

Phosphorus excretion and the measurement of feeding and assimilation by zooplankton

Abstract—A previously described model of the rate of P excretion by zooplankton shows that the excretion of recently ingested P can significantly affect estimates of assimilation but that short term measurements of ingestion are almost unchanged.

Excretion of assimilated label may lower tracer estimates of feeding or assimilation by zooplankton (Conover and Francis 1973; Rigler 1971a,b). Rigler (1961) and McMahon (1962) made rough estimates of this effect in short term feeding experiments and found the error to be negligible; less than 3.6% of the ingested ^{32}P was released. Since assimilation measurements necessitate longer experiments, excretion is potentially a greater source of error than in feeding experiments. It is now possible to improve the short term estimate and to calculate the error that P excretion introduces into assimilation measurements.

Peters and Rigler (1973) used the rate of release of ^{32}P from fully labeled *Daphnia rosea* to develop an equation which predicts the rate of P excretion; this model also describes the apparent decrease of P excretion rate with time after the animals are placed in a nonradioactive food suspension:

$$E_m = ae^{-0.0119M}, \quad (1)$$

where E_m is the apparent P excretion rate in $\mu\text{g P mg}^{-1}$ dry wt min^{-1} , M is time in minutes, and a is a constant that depends on animal dry weight (W , in mg), temperature (T , in degrees Celsius), food concentration (C , in yeast cells ml^{-1}), and food phosphorus content (P , in $\mu\text{g ml}^{-1}$) according to the equation

$$a = 0.00047e^{0.0387T + 0.00001C - 3.34PW^{-0.383}}. \quad (2)$$

[The exponent of W is misprinted as “-3.383” in Peters and Rigler (1973).] We interpreted the decline in excretion rate as the reduction of the specific activity of excreted P through the excretion of unlabeled P derived from the food. Thus the difference between the initial excretion rate ($E_0 = E_M$, when $M = 0$) and the apparent

excretion rate at some later time ($M > 0$) is the rate of excretion (E') of recently ingested unlabeled P:

$$E' = E_0 - ae^{-0.0119M}. \quad (3)$$

The total amount of recently ingested P which has been excreted is found by integrating Eq. 3 with respect to M :

$$\int_0^M E' = E_0M + \frac{a}{0.0119}(e^{-0.0119M} - 1). \quad (4)$$

Since radiophosphorus estimation of ingestion and assimilation is essentially the converse of our excretion experiment, in that unlabeled animals are placed in ^{32}P -labeled food and the accumulation of tracer followed over time, these equations can be used to estimate the error introduced by the excretion of incoming tracer. Figure 1 shows the magnitude of this effect in a typical experiment. Representative values were chosen for W (0.01 mg), T (20°C), C (10^5 cells ml^{-1}) and P ($0.021 + 0.004 = 0.025 \mu\text{g P ml}^{-1}$, where 0.021 is the P content of 10^5 yeast cells and 0.004 is a correction factor for nonyeast P available to the animals in our experiments), and estimates of ingestion and assimilation were made from Peters and Rigler (1973). Our tracer measurement of ingestion rate ($0.031 \mu\text{g P mg}^{-1} \text{min}^{-1}$) was corrected for ^{32}P excretion to give the “calculated” uptake of $0.157 \mu\text{g P mg}^{-1}$ at 5 min. By about 5 min, the gut of *D. rosea* is filled with labeled food (Burns 1966; Haney 1971; Peters 1972) and further P uptake is due to assimilation, calculated here from the sum of growth rate ($0.38 \times 10^{-3} \mu\text{g P mg}^{-1} \text{min}^{-1}$), reproductive rate ($3.15 \times 10^{-3} \mu\text{g P mg}^{-1} \text{min}^{-1}$), and excretion rate ($E_0 = 1.5 \times 10^{-3} \mu\text{g P mg}^{-1} \text{min}^{-1}$) as $0.157 + 0.0185 M \mu\text{g P mg}^{-1}$. The amount of labeled P which would be excreted was determined from Eq. 4 and subtracted from these calculated uptakes to give the uptake which would be “measured” with tracer techniques in experiments lasting up to 5 h. As Fig. 1 shows,

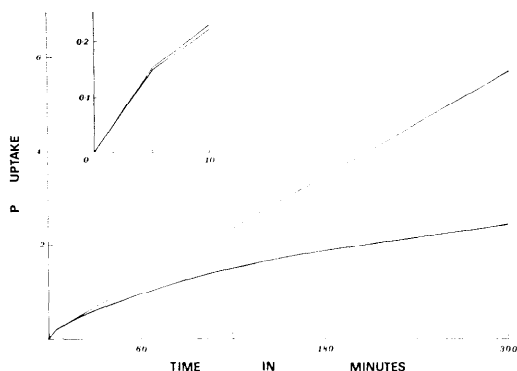


Fig. 1. The effect of P excretion on the uptake ($\mu\text{g P mg dry wt}^{-1}$) of labeled P in feeding and P assimilation measurements. The upper curve is calculated from independent estimates of ingestion, growth, reproduction, and excretion. The lower curve indicates the P accumulation which would be measured using the uptake of label as a tracer and the difference between the curves indicates the error tracer excretion introduces into uptake measurements. The inset shows the same curves in the brief, initial period such as might be used to measure ingestion rate. The determination of each curve is detailed in the text.

tracer excretion produces a negligible underestimate of 1.4% in a 5-min experiment used to measure feeding or filtering rate. However assimilation measurements can be significantly affected. After 30 min the measured uptake is 11% low and this underestimate will reach 53% in a 4-h experiment. If Eq. 3 continues to hold in such long experiments, at 4 h 94% of the P then being excreted will be derived from labeled food and further accumulation approaches the sum of growth and reproduction.

It is probable that this source of error exists for other taxa and other radiotracers. Equation 1 adequately predicted the excretion rate of other daphnids (Peters and Rigler 1973) and of cyclopoid and calanoid copepods (Peters in press). The rate constants of decline in those experiments were of the same magnitude as -0.0119 . Schindler (1968) reported that assimilated ^{14}C was not respired by *Daphnia magna* for 16 to 24 h, but Lampert (in press) found that recently ingested ^{14}C was rapidly released by *Daphnia pulex*. Lampert gave compartment sizes and rate constants that are re-

markably similar to those determined with ^{32}P . His work suggests that, at least in some cases, carbon uptake may be subject to similar errors.

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