

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 of solar radiation and can also lead to increased cloud formation; the CLAW hypothesis proposes that these mechanisms could regulate climate.

In this research, we consider the effect of DMS feedbacks on a simple NPZ ecosystem model. This continues research described in Cropp et al. (2007, Glob Biogeochem. Cycles: GB2024, doi: 10.1029/2006GB002812) with a model that has a greater range of dynamical behaviour than the model used in 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.

The new model that is the focus of this research differs from the original model only in that the Lotka-Volterra predation term for zooplankton grazing of phytoplankton is replaced by a Michaelis-Menten term. Consequently we will refer to the original model as the 'LV model' and the new model as the 'MM model'.

Changing the form of the zooplankton grazing parameterization results in a model with more complex dynamics: the original model had only a

spirally stable node that controlled its dynamical behaviour, whereas the new model may have limit cycle or spirally stable dynamics depending on the parameter values used in the simulation (Figure A).

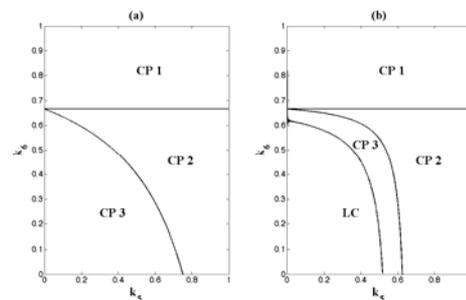


Figure A. Dynamical regimes for the LV model (a) and MM model (b) as a function of the Z and P mortality parameters k_5 and k_6 revealing a new type of survival in the lower left region.

The response of the new MM model to the biogenic feedback is quite different to that of the original LV model (Figure B).

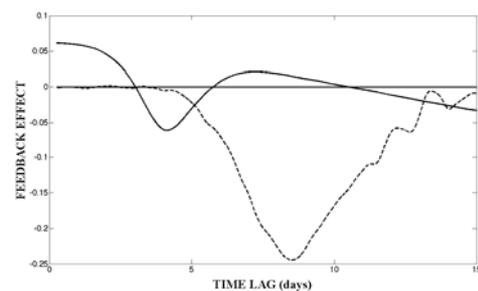


Figure B. Normalised feedback effects for the LV (solid line) and the MM model (dashed line).

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 (LV or MM) is 'correct' before the significance of these results can be assessed.

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 of solar radiation and can also lead to increased cloud formation; the CLAW hypothesis proposes that these mechanisms could regulate climate.

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). 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 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 consider 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), which will be referred to as the LV model here due to its Lotka-Volterra zooplankton grazing formulation, was composed of nutrient (N), phytoplankton (P) and zooplankton (Z), and is given by equations (1)-(3):

$$\frac{dN}{dt} = k_6 P + k_5 Z + k_3 k_4 PZ - Ek_1 \left(\frac{N}{N + k_2} \right) P, \quad (1)$$

$$\frac{dP}{dt} = Ek_1 \left(\frac{N}{N + k_2} \right) P - k_3 PZ - k_6 P, \quad (2)$$

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

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 $P + Z + N = N_T$ (Table 1). E is an environmental forcing term that is set to 1 in the basic model, but is replaced with irradiance, temperature or feedback forcing functions in the analyses.

The 'new' model that is the focus of 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 ($k_3 \left(\frac{P}{P + k_7} \right) Z$). The new model, which we will refer to as the MM model, is given by equations (4) - (6):

$$\frac{dN}{dt} = k_6 P + k_5 Z + k_3 k_4 \left(\frac{P}{P + k_7} \right) Z - Ek_1 \left(\frac{N}{N + k_2} \right) P, \quad (4)$$

$$\frac{dP}{dt} = Ek_1 \left(\frac{N}{N + k_2} \right) P - k_3 \left(\frac{P}{P + k_7} \right) Z - k_6 P, \quad (5)$$

$$\frac{dZ}{dt} = k_3 (1 - k_4) \left(\frac{P}{P + k_7} \right) Z - k_5 Z. \quad (6)$$

The extra ecosystem parameter definitions and values required for this model are also given in Table 1.

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-Volterra term is shown in Figure 1.

The MM zooplankton grazing term (Figure 2) has a similar grazing surface to the LV term, but has a slightly lower maximum value for the parameter values used in this analysis. The LV grazing surface is symmetric with respect to $P = Z$, whereas the MM surface has the maximum values shifted towards low P values. The maximum value for the LV function for the LV parameter values given in Table 1 (12.5) occurs when $P = Z = 25$,

whereas the MM maximum (8.5) occurs at $P = 14$, $Z = 36$ where the total mass $N_T = 50$.

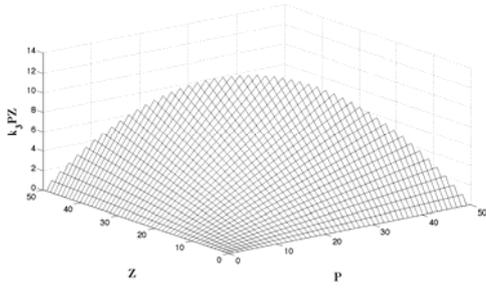


Figure 1. Zooplankton grazing term as a function of P and Z population levels for the LV model.

The effect of changing the grazing formulation is therefore to increase the relative grazing rate by up to 85% when P population levels are low and reduce it by up to 65% when P population levels are high.

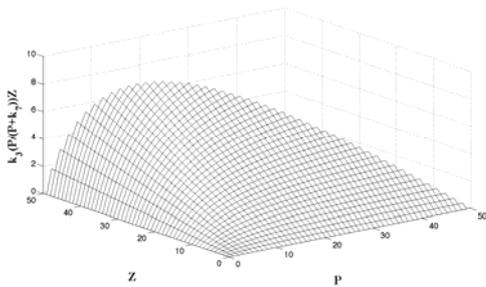


Figure 2. Zooplankton grazing term as a function of P and Z population levels for the MM model.

The parameter values used for the LV model (Table 1) 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 dynamics similar to those of the LV model. The LV and MM models therefore have different parameter and critical point values, but similar slowly exponentially-decaying oscillatory dynamics.

3. METHODS

3.1. Model Validation

The ability to reproduce observed data is a necessary, but not sufficient test of model correctness, but is often the only test available to determine whether ecosystem models are reasonable representations of the processes they model (Franks 2002). This basic test was applied to the two models. A chlorophyll concentration climatology was derived from five years of weekly

composite data measured by the SeaWiFS satellite in the Southern Ocean. Chlorophyll concentrations over the area $60 - 65^{\circ}\text{S}$, $123 - 145^{\circ}\text{E}$ were averaged over the five images each week to produce the climatology. The chlorophyll concentrations were converted to equivalent nitrogen concentrations for comparison with the model data using a typical C:CHL ratio for Antarctic waters of 50 and a constant Redfield C:N ratio of 5.7 (Gabric et al. 2003).

We modified the basic models to compare their predictions with the satellite chlorophyll climatology by formulating them as zero-dimensional slab models that represent quantities averaged over the depth of the mixed layer. In doing so we formulated $E = F_L F_T$ to represent light and temperature forcing functions that operated on the P growth coefficient in each model. The relationship used to model light limitation of P growth in the models was that used in simulations by Gabric et al. (1995) using a similar model in the Southern Ocean:

$$F_L = \frac{I_{av}}{I_0} \left[1 + \left(\frac{I_{av}}{I_0} \right)^2 \right]^{-\frac{1}{2}}, \quad (7)$$

where I_{av} is the average light over a mixed layer of depth Z metres, given by:

$$I_{av} = \frac{I_0}{Z} \int_0^Z e^{-k_w z} dz = \frac{I_0}{k_w Z} (1 - e^{-k_w Z}), \quad (8)$$

and k_w is the light attenuation of seawater (set to 0.05 m^{-1}), z is depth in metres, Z is the depth of the mixed layer in metres and I_0 is the incident surface irradiation (W/m^2). The temperature dependence of phytoplankton growth used in the models was that estimated by Eppley (1972):

$$F_T = e^{0.063(T - T_{max})}, \quad (9)$$

where T is the ambient water temperature ($^{\circ}\text{C}$) and T_{max} is the maximum annual temperature (equal to 2.0°C in the region of the Southern Ocean sampled).

Climatological time series of sea surface temperature (SST), photosynthetically active radiation (PAR) and mixed layer depth (MLD) data were developed for the same region of the Southern Ocean as the chlorophyll data. The SST climatology was created from data obtained from the AVHRR satellite and the PAR climatology

from the SeaWiFS satellite. The MLD data was obtained from the World Oceanographic Atlas.

A genetic algorithm (GA) (Mitchell 1997) was used to simultaneously fit each model's dynamics to the observed data using a least squares fitness metric:

$$M = \sum_{\text{models}} \left(\sum_{\text{observations}} (\text{Chl}_{\text{observed}} - \text{Chl}_{\text{model}})^2 \right). \quad (10)$$

This metric was used to find a single parameter set that resulted in both models fitting the data reasonably well, rather than individual parameter sets that gave optimal fits for each model. The optimal parameter set found by the GA is listed under GA in Table 1.

3.2. Stability Analysis

The dynamical regimes available to the two models were assessed by obtaining analytic expressions for the critical points of the models and for the eigenvalues of linearised systems around each of the critical points. The bifurcations of the systems were plotted against the phytoplankton and zooplankton mortality coefficients to generate stability diagrams for the various dynamical behaviours.

3.3. Feedback Analysis

A biogenic feedback term $E = R$, representing the atmospheric processing of dimethylsulphide and its effect on the irradiance experienced by the phytoplankton was derived for the feedback analysis. The derivation of this term is described in Cropp et al. (2007) and will not be repeated here. R is a function of the phytoplankton and zooplankton concentrations (P and Z) and is given by:

$$R = \frac{(1 + 2m_8)\xi}{m_8\xi^2 + \xi + m_8}, \quad (11)$$

$$\xi = 1 - \frac{m_7}{N_0} \{m_5 \ln \psi - m_6 - N_0\}, \quad (12)$$

$$\psi = \left[m_3 (m_1 P(t - \tau) + m_2 Z(t - \tau)) - m_4 \right]. \quad (13)$$

It is useful to note that R is a biphasic function (Figure 3) 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 Lyapunov stability of the models. The parameters involved in the feedback term R are described in Cropp et al. (2007) and are not the focus of this paper.

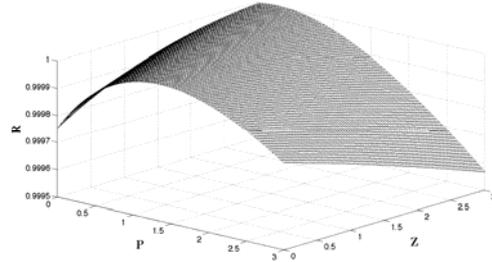


Figure 3. The R function as a function of the scaled P and Z populations relative to the steady state values. Note $R = 1$ when $P = Z = 1$.

The methods of assessing the effects of the feedback employed in this analysis 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 4) for the LV and MM 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. A scalar metric describing the effect of the feedback was calculated by subtracting the return time surface of the MM model from that of the LV model and normalising by the LV model surface, and then summing the difference surface:

$$M = \sum_i \sum_j \frac{RLV_{i,j} - RMM_{i,j}}{RLV_{i,j}}, \quad i, j = 1 \dots 20, \quad (14)$$

where RLV is the return time surface for the LV model, etc.

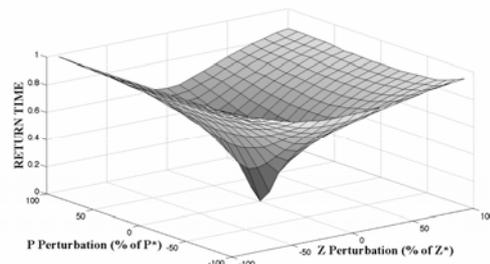


Figure 4. Typical return time surface for the LV model.

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

Table 1. Parameter values for the LV and MM models.

PAR	PROCESS	UNITS	GA	LV Model	MM Model
k_1	Maximum rate of N uptake by P	d^{-1}	0.270	0.270	0.270
k_2	Half-saturation constant for N uptake by P	$mgNm^{-3}$	13.70	12.60	25.00
k_3	Maximum rate of Z grazing on P	d^{-1}	0.0075	0.020	0.405
k_4	Z assimilation efficiency	-	0.370	0.300	0.500
k_5	Z specific mortality rate	d^{-1}	0.0075	0.050	0.120
k_6	P specific mortality rate	d^{-1}	0.0006	0.000	0.108
k_7	Half-saturation constant for P uptake by Z		1.630		10.00
N_T	Total nutrient	$mgNm^{-3}$	3.250	50	50
τ	Feedback time lag	d	-	0-15	0-15

4. RESULTS

4.1. Model Validation

The model ‘validation’ was only undertaken to the extent of testing whether both models could produce ‘reasonable’ reproductions of observed

could have a significant impact on the location of the third critical points (3) of the models. The properties of these critical points are particularly important to the dynamics of the models, as they are the only critical points of the models for which all biota are extant.

Table 2. Critical points of the models.

	CP	P^*	Z^*	N^*
LV MODEL	1	$P_{LV-1}^* = 0$	$Z_{LV-1}^* = 0$	$N_{LV-1}^* = N_T$
	2	$P_{LV-2}^* = 1 - \frac{k_2 k_6}{k_1 - k_6}$	$Z_{LV-2}^* = 0$	$N_{LV-2}^* = \frac{k_2 k_6}{k_1 - k_6}$
	3	$P_{LV-3}^* = \frac{k_5}{k_3(1 - k_4)}$	$Z_{LV-3}^* = \frac{k_1}{k_3} \left(\frac{N_{LV-3}^*}{N_{LV-3}^* + k_2} \right) - \frac{k_6}{k_3}$	$N_{LV-3}^* = N_T - P_{LV-3}^* - Z_{LV-3}^*$
MM MODEL	1	$P_{MM-1}^* = 0$	$Z_{MM-1}^* = 0$	$N_{MM-1}^* = N_T$
	2	$P_{MM-2}^* = 1 - \frac{k_2 k_6}{k_1 - k_6}$	$Z_{MM-2}^* = 0$	$N_{MM-2}^* = \frac{k_2 k_6}{k_1 - k_6}$
	3	$P_{MM-3}^* = \frac{k_7 k_5}{k_3(1 - k_4) - k_5}$	$Z_{MM-3}^* = \frac{k_1}{k_3} (P_{MM-3}^* + k_7) \left(\frac{N_{MM-3}^*}{N_{MM-3}^* + k_2} \right) - \frac{k_6}{k_3} (P_{MM-3}^* + k_7)$	$N_{MM-3}^* = N_T - P_{MM-3}^* - Z_{MM-3}^*$

chlorophyll data. Figure 5 demonstrates that both models do a reasonable job in the Antarctic study region where chlorophyll dynamics are positively correlated with irradiance and temperature.

Figure 5 reveals that the LV model produces a slightly better representation of chlorophyll dynamics, as the MM model does not capture the decay of the bloom well. However, for the purposes of this research we consider both models to represent the processes involved in the ecosystem dynamics sufficiently well.

4.2. Critical Points

The critical points of the two models are shown in Table 2. The change in grazing formulation has a subtle effect on the expressions defining the locations of the critical points, and there is no difference between the first two critical points (1 and 2) of the two models. However, it can be seen in Table 2 that changing the grazing formulation

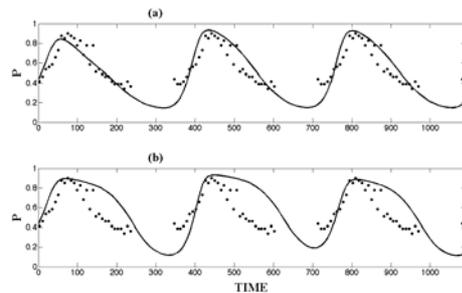


Figure 5. Model phytoplankton concentrations (solid lines) and satellite-measured chlorophyll data (dots) for the LV (a) and MM (b) models.

4.3. Stability

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 6 which reveals that an entirely new dynamical

behaviour (a limit cycle), that is not possible in the LV model has appeared in the MM model.

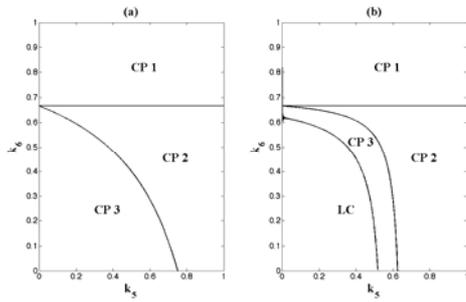


Figure 6. Dynamical regimes for the LV model (a) and MM model (b) as a function of the Z and P mortality parameters k_5 and k_6 . The new limit cycle regime is shown in (b) occupying most of the CP 3 space. Parameter values have been non-dimensionalised for this figure.

The labels in Figure 6 refer to different dynamical regimes that occur for the parameter values delineated in the parameter space. CP 1 refers to critical points one (Table 2), asymptotically stable states where no biota exist. CP 2 refers to critical points two (Table 2), asymptotically stable states where only P exists, while CP 3 refers to critical points three (Table 2) and indicates regions with spirally stable nodes that have both P and Z in existence. Figure 6(b) reveals that the MM model has an extra dynamical regime, denoted by LC, where a limit cycle involving P and Z occurs.

The lines separating the CP 1 and CP 2 regions in Figure 6 are the locations of transcritical bifurcations where critical points 1 and 2 collide and exchange stability, and is given by:

$$k_6 = \frac{k_1}{1 + k_2}. \quad (15)$$

Similarly the line between the CP 2 and CP 3 regions represents the transcritical bifurcation of critical points 2 and 3 which is given for the LV model by:

$$k_6 = k_1 \left[\frac{k_5 - k_3(1 - k_4)}{k_5 - k_3(1 + k_2)(1 - k_4)} \right], \quad (16)$$

and for the MM model by:

$$k_6 = k_1 \left[\frac{k_5(1 + k_7) - k_3(1 - k_4)}{k_5(1 + k_2 + k_7) - k_3(1 + k_2)(1 - k_4)} \right]. \quad (17)$$

An analytic expression for the location of the Hopf bifurcation between the LC and CP 3 regions in Figure 6(b) is not useful, and the boundary has been calculated numerically.

4.4. Feedback Effects

The results of the feedback analysis are shown in a single plot of the time lag analysis (Figure 7). 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).

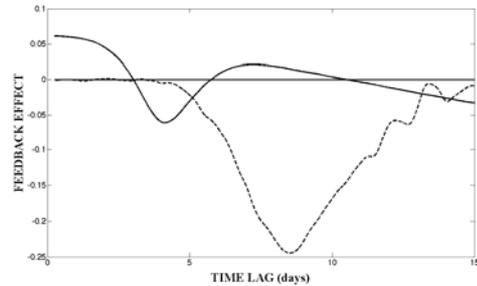


Figure 7. Normalised feedback effects for the LV model (solid line), the MM(LC) model (dotted line) and the MM(SS) model (dashed line).

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 is most pronounced on the return times of the MM model (Figure 7, 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 model taking up to 25% longer than the equivalent model without feedback to return to steady state.

5. DISCUSSION AND CONCLUSION

We find that changing the zooplankton grazing term in the ecosystem model from a Lotka-Volterra formulation to a Michaelis-Menten formulation produces several interesting effects. The locations of the critical points of the two models are similar, but could be quite different for some parameter sets. Further, the stability properties of the two models are similar, but the MM model has an extra dynamical behaviour available to it, having the potential to exhibit limit cycle behaviour. The biogenic feedback is the most sensitive attribute of the models to change of the

grazing term. The MM model reveals a significantly different influence of the feedback than the LV model originally examined by Cropp et al. (2007).

The original work by Cropp et al. (2007) investigating the effect of the biogenic feedback on ecosystems resulting from the production and release of dimethylsulphide revealed that the feedback initiated by the ecosystem caused it to return to its prior 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 significance of the work described in this paper is that it reveals that the effect of the feedback is critically dependent on the formulation of the grazing term in the model, and that the implication of the biogenic feedback for the ecosystem cannot therefore be reliably evaluated until there exists unequivocal evidence constraining the formulations that correctly represent the ecosystem processes.

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. At this stage, there is little evidence to suggest that one formulation is preferable to the other, although anecdotal evidence suggests a current trend to prefer Michaelis-Menten over Lotka-Volterra grazing terms in ecosystem models.

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