L. C. FOLMAR. 1981. Lunar phasing of thyroxine surge preparatory to seaward migration of salmonid fish. Science 211: 607-609.

- HEARD, W. R. 1964. Phototactic behaviour of emerging sockeye salmon frv. Anim. Behav. 12: 382-388.
- HOAR, W. S. 1958. The evolution of migratory behavior among juvenile salmon of the genus Oncorhynchus. J. Fish. Res. Board Can. 15: 391-428.
- HOBBS, D. F. 1937. Natural reproduction of quinnat salmon, brown
- Can. 15: 391–428.
 HOBBS, D. F. 1937. Natural reproduction of quinnat salmon, brown and rainbow trout in certain New Zealand waters. N.Z. Mar. Dep. Fish. Bull. 6: 104 p.
 HOFFMAN, K. 1976. The adaptive significance of biological rhythms corresponding to geophysical cycles, p. 63–75. *In J.* W. Hastings and H. G. Schweiger [ed.] The molecular basis of circadian rhythms. Dahlem Konferenzen, Berlin.
 HUNTER, J. G. 1959. Survival and production of pink and chum salmon in a coastal stream. J. Fish. Res. Board Can. 16: 835–886.
 HORDAN, R. M. 1981. Atlantic salmon spawning survey and evaluation of natural spawning success. Maine Dep. Inland Fish. Wildl. Final Rep., Fed. Aid Proj. AFS-20-R: 26 p.
 KALLEBERG, H. 1988. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). Rep. Inst. Freshw. Res. Drottningholm 39: 55–98.
 KEEENLEYSIDE, M. H. A., AND F. T. YAMAMOTO. 1962. Territorial behavior of juvenile Atlantic salmon (*Salmo salar* L.). Behavior 19: 139–169.
 MASON, J. C. 1975. Seaward movement of coho salmon (*Oncorrhythack issutch*) fry. J. Fish. Res. Board Can. 32: 2542–2547.
 MCDONALD, J. 1960. The behavior of Pacific salmon fry during their downstream migration to freshwater and saltwater nursery areas. J. Fish. Res. Board Can. 17: 655–676.
 MASON, F. 1955. Notes on the seaward migration of pink and chum salmon fry. J. Fish. Res. Board Can. 12: 369–374.
 MORTHCOTE, T. G. 1962. Migratory behavior of juvenile rainbow trout, *Salmo gairdneri*, in outlet and inlet streams of Loon Lake, Department of Biology, University of Oligotrophic lake using radiophosph 40: 817–821.
 We used ³²P uptake kinetics as a mean toplankton growth in an ultraoligotrophic lakk weekly in 1975 and 1976, respectively, yie phosphorus over the sampling seasons. Am. concentrations were not as informative as upta toplankton gr

British Columbia. J. Fish. Res. Board Can. 19: 201-270.

1969. Lakeward migration of young rainbow trout (Salmo gairdneri) in the Upper Lardeau River, British Columbia. J. Fish. Res. Board Can. 26: 33-45.

- OTTAWAY, E. M., AND A. CLARKE. 1981. A preliminary investigation into the vulnerability of young trout (Salmo trutta L.) and Atlantic salmon (Salmo salar L.) to downstream displacement by high water velocities. J. Fish Biol. 19: 135-145.
- PALMER, J. D. 1976. An introduction to biological rhythms. Academic Press, New York-San Francisco-London. 375 p.
- PETERMAN, R. M., AND M. GATTO. 1978. Estimation of functional responses of predators on juvenile salmon. J. Fish. Res. Board Can. 35: 797-808.
- PITTENDRIGH, C. S. 1954. On temperature independence in the clock system controlling emergence time in Drosophila. Proc. Nat. Acad. Sci. USA 40: 1018-1029.
- PORTER, T. R. 1973. Fry emergence trap and holding box. Prog. Fish-Cult. 35: 104-106.
- SNEDECOR, G. W., AND W. G. COCHRAN. 1967. Statistical methods. Iowa State University Press, Ames, IA. 593 p.
- SYMONS, P. E. K. 1974. Territorial behavior of juvenile Atlantic salmon reduces predation by brook trout. Can. J. Zool. 52: 677-679.

1976. Behavior and growth of juvenile Atlantic salmon (Salmo salar) and three competitors at two stream velocities. J. Fish. Res. Board Can. 19: 625-634.

- TERHUNE, L. D. B. 1958. The Mark VI groundwater standpipe for measuring seepage through salmon spawning gravel. J. Fish. Res. Board Can. 15: 1027-1063.
- WANKOWSKI, J. W. J., AND J. E. THORPE. 1979. Spatial distribution and feeding in Atlantic salmon, Salmo salar L. juveniles. J. Fish Biol. 14: 239-247.
- WATERS, T. F. 1962. Diurnal periodicity in the drift of stream invertebrates. Ecology 43: 316-320.
- WILLIAMS, D. D. 1981. The first diets of postemergent brook trout (Salvelinus fontinalis) and Atlantic salmon (Salmo salar) alevins in a Quebec river. Can. J. Fish. Aquat. Sci. 38: 765-771.

Assessment of Phosphorus Limitation in an Oligotrophic Lake Using Radiophosphorus Uptake Kinetics¹

PATRICIA CHOW-FRASER² AND HAMISH C. DUTHIE

Department of Biology, University of Waterloo, Waterloo, Ont. N2L 3G1

CHOW-FRASER, P., AND H. C. DUTHIE. 1983. Assessment of phosphorus limitation in an oligotrophic lake using radiophosphorus uptake kinetics. Can. J. Fish. Aquat. Sci.

We used ³²P uptake kinetics as a means of assessing periods of P limitation to phytoplankton growth in an ultraoligotrophic lake. Tracer experiments, conducted biweekly and weekly in 1975 and 1976, respectively, yielded information regarding the availability of phosphorus over the sampling seasons. Analytical measurements of ambient phosphorus concentrations were not as informative as uptake kinetic data in the assessment of phosphorus demands in the lake. Whereas analytical methods identified probable periods of P limitation at the end of summer, radiophosphorus data indicated that P limitation was prevalent throughout most of the summer.

¹Contribution No. 67 of the Matamek Research Station.

²Present address: University of Toronto, Erindale College, Mississauga, Ont. L5L IC6.

CHOW-FRASER, P., AND H. C. DUTHE. 1983. Assessment of phosphorus limitation in an oligotrophic lake using radiophosphorus uptake kinetics. Can. J. Fish. Aquat. Sci. 40: 817-821.

La cinétique de l'absorption de ³²P a servi à évaluer les périodes durant lesquelles le phosphore est le facteur limitatif de croissance du phytoplancton dans un lac ultraoligotrophe. Des essais avec marqueurs, effectués à intervalles bihebdomadaires en 1975 et hebdomadaires en 1976, ont fourni des données sur l'accessibilité du phosphore pendant les saisons d'échantillonnage. Les mesures de concentrations du phosphore ambiant n'ont pas donné autant d'information que la cinétique de l'absorption dans l'évaluation de la demande en phosphore dans le lac. Alors que les méthodes analytiques permirent d'identifier des périodes probables de limitation du phosphore à la fin de l'été, celle du phosphore radioactif indiqua que la limitation du phosphore prédominait durant la majeure partie de l'été.

Received February 12, 1982 Accepted March 8, 1983

UNTIL recently, assessment of phosphorus demands in lakes has been limited to the correlation of conventional characteristics such as total phosphorus (TP), soluble reactive phosphorus (SRP), or soluble unreactive phosphorus (SUP) to the phytoplankton biomass or chlorophyll a. This approach produced results that were difficult to interpret and often misleading. One explanation for this inaccuracy has been attributed to the inappropriateness of employing a static measurement to describe a dynamic system that exhibits a constant flux among various P compartments (Lean 1973a, 1973b; Lean and Rigler 1974; Halfon 1979). Static measurements, in addition to being inappropriate, have also been problematic when applied to ultraoligotrophic systems. The forms of P exist in such low concentrations that they often escape detection or are inaccurately measured owing to sensitivity limitations. Also, some organic P may be hydrolyzed by acidic reagents, giving overestimates of SRP (Rigler 1968; Downes and Paerl 1978; White et al. 1981). A dynamic system is more appropriately measured by a kinetic term (e.g. the "turnover time" of an uptake curve) that indicates the rate of P uptake.

Lean and Nalewajko (1979) were able to use ³²P uptake experiments to assess periods of P limitation in small and large lakes, and Levine and Schindler (1980) measured seasonal changes in the flux of orthophosphate to seston in two Canadian Shield lakes. Recently, White et al. (1982) identified factors affecting orthophosphate turnover times in New Zealand and Canadian lakes. In none of these studies are turnover times compared with parallel changes in phytoplankton abundance.

The objective of our study was to test the effectiveness of P kinetics for assessing P demand in an ultraoligotrophic lake. We were particularly interested in comparing P kinetics and standard analytical methods to observed changes in phytoplankton abundance in hopes that kinetics may be used as an alternate means for the identification of P limitation in oligotrophic systems.

Lake Matamek ($65^{\circ}50'W$, $50^{\circ}20'N$) is a Precambrian Shield lake with an area of 1320 ha and a maximum depth of 100 m (Janus and Duthie 1979a). The lake is acidic, with a summer pH of 5.5–6.0, and is very low in dissolved solids. Conductivity is in the range $10-20 \ \mu$ mho/cm, and total Reçu le 12 février 1982 Accepté le 8 mars 1983

cations do not exceed 4 mg/L. The mean summer chlorophyll *a* concentration of about 1.5 mg/m³ and the summer phytoplankton biomass of generally between 100 and 150 mg/m³ attest to its ultraoligotrophic nature. The phytoplankton and primary productivity of Lake Matamek have been described (Janus and Duthie 1979b; Ross and Duthie 1981), and a P budget has been calculated (Chow-Fraser and Duthie 1983).

Methods — Biwcekly ³²PO₄ uptake experiments were carried out during 1975 at a central station in Lake Matamek (Matamek Centre) from the beginning of June until late August. Surface water samples were brought back to the laboratory within 30 min of collection. Samples were also taken for SRP and phytoplankton biomass determinations. The SRP and TP samples were obtained from a depth of 0.5 m, and the integrated phytoplankton samples were collected by means of a 2-m-long rubber hose lowered vertically into the water. In 1976 the same sampling methodology was carried out weekly at a station approximately 2 km to the east (East Basin) of Matamek Centre.

The method of Lean (1973b) was used to estimate P turnover times. To a 600-mL sample of lakewater was added 9.25 MBq of carrier-free ${}^{32}PO_4$. At various time intervals, 10-mL aliquots were withdrawn and immediately filtered through 0.45-µm pore size membrane filters. The filters were rinsed with 20 mL of distilled water and then placed in scintillation vials. All incubations were carried out for 4-h periods. The logarithm of the percentage of total radioactivity remaining in the filtrate was plotted against time. The reciprocal of the initial slope of the curve yielded the turnover time. Samples for TP (in 1976) and SRP (in 1975) were analyzed by the methods in Strickland and Parsons (1972). Phytoplankton enumeration was carried out using an inverted microscope and freshweight biomass estimated by the method described by Janus and Duthie (1979a).

Results and discussion — Interpretation of radiophosphorus uptake curves — Figure 1 shows representative uptake curves that were obtained in Lake Matamek over the two sampling years and describes approximately 75% of our observations. The three curves correspond to types described by Lean and Nalewajko (1979). Figure 1a corresponds to the NOTES



Realewajko 1979). Type 1 (9 June 1975, Matamek Centre); type 2 E(20 July 1976, East Basin); type 3 (4 August 1975, Matamek Centre).

type 1 curve; the long turnover time of 121.1 min suggests Sthat P was abundant or in low demand. Figure 1b corresponds to the monophasic type 2 curve where P is depleted and/or in High demand. The kinetics can be described using a two-Scompartment model: phosphate exchanging with cellular P ĭwith insignificant formation of organic P. Figure 1c, however, corresponds to Lean and Nalewajko's (1979) diphasic Hype 3 curve thought to represent extreme P depletion or very High demand and occurs at times when colloidal P and a Ephosphorus compound (XP) of low molecular weight become Isolabeled in less than 1 min.

Figure 2a appears to be a transition type between type 1 \pm and type 2 (type 1-2). The initial portion of the curve slopes -very gently and is followed by a gradual asympote. In this Eparticular case there is a possibility that even after 4 h of Sincubation, the system has not reached an asymptotic level.

Figure 2b is an example of a curve that cannot be explained using a two-compartment model even though the curve is log-linear. Were it not for the relatively low turnover time this curve could be mistaken for type 1 kinetics. However, a turnover time of 6.9 min implies a very rapid incorporation of P, characteristically associated with a P-depleted condition. Figure 2c presents yet another situation in which the uptake kinetics appear to be intermediate between two curve types. The oscillation of points about the asymptote renders the task of distinguishing between curve types 2 and 3 extremely



Fig. 2. Examples of transitional P uptake curves. Type 1-2(1 September 1975, Matamek Centre); type ? (27 August 1976, East Basin): type 2-3 (30 August 1976, East Basin).

difficult.

Paramount to a proper understanding of P demands in lakes is the recognition that there is a constant exchange of P between two or more compartments. Our suggestion that there are transition types between the types of uptake curves described by Lean and Nalewajko (1979) is totally in keeping with the dynamic nature of the model.

Interpretation of P limitation ---- Figure 3 summarizes the seasonal variations in uptake curve types for Matamek Centre in 1975 and corresponding measurements of turnover times, SRP concentrations, and algal biomass. In the beginning of June, both biomass and SRP measurements were relatively high. Both decreased until early July and then increased again, but by mid-August the curves had diverged, with SRP being minimal and biomass being maximal. Since algal biomass was high and SRP was very low in August, P limitation was likely. The low biomass and relatively high SRP values from June to mid-July could be interpreted to mean a non-Plimiting system.

The type 2 curve and the relatively rapid turnover time in the early part of June imply the existence of a moderately depleted system; the type 3 curves and low turnover times



FIG. 3. Summary of uptake curve types, turnover times, soluble reactive phosphorus concentrations (SRP), and phytoplankton biomass concentrations (biomass) for Matamek Centre, 1975.

exhibited from mid-July to mid-August also corroborate with the interpretation of SRP that the system was P limited. However, interpretations of the kinetic data diverge from those of SRP measurements from mid-June to mid-July. Whereas the types 3 and 2 together with corresponding low turnover times were indicative of P limitation, SRP and biomass measurements were not. In summary, while uptake kinetics revealed that Matamek Centre was P limited, or at least P depleted for most of the summer in 1975, analytical measurements implied limitation only at the end of the summer.

The data for the East Basin is summarized in Fig. 4 and may be interpreted in a fashion similar to those for Matamek Centre. The inverse relationship between TP and algal biomass in June and August is clear. These trends suggest that initially there was an abundance of P, probably as a result of spring overturn, but as biomass increased, P became depleted and the system was probably P limited by late June. The very high algal biomass and low TP measurements in mid-August also imply P limitation.

With reference to the corresponding P uptake kinetic data for June, the type 1 curve and extremely high turnover times (in excess of 100 min) substantiate our interpretation that P was not in high demand. A more concentrated sampling effort in East Basin permitted the observation of the transition



FIG. 4. Summary of uptake curve types, turnover times, total phosphorus concentrations (TP), and phytoplankton biomass concentrations (biomass) for East Basin, 1976.

curve type 1-2. By late June, the occurrence of type 2 and shorter turnover times indicated that P was in higher demand. In mid-August, transition type 2-3 and type 3 curves, together with extremely shortened turnover times and high algal biomass, strongly indicated a very high P demand in the lake. Up to this point, uptake kinetics in East Basin concur with the interpretation reached by conventional measurements. The discrepancy occurs in the period between late June and early August. Type 2 and 3, in conjunction with very short turnover times, are indicative of a very high P demand, not revealed by TP and algal biomass measurements. As in Matamek Centre, the kinetic data inferred that P was in high demand throughout most of the summer in 1976, even though conventional measurements did not.

The foregoing comparison of algal biomass, analytical, and kinetic data points out the interpretive difficulties with measurements of SRP and TP. These appear adequate for indentifying P limitation during periods of low P concentrations, but can be misleading during other periods. The basic problem is that a P measurement, regardless of the algal biomass, can be equally associated with a high or low P demand. Therefore, the moderately high SRP and TP measurements in midsummer in Matamek Centre and East Basin could not accurately reflect the P-limited condition in the lake. On the other hand, corresponding kinetic data were capable of describing the high P demand in both instances. Seasonal trends of the measured parameters are more important than their respective mean values when assessing P availability in a particular lake. The use of uptake curve types to distinguish the degree of P demand at specific times enhances the sensitivity of using turnover times alone.

Acknowledgments --- The research was supported by grants to H. C. Duthie from the Woods Hole Oceanographic Institution and from the Natural Sciences and Engineering Research Council of Canada. G. McLachlan and I. Jordan provided field assistance. We hank W. D. Taylor for a critical reading of the manuscript.

- CHOW-FRASER, P., AND H. C. DUTHIE. 1983. An interpretation of

LEAN, D. R. S. 1973a. Phosphorus dynamics in lakewater. Science (Washington, DC) 179: 678-680.

1973b. Phosphorus movement between biologically important forms in lakewater, J. Fish. Res. Board Can. 30: 1525-1536.

- LEAN, D. R. S., AND F. H. RIGLER. 1974. A test of the hypothesis that abiotic phosphorus complexing influences phosphorus kinetics in epilimnetic lake water. Limnol. Oceanogr. 19: 784-788.
- LEAN, D. R. S., AND C. NALEWAJKO. 1979. Phosphorus turnover time and phosphorus demand in large and small lakes. Arch. Hydrobiol. Beih. Ergebn. Limnol. 13: 120-132.
- LEVINE, S. N., AND D. W. SCHINDLER. 1980. Radiochemical analysis of orthophosphate concentrations and seasonal changes in the flux of orthophosphate to seston in two Canadian Shield lakes. Can. J. Fish. Aquat. Sci. 37: 479-487.
- RIGLER, F. H. 1968. Further observations inconsistent with the hypothesis that the molybdenum blue method measures orthophosphate in lake water. Limnol. Oceanogr. 13: 7-13.
- Ross, P. E., AND H. C. DUTHIE. 1981. Ultraplankton biomass, productivity and efficiency in Lac Matamec, a Precambrian Shield lake. J. Phycol. 17: 181-186.
- STRICKLAND, J. D. H., AND T. R. PARSONS. 1972. A practical handbook of seawater analysis. Bull. Fish. Res. Board Can. 67: 311 p.
- WHITE, E., G. PAYNE, S. PICKMERE, AND F. R. PICK. 1981. Orthophosphate and its flux in lake waters. Can. J. Fish. Aquat. Sci. 38: 1215-1219.
 - 1982. Factors influencing orthophosphate turnover times: a comparison of Canadian and New Zealand lakes. Can. J. Fish. Aquat. Sci. 39: 469-474.

Eubothrium salvelini (Cestoda: Pseudophyllidea) Impairs Seawater Adaptation of Migrant Sockeye Salmon Yearlings (Oncorhynchus nerka) from Babine Lake, British Columbia

N. P. BOYCE¹ AND W. CRAIG CLARKE

Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6

BOYCE, N. P., AND W. C. CLARKE. 1983. Eubothrium salvelini (Cestoda: Pseudophyllidea) impairs seawater adaptation of migrant sockeye salmon yearlings (Oncorhynchus nerka) from Babine Lake, British Columbia. Can. J. Fish. Aguat. Sci. 40:

 Plank W. D. Taylor for a Cinteen reading of the manuscript.
 CHOW-FRASER, P., AND H. C. DUTHIE. 1983. An interpretation of phosphorus loadings in dystrophic lakes. Arch. Hydrobiol. (In press)
 COMNES, M. T., AND H. W. PAERL. 1978. Separation of two dissolved phosphorus fractions in lake water. J. Fish. Res. Board Can. 35: 1636–1639.
 THALFON, E. 1979. Mathematical modelling of phosphorus dynamics through integration of experimental work and system theory, p. 75–83. *In* D. Scavia and A. Robertson [ed.] Perspectives on lake ecosystem modelling. Ann Arbor, MI.
 TAMUS, L. L., AND H. C. DUTHIE. 1979a. Phytoplankton composition and periodicity in a northeastern Quebec lake. Hydrobiologia 63: 129–134.
 1979b. Phytoplankton and primary production of lakes in the Matamek Watershed, Quebec. Int. Rev. Gesamten Hydrobiol. 64: 89–98.
 Eubothrium salvelini (Cestoda: Pseudoppi Migrant Sockeye Salmon Yearlings (*O British Cost Salman Sockeye Salmon Yearlings (O British Cost Salman Sockeye Salmon Yearlings (O British Cost Salman Sockeye Salmon Yearlings (<i>Oncost Salman Sockeye Salmon Yearlings (Oncost Salman Sockeye Salmon Yearlings (Oncost Salman Sockeye Salmon Yearlings (<i>Oncost Salman Sockeye Salmon Yearlings (Oncost Salman Sockeye Salmon Yearlings (Oncost Salman Sockeye Salmon Yearlings (<i>Oncost Salman Sockeye Salmon Yearlings (Oncost Salman Sockeye Salmon Yearlings (Oncost Salman Sockeye Salmon Yearlings (Oncost Salman Sockeye Salmon Yearlings (<i>Oncost Salma Sal* Migrant sockeye salmon yearlings (Oncorhynchus nerka) were captured at the outlet of Babine Lake, British Columbia, in 1979 and 1980 and transported to the laboratory for evaluation of their seawater adaptability in a 24-h challenge test. Fish infected with the cestode Eubothrium salvelini had a reduced ability to adapt to salt water, as evidenced by greater mortality and elevated plasma sodium levels after challenge. The prevalence of infection was 60% in 1979 and 30% in 1980. In 1979, mortality during challenge was significantly higher among infected than among noninfected fish; the elevation of plasma sodium levels in the infected fish was not statistically significant. In 1980, both infected and noninfected fish had improved seawater adaptability compared with the previous year; infected fish did not suffer significantly higher mortality after challenge but their plasma sodium levels were elevated significantly compared with the noninfected fish. The reduced seawater adaptability of infected fish is likely to reduce their ocean survival considerably.

Present address: Department of Fisheries and Oceans, Resource Research Branch, Ottawa, Ont. KIA 0E6.