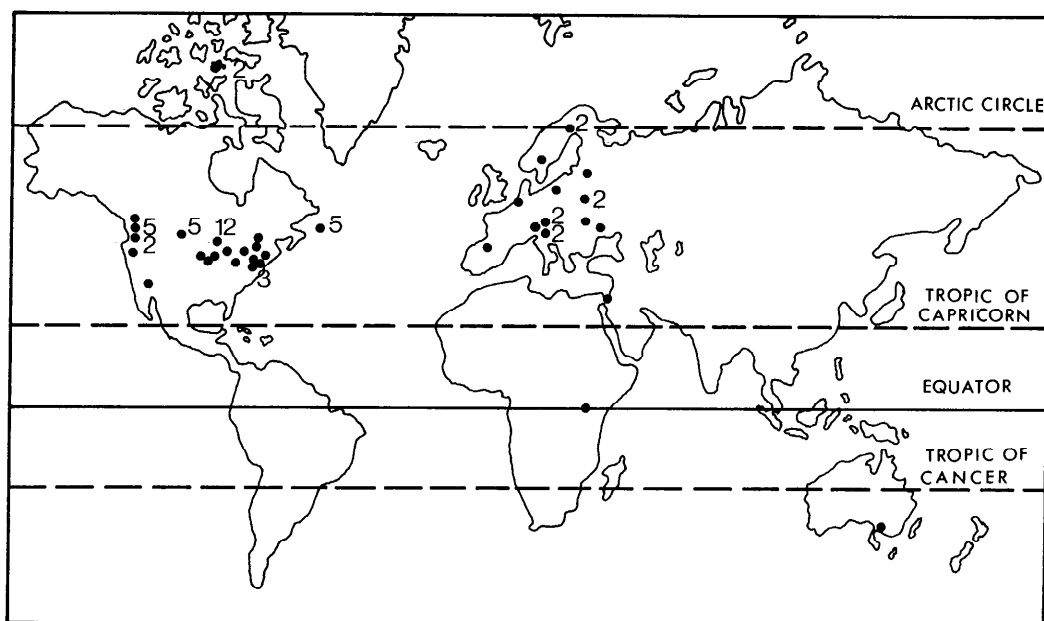


Fig. 1. Approximate locations of lakes and reservoirs in analysis. Numbers indicate several lakes in same locality.

available. On the other hand, I was able to obtain more results from arctic regions than were used in the earlier summaries, plus data for one temperate site in the southern hemisphere (Fig. 1). The difference in upper production values between the analyses is probably not as great as it would first seem from Table 1. Brylinsky used gross production in his analysis, correcting ^{14}C data for respiration by adding a constant proportion. I used net production, defined as discussed above.

Results

Latitude and phytoplankton production—A correlation coefficient of only 0.20 (not significant) was found between net production and latitude. To some extent this is due to the abundance of data from productive north-temperate lakes, where studies of eutrophication are most common, and the paucity of tropical lakes with good data for nutrient input.

Phosphorus and phytoplankton production—One of the most popular indices of eutrophication has been annual

phosphorus input (Vollenweider 1968). If production is truly a measure of eutrophication, one would expect a good relationship between annual production and annual phosphorus input. Vollenweider et al. (1974) found such a relationship for the St. Lawrence Great Lakes. I did not find it for the lakes examined here: the correlation coefficient of 0.23 was not significant.

In the treatment of lakes with drainage from the Precambrian Shield, Schindler et al. (1978) found that two extremely simple and logical equations could be used to relate phytoplankton standing crop and production to phosphorus input and water renewal. The first of these is the steady state equation for a conservative element:

$$C^*_c = \frac{I_c}{V_o}, \quad (1)$$

where C^*_c is the steady state concentration of chemical (c) in the lake, I_c is the amount of chemical entering in a given period, and V_o is the outflow volume during the period. The second equation,

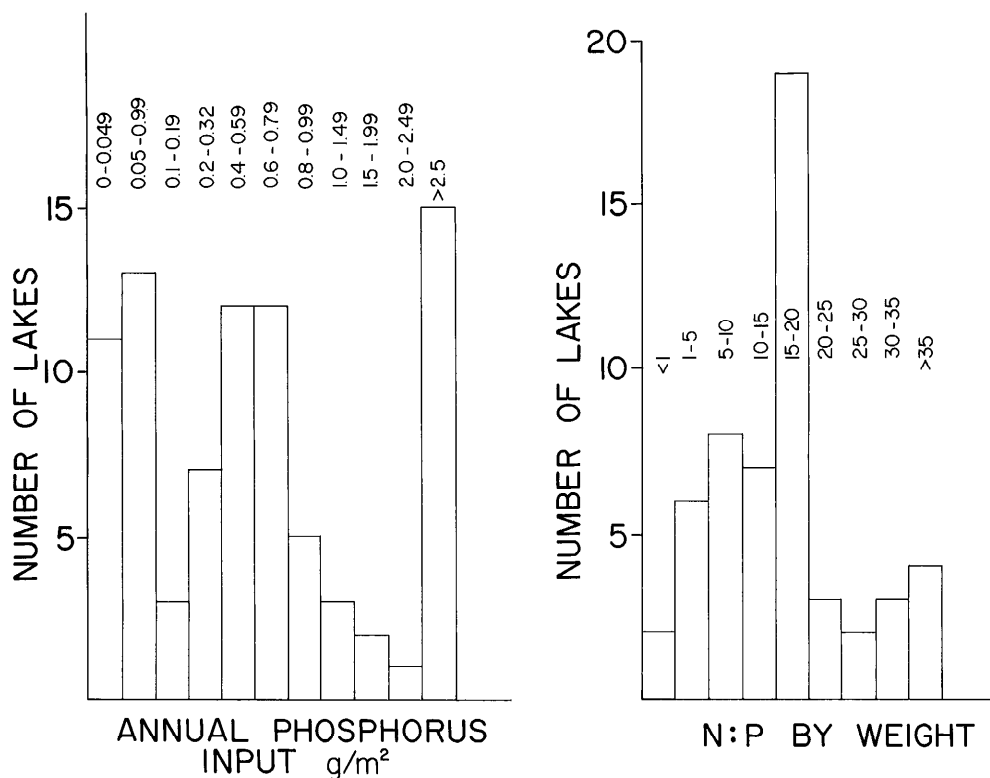


Fig. 2. Frequency distribution of nutrient loading for lakes studied.

$$C^*_c = \frac{M_c + I_c(t)}{V_L + V_o(t)}, \quad (2)$$

where M_c is the mass of chemical in the lake at the beginning of the period, V_L is the lake volume, and t is the time period under examination, is a simple modification to incorporate lakes where nutrient inputs are rapidly increased or reduced. At steady state, the two equations should give equal results. Both equations performed well for Schindler et al. (1978). Both also worked very well here, but Eq. 2 clearly performed better, perhaps because of the fact that several lakes had recently undergone rapid increases or decreases in phosphorus input. For the sake of brevity I will therefore discuss only the results of Eq. 2.

Before using Eq. 2 to relate C^*_p (where P is total phosphorus) and annual production, a second adjustment to the data was made. One would not expect to find

a relationship between phosphorus and phytoplankton production when the ratio of nitrogen to phosphorus in input is extremely low, i.e. where phosphorus is not the limiting nutrient. Most algae seem to require N:P at at least 10:1 by weight (Vallentyne 1974), and a severe reduction in the ratio should cause the system to be nitrogen limited. In a detailed study of relative nutrient requirements, Chian-dani and Vighi (1974) found phosphorus to be limiting at above 10:1, nitrogen below 5:1, and a proportional relationship in between these values. Schindler (1976, 1977) found that fixation of atmospheric N_2 would allow phosphorus-proportional development of phytoplankton in lakes with ionic N:P ratios in input as low as 5:1. Only lakes with N:P ratios in input greater than 5:1 were therefore included in this analysis. The frequency distributions of P loading and N:P ratios encountered are given in Fig. 2.

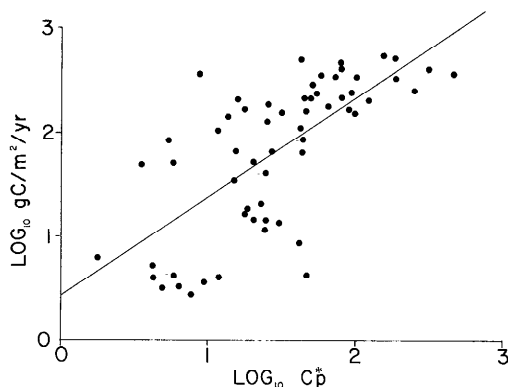


Fig. 3. Relationship between net primary production and C^*_P , as calculated from Eq. 1. Lakes where N:P in input is $<5:1$ are not included in analysis. Correlation coefficient, $r = 0.69$, is highly significant. $\log P_N = 0.83 \log C^*_P + 0.56$.

A linear regression of production on C^*_P explained a highly significant proportion of the variance ($r = 0.59$) but this could presumably be improved if more data were available in the upper C^*_P range. Using a log-log plot improved the correlation to $r = 0.65$ (Fig. 3).

Inspection suggested that the relationship between production and C^*_P reached some upper limit, where production did not increase as C^*_P got larger. This would be expected logically: chlorophyll concentrations in lakes with the highest C^*_P were high enough to restrict severely the depth of the eutrophic zone, so that light should have limited further increases in production, regardless of nutrient conditions. This apparent upper asymptote is too roughly defined to treat in detail because of the paucity of lakes with high C^*_P . It is also probable that the asymptote of this relationship would be lower in lakes where light attenuation is caused largely by tripton or dissolved material. Only further investigations in productive lakes can clarify this point.

Phosphorus and standing crop—From the standpoint of managing eutrophication, the concentration of the algal standing crop supported is often of greater interest than the production. It therefore seemed worthwhile to try to analyze nutrient factors affecting standing crop di-

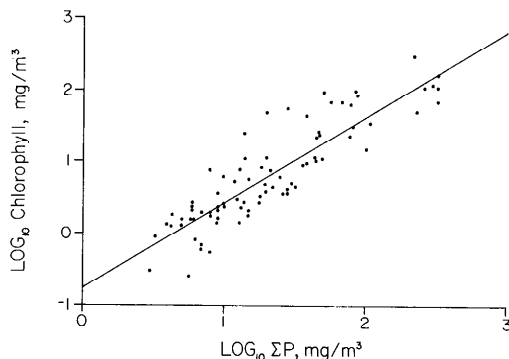


Fig. 4. Relationship between mean annual chlorophyll concentration and mean annual concentration of total phosphorus. Value for r (0.88) is highly significant. $\log [\text{Chl}] = 1.213 \log [\Sigma P] - 0.848$.

rectly, even though production and standing crop must be related to some degree.

Sakamoto (1966) and Dillon and Rigler (1974) have shown that the summer chlorophyll concentration of temperate lakes may be predicted quite accurately from the concentration of total phosphorus (ΣP) at spring overturn. A similar treatment was not possible for the lakes studied here, because it was impossible to assign a "spring" value to tropical and arctic lakes. Instead, the relationship between mean annual chlorophyll concentration and mean annual concentration of total phosphorus was examined (Fig. 4) and found to be as good as correlations in the above-mentioned papers ($r = 0.89$).

In turn, our results show that the mean annual concentration of total phosphorus could be quite accurately related to the phosphorus input corrected for water renewal ($r = 0.88$, Fig. 5). In fact, when the chlorophyll-phosphorus relationship of Dillon and Rigler (1974), the Pacific Northwest Environmental Research Laboratory (1974), and this study are compared, there is no significant difference between them (Schindler 1976). This is of obvious interest to managers, because knowing either phosphorus input and water renewal time or mean concentration of P allows one to predict the mean phytoplankton standing crop quite accurately in the majority of cases, or, con-

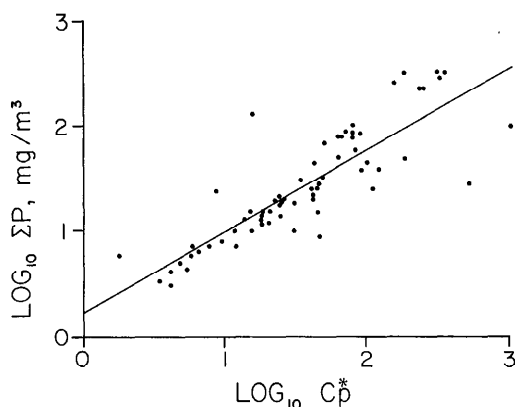


Fig. 5. Relationship between mean annual concentration of total phosphorus and corrected annual phosphorus input, C_p^* from Eq. 1. Correlation ($r = 0.88$) is highly significant. $\log [\Sigma P] = 0.779 \log C_p^* + 0.214$.

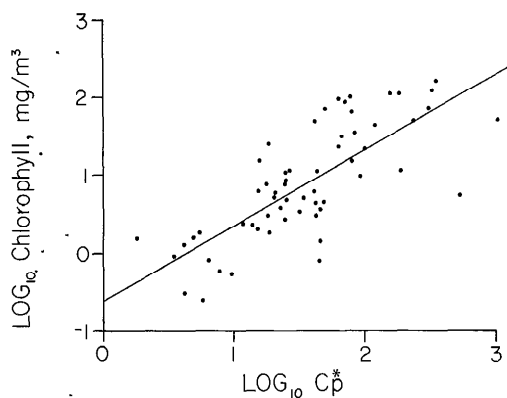


Fig. 6. Relationship between C_p^* and mean annual chlorophyll concentration. Correlation ($r = 0.76$) is highly significant. $\log [Chl] = 0.968 \log C_p^* - 0.620$.

versely if a certain reduction in standing crop is desired, the necessary reduction in loading can be calculated and the feasibility of obtaining it by regulating phosphorus input studied. Such a plan has recently been suggested for lakes of Ontario by Dillon and Rigler (1975).

Since there are good relationships between C_p^* and ΣP , and between ΣP and chlorophyll, it follows that chlorophyll should be predictable directly from C_p^* . This is shown in Fig. 6 ($r = 0.76$).

The effect of thermal stratification on phytoplankton production and standing crop—One statement often debated by limnologists is whether shallow, holomictic lakes are more productive than stratified ones which circulate only periodically (e.g. Richardson 1975). It was therefore of interest to compare C_p^* vs. annual average ΣP for stratified and unstratified lakes. Presumably if "internal loading" (return from sediments) caused significantly more phosphorus to become available in the shallower lakes, the slope of ΣP on C_p^* would be greater than for deeper, stratified ones. The data were therefore separated into a stratified and an unstratified group and the regressions were rerun. The difference detected (Fig. 7) was not significant, and we as-

sume that for our purposes only external loading of this element is of overwhelming importance.

Nitrogen and primary production—Because we failed to ask contributors for average concentrations of total nitrogen, it was impossible to calculate a C_N^* value for water renewal-corrected nitrogen loading, as we did for phosphorus. By using the same rationale, i.e. by not including data where the N:P ratio input would render phosphorus limiting ($>10:1$ according to Chiandani and Vighi 1974), we predict that good correlations between production and nitrogen input would be found. Fewer data would, however, be available, because many investigators did not collect nitrogen input data, and for many lakes the N:P ratio exceeds the 10:1 critical value mentioned earlier.

Light and primary production—The difference in total annual light reaching Char Lake, the most northerly lake studied here, and Lake George at the equator, was less than 50×, even when winter darkness and attenuation by ice and snow were accounted for. It therefore seems unlikely that the much greater (1,000×) range in production with latitude observed by Brylinsky was due to light alone.

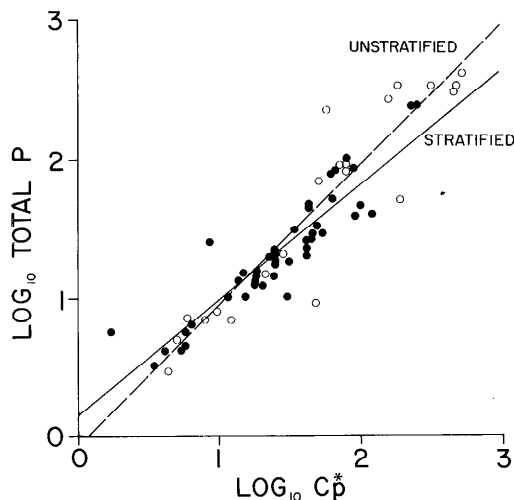


Fig. 7. Separation of regressions of total P on C^*_P into stratified and unstratified group. Lack of significant difference between slopes and asymptotes indicates that increased contact (and presumed exchange) with sediments has little influence on phosphorus concentration. ○—Unstratified lakes; ●—stratified lakes.

The question then remains—why did Brylinsky find a high correlation between production and latitude, if light is not of primary importance? A few scraps of evidence suggest a hypothesis which can be simply tested in a few years if the required data are collected. When nutrient in rainfall is compared for the few sites where such data are available and where cultural contamination is probably slight, there is a $100\times$ increase in nutrient influx from polar regions to the equator (Schindler and Fee 1974). Due to increased amounts of precipitation, higher runoff, more organic and inorganic acids, more diverse and efficient communities of soil decomposers, longer period when soils are not frozen, and higher temperature, one might also expect the nutrient inflow via runoff and streamflow to be higher at more equatorial latitudes. Latitude and input of nutrients could therefore be correlated, as well as latitude and light.

Data collected and analyzed from a large number of sites would be needed to rigorously test the above hypothesis, due to geological, geographical, and cul-

tural factors. If controlling world aquatic productivity is seriously contemplated, such a study must be undertaken. S. Odén and T. Ahl (pers. comm.) showed that input of nutrients to north-temperate regions of Europe via precipitation is increasing rapidly due to the effects of industry and agriculture. Outside Europe, such data are scarce and not usually collected and analyzed in comparable fashion.

Talling (1975) doubts that the accuracy of any net production measurement is better than $\pm 50\%$. Measurement of nutrient input is probably subject to even larger errors, because many lakes have diffuse nutrient sources that are nearly impossible to estimate. The relationships found here were possible only because the data treated embraced a range of 100 to $1,000\times$ so that even quite large errors would not obscure relationships if they existed.

When all data used are obtained by similar methods, and when a relatively narrow range of production and nutrient input values are compared, the above methods give much more precise results (Schindler et al. 1978). A global standardization of methodology would probably allow better interpretation to be made.

Discussion

It is obvious that work on lake productivity and on eutrophication is really inseparable—the only difference is in the emphasis on the fate of the photosynthesized material. Two variables, phosphorus input and water renewal time, which have recently become central to interpreting eutrophication problems, appear to serve equally well for interpreting production results and are the key to managing a wide variety of aquatic productivity problems.

It may not be a geochemical accident that production and standing crop in the majority of the world's lakes are predictable from phosphorus-based models, even when ratios of C and N to P in input are lower than those apparently favored by plankton. Input calculations almost

never take into account N_2 fixation by both phytoplankton and periphyton. Atmospheric contributions of CO_2 can be quite large. Furthermore, once sedimentation and outflow are subtracted from input, it is almost invariably found that a higher proportion of incoming nitrogen than of incoming phosphorus is retained in the water column of the lake. These factors appear to allow lakes to correct deficiencies of nitrogen and carbon to the point where standing crop is proportional to phosphorus (Schindler 1976, 1977; Persson et al. 1975). No such mechanisms appear to assist the phosphorus cycle, and while we do not have comparable investigations of other elements, it seems unlikely that they would be of primary importance in controlling the production of natural systems.

M. Brylinsky (pers. comm.) performed calculations on the precipitation data from IBP sites which partially support my hypothesis about latitudinal effects in nutrient input. He found a significant correlation between latitude and amount of precipitation ($r = 0.43$, $n = 89$), but no significant relationship between concentration of nutrients in precipitation and latitude. He was unable to separate differences in the effects of cultural sources or collection techniques, while in our much smaller analysis we were able to minimize such differences. Careful studies of global precipitation chemistry are necessary before the relationship between latitude, cultural pollutants, and concentration can be accurately assessed, and such knowledge is necessary before a rational management strategy can be devised for production and eutrophication in all climatic and geological settings.

The above treatment suggests general strategies for the management of water bodies which should be widely applicable. However, when management of a specific water body is discussed, light, temperature, hydrology, and morphology as well as nutrients may play important roles. For example, low light availability in very shallow lakes may be due to high wind-induced turbidity or to the inflow

of a large, highly turbid river. For this reason Lake Chad, at only $13^\circ N$ and presumably with quite a high nutrient input, is as unproductive as most subarctic lakes (Brylinsky and Mann 1973). Although one can devise predictive management strategies that will apply to the majority of lakes, there will always be a small proportion of water bodies which will not conform to any generalized pattern.

References

- AHLGREN, G. 1970. Limnological studies of Lake Norrviken, a eutrophicated Swedish lake. 2. Phytoplankton and its production. Schweiz. Z. Hydrol. **32**: 353-396.
- BARICA, J. 1975. Geochemistry and nutrient regime of saline eutrophic lakes in the Erickson-Elphinstone district of southwestern Manitoba. Environ. Can., Fish. Mar. Serv. Tech. Rep. 511. 82 p.
- BINDLOSS, M. E. 1974. Primary productivity of phytoplankton in Loch Leven, Kinross. Proc. R. Soc. Edinb. Ser. B **74**: 157-182.
- BRYLINSKY, M. In press. Estimating the productivity of lakes and reservoirs. In E. D. LeCren [ed.], The functioning of freshwater ecosystems. IBP Synthesis Vol. Cambridge.
- , AND K. H. MANN. 1973. An analysis of factors governing productivity in lakes and reservoirs. Limnol. Oceanogr. **18**: 1-14.
- CHIANDANI, G., AND M. VIGILI. 1974. The N:P ratio and tests with *Selenastrum* to predict eutrophication in lakes. Water Res. **8**: 1063-1069.
- DILLON, P. J. 1975. The application of the phosphorus-loading concept of eutrophication research. CCIW Sci. Ser. 46, Burlington, Ontario. 14 p.
- , AND F. H. RIGLER. 1974. The phosphorus-chlorophyll relationship in lakes. Limnol. Oceanogr. **19**: 767-773.
- , AND ———. 1975. A simple method for predicting the capacity of a lake for development based on lake trophic status. J. Fish. Res. Bd. Can. **32**: 1519-1531.
- GANE, C. G., AND A. J. HORNE. 1975. Diurnal stratification, photosynthesis and nitrogen-fixation in a shallow, equatorial lake (Lake George, Uganda). Freshwater Biol. **5**: 13-39.
- KALFF, J., AND H. E. WELCH. 1974. Phytoplankton production in Char Lake, a natural polar lake, and in Meretta Lake, a polluted polar lake, Cornwallis Island, Northwest Territories. J. Fish. Res. Bd. Can. **31**: 621-636.
- MATTHESEN, H. 1971. Summer maxima of algae and eutrophication. Mitt. Int. Ver. Theor. Angew. Limnol. **19**, p. 161-181.
- PACIFIC NORTHWEST ENVIRONMENTAL RESEARCH LABORATORY. 1974. The relationships of phosphorus and nitrogen to the trophic state of northeast and north-central lakes and reser-

- voirs. Working Pap. 23. 28 p. PNWERL, Corvallis, Oregon.
- PERSSON, G., S. K. HOLMGREN, M. JANSSON, A. LUNDGREN, B. NYMAN, D. SOLANDER, AND C. ANELL. 1975. Phosphorus and nitrogen and the regulation of lake ecosystems: Experimental approaches in subarctic Sweden. Proc. Circumpolar Conf. Northern Ecol. Sect. 2, p. 1-20. September 1975, Ottawa. Natl. Res. Council. Can.
- RICHARDSON, J. L. 1975. Morphometry and lacustrine productivity. *Limnol. Oceanogr.* **20**: 661-663.
- SAKAMOTO, M. 1966. Primary production by phytoplankton community in some Japanese lakes and its dependence on lake depth. *Arch. Hydrobiol.* **62**: 1-28.
- SCHINDLER, D. W. 1976. Biogeochemical evolution of phosphorus limitation in nutrient-enriched lakes of the Precambrian Shield, p. 647-664. *In* J. O. Nriagu [ed.], *Environmental biogeochemistry*. Ann Arbor Sci.
- . 1977. The evolution of phosphorus limitation in lakes. *Science* **195**: 260-262.
- , AND G. W. COMITA. 1972. The dependence of primary production upon physical and chemical factors in a small, senescing lake, including the effects of complete winter oxygen depletion. *Arch. Hydrobiol.* **69**: 413-451.
- , AND E. J. FEE. 1973. Diurnal variation of dissolved inorganic carbon and its use in estimating primary production and CO₂ invasion in lake 227. *J. Fish. Res. Bd. Can.* **30**: 1501-1510.
- , AND ———. 1974. Primary production in freshwater, p. 155-158. Proc. Int. Congr. Ecol. (1st), The Hague, September 1974. PUDOC, Wageningen.
- , ———, AND T. RUSZCZYNSKI. 1978. Phosphorus input and its consequences for phytoplankton standing crop and production in the Experimental Lakes Area and in similar lakes. *J. Fish. Res. Bd. Can.* **35**: 190-196.
- , J. KALFF, H. E. WELCH, G. J. BRUNSKILL, H. KLING, AND N. KRITSCH. 1974. Eutrophication in the high arctic—Meretta Lake, Cornwallis Island (75°N lat.). *J. Fish. Res. Bd. Can.* **31**: 647-662.
- TALLING, J. 1975. Primary production of freshwater microphytes, p. 227-247. *In* J. P. Cooper [ed.], *Photosynthesis and productivity in different environments*. Cambridge.
- VALENTYNE, J. R. 1974. The algal bowl. Misc. Spec. Publ. 22. 186 p. Dep. Environ., Fish. Mar. Serv., Ottawa.
- VOLLENWEIDER, R. A. 1968. Water management research. OECD Paris. DAS/CS1/68.27. 183 p.
- . 1975. Input-output models. *Schweiz. Z. Hydrol.* **37**: 53-84.
- . 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. *Mem. Ist. Ital. Idrobiol.* **33**: 53-83.
- , M. MUNAWAR, AND P. STADELMANN. 1974. A comparative review of phytoplankton and primary production in the Laurentian Great Lakes. *J. Fish. Res. Bd. Can.* **31**: 739-762.
- WETZEL, R. G. 1966. Variations in productivity of Goose and hypereutrophic Sylvan lakes, Indiana. *Invest. Indiana Lakes Streams* **7**: 147-184.

Submitted: 29 December 1975
Accepted: 15 November 1977