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Equilibria, stability and excitability in a general class of plankton population models†

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In a recent paper we proposed a simple ODE model for the behaviour of populations of phytoplankton and zooplankton which had a mathematical structure analogous to models of excitable media. That model comprised a two-component system, in which limiting effects on the phytoplankton growth rate such as nutrient shortage and self-shading were represented parametrically. Here, we demonstrate the relationship of such a two-component system to a general class of three-component models in which nutrient is more realistically regarded as a third evolving variable, and self-shading is included as a growth rate modulation. We derive conditions for the existence and stability of equilibrium states which are generally valid for this class, and interprete the behaviour of particular models, proposed elsewhere, within this picture.

1. Introduction

The study of the dynamics of plankton ecosystems is an interdisciplinary field, combining influences from the biological sciences, oceanography, physics and mathematics. This diversity of interest is reflected in the great variety of motivations and goals for research as well as in the modelling tools used to tackle them. Interest ranges from the detailed modelling of taxonomically complex ecosystems in specific regions, to more general and simpler models for describing features such as annual cycles and atmosphere–ocean fluxes. Modelling techniques include stochastic and deterministic approaches, and both lagrangian and eulerian representations of plankton communities. While some attempts are being made to use temporally and spatially discrete methods such as cellular automata, the great majority of work has been done by using partial differential equation (PDE) and ordinary differential equation (ODE) models. The volume of published work is vast, but the essentials are covered in an excellent recent survey and bibliography in Fasham (1993).

PDE models allow a description of how the density fields of the population components vary with space and time. They have the advantage that spatial phenomena such as sinking, light penetration, currents and turbulence can be addressed directly, and they enable spatial structures to be investigated. While it is clear that PDEs give a more accurate and 'realistic' description of the ecosystem

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dynamics than ODE models, the latter are often more useful for testing scientific hypotheses.

In fact, for many applications, such as modelling annual population cycles or biological carbon fluxes across the ocean–atmosphere interface, spatial detail is less important than the temporal variations of populations and parameters, and these can be adequately captured using ODEs. The difficulties in obtaining spatial data mean that PDE models are much harder to test, and their use tends to be restricted to the simulation of specific geographical locations or experimental enclosures (Andersen *et al.* 1987). For this reason, ODE models are usually used (Wroblewski *et al.* 1988; Fasham *et al.* 1988; Belyaev 1984). It is important that ODE systems model successfully the effects of sinking, varying mixed layer depth and turbulent diffusion. If this can be done, however, these systems equate more closely to the level and quality of data presently available from experiment.

From a mathematical viewpoint, ODE systems are more easily handled both numerically and analytically. However, the extent of numerical work far outweighs the analytical. Questions of the stability and bifurcational behaviour of solutions are not often addressed. While it is true that for systems with large numbers of components analysis is often intractable, we are able to show here that for a fairly general three-component system an understanding of the bifurcational structure of the solutions can be achieved which will usefully inform more complex numerical work.

Among ODE models, most operate with a fairly limited number of taxonomic categories, given the incredible complexity of the ecosystems they represent. As any particular taxonomic category interacts with most others in a planktonic food-web, the number of parameters tend to proliferate as the square of the number of components within the model, increasing the data required for operation and obscuring the mechanisms involved. Most models are limited to about seven components (Fasham *et al.* 1988; Belyaev 1984; Belyaev & Konduforova 1992). Others sacrifice diversity of species for a degree of parametrization of the vertical structure of the ocean, such as the existence and movement of the thermocline (Taylor *et al.* 1991).

In contrast to these approaches, valuable results can still be achieved using very simple systems and exploiting the nonlinearity of their dynamics (Beltrami 1989). The most basic categorization for ocean systems, and that most widely used (Franks *et al.* 1986; Wroblewski *et al.* 1988; Evans & Parslow 1985; Busenberg *et al.* 1990; Steele & Henderson 1992) has three components: nutrients (N), phytoplankton (P), and herbivorous grazers (Z). An even simpler model is suggested by the behaviour of populations of phytoplankton and zooplankton *during* blooms or tides, which bears a phenomenological resemblance to the behaviour of the excitable and refractory variables in a model of an excitable medium. We have proposed in a previous paper (Truscott & Brindley 1994) a two-component mathematical model which displays this behaviour in a qualitative sense, and which yields sensible quantitative results when parameters are calibrated by comparison with observations. A weakness of this model is, of course, its restriction to two components, phytoplankton and zooplankton, and its tacit assumption of an instantaneously replenished nutrient supply.

In this paper we therefore consider a wide class of three-component models, in which the nutrient is regarded as a third variable. In the sections below, we outline the nature of the interactions between these elements, and show that, by

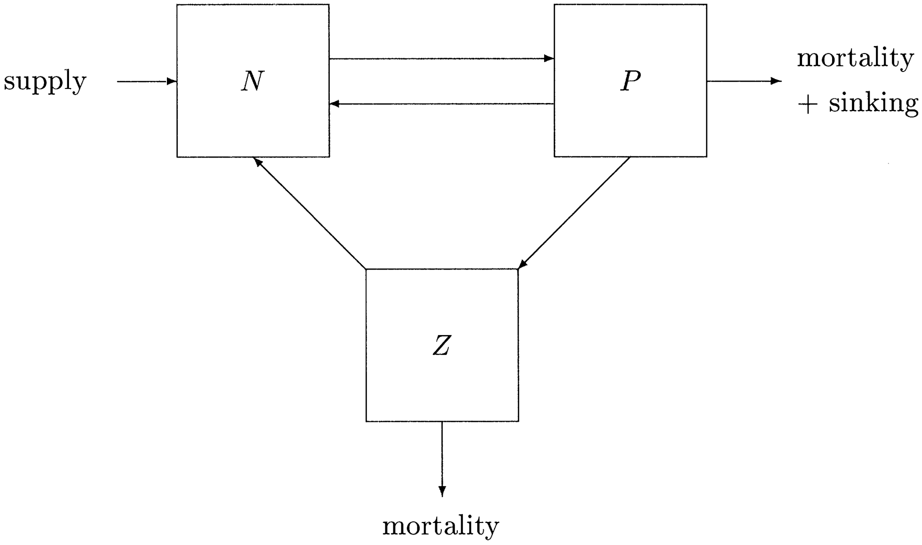

Figure 1. Relation between nutrients (N), phytoplankton (P), and herbivorous grazers (Z) (after Wroblewski *et al.* 1988).

considering the most general functional forms for these interactions within an ODE framework, conditions for the existence and stability of the equilibrium solutions can be obtained. These global results throw light on a number of specific results obtained by earlier researchers, such as the existence of limit-cycle behaviour. In particular, we demonstrate the relationship of the earlier two-component model to this class of three-component models, and assess their utility as simple scientific test beds.

2. Model

For three-component N–P–Z systems, the interactions found within models usually include most, if not all, of those illustrated in figure 1.

As a system of ODEs, these interactions can be expressed as

$$\begin{aligned} \mathrm{d}N/\mathrm{d}t &= \text{input} - \text{uptake} + Z \times \text{regeneration} + P \times \text{regeneration}, \\ \mathrm{d}P/\mathrm{d}t &= \text{uptake} - \text{grazing} - P \times \text{mortality} - \text{sinking}, \\ \mathrm{d}Z/\mathrm{d}t &= \text{growth} - Z \times \text{mortality}. \end{aligned}$$

To analyse the existence, stability and bifurcational properties of the solutions of such models, it is necessary to try to ascribe general functional forms to the above interactions, in terms of the variables N, P, Z, and appropriate parameters. We want to keep the forms as general as possible while still describing the essentials of the biological and physical mechanisms. It is also important that the properties of any general functional relationship must embrace those of specific forms in use in models.

(a) *Functional forms*

(i) *Input*

In ODE models of mixed layer ecosystems, the mixed layer is usually seen as resting on top of an infinite reservoir of nutrient with concentration, N_0 (Evans & Parslow 1985). The rate of mixing is assumed to be proportional to the difference in concentration between the mixed layer and the reservoir. The functional form used to describe the input of nutrient in most models (Steele & Henderson 1992) is the same as that used in models of chemostat experiments:

$$\text{input} = S(N_0 - N),$$

where S is a mixing rate.

(ii) *Uptake*

There are two main mechanisms for nutrient uptake and growth by phytoplankton. The Droop mechanism (Droop 1977) splits the nutrient into two parts: the 'ambient' nutrient in the surrounding water, and the internal nutrient reservoir of each phytoplankton cell. Phytoplankton growth rate responds to the internal reservoir state, rather than the ambient nutrient as in the standard Monod approach. While the Droop mechanism is arguably a more accurate and intuitively reasonable model of phytoplankton-nutrient dynamics, we do not use it here. Instead we follow the majority of models in using the standard Monod mechanism, since the Droop model would add considerably to the difficulty of analysis.

For the Monod mechanism, the general form of the interaction is

$$\text{uptake} = f(N)P.$$

Clearly growth must cease when nutrient is absent and must saturate as nutrient concentrations become excessive. It is also reasonable to assume that an *increase* in nutrient concentration never leads to a *decrease* in growth rate. These properties translate into the following conditions on $f(N)$:

$$f(0) = 0, \quad \frac{\mathrm{d}f}{\mathrm{d}N} > 0, \quad \forall N > 0, \quad \lim_{N\to\infty} f(N) = f_{\max} > 0.$$

The effects of self-shading can also be included by a change in the functional form describing the growth rate. This adaptation and its consequences are discussed in § 3*c* (ii).

(iii) *Grazing*

The functional form for grazing on phytoplankton is expressed as a rate proportional to the herbivore population. The proportionality is dependent on the phytoplankton population through a function, $g(P)$, namely

$$\text{grazing} = g(P)Z,$$

where $g(P)$ is subject to similar conditions to those for $f(N)$. When phytoplankton are absent their rate of consumption must be zero, and we assume that an increase in phytoplankton population will not lead to a decrease in the rate of consumption. This leads to the following conditions on $g(P)$:

$$g(0) = 0, \qquad \frac{\mathrm{d}g}{\mathrm{d}P} > 0, \quad \forall P > 0,$$

The behaviour of $g(P)$ for large values of P has a critical effect on the behaviour of solutions, and so is left until § 3*c*.

(iv) *Growth and herbivore related recycling*

Herbivore growth is taken to be proportional to the rate of grazing on phytoplankton. The constant of proportionality, γ, will clearly be less than one. Recycling from the feeding activities of the herbivores, a common model feature (Wroblewski *et al.* 1988; Busenberg *et al.* 1990; Evans & Parslow 1985) is also proportional to the grazing rate, with a constant, ζ, giving

$$\text{growth} = \gamma g(P)Z, \qquad \text{recycling} = \zeta g(P)Z.$$

From a consideration of the flow of nutrients through the system, it is clear that $\zeta + \gamma \leqslant 1$ and $0 \leqslant \gamma, \zeta \leqslant 1$. Some models also include the complete recycling of dead herbivores back into nutrient (Wroblewski *et al.* 1988; Franks *et al.* 1986; Busenberg *et al.* 1990), introducing a further term, $+\mu Z$, into the equation governing N. To cover this possibility, we include an extra recycling term, $+\rho\mu Z$, in the nutrient equation, where $0 \leqslant \rho < 1$.

(v) *Mortality and sinking*

Mortality for both Z and P is linear in form. This is the case in the majority of models. Steele & Henderson (1992) draw attention to the importance of this term in the system's behaviour, in particular the change in dynamics resulting from the use of a quadratic mortality term. In the case of phytoplankton, the mortality has been combined with a sinking term, which is also linear. The rationale for this can be easily seen. If we consider phytoplankton to be evenly distributed throughout the layer at a concentration P, in a layer of depth M, then a sinking velocity, v, will result in a flux, F, from the bottom of the layer, where $F = vP/M$, a linear relation. This results in the following forms:

$$Z \times \text{mortality} = \mu Z, \qquad P \times \text{mortality} + \text{sinking} = -qP.$$

Nutrient recycling from the mortality and respiration of phytoplankton is some fraction of that lost from the phytoplankton community, so

$$P \times \text{recycling} = -cP,$$

where $c < q$. Gathering together all the terms above gives the final form:

$$\mathrm{d}N/\mathrm{d}t = S(N_0 - N) - f(N)P + cP + \zeta g(P)Z + \rho\mu Z = \hat{N}, \tag{2.1}$$

$$\mathrm{d}P/\mathrm{d}t = f(N)P - qP - g(P)Z = \hat{P}, \tag{2.2}$$

$$\mathrm{d}Z/\mathrm{d}t = \gamma g(P)Z - \mu Z = \hat{Z}, \tag{2.3}$$

where all parameters are positive.

3. Analysis

(*a*) *An invariant set*

Since N, P, Z represent real concentrations, it is an essential property of the system that solutions with $N, P, Z \geqslant 0$ initially remain in the positive octant for all time. For this system it is possible to construct an invariant set in the positive octant. An invariant set for an ODE is a region, $\boldsymbol{D}$, of phase space (in this case, the three-dimensional space with orthogonal axes N, P, Z) with the property that any solution starting within $\boldsymbol{D}$ remains within it for all time. If we express equations (2.1)–(2.3) as

$$\mathrm{d}\boldsymbol{x}/\mathrm{d}t = \boldsymbol{f}(\boldsymbol{x}), \tag{3.1}$$

where

$$\boldsymbol{x} = \begin{pmatrix} N \\ P \\ Z \end{pmatrix},$$

we can ensure that $\boldsymbol{D}$ is an invariant set by showing that

$$\boldsymbol{f}(\boldsymbol{x}) \cdot \boldsymbol{n} \leqslant 0, \quad \boldsymbol{x} \in \partial \boldsymbol{D}, \tag{3.2}$$

where $\partial \boldsymbol{D}$ is the boundary of the set, and $\boldsymbol{n}$ is the outward normal on $\partial \boldsymbol{D}$. Condition (3.2) means that all trajectories on the surface of $\boldsymbol{D}$ are entering the set, and therefore none can leave. On the boundaries of the positive octant,

$$\begin{aligned} N &= 0, \quad \mathrm{d}N/\mathrm{d}t = SN_0 > 0, \\ P &= 0, \quad \mathrm{d}P/\mathrm{d}t = 0, \\ Z &= 0, \quad \mathrm{d}Z/\mathrm{d}t = 0, \end{aligned}$$

so clearly no trajectory can leave the positive octant, ensuring non-negative solutions. It will be assumed therefore that all analysis is confined to $N, P, Z \geqslant 0$. We now find the enclosing surface for $\boldsymbol{D}$. Adding equations (2.1), (2.2) and (2.3) we get

$$\frac{\mathrm{d}}{\mathrm{d}t}(N + P + Z) = SN_0 - SN - (q - c)P - (1 - (\zeta + \gamma))g(P)Z - \mu(1 - \rho)Z.$$

Since $(1 - (\zeta + \gamma))g(P)Z \geqslant 0$, we can define the function, $h(N, P, Z)$, in the following inequality,

$$\frac{\mathrm{d}}{\mathrm{d}t}(N + P + Z) \leqslant SN_0 - SN - (q - c)P - \mu(1 - \rho)Z = \psi(N, P, Z). \tag{3.3}$$

Next consider the function, $\phi(N, P, Z)$, given by

$$\phi(N, P, Z) = N + P + Z - \xi,$$

where

$$\xi = \max[N_0, SN_0/(q - c), SN_0/\mu] > 0.$$

Within the positive octant,

$$\psi(N, P, Z) < 0, \quad \text{on the surface } \phi(N, P, Z) = 0.$$

But the outward normal, $\boldsymbol{n}$, where $\boldsymbol{n} = \nabla \phi$, is given by

$$\boldsymbol{n} = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix},$$

and therefore, writing condition (3.2), and inequality (3.3) on $\phi(N,P,Z)=0$,

$$\boldsymbol{f}(\boldsymbol{x})\cdot\boldsymbol{n}=\frac{\mathrm{d}}{\mathrm{d}t}\begin{pmatrix}N\\P\\Z\end{pmatrix}\cdot\begin{pmatrix}1\\1\\1\end{pmatrix}=\frac{\mathrm{d}}{\mathrm{d}t}(N+P+Z)\leqslant\psi(N,P,Z)\leqslant 0.$$

Thus the surface $\phi(N,P,Z)=0$ satisfies the condition for the boundary of an invariant set. This surface forms a plane cutting each of the P, N, Z axes at ξ, enclosing a tetrahedron, so we can always construct an invariant set, $\boldsymbol{D}$, where

$$\boldsymbol{D}=\{(N,P,Z)|N,P,Z\geqslant 0,\ \phi(N,P,Z)\leqslant 0\}.$$

The existence of this set is necessary for ascertaining the stability of solutions, as discussed in § 3*c*.

(*b*) *Solutions*

The equilibrium solutions of the system are the solutions to the equations,

$$S(N_0-N)-f(N)P+cP+\zeta g(P)Z+\rho\mu Z=0, \tag{3.4}$$

$$f(N)P-qP-g(P)Z=0, \tag{3.5}$$

$$\gamma g(P)Z-\mu Z=0. \tag{3.6}$$

We first note that for any solution of the above system, $N\leqslant N_0$. Otherwise, since $c<q$ and $\zeta<1$, either P or Z would have to be less than zero, which is physically inadmissible. From equation (3.6) we can see that solutions must have either $Z=0$ or $P=\tilde{P}$ where,

$$\gamma g(\tilde{P})=\mu.$$

Since $\mathrm{d}g/\mathrm{d}p>0$, the value of $\tilde{P}$ is unique. For solutions with $Z=0$, N and P must satisfy

$$S(N_0-N)-f(N)P+cP=0, \tag{3.7}$$

$$(f(N)-q)P=0. \tag{3.8}$$

Clearly, for the above equations, $(N,P,Z)=(N_0,0,0)$ is a always a solution. The alternative solution, $(N^*,P^*,0)$, where

$$f(N^*)=q, \tag{3.9}$$

$$P^*=S(N_0-N^*)/(q-c), \tag{3.10}$$

is only possible if the condition

$$f(N_0)\geqslant q \tag{3.11}$$

is satisfied. Again, since $f(N)$ is monotonic in P, N^* and P^* are unique.

For the case, $P=\tilde{P}$, N and Z must satisfy

$$S(N_0-N)-(q-c)\tilde{P}-(1-\zeta-\rho\gamma)g(\tilde{P})Z=0, \tag{3.12}$$

$$(f(N)-q)\tilde{P}-g(\tilde{P})Z=0, \tag{3.13}$$

where equation (3.12) comes from adding equations (3.13) and (3.4). In (3.13), Z is clearly a monotonically increasing function of N, such that Z is zero at N^* and

$Z > 0$ at $N = N_0$. In (3.12), however, Z is a monotonically decreasing function of N, with

$$Z = \frac{1}{(1-\zeta-\rho\mu)g(\tilde{P})}(SN_0 - SN^* - (q-c)\tilde{P}),$$

at $N = N^*$ and $Z < 0$ at $N = N_0$. This together with the monotonicity of the functions guarantees the existence of a unique solution, $(\tilde{N}, \tilde{P}, \tilde{Z})$, if and only if

$$S(N_0 - N) > (q-c)\tilde{P}.$$

Without this condition, no solution is possible in the positive octant. From (3.10), it can be seen that the above is equivalent to

$$\tilde{P} < P^*. \tag{3.14}$$

The behaviour of the $(\tilde{N}, \tilde{P}, \tilde{Z})$ solution as $\tilde{P} \Rightarrow 0$ depends critically on the form of $g(P)$. From equation (3.12), it is clear that as $\tilde{P} \Rightarrow 0$, $\tilde{N} \Rightarrow N_0$. The value of $\tilde{Z}$, however, is given by

$$\lim_{P\Rightarrow 0} \tilde{Z} = \frac{P}{g(P)}(f(N_0 - q) = \begin{cases} \infty, & g'(0) = 0, \\ (f(N_0 - q)/g'(0), & g'(0) > 0. \end{cases}$$

Equations (3.4), (3.5) and (3.6) have only three equilibrium solutions. The solution $(N_0, 0, 0)$ is always possible. The solution $(N^*, P^*, 0)$ is only possible if condition (3.11) is satisfied. The solution $(\tilde{N}, \tilde{P}, \tilde{Z})$ requires that condition (3.14) is satisfied, which first requires that $\tilde{P}$ exists. Therefore if we consider some space of all parameters governing the functional forms of the system, the surface, $f(N_0) = q$, separates regions in which only $(N_0, 0, 0)$ is possible from those where two or more solutions exist. The condition $\tilde{P} = P^*$ then represents a surface entirely within the latter region, separating the 2-equilibria solution part from the 3-equilibria part. Having found the solutions and the conditions necessary for each to exist, we must next examine their stability.

(*c*) *Stability*

To calculate the stability of the solutions, we need to calculate the signs of the eigenvalues of their stability matrices. The stability matrix, $\boldsymbol{J}$, of a solution is given by

$$\boldsymbol{J} = \begin{pmatrix} \hat{N}_N & \hat{N}_P & \hat{N}_Z \\ \hat{P}_N & \hat{P}_P & \hat{P}_Z \\ \hat{Z}_N & \hat{Z}_P & \hat{Z}_Z \end{pmatrix},$$

where $\hat{N}_N = \partial\hat{N}/\partial N$, etc., and

$$\begin{aligned} \hat{N}_N &= -S - f'(N)P, \\ \hat{N}_P &= -f(N) + c + \zeta g'(P)Z, \\ \hat{N}_Z &= \zeta g(p) + \rho\mu, \\ \hat{P}_N &= f'(N)P, \\ \hat{P}_P &= f(N) - q - g'(P)Z, \end{aligned}$$

$$\begin{aligned}\hat{P}_Z &= -g(P),\\ \hat{Z}_N &= 0,\\ \hat{Z}_P &= \gamma g'(P)Z,\\ \hat{Z}_Z &= \gamma g(P) - \mu.\end{aligned}$$

For the $(N_0, 0, 0)$ solution, $\boldsymbol{J}$ is given by

$$\boldsymbol{J} = \begin{pmatrix} -S & -f(N_0)+c & \rho\mu \\ 0 & f(N_0)-q & 0 \\ 0 & 0 & -\mu \end{pmatrix}.$$

The eigenvalues of this matrix are $-S, -\mu, f(N_0) - q$. The eigenvectors of $-\mu$ and $-S$ both lie in the $P = 0$ plane. Since $\hat{P} = 0$ in this plane, it forms a stable manifold for the solution for all non-zero values of $-\mu$ and $-S$. The stability of the point is dependent upon the sign of $f(N_0) - q$. For $f(N_0) < q$, it is a saddle point and unstable. For $f(N_0) > q$, the solution is a stable node. From § 3*b*, we can see that the condition for the existence of $(N^*, P^*, 0)$ is also the condition for the instability of $(N_0, 0, 0)$.

For the $(N^*, P^*, 0)$ solution, the stability matrix is given by

$$\boldsymbol{J} = \begin{pmatrix} -S - f'(N^*)P^* & -f(N^*)+c & \zeta g(P^*) + \rho\mu \\ f'(N^*)P^* & f(N^*)-q & -g(P^*) \\ 0 & 0 & \gamma g(P^*) - \mu \end{pmatrix}.$$

The characteristic equation for the eigenvalues of this matrix is

$$(\hat{Z}_Z - \lambda)(\lambda^2 - \hat{N}_N - \hat{N}_P\hat{P}_N) = 0,$$

giving

$$\lambda = \hat{Z}_Z, \quad \text{or} \quad \tfrac{1}{2}\hat{N}_N \pm \tfrac{1}{2}\sqrt{\hat{N}_N^2 + 4\hat{N}_P\hat{P}_N}.$$

Since $\hat{N}_P\hat{P}_N < 0$ for this equilibrium point, the last two eigenvalues have $\mathrm{Re}(\lambda) < 0$. It can easily be shown that the eigenvectors associated with these last two eigenvalues both lie in the $Z = 0$ plane. As before, since $\hat{Z} = 0$ on this plane, it is a stable manifold of this equilibrium point. The stability of the solution is dependent upon the sign of $\hat{Z}_Z$, giving

$$\begin{aligned} 0 < P^* < \tilde{P}, \quad & \hat{Z}_Z < 0 \Longrightarrow \text{ stable node or spiral,}\\ P^* > \tilde{P}, \quad & \hat{Z}_Z > 0 \Longrightarrow \text{ saddle point.}\end{aligned}$$

Analogously with the previous solution, the condition for the instability of $(N^*, P^*, 0)$ is the same as that for the existence of the $(\tilde{N}, \tilde{P}, \tilde{Z})$ solution.

For the $(\tilde{N}, \tilde{P}, \tilde{Z})$ solution, the $\boldsymbol{J}$ matrix has the form,

$$\boldsymbol{J} = \begin{pmatrix} -S - f'(\tilde{N})\tilde{P} & -f(\tilde{N}) + c + \zeta g'(\tilde{P})\tilde{Z} & \zeta g(\tilde{P}) + \rho\mu \\ f'(\tilde{N})\tilde{P} & f(\tilde{N}) - q - g'(\tilde{P})\tilde{Z} & -g(\tilde{P}) \\ 0 & \gamma g'(\tilde{P})\tilde{Z} & 0 \end{pmatrix},$$

yielding the characteristic equation,

$$\lambda^3 - (\hat{P}_P + \hat{N}_N)\lambda^2 + (\hat{N}_N\hat{P}_P - \hat{Z}_P\hat{P}_Z - \hat{N}_P\hat{P}_N)\lambda + \hat{Z}_P\hat{P}_Z\hat{N}_N - \hat{N}_Z\hat{P}_N\hat{Z}_P = 0.$$

Within this expression, only $\hat{P}_P$ and $\hat{N}_P$ are not of definite sign. The solutions of this cubic have $\mathrm{Re}(\lambda) < 0$ if and only if they satisfy the Routh–Hurwitz conditions (Murray 1990), which for a cubic,

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0,$$

are $a_1, a_3 > 0$, and $a_1a_2 - a_3 > 0$. For this cubic, assuming only $\hat{P}_P < 0$,

$$a_1 = -(\hat{P}_P + \hat{N}_N) > 0,$$

$$\begin{aligned} a_3 &= \hat{Z}_P\hat{P}_Z\hat{N}_N - \hat{N}_Z\hat{P}_N\hat{Z}_P \\ &= \hat{Z}_P g'(\tilde{P})[S + (1 - \zeta - \rho\gamma)f'(\tilde{N})\tilde{P}] > 0, \end{aligned}$$

and

$$a_1a_2 - a_3 = \hat{P}_P\hat{Z}_P\hat{P}_Z + \hat{Z}_P\hat{N}_Z\hat{P}_N - \hat{N}_N\hat{P}_P^2 - \hat{N}_N^2\hat{P}_P + \hat{N}_P\hat{P}_N\hat{P}_P + \hat{N}_P\hat{P}_N\hat{N}_N. \quad (3.15)$$

Noting that $\hat{N}_P + \hat{P}_P < 0$, we can re-arrange (3.15) to the form,

$$a_1a_2 - a_3 = \hat{P}_P\hat{Z}_P\hat{P}_Z + \hat{Z}_P\hat{N}_Z\hat{P}_N + (\hat{P}_P + \hat{N}_N)[\hat{P}_N(\hat{N}_P + \hat{P}_P) - \hat{P}_P(\hat{P}_N + \hat{N}_N)]. \quad (3.16)$$

Examination of this expression, term by term, reveals it to be positive-definite provided $\hat{P}_P < 0$. Therefore the Routh–Hurwitz conditions are satisfied and the solution $(\tilde{N}, \tilde{P}, \tilde{Z})$ is stable.

(i) *Hopf bifurcation*

The coefficient, a_3, is positive definite for the $(\tilde{N}, \tilde{P}, \tilde{Z})$, and this dictates that the only possible signs for the $\mathrm{Re}(\lambda)$ are $-, -, -$ or $+, +, -$. For $\hat{P}_P > 0$, the Routh–Hurwitz conditions are not guaranteed and the latter choice is possible, resulting in all equilibria being unstable. Assuming that the solution does not lie on one of the stable manifolds already identified, the existence of an invariant set implies a periodic solution (barring the possibility of chaos). So we can state a necessary condition for limit cycle behaviour to occur,

$$\hat{P}_P > 0, \quad \text{at } (\tilde{N}, \tilde{P}, \tilde{Z}). \quad (3.17)$$

Sustituting (3.13) into the expression for $\hat{P}_P$ gives,

$$\hat{P}_P = [g(\tilde{P}) - \tilde{P}g'(\tilde{P})]\tilde{Z}/\tilde{P}. \quad (3.18)$$

The sign of $\hat{P}_P$ is therefore determined by the sign of $g(\tilde{P}) - \tilde{P}g'(\tilde{P})$ and a Hopf bifurcation is possible only if

$$g(\tilde{P}) - \tilde{P}g'(\tilde{P}) > 0, \quad 0 < \tilde{P} < P^*. \quad (3.19)$$

From this stability analysis we have built up a complete picture of the bifurcational behaviour of this system. For $f(N_0) < q$, only the $(N_0, 0, 0)$ solution exists and is stable. The surface, $f(N_0) = q$, represents a bifurcation surface at which a transcritical bifurcation occurs and stability is transferred to the $(N^*, P^*, 0)$ solution, which now exists. This solution remains stable as long as $\tilde{P} > P^*$. On the surface $\tilde{P} = P^*$, a further transcritical bifurcation occurs at which stability is transferred to the $(\tilde{N}, \tilde{P}, \tilde{Z})$ solution, which is now positive definite. Within this region, this solution remains stable provided $g(\tilde{P}) - \tilde{P}g'(\tilde{P}) < 0$. Where this condition does not apply, there is the possibility of a Hopf bifurcation to a stable limit cycle.

(ii) *Self-shading*

The shading effect of the phytoplankton community on itself is included in many ODE models (Evans & Parslow 1985; Steele & Henderson 1981; Frost 1987). Its effect is to reduce the specific rate of production of the population, due to a reduction in the amount of photosynthetically active radiation reaching organisms at depth. These effects are usually included as a modification in the growth rate of the depth averaged plankton population (Steele & Henderson 1992), namely

$$\text{growth rate} = F(N)H(P),$$

where $F(N)$ and $H(P)$ are the nutrient- and light-controlled elements of the growth rate, respectively. To fit in with the analysis of the previous sections, it is convenient to 'normalize' this expression to a form $f(N)h(P)$, such that as $P \to 0$ and self-shading becomes negligible, the growth rate term reverts to the form in § 2*a*, namely

$$\lim_{P\to 0} f(N)h(P) = f(N)P.$$

This is ensured if

$$h(P) = H(P)/H'(0) \quad \text{and} \quad f(N) = F(N)H'(0).$$

Thus $h(0) = 0$ and $h'(0) = 1$. Given the assumption that any increase in P will not increase the *specific* growth rate of the community,

$$\frac{\mathrm{d}}{\mathrm{d}P}\left(\frac{f(N)h(P)}{P}\right) = f(N)\frac{h'(P)P - h(P)}{p^2} \leqslant 0,$$

and hence

$$h'(P) \leqslant h(P)/P. \tag{3.20}$$

From the limit as $P \to 0$ we also have

$$h(P)/P \leqslant 1. \tag{3.21}$$

It is easy to show that specific examples obey these constraints. In particular, for those of the form, $H(P) = G(P)P$, such as Steele & Henderson (1992), it is sufficient that

$$\partial G/\partial P \leqslant 0, \quad \forall P \geqslant 0.$$

Equations (2.1) and (2.2) now have the form,

$$\frac{\mathrm{d}N}{\mathrm{d}t} = S(N_0 - N) - f(N)h(P) + cP + \zeta g(P)Z + \rho\mu Z = \hat{N}, \tag{3.22}$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = f(N)h(P) - qP - g(P)Z = \hat{P}, \tag{3.23}$$

How does this adaptation affect the dynamics of the system? Since equation (2.3) is not altered by the addition, all solutions have either $Z = 0$ or $P = \tilde{P}$, as before. Looking first at the $Z = 0$ solutions, it is clear that the $(N_0, 0, 0)$ still exists. From (3.23), we can see that a solution of the form $(N^*, P^*, 0)$ is only possible if

$$f(N)/q = P/h(P) \leqslant 1.$$

This is identical to inequality (3.11), and so the condition for the existence of this solution is unchanged. From (3.22) and (3.23), $(N^*, P^*, 0)$ is now the solution of

$$S(N_0 - N) - f(N)h(P) + cP = 0, \tag{3.24}$$

$$f(N)h(P) - qP = 0. \tag{3.25}$$

Does a unique solution still exist to the above? Assuming the solutions of these two equations to be curves $N \equiv N(P)$, adding (3.24) and (3.25) gives

$$N(P) = N_0 - \frac{(q-c)}{S}P,$$

a straight line with negative gradient with $N(0) = N_0$. Differentiating (3.25) with respect to P gives

$$\frac{\partial N}{\partial P} = \frac{q}{f'(N)h^2(P)}[h(P) - Ph'(P)] > 0.$$

In addition, it is clear from (3.25) that $N(P) \to N^*$ as $P \to 0$. Therefore from the monotonicities of these two functions, there is a unique solution of the form $(N, P, 0)$ if and only if $f(N_0) \leqslant q$, once again in agreement with inequality (3.11). For solutions with $P = \tilde{P}$, $h(\tilde{P})$ is effectively just a constant multiplying $f(N)$ and so the conditions for uniqueness and existence are unchanged. It is clear that the inclusion of the self-shading effect makes no difference to the number or type of the solutions or their regions of stability.

The addition of the new term changes some of the elements of the stability matrices as shown below:

$$\begin{aligned}\hat{N}_N &= -S - f'(N)h(P),\\ \hat{N}_P &= -f(N)h'(P) + c + \zeta g'(P)Z,\\ \hat{P}_N &= f'(N)h(P),\\ \hat{P}_P &= f(N)h'(P) - q - g'(P)Z.\end{aligned}$$

For the $(N_0, 0, 0)$ solution, the stability matrix is unchanged and therefore the stability of the solution is identical, i.e. stable for $f(N_0) < q$ only. For the $(N, P, 0)$ solution, the characteristic equation for the stability eigenvalues is

$$(\hat{Z}_Z - \lambda)[\lambda^2 - (\hat{N}_N + \hat{P}_P)\lambda + \hat{N}_N\hat{P}_P - \hat{N}_P\hat{P}_N] = 0.$$

Substituting (3.25) into $\hat{P}_P$, we find

$$\hat{P}_P = \frac{f(N)}{P}[Ph'(P) - h(P)] \leqslant 0.$$

As before, using the condition $\hat{N}_P + \hat{P}_P < 0$, we can arrange the quadratic into the form,

$$\lambda^2 - (\hat{N}_N + \hat{P}_P)\lambda + \hat{P}_P(\hat{N}_N + \hat{P}_N) - \hat{P}_N(\hat{N}_P + \hat{P}_P) = 0,$$

in which all the terms are clearly positive definite, ensuring roots with $\mathrm{Re}(\lambda) < 0$. The stability is hence governed by the value of $\hat{Z}_Z$, as before, and the stability condition for this solution is unchanged. For the $P = \tilde{P}$ solution, the analysis is also essentially unchanged. Stability is guaranteed if $\hat{P}_P < 0$, where

$$\hat{P}_P = \frac{f(N)}{P}[Ph'(P) - h(P)] + [g(P) - Pg'(P)]\frac{Z}{P}.$$

Since the first bracketed term is negative definite, the effect of self-shading is to increase the stability of the solution and help ‘damp out’ any autonomous limit cycle behaviour that might arise.

(iii) *Conservative systems*

Some models (Wroblewski *et al.* 1988; Franks *et al.* 1986) take a form which implies that the system is conservative,

$$N + P + Z = N_T, \tag{3.26}$$

where N_T a constant. In the case of our generalized system, this is equivalent to choosing $S = 0$, $1 = \zeta + \gamma$, $\rho = 1$, and $c = q$. The result of this conservative property is that the number of degrees of freedom of the system is reduced from three to two. The value of the third variable is always dictated by equation (3.26), where N_T is determined by initial conditions. The effect of this on the preceding analysis is to introduce degeneracies into the solutions and zero eigenvalues into the stability matrices. A better analysis of such a system could be achieved following the method as used in Busenberg *et al.* (1990). However, their findings for this more constrained system are consistent with those obtained in this paper concerning existence and stability. In any case, the possibility of such precise parameter values occurring in practice seems remote and, more importantly, it can be argued that a system without this conservative property is more realistic, since nutrient clearly must escape from this limited system to ‘fuel’ the rest of the food web.

4. Discussion

(*a*) *General properties*

Analysis of this system has revealed a number of general properties which will also be possessed by more specific systems which satisfy the conditions in § 2*a*. The stability analysis of § 3*c* shows that the conditions for the existence of positive-definite solutions in equations (3.11) and (3.14) also describe the surfaces in parameter space on which bifurcations occur. Although the system has multiple solutions, no more than one is ever stable for any combination of parameter values. The bifurcations on the surfaces $f(N_0) = q$ and $\tilde{P} = P^*$ are of the transcritical type, which means that as the parameter values pass through them, stability is exchanged between the solutions but the number of stable solutions is unchanged, in contrast to a pitchfork or saddle-node bifurcation in which the number of stable solutions will change. This model is therefore different from models such as Beltrami (1989), which exhibit saddle-node bifurcations, and as a consequence, changes in the number of stable equilibria.

(*b*) *Two-component models*

A common analytical technique to examine the behaviour of three-dimensional systems is to remove the explicit nutrient dependence and replace it with a logistic growth function in a two-component model (Evans & Parslow 1985; Steele & Henderson 1992). This leads to equations of the form,

$$\frac{\mathrm{d}P}{\mathrm{d}t} = rP\left(1 - \frac{P}{K}\right) - g(P)Z, \quad \frac{\mathrm{d}Z}{\mathrm{d}t} = \gamma g(P)Z - \mu Z.$$

An important question is to what extent is the two-component model a good representation of the three-component system? Can we identify parameters in the three-dimensional system with those in the reduced version?

The non-zero equilibrium solutions of the above are $(P, Z) = (P_0, Z_0)$ or $(P_0, 0)$, where

$$rP_0(1 - P_0/K) = g(P_0)Z_0, \quad \gamma g(P_0) = \mu.$$

Bifurcation analysis of the two-dimensional system shows that as P_0 increases through K, the stability of solutions changes from an unstable $(P_0, 0)$ and stable (P_0, Z_0), to a stable $(K, 0)$ with $Z_0 < 0$, which is physically inadmissible. This is analogous to the behaviour of the three-dimensional system as $\tilde{P}$ increases through P^*, with the $(\tilde{N}, \tilde{P}, \tilde{Z})$ solution exchanging stability with the $(N^*, P^*, 0)$ solution. The parameter, K, can therefore be associated with P^*,

$$K \equiv P^*.$$

The two systems also share similar behaviour for low values of P_0 (or $\tilde{P}$ respectively). For the two-dimensional system, as P_0 approaches zero,

$$\lim_{P_0 \to 0} \tilde{Z} = \frac{r}{g'(0)} = \begin{cases} \infty, & g'(0) = 0, \\ r/g'(0), & g'(0) > 0. \end{cases}$$

Again the analogy can be seen with the expressions for $\tilde{Z}$ in § 3*b*. The dependence of the solutions on the value of $g'(0)$ is the same. We can further see that, following the analogy through,

$$r \equiv f(N_0) - q.$$

The logistic function, therefore, qualitatively reflects the dynamics of the growth rate in the three-dimensional system: it is proportional to P for small population levels, and falls to zero again at some finite cut-off point, K. To what extent it quantitatively reflects the behaviour of the three-dimensional system is a matter for numerical analysis.

(*c*) *Hopf bifurcations*

Possibly the most useful results of the stability analysis is the necessary condition for Hopf Bifurcations to occur,

$$Q(\tilde{P}) = g(\tilde{P}) - \tilde{P}g'(\tilde{P}) > 0, \quad 0 < \tilde{P} < P^*. \tag{4.1}$$

This condition can be applied to previous umerical work. For example, in the paper by Franks *et al.* (1986), a numerical comparison is made between the behaviour of an ecosystem model with two different grazing terms:

$$g_1(P) = R_m(1 - \mathrm{e}^{-\lambda P}) \quad \text{and} \quad g_2(P) = R_m\lambda P(1 - \mathrm{e}^{-\lambda P}).$$

They found that using g_2, no oscillations where found, while with g_1, autonomous oscillations did arise. The system used by Franks *et al.* is of the degenerate, conservative type described in § 3*c* (iii), but the present analysis enables us to make general remarks about the class of models of which it is a member. Testing $g_2(P)$ with condition (4.1), we find

$$Q(P) = -R_m \lambda^2 P e^{\lambda P} < 0, \quad \forall P > 0.$$

It is therefore certain that this particular grazing function can never lead to oscillatory behaviour for any parameter values. However, with g_1,

$$Q(P) = R_m(1 - e^{\lambda P} - \lambda P e^{\lambda P}) > 0, \quad \forall P > 0.$$

so there is a possibility of limit cycle behaviour for all values of P. Other Hollings type II functions give similar results, e.g.

$$g(P) = P/(a+P) \quad \text{gives} \quad Q(P) = P^2/(a+P)^2 > 0.$$

Hollings type III functions exhibit slightly richer behaviour. For a typical Hollings III function, $g(P) = P^2/(\alpha^2 + P^2)$,

$$Q(P) = \frac{P^2(P^2 - \alpha^2)}{(\alpha^2 + P^2)^2}.$$

So for this function, oscillatory behaviour is only possible for values of $\tilde{P} > \alpha$. This lower cut-off behaviour can be shown to be a general property of Hollings type III functions.

(*d*) *Conclusions*

The principal contribution of this paper is the set of results contained in § 3, pertaining to a very wide class of three-component models for plankton dynamics. Essentially we are able to delineate regions of the total parameter space of the model within which certain *qualitative* patterns of behaviour are produced. The dimensionality of the parameter space depends on the detail of the model, but it seems likely that any absolute minimum model must contain parameters to describe the mixed-layer depth, the efficiency of mixing, and the radiation input.

The second important result is the establishment of a clear relationship between three-dimensional models, in which phytoplankton, zooplankton and nutrient are all accorded the status of a variable, and two-dimensional models, in which the nutrient is relegated to parametric status (usually constant conditions are assumed). This relationship makes clear the regions of validity in parameter space of our earlier excitable medium model, and, at the same time, emphasises its limitations and potential pitfalls. It implies that *excitability* will be a characteristic of a wide class of three-dimensional models over substantial regions of parameter space. Moreover the simple form of the results obtained in § 3 will permit early recognition of the possibility of blooms or tides in specific models, with clear attribution to physical effects, such as changes in radiation, mixing, nutrients, grazing, mortality, etc. We shall explore these particular possibilities elsewhere.

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