ELSEVIER

Marine Geology 139 (1997) 109–122

MARINE GEOLOGY
INTERNATIONAL JOURNAL OF MARINE GEOLOGY, GEOCHEMISTRY AND GEOPHYSICS

Phosphorus and ammonia excretion by planktonic protists

J.R. Dolan[1]

Observatoire des Sciences de l'Univers, Université Paris VI, INSU/CNRS URA 716, Station Zoologique, B.P. 28, F-06230 Villefranche-Sur-Mer, France

Received 1 December 1994; revision 1 January 1996; accepted 2 February 1996

Abstract

Excretion by grazers is an important source of the nutrients orthophosphate and ammonia to producers of organic particles (phytoplankton and bacteria). Excretion may be dominated by the smallest of particle consumers, planktonic protists, because metabolic rates per unit weight are usually inversely related to size. However, protist taxa are a heterogenous assemblage, ranging over 3 orders of magnitude in size, and include forms which are mixotrophic, profiting simultaneously from photosynthesis and ingestion of particulate matter. Excretion rates from laboratory studies of protists, ciliates and flagellates, both heterotrophic and mixotrophic, were analysed to determine relationships with both cell size and growth rate. Smaller protists, such as flagellates, showed higher weight-specific excretion rates than larger protists like ciliates. Equations relating maximal excretion rate (excr) to size in terms of dry weight (DW) were, for orthophosphate, log excr (μg P cell^{-1} h^{-1}) = −2.101 + 0.570 log size (mg DW cell^{-1}), $r = 0.847$, $n = 12$ and for ammonia, log excr (μg N cell^{-1} h^{-1}) = −1.388 + 0.622 log mg DW cell^{-1}, $r = 0.899$, $n = 15$. Mixotrophic protists showed maximum excretion rates similar to like-sized heterotrophic protists. For phosphorus, the maximum weight-specific excretion rates of protists were higher than predicted by extrapolation of most size–excretion rate relationships established for metazoan zooplankton. Maximum excretion rates for ammonia approached the average of reported relationships for metazoan-based equations.

Rapidly growing protozoa appear to excrete orthophosphate (measured as soluble reactive phosphorus) relative to ammonia well in excess of the Redfield atom ratio of 16:1, i.e., excretory N:P ratios of 2:1–8:1. For orthophosphate, excretion rate may be predictable based on cell size and growth rate. In contrast, ammonia excretion appeared weakly related to growth rate in five out of ten species, and independent of growth rate in the remaining species, probably due to variability of the form of nitrogenous excretion. Consequently, planktonic protists may be much more important in the regeneration of orthophosphate than ammonia. However, the apparent magnitude and simplicity of phosphorous excretion may be an artefact of considering the dominant excretory compound, soluble reactive phosphorus, as entirely orthophosphate.

Keywords: Nutrients; Recycling

1. Introduction

In marine systems, organic matter is predominately formed via photosynthesis which is often dependant on the supply of nutrient salts to phytoplankton in the surface ocean. Nutrients utilised for the formation of biomass have either been recycled, (that is are derived from consumption and excretion by consumers of particulate matter–primarily grazers on phytoplankton and bacteria), or have been delivered to the surface

[1]E-mail: dolan@ccrv.obs-vlfr.fr.

PII S0025-3227(96)00106-5

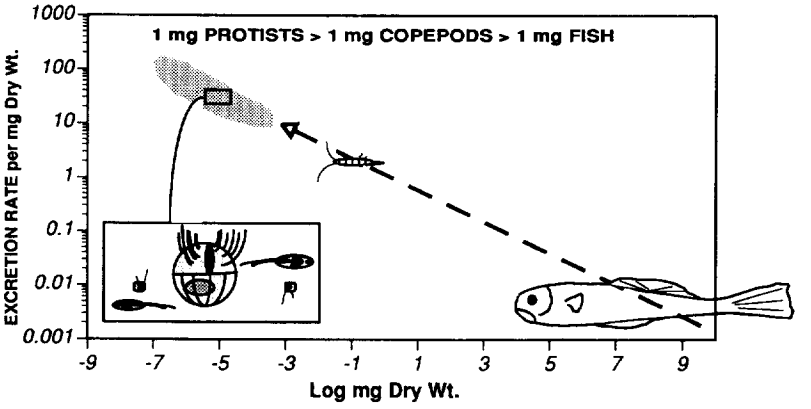

Fig. 1. Cartoon showing the relationship between organism size and weight-specific excretion rate. From general relationships relating metabolic rates to body size (e.g., Peters, 1983), 1 mg of protists should excrete much more phosphorus or nitrogen than 1 mg of copepods or 1 mg of anchovies.

waters either from deeper waters, the atmosphere or coastal areas. In contrast to phosphorus, different chemical forms of nitrogen, usually derived from different source pathways are absorbed by algae and bacteria. Ammonia, the common form of nitrogen excreted, is considered as "recycled", while nitrate represents a nutrient mixed into the surface layer from outside (Dugdale and Goering, 1967). Primary production fuelled by nutrients mixed into the surface layer from outside is defined as "new production", in contrast to "old production" which is based on excreted or recycled nutrients. Estimates of the relative quantity of new production to total production, the *f*-ratio (Eppley and Peterson, 1979), are often in the range of a few percent for open ocean areas, thus indicating the importance of recycled or excreted nutrients.

In pelagic ecosystems, heterotrophic (particle consuming) organisms occur in fairly distinct size-classes of approximately equal aggregate weight, in marked contrast to benthic ecosystems (e.g., Warwick and Joint, 1987). Thus, in a cubic meter of open ocean water one might expect to find, in terms of dry weight, 1 mg of flagellate protists, 1 mg of ciliate protists, 1 mg of crustacean filter feeders such as copepods and a 1 mg fraction of a small fish — each more or less characteristic of a distinct size-class. When comparing organisms of different sizes, it has long been known that a variety of metabolic rates, from respiration to reproduction, are generally higher in small organisms relative to large organisms. Thus, based on both solid theoretical grounds and some experimental data, Johannes (1964a) pointed out that planktonic protists, members of the microzooplankton defined as 20–200 μm (mostly ciliates), and nanozooplankton, defined as organisms 2–20 μm (mostly flagellates), are probably very important in nutrient excretion, specifically phosphorus dynamics in marine systems (Fig. 1).

The basic conclusion of Johannes has rarely been questioned, but his data on protozoa (1964a, b) were very limited, consisting of 4 ciliates of genera more typical of benthic than planktonic communities (*Euplotes*, *Uronema*). Furthermore, the accuracy of his rate estimates, some of the first using ^{32}P-tracer techniques, have been reasonably criticised (with hindsight) as overestimates because of non-equilibrium conditions in the cellular pools (Taylor and Lean, 1981; Caron and Goldman, 1990). More importantly, it has not been shown that the allometric, or size-based, rate relationship Johannes (1964a,b) presented, which predicted high excretion rates for protists relative to larger organisms, holds for protists of different sizes. Within individual taxa, metabolic rates do not always scale with body size. Among the larger crustacean zooplankton, i.e. copepods, body size has been termed a poor predictor of several physiological processes (Frost, 1980). For some metabolic processes, such as growth, differences in

maximal rates may be closely related to genome size, which need not be related to body size in organisms such as ciliated protists (Taylor and Shuter, 1981).

Planktonic protists are a heterogeneous assemblage of single-celled organisms which not only span 3 orders of magnitude in size but also include forms which are mixotrophic, species which profit from photosynthesis as well as the ingestion of particulate matter. Many flagellate species, which posses chloroplasts and would normally be considered algae, ingest particulate matter either to supplement photosynthesis or obtain nutrients (Nygaard and Tobiesen, 1993; Arenovski et al., 1995). Among planktonic ciliates, the dominant component of the microzooplankton in most systems, mixotrophic species which sequester and then exploit functional chloroplasts from ingested algae, often form the majority of ciliate biomass in near-surface waters (Dolan and Marassé, 1995). Mixotrophic ciliates can supply about 50% of their carbon requirements through photosynthesis (Stoecker and Michaels, 1991). Mixotrophic protists which fix carbon via photosynthesis might be expected to ingest particulate matter largely to obtain other essential elements, such as P or N. Therefore they likely excrete P or N at lower rates than strictly heterotrophic species.

Many studies have related the size of marine metazoan zooplankton (crustaceans and gelatinous form) to excretory rates to permit estimation of the quantities excreted, based on knowledge of the size structure of the fauna (e.g., Hargrave and Geen, 1968; Mullen et al., 1975; Ikeda et al., 1982). This approach also permits determination of the relative importance of distinct organisms. For protists, investigations of cell size and respiration rate (Laybourn and Finlay, 1976; Klekowski, 1981; Fenchel and Finlay, 1983; Caron et al., 1990) or growth rate (Fenchel, 1968; Finlay, 1977; Taylor, 1978; Taylor and Shuter, 1981; Montagnes et al., 1988; Müller and Geller, 1993; Montagnes, 1995) are common, whereas studies relating cell size to excretion rate are rare.

In the present study, experimental laboratory data were examined to determine the relationship between organism size and excretion rate in planktonic protozoa. The data base constructed includes flagellates and ciliates, both heterotrophic and mixotrophic; there are apparently no data at present for planktonic sarcodines (e.g., Foraminifera, radiolaria). First, size–excretion rate trends are compared in terms of maximum reported excretion rates with the intent to see if, within the protists, cell size could be used to predict excretion rate, and to compare the (size–excretion rate) relationship with those of metazoan zooplankton. Additional comparisons are made with a (size–excretion rate) relationship developed from equations relating cell size to maximum potential growth rate. Second, the relationship between growth (which integrates ingestion, food quality and temperature) and the excretion of phosphorus and ammonia is examined to assess the possibility that the excretion and growth rates could be used as proxies for one another.

2. Methods and materials

2.1. Maximum excretion and cell size

The data used to examine cell-size and excretion rates are given in Tables 1 and 2 for phosphorus and ammonia, respectively. Maximum rates were chosen as a means of comparison because excretion rates vary, down to near-zero, depending on culture conditions. Data on both mixotrophic forms and strict heterotrophs were included. In the original reports, when ranges of excretion rates were given, maximum values were used. If single values were reported but graphs were presented with time-course concentrations of organisms and PO_4 or NH_4, a maximum rate was calculated based on the graph data alone or in combination with tabular data. In all cases, maximum excretion rates were found to correspond with early exponetial growth phases. If a single estimate of excretion rate was presented without graphs or tables the single value was used. For cell size comparisons, all organism masses were transformed into dry weight. If the author(s) gave a dry weight estimate, it was used. If a volume estimate was given, dry weight was calculated assuming 0.2 pg dry weight per μm^3 (Sherr et al., 1983). If no volume estimates were given, a size was assigned based on the

Table 1
Maximum PO_4 excretion rate and cell size

Organism (type)	Dry weight/pg per cell	D.W. estimation source (Conversion factor x = CF x)	Maximum excretion/μg PO_4–P per cell per h	Excretion estimation source	Temp (°C)	Food type	Reference
Ochromonas flagellate, mixotrophic	2.00	text $\mu m^3 \times$ CF A	1.80×10^{-7}	table 3 and fig. 3b	ND	Bacteria	Andersson et al., 1985
chrysomonad flagellate, heterotrophic	8	text $\mu m^3 \times$ CF A	4.0×10^{-8}	text	22	Bacteria	Berman et al., 1987
Spumella sp. flagellate, heterotrophic	6.6	text carbon $cell^{-1} \times$ CF B	3.8×10^{-9}–6.6×10^{-7}	fig. 3 and table 4	25	Bacteria	Nakano, 1994
Paraphysomonas flagellate, heterotrophic	54	text $\mu m^3 \times$ CF A (μm^3 from Goldman and Caron, 1985)	8.3×10^{-9}–1.38×10^{-7}	table 2	20	Bacteria	Andersen et al., 1986
Poterioochromonas flagellate, mixotrophic	76	text cell dimensions for vol. × CF A	4.96×10^{-8}– 2.16×10^{-7}	fig. 1, h 120–140 and h 48–62	20	Bacteria	Caron et al., 1990
Cyclidium ciliate, heterotrophic	80	text DW	1.20×10^{-6} excr (mg^{-1} DW) ÷ cells mg^{-1} DW	text	22	Bacteria	Berman et al., 1987
Codonella cratera ciliate, heterotrophic	2000	assumed 20 × 50 μm lorica × CF C × CF B	6.3×10^{-6}	table 1 and fig. 8	8.6	algae	Taylor, 1984
Strombidium viride ciliate, mixotrophic	3300	assumed 40 × 40 μm cone × CF A	2.9×10^{-6}	table 1 and fig. 8	8.6	algae	Taylor, 1984
Strombidium sulcatum ciliate, heterotrophic	3250	text DW	0–8.0×10^{-5}	text	18	bacteria	Allali et al., 1994
Strobilidium velox ciliate, heterotrophic	4800	assumed 45 × 45 μm cone × CF A	$5.36 \times 10 - 6$	table 1 and fig. 8	8.6	algae	Taylor, 1984
Colpidium colpoda ciliate, heterotrophic	15224	vol. from Taylor, 1978 × CF A	7.8×10^{-6}–1.23×10^{-5}	text	20	bacteria	Taylor, 1986
Stokesia vernalis ciliate, heterotrophic	40200	assumed 120 × 80 cone × CF A	1.3×10^{-5}	table 1 and fig. 8	8.6	algae	Taylor, 1984

Conversion factors: A = 0.2 pg DW μm^3 cell volume, Sherr et al., 1983; B: DW is carbon × 2.5, Beers and Stewart, 1970; C: lorica or shell vol (μm^3) × 0.053 = pg carbon, Verity and Langdon, 1984).

Table 2
Maximum NH_4 excretion rate and cell size

Organism(type)	Dry Weightpg per cell	D.W. estimation source (Conversion Factor x = CF *x*)	Maximum Excretionμg NH4–N per cell per h	Excretion estimation source	Temp (C)	Food Type	Reference
"flagellate" heterotrophic	1.74	text $\mu m^3 \times CF$ *A*	3.08×10^{-7}	table 7	10	Bacteria	Van Wambeke and Bianchi, 1985
Ochromonas flagellate, mixotrophic	2.00	text $\mu m^3 \times CF$ *A*	6.80×10^{-7}	table 3 and fig. 3b	ND	Bacteria	Andersson et al., 1985
Monas sp. flagellate, heterotrophic	7.00	text DW	4.4×10^{-6}–3.5×10^{-7}	table 3	30	Bacteria	Sherr et al., 1983
chrysomonad flagellate, heterotrophic	8	text $\mu m^3 \times CF$ *A*	4.10×10^{-6}–3.08×10^{-7}	text	22	Bacteria	Berman et al., 1987
Spumella sp. flagellate, heterotrophic	8.6	text $\mu m^3 \times CF$ *A*	8.7×10^{-7}	fig. 3 and table 4	25	Bacteria	Nakano, 1994
Pseudobodo sp. flagellate, heterotrophic	12.7	text DW (excr. mg^{-1} DW) ÷ (excr. $cell^{-1}$)	7.0×10^{-9}–1.08×10^{-7}	text	12	Bacteria	Ferrier-Pages and Rassoulzadegan, 1994
Paraphysomonas flagellate, heterotrophic	54	text $\mu m^3 \times CF$ *A* (μm^3 from Goldman and Caron, 1985)	7.08×10^{-7}	fig. 6	20	Bacteria	Goldman et al., 1985
Poterioochromonas flagellate, mixotrophic	76	text cell dimensions for vol. × CF *A*	1.7×10^{-7}–7.6×10^{-7}	fig. 1, h 62–75	20	Bacteria	Caron et al., 1990
Cyclidium ciliate, heterotrophic	80	text DW	1.59×10^{-7}–5.92×10^{-7} excr (mg^{-1} DW) ÷ cells mg^{-1} DW	text	22	Bacteria	Berman et al., 1987
Oxyrrhis flagellate, heterotrophic	1260	text $\mu m^3 \times CF$ *A*	1.25×10^{-6}	text	20	Algae	Goldman et al., 1989
Tintinnopsis acuminata ciliate, heterotrophic	2055	text carbon $cell^{-1} \times CF$ *B*	9.0×10^{-6}–2.1×10^{-5}	text	25	Algae	Verity, 1985a
Strombidium sulcatum ciliate, heterotrophic	4360	text DW (excr. mg^{-1} DW) ÷ (excr. $cell^{-1}$)	8.9×10^{-6}–1.2×10^{-4}	text	12	Bacteria	Ferrier-Pages and Rassoulzadegan
Paramecium aurelia ciliate, heterotrophic	17600	text DW	1.0×10^{-6}–3.8×10^{-5}	fig. 2, day 9–11, day 3–4	27	Bacteria	Soldo and van Wagtendonk, 1961
Tintinnopsis vasculum ciliate, heterotroph	20800	text carbon $cell^{-1} \times CF$ *B*	3.8×10^{-5}–8.2×10^{-5}	text	15	Algae	Verity, 1985a
Euplotes vannus ciliate, heterotrophic	20535	text (excr. mg^{-1} WW = 0.2 mg^{-1} DW) ÷ (excr. $cell^{-1}$)	5.74×10^{-5}	text	25	Bacteria	Gast and Horstman, 1983

Conversion factors: $A = 0.2$ pg DW μm^3 cell volume, Sherr et al., 1983; B = DW is carbon × 2.5, Beers and Stewart, 1970.

author's description of the species and then transformed into dry weight. All of the studies, with the exception of Taylor (1984), employed a batch culture approach in which time course changes in prey, protist and excretory products were monitored. In general, the studies employed standard autoanalyser techniques for PO_4 or NH_4 analysis. Taylor (1984) estimated excretion based on the appearance of $^{32}PO_4$ in solution following the feeding of protists with $^{32}PO_4$-labelled algae. Least-squares regressions were used to generate the equations relating cell size to maximum excretion rate using log transformed data. For both phosphorus and ammonia, the relationships derived describing reported maximum excretion rates were compared to two types of predictions of excretion rates: extrapolations of equations describing metazoan excretion rates and a simple equation relating cell size to growth rate and excretion.

(Weight–excretion rate) relationships of metazoan zooplankton considered are given in Table 3. Excretion rates were extrapolated down to protozoan weight values for comparison. It should be noted that the equations for metazoans were based on studies of natural populations, not cultures, and were not meant to represent maximum metazoan rates nor protozoan rates.

The relationship between cell size, maximum growth rate and maximum excretion rate was constructed based on an estimated maximum growth rate and the assumption that assimilated phosphorus or nitrogen equalled the excreted phosphorus or nitrogen. These calculations involved the following steps: (A) estimation of a maximum growth rate (at 20°C) using the empirical relationship between cell size and maximum growth rate presented by Müller and Geller (1993):

$$\ln[\text{growth rate, } r\,(\text{h}^{-1})] = -1.44 + 1.52 \ln \times [\text{temperature } (^{\circ}\text{C})] - 0.27 \ln [\text{cell volume } (\mu\text{m}^3)] \quad (1)$$

(B) biovolume production calculated as growth rate multiplied by cell size, (C) biomass production in terms of dry weight as 0.2 pg per μm^3 (Sherr et al., 1983), (D) biomass production in terms of carbon as dry weight divided by 2.5 (Beers and Stewart, 1970), (E) production in terms of N and P using the Redfield ratio of C:N:P of 106:16:1, (F) production as equal to excretion, based on a gross growth efficiency of 50% (Verity, 1985a,b). For the purpose of these calculations, I have assumed that growth is "balanced", meaning that biomass production is proportional to growth rate (Legner, 1980), or that the average cell size does not change appreciably with growth rate and that the elemental ratio of the biomass produced is constant.

2.2. Excretion and growth rates

Sources of data used to examine the relationships between excretion rates of phosphorus and nitrogen are given in Table 4. Graphs and tables in the original reports were scanned for estimates of growth rates which could be matched with excretion rates. The purpose of the analysis was to see if growth and excretion rates could be related in a simple fashion, regardless of the source of growth rate variability. Consequently, the actual source of growth rate variability for a given species from a given study, which varied according to the growth phase of a batch culture or food quality or temperature, was purposefully ignored. In cases where studies followed excretion in batch cultures, data from early periods in batch cultures (lag) in which cell densities were low, and hence difficult to accurately estimate, were not used.

Stepwise regression was used to generate an equation relating excretion rate to cell size and growth rate for phosphorus. Data on phosphorus excretion and growth rate (sources in Table 4) and cell sizes (Table 1) were pooled yielding a total of 24 estimates for four species. Data were log transformed (size to log mg dry weight, excretion to log μg P cell^{-1} h^{-1}) before analysis. As in the analysis of maximal rates, rates from early (lag) periods in batch cultures were not included. Excretion rates from periods in which negative growth was recorded were also not included. No attempt was made to generate an equation relating cell size and growth rate to ammonia excretion as simple plots revealed no relationships between growth rate and excretion for at least half the species for which data were available (see results).

Table 3
Equations relating body size to excretion rates

Organisms	Equation	Reference
Phosphorus		
Mixed marine metazoan zooplankton	log excr (ng P animal^{-1} h^{-1}) = −0.174 + 0.429 log size (μg DW animal^{-1})	Ikeda et al., 1982
Mixed marine metazoan zooplankton	log excr (ng at P animal^{-1} h^{-1}) = 0.405 + 0.915 log size (mg DW animal^{-1})	Mullin et al., 1975
Mixed estuarine metazoan zooplankton	log excr (μg at × 10^{-5} mg^{-1} DW d^{-1}) = 3.705 + −0.295 log size (μg DW animal^{-1})	Hargrave and Geen, 1968
Freshwater metazoan zooplankton (Cladocera)	excr (μg P mg^{-1} DW h^{-1}) = 0.021 size (mg DW animal^{-1})$^{-0.30}$	Wen et al., 1994
Protists: maximum reported rates	log excr (μg P animal^{-1} h^{-1}) = −2.101 + 0.570 log size (mg DW animal^{-1})	This study[1] Table 1 data
Protists: calculated from predicted "r-max"	log excr (μg P animal^{-1} h^{-1}) = −1.653 + 0.731 log size (mg DW animal^{-1})	This study, see methods
Ammonia		
Mixed marine metazoan zooplankton	log excr (ng N animal^{-1} h^{-1}) = 0.518 + 0.525 log size (μg DW animal^{-1})	Ikeda et al., 1982
Marine metazoan zooplankton (copepods)	log excr (μg N mg^{-1} DW d^{-1}) = 0.686 − 0.402 (log size (mg DW animal^{-1})	Verity, 1985a
Protists: maximum reported rates	log excr (μg N animal − 1 h^{-1}) = −1.388 + 0.622 log size (mg DW animal^{-1})	This study[2] Table 2 data
Protists: calculated from predicted "r-max"	log excr (μg N animal^{-1} h^{-1}) = −0.455 + 0.729 log size (mg DW animal^{-1})	This study, see methods
Marine metazoan zooplankton (crustaceans)	log excr (μg N animal^{-1} d^{-1}) = 1.867 + 0.837 log size (μg DW animal^{-1})	Vidal and Whitledge, 1982
Mixed marine metazoan zooplankton	log excr (ng at N animal^{-1} h^{-1}) = 1.237 + 0.928 log size (mg DW animal^{-1})	Mullin et al., 1975

[1]For P: $n = 12$, $r = 0.847$, $p = 0.0005$, 95% C.I. for slope = 0.318–0.821.
[2]For N: $n = 15$, $r = 0.899$, $p = 0.0001$, 95% C.I. for slope = 0.441–0.804.

3. Results

3.1. P-excretion and cell size

The maximum reported excretion rate of phosphorus (as soluble reactive phosphorus) as a function of cell dry weight is shown in Fig. 2. Mixotrophic species did not appear to form a distinct group. The equation and associated regression parameters are given in Table 3. A comparison of (maximum reported excretion rate as a function of cell dry weight) with the two types of predictions, extrapolations of published excretion equations for metazoan zooplankton, and excretion rates calculated from theoretical maximum growth rates (Eq. 1), appears in Fig. 3. A wide range of predicted excretion values for organisms in the size range of common planktonic protists (log mg dry weight of −9 to −4) resulted. All but one of the equations underestimates maximal excretion. In the upper end of the protistan size range, log mg dry weights of −6 to −4 which corresponds to ciliates, excretion rates predicted from freshwater metazoan zooplankton (Wen et al., 1994; Fig. 3: line C) and rates predicted from theoretical maximal growth rate (Fig. 3: line D) fall within the 95% confidence envelope (lines not plotted). It should be noted that the relationships for metazoa were not based on maximal metazoan rates; estimates were made with natural populations which may or may not have been excreting at maximal rates.

Table 4
Excretion and growth rates

Organism	Source of growth rate variabilty	Reference (data from)
Phosphorus		
Strombidium sulcatum	growth phases of batch cultures	Allali et al., 1994 (figs. 1 and 5)
Poterioochromonas malhamensis	growth phase of a batch culture	Caron et al., 1990 (fig. 1)
Paraphysomonas imperforata	diet (algae, bacteria, prey N:P ratios)	Andersen et al., 1986 (tables 1 and 2)
Spumella sp.	diet (C:N:P ratios of bacterial food)	Nakano, 1994 (tables 3, 4 and fig. 4)
Ammonia		
Tintinnopsis vasculum	temperature	Verity, 1985a (table 3)
Tintinnopsis acuminata	temperature	Verity, 1985a (table 3)
Pseudobodo sp.	growth phases of batch cultures	Ferrier-Pages and Rassoulzadegan, 1992 (fig. 4)
Poterioochromonas malhamensis	growth phases of a batch culture	Caron et al., 1990 (fig. 1)
Paramecium aurelia	growth phases of a batch culture	Soldo and van Wagtendonk, 1961 (fig. 2)
Strombidium sulcatum	growth phases of batch cultures	Ferrier-Pages and Rassoulzadegan, 1992 (fig. 2)
Paraphysomonas imperforata	diet (algae, bacteria, prey N:P ratios) and temperature	Goldman et al., 1985(figs. 6 and 7); Caron et al., 1986 (table 1)
Oxyrrhis marina	diet (algae C:N ratio)	Goldman et al., 1989 (table 2)
Monas sp.	diet and temperature	Sherr et al., 1983 (tables 2 and 3)
Euplotes vannus	diet (bacteria, algae)	Gast and Horstman, 1983 (figs. 1 and 3, 24–48 h)

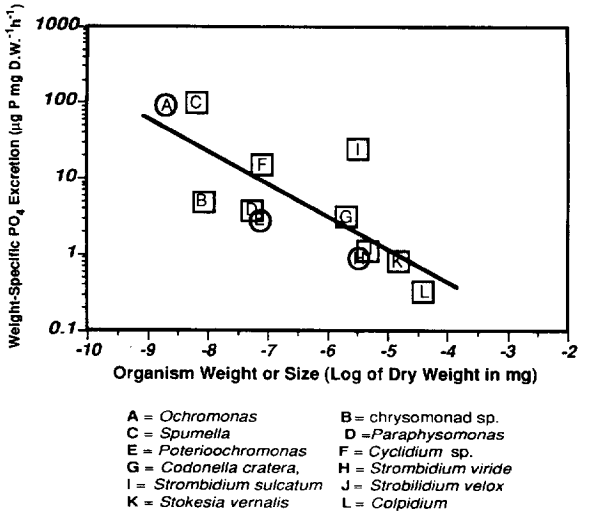

Fig. 2. Maximum weight-specific phosphorus excretion rates of protozoa (flagellates and ciliates) as a function of dry weight. Circles represent mixotrophic species, squares represent heterotrophic species. Data in the form of dry weight and excretion per cell appears in Table 1.

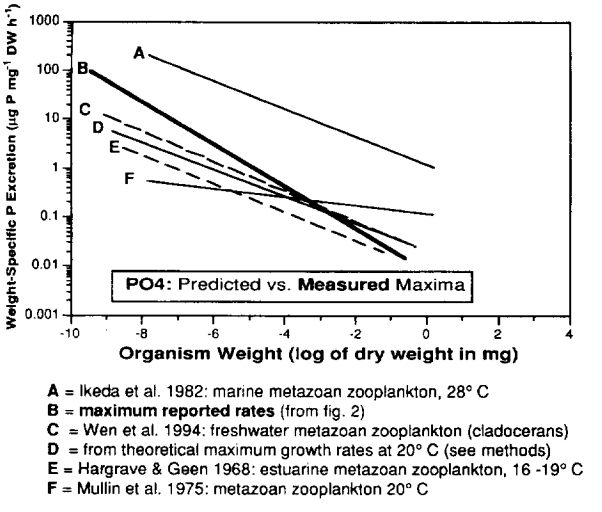

Fig. 3. Maximum weight-specific phosphorus excretion rates of protists compared to predicted rates from extrapolating published relationships for metazoans and calculations based on cell size and maximum predicted growth rate. Bold line represents the relationship shown in Fig. 2. Lines based on equations given in Table 3.

3.2. N-excretion and cell size

Plotting maximum reported excretion rates of ammonia as a function of cell dry weight (Fig. 4) gave results similar to those obtained for phosphorus: smaller protists show higher weight-specific excretion rates relative to larger protists. The equation, and associated regression parameters, relating dry weight to maximal excretion are

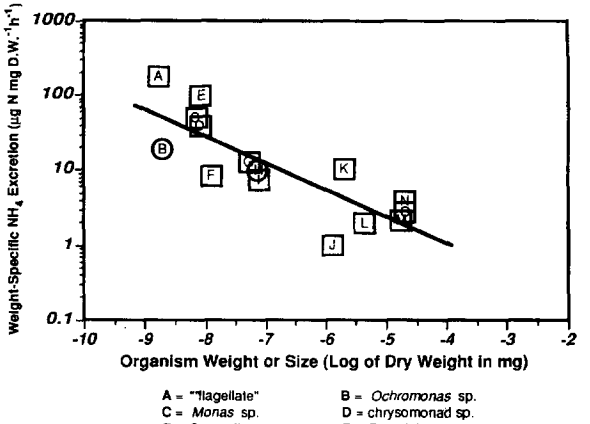

Fig. 4. Maximum weight specific ammonia excretion rates of protozoa (flagellates and ciliates) as a function of dry weight. Circles represent mixotrophic species, squares represent heterotrophic species. Data for in the form of dry weight and excretion per cell appears in Table 2.

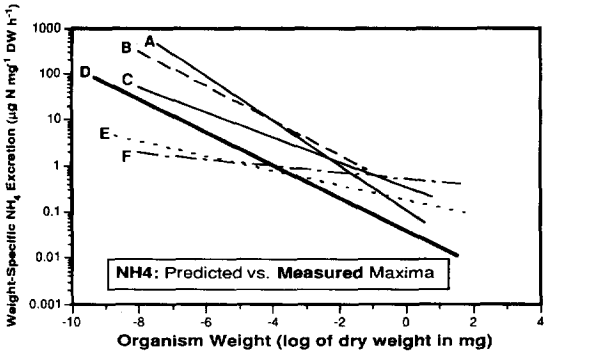

Fig. 5. Maximum weight-specific phosphorus excretion rates of protists compared to predicted rates from extrapolating published relationships for metazoans and calculations based on cell size and maximum predicted growth rate. Bold line represents the relationship shown in Fig. 4. Lines based on equations given in Table 3.

given in Table 3. In contrast to the relationship observed for phosphorus excretion rates, the equation relating maximal reported ammonia excretion rates (Fig. 5, line D) approached the average of the relationships extrapolated from equations based on metazoans. The excretion rates predicted from theoretical maximum growth rates (Fig. 5, line C), using the simple relationship given in Eq. (1), fall entirely within the 95% confidence envelope of the regression of reported rates (lines not plotted) throughout the range of common protozoan sizes (log mg dry weight −4 to −9). Again, it should be recalled that the equations relating metazoan excretion rates to organism size for ammonia were not meant to describe maximum rates.

3.3. Excretion and growth rates

Phosphorus excretion rate as a function of growth rate for four species is shown in Fig. 6; for all four species, excretion increased exponentially with growth rate. A stepwise regression of phosphorus excretion (log transformed) vs. dry weight (log mg) and growth rate (r h^{-1}) yielded the equation: log excretion (µg P animal^{-1}) = 3.3 + 1.498 log mg dry weight + 6.391 r h^{-1} (n = 24, r^2 = 0.87).

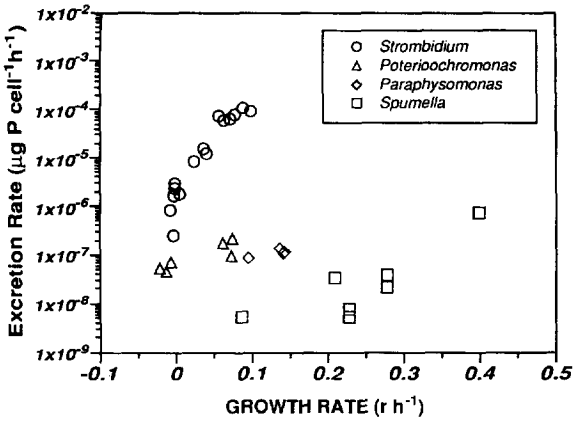

Fig. 6. Phosphorus excretion rate per cell as a function of growth rate. Estimates of excretion rates from sources given in Table 4. A stepwise multiple regression of excretion rate as a function of cell size and growth rate yielded the following relationship: log excretion (µg P cell^{-1}) = 3.3 + 1.498 log mg DW + 6.391 r h^{-1}.

For ammonia excretion rate, there was no clear pattern of increasing excretion rate with growth rate for most of the ten species for which data

were available. Species in which ammonia excretion appears to increase regularly with growth rate appear in Fig. 7a and those in which ammonia excretion appeared unrelated to growth rate are shown in Fig. 7b. The two distinct ammonia excretion patterns do not correspond with taxonomic grouping (Table 2) or source of excretion variability (Table 3).

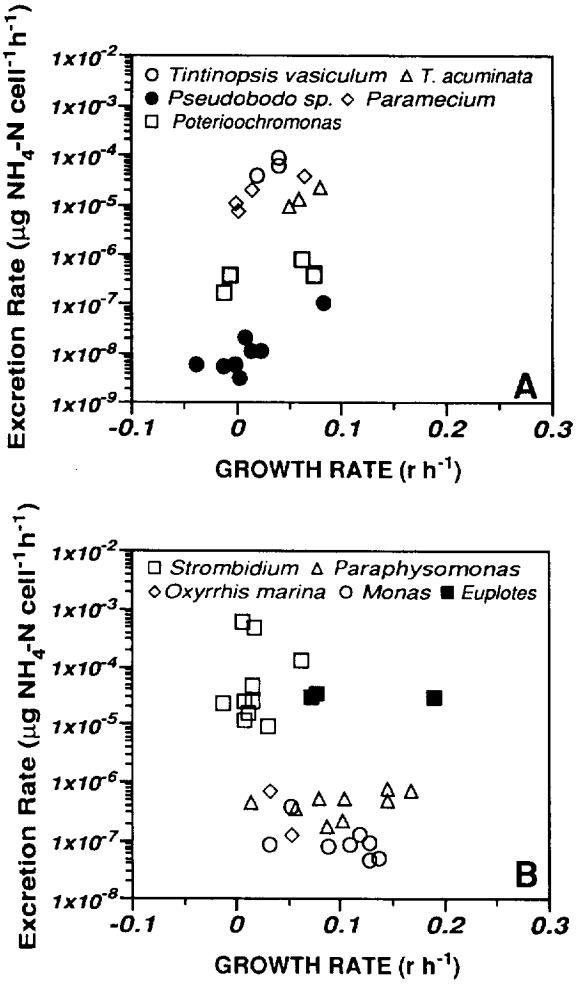

Fig. 7. Ammonia excretion rate per cell as a function of growth rate based on data sources given in Table 4. Data for species which show a positive relationship of excretion with growth are plotted in (A), data for species which showed no apparent relationships are shown in (B). The two sets of species do not correspond with taxonomic groups or sources of growth rate variability (see Table 4).

4. Discussion

Maximal excretion rates were examined as a means of comparison because the excretion rate of a given species can vary dramatically, over 2–3 orders of magnitude down to minimal rates of zero, with factors such as the growth phase of a population, food composition, temperature, or combinations of such factors (Tables 1 and 2). Calculation and comparison of average rates poses the problem of defining an "average" condition among the studies; comparing minimal rates would be meaningless as the minimal rates were often zero. Thus, maximal rates were compared and no attempt was made to adjust for temperature or other factors. While an equation relating maximal excretion rate to cell size can not be used directly to predict excretion in natural populations, it is nonetheless valuable as it allows estimation of upper limits, given data on the size structure of a natural population. Such estimates can then be used both to constrain models and in model validation and verification (Silvert, 1981).

The positive, exponential relationship between maximal weight-specific excretion rates and cell size follows general allometric, or size-scaled relationships, between organisms of different sizes (e.g., Peters, 1983). The finding that the magnitudes of protozoan maximal rates fall somewhere within the range of excretion rates extrapolated from metazoan zooplankton size–excretion equations was expected given the very wide range of reported metazoan size–excretion relationships (Table 3). However, two findings concerning maximal excretion rates were unexpected: the magnitude of P excretion, and the lack of a marked difference between mixotrophic and heterotrophic protists.

Protistan P excretion rates (Fig. 3, line B) exceeded, in general, rates predicted from metazoan-derived equations (Fig. 3, lines C, E, F) or theoretical maximum growth (Fig. 3, line D). This is not the case for the ammonia excretion rates (Fig. 5). Comparing the two lines for maximum excretion, phosphorus, relative to ammonical nitrogen, is excreted in an atom ratio of ~2 N: 1 P, in considerable excess of the Redfield atom ratio (16 N: 1 P). These findings, which must be

considered quite tentative as P and N excretion were generally measured in different studies, are none the less intriguing as they suggest that protists may recycle P much more efficiently than N.

Recently, N:P ratios of "seston" (particulate matter, 0.7–83 μm = algae and protists) for marine and freshwaters were compared to "metazoan zooplankton" N:P ratios (organisms ≥153 μm smallest dimension); marine "seston", which in general contains a much larger protistan component than in freshwater, was found to be relatively P-rich or N-poor compared to metazoan zooplankton (Elser and Hasset, 1994). Possibly, protists have high N to P requirements, higher than those of metazoan zooplankton, which could explain low assimilation rates, or high excretion rates, of P. Use of the Redfield ratio (i.e., Eq. 1) to predict excretion based on growth or carbon biomass production is probably incorrect. Unfortunately, basic data on the C:N:P ratio of individual protists, needed to examine such questions, are largely lacking.

The mixotrophic protists considered here are limited to three species, two chloroplast-containing flagellates and one ciliate, but still of interest as mixotrophs could potentially function as nutrient absorbers or regenerators (Dolan, 1992). For flagellates capable of photosynthesis, mixotrophy (the ingestion of particulate food), has been considered as a strategy to either acquire carbon under low light conditions or to acquire nutrients in short supply (Nygaard and Tobiesen, 1993; Arenovski et al., 1995). Based on the limited data presented here, mixotrophic flagellates appear indistinguishable from heterotrophs in terms of their maximal excretion rates. However, the mixotrophic flagellates considered here may be atypical. Caron et al. (1990) concluded that although *Poterioochromonas malhamensis* always has chloroplasts, it is primarily heterotrophic; Andersen et al. (1986) described their *Ochromonas* sp. as heterotrophic but chloroplast-containing.

In ciliates, mixotrophy can be either a symbiosis, with complete algal cells harbored within the ciliate cytoplasm, or the temporary exploitation of individual chloroplasts from partially digested algae; the two are distinct physiologically and found in different ciliate taxa (Dolan, 1992). For both types of mixotrophy, phosphorus has been found to enter the ciliates primarily through the ingestion of particulate phosphorus (Buechler and Dillon, 1974; Taylor and Lean, 1981). The only mixotrophic ciliate for which excretion rate data exists is *Strombidium viride*, which uses chloroplast mixotrophy, and whose maximal phosphorus excretion rate is in line with heterotrophic ciliates (Fig. 2).

Other mixotrophic protozoa, such as Foraminifera, which ingest food as well as profit from a symbiosis with complete algal cells, may play a different role in nutrient cycles. Recent studies have suggested that mixotrophic Foraminifera, in contrast to mixotrophic ciliates, directly absorb dissolved phosphate and nitrates (Lee et al., 1991) similar to metazoans with endosymbiotic algae such as corals (reviewed in Wilkerson and Kremer, 1992). Given that Foraminifera absorb dissolved P and N, it would seem unlikely that they would excrete phosphorus and nitrogen at rates comparable to heterotrophic protozoa.

The maximum P excretion rates which have been reported for protists exceed most of the extrapolations of metazoan excretion rates. Comparison of phosphorus and ammonia excreted, based on reported maximum rates, showed an excess of phosphorus excreted compared to the Redfield ratio of N:P (Figs. 2 and 4). These observations suggest that rapidly growing protozoa could be more important in phosphorus, compared to ammonical nitrogen, remineralization. An apparent excess of phosphorus remineralization could reflect the fact that nitrogen is excreted by protozoa in organic forms such as amino acids and urea (reviewed in Caron et al., 1990) so that nitrogen excretion is underestimated when only ammonia is considered. However, the same argument applies to phosphorus, as dissolved organic forms are excreted and can account for a large portion of phosphorus excreted. Andersen et al. (1986) found that organic phosphorus represented up to 70% of total dissolved phosphorus excreted by a microflagellate feeding on bacteria. In contrast, analysis of phosphorus excreted by the ciliate *Strombidium viride* using gel filtration revealed largely phosphate (Taylor and Lean, 1981). In general, organic forms are thought to

represent a minor fraction of phosphorus excretion in protozoa studied thus far (Caron et al., 1990).

The differences between correspondences in growth and excretion rates of phosphorus vs. ammonia may also reflect the relative simplicity of phosphorus metabolism. While the data set is small (four species for phosphorus, ten species for ammonia), ammonia excretion had no apparent relationship with growth rate in five out of ten species. In contrast, phosphorus excretion increased with growth rate, and 87% of excretion rate variability was attributable to cell size and growth rate (Fig. 6). Such differences are understandable if, in some species, the composition of nitrogenous excretory products vary with growth rate. For at least one flagellate species, *Paraphysomonas imperforata*, the ratio of ammonia to amino acids excreted does differ in cells from lag phase to log phase to stationary phase in batch cultures; the highest proportion of nitrogen excretion as dissolved free amino acids occurs in early exponential phase cells (Nagata and Kirchman, 1991). Interestingly, in the same species, organic phosphorus, as a percent of phosphorus excretion, also changes with growth phase with the greatest relative excretion of organic phosphate occurring during exponential growth (Andersen et al., 1986).

It is not unreasonable to postulate that the composition of excretory products should vary, especially with growth rate. In rapidly growing populations, for which food is not limiting and ingestion rates are maximal, processing of ingested matter by protozoa is thought to be limited by the availability of membrane to form food vacuoles. However, digestion may also be effected by the availability of digestive enzymes (Dolan and Coats, 1991). At least in part, variability of excretion products could result from incomplete digestion of food. If food availability is not limiting, processing ingested matter incompletely but rapidly, analogous to "creaming", can be an efficient digestive strategy (Jumars et al., 1989).

Excretion of phosphorus by protozoa may be more complex than is generally suspected and the apparent predictability and simplicity of phosphorus remineralization (relative to nitrogen) partially an artefact of analytical techniques. Commonly, orthophosphate phosphorus is equated with dissolved inorganic phosphorus (DIP) or soluble reactive phosphorus (SRP); organic phosphorus is estimated as the difference between SRP or DIP and total dissolved phosphorus which is measured after an oxidation and /or acid hydrolysis (i.e., Strickland and Parsons, 1972). It has long been suspected that SRP measurements overestimate DIP or biologically available phosphorus concentrations (Nürnberg and Peters, 1984; Thingstad et al., 1993). This is not unreasonable considering that SRP includes any phosphorus held in organic compounds which hydrolyses and reacts rapidly in acidic molybdate (Strickland and Parsons, 1972, p. 45). Thus, variability in phosphorus excretion products with growth rate, or between different species of similar size, if in the form of easily hydrolyzable organic compounds, would not be detected with the commonly employed technique.

5. Conclusions

Thirty years ago Johannes (1964a,b) argued, based on data from four ciliated protists compared to a variety of larger organisms, that weight-specific excretion rates of phosphorus increase with decreasing body size and therefore protists, the smallest particle-ingesting organisms in the oceans, likely play a key role in phosphorus remineralization. Data presented here, drawn from a large number of laboratory studies, extend the pattern of higher weight-specific phosphorus excretion rates in small protozoa relative to large protozoa. Considering maximal rates, protists may excretion may exceed the Redfield ratio of N:P in terms of ammonia to orthophosphate. This finding suggests that protozoa may be a more important source of remineralized P than remineralized N. A comparison of maximal weight-specific excretion rates of phosphorus and ammonia, and relationships between excretion rates and growth rates, suggests that the excretion of phosphorus as SRP may be much more predictable than excretion of nitrogen as ammonia.

Acknowledgements

Parts of this work were presented in the special session "Phosphorus Cycling and Sedimentation", organised by Gabriel Filippelli and Kathleen Ruttenburg at the 1994 AGU-ASLO Ocean Sciences Meeting. The analysis presented was provoked by offhand remarks of Paul Falkowski who questioned if protozoan excretion rates were worth measuring since they could probably be predicted from allometry, and Tim Hollibaugh who suggested that perhaps excretion could be measured instead of growth. While comments by D.A. Caron, K. Ruttenberg, R.H. Peters, W.D. Taylor and three anonymous reviewers on earlier versions of this manuscript are gratefully acknowledged, all errors of fact and interpretation are my own. Financial support was provided by the Commission of the European Communities, MAST II grant MAS 2 - CT93-0063 "Medipelagos", the *Centre National de Recherche Scientifique*, URA 716 and the *Université Pierre et Marie Curie*, Paris VI (France). **(K.C.R.)**

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