Phosphate concentrations in lakes

Jeff J. Hudson*†, William D. Taylor‡ & David W. Schindler*

** Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada*
‡ Department of Biology, University of Waterloo, Waterloo, Ontario N2L 3G1, Canada

Phosphate is an important nutrient that restricts microbial production in many freshwater[1–3] and marine environments[4–6]. The actual concentration of phosphate in phosphorus-limited waters is largely unknown because commonly used chemical and radiochemical techniques overestimate the concentration[7,8]. Here, using a new steady-state radiobioassay to survey a diverse set of lakes, we report phosphate concentrations in lakes that are orders of magnitude lower than estimates made spectrophotometrically or with the frequently used Rigler radiobioassay. Our results, combined with those from the literature, indicate that microbes can achieve rapid turnover rates at picomolar nutrient concentrations. This occurs even though these concentrations are about two orders of magnitude below the level where phosphate uptake is estimated to be half the saturation level for the picoplankton community. Also, while phosphate concentration increased with the concentration of total phosphorus and soluble reactive phosphorus in the lakes we sampled, the proportion of phosphate in the total phosphorus pool decreased from oligotrophic to eutrophic lakes. Such information, as revealed by the phosphate assay that we use here, should allow us to address hypotheses concerning the concentration of phosphate available to planktonic microorganisms in aquatic systems.

Phosphate, that is, PO_4^{3-}, has been routinely measured for decades in aquatic environments[9]. However, such measurements are widely recognized to overestimate phosphate[7,8,10] when phosphate is at low concentrations. For example, although recent modifications to the Rigler radiobioassay[11] produce relatively low estimates of phosphate compared to spectrophotometric techniques, this assay estimates phosphate to be the sum of phosphate and the apparent half-saturation constant for phosphate transport for the mixed community, and so these components cannot be separated[10]. Although there are many hypotheses concerning the effects of grazers, light, mixing, carbon sources and other factors on the availability of phosphorus to microorganisms, direct assessment of phosphate concentration is not possible. A new approach is clearly required if we wish to test hypotheses concerning phosphate concentration in aquatic ecosystems.

Illuminated surface waters where photosynthesis occurs are often isolated from underlying nutrient-rich waters by distinct thermoclines, and rely on rapid phosphorus recycling to sustain productivity. In such environments, inputs of phosphate from the atmosphere, from horizontal and vertical transport and from larger organisms (for example, fish) are small compared to planktonic regeneration[12]. Under these conditions, the concentration of phosphate is usually too small to be estimated with chemical measurements, the turnover of phosphate is rapid and the flux of phosphate into (uptake) and out of (regeneration) the plankton must be approximately equal[13,14]. This relationship can be used to solve for concentrations of phosphate.

We have employed a new method for estimating the regeneration of dissolved phosphorus[15] (defined as that phosphorus which passes through a filter of 0.2-μm pore size). Most of the phosphorus regenerated by the plankton is phosphate[16–19], and the rest is likely to be substrates for phosphatases[20]. Although phosphate uptake cannot be directly measured, the uptake constant (k) for phosphate can be easily and accurately measured[10]. Therefore, with the regeneration rate and the uptake constant measured, we can solve for the concentration of phosphate (that is, phosphate uptake = $k \times [PO_4^{3-}]$ = regeneration rate). We refer to this measure of phosphate as a steady-state estimate.

Phosphate concentrations were determined for 56 lakes from three major physiographic regions of North America (Rocky Mountains, Interior Plains and Canadian Shield), spanning a nutrient gradient of 0.058–4.5 μM of total phosphorus (TP, which is the concentration of all phosphorus in the water, including dissolved phosphorus and phosphorus in plankton). In addition, we obtained concentrations of soluble reactive phosphorus (SRP) for 14 of these lakes from the literature. The colorimetric determination of SRP is still widely used as an estimate of phosphate concentration (for example, see APHA[21]) and provides a contrast with our steady-state estimates. We also compare the steady-state phosphate with Rigler bioassay determinations of phosphate in two Canadian Shield lakes.

Uptake constants (k) for phosphate were rapid, 0.02–1.1 min^{-1}, and indicate that phosphorus was limiting in all lakes[10,22]. Dissolved phosphorus regeneration had a range of 210–26,000 pM h^{-1}. The steady-state estimates of phosphate concentration were between 27 and 16,800 pM (Fig. 1). This range narrowed to 27–885 pM when three lakes were removed from the data set. These lakes were identified as outliers in the regression analysis of phosphate on TP. Phosphate concentrations in these lakes were orders of magnitude greater than the 53 other lakes and are probably not a result of analytical error. Instead, we suspect that these lakes were not phosphorus-limited to the same extent as the other lakes, and that therefore phosphate concentrations were elevated due to low demand. The slow turnover times of phosphate in these lakes (range 31–64 min) compared to the other 53 lakes (range 1–10 min) supports this interpretation.

Phosphate concentration tended to increase with TP, but the proportion of phosphate declined with increasing TP (the slope of the relationship in Fig. 1 is 0.745). Our results illustrate that even at

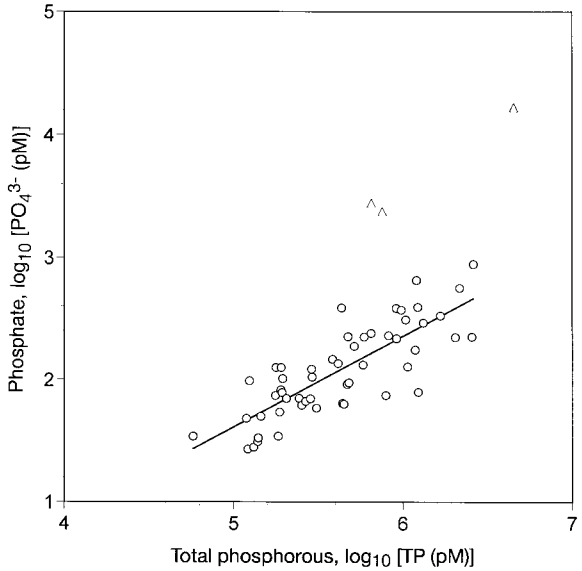

Figure 1 Steady-state phosphate estimates as a function of total phosphorus for 56 lakes. Phosphate concentration, $[PO_4^{3-}]$ in units of pM, tended to increase with total phosphorus (TP) concentration, [TP] in units of pM: $n = 53$, $r^2 = 0.66$, $P < 0.0001$, $\log_{10}[PO_4^{3-}\text{ (pM)}] = 0.745(\log_{10}[\text{TP (pM)}] - 2.11)$. Data points are shown as circles, except for estimates from three lakes, which are considered to be outliers (triangles) and were not included in the model I least-squares regression analysis.

† Present address: Dorset Environmental Sciences Centre & Trent University, PO Box 39, Bellwood Acres Road, Dorset, Ontario POA 1E0, Canada.

minute concentrations, rapid cycling of phosphate can support high rates of production. That is, the turnover rate of particulate phosphorus (phosphorus bound in plankton) is not a function of TP (ref. 12), implying that the productivity of plankton on a per unit biomass basis remains similar across a broad range in biomass.

Although our steady-state estimates of phosphate are not contemporaneous with measurements of SRP, the magnitude of the differences and the consistency of our phosphate estimates indicate that there is a large discrepancy between phosphate and SRP (Fig. 2). In no instance, even in eutrophic Halfmoon Lake (with a TP value of 2.6 μM), did SRP concentrations approximate the steady-state concentrations. There are two well-documented explanations for this discrepancy. First, the SRP approach requires a water-filtration step to isolate the soluble phosphorus from the particulate phosphorus (phosphorus bound in plankton). During this step an error is introduced because a portion of the particulate phosphorus is released into the soluble pool, probably as a result of cell damage[23]. Second, the reagents that are used to determine SRP acidify the filtrate and lead to the release of bound phosphate[8]. Both steps lead to overestimates of actual phosphate. In past studies, TP and SRP were routinely measured together. The TP measured in these studies may be substituted into the relationship in Fig. 1 to convert past SRP measurements to steady-state phosphate. However, this relationship would only provide an approximate measure.

Rigler bioassay estimates of phosphate in Mouse and Ranger Lakes were between 6 and 38 nM and represent concentrations that are approximately two orders of magnitude greater than the concurrent steady-state estimates (Fig. 3). There is an obvious explanation for this discrepancy. The Rigler bioassay uses the Michaelis–Menten equation and uptake velocities for different additions of phosphate to determine the sum of the half-saturation constant for uptake (K_s) of the added phosphate and the unknown ambient phosphate concentration[24]. Therefore, the assay can only provide a potential upper limit of phosphate, because the phosphate concentration cannot be separated mathematically from the apparent K_s for the mixed community. Our results suggest that this apparent K_s is much greater than the phosphate concentration. Therefore, the Rigler bioassay is essentially an estimate of K_s and not of phosphate. Despite these shortcomings, this assay has been used extensively for the past three decades to provide the lowest routine estimates of phosphate. Bentzen and Taylor[10] provide a complete description of the assay.

One of the assumptions of the steady-state technique is that uptake of phosphate is equal to regeneration of phosphate. There are instances when this assumption may not be appropriate. When the turnover rate of phosphate by plankton is slow, indicating that the phosphate pool is large relative to the rate of phosphate uptake, regeneration and uptake may not be in balance. In addition, when the plankton community is increasing in biomass and drawing down the phosphate concentration, uptake would presumably exceed regeneration. More generally, our technique will underestimate phosphate in proportion to the relative importance of new versus recycled phosphate. Therefore, it should be applied only when the turnover rate of the phosphate is rapid relative to the supply from external sources. We do not know the extent of these errors in the current data set; however, we suspect that they are small because total planktonic biomass does not change rapidly relative to the turnover rate of phosphate during stratified conditions when phosphate concentration is low.

We report the smallest concentrations of phosphate for any aquatic system (that is, 27 pM). These concentrations are extremely low for a macronutrient, but equivalent concentrations exist for micronutrients. For example, dissolved Fe, Mn and Zn have been reported at picomolar concentrations in open-ocean surface waters[25,26]. With a modified Rigler bioassay, phosphate concentrations have been measured in the 5 to 10 nM range in the phosphorus-limited Sargasso Sea[4]. If the modified Rigler bioassay consistently overestimates phosphate by two orders of magnitude, then these Sargasso Sea concentrations would be equivalent to 50 to 100 pM of steady-state phosphate. The low concentration and rapid turnover of phosphate supports the idea that biological processes (that is, uptake and regeneration) regulate limiting nutrient concentrations. Interestingly, the smallest concentrations reported for micro- and macronutrients appear to be in the low picomolar range. These concentrations may reflect the physiological limits to microbial scavenging of nutrients.

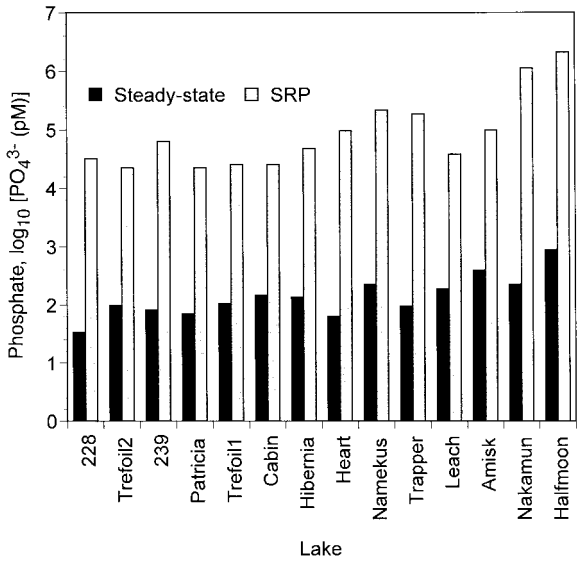

Figure 2 Comparison of steady-state and soluble reactive phosphorus estimates of phosphate concentration in a subset of 14 lakes. Lakes increase in nutrient content from the left (TP = 0.06 μM) to the right (TP = 2.6 μM). Soluble reactive phosphorus (SRP) concentrations are 2–3 orders of magnitude greater than steady-state concentrations. Summer SRP concentrations were obtained from the literature and government documents, and were not sampled concurrently with steady-state concentrations.

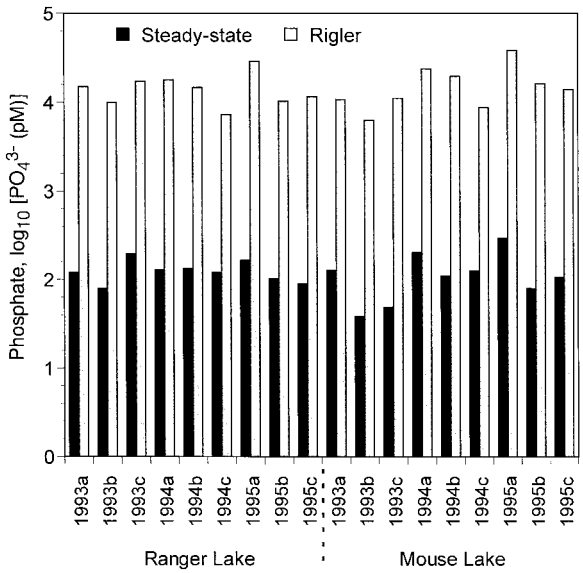

Figure 3 Comparison of steady-state and Rigler bioassay estimates of phosphate concentration in Mouse and Ranger Lakes. The comparison is based on concurrent measurements. Letters that follow each year on the *x*-axis refer to the time of sampling within a year: early summer (a), mid-summer (b) and late summer (c). Rigler bioassay concentrations are approximately two orders of magnitude greater than steady-state concentrations.

There are few studies that directly support the low estimates of phosphate that we have obtained with our steady-state bioassay; however, two single-lake studies made similar observations. Fisher and Lean[7] measured phosphate concentrations by dialysis of radiolabelled lake water followed by column chromatography. With this elegant approach, concentrations of 500 pM were measured in mesotrophic Jacks Lake. In the same lake, a model of plankton interactions and a mass balance approach were used to deduce that the phosphate concentration must be about 300 pM (ref. 23). Dodds[13] used a modified Michaelis–Menten model in combination with regeneration measurements by isotope dilution, and reported phosphate concentrations between 80–140 pM in oligotrophic Flathead Lake.

Although our steady-state bioassay is not suitable for routine monitoring, it is appropriate for testing hypotheses that address the phosphate concentration in phosphorus-limited pelagic systems. Our approach may also be adopted to examine the concentration of other nutrients. Most important, our results indicate that phosphate is at picomolar concentrations in lakes across a broad range in total phosphorus, and orders of magnitude lower than measured with the best widely used methods. □

Methods

Each lake was sampled once, except for Mouse and Ranger Lakes and three alpine lakes, which were sampled more frequently and over multiple years. Mean values are presented for these lakes. Only lakes that had a maximum depth equal to, or greater than 4 m were considered, in order to minimize benthic effects on the pelagic zone. We intended to sample only lakes with TP concentrations below 3.2 μM; however, one lake was sampled that exceeded this concentration (Islet). The water columns of 47 lakes were thermally stratified and the remaining lakes ($n = 9$) had isothermal water columns. Water (20 litres) was removed from a central location at the mid-epilimnetic depth of each lake with a Van Dorn sampler and placed in 20-litre polyethylene containers (acid washed) that were held in coolers. Isothermal lakes were sampled just below the surface (<1 m). Rigler bioassay[10] determinations of phosphate were conducted on mid-epilimnetic water collected from a central station in Mouse and Ranger Lakes[15]. This water was collected at the same depth on the same day, or one day before the collection of water for the measurement of phosphorus regeneration[15]. Phosphate uptake constants[10] and phosphorus regeneration rates[15] were determined for all lakes. Standard chemical estimates of phosphate (SRP) were obtained from the literature for 14 of the study lakes (Fig. 2). SRP concentrations were provided by ref. 27 for Lake 239; ref. 28 for Heart, Namekus and Trapper Lakes; ref. 29 for Amisk and Nakamun Lakes; The Freshwater Institute (Winnipeg, Manitoba) for Lake 228; Environment Canada (Regina, Saskatchewan) for Trefoil 1 and 2, Patricia, Cabin, Hibernia, and Leach Lakes; and Alberta Environment (Edmonton, Alberta) for Halfmoon Lake.

Received 8 November 1999; accepted 18 May 2000.

1. Schindler, D. W. Evolution of phosphorus limitation in lakes. *Science* **195,** 260–262 (1977).
2. Wetzel, R. G. *Limnology* 2nd edn (Saunders, New York, 1983).
3. Edmondson, W. T. *The Uses Of Ecology: Lake Washington And Beyond* 1st edn (Univ. Washington Press, Seattle, 1991).
4. Cotner, J. B. *et al.* Phosphorus-limited bacterioplankton growth in the Sargasso Sea. *Aquat. Microb. Ecol.* **13,** 141–149 (1997).
5. Karl, D. *et al.* The role of nitrogen fixation in biogeochemical cycling in the subtropical North Pacific Ocean. *Nature* **388,** 533–538 (1997).
6. Thingstad, T. F., Zweifel, U. L. & Rassoulzadegan, F. P limitation of heterotrophic bacteria and phytoplankton in the northwest Mediterranean. *Limnol. Oceanogr.* **43,** 88–94 (1998).
7. Fisher, T. R. & Lean, D. R. S. Interpretation of radiophosphate dynamics in lake waters. *Can. J. Fish. Aquat. Sci.* **49,** 252–258 (1992).
8. Baldwin, D. S. Reactive "organic" phosphorus revisited. *Wat. Res.* **32,** 2265–2270 (1998).
9. Atkins, W. R. G. The phosphate content of fresh and salt waters in its relationship to the growth of the algal plankton. *J. Mar. Biol. Assoc.* **13,** 119–150 (1923).
10. Bentzen, E. & Taylor, W. D. Estimating Michaelis-Menton parameters and lake water phosphate by the Rigler bioassay: importance of fitting technique, plankton size and substrate range. *Can. J. Fish. Aquat. Sci.* **48,** 73–83 (1991).
11. Rigler, F. Radiobiological analysis of inorganic phosphorus in lakewater. *Verh. Int. Verein. Theor. Angew. Limnol.* **16,** 465–470 (1966).
12. Hudson, J. J., Taylor, W. D. & Schindler, D. W. Planktonic nutrient regeneration and cycling efficiency in temperate lakes. *Nature* **400,** 659–661 (1999).
13. Dodds, W. K. What controls levels of dissolved phosphate and ammonium in surface waters. *Aquat. Sci.* **55,** 132–142 (1993).
14. Harrison, W. G. Nutrient recycling in production experiments. *ICES Mar. Sci. Symp.* **197,** 149–158 (1993).
15. Hudson, J. J. & Taylor, W. D. Measuring regeneration of dissolved phosphorus in planktonic communities. *Limnol. Oceanogr.* **41,** 1560–1565 (1996).
16. Peters, R. H. & Lean, D. R. S. The characterization of soluble phosphorus released by limnetic zooplankton. *Limnol. Oceanogr.* **18,** 270–279 (1973).
17. Peters, R. H. & Rigler, F. H. Phosphorus release by *Daphnia*. *Limnol. Oceanogr.* **18,** 821–839 (1973).
18. Ferrante, J. G. The characterization of phosphorus excretion products of a natural population of limnetic zooplankton. *Hydrobiologia* **50,** 11–15 (1976).
19. Taylor, W. D. & Lean, D. R. S. Radiotracer experiments on phosphorus uptake and release by limnetic microzooplankton. *Can. J. Fish. Aquat. Sci.* **38,** 1316–1321 (1981).
20. Bentzen, E. & Taylor, W. D. Estimating organic P utilization by freshwater plankton using (32P) ATP. *J. Plank. Res.* **13,** 1223–1238 (1991).
21. American Public Health Association *Standard Methods for the Examination of Water and Wastewater* 19th edn (APHA, Washington, DC, 1995).
22. Lean, D. R. S., Abbott, A. A. & Pick, F. R. Phosphorus deficiency of Lake Ontario plankton. *Can. J. Fish. Aquat. Sci.* **44,** 2069–2076 (1987).
23. Taylor, W. D. & Lean, D. R. S. Phosphorus pool sizes and fluxes in the epilimnion of a mesotrophic lake. *Can. J. Fish. Aquat. Sci.* **48,** 1293–1301 (1991).
24. Tarapchak, S. J. & Herche, L. R. Orthophosphate concentrations in lake water: analysis of Rigler's radiobioassay method. *Can. J. Fish. Aquat. Sci.* **45,** 2230–2237 (1988).
25. Bruland, K. W., Donat, J. R. & Hutchins, D. A. Interactive influences of bioactive trace metals on biological production in oceanic waters. *Limnol. Oceanogr.* **36,** 1555–1577 (1991).
26. Landry, M. R. *et al.* Iron and grazing constraints on primary production in the central equatorial Pacific: An EqPac synthesis. *Limnol. Oceanogr.* **42,** 405–418 (1997).
27. Schindler D. W. in *Proc. IBP-UNESCO Symposium on Productivity Problems of Freshwaters* (eds Kajak, Z. & Hillbright-Ilkowska, A.) 303–331 (UNESCO, Warsaw, 1972).
28. Canadian Park Service. *Prince Albert National Park Resource Description and Analysis*. Vol. 2, p. 4–40 (Environment Canada, Parks, Prairie and Northern Region, Winnipeg, Manitoba, 1986).
29. Prepas, E. E. Orthophosphate turnover time in shallow productive lakes. *Can. J. Fish. Aquat. Sci.* **40,** 1412–1418 (1983).

Acknowledgements

We thank T. Paul, W. Bell, R. Hazewinkel, J. Almond, S. Leung, T. MacDonald, J. Huvane, B. Parker and N. McMaster for field and laboratory assistance. We also thank the Dorset Environmental Sciences Centre, D. McQueen and the Freshwater Institute for assistance, laboratory space, equipment and accommodation. D. Lean, P. Dillon, G. Mierle and K. Somers provided constructive criticism of the manuscript. A scholarship (NSERC) and a Killam Post-Doctoral Fellowship (University of Alberta) to J. J. H. and NSERC research grants to W. D. T. and D. W. S. supported this research.

Correspondence and requests for materials should be addressed to J. J. H. (e-mail: hudsonje@ene.gov.on.ca).

The sedimentary structure of linear sand dunes

C. S. Bristow*, S. D. Bailey* & N. Lancaster†

**School of Earth Sciences, Birkbeck College, University of London, Malet Street, London WC1E 7HX, UK*

† Desert Research Institute, UCCSN, 2215 Raggio Parkway, Reno, Nevada 89512, USA

Linear sand dunes—dunes that extend parallel to each other rather than in star-like or crescentic forms—are the most abundant type of desert sand dune[1]. But because their development and their internal structure are poorly understood, they are rarely recognized in the rock record[2]. Models of linear dune development[2–6] have not been able to take into account the sub-surface structure of existing dunes, but have relied instead either on the extrapolation of short-term measurements of winds and sediment transport or on observations of near-surface internal sedimentary structures. From such studies, it has not been clear if linear dunes can migrate laterally[2,7,8]. Here we present images produced by ground penetrating radar showing the three-dimensional sedimentary structure of a linear dune in the Namib sand sea, where some of the world's largest linear dunes are situated. These profiles show clear evidence for lateral migration in a linear dune. Moreover, the migration of a sinuous crest-line along the dune produces divergent sets of cross-stratification, which can become stacked as the dune height increases, and large linear dunes can support superimposed dunes that produce stacked sets of trough cross-stratification. These clear structural signatures of linear dunes should facilitate their recognition in geological records.