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Time-courses of size-fractionated phosphate uptake: are larger cells better competitors for pulses of phosphate than smaller cells?

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Summary. Time-course experiments of phosphate uptake by size-fractionated phytoplankton were conducted in oligotrophic Kennedy and Sproat Lakes. The objective was to determine if large phytoplankton obtained more phosphate than smaller cells, when the nutrient was present at higher concentrations. Studies at Kennedy Lake revealed that uptake rates in the 0.2–3.0 μm fraction were very sensitive to the time they were exposed to elevated concentrations; rates determined over the 60–120 min interval were less than 30% of those recorded over the 0–60 min interval. In contrast, there was little difference in uptake rates over these intervals for cells >3.0 μm. At Sproat Lake phosphate incorporation into the two size fractions was followed after the aerial fertilization of the lake with inorganic nutrients. Following nutrient addition the proportion of phosphate entering the >3.0 μm size fraction increased from ca. 35% to ca. 85%. Despite these observations, it is doubtful that larger cells are able to sequester enough phosphate from pulses to realize the same specific growth rates as their smaller counterparts.

Key words: Phosphate uptake – Nutrient pulses – Size-fractionated phosphate uptake – Nutrient patches – Lake fertilization

Previous observations that ambient phosphate (PO_4^{-3}) flux frequently goes into smaller sized cells have been made for marine (Berman 1983), estuarine (Friebele et al. 1978; Berman 1983) and freshwater (Schindler et al. 1979; Lean and White 1983; Berman 1985) habitats. In addition, thorough studies by Currie and coworkers (Currie and Kalff 1984a, 1984b; Currie 1986; Currie et al. 1986) indicate that larger phytoplankton (>3.0 μm), in phosphorus-limited systems are not able to meet their requirements by uptake of PO_4^{-3} at low ambient levels. These findings are consistent with arguments that small cells should be superior nutrient competitors (Laws 1975; Smith and Kalff 1983), and general observations of decreasing cell size with decreasing nutrient availability in both freshwater (Watson and Kalff 1981) and marine systems (Hulburt 1970; Herbland et al. 1985). However, it is well known that populations of larger cells are frequently observed in nutrient depleted areas. The significance of phytoplankton cell size to processes occurring in aquatic ecosystems (Malone 1980; Azam et al. 1983; Suttle et al. 1986) and the existence of an apparently ubiquitous community of picophytoplankton (Stockner and Antia 1986), once again raises questions concerning the factors responsible for the maintenance of size structure in phytoplankton communities. Although by no means a unanimous view (Hulburt 1970; Goldman et al. 1979), the consensus is that oligotrophic aquatic habitats represent nutrient-limited systems (Maestrini and Bonin 1981) in which selection for small cells would be expected.

Theoretical models (Grenney et al. 1973) and empirical observations (Turpin and Harrison 1979; Robinson and Sandgren 1983; Scavia et al. 1984; Sommer 1984, 1985; Gaedeke and Sommer 1986; Suttle et al. 1987) demonstrate that the frequency of addition of a limiting resource can affect the species composition of phytoplankton communities. As well, studies by Turpin and Harrison (1980) and Suttle et al. (1987) show that the frequency of nutrient addition can affect cell size, with pulses which are less frequent but of higher resource concentration, selecting for larger cells. These findings, in conjunction with reports that as the concentration of PO_4^{-3} increases a greater proportion is taken up into larger size fractions (Schindler et al. 1979; Lean and White 1983; Lean 1984), suggests that pulses of PO_4^{-3} may provide a mechanism whereby larger cells are able to obtain sufficient phosphorus to allow coexistence with smaller ones. Presumably, such pulses could range in size from excretion events by zooplankton (Lehman and Scavia 1982) to major mixing due to storms or seasonal events. However, contradicting data of Lehman and Sandgren (1982) indicate that cells which pass through a 5.0 μm filter have much higher chlorophyll-specific initial uptake rates than larger cells. Yet these data also show that smaller cells can only sustain greatly elevated uptake rates for a short period of time; uptake rates in the 60–90 min interval were approximately 30% of those in the 0–5 min period. Suttle et al. (1987) note that under phosphorus-limited conditions the duration over which elevated uptake rates are sustainable, during PO_4^{-3} pulses, can be of important competitive advantage. Perhaps larger cells sequester adequate PO_4^{-3} to overcome their larger cellular requirements (Shuter 1978) by sustaining high uptake

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rates, during nutrient pulses, for a longer time than their smaller counterparts.

The purpose of this study was to examine time-courses of PO_4^{-3} partitioning between the less than and greater than 3.0 μm size fractions of plankton communities from two oligotrophic lakes. The objective was to ascertain if results were consistent with the hypothesis that larger cells can sequester sufficient phosphorus during an elevated pulse to meet their growth requirements. Experiments were carried out in one instance by enriching samples of lake water with various levels of ^{32}P–PO_4^{-3} and following incorporation into the two size-fractions. In the other instance ^{32}P–PO_4^{-3} was added to lake water before and after the addition of inorganic nutrients to a lake from an aircraft. Nutrients are routinely added to several western Canadian lakes in this manner for the purpose of enhancing growth rates of juvenile anadromous salmon (Stockner 1981; Stockner and Shortreed 1985). This provided an unusual opportunity to quantify, in situ, the partitioning of a PO_4^{-3} pulse into small and large phytoplankton fractions.

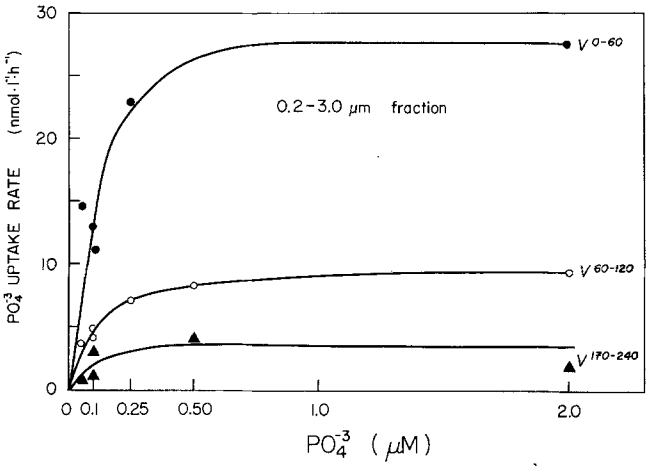

Fig. 1. Phosphate uptake rates (0.2–3.0 μm size fraction) for the three time intervals 0–60, 60–120 and 170–240 min. Rates are plotted against the PO_4^{-3} concentration added at the beginning of the incubation. The 0.1 μM treatment was duplicated; other treatments were unreplicated. Data are from Kennedy Lake in May 1984. Curves were fitted by eye

Materials and Methods

Experiments were carried out on Kennedy and Sproat Lakes (surface areas; 47 km^2 and 41 km^2, respectively), two oligotrophic lakes located on Vancouver Island in southwestern British Columbia, Canada. The limnology of these lakes, location of the sampling stations and details of the methods used are elaborated upon in Suttle and Harrison (1987a). Phosphate uptake experiments at Kennedy Lake were conducted in May 1984, and those at Sproat Lake in May 1985. Water was collected from 1 m at stations greater than 1 km from shore, and filtered through 120 μm screening to remove large grazers. At Kennedy Lake, water was dispensed into 1- or 2-liter flat-bottomed boiling flasks and, ^{32}P–PO_4 (ca. 30000 dpm·ml^{-1}) was used to determine PO_4^{-3} uptake rates at ambient (carrier-free addition) and five added concentrations (0.05, 0.10, 0.25, 0.50 and 2.0 μM); the 0.1 μM treatments were duplicated. Samples were incubated in flowing water, under natural light, at lake temperature. Screening as used to decrease the light to the approximate level at 1 m (425 μE·m^{-2}·s^{-1}). At the end of 60, 120, 170 and 240 min, two-25 ml subsamples were removed from the 500 ml lakewater samples and filtered through either a 0.2 or 3.0 μm pore size, polycarbonate filter (Nuclepore). Radioactivity on the filters was determined by liquid scintillation counting and uptake rates were calculated from the amount of ^{32}P incorporated into the particulate material in each size fraction, as outlined in Suttle and Harrison (1987a). Uptake rates were calculated assuming an ambient PO_4^{-3} concentration of zero. The amount of uptake in the 0.2–3.0 μM fraction was estimated by subtraction of the isotope uptake on the 3.0 μm filter from that on the 0.2 μm filter.

At Sproat Lake carrier-free additions of ^{32}P–PO_4 were added to samples of lakewater taken 1 h prior to and several times following (0.3, 3.0, 5.3 h) the aerial fertilization of the lake with ammonium nitrate and ammonium phosphate (3.0 mg·m^{-2} of PO_4^{-3}). At times of 0, 2, 5, 10, 15, 20 and 30 min after the addition of ^{32}P to lakewater samples, two-25 ml subsamples were filtered and processed as described for Kennedy Lake. These data were used to estimate the proportion of PO_4^{-3} incorporated into each size fraction.

Phosphate turnover times in the lakewater were calculated as described in Lean and White (1983). Briefly, turnover time is derived by following the incorporation of a ^{32}P–PO_4^{-3} addition into particulate material over time. The percentage of the initial ^{32}P–PO_4^{-3} addition which remains in solution at each sampling time is then calculated, and plotted on semi-logarithmic graph paper, against time. The initial slope of this line multiplied by 2.303 (= ln 10) is an estimate of the uptake rate constant (h^{-1}), the reciprocal is the turnover time. In many instances the percentage of ^{32}P–PO_4^{-3} remaining in solution will approach an asymptote with time; in such cases it is necessary to subtract the asymptote from the measured values to yield a straight line, before calculating the slope. The above analysis assumes ^{32}P–PO_4^{-3} exchanges with only two compartments, a PO_4^{-3} pool and a particulate pool (plankton). Lean (1973) has shown that this assumption is not always valid under very P-deplete conditions when a third compartment can be involved. There was no indication that the ^{32}P–PO_4^{-3} kinetics in Sproat Lake could be resolved into three components, although the sampling frequency was probably inadequate to permit resolution of such a pool.

Soluble reactive phosphorus and total phosphorus were estimated by reaction with ammonium molybdate as outlined in Stainton et al. (1977) and Stephens and Brandstaetter (1983), respectively.

Results

The concentration of soluble reactive phosphorus in Kennedy Lake was below the limit of chemical hydrolytic detection (< 0.03 μM). Uptake rates in the 0.2–3.0 μm fraction were very sensitive to the time which they were exposed to elevated concentrations of PO_4^{-3} (Fig. 1). Rates determined over the 60–120 min interval were less than 30% of those recorded over the 0–60 min interval, and those measured over 170–240 min were only half those for the 60–120 min interval. In contrast, there was little difference in uptake rates measured over the first two time intervals

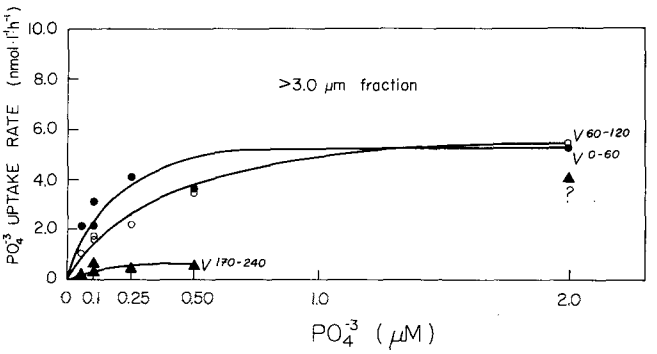

Fig. 2. As for Fig. 1 except that the data are for the >3.0 μm size fraction. See text for an explanation of the question mark

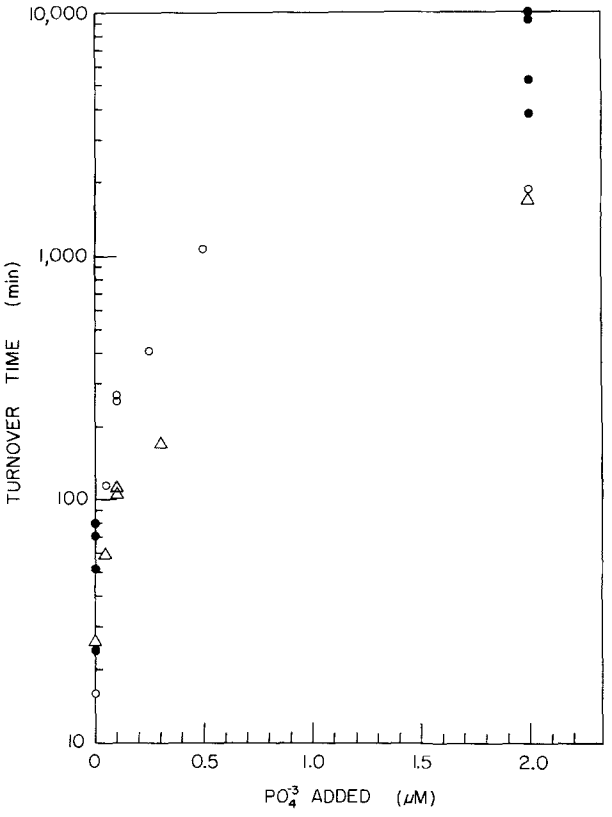

Fig. 3. Phosphate turnover times are sensitive to the addition of PO_4^{-3} and as such can be used to indicate sudden increases in PO_4^{-3} concentration in Sproat Lake (●-May); Kennedy Lake (o-May, △-July)

for the larger size fraction (Fig. 2); however, in the 170–240 min interval uptake rates had declined to less than 20% of the rate over the previous time periods. The apparent slight decline in uptake rate at the highest substrate level was probably the result of an error in the 3.0 μm filtration. This is supported by the observation that if the rate (170–240 min) in the >3.0 μm fraction, for the 2.0 μM concentration, is assumed to equal that for the 0.5 μM concentration, then the calculated rate (170–240 min) for the 2.0 μM concentration, in the 0.2–3.0 μm fraction, is no longer underestimated. Uptake rates have been plotted against the initial concentration added as less than 4% (77 nM) of the 2.0 μM addition was taken up over the course of the 240 min incubation.

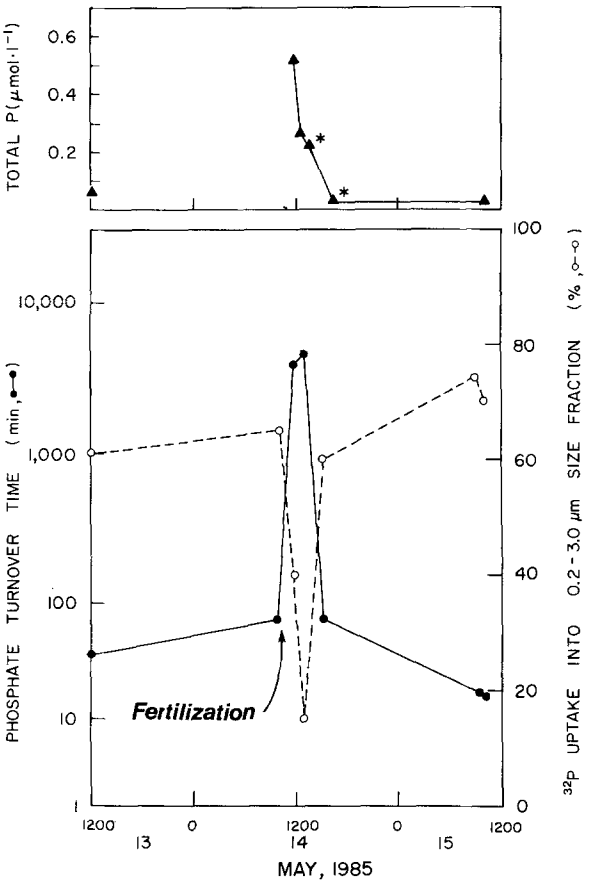

Fig. 4. Phosphate turnover times, proportion of ^{32}P uptake into the 0.2–3.0 μm size fraction, and changes in the total phosphorus concentration preceding and following the aerial fertilization of Sproat Lake with inorganic nutrients. The asterisk indicates surface concentrations, as data from 1 m were not collected

Figure 3 summarizes the relationship between the PO_4^{-3} turnover time in water from Kennedy and Sproat lakes and the concentration of substrate added. Data from Kennedy Lake in July and the 2.0 μM Sproat Lake additions were derived independently of the experiments reported here, although the latter were conducted concurrently. As would be intuitively expected the turnover times are longest when the added PO_4^{-3} concentrations are greatest. The effect of the aerial fertilization on PO_4^{-3} turnover time in Sproat Lake is illustrated in Fig. 4. Immediately following nutrient addition the turnover time increased approximately two orders of magnitude, suggesting a significant increase in the ambient PO_4^{-3} concentration. As can be seen from Fig. 3, turnover times greater than 1000 min were only associated with nutrient additions of at least 0.5 μM. Turnover time remained elevated at 3 h post-fertilization but decreased to prefertilization levels by 5.3 h. If these turnover times are used as an indicator of increased PO_4^{-3} concentration (cf. Fig. 3), it is apparent that partitioning between the size fractions was dependent on the aerial addition of PO_4^{-3} to Sproat Lake. The proportion going into the 0.2–3.0 μm plankton was almost the mirror image of the turnover times; when concentrations were elevated uptake into the large size-fraction was strongly favoured. Although concomitant SRP data were not collected, the increase in total phosphorus following fertilization (Fig. 3) also indicates a significant input of phosphorus into the system.

Discussion

Kennedy Lake

The Kennedy Lake data support the hypothesis that larger cells are able to maintain elevated uptake rates for longer than smaller cells. Uptake rates in the small size fraction were approximately 70% lower in the second hour than in the first, whereas they remained virtually unchanged in the larger size class (Figs. 1 and 2). Closer scrutiny of the data indicate, however, that despite the ability to sustain elevated uptake rates for longer, the larger size class may not be able to sequester enough PO_4^{-3} to realize the same phosphorus specific growth rate as the smaller cells. In Kennedy Lake, 55% of the chlorophyll a was in the >3.0 μm fraction and a similar proportion of the particulate P, assuming particulate P and chlorophyll are distributed similarly between the fractions; data from Suttle and Harrison (1987b; Table 1) indicate that this is a reasonable approximation. Therefore, if the particulate P is in the plankton and the larger cells are able to obtain more than 55% of a PO_4^{-3} pulse, they should be able to realize a higher P specific growth rate than smaller competitors. In fact after 4 h only 28% of the isotope was incorporated into the larger fraction. As the data show, maximum uptake rates per liter (and approximately per chlorophyll) are initially much higher in the small size class than in the larger one. It is only in the last time interval (170–240 min) that the uptake rates of the smaller cells decrease to the level where they are similar to the 'elevated' uptake rates associated with the larger cells. Consequently, the smaller cells benefit more from the nutrient pulse than do the larger ones. The above analysis rests on the assumption that the proportion of particulate P in cells is the same for the two size fractions. This may not be true as significant amounts of P have been found to occur in colloids and fibrils in lakewater (Lean 1976, Paerl and Lean 1976). If such colloids or fibrils were present in Kennedy Lake they would likely pass a 3.0 μm filter, but may be trapped on the Whatman GF/F glassfiber filters used for particulate P analysis. This would result in an overestimate of the particulate P in the small fraction and, therefore, cause an underestimate of their P specific uptake rates. Hence the advantage of the smaller cells may be even larger than indicated here.

Sproat Lake

Data from Sproat Lake (Fig. 4) also show that cells in the larger size-fraction are able to sustain elevated uptake rates for longer than small cells. Two hours following nutrient addition the proportion of PO_4^{-3} entering the >3.0 μm fraction had increased from 35 to 60% of the total, and another hour later had further increased to 85%. When the nutrient concentration decreased (presumably as a result of mixing), as indicated by the shorter turnover times and decrease in total phosphorus concentration, the proportion entering the large size class declined to 40%, similar to what it was pre-fertilization. However, when biomass is taken into consideration the results from the experiments conducted at Sproat Lake are quite different from those at Kennedy Lake. Prior to nutrient addition the proportion of PO_4^{-3} entering each size fraction was similar when expressed on a chlorophyll basis (ca. 65% of the chlorophyll was in the small fraction), but after fertilization the principle flux was into the larger cells (Fig. 4). Two hours after the nutrients were added about 40% of the uptake was into the small fraction; this had decreased to less than 15% after 3 h. Subsequent to 5 h, when the turnover time had returned to pre-fertilization rates, the amounts of isotope going into each size-class were again similar on a chlorophyll specific basis. Clearly, in this instance the large fraction was getting most of the pulse.

Do Phosphorus Pulses Favour Larger Cells?

There are two arguments that can be used to resolve the discrepant results from the two experiments. The first is that because the time scales over which the experiments were conducted are different, it is conceivable that the uptake rates in the 0.2–3.0 μm fraction would have continued to decline in the Kennedy Lake samples, such that after 3 h most of the PO_4^{-3} would be entering the large fraction, as was the case in Sproat Lake. This implies that elevated concentrations of PO_4^{-3} would have to be present for several hours in order for the larger cells to obtain enough to maintain a growth rate similar to the small cells. Such a strategy would not permit large cells to meet their phosphorus requirements through utilizing nutrient patches produced by individual zooplankton, but perhaps could be of some significance when large amounts of nutrients enter the euphotic zone via upwelling or storm events.

An alternative explanation is that the two size fractions may have been competing for different resources in Sproat Lake, but not in Kennedy Lake. The rationalization behind this rests on two observations. The first of these is that estimates of in situ N:P supply ratios (by atoms), derived from experiments examining the ratio of saturated PO_4^{-3} to saturated ammonium uptake rates (Suttle and Harrison 1987a), range from 36:1 to >45:1 in Kennedy Lake, and from 18:1 to 24:1 in Sproat Lake (Suttle and Harrison 1987a). Secondly, most of the cell volume in the larger size fraction consists of diatoms, while in the smaller range it consists largely of small cyanobacteria, probably *Synechococcus* (K.S. Shortreed and J.G. Stockner, unpublished work). The 'critical' supply ratios at which phytoplankton shift between phosphorus and nitrogen limitation range between 7:1 and 25:1 for diatoms (Rhee and Gotham 1980), and between 25:1 and 45:1 for *Synechococcus,* depending upon the light conditions under which it is grown (Healey 1985). Consequently, in Kennedy Lake both size fractions would be limited by PO_4^{-3}, whereas, in Sproat Lake, *Synechococcus* may have been nitrogen limited and the diatoms phosphorus limited. Therefore, in Sproat Lake, most of the PO_4^{-3} during a large pulse went into the larger cells not because they were better competitors, but because the small cells were not phosphorus limited.

The greater than 3.0 μm fraction from Kennedy Lake was able to sustain elevated PO_4^{-3} uptake rates for longer than the smaller fraction, when both size classes were likely limited by phosphorus. It appears unlikely, however, that the larger cells would have been able to sequester enough phosphorus to realize the same specific growth rate as the smaller cells, in pulses of less than 2 h duration. Interpretation of the results is complicated because one cannot be certain that the physiological status of cells in the two size fractions was equivalent. Suttle and Harrison (1986) have demonstrated that a unicellular cyanophyte, probably *Synechococcus,* isolated from Kennedy Lake was able to sustain greatly elevated maximum uptake rates for PO_4^{-3}, for at

least 2 h. Therefore, the possibility remains that in Kennedy Lake internal pools of phosphorus were less depleted in the smaller cells and, consequently, high uptake rates could not be sustained for as long. This would be consistent with the smaller cells being better PO_4^{-3} competitors and is supported by observations that *Synechococcus* can outcompete other organisms in phosphorus-limited cultures (Suttle and Harrison 1987a).

The experiments presented here do little towards elucidating a mechanism whereby larger cells are able to obtain adequate resources under nutrient limited conditions. Conceivably, some large cells may be 'physiologically small'. Certain diatoms would seem most likely to fit this criterion; their large vacuoles (Strathmann 1967) would result in a relatively small cytoplasm relative to their surface area. This is in agreement with many competition experiments (Smith and Kalff 1983; Sommer 1986; Kilham 1986; Tilman et al. 1986; Suttle et al. 1987) which have found species of *Synedra* to be good competitors for PO_4^{-3}. Yet Smith and Kalff (1983) maintain that even correcting for cytoplasmic volume certain species of *Synedra* were better PO_4^{-3} competitors than expected. Another point to consider is that it may be presumptuous to assume that organisms of different sizes are competing for the same resources. Nutrient bioassay experiments have suggested that multiple resource limitation may occur in some oligotrophic areas (Menzel et al. 1963; Thomas 1969; de Haan et al. 1982; Lane and Goldman 1984; Wurtsbaugh et al. 1985). If this is true it is possible that smaller cells may not be the best competitors for all nutrients. Finally, it must be remembered that in nature different size classes may not need to achieve the same specific growth rates. If loss rates are less in the larger cells a lower nutrient specific uptake may support a higher net population growth rate.

In conclusion, the results from this study do not support the contention that larger cells are able to meet their PO_4^{-3} requirements by sequestering phosphorus from pulses of elevated concentration, unless their loss rates are much lower than cells less than 3.0 μm. In Kennedy Lake the maximum uptake rates of larger cells did not decrease as rapidly as those in the smaller fraction, however, the degree of enhancement on a phosphorus specific basis was much higher for the smaller cells. Consequently, the phosphorus doubling time was much shorter in the smaller size fraction. In Sproat Lake most of the PO_4^{-3} uptake was into the larger size class; however, the estimated N:P supply ratios in the lake are such that the smaller cells may be nitrogen limited. As a result the greater uptake by the large cells was likely not an indication of better competitive ability at elevated concentrations, but rather, evidence of PO_4^{-3} sufficiency in the smaller cells.

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