1   **Running Head**:   Heuristic climate bio-regulation modelling

2

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4   # Dimethylsulphide, clouds and phytoplankton: insights

5   # from a simple plankton ecosystem feedback model.

6

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18 **ABSTRACT**

19 The hypothesis that marine plankton ecosystems may effectively regulate climate by

20 the production of dimethylsulphide (DMS) has attracted substantial research effort

21 over recent years. This hypothesis suggests that DMS produced by marine ecosystems

22 can affect cloud properties and hence the averaged irradiance experienced by the

23 phytoplankton that produce DMS's precursor dimethylsulphoniopropionate (DMSP).

24 This paper describes the use of a simple model to examine the effects of such a

25 biogenic feedback on the ecosystem that initiates it. We compare the responses to

26 perturbation of a simple marine nitrogen – phytoplankton – zooplankton (*NPZ*)

27 ecosystem model with and without biogenic feedback. Our analysis of this heuristic

28 model reveals that the addition of the feedback can increase the model's resilience to

29 perturbation and hence stabilise the model ecosystem. This result suggests the

30 hypothesis that DMS may play a role in stabilising marine plankton ecosystem

31 dynamics through its effect on the atmosphere.

32

33 **INDEX TERMS:** 0315, 0439, 0444, 0466

34

35 **KEYWORDS:** DMS, climate change, CLAW, biofeedback, NPZ model.

36

37 **INTRODUCTION**

38 The prospect of human-induced climate change has stimulated research into several

39 biological processes that might affect climate. One such process that has attracted a

40 substantial research effort is the so-called CLAW hypothesis [*Charlson, et al.*, 1987].

41   This hypothesis suggests that marine plankton ecosystems may effectively regulate

42   climate by a feedback associated with the production of dimethylsulphide (DMS).

43   Charlson et al. [1987] observed that some of the DMS produced by marine

44   ecosystems is transferred from the ocean to the atmosphere where it is the major

45   source of cloud condensing nuclei (CCN) over the remote oceans. The aerosols

46   resulting from biogenic DMS emissions can have a direct effect on the solar radiative

47   forcing experienced by the Earth through scattering, absorption and reflection and can

48   also lead to increased cloud formation; the CLAW hypothesis proposes that these

49   mechanisms could regulate climate. Charlson et al [1987] argued that an increase in

50   global temperature would lead to increased biogenic DMS emissions from the ocean

51   and result in an increase in scattering, cloud cover and cloud albedo that would

52   increase the proportion of the incoming solar radiation reflected back into space (thus

53   changing the global albedo), and thereby cooling the planet.

54

55   DMS is an ecosystem product. Many species of marine phytoplankton synthesise

56   dimethylsulphoniopropionate (DMSP), the precursor to DMS. However, most DMSP

57   that is converted to DMS is done so by ecosystem processes that occur outside the

58   phytoplankton cell [*Simo*, 2001]. In addition to the climatic role postulated for DMS

59   by the CLAW hypothesis, DMSP is a compatible solute that can protect cells from the

60   osmotic effects of seawater and the effects of freezing, may deter predation by

61   zooplankton, may act as an antioxidant, and has also been proposed to assist in the

62   long range dispersal of marine phytoplankton [*Hamilton and Lenton*, 1998; *Kiene, et*

63   *al.*, 2000; *Sunda, et al.*, 2002; *Wolfe, et al.*, 1997].

64

65   The objective of this paper is to examine the implications of the climate regulation

66   process proposed by Charlson et al. [1987] for the dynamics of the ecosystems that

67   produce it. To do this we develop a simple plankton model that incorporates the DMS

68   feedback mechanism and compare its dynamics to the same ecosystem model without

69   the feedback. The plankton model is composed of nutrient (N), phytoplankton (P) and

70   zooplankton (Z), and is one of a class of *NPZ* models that have proved powerful

71   heuristic tools in biological oceanography [*Franks*, 2002]. The feedback processes

72   quantified by Charlson et al. [1987] (a changed light environment arising from a

73   modified albedo due to DMS production, where the changed light environment then

74   influences the phytoplankton growth rate) were incorporated into the *NPZ* model to

75   build a biogenic feedback model that was not intrinsically constrained to any specific

76   oceanic environment. The structure of this model is shown in Figure 1. Our whole-of-

77   system modelling approach is similar to that of Lawrence [1993], who used a similar

78   model to assess the impact of the feedback on climate. Our approach and intention is

79   substantially different: we close the feedback cycle on the ecosystem, and examine the

80   implications of the feedback for the ecosystems that generate it.

81

82   Comparisons between simulations of the *NPZ* model with and without feedback were

83   undertaken to elucidate the influence of the feedbacks for the ecosystem. The

84   simulations revealed that the presence of the feedback generally enhanced the stability

85   of the ecosystem by making it more resilient to perturbation. Resilience is a form of

86   stability that may be analytically evaluated for many simple ecosystem models. The

87   resilience of model ecosystems is defined as the negative of the dominant eigenvalue

88   of the linearised system about the steady state [*DeAngelis*, 1980], and is inversely

89   related to the time the model ecosystem will take to return to its equilibrium state after

90   a perturbation.

91

92   A sensitivity analysis of the model with instantaneous feedback (the reason we

93   examine instantaneous feedback is discussed) indicated that such feedback always

94   stabilised the system, that is no parameter values or combination of parameter values

95   used in the sensitivity analysis caused the system to become less stable than the

96   equivalent system without the feedback. We note that the feedback system is more

97   sensitive to the magnitude and direction of zooplankton perturbations than to

98   phytoplankton perturbations. We also note the sensitive dependence of the feedback

99   effect on time lags in the feedback process, and the influence of the biometric rate

100   parameters on these effects. These parameters are also important determinants of the

101   resilience of the ecosystem model

102

103   **THE ECOSYSTEM MODEL**

104

105   We first describe the basic *NPZ-DMS* model without feedback, summarised in

106   equations (1) - (5), and the methods used in this analysis. We then develop the

107   feedback model (equation (34) and equations (35) - (37)).

108

109   **The *NPZ-DMS* model**

110   A simple model of a planktonic ecosystem that produces DMS is used as the starting

111   point for this analysis. The model is a simplification of the GMSK model proposed by

112   Gabric et al. [1993], in which a DMS - DMSP model was coupled to the plankton

113   ecosystem model of Moloney et al. [1986]. This model is shown in Figure 1, where it

114   comprises all the model components in the ocean. The ecosystem model has been

115   simplified to a nutrient – phytoplankton - zooplankton (*NPZ*) model, a valuable tool in

116   biological oceanography [*Franks*, 2002], for this analysis and coupled to the DMS

117   equations of Gabric et al. [1993]. A schematic of the resulting simple *NPZ-DMS*

118   model comprises the model components shown as solid lines in the ocean in Figure 1.

119

120   The *NPZ-DMS* model is defined by the following equations:

121

122
$$\frac{dN}{dt} = k_5 Z + k_3 k_4 PZ - k_1 \left(\frac{N}{N+k_2} \right) P , \tag{1}$$

123
$$\frac{dP}{dt} = k_1 \left(\frac{N}{N+k_2} \right) P - k_3 PZ , \tag{2}$$

124
$$\frac{dZ}{dt} = k_3 \left(1 - k_4 \right) PZ - k_5 Z , \tag{3}$$

125
$$\frac{dDMSP}{dt} = m_1 \gamma P + m_2 \gamma Z - m_3 DMSP - m_4 DMSP , \tag{4}$$

126
$$\frac{dDMS}{dt} = \gamma m_5 P + m_3 DMSP - m_6 DMS - m_7 DMS . \tag{5}$$

127

128   Equations (1) - (3) represent the ecosystem component of the model. These equations

129   are written in a currency of nitrogen (where N, P and Z represent the concentrations of

130   dissolved inorganic nutrient, phytoplankton and zooplankton respectively in units of

131   atomic nitrogen). These equations conserve mass so that $N + P + Z = N_T$ always,

132   where N_T is the total nutrient in the system. Equations (4) and (5) represent the DMS

133   production generated by the ecosystem and are written in a currency of sulphur

134   (where *DMSP* and *DMS* represent the concentrations of dimethylsulphoniopropionate

135   and dimethylsulphide respectively in units of atomic sulphur) and these equations do

136   not conserve mass. The *k* and *m* parameters represent the attributes of biota in the

137   ecosystem model and the rates of chemical reactions and physical processes in the

138   DMS model. The parameter γ in equations (4) and (5) represents the sulphur :

139   nitrogen ratio of marine plankton. The parameter set used by Gabric et al. [1999],

140   derived from measured values reported in the literature, was selected as a starting

141   point for this analysis (Table 1, G99). The equations derived by Gabric et al [1993]

142   were used as the basis for developing a feedback process to incorporate in the *NPZ*

143   model to create the biofeedback model. This is described below in The Feedback

144   Model.

145

146   ***NPZ* model resilience**

147   The nitrogen-based components of the *NPZ-DMS* model may be isolated to form an

148   ecosystem (*NPZ*) model. This model has four critical (equilibrium) points defined by

149    $\dfrac{dN}{dt} = \dfrac{dP}{dt} = \dfrac{dZ}{dt} = 0$ of which one is ecologically infeasible and two are unstable and

150 not relevant to this analysis (see Cropp and Norbury [2007] for details). The fourth

151 point is an asymptotically stable node located at:

152

$$P^* = \frac{k_5}{k_3\left(1 - k_4\right)}, \tag{6}$$

$$Z^* = \frac{k_1}{k_3}\left(\frac{N^*}{N^* + k_2}\right), \tag{7}$$

$$N^* = \frac{1}{2}\left[-\left(k_2 + P^* + \frac{k_1}{k_3} - N_T\right) \pm \sqrt{\left(k_2 + P^* + \frac{k_1}{k_3} - N_T\right)^2 - 4k_2\left(P^* - N_T\right)}\right]. \tag{8}$$

156

157 The eigenvalues of the linearised *NPZ* model about this point are:

158

$$\lambda = -\frac{k_1 P^*}{2}\left[\frac{k_2}{\left(N^* + k_2\right)^2}\right]\left\{1 \pm \sqrt{1 - \left(N^* + k_2\right)\left[1 + \frac{\left(N^* + k_2\right)^2}{k_1 k_2 P^*}\right]\left(\frac{4k_4 N^*}{k_2 P^*}\right)}\right\}. \tag{9}$$

160

161 For the parameter values used in this study (and for most reasonable values) this point

162 is an asymptotically stable spiral node, indicating that when the model is perturbed

163 from this steady state it will oscillate in "boom-and-bust" cycles of decreasing

164 amplitude until it regains equilibrium. The amplitude and rate of decay of these cycles

165   is determined by the magnitude of the real part of the eigenvalue of this point, the

166   basis of DeAngelis' [1980] resilience measure:

167

168
$$Res = \frac{k_1}{2}\left(\frac{k_2}{\left(N^* + k_2\right)^2}\right)\left(\frac{k_5}{k_3\left(1 - k_4\right)}\right).$$
(10)

169

170   This resilience metric is inversely proportional to the time required for the model to

171   return to equilibrium after a perturbation and we will use this metric to describe the

172   stability of the model.

173

174   High resilience means that a system will rapidly return to its steady state after a

175   perturbation. Johnson [1990] studied isolated Arctic lake ecosystems and proposed the

176   hypothesis that ecosystems adapt to acquire attributes that endow the system with

177   high resilience. Cropp and Gabric [2002] simulated the adaptation of a simple

178   plankton ecosystem model under thermodynamic constraints and modified Johnson's

179   hypothesis to propose that ecosystems adapted to states of maximum resilience within

180   genetic and environmental constraints. Laws [2003] reported that the concept of

181   maximum resiliency was a useful heuristic for fitting ecosystem models to observed

182   plankton data in many regions of the global oceans.

183

184

185   **THE FEEDBACK MODEL**

186   The feedback model is based on the simplified GMSK model and is comprised of the

187   *NPZ* model described above coupled to a model of the sulphur and atmospheric

188   processes. The feedback model is also shown in Figure 1, and comprises all the model

189   components drawn with solid lines in both the ocean and the atmosphere.

190

191   A *DMS* sub-model may be extracted from the sulphur-based components of the *NPZ-*

192   *DMS* model (equations (4) - (5)) for analysis. A steady state of the *DMS* sub-model

193   may be obtained where the aqueous *DMS* concentration is defined in terms of *P, Z*

194   and some parameters:

195

$$DMS^* = \gamma \left(\frac{P\left(m_1 m_3 + m_5 m_3 + m_5 m_4\right) + m_2 m_3 Z}{\left(m_3 + m_4\right)\left(m_6 + m_7\right)} \right). \tag{11}$$

197

198   This steady state is always an asymptotically stable node, and for measured parameter

199   values the eigenvalues of this point are large and negative, indicating that the steady

200   state is a strong attractor and the *DMS* model is highly resilient. This means that the

201   system will return to its steady state very rapidly after any perturbation, and that the

202   steady state values are a therefore a good description of the system. Analytic

203   expressions describing *P(t)* and *Z(t)* are not derivable, but it is clear that the *DMS*

204   model is essentially slaved to the *NPZ* model, and the state of the ecosystem model

205   will determine the state of the *DMS* model. These properties of the *NPZ-DMS* model

206   allow the effects of the system's feedback on its own environment to be included in a

207   simple ecosystem biofeedback model. The derivation of this model is now described.

208

209   **DMS sea-air transfer**

210   The flux of DMS from the ocean to the atmosphere (DMS_{flux}) may be modeled as a

211   linear function of the aqueous concentration of DMS (DMS_{aq}) and the DMS piston

212   velocity (k_{tr}) [*Liss and Merlivat*, 1986]:

213

214    $$DMS_{flux} = k_{tr} DMS_{aq}.$$ (12)

215

216   Although this flux occurs only at the ocean surface, when applied in a zero-

217   dimensional (i.e. depth-averaged over the mixed layer) model as in this analysis, the

218   loss of DMS_{aq} is also averaged over the depth of the mixed layer (MLD):

219

220    $$DMS_{flux} = \left(\frac{k_{tr}}{MLD} \right) DMS_{aq}.$$ (13)

221

222   The DMS piston velocity parameterises the rate at which DMS is transferred from the

223   ocean to the atmosphere, and the empirically derived estimate of Nightingale et al.

224   [2000] was used in this analysis:

225

$$k_{tr} = 0.005\left(5.88u_{10}^2 + 1.49u_{10}\right)Sc^{-\frac{1}{2}}, \tag{14}$$

227

228 where k_{tr} (day^{-1}) is for a notional 48 metre deep mixed layer, u_{10} is the 10 metre wind

229 speed (ms^{-1}) and Sc is the dimensionless Schmidt number. The Schmidt number is

230 temperature dependent, and the experimentally derived relationship of Saltzman et al.

231 [1993] was used:

232

$$Sc = 2764 - 147.12\,SST + 3.726\,SST^2 - 0.038\,SST^3, \tag{15}$$

234

235 where SST is the sea surface temperature (^{0}C). The sea surface temperature has little

236 influence on the piston velocity, which is mostly controlled by the wind speed. A

237 global average wind speed of 8.2 ms^{-1} (derived from two years of SeaWinds 12 hourly

238 measurements) and a global average sea surface temperature of 16.7^{0}C (derived from

239 15 years of Advanced Very High Resolution Radiometer (AVHRR) data) were used

240 for this analysis, giving a representative DMS piston velocity of $k_{tr} = 2.88$ md^{-1}. This

241 is consistent with the estimates of Simo and Dachs [2002] who used a non-linear

242 correction to zonal monthly climatological wind speeds and obtained global estimates

243 of piston velocity between 1 and 4 md^{-1}.

244

245   A relationship between *P*, *Z* and *DMS* flux from the ocean to the atmosphere can be

246   derived by substituting equation (11) into equation (12):

247

248

$$
\begin{aligned}
DMS_{flux} &= k_{tr}\gamma\left[\frac{(m_1m_3 + m_3m_5 + m_4m_5)}{(m_3 + m_4)(m_6 + m_7)}P + \frac{m_2m_3}{(m_3 + m_4)(m_6 + m_7)}Z\right], \quad (16)\\
&= k_6 P + k_7 Z
\end{aligned}
$$

249

250   where $k_6 = \dfrac{\gamma k_{tr}(m_1m_3 + m_3m_5 + m_4m_5)}{(m_3 + m_4)(m_6 + m_7)}$, and $k_7 = \dfrac{\gamma k_{tr}m_2m_3}{(m_3 + m_4)(m_6 + m_7)}$ where k_6 and k_7

251   have units of mgS m mgN^{-1} day^{-1} and *DMS$_{flux}$* has units of mgS m^{-2} day^{-1}.

252

253   **DMS flux and cloud condensation nuclei**

254   Pandis et al. [1994] estimated a long-term average cloud condensation nuclei (CCN) -

255   DMS flux relationship over the remote ocean from the steady state of a model of the

256   principal gas-, aerosol- and aqueous-phase processes in the marine atmospheric

257   boundary layer. They predicted that when DMS emission flux is smaller than 1.3

258   μmoles m^{-2} d^{-1} the CCN concentration is essentially constant at 20 particles cm^{-3}. In a

259   second DMS flux regime, extending between 1.3 and 2.3 μmoles m^{-2} d^{-1} only a few

260   particles become CCN each day. A third region corresponds to DMS emission fluxes

261   larger than 2.3 μmoles m^{-2} d^{-1}. The CCN concentration in this regime is a linear

262   function of the DMS flux:

263

264
$$CCN = 22.7\,DMS_{flux} - 15.0\,,\qquad(17)$$

265

266 where *DMS* emission flux is in µmoles m^{-2} d^{-1} and *CCN* is in particles cm^{-3}. Simo and

267 Dachs [2002] estimated a conservative global mean annual flux of DMS from the

268 ocean to the atmosphere of 6.8 µmoles m^{-2} d^{-1} ($\sigma = 2.49$ µmoles m^{-2} d^{-1}) suggesting

269 that equation (17) is appropriate for a globally representative model. Converting this

270 relationship to represent *DMS* in mg S m^{-2} d^{-1} using 1 µmol S m^{-2} d^{-1} = 0.032 mgS m^{-2}

271 d^{-1} gives approximately:

272

273
$$CCN = 710\,DMS_{flux} - 15\,.\qquad(18)$$

274

275 When applied using Simo and Dachs' [2002] global mean DMS flux estimate

276 equation (18) produces a CCN estimate of 140 particles cm^{-3}, comparable to CCN

277 observations of 50-250 particles cm^{-3} reported for the Northeast Atlantic Ocean by

278 Hegg [1994]. Substituting equation (16) into equation (18) then gives:

279

280
$$\begin{aligned} CCN &= 710\left(k_6 P + k_7 Z\right) - 15 \\ &= k_8\left(k_6 P + k_7 Z\right) - k_9 \end{aligned}\qquad(19)$$

281

282 where $k_8 = 710$ and $k_9 = 15$.

283

Cloud condensation nuclei and cloud droplets

285   Several authors have derived relationships between *CCN* and cloud droplet number

286   concentration (N_C) (see Gondwe [2004] for a summary). The empirically measured

287   relationships reported in the literature take several forms, although they all describe

288   similar (hyperbolic-like) relationships. In keeping with our heuristic approach, we

289   have used the simple non-linear relationship between cloud droplet number (N_C) and

290   the number of *CCN* measured by Saxena and Menon [1999] over the south-eastern

291   United States:

292

$$
\begin{aligned}
N_C &= 183\ln\left(CCN\right) - 334 \\
&= k_{10}\ln\left(CCN\right) - k_{11}
\end{aligned}
\tag{20}
$$

294

295   where $k_{10} = 183$ and $k_{11} = 334$. This relationship is similar (differing only slightly in

296   the coefficients) to the relationship between *CCN* and the sub-cloud aerosol number

297   concentration measured over the North Atlantic Ocean by Gultepe and Isaac [1996]. It

298   also produces estimates of N_C similar to the theoretical derivation of Chuang and

299   Penner [1995] (when applied with the associated relationship between *CCN* and

300   sulphate aerosol mass concentration given by Saxena and Menon [1999]) suggesting

301   equation (20) is a robust parameterisation. Substituting equation (19) into equation

302   (20) gives an estimate of the number of cloud droplets that will result from *DMS*

303   ventilated into the atmosphere from the ecosystem:

304

305
$$N_C = k_{10} \ln \left[k_8 \left(k_6 P + k_7 Z \right) - k_9 \right] - k_{11} .$$
(21)

306

307 **Cloud droplets, albedo and irradiance**

308 Relationships between changes in cloud droplet number and changes in cloud top

309 albedo (α), assuming constant atmospheric liquid content, have been provided by

310 several authors [*Han, et al.*, 1998]. These are all similar linear relationships, varying

311 only in the slope, and the most recent, given by Schwartz and Slingo [1996], and valid

312 for albedos between 0.28 and 0.72, is used here:

313

314
$$\begin{aligned} \Delta \alpha &\approx 0.075 \left(\frac{\Delta N}{N_0} \right) \\ &\approx 0.075 \left(\frac{N_C - N_0}{N_0} \right) , \end{aligned}$$
(22)

315

316 where N_0 is the reference cloud droplet number density and ΔN is the change in cloud

317 droplet concentration from the reference. The change in cloud top albedo due to

318 change in the flux of DMS from the ocean to the atmosphere can then be

319 approximated by substituting equation (21) into equation (22):

320

321

$$\Delta\alpha = 0.075\left\{\frac{k_{10}\ln\left[k_8\left(k_6 P + k_7 Z\right) - k_9\right] - k_{11} - N_0}{N_0}\right\}$$

$$= k_{12}\left\{\frac{k_{10}\ln\left[k_8\left(k_6 P + k_7 Z\right) - k_9\right] - k_{11} - N_0}{N_0}\right\}$$ (23)

322

323   where $k_{12} = 0.075$.

324

325   If it is assumed that the reference number of droplets (N_0) is equated with the steady

326   state of the ecosystem (i.e. the reference number of droplets includes a contribution

327   from the ecosystem at steady state), then N_0 can be described in terms of the steady

328   state values of the *NPZ* model:

329

330    $$N_0^* = k_{10}\ln\left[k_8\left(k_6 P^* + k_7 Z^*\right) - k_9\right] - k_{11},$$ (24)

331

332   where P^* and Z^* are defined by equations (6) and (7) respectively. The change in

333   cloud top albedo attributable to a change in DMS production by the ecosystem is then

334   given by:

335

336    $$\Delta\alpha = \frac{k_{12}}{N_0^*}\left\{k_{10}\ln\left[k_8\left(k_6 P + k_7 Z\right) - k_9\right] - k_{11} - N_0^*\right\}.$$ (25)

337

338   **Irradiance and photosynthesis**

339   The depth of mixing in the upper ocean influences the average irradiance experienced

340   by phytoplankton. This also varies latitudinally, seasonally and daily with values of

341   30m typical of equatorial regions, and 100m typical of high latitudes. The average

342   mixed layer irradiance at any latitude may be approximated by:

343

344
$$I_A = \frac{I_\theta}{MLD} \int_0^{MLD} e^{-k_L z} \, dz = \frac{I_\theta}{MLD} \left(\frac{1 - e^{-k_L MLD}}{k_L} \right),$$
(26)

345

346   where I_A is the average irradiance over the mixed layer,

347                    $I_\theta = I_E \cos(\theta)$ is the incident surface irradiance at latitude θ,

348   I_E is the incident surface irradiance at the equator,

349   MLD is the depth of the mixed layer,

350   z is depth in the water column in metres, and

351   k_L is the seawater light extinction coefficient (typically 0.04 m^{-1} for

352   ocean water).

353

354   Zonneveld [1998] derived a photosynthesis-irradiance (*PI*) curve of the general form:

355

18

356
$$P_{photo} = \frac{aI_P}{bI_P^2 + I_P + c},$$
(27)

357

358 where P_{photo} denotes photosynthesis, I_P denotes irradiance measured as the average

359 number of photons per area per time, a represents the maximum rate quantum yield

360 per photosynthetic unit, b represents the ratio of the cell absorption cross-section to

361 the specific recovery rate of damaged d-protein, and c represents the excitation

362 requirements of the cell. Zonneveld observed that other researchers had derived

363 relationships of the same general form from different premises.

364

365 Phytoplankton acclimate to the average light intensity in which they grow [*Zonneveld*,

366 1998], and it is therefore reasonable to assume that phytoplankton throughout the

367 global oceans are adapted to their local irradiance. The average irradiance experienced

368 by endemic phytoplankton at any latitude on the globe (I_A) may then be scaled by

369 their saturating irradiance (I_S, at which phytoplankton photosynthesis is a maximum),

370 and the effect of variations in irradiance on phytoplankton growth at any latitude may

371 then be approximated by:

372

373
$$P_{photo} = \frac{aI}{bI^2 + I + c},$$
(28)

374

375 where $I = \dfrac{I_A}{I_S}$. The maximum value of equation (28) occurs when:

376

$$I = \sqrt{\frac{c}{b}} \, , \qquad (29)$$

378

379 and the maximum value of P_{photo} is now by definition achieved when $I = 1$, which

380 from equation (29) stipulates that $c = b$. The *PI* relationship may be applied to a

381 particular phytoplankton species by scaling it to be a function between 0 and 1 that

382 operates on the maximum phytoplankton growth rate (k_I) of the phytoplankton

383 species. This condition specifies that $P_{photo}(I = 1) = 1$, and therefore equation (28)

384 stipulates that $a = 1 + 2b$. The photosynthesis-irradiance relationship may then be

385 written as a general non-dimensional operator on the maximum phytoplankton growth

386 rate:

387

$$R = \frac{(1 + 2b)I}{bI^2 + I + b} \, , \qquad (30)$$

389

390 where b is now a photo-inhibition parameter that controls the shape of the *PI* curve

391 (Figure 2) and is likely to be species dependent. Note that R is relatively insensitive to

392 b once $b > 1$. As b tends towards infinity R tends to $\dfrac{2I}{I^2 + 1}$, so when $b = \infty$, $R = 0.385$

393 at $I = 5$, not appreciably different to its value when for example $b = 10$, when $R =$

394 0.396.

395

396   The *R* curves in Figure 2 represent a dimensionless operator on the maximum

397   phytoplankton growth rate, and equation (2) in the ecosystem model becomes:

398

$$\frac{dP}{dt} = k_1 R\left(\frac{N}{N + k_2}\right) P - k_3 PZ,$$ (31)

399

400

401   and the appropriate modification is also made to equation (1):

402

$$\frac{dN}{dt} = k_5 Z + k_3 k_4 PZ - k_1 R\left(\frac{N}{N + k_2}\right) P.$$ (32)

403

404

405   The usual condition when the climate is unperturbed (by anthropogenic or biogenic

406   activities) has $I = 1$ (as we have previously assumed $I = \dfrac{I_A}{I_S}$ in equation (28)). Any

407   perturbations to this steady state due to ecosystem feedbacks such as described by

408   equation (23) will affect the irradiance experienced by the phytoplankton, and can be

409   modelled by replacing the irradiance in equation (30) with the term $1 - \Delta\alpha$,

410   representing the change in irradiance due to changes in albedo:

411

412
$$R = \frac{(1+2b)(1-\Delta\alpha)}{b(1-\Delta\alpha)^2 + (1-\Delta\alpha) + b}.$$
(33)

413

414   This feedback effect may be written in terms of P and Z by substituting for $\Delta\alpha$ from

415   equation (25) giving an expression describing the effect on a marine planktonic

416   ecosystem of its production of DMS:

417

418
$$R = \frac{(1+2k_{13})\left(1 - \frac{k_{12}}{N_0}\left\{k_{10}\ln\left[k_8\left(k_6 P + k_7 Z\right) - k_9\right] - k_{11} - N_0\right\}\right)}{k_{13}\left(1 - \frac{k_{12}}{N_0}\left\{k_{10}\ln\left[k_8\left(k_6 P + k_7 Z\right) - k_9\right] - k_{11} - N_0\right\}\right)^2 + \left(1 - \frac{k_{12}}{N_0}\left\{k_{10}\ln\left[k_8\left(k_6 P + k_7 Z\right) - k_9\right] - k_{11} - N_0\right\}\right) + k_{13}},$$
(34)

419

420   where k_{13} has been substituted for b.

421

422   **The feedback model**

423   A global biogeochemical feedback model incorporating the effects of DMS produced

424   by marine ecosystems on climate and irradiance, and therefore their own environment,

425   can now be written by incorporating equation (34) into the *NPZ* model (equations (1)

426   - (3)):

427

428
$$\frac{dN}{dt} = k_5 Z + k_3 k_4 PZ - R k_1 \left(\frac{N}{N + k_2}\right) P,$$
(35)

22

$$\frac{dP}{dt} = Rk_1\left(\frac{N}{N+k_2}\right)P - k_3 PZ,$$ (36)

$$\frac{dZ}{dt} = k_3\left(1 - k_4\right)PZ - k_5 Z,$$ (37)

where R is given by equation (34). The values of the additional parameters ($k_6 - k_{13}$) used for the feedback model simulations are listed in Table 2. The nature of the scaling described in the model formulation ensures that the steady states of the simple and feedback models are identical (i.e. at steady state $R = 1$).

The time-lagged feedback model

The time-lagged feedback model was developed by including a time lag (τ) in the feedback term:

$$R = \frac{\left(1 + 2k_{13}\right)\left(1 - \frac{k_{12}}{N_0}\left\{k_{10}\ln\left[k_8\left(k_6 P(t-\tau) + k_7 Z(t-\tau)\right) - k_9\right] - k_{11} - N_0\right\}\right)}{k_{13}\left(1 - \frac{k_{12}}{N_0}\left\{k_{10}\ln\left[k_8\left(k_6 P(t-\tau) + k_7 Z(t-\tau)\right) - k_9\right] - k_{11} - N_0\right\}\right)^2 + \left(1 - \frac{k_{12}}{N_0}\left\{k_{10}\ln\left[k_8\left(k_6 P(t-\tau) + k_7 Z(t-\tau)\right) - k_9\right] - k_{11} - N_0\right\}\right) + k_{13}},$$ (38)

so that phytoplankton growing at time (t) experience light conditions determined by *DMS* emissions generated by the P and Z populations at some earlier time $(t - \tau)$.

446   **METHODS**

447

448   *NPZ-DMS* **model validation**

449   Often the only model validation available for ecosystem models is to test whether a

450   model can reproduce observed data [*Franks*, 2002], and the *NPZ-DMS* model

451   (equations (1) - (5)) used in this analysis was evaluated against this criteria in a study

452   region in the Southern Ocean off the eastern Antarctic coast (60-65° S, 125-140° E).

453   The model was formulated as a seasonally-forced, depth-averaged model for the

454   validation, where the state variables were averaged over the depth of the surface

455   ocean mixed layer and the model was forced with climatologies of environmental

456   data. The forcings comprised ocean mixed layer depth (*MLD*), sea surface

457   temperature (*SST*), photosynthetically active radiation (*PAR*) and sea surface wind

458   speed (*WIN*), and were sourced from the World Oceanographic Atlas, and from the

459   Pathfinder, SeaWiFS and SeaWinds satellite sensors respectively. Time series of the

460   forcings are shown in Figure 3.

461

462   Annual climatologies of ocean surface chlorophyll and DMS concentrations for the

463   study region were developed from SeaWiFS satellite data and the Kettle et al [1999]

464   database respectively. Model *P* values in mg N m^{-3} were converted to mg Chl *a* m^{-3}

465   assuming a Redfield C:N ratio of 5.7 (by weight) and a typical carbon : chlorophyll

466   ratio of 50 [*Walsh, et al.*, 2001] for the comparison. A genetic algorithm, an efficient

467   non-linear optimisation technique that does not require any derivative information

468   [*Holland*, 1975; *Mitchell*, 1997], was used to fit the model to observed data by

469   minimising the squared error between the model predictions and the observed data. A

470   parameter set was derived for the forced *NPZ* model so that the *P* population

471   reproduced the surface ocean chlorophyll concentrations climatology. The *NPZ-DMS*

472   model was then fitted to the DMS climatology

473

474   Seasonal forcing is implemented in the depth-averaged form of the *NPZ-DMS* model

475   by replacing k_1 in equations (1) and (2) with k_1', where:

476

477
$$k_1' = R_L R_T k_1 , \qquad (39)$$

478

479   where R_T is the temperature limitation of the phytoplankton growth rate and R_L is the

480   light limitation of the phytoplankton growth rate. The light limitation factor R_L is used

481   to explicitly represent the measured seasonal forcing of light in driving chlorophyll and

482   hence DMS dynamics for the model validation (where it must reproduce seasonal

483   variations in chlorophyll and DMS). In contrast the light factor *R* (equation (34))

484   represents the feedback light limitation due to changes in albedo, and is free of seasonal

485   effects in an unforced model.

486

487   Laboratory studies of phytoplankton have revealed a dependence of phytoplankton

488   growth rates on temperature [*Eppley*, 1972; *Goldman and Carter*, 1974]. The

489   temperature dependence of phytoplankton growth used in the model validation was

490   estimated by Eppley [1972] to be:

491

$$R_T = e^{0.063(T-T_{\max})},\qquad(40)$$

493

494   where T is the ambient temperature (^{0}C) and T_{max} is the maximum annual temperature.

495   R_T was forced with the climatology of SST (Figure 3a) for the validation.

496

497   As noted previously, the average irradiance in the ocean mixed layer (I_A) can be

498   approximated by equation (26). For the purposes of the model validation, a form of

499   light limitation on the phytoplankton growth rate proposed by Walsh et al. [2001] was

500   used:

501

$$R_L = \frac{I_A}{I_S}e^{\left(1-\frac{I_A}{I_S}\right)},\qquad(41)$$

503

504   where I_S the phytoplankton saturating irradiance (assumed to be 35 W m^{-2} for this

505   analysis ([*Walsh, et al.*, 2001], and references cited therein). R_L was forced with the

506   climatologies of MLD and PAR (Figure 3 b and c) for the validation.

507

508   The *DMS* model (equations (4) - (5)) was modified for the validation exercise by

509   including a term parameterising the transfer of DMS from the ocean to the atmosphere

510   identical to that used in the feedback model (equations (12) - (15)). However, the *DMS*

511   sea-air transfer velocity (k_{tr}) was forced by the climatologies of SST and WIN (Figure 3

512   a and d) for the validation exercise.

513

514   **Perturbation analysis**

515

516   The eigenvalues of the *NPZ* model are easily derived and informative, however, the

517   eigenvalues of the biofeedback model are not. The effect of including the feedback on

518   the model dynamics was therefore evaluated by numerically calculating the time

519   required for each model took to return to steady state after a perturbation. The return

520   time of a system provides a useful measure of its resilience as defined by DeAngelis

521   [1980], to which it is inversely proportional.

522

523   The models are reactive in the sense of Neubert and Caswell [1997] in that they

524   respond to almost all perturbations by initially amplifying the magnitude of the

525   perturbation, after which the perturbation exponentially decays as the model returns to

526   its steady state. A simple metric measuring the closeness of the model trajectory to

527   steady state was not therefore possible, and the time required for the whole of the

528   model's trajectory to be confined within a circle of 0.05% of the area of the model's

529   state space was therefore used. The accuracy of this metric is determined by the

530   period of oscillation of the system and is approximately controlled by the imaginary

531   part of the linearised non-feedback system's eigenvalue given by:

532

533
$$Err \approx \pm \frac{2\pi}{\mathrm{Im}(\lambda)} = \pm 4\pi \sqrt{\left[k_1 \left(\frac{k_2}{\left(N^* + k_2\right)^2} \right) P^* \right]^2 - 4P^* \left[k_3 k_4 Z^* - k_1 \left(\frac{N^*}{N^* + k_2} \right) \right] \left[k_3 - k_1 \left(\frac{k_2}{\left(N^* + k_2\right)^2} \right) P^* \right]}. \quad (42)$$

534

535   Return time surfaces were calculated for each of the models to demonstrate the effect

536   of the inclusion of the feedback process on the model resilience. These surfaces were

537   generated by perturbing each model 400 times using combinations of perturbations of

538   -90 to +100 % (in steps of 10%) of the steady state values of P and Z (equations (6)

539   and (7) respectively). The models were integrated forward in time using the perturbed

540   steady state values as initial conditions for the integration. Return time surfaces were

541   generated for each model and normalised by the largest return time of the non-

542   feedback model. A difference surface describing the effect of the feedback was also

543   calculated. Although the return time surfaces appear quite smooth, the accuracy

544   constraints of the metric used to build them meant that the difference surface was not

545   smooth. The difference surface was therefore smoothed for display; however, the

546   smoothing did not change the fundamental characteristics of the surface.

547

548   **Sensitivity analysis**

549   A sensitivity analysis of the biofeedback model was undertaken to ascertain the most

550   important parameters and processes in the model and to evaluate its behaviour. The

551   New Morris Method, an efficient second order screening method,[*Campolongo and*

552   *Braddock*, 1999; *Cropp and Braddock*, 2002] was used for the sensitivity analysis.

553   The sensitivity analysis measured the difference in return time surfaces of the models.

554   This analysis quantified the sensitivity of the feedback effect to the model parameters,

555   and is an important part of the analysis because, as was evident in the development of

556   the feedback model, the empirical relationships used have poorly known parameter

557   values. Two sensitivity metrics were calculated; the sum of the differences between

558   the return times of the models for each perturbation:

559

560
$$F = \sum_{i=1}^{20} \sum_{j=1}^{20} \left(R_{N:i,j} - R_{F:i,j} \right),$$
(43)

561

562   where $R_{N:i,j}$ is the return time for the *NPZ* model from perturbation (i, j) and $R_{F:i,j}$ is

563   the equivalent return time of the feedback model, and the normalised equivalent:

564

565
$$F_N = \sum_{i=1}^{20} \sum_{j=1}^{20} \left(\frac{R_{N:i,j} - R_{F:i,j}}{R_{N:i,j}} \right).$$
(44)

566

567   The sensitivity analysis was implemented to examine the influence of the twenty-two

568   parameters of the feedback model ($k_1 - k_5$, $k_8 - k_{13}$, $m_1 - m_7$ and γ, see Tables 1 and

569   2) and was implemented using parameter ranges of ±25% of the values listed in

570   Tables 1 (G99) and 2. The analysis made 48,400 comparisons of return time surfaces

571   and required 3.87 x 10^7 model evaluations.

572

573 **Time lag analysis**

574 The inclusion of the feedback time lag analysis recognises that a delay between a

575 phytoplankton bloom and increased DMS concentration in the water has been

576 observed [*Turner, et al.*, 2004; *Turner, et al.*, 1996] and that time lags between the

577 transfer of DMS to the atmosphere and modification of irradiance are likely to be

578 significant. As none of the relationships used to build the feedback model are reported

579 with associated time scales, the feedback model by default includes the assumption

580 that the atmospheric processes of the feedback occur instantaneously. Clearly this

581 assumption is untenable, and hence we have also examined the effect of time lags in

582 the feedback process on our simulation results.

583

584 The effect of time lags in the feedback processes was examined by modifying the

585 feedback model to include a time lag into the feedback *R* that operates on the *P*

586 growth term (see feedback model description above). However, there is little

587 conclusive evidence indicating the magnitude of the time lags involved in these

588 processes [*Ayers and Gillett*, 2000]. In situ correlations of ocean-atmosphere DMS

589 flux, atmospheric DMS concentration and condensation nuclei [*Andreae, et al.*, 1995]

590 have suggested that some pathways may be as short as six hours [*Lin and Chameides*,

591 1993]. In the absence of definitive evidence to the contrary, a reasonable first

592 approximation is to commence the time lags at zero and increase them until

593 interesting model behaviour appears exhausted.

594

595   A numerical analysis of the difference between the return time surfaces of the *NPZ*

596   model and the time–lagged feedback model was conducted for time lags between 0

597   and 15 days. The perturbation metric selected ensured that the model was integrated

598   for approximately 1,500 days, about a hundred times longer than the largest time lag,

599   ensuring the discontinuities related to the initial conditions did not affect the return

600   times. Return time surfaces were calculated for 60 time lags between 0.25 and 15 days

601   in increments of 0.25 days. These return time surfaces were each subtracted from the

602   return time surface of the *NPZ* model and the resulting difference surface was

603   summed to give a scalar metric of the feedback effect for each time lag. This metric

604   was scaled by the sum of the return time surface of the equivalent *NPZ* model to

605   provide a proportional measure of the feedback effect. This enabled comparison of the

606   feedback effects between different parameterisations as they have very different

607   magnitude return time surfaces.

608

609   The ecosystem model contains three rate parameters: the phytoplankton maximum

610   growth rate (k_1), the rate of zooplankton grazing on phytoplankton (k_3) and the rate of

611   zooplankton mortality (k_5). Previous sensitivity analysis of the major determinants of

612   DMS flux to the atmosphere [*Cropp, et al.*, 2004] have identified the importance of k_1

613   and k_3. These results are confirmed by the importance of these parameters to the

614   feedback effect examined in this research (see below), which also identified k_5 as an

615   important determinant of the magnitude of the feedback effect. The time lag analysis

616   was therefore conducted for the basic parameter set and also for parameter sets with

617   doubled k_1, doubled k_3 or doubled k_5.

618

619 **RESULTS**

620

621 *NPZ-DMS* **model validation**

622 The *P* concentration predicted by the depth-averaged *NPZ* model for the best-fit

623 parameter set derived by the genetic algorithm is shown in Figure 4 (a) with the

624 SeaWiFS chlorophyll data. Similarly, the best fit to the interpolated DMS data derived

625 by Kettle et al (1999) is shown in Figure 4 (b). (The environmental forcings used in

626 the simulation are shown in Figure 3.) The parameter values used to generate the

627 predictions in Figure 4 are listed in Table 1 (GA). The model produces a prediction

628 that matches the observed data well, suggesting that the *NPZ* model is a valid

629 representation of the generic plankton seasonal dynamics in the region of the Southern

630 Ocean off the east Antarctic coast, and similarly that the *DMS* model is a valid

631 representation of the seasonal DMS dynamics in this region.

632

633 **Return time surfaces**

634 The return time surface for the simple *NPZ* model without biogenic feedback on its

635 environment is shown in Figure 5. This reveals that the model is more sensitive to

636 perturbations in *Z* than to perturbations in *P*, in fact perturbations in *P* have almost no

637 effect on the return time of the system if *Z* has suffered a large perturbation in either

638 direction. This return time surface is characteristic of the *NPZ* model and is robust to

639 substantial (but not all) parameter variations

640

641   The return time surface for the feedback model is shown in Figure 6. This return time

642   surface is very similar to the surface for the *NPZ* model without biogenic feedback,

643   the principal difference being that the feedback model returns to equilibrium more

644   rapidly than the non-feedback model.

645

646   The surface representing the difference in return times to equilibrium for each of the

647   models is shown in Figure 7. This surface clearly demonstrates that the inclusion of

648   the biogenic feedback on its environment has endowed the *NPZ* model with increased

649   resilience. The time the system requires to recover its equilibrium state after

650   perturbations of any magnitude in any direction is substantially reduced by the

651   inclusion of the feedback process. Similarly to the models' return time surfaces, the

652   magnitude of the *P* perturbation does not have a substantial effect on the difference

653   between the two return time surfaces. The magnitude by which the resilience is

654   enhanced by the feedback process appears to be largely determined by the *Z*

655   perturbation. For each *Z* perturbation, the *P* perturbations appear to have little

656   influence on the return time of the system.

657

658   This increased resilience is an interesting result as the feedback (*R*) is formulated so

659   that at steady state $R = 1$ (its maximum possible value) and the resilience of the

660   feedback model is identical to that of the non-feedback model. Therefore including

661   the feedback into the model cannot increase the resilience (as defined by equation (10)

662   ) of the model. The effect of the feedback when the *P* and *Z* populations are greater

663   than their steady state values, the effect of the feedback is intuitive – it serves to

664   reduce the irradiance the *P* receive and slows their growth rate, helping them to

33

665   decline back to the steady state value. The effect on the system when the P and Z

666   populations are smaller than their steady state values is not so intuitive – the P growth

667   rate is again slowed, but it is not clear how this helps them to achieve their steady

668   state values more rapidly.

669

670   **Sensitivity analysis**

671   All of the 48,400 comparisons of un-lagged return time surfaces indicated that the

672   biofeedback model returned to steady state more rapidly than the non-feedback

673   model, that is that the addition of the biogenic feedback always reduced the time taken

674   for the system to recover from perturbation. This result indicates that the stabilising

675   effect of adding the instantaneous feedback to the ecosystem model is robust to

676   substantial parameter variations of both ecosystem and atmospheric processes.

677

678   The sensitivity analysis indicated that the model return times after perturbation were

679   sensitive to both biological parameters describing the ecosystem and physical

680   parameters describing the atmospheric processes. Both the raw and normalised

681   metrics used to measure the sensitivities (equations (43) and (44)) revealed almost the

682   same sensitivities to the parameters. Only one of these, the raw sensitivities, are

683   therefore presented, with Figure 8 describing the first order effects and Figure 9 the

684   second order or two-parameter interaction effects. Two of the most influential

685   parameters were k_{10} and k_{11}, describing the cloud droplet to CCN relationship

686   (equation (20)), followed by k_3, the Z grazing rate, k_1, the P growth rate, and k_5, the Z

687   mortality rate. It is apparent from equation (10) that these ecosystem rate parameters

688   also have significant impacts on the model resilience.

689

690   Combinations of these parameters were also important in the two-factor effects shown

691   in Figure 9. While the two most influential parameter interactions, k_{10}, k_{11} and k_1, k_3

692   are atmospheric and biological pairs respectively, the next most important pair k_3, k_{10}

693   and several other important pairs involving k_1, k_5, k_{11} and k_{12} reveal that interactions

694   between the marine ecological processes and the atmospheric physical and chemical

695   processes are important determinants of the magnitude of the feedback effect.

696

697   The three important results from the sensitivity analysis are therefore that the

698   consequences of the feedback for the ecosystem depend on both biological and

699   atmospheric properties, that an instantaneous feedback always acts to stabilise the

700   ecosystem dynamics, and that it is critically important to the determination of the

701   actual magnitude of this feedback process that both the atmospheric and biological

702   components of the process noted above are better quantified by field measurements.

703

704   **Time lag analysis**

705   The time lag analysis reveals that the magnitude and direction of the feedback effect

706   is dependent on the time lag between the ecosystem dynamics and the change in

707   irradiance experienced by the phytoplankton as a result of the atmospheric feedback

708   (Figure 10). The solid line in Figure 10 shows the effect of feedback time lags on the

709   return time of the feedback model for the basic parameter set. This reveals that the

710 initial stabilising effect (by which is meant that the resilience the system is increased)

711 of the feedback, where it reduces the return time of the model by about 6%, rapidly

712 declines once a lag of two days is introduced into the feedback. The feedback has no

713 effect on the resilience of the model if the feedback is lagged by three days, and for

714 lags of three to six days, the feedback destabilises (reduces the resilience of) the

715 model, increasing the return time by up to about 6%.

716

717 Time lags of six to ten days once again increase the resilience of the feedback model

718 (by up to about 2%). This recovery of the stabilising effect of the feedback, with a

719 maximum in the second stabilising region at a time lag of about seven days is

720 especially interesting given that ocean in situ ecosystem-scale experiments that

721 stimulated phytoplankton blooms measured a peak in DMS aqueous concentrations

722 about a week after the bloom [*Turner, et al.*, 1996]. Time lags greater than ten days

723 again result in destabilisation of the feedback model. It should be noted, however, that

724 while the lagged feedback sometimes makes this model less resilient, causing it to

725 take up to 10% longer to reach steady state than the non-feedback model (Figure 10),

726 it never reduces the resilience to zero (i.e. the system always returns to the steady

727 state). For the realistic (i.e. based on measured values) parameter values used (Tables

728 1 and 2) both models are always stable – only the resilience, and hence the time taken

729 to return to steady state after a perturbation, is affected by the feedback.

730

731 The time lag analysis also reveals the influence that the properties of the biota in the

732 ecosystem can have on the feedback process. The simulation with k_1 doubled (Figure

733 10, dotted line) reveals that the increased phytoplankton growth rate both greatly

734   reduces the time lags for which the feedback model is initially more resilient (two

735   days rather than three) and also reduces the magnitude of the stabilising or

736   destabilising effects (a 4% reduction in return time). Similarly the recovery of the

737   stabilising effect occurs earlier (around four days), but lasts for only two days and

738   produces only a 1% reduction in return time.

739

740   The simulation with doubled zooplankton grazing (k_3) reveals quite the opposite effect

741   (Figure 10, dashed line). In this case the increase in resilience for lags of up to three

742   days is substantially increased with return times being up to 12.5% shorter than the

743   non-feedback model. The region of reduced resilience is smaller and the stabilising

744   effect is recovered much sooner at about 4 days. This variant also recovers resilience

745   to a greater extent than the base parameter feedback model, with reductions in return

746   time of up to 6%. The reduction in resilience that subsequently occurs is again very

747   similar to the base parameter feedback model. The distinctive feature of the increased

748   zooplankton grazing model is that its region of reduced resilience in Figure 10 is

749   much smaller (in magnitude and duration) compared to both other parameter options.

750

751   An increase in the rate of zooplankton mortality (k_5) also reduces the stabilising effect

752   of the feedback, reducing its initial increase in resilience to about 2%, but providing

753   the largest reduction in resilience of over 7.5% at about day three. This variant also

754   reduces the duration of the initial stabilising feedback to less than 2 days. The

755   feedback again produces increased resilience after a time lag of 5 days, and remains

756   so up to about 8 days, but only marginally (less than 1% reduction in return time).

757   However, subtle effects that operate for long periods of time may still be influential.

758

759   An interesting aspect of the response of the feedback effect to these parameter

760   variations is that the feedback process provides the ecosystem with a mechanism to

761   recover resilience if the attributes of the biota change to reduce it. Increases in the

762   phytoplankton growth rate (k_1) and the zooplankton mortality rate (k_5) reduce the

763   stabilising effect of the feedback, but it is apparent from equation (10) that they

764   simultaneously must increase the resilience of the ecosystem. Similarly, increases in

765   the zooplankton grazing rate (k_3) reduce the resilience of the ecosystem, but increase

766   the stabilising effect of the feedback. Of these two processes, the ecosystem resilience

767   is the principal determinant of the response to perturbation; the feedback system with

768   increased phytoplankton growth rate has shorter return times than the system with

769   increased zooplankton grazing, even though the latter provides a much greater

770   stabilising feedback effect. An interesting heuristic gained from this analysis is that

771   the feedback process provides a "resilience insurance policy" in that changes in the

772   properties of the ecosystem that tend to reduce its resilience are countered by an

773   increase in resilience delivered by the feedback, and *vice versa*.

774

775   **DISCUSSION**

776   This research essentially generates a hypothesis that the DMS feedback process may

777   serve to stabilise (that is, increase the resilience of) some ecosystems. The

778   geographical extent to which this hypothesis may apply is as yet unclear, as the *NPZ-*

779   *DMS* model is not able to reproduce chlorophyll and DMS dynamics over the whole

780   of the global oceans. The stability attributes of the *NPZ* and *DMS* models suggest that

781   the model will be best able to reproduce observed dynamics in regions of the oceans

782   where the chlorophyll seasonal variation closely follows the physical forcings of

783   irradiance, temperature and mixed layer depth, and the DMS concentration is closely

784   coupled to the chlorophyll signal. This is generally the situation in high latitudes

785   where the forcings are very strong and drive the plankton dynamics, but is not the

786   case in many parts of the oceans. In the equatorial oceans, for example, chlorophyll is

787   often out of phase with the physical forcings, and this model cannot reproduce the

788   temporal chlorophyll dynamics in these regions. Similarly, the model cannot

789   reproduce DMS dynamics if there is a substantial time lag between the chlorophyll

790   maximum and the DMS maximum, for example the "summer paradox" observed at

791   some mid and low latitude locations [*Simo and Pedros-Alio*, 1999].

792

793   These caveats constrain the spatial range where the model can competently reproduce

794   measured data, but do not necessarily degrade the heuristic value of the model. Work

795   in progress by the authors suggests that the dynamics of the *NPZ* model used in this

796   analysis is a subset of a slightly more complicated *NPZ* model that can fit chlorophyll

797   dynamics that are out of phase with their physical forcings. (The dynamics of this

798   slightly more complicated model are such that at this stage it does not have the

799   heuristic value of the model we have used.) Similarly, Vallina et al (in preparation)

800   show that the DMS summer paradox may be explained by including an extra DMS

801   source term, reflecting the exudation of DMS by phytoplankton under UV stress, that

802   effectively loosens the coupling between the ecosystem and chemical models.

803

804   Although there are no assumptions in the model that intrinsically limit its application

805   to any part of the globe, the validation exercise suggests that inferences and

806 hypotheses drawn from this exercise may only be directly relevant to high latitude

807 regions. Never-the-less, this research contributes a new dimension to the DMS

808 hypothesis of Charlson et al [1987] in particular, and to the field of Earth System

809 Science in general. Our results show that an instantaneous biogenic feedback on the

810 planktonic ecosystem model's irradiance environment can make the model more

811 resilient to perturbation. The time that the system requires to return to its equilibrium

812 state after any perturbation is therefore reduced by the addition of the instantaneous

813 feedback.

814

815 The stabilising effect of the feedback is largest for perturbations that reduce the *Z*

816 population. This is an interesting result, as recent work on model *NPZ* ecosystems

817 [*Cropp and Norbury*, 2007] suggests that extinction processes in climate change

818 scenarios will progress sequentially commencing with the extinction of *Z*. The

819 presence of the feedback mechanism in the model therefore provides the system with

820 an additional safeguard against extinction: the smaller the *Z* population gets, the

821 stronger the feedback restoring the system to its equilibrium state becomes. This

822 suggests the heuristic that the stability properties engendered by the feedback act most

823 strongly in the manner required to both save the species and to maintain the

824 ecosystem in its original form.

825

826 The sensitivity analysis revealed two important properties of the instantaneous

827 feedback effect: that it always serves to increase the resilience of the model, and that

828 it is a function of both the biological and physical-chemical factors involved in the

829 process. Two important parameters controlling the magnitude of the feedback effect

830   are the slope (k_{10}) and intercept (k_{11}) values of the regression relating the number of

831   cloud droplets in the atmosphere to the number of cloud condensing nuclei in the

832   atmosphere. The second most influential parameter is the rate of zooplankton grazing

833   on phytoplankton (k_3). This parameter was identified by Cropp et al. [2004] as the

834   most important determinant of annual integrated DMS flux to the atmosphere.

835

836   The time lag analysis revealed that the magnitude of the feedback effect, and whether

837   it increases or reduces the resilience of the system, depends on the time lags

838   associated with the feedback processes. This analysis revealed that the feedback could

839   make the system more sensitive to perturbation if the effect of the feedback took

840   several days to impact on the ecosystem. However, the most interesting and perhaps

841   important result of the time lag analysis is that for time lags of about 7-10 days the

842   feedback effect again increases the resilience of the ecosystem; that is the feedback

843   causes the ecosystem to return to its equilibrium state more rapidly than if the

844   feedback was not present. The time lags that lead to this recovered stabilising effect

845   correspond with time lags observed in *in situ* ocean ecosystem experiments between

846   phytoplankton blooms and subsequent maximum aqueous DMS concentrations

847   [*Turner, et al.*, 2004; *Turner, et al.*, 1996]. This analysis also identified an important

848   modification to the results of the sensitivity analysis that also serves to further reflect

849   the importance of k_1, k_3 and k_5 on the stabilising effects of the feedback, and suggest

850   that the timing and magnitude of the feedback effects will vary between ecosystems.

851

852   The time-lagged feedback model we have used does not account for spatial factors,

853   and the rapid advection rates in the atmosphere compared to the ocean suggest that

854 only in periods of calm weather would the atmospheric effects generated by a

855 phytoplankton bloom affect the originating population. However, as the atmospheric

856 processes involved in the feedback may be rapid [*Hamilton and Lenton*, 1998], for

857 some pathways perhaps as short as six hours [*Lin and Chameides*, 1993], couplings

858 on local and regional scales may be close.

859

860 The influence of the feedback on the ecosystem model's stability characteristics leads

861 to the interesting hypothesis that the DMS feedback cycle may not be just an artefact

862 of plankton biochemistry, but an intrinsic component of marine planktonic

863 ecosystems. Such a hypothesis would suggest that marine phytoplankton gained a

864 benefit from the production of DMSP as it initiated processes that stabilised the

865 plankton ecosystem and consequently buffered the population from the effects of

866 perturbations. Many authors, perhaps beginning with Dunbar [1960], have pointed to

867 the susceptibility of populations to extinction due to stochastic events when at the

868 nadir of extended "boom and bust" cycles that many low resilience systems

869 experience after perturbation.

870

871 Such a hypothesis would require the invocation of group selection, a concept

872 extensively attacked in the 1970's (see for example Dawkins [1976]). While it is not

873 the intent of this research to debate the merits of group selection, we note that group

874 selection is attracting new interest in Western evolutionary debate [*Borello*, 2005] and

875 that ecosystem evolution is an accepted paradigm in Russian science [*Lekiavichius*,

876 2003]. As noted by Loreau et al. [2004] "Species traits and their evolution are

877   ultimately constrained by ecosystem processes, just as ecosystem properties are

878   constrained by the ecological and evolutionary history of interacting species."

879

880   Our results clearly show that the influence of the feedback is dependent on the time

881   lags in the ocean and atmospheric processes, and on the characteristics of the

882   ecosystem. Our theoretical analysis suggests that clarification of the time scales of the

883   feedback processes, and better knowledge of all the parameters in the model, would

884   be a very useful contribution to the whole DMS hypothesis.

885

886   **CONCLUSION**

887   This research has modelled a process whereby production of a precursor compound

888   by individual phytoplankton, coupled with subsequent biological processing by co-

889   constituents of a plankton ecosystem, results in a product that modifies the properties

890   of the atmosphere. The changes in albedo we have modelled subsequently influence

891   the irradiance experienced by the phytoplankton that initiated the process. Our results

892   demonstrate that this change in environment modifies the population dynamics of the

893   phytoplankton and may make the ecosystem to which they belong more resilient to

894   perturbation. Our results also suggest that the magnitude and timing of the feedback

895   effects are highly dependent on the characteristics the ecosystems and the atmospheric

896   processes involved. Although the feedback effect can reduce the resilience of the

897   ecosystem when time lags are introduced, the feedback increases the resilience of the

898   system at time lags similar to those observed in real ocean plankton ecosystems.

899

900   The coherence of these theoretical and observed relationships then raises the question

901   of whether the phytoplankton – DMS – cloud relationship reflects a fortuitous artefact

902   of phytoplankton metabolism or an evolved property that improves phytoplankton

903   fitness by stabilising the dynamics of their ecosystem. Because the benefits derived by

904   an individual phytoplankton from producing DMSP are accrued by the group, and

905   perhaps even the ecosystem as a whole, the option that phytoplankton have evolved

906   the ability to influence the properties of the atmosphere invokes group-level selection.

907   Hamilton and Lenton [1998] have argued just such a case for these systems, although

908   in support of a different hypothesis. The stabilising effects observed in this study,

909   although subtle, would act over long time scales and may therefore have profound

910   implications for the characteristics of the ecosystems that generate them.

911

912   Our research indicates a pressing need for clarification of the time scales of the

913   atmospheric processes involved in the DMS feedback. Although the feedback effects

914   we have documented appear robust to substantial parameter variations the

915   implications of the feedback process for marine plankton ecosystems may not be fully

916   assessed, nor our hypothesis refined, until these details are elucidated. If the time lags

917   observed in real systems do indeed correspond with the time lags that stabilise our

918   model ecosystem, then such further research may yield rich results relating to

919   fundamental properties of living systems.

920

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937

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1069 **TABLES**

1070 **Table 1: Parameters and values for the *NPZ-DMS* model.**

PAR	PROCESS	UNITS	VALUES	
			G99	GA
k_1	Maximum rate of N uptake by P	d^{-1}	0.27	0.9918
k_2	Half-saturation constant for P uptake of N	$mgNm^{-3}$	12.6	19.1230
k_3	Z grazing rate (per individual) on P	$m^3mgN^{-1}d^{-1}$	0.02	0.0256
k_4	Proportion of N uptake excreted by Z	-	0.3	0.0287
k_5	Z specific mortality rate	d^{-1}	0.050	0.3720
m_1	Rate of release of *DMSP* by P	d^{-1}	0.01	0.0076
m_2	Rate of *DMSP* excretion rate by Z	d^{-1}	0.01	0.3050
m_3	*DMSP – DMS* conversion rate	d^{-1}	0.5	0.9226
m_4	Rate of *DMSP* consumption by bacteria	d^{-1}	0.53	0.1201
m_5	Rate of release of *DMS* by P	d^{-1}	0.0085	0.0045
m_6	Rate of *DMS* consumption by bacteria	d^{-1}	0.29	0.2664
m_7	Maximum *DMS* photo-oxidation rate	d^{-1}	1.3	0.5752
γ	Phytoplankton *S(DMSP):N* ratio	mg S/mg N	0.3	0.3580
N_T	Total nutrient as dissolved inorganic nitrogen	$mgNm^{-3}$	50	3.0761

1071   G99 represents Gabric et al [1999]; GA represents derived by GA for model

1072   validation in this paper.

1073

1074

1075   **Table 2: Additional parameters derived for the biofeedback model.**

PAR.	PROCESS	UNITS	VALUE
k_6	*P-DMS* flux parameter	mgS m mgN^{-1} d^{-1}	0.0128
k_7	*Z-DMS* flux parameter	mgS m mgN^{-1} d^{-1}	0.0035
k_8	*CCN-DMS* flux ratio	m^{2}d mgS^{-1}	710
k_9	*CCN* background level	-	15
k_{10}	N_C - *CCN* ratio	-	183
k_{11}	N_C - *CCN* regression constant	-	334
k_{12}	$\Delta\alpha$ - N_C ratio	-	0.075
k_{13}	Phytoplankton *PI* curve parameter	-	0 - ∞
N_0	$\Delta\alpha$ - N_C reference droplet number (N_0)	-	-

1076

1077

1077 **FIGURE LEGENDS**

1078

1079 Figure 1. Schematic diagram of the *NPZ-DMS* feedback model. Dotted lines indicate

1080 the components of the original GMSK model that have been omitted for this analysis.

1081

1082 Figure 2: Photosynthesis-irradiance curve described by equation (30). Solid line has b

1083 $= 0.10$, dotted line is $b = 1$ and dashed line is $b = 10$.

1084

1085 Figure 3. Forcing data for depth-averaged *NPZ-DMS* model validations: (a) sea

1086 surface temperature (SST); (b) mixed layer depth (MLD), (c) photosynthetically

1087 active radiation (PAR) and (d) sea surface wind speed (WIN) for the Southern Ocean

1088 region 60-65^{0}S, 125-140^{0}E.

1089

1090 Figure 4. Best fits derived for depth-averaged *NPZ-DMS* model validations: (a) model

1091 *P* (line) and SeaWiFS chlorophyll data (dots) and (b) model *DMS* (line) and Kettle et

1092 al [1999] DMS data (dots). Data is for the same Southern Ocean region as Figure 3.

1093

1094 Figure 5. Normalised return time surface for the *NPZ-DMS* model without feedback

1095 showing the times the system takes to return to its equilibrium state after perturbation.

1096

1097   Figure 6. Normalised return time surface for the *NPZ-DMS* model with feedback

1098   showing the times the system takes to return to its equilibrium state after perturbation.

1099

1100   Figure 7. Normalised return time difference surface for the *NPZ-DMS* model with and

1101   without biogenic feedback. This surface is calculated by subtracting the return time

1102   surface of the *NPZ-DMS* model with feedback from the return time surface of the

1103   *NPZ-DMS* model with no feedback. This surface has been smoothed for clarity of

1104   presentation.

1105

1106   Figure 8. Sensitivity of feedback effect to first order parameters identified by the New

1107   Morris Method. Light region of bar is sensitivity to each parameter alone; dark region

1108   is the influence of each parameter in association with all other parameters (i.e.

1109   indicates the existence of second and higher order interaction effects).

1110

1111   Figure 9. Sensitivity of feedback effect to second order parameter interactions

1112   identified by the New Morris Method. Light region of bar is sensitivity to each

1113   parameter pair alone; dark region is the influence of each parameter pair in association

1114   with all other parameters (i.e. indicates the existence of third and higher order

1115   interaction effects).

1116

1117   Figure 10. The effect of time lags on the feedback for the return time of the *NPZ-DMS*

1118   feedback model. The feedback effect is measured as the proportion by which sum of

1119   non-feedback model's return time surface exceeds the sum of the feedback model's

1120   return time surface. The thick solid line is the feedback model with the default

1121   parameter set, the dotted line is with the maximum phytoplankton growth rate (k_1)

1122   doubled, the dashed line is with the zooplankton grazing rate (k_3) doubled and the thin

1123   solid line is with the zooplankton mortality rate (k_5) doubled.

1124