

## The role of higher predation in plankton population models

Andrew M. Edwards and Andrew Yool<sup>1</sup>

*Biological Oceanography Division, Bedford Institute of Oceanography B240, Dartmouth, Nova Scotia B2Y 4A2, Canada and <sup>1</sup>School of Ocean and Earth Sciences, Southampton Oceanography Centre, European Way, Southampton SO14 3ZH, UK*

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**Abstract.** Zooplankton mortality in plankton population models is often represented by the so-called closure term. Recently, much attention has been paid to the choice of functional form used for the closure term, primarily due to the influential paper by Steele and Henderson (*J. Plankton Res.*, **14**, 157–172, 1992). Here we reveal an inconsistency in the normalization of Steele and Henderson's models, and show that unforced short-term oscillations (limit cycles) can occur when a quadratic closure term is used. Furthermore, we contradict the hypothesis regarding the relationship between nutrient steady-state values and the choice of closure term: using the seven-component plankton model of Fasham (*The Global Carbon Cycle*, Heimann, M. (ed.), pp. 457–504, 1993) with four alternative closure terms, we find the nutrient value to depend more upon the choice of parameter values than on the choice of closure term. However, our results agree with and strengthen the general conclusion of Steele and Henderson's work: that the choice of closure term can strongly influence the dynamics of models.

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### Introduction

Models of the oceanic plankton ecosystem are used to improve our understanding of biogeochemical cycles. Usually, the highest trophic level of the food web that is explicitly modelled is that comprising zooplankton [e.g. (Fasham, 1993; Sarmiento *et al.*, 1993)]. This requires that the rate of zooplankton mortality due to consumption by higher predators be represented by some mathematical function that does not explicitly depend upon the population level of the higher predators, since such predators are not being modelled. Steele and Henderson (1992) referred to this function as the closure term.

Recently, the choice of closure term has attracted considerable interest (Edwards and Brindley, 1996, 1999; Caswell and Neubert, 1998; Pitchford and Brindley, 1998; Yool, 1998; Sharada and Yajnik, 1999). Much motivation for these studies came from the paper entitled 'The role of predation in plankton models' by Steele and Henderson (1992). The results from this paper are often considered by modellers when they formulate plankton models [e.g. (Fasham, 1993, 1995; Fasham *et al.*, 1993)] and the paper has been cited >50 times in the literature.

Steele and Henderson (1992) showed how alternative closure terms, and parameter values used in those closure terms, can significantly affect the dynamics of simple models. The changes in dynamics were characterized by the presence or absence of short-term oscillations of the state variables (nutrient, phytoplankton and zooplankton), and by the shift between the so-called 'North Pacific' (constant, low phytoplankton population) and 'North Atlantic' (phytoplankton bloom) patterns of annual plankton abundance. The authors focused their analysis on variants of one of their own models (Steele and Henderson, 1981) and on results from four other models.

By performing numerical integrations of a nutrient–phytoplankton–zooplankton (*NPZ*) model, Steele and Henderson (1992), hereafter abbreviated to SH92, found short-term oscillations (limit cycles) to occur when zooplankton mortality was modelled using a linear form, but not with a quadratic form. Edwards and Brindley (1996) have since shown that limit cycles can occur across wide ranges of parameters for an *NPZ* model [based on that of Steele and Henderson (1981)] when the quadratic mortality term is used. SH92 also concluded that the ratio of nutrient steady-state value to the half-saturation constant for nutrient uptake by phytoplankton is determined by the choice of closure term for five models taken from the literature.

Here we take a formal approach to non-dimensionalizing SH92's models, which reveals an inconsistency in their normalization. By recomputing SH92's simulations, we find that, in general, their results are not greatly affected by the inconsistency, and where differences do occur, we explain these by constructing bifurcation diagrams. However, we do find that limit cycles can occur with quadratic zooplankton mortality for the SH92 model. We then investigate the effects of four alternative closure terms on the behaviour of the Fasham (1993) model, which is a more complex plankton ecosystem model than that of SH92. Finally, we re-evaluate the conclusions of SH92 regarding nutrient steady-state values, in the context of the Fasham (1993) model; we find these conclusions to be invalid.

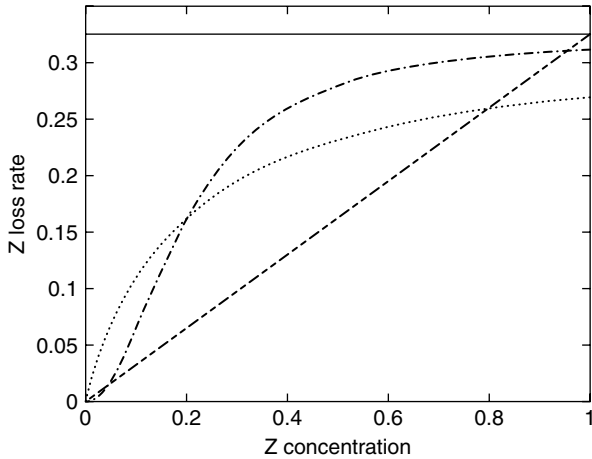
Overall, however, our results strengthen the general message conveyed by SH92: that the choice of closure term and its parameter values can have an important influence upon the dynamics of models. SH92 emphasized the additional importance of the closure term 'because it determines a major component of the organic flux out of the system—a factor of prime concern for the overall physical–biological programmes using these models'. Thus, an improved understanding of the effects of the choice of closure term is desirable.

## Definitions of closure terms

In Table I, we list four types of closure terms, together with examples of their use in models. In Figure 1, we show the different shapes of the four closure terms, with the specific zooplankton loss rate ( $\text{day}^{-1}$ ) plotted against zooplankton concentration ( $\text{mmol N m}^{-3}$ ). Note that  $\mu_1$  [ $(\text{mmol N m}^{-3})^{-1} \text{day}^{-1}$ ] has a different definition and different units for the quadratic form than  $\mu_2$  ( $\text{day}^{-1}$ ) has for the other forms, but we use the same numerical value for  $\mu_1$  and  $\mu_2$  in Figure 1 since  $Z$  is often of the order of  $1 \text{ mmol N m}^{-3}$  [e.g. Figure 9 of Fasham (1993)]. For the hyperbolic and sigmoid terms,  $k_6$  ( $\text{mmol N m}^{-3}$ ) is the half-saturation constant for the zooplankton loss.

The linear form has a specific rate independent of zooplankton concentration, and may be interpreted as representing a predator whose biomass does not fluctuate. Although this is perhaps unrealistic, the linear form is commonly used since it is the most simple form (SH92), and often there is insufficient information to justify the use of a more complex form.

The quadratic form has a specific rate dependent on the zooplankton biomass



**Fig. 1.** Specific zooplankton loss rate ( $\text{day}^{-1}$ ) versus zooplankton concentration ( $\text{mmol N m}^{-3}$ ) for the four closure terms: linear (solid line), quadratic (dashed), hyperbolic (dotted) and sigmoid (dot-dash). We use the Fasham (1993) values of  $k_6 = 0.2 \text{ mmol N m}^{-3}$  for the hyperbolic and sigmoid cases, with  $\mu_2 = 0.325 \text{ day}^{-1}$  for these plus the linear case, and  $\mu_1 = 0.325 (\text{mmol N m}^{-3})^{-1} \text{ day}^{-1}$  for the quadratic case.

**Table I.** Definitions of closure terms, plus examples of their use by modellers, retaining the notation of Fasham (1993).  $Z$  represents the zooplankton concentration ( $\text{mmol N m}^{-3}$ ). The parameter  $\mu_2$  is the specific zooplankton loss rate ( $\text{day}^{-1}$ ) for the linear form and is the maximum specific zooplankton loss rate ( $\text{day}^{-1}$ ) for the hyperbolic and sigmoid forms, for which  $k_6$  is the half-saturation constant ( $\text{mmol N m}^{-3}$ ). For the quadratic form,  $\mu_1$  is the loss rate, with units  $(\text{mmol N m}^{-3})^{-1} \text{ day}^{-1}$

Closure term	Function	Literature examples
Linear	$dZ/dt = \dots - \mu_2 Z$	(Evans and Parslow, 1985; Wroblewski, 1989; Fasham <i>et al.</i> , 1990; Beltrami and Carroll, 1994; Edwards and Brindley, 1999)
Quadratic	$dZ/dt = \dots - \mu_1 Z^2$	(Steele and Henderson, 1981; Denman and Gargett, 1995; Fasham, 1995; Edwards and Brindley, 1996)
Hyperbolic	$dZ/dt = \dots - \mu_2 Z^2 / (k_6 + Z)$	(Frost, 1987; Fasham, 1993; Ross <i>et al.</i> , 1994)
Sigmoid	$dZ/dt = \dots - \mu_2 Z^3 / (k_6^2 + Z^2)$	(Malchow, 1994)

itself. This may be interpreted as representing either cannibalism within the zooplankton compartment, or a predator whose biomass is proportional to that of the zooplankton. As such, this form is more realistic since predator populations commonly vary with those of their prey. Note that here cannibalism may represent either true cannibalism (species X eats species X) or intratrophic predation [zooplankton species X eats zooplankton species Y; (Kohlmeier and Ebenhö, 1995; Pitchford and Brindley, 1998)], because all of the zooplankton species have been combined into a single compartment where they are assumed to be functionally identical.

In a sense, the hyperbolic and sigmoid forms lie between the linear and quadratic forms. At low zooplankton concentrations, both behave somewhat similarly to the quadratic form (i.e. with a specific rate proportional to zooplankton biomass), whereas at high zooplankton concentrations both plateau and behave similarly to the linear form (i.e. with an invariant specific rate). Both forms represent satiable predators. This ‘satiation’ may parameterize a number of different ecological processes. Following Holling’s original derivation, it may represent handling time, namely the minimum period of time that a predator spends processing each food item before it can capture another one. Alternatively, it may represent a limit on predator density, caused either by some other factor in the environment (e.g. the availability of suitable mating sites), or by direct interference between the predators themselves (deliberate or accidental).

The sigmoidal form differs from the hyperbolic form in its behaviour at very low zooplankton concentrations. At these densities (using the same half-saturation constant), the sigmoidal response leads to lower rates of predation than the hyperbolic form. However, as zooplankton density increases, the sigmoidal response leads to a more-than-linear increase in predation rate. This is why the form is referred to as sigmoidal or ‘S-shaped’. One of the ways such a response may occur in a biological system is when the predator ‘switches’ between different prey types (Begon *et al.*, 1986). Alternatively, the lowering of predation rate at very low zooplankton density may parameterize a predator with a prey threshold concentration. Below a certain prey concentration, the predator reduces its searching efforts to save resources until prey density becomes sufficient to make a net gain for effort expended.

Although these latter two functional forms allow modellers to specify a more complex response, they require much more information about the predators that they aim to model implicitly. By contrast, the linear and quadratic forms require only that predator numbers be either independent of prey, or increase with prey. SH92 note that the more complex forms are often used to model situations for which no data for such predation are available. The  $\mu_2$  and  $k_6$  parameters are then used to fine-tune the model so that it fits the data (on, say, phytoplankton populations) which are available.

Note that the words ‘linear’ and ‘quadratic’ refer to the absolute rate as it appears in the  $dZ/dt$  equation (i.e.  $\mu_2 Z$  for the linear form), whereas the words ‘hyperbolic’ and ‘sigmoid’ refer to the specific rate [i.e.  $\mu_2 Z/(k_6 + Z)$  for the hyperbolic form]—there appears to be no concise phrase for the absolute rates corresponding to the latter two closure terms. Since different researchers use different definitions, the mathematical expressions should always be checked to verify which type of function is being discussed. Natural mortality is often not explicitly mentioned by modellers, but since zooplankton do not live forever such mortality is implicitly included in the closure term.

### The Steele and Henderson (1992) models

In SH92,  $PZ$  and  $NPZ$  models with and without temporal forcing were studied. First, SH92 took a two-compartment  $PZ$  model, without nutrient limitation, and

‘normalized’ the two ordinary differential equations to concentrate on the effects of changes in the rate of zooplankton mortality. They then introduced nutrient limitation, adding a third variable,  $N$ , and a third ordinary differential equation to the model. SH92 then normalized the new three-component model in the same way as they did the two-component model. However, we show here that this is not valid. Their normalization, which is essentially a non-dimensionalization of the original model, results in a three-component model which is inconsistent with the original model.

First, we describe the dimensional  $PZ$  model of SH92, and then show (in the Appendix) how their ‘normalization’ is equivalent to a unique non-dimensionalization of the equations. However, contrary to what SH92 assumed, the  $NPZ$  model cannot be normalized, or non-dimensionalized, in the same way as for the  $PZ$  model. We show that an extra parameter is needed in the non-dimensional  $NPZ$  model, and then determine how this affects the numerical simulations presented by SH92.

The dimensional two-component unforced  $PZ$  system has the form:

$$\frac{dP}{dt} = \beta P \left( 1 - \frac{P}{\gamma} \right) - \frac{\lambda P^{\nu}}{\mu^{\nu} + P^{\nu}} Z \quad (1)$$

$$\frac{dZ}{dt} = \alpha \frac{\lambda P^{\nu}}{\mu^{\nu} + P^{\nu}} Z - \alpha \delta Z^m \quad (2)$$

where  $P$  and  $Z$  represent the phytoplankton and zooplankton concentrations,  $t$  is time, and all parameters are positive. The value of  $m$  equals 1 to give the linear closure term or 2 for the quadratic term, and  $\nu$  equals 1 or 2 to represent Holling Type II or III grazing functions. Parameters  $\beta$  and  $\gamma$  are the intrinsic growth rate and carrying capacity of the logistic phytoplankton growth term,  $\alpha$  is the zooplankton growth efficiency,  $\lambda$  is the maximum zooplankton grazing rate,  $\mu$  is the half-saturation coefficient for zooplankton grazing and  $\alpha\delta$  gives the rate of zooplankton mortality. Note that SH92 actually have the form  $\mu + P^{\nu}$ , but this must be a misprint and it should be  $\mu^{\nu} + p^{\nu}$  [the form used by Steele and Henderson (1981)] so that  $\mu$  has the same definition and dimensions for both  $\nu = 1$  and  $\nu = 2$ .

SH92 ‘normalized’ these equations by taking  $\beta = \lambda = \mu = 1$ , so that at equilibrium the new rescaled  $P$  and  $Z$ , which we shall call  $p$  and  $z$  for clarity, satisfy:

$$p \left( 1 - \frac{p}{c} \right) = \frac{p^{\nu}}{1 + p^{\nu}} z \quad (3)$$

$$az^{m-1} = \frac{p^{\nu}}{1 + p^{\nu}} \quad (4)$$

where  $c = \gamma/\mu$ , and  $a$  depends on  $\delta$  and other parameters. This normalization is equivalent to rescaling the equations by a unique non-dimensionalization, which we derive in the Appendix. SH92 then added a nutrient equation to the  $PZ$

system, and stated that the new *NPZ* system could be rescaled in the same way as the *PZ* system.

However, the *NPZ* system cannot be rescaled in the way stated by SH92, and an extra parameter is required in the non-dimensional equations. The mathematical details are given in the Appendix, where it is shown that the non-dimensional system used by SH92 for their computations is structurally different from their original *NPZ* system, in that it makes different assumptions concerning the regeneration of zooplankton excretion. The resulting consistent non-dimensional equations are:

$$\frac{dn}{d\tau} = -\frac{n}{\tilde{k} + n} p \left(1 - \frac{p}{c}\right) + (1 - \alpha) \frac{p^2}{1 + p^2} z + s (n_0 - n) \quad (5)$$

$$\frac{dp}{d\tau} = \frac{n}{\tilde{k} + n} p \left(1 - \frac{p}{c}\right) - \frac{p^2}{1 + p^2} z \quad (6)$$

$$\frac{dz}{d\tau} = \hat{\alpha} \frac{p^2}{1 + p^2} z - \hat{\alpha} a z^m \quad (7)$$

where  $n$  represents the non-dimensional nutrient concentration,  $\tau$  represents non-dimensional time,  $\tilde{k}$  corresponds to the half-saturation constant for nutrient uptake,  $s$  is the cross-thermocline exchange rate of water,  $n_0$  is the nutrient concentration below the mixed layer,  $\hat{\alpha}$  relates to the zooplankton growth efficiency and  $\nu$  has been set to 2, since the  $\nu = 1$  case is considered no further.

The incorrect normalization by SH92 resulted in the  $\alpha$  term in (5) being  $\hat{\alpha}$ , the same parameter as appears in equation (7). However, in the Appendix, we show that  $\hat{\alpha}$  is defined by  $\hat{\alpha} = \lambda\alpha/\beta$ , and so  $\alpha$  and  $\hat{\alpha}$  cannot be assigned values independently of one another. The SH92 simulations used  $\alpha = \hat{\alpha} = 0.5$ , which does not satisfy  $\hat{\alpha} = \lambda\alpha/\beta$ . The correct values (derived from the parameters of the SH92 dimensional model) are  $\hat{\alpha} = 0.5$  and  $\alpha = 0.29$ , which we use shortly to investigate how the erroneous rescaling by SH92 affects their results.

## Simulations

The three-component model used in the numerical simulations presented by SH92 in their Figures 5 and 6 is the incorrect normalized model given by equations (21), (22) and (23) in the Appendix, which is equivalent to equations (5), (6) and (7) with  $\alpha = \hat{\alpha}$ . In their simulations, SH92 forced the phytoplankton growth rate, which had been normalized to one, to represent seasonal changes through the year. They used the following sinusoidal forcing function, which has a period of 100 time units ( $\approx 1$  year):

$$\text{forcing} = 1 + \frac{1}{2} \sin \frac{2\pi\tau}{100} \quad (8)$$

The parameter values used by SH92 for their Figure 5C were  $s = 0.3$ ,  $\alpha = \hat{\alpha} = 0.5$ ,  $n_0 = 4$ ,  $m = 1$ ,  $\tilde{k} = 0.5$ ,  $a = 0.7$  and  $c = 10$ . We have recomputed the  $npz$  simulations given by SH92 for the following two situations: (i)  $\hat{\alpha} = \alpha = 0.5$  – the original (incorrect) SH92 values; (ii)  $\hat{\alpha} = 0.5$  and  $\alpha = 0.29$ , to see whether the difference in the value of  $\alpha$  is important.

### *Linear zooplankton mortality*

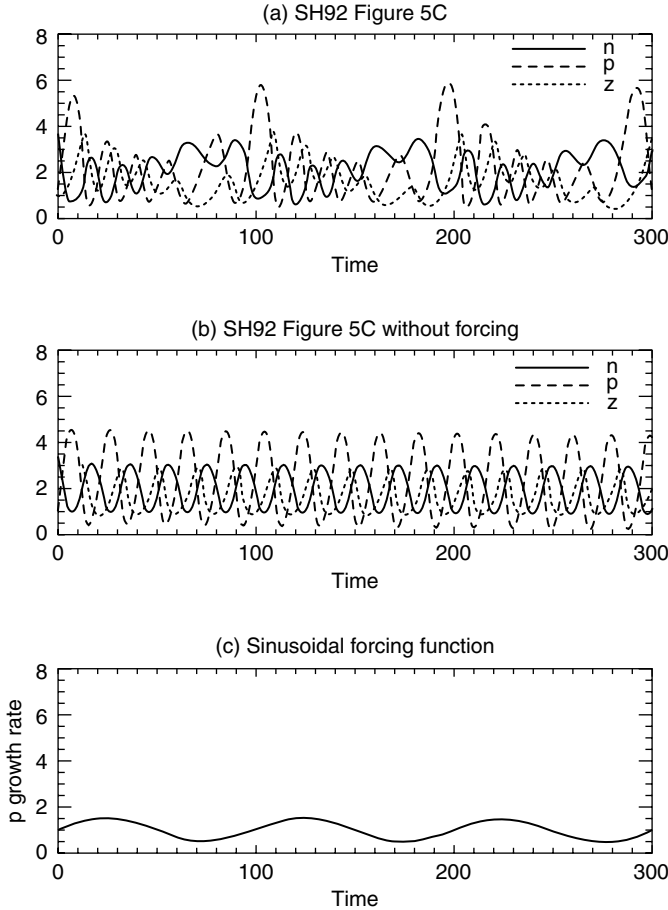
First, SH92 had  $m = 1$ , representing linear zooplankton mortality, for their Figure 5B and C. We have recomputed Figure 5B and found some minor differences when the  $\alpha$  anomaly is corrected [in particular, short-term oscillations can occur with a low cross-thermocline mixing rate (Edwards, 1997)], but here we focus on the simulations in Figures 5C and 6 of SH92.

In Figure 2a, we reproduce Figure 5C of SH92, and in Figure 2b show what happens when the phytoplankton growth rate is not forced but is held constant. The forcing function of the phytoplankton growth rate is shown in Figure 2c. The initial conditions, as used by SH92, are  $(n, p, z) = (4, 1, 1)$  for all simulations. The forced system exhibits large oscillations of  $n$ ,  $p$  and  $z$ , at a frequency of roughly five cycles per year (100 time units  $\approx$  1 year). By switching off the forcing to hold the growth rate constant (Figure 2b), we can better understand the factors controlling the dynamics of the forced system. The unforced system shown in Figure 2b settles down to a repeating oscillatory cycle, known as a limit cycle. Thus, the forced system in Figure 2a results from the interaction of the frequency of the sinusoidal forcing and the natural frequency of the oscillations of the unforced system. With the corrected value of  $\alpha = 0.29$  (not shown), there is little difference from Figure 2 for  $\alpha = 0.5$ .

### *Quadratic zooplankton mortality*

In their Figure 6, SH92 set  $m = 2$ , to investigate the effects of using the quadratic zooplankton mortality function. In Figure 3a, we reproduce Figure 6A of SH92, for which they set  $a = 0.1$ , where  $a$  is the zooplankton mortality parameter. The forced system shows fairly constant low phytoplankton values, higher zooplankton values which oscillate with the forcing, and high nutrient values. SH92 compared this to the general situation in the North Pacific Ocean, shown in their Figure 2. If we omit the forcing, then  $n$ ,  $p$  and  $z$  settle down to constant values, as shown in Figure 3b—the system is thus attracted to a steady state or equilibrium. The system quickly reaches the steady state, with low  $p$  and high  $n$  and  $z$ . With the forcing, the values of  $n$ ,  $p$  and  $z$  vary slowly, with a frequency (or period) the same as that of the forcing. The forced system thus appears to track the steady state, which is moved around due to the forcing. For the corrected value of  $\alpha = 0.29$ , the diagrams change very little and so are not shown here.

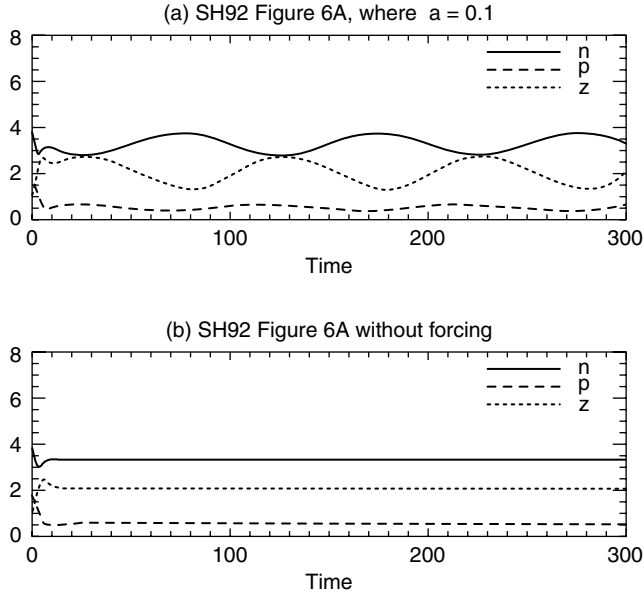
SH92 then increased the value of  $a$  to 0.5, to give their Figure 6B, reproduced in Figure 4a. We see that  $p$  undergoes large-amplitude fluctuations, and the minima of  $n$  are close to the value of the half-saturation constant  $\tilde{k} = 0.5$ . SH92 compared this situation to the North Atlantic Ocean. For the unforced system,



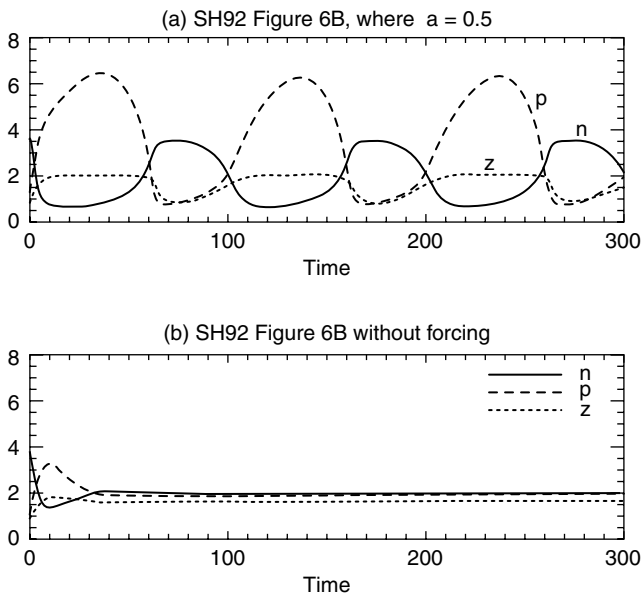
**Fig. 2.** (a) Figure 5C of SH92 shows that  $n$ ,  $p$  and  $z$  undergo oscillations when the phytoplankton growth rate is forced by the sinusoidal function shown in (c) (100 time units  $\approx$  1 year). (b) If we hold the phytoplankton growth rate constant, then the system settles onto a large-amplitude limit cycle.

we see that the system settles down to a steady state, with  $n$ ,  $p$  and  $z$  all taking similar values. However, note that the steady-state value of  $p$  is much less than the average of the  $p$  values throughout the cycles of the forced system. This is unlike Figure 3 for  $a = 0.1$ , where the average of  $p$  in the forced system equals the unforced steady-state value. We elaborate on this below.

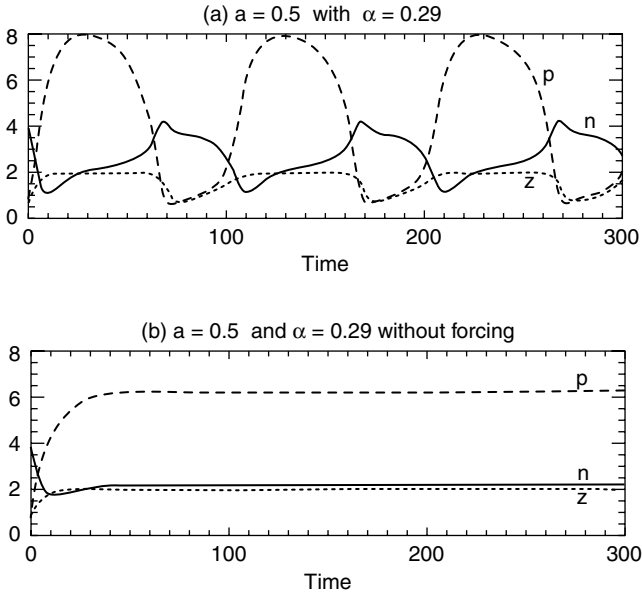
With the corrected value of  $\alpha = 0.29$ , we obtain Figure 5a, for which  $p$  reaches much higher values than for  $\alpha = 0.5$  (Figure 4a), and  $n$  only gets as low as 1.0, twice the value of the half-saturation constant. The behaviour of  $z$  is practically identical to that for  $\alpha = 0.5$ . For the unforced system (Figure 5b), we find a 3-fold increase in the steady-state value of  $p$ , compared to Figure 4b for  $\alpha = 0.5$ . The  $n$  value increases marginally, and the  $z$  value actually increases by a third, despite



**Fig. 3.** (a) Figure 6A of SH92 shows that with quadratic zooplankton mortality ( $m = 2$ ) at a rate of  $a = 0.1$ , the forced system has fairly constant low  $p$  values, and slowly oscillating  $n$  and  $z$ , which is the general situation for the North Pacific Ocean. (b) The unforced system settles down to a steady state.



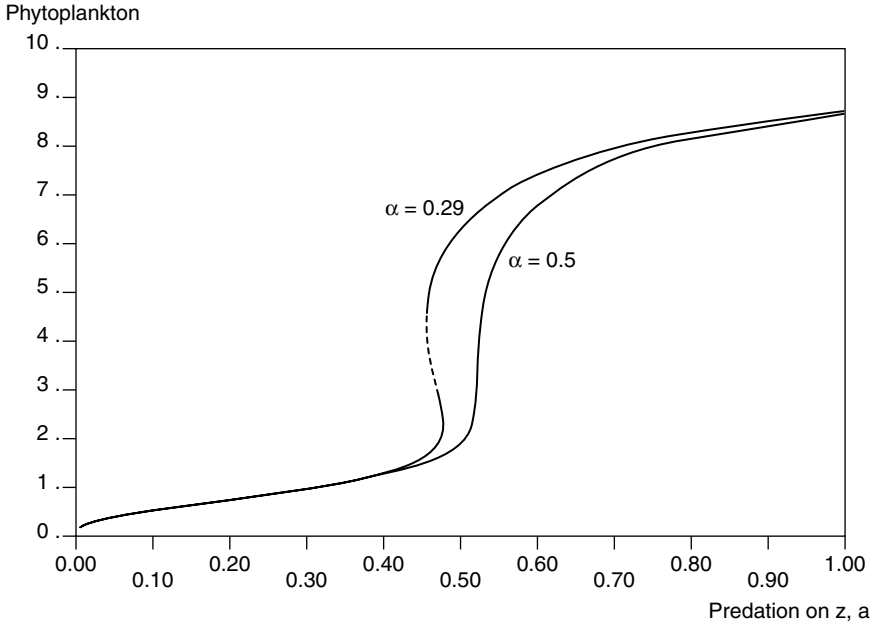
**Fig. 4.** (a) Figure 6B of SH92 shows that with an increase in the rate of zooplankton mortality,  $a = 0.5$ ,  $p$  undergoes large-amplitude fluctuations, and  $n$  gets close to the value of the half-saturation constant  $\bar{k}$ , corresponding to the situation in the North Atlantic Ocean. (b) The unforced system settles down to a steady state.



**Fig. 5.** (a) With the corrected  $\alpha = 0.29$ , and  $a = 0.5$ ,  $p$  reaches higher values than for  $\alpha = 0.5$ . (b) The steady-state value of  $p$  is three times that for  $\alpha = 0.5$ , explaining why the forced system shows higher  $p$  values.

showing no change for the forced equations. So the  $\alpha$  anomaly does, in this case, make a significant difference.

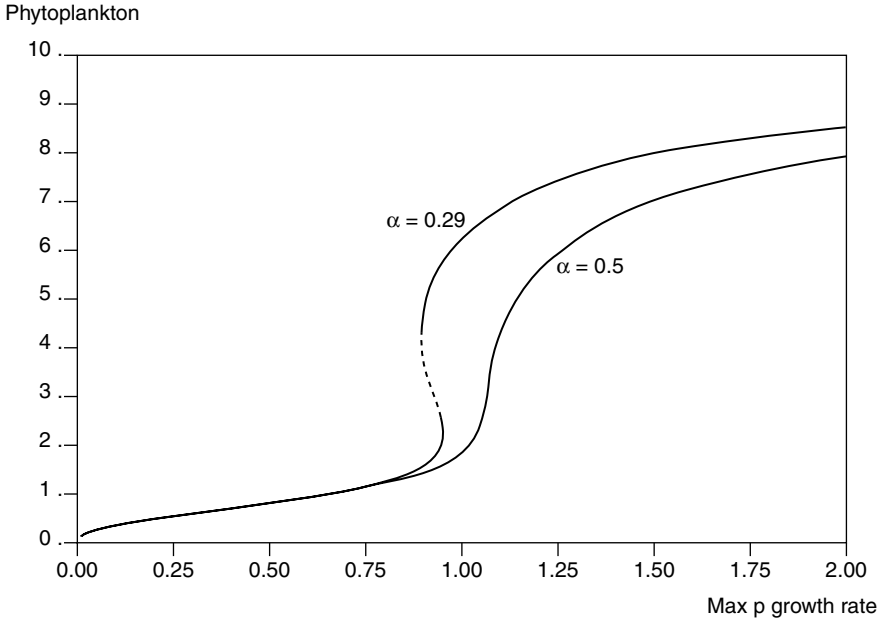
In Figure 6, computed using the dynamical-systems package AUTO (Doedel *et al.*, 1994), we show how the steady-state value of  $p$  for the unforced system changes in magnitude as we vary  $a$ , the predation on the zooplankton. We plot the curves for both  $\alpha = 0.5$  and  $\alpha = 0.29$ ; a solid line indicates that a steady state is stable and a dashed line that it is unstable (and so does not attract trajectories). The situations that we have just discussed are for  $a = 0.1$  (Figure 3), and then  $a = 0.5$  (Figures 4 and 5). In Figure 6, we see that at  $a = 0.1$ , the steady-state value of  $p$  is the same for both  $\alpha = 0.5$  and  $\alpha = 0.29$ , at the value shown in Figure 3. In addition, we see that at  $a = 0.5$ , the steady-state value of  $p$  is just below 2 for  $\alpha = 0.5$  and just above 6 for  $\alpha = 0.29$ . This explains the large difference in  $p$  values that we found in Figures 4 and 5. The reason for the difference is that the  $\alpha = 0.29$  curve in Figure 6 shows a hysteresis effect, whereby it doubles back on itself. For a narrow range of  $a$  values, there exist two stable steady states plus the unstable one given by the dashed line—the stable steady state that a simulation reaches will depend upon the initial conditions. The two points where the branch of unstable steady states (dashed line) becomes stable (solid line) are known technically as fold or saddle-node bifurcations [e.g. (Guckenheimer and Holmes, 1983; Glendinning, 1994; Kuznetsov, 1995)]. For  $\alpha = 0.5$ , the hysteresis does not occur, although high  $p$  values are reached at higher  $a$  values. So, for example, if  $a = 0.7$ , then  $\alpha = 0.5$  and  $\alpha = 0.29$  again have similar  $p$  steady-state values.



**Fig. 6.** The phytoplankton steady-state value changes as the predation on zooplankton,  $a$ , is increased. A solid line indicates where a steady state is stable, and a dashed line where it is unstable. Hysteresis occurs for  $\alpha = 0.29$ , but not for  $\alpha = 0.5$ . At  $a = 0.1$ , the  $p$  values are the same for both values of  $\alpha$ , but at  $a = 0.5$ , the  $\alpha = 0.29$  value is much higher than for  $\alpha = 0.5$ , explaining the difference between Figures 4 and 5.

In Figure 7, we show how the steady-state value of  $p$  for the unforced system changes as the maximum growth rate of  $p$  is varied, with  $a$  set to 0.5. The maximum growth rate, which has been ‘normalized’ to 1.0 and is not specified explicitly as a parameter, is what is forced in the preceding diagrams. In the unforced diagrams it equals 1.0, and when forced it ranges from 0.5 to 1.5, as implied from its formulation given by equation (8). When the maximum growth rate equals 1.0, we have the same steady-state values for  $p$  as we have at  $a = 0.5$  in Figure 6. Again we find hysteresis for  $\alpha = 0.29$ , but not for  $\alpha = 0.5$ . As the forcing increases the growth rate, we see that, for  $\alpha = 0.5$ , the steady-state value of  $p$  is pushed up to values much greater than when the growth rate equals 1.0. This explains why, in Figure 4, for  $\alpha = 0.5$ , the average value of  $p$  during the forced cycles (Figure 4a) is much greater than the unforced steady-state value shown in Figure 4b. The forcing pushes the system through a region where  $p$  increases sharply, namely the near vertical part of the  $\alpha = 0.5$  curve in Figure 7. For  $\alpha = 0.29$ , Figure 7 explains how  $p$  reaches much lower values in the forced simulation in Figure 5a than the steady-state value in Figure 5b.

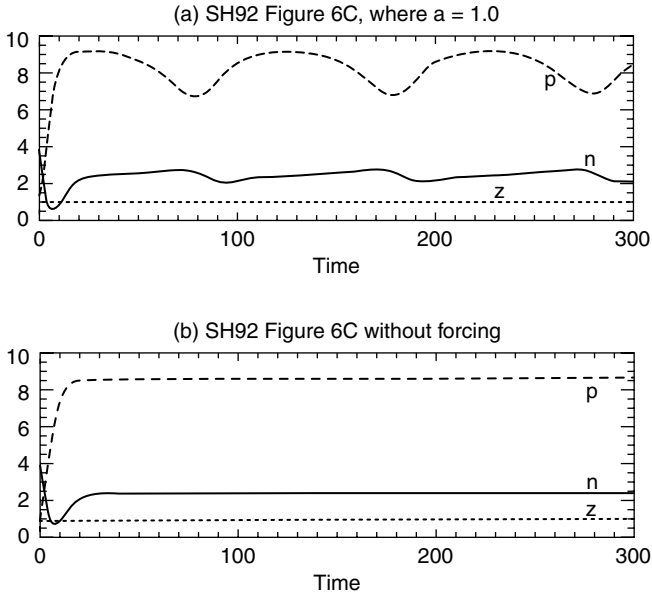
For their final numerical simulation, SH92 set  $a$  to the high value of 1.0, to produce their Figure 6C, which we reproduce in Figure 8a. Throughout the cycles,  $p$  remains fairly high. In Figure 8b, we see that the unforced system settles down to a steady state with a high  $p$  value. We already know this—it is given by the



**Fig. 7.** In the unforced system, the maximum phytoplankton growth rate is set to 1.0, but in the forced system it varies sinusoidally between 0.5 and 1.5. This diagram (for which  $a = 0.5$ ) shows that for  $\alpha = 0.5$ , the forcing pushes the system into a region where the steady-state value of  $p$  is much higher than in the unforced system, thus explaining the large peaks of  $p$ , relative to the unforced steady-state value, reached in Figure 4a. For  $\alpha = 0.29$ , the unforced steady state is already at a high value of  $p$ .

point with  $a = 1.0$  on the bifurcation diagram of Figure 6. For  $\alpha = 0.29$ , the simulations (not shown) are very similar to Figure 8a and b for  $\alpha = 0.5$  (note that the  $\alpha = 0.29$  and  $\alpha = 0.5$  curves of Figure 6 are very close at  $a = 1.0$ ).

Thus, we have recomputed the numerical simulations of SH92 with the corrected value of  $\alpha = 0.29$ . For quadratic zooplankton mortality, when  $a = 0.5$  the ‘alpha’ anomaly makes a difference, as shown by Figures 4 and 5, which show different  $p$  values for  $\alpha = 0.5$  and  $\alpha = 0.29$ . In Figure 6, we show how this difference can be explained, and that if an alternative value of  $a$  is used, such as  $a = 0.4$  or  $a = 0.6$ , then the steady-state values of  $p$  would be similar. It just happens to be that  $a = 0.5$ , the value chosen by SH92, gives a large difference. This is a good example of how a dynamical-systems approach, namely the construction of the bifurcation diagram in Figure 6, is more powerful than simple computation of trajectories in producing a more complete picture of the behaviour. The time series of Figures 4 and 5 show a large difference when  $\alpha$  is changed, but Figure 6 shows that this only occurs within a narrow range of values of  $a$ , and this range just happens to contain the value  $a = 0.5$ . Figure 7 explains how the forcing of the phytoplankton growth rate can lead to values of  $p$  far greater than the steady-state value for the unforced system. Overall, it appears that the results of SH92 are not drastically altered when the ‘alpha’ anomaly is corrected, but nevertheless our



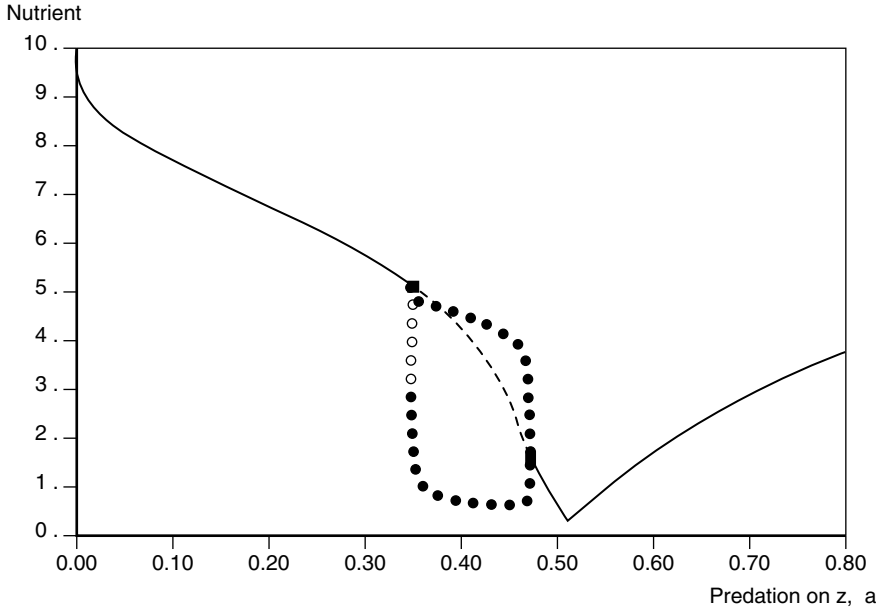
**Fig. 8.** (a) Figure 6C of SH92 shows that with a very high rate of zooplankton mortality,  $a = 1.0$ ,  $p$  remains large and fairly close to the carrying capacity ( $c = 10$ ), and  $z$  remains low and constant. (b) The unforced system settles down to a steady state with a high  $p$  value, as predicted by the bifurcation diagram of Figure 6.

investigation has improved the understanding of the mechanisms underlying the dynamics of the models.

### Do oscillations occur for the SH92 model with quadratic zooplankton mortality?

Thus far, we have not come across any unforced oscillations when the quadratic zooplankton mortality is used, in agreement with the findings of SH92, but Edwards and Brindley (1996) showed that oscillations occur across wide ranges of parameter values in a similar NPZ model, which uses the quadratic zooplankton mortality. So, is this difference due to slight differences in the structure of the two models? Or, is it the case that the SH92 model can exhibit oscillations, but the parameter space has not been explored fully enough to find them?

To investigate these questions, we continue using the corrected non-dimensionalized SH92 model, as given by equations (5), (6) and (7), but with the parameter values from Steele and Henderson (1981), which Edwards and Brindley (1996) used. These values are equivalent to the following values for the dimensional parameters of the dimensional SH92 model, given by equations (18), (19) and (20):  $S = 0.05$ ,  $\alpha = 0.25$ ,  $N_0 = 0.6$ ,  $\lambda = 0.6$ ,  $k = 0.03$ ,  $\mu = 0.035$ ,  $\beta = 1$ ,  $\delta = 4$  and  $\gamma = 1$ .



**Fig. 9.** For  $n_0 = 10$  and the remaining parameters set to the values of Steele and Henderson (1981), oscillations do occur in the unforced SH92 model with quadratic zooplankton mortality. The solid and dashed lines represent stable and unstable steady states, respectively, the solid squares (where the solid lines become dashed) are Hopf bifurcations, and solid (open) circles indicate the maximum and minimum nutrient values along stable (unstable) cycles.

Most of the parameters have equivalent definitions to parameters in the Steele and Henderson (1981) model, but Steele and Henderson (1981) had a phytoplankton growth rate, excluding nutrient limitation, of the form  $A_3P/(A_4 + A_5P)$ , whereas in the SH92 model it is the logistic form  $\beta P(1 - P/\gamma)$ . We thus equate  $\beta$  to the Steele and Henderson (1981) maximum specific phytoplankton growth rate:  $A_3/A_4 = 1$ . The half-saturation constant in  $A_3P/(A_4 + A_5P)$  is  $A_4/A_5$ , and for  $\beta P(1 - P/\gamma)$  half of the maximum specific growth rate is reached when  $P = \gamma/2$ , and so we choose to set  $\gamma = 2A_4/A_5$ . These values result in the following parameters (to two significant figures) for the non-dimensionalized model, as given by equations (5), (6) and (7):  $s = 0.05$ ,  $\alpha = 0.25$ ,  $n_0 = 17$ ,  $\hat{\alpha} = 0.15$ ,  $\tilde{k} = 0.86$ ,  $a = 0.39$  and  $c = 29$ .

As we have just shown, SH92 considered different levels of zooplankton mortality,  $a$ , in their numerical simulations. We shall do likewise, and following Edwards and Brindley (1996) we consider a maximum value for  $a$  of double the default value of 0.39. Edwards (1997) has found that stable unforced oscillations do not occur as  $a$  is varied with all the other parameters fixed at their given values. However, if  $n_0$  is reduced to  $n_0 = 10$  (a value well within the range used by other modellers), then oscillations do occur, which we now show.

In Figure 9, we demonstrate the existence of unforced oscillations across a range

of values of  $a$  by means of a bifurcation diagram constructed using AUTO (Doedel *et al.*, 1994). In Figure 9, there is no annual forcing, and  $n_0$  is fixed at 10. The solid circles indicate the existence of stable limit cycles (unforced oscillations) such as those in Figure 2b. At each value of  $a$ , the location of the circles gives the maximum and minimum nutrient levels reached along a cycle. The open circles indicate the extremely narrow range of  $a$  for which unstable cycles occur (such cycles are of little ecological significance). The two black squares indicate the location of *Hopf bifurcations* [e.g. (Glendinning, 1994; Kuznetsov, 1995; Edwards and Brindley, 1999)]. By definition, these occur where the steady states go from being stable (solid line) to unstable (dashed line) and the limit cycles emerge.

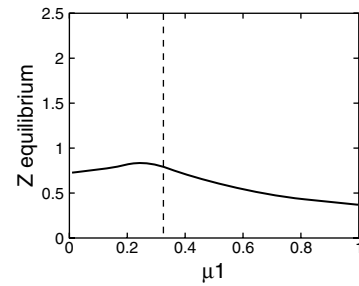
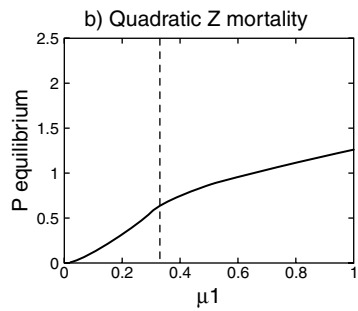
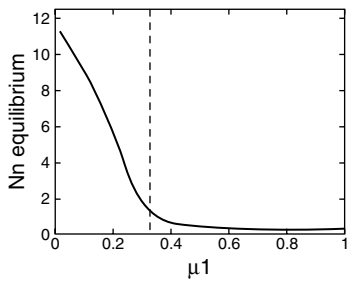
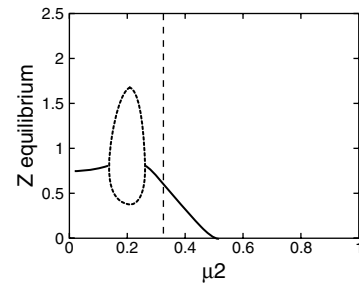
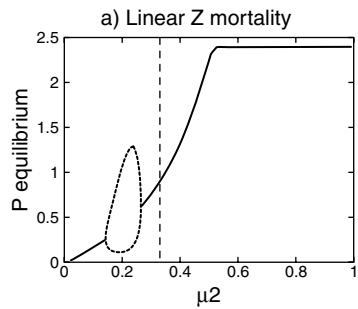
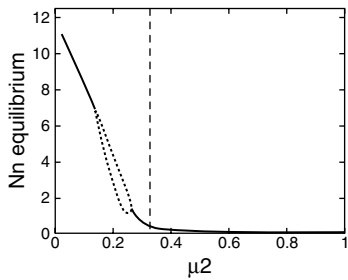
So, we have found that unforced oscillations do occur in the SH92 model with quadratic zooplankton mortality. As mentioned in the Introduction, the fact that SH92 found such unforced oscillations only when linear mortality was used has influenced the thinking of other modellers, in particular Fasham, during the construction of their models. This prompts us now to investigate the effects of alternative closure terms on the behaviour of the Fasham (1993) model, which is a more complex plankton ecosystem model than that of SH92.

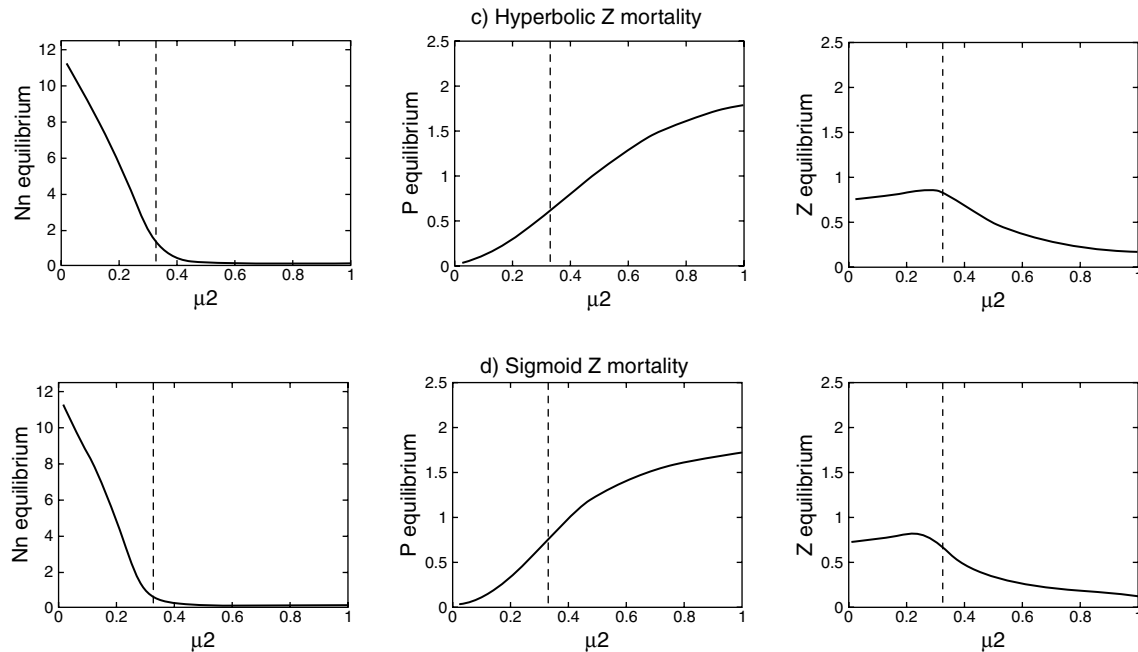
### Alternative closure terms in the seven-component Fasham (1993) model

The Fasham (1993) model of the marine ecosystem is one of several which aim to describe the seasonal dynamics of the open-ocean planktonic ecosystem of the North Atlantic [e.g. (Wroblewski, 1989; Taylor *et al.*, 1991; Bauer *et al.*, 1993; Dadou *et al.*, 1996)]. The model consists of seven compartments, explicitly representing concentrations of nitrate, phytoplankton, zooplankton, bacteria, dissolved organic nitrogen, ammonium and detritus in the mixed layer. Changes in the concentrations of these variables are modelled by seven coupled ordinary differential equations, which contain  $>30$  parameters. Furthermore, the system is forced by two forcing functions, representing the annual cycles of mixed-layer depth and solar irradiance.

For the zooplankton loss term (which included excretion plus mortality) Fasham (1993) used the hyperbolic form shown in Table I. In an earlier version of the model, Fasham *et al.* (1990) used the linear form. We now use all four closure terms given in Table I.

Figure 10 shows the steady-state values of phytoplankton ( $P$ ), zooplankton ( $Z$ ) and nitrate ( $N_n$ ) for the Fasham model with the four alternative closure terms, across a range of  $\mu_1$  and  $\mu_2$  values. The time-dependent forcing of the Fasham model (related to irradiance and mixed-layer depth) has been fixed to the values that Fasham used for OWS 'India' on day 197, the day on which the mixed layer is shallowest. All parameters are set to Fasham's values, except for the cross-thermocline mixing rate, which is set to  $0.30 \text{ m day}^{-1}$  [see (Yool, 1998)]. The solid lines indicate stable steady states, and dotted lines indicate the amplitudes of limit cycles, just like the solid circles in Figure 9. Figure 10 was computed by running trajectories until either a steady state or a limit cycle was reached. The vertical dashed lines indicate the baseline value of  $\mu_2$  [that used by Fasham (1993)] or  $\mu_1$ .





**Fig. 10.** Nitrate, phytoplankton and zooplankton equilibria for each of the four functional forms across ranges of the appropriate zooplankton mortality parameter  $\mu_1$  or  $\mu_2$ . Solid lines indicate stable equilibrium solutions, dotted lines indicate the range of limit cycle amplitude, and dashed lines mark the baseline value of  $\mu_2$  used in Fasham (1993). Concentrations are in  $\text{mmol N m}^{-3}$ .

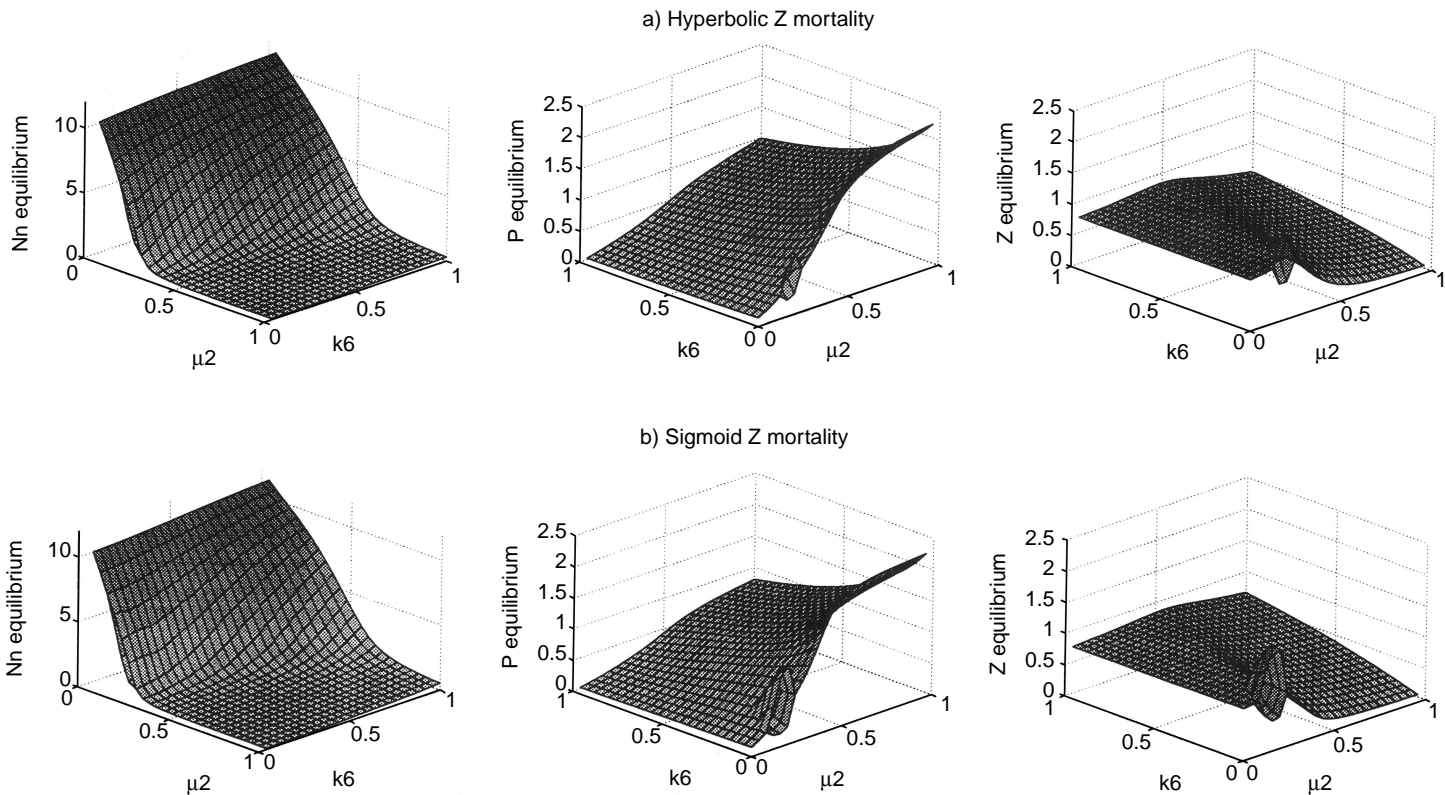
The most significant difference between the four rows of plots is the occurrence of limit cycles with the linear mortality term. These cycles occur just below the baseline value of  $\mu_2$ , across the range  $0.14 \leq \mu_2 \leq 0.26$ , and have periods which decrease from 37.5 to 30.8 days as  $\mu_2$  is increased. The maximum zooplankton concentration reached for the cycles is more than double the highest steady-state value, illustrating that the cycles are important in a quantitative sense, and not just a qualitative sense.

Aside from the limit cycles, the four terms show somewhat similar behaviour in response to increasing  $\mu_1$  or  $\mu_2$ . In all four cases, the zooplankton equilibria increase with  $\mu_1$  or  $\mu_2$  to a point just below the baseline value, and then decline to lower values. For the linear form, this decline is extreme, and for values of  $\mu_2 > 0.50$  the zooplankton become extinct (note that in practice  $Z$  never quite reaches zero). The analyses by Truscott and Brindley (1994), Edwards (1997) and Edwards and Brindley (1999) suggest that the steady state now has a negative zooplankton value (and is therefore ecologically unrealistic), and trajectories are now attracted to a stable steady state with  $Z = 0$  and high  $P$ . The  $Z$  mortality remains high at low  $Z$  values (Figure 1), and so  $Z$  die out. In the other three cases, the equilibria fall, but to a much lesser degree. This shared response to increasing  $\mu_1$  or  $\mu_2$  is also found with the phytoplankton and nutrient compartments, which display opposing trends to increases in  $\mu_1$  or  $\mu_2$ .

No limit cycles are found here with the quadratic term, in agreement with the original results of SH92. However, we have not considered as large an area of parameter space as Edwards and Brindley (1996), who did find such cycles with the quadratic term. With the hyperbolic and sigmoid closure terms, although no limit cycles were found in the range of  $\mu_2$  examined, it is clear from the formulae in Table I that as  $k_6 \rightarrow 0$ , both terms collapse to the linear term. Therefore, at some low values of  $k_6$  we would expect the behaviours for the hyperbolic and sigmoid terms to approach that of the linear term [unless the model is structurally unstable, in the sense of Wiggins (1990)].

To examine the significance of the value of  $k_6$  on the behaviours, in Figure 11 we show the phytoplankton, zooplankton and nitrate equilibria plus limit cycle amplitudes as  $k_6$  and  $\mu_2$  are varied. The remaining parameter values are the same as for Figure 10. For both terms, oscillatory behaviour is found as  $k_6 \rightarrow 0$ . The hyperbolic term yields such behaviour only at values of  $k_6 \leq 0.02$ , a value one-tenth that of the baseline value used by Fasham (1993). The sigmoid term found oscillations up to values of 0.16, only slightly lower than the baseline. Other than the difference in the range of values over which limit cycles occur, both mortality terms show very similar equilibrium densities across parameter space.

The reason for the difference in the extent of limit cycle regions can be seen from the shapes of the two response curves (Figure 1). For the same half-saturation constant and for zooplankton concentrations above that constant (which, in the case of this model and its baseline parameter values, is normal for the summer zooplankton population), the sigmoid term results in greater levels of predation on zooplankton (i.e. levels of predation closer to those of the linear term) than the hyperbolic term. Consequently, the region of  $\mu_2 - k_6$  space in which limit cycle behaviour occurs is larger for the sigmoid than for the hyperbolic form.



**Fig. 11.** Nitrate, phytoplankton and zooplankton equilibria across ranges of maximum zooplankton mortality rate,  $\mu_2$ , and mortality half-saturation constant,  $k_6$ , for the hyperbolic and sigmoid functional forms. Where limit cycles occur (at some values of  $\mu_2$  when  $k_6$  is low), the maximum and minimum values are indicated. The baseline values of predation parameters are  $\mu_2 = 0.325 \text{ day}^{-1}$ ,  $k_6 = 0.2 \text{ mmol N m}^{-3}$ . Note that the plots of nitrate equilibria have been rotated clockwise by  $90^\circ$  (relative to the other plots) for clarity. Concentrations are in  $\text{mmol N m}^{-3}$ .

**Table II.** Values of the  $N^*/k$  ratios estimated by SH92 for five models, plus our computed ratios for the Fasham (1993) model with each closure term. The five SH92 ratios correspond, respectively, to the models by Sarmiento *et al.* (1989), Wroblewski *et al.* (1988), Steele and Henderson (1981), Frost (1987) and Hofmann and Ambler (1988)

Closure term	SH92 ratio	Fasham (1993) ratio
Linear	0.2, $\leq 0.5$	0.93
Quadratic	3.3	3.04
Hyperbolic	6.0, 8.0	3.40
Sigmoid	–	1.42

### Four closure terms and a nutrient index

SH92 estimated the nutrient equilibrium values,  $N^*$ , for five models from the literature, and compared them with the nutrient uptake half-saturation constant,  $k$ , for each model. They concluded that:

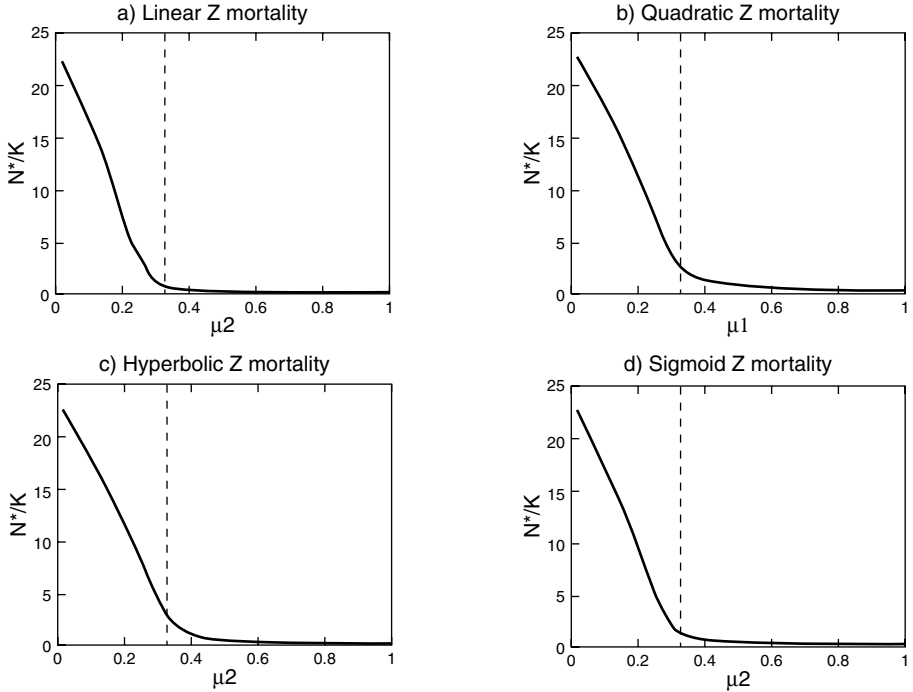
$$\frac{N^*}{k} < 1 \quad \text{for linear } Z \text{ mortality}$$

$$\frac{N^*}{k} > 1 \quad \text{for quadratic } Z \text{ mortality}$$

and for the hyperbolic mortality term, the ratio  $N^*/k$  is largest. The inference drawn from this was that the different choices of closure terms may directly influence the equilibrium state of plankton systems. In Table II, we show the ratio, or nutrient index, SH92 obtained for each model, together with ratios for the four alternative closure terms that we have just used for the Fasham model, for which  $k = 0.5$  (and all parameters are as for Figure 10, with  $\mu_1$  and  $\mu_2$  at the baseline values).

The value of  $N^*/k$  produced by the Fasham (1993) model with linear mortality is not as low as those found by SH92, and it only just falls below one. The values produced by the other forms fall markedly above one, but the quadratic and hyperbolic show only a minor difference, in contrast to the findings of SH92.

Figure 12 shows how the  $N^*/k$  ratio depends on  $\mu_1$  and  $\mu_2$ , and that the ratio can be above or below one, solely due to the value of  $\mu_1$  and  $\mu_2$ . Where a limit cycle occurs, the nitrate equilibrium is set to the midway point between the oscillation maximum and minimum. The ratio can take a wide range of values for each of the closure terms, and there seems to be no clear distinction between them. Furthermore, we have set the forcing functions to correspond to summertime conditions. Simulations incorporating the annual forcing show that with the linear zooplankton mortality and the baseline level of  $\mu_2$  used above, the zooplankton die out in the winter (Yool, 1998). This is due to the specific zooplankton mortality rate remaining high for low zooplankton concentrations, causing a steady state with zero zooplankton to become stable (Edwards and Brindley, 1999). This suggests



**Fig. 12.** Plots of the  $N^*/k$  ratio across a range of zooplankton mortality rates, using each of the four closure terms for the Fasham (1993) model. The ratio can be greater or less than one for all four terms, and depends more on the value of  $\mu_1$  or  $\mu_2$  than on the choice of closure term, in contrast to the conclusions of SH92.

that  $\mu_2$  for the linear closure term should be set to a lower value than for the other terms. However, Figure 12 shows that at such lower values the  $N^*/k$  ratio is always above one, contradicting the conclusions of SH92 regarding this ratio.

Furthermore, Edwards and Brindley (1996, 1999) computed diagrams of  $N^*$  against  $\mu_1$  and  $\mu_2$  from which we infer that  $N^*/k > 1$  for linear and quadratic closure terms across a wide spectrum of parameter values (except for the very highest values of  $\mu_2$  in the linear case, just like Figure 10). The models were based on the Steele and Henderson (1981) model, one of the models examined by SH92 (Table II). Moreover, Edwards (1997) showed diagrams from which we calculate that  $N^*/k < 1$  can hold for the quadratic closure term, as for Figure 10, when  $\mu_1$  is high and the sub-mixed-layer nutrient concentration is low.

Thus, in general, we find the value of  $N^*/k$  to depend more upon the value of  $\mu_1$  or  $\mu_2$  than on the choice of closure term, and that the ratio can be smaller or greater than one for a variety of models and closure terms. The SH92 conclusions may be due to other differences between the five models that they considered, which ranged from their 1981 NPZ model to the 10-equation model of Hofmann and Ambler (1988).

## Discussion

We have re-examined the influential paper by Steele and Henderson (1992) concerning the choice of closure terms in plankton population models. Steele and Henderson found that this choice can greatly affect the output of models. We have corrected an erroneous normalization of SH92's NPZ model, and recomputed their simulations with the corrected model. The results are generally unaffected, but where discrepancies do occur we have investigated their extent by constructing bifurcation diagrams, and found them to occur only for limited parameter ranges. In so doing, we have improved the understanding of the fundamental mechanisms controlling the dynamics of the models, and we have demonstrated that caution needs to be taken when 'normalizing' or non-dimensionalizing models. Furthermore, we have shown limit cycles to occur when the quadratic mortality function is used in the SH92 NPZ model. SH92 did not find these limit cycles because they varied only the zooplankton mortality parameter, and none of the other parameters. Note, however, that SH92 were not looking specifically for such oscillations. Rather, by changing the zooplankton mortality, the simple system, when seasonally forced, was shown to simulate the qualitative differences in  $N$ ,  $P$  and  $Z$  between the general situations in the North Pacific and the North Atlantic Oceans.

We then investigated the effects of using alternative closure terms in the Fasham (1993) model, a seven-component model that has been used to simulate the dynamics of various marine ecosystems, including the North Atlantic Ocean (Sarmiento *et al.*, 1993) and the Arabian Sea (Sharada and Yajnik, 1997; Ryabchenko *et al.*, 1998). With the physical conditions held constant at summertime values, we found limit cycles to occur for the linear closure term, and for the hyperbolic and sigmoid terms when the half-saturation coefficient ( $k_6$ ) takes low values. Finally, we reassessed the hypothesis of SH92 that the ratio of nutrient steady-state value to half-saturation coefficient for nutrient uptake (the nutrient index) could be related to the closure term. We found no such correlation when testing this hypothesis on the Fasham model, and conclude that the ratio is determined more by the parameter values used in the closure term than by the actual choice of closure term.

A primary consequence of the work here is that the quadratic mortality term should not be seen as a foolproof way to reduce the occurrence of limit cycles and thereby increase model stability. In the case of the models examined here, all four mortality terms were found to produce oscillatory behaviour, if not actually at baseline parameter values then at values in neighbouring parameter space. This latter point underlines the importance of sensitivity studies in ecological modelling. As both the form and parameterization of the mortality term are usually difficult to assign from ecological observations and experiments, this source of model uncertainty should be explored to ascertain its significance in a given model (especially given its role in modelling the export flux).

Overall though, the results presented here suggest that oscillations occur more commonly with the linear closure term than for the other closure terms. This concurs with Edwards and Brindley (1999), who found oscillations to be more

common across parameter space for linear closure than for the quadratic. Thus, although replacing a linear closure term with a quadratic one will not guarantee elimination of oscillations, it may certainly reduce the likelihood of them occurring—this is consistent with SH92's original findings.

Another choice of closure term is the combination of the linear and quadratic terms,  $\mu_2 Z + \mu_1 Z^2$ , used by McGillicuddy *et al.*, (1995) and Broström (1998). Such a form eliminates unfavourable consequences of using either the linear or quadratic form on their own (Edwards and Brindley, 1999). In particular, for the linear form the phytoplankton steady-state value depends only upon parameters in the zooplankton equation, and does not change with, say, an increase in nutrients. The combined form avoids this, but requires the estimation of two poorly known parameters rather than one, an objection cited by SH92 against forms such as the hyperbolic and sigmoid.

Using an alternative approach to construct models, Baird and Emsley (1999) attempted to derive interaction terms for plankton models from a 'first principles' perspective (given organism shape, size, buoyancy, swimming velocity, etc.), rather than rely on experimental work. Although these derivations currently apply only to passive predators (rather than those with more active, hunting behaviour), future extension of this work may provide a less arbitrary approach to assigning functional forms [see also (Rothschild and Osborn, 1988)].

In summary, although we have contradicted some of the results of SH92, our work essentially supports their conclusion—that the choice of zooplankton mortality term can have a profound impact upon the dynamics of plankton ecosystem models. Future work should therefore consider the influence of this term.

## Acknowledgements

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## References

- Baird, M.E. and Emsley, S.M. (1999) Towards a mechanistic model of plankton population dynamics. *J. Plankton Res.*, **21**, 85–126.
- Bauer, P., Gaito, S., McGlade, J.M. and Winter, D. (1993) Estimation of net photosynthetically available radiation over oceans from satellite data—application to a dynamic model of a plankton bloom in the Atlantic Ocean. *Photogramm. Eng. Remote Sensing*, **59**, 323–329.

- Begon,M., Harper,J.L. and Townsend,C.R. (1986) *Ecology: Individuals, Populations and Communities*. Blackwell Scientific, Oxford.
- Beltrami,E. and Carroll,T.O. (1994) Modelling the role of viral disease in recurrent phytoplankton blooms. *J. Math. Biol.*, **32**, 857–963.
- Broström,G. (1998) A note on the C/N and C/P ratio of the biological production in the Nordic seas. *Tellus*, **50B**, 93–109.
- Caswell,H. and Neubert,M.G. (1998) Chaos and closure terms in plankton food chain models. *J. Plankton Res.*, **20**, 1837–1845.
- Dadou,I., Garçon,V., Andersen,V., Flierl,G.R. and Davis,C.S. (1996) Impact of the north equatorial current meandering on a pelagic ecosystem—a modelling approach. *J. Mar. Res.*, **54**, 311–342.
- Denman,K.L. and Gargett,A.E. (1995) Biological-physical interactions in the upper ocean: the role of vertical and small scale transport processes. *Annu. Rev. Fluid Mech.*, **27**, 225–255.
- Doedel,E., Wang,X. and Fairgrieve,T. (1994) AUTO: Software for continuation and bifurcation problems in ordinary differential equations. Applied Mathematics Report, California Institute of Technology.
- Edwards,A.M. (1997) A rational dynamical-systems approach to plankton population modelling. PhD Thesis, University of Leeds, Leeds, UK.
- Edwards,A.M. and Brindley,J. (1996) Oscillatory behaviour in a three-component plankton population model. *Dyn. Stabil. Syst.*, **11**, 347–370.
- Edwards,A.M. and Brindley,J. (1999) Zooplankton mortality and the dynamical behaviour of plankton population models. *Bull. Math. Biol.*, **61**, 303–339.
- Evans,G.T. and Parslow,J.S. (1985) A model of annual plankton cycles. *Biol. Oceanogr.*, **3**, 327–347.
- Fasham,M.J.R. (1993) Modelling the marine biota. In Heimann,M. (ed.), *The Global Carbon Cycle*. Springer-Verlag, Berlin, pp. 457–504.
- Fasham,M.J.R. (1995) Variations in the seasonal cycle of biological production in subarctic oceans: A model sensitivity analysis. *Deep-Sea Res. I*, **42**, 1111–1149.
- Fasham,M.J.R., Ducklow,H.W. and McKelvie,S.M. (1990) A nitrogen-based model of plankton dynamics in the oceanic mixed layer. *J. Mar. Res.*, **48**, 591–639.
- Fasham,M.J.R., Sarmiento,J.L., Slater,R.D., Ducklow,H.W. and Williams,R. (1993) Ecosystem behavior at Bermuda Station ‘S’ and Ocean Weather Station ‘India’: a general circulation model and observational analysis. *Global Biogeochem. Cycles*, **7**, 379–415.
- Frost,B.W. (1987) Grazing control of phytoplankton stock in the open subarctic Pacific Ocean: a model assessing the role of mesozooplankton, particularly the large calanoid copepods *Neocalanus* spp. *Mar. Ecol. Prog. Ser.*, **39**, 49–68.
- Glendinning,P. (1994) *Stability, Instability and Chaos: An Introduction to the Theory of Nonlinear Differential Equations*. Cambridge Texts in Applied Mathematics. Cambridge University Press, Cambridge.
- Guckenheimer,J. and Holmes,P. (1983) *Nonlinear Oscillations, Dynamical Systems, and Bifurcations of Vector Fields*. Applied Mathematical Sciences Vol. 42. Springer-Verlag, New York.
- Hofmann,E.E. and Ambler,J.W. (1988) Plankton dynamics on the outer southeastern U.S. continental shelf. Part II: A time-dependent biological model. *J. Mar. Res.*, **46**, 883–917.
- Kohlmeier,C. and Ebenhöf,W. (1995) The stabilizing role of cannibalism in a predator–prey system. *Bull. Math. Biol.*, **57**, 401–411.
- Kuznetsov,Y.A. (1995) *Elements of Applied Bifurcation Theory*. Applied Mathematical Sciences Vol. 112. Springer-Verlag, New York.
- Malchow,H. (1994) Non-equilibrium structures in plankton dynamics. *Ecol. Model.*, **75**, 123–134.
- McGillicuddy,D.J., McCarthy,J.J. and Robinson,A.R. (1995) Coupled physical and biological modeling of the spring bloom in the North Atlantic (I): model formulation and one dimensional bloom process. *Deep-Sea Res. I*, **42**, 1313–1357.
- Pitchford,J. and Brindley,J. (1998) Intratrophic predation in simple predator–prey models. *Bull. Math. Biol.*, **60**, 937–953.
- Ross,A.H., Gurney,W.S.C. and Heath,M.R. (1994) A comparative study of the ecosystem dynamics of four fjords. *Limnol. Oceanogr.*, **39**, 318–343.
- Rothschild,B.J. and Osborn,T.R. (1988) Small-scale turbulence and plankton contact rates. *J. Plankton Res.*, **10**, 465–474.
- Ryabchenko,V.A., Gorchakov,V.A. and Fasham,M.J.R. (1998) Seasonal dynamics and biological productivity in the Arabian Sea euphotic zone as simulated by a three-dimensional ecosystem model. *Global Biogeochem. Cycles*, **12**, 501–530.
- Sarmiento,J.L., Fasham,M.J.R., Siegenthaler,U., Najjar,R. and Toggweiler,J.R. (1989) Models of chemical cycling in the ocean: Progress Report II. Ocean Tracers Laboratory Technical Report No. 6, Princeton University.

- Sarmiento, J.L., Slater, R.D., Fasham, M.J.R., Ducklow, H.W., Toggweiler, J.R. and Evans, G.T. (1993) A seasonal three-dimensional ecosystem model of nitrogen cycling in the North Atlantic euphotic zone. *Global Biogeochem. Cycles*, **7**, 417–450.
- Sharada, M.K. and Yajnik, K.S. (1997) Seasonal variation of chlorophyll and primary productivity in central Arabian Sea: A macrocalibrated upper ocean ecosystem model. *Proc. Indian Acad. Sci. (Earth Planet. Sci.)*, **106**, 33–42.
- Sharada, M.K. and Yajnik, K.S. (1999) Effect of nonlinear mortality and self-grazing on the dynamics of a marine ecosystem. *Sādhanā*, **24**, 17–24.
- Steele, J.H. and Henderson, E.W. (1981) A simple plankton model. *Am. Nat.*, **117**, 676–691.
- Steele, J.H. and Henderson, E.W. (1992) The role of predation in plankton models. *J. Plankton Res.*, **14**, 157–172.
- Taylor, A.H., Watson, A.J., Ainsworth, M., Robertson, J.E. and Turner, D.R. (1991) A modelling investigation of the role of phytoplankton in the balance of carbon at the surface of the North Atlantic. *Global Biogeochem. Cycles*, **5**, 151–171.
- Truscott, J.E. and Brindley, J. (1994) Equilibria, stability and excitability in a general class of plankton population models. *Philos. Trans. R. Soc. London Ser. A*, **347**, 703–718.
- Wiggins, S. (1990) *Introduction to Applied Nonlinear Dynamical Systems and Chaos. Texts in Applied Mathematics Vol. 2*. Springer-Verlag, New York.
- Wroblewski, J.S. (1989) A model of the spring bloom in the North Atlantic and its impact on ocean optics. *Limnol. Oceanogr.*, **34**, 1563–1571.
- Wroblewski, J.S., Sarmiento, J.L. and Flierl, G.R. (1988) An ocean basin scale model of plankton dynamics in the North Atlantic. (1) Solutions for the climatological oceanographic conditions in May. *Global Biogeochem. Cycles*, **2**, 199–218.
- Yool, A. (1998) The dynamics of open-ocean plankton ecosystem models. PhD Thesis, University of Warwick, UK; [www.oikos.warwick.ac.uk/ecosystems/ThesisArchive](http://www.oikos.warwick.ac.uk/ecosystems/ThesisArchive).

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## Appendix: The erroneous Steele and Henderson (1992) normalization

### Non-dimensionalizing the PZ system

The setting of  $\beta = \lambda = \mu = 1$  by SH92 in order to normalize equations (1) and (2) is a rescaling of  $P$ ,  $Z$  and  $t$ , such that the new equations have the form:

$$\frac{dp}{d\tau} = p \left( 1 - \frac{p}{c} \right) - \frac{p^v}{1 + p^v} z \quad (9)$$

$$\frac{dz}{d\tau} = \hat{\alpha} \frac{p^v}{1 + p^v} z - \hat{\alpha} a z^m \quad (10)$$

where  $\tau$  is non-dimensional time, and  $c$ ,  $\hat{\alpha}$  and  $a$  are non-dimensional parameters to be determined. Setting  $\beta = \lambda = \mu = 1$  in equations (1) and (2) thus gives equations of the form (9) and (10). SH92 had no mention of an  $\hat{\alpha}$  term because they only showed a steady-state version of the normalized system, their equations (3) and (4), for which any such  $\hat{\alpha}$  term cancels out.

This transformation can be made explicit by defining the new non-dimensional variables  $p$  and  $z$ , plus non-dimensional time,  $\tau$ , as:

$$\tau = \frac{t}{T}, \quad p = \frac{P}{\tilde{P}}, \quad z = \frac{Z}{\tilde{Z}} \quad (11)$$

and finding expressions for  $T$ ,  $\tilde{P}$  and  $\tilde{Z}$ . This gives:

$$\frac{d}{dt} = \frac{d\tau}{dt} \frac{d}{d\tau} = \frac{1}{T} \frac{d}{d\tau} \quad (12)$$

and substitution into equation (1) leads to:

$$\frac{dp}{d\tau} = \beta T p \left( 1 - \frac{\tilde{P} p}{\gamma} \right) - \frac{\lambda \tilde{Z} T}{\tilde{P}} \frac{\tilde{P}^v p^v}{\mu^v + \tilde{P}^v p^v} z \quad (13)$$

To make this into the form of equation (9) uniquely requires:

$$T = \frac{1}{\beta}, \quad \tilde{P} = \mu, \quad \tilde{Z} = \frac{\beta\mu}{\lambda} \quad (14)$$

Defining  $c = \gamma/\mu$  gives the required equation (9). The transformations (11) therefore become:

$$\tau = \beta t, \quad p = \frac{P}{\mu}, \quad z = \frac{\lambda Z}{\beta\mu} \quad (15)$$

Using these substitutions, equation (2) becomes

$$\frac{dz}{d\tau} = \frac{\alpha\lambda}{\beta} \frac{p^v}{1+p^v} z - \frac{\alpha\delta}{\beta} \cdot \left( \frac{\beta\mu}{\lambda} \right)^{m-1} z^m \quad (16)$$

and so to obtain the form (10) requires  $\hat{\alpha}$  and  $a$  to be defined as:

$$\hat{\alpha} = \frac{\lambda\alpha}{\beta}, \quad a = \frac{\delta\beta^{m-1}\mu^{m-1}}{\lambda^m} \quad (17)$$

The rescalings, or non-dimensionalizations, (15) and (17) are unique in that they are the only transformations that will turn equations (1) and (2) into the required forms (9) and (10).

In the non-dimensional system with time,  $\tau$ , one unit of time is equivalent to  $1/\beta$  days (the old time scale was days). SH92 took an average doubling time for the phytoplankton of 2 days, which means that  $\beta = \ln 2/2$ . Thus one new unit of time =  $2/\ln 2 = 2.88$  days, and so 100 new time units are approximately equal to 1 year.

### *Non-dimensionalizing the NPZ system*

The full three-component system considered by SH92 has the original dimensional form:

$$\frac{dN}{dt} = -\beta \frac{N}{k+N} P \left( 1 - \frac{P}{\gamma} \right) + (1-\alpha) \frac{\lambda P^2}{\mu^2 + P^2} Z + S(N_0 - N) \quad (18)$$

$$\frac{dP}{dt} = \beta \frac{N}{k+N} P \left( 1 - \frac{P}{\gamma} \right) - \frac{\lambda P^2}{\mu^2 + P^2} Z \quad (19)$$

$$\frac{dZ}{dt} = \alpha \frac{\lambda P^2}{\mu^2 + P^2} Z - \alpha\delta Z^m \quad (20)$$

where  $S$  is the cross-thermocline exchange rate,  $N_0$  is the nutrient concentration below the mixed layer and  $k$  is the half-saturation coefficient for nutrient uptake. In their numerical simulations, SH92 only considered the Holling Type III grazing function, and so we have set  $v = 2$  in the grazing expression  $\lambda P^v/(\mu^v + P^v)$ . SH92 then expressed the three equations in the following form, and stated that equations (22) and (23) had been normalized in the same way as for the two-component system [requiring equation (23) to be identical to equation (10)]:

$$\frac{dn}{d\tau} = -\frac{n}{\tilde{k}+n} p \left( 1 - \frac{p}{c} \right) + (1-\hat{\alpha}) \frac{p^2}{1+p^2} z + s (n_0 - n) \quad (21)$$

$$\frac{dp}{d\tau} = \frac{n}{\tilde{k}+n} p \left( 1 - \frac{p}{c} \right) - \frac{p^2}{1+p^2} z \quad (22)$$

$$\frac{dz}{d\tau} = \hat{\alpha} \frac{p^2}{1+p^2} z - \hat{\alpha} a z^m \quad (23)$$

where  $s$ ,  $n_0$  and  $\tilde{k}$  are new non-dimensional parameters, and  $n$  is the non-dimensionalized nutrient variable. Note that SH92 had  $\alpha$  in their form of the above equations instead of  $\hat{\alpha}$  because they did not

rename their parameters or variables in their normalized equations. We have  $\hat{\alpha}$  because the *NPZ* system is required to be normalized in the same way as the *PZ* system, which we have shown earlier to require the  $\hat{\alpha}$  term.

Since equations (22) and (23) have been normalized, equation (21) must clearly have been rescaled in the same way, so that the units of time,  $p$  and  $z$  are consistent in all three equations. However, we now show that equations (18), (19) and (20) cannot be rescaled into exactly the form of equations (21), (22) and (23) using the same non-dimensionalizations as those used for the two-component system.

Using the substitutions for  $t$ ,  $P$  and  $Z$  given by (15), and defining  $n$  as:

$$n = \frac{N}{\tilde{N}} \quad (24)$$

the three dimensional equations (18), (19) and (20) become:

$$\frac{dn}{d\tau} = -\mu \frac{n}{k + \tilde{N}n} p \left(1 - \frac{p}{c}\right) + (1 - \alpha) \frac{\mu}{\tilde{N}} \frac{p^2}{1 + p^2} z + \frac{S}{\beta} \left(\frac{N_0}{\tilde{N}} - n\right) \quad (25)$$

$$\frac{dp}{d\tau} = \frac{\tilde{N}n}{k + \tilde{N}n} p \left(1 - \frac{p}{c}\right) - \frac{p^2}{1 + p^2} z \quad (26)$$

$$\frac{dz}{d\tau} = \hat{\alpha} \frac{p^2}{1 + p^2} z - \hat{\alpha} a z^m \quad (27)$$

The zooplankton equation (27) is the same as equation (23). We require that equations (25) and (26) are in the same form as equations (21) and (22). In order for the phytoplankton uptake terms to be the same in the nutrient and phytoplankton equations [the first terms in equations (25) and (26)], we require  $\tilde{N} = \mu$ . Note that  $N$  and  $P$  must be scaled by the same factor, namely  $\mu$ , since the uptake terms have the same form in the dimensional  $dN/dt$  and  $dP/dt$  equations, plus they have the same form in the non-dimensional  $dn/d\tau$  and  $dp/d\tau$  equations. The definitions  $s = S/\beta$ ,  $n_0 = N_0/\mu$  and  $\tilde{k} = kl\mu$  are clearly required.

This leaves only the regeneration term, the penultimate term in equation (25), not in the required form given in equation (21). In equation (25) there is a  $(1 - \alpha)$  term ( $\tilde{N} = \mu$ , so  $\mu/\tilde{N} = 1$ ), but in equation (27) we have  $\hat{\alpha}$ , which is given by  $\hat{\alpha} = \lambda\alpha/\beta$ . This shows that equations (21), (22) and (23) are inconsistent, since they have  $(1 - \hat{\alpha})$  for the regeneration in equation (21), and  $\hat{\alpha}$  in equation (23), but we have just shown that it cannot be the same ‘alpha’ in both equations. The value of  $\beta$  used by SH92 was  $\ln 2/2 = 0.35$ , and they did not actually give a value for  $\lambda$  (because it became ‘normalized’), but in an earlier paper (Steele and Henderson, 1981) they used 0.6, and so  $\lambda/\beta \neq 1$  and  $\hat{\alpha} \neq \alpha$ .

The full consistent non-dimensional equations are therefore:

$$\frac{dn}{d\tau} = -\frac{n}{\tilde{k} + n} p \left(1 - \frac{p}{c}\right) + (1 - \alpha) \frac{p^2}{1 + p^2} z + s(n_0 - n) \quad (28)$$

$$\frac{dp}{d\tau} = \frac{n}{\tilde{k} + n} p \left(1 - \frac{p}{c}\right) - \frac{p^2}{1 + p^2} z \quad (29)$$

$$\frac{dz}{d\tau} = \hat{\alpha} \frac{p^2}{1 + p^2} z - \hat{\alpha} a z^m \quad (30)$$

and contain both  $\alpha$  and  $\hat{\alpha}$ . Since  $\alpha$  is a dimensionless constant, the equations are non-dimensional and consistent. These are equations (5), (6) and (7) given in the main text, as used for our simulations.

For their numerical simulations, SH92 used  $\hat{\alpha} = 0.5$  in the (incorrect) equations (21), (22) and (23), which is equivalent to setting  $\alpha = \hat{\alpha} = 0.5$  in the corrected system given by equations (28), (29) and (30). Setting  $\alpha = 0.5$  in equation (28) is equivalent to setting  $\alpha = 0.5$  in equation (18), the original dimensional  $dN/dt$  equation. Setting  $\hat{\alpha} = 0.5$  in equation (30) means that the corresponding  $\alpha$  in equation (20), the dimensional  $dZ/dt$  equation, is given by  $\beta\hat{\alpha}/\lambda$ . With  $\beta = 0.35$  and  $\lambda = 0.6$ , this gives  $\alpha = 0.29$ . So the SH92 value of  $\hat{\alpha} = 0.5$  in their normalized equations (21), (22) and (23) corresponds to setting  $\alpha = 0.5$  in equation (18), but  $\alpha = 0.29$  in equation (20). This means that a proportion 0.29 of zooplankton grazing fuels zooplankton growth, a proportion 0.5 ( $= 1 - 0.5$ ) is recycled as nutrient, and

the remaining 0.21 is lost from the system, but the way that SH92 wrote their original dimensional equations (18), (19) and (20), with the same ‘alpha’ in equation (18) and equation (20), implies that they intended a proportion  $\alpha$  of zooplankton grazing to fuel zooplankton growth, with the remaining proportion  $1 - \alpha$  to be recycled into nutrient, with no external loss from the system. However, the values of the non-dimensional parameters that they used does give a loss, due to the inconsistencies in the non-dimensionalization, giving a slight structural difference to their original dimensional model. The value  $\hat{\alpha} = 0.5$  was used by SH92 for both the  $pz$  and  $npz$  models, and so we take this to be the ‘true’ intended value, and use this plus the corrected value of  $\alpha = \beta\hat{\alpha}/\lambda = 0.29$  to recompute the simulations of SH92.

The reason that the SH92 normalization does not work is that the concept of normalizing the equations is used in two subtly different manners. In normalizing the  $PZ$  system, SH92 set three of the parameters equal to one. This reduces the number of parameters in the model by three, which means that  $P$ ,  $Z$  and time have been scaled independently with the aim of reducing the total number of parameters. However, for the  $NPZ$  system, the extra variable  $N$  is not scaled independently of the others. This is because SH92 wrote the original  $NPZ$  equations such that  $N$  and  $P$  are measured in the same units, and then wrote the normalized  $npz$  equations such that the phytoplankton growth term has the same form in the  $dn/dt$  and  $dp/dt$  equations, i.e. the first two terms in equations (5) and (6) have the same formulation. Therefore,  $N$  and  $P$  must be scaled by the same factor to obtain  $n$  and  $p$ , and so the number of parameters is not reduced further by one. In actual fact, non-dimensionalizing the  $NPZ$  equations only reduces the number of parameters by two: from nine to seven. The subtle reason for this is that when the  $PZ$  model was normalized,  $\hat{\alpha}$  replaced the zooplankton growth efficiency  $\alpha$  and absorbed the rescaling of  $Z$ , but the original  $\alpha$  is still required in the normalized  $npz$  equations (in the  $n$  equation), and  $\hat{\alpha}$  is also required. Thus, the number of parameters reduced by the non-dimensionalization is three for the  $PZ$  model, but only two for the  $NPZ$  model.