

On the mathematical formulation and parameter estimation of the Norwegian Sea plankton system

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SARSIA



Broström G, Drange H. 2000. On the mathematical formulation and parameter estimation of the Norwegian Sea plankton system. *Sarsia* 85:211-225.

The mathematical description of the oceanic plankton system is often characterised by a simple structure where the major components of the system are governed by the dissolved nutrient concentration N , the phytoplankton biomass P , and the zooplankton biomass Z (also known as the NPZ model). The flows between the variables can be formulated in a variety of ways that, in general, alter the time development of the model. In this study we investigate how the numerical value of model parameters that are hard to determine experimentally can be estimated from *in situ* field observations. By that, we can assign parameter values to each model formulation such that they should follow a prescribed time development that is consistent with data. Accordingly, this gives us a tool to compare model formulations in a consistent way. The study emphasises the importance of analysing the model with respect to stability and multiple solutions. The study is exemplified using observations from Ocean Weather Station Mike (66°N, 2°E) in the Norwegian Sea, illustrating the need for a proper model formulation in order to reproduce measurements.

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Keywords: Ecosystem modelling; parameter estimation; stability properties; Norwegian Sea.

INTRODUCTION

A theoretical formulation of the oceanic plankton system usually includes descriptions of biological and ocean dynamical quantities like species composition, nutrient availability, advective transport, vertical mixing, solar radiation, and temperature. A complete mathematical formulation of the plankton system is therefore very complicated and highly non-linear. Thus, existing ecosystem models by necessity represent a simplification of the actual properties of the marine biota.

Although we conclude that the ocean plankton system is complex there are, nevertheless, some features of the plankton system that are fairly predictable. An example is provided by the importance of physical factors for high latitude spring blooms. Sverdrup (1953) showed that the major plankton blooming in the spring cannot proceed unless the available light over the well-mixed upper ocean layer is such that the integrated growth of phytoplankton in the mixed layer is above the respiration rate of the organisms. These quantities are well predictable illustrating that the integrated behaviour of the plankton system can be described even if the details are not known.

The physical properties of the upper ocean can be described by means of physical models (for instance,

Gaspar 1988; Oberhuber 1993). The coupling between physical properties of the ocean and the plankton system can therefore be studied by coupled physical-biological models. It is interesting and encouraging that it is possible to simulate the major (or integrated) features of the marine ecosystem over large areas such as the North Atlantic ocean using ecosystem models with essentially uniform biological parameters (Oschlies & Garçon 1998) or with ecosystem models designed to describe the seasonal cycling of plankton and plant nutrients at specific locations (Fasham & al. 1993; Drange 1996).

One of the fundamental topics in mathematical modelling deals with the robustness of the model formulation. It is well known that even small changes in the model formulation and parameter values may completely change the time development of the model (Truscott & Brindley 1994; Edwards & Brindley 1996, 1999). Furthermore, it appears that a model can be robust in one parameter regime but highly sensitive in another parameter regime. Thus, a detailed analysis of the model may be necessary to fully comprehend the model behaviour. Unfortunately, it appears that thorough discussions of the mathematical properties of marine ecosystem models are more an exception (see for instance Busenberg & al. 1990) than a rule.



The aim of this study is to investigate the *mathematical* behaviour of a simple model for the biological cycle during the productive season at high latitudes. To construct a model for the ecosystem we must:

- formulate the mathematical model;
- find parameter values that reproduce measurements; and
- evaluate the properties of the model, including search for multiple solutions, examine sensitivity to parameter values, and study the stability of the time development of the modelled variables.

We do not intend to make a full investigation of the model system in this study. Instead, we concentrate on certain solutions and the associated behaviour of the system that may be of practical concern in the modelling attempt. Accordingly, the guideline for this study is simplicity rather than completeness; a more complete discussion on the stability properties of a similar model may be found in Truscott & Brindley (1994) and Edwards & Brindley (1996, 1999). To exemplify the model features we use data from Station Mike (66°N, 2°E) in the Norwegian Sea as a testbed for ascribing parameters to the model.

The paper is outlined as follows: In Sec. 2 we describe the basic structure of the model. Parameter values that allow the model to reproduce measurements can be found from an analysis of the model equations and data, and a description of this procedure is given in Sec. 3. The sensitivity to changes in parameters is also an important model feature, and it is briefly covered in Sec. 4. The stability aspect of the model is described in Sec. 5, whereas the time evolution of the model compartments for Station M is presented in Sec. 6. Discussions are devoted to Sec. 7.

2. FORMULATION OF THE PLANKTON SYSTEM

The most basic properties of the oceanic plankton system can be described with the dissolved nutrient concentration N , the phytoplankton concentration P , and the zooplankton concentration Z . Further, we temporarily include the detritus concentration D to describe the export of organic material from the euphotic zone. The variables P and Z should be regarded as integrated, or distribution probabilities, of the entire phyto- and zooplankton populations, respectively (Radach & Maier-Reimer 1975). Some major features of the system are:

- Phytoplankton consumes dissolved nutrients during growth.
- Zooplankton uses phytoplankton as food source.
- Both phyto- and zooplankton have a metabolism in which they consume body weight and release nutrients to the water. The grazing of zooplankton on other zooplankton will result in a loss of organic

material from the zooplankton pool due to the, say 20-40 %, losses in the zooplankton feeding process. We will describe these “self-grazing” losses as a metabolic process.

- Import and export of nutrients and biomass to/from the upper layer. Mixing of nutrients from deeper layers to the upper layer represents an import of dissolved nutrients. Phytoplankton may sink out of the upper layer and be lost from the system representing a loss term. Further, movements of zooplankton may create a vertical flow in the model. However, the most important export process is probably the sinking of faecal pellets produced by zooplankton. We represent this flux by introducing the detritus concentration D .

EQUATIONS OF THE SYSTEM

Conservation equations that describe the evolution of the system may be put in the form

$$\begin{aligned} \frac{dN}{dt} &= -G_p(N, P) + M_z(Z) + M_D(D) + S, \\ \frac{dP}{dt} &= G_p(N, P) - G_z(P, Z) - W_p(P), \\ \frac{dZ}{dt} &= \varepsilon G_z(P, Z) - M_z(Z), \\ \frac{dD}{dt} &= (1 - \varepsilon)G_z(P, Z) - M_D(D) - W_D(D). \end{aligned} \quad (1 \text{ a-d})$$

Here $G_p(N, P)$ is the net growth of phytoplankton (depends on the nutrient concentration N , and the phytoplankton concentration P); M_z is the metabolism for zooplankton; M_D represents mineralisation of detritus; S represents sources/sinks in the nutrient equation due to external processes like mixing; G_z is the growth of zooplankton; W_p is the loss of phytoplankton from the upper layer caused by sinking phytoplankton; W_D is the loss of sinking particles; and ε represents an assimilation efficiency for zooplankton (i.e., $1 - \varepsilon$ represents the production of large detritus particles with high sinking speeds, the egestion of small particles is, accordingly, described through M_z). See Evans & Garçon (1997) for detailed formulations on ecosystem models based on Eqs 1a-d.

SOME SIMPLIFICATIONS

Although Eqs 1a-d are general enough to describe the time development of many ecosystems, the equations are too complicated to admit a simple analysis of the system. Therefore, we introduce the following simplifications:

- We assume that the plankton sinking term $W_p(P)$ is small compared to the other terms in the



phytoplankton equation, at least as long as the nutrient concentration N is above a certain minimum value. Accordingly, we put $W_p(P) = 0$.

- If the sinking velocity of detritus is sufficiently large, the nutrients that are converted to detritus will be exported to deeper layers. Thus, the export of nutrients can be calculated directly from $(1 - \epsilon)G_z(P, Z)$.

With these simplifications the equations describing the system can be put in the form

$$\begin{aligned} \frac{dN}{dt} &= -G_p(N, P) + M_z(Z) + S, \\ \frac{dP}{dt} &= G_p(N, P) - G_z(P, Z), \\ \frac{dZ}{dt} &= \epsilon G_z(P, Z) - M_z(Z). \end{aligned} \tag{2 a-c}$$

MODEL FLUXES

The fluxes in Eqs 2a-c may be written as

$$\begin{aligned} G_p(N, P) &= \gamma_p \cdot \frac{N}{\kappa_N + N} \cdot P - \mu_p \cdot P, \\ G_z(P, Z) &= \gamma_z \cdot \frac{P^n}{\kappa_p^n + P^n} \cdot Z, \\ M_z(Z) &= \mu_z \cdot Z^m, \end{aligned} \tag{3 a-c}$$

where γ represents the growth rate, κ the half-saturation constant, and μ the metabolism. For phytoplankton, γ_p includes the effect of light on growth. Furthermore, n and m are constants that may take values of 1 or 2 depending on the ecosystem formulation (Steele & Henderson 1981, 1992, 1995; and Sec. 4.3).

If the nutrient concentration is much larger than the half-saturation constant, i.e., if $N/(\kappa_N + N) \approx 1$, we may write $G_p(N, P) \approx G_p(P)$, where

$$G_p(P) = (\gamma_p - \mu_p)P, \tag{4}$$

Eq. 4 is useful when analysing the sensitivity of the system to changes in parameter values in the case where there are plenty of dissolved nutrients.

The typical phytoplankton growth rate in the upper layer, γ_{ps} , can be calculated as

$$\gamma_{ps} = \langle \Gamma_{p, \max} I_{\lim}(I) \rangle, \tag{5}$$

where $\langle \rangle$ represents a mean value over 24 hours and the mixed layer depth, $\Gamma_{p, \max}$ is the phytoplankton growth rate at optimal growth conditions, it depends on the temperature (Eppley 1972), and $\Gamma_{p, \max} \approx 1.1 \text{ day}^{-1}$ at 10 °C. The growth rate depends on the light intensity according to

$$I_{\lim}(I) = \frac{I}{\kappa_I + I}, \tag{6}$$

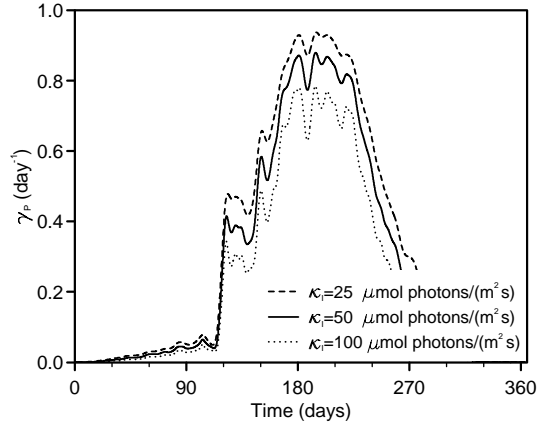


Fig. 1. An estimate of the phytoplankton growth rate γ_p at Station M in 1991 for different values of the phytoplankton light sensitivity parameter κ_I . γ_p represents the mean potential growth rate for phytoplankton over the mixed layer, i.e., it represents the averaged growth rate at high nutrient concentration (see Eq. 5).

where κ_I is the half-saturation constant for light. Typical values of κ_I range between 25-100 $\mu\text{mol photons}/(\text{m}^2\text{s})$ reflecting the light sensitivity of the organisms (Rhee & Gotham 1981; Sakshaug & Slagstad 1991). Finally, the penetration of light in the ocean can be written

$$\frac{dI}{dz} = k_d \cdot I, \tag{7}$$

where z is depth (z is positive upwards) and k_d is the extinction coefficient for oceanic water.

Some calculations of γ_p are shown in Fig. 1. The calculations are based on observed cloudiness at Station M and mixed layer depths taken from a one dimensional turbulence model that has been forced by observed atmospheric conditions at Station M (Broström 1997). Fig. 1 illustrates the physical control on primary production, i.e., it essentially reflects the annual cycles of the radiation conditions, the temperature and the thickness of the mixed layer. There is, however, a feed back from the biological system through self-shading. We have therefore ascribed a typical summer value, $k_d = 0.1 \text{ m}^{-1}$, to the extinction coefficient in the calculation presented in Fig. 1.

3. ESTIMATING MODEL PARAMETERS

There are three factors that influence the model behaviour: The model structure; the mathematical formulation of the flows; and the parameters that describe the strength of the flow functions. Given a model structure, the time development of the ecosystem model will depend on the mathematical formulation and the parameter values,



implying that different flow formulations need different parameter values to describe a similar time development.

If the model parameters are known, it is possible to solve the system and determine the time evolution of the model. It is therefore a direct coupling between the parameters of the model and the model solution. Accordingly, for each independent observational set we have of the system, it is possible to determine the numerical value of one parameter. We will use this approach to determine the numerical value of the least known parameters of the ecosystem model.

We consider the phytoplankton dynamics as to be more comprehensively described in the literature than the dynamics of the zooplankton (Eppley 1972; Sakshaug & Slagstad 1991). Accordingly, we assume that the phytoplankton growth and metabolism rate, i.e., γ_p , κ_N , and μ_p are known (see Table 1 for the numerical values used in this study, and Broström (1997) for a motivation of the choices).

The situation is more complicated for the zooplankton compartment for several reasons. Zooplankton may have “advanced” survival strategies and life cycles that make their behaviour difficult to study. In addition, the zooplankton compartment represents the highest trophic level in our model, so the zooplankton loss term also includes grazing from higher trophic levels, a process that is hard to parameterise. The response of zooplankton grazing on phytoplankton has been studied in a number of investigations (Frost 1977; Hansen & al. 1990). We believe that the functional form of the grazing is easier studied than the magnitude of the grazing capacity and assign a prescribed value to κ_p rather than to γ_z . Accordingly we assume that the parameters of the zooplankton equation are the parameters for which little is known and we intend to determine γ_z , μ_z , and ε from observations. For κ_p we use a value of $0.5 \mu\text{mol/kg}$ that is typical for *Calanus finmarchicus* which dominates the population at station M (Tande & Slagstad 1992). However, for NPZ

models for the North Atlantic, $\kappa_p = 1 \mu\text{mol/kg}$ is a more typical value (Evans & Parslow 1985; Fasham & al. 1990; Evans & Garçon 1997).

OBSERVATIONS TO FIT

The zooplankton parameters γ_z , μ_z , and ε are considered as *a priori* unknowns. To determine these parameters we use three empirical observations of the ecosystem. The observations are based on data from the period immediately after the transient part of the spring bloom in the Norwegian and the surrounding seas. This period starts in early May, ends three months later in early August, and is characterised by a steady decrease in the nitrate concentration. We refer to this period as the decay phase and the observations can be summarised as:

1. According to upper ocean measurements at Station M for 1991, the decrease in nitrate concentration during the decay phase, d , is about $12 \mu\text{mol/kg}$ in 90 days (F. Rey, Marine Research Institute, Bergen, Norway; see also Fig. 9a), so $d(\text{NO}_3) = -0.13 \mu\text{mol N}/(\text{kg day})$.
2. The phytoplankton concentration appears to vary around a reasonably well-defined mean value P_S during the decay phase (F. Rey, Marine Research Institute, Bergen, Norway; see also Fig. 9b). The chlorophyll concentration is approximately $1 \text{ mg}/\text{m}^3$, thus assuming C:Chl = 50 and C:N = 106:16 ratios we have $P_S \approx 0.6 \mu\text{mol N}/\text{kg}$.
3. The zooplankton concentration varies around a mean value Z_S during the decay phase. From observations we have the rough estimate $Z_S \approx 0.9 \mu\text{mol N}/\text{kg}$.

The estimate of Z_S is based on the following findings:

- Sakshaug & Slagstad (1992) estimated the averaged ratio of phytoplankton and zooplankton biomass to 2/3 in the Barents Sea.

Table 1. The constants in the standard parameter setup of the model.

Constant	Meaning	Value
γ_p	Phytoplankton growth rate	0.7 day^{-1}
μ_p	Phytoplankton metabolism	0.1 day^{-1}
κ_N	Half-saturation constant for phytoplankton growth on nutrients	$0.1 \mu\text{mol/kg}$
$^1\gamma_z$	Zooplankton growth rate ($n = 1$)	0.733 day^{-1}
$^2\gamma_z$	Zooplankton growth rate ($n = 2$)	0.677 day^{-1}
$^1\mu_z$	Zooplankton metabolism ($m = 1$)	0.244 day^{-1}
$^2\mu_z$	Zooplankton metabolism ($m = 2$)	$0.272 (\mu\text{mol/kg})^{-1} \text{ day}^{-1}$
κ_p	Half-saturation constant for zooplankton grazing on phytoplankton	$0.5 \mu\text{mol/kg}$
ε	Zooplankton feeding efficiency	0.611



- Lenz & al. (1993) made observations in the beginning of June at 58°N, 23°W and obtained the estimates: A phytoplankton standing stock of 2056 mg C/m², a mesozooplankton stock of 1933 mg C/m², and a microzooplankton stock of 110 mg C/m². However, the mesozooplankton stock could only account for 50 % of the estimated grazing rate suggesting that the nano- and microzooplankton population must be significant.
- Burkill & al. (1993) estimated the microzooplankton population to 428 mg C/m² at 60°N, 20°W, suggesting that the microzooplankton biomass may be higher than the 110 mg C/m² observed by Lenz & al. (1993).

Taken together, a reasonable estimate of the phytoplankton to zooplankton ratio is 2/3 for the Nordic seas. Thus, given that $P_s \approx 0.6 \mu\text{mol N/kg}$, we obtain the estimate $Z_s \approx 0.9 \mu\text{mol N/kg}$ for Station M.

THE APPROXIMATE BALANCE DURING THE DECAY PHASE

During the decay phase, the biological system is characterised by variations around relatively constant mean levels for zoo- and phytoplankton, while the level of dissolved nitrate decays at a reasonably constant rate (Fig. 9a). In this state we have coexistence of substantial zoo- and phytoplankton populations characterised by approximate balance between rates of growth and decay.

According to the above given considerations regarding the properties of the decay state we assume that the right hand sides of Eqs 2b-c vanish if we consider the mean value over the mixed layer depth and a substantial portion of the decay phase, say 10 or 20 days. Somewhat intuitively we assume that the contribution provided by mixing is small, and we set $S = 0.01 \mu\text{mol}/(\text{kg day})$.

Inserting the known properties of the solutions into Eqs 2, using Eqs 3, we arrive at

$$\begin{aligned}
 d(NO_3) &= -(\gamma_p - \mu_p)P_s + \mu_z Z_s^m + S, \\
 0 &= (\gamma_p - \mu_p)P_s - \gamma_z \frac{P_s^n}{\kappa_p^n + P_s^n} Z_s, \\
 0 &= \epsilon \gamma_z \frac{P_s^n}{\kappa_p^n + P_s^n} Z_s - \mu_z Z_s^m,
 \end{aligned}
 \tag{8 a-c}$$

where P_s and Z_s represent mean values for P and Z for the decay phase. In deriving Eq. 8b we have made the assumption that production is not limited by nutrient, which is presumably true at least in the early part of the decay phase.

These three equations can be used to determine the values of γ_z , μ_z and ϵ , given that κ_p , γ_p , and μ_p are known (parameter values given in Table 1). With $\gamma_p = 0.7 \text{ day}^{-1}$ (Fig. 1) and the prescribed values of $d(NO_3)$, P_s , and Z_s , we get the following approximate values of γ_z , μ_z and ϵ :

$$\begin{aligned}
 {}^1\gamma_z &= 0.733 \text{ day}^{-1}, \\
 {}^2\gamma_z &= 0.677 \text{ day}^{-1}, \\
 {}^1\mu_z &= 0.244 \text{ day}^{-1}, \\
 {}^2\mu_z &= 0.272 (\mu\text{mol/kg})^{-1} \text{ day}^{-1}, \\
 \epsilon &= 0.611,
 \end{aligned}$$

where the superscripts 1 and 2 on γ_z and μ_z refer to the value of n and m , respectively. The fact that we get similar numerical values for each n and m arises since $\kappa_p \approx P_s$ and $Z_s \approx 1 \mu\text{mol/kg}$. It should be noted that with $\kappa_p = 1 \mu\text{mol/kg}$, we obtain ${}^1\gamma_z \approx 1.1 \text{ day}^{-1}$ and ${}^2\gamma_z = 1.5 \text{ day}^{-1}$. However, all these cases correspond to an apparent zooplankton growth rate that is approximately 0.2-0.25 day^{-1} for the given phytoplankton concentration.

The obtained parameter values are quite similar to values found in the literature for comparable types of ecosystem models. For instance, for Bermuda Station S and Ocean Weather Station India in the Atlantic Ocean, Fasham & al. (1990) and Fasham (1993) used a zooplankton assimilation efficiency ϵ of 0.75, and a maximum zooplankton growth rate γ_z of 1 day^{-1} (using $\kappa_p = 1 \mu\text{mol/kg}$). In addition, Fasham & al. (1990) used the value 0.15 day^{-1} for μ_z for the case of a linear metabolism (see also Evans & Garçon 1997).

4. STEADY STATE SOLUTIONS AND SENSITIVITY ANALYSIS

We have already found the relation between the steady state solution of the model and the parameter values. It is, however, still interesting to know the sensitivity of the solution to variations in the parameter space. As described in Sec. 3, the system is in a quasi-steady state after the initial part of the bloom and we will investigate the sensitivity of the steady-state solutions. However, it should be mentioned that although there exists a steady state solution, it may be unstable to infinitesimal disturbances; thus the analysis of the steady state solutions must be complemented with the stability analysis in the next section before a final understanding of the model is reached.

Let us assume that the greatest variability of the system is caused by

- solar radiation;
- mixing intensity (i.e., the depth of the mixed layer); and
- input and export of nutrients.

These factors mainly influence the biological system through the phytoplankton dynamics, implicitly by the nutrient concentration or directly by the phytoplankton growth rate. We therefore investigate the response of the system to changes in the total nutrient concentration, defined as $N_T \equiv N + P + Z$, and the phytoplankton growth rate.

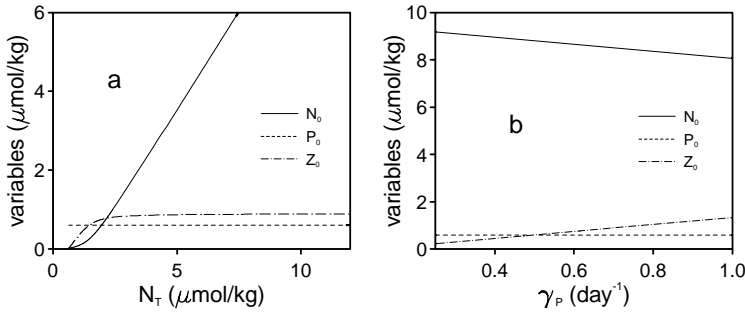


Fig. 2. Steady state solution to the model for the $n = m = 1$ case as a function of a) the total nutrient concentration and b) the phytoplankton growth rate. Below $N_T \approx 0.6 \mu\text{mol/kg}$ the solution changes to a state where $Z_0 = 0$ (not shown). Changing the value of n to 2 will not significantly alter the figure. Panel a is drawn for $\gamma_p = 0.7 \text{ day}^{-1}$, and panel b is drawn for $N_T = 10 \mu\text{mol/kg}$.

THE STEADY STATE SOLUTION

The properties of the steady state solution and its stability are investigated for a system where the total nutrient concentration is considered as constant. Thus, we consider a system where the export from the system is balanced by an import of dissolved nutrients; or where all nutrients are mineralised to dissolved nutrient immediately as they leave the planktonic states and where $S = 0$. The dissolved nutrient concentration in the system can be expressed as a function of the total nutrient concentration and Eqs 2b-c may be written as

$$\begin{aligned} \frac{dP}{dt} &= G_P(N_T - P - Z, P) - G_Z(P, Z), \\ \frac{dZ}{dt} &= \epsilon G_Z(P, Z) - M_Z(Z). \end{aligned} \tag{9 a, b}$$

The steady state solutions, denoted P_0 and Z_0 , are defined from Eqs 9 by dropping the time derivatives

$$\begin{aligned} 0 &= G_P(N_T - P_0 - Z_0, P_0) - G_Z(P_0, Z_0), \\ 0 &= \epsilon G_Z(P_0, Z_0) - M_Z(Z_0). \end{aligned} \tag{10 a, b}$$

The solutions to these algebraic equations are not easily found, and an analytical solution is only found for the $n = m = 1$ case, for the other cases we use numerical solutions. The solutions to Eqs 10 are shown in Figs 2-4. Recall that the dissolved nutrient concentration in the steady state, denoted N_0 , can be calculated from $N_0 = N_T - P_0 - Z_0$.

An analysis of the solutions with high dissolved nutrient concentrations

During a significant part of the spring-summer at station M there are plenty of nutrients in the productive layer and the behaviour of the model under such conditions is crucial to its success. Further, there are some interesting dynamical features at high dissolved nutrient concentra-

tions, e.g., the multiple solutions for the $m = 2$ case (Figs 3 and 4). Accordingly we will discuss the solutions presented in Figs 2-4 for the case of $N_0/(\kappa_N + N_0) \approx 1$, which allows some analytical solutions that give guidance to a more thorough understanding of the system. Among other things, the analytical solutions give a better understanding of the sensitivity of the solution in the parameter space.

Let us consider the case with $N_0/(\kappa_N + N_0) \approx 1$, with this assumption we can write

$$\begin{aligned} 0 &= G_P(P_0) - G_Z(P_0, Z_0), \\ 0 &= \epsilon G_Z(P_0, Z_0) - M_Z(Z_0), \end{aligned} \tag{11 a, b}$$

where $G_P(P_0)$ is given by Eq. 4.

The phytoplankton concentration is given by the following polynomial (note that the $P_0 = 0$ solution has been removed)

$$\begin{aligned} P_0^{1-n-1/m} (\kappa_P^n + P_0^n) - \left(\frac{\gamma_Z}{\gamma_P - \mu_P} \right) \left(\frac{\epsilon(\gamma_P - \mu_P)}{\mu_Z} \right)^{1/m} &= 0, \\ Z_0^m = \left(\frac{\epsilon(\gamma_P - \mu_P)}{\mu_Z} \right) P_0. \end{aligned} \tag{12 a, b}$$

Introducing $P_* = P_0/\kappa_P$, we may write Eq. 12a as

$$P_*^{m-1} (P_*^{-n} + 1)^m - \chi = 0, \tag{13}$$

where

$$\chi = \frac{\epsilon \gamma_Z}{\kappa_P^{m-1} \mu_Z} \left(\frac{\gamma_Z}{\gamma_P - \mu_P} \right)^{m-1}.$$

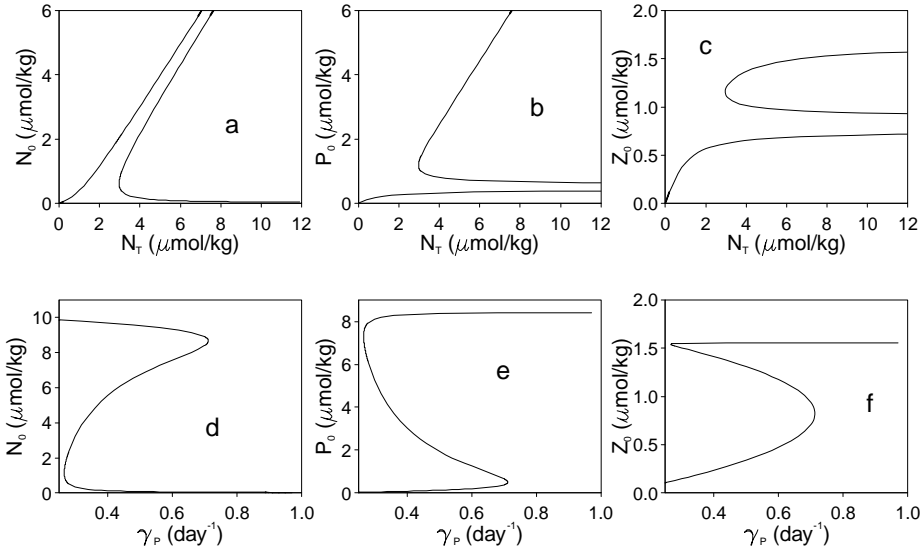


Fig. 3. Steady state solution to the model for the $n = 1, m = 2$ case as a function of the total nutrient concentration for $\gamma_p = 0.7 \text{ day}^{-1}$ (upper row), and as function of the phytoplankton growth rate for $N_T = 10 \text{ }\mu\text{mol/kg}$ (lower row). Multiple solutions are possible above $N_T = 3 \text{ }\mu\text{mol/kg}$ for $\gamma_p = 0.7 \text{ day}^{-1}$, and between $\gamma_p \approx 0.25 \text{ day}^{-1}$ and $\gamma_p \approx 0.7 \text{ day}^{-1}$ for $N_T = 10 \text{ }\mu\text{mol/kg}$. Note that the model solution is very sensitive to small changes in γ_p around the value $\gamma_p = 0.7 \text{ day}^{-1}$.

Some solutions to Eq. 13, valid for $N_0 / (\kappa_N + N_0) \approx 1$, are given below.

Case with $m = 1$

Inserting $m = 1$ in Eq. 13 gives

$$P_* = \left({}^1\chi - 1 \right)^{-1/n}, \tag{14}$$

where

$${}^1\chi = \frac{\varepsilon\gamma_Z}{\mu_Z}.$$

It is interesting that the phytoplankton concentration is fully described by parameters of the zooplankton equation. Thus P_0 does not depend on the phytoplankton growth rate which explains the insensitivity to N_T and γ_p as shown in Fig. 2. Continuing, since P_0 only depends on the parameters in the zooplankton equation, the model case with $n = 2$ will show a similar sensitivity to N_T and γ_p (parameters that only influence the phytoplankton growth rate) as the $n = 1$ case. Further, for high total nutrient concentration, the zooplankton concentration is directly proportional to γ_p (Eq. 12b and Fig. 2b).

Case with $m = 2$

The solutions with $m = 2$, displayed in Figs 3-4, show that there may be multiple solutions for some parameter regimes. An important task is to find how the multiple

solutions relate to parameter space. With $m = 2$, Eq. 13 does not have a simple solution for P_0 for an arbitrary value of n , and the different cases are treated separately. For $n = 1$, we get

$$P_* = \frac{{}^2\chi - 2 \pm \sqrt{{}^2\chi({}^2\chi - 4)}}{2}, \tag{15a}$$

where

$${}^2\chi = \frac{\varepsilon\gamma_Z}{\mu_Z\kappa_P} \left(\frac{\gamma_Z}{\gamma_P - \mu_P} \right). \tag{15b}$$

For $n = 1$ there are only real solutions if ${}^2\chi$ is larger than 4, further, these solutions are multiple solutions (Fig. 5). An analytical solution to Eq. 13 also exists for $n = 2$, but due to its complexity it is only presented graphically in Fig. 5. For $n = 2$, multiple solutions appear at ${}^2\chi \approx 3$.

The solutions described in Fig. 5 correspond to the solutions in Figs 3 and 4 with the lowest phyto- and zooplankton concentrations. For the $n = 1$ ($n = 2$) case, these solutions vanish at $\gamma_p \approx 0.7 \text{ day}^{-1}$ ($\gamma_p \approx 0.8 \text{ day}^{-1}$), corresponding to ${}^2\chi \approx 4$ (${}^2\chi \approx 3$) by means of Eq. 15b, which follows the results presented in Fig. 5. Thus, ${}^2\chi$ is a valuable quantity in estimating the disappearance of the solution with low phytoplankton concentration.

We have concentrated our investigation to the case with $\gamma_p = 0.7 \text{ day}^{-1}$ and for this phytoplankton growth rate both

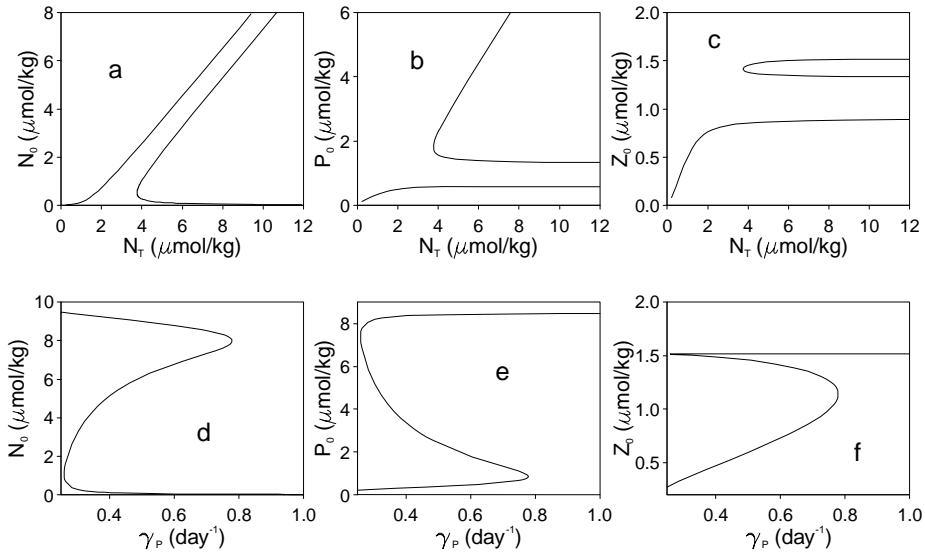


Fig. 4. As Fig. 3, but for $n = 2$, $m = 2$. Multiple solutions exist above $N_T = 4 \mu\text{mol/kg}$ for $\gamma_p = 0.7 \text{ day}^{-1}$, and between $\gamma_p \approx 0.3 \text{ day}^{-1}$ and $\gamma_p \approx 0.8 \text{ day}^{-1}$ for $N_T = 10 \mu\text{mol/kg}$. Note that the model is particularly sensitive to small changes in γ_p around the value $\gamma_p = 0.8 \text{ day}^{-1}$.

$n = 1$ and $n = 2$ cases have solutions with low phytoplankton concentration. However, the model solutions are very sensitive to changes in γ_p around ${}^2\chi = 4$ for the $n = 1$ case, and around ${}^2\chi = 3$ for the $n = 2$ case. Thus, in a more realistic situation where the phytoplankton growth rates varies during the year (e.g., Fig. 1), with growth rates exceeding $\gamma_p = 0.7 \text{ day}^{-1}$, the system can move into a regime where the solution with high phytoplankton concentrations is the only existing solution. In this case, the system will move rapidly towards the solution with high phytoplankton concentration.

According to measurements from Station M, the phytoplankton concentrations are generally below $1 \mu\text{mol N/kg}$ and we find no evidence that the solution with the high phytoplankton concentration has a counterpart in observations. Therefore, this solution probably represents an unwanted feature of the model. Comparing the $n = 1$ case (Fig. 3) with the $n = 2$ case (Fig. 4), we see that the disappearance of the solution with low P concentrations is highly dependent upon the model formulation. If the solution with high phytoplankton concentration is an unwanted feature of the model, it appears that the model case with $n = 2$ may be the preferred one.

The solutions with low dissolved nutrient concentrations

In the last section, we stated that for $m = 1$, the phytoplankton concentration is fully described by the parameters in the zooplankton equation at high nutrient concentrations (Eq. 14). However, this conclusion on P_0 is not restricted to high nutrient concentrations, it is in fact

valid as long as there are zooplankton in the system. Accordingly, the phytoplankton concentration is independent of N_T and γ_p down to approximately $N_T \approx 0.6 \mu\text{mol/kg}$. Below this concentration the zooplankton concentration becomes zero; this case is not covered by our analysis but it is characterised by having the main parts of the nutrients in the form of phytoplankton (until very low values of N_T when phytoplankton also vanishes from the system).

The solution with the high phytoplankton concentration, and low dissolved nutrient concentration, can be understood if we consider phytoplankton concentrations high enough to saturate G_Z , i.e., $P^n / (\kappa_p^n + P^n) \approx 1$. The zooplankton grazing can no longer respond to the phytoplankton growth and the phytoplankton population will grow until most of the dissolved nutrient has been used. Thus, we reach a state where the dissolved nutrient is at a low level and the phytoplankton growth is severely limited by low nutrient concentration. The dissolved nutrient concentration is set by the level where the production of phytoplankton is matched by zooplankton grazing. The zooplankton is, as in the earlier cases, set internally from “self grazing”. For high enough phytoplankton growth rates, zooplankton is not able to control the phytoplankton population and this state becomes the only existing solution (Figs 3 and 4).

The cases with $m = 2$ (Figs 3 and 4) show some very different behaviours from the $m = 1$ case (Fig. 2) at low total nutrient concentration. For $m = 1$ the phytoplankton concentration is set at a constant level whereas for $m =$

2, the concentrations for N , P and Z depend almost linearly on the total nutrient concentration up to, say, $N_T \approx 2 \mu\text{mol/kg}$ (Steele & Henderson 1981, 1992, 1995). Burkill & al. (1993) noted that there was a linear relation between the microzooplankton biomass and the phytoplankton biomass during the U.K. Biogeochemical Ocean Flux Study giving some credit to the $m = 2$ model case. However, with or without direct empirical evidence we may conclude that the linear relation between phyto- and zooplankton is an attractive feature of the model case with $m = 2$ (Steele & Henderson 1995).

5. INVESTIGATING THE STABILITY OF THE SYSTEM

The stability of the steady state solutions is found by investigating the time-development for small perturbations in the phyto- and zooplankton concentrations. This may be achieved by describing the properties of the equations in the vicinity of the steady-state solution using a Taylor series expansion of the basic equations (May 1975; Murray 1989). This method allows us to keep the general formulation of the flow formulations to the final stage of the stability analysis, which is advantageous for a thorough understanding of the system.

THE PERTURBATION EQUATIONS

We will now investigate how small changes from the steady state solutions, denoted δP and δZ , affect the time dependence of the phyto- and zooplankton concentrations. The Taylor expansion of Eqs 9 can to the lowest order be written as (using the definition of the steady state solution Eqs 10 to remove the steady state solution from the expression)

$$\begin{aligned} \frac{d\delta P}{dt} &= \left(\frac{\partial G_P}{\partial P} - \frac{\partial G_Z}{\partial P} \right) \delta P + \left(\frac{\partial G_P}{\partial Z} - \frac{\partial G_Z}{\partial Z} \right) \delta Z, \\ \frac{d\delta Z}{dt} &= \varepsilon \frac{\partial G_Z}{\partial P} \delta P + \left(\varepsilon \frac{\partial G_Z}{\partial Z} - \frac{\partial M_Z}{\partial Z} \right) \delta Z, \end{aligned} \quad (16 \text{ a, b})$$

where $G_p = G_p(N_T - P - Z, P)$, and where the differentiation on the right-hand side are evaluated at $P = P_0$, $Z = Z_0$. The solutions to the equations are in the form (for instance Braun 1983, Chap. 3.6)

$$(\delta P, \delta Z) = Ae^{q_+ t} + Be^{q_- t}, \quad (17)$$

where A and B are constants and

$$\begin{aligned} 2(q_+, q_-) &= \left(\frac{\partial G_P}{\partial P} - \frac{\partial G_Z}{\partial P} \right) + \left(\varepsilon \frac{\partial G_Z}{\partial Z} - \frac{\partial M_Z}{\partial Z} \right) \\ &\pm \sqrt{\left[\left(\frac{\partial G_P}{\partial P} - \frac{\partial G_Z}{\partial P} \right) - \left(\varepsilon \frac{\partial G_Z}{\partial Z} - \frac{\partial M_Z}{\partial Z} \right) \right]^2 + 4 \left(\frac{\partial G_P}{\partial Z} - \frac{\partial G_Z}{\partial Z} \right) \left(\varepsilon \frac{\partial G_Z}{\partial P} \right)}. \end{aligned} \quad (18)$$

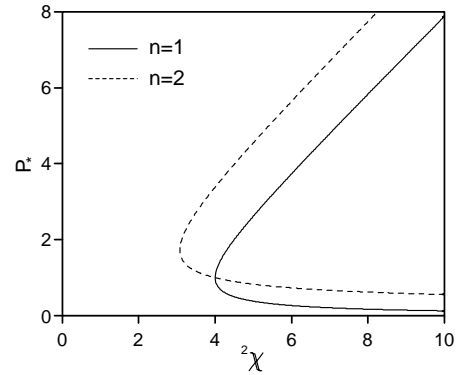


Fig. 5. Steady state solution for P_* as a function of the non-dimensional parameter 2χ . The solution is valid for the cases with $m = 2$, and for $N_0/(\kappa_N + N_0) \approx 1$.

The system is stable if q_+ and q_- take on negative values, it is unstable if either q_+ or q_- is positive, and we get oscillatory solutions if q_+ and q_- have an imaginary part. We see that q_+ represents the most unstable solution, that a positive value of the first four terms always makes the system unstable, whereas a negative value of these terms implies that the magnitude of the root must be evaluated before the stability of the system can be found. As already stated, q_+ is the most unstable part and the real and the imaginary parts of q_+ for the different model cases are shown in Figs 6 and 7. To explain the value of q_+ for the different cases, we will discuss the different terms on the right-hand side of Eq. 18.

The net growth of phytoplankton G_p tends to destabilise the system. The net growth rate depends on the dissolved nutrient concentration, which is low at low total nutrient concentrations. The system is therefore most stable at low total nutrient concentrations. Even the $n = m = 1$ case, which otherwise is the most unstable case, shows stable properties if the total nutrient concentration is below $2 \mu\text{mol/kg}$ (Fig. 6a). However, at small N_T concentrations, the root function becomes positive and its root will contribute to the stability (i.e., the imaginary part disappears and becomes a real part). To analyse the system with a positive root is rather complicated but we may notice that the stability of the system decreases rapidly as the total nutrient concentration is below the breaking point, say $1\text{--}2 \mu\text{mol/kg}$.

The functions $\partial G_p / \partial Z$ and $\partial G_p / \partial P$ are shown in Fig. 8. Starting with $\partial G_p / \partial Z$, which represents a destabilising factor, we see that there is a switch in the magnitude of the derivative at the phytoplankton concentration $P = \kappa_p$. Below this concentration the function with $n = 1$ is larger than the function with $n = 2$, whereas the opposite holds for P larger than κ_p . Thus, from the view of the $\partial G_p / \partial Z$ function, the $n = 1$ case is “more stable” for phytoplankton

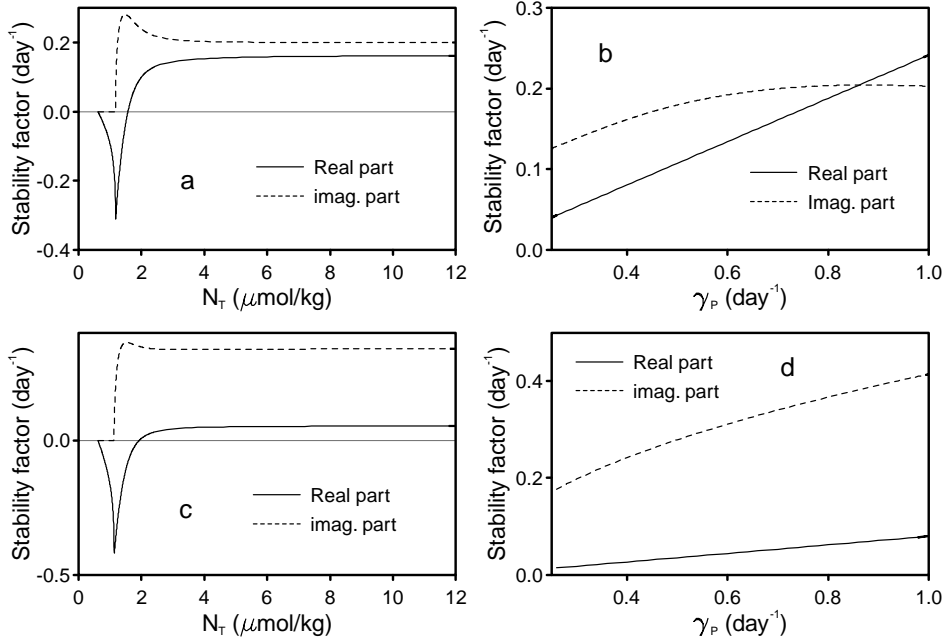


Fig. 6. The real and imaginary parts of q_+ for the $n = m = 1$ case (a-b), and for the $n = 2$ and $m = 1$ case (c-d). The concentrations needed to evaluate Eq. 22 are taken from Fig. 2 for the $n = 1$ case. For the $n = 2$ case we use a steady state solution that is similar to Fig. 2.

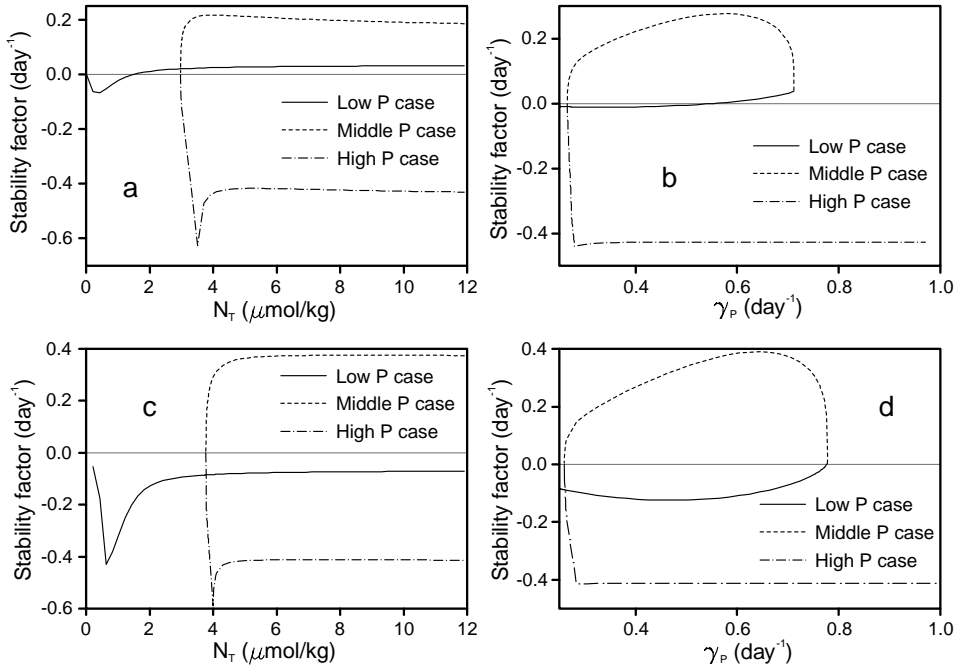


Fig. 7. The real part of q_+ for the model case $n = 1, m = 2$ (a-b), and for $n = 2, m = 2$ (c-d). The concentrations needed to evaluate Eq. 22 for the $n = 1, m = 2$, and the $n = 2, m = 2$ cases are taken from Figs 3 and 4, respectively.

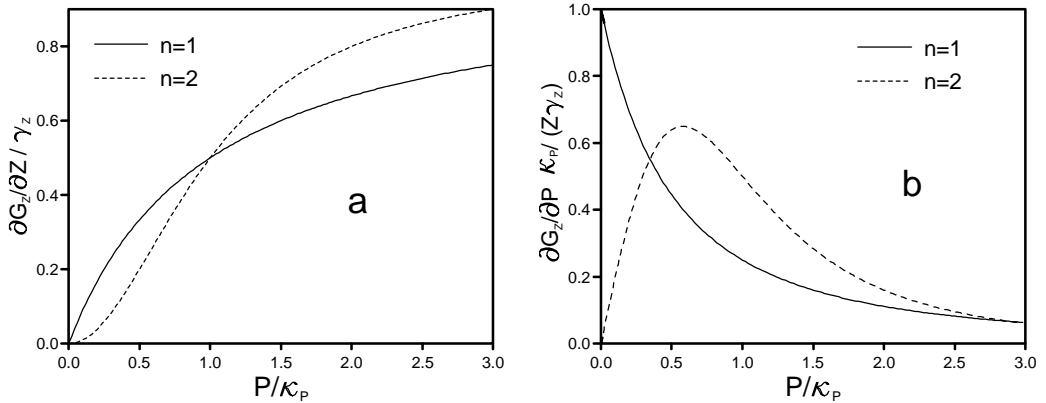


Fig. 8. The form of a) normalised dG_z/dZ , and b) normalised dG_z/dP for different values of n .

concentrations above κ_p , and the $n = 2$ case is “more stable” below this concentration.

For $n = 1$, the $\partial G_z/\partial P$ function, which represent a stabilising factor, has a high value at small concentrations and decreases monotonically with increasing value of P . With $n = 2$ the function is small at low concentrations and it increases fast until it reaches a maximum value at $P \approx 0.5\kappa_p$, above this value the function decreases with increasing P . Comparing the two cases, the $n = 1$ case has highest values, and thereby the most stabilising effect, for concentrations below approximately $0.5\kappa_p$. Above this concentration, the $n = 2$ function has higher values and, notably, it has significantly higher values between, say $P = 0.6\kappa_p$ and $P = 1.5\kappa_p$, which represent the phytoplankton concentrations that are normally found in the productive season.

We can see the stabilising effect of $\partial G_z/\partial P$ on the system when comparing the $n = m = 1$ case with the $n = 2, m = 1$ case (Fig. 6) (the function $\partial G_z/\partial Z$ does not depend significantly on n for the given steady solution where $P_0 \approx \kappa_p$). Although both cases are generally unstable we see that the $n = 2$ case has smaller values on the real part of q_+ . The case with $n = 2$ simply has larger derivatives at the given concentrations showing the importance of the form of the G_z function for the stability. We also note that the low P solution in the $n = m = 2$ case is more stable than the low P solution in the $n = 1, m = 2$ case which is unstable in the main part of the illustrated parameter domains (Fig. 7).

The zooplankton metabolism appears in the fourth term and it acts to stabilise the system. Given the parameter set up and steady state solutions of the model, the system becomes more stable with increasing value of m . The stabilising effect of the $m = 2$ case can be seen when comparing the stability factors in Fig. 7 with those in Fig. 6. However, the $m = 2$ case also trigger new solutions of the model. Fig. 7 shows that the solution with

the highest phytoplankton concentrations is always stable whereas the middle solution is always unstable. The stability of the solution with the lowest phytoplankton concentration depends on the value of n and the parameter values. For $n = 1$ and $\gamma_p = 0.7 \text{ day}^{-1}$ it is stable below, say $N_T = 1.8 \mu\text{mol/kg}$ (Fig. 7a) and for $N_T = 10 \mu\text{mol/kg}$ it is stable below $\gamma_p = 0.5 \text{ day}^{-1}$. For $n = 2$ the low P solution is stable in the entire parameter regime.

6. SIMULATING THE SEASONAL CYCLE AT STATION M

Of the four different model cases, we will restrict the investigation to the $n = m = 1$, the $n = 1, m = 2$, and the $n = m = 2$ cases. We start the integration at beginning of May (day 110), and initialise the model with observed nitrate and phytoplankton concentrations. The value of the zooplankton concentration is more uncertain, and the model is initialised with a concentration of $0.7 \mu\text{mol/kg}$.

The high zooplankton concentration at the start of the spring bloom is assumed to be the result of vertical zooplankton movements that occur in early spring (Østvedt 1955; Lie 1968; Wiborg 1978; Bathmann & al. 1990). The zooplankton concentration in the early part of the spring bloom is an important model parameter, possibly controlling if there will be a strong bloom of phytoplankton or not. The model is able to reproduce the observed nitrate and phytoplankton concentrations, indicating that the initial zooplankton concentration is reasonable.

The growth rate for phytoplankton is fixed to $\gamma_p = 0.7 \text{ day}^{-1}$ (see Fig. 1 for a more realistic time development of γ_p), and the time development for the first 130 days is shown in Fig. 9. All model compartments in the $n = m = 1$ and $n = 1, m = 2$ cases show strong oscillations as predicted by the stability analysis. The oscillations have no counterpart in the observations and we conclude that the oscillations are an unwanted feature of the model for-

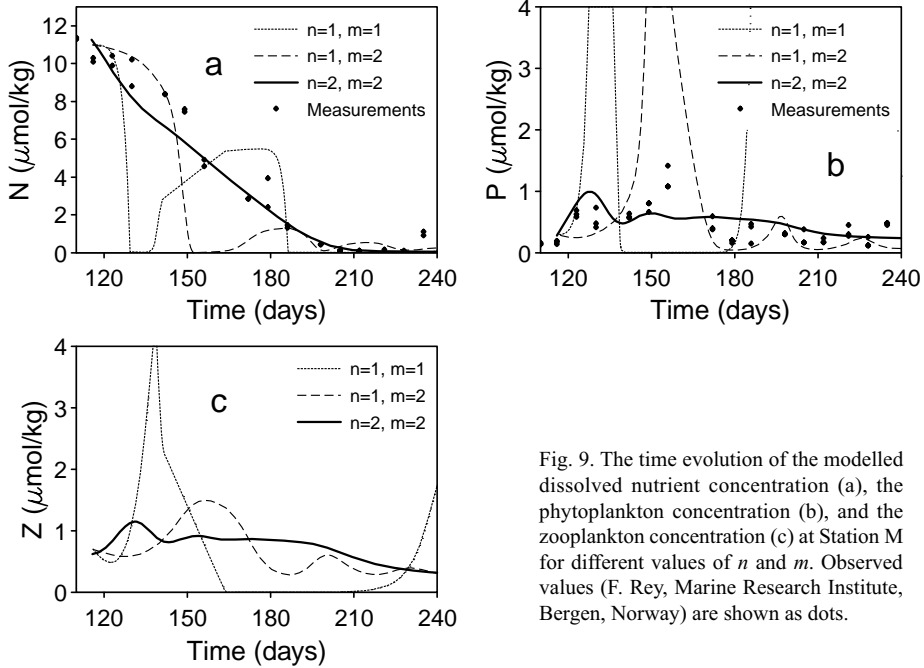


Fig. 9. The time evolution of the modelled dissolved nutrient concentration (a), the phytoplankton concentration (b), and the zooplankton concentration (c) at Station M for different values of n and m . Observed values (F. Rey, Marine Research Institute, Bergen, Norway) are shown as dots.

mulation. The model with $n = m = 2$ has a stable time development and model concentrations that are in fair agreement with data.

The agreement between data and the model experiment with $n = m = 2$ illustrates that model parameters can be achieved as discussed in Sec. 3. However, the $m = 2$ case also has a solution with high phytoplankton concentration that is stable. Although this solution is not reached in Fig. 9, it may be reached if we encounter high phytoplankton concentrations in the system. Let us imagine a calm sunny period, say 5 days long, giving high growth rates for phytoplankton. This situation is described in Fig. 10 where we force the model with a spike in the phytoplankton growth rate located around day 120. The time-development of the system is drastically changed from the case without the spike, illustrating that the system may switch to the “high phytoplankton concentration” solution given a small disturbance of the system. This may also be seen as an example of the excitable nature of the marine plankton system (Truscott & Brindley 1994).

The possibility of the model to switch from one to another state clearly illustrates the need and importance of appropriate description of the vertical mixing processes in coupled physical-biochemical models. In fact, over-simplified mixing schemes may lead to switching from low to high phytoplankton concentration solutions, or vice versa, compared to more sophisticated mixing schemes.

Without doubt, there are fluctuations in the time development of the system creating random disturbances in the concentrations. These small changes in the concentration distribution of the compartments may lead to abrupt changes in the solution regime. Such feature of the model behaviour cannot, in general, be found from infinitesimal perturbation theory. To give an idea of the sensitivity of the system, we perform a set of experiments with a closed system where all exported material is returned to the dissolved nutrient pool and where $S = 0$. Further, we assume that the total nutrient concentration in the system is $10 \mu\text{mol/kg}$. The experiments are started with different initial conditions, and the solution trajectories in the P, Z -space are presented in Fig. 11. We see that small changes in the P and Z concentrations can lead to very different time developments. Note that two pairs of initial conditions are indistinguishable in the figure (marked with two circles), albeit that, the system develops to different steady state solutions. Under constant conditions, solution trajectories can never cross each other and the trajectories in Fig. 11 may be used to evaluate how the different steady state points attract solutions in P, Z -space. We see that the main part of the P, Z space shown in Fig. 11 ends up in the high P concentration solution. Nevertheless, there is a distinct area in P, Z space, centred around the low P concentration solution, where the system ends up in the low P concentration solution implying that this solution is relatively stable against finite disturbances. However, if some random

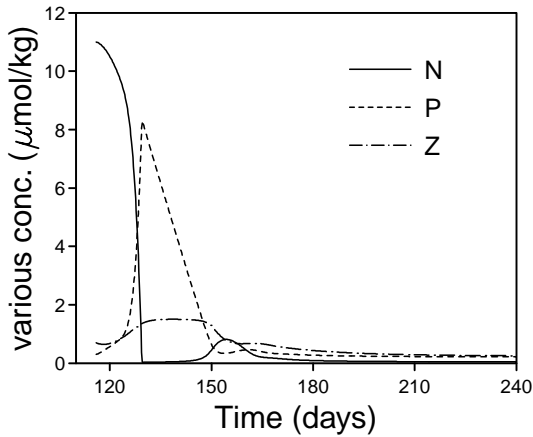


Fig. 10. The time development for the $n = m = 2$ model case with a “spike” in the phytoplankton growth rate at day 120.

fluctuation moves the system over any of the trajectories separating the different solution regimes, the system will have a switch in the steady state behaviour.

7. RESULT AND DISCUSSION

In this study we examine some properties of a mathematical formulation of the marine ecosystem known as the NPZ system, implying that we use the variables dissolved nutrient, phyto- and zooplankton concentrations to describe the system. Although such a system represents a very crude description of the real ecosystem, this kind of model can reproduce the major features of the seasonal cycling of biomass and nutrient concentration in the ocean. However, to formulate an ecosystem model, several choices have to be made. First, model variables and the flow structure must be described. Further, the formulations of the flows and the parameters that determine the strength of the flows must be quantified.

In this study we use a fixed model structure and investigate how different flow structures and parameter values influence the time evolution of the model. In doing so, it is important to realise that different flow formulations give different time evolution of the model and are therefore not directly comparable. To overcome this problem we use parameters that have been chosen to give a similar time evolution of the model. However, it must be noted that not all model cases are able to reproduce the characteristic features of the developing ecosystem (actually, only one of the proposed model formulations can reproduce measurements).

The way we have estimated the parameters is powerful and arises from the fact that there is a direct connec-

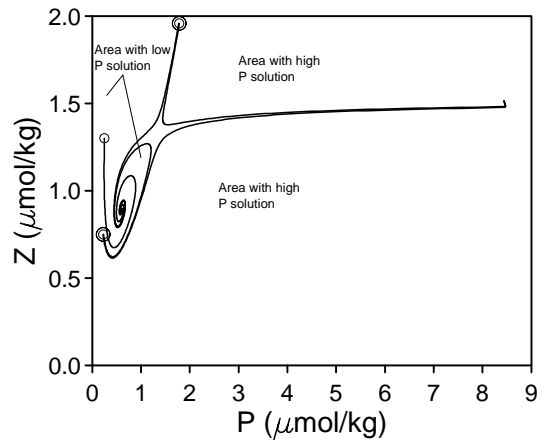


Fig. 11. The time development for the $n = m = 2$ model for five initial values (marked with a circle of initial P and Z concentrations). Note that two pairs of trajectories start with almost similar initial conditions that cannot be distinguished in the figure (shown with two circles). Solution trajectories cannot cross each other and it is possible to find how the different steady state points attract solutions. The areas “belonging” to each steady state point are given in the figure.

tion between the parameters of the model and the model solution. Thus, it is possible to analyse the behaviour of the equations over a given period and insert the observations directly into the equations. With this method, it is possible to derive numerical value of the (poorest known) model parameters. Further, if there are observations of the seasonal cycle under various conditions, it may be possible to make some predictions on the model formulation as well as on the model parameters, although this hypothesis remains to be tested.

An important aspect of the model is the sensitivity to changes in the value of model parameters. An example is provided by the model behaviours with $m = 1$ and $m = 2$ at low total nutrient concentrations. For $m = 1$, the model predicts that the phytoplankton concentration is constant down to a total nutrient concentration of approximately $0.6 \mu\text{mol/kg}$. The case with $m = 2$ predicts that N , P and Z depend linearly on the total nutrient concentration for low concentrations. Intuitively we may expect that the case with $m = 2$ describes the natural ecosystem more accurate than the $m = 1$ case, although it is hard to find empirical evidences for such a statement.

Further, it is necessary to look for the stability of the system and the possibility that the system has multiple solutions. Although the model cases with $m = 1$, $n = 1$, and $m = 2$, $n = 1$ have quasi-steady state solutions that should give reasonable results for the annual cycle, these model cases are not realised; instead the model solution



is characterised by strong oscillations. The oscillations have no counterpart in the data, illustrating that the actual choices of model flows and model parameter values should be carefully examined. In this study we have only analysed the stability of the system from a rather practical point of view and for a more general discussion on stability properties of a similar system we refer to other more complete studies (May 1975; Steele & Henderson 1981, 1992; Murray 1989; Truscott & Brindley 1994; Edwards & Brindley 1996, 1999).

The model with $n = m = 2$ shows good agreement with data. However, this model case has a stable solution with high phytoplankton concentration that may be reached if the phytoplankton growth rate is high enough or if the system is significantly disturbed from the quasi steady state solutions. An important model feature is therefore the parameter regimes in which multiple solutions exist. Especially important is the point where the solution with low phytoplankton concentration disappears. The switching point is related to the parameter $^2\chi$ (Eq. 15b) which can be used to analyse the system. It should be mentioned that it is also possible to describe the zooplankton metabolism as a combination of a linear and a quadratic term (Broström 1998). With such a model formulation, the parameter regime for the multiple solutions may move to higher values of the phytoplankton growth rates. For the combined case, the linear term reflects the direct metabolism of zooplankton, and the quadratic term reflects the effect of internal grazing in the zooplankton pool.

More advanced models may easily be developed from the NPZ system. An example is to divide the nutrient N into nitrate NO_3^- , and ammonia NH_4^+ . Depending on how phytoplankton use NO_3^- and NH_4^+ there can be slightly

different phytoplankton growth rates for the same amount of dissolved nitrogen (Wroblewski 1977). If there are only small changes in the phytoplankton growth rate for different combinations of nitrate and ammonium, the general properties of the system will probably not change in any important way from the simple NPZ model. However, if different combinations of nitrate and ammonium concentrations imply that the phytoplankton growth rate changes considerably, a thorough investigation of its stability, both for infinitesimal disturbances and for small disturbances, may be needed.

The divisions of P and Z into different categories, i.e., different taxonomic species, imply that the system cannot be described as a NPZ system. However, the characteristic behaviour of the more complex model, e.g., its stability and the possible existence of multiple solutions, can in many regards be analysed from the results of the NPZ model. The same conclusion is valid if we include a microbial loop to the NPZ model (Taylor & Joint 1990). However, it is important to check that the microbial loop does not have a cyclic solution.

ACKNOWLEDGEMENTS

We would like to thank Prof. Gösta Walin for the interest in the subject and many discussions on the formulation of the biological model. We are also in debt to Francisco Rey at the Institute of Marine Research, Bergen, Norway, who handed us unpublished data from Station M. Andy Edwards and John Steele provided valuable comments on an earlier version of this manuscript. The work is a part of the project *Surface water carbon fluxes in the Nordic Seas*, sponsored by the Nordic Council of Ministers. Parts of the work have been supported through the *ESOP-II* project (MAS2-CT95-0015) of the European Community programme MAST-III (HD).

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