

Process-dependence of biogenic feedback effects in models of plankton dynamics.

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EXTENDED ABSTRACT

The prospect of human-induced climate change has stimulated research into several biological processes that might affect climate. One such process that has attracted a substantial research effort is the so-called CLAW hypothesis (Charlson et al. 1987). This hypothesis suggests that marine plankton ecosystems may effectively regulate climate by a feedback associated with the production of dimethylsulphide (DMS). Charlson et al. (1987) observed that some of the DMS produced by marine ecosystems is transferred from the ocean to the atmosphere where it is the major source of cloud condensing nuclei (CCN) over the remote oceans. The aerosols resulting from biogenic DMS emissions can have a direct effect on the solar radiative forcing experienced by the Earth through scattering, absorption and reflection and can also lead to increased cloud formation; the CLAW hypothesis proposes that these mechanisms could regulate climate. Charlson et al (1987) argued that an increase in global temperature would lead to increased biogenic DMS emissions from the ocean and result in an increase in scattering, cloud cover and cloud albedo that would increase the proportion of the incoming solar radiation reflected back into space (thus changing the global albedo), and thereby cooling the planet.

The objective of this paper is to examine the implications of the climate regulation process proposed by Charlson et al. (1987) for the dynamics of the ecosystems that produce it. Cropp et al. (2007) developed a simple plankton model that incorporated the DMS feedback mechanism and compared its dynamics to the same ecosystem model without the feedback. These simulations revealed that the presence of the feedback generally enhanced the stability of the ecosystem by making it more resilient to perturbation. In this research, we compare the effect of the feedbacks on a similar NPZ ecosystem model that has a greater range of dynamical behaviour than the model used by Cropp et al. (2007). The results of

simulations with the new feedback model are compared to the results of Cropp et al. (2007) to elucidate the influence of the model formulation on the effects of the feedback.

In this research, we compare the effect of the feedbacks on a similar NPZ ecosystem model that has a greater range of dynamical behaviour than the model used by Cropp et al. (2007). The model used in this research differs from the model used by Cropp et al. (2007) only in that the Lotka-Volterra predation term for zooplankton grazing of phytoplankton ($k_3 PZ$) is replaced by a Michaelis-Menten term ($k_3 (P/P + k_r) Z$). Changing the form of the zooplankton grazing parameterization results in a model with more complex dynamics: the original (LV) model had only a spirally stable node that controlled its dynamical behaviour, whereas the new (MM) model may have limit cycle (MM-LC) or spirally stable (MM-SS) dynamics depending on the parameter values used in the simulation. These two models respond quite differently to the biogenic feedback than does the original LV model (Figure A).

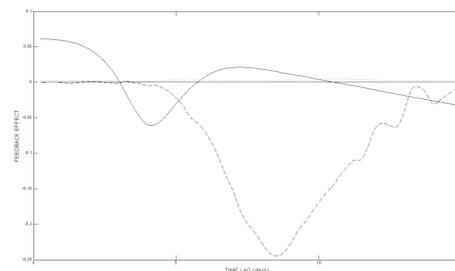


Figure A. Normalised feedback effects for the LV model (solid line), the MM-LC model (dotted line) and the MM-SS model (dashed line).

The conclusions that might be drawn from simulating the effect of the biogenic feedback for the ecosystem that initiates it are therefore critically sensitive to the formulation of the ecosystem model.

1. INTRODUCTION

The prospect of human-induced climate change has stimulated research into several biological processes that might affect climate. One such process that has attracted a substantial research effort is the so-called CLAW hypothesis (Charlson et al. 1987). This hypothesis suggests that marine plankton ecosystems may effectively regulate climate by a feedback associated with the production of dimethylsulphide (DMS). Charlson et al. (1987) observed that some of the DMS produced by marine ecosystems is transferred from the ocean to the atmosphere where it is the major source of cloud condensing nuclei (CCN) over the remote oceans. The aerosols resulting from biogenic DMS emissions can have a direct effect on the solar radiative forcing experienced by the Earth through scattering, absorption and reflection and can also lead to increased cloud formation; the CLAW hypothesis proposes that these mechanisms could regulate climate. Charlson et al (1987) argued that an increase in global temperature would lead to increased biogenic DMS emissions from the ocean and result in an increase in scattering, cloud cover and cloud albedo that would increase the proportion of the incoming solar radiation reflected back into space (thus changing the global albedo), and thereby cooling the planet.

DMS is an ecosystem product. Many species of marine phytoplankton synthesise dimethylsulphoniopropionate (DMSP), the precursor to DMS. However, most DMSP that is converted to DMS is done so by ecosystem processes that occur outside the phytoplankton cell (Simo 2001). In addition to the climatic role postulated for DMS by the CLAW hypothesis, DMSP is a compatible solute that can protect cells from the osmotic effects of seawater and the effects of freezing, may deter predation by zooplankton, may act as an antioxidant, and has also been proposed to assist in the long range dispersal of marine phytoplankton (Wolfe et al. 1997, Hamilton and Lenton 1998, Kiene et al. 2000, Sunda et al. 2002).

The objective of this paper is to examine the implications of the climate regulation process proposed by Charlson et al. (1987) for the dynamics of the ecosystems that produce it. Cropp et al. (2007) developed a simple plankton model that incorporated the DMS feedback mechanism and compared its dynamics to the same ecosystem model without the feedback. The plankton model was composed of nutrient (N), phytoplankton (P) and zooplankton (Z), and was one of a class of NPZ models that have proved powerful heuristic tools in biological oceanography (Franks 2002).

The simulations revealed that the presence of the feedback generally enhanced the stability of the ecosystem by making it more resilient to perturbation. Resilience is a form of stability that may be analytically evaluated for many simple ecosystem models, and is defined as the negative of the dominant eigenvalue of the linearised system about the steady state (DeAngelis 1980).

In this research, we compare the effect of the feedbacks on a similar NPZ ecosystem model that has a greater range of dynamical behaviour than the model used by Cropp et al. (2007). The results of simulations with the new feedback model are compared to the results of Cropp et al. (2007) to elucidate the influence of the model formulation on the effects of the feedback.

2. THE MODELS

The biogeochemical feedback model of Cropp et al. (2007) is given by equations (1) - (6):

$$\frac{dN}{dt} = k_6 P + k_5 Z + k_3 k_4 PZ - Rk_1 \left(\frac{N}{N + k_2} \right) P, \quad (1)$$

$$\frac{dP}{dt} = Rk_1 \left(\frac{N}{N + k_2} \right) P - k_3 PZ - k_6 P, \quad (2)$$

$$\frac{dZ}{dt} = k_3 (1 - k_4) PZ - k_5 Z \quad (3)$$

where:

$$R = \frac{(1 + 2m_8)\xi}{m_8\xi^2 + \xi + m_8}, \quad (4)$$

$$\xi = 1 - \frac{m_7}{N_0} \{m_5 \ln \psi - m_6 - N_0\} \quad (5)$$

$$\psi = \left[m_3 (m_1 P(t - \tau) + m_2 Z(t - \tau)) - m_4 \right] \quad (6)$$

The model is written in a currency of nitrogen and the state variables (P , Z and N) are expressed as concentrations of nitrogen (mgNm^{-3}). The model conserves mass so that $P + Z + N = N_T$.

The additional model used in this research differs from the above model only in that the Lotka-Volterra predation term for zooplankton grazing of phytoplankton ($k_3 PZ$) is replaced by a Michaelis-Menten term ($k_3 (P/P + k_7) Z$). The new model is given by equations (7) - (9):

$$\frac{dN}{dt} = k_6 P + k_5 Z + k_3 k_4 \left(\frac{P}{P + k_7} \right) Z - R k_1 \left(\frac{N}{N + k_2} \right) P, \quad (7)$$

$$\frac{dP}{dt} = R k_1 \left(\frac{N}{N + k_2} \right) P - k_3 \left(\frac{P}{P + k_7} \right) Z - k_6 P, \quad (8)$$

$$\frac{dZ}{dt} = k_3 (1 - k_4) \left(\frac{P}{P + k_7} \right) Z - k_5 Z, \quad (9)$$

where R is again given by equations (4) - (6). The derivation of R , which represents atmospheric processing of dimethylsulphide and its effect on the irradiance experienced by the phytoplankton is described in Cropp et al. (2007) and will not be repeated here. However, it is useful to note that R is a biphasic function (Figure 1) that acts to reduce the irradiance field of the phytoplankton. The function is formulated such that when the ecosystem is at steady state $R = 1$ and has no effect on the dynamics or Lyapunov stability of the models.

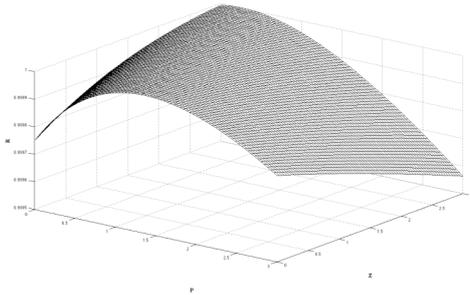


Figure 1. The R function as a function of the scaled P and Z populations relative to the steady state values. In this figure $R = 1$ when $P = Z = 1$.

Table 1. Parameter definitions.

PAR	PROCESS
k_1	Maximum rate of N uptake by P
k_2	Half-saturation constant for N uptake by P
k_3	Maximum rate of Z grazing on P
k_4	Z assimilation efficiency
k_5	Z specific mortality rate
k_6	P specific mortality rate
k_7	Half-saturation constant for P uptake by Z
N_T	Total nutrient
τ	Feedback time lag

We will refer to the original model as the LV model and the new model as the MM model. The ecosystem parameter definitions and values are given in Tables 1 and 2 respectively.

The parameters involved in the feedback term R are described in Cropp et al. (2007) and are not the focus of this paper.

Both Lotka-Volterra and Michaelis-Menten grazing formulations are common in ecosystem models, and provide similar grazing responses to population levels. The grazing surface for the Lotka form is shown in Figure 2.

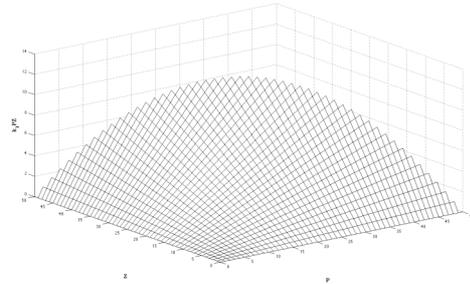


Figure 2. Zooplankton grazing term as a function of P and Z population levels for the LV model.

The MM zooplankton grazing term has a similar grazing surface to Figure 2, but has a slightly lower maximum value for the parameter values used in this analysis. The LV grazing surface is symmetric, whereas the MM surface has the maximum values shifted towards low P values (Figure 3). The maximum value for the LV function (12.5) occurs when $P = Z = 25$, whereas the MM maximum (8.5) occurs at $P = 14$, $Z = 36$.

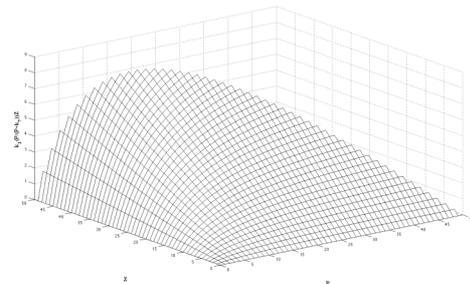


Figure 3. Zooplankton grazing term as a function of P and Z population levels for the MM model.

The effect of changing the grazing formulation is therefore to slightly increase the relative grazing rate when P population levels are low and substantially reduce it when P population levels are high. However, changing the grazing formulation has a dramatic impact on the location of the critical points of the model. For example, the phytoplankton equilibrium for the LV model using the MM(SS) parameter set (Table 2) is:

$$P^* = \frac{k_5}{k_3(1-k_4)} = 0.59, \quad (10)$$

whereas the equivalent point for the MM model is:

$$P^* = \frac{k_5 k_7}{k_3(1-k_4) - k_5} = 14.55. \quad (11)$$

Further, changing the form of the zooplankton grazing parameterization results in a model with more complex dynamics. This is demonstrated in the dynamical regimes of the two models in Figure 4 which reveals that an entirely new dynamical behaviour (a limit cycle), that is not possible in the LV model has appeared.

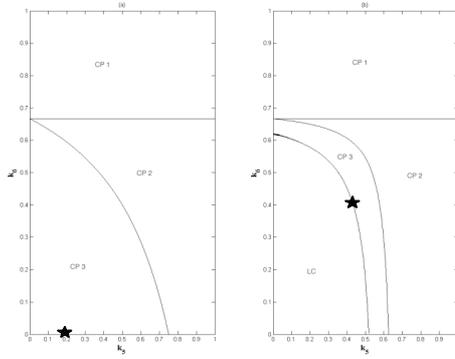


Figure 4. Dynamical regimes for the LV model (a) and MM model (b) as a function of the Z and P mortality parameters k_5 and k_6 . Parameter values have been non-dimensionalised for this figure.

Table 2. Parameter values.

PAR	UNITS	LV model	MM model	
			LC	SS
k_1	d^{-1}	0.270	0.270	0.270
k_2	$mgNm^{-3}$	12.60	25.00	25.00
k_3	d^{-1}	0.020	0.405	0.405
k_4	-	0.300	0.500	0.500
k_5	d^{-1}	0.050	0.108	0.120
k_6	d^{-1}	0.000	0.108	0.108
k_7	$mgNm^{-3}$	-	10.00	10.00
N_T	$mgNm^{-3}$	50	50	50

The labels in Figure 4 refer to different dynamical regimes that occur for the parameter values delineated in the parameter space. CP 1 refers to an asymptotically stable state where no biota exist, CP 2 is an asymptotically stable state where only P exists, while CP 3 indicates a region with a spirally stable node with both P and Z in existence. Figure 4(b) reveals that the MM model has an extra

dynamical regime, denoted by LC, where a limit cycle with both P and Z occurs.

The parameter values used for the LV model (Table 2) were based on measured values as described in Cropp et al. (2007). Similar values were used for the MM model with the exception that values of k_5 were chosen to produce spirally stable steady state (SS) dynamics similar to those of the LV model. Limit cycle (LC) dynamics in the MM model were then generated by choosing a nearby second value of k_5 within the limit cycle region of the parameter space. The values chosen for k_5 and k_6 were selected to locate the models either side of the star in Figure 3 (b). For comparison, the ‘equivalent’ value for k_5 in the LV model is shown by the star in Figure 3 (a). The LV and MM(SS) models therefore have very different sets of parameter values and very different critical point values, but similar slowly exponentially-decaying oscillatory dynamics.

3. METHODS

The methods employed in this research are based on the perturbation and time-lag analyses described in Cropp et al. (2007) and will not be repeated in detail here. Briefly, return time surfaces (i.e. Figure 5) for the LV and MM(SS) models were generated by perturbing the model from its steady state 400 times (between -90% and +100% of the steady-state P and Z values in steps of 10%) and compared to determine the effects of the feedback.

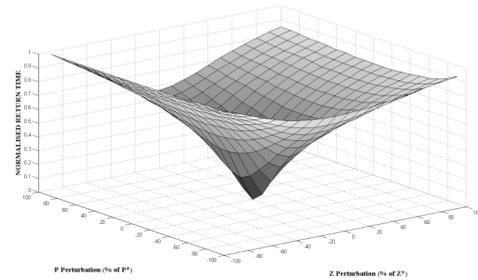


Figure 5. Typical return time surface for the LV model.

The time lag analysis was implemented by calculating the feedback effect metrics for the LV, MM(LC) and MM(SS) models for 60 time lags (τ) in increments of 0.25 days, resulting in an analysis of the feedback effects for time lags up to 15 days.

The return time surfaces for the LV and MM(SS) models were calculated for each time lag and were subtracted their equivalents without the feedbacks (i.e. with $R = 1$) and then normalised to provide a

scalar metric quantifying the effect of the feedback for the time lag analysis.

A new metric to quantify the effect of the feedback on the MM(LC) model dynamics was developed for the time lag analysis of this model (no perturbation analysis was conducted for this model). This metric reflected the amplitude of the limit cycle and was calculated by finding the maximum and minimum values of P and Z over the last 10% of a 2,000 day simulation and calculating their Euclidean separation. The time lag analysis metrics were normalised by the magnitude of their effect on the model dynamics to enable comparison between models with different dynamics.

4. RESULTS

The results of the analysis are shown in a single plot of the time lag analysis (Figure 6). In this figure, the solid line shows the feedback effect for the LV model as reported in Cropp et al. (2007). For time lags up to about four days the feedback causes the model to return to steady state more rapidly after perturbation than the equivalent model without feedback (up to 6% faster).

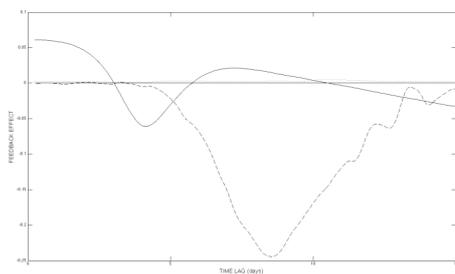


Figure 6. Normalised feedback effects for the LV model (solid line), the MM(LC) model (dotted line) and the MM(SS) model (dashed line).

Time lags of four to six days in the feedback cause the model to return to steady state more slowly after perturbation compared to the model without feedback (up to 6% slower). However, time lags of six to ten days in the feedback cause the model to again return to steady state more rapidly after perturbation than the equivalent model without feedback (up to 2% faster).

The effect of the feedback on the MM(LC) model is very subtle, and can be observed in the dotted line just above zero in Figure 5. The feedback results in a slight (less than 0.5%) reduction in the amplitude of the limit cycle. This feedback effect

is only slightly sensitive to variations in the time lag of the feedback.

The effect of the feedback is most pronounced on the return times of the MM(SS) model (Figure 5, dashed line). Feedbacks with time lags of up to five days have little effect on the return time with increases or decreases of less than 0.5% evident. However, time lags greater than five days result in the MM(SS) model taking up to 25% longer than the equivalent model without feedback to return to steady state.

5. DISCUSSION

This research extends the work of Cropp et al. (2007) investigating the effect of the biogenic feedback on ecosystems resulting from the production and release of dimethylsulphide. We find that changing the zooplankton grazing term in the ecosystem model from a Lotka-Volterra formulation to a Michaelis-Menten formulation results in a significantly different impact of the biogenic feedback. The new model with the Michaelis-Menten formulation reveals a significantly different influence of the feedback than the Lotka-Volterra formulation originally examined by Cropp et al. (2007).

The original work by Cropp et al. (2007) revealed that the feedback caused the ecosystem to become more resilient to perturbation (i.e. it returned to its previous state more rapidly after perturbation) when the feedback occurred approximately seven to ten days after the phytoplankton bloom. This result was interesting because the typical delays between phytoplankton blooms and maximum emissions of dimethylsulphide to the atmosphere have been measured in ocean fertilization experiments to be in the order of seven to ten days (Turner et al. 1996).

The significant difference of the work described in this paper is that it reveals that the feedback has exactly the opposite effect in the modified model: the feedback causes the ecosystem to become less resilient to perturbation at the time lags observed in real systems.

The reason for this difference in the effect of the feedback is not clear, but we note:

- the response surfaces of the Lotka-Volterra and Michaelis-Menten grazing terms are very similar (Figures 2 and 3).
- the critical points of the Lotka-Volterra and Michaelis-Menten models are very different for the same parameter sets (equations (10) and (11)).

- the dynamics of the Lotka-Volterra and Michaelis-Menten models are very different for the same parameter sets, with the Michaelis-Menten model capable of limit cycle dynamics that the Lotka-Volterra model is not (Figure 4).

We also note that in order to have the Michaelis-Menten model exhibit similar dynamics to the Lotka-Volterra model the maximum zooplankton grazing rate (k_3) was increased by a factor of twenty from the value used in the Lotka-Volterra model (0.020 cf 0.405). The maximum zooplankton grazing rate is an important determinant of the dimethylsulphide flux to the atmosphere (Cropp et al. 2004) and such an increase would therefore be expected to have a substantial impact on the magnitude of the feedback effect. However, any such impact appears to be counter-intuitive as an increase in k_3 results in a decrease in dimethylsulphide emissions.

The mechanism by which the feedback effect influences the return time of the system is also not clear and appears counter-intuitive. The effect of R is to reduce phytoplankton growth rates when it is both greater than and less than its steady state value. When the phytoplankton population is greater than its sustainable population (P^*), the ecosystem produces more dimethylsulphide which results in increased cloud cover and a reduced irradiance regime for the phytoplankton. This slows phytoplankton growth as they do not receive sufficient photons to maximise photosynthesis (Zonneveld 1998).

Conversely, when the phytoplankton population is less than its sustainable population (P^*), less dimethylsulphide is produced, leading to reduced cloud cover and increased irradiance. As an assumption of the feedback function (R) is that phytoplankton are adapted to the average ambient irradiance, and that this includes a component derived from the influence of the dimethylsulphide contribution to irradiance, low phytoplankton population levels will experience irradiance levels that inhibit their growth.

In order that such a reduction in phytoplankton growth rate could produce a reduction in the time taken to return to equilibrium, the oscillations of the phytoplankton and zooplankton populations must be damped by a concomitant reduction in the phytoplankton losses due to grazing. This must occur more rapidly than the reduction in phytoplankton growth due to the feedback for the return time to be reduced. This suggests that the formulation of the phytoplankton grazing term

may be an important determinant of the response to the feedback. In order for the feedback to be 'stabilising' the phytoplankton grazing term must reduce more rapidly than the phytoplankton growth term. Comparison of Figures 2 and 3 reveals that the Michaelis-Menten grazing term is larger at low phytoplankton levels than the Lotka-Volterra grazing term, suggesting that this may be the source of the difference in the effect of the feedback between the Lotka-Volterra model and the Michaelis-Menten model. This relationship will be the focus of further research.

6. CONCLUSION

This paper extends the work of Cropp et al. (2007) into the effect of feedbacks associated with the production and release to the marine atmosphere of dimethylsulphide synthesised by marine planktonic ecosystems. This process has been postulated to have a significant effect on global climate (Charlson et al. 1987), but little research has considered the effect of such feedbacks on the ecosystems that initiate it. Cropp et al. (2007) was the first paper to do so, and this work revealed that the feedback produced a stabilising effect on the ecosystem dynamics at time lags consistent with those observed in ocean iron fertilization experiments (see de Baar et al. (2005) for a summary).

The work presented in this paper however indicates that a subtle change in the formulation of the ecosystem model, specifically changing the Lotka-Volterra zooplankton grazing term in the original model to a Michaelis-Menten term, has a dramatic effect on the implications of the feedback. Rather than stabilising the ecosystem model dynamics at time lags of about one week, the revived model indicates that the feedback would make the ecosystem less resilient to perturbation.

This work therefore reveals that the effects of the feedbacks associated with dimethylsulphide are critically dependent on the model formulation. These results suggest that it is necessary to determine which of the two model formulations is 'correct' before the significance of these results can be assessed.

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