

Simulating the impacts of climate change on ecosystems: the importance of mortality.

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EXTENDED ABSTRACT

The potential for marine plankton ecosystems to influence climate by the production of dimethylsulphide (DMS) has been an important topic of recent research into climate change. Several general circulation models used to predict climate change have or are being modified to include interactions of ecosystems with climate. Climate change necessitates that parameters within ecosystem models must change during long-term simulations, especially mortality parameters that increase as organisms are pushed toward the boundaries of their thermal tolerance. There is therefore a pressing need to understand the influence of varying mortality parameters on the long-term behaviour of ecosystem models.

Mortality terms have been identified as important determinants of ecosystem model dynamics. Although many forms of mortality have been proposed for use in ecosystem models, linear mortality forms are often used because they are simple, require only one parameter each (parameters are often poorly known), and there is little empirical data to support alternative forms. Mortality parameters have also proved to be useful bifurcation parameters for simple ecosystem models.

We consider an ecosystem model originally developed to reproduce marine plankton and microbial dynamics that was subsequently developed to include dimethylsulphoniopropionate (DMSP) and DMS for use in climate change simulations. This model has proved useful in reproducing spatial distributions and depth profiles of DMS observed in the ocean and in predicting the potential for biogenic DMS to ameliorate climate change. Reproducing observed data is often the only validation available for ecosystem models.

The model is composed of five biotic compartments: phytoplankton (P), zooplankton (Z),

dissolved inorganic nitrogen (N), bacteria (B) and zooflagellates (F). The model is composed of five coupled differential equations that together with the mass conservation constraint $B + F + N + P + Z = 1$ form a four degrees of freedom system where each scaled variable is a concentration satisfying $0 \leq B, F, N, P, Z \leq 1$ for all time $t > 0$. The model has fourteen critical points of which seven lie in the ecologically feasible region of the state space for measured parameter values. The location and stability properties of these critical points substantially control the dynamics of the model. The model has a very complicated, robust and highly nonlinear limit cycle attractor. This attractor is composed of two distinct components; a BFN component and an NPZ component. Mostly the model circulates on planes where $B + F + N = 1$ and $N + P + Z = 1$ rather than in the full four-dimensional state space.

We examine the effects of varying three linear mortality coefficients. Although the limit cycle of the model is very robust with respect to variations in the values of the mortality parameters, significant changes in dynamics can be induced by parameter variations. Stable spiral points and asymptotically stable nodes are observed for moderate one-at-a-time variations in mortality. A climate change scenario, in which all mortality parameters are increased simultaneously, indicates the ecosystem will reach a final stable state where only phytoplankton exist. This state is a result of the model not containing an explicit phytoplankton mortality term. The inclusion of a phytoplankton mortality term to the model has little effect on the dynamics, and hence its ability to reproduce observed data, but has a significant effect on the bifurcation behaviour. Rather than predict an phytoplankton-dominated final state, the model now predicts the extinction of all biota. This research suggests that the specific formulation of ecosystem models must be considered very carefully if they are to be applied in simulations of climate change.

1. INTRODUCTION

Dimethylsulphide (DMS) molecules in the atmosphere have been identified as a potentially significant modifier of solar radiation reflectance and hence climate (Charlson et al. 1987). The production and emission to the atmosphere of DMS from plankton blooms in the upper regions of the oceans has consequently been a subject of growing interest observationally, experimentally, and by modelling. We consider a model introduced by Moloney et al. (1986) and subsequently developed by Gabric et al. (1993) to include dimethylsulphoniopropionate (DMSP) and DMS. This model has proved useful in reproducing spatial distributions and depth profiles of DMS observed in the ocean and in predicting the potential for biogenic DMS to ameliorate climate change (Cropp et al. 2004). This work showed that understanding the inherent dynamics of the GMSK model is important in understanding more detailed and realistic models. It also demonstrated that the sulphur compartments of the model may be considered as a separate sub-model that is slaved to the nitrogen-based ecosystem model, and therefore when considering the determinants of DMS we need only consider the dynamics of the ecosystem model.

Mortality terms have been identified as important determinants of ecosystem model dynamics (Steele and Henderson 1992). Although many forms of mortality have been proposed for use in ecosystem models, linear mortality forms are often used because they are simple, require only one parameter each (parameters are often poorly known), and there is little empirical data to support alternative forms (Edwards and Brindley 1999). The coefficients of mortality terms have served as effective bifurcation parameters in studies of simple ecosystem dynamics (Edwards and Brindley 1999). The choice of the form of the mortality terms has also been shown to have an important influence on the dynamics of simple ecosystem models (Steele and Henderson 1992, Edwards and Yool 2000). We therefore chose to examine the influence of all the linear mortality terms in the model.

Examination of the influence of mortality parameters on ecosystem model dynamics is also interesting and important in the context of modelling ecosystem responses to climate change. It is reasonable to assume that most anthropogenically unperturbed ecosystems, and most organisms within them, are well adapted to their ambient environment, and in particular to the ambient temperature. Generally therefore, species are maintained near the centre of their ecological niches. Any change in climate will have the effect of moving species from the optimal position in their ecological niche to a less-optimal position where reproduction is reduced and mortality increased. The response of ecosystem models to

increases in mortality rate is therefore useful as an indicator of the influence of climate change, and also of the suitability of particular ecosystem models for applications in earth system models used to predict global climate change.

2. THE MODEL

The model is composed of five biotic compartments: phytoplankton (P), zooplankton (Z), dissolved inorganic nitrogen (N), bacteria (B) and zooflagellates (F). Our five coupled differential equations model together with the mass conservation constraint $P + Z + N + B + F = 1$ forms a four degrees of freedom system where each variable is a concentration satisfying $0 \leq P, Z, N, B, F \leq 1$ for all time $t \geq 0$. The model is composed of the following equations:

$$\frac{dP}{dt} = k_{23} \left(\frac{N}{N + k_{24}} \right) P - k_1 \left(\frac{P}{P + k_2} \right) B - k_4 PZ, \quad (1)$$

$$\frac{dB}{dt} = k_1 (1 - k_{11}) \left(\frac{P}{P + k_2} \right) B - k_8 \left(\frac{B}{B + k_9} \right) F + k_{25} (1 - k_{11}) \left(\frac{N}{N + k_{26}} \right) B - k_{10} B, \quad (2)$$

$$\frac{dF}{dt} = k_8 (1 - k_{14}) \left(\frac{B}{B + k_9} \right) F - k_{13} F, \quad (3)$$

$$\frac{dZ}{dt} = k_4 (1 - k_{20}) PZ - k_{19} Z, \quad (4)$$

$$\begin{aligned} \frac{dN}{dt} = & k_{10} B + k_{11} \left[k_{25} \left(\frac{N}{N + k_{26}} \right) B + k_1 \left(\frac{P}{P + k_2} \right) B \right] \\ & + k_{13} F + k_8 k_{14} \left(\frac{B}{B + k_9} \right) F + k_{19} Z + k_4 k_{20} PZ \quad (5) \\ & - k_{23} \left(\frac{N}{N + k_{24}} \right) P - k_{25} \left(\frac{N}{N + k_{26}} \right) B \end{aligned}$$

The parameter set for the ecosystem model (Table 1) is composed of parameter values from station one of Gabric et al (1999) and literature values cited by Gabric et al (1993).

Equations (1)-(5) are non-dimensionalised and the state variables replaced by their scaled equivalents:

$$C' = \frac{C}{N_0} \quad \text{for } C = B, F, N, P \text{ and } Z \text{ while time is}$$

scaled by the maximum phytoplankton growth rate $t' = k_{23} t$. The resultant scaled parameter values are listed in Table 1. These values will be used throughout this analysis unless otherwise specified.

Table 1: Measured parameter values.

| PAR | UNITS | MEAS. VALUE | SCALED VALUE |
|----------|---------------------|-------------|--------------|
| k_1 | d^{-1} | 0.31 | 1.148 |
| k_2 | $mgNm^{-3}$ | 34.65 | 0.693 |
| k_4 | $m^3mgN^{-1}d^{-1}$ | 0.01 | 1.852 |
| k_8 | d^{-1} | 1.67 | 6.185 |
| k_9 | $mgNm^{-3}$ | 9.10 | 0.182 |
| k_{10} | d^{-1} | 0.07 | 0.259 |
| k_{11} | - | 0.63 | 0.630 |
| k_{13} | d^{-1} | 0.05 | 0.185 |
| k_{14} | - | 0.65 | 0.650 |
| k_{19} | d^{-1} | 0.05 | 0.185 |
| k_{20} | - | 0.40 | 0.400 |
| k_{23} | d^{-1} | 0.27 | 1.000 |
| k_{24} | $mgNm^{-3}$ | 12.60 | 0.252 |
| k_{25} | d^{-1} | 0.31 | 1.148 |
| k_{26} | $mgNm^{-3}$ | 3.45 | 0.069 |
| N_0 | $mgNm^{-3}$ | 154 | 1 |

The non-dimensionalisation implemented on the model scales the mortality rates of B , F and Z relative to the maximum P growth rate. We explore varying three key mortality parameters, k_{10} , k_{13} and k_{19} over a range of 4 - 1,000% of measured values. As moving species from their optimal niche positions simultaneously reduces their reproduction rate and increases their mortality rate it is reasonable to examine the influence of quite large increases in scaled mortality rates.

3. ANALYSIS

3.1. Dynamics

The model has seven critical points (labelled CP 1 – 7, see 3.2 below) that appear to substantially control the shape of its limit cycle. The dynamics of the model are confined to a very structurally stable and highly nonlinear periodic orbit shown in NPZ and BFN state spaces in Figures 1 and 2. The combination of these figures describes the dynamics of the model in the five dimensional state space. Dotted lines show the triangular planes defined by mass conservation in each state space. The locations of the critical points are marked by stars, and some eigenvectors of important positive (outward pointing) and negative (inward pointing) eigenvalues are shown for each critical point.

We note that the system is never actually on the simplex planes as B and F in the case of the NPZ plane, and P and Z in the case of the BFN plane are very small but never exactly zero; for ease of discussion we will not labour this distinction.

Figures 2 and 3 reveal that six of the seven feasible critical points of the model form three pairs of closely aligned points: CP 1 and 7 lie very close, as

do CP 3 and 4, and CP 5 and 6. CP 2 is unique in the model in that it is a lone feasible critical point for measured parameter values. The locations of most of the critical points can, however, be expected to change in response to variations in k_{10} , k_{13} and k_{19} .

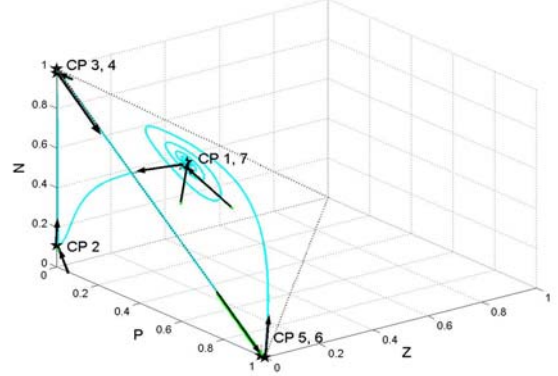


Figure 1: Model dynamics in NPZ state space.

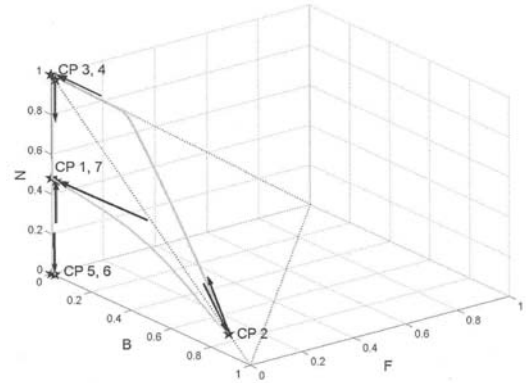


Figure 2: Model dynamics in BFN state space.

3.2. Critical Points

The model has fourteen critical points of which seven lie in the ecologically feasible region of the state space for measured parameter values. The first critical point (CP 1), and the only critical point to have all non-zero state variables is:

$$P_1^* = \left(\frac{k_{19}}{k_4(1-k_{20})} \right), \quad (6)$$

$$B_1^* = \frac{k_9 k_{13}}{k_8(1-k_{14}) - k_{13}}, \quad (7)$$

$$F_1^* = \left(\frac{B_1^* + k_9}{k_8} \right) \begin{bmatrix} k_1(1-k_{11}) \left(\frac{P_1^*}{F_1^* + k_2} \right) - k_{10} \\ + k_{25}(1-k_{11}) \left(\frac{N_1^*}{N_1^* + k_{26}} \right) \end{bmatrix}, \quad (8)$$

$$Z_1^* = \left(\frac{k_{23}}{k_4} \right) \left(\frac{N_1^*}{N_1^* + k_{24}} \right) - \left(\frac{k_1}{k_4} \right) \left(\frac{B_1^*}{F_1^* + k_2} \right), \quad (9)$$

$$N_1^* = 1 - B_1^* - F_1^* - P_1^* - Z_1^*. \quad (10)$$

The second critical point (CP 2) is given by:

$$B_2^* = 1 - \frac{k_{10}k_{26}}{k_{25}(1-k_{11}) - k_{10}}, \quad (11)$$

$$N_2^* = \frac{k_{10}k_{26}}{k_{25}(1-k_{11}) - k_{10}}, \quad (12)$$

$$P_2^*, Z_2^*, F_2^* = 0. \quad (13)$$

Useful expressions for two of the eigenvalues of CP 2 are obtainable:

$$\lambda_{CP_{2-1}} = k_{23} \left(\frac{N_2^*}{N_2^* + k_{24}} \right) - \left(\frac{k_1}{k_2} \right) B_2^*, \quad (14)$$

$$\lambda_{CP_{2-2}} = -k_{19}, \quad (15)$$

while the other two are given by the roots of a quadratic that are not enlightening. The third critical point (CP 3) is located at:

$$B_3^* = \frac{k_9 k_{13}}{k_8(1-k_{14}) - k_{13}}, \quad (16)$$

$$F_3^* = \frac{k_{25}(1-k_{11})(B_3^* + k_9)}{k_8} \left(\frac{N_3^*}{N_3^* + k_{26}} \right) - \frac{k_{10}}{k_8} (B_3^* + k_9), \quad (17)$$

$$N_3^* = \frac{1}{2} \left[\begin{array}{l} - \left(k_{26} + B_3^* + \left(\frac{B_3^* + k_9}{k_8} \right) (k_{25}(1-k_{11}) - k_{10}) - 1 \right) \\ \pm \sqrt{\left(k_{26} + B_3^* + \left(\frac{B_3^* + k_9}{k_8} \right) (k_{25}(1-k_{11}) - k_{10}) - 1 \right)^2} \\ - 4k_{26} \left(B_3^* - 1 + k_{10} \left(\frac{B_3^* + k_9}{k_8} \right) \right) \end{array} \right], \quad (18)$$

$$P_3^*, Z_3^* = 0. \quad (19)$$

For measured parameter values CP 3 lies very close to the fourth critical point (CP 4) at the origin of the system where no biota are extant:

$$N_4^* = 1, \quad (20)$$

$$P_4^*, Z_4^*, B_4^*, F_4^* = 0. \quad (21)$$

Useful eigenvalues expressions may also be obtained for CP 4:

$$\lambda_{CP_{4-1}} = \frac{k_{23}}{1+k_{24}}, \quad (22)$$

$$\lambda_{CP_{4-2}} = \frac{k_{25}(1-k_{11})}{1+k_{26}} - k_{10}, \quad (23)$$

$$\lambda_{CP_{4-3}} = -k_{19}, \quad (24)$$

$$\lambda_{CP_{4-4}} = -k_{13}. \quad (25)$$

The fifth critical point (CP 5) is the phytoplankton-only critical point:

$$P_5^* = 1, \quad (26)$$

$$Z_5^*, N_5^*, B_5^*, F_5^* = 0. \quad (27)$$

Again, useful eigenvalues expressions may be obtained for CP 5:

$$\lambda_{CP_{5-1}} = k_4(1-k_{20}) - k_{19}, \quad (28)$$

$$\lambda_{CP_{5-2}} = \frac{k_1(1-k_{11})}{1+k_2} - k_{10}, \quad (29)$$

$$\lambda_{CP_{5-3}} = -\frac{k_{23}}{k_{24}}, \quad (30)$$

$$\lambda_{CP_{5-4}} = -k_{13}. \quad (31)$$

The system has a further critical point (CP 6) that lies very close to CP 5 for measured parameter values, given by:

$$P_6^* = \frac{k_1}{k_{23}} \left(\frac{N + k_{24}}{N} \right) B_6^* - k_2, \quad (32)$$

$$B_6^* = \frac{k_9 k_{13}}{k_8(1-k_{14}) - k_{13}}, \quad (33)$$

$$F_6^* = \frac{k_{25}(1-k_{11})(B_6^* + k_9)}{k_8} \left(\frac{N_6^*}{N_6^* + k_{26}} \right) - \frac{k_{10}}{k_8} (B_6^* + k_9), \quad (34)$$

$$Z_6^* = 0, \quad (35)$$

$$N_6^* = 1 - B_6^* - F_6^* - P_6^*. \quad (36)$$

A seventh critical point (CP 7), which lies very close to CP 1 for measured parameter values, is given by:

$$P_7^* = \frac{k_{19}}{k_4(1-k_{20})}, \quad (37)$$

$$Z_7^* = \frac{k_{23}}{k_4} \left(\frac{N_7^*}{N_7^* + k_{24}} \right), \quad (38)$$

$$N_7^* = \frac{1}{2} \left[\begin{array}{l} - \left(k_{24} + P_7^* + \frac{k_{23}}{k_4} - 1 \right) \\ \pm \sqrt{\left(k_{24} + P_7^* + \frac{k_{23}}{k_4} - 1 \right)^2 - 4k_{24}(P_7^* - 1)} \end{array} \right], \quad (39)$$

$$B_7^*, F_7^* = 0. \quad (40)$$

3.3. Variations in B mortality (k_{10})

The locations of critical points CP 1, 2, 3, 6 and 7 are sensitive to variations in k_{10} . Critical points CP 1, 2, 3 and 6 lose feasibility as k_{10} increases, and CP 7 eventually becomes stable. As k_{10} increases from its measured value CP 2 approaches CP 3 and F_3^* slowly reduces until the two critical points collide when F_3^* becomes zero and a “transcritical” bifurcation occurs, although no transfer of stability takes place (both critical points are unstable before and after the collision), which occurs when:

$$k_{10} = k_{25} (1 - k_{11}) \left(\frac{1 - B_2^*}{1 - B_2^* + k_{26}} \right) = 0.396, \quad (41)$$

where $B_2^* = B_3^* = \frac{k_9 k_{13}}{k_8 (1 - k_{14}) - k_{13}}$. CP 3 is now infeasible and as k_{10} is increased further CP 2 also becomes infeasible when B_2^* becomes zero, which occurs when:

$$k_{10} = \frac{k_{25} (1 - k_{11})}{1 + k_{26}} = 0.397. \quad (42)$$

At this point the eigenvalue λ_{CP_4-2} of CP 4 (equation (23)) becomes negative and CP 2 and CP 4 collide. However, λ_{CP_4-1} of CP 4 is never negative, so no change of stability occurs.

If k_{10} exceeds the value defined by equation (42) the system is in NPZ state space most of the time, taking short excursions into the BFN state space. However when:

$$k_{10} = (1 - k_{11}) \left(k_1 \left(\frac{P_{1,7}^*}{P_{1,7}^* + k_2} \right) + k_{25} \left(\frac{N_{1,7}^*}{N_{1,7}^* + k_{26}} \right) \right) \approx 0.453, \quad (43)$$

CP 1 and CP 7 closely approach and the system changes from a limit cycle to an asymptotically stable node at CP 7. Stability in this case is conferred

by the single positive real eigenvalue of CP 7 becoming negative, rather than a true Hopf bifurcation.

When $k_{10} > 0.453$ we can see from equation (2) that $\frac{dB}{dt}$ is always negative when the system is in the vicinity of CP 1 or 7. The system is now prevented from flipping to the BFN plane.

3.4. Variations in F mortality (k_{13})

The locations of critical points CP 1, 3 and 6 are sensitive to variations in k_{13} (note that CP 6 has two feasible roots for some values of k_{13}). The location of CP 2 is insensitive to variations in k_{13} but the eigenvalues of this point are affected by variations in the parameter. Critical points CP 1, 3 and 6 all become infeasible as k_{13} increases.

The first change that occurs as k_{13} increases is at $k_{13} = 1.508$, when a second root of CP 6-2, becomes feasible. CP 6 has two positive roots for values of k_{13} less than 1.508, but the second root is ecologically infeasible. This second critical point however soon disappears along with CP 6-1 in a saddle-node bifurcation when $k_{13} = 1.537$. This change in CP 6 coincides with the loss of feasibility of CP 1. The Z population reduces as k_{13} increases and eventually $Z_1^* = 0$ when:

$$k_{13} = \frac{k_8 k_{23} (1 - k_{14}) \left(\frac{k_{19}}{k_4 (1 - k_{20})} + k_2 \right)}{k_1 k_9 \left(1 + \frac{k_{24}}{N_1^*} \right) + k_{24} \left(\frac{k_{19}}{k_4 (1 - k_{20})} + k_2 \right)} = 1.537. \quad (44)$$

These events are not accompanied by any change in the stability properties of the system. However as k_{13} approaches this value the magnitude of the P blooms decreases and the system progressively spends more time in the BFN state space until at $k_{13} = 1.537$ it appears that P no longer blooms and the system is effectively confined to the BFN state space.

As k_{13} increases further the real parts of the eigenvalues of CP 3 all become negative when $k_{13} = 1.653$. At this point CP 3 becomes an asymptotically stable spiral node, a change in stability that apparently is not accompanied by any qualitative change in the critical points. This point remains stable until CP 3 collides with CP 2 in a transcritical bifurcation that occurs when $F_3^* = 0$ and:

$$k_{13} = k_8 (1 - k_{14}) \left(\frac{B_3^*}{B_3^* + k_9} \right) = 1.799, \quad (45)$$

where $B_3^* = B_2^* = 1 - \frac{k_{10}k_{26}}{k_{25}(1-k_{11})-k_{10}} = 0.892$. At

this point CP 3 becomes a saddle point, while CP 2 acquires stability and remains a stable node for further increases in k_{13} .

3.5. Variations in Z mortality (k_{19})

Increases in k_{19} engender a bifurcation when:

$$k_{19} = k_4(1-k_{20}) = 1.111, \quad (46)$$

at which point CP 7 collides, and CP 1 “almost collides” with CP 5. When this occurs the positive eigenvalue of CP 5 becomes negative and CP 5 becomes an asymptotically stable node. In this case the system changes from a limit cycle to a stable node. As noted above, all the eigenvalues of the system have become real by this point.

3.6. Simultaneous variations in all mortality parameters

Simultaneous variation in k_{10} , k_{13} and k_{19} leads to similar bifurcation behaviour to that described above. The salient effect of varying all the mortality parameters together is that the critical points CP 2 and 3, that previously became stable for perturbations of k_{10} singly, no longer do so. The only critical points that now become stable are CP 7, which now becomes stable when k_{10} , k_{13} and k_{19} all equal 0.506 and CP 5 ($P_5^* = 1$), which acquires stability at 1.111. At this point the eigenvalues of all the critical points all become real. For mortality parameter values greater than 1.111, the only other ecologically feasible critical point is CP 4 ($N_4^* = 1$). This critical point has one positive eigenvalue that appears insensitive to all mortality parameter perturbations, indicating that CP 4 is always unstable.

3.7. An amended model

The stability scenario for a simultaneous increase in mortality parameters is exactly the circumstance that ensues when ecosystems are subject to climate change, and species are pushed to the limits of their thermal ecological niches and beyond. Our results that predict that P is the only survivor appears to be a result of the model formulation not including an explicit mortality term for P . We amended the model by subtracting an explicit P linear mortality term (k_5P) from equation (1) and adding it to equation (5). Considering the equivalent of CP 5 of the original model in the new model (CP 5_{alt}), we find that this critical point has become:

$$P_{5_alt}^* = \frac{k_{23} - k_5(1 + k_{24})}{k_{23} - k_5}, \quad (47)$$

$$N_{5_alt}^* = 1 - \frac{k_{23} - k_5(1 + k_{24})}{k_{23} - k_5}, \quad (48)$$

$$B_{5_alt}^*, F_{5_alt}^*, Z_{5_alt}^* = 0. \quad (49)$$

The eigenvalues of this point are:

$$\lambda_{CP_5alt-1} = k_4(1 - k_{20}) - k_{19}, \quad (50)$$

$$\lambda_{CP_5alt-2} = \frac{k_1(1 - k_{11})}{1 + k_2} - k_{10}, \quad (51)$$

$$\lambda_{CP_5alt-3,4} = - \left(k_5 + k_{13} + \frac{k_{23}}{k_{24}} \right) \left(1 \pm \sqrt{1 - \frac{4k_{13}k_{23}k_{24}}{[k_{24}(k_5 + k_{13}) + k_{23}]^2}} \right). \quad (52)$$

λ_{CP_5alt-1} is negative when:

$$k_{19} > k_4(1 - k_{20}) = 1.111, \quad (53)$$

while λ_{CP_5alt-2} is positive when:

$$k_{10} < \frac{k_1(1 - k_{11})}{1 + k_2} = 0.251. \quad (54)$$

λ_{CP_5alt-1} and λ_{CP_5alt-2} are therefore identical to λ_{CP_5-1} and λ_{CP_5-2} of the original model. $\lambda_{CP_5alt-3,4}$ are always negative and CP 5_{alt} will be an asymptotically stable node when $k_{19} > 1.111$. However, as k_5 increases, $P_{5_alt}^*$ reduces, and CP 5_{alt} becomes ecologically infeasible when:

$$k_5 = \frac{k_{23}}{1 + k_{24}} = 0.799, \quad (55)$$

well before it acquires stability. The location of the fourth critical point (CP 4_{alt}) at the origin of the system where no biota are extant is unchanged by the addition of P mortality:

$$N_{4_alt}^* = 1, \quad (56)$$

$$P_{4_alt}^*, Z_{4_alt}^*, B_{4_alt}^*, F_{4_alt}^* = 0. \quad (57)$$

While three of the eigenvalues of CP 4_{alt} are identical to those of CP 4, one (λ_{CP_4alt-1}) is different:

$$\lambda_{CP_4alt-1} = \frac{k_{23}}{1+k_{24}} - k_5, \quad (58)$$

$$\lambda_{CP_4alt-2} = \frac{k_{25}(1-k_{11})}{1+k_{26}} - k_{10}, \quad (59)$$

$$\lambda_{CP_4alt-3} = -k_{19}, \quad (60)$$

$$\lambda_{CP_4alt-4} = -k_{13}. \quad (61)$$

λ_{CP_4alt-1} , λ_{CP_4alt-3} and λ_{CP_4alt-4} are always negative and λ_{CP_4alt-2} is negative for:

$$k_{10} > \frac{k_{25}(1-k_{11})}{1+k_{26}} = 0.397. \quad (62)$$

CP_{4alt} becomes an asymptotically stable node when $k_{10} = 0.397$ and becomes the long term state of the system for high mortality rates. This is fundamentally different to the climate change response of the original model. This result suggests that great care must be taken in selecting ecological models used to predict the impacts of events such as climate change that affect the attributes of organisms represented in the models. The veracity of an ecosystem model is often assessed by testing whether it can reproduce observed data (Franks 2002). While the original and modified models are capable of reproducing the same data, these models will produce very different results if used to simulate the effects of global warming.

4. CONCLUSIONS

Our model has a complicated, interesting and quite robust limit cycle that essentially comprises two modes of behaviour, a *BFN* cycle and a *NPZ* cycle. This limit cycle is largely determined by the location and stability properties of the critical points. The robustness of this limit cycle is of profound importance to the model's application in simulations of climate change. Scenarios of climate change lead to manipulation of mortality parameters, and we find that mortality parameters have a dramatic influence on the model's dynamics.

We also observe the importance of microbial factors in destabilising plankton dynamics. Bacterial blooms occur more frequently if bacterial mortality is low or nutrient levels are high. The presence of a bacterial predator however effectively controls the bacterial population, and restricts the potential for bacteria to dominate the system to a small region of parameter space.

We have also highlighted the importance of subtle variations in model formulation if the model is to be used in scenarios such as climate change. The

inclusion of an explicit linear *P* mortality term to the model produces only subtle modifications to the dynamics for measured parameter values. Such a modification does not affect the model's ability to reproduce observed ecosystem dynamics, and both models would satisfy the usual ecological model validation criteria of reproducing observed data. However our analysis indicates small differences in ecosystem model formulation may have profound impacts on climate change scenario predictions.

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