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The analysis of alternative formulations in a simple model of a coastal ecosystem

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Abstract

Ecosystems are complex and often require complex models if their detailed behaviour is to be replicated. However, such complex models are difficult to analyse due to their nonlinearities and the large number of parameters that most such models have. One approach that allows greater understanding of basic process is the development of simplified models. We have developed a series of simple models describing alternative formulations of a coastal ecosystem, as a tool to aid development and analysis of more sophisticated models. Sediment biogeochemistry plays a critical role in many coastal ecosystems, and much of the nitrogen input load is lost through denitrification, provided eutrophication has not set in. We have dealt with the sediment and water column response separately in simple models by exploiting the different time scales of sediment and water column response. In simple water column models, we have considered a variety of common formulations of phytoplankton–zooplankton interactions, and their implications for the steady-state response of phytoplankton and nutrients to increased nutrient load. For most formulations, we have derived explicit formulae linking model parameters to predicted mean, steady-state concentration and biomass. The simple model results provide considerable insight into the response of the bay to changes in nutrient load. In particular, the sediment model identifies a maximum denitrification capacity for the bay. Once loads exceed this capacity, denitrification declines, and nutrients are instead lost through export. This decline in denitrification results in a switch from mesotrophic to eutrophic conditions. The water column model analysis confirms the importance of the zooplankton mortality formulation in N–P–Z models in determining the dependence of steady-state phytoplankton biomass on nutrient load, and the stability of steady-state solutions. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Simple models; Coastal; Plankton; Denitrification

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1. Introduction

There has been a rapid growth over the last decade in the development of ecosystem models for both scientific understanding and applied management support (Jørgensen et al., 1996). With the parallel growth in cheap computational power, it has become possible to build and run numerical simulation models with increasing spatial and temporal resolution and process complexity.

However, the increased model complexity makes it more difficult to understand model behaviour and its dependence on model assumptions and parameter values, and on environmental forcing. Sensitivity analysis around a particular solution can be useful in identifying parameters to which the model is sensitive, particularly if a few parameters, or pairs of parameters, can be selected a priori for investigation (Fasham, 1995), and a simple sensitivity analysis has been done for the full Port Phillip Bay model (Murray and Parslow, 1997). Most ecological models are strongly nonlinear, and parameter values are subject to considerable uncertainty; the failure to investigate interaction of parameters can grossly distort the analysis of sensitivity (Elston, 1992). For even moderate numbers of parameters, and moderate run times, systematic sampling of the potential parameter space is not feasible (the 'curse of dimensionality'), and sensitivity analysis in nonlinear systems is only locally informative. For management applications as well as scientific understanding, there is a strong need to understand, at least at a qualitative level, the way in which uncertainty in process formulation or parameter values propagates through the model to affect model predictions.

These problems of complexity and uncertainty are also apparent in model calibration. There are now a variety of formal statistical procedures for fitting models to data, and estimating parameter values (Marsili-Libelli, 1992; Matear, 1995). However, these generally require large numbers of model runs, and are not computationally feasible for large two-dimensional or three-dimensional models. For example, the most robust and powerful Bayesian techniques require tens of thousands of simulations (Harmon and Challenor, 1997). If calibration of complex models is not to be a completely hit or miss affair, then again qualitative or semi-quantitative understanding of the dependence of predictions on parameter values is required.

A powerful tool available to ecosystem modellers is the derivation and analysis of simpler models as analogues for complex simulation models through a process of approximation and simplification. These simple models are then susceptible to mathematical analysis, including classical techniques such as identification of explicit steady-state solutions, stability analysis and graphical techniques (May, 1981). This approach has been commonly used to analyse the effects of the formulation of single processes such as grazing (Franks et al., 1986) or the effects of zooplankton mortality (Steele, 1976; Steele and Henderson, 1992) upon plankton populations. It has also been used to investigate the response to stresses, such as eutrophication, of simple ecosystems (Rosenzweig, 1971; May, 1974). Simple ecosystem models of both pelagic (Evans and Parslow, 1985; Taylor, 1988; Taylor and Joint, 1990; Klepper, 1995), and coastal (Ross and Nival, 1976; Kishi et al., 1981; Kimmerer et al., 1993) ecosystems are also used to analyse their fluxes and structures. These simple models may be an end in themselves or they can be used as a qualitative or quantitative guide in choosing among process formulations, or estimating parameter values during the development and tuning of such models. A classic example of this approach is the analysis of the spruce budworm model by Ludwig et al. (1978). Similarly, Armstrong (1994), derived a simplified version of a plankton food-chain model developed by Moloney and Field (1991) in order to simplify the numerical investigation of its behaviour.

In this paper we apply the derivation and analysis of simplified models to increase our understanding of nutrient cycling in a coastal marine ecosystem. The ecosystem that we have based the analysis on is that of Port Phillip Bay in south-eastern Australia. This bay has been the subject of a large integrated study that addressed the environmental impact of nutrient and toxicant loads

(Harris et al., 1996). As part of this study, we developed a range of models of nutrient cycling in the bay using simple models to design and analyse more detailed ones. Details of the Port Phillip Bay environment and our application of the simple model to its analysis are presented in Murray and Parslow (1997).

Port Phillip Bay has a number of features which simplify modelling (Harris et al., 1996). The bay's water exchanges only slowly with the ocean but is internally well mixed, both horizontally and vertically, and these properties allow us to concentrate on the modelling of local biogeochemical processes using simplified physical modelling (Mahamah, 1998). Over most of the bay, production is N limited, allowing us to limit the model to N cycling. Most N inputs are regulated, and this, combined with the large volume of the bay, buffers against perturbation, particularly in the central basin which contains 70% of the bay's volume. This lack of perturbation strengthens the value of steady-state solutions in understanding of the ecosystem.

We have separated the water column and sediment compartments; these are linked only by a sedimentary flux of detritus from the water column to sediment, and a net flux of Dissolved Inorganic Nitrogen (DIN) from the sediment to the water column. We can derive solutions of the water column model, after specifying a given flux of DIN from the sediment. Conversely, if we assume the water column pools are at steady-state, we can specify the load of organic detritus to the sediment through mass balance, without consideration of plankton dynamics. This separation is obviously justified if we consider only steady-state solutions of both systems. However, given that the time scales associated with sediment pools are typically long compared with those associated with the key water column pools, this approach can also be used for analysis of dynamical behaviour, on the basis of separation of time scales (Ludwig et al., 1978; Evans and Parslow, 1985; Klepper, 1995).

Our simple model is designed to help us understand the response of coastal waters to external nutrient loads. We define a specific level of nutrient input which the model itself balances by means of denitrification, or, if eutrophic, export; this means the total nutrient in the system varies nonlinearly in response to inputs as denitrification efficiencies change. Other models of marine ecosystems use fixed bottom boundary conditions (Evans and Parslow, 1985; Taylor and Joint, 1990; Klepper, 1995) or a fixed total mass of nutrient (Kishi et al., 1981; Armstrong, 1994) and so are not able to fully explore these nonlinear interactions between external nutrient supplies and total nutrient availability, which are such a feature of coastal eutrophication. Kimmerer et al. (1993) did include denitrification in their nutrient cycling model of Tomales Bay, but only as a fixed proportion of mineralisation; their model includes nitrogen fixation and has very different behaviour to that observed and modelled in Port Phillip Bay.

1.1. The steady-state sediment model

Denitrification in the sediments of coastal waters leads to the removal of a large proportion of the N input to coastal waters (Seitzinger, 1988). In the semi-enclosed Port Phillip Bay the denitrification loss is so large that there is little net export of nitrogen to the ocean (Harris et al., 1996). We were thus able to assume for the simple model that export from the bay is zero, and that the external nitrogen load (I_e) is balanced exactly by the loss to denitrification in sediments. We assume further that bay-wide water column and sediment N pools are at steady-state. At steady-state, the net production of organic nitrogen in the water column must equal both the net supply of DIN to the water column (I_x), and the net export of organic N from the water column to the sediment. This export of organic matter to the sediment must in turn support net sediment respiration. The denitrification efficiency d is defined as the fraction of organic N involved in net sediment respiration which is lost as N_2 gas. It follows that:

$$I_e = I_x \cdot d \tag{1}$$

In highly oxic sediments denitrification may be inhibited, but for moderate to low oxygen levels denitrification efficiency tends to drop as oxygen levels fall due to inhibition of nitrification (Kemp et al., 1990). Benthic chamber studies in Port Phillip Bay showed that denitrification efficiency decreased linearly as sediment respiration rate increased (see Murray and Parslow, 1997). Although we have included a decline in denitrification efficiency at very low loads in the full model, this feature only occurs in some very oligotrophic regions of the bay and has a minimal role in the regions of the bay were most of the denitrification occurs. Phosphate is always present in excess and does not play the role of controlling net denitrification that it does in Tomales Bay (Kimmerer et al., 1993). For this simple analysis, we therefore adopt an empirical model which relates denitrification efficiency to sediment net respiration rate R:

$$d = \max[D_{\max}\ (1 - R/R\_0),\ 0] \qquad (2)$$

where $D_{\max}$ is a maximum possible denitrification efficiency, R is the net benthic respiration rate and R_0 is a level of respiration at which nitrification ceases due to lack of oxygen (anoxia). Because R and R_0 are expressed on a per unit area basis (mg N m^{-2} d^{-1}), whereas I_e and I_x are expressed on a per unit volume basis (mg N m^{-3} d^{-1}), $R = I_x \cdot h$, where h is the mean water depth. This simple model could create problems in the analysis of the effects of large cuts in nutrient input, but it is admirably suited to analysis of eutrophication.

1.2. The plankton model

We have considered a number of alternative plankton models, all focused on the implications of alternative assumptions for zooplankton grazing and mortality. In these simple models, we have ignored the terms associated with physical exchange the ocean. The observed turnover time for phytoplankton and DIN within the bay is short, of order a few days (Harris et al., 1996), compared with a flushing time of 1 year, so that the export term is negligible for these variables. Grazing in most of Port Phillip Bay appears to be dominated by microzooplankton, which are likely to turn over on comparably short time scales.

The simplest version of the model contains only two variables: DIN (N) and phytoplankton (P). The corresponding equations are:

$$dP/dt = \frac{\mu_{pI} NP}{N + K_N} - m_p P - C_z P^n \qquad [P1] \qquad (3)$$

$$dN/dt = I_x + fC_z P - \frac{\mu_{pI} PN}{N + K_N} \qquad [N1], \qquad (4)$$

where μ_{pI} is the light limited, nutrient saturated phytoplankton growth rate, K_N is the nutrient half-saturation concentration for phytoplankton growth, m_p is the phytoplankton 'natural' mortality rate, and C_z is a grazing loss parameter. The grazing loss can be either linear ($n = 1$) or quadratic ($n = 2$) in P. As described above, I_x is the total DIN load to the water column from both external sources and sediment release. A fraction f of the grazing loss is assumed to be recycled as DIN in the water column, but all of the loss due to 'natural mortality' is assumed to be exported to the sediment.

The other plankton models represent zooplankton biomass Z explicitly. Now grazing losses are assumed to be proportional to Z, and e is the gross growth efficiency for zooplankton. A fraction f_g of the growth inefficiency is recycled as DIN while the rest is assumed to be exported to the sediment. Similarly, a fraction f_m of the zooplankton mortality is recycled as DIN.

$$dP/dt = \frac{\mu_{pI} PN}{N + K_N} - m_p P - GZ \qquad [P2] \qquad (5)$$

$$dN/dt = I_x + f_m m_z Z^n + f_g (1 - e) GZ - \frac{\mu_{pI} PN}{N + K_N}$$

$$[N2] \qquad (6)$$

$$dZ/dt = GeZ - m_z Z^n \qquad [Z2] \qquad (7)$$

The zooplankton mortality parameter m_Z is introduced, and again, the exponent n can take the value 1 (linear mortality) or 2 (quadratic mortality).

The function G represents the zooplankton grazing functional response. We consider four options for G.

1. The linear formulation:

$$G = cP \qquad [G1] \qquad (8)$$

where c is a constant clearance rate.

2. A bilinear formulation:

$$G = \min[cP,\ g_{\max}] \qquad [G2], \qquad (9)$$

where $g_{\max}$ is the maximum (saturated) grazing rate.

3. The rectangular hyperbola:

$$G=\frac{cP}{1+cP/g_{\max}} \qquad [\text{G3}]. \tag{10}$$

4. Rectangular hyperbola with a minimum threshold for grazing, P_t:

$$G=\frac{c(P-P_t)}{1+c(P-P_t)/g_{\max}} \qquad [\text{G3}]. \tag{11}$$

G1 and G2 are variants of Holling's Type 1 functional response, while G3 and G4 correspond to Types 2 and 3, respectively (Holling, 1966).

Appropriate values and ranges for the introduced parameters are discussed in Murray and Parslow (1997), but for this analysis we are mostly concerned with overall behaviour of the models and not their behaviour at specific points in parameter space. For this reason, the specific parameter values are usually not important. The parameters used in the model are summarised in Table 1; the model formulations are summarised in Table 2.

2. Steady-state solutions

2.1. Sediment model

Recall that $I_x = I_e/d$, while denitrification efficiency d depends on sediment respiration rate R:

$$d=\max[D_{\max}.(1-R/R\_0),\ 0] \tag{12}$$

and $R = I_x \cdot h$. It follows that, for $R < R\_0$, there is a quadratic relationship between I_x and I_e:

$$I_e = D_{\max}(1-I_x \cdot h/R\_0)I_x, \tag{13}$$

or:

$$I_x=\frac{D_{\max}-\sqrt{D_{\max}^2-4I_e hD_{\max}/R\_0}}{2hD_{\max}/R\_0} \tag{14}$$

As external load I_e increases, sediment respiration rate increases, denitrification efficiency decreases, and load to the water-column increases at an accelerating rate (Fig. 1). There is a maximum denitrification capacity for the system which occurs at $R = 0.5R\_0$, given by $0.25D_{\max}\ R\_0/h$. When I_e exceeds this maximum denitrification capacity, the nitrogen load can no longer be assimilated internally, and nitrogen accumulates in

Table 1
Model variables

Variable	Description	Unit type
c	Unsaturated grazing rate	$\mathrm{m^3\ mg\ N^{-1}\ d^{-1}}$
C_z	grazing constant for N–P model	$\mathrm{d^{-1}}$ or $\mathrm{d^{-1}\ (mg\ N\ m^{-3})^{-1}}$
d	denitrification efficiency	
D	Exchange with oceanic water	$\mathrm{d^{-1}}$
$D_{\max}$	Maximum denitrification efficiency	
e	Assimilation efficiency	
f	Recycling of grazing in N–P model	
f_g	Recycling of unassimilated grazing	
f_m	Recycling of zooplankton mortality	
G	Grazing	$\mathrm{d^{-1}}$
G^*	Grazing at P^*	$\mathrm{d^{-1}}$
$g_{\max}$	Maximum grazing rate	$\mathrm{d^{-1}}$
h	Height of water-column	m
K_N	P nutrient half saturation	$\mathrm{mg\ N\ m^{-3}}$
m_p	P mortality	$\mathrm{d^{-1}}$
m_z	Z mortality	$\mathrm{d^{-1}}$ or $\mathrm{d^{-1}\ (mg\ N\ m^{-3})^{-1}}$
n	Linear (1) or quadratic (2) mortality	
P_t	Grazing threshold	$\mathrm{mg\ N\ m^{-3}}$
r	Recycling efficiency	
R	Sediment respiration	$\mathrm{mg\ N\ m^{-2}\ d^{-1}}$
R_0	Anoxia inducing sediment respiration	$\mathrm{mg\ N\ m^{-2}\ d^{-1}}$
μ_{pI}	P light limited growth rate	$\mathrm{d^{-1}}$
I_e	External nutrient inputs	$\mathrm{mg\ N\ m^{-3}\ d^{-1}}$
I_x	Total nutrient input	$\mathrm{mg\ N\ m^{-3}\ d^{-1}}$
N	Nutrients	$\mathrm{mg\ N\ m^{-3}}$
P	Phytoplankton	$\mathrm{mg\ N\ m^{-3}}$
Z	Zooplankton	$\mathrm{mg\ N\ m^{-3}}$
N^*	Nutrients steady state solution	$\mathrm{mg\ N\ m^{-3}}$
P^*	Phytoplankton steady state solution	$\mathrm{mg\ N\ m^{-3}}$
Z^*	Zooplankton steady state solution	$\mathrm{mg\ N\ m^{-3}}$
$P_{\max}$	Maximum possible P^* under P^2 mortality	$\mathrm{mg\ N\ m^{-3}}$
$Z_{\max}$	Maximum possible Z^* under Z^2 mortality	$\mathrm{mg\ N\ m^{-3}}$

Table 2
Responses to increased nutrient loads of N^*, P^* and Z^* under different mortality assumption[a]

Condition	N^*	P^*	Z^*
No Zooplankton			
a. Linear P mortality	Constant	Linear increase	
b. Quadratic P mortality	Accelerating increase	Square root increase	
Linear Z Mortality			
a. Moderate load	Accelerating increase	Constant	Linear increase
b. High load	Linear increase	Constant	Constant
Quadratic Z mortality			
a. Moderate load	Accelerating increase	Square root increase	Square root increase
b. P growth saturated	Linear increase	Constant	Constant
c. Grazing saturated	Decrease	Linear increase	Constant

[a] At low loads under linear Z mortality Z^* can fall to zero, in which case the solutions under no zooplankton and linear P mortality apply to P^* and N^*.

the system. There is no longer any steady-state solution, and the simple sediment model fails. Simple models can easily be extended to cover high loads, by allowing for exchange with the ocean. At high loads, denitrification ceases, and the external load of nitrogen is balanced by export to the ocean. Because the flushing rate of the Bay is very low, large pools of DIN or phytoplankton N are required for export to balance this additional load. These large pools in turn imply very high sediment respiration rates, exceeding R_0. In fact, an extended simple model, incorporating export as well as denitrification, predicts a catastrophic transition from a mesotrophic system with load balanced by denitrification, to a highly eutrophic system with denitrification switched off and load balanced by export, as I_e exceeds the denitrification capacity.

This is an important and robust result, with implications for any large shallow N-limited marine system with inefficient tidal flushing. In systems of this kind, denitrification provides a rigorous scientific basis for defining an assimilative capacity for nitrogen load. The full spatially-resolved simulation model also shows a rapid increase in water column total N and primary production as loads approach the bay-wide denitrification capacity. However, because of spatial variation in water column production and sediment respiration within the Bay, the catastrophic failure of denitrification in the 1-box model is replaced by a more gradual and reversible decline in the full model (Murray and Parslow, 1997).

2.2. Water-column steady state solutions without zooplankton (Eqs. P1 and N1)

A number of eutrophication models do not represent zooplankton explicitly, and represent their effect implicitly as phytoplankton mortality. It is commonly assumed that phytoplankton specific mortality rates are constant, linear mortality (Taylor, 1988). This is equivalent to assuming that zooplankton biomass and clearance rates are fixed. Alternatively, one can try to allow for the effect of changes in zooplankton clearance rates and/or biomass with phytoplankton abundance by making the specific mortality rate a function of phytoplankton biomass (Kimmerer et al., 1993). We consider here the case where specific mortality rate increases with biomass (quadratic mortality). Arguments can be made for other functional forms, based on assumptions about zooplankton functional and numerical responses. While implicit and explicit models of zooplankton may be equivalent at steady-state, the implicit models cannot represent the time lag in zooplankton numerical response to changes in phytoplankton abundance, so that the models may differ in transient behaviour and stability properties.

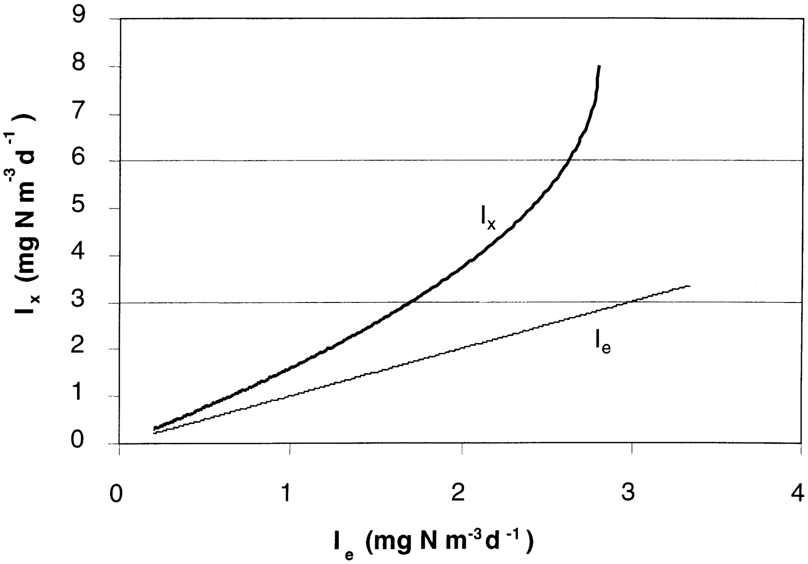

Fig. 1. Relationship between external nutrient load (I_e) and total load (I_x). In the example shown $D_{max} = 0.75$ and $R\_0/h = 250/14$ mg N m^{-3} d^{-1}.

2.2.1. Grazing proportional to *P* (Eqs. N1 and P1, $n = 1$)

For steady state solutions we set $dP/dt = 0$ and $dN/dt = 0$, and rearrange to obtain:

$$N^* = \frac{K_N(C_z + m_p)}{\mu_{pI} - C_z - m_p} \quad \text{[N1a]} \qquad (15)$$

$$P^* = I_x/[C_z(1-f) + m_p] \quad \text{[P1a]}. \qquad (16)$$

According to this model, the nutrient concentration under steady-state conditions is a constant, determined by the imposed phytoplankton mortality rate, but independent of external load, while phytoplankton biomass increases linearly with load (Fig. 2). This is comparable to the result obtained by Taylor (1988) who observed that *N* in the mixed layer was independent of deep water *N* (N inputs) while *P* increased with deep water *N* in his N–P modelling investigations of vertical phytoplankton distribution.

At very high loads, *P* concentration gradients across the entrance of the bay become larger. However, since the flushing rate is still small relative to m_p, this loss term (export to the ocean) can still be neglected when solving for N^* and P^* in terms of I_x, although, as discussed above, this loss becomes important in the relationship between I_x and I_e.

2.2.2. Grazing proportional to P^2 (Eqs. N1 and P1, $n = 2$)

The steady-state solutions are:

$$P^* = \frac{-m_p + \sqrt{m_p^2 + 4C_z(1-f)I_x}}{2C_z(1-f)} \quad \text{[P1b]} \qquad (17)$$

$$N^* = \frac{K_N(m_p + C_zP^*)}{\mu_{pI} - m_p - C_zP^*} \quad \text{[N1b]} \qquad (18)$$

P^* increases essentially with the square root of loading, while N^* increases at an accelerating rate,

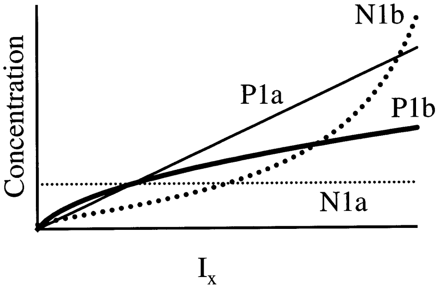

Fig. 2. Analytical steady-state solutions of the N–P model as a function of load under linear (1a, thin) and quadratic (1b, thick) grazing mortality formulations. P^* is given by the solid lines and N^* by dotted lines.

since the numerator increases and the denominator decreases, as P^* increases (Fig. 2). These solutions are similar to those obtained with respect to phosphate load for the model used by Kimmerer et al. (1993) who used density dependent P mortality in an N–P model of phytoplankton in Tomales Bay. When $\mu_{\mathrm{pI}} = m_{\mathrm{p}} + C_{\mathrm{z}}P^*$, the specific mortality rate of the phytoplankton reaches their maximum possible growth rate. The quadratic grazing formulation therefore sets a maximum phytoplankton biomass given by $P_{\max} = (\mu_{\mathrm{pI}} - m_{\mathrm{p}})/C_{\mathrm{z}}$. As P^* approaches $P_{\max}$, N^* becomes large and nutrient loads are increasingly balanced by export of DIN to the ocean. These steady-state solutions are similar to those obtained under the N–P–Z model with quadratic zooplankton mortality (see below). As we show later, under that model, Z^* increases with P^* and hence the mortality on phytoplankton due to grazing, cP^*Z^*, is a function of P^{*2}. These solutions to the equations N1 and P1 are highly stable and the effect of any perturbation is rapidly attenuated.

2.3. *Water-column steady state analysis under linear zooplankton mortality (Eqs. P2, N2, Z2, n = 1)*

In the full model, we have used formulations that do explicitly include zooplankton. This is necessary for the modelling of some of the local dynamic features of the bay, but, as we show here, both the steady-state and dynamical behaviour of plankton models can be quite sensitive to the formulation of zooplankton–phytoplankton interactions. In particular, the significance of the zooplankton mortality formulation for model behaviour (Steele and Henderson, 1992) is clearly demonstrated by this analysis.

2.3.1. *Linear grazing models*

We begin with an analysis of the model version with linear zooplankton mortality and G1, the (linear) grazing formulation. This is the simplest model to analyse, and results are later extended to consider other more realistic versions. The phytoplankton–zooplankton interaction in this version of the model resembles the classical Lotka–Voltera equations which are recognised as unsatisfactory as a description of 'predator–prey' interactions, because they are neutrally stable, and consequently sensitive to small changes in process formulation (May, 1981). Because nutrient limitation is included, this model does not show the same neutral stability, except at high loads, where nutrients no longer limit growth.Setting $dZ/dt = 0$ gives:

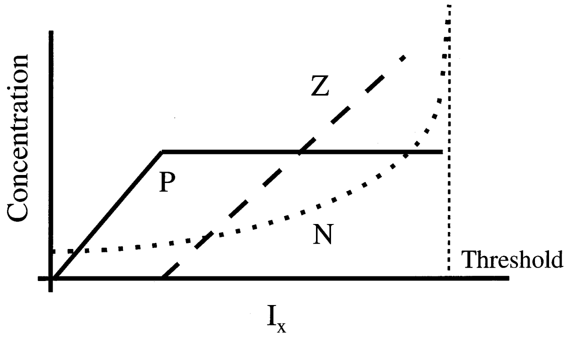

Fig. 3. Analytical steady-state solution of the N–P–Z model with linear zooplankton mortality and G1 grazing (N2a, P2a and Z2a) as a function of load. P^* is given by the solid line, Z^* by the dashed line and N^* by the dotted line.

$$P^* = m_z/ec. \qquad [\mathrm{P2a}] \qquad (19)$$

Thus, the steady-state phytoplankton biomass is independent of external nutrient load, a well-known result (e.g. Steele, 1976; Evans and Parslow, 1985), which is independent of the formulation of the grazing functional response G.Setting $d(P+N)/dt = 0$ gives:

$$Z^* = \frac{I_x - m_p P^*}{cP^*[1-(1-e)f_g] - f_m m_z} \qquad [Z2a], \qquad (20)$$

and setting $dP/dt = 0$,

$$N^* = \frac{K_N(cZ^* + m_p)}{\mu_{\mathrm{pI}} - m_p - cZ^*} \qquad [\mathrm{N2a}]. \qquad (21)$$

According to these solutions P^* is constant, N^* increases asymptotically and Z^* increases linearly with loading (Fig. 3).

This solution breaks down at very low and very high loads. After substituting for P^* from P2a in Z2a, we find that Z^* is negative for $I_x < m_z m_p/ec$. At very low loads, there is insufficient nutrient supply to support phytoplankton 'natural mortality' at the phytoplankton biomass required to sustain zooplankton. Instead, zooplankton are eliminated, and one obtains the solution:

$$P^* = I_x/m_p \qquad [\mathrm{P2a}^-] \tag{22}$$

$$Z^* = 0 \qquad [\mathrm{Z2a}^-] \tag{23}$$

$$N^* = \frac{K_N(m_p)}{\mu_{pI} - m_p} \qquad [\mathrm{N2a}^-]. \tag{24}$$

Above the minimum threshold, Z^* increases linearly with load (Z2a), but N2a only defines N^* for $\mu_{pI} > m_p + cZ^*$. Provided P^* is regulated by zooplankton grazing, there is a maximum uptake capacity for DIN given by $\mu_{pI}P^*$. If the DIN load I_x exceeds this, DIN must accumulate to levels where it becomes nonlimiting. It is possible to obtain a steady-state solution at high loads, if we allow for export to the ocean. If we approximate $P\mu_{pI}N/(N+K_N)$ by $P\mu_{pI}$ and include an export flux to the ocean in the nutrient equation, with a dilution rate D, we obtain:

$$\mu_{pI}P^* = I_x + f_m m_z Z^* + (1-\mathrm{e})f_g cP^*Z^* - DN^*. \tag{25}$$

Then:

$$P^* = m_z/ec \qquad [\mathrm{P2a}^+] \tag{26}$$

$$Z^* = P^*e(\mu_{pI} - m_p)/m_z \qquad [\mathrm{Z2a}^+] \tag{27}$$

$$N^* = [I_x + f_m m_z Z^* + (1-e)f_g cP^*Z^* - \mu_{pI}P^*]/D \quad [\mathrm{N2a}^+]. \tag{28}$$

Thus, at high loadings, Z^* is constant and N^* increases linearly with increased loading, while P^* remains constant as before.

At high loads, phytoplankton growth is no longer nutrient-limited, and the stability of the steady-state solution is no longer assured. To check this, we considered numerical solutions of the dynamical model described by P2, N2, Z2, including exchange with oceanic water. The dynamical model produced steady-state solutions at all loads, and these agreed well with the analytical solutions (Fig. 4). The ocean boundary acts as a weak source of zooplankton in the numerical model, so that zooplankton concentrations fall to low levels, but not the zero levels predicted without exchange at very low loads. The transition at high loads is also less abrupt, because in the equations 2a$^+$, we approximated $N/(N+K_N)$ by 1. The analytical solution of N^* has a problem at the transition too. Since at or below this load phytoplankton growth is equal to nutrient supply: $\mu_{pI}P^* = I_x + f_m m_z Z^* + (1-e)f_g cP^*Z^*$, so the value of N^* at the transition point according to N2a$^+$ is zero. However, the analytical solution rapidly converges on the steady-state solution of the dynamic model—this behaviour is a product of our simplifying assumptions.

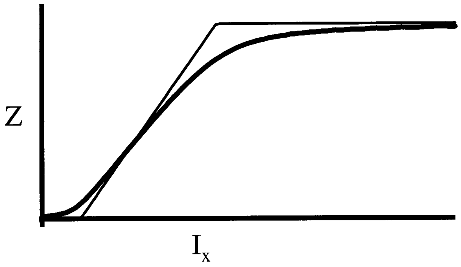

Fig. 4. Analytical (thin line) and numerical (thick line) steady-state solutions for Z for the N–P–Z model with linear zooplankton mortality and G1 grazing.

At higher loads, instabilities appeared in the dynamical model (Fig. 5). Instability is a recognised feature of enrichment in simple ecosystem models (Rosenzweig, 1971). In this particular case, instability is a numerical effect and the numerical model solution does approach the steady-state solution at higher loadings if the time step is small enough. This reflects the near-neutral stability of the phytoplankton–zooplankton inter-

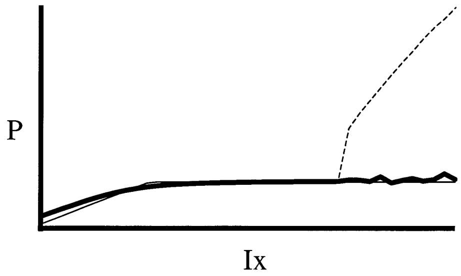

Fig. 5. Analytical steady-state (thin line) and mean numerical (thick line) solutions of P for the N–P–Z model with linear zooplankton mortality and G1 grazing. In this case, limit cycles are predicted by the dynamical (numerical) model at higher loads; maximum values are shown with a dashed line.

action at near-saturating nutrient concentrations. Because the underlying differential equations are almost neutrally stable, the difference equations used in the numerical model are unstable if the time step is too long (May and Oster, 1976). Thus, at least at high nutrient loads, this simplest N–P–Z model suffers from the same deficiency as the Lotka–Volterra model.

In practice all grazers have a maximum food intake level $g_{\max}$ at which they become satiated. In the G2 (bilinear) formulation, the transition from a linear functional response (constant clearance rate) to satiated grazing takes place abruptly. The steady-state implications are almost trivial. The maximum zooplankton growth rate is just $eg_{\max}$. If $eg_{\max} > m_Z$, then the steady-state solution described in the preceding subsection applies. If $eg_{\max} < m_Z$, then zooplankton cannot be sustained, and will be lost from the system. The solution $2a^-$ then applies.

While the introduction of zooplankton satiation in this form has trivial consequences at steady-state, it has important consequences for the dynamical behaviour of the model. Provided P^* remains less than $g_{\max}/c$, the steady-state remains neutrally stable at high loads. However, perturbations which result in larger values of P may grow in amplitude. The effects of satiation on stability under G3 are discussed below.

2.3.2. Rectangular hyperbola (Michaelis–Menten) grazing model

Analytical solutions can be obtained using the G3 grazing model as for G1, except that where previously $G^* = m_Z/e$, the equation is now replaced with $G^* = cP^*/(1 + cP^*/g_{\max})$. It follows that:

$$P^* = \frac{m_z}{ce - m_z c/g_{\max}} \qquad [\text{P2b}] \qquad (29)$$

$$Z = \frac{I_x - m_p P^*}{G^* - (1-e) f_g G^* - f_m m_z} \qquad [\text{Z2b}] \qquad (30)$$

$$N^* = \frac{K_N(G^* Z^*/P^* + m_p)}{\mu_{pI} - m_p - G^* Z^*/P^*} \qquad [\text{N2b}]. \qquad (31)$$

The qualitative dependence of the steady-state solution on load I_x is unchanged; P^* is constant, Z^* increases linearly and N^* increases at an accelerating rate.

As before, if I_x/m_p is less than P^*, then grazing cannot be supported and the zooplankton biomass is zero. In the absence of zooplankton, grazing formulation makes no difference and so the previously determined solutions (P2a^-, Z2a^-, N2a^-) apply.

$$P^* = I_x/m_p \qquad [\text{P2b}^-] \qquad (32)$$

$$Z^* = 0 \qquad [\text{Z2b}^-] \qquad (33)$$

$$N^* = \frac{K_N m_p}{\mu_{pI} - m_p} \qquad [\text{N2b}^-] \qquad (34)$$

If loadings are high then steady-state solutions to Z^* and N^* are determined using the same approximations that we used to solve the model with G1 grazing (phytoplankton growth rate equals μ_{pI} and export of N is included).

$$P^* = \frac{m_z}{ce - m_z c/g_{\max}} \qquad [\text{P2b}^+] \qquad (35)$$

$$Z^* = P^* e(\mu_{pI} - m_p)/m_z \qquad [\text{Z2b}^+] \qquad (36)$$

$$N^* = [I_x + f_m m_z Z^* + (1-e) f_g G Z^* - \mu_{pI} P^*]/D \qquad [\text{N2b}^+] \qquad (37)$$

However, the hyperbolic grazing formulation does significantly change the stability properties of solutions at high loads. Under nutrient saturation, the phytoplankton–zooplankton interaction is intrinsically unstable for G3, whereas it is neutrally stable for G1. Numerical analysis of the N–P–Z model including exchange with the ocean shows that there is a threshold load, beyond which steady-state solutions become dynamically unstable, and are replaced by limit cycle solutions.

Our results are similar to those obtained by Franks et al. (1986) for an analysis of two grazing models. The Ivlev model, like G3, saturates as P becomes large, and like G3 exhibits large instabilities at high loads. Mayzaud and Poulet's model, like G1, becomes linear as P1 becomes large; this model showed little instability, and our G1 model shows only numerical instability.

This onset of instability is a potentially important result. Under this formulation, the system can tolerate increasing nutrient inputs with no effect on phytoplankton biomass until a threshold is crossed, and there is a sudden transition to episodic blooms of increasing amplitude. While this may not involve a dramatic increase in mean phytoplankton biomass, episodic dense blooms are generally environmentally undesirable. If this transition occurred in real systems, the threshold load would be of great interest to environmental managers. We will later discuss how such instability matches the observations made in Port Phillip Bay.

2.3.3. Grazing thresholds

As in the case of the G3 formulation, the introduction of a grazing threshold under G4 grazing does not change the qualitative form of the steady-state solutions, all it does is increase P by the threshold P_t, and in fact Z2b and N2b still apply, with the new value of P^*.

$$P^* = P_t + \frac{m_z}{ce - m_z c/g_{\max}} \qquad [\text{P2c}] \qquad (38)$$

As under other versions of this model that use the linear zooplankton mortality assumption, P^* is constant, Z^* increases linearly and N^* increases asymptotically with load. If $I_x < m_p P^*$ (by P2c) then Z^* is 0 and the previously derived (N2a$^-$, P2a$^-$, Z2a$^-$) solutions apply. This lack of a significant role for grazing thresholds was also noted by Kishi et al. (1981).

The introduction of a grazing threshold can have a significant effect on the stability properties of the phytoplankton–zooplankton interaction at high loads, under nutrient saturation. Provided P^* is close to P_t, the steady-state solution is asymptotically stable (cf. Evans and Parslow, 1985), and it is possible in principal to have a solution in which P^* is low and grazing-regulated at high loads, while most of the DIN load is not utilised and exported directly to the offshore ocean.

2.4. Water-column steady-state solutions with quadratic zooplankton mortality (Eqs. P2, N2, Z2, $n = 2$)

The formula used to describe zooplankton mortality is shown to play a critical role in the model's behaviour. Naïvely, this might seem surprising since zooplankton graze only some of the phytoplankton; the rest fall out; while all inputs pass through the N and P pools. In fact, the exact specification of zooplankton mortality is critical in determining relative sizes of DIN and phytoplankton pools and their response to changes in input nutrient loads, and the stability of steady-state solutions at high nutrient loads (Steele, 1976; Steele and Henderson, 1992). In this section, we consider an alternative formulation in which zooplankton mortality is proportional to the square of zooplankton biomass. This formulation can be based on an argument similar to that used to justify quadratic mortality for phytoplankton: that is, that both carnivore-specific ingestion rates and carnivore biomass increase linearly with zooplankton biomass. It can alternatively be justified by arguing that switching or spatial aggregation by carnivores leads to an effective quadratic dependence in their functional response. Arguments can be made for other functional forms, involving different mixes of functional and numerical responses.

We start by examining the model with G1 grazing. We can simply take the existing solutions and replace the term m_z by $m_z Z^*$:

$$P^* = m_z Z^*/ec \qquad [\text{P2d}] \qquad (39)$$

$$Z^* = \frac{I_x - m_p P^*}{cP(1-(1-e)f_g) - f_m m_z Z^*}$$

$$N^* = \frac{K_N(cZ^* + m_p)}{\mu_{pI} - m_p - cZ} \qquad [\text{N2d}]. \qquad (40)$$

However, all these solutions depend on the unknown Z^*. We can solve for Z^* from this point by substituting $m_z Z^*/ec$ for P^* in the zooplankton equation. After some algebra, one can obtain:

$$Z^* = \frac{-m_p/c + \sqrt{(m_p/c)^2 + 4\gamma e I_x/m_z}}{2\gamma} \qquad [\text{Z2b}] \qquad (41)$$

where $\gamma = 1 - (1-e)f_g - ef_m$. According to this result, at very low loads, where $m_p P^*$ predominates over cP^*Z^*, and Z^* and P^* increase linearly with load. (Note that the model no longer predicts disappearance of zooplankton at very low loads.) As load increases further, and grazing losses predominate over natural mortality, Z^* and P^* increase in proportion to the square root of

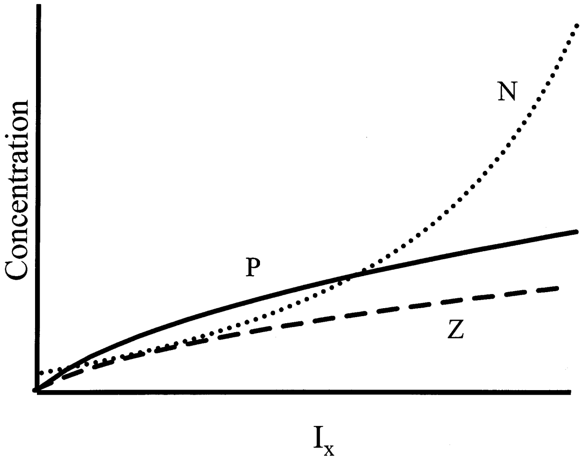

Fig. 6. Analytical steady-state solutions of the N–P–Z model with quadratic Z mortality and G1 grazing (N2d, P2d, Z2d) vs. load. P^* is given by the solid line, Z^* by the dashed line and N^* by the dotted line.

load. The value of N^* increases in an accelerating way (Fig. 6). As before, this solution breaks down at very high loads, when $\mu_{pI} < m_p + cZ^*$. Although P^* is not constant, it increases only like the square root of the load, so that eventually the N load must exceed the maximum phytoplankton uptake capacity and nitrogen starts to accumulate. As before, the model then needs to be extended to allow for export of N through flushing. This restores the steady-state solution in which N^* is large, phytoplankton growth is nutrient saturated, P^* and Z^* approach asymptotic maximum values, and the DIN load is predominantly balanced by export:

$$Z^* = (\mu_{pI} - m_p)/c \qquad [\mathrm{Z2d}^{+a}] \tag{42}$$

$$P^* = m_z Z^*/ec \qquad [\mathrm{P2d}^{+a}] \tag{43}$$

$$N^* = [I_x + (1-e)f_g cP^*Z^* + f_m m_z Z^{*2} - \mu_{pI}P^*]/D \quad [\mathrm{N2d}^{+a}]. \tag{44}$$

The introduction of quadratic zooplankton mortality changes the phytoplankton–zooplankton interaction under nutrient saturation from neutrally stable to asymptotically stable, and numerical analysis shows that solutions of the dynamical model under very high loads approach the steady-state solution 2d^{+a}.

If we replace the simple and unrealistic linear grazing formulation G1 by a bilinear (G2) functional response, the model behaviour at high loads becomes more complicated. There is now a maximum possible zooplankton biomass, given by $Z_{max} = eg_{max}/m_z$, and consequently a maximum grazing loss eg_{max}^2/m_z. If the maximum steady-state value of Z^* for the corresponding G1 solution (Z2d^{+a}) is greater than Z_{max}, then phytoplankton will escape grazing control at high loads. The system will then approach a steady-state solution in which zooplankton biomass equals Z_{max}, phytoplankton biomass is high and increases linearly with load, and phytoplankton growth is balanced predominantly by 'natural mortality':

$$Z^* = eg_{max}/m_z \qquad [\mathrm{Z2d}^{+b}] \tag{45}$$

$$P^* = [I_x + Z^*(f_m m_z Z^* + ((1-e)f_g - 1)g_{max}]/m_p \quad [\mathrm{P2d}^{+b}] \tag{46}$$

$$N^* = K_N(g_{max}Z^* + m_pP^*) /(\mu_{pI}P^* - m_pP^* - g_{max}Z^*) \qquad [\mathrm{N2d}^{+b}]. \tag{47}$$

Note that, according to N2d^{+a}, N^* declines as nutrient load increases. This counter-intuitive result occurs because, as the relative role of grazing declines at high values of P, phytoplankton specific mortality rate, and therefore phytoplankton specific growth rate, decreases. (In a more sophisticated model incorporating light attenuation and self-shading (e.g. Murray and Parslow, 1997), the growth rate μ_{pI} would eventually decline at very high P, owing to self-shading, and N^* would increase again. Eventually a maximum phytoplankton biomass would be reached when $\mu_{pI} = m_p$, and further inputs would be balanced by DIN export to the ocean.)

If the maximum value of Z^* according to Z2d^{+a} is less than Z_{max}, then there are two alternative steady-state solutions possible at high loads, a high nutrient solution, grazing regulated solution (2d^{+a}), and a low nutrient solution (2d^{+b}).

The hyperbolic functional response (G3) also approaches a maximum g_{max} for P^* large, and so there is still an upper bound to zooplankton biomass, given by $Z_{\max} = eg_{\max}/m_z$. A steady-state solution with $Z^* \approx Z_{\max}$, high P^* and low N^* (similar to 2d$^{+\mathrm{b}}$) therefore exists at very high loads. A high N^* steady-state solution, similar to 2d$^{+\mathrm{a}}$, also exists at high loads. For this solution, $Z^* = eG^*/m_z$ is always less than $Z_{\max}$, and so both high N^* and low N^* solutions always exist.

The steady-state solution at low loads is also similar under the two grazing models since G3 approaches cP^* when P^* is small. The expressions for steady-state solutions at intermediate loadings are more complicated in the case of G3, but qualitatively similar to those derived for G2. We have not derived explicit expressions for these solutions. However, due to the saturation of grazing, P^* increases faster than Z^*:

$$P^* = \frac{m_z Z^*}{c(e - m_z Z^*/g_{\max})} \qquad \text{[P2e].} \qquad (48)$$

N^*, as a function of P^* and Z^* is given by the same formula as N2b.

$$N^* = \frac{K_N(G^*Z^*/P^* + m_\mathrm{p})}{\mu_\mathrm{pI} - m_\mathrm{p} - G^*Z^*/P^*} \qquad \text{[N2e]} \qquad (49)$$

We have obtained iterative steady-state solutions for this model and compared these with solutions of the full dynamical model.

The dependence on loads of the steady-state solutions of the quadratic zooplankton mortality N–P–Z model can be summarised as follows. P^* and Z^* increase linearly at very low loads, and with the square root of loads as these increase further, while N^* increases at a rate which is faster than P^* or Z^*. Then, either the zooplankton reach their maximum biomass and phytoplankton escape grazing control, or the phytoplankton reach their maximum growth rate, and grazing controls phytoplankton biomass. In the latter case N^* increases linearly with further increases in loads, which are balanced primarily by export of DIN through flushing. In the former case, P^* increases linearly with load, N^* declines, and loads are balanced primarily by the export of P. In more realistic models, factors such as self-shading also limit the growth rate of phytoplankton, arresting and then reversing the fall in N^*.

The analytical solutions under G2 grazing have been compared with steady-state results obtained by running the numerical dynamical model to equilibrium. In both cases (grazer escaped or grazer controlled) analytical and numerical solutions for P^*, Z^* and N^* are in good agreement at high and at low loadings. At loads close to the point where nutrients become saturating, there are discrepancies. The grazer controlled numerical solution is similar to the analytical solution, except that there is a smooth transition from low to high loadings in the numerical solution (Fig. 7). This results in only slight disagreement for P^* and Z^*, but the analytical solution for N^* falls to zero at the transition, as discussed for N2a$^+$. As loading increases, the analytical solution for N^* converges with the dynamical model's result. The analytical solution gives a very good match with the numerical results for parameter sets in which phytoplankton escape grazing control. However, at loads close to the transition between low load and high load regimes, instabilities occur in the dynamical solution (Fig. 8). These instabilities are partly numerical and depend on time step size. For large time steps, the oscillation amplitude is so large that the numerical mean diverges from the analytical solution (a small divergence is visible in Fig. 8). Stability also depends on the closeness of the two maximum Z^* solutions (Z2d$^{+\mathrm{a}}$ and Z2d$^{+\mathrm{b}}$); in the example shown (Fig. 8) N is rising rapidly as Z2d$^{+\mathrm{b}}$ is reached (the N^* peak), this is because Z^* is also approaching Z2d$^{+\mathrm{a}}$. Real (as opposed to numerical) instability results from the interaction of these two values of Z^*. If the solutions are more distant, only one Z^* influ-

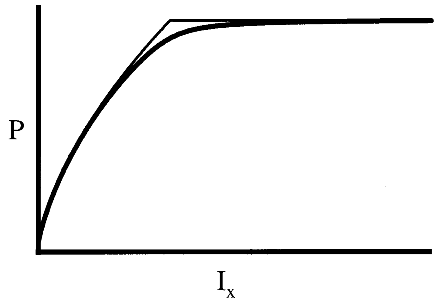

Fig. 7. Analytical (thin line) and numerical (thick line) steady-state solutions for P for the N–P–Z model with quadratic Z mortality and G2 grazing, for a case where grazing limits maximum production.

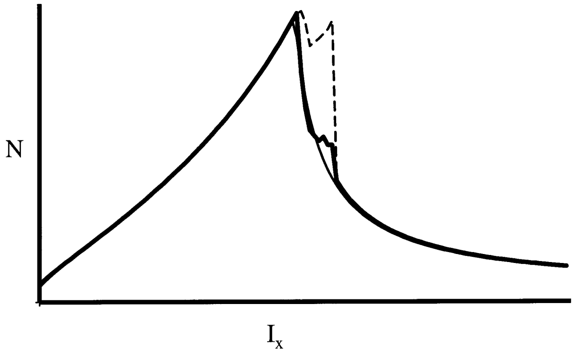

Fig. 8. Analytical steady-state (thin line) and mean numerical (thick line) solutions for *N* for the N–P–Z model with quadratic *Z* mortality and G2 grazing, for a case where *P* escapes grazing control at high loads. Maximum values of *N* from the dynamic model are shown with a dashed line where instabilities occur.

ences the model's steady state and there is no instability.

3. Discussion

Our analysis of simple models condenses the basic behaviour of a complex coastal ecosystem model into a form that is easily comprehensible without the need for extensive computation. Although not a substitute for a more detailed model, this set of analyses has given us a powerful tool (a meta-model) for use in the analysis of the full model and as a tool in its development (Murray and Parslow, 1997).

We have used this qualitative analysis of simplified models to examine the effects of alternative process formulations on model behaviour. In particular, we have considered plankton models with and without zooplankton, and compared different mortality and grazing formulations.

The most significant result is the dependence of the model's behaviour on the formulation of zooplankton mortality or, in the absence of an explicit zooplankton component, upon phytoplankton mortality (Table 2). Linear and quadratic zooplankton mortalities produce different behaviour. Under linear mortality, phytoplankton biomass remains constant as loading increases until the steady-state solution becomes unstable, and there is a transition to limit cycle behaviour, with periodic blooms. Under quadratic mortality, steady-state phytoplankton biomass increases with the square root of loading until, at high loads, either phytoplankton growth is nutrient-saturated and phytoplankton biomass approaches a grazing-controlled maximum, or grazing is saturated and phytoplankton increases linearly with load.

The radically different behaviour of the two formulations is certainly not unknown (Steele, 1976) but it is surprisingly under-emphasised. Published models do not generally justify the selection of a particular mortality formulation. There are two key questions involved in choosing the mortality formulation. Is the prediction that steady-state phytoplankton biomass should remain constant over a wide range of nutrient loads consistent with observations? If we include both oceanic and coastal systems, marine planktonic ecosystems ranging from oligotrophic to eutrophic status exhibit near steady-state behaviour with phytoplankton biomass ranging over about two orders of magnitude.

The second question is whether observations are consistent with a qualitative transition from steady-state behaviour under low nutrient loads, to large amplitude phytoplankton–zooplankton oscillations under high loads. While episodic blooms certainly occur in eutrophic systems, these seem to be driven more by episodic loads or environmental forcing, rather than intrinsic limit cycles. In highly eutrophic systems, zooplankton grazing tends to become unimportant compared with other phytoplankton loss terms. While this may be due to changes in community composition to large, grazing-resistant forms, it is again more compatible with the quadratic mortality model. Mesocosm experiments show that predatory–prey oscillations do not appear to be realistic (Franks et al., 1986).

In general, both the steady-state and transient behaviours appear to be more realistic under the quadratic zooplankton mortality formulation. We discuss the applicability of this formulation to Port Phillip Bay in the light of observations, and the reproduction of features in a dynamic spatially structured model of the bay elsewhere (Parslow and Murray, 1997).

The formulation of the grazing functional response generally does not prove to be important in controlling model behaviour, provided that there is a saturating maximum ingestion rate for zooplankton (and even this is only important if zooplankton mortality is quadratic). Although at first sight perhaps this is surprising, given the critical role of zooplankton mortality, the small difference (particularly at low or high P^*) between the main models, the rectilinear (G2, Lotka–Voltera with $g_{\max}$) and the hyperbolic rectilinear (G3, Michaelis–Menten), explains this lack of difference. Grazing thresholds, too, are not particularly important at steady-state, although they can have important effects on the stability properties at low phytoplankton biomass (Franks et al., 1986). Differences between the formulae do occur for intermediate phytoplankton populations. Instabilities can result under G3 grazing due to relaxation in grazing pressure as phytoplankton population increases. The more gradual approach to grazer saturation also means that phytoplankton are more likely to escape grazer control at high loads ($\mathrm{P2d}^{+\mathrm{b}}$), because $Z_{\max}$ is effectively lowered.

Many simple phytoplankton models do not include zooplankton explicitly (e.g. Taylor, 1988; Kimmerer et al., 1993). Without zooplankton, grazing must be defined as a function of P alone. A version of the N–P model with a cap on quadratic P mortality could reproduce much of the N–P–Z model's results. However, an N–P dynamical model cannot reproduce transient and local behaviour where the time lag in the numerical response of zooplankton is important. Before deciding whether to use an N–P formulation, modellers should decide whether these transients are important for management decisions.

The N–P–Z models have alternative steady-state solutions where $P^* = 0$ and $Z^* = 0$ or where $Z^* = 0$, and the N–P models have a solution where $P^* = 0$. However, these solutions are highly unstable and the variables will tend to the solutions described above following any perturbation.

We have used the steady-state analysis described here to assist in calibration of the full simulation model. Using the explicit steady-state solutions described above, it was a straightforward matter to choose parameter values in the full model so that predicted phytoplankton and nutrient pools and fluxes matched observed pools and fluxes at bay-wide annual scales. The simple model analysis does not address plankton size fractions or spatial and temporal pattern. Understanding the full model simulation of these phenomena and their dependence on parameter values was achieved through extensive computation and analysis. This numerical analysis was feasible because it rested on a solid foundation provided by the analysis of simpler models.

For a given model formulation, the steady-state solutions allow us to identify the critical parameters controlling steady-state pools and fluxes. For example, it might seem intuitively obvious that we could adjust phytoplankton biomass by changing phytoplankton maximum growth. In fact, phytoplankton maximum growth rates and half-saturation values for nutrient-limitation do not affect modelled phytoplankton biomass at steady-state. Maximum phytoplankton growth rate does influence the transient response to perturbations, and the outcome of competition between different primary producers, but it is the wrong parameter to adjust if we wish to alter offshore chlorophyll levels. Conversely, if we wished to alter phytoplankton maximum growth rates for some reason, but to leave background N, P and Z concentrations the same, the analysis shows us that we could compensate by adjusting the half-saturation constant for growth on DIN.

The steady-state solutions relate observables such as phytoplankton biomass to combinations of model parameters. We can then use observations to constrain these combinations directly, and the model parameters indirectly. As an example, for the N–P–Z model with linear Z mortality and G1 grazing, $P^* = ec/m_z$. Given observations of P, and reasonable literature estimates of growth efficiency e, we can constrain the ratio c/m_z. As a second example, under quadratic mortality (with G1 grazing), the ratio of P:Z at steady-state is equal to m_z/ec, and independent of load. If, after Sheldon et al. (1972), we assume this ratio to be close to 1, then:

$$m_z \approx ec \tag{50}$$

Although the P:Z ratio may vary, this is still a very useful constraint, particularly given the uncertainty introduced by the biomass dependent nature of m_z under quadratic Z mortality.

This method of analysis has proved effective because Port Phillip Bay is internally well mixed, has limited exchange with offshore water, and is generally subject to only relatively mild perturbations. These conditions make local steady-state solutions ecologically meaningful. The approach can be applied to models of other environments that meet these conditions, such as many lagoons and lakes. The method can also be applied to investigation of models of offshore areas where effects of horizontal advection and mixing are weak. The area of the marine environment in which this approach is least likely to be applicable is, ironically, exposed coastal waters, where horizontal gradients and exchanges are often dominant.

The assumption of approximately steady-state conditions is critical to the solution of the simple models. However, systems which vary at time scales that are longer than the plankton turn-over times, e.g. seasonal variation, can be analysed using quasi-steady-state models (Klepper, 1995). The modelled water-column components turnover in periods of days (N and P) to weeks (Z) and therefore steady-state can return within a few weeks after even quite large perturbations (Taylor, 1988). The organic sediments have a much slower turnover and may take much longer to return to steady-state. However, if fluxes from the sediment are known, an analysis of the water-column model can still be made using this assumption that fluxes from the sediment change slowly relative to the time required for the plankton to reach steady-state (Ludwig et al., 1978).

Many other workers have applied simple modelling techniques to analyse specific problems such as the dependence of models on grazing formulation (Franks et al., 1986) or zooplankton mortality formulation (Steele and Henderson, 1992). Modellers also use simple steady-state models to describe and analyse ecosystems (Evans and Parslow, 1985; Taylor and Joint, 1990) or analyse the steady-state solutions of simple dynamic models (Ross and Nival, 1976; Kishi et al., 1981). These simple models can be used to analyse the behaviour of more complex models (Ludwig et al., 1978; Armstrong, 1994; Klepper, 1995). We have developed our simple model specifically as a tool to analyse a more detailed coastal ecosystem model (Murray and Parslow, 1997). We have extended the simplified modelling approach to include sediments, allowing an investigation of the nonlinear responses of coastal ecosystems to nutrient enrichment. We identify testable differences in model predictions, which we elsewhere apply to an extensive observational data set (Parslow and Murray, 1997). We have used this model as a practical tool in the design and calibration of a spatially structured dynamic model with considerable success.

Direct comparison of the behaviour of our model with that of other simple marine ecosystem models is instructive. In pelagic marine ecosystem models total nutrient usually is either fixed (Armstrong, 1994) or depends upon input base on exchanged of fixed concentration deep water with water from the surface layer (Evans and Parslow, 1985; Taylor, 1988; Fasham, 1995), which are very similar in effect. Such models limit total nutrient concentration to approximately that found in the deep layer and are inappropriate for coastal ecosystems in which nutrients are supplied as inputs from the sediments and external sources and accumulate unless explicitly removed. Coastal ecosystem models are more directly relevant.

A simple coastal ecosystem model was developed by Kishi et al. (1981). This model maintains a constant total mass of nutrient and so can behave quite differently to that of our model. An illustration of this is in their respective responses to changes in the phytoplankton growth rate parameter, once μ_{pI} exceeds m_{p} (if $\mu_{\mathrm{pI}} < m_{\mathrm{p}}$ then P^* and Z^* must be zero in any model). In our model, Z^* is independent of further changes in μ_{pI}, while in the model employed by Kishi et al. (1981) Z^* increases linearly with this parameter. In this earlier model, the total nutrient (phosphorous) is constant so reduced turnover of inorganic nutrient effectively reduces I_{x}, leading to a cut in Z^*. In our model, DIN accumulates to a level that gives a similar primary productivity regardless of μ_{pI}, and so the value of this parameter has no effect on Z^*. The value of P^* is independent of load in the Kishi et al. (1981) model which has linear Z mortality; this is similar to the linear m_z versions of our model. The difference in behaviour between the models illustrates the differences between systems in which removal of external nutrient inputs is dominated by advection and removal by local denitrification. Under advection loss the total mass of the summed pools remains constant, so any slowing in the turnover of one pool leads to impoverishment of all the other pools. Under a local denitrification regime the total flux remains constant (except to changes in recycling efficiency), so any decrease in turnover rate of a pool must leads to accumulation in that pool thus maintaining the fluxes and having minimal effect upon other pools. At high loads, our model does behave like the model employed by Kishi et al. (1981), because denitrification is inhibited and advection (export) is then the controlling loss term.

Ross and Nival (1976) produced a simple P–Z model of another coastal ecosystem, the Bay of Villefranche. Their model is essentially a complicated Lotka–Voltera model with a quadratic P mortality term, limiting maximum phytoplankton biomass. In this case production is limited by the value of P and is independent of nutrient inputs, which are not explicitly described. This model is inappropriate for our main purpose, which is the investigation of the effect of nutrient loads upon the ecosystem.

A simple coastal model that does include denitrification is that derived by Kimmerer et al. (1993) for Tomales Bay. In this model phosphate is the nutrient that controls the behaviour of the ecosystem. The model responds weakly to increases in N input, since excess N is, while excess phosphate input leads to increased production by nitrogen fixing organisms. Increase phosphate loads lead to increased organic matter, but at a declining rate which eventually saturates, while DIP increases at an accelerating rate. This response to phosphate loads is similar to our models' P1b and N1b response to increased total nitrogen load I_x. Net nitrogen fixation in response to phosphate availability is clearly not the case in Port Phillip Bay, which, on average in 1993–1995, contained 1460 tonnes phosphate and only 253 tonnes nitrogen as inorganic nutrients, with no evidence of net N fixation (Harris et al., 1996). In general, observed denitrification exceeds nitrogen fixation in coastal waters (Seitzinger, 1988) and so these waters are usually nitrogen limited. Port Phillip Bay is a good example of an autotrophic marine system with a long residence time, which should theoretically be phosphate limited (Kimmerer et al., 1993). Because it is, in fact, nitrogen limited, Port Phillip Bay responds strongly to nitrogen loads and not at all to changes in phosphate load. Due to changes in denitrification efficiency the response of our model to changed external nitrogen load is nonlinear, whereas the model employed by Kimmerer et al. (1993) responds linearly to external phosphate loads.

Our model responds quite differently to changes in nutrient loads to the model of Kimmerer et al. (1993), for reasons of different biology, and differs from the Kishi et al. (1981) model due to different physical transport processes. The model of Ross and Nival (1976) does not explicitly deal with nutrients. The physical difference is due to the very slow exchange Port Phillip Bay has with the ocean; the biological difference is the bay's efficient net denitrification (Harris et al., 1996). Should nitrogen fixation become an important process, then the bay's ecosystem would be very different.

In summary, we present here a method of analysis that provides insight into detailed modelling at the level of individual parameters, process formulations and model structure. The dependence of solutions on parameters can be derived and investigated in minutes, as opposed to the days of computation required by long series of runs of the full model (and the additional time needed to process and interpret model output). These analytical solutions may be regarded as a sort of meta-model, a model of the model, rather than as a model in itself, and results must be referred back to the full model for detailed investigation (and to investigate dynamic or local features). Existing simple models do not appear to be able to simulate the appropriate nonlinear accumulation of total nutrient in response to external loads. This approach should be applicable in locations where advection and transient perturbations do not overwhelm local processes.

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