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DOI

[10.1016/0040-5809\(91\)90050-P](https://doi.org/10.1016/0040-5809(91)90050-P)

Publication date

1991

Published in

Theoretical Population Biology

[Link to publication](#)

Citation for published version (APA):

Nisbet, R. M., McCauley, E. M., de Roos, A. M., Murdoch, W. W., & Gurney, W. S. C. (1991). Population dynamics and element recycling in an aquatic plant-herbivore system. *Theoretical Population Biology*, 40(2), 125-147. [https://doi.org/10.1016/0040-5809\(91\)90050-P](https://doi.org/10.1016/0040-5809(91)90050-P)

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Population Dynamics and Element Recycling in an Aquatic Plant–Herbivore System

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Received September 18, 1990

We construct a model of an aquatic plant–herbivore system which takes explicit account of the cycling of the element limiting plant growth. The work is motivated by experiments on the population dynamics of the waterflea *Daphnia* where the *Daphnia* population is regulated by the availability of algal food, but the algae are phosphorus limited. The model is used to investigate the possibility that the system may be stabilised by a mechanism in which the *Daphnia* constitute a temporary phosphorus “sink.” We conclude that this is unlikely if the system is closed to external input of the nutrients limiting plant growth. © 1991 Academic Press, Inc

INTRODUCTION

Population dynamics makes use of both mechanistic and non-mechanistic population models. Structured population models (Metz and Diekmann, 1986; McCauley, 1992; McCauley *et al.*, 1992), which predict population behaviour from assumptions about individuals, are the obvious

example of mechanistic models. The logistic model, which characterises density-dependence through a parameter K (carrying capacity) with no immediate interpretation other than as a fitting parameter is a well-used non-mechanistic model. In spite of a growing awareness that any theory that aims to elucidate the causes of broad patterns in nature should explicitly incorporate environmental and physiological constraints (Tilman, 1989), few current population models stick rigourously to this ideal. For example, we have recently (Nisbet *et al.*, 1989; de Roos *et al.*, 1990) developed models of a *Daphnia* population, regulated through its algal food supply, in which the representation of *Daphnia* takes account of a wide body of information on the physiology of feeding, maintenance, growth, development, reproduction and mortality, while the phytoplankton assemblage is treated as a single species with logistic dynamics, parameterised in the time-honoured manner by r (intrinsic growth rate) and K . This approach may be justified by appealing to separation of space or time scales, especially in system-specific models that make no claim to generality; however, there is a compelling argument that attempts to understand widely observed dynamic patterns may be flawed if they rely (for example) on classification of systems by some vague population parameter such as K .

We are currently engaged in a programme whose objectives include identification of the causes of low amplitude *Daphnia* population cycles with a period of 25–40 days that have been identified in the laboratory, in mesocosms, and in lakes (Murdoch and McCauley, 1985; McCauley and Murdoch, 1987). Recent experiments (McCauley and Murdoch, 1990) in large (over 750 liter) tanks establish that the amplitude of the cycles is not significantly affected by enrichment with inorganic nutrients, in apparent disagreement with the so-called “paradox of enrichment” predicted by many models (Rosenzweig, 1971; May, 1972; Gilpin, 1972). The mathematics supporting the prediction is unambiguous; in a wide range of predator–prey models the effect of increasing K , the prey carrying capacity, is to destabilise any equilibrium and produce cycles of very large amplitude. The large amplitude occurs partly because saturation in the predator response implies that there is a portion of the cycle through which the prey are not controlled by the predator; for this reason we shall refer to the cycles as “prey escape cycles” (de Roos *et al.*, 1990). However, because K is ill-defined, the relevance of the mathematics to the real world is not clear.

One particular constraint that is commonly ignored in simple plant–herbivore population models is conservation of elemental matter. This neglect can be defended on the grounds that plant population growth is commonly limited by inorganic nutrients (e.g., Likens, 1972; Schindler, 1974), while reproduction of herbivores, and higher predators, is more

commonly limited by energy (or equivalently carbon). Yet there remains a problem, namely, that limiting nutrient bound in animals is unavailable for plants. In logistic language, " K " may be a function of the densities of other species in a system and not a property of the abiotic environment.

In this paper we construct a model of an aquatic plant-herbivore system which takes account of the cycling of the element (phosphorus) limiting plant growth. It is *not* a "realistic" phosphorus model for a lake ecosystem with compartments for all components of the biota (e.g., edible and inedible algae, herbivorous and carnivorous zooplankton, and bacteria), but is a deliberately simple representation of a closed system which was originally motivated by an attempt to understand the absence of large amplitude cycles in the experiments on *Daphnia* in stock tanks. We explore the possibility that *Daphnia* may act as a temporary sink for phosphorus, with the resulting inhibition of algal growth being sufficiently great to stop the "prey escape" mechanism.

Where "default" values for the parameters that appear in various formulae are required, we obtain them by assuming that the phytoplankton are *Chlamydomonas reinhardtii* and the zooplankton *Daphnia pulex*, both at 20° C (Table I and Appendix).

However, our model has wider relevance as an addition to the repertoire of abstract or "strategic" population models. Complementing the traditional producer-consumer models discussed above, there is a considerable literature on models of nutrient recycling (de Angelis *et al.*, 1989, and references therein). These models lead to apparently robust hypotheses relating stability or resilience of a system to nutrient turnover rate, but are

TABLE I
Default Parameter Set Based on *Chlamydomonas reinhardtii*
and *Daphnia pulex*, both at 20° C

Parameter	Value	Units
k_O	2.440	day ⁻¹
k_Z	1.400	day ⁻¹
k_J	1.000	day ⁻¹
$r_{\max}$	1.000	day ⁻¹
k_Q	2.5×10^{-7}	mol P(mg C) ⁻¹
b	0.120	day ⁻¹
$I_{\max}$	1.000	day ⁻¹
C_0	0.164	mg C liter ⁻¹
e	0.500	Dimensionless
m	0.020	day ⁻¹

Note. Details of the parameter estimation are in the Appendix.

limited by their emphasis on a single element. The model presented in this paper provides a modelling framework for systems effectively closed for one element, but open for another.

A MODEL OF CARBON FLOW IN A PLANT-HERBIVORE SYSTEM

One of the simplest and most commonly quoted models of a producer-consumer system assumes logistic growth of the plant in the absence of the herbivore, a herbivore feeding rate that is a saturating function of food density, and density-independent mortality of the herbivore (McCauley *et al.*, 1988, and references therein). The model has been used to describe changes in population numbers, biomasses, or carbon content.

We choose to work with carbon, and let C_P and C_Z represent the carbon content per unit volume of phytoplankton and zooplankton, respectively. The carbon flows are illustrated in Fig. 1. As already noted we assume logistic renewal of phytoplankton implying that the per capita growth rate (r) of phytoplankton varies with standing carbon as

$$r = r_{\max}(1 - C_P/K). \quad (1)$$

We require four assumptions on ingestion, assimilation, and utilisation of carbon by zooplankton. The first three of these [(a)–(c)] are based on our previous modelling of *Daphnia* (Nisbet *et al.*, 1989; McCauley *et al.*, 1990; Gurney *et al.*, 1990, and work cited in these papers). The final assumption (d) is made for convenience. We assume:

(a) Individual zooplankton have an ingestion rate proportional to their carbon content (broadly in agreement with experiments on *Daphnia* but wrong in detail: McCauley *et al.*, 1990), and uptake of algal food involves a type II functional response (a reasonable assumption for *Daphnia*: Porter *et al.*, 1982; de Mott, 1982). Thus the ingestion rate per unit of zooplankton carbon is

$$I = I_{\max} C_P / (C_0 + C_P). \quad (2)$$

(b) A time-invariant fraction e of intake is assimilated and represents new zooplankton biomass. We use the same assimilation efficiency, irrespective of whether the assimilate is eventually committed to body growth or to reproduction.

(c) Zooplankton meet maintenance by burning carbon, and an individual's respiration rate is proportional to its carbon content. Again this assumption is broadly consistent with what is found in *Daphnia*, but wrong in detail; over the full range of animal sizes, respiration rate scales

FIG. 1. (a) Schematic representation of phosphorus and carbon flows in a closed phytoplankton-zooplankton system. (b) Notation used to describe the standing masses and flows in the models. The "carbon" model (Eqs. (4) and (5)) incorporates only the carbon flows; the full model (Eqs. (9)-(15)) incorporates flows of both carbon and phosphorus.

as dry weight to the power 0.9, and carbon is an approximately constant fraction of dry weight (McCauley *et al.*, 1990, and references therein). Thus in the model, the total rate of zooplankton respiration (R) is given by

$$R = bC_Z. \quad (3)$$

(d) A zooplankter's per capita death rate (m) is independent of its carbon content, of density, and of food supply. Thus the total rate of loss of zooplankton carbon due to mortality is mC_Z .

The phytoplankton and zooplankton carbon densities obey the familiar differential equations

$$dC_P/dt = r_{\max} C_P (1 - C_P/K) - I_{\max} C_P C_Z / (C_0 + C_P) \quad (4)$$

$$dC_Z/dt = e I_{\max} C_P C_Z / (C_0 + C_P) - (m + b) C_Z. \quad (5)$$

The equilibrium carbon levels are

$$\begin{aligned} C_P^* &= (m + b) C_0 / (e I_{\max} - m - b), \\ C_Z^* &= (r/I_{\max})(1 - C_P^*/K)(C_0 + C_P^*) \end{aligned} \quad (6)$$

FIG. 2. Stability and extinction conditions for the carbon flow model (Eqs. (4) and (5)) with logistic renewal of phytoplankton. All parameters other than m and T have the values in Table I.

with C_{Z^*} being positive provided

$$K > (m + b) C_0 / (eI_{\max} - m - b). \quad (7)$$

The equilibrium is locally stable if in addition

$$K < C_0(eI_{\max} + m + b) / (eI_{\max} - m - b). \quad (8)$$

With plausible values for *D. pulex* at 20° C (Table I) assigned to the zooplankton feeding parameters, the equilibrium and stability conditions can be represented by curves in the m - K plane (Fig. 2). This figure gives a stark representation of the fragility of the system: only a very narrow range of carrying capacities yields stable equilibria except when zooplankton mortality is sufficiently high for its viability to be threatened.

A MODEL OF PLANT-HERBIVORE DYNAMICS WITH ELEMENT CYCLING

Phosphorus in Lakes

Phosphorus can be found in several forms in lakewater, and it is common practice to distinguish two components: *soluble* phosphorus which is not bound in living tissue, and *particulate* phosphorus which is bound in living tissue (Rigler, 1973; Lean, 1973a, b). Within the soluble fraction, it is useful to distinguish two forms: *organic* (bound to a carbon chain) and *inorganic* (Rigler, 1973; Lean and Nalewajko, 1976). Phytoplankton take up phosphorus predominantly from the inorganic, soluble pool, mainly as PO_4-P (orthophosphate). They can also obtain phosphorus from the soluble organic fraction by trapping organic molecules on the cell surface and using the enzyme alkaline phosphatase to cleave the PO_4-P from the molecule (e.g., Smith and Kalff, 1981). This process is energetically expensive and slow, and we neglect it in our modelling.

Herbivorous zooplankton obtain phosphorus by eating phytoplankton, and release it by excretion, defecation, and decomposition. Excreted phosphorus is largely orthophosphate (Peters and Lean, 1973; Peters and Rigler, 1973), and is thus readily available for phytoplankton. Fecal pellets and zooplankton corpses contain both organic phosphorus and orthophosphate released by cell lysis within the gut.

Within a closed system (e.g., the tanks of McCauley and Murdoch, 1990), a minimal representation of the phosphorus cycle is thus as shown in Fig. 1a. The compartments used in that figure have been recognised in many limnological radiotracer studies, and as a result it is possible to

identify appropriate ranges of values for model parameters (Table I and Appendix). We discuss these in detail later; however, for the present it is useful to note that in a "typical" oligotrophic lake, the concentration of total phosphorus is of order of magnitude 10^{-8} kg P liter $^{-1}$ (3×10^{-7} mol P liter $^{-1}$), and may rise as high as 10^{-5} mol P liter $^{-1}$ in eutrophic lakes (McCauley *et al.*, 1989). In the stock tanks of McCauley and Murdoch, the phosphorus densities were around 3×10^{-7} and 3×10^{-6} mol P liter $^{-1}$.

These numbers have implications for the "carbon-flow" model in the previous section. For that model, we might naively argue that K should be proportional to the total phosphorus (T) in the system. If k_Q represents the minimum quota of phosphorus per unit carbon in algal cells (i.e., that quota which reduces specific growth rate to zero), then an upper bound on K is T/k_Q . If we set the carrying capacity K equal to this upper bound, and take a value of k_Q appropriate to *C. reinhardtii* (Table I), it follows that unless mortality rates are very high, even the most oligotrophic systems have phosphorus content in excess of the minimal level required for instability. For example, using the stability boundary in Fig. 2 ($m = 0.002$ day $^{-1}$), instability would occur with $T > 0.75 \times 10^{-7}$ mol P liter $^{-1}$.

Phosphorus and Carbon Balance Equations

We now construct a model which takes explicit account of phosphorus cycling, in order to assess the effects of this cycling on the dynamics of a system where phytoplankton growth is phosphorus limited while zooplankton growth is limited by carbon or other quantities tightly correlated with carbon. As before we define a *carbon density* (C_P , C_Z —mass of bound carbon per unit volume of water) for both the phytoplankton and zooplankton. We also introduce a *phosphorus density* (P_P , P_Z —units: moles of bound phosphorus per unit volume of water) for phytoplankton and zooplankton. Phosphorus *quotas* (Q_P , Q_Z —units: moles phosphorus per unit mass of carbon) are then defined as the ratios P_P/C_P and P_Z/C_Z . We recognise three forms of phosphorus: soluble inorganic, soluble organic, and a third component which we call "junk" which is made up of feces plus corpses. The densities of standing phosphorus in the three compartments are denoted by P_I , P_O , and P_J , respectively.

The notation used to describe the carbon and phosphorus flows is illustrated in Fig. 1b. From book-keeping on carbon and phosphorus, it is possible to derive the following equations relating changes in each of the state variables to flows of carbon or phosphorus in and out of the compartments:

$$dP_I/dt = F_O + E_P + E_Z - U \quad (9)$$

$$dP_P/dt = U - IQ_P C_Z - E_P \quad (10)$$

$$dP_Z/dt = eIQ_P C_Z - E_Z - mP_Z \quad (11)$$

$$dP_J/dt = (1 - e) IQ_P C_Z + mP_Z - F_J \quad (12)$$

$$dP_O/dt = F_J - F_O \quad (13)$$

$$dC_P/dt = rC_P - IC_Z \quad (14)$$

$$dC_Z/dt = eIC_Z - R - mC_Z. \quad (15)$$

It is a routine exercise to check that the above equations imply constancy of total phosphorus (T) in the system, i.e.,

$$dT/dt = d/dt \{ P_I + P_P + P_Z + P_J + P_O \} = 0. \quad (16)$$

To complete the model specification, we require formulae that relate the various rate processes to the state variables. To obtain these formulae, we retain our previous assumptions on carbon flow, but require further assumptions on the cycling and utilisation of phosphorus.

Assumptions on Phosphorus Utilisation and Cycling

We assume:

- (e) All excretion processes obey first-order kinetics. Thus

$$E_P = k_P P_P, \quad E_Z = k_Z P_Z. \quad (17)$$

The form chosen for these relations merits comment. Although data are available (Peters and Rigler, 1973) on phosphorus excretion per unit time *per unit of dry weight*, there is no detailed information on the metabolic processes responsible for the measured excretion. In the absence of hard biochemical information, it seems most sensible to assume a constant rate of loss *per unit of phosphorus*; otherwise the model might allow the phosphorus quota of zooplankton to become negative.

(f) Uptake of inorganic phosphorus by phytoplankton obeys Michaelis-Menten kinetics. Thus

$$U = v_{\max} P_I B_P / (k_M + P_I). \quad (18)$$

We argue later that this process is normally very fast, so in most of the work, we use an approximation that avoids the need to estimate the parameters in this formula.

(g) Phytoplankton growth rate depends on phosphorus quota. Following Droop (1973), we hypothesize

$$r = r_{\max} [(Q_P - k_Q)/Q_P] \quad (19)$$

in which $r_{\max}$ is the maximum observable growth rate and k_Q is the minimum cell quota for growth to occur. This form is particularly appropriate for comparison with the simple "carbon" model (Eqs. (4) and (5)) since in the limiting situation where *all* phosphorus is bound in the phytoplankton, it gives logistic growth.

(h) "Junk" decomposition obeys first-order kinetics. Thus

$$F_J = k_J P_J. \quad (20)$$

(i) Conversion of organic phosphorus to inorganic form proceeds by first-order kinetics. Thus

$$F_O = k_O P_O. \quad (21)$$

Assumptions (h) and (i) are made for maximum simplicity, given the lack of detailed information on these processes. An alternative hypothesis (Ilyichev and Blokhin, 1987) is to approximate the kinetics as a (parallel) set of discrete delays; this makes the stability analysis much harder. While defensible in specific instances, we know of no experimental evidence that suggests that the more elaborate form is likely to be more generally applicable than its simple counterpart.

Separating Time Scales

The time constants for the various processes described above differ greatly: for example, the time constant for *Daphnia* growth is of the order of several days while that for phosphorus uptake may be as low as a few minutes (Rigler, 1964; Lean and Nalewajko, 1979; McCauley and Kalff, 1987). The model equations are thus "stiff" (a minor technical nuisance), and involve parameters whose precise values are unlikely to affect the dynamics of the system over time scales that are significant from a population dynamics perspective.

We can take advantage of this separation of time scales to reduce the number of differential equations and the number of model parameters. If uptake of phosphorus by the phytoplankton is very fast compared with all other time scales in the model, then we expect the density of free inorganic phosphorus (P_I) to be very small and in pseudoequilibrium (i.e., the rates of creation and removal, which may be appreciable in magnitude, are approximately equal at all times). Equation (9) is then no longer needed, and Eq. (10) is simplified by substituting

$$U - E_P = F_O + E_Z. \quad (22)$$

EQUILIBRIA, STABILITY, AND PREY-PREDATOR CYCLES

Equilibrium values of the various state variables can be computed in the usual way by setting all time derivatives to zero and (numerically) solving the resulting set of equations. As in the models that ignore phosphorus cycling, equilibrium phytoplankton carbon density is determined solely by parameters associated with zooplankton and is thus independent of total phosphorus. With our default parameter set (Table I), we obtain a value of C_{P^*} of around $0.06 \text{ mg C liter}^{-1}$, which is a factor of 2 higher than the lowest measured edible algal densities in stock tank experiments. This is a larger error than can be accounted for by experimental uncertainty (for example, through variations in the carbon content of a *C. reinhardtii* cell). We believe that this reflects the inadequacy of one of our model assumptions, namely, that the conversion efficiency of assimilate to new zooplankton biomass is constant, whether it is to growth or reproduction. This is not true; there are several mechanisms that reduce the efficiency of biomass production at high food density (Gurney *et al.*, 1990). Thus if, as in this paper, we estimate the parameters from high food measurements, we shall underestimate the value of the product $eI_{\max}$ that is appropriate to the size structure of a population at low food density and hence overestimate C_{P^*} ; indeed good agreement might indicate a problem! We are currently making a detailed study of the performance of simple models of *Daphnia*/phytoplankton systems, and shall elaborate on this problem in a subsequent publication (Murdoch *et al.*, in preparation).

Figure 3 illustrates the model predictions of equilibrium zooplankton carbon density, phosphorus quotas, and junk as a function of total phosphorus. These are given for three different values of k_j , the parameter about whose value we are least certain. Zooplankton carbon varies in essentially the same manner as in the models without cycling, increasing with total phosphorus. The phosphorus quotas also increase with increasing total phosphorus, and are reduced if the parameter k_j is decreased (as phosphorus is then held longer in the "junk" pool). The wide range of the equilibrium zooplankton phosphorus quota is significant as it points to a potential difficulty with our method for estimation of the parameter k_z (Appendix). However, in the absence of any information on the thermodynamic "force" driving the excretion of phosphorus (cf. Eq. (17)) we can do no better; at least the combination of Eq. (17) and our nominal value of k_z gives reasonable values for the total excretion rate.

Local stability of the equilibria may be investigated by traditional methods—local linearisation and determination of conditions under which the roots of the characteristic equation have negative real parts (e.g., Nisbet and Gurney, 1982, Chap. 4; McDonald, 1989, Chap. 2 and 4). Figure 4a shows the stability boundaries in terms of T (the parameter characterising

FIG. 3. Variation with total phosphorus of the equilibrium values of (a) phosphorus quota of phytoplankton, (b) zooplankton carbon, (c) phosphorus quota of zooplankton, and (d) junk, for three different values of k_j . In every case the per capita zooplankton death rate is 0.02 day^{-1} .

FIG. 3—Continued

FIG. 4. Stability boundaries in (a) the T/k_J plane and (b) the T/k_Z plane. In each case all parameters other than those plotted have the values from Table I. The curves shown correspond to two different values of zooplankton per capita death rate: $m = 0.02$ day $^{-1}$ (continuous line), and $m = 0.12$ day $^{-1}$ (broken line).

FIG. 5. Stability boundaries in the T/m plane for the phosphorus cycling model with: (a) default value of k_j and a 10-fold increase in this value and (b) default value of k_z and a 10-fold increase in this value. The broken line in each figure is the corresponding boundary (calculated from Fig. 1 using the value of k_Q in Table I) for the simple carbon-flow model.

the degree of enrichment) and k_j (the parameter about which we are most ignorant), with all other model parameters assigned their default values, and two different zooplankton mortality rates. From this figure we conclude that except when k_j is very small, the system is unstable with most plausible levels of total phosphorus. Very low total phosphorus (under 1×10^{-7} mol P liter $^{-1}$), comparable with ultraoligotrophic lakes is needed for stability with $m = 0.02$ day $^{-1}$. The stabilising effect of very low values of k_j reflects a situation where phytoplankton growth is held back through retention of much of the phosphorus in the "junk" pool.

One reason for the instability at most plausible phosphorus levels is the use of the relatively large value of the rate constant (k_z) for phosphorus excretion by *Daphnia*, which signifies that the half-life for retention of phosphorus is only a few hours. To assess the importance of this, we have plotted in Fig. 4b stability boundaries on a T - k_z plane, with all other parameters (including k_j) assigned their default values. It is clear that while a large reduction of k_z is sufficient to dampen cycles under highly oligotrophic conditions, with even mild eutrophication ($T > 8 \times 10^{-7}$ mol P liter $^{-1}$), the recycling via the junk pool supports sufficiently fast phytoplankton growth for instability irrespective of the value of k_z . In view of the problems with our estimate of k_z (see above), it is reassuring to find this robustness of system dynamics against changes in the value of this parameter.

Finally we compare the stability properties of the model with those of its counterpart without elemental cycling. Figure 5a contains stability boundaries on the T/m plane for two values of k_j together with that for

FIG. 6. An example of "prey-escape" cycles in the phosphorus cycling model. All parameters have their default values. The total phosphorus $T = 1.0 \times 10^{-6}$, and the per capita zooplankton death rate $m = 0.02$ day $^{-1}$.

the simple carbon-flow model. Figure 5b contains the results of a similar computation but with k_Z varying. These figures reinforce our conclusion from the previous calculations, namely, that phosphorus cycling has a significant effect on the population dynamics only if one or more of the recycling constants (k_O , k_J , or k_Z) is small, and/or the total phosphorus is very low. In fact the carbon model emerges naturally as a limiting case of the full model when k_Z , k_J , and k_O all become very large.

We have computed a number of numerical solutions to the model equations with parameter values that produce locally unstable equilibria. The broad conclusion from these computations is that except very close to stability boundaries, the populations rapidly settle down to large amplitude limit cycles of exactly the type associated with the "prey escape mechanism" (see Fig. 6).

DISCUSSION

The most striking conclusion from the model in which all phosphorus for phytoplankton comes from recycling is that with plausible parameters, the traditional picture inferred from models of phytoplankton-zooplankton dynamics survives. The sole exceptional cases are ultraoligotrophic systems and systems in which the junk pool has a long residence time and thus constitutes an effective phosphorus "sink." In particular, because of high rates of excretion, phosphorus bound in the *zooplankton* will not normally remain there long enough to significantly inhibit phytoplankton growth.

It follows that phosphorus bound in the zooplankton or in detritus is unlikely to be the explanation of the absence of "prey escape" behaviour in truly closed systems like the stock tanks of McCauley and Murdoch (1990) or in earlier experiments by Murdoch (Murdoch and McCauley, 1985). There remains of course the possibility that significant quantities of phosphorus are bound in inedible phytoplankton (see McCauley *et al.*, 1988; also McCauley *et al.*, 1989), a mechanism we shall discuss in a later paper. Murdoch and McCauley (1985) conjectured that *Daphnia* cycles in lakes and stock tanks might have a common cause. If, as we have argued above, phosphorus dynamics are not the key to the stability of *Daphnia* in stock tanks, it is then natural to ask if this conclusion also applies to lake populations in the months between the spring and autumn turnovers? It is possible that the stabilizing role of the "junk" pool may be somewhat greater in lakes than in tanks; in particular we expect a steady increase in hypolimnetic phosphorus during the summer months with little transport back to the epilimnion. In the language of our model, stratification in lakes will cause a somewhat lower value of k_J than in tanks. However Fig. 4 shows that the reduction in k_J would need to be very substantial (to less

than 0.1 day^{-1}) before the effect on stability was significant. We doubt if a strong, general case can be made for such a reduction.

However, once we start considering lakes, it is no longer reasonable to restrict the discussion to closed systems. A large throughput of inorganic nutrient can have a stabilizing effect in models which consider flow and recycling of a single element (de Angelis, 1980), a phenomenon which is well documented for the particular case of microbial prey-predator models where throughput is determined by a chemostat dilution rate (Cunningham and Nisbet, 1983, and references therein). Furthermore, in open systems the instability associated with prey escape may appear very abruptly (Nakajima and de Angelis, 1989; de Angelis *et al.*, 1989), and the apparent absence of this type of behaviour in real open systems is thus potentially a matter of parameter values rather than one of fundamental mechanism. Yet the fundamental problem of the absence of cycles in the phosphorus-rich *closed* systems of McCauley and Murdoch (1990) remains unsolved. The take-home message from the present work is that if there is a common cause for the low amplitude of cycles in lakes and tanks, it is unlikely to be phosphorus immobilisation in a predator compartment or junk pool.

APPENDIX: PARAMETERS FOR THE "PHOSPHORUS" MODEL

This appendix contains details of the judgements made in choosing values for some of the parameters in Table I in the text.

Estimate of k_o

Lean (1983b) gives a value of 0.0017 min^{-1} for hydrolysis of colloidal phosphorus. This is equivalent to 2.44 day^{-1} .

Estimate of k_z

The excretion rate of *Daphnia* is around $1 \mu\text{g P}$ per milligram dry weight per hour (Peters, 1987). The mean phosphorus quota of *Daphnia* is around $17/450 \text{ mg P/mg C}$ (Peters, 1987). If carbon is approximately 40% of dry weight, this implies $k_z = 1.58 \text{ day}^{-1}$. Of the excretion, 90% is inorganic phosphate, so we revise this estimate downwards to 1.4 day^{-1} .

Estimate of k_d

McCauley (unpublished work) has studied laboratory populations of *D. pulex* which were sampled three times per week. There was significant mortality, but only empty carapaces were found. This implies a rate constant for decomposition not significantly less than 1 day^{-1} .

Estimate of $r_{\max}$

For a *Chlamydomonas* cell of $3\ \mu\text{m}$ radius, cell volume = $113\ (\mu\text{m})^3$. An estimate of $r_{\max}$ can then be read off Fig. 6 of Smith and Kalff (1982).

Estimate of k_Q

From Smith and Kalff (1982) (Fig. 4) we estimate the minimum quota for a cell of volume $113\ (\mu\text{m})^3$ in units of mol P per cell. We take the carbon content of a *Chlamydomonas* cell to be 20 pg. The result follows.

Estimate of b

There are two approaches, one based on respiration measurements, the other on weight loss during bouts of starvation:

The most detailed data on respiration is that of Bohrer and Lampert (1989). After assuming a constant ratio (40%) of carbon to dry weight, their data show that respiration rate per unit carbon for *D. magna* is related to A , the assimilation rate per unit carbon, by

$$R/C_Z = c_1 + c_2 A$$

and

$$c_1 = 0.1\ \text{day}^{-1}; \quad c_2 = 0.17\ \text{day}^{-1}.$$

Here c_1 represents minimal metabolism which continues in the absence of feeding, i.e., the parameter b we require for our model. The parameter c_2 describes increased respiration rate for feeding animals; this phenomenon can be incorporated in our "assimilation efficiency" parameter e (see below).

There have been several studies of weight loss by daphnids during starvation: e.g., Smith (1963) and Schindler (1974) for *D. magna*, and Richman (1954) for *D. pulex*. The first two data sets are consistent with the above value of b for *D. magna*. Richman's data give estimates for *D. pulex* between 0.11 and $0.15\ \text{day}^{-1}$ depending on how we interpret his description of his data. Since starved *D. pulex* can survive as long as 8 days (E. McCauley, unpublished work), we favour the lower value. To be any more precise involves discussing size dependence and the effect of cast skin (McCauley *et al.*, 1990).

The above results point to a value of b of around $0.1\ \text{day}^{-1}$ for *D. magna*. On general grounds (Peters, 1983) and on the basis of our own studies (McCauley *et al.*, 1990), we except a slightly higher value for *D. pulex*. We therefore take as a plausible working value

$$b = 0.12\ \text{day}^{-1}.$$

Working Value of m

The per capita death rate m is of course largely set by the biotic and abiotic environment in any natural system. However, for estimation of the parameter $I_{\max}$ (see below) we require a value appropriate to laboratory and stock tank conditions. We assume $m = 0.02 \text{ day}^{-1}$ (corresponding to a mean lifetime of 50 days).

Estimate of $I_{\max}$ and e

To estimate these parameters, we considered two approaches:

First we used the result that the maximum possible specific growth rate of *Daphnia* biomass (or numbers), r_{Daph} , is given in our model by

$$r_{\text{Daph}} = eI_{\max} - b - m.$$

Taylor and Gabriel (1986) propose $r_{\text{Daph}} = 0.35 \text{ day}^{-1}$ for *D. pulex* on the basis of experiments on individuals, a result consistent with (unpublished) experiments by one of us (E.M.) on laboratory populations.

Our second approach was to use the structured model of Nisbet *et al.* (1989). The parameters of this model are all derived from experiments on individuals; a straightforward calculation gives the value $r_{\text{Daph}} = 0.6 \text{ day}^{-1}$. This model has never been tested at high food densities, but we know that a detailed individual model (Gurney *et al.*, 1990) needed an ad hoc adjustment (!) to avoid predicting impossibly large fecundities at high food. Therefore we distrust the second argument and accept the direct measurements which imply

$$r_{\text{Daph}} = 0.35 \text{ day}^{-1}.$$

With this value of r_{Daph} and our previously agreed values of b and m , we obtain

$$eI_{\max} = 0.5.$$

To obtain individual values for e and $I_{\max}$, we let e_A be the traditional assimilation efficiency (fraction of ingested food that crosses the gut wall) which we know has a value of around 0.6 (McCauley *et al.*, 1990) for *D. pulex*. If respiration per unit weight has the form given above, then

$$e = e_A(1 - c_2).$$

As noted above $c_2 = 0.167$, and we conclude

$$e = 0.5; \quad I_{\max} = 1.0 \text{ day}^{-1}.$$

It is possible to check the above calculation for consistency with values deduced from feeding experiments. We cannot demand perfect agreement since feeding/assimilation data are not mutually consistent (cf. McCauley *et al.*, 1990). However, error by more than a factor of 2 would indicate something badly wrong. Paloheimo *et al.* (1982) give (their Eq. (1'))

$$I_{\max} = 721 \times 10^3 \text{ cells mg}^{-1} \text{ h}^{-1},$$

where the cells are *C. reinhardtii* and the measurement is dry weight. Using the conversion (1 cell = 2×10^{-8} mg C; E. McCauley, unpublished work), this yields

$$I_{\max} = 0.87 \text{ day}^{-1},$$

which is acceptably close (13%) to our previous value. The consistency looks less good if we adopt Paloheimo's measured dry weight for a *C. reinhardtii* cell (9.5×10^{-8} mg) which gives a carbon content almost twice our value and thus implies an $I_{\max}$ of around 1.7 day^{-1} . Nevertheless, we conclude that our proposed $I_{\max}$ lies in the range allowed by uncertainty in algal cell weight.

Estimation of C_0

The value used is taken from McCauley *et al.* (1990b).

ACKNOWLEDGMENTS

This research is supported by SERC (UK), NSERC (Canada), the U.S. Department of Energy (Grant DE-FG03-89ER60885), and a NATO Award for International Collaborative Research. A.d.R. was supported by a postdoctoral fellowship and RMN received a Distinguished Visiting Lectureship from the University of Calgary.

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