Excitability of an age-structured plankton ecosystem

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Abstract. We adapt a simple two-component model of a plankton ecosystem to account for the life spans of individual predatory organisms. We investigate the system's short-term dynamics, in particular its excitability, and its long-term dynamics, and show how both can be highly sensitive to initial conditions. We discover that this effect is enhanced by imposing age structure on the system.

Key words: Plankton blooms – Structured populations – Excitable medium – Bifurcation diagram – Overwintering populations

1. Introduction

It is well-known that plankton ecosystems can sometimes exhibit the behaviour characteristic of excitable media. The populations which comprise such ecosystems can exist at relatively stable levels; however, small changes in the environment have been observed to induce sudden population explosions. Typically, the phytoplankton population increases by a factor of 10 to 20 and stays in this range for several weeks before diminishing rapidly to its original order of magnitude.

Sudden, large excursions from an equilibrium, followed after a time lapse by a return to that (usually unique) equilibrium are characteristic of excitable systems. When in its excitable state, the system may, given a suitable small perturbation, exhibit a large and rapid response. However, in the absence of further perturbations, the system will return to its equilibrium state and remain there undisturbed (see, for example, [13]). This seems to be a very common mechanism in mathematical biology: it occurs widely in physiology, governing, for example, the

function of cardiac muscle or nerve fibres, and in cell biology, for example in dichtostelium. The form of behaviour of phytoplankton and zooplankton populations during many blooms suggests a similar mechanism, which was proposed in [21]. Interestingly, excitability turned out to be only one of a range of different forms of dynamical behaviour which manifested themselves as the model parameters were varied. Of the other dynamics which were observed, two types in particular appeared to predominate: bistability, in which the system tended to one of two coexisting stable equilibria, and periodicity, in which the system oscillated around a single unstable equilibrium. This raised the pertinent question: which, if any, of the three mathematical phenomena comes close to modelling the biological phenomenon of phytoplankton blooms?

From a mathematician's point of view, a sensible approach is to investigate the robustness of the behaviour to improvements in the model, in other words, to add extra features to the model and then to assess their effect on its dynamical properties. This strategy suggests several different approaches: for example, nutrient upwelling has been investigated by Edwards [6, 7], spatial patchiness by Matthews [10] and species diversity by Pitchford [14, 15]. By scrutinising the effect of each of these features on the qualitative behaviour of the system, these authors drew various conclusions relating to the robustness of the mechanisms present in the general model. Their inferences are summarised very briefly in Table 1.

Perhaps the most obvious omission in this body of work is the consideration of physiological heterogeneity within a population. Specifically, only a limited (and variable) proportion of the biomass of any population is available for reproduction at any one time. The models summarised in Table 1 all rest on the assumption that the birth rate of each population is independent of its composition. However, during a plankton bloom, which takes place over a relatively short time scale

Table 1. Previous extensions of the excitable model

Nutrient upwelling	Nutrient feedback loop induces stable limit cycles and chaotic attractors in a limited region of parameter space. Bistability is suppressed.
Species diversity	Interaction between populations of organisms of different sizes induces bistability. The domains of excitability and periodicity are modified.
Spatial heterogeneity	Can be promoted by different relative motion of P and Z in a shear flow. Excitability can enhance patchiness.

(comparable to the life span of the organisms present), the composition of each population may be expected to vary considerably (see, for example [3]). This may well have a significant effect on the dynamics of the population during and after the bloom: the main goal of this article is to establish precisely how physiological structure can affect the mechanisms that drive these dynamics.

One way to account for physiological heterogeneity is to introduce a delay into the system, representing the time lapse C between the birth of an organism and its onset of fertility. At a given time, the birth rate of the population is determined by its total biomass C days earlier. This method has been employed in [20]. Its main advantage lies in the large body of analytical tools and numerical techniques available for studying delay equations. On the other hand, it suffers from the disadvantage of inflexibility. While a delay system can account for physiological features which depend on the age of an individual, the connection between individual biology and population behaviour is often obscured.

In earlier work, the excitable behaviour of plankton ecosystems has been explained by assuming that the rate at which zooplankton convert biomass consumed into biomass of new organisms is very low. In [21], for example, it is assumed that 0.05 units of zooplankton are produced for every unit of phytoplankton that is consumed. This assumption does not account for the fact that reproductive capacity is an age-dependent phenomenon. A typical zooplankton organism can reproduce only after passing a certain stage in its life-cycle. After this stage, it may be expected to produce new organisms with greater efficiency than has previously been accounted for. However, such behaviour is difficult to simulate using classical type population models, which make the highly restrictive assumption that each population is a homogeneous collection of identical individuals.

It is not possible, or even desirable, to create a model which accounts for all possible variations amongst all individuals within each population. Nevertheless, a model which specifies even a small number of characteristics and identifies them as purely age-dependent will be more realistic than the unstructured model, while at the same time it will retain the capacity to pinpoint those factors which significantly affect the behaviour of the system.

2. A review of an unstructured model

The phenomenon of excitability is captured neatly by an unstructured two-component model of Truscott and Brindley [21], which simulates

the evolution of the total phytoplankton biomass P and the total zooplankton biomass Z. The model is based on the logistic phytoplankton growth rate

$$F(P) = rP\left(1 - \frac{P}{K}\right)$$ (2.1)

with maximum growth rate r and carrying capacity K, the Holling type-III functional response

$$G(P) = R_m \frac{P^2}{v^2 + P^2}$$ (2.2)

with maximum specific grazing rate R_m, and either linear or quadratic zooplankton mortality:

$$\delta_1 Z \quad \text{or} \quad \delta_2 Z^2.$$ (2.3)

The governing equations of the system take the form

$$\frac{dP}{dt} = F(P) - G(P)Z := f(P, Z),$$ (2.4a)

$$\frac{dZ}{dt} = \Gamma G(P)Z - \delta Z^m := g(P, Z),$$ (2.4b)

with the choice of m determining the linear or quadratic nature of zooplankton mortality.

Since both the mortality δ and the conversion efficiency

$$\Gamma := \frac{\text{Rate at which new biomass is produced}}{\text{Rate at which biomass is consumed}}$$ (2.5)

are significantly lower than one, the variables P and Z evolve according to different time scales, despite their mutual dependence. This implies that Z is slow to respond to any sudden change in the dynamics of P, which is one of the crucial factors in the excitability of the model.

Another crucial factor is the relative behaviour of the functional response G and the logistic growth curve F, as this determines the shape of the P-nullcline $f(P, Z) = 0$. Because the P-nullcline admits a sigmoidal shape, the sign of $f(P, Z)$ can change repeatedly as P varies whilst Z (which evolves on a slower time scale) remains within a narrow interval. In certain cases, this means that P can be forced out of the local basin of attraction of a stable steady state $(\hat{P}, \hat{Z})$. If the slower dynamics of Z eventually cause P to return to $(\hat{P}, \hat{Z})$ after occupying a different region of phase space, the system is classified as excitable. A typical example is illustrated in Fig. 1.

Any steady state $(\hat{P}, \hat{Z})$ must lie at a point of intersection of the P-nullcline and the Z-nullcline $g(P, Z) = 0$. In the linear case, the slow
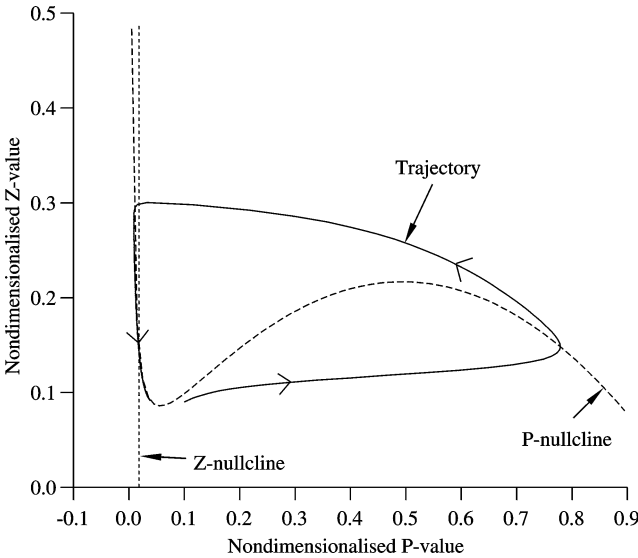
The Phase Plane

Fig. 1. The nullclines in the linear unstructured case

variation of Z suggests that its stability depends on the gradient of the P-nullcline: if it is negative at $(\hat{P}, \hat{Z})$ then the steady state is stable and conversely. This may be inferred from a close examination of Fig. 1.

More generally, the stability of $(\hat{P}, \hat{Z})$ is determined by the eigenvalues of the stability matrix

$$D := \begin{bmatrix} F'(\hat{P}) - G'(\hat{P})\hat{Z} & -G(\hat{P}) \\ \Gamma G'(\hat{P})\hat{Z} & \Gamma G(\hat{P}) - m\delta\hat{Z}^{m-1} \end{bmatrix},$$

which reduces to

$$D = \begin{bmatrix} F'(\hat{P}) - G'(\hat{P})\hat{Z} & -G(\hat{P}) \\ \Gamma G'(\hat{P})\hat{Z} & -(m-1)\Gamma G(\hat{P}) \end{bmatrix}$$

since $g(\hat{P}, \hat{Z}) = 0$. The determinant of D is given by

$$\det D = -\Gamma G(\hat{P}) \begin{vmatrix} F'(\hat{P}) - G'(\hat{P})\hat{Z} & 1 \\ G'(\hat{P})\hat{Z} & m-1 \end{vmatrix},$$

which implies that the real parts of the eigenvalues have the same sign if and only if

$$(m-1)(F'(\hat{P}) - G'(\hat{P})\hat{Z}) - G'(\hat{P})\hat{Z} \leqq 0.$$
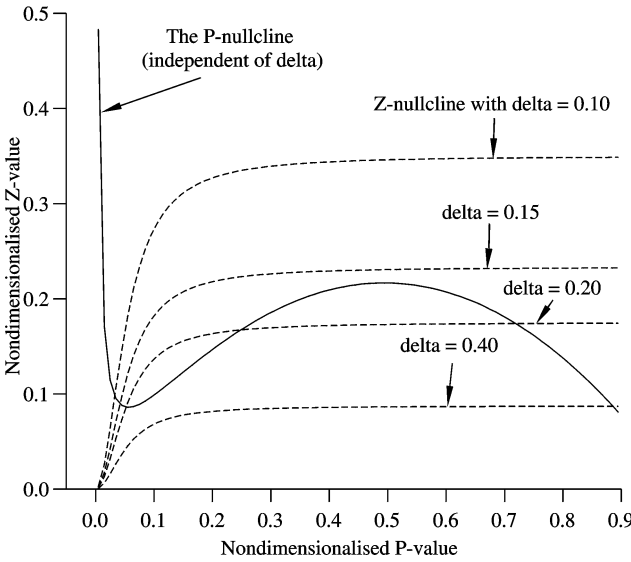
The Nullclines

Fig. 2. The nullclines in the quadratic unstructured case

In the case of linear zooplankton mortality ($m = 1$), this condition necessarily holds, and the stability of $(\hat{P}, \hat{Z})$ is determined by the sign of

$$\text{trace } D = F'(\hat{P}) - G'(\hat{P})\hat{Z}. \tag{2.6}$$

In accord with geometrical intuition, this agrees with the sign of the gradient of the *P*-nullcline.

In both the linear and quadratic cases, it is clear that the qualitative behaviour of the system is very sensitive to the position and shape of the *Z*-nullcline. Since this depends to a great extent on the ratio Γ/δ, it makes sense to analyse the system using δ as a bifurcation parameter.

2.1. Linear mortality

The case $m = 1$ is straightforward: the equilibrium equations give

$$\delta = \Gamma G(\hat{P})$$

$$\hat{Z} = \frac{F(\hat{P})}{G(\hat{P})},$$

and bifurcations occur at the two roots of the equation

$$G(\hat{P}) \frac{d}{dP} \left(\frac{F(P)}{G(P)} \right) \bigg|_{P=\hat{P}} = F'(\hat{P}) - G'(\hat{P}) \frac{F(\hat{P})}{G(\hat{P})} = F'(\hat{P}) - G'(\hat{P})\hat{Z} = 0, \quad (2.7)$$

which correspond to the turning points of the P-nullcline.

At each bifurcation point, the eigenvalues of D satisfy the equation

$$\lambda^2 + \Gamma G(\hat{P})G'(\hat{P})\hat{Z} = 0.$$

Since $(\hat{P}, \hat{Z})$ is a non-trivial equilibrium, the roots of this equation form a non-zero complex conjugate pair with zero real part. Therefore both bifurcations are Hopf bifurcations. If $\delta_1 < \delta_2$ denote the bifurcation points, then the system is excitable in the region $(0, \delta_1]$, and admits a stable periodic orbit in the region (δ_1, δ_2).

2.2. Quadratic mortality

In the case $m = 2$, one of the two eigenvalues crosses between the left and right half planes when the equation

$$F'(\hat{P}) - 2G'(\hat{P}) \frac{F(\hat{P})}{G(\hat{P})} = F'(\hat{P}) - 2G'(\hat{P})\hat{Z} = 0 \qquad (2.8)$$

is satisfied. As we shall see in Sect. 7, this coincides with the appearance of two further equilibria, which arise when the Z-nullcline first meets a portion of the P-nullcline. In addition, it is possible (though not inevitable) that, in some point of parameter space, $\det D > 0$ and trace $D = 0$, indicating the presence of a Hopf bifurcation. Clearly, this can only happen if

$$F'(\hat{P}) - 2G'(\hat{P})\hat{Z} < 0 = \text{trace } D = F'(\hat{P}) - (\delta + G'(\hat{P}))\hat{Z},$$

which imposes the draconian constraint $\delta < G'(\hat{P})$.

To summarise, the dynamics of the system are determined by the parameter

$$\alpha_1 = F'(\hat{P}) - G'(\hat{P})\hat{Z}$$

in the case of linear mortality, and by the parameters

$$\alpha_2 = F'(\hat{P}) - 2G'(\hat{P})\hat{Z},$$
$$\beta_2 = G'(\hat{P}) - (\delta + G'(\hat{P}))\hat{Z}$$

in the case of quadratic mortality.

This analysis demonstrates that we have considerable analytical control over equations (2.4). Given their lack of biological sophistication, this is only to be expected. The relevance of the model lies in the

fact that it clearly exhibits dynamics which have been observed in ocean plankton populations. This provides evidence (and no more than evidence) that the quantitative mechanism of excitability could be the underlying mechanism of spring blooms and red tides. The next step is to test the robustness of the model by modifying or discarding its simplifying assumptions.

By introducing age structure into the model, one can begin to address the assumption of homogeneity. The dynamics of any system are determined by individual interactions, and unstructured models do not allow for variation among members of a single population. An age-structured model is only a partial improvement, though: while an individual's age affects its behaviour, which in turn affects the environment, the environment cannot have any effect on the aging rate of its resident organisms! Thus, assuming that individual behaviour is solely dependent on age is still an oversimplification.

On the other hand, it is possible to gain considerable analytical control over an age-structured model, even though it is infinite-dimensional. In fact, the results that follow lead to the unexpected conclusion that the stability properties of the plankton model persist when fertility is delayed by a fixed time interval.

3. The age-structured model

One of the most obvious limitations of the model represented by equations (2.4) is the requirement of a low value of the conversion efficiency Γ in order to achieve excitability. Experiments on individual organisms suggest a value between 0.3 and 0.8, as opposed to the value of 0.05 used in [21]. However, this is not a fatal flaw, as only a small proportion of the zooplankton population is available for reproduction. Hence, if the definition (2.5) is interpreted on the *population* level (or the *p*-level), rather than the *individual* level (the *i*-level), the value 0.05 may not be unfeasibly low.

In order to resolve the ambiguity in the definition of Γ it is necessary to distinguish between the *p*-level and the *i*-level. The *p*-level parameter is defined as

$$\Gamma_p := \frac{\text{Total rate of production of new zooplankton biomass}}{\text{Total rate of consumption of phytoplankton biomass}}, \quad (3.1)$$

while the *i*-level parameter is defined, for an individual organism ω, by

$$\gamma_i(\omega) := \frac{\text{Rate at which } \omega \text{ produces new biomass}}{\text{Rate at which } \omega \text{ consumes phytoplankton biomass}}. \quad (3.2)$$

If every newborn organism has equal biomass, an equivalent definition of i-level conversion efficiency is

$$b(\omega) := \frac{\text{Rate at which } \omega \text{ produces new born individuals}}{\text{Rate at which } \omega \text{ consumes phytoplankton biomass}}. \quad (3.3)$$

This is an individual-based parameter, and since the paradigm of structured population theory involves monitoring individual inter-actions and then lifting the results to the population level, $b(\omega)$ is more of a natural choice than $\gamma_i(\omega)$. The two are related by the expression

$$\gamma_i(\omega) = b(\omega) \times \text{mass of a newborn individual.} \quad (3.4)$$

In an age-structured model, age is the only characteristic which distin-guishes between individuals, so each individual ω is identified with its age a. In particular, the i-level parameters $\gamma_i(\omega)$ and $b(\omega)$ may be realised as mathematical functions $a \mapsto \gamma_i(a)$ and $a \mapsto b(a)$ respectively.

If γ_i is not a constant function then, since the age distribution of the population may fluctuate over time, the p-level parameter Γ_p can no longer be assumed to be constant in time. In fact, when phenomena such as excitability and periodicity are being investigated, one expects to see considerable changes in the populations over a short time scale, which may profoundly affect the value of Γ_p. Were this not the case, there would be little point in imposing age structure on the original model, as its properties would persist vacuously!

Delayed zooplankton fertility is the only new feature that will be introduced into the unstructured model. Consequently, while the phytoplankton population need not be structured, it is necessary to use a time-dependent distribution ρ to monitor the age profile of the zooplankton population.

At any given time t, $\rho(\,\cdot\,, t)$ is an integrable function on the half line $(0, \infty)$ which describes the population in the sense that

● for any interval $(a_1, a_2) \subseteq (0, \infty)$,

$$\int_{a_1}^{a_2} \rho(a, t) da$$

$= $ number of members of the population whose ages lie between a_1 and a_2;

● the boundary value $\rho(0, t)$ satisfies

$$\rho(0, t) = \text{total birth rate of the population.}$$

As has already been observed, the variable Z is a measure not of number of organisms, but rather of total biomass. Therefore to

translate from ρ to Z it is necessary to integrate against a time-invariant weight function m. That is,

$$Z = \int_0^\infty m(a)\rho(a, t)\, da,$$

where $m(a)$ represents the biomass of a single organism of age a. At this point, the major shortcoming of the age-structured approach becomes clear. The weight function m is time-invariant, which means that the growth rate of every individual is independent of the environment. This is a manifestation of the one-way interaction between age profile and environment alluded to at the end of Sect. 2.

The equations of the age-structured system are now easily obtained. Assuming that an individual of age a consumes phytoplankton at a rate of $G(P)m(a)$ units per day and summing over individuals of all ages gives

$$\frac{dP}{dt} = F(P) - G(P)\int_0^\infty m(a)\rho(a, t)\, da$$

$$= F(P) - G(P)Z, \tag{3.5}$$

as in the unstructured case. For the zooplankton population, it is necessary to derive an internal continuity equation and a condition specifying the boundary value $\rho(0, t)$. The latter is derived by appealing to the definition of b and summing as before:

$$\rho(0, t) = G(P)\int_0^\infty b(a)m(a)\rho(a, t)\, da$$

$$:= G(P)Z_b. \tag{3.6}$$

For the continuity equation, a short heuristic argument suffices. As time progresses from t to $t + h$, the age-band $[a, a + da)$ evolves to $(a + h, a + h + da)$, and the number of organisms lying within this age-band decreases due to predation. The magnitude of this decrease may be obtained by viewing predation as a Poisson process with probability δZ^{m-1}:

$$\rho(a + h, t + h)\, da - \rho(a, t)\, da = -\,\delta Z^{m-1}\rho(a, t)\cdot h\, da + o(h\, da).$$

Dividing this equation by $h\, da$, and letting h and da tend to zero independently, gives

$$\frac{\partial\rho}{\partial a} + \frac{\partial\rho}{\partial t} = -\,\delta Z^{m-1}\rho. \tag{3.7}$$

The system, then, is defined explicitly by the equations

$$\frac{dP}{dt} = F(P) - G(P)Z \tag{3.8a}$$

$$\frac{\partial \rho}{\partial a} + \frac{\partial \rho}{\partial t} = - \delta Z^{m-1} \rho \tag{3.8b}$$

$$\rho(0, t) = G(P)Z_b, \tag{3.8c}$$

where Z and Z_b are integrals of the distribution $\rho(a, t)$, weighted against the functions $m(a)$ and $b(a)m(a)$ respectively. The precise form of the functions $b(a)$ and $m(a)$ is more of a biological consideration than a mathematical one, although the modeller's desire for analytical tractability motivates the choice of piecewise linear or constant functions.

Fertility is assumed to begin at a fixed age C. After this age, growth ceases and biomass remains at a constant level M, while reproduction occurs in proportion to the biomass of phytoplankton consumed. If B denotes the constant of proportionality, this gives

$$m(a) = M \quad \text{and} \quad b(a) = B \quad \text{for } a \in [C, \infty).$$

Up until the threshold age, C, there is no reproduction and growth is linear from 0 to M. Hence b and m have the forms

$$b(a) = \begin{cases} 0 & \text{for } a \in (0, C); \\ B & \text{for } a \in [C, \infty) \end{cases} \tag{3.9}$$

and

$$m(a) = \begin{cases} Ma/C & \text{for } a \in (0, C); \\ M & \text{for } a \in [C, \infty) \end{cases} \tag{3.10}$$

respectively. In particular, in the limiting case $C = 0$, b and m reduce to constant functions on $(0, \infty)$ and the model itself reduces to the unstructured model (2.4) with $\Gamma = BM$.

The formulation of an age-structured population model in terms of a partial differential equation dates back to Lieutenant-Colonel A. G. McKendrick. In his 1926 paper [11], McKendrick turned his attention to a single population and considered the linear case, in which the birth and mortality terms were both linear functions of the state variable: the instantaneous distribution of the population. Later on, Gurtin and MacCamy [8] worked on the semilinear case, in which the birth rate was still linear but the mortality rate was dependent on the dynamic states of the populations involved. This generalisation provided the scope for age-structured models to represent systems of competing or

cooperating populations. If the total magnitude of one population affected the survival rate of another, the Gurtin/MacCamy model could be used to analyse the situation.

Biologically, it is a simple and natural step to move from the idea of population interactions affecting death rates to that of population interactions affecting birth rates. Mathematically, this is still possible even when the birth function is linear. However, the range of interactions that can be described using linear birth rates is limited, and falls well short of covering the current example. Unfortunately, as the birth function appears in the boundary condition of the PDE formulation (equation (3.8c) in this case), nonlinear birth rates introduce technical problems that are not present in the semilinear case. These problems are of a mathematical nature. While they hinder the rigorous verification of stability criteria, they do not stand in the way of the formal analysis that will be the subject of this paper. The primary goal will be to derive expressions for the stability matrices in the linear and quadratic cases, and to test the resulting bifurcation diagrams using a numerical integration scheme. It should be emphasised that the analysis, while formally correct, is by no means rigorous. We avoid potentially hazardous questions about the space of functions we are working in (a finite number of individuals of identical ages, for example, cannot be represented as an L^1-function), and concentrate instead on the local behaviour of the terms that define the system, such as the birth function

$$(P, \rho) \mapsto G(P)\int bm\rho$$

and the mortality function

$$\rho \mapsto \delta \hat{Z}^{m-1}\rho.$$

The question of mathematical rigour is one that will be addressed in a later paper: recent developments in the theory of nonlinear age-dependent population dynamics (see [4]) have laid a framework within which the difficulties associated with the boundary condition (3.8c) may be circumvented. The ultimate aim is to obtain a general mathematical theory which fails only when its concrete interpretation ceases to make biological sense. This paper constitutes a preliminary first step in this direction. If, under certain conditions, the formal approach to stability analysis fails, this may be detected numerically, helping to lead to an appreciation of the most critical mathematical and biological issues.

Each bifurcation diagram will admit two free parameters and two classes of curves. One class of curves will specify the positions of the equilibria, while the other will mark the stability boundaries of the

system. The former will be derived in the next section; the latter in the following sections.

4. Location of equilibria

At equilibrium, the distribution $\rho(\cdot, t)$ and the variables P, Z and Z_b are given by the time-independent quantities

$$\rho(\cdot, t) = \hat{\phi}$$

$$P = \hat{P},$$

$$Z = \hat{Z}$$

and

$$Z_b = \hat{Z}_b.$$

Since $\hat{\phi}$ is time-independent, the differential operator $\partial/\partial a + \partial/\partial t$ reduces to the age derivative and equation (3.8b) becomes an ordinary differential equation. Thus the state of the system at equilibrium is given by the equations

$$F(\hat{P}) - G(\hat{P})\hat{Z} = 0 \tag{4.1a}$$

$$\frac{d\hat{\phi}}{da} = -\delta \hat{Z}^{m-1}\hat{\phi} \tag{4.1b}$$

$$\hat{\phi}(0) = G(\hat{P})\hat{Z}_b. \tag{4.1c}$$

From the differential equation (4.1b) and the boundary condition (4.1c), the form of $\hat{\phi}$ is given by

$$\hat{\phi}(a) = \hat{\phi}(0) \exp(-\delta \hat{Z}^{m-1} a)$$

$$= G(\hat{P})\hat{Z}_b \exp(-\delta \hat{Z}^{m-1} a), \tag{4.2}$$

which means that the values of $\hat{P}, \hat{Z}$ and $\hat{Z}_b$ are enough to specify the state of the system at equilibrium.

Integrating both sides of equation (4.2) against the weight $m(a)$ gives

$$\hat{Z} = G(\hat{P})\hat{Z}_b \int_0^\infty m(a) \exp(-\delta \hat{Z}^{m-1} a) \, da$$

$$= \frac{MG(\hat{P})\hat{Z}_b}{\delta \hat{Z}^{m-1}} E^{(0)}(\delta \hat{Z}^{m-1} C) \cdot \frac{1 - \exp[-\delta \hat{Z}^{m-1} C]}{\delta \hat{Z}^{m-1} C}.$$

Rearranging this expression yields the equation

$$\delta\hat{Z}^m = MG(\hat{P})\hat{Z}_b \frac{1 - \exp[-\delta\hat{Z}^{m-1}C]}{\delta\hat{Z}^{m-1}C}, \tag{4.3}$$

which determines $\hat{Z}_b$ uniquely in terms of $\hat{P}$ and $\hat{Z}$.

On the other hand, integrating both sides of equation (4.2) against the weight $b(a)m(a)$ gives

$$\hat{Z}_b = G(\hat{P})\hat{Z}_b \int_0^\infty b(a)m(a)\exp(-\delta\hat{Z}^{m-1}a)\,da,$$

which reduces to

$$1 = BG(\hat{P}) \int_C^\infty M \exp(-\delta\hat{Z}^{m-1}a)\,da$$

$$= \frac{BG(\hat{P})}{\delta\hat{Z}^{m-1}} M \exp(-\delta\hat{Z}^{m-1}C),$$

and may be rearranged to give the equation

$$\delta\hat{Z}^{m-1} = M\,BG(\hat{P})\exp(-\delta\hat{Z}^{m-1}C). \tag{4.4}$$

Together with equation (4.1a), equation (4.4) gives finitely many values of the pair $(\hat{P}, \hat{Z})$, each of which determines a unique equilibrium state.

5. Formal stability analysis

An equilibrium $(\hat{P}, \hat{\phi})$ is stable if there is a neighbourhood in phase space within which every set of initial conditions (P_0, ϕ_0) leads to dynamics converging to $(\hat{P}, \hat{\phi})$. The notion of convergence can, of course, only make sense once the phase space has been defined and equipped with a suitable norm. In the context of age-structured population biology, a common choice is the Banach space

$$B = \mathbb{R} \times L^1(0, \infty),$$

endowed with the norm

$$\|(P, \phi)\|_B = |P| + \int_0^\infty |\phi(x)|\,dx.$$

Within this setting, it is possible to define the *solution operators*. For any $t > 0$, the solution operator $S(t): B \to B$ is defined by

$$S(t)(P_0, \phi_0) = \frac{\text{solution of equations (3.8) with initial conditions}}{P(0) = P_0, \ \rho(\cdot, 0) = \phi_0, \text{ evaluated at time } t,}$$

with $\mathscr{D}(S(t)) = B_+$, the positive cone in B defined by

$$B_+ := \{(P, \phi) \in B : P \geqq 0 \text{ and } \phi \geqq 0 \text{ a.e.}\}$$

By checking regularity conditions, it is a straightforward exercise to demonstrate that the family of operators $S(t), t \geqq 0$, forms a C_0-*semigroup* on B_+. This means that

1. for every $t > 0$, $S(t)$ is a continuous map from B_+ into B_+;
2. $S(0)$ acts as the identity on B_+;
3. for any $\Phi \in B_+$ and any $t_1, t_2 \geqq 0$, $S(t_1 + t_2)\Phi = S(t_1)S(t_2)\Phi$;
4. for each fixed $\Phi \in B_+$, the mapping $t \mapsto S(t)\Phi$ is continuous from $[0, \infty)$ into B_+.

The *generator* T of the semigroup $\{S(t)\}_{t \geqq 0}$, is an operator on B, defined as

$$T : \Phi \mapsto \lim_{h \to 0} \frac{S(h)\Phi - \Phi}{h},$$

whose domain consists of all those elements of B_+ for which this limit exists.

The significance of the generator is that it can be used to recast the system as an abstract ODE, in which context formal linear stability analysis can proceed naturally. Given an initial value $\Phi_0 = (P_0, \phi_0)$ lying in the domain of T, the dynamics of the subsequent state $\Phi = (P, \phi)$ are given simply by the equation

$$\frac{d}{dt} \Phi = T \cdot \Phi. \tag{5.1}$$

In this formulation, the stability of an equilibrium is usually addressed in terms of the Fréchet derivative of T at that equilibrium. By definition, T is Fréchet differentiable at $\hat{\Phi} := (\hat{P}, \hat{\phi})$ if there is a linear functional $T' : B \to B$ such that

$$T(\hat{\Phi} + K) = T(\hat{\Phi}) + T'(\hat{\Phi})K + O(\|K\|_B^2)$$

for every $K \in \mathscr{D}(T) - \hat{\Phi}$ lying in some neighbourhood of zero. Clearly, the Fréchet differentiability of T is dependent not only on its action close to $\hat{\Phi}$, but also on the regularity of its domain. The linear operator $T'(\hat{\Phi})$ will have its own domain: a linear space embedded inside $\mathscr{D}(T) - \hat{\Phi}$. This highlights the potential problems associated with the Fréchet derivative: there is no guarantee that $\mathscr{D}(T)$ is a linear space. Hence there is no guarantee that the domain of $T'(\hat{\Phi})$ is non-trivial, regardless of the smoothness of the action of T close to $\hat{\Phi}$.

Motivated by these observations, we relax the definition of $T'(\hat{\Phi})$: instead of requiring that its domain be embedded inside $\mathscr{D}(T) - \hat{\Phi}$, we stipulate only that its domain approach $\mathscr{D}(T) - \hat{\Phi}$ asymptotically at zero. That is, $T'(\hat{\Phi})$ is defined as the unique linear operator satisfying

$$T(\hat{\Phi} + K) = T(\hat{\Phi}) + T'(\hat{\Phi})(K + O_1(\|K\|_B^2)) + O_2(\|K\|_B^2)$$

for every $K \in \mathscr{D}(T) - \hat{\Phi}$ lying in some neighbourhood of zero. The functions O_1 and O_2 are continuous and vanish at the origin, and the equation carries the implicit requirement that $K + O_1(\|K\|_B^2)$ lies in the domain of $T'(\hat{\Phi})$.

Given this weaker definition of $T'(\hat{\Phi})$, the linearisation of equation (5.1) is given by

$$\frac{d}{dt} K = T'(\hat{\Phi})K, \tag{5.2}$$

which is the starting point in our linear stability analysis.

Without further analysis, it cannot be proved that the location of the spectrum of $T'(\hat{\Phi})$ establishes an exponential dichotomy on the linearised system. Hence it cannot be assumed that the stability of $\hat{\Phi}$ depends on the spectrum of $T'(\hat{\Phi})$. Nevertheless, since this section constitutes a formal procedure rather than watertight mathematical theory, we shall make just this assumption and go on to calculate $T'(\hat{\Phi})$ and search for its spectrum.

To follow this procedure, we must first find the infinitesimal generator T. Noting that the solution operator $S(t)$ may be split up into two components:

- $S_1(t)$, the phytoplankton component and
- $S_2(t)$, the zooplankton component.

we see that, given a point $\Phi = (P, \phi) \in \mathscr{D}(T)$, the first component $T_1(\Phi)$ of $T(\Phi)$ is given by

$$T_1(\Phi) = \lim_{h \to 0} \frac{S_1(h)P - P}{h} = \lim_{h \to 0} \frac{P(t + h) - P(t)}{h} = \frac{dP}{dt} = F(P) - G(P)Z,$$

and the second component T_2 is given by evaluating $T_2(\Phi)$ at a point a:

$$T_2(\Phi)(a) = \lim_{h \to 0} \frac{S_2(h)\phi(a) - \phi(a)}{h}$$

$$= \lim_{h \to 0} \frac{S_2(h)\phi(a) - S_2(h)\phi(a + h) + S_2(h)\phi(a + h) - \phi(a)}{h}$$

$$= -\lim_{h \to 0} \frac{S_2(h)\phi(a+h) - S_2(h)\phi(a)}{h} + \lim_{h \to 0} \frac{S_2(h)\phi(a+h) - \phi(a)}{h}$$

$$= -\phi'(a) + \left(\frac{\partial \phi}{\partial a} + \frac{\partial \phi}{\partial t}\right)(a)$$

$$= -\phi'(a) - \delta Z^{m-1}\phi(a).$$

It remains to determine the domain of T. For $T_2(\Phi)$ to exist and lie in $L^1(0, \infty)$, it is necessary that ϕ be absolutely continuous and ϕ' be integrable over $(0, \infty)$. Further, since continuous functions which converge in L^1 must also converge pointwise, and since each $S_2(h)\phi$ satisfies the boundary condition

$$S_2(h)\phi(0) = G(P(t+h))Z_b(t+h),$$

it is also necessary for ϕ to satisfy the boundary condition

$$\phi(0) = G(P)Z_b. \tag{5.3}$$

Conversely, given any $\Phi = (P, \phi) \in B_+$ which satisfies the conditions

$$\phi \in \mathrm{AC}[0, \infty), \quad \phi' \in L^1(0, \infty), \qquad \phi(0) = G(P)Z_b,$$

the limit

$$\lim_{h \to 0} \frac{S_2(h)\phi - \phi}{h}$$

exists in L^1, and so $\Phi \in \mathscr{D}(T)$.

It is necessary to find $T'(\hat{\Phi})$ now that the operator

$$\mathscr{D}(T) = \{(P, \phi) \in B_+ : \phi \in \mathrm{AC}[0, \infty), \phi' \in L^1(0, \infty),$$

$$\phi(0) = G(P)Z_b\} \tag{5.4a}$$

$$T : (P, \phi) \mapsto (F(P) - G(P)Z, -\phi' - \delta Z^{m-1}\phi), \tag{5.4b}$$

has been identified. To do this, let $(P, \phi) = (\hat{P} + p, \hat{\phi} + \psi)$ be a point in a neighbourhood of $(\hat{P}, \hat{\phi})$, so that $Z = \hat{Z} + z$ and $Z_b = \hat{Z}_b + z_b$, where

$$z = \int_0^\infty m(a)\psi(a)da \quad \text{and} \quad z_b = \int_0^\infty b(a)m(a)\psi(a)da.$$

Then, for every point (p, ψ) inside the domain of $T'(\hat{\Phi})$,

$$T'(\hat{\Phi})(p, \psi) = (F'(\hat{P})p - G'(\hat{P})\hat{Z}p - G(\hat{P})z,$$

$$-\psi' - \delta\hat{Z}^{m-1}\psi - (m-1)\delta\hat{Z}^{m-2}z\hat{\phi}).$$

To find the domain of $T'(\hat{\Phi})$, notice that, for any $K = (p, \psi) \in \mathscr{D}(T'(\hat{\Phi}))$,

$$T'(\hat{\Phi})K = \lim_{h \to 0} \frac{T(\hat{\Phi} + hK + O(h^2)) - T(\hat{\Phi})}{h},$$

so ψ must be absolutely continuous and ψ' must be integrable; moreover, $\hat{\Phi} + hK + O(h^2)$ must lie in $\mathscr{D}(T)$ for all $h > 0$. But this implies that

$$G(\hat{P})\hat{Z}_b + h\psi(0) + O(h^2)(0) = (\hat{\phi} + h\psi + O(h^2))(0)$$
$$= G(\hat{P} + hp + O(h^2))(\hat{Z}_b + hz_b + O(h^2))$$
$$= G(\hat{P})\hat{Z}_b + (G'(\hat{P})\hat{Z}_b p + G(\hat{P})z_b)h + O(h^2).$$

Subtracting $G(\hat{P})\hat{Z}_b$ from both sides, dividing by h and taking the limit as h tends to zero gives the boundary condition

$$\psi(0) = G'(\hat{P})\hat{Z}_b p + G(\hat{P})z_b.$$

Conversely, if $K = (p, \psi) \in B$ satisfies the conditions

$$\psi \in \mathrm{AC}[0, \infty), \quad \psi' \in L^1(0, \infty), \qquad \psi(0) = G'(\hat{P})\hat{Z}_b p + G(\hat{P})z_b,$$

then there is a function $O : \mathbb{R} \to B$, which is continuous and vanishes at the origin, such that the limit

$$\lim_{h \to 0} \frac{T(\hat{\Phi} + hK + O(h^2)) - T(\hat{\Phi})}{h},$$

exists. Hence K lies in the domain of $T'(\hat{\Phi})$.

Consequently, the linearised operator $T'(\hat{\Phi})$ is given by

$$\mathscr{D}(T'(\hat{\Phi})) = \{(p, \psi) \in B : \psi \in \mathrm{AC}[0, \infty), \quad \psi' \in L^1(0, \infty),$$
$$\psi(0) = G'(\hat{P})\hat{Z}_b p + G(\hat{P})z_b\}, \tag{5.5a}$$
$$T'(\hat{\Phi})(p, \psi) = (F'(\hat{P})p - G'(\hat{P})\hat{Z}p - G(\hat{P})z,$$
$$- \psi' - \delta\hat{Z}^{m-1}\psi - (m-1)\delta\hat{Z}^{m-2}z\hat{\phi}). \tag{5.5b}$$

The location of its spectrum, which consists entirely of its eigenvalues, involves laborious but straightforward computation. This is carried out in Appendix A.

6. Linear zooplankton mortality

In the case of linear zooplankton mortality ($m = 1$), equation (A.6) shows that the spectrum coincides precisely with the set of zeroes of the

determinant

$$\Delta_1(\lambda) := \begin{vmatrix} F'(\hat{P}) - G'(\hat{P})\hat{Z} - \lambda & -G(\hat{P}) & 0 \\ MG'(\hat{P})\hat{Z}_b \dfrac{1 - e^{-(\lambda+\delta)C}}{(\lambda+\delta)C} & -\delta - \lambda & MG(\hat{P})\dfrac{1 - e^{-(\lambda+\delta)C}}{(\lambda+\delta)C} \\ MBe^{-(\lambda+\delta)C}G'(\hat{P})\hat{Z}_b & 0 & \delta(e^{-\lambda C} - 1) - \lambda \end{vmatrix}.$$

Note that, in the limiting case $C = 0$, organisms are effectively born with mass M, so $\Gamma_p = BM$, and the equilibrium equations give $\hat{Z}_b = B\hat{Z}$ and $MBG(\hat{P}) = \delta$. Consequently, the determinant $\Delta_1(\lambda)$ reduces to

$$\Delta_1^{(0)}(\lambda) := \begin{vmatrix} F'(\hat{P}) - G'(\hat{P})\hat{Z} - \lambda & -G(\hat{P}) & 0 \\ MG'(\hat{P})\hat{Z}_b & -\delta - \lambda & MG(\hat{P}) \\ MBG'(\hat{P})\hat{Z}_b & 0 & -\lambda \end{vmatrix}$$

$$= \begin{vmatrix} F'(\hat{P}) - G'(\hat{P})\hat{Z} - \lambda & -G(\hat{P}) & 0 \\ MBG'(\hat{P})\hat{Z} & -\delta - \lambda & MG(\hat{P}) \\ 0 & B(\delta + \lambda) & -\delta - \lambda \end{vmatrix}$$

$$= \begin{vmatrix} F'(\hat{P}) - G'(\hat{P})\hat{Z} - \lambda & -G(\hat{P}) & 0 \\ \Gamma_p G'(\hat{P})\hat{Z} & -\lambda & MG(\hat{P}) \\ 0 & 0 & -\delta - \lambda \end{vmatrix}$$

$$= -(\delta + \lambda) \begin{vmatrix} F'(\hat{P}) - G'(\hat{P})\hat{Z} - \lambda & -G(\hat{P}) \\ \Gamma_p G'(\hat{P})\hat{Z} & -\lambda \end{vmatrix},$$

whose zeroes agree, modulo the root $\lambda = -\delta$, with those of the stability matrix associated with the unstructured model. Since the extra root $-\delta$ necessarily lies in the left half-plane $\mathbb{C}_0^-$, it can have no effect on the stability of the system and may safely be ignored. Hence the stability matrix $\Delta_1(\lambda)$ behaves as should be expected when the delay between birth and onset of fertility is excluded from the model.

In the general case, the equilibrium $\hat{\Phi}$ is locally asymptotically stable when all of the zeroes of $\Delta_1(\lambda)$ lie in the left half-plane $\mathbb{C}_0^-$, and unstable when $\Delta_1(\lambda)$ admits any zeroes in the right half-plane $\mathbb{C}_0^+$. Furthermore, by virtue of the equations

$$F(\hat{P}) = G(\hat{P})\hat{Z} \tag{6.1a}$$

$$\delta e^{\delta C} = MBG(\hat{P}), \tag{6.1b}$$

the equilibrium $(\hat{P}, \hat{Z})$ exists uniquely and is continuously dependent on the parameters that specify the system. Consequently the matrix $\Delta_1(\lambda)$ varies continuously with each of the parameters, and the stability boundaries of the system coincide with purely imaginary roots $\lambda = i\omega$ of Δ_1.

This fact can be exploited to calculate the stability boundaries: by taking the real and imaginary parts of the equation

$$\Delta_1(i\omega) = 0 \tag{6.2}$$

and solving them simultaneously for two free parameters, one obtains a single point on a boundary. Other points are then obtained by varying the initial choice of ω, and the boundary is thus established constructively.

There is one initial choice of ω for which this procedure breaks down, however: when $\omega = 0$, the stability matrix evaluates to

$$\Delta_1(0) = \begin{vmatrix} F'(\hat{P}) - G'(\hat{P})\hat{Z} & -G(\hat{P}) & 0 \\ MG'(\hat{P})\hat{Z}_b \dfrac{1 - e^{-\delta C}}{\delta C} & -\delta & MG(\hat{P})\dfrac{1 - e^{-\delta C}}{\delta C} \\ MBe^{-\delta C}G'(\hat{P})\hat{Z}_b & 0 & 0 \end{vmatrix}$$

$$= -M^2 Be^{-\delta C}(1 - e^{-\delta C})G'(\hat{P})G(\hat{P})^2\hat{Z}_b$$

$$< 0,$$

which clearly has no roots. In other words, the stability of the system can only change when a non-zero complex conjugate pair of eigenvalues crosses the imaginary axis: every possible bifurcation of the system is a Hopf bifurcation!

In the unstructured case $C = 0$, the full range of dynamics of the system is obtained by varying the mortality parameter δ. As was illustrated in Sect. 2, the critical value δ_c of δ occurs precisely when the parameter

$$\alpha := F'(\hat{P}) - G'(\hat{P})\hat{Z} \tag{6.3}$$

vanishes. Stable limit cycles appear when α is positive, in contrast to the stable steady state that dominates the system when α is negative. This phenomenon has a biological interpretation, as noted by De Roos et al. [3]. As P increases in a neighbourhood of its equilibrium value $\hat{P}$, both $F(P)$ and $G(P)$ increase in response. If the rate if increase of reproduction $F'(P)$ exceeds the rate of increase of predation $G'(\hat{P})\hat{Z}$, then the phytoplankton can escape zooplankton control close to $(\hat{P}, \hat{Z})$. The name coined for this process is the *prey escape mechanism*; it is the only destabilising mechanism in the unstructured system. Thus, if $F'(\hat{P})$ is smaller in magnitude than $G'(\hat{P})\hat{Z}$, the steady state $(\hat{P}, \hat{Z})$ must be stable, as the prey escape mechanism can no longer take hold.

In order to understand which other mechanisms take effect when zooplankton fertility is delayed, it is worth investigating the unstructured model in greater depth. Following Truscott and Brindley [21],

the values of P and Z are non-dimensionalised by setting

$$\tilde{P} = \frac{P}{K}, \qquad \tilde{Z} = \frac{Z}{K},$$

which is equivalent to setting $K = 1$. Adopting the fixed parameters

$$K = 1, \tag{6.4a}$$

$$v = 0.053, \tag{6.4b}$$

$$R_m = 0.7 \text{ day}^{-1}, \tag{6.4c}$$

$$r = 0.6 \text{ day}^{-1}, \tag{6.4d}$$

$$\Gamma = BM = 0.05, \tag{6.4e}$$

(see equations (2.1), (2.2) and (2.4)), it is a straightforward matter to find the critical value δ_c. Since $\hat{Z}$ is given uniquely in terms of $\hat{P}$ by the relation

$$F(\hat{P}) - G(\hat{P})\hat{Z} = 0,$$

δ_c is found by solving the equation

$$F'(\hat{P}) - G'(\hat{P})\frac{F(\hat{P})}{G(\hat{P})} = 0$$

for $\hat{P}$ and substituting the resulting value into the expression

$$\Gamma G(\hat{P}) = \delta.$$

This leads to a value (correct to six decimal places) of

$$\delta_c = 0.018543. \tag{6.5}$$

By the Hopf Bifurcation Theorem, the direction of the bifurcation at δ_c is determined by the quadratic component δ_2 of the function

$$\varepsilon \mapsto \delta^*(\varepsilon),$$

which admits the following properties:

(P1) δ^* is even;
(P2) $\delta^*(0) = \delta_c$;
(P3) when $\delta = \delta^*(\varepsilon)$, there is a periodic solution $[P_\varepsilon, Z_\varepsilon]$ of the system satisfying

$$\begin{bmatrix} P_\varepsilon \\ Z_\varepsilon \end{bmatrix} = \varepsilon\Re\left(e^{i\omega_o t}\begin{bmatrix} p_c \\ z_c \end{bmatrix}\right) + o(\varepsilon), \tag{6.6}$$

where $[p_c, z_c]^T$ is an eigenvector of the matrix

$$D_1 := \begin{bmatrix} 0 & -G(\hat{P}) \\ \Gamma G'(\hat{P})\hat{Z} & 0 \end{bmatrix} \tag{6.7}$$

corresponding to the purely imaginary eigenvalue $i\omega_0$.

The formula for δ_2, and the results of the MAPLE code the authors used to calculate it, are given in Appendix B. Since its computed value is positive, it follows that the local direction of the Hopf bifurcation δ_c is supercritical. That is, stable periodic solutions of the system bifurcate away from δ_c in the same direction as the branch of unstable equilibria that starts at δ_c.

However, the fact that the local direction of δ_c is supercritical is no guarantee that the branch of bifurcating solutions will not change direction somewhere to the right of δ_c and then return to the subcritical region to the left of δ_c. Such behaviour could give rise to the coexistence of stable equilibria and stable periodic orbits in the subcritical region. To investigate this possibility, the numerical path-following package AUTO was used. As illustrated in Fig. 8, it confirmed the most believable hypothesis: that no such change of direction takes place.

An immediate consequence of this analysis is that, regardless of initial conditions, the value of δ determines the long-term behaviour of the system uniquely. Below δ_c, the system approaches its steady state $(\hat{P}, \hat{Z})$. Depending on the starting conditions, it may or may not begin with an excursion characteristic of excitable media; however, the convergence to $(\hat{P}, \hat{Z})$ is inevitable. Above δ_c, the system approaches a stable periodic orbit. Once again, no starting conditions can be chosen in order to avoid this behaviour. The prey escape mechanism cannot be overridden.

This is illustrated numerically from two separate standpoints. First of all, the critical value δ_c is located graphically by plotting the curves

$$\Gamma G(\hat{P}) = \delta$$

and

$$0 = |\Delta_1^{(0)}(i\omega)|$$

on the same set of axes, as illustrated in Fig. 3. This is, of course, not strictly necessary, as the value of δ_c is already known. However, it is done for the sake of completeness, since it is the only technique available for locating δ_c in the unstructured case.

The other line of investigation is numerical integration of the system. This is done using the *Escalator Boxcar Train* (or EBT) package [2], which was developed precisely for the purpose of integrating general systems of physiologically structured populations. The independence of the system's long-term dynamics from its initial conditions is illustrated well using this tool. Figure 4 shows results obtained with various initial conditions when δ takes the value 0.018540 (marginally less than δ_c), and Fig. 5 shows results obtained when δ takes the value 0.018546 (marginally greater).
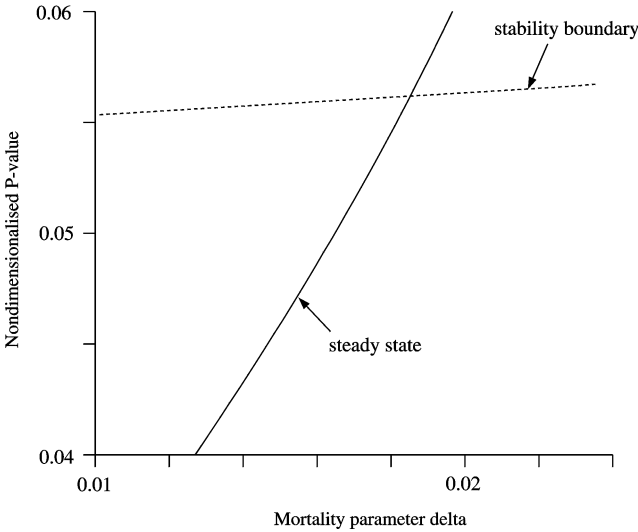
Stability Switch

Fig. 3. The stability boundary in the linear unstructured case

By contrast, the structured case exhibits richer dynamics. Setting the threshold age C to the reasonable value of 20 days offers scope to increase the value of BM from 0.05 to 0.25. Hence, in the structured case, the fixed parameters are given by

$$K = 1, \tag{6.8a}$$

$$v = 0.053, \tag{6.8b}$$

$$R_m = 0.7 \text{ day}^{-1}, \tag{6.8c}$$

$$r = 0.6 \text{ day}^{-1}, \tag{6.8d}$$

$$B = 0.25, \tag{6.8e}$$

$$M = 1.0, \tag{6.8f}$$

$$C = 20 \text{ days}. \tag{6.8g}$$

In order to obtain the curves

$$MBG(\hat{P}) = \delta e^{\delta C}$$

and

$$0 = |\Delta(i\omega)|,$$

a predictor-corrector method (using a tangent predictor and a Newton-like corrector) was employed. A close view of the point of intersection of the resulting curves (see Fig. 6) reveals that the critical value δ_c lies between 0.0382 and 0.0384.

Whereas the long-term behaviour of the unstructured system was independent of its initial state, the structured system allows a stable limit cycle to coexist with a stable steady state for values of δ just below
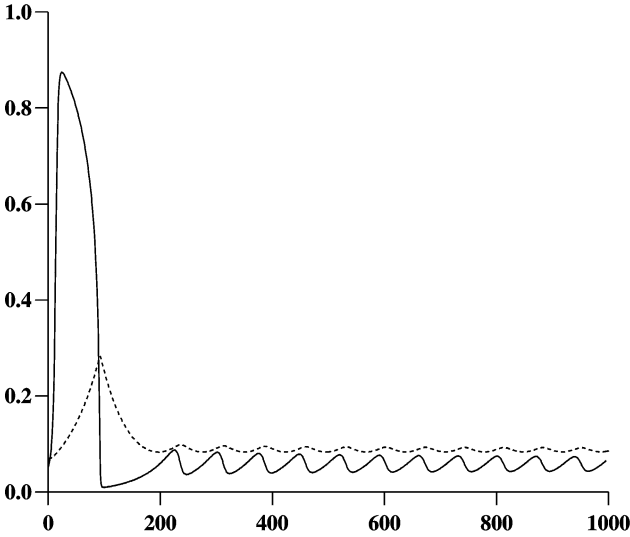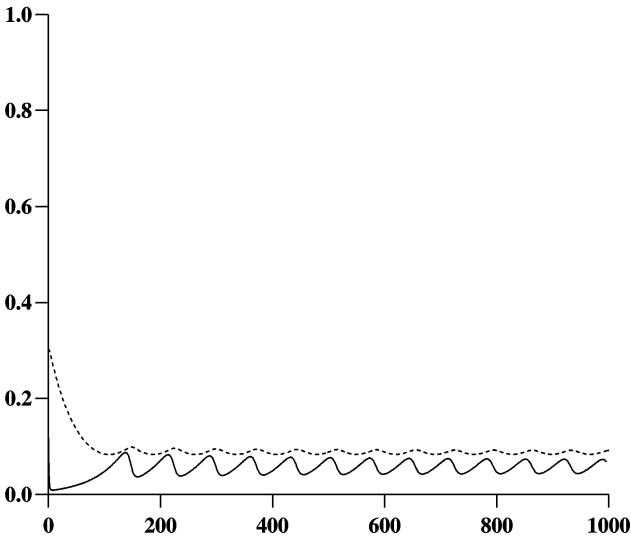
Fig. 4. Dynamics of the linear unstructured system with $\delta = 0.018540$ Solid lines represent phytoplankton biomass, broken lines represent zooplankton biomass.

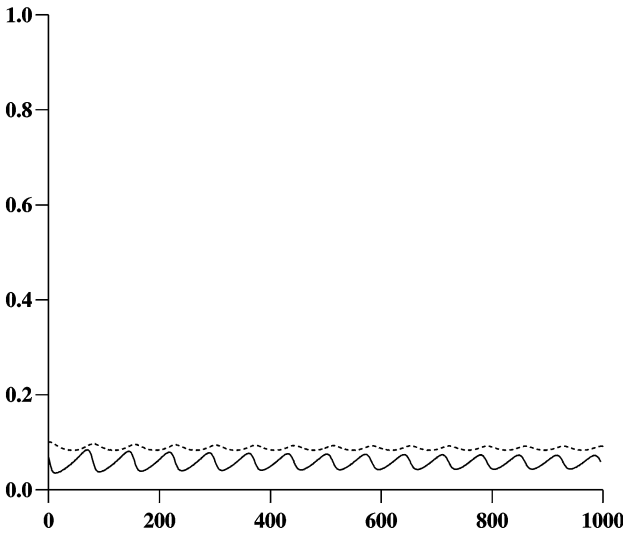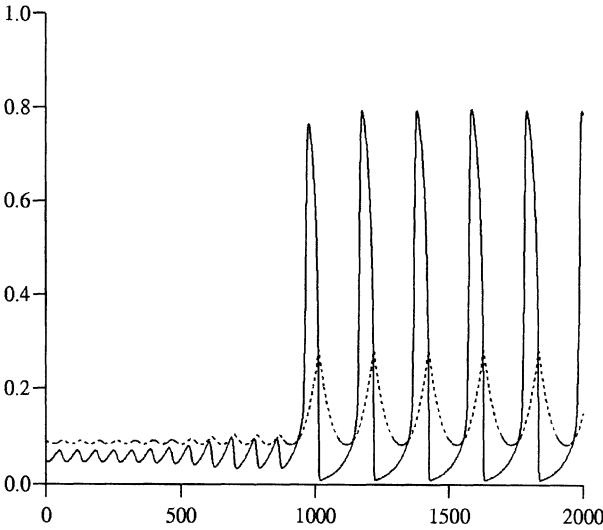## P(0) = 0.07, Z(0) = 0.07
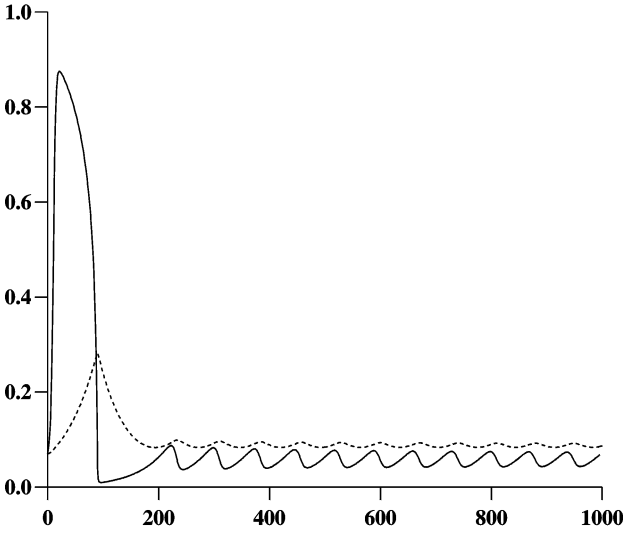
P(0) = 0.07, Z(0) = 0.1

Fig. 4. (continued)

δ_c. This can be seen by observing Fig. 7, which shows the results of two EBT simulations with $\delta = 0.0382$. In each case, the initial zooplankton population was concentrated into a single cohort of 30-day old

individuals; hence Z_0, the initial value of Z, represented the total biomass within this cohort.

Although the only difference between the systems lies in their initial conditions, they display notably different dynamics. The most likely

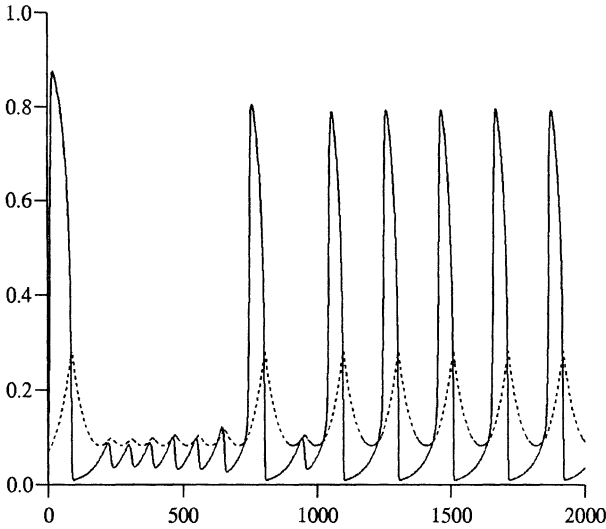## $P(0) = 0.05, \ Z(0) = 0.09$

$P(0) = 0.1, \ Z(0) = 0.09$
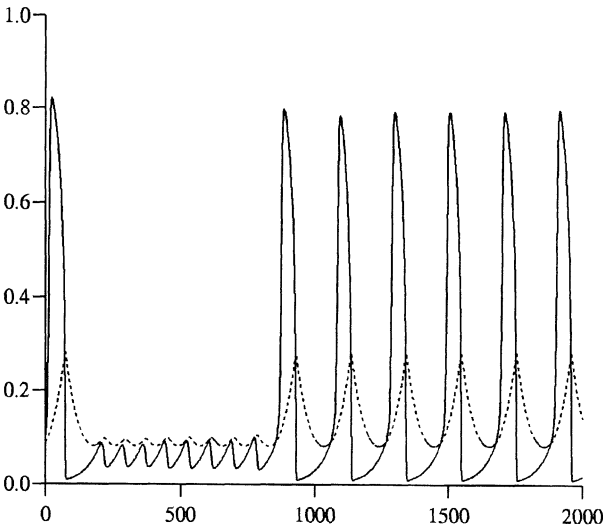
Fig. 5. Dynamics of the linear unstructured system with $\delta = 0.018546$

$P(0) = 0.09, \ Z(0) = 0.07$
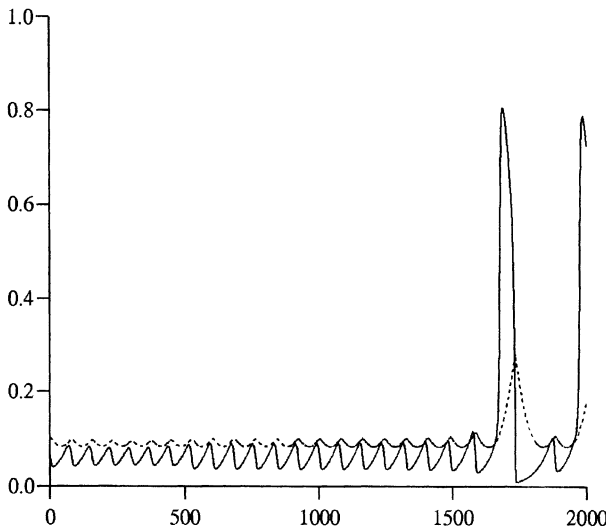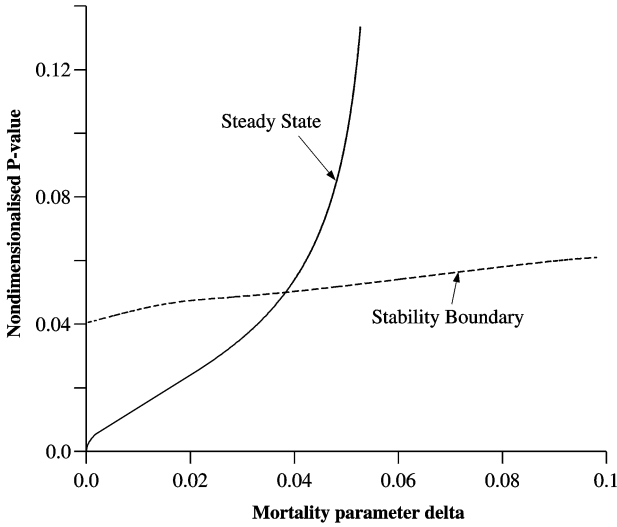

$P(0) = 0.07, \ Z(0) = 0.1$

Fig. 5. (continued)

explanation for this behaviour is a change in the direction of the bifurcation δ_c, induced by the delay in zooplankton fertility. There are, in fact, techniques available for calculating the local direction of δ_c; however, it is not necessary to employ them in this case. The crucial

Stability Switch
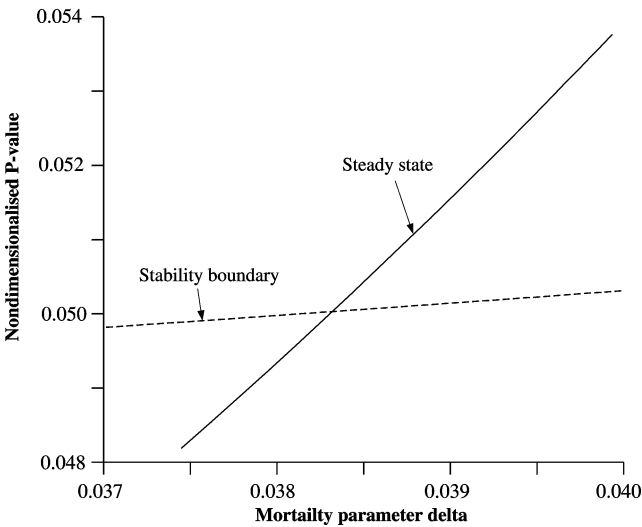

Stability Switch

Fig. 6. The stability boundary in the linear structured case

issue is the coexistence of stable limit cycles with a stable equilibrium in the subcritical region, in contrast to the unique dynamics characteristic of the unstructured system. The consequent dependence of the dynamics on initial conditions is in accord with the experience of field
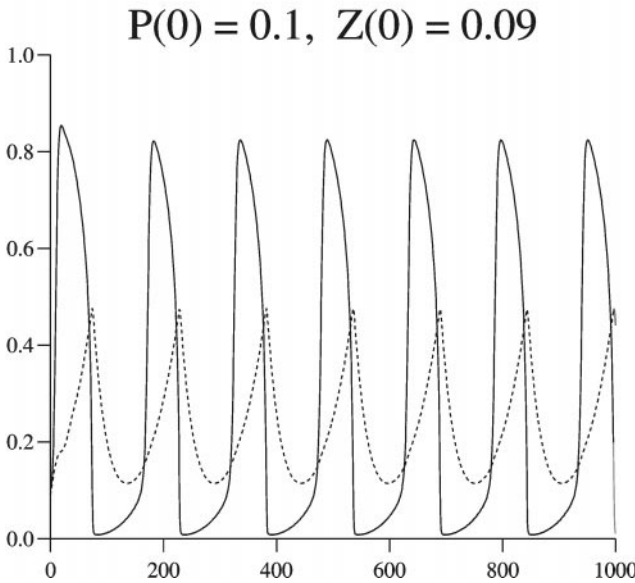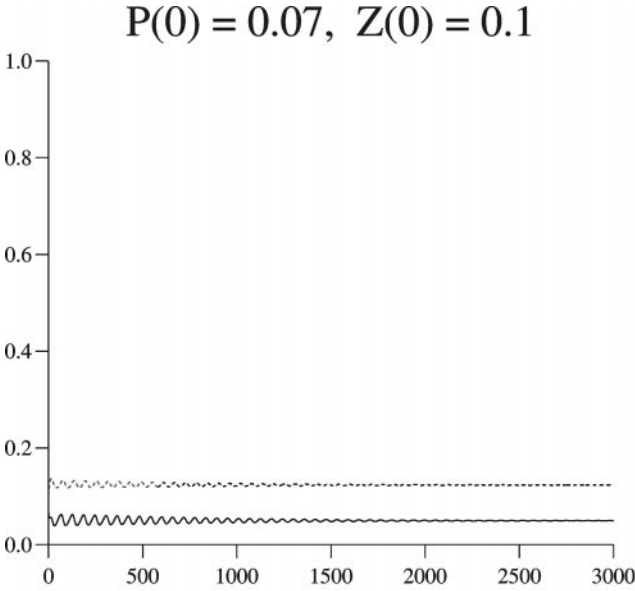
P(0) = 0.07, Z(0) = 0.1

P(0) = 0.1, Z(0) = 0.09

Fig. 7. Dynamics of the linear structured system with $\delta = 0.0382$

biologists, who stress the importance of the "overwintering popula-
tions" of phytoplankton and zooplankton in determining the average
plankton concentrations (and, by implication, the fish stocks) during
the coming year.
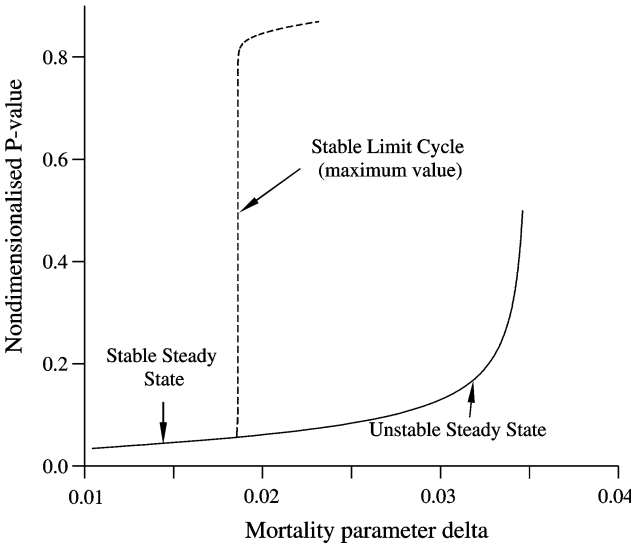
The Direction of the Bifurcation

Fig. 8. The supercritical Hopf bifurcation in the linear unstructured case

7.   Quadratic zooplankton mortality

To a great extent, the analysis of the previous section relied upon the uniqueness of the equilibrium $(\hat{P}, \hat{Z})$ once the set of parameters had been specified. In the case of quadratic zooplankton mortality, this uniqueness is foregone. It is easiest to see this in the unstructured case, where equilibria occur at the points of intersection of the nullclines

$$F(P) - G(P)Z = 0 \tag{7.1a}$$

$$\Gamma G(P) - \delta Z = 0. \tag{7.1b}$$

As the parameter δ is varied, the Z-nullcline (7.1b) is dilated vertically about the P-axis while the sigmoidal P-nullcline (7.1a) remains invariant. Under relatively mild conditions on the fixed parameters, this implies that there will be two critical values of δ between which the system admits three equilibria, and outside which it admits only one. This is easily seen on consulting Fig. 2.

     Given the algebraic representation of the P-nullcline (7.1a), it is plain to see that each value of $\hat{P}$ corresponds to at most one

equilibrium $(\hat{P}, \hat{Z})$. In other words, each equilibrium $(\hat{P}, \hat{Z})$ is characterised uniquely by the value of $\hat{P}$, and the response of the system to the variable parameter δ is best illustrated by varying $\hat{P}$ and plotting it against the value of δ given by equations (7.1).

On the same set of axes, the stability boundary may be constructed, as in the linear case, by calculating the roots of the equation

$$\Delta_2(i\omega) = 0 \qquad (7.2)$$

for a range of values of ω in the positive real line. The resulting curves will define an interval of instability on the $\hat{P}$-axis, which may be compared qualitatively in the structured and unstructured cases.

From Appendix A, the characteristic equation $\Delta_2(\lambda)$ is given by

$$0 = \Delta_2(\lambda) := \begin{vmatrix} q_{11} & q_{12} & q_{13} \\ q_{21} & q_{22} & q_{23} \\ q_{31} & q_{32} & q_{33} \end{vmatrix}$$

with

$$q_{11} = F'(\hat{P}) - G'(\hat{P})\hat{Z} - \lambda$$

$$q_{12} = -G(\hat{P})$$

$$q_{13} = 0$$

$$q_{21} = G'(\hat{P})\hat{Z}_b M \left\{ \frac{1 - \mathrm{e}^{-(\lambda + \delta\hat{Z})C}}{(\lambda + \delta\hat{Z})C} \right\}$$

$$q_{22} = \frac{\delta G(\hat{P})\hat{Z}_b M}{\lambda} \left(\left\{ \frac{1 - \mathrm{e}^{-(\lambda + \delta\hat{Z})C}}{(\lambda + \delta\hat{Z})C} \right\} - \frac{\lambda + \delta\hat{Z}}{\delta\hat{Z}} \left\{ \frac{1 - \mathrm{e}^{-\delta\hat{Z}C}}{\delta\hat{Z}C} \right\} \right) - \delta\hat{Z} - \lambda$$

$$q_{23} = G(\hat{P})M \left\{ \frac{1 - \mathrm{e}^{-(\lambda + \delta\hat{Z})C}}{(\lambda + \delta\hat{Z})C} \right\}$$

$$q_{31} = G'(\hat{P})\hat{Z}_b M B \mathrm{e}^{-(\lambda + \delta\hat{Z})C}$$

$$q_{32} = \frac{\delta G(\hat{P})\hat{Z}_b M B}{\lambda} \mathrm{e}^{-\delta\hat{Z}C} \left(\mathrm{e}^{-\lambda C} - \frac{\lambda + \delta\hat{Z}}{\delta\hat{Z}} \right)$$

$$q_{33} = \delta\hat{Z}(\mathrm{e}^{-\lambda C} - 1) - \lambda.$$

The unstructured case $C = 0$ is of particular interest. In this case, as before, $M\hat{Z}_b = MB\hat{Z} = \Gamma_p\hat{Z}$ and, in view of the equilibrium condition

$\delta\hat{Z} = \Gamma_p G(\hat{P})$, the determinant $\Delta_2(\lambda)$ reduces to

$$\Delta_2^{(0)}(\lambda) = \begin{vmatrix} F'(\hat{P}) - G'(\hat{P})\hat{Z} - \lambda & -G(\hat{P}) & 0 \\ MG'(\hat{P})\hat{Z}_b & -2\delta\hat{Z} - \lambda & MG(\hat{P}) \\ M(\hat{P})B\hat{Z}_b & -\delta B\hat{Z} & -\lambda \end{vmatrix}$$

$$= \begin{vmatrix} F'(\hat{P}) - G'(\hat{P})\hat{Z} - \lambda & -G(\hat{P}) & 0 \\ \Gamma_p G'(\hat{P})\hat{Z} & -2\delta\hat{Z} - \lambda & MG(\hat{P}) \\ 0 & \delta B\hat{Z} + B\lambda & -\delta\hat{Z} - \lambda \end{vmatrix}$$

$$= \begin{vmatrix} F'(\hat{P}) - G'(\hat{P})\hat{Z} - \lambda & -G(\hat{P}) & 0 \\ \Gamma_p G'(\hat{P})\hat{Z} & \delta\hat{Z} - \lambda & MG(\hat{P}) \\ 0 & 0 & -\delta\hat{Z} - \lambda \end{vmatrix}$$

$$= -(\delta\hat{Z} + \lambda) \begin{vmatrix} F'(\hat{P}) - G'(\hat{P})\hat{Z} - \lambda & -G(\hat{P}) \\ \Gamma_p G'(\hat{P})\hat{Z} & \delta\hat{Z} - \lambda \end{vmatrix}.$$

Its zeroes are, as expected, identical to those of the unstructured model provided the superfluous (and, from the point of view of linear stability analysis, irrelevant) root $\lambda = -\delta\hat{Z}$ is disregarded.

One special property of this degenerate case is that the stability switch, which occurs when a zero of $\Delta_2^{(0)}(\lambda)$ crosses the imaginary axis, coincides exactly with the appearance of two extra equilibria. In other words, the interval of instability begins and ends at the turning points of the equilibrium curve (at which the slope of the curve is vertical).

To see this, observe that the turning points of the equilibrium curve occur when δ, determined as a function of $\hat{P}$, passes through a stationary value. From equations (7.1), the function which determines δ is given by

$$\delta = \Gamma G(\hat{P})^2 / F(\hat{P}),$$

and its stationary points occur at the zeroes of the derivative

$$\frac{d\delta}{d\hat{P}} = -\Gamma \left(\frac{G(\hat{P})}{F(\hat{P})}\right)^2 \left[F'(\hat{P}) - 2G'(\hat{P})\frac{F(\hat{P})}{G(\hat{P})}\right],$$

which comprise the bifurcation points, as defined by equation (2.8).

The coincidence of the stability switch and the appearance of extra equilibria does not survive the introduction of delayed fertility. Nevertheless, in most practical cases the deviation from this behaviour is almost imperceptible. With the parameters given by

$$K = 1, \tag{7.3a}$$

$$v = 0.053, \tag{7.3b}$$

$$R_m = 0.7 \text{ day}^{-1}, \tag{7.3c}$$

$$r = 0.6 \text{ day}^{-1}, \tag{7.3d}$$

$$B = 0.25, \tag{7.3e}$$

$$M = 1.0, \tag{7.3f}$$

$$C = 20 \text{ days}, \tag{7.3g}$$

Fig. 9 shows that the system is very slightly destabilised: the interval of instability extends beyond the turning points of the equilibrium curve. However, the magnitude of this destabilisation is negligibly small.

Although the change in the value of C did not appear to affect the global stability properties of the quadratic system, it should be emphasised that the simultaneous presence of two stable equilibria automatically implies dependence on initial conditions. Interestingly, the region of coexistence of stable equilibria spans a narrower interval of δ-values in the structured case than in the unstructured case. This does not imply that delayed fertility reduces dependence on initial conditions, as the shape of the equilibrium curve

$$\delta \hat{Z} e^{\delta \hat{Z} C} = MBG(\hat{P}) \tag{7.4}$$

is altered not only by changes in C, but also by corresponding changes in B. Increasing the value of C narrows the region of coexistence; increasing the value of B stretches it.
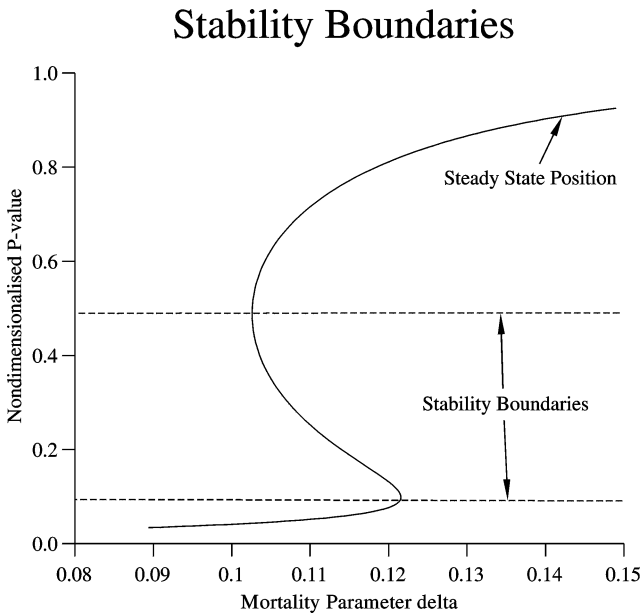

Fig. 9. The phase plane in the quadratic structured case

8. Summary

The research contained in this paper has demonstrated that the central concept of *excitability*, focused on explicitly in the earlier papers by Truscott and Brindley [21, 22], but implicit in many earlier models for plankton populations [17, 18], readily survives the important extension from uniform to age-structured zooplankton populations. Establishment of the existence and especially the stability of static or dynamic equilibria in the multi-dimensional age-structured model is a non-trivial mathematical problem, and we have adopted a constructive procedure rather than attempting a fully rigorous proof of our results. Our investigations have been based on a simple model for the evolution of Z in which each individual grows linearly to a certain size M (at age C), after which it reproduces at a steady rate until its death, which is determined at the population level by a Poisson process.

The principal conclusions may be summarised as

- The qualitative phenomenon of excitability survives as C varies from zero upwards.
- The stringent conditions on the net conversion rate required for excitability are relaxed (since a large fraction of this population is not reproductive).
- Regions of parameter space exist for which stable limit cycles occur, as well as those in which a single stable equilibrium dominates.
- When the Z-mortaility is assumed to be linear, there is a region of parameter space in the age-structured model for which stable steady states coexist with stable limit cycles. Thus, depending on initial conditions, two quite different final states may be reached. This phenomenon is absent in the earlier unstructured model, in which the long-term dynamics of the system were independent of its initial state.
- When the Z-mortality is assumed to be quadratic, there are regions of parameter space in both the structured and unstructured models for which two stable steady states coexist. This automatically implies dependence of the long-term dynamics on initial conditions, as observed in the linear age-structured model.

The final results emphasise the sensitivity of the behaviour shown by the model to initial conditions. Not only is the occurrence of an initial bloom, but, in some cases, also the long-term state of the population, dependent on small differences in initial state. It is significant that the (often very small) size of the overwintering populations has long been known by marine biologists to be of crucial importance in determining productivity in the following season, which can vary by

an order of magnitude from year to year in apparently very similar physical conditions.

Appendix A: Location of the spectrum

For convenience of notation, let T' denote the linear operator $T'(\hat{\Phi})$. Its spectrum consists of all values of λ for which the operator

$$\lambda I - T' = \lambda I - T'(\hat{\Phi})$$

fails to have an inverse.

Given elements

$$K = \begin{bmatrix} p^K \\ \psi^K \end{bmatrix} \quad \text{and} \quad M = \begin{bmatrix} p^M \\ \psi^M \end{bmatrix}$$

of B, necessary and sufficient conditions for the relationship

$$(\lambda I - T')K = M \tag{A.1}$$

to hold are given by those determined by the action of $\lambda I - T'$,

$$\lambda p^K - (\alpha_1 p^K - \alpha_2 z^K) = p^M \tag{A.2a}$$

$$\lambda \psi^K(a) + \psi^{K'}(a) + \alpha_3 \psi^K(a) + \alpha_4 z^K \hat{\phi}(a) = \psi^M(a), \tag{A.2b}$$

together with those determined by its domain:

$$\psi^K(0) = \beta_1 p^K + \beta_2 z_b^K \tag{A.2c}$$

$$\psi^K \in AC[0, \infty) \quad \text{and} \quad \psi^{K'} \in L^1(0, \infty). \tag{A.2d}$$

The coefficients α_i and β_j, $1 \leq i \leq 4$, $1 \leq j \leq 2$, are given in terms of the equilibrium $\hat{\Phi}$ by

$$\alpha_1 = F'(\hat{P}) - G'(\hat{P})\hat{Z}$$

$$\alpha_2 = G(\hat{P})$$

$$\alpha_3 = \delta \hat{Z}^{m-1}$$

$$\alpha_4 = (m-1)\delta \hat{Z}^{m-2}$$

$$\beta_1 = G'(\hat{P})\hat{Z}_b,$$

$$\beta_2 = G(\hat{P}).$$

Equations (A.2b) and (A.2c) comprise an inhomogeneous linear first order ODE with a linear boundary condition. They may be solved analytically to yield an expression for ψ^K which is linear in p^K, z^K, z_b^K and ψ^M. By integrating this expression against the weights $m(a)$ and $m(a)b(a)$ respectively, expressions for z^K and z_b^K may be derived. From these, it will be possible to obtain the spectrum of T' as the set roots of a determinant.

Multiplying both sides of equation (A.2b) by the integrating factor $\exp[(\lambda + \alpha_3)a]$ gives

$$\frac{d}{da}\left\{\exp[(\lambda + \alpha_3)a]\psi^K(a)\right\} = -\alpha_4 \exp[(\lambda + \alpha_3)a]\hat{\phi}(a)z^K + \psi^M(a),$$

which may be integrated from 0 to a. In view of the boundary condition (A.2c), this yields

$$\psi^K(a) = \beta_1 p^K \exp[-(\lambda + \alpha_3)a] + \beta_2 z_b^K \exp[-(\lambda + \alpha_3)a]$$

$$- \alpha_4 z^K \exp[-(\lambda + \alpha_3)a] \int_0^a \exp[(\lambda + \alpha_3)\zeta]\hat{\phi}(\zeta)\,d\zeta$$

$$+ \int_0^a \exp[-(\lambda + \alpha_3)(a - \zeta)]\psi^M(\zeta)\,d\zeta.$$

However, since $\hat{\phi}(\zeta) = \beta_3 \exp[-\alpha_3\zeta]$, where $\beta_3 = G(\hat{P})\hat{Z}_b$, this in turn reduces to

$$\psi^K(a) = \beta_1 p^K \exp[-(\lambda + \alpha_3)a] + \beta_2 z_b^K \exp[-(\lambda + \alpha_3)a]$$

$$- \frac{\alpha_4\beta_3 z^K}{\lambda}\exp[-\alpha_3 a] + \frac{\alpha_4\beta_3 z^K}{\lambda}\exp[-(\lambda + \alpha_3)a]$$

$$+ \int_0^a \exp[-(\lambda + \alpha_3)(a - \zeta)]\psi^M(\zeta)\,d\zeta. \tag{A.3}$$

This is an equivalent representation of the conditions (A.2), which are, in turn, equivalent to equation (A.1).

Integrating equation (A.3) against the weight $m(a)$ gives

$$z^K = \beta_1 p^K \int_0^\infty m(a)\exp[-(\lambda + \alpha_3)a]da$$

$$+ \beta_2 z_b^K \int_0^\infty m(a)\exp[-(\lambda + \alpha_3)a]\,da$$

$$- \frac{\alpha_4 \beta_3 z^K}{\lambda} \int_0^\infty m(a) \exp[-\alpha_3 a]$$

$$+ \frac{\alpha_4 \beta_3 z^K}{\lambda} \int_0^\infty m(a) \exp[-(\lambda + \alpha_3)a]$$

$$+ \int_0^\infty m(a) \int_0^a \exp[-(\lambda + \alpha_3)(a - \zeta)] \psi^M(\zeta) \, d\zeta \, da$$

$$= \beta_1 p^K \frac{M}{\lambda + \alpha_3} \left\{ \frac{1 - \exp[-(\lambda + \alpha_3)C]}{(\lambda + \alpha_3)C} \right\}$$

$$+ \beta_2 z_b^K \frac{M}{\lambda + \alpha_3} \left\{ \frac{1 - \exp[-(\lambda + \alpha_3)C]}{(\lambda + \alpha_3)C} \right\}$$

$$- \frac{\alpha_4 \beta_3 z^K}{\lambda} \frac{M}{\alpha_3} \left\{ \frac{1 - \exp[-\alpha_3 C]}{\alpha_3 C} \right\}$$

$$+ \frac{\alpha_4 \beta_3 z^K}{\lambda} \frac{M}{\lambda + \alpha_3} \left\{ \frac{1 - \exp[-(\lambda + \alpha_3)C]}{(\lambda + \alpha_3)C} \right\}$$

$$+ \int_0^\infty m(a) \int_0^a \exp[-(\lambda + \alpha_3)(a - \zeta)] \psi^M(\zeta) \, d\zeta \, da,$$

and integrating it against $b(a)m(a)$ gives

$$z_b^K = \beta_1 p^K \int_0^\infty b(a)m(a) \exp[-(\lambda + \alpha_3)a] \, da$$

$$+ \beta_2 z_b^K \int_0^\infty b(a)m(a) \exp[-(\lambda + \alpha_3)a] \, da$$

$$- \frac{\alpha_4 \beta_3 z^K}{\lambda} \int_0^\infty b(a)m(a) \exp[-\alpha_3 a]$$

$$+ \frac{\alpha_4 \beta_3 z^K}{\lambda} \int_0^\infty b(a)m(a) \exp[-(\lambda + \alpha_3)a]$$

$$+ \int_0^\infty b(a)m(a) \int_0^a \exp[-(\lambda + \alpha_3)(a - \zeta)] \psi^M(\zeta) \, d\zeta \, da$$

$$= \beta_1 p^K \frac{MB}{\lambda + \alpha_3} \exp[-(\lambda + \alpha_3)C]$$

$$+ \beta_2 z_b^K \frac{MB}{\lambda + \alpha_3} \exp[-(\lambda + \alpha_3)C]$$

$$-\frac{\alpha_4\beta_3 z^K}{\lambda}\frac{MB}{\alpha_3}\exp[-\alpha_3 C]$$

$$+\frac{\alpha_4\beta_3 z^K}{\lambda}\frac{MB}{\lambda+\alpha_3}\exp[-(\lambda+\alpha_3)C]$$

$$+\int_0^\infty b(a)\,m(a)\int_0^a \exp[-(\lambda+\alpha_3)(a-\zeta)]\psi^M(\zeta)\,d\zeta\,da.$$

These two expressions may be rearranged to give

$$(\lambda+\alpha_3)z^K = \beta_1 M\left\{\frac{1-\exp[-(\lambda+\alpha_3)C]}{(\lambda+\alpha_3)C}\right\}p^K$$

$$+\frac{\alpha_4\beta_3 M}{\lambda}\left(\left\{\frac{1-\exp[-(\lambda+\alpha_3)C]}{(\lambda+\alpha_3)C}\right\}\right.$$

$$\left.-\frac{\lambda+\alpha_3}{\alpha_3}\left\{\frac{1-\exp[-\alpha_3 C]}{\alpha_3 C}\right\}\right)z^K$$

$$+\beta_2 M\left\{\frac{1-\exp[-(\lambda+\alpha_3)C]}{(\lambda+\alpha_3)C}\right\}z_b^K$$

$$+(\lambda+\alpha_3)\int_0^\infty m(a)\int_0^a \exp[-(\lambda+\alpha_3)(a-\zeta)]\psi^M(\zeta)\,d\zeta\,da,$$

$$\text{(A.4)}$$

and

$$(\lambda+\alpha_3)z_b^K = \beta_1 MB\exp[-(\lambda+\alpha_3)C]p^K$$

$$+\frac{\alpha_4\beta_3 MB}{\lambda}\exp[-\alpha_3 C]\left(\exp[-\lambda C]-\frac{\lambda+\alpha_3}{\alpha_3}\right)z^K$$

$$+\beta_2 MB\exp[-(\lambda+\alpha_3)C]z_b^K$$

$$+(\lambda+\alpha_3)\int_0^\infty b(a)m(a)\int_0^a \exp[-(\lambda+\alpha_3)(a-\zeta)]\psi^M(\zeta)\,d\zeta\,da,$$

$$\text{(A.5)}$$

respectively.

Taking stock, equations (A.2a), (A.4) and (A.5) may be expressed as a linear system

$$\begin{bmatrix} q_{11} & q_{12} & q_{13} \\ q_{21} & q_{22} & q_{23} \\ q_{31} & q_{32} & q_{33} \end{bmatrix}\begin{bmatrix} p^K \\ z^K \\ z_b^K \end{bmatrix} = \begin{bmatrix} p^M \\ \tilde{z}^M \\ \tilde{z}_b^M \end{bmatrix},$$

where the entries of the characteristic matric $Q := [q_{ij}]_{3 \times 3}$ are given by

$$q_{11} = \alpha_1 - \lambda$$

$$q_{12} = -\alpha_2$$

$$q_{13} = 0$$

$$q_{21} = \beta_1 M \left\{ \frac{1 - \exp[-(\lambda + \alpha_3)C]}{(\lambda + \alpha_3)C} \right\}$$

$$q_{22} = \frac{\alpha_4 \beta_3 M}{\lambda} \left(\left\{ \frac{1 - \exp[-(\lambda + \alpha_3)C]}{(\lambda + \alpha_3)C} \right\} \right.$$

$$\left. - \frac{\lambda + \alpha_3}{\alpha_3} \left\{ \frac{1 - \exp[-\alpha_3 C]}{\alpha_3 C} \right\} \right) - \alpha_3 - \lambda$$

$$q_{23} = \beta_2 M \left\{ \frac{1 - \exp[-(\lambda + \alpha_3)C]}{(\lambda + \alpha_3)C} \right\}$$

$$q_{31} = \beta_1 M B \exp[-(\lambda + \alpha_3)C]$$

$$q_{32} = \frac{\alpha_4 \beta_3 M B}{\lambda} \exp[-\alpha_3 C] \left(\exp[-\lambda C] - \frac{\lambda + \alpha_3}{\alpha_3} \right)$$

$$q_{33} = \beta_2 M B \exp[-(\lambda + \alpha_3)C] - \alpha_3 - \lambda$$

and the entries $\tilde{z}^M$ and $\tilde{z}_b^M$ of the right-hand vector are given by

$$(\lambda + \alpha_3) \int_0^\infty m(a) \int_0^a \exp[-(\lambda + \alpha_3)(a - \zeta)] \psi^M(\zeta) \, d\zeta \, da$$

and

$$(\lambda + \alpha_3) \int_0^\infty b(a)m(a) \int_0^a \exp[-(\lambda + \alpha_3)(a - \zeta)] \psi^M(\zeta) \, d\zeta \, da$$

respectively.

If Q is singular then, given a nonzero element $[p, z, z_b]^T$ of its nullspace, the nonzero distribution

$$\psi(a) = \beta_1 p \exp[-(\lambda + \alpha_3)a] + \beta_2 z_b \exp[-(\lambda + \alpha_3)a]$$

$$- \frac{\alpha_4 \beta_3 z}{\lambda} \exp[-\alpha_3 a] + \frac{\alpha_4 \beta_3 z}{\lambda} \exp[-(\lambda + \alpha_3)a]$$

satisfies equations (A.2) with $M = 0$. Hence the nullspace of $\lambda I - T'$ is nonzero and λ lies in the spectrum of T'.

Conversely, if Q is invertible, then, for any nonzero $M \in B$, the vector $[p^K, z^K, z_b^K]^T$, given by

$$\begin{bmatrix} p^K \\ z^K \\ z_b^K \end{bmatrix} = Q^{-1} \begin{bmatrix} p^M \\ z^M \\ \tilde{z}_b^M \end{bmatrix},$$

defines a distribution

$$\psi^K(a) = \beta_1 p^K \exp[-(\lambda + \alpha_3)a] + \beta_2 z_b^K \exp[-(\lambda + \alpha_3)a]$$

$$- \frac{\alpha_4 \beta_3 z^K}{\lambda} \exp[-\alpha_3 a] + \frac{\alpha_4 \beta_3 z^K}{\lambda} \exp[-(\lambda + \alpha_3)a]$$

$$+ \int_0^a \exp[-(\lambda + \alpha_3)(a - \zeta)]\psi^M(\zeta)\,d\zeta,$$

lying in the domain of T', for which

$$(\lambda I - T')K := (\lambda I - T') \begin{bmatrix} p^K \\ \psi^K \end{bmatrix} = \begin{bmatrix} p^M \\ \psi^M \end{bmatrix} = M.$$

That is, $\lambda I - T'$ is invertible and λ lies outside the spectrum of T'.

This demonstrates that the spectrum of T' consists solely of its eigenvalues, which are precisely the roots of the determinant $\Delta(\lambda) := \det(Q)$.

In the case of linear zooplankton mortality, the characteristic matrix Q simplifies considerably, as the coefficient α_4 vanishes. The characteristic equation acquires the form

$$0 = \Delta_1(\lambda) := \begin{vmatrix} F'(\hat{P}) - G'(\hat{P})\hat{Z} - \lambda & -G(\hat{P}) & 0 \\ MG'(\hat{P})\hat{Z}_b \dfrac{1-\mathrm{e}^{-(\lambda+\delta)C}}{(\lambda + \delta)C} & -\delta - \lambda & MG(\hat{P}) \dfrac{1-\mathrm{e}^{-(\lambda+\delta)C}}{(\lambda + \delta)C} \\ MB\mathrm{e}^{-(\lambda+\delta)C}G'(\hat{P})\hat{Z}_b & 0 & \delta(\mathrm{e}^{-\lambda C} - 1) - \lambda \end{vmatrix}$$

$$\text{(A.6)}$$

by virtue of the identity $\delta \mathrm{e}^{\delta C} = MBG(\hat{P})$.

In the case of quadratic zooplankton mortality, the entries of the characteristic matrix Q take the form

$$q_{11} = F'(\hat{P}) - G'(\hat{P})\hat{Z} - \lambda$$

$$q_{12} = -G(\hat{P})$$

$$q_{13} = 0$$

$$q_{21} = G'(\hat{P})\hat{Z}_b M \left\{ \frac{1 - e^{-(\lambda + \delta\hat{Z})C}}{(\lambda + \delta\hat{Z})C} \right\}$$

$$q_{22} = \frac{\delta G(\hat{P})\hat{Z}_b M}{\lambda} \left(\left\{ \frac{1 - e^{-(\lambda + \delta\hat{Z})C}}{(\lambda + \delta\hat{Z})C} \right\} - \frac{\lambda + \delta\hat{Z}}{\delta\hat{Z}} \left\{ \frac{1 - e^{-\delta\hat{Z}C}}{\delta\hat{Z}C} \right\} \right) - \delta\hat{Z} - \lambda$$

$$q_{23} = G(\hat{P}) M \left\{ \frac{1 - e^{-(\lambda + \delta\hat{Z})C}}{(\lambda + \delta\hat{Z})C} \right\}$$

$$q_{31} = G'(\hat{P})\hat{Z}_b M B e^{-(\lambda + \delta\hat{Z})C}$$

$$q_{32} = \frac{\delta G(\hat{P})\hat{Z}_b M B}{\lambda} e^{-\delta\hat{Z}C} \left(e^{-\lambda C} - \frac{\lambda + \delta\hat{Z}}{\delta\hat{Z}} \right)$$

$$q_{33} = \delta\hat{Z}(e^{-\lambda C} - 1) - \lambda,$$

and the characteristic equation is then given by

$$0 = \Delta_2(\lambda) := \det[q_{ij}]. \tag{A.7}$$

Given these characteristic equations, it is now possible to create bifurcation diagrams using standard continuation algorithms.

Appendix B: The direction of the bifurcation

The formula for δ_2, the quadratic compenent of the even function δ^*, is given in terms of an eigenvector $[p_c, z_c]^T$ of the matrix

$$D_1 := \begin{bmatrix} F'(\hat{P}) - G'(\hat{P})\hat{Z} & -G(\hat{P}) \\ \Gamma G'(\hat{P}) & 0 \end{bmatrix} = \begin{bmatrix} 0 & -G(\hat{P}) \\ \Gamma G'(\hat{P}) & 0 \end{bmatrix}, \tag{B.1}$$

corresponding to the eigenvalue $i\omega_0$ ($\omega_0 > 0$), and an eigenvector $[p_c^*, z_c^*]$ of the transposed matrix D_1^T. Provided the relation

$$\begin{bmatrix} p_c \\ z_c \end{bmatrix} \cdot \begin{bmatrix} p_c^* \\ z_c^* \end{bmatrix} := p_c p_c^* + z_c z_c^* = 1 \tag{B.2}$$

is satisfied, there is no restriction on the choices of $[p_c, z_c]^T$ and $[p_c^*, z_c^*]^T$.

Notice that D_1 is a representation of the first derivative $\mathbf{f}^{(1)}(\hat{P}, \hat{Z})$ of the function

$$\mathbf{f}: \begin{bmatrix} P \\ Z \end{bmatrix} \mapsto \begin{bmatrix} F(P) - G(P)Z \\ \Gamma G(P)Z - \delta Z \end{bmatrix}, \tag{B.3}$$

evaluated at $(\hat{P}, \hat{Z})$. It is logical that the position of the bifurcation δ_c should depend on $\mathbf{f}^{(1)}(\hat{P}, \hat{Z})$, as this represents the linearisation of the

original system about $(\hat{P}, \hat{Z})$. However, to obtain the direction of δ_c, which is closely related to the curvature of the branch of bifurcating solutions, one would expect to have to compute higher derivatives of **f**.

In fact, the formula for δ_2, as derived in a set of exercises in [4], takes the form

$$\delta_2 = -\left[\pi\left(\begin{bmatrix} p_c^* \\ z_c^* \end{bmatrix} \cdot \frac{\partial}{\partial\delta}\mathbf{f}^{(1)}(\hat{P}, \hat{Z})\Big|_{\delta=\delta_c}\begin{bmatrix} p_c \\ z_c \end{bmatrix}\right)\right]^{-1}\mathfrak{R}(c), \qquad \text{(B.4)}$$

where the complex number c is defined by

$$c = \frac{1}{2}\begin{bmatrix} p_c^* \\ z_c^* \end{bmatrix} \cdot \mathbf{f}^{(3)}(\hat{P}, \hat{Z})\left(\begin{bmatrix} p_c \\ z_c \end{bmatrix}, \begin{bmatrix} p_c \\ z_c \end{bmatrix}, \begin{bmatrix} \overline{p_c} \\ \overline{z_c} \end{bmatrix}\right)$$

$$+ \begin{bmatrix} p_c^* \\ z_c^* \end{bmatrix} \cdot \mathbf{f}^{(2)}(\hat{P}, \hat{Z})\left(-D_1^{-1}\mathbf{f}^{(2)}(\hat{P}, \hat{Z})\left(\begin{bmatrix} p_c \\ z_c \end{bmatrix}, \begin{bmatrix} \overline{p^c} \\ \overline{z_c} \end{bmatrix}\right), \begin{bmatrix} p_c \\ z_c \end{bmatrix}\right)$$

$$+ \frac{1}{2}\begin{bmatrix} p_c^* \\ z_c^* \end{bmatrix} \cdot \mathbf{f}^{(2)}(\hat{P}, \hat{Z})\left((2i\omega_0 - D_1)^{-1}\mathbf{f}^{(2)}(\hat{P}, \hat{Z})\left(\begin{bmatrix} p_c \\ z_c \end{bmatrix}, \begin{bmatrix} p_c \\ z_c \end{bmatrix}\right), \begin{bmatrix} \overline{p_c} \\ \overline{z_c} \end{bmatrix}\right).$$

$$\text{(B.5)}$$

If the eigenvectors $[p_c, z_c]^T$ and $[p_c^*, z_c^*]^T$ are set to

$$\begin{bmatrix} p_c \\ z_c \end{bmatrix} = \begin{bmatrix} 1 \\ i\omega_0/\Gamma G'(\hat{P})\hat{Z} \end{bmatrix}$$

and

$$\begin{bmatrix} p_c^* \\ z_c^* \end{bmatrix} = \begin{bmatrix} 1/2 \\ \Gamma G'(\hat{P})\hat{Z}/2i\omega_0 \end{bmatrix}$$

repectively, then the necessary relation (B.2) is satisfied and, since

$$\frac{\partial}{\partial\delta}\mathbf{f}^{(1)}(\hat{P}, \hat{Z}) = \begin{bmatrix} 0 & 0 \\ 0 & -1 \end{bmatrix},$$

it follows that the first factor of δ_2 evaluates to

$$-\left[\mathfrak{R}\left(\begin{bmatrix} p_c^* \\ z_c^* \end{bmatrix} \cdot \frac{\partial}{\partial\delta}\mathbf{f}^{(1)}(\hat{P}, \hat{Z})\Big|_{\delta=\delta_c}\begin{bmatrix} p_c \\ z_c \end{bmatrix}\right)\right]^{-1} = -\left[\mathfrak{R}(-z_c z_c^*)\right]^{-1}$$

$$= -\mathfrak{R}(-\tfrac{1}{2})^{-1}$$

$$= 2.$$

The value of the second factor, $\mathfrak{R}(c)$, was calculated using a MAPLE routine which may be obtained on request from the first author. To six

significant figures, the computed value of $\Re(c)$ was 1275.69, which, in turn, gave

$$\delta_2 = 2551.38. \tag{B.6}$$

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