

Accounting for grazing dynamics in nitrogen-phytoplankton-zooplankton models

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Abstract

Nitrogen-phytoplankton-zooplankton (NPZ)-type models are widely used to explore the dynamics of marine planktonic ecosystems. Within these models, grazing by zooplankton on phytoplankton that are subjected to varying degrees of nitrogen limitation is described using N-based grazing kinetics together with fixed N assimilation efficiency. There is no empirical evidence for zooplankton displaying such behavior; on the contrary, there is evidence for a decline in zooplankton growth rates on consumption of N-impooverished prey, with decreased assimilation efficiencies coupled with decreased ingestion rates of nutrient-limited (i.e., poor quality, low N:C) prey. Unwittingly, then, traditional NPZ models make unjustified assumptions concerning changes in predator-prey interactions on consumption of low-quality prey. We explore the effects of this flawed description, also asking why NPZ models can still give reasonable descriptions of field data. Our conclusion is that one flaw may be countered by another, namely, by an inadequate description of nongrazing phytoplankton losses. In nature, these nongrazing losses are enhanced within nutrient-depleted phytoplankton populations. In models, a decline in grazing losses on nutrient-depleted phytoplankton is, de facto, compensated for by enhanced nongrazing losses. While the fit of the revised model to the data is not dissimilar to that of the original model (with its inappropriate descriptions of grazing and nongrazing phytoplankton mortality), the fate of primary production is very different. With the biologically more acceptable description, more material flows through the detrital compartment, with important implications for trophic dynamics. Care must be taken not to oversimplify descriptions of biology in models, as these may directly or indirectly mask the simulation of other important ecological processes.

Over the past decade there has been a concerted effort to increase the realism of ecosystem models that describe plankton production. Most of this effort has been expended on the description of phytoplankton; thus, multinutrient, photoacclimation models are now not uncommon (e.g., Fasham et al. 2006). Zooplankton grazing functions have been shown to be important determinants for plankton system dynamics (Steele 1976; Steele and Henderson 1992; Strom and Loukos 1998; Mitra and Flynn 2006). Thus, it is just as important to justify the construction of zooplankton models for incorporation within ecosystem models as it is to do so for phytoplankton models (Flynn 2003, 2005b). However, the description of zooplankton models has changed little, other than by the inclusion of more zooplankton groups (micro-, mesozooplankton and so on; e.g., Blackford et al. 2004) and by the greater appreciation of the importance of stoichiometry (e.g., carbon:nitrogen:phosphorus [C:N:P] in affecting assimilation and hence gross growth efficiency of the zooplankton predator (e.g., Sterner and Elser 2002; Anderson et al. 2005). These zooplankton models do not consider the effects of prey quality and availability on prey selection, ingestion kinetics, and growth dynamics.

Recently, we have developed models to enable a consideration of the effects of prey of different quality and quantity on zooplankton ingestion and growth kinetics (Mitra 2006; Mitra and Flynn 2006a, 2006b). These factors are important because changes in phytoplankton nutrient status, typically associated with nutrient exhaustion and often with the accumulation of toxins (Cembella 2003), can stimulate changes in zooplankton predation behavior (Irigoiien et al. 2005; Mitra and Flynn 2005). Such changes in behavior, associated with stoichiometric disparity between predator and prey, have been termed stoichiometric modulation of predation (SMP; Mitra and Flynn 2005). In this paper we consider the implications of SMP for the performance of what can probably be considered the classic modeling description of marine planktonic ecosystems, namely, the nitrogen-phytoplankton-zooplankton (NPZ) model (Fasham et al. 1990; Evans and Garçon 1997; Franks 2002).

Predation operates at the level of the particle; individual food items are selected, captured, and ingested. However, most planktonic ecosystem models do not use the individual as a state variable but use biomass instead; NPZ models describe biomass in terms of nitrogen. Generally, carbon biomass correlates well with the number of individuals for a given type of organism. Phytoplankton carbon per cell ($C \text{ cell}^{-1}$) is more constant for a given species than is their nitrogen content during N deprivation (e.g., Davidson et al. 1992). Phytoplankton N:C varies with the availability of nutrient N over a three- to fivefold range, depending on the phytoplankton type (e.g., Flynn et

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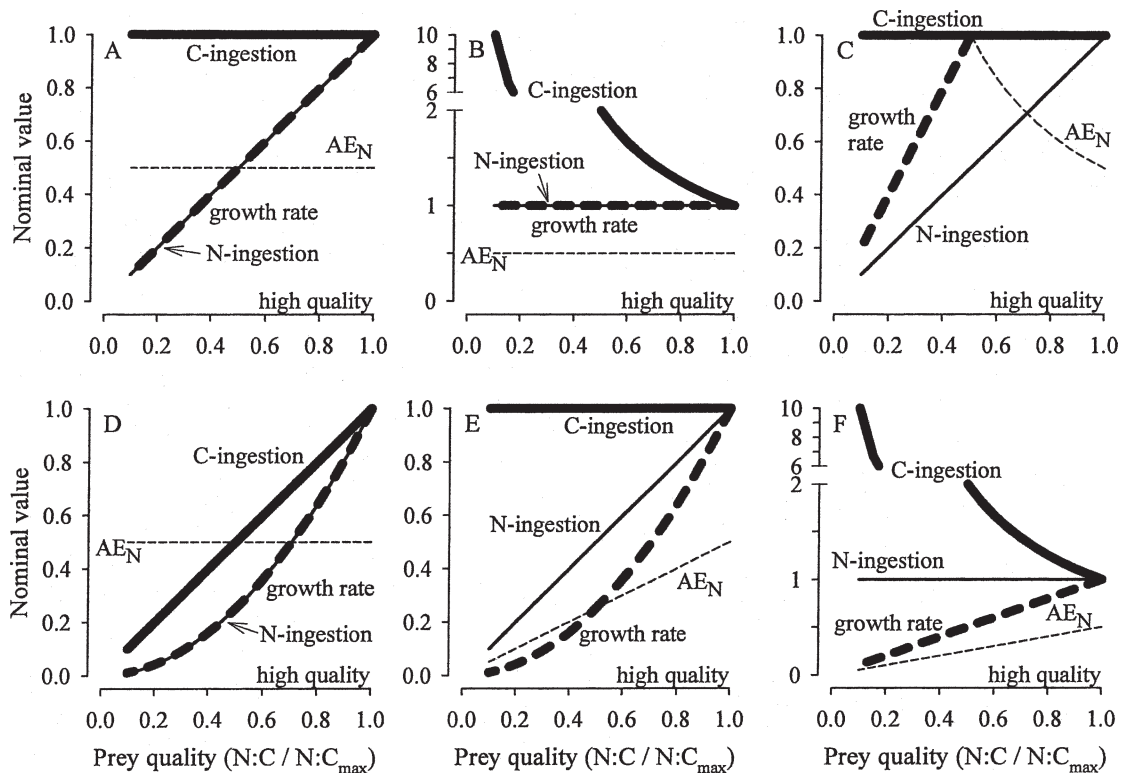


Fig. 1. Effects of prey quality on predator growth. (A) Neutral stoichiometric modulation of predation (SMP) for ingestion and assimilation (0 SMP_{Ing} and 0 SMP_{AE} , respectively), with no modification of the ingestion behavior or assimilation efficiency for the limiting nutrient (nitrogen; AE_N) in response to the presence of poor-quality prey. (B) +ve SMP_{Ing} with 0 SMP_{AE} ; ingestion of prey C is increased, so maintaining N ingestion. (C) 0 SMP_{Ing} with +ve SMP_{AE} ; AE_N is enhanced to a maximum of 100%. (D) -ve SMP_{Ing} with 0 SMP_{AE} ; C ingestion decreases, decreasing further N ingestion. (E) 0 SMP_{Ing} with -ve SMP_{AE} ; as panel (A) but with AE_N decreasing. (F) +ve SMP_{Ing} with -ve SMP_{AE} ; as panel (B) but with AE_N decreasing. The original configuration of NPZ-type models for phytoplankton predation accords with the pattern in panel (B). Y-axis units are indicative of relative change with food quality only.

al. 1993; John and Flynn 2002). Transformations from cell volume are used to yield carbon rather than nitrogen biomass (e.g., Postel et al. 2000). Let us, therefore, assume that C cell⁻¹ indeed remains constant regardless of N:C in phytoplankton. The default, simplest expectation is that as phytoplankton N:C declines during nutrient exhaustion, there is no change in cell-based and hence C-based capture kinetics. Likewise, the simplest expectation is that assimilation efficiency for the limiting nutrient (in this instance AE for N [AE_N]) is unaffected. This behavior, with no response by the predator to the consumption of poor-quality (low N:C) prey, is neutral stoichiometric modulation of predation (0 SMP; Mitra and Flynn 2005).

The implications of 0 SMP are shown in Fig. 1A; if predation rate in terms of cell number and hence C ingestion is unaffected by prey N:C and all other factors (such as AE_N) remain constant, then there is a decline in predator growth rate pro rata with the decline in N ingestion. Most zooplankton models make such assumptions in their construct or exhibit no functional relationship between ingestion and prey quality (e.g., Sterner and Elser 2002; Anderson et al. 2005; cf. Mitra 2006).

When confronted with prey of low N:C, predators may be expected to modify their behavior in order to counter the decline in prey quality; this is termed positive SMP (+ve SMP; Mitra and Flynn 2005). This could be accomplished

by enhancing the ingestion rate and/or by enhancing the assimilation efficiency of what is ingested. These behavioral responses are termed +ve SMP_{Ing} (Fig. 1B) and +ve SMP_{AE} (Fig. 1C), respectively. Other factors (such as reproduction costs) may also be affected by changes in behavior (Mitra 2006), but as these are not described in NPZ models, we will restrict discussion to changes in AE. AE is in any case the major determinant of post-ingestion growth dynamics; a consumer can use only what it assimilates. Assimilation efficiency can be increased only within a restricted range; it cannot exceed 100% and is often less than 80% (Tang and Dam 1999).

On the contrary, consumption of poor-quality prey may lead to behavior, at the extreme leading to prey rejection, that exacerbates the decline in nutritional value; this is termed negative SMP (-ve SMP). This may be associated with a decreased ingestion rate of the predator (-ve SMP_{Ing} ; Fig. 1D) and/or decreased assimilation efficiency (-ve SMP_{AE} ; Fig. 1E). The effect of -ve SMP (Fig. 1D,E) has a powerful effect on predator-prey interactions because it promotes the development of poorly grazed nutrient-stressed phytoplankton populations (Mitra and Flynn 2006a). These consequences of -ve SMP contrast with the effect of +ve SMP, which enhances nutrient cycling in a way that is not expected according to conventional stoichiometric theory (Hessen and Andersen 1992).

Turning now to the assumptions made in NPZ models, the base nutrient in these models is nitrogen, with all dynamics, including predation kinetics, being described in terms of N. Nitrogen-limited growth of phytoplankton is described using Monod functions in NPZ models, and while in reality during N exhaustion phytoplankton N:C declines, there is no explicit description of this decline in these N-based models. As phytoplankton N:C (and hence N cell⁻¹) declines and assuming that the predators continue to feed using the same particle capture kinetics and with a constant assimilation efficiency, the simplest (default) expectation must be a decline in prey N consumption during the N-limited period of the production cycle. Hence, one would expect 0 SMP (Fig. 1A). However, this is not what NPZ models describe at all. By describing grazing in terms of nitrogen, there is an implicit assumption in NPZ models that as phytoplankton become nitrogen limited, which would inevitably result in a decline in N:C, predators will continue to consume and assimilate prey N with the same kinetics. The only way this could be accomplished in reality is by a behavioral response in which zooplankton increase their ingestion of prey carbon as prey quality declines. De facto, then, NPZ models inherently display +ve SMP_{Ing} together with a fixed assimilation efficiency for N ($\equiv 0$ SMP_{AE}); this combination is described in Fig. 1B.

The question is whether one can justify the behavior of zooplankton feeding as described in NPZ models. The answer appears to be no. Not only does the description of zooplankton in these models not conform to the simplest expectation (i.e., 0 SMP; Fig. 1A), but they use a pattern (Fig. 1B) for which there is no supporting evidence. That zooplankton should not be assumed to be able to counter a decline in phytoplanktonic prey N:C by altering their behavior is quite clear (Flynn and Davidson 1993; Jones and Flynn 2005), with copepod egg viability and juvenile growth particularly at risk (Jónasdóttir 1994; Koski et al. 2006). While consumption of poor-quality prey can result in increased ingestion rates (+ve SMP_{Ing}) in some zooplankton, this is allied to decreased assimilation efficiencies (-ve SMP_{AE}) along with increased voiding rates (e.g., freshwater *Daphnia*; Darchambeau 2005). This pattern, Fig. 1F, is very different to those in Fig. 1A or Fig. 1B. Alternatively, there is evidence for both microzooplankton and copepods (Flynn and Davidson 1993; Jones et al. 2002; Jones and Flynn 2005) to support the contrary behavior, that consumption of poor-quality prey leads to a decreased ingestion rate (-ve SMP_{Ing}; Fig. 1D) and/or decreased AE (-ve SMP_{AE}; Fig. 1E).

In addition to the unsupportable description of +ve SMP_{Ing} plus 0 SMP_{AE} in NPZ-type models, the most widely used description of the partition of grazing effort between different food items (typically between phytoplankton, bacteria, and detritus) in more complex NPZ variants is the ratio-based prey selectivity function of Fasham et al. (1990), hereafter RS. The RS function is known to exhibit anomalous behavior (Fasham et al. 1990; Gentleman et al. 2003) such that consumption of a mixed diet leads to decreased growth rates, while experimental evidence indicates the opposite (e.g., Jones and Flynn

2005). Further, the description of RS (Fasham et al. 1990) assumes fixed grazing kinetics for all prey items (i.e., fixed maximum grazing rate and half-saturation constant for grazing), with fixed prey preferences that sum to unity. RS cannot correctly represent zooplankton behavior when confronted with prey of variable quality and/or quantity (Mitra and Flynn 2006b).

Given the anomalous description of zooplankton behavior in NPZ-type models, as identified previously, it is important to assess the effect of these on whole-system dynamics. In order to achieve this, two things are required. First, it is necessary to explicitly describe the changes in phytoplankton quality (N:C) that accompany nitrogen exhaustion. For this purpose, phytoplankton growth may be described using a N:C quota model, where algal growth is a function of N:C; this replaces the Monod-type description typically used (Evans and Garçon 1997). Second, when using a multiprey variant of the model, the zooplankton grazing function (RS) needs to be replaced with an alternative function that does not introduce the anomalous characteristics inherent in the RS formulations. To achieve this aim, we have employed an alternative selectivity function (Mitra and Flynn 2006b).

Using such a modified model, we consider here the consequences of replacing the enhanced ingestion of low-quality phytoplankton (+ve SMP_{Ing}) implicit in the original nitrogen-phytoplankton-zooplankton-bacteria-detritus (NPZBD) model of Fasham et al. (1990) with the default expectation of 0 SMP_{Ing}. Further, because consumption of poor-quality prey can decrease AE in zooplankton (Darchambeau 2005; Jones and Flynn 2005), we consider the effect of replacing the default 0 SMP_{AE} with -ve SMP_{AE}. Finally, we attempt to redress the effect of decreased grazing losses on phytoplankton of poor nutritional quality by describing enhanced death and sedimentation of such nutrient-stressed phytoplankton (Smayda 1970).

Methods

Model description—The NPZBD model of Fasham (1993) was used with the modifications described here. A schematic of the model is given in Fig. 2.

Phytoplankton component—Phytoplankton N uptake and the interaction between ammonium and nitrate uptakes were described using equations 19 to 22 in Flynn (2003); this replaced the original NPZBD description, which incorrectly assumes an inhibition of nitrate consumption. The maximum possible growth rate under saturating light and nutrients (μ_{max}) was restricted by the nitrogen status of the phytoplankton (as indicated by its N:C varying over a fourfold range) via a quotient, NCu , generated by a quota-style function (equation 9 in Flynn 2003). This replaced the original Monod-type description of N-limited growth. When $NCu = 0$, phytoplankton growth is zero and N:C is minimal (prey quality is lowest), while at $NCu = 1$, growth is controlled only by light availability. The maximum N-limited growth rate for phytoplankton, Vp in Fasham (1993), was given by the product of μ_{max} and NCu ; this was used within equation A6 of the NPZBD description in

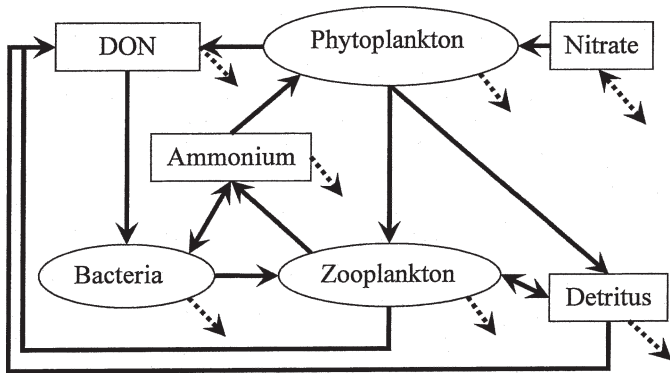


Fig. 2. Schematic of the NPZBD model described in Fasham (1993). Solid arrows indicate flows of nitrogen between model compartments within the mixed layer. Dashed lines indicate input and output from the mixed layer. DON, dissolved organic nitrogen.

Fasham (1993), providing an interaction with N for the calculation of N-specific primary production. There was no longer a need for equation A9 in Fasham (1993).

Zooplankton component—Zooplankton were described using a single state variable with units of N biomass, with inputs from grazing on phytoplankton, bacteria, and detritus (Fig. 2; Fasham 1993). The ingested material is assimilated with a fixed efficiency (β in Fasham 1993; Table 1) and the remainder, $1-\beta$, is voided to detritus.

Other losses from the zooplankton state variable are associated with excretion by and predation on the zooplankton; these contribute to the ammonium, dissolved organic N (DON), and detrital pools (Fig. 2).

Typically, grazing in NPZBD models is described using the ratio-based prey selectivity function (RS; Eq. 1; Fasham et al. 1990; Fasham 1993; Evans and Garçon 1997). Grazing on the i th prey item (G_i) is a function of prey (food) availability (F_i , as N biomass) and a relative preference index (p_i) such that

$$\sum p_i = 1$$

G_{max} and K_{pred} describe the maximum grazing rate and the half-saturation constant for grazing, respectively:

$$G_i = G_{max} \cdot p_i \cdot F_i^2 \div [K_{pred} \cdot (p_1 \cdot F_1 + p_2 \cdot F_2 + p_3 \cdot F_3 + \dots) + p_1 \cdot F_1^2 + p_2 \cdot F_2^2 + p_3 \cdot F_3^2 + \dots] \quad (1)$$

Because of the problems inherent with the use of RS (Fasham et al. 1990; Gentleman et al. 2003), an alternative prey selectivity function was used that does not display the aberrant behavior of RS. In the “ingestion control selectivity function” (IS; Eq. 2; Mitra and Flynn 2006b), the potential capture rate of a particular food type is a linear function of its availability (F_i) and a capture rate parameter, Cr_i . The summed assimilation of all captured

Table 1. Definitions of constant parameters used. Where possible, the original parameter names used by Fasham (1993) and Flynn (2003) have been retained. Nonzooplankton parameters share common values. Values listed under Dqd and Tqd are additional and changed values for the default +qd and test 1 +qd configurations, respectively, used in Figs. 5, 6, and 7; see also Table 2.

Parameter	Description	Common	RS	IS	Dqd	Tqd
Cr_{phyto}	Capture rate for phytoplankton for IS ($[\text{mol N} (\text{mol N}^{-1}) \text{d}^{-1}] \cdot [\text{m mol N m}^{-3}]^{-1}$)			2.0	2.0	2.0
$Cr_{bacteria}$	Capture rate for bacteria for IS ($[\text{mol N} (\text{mol N}^{-1}) \text{d}^{-1}] \cdot [\text{m mol N m}^{-3}]^{-1}$)			1.16		
$Cr_{detritus}$	Capture rate for detritus for IS ($[\text{mol N} (\text{mol N}^{-1}) \text{d}^{-1}] \cdot [\text{m mol N m}^{-3}]^{-1}$)			0.98		
G_{max}	Maximum grazing rate (d^{-1})		0.93	0.83		
K_I	Half-saturation for ingestion feedback for IS (d^{-1})			0.85		
k_3	Half-saturation for grazing (K_{pred}) for RS (m mol N m^{-3})		0.55			
p_{phyto}	Preference for phytoplankton for RS (dimensionless)		0.40			
$p_{bacteria}$	Preference for bacteria for RS (dimensionless)		0.47			
$p_{detritus}$	Preference for detritus for RS (dimensionless)		0.13			
KgN	Half-saturation for phytoplankton N uptake (m mol N m^{-3})	1.00				
KQN	Normalized quota control constant (dimensionless)	1.00				
k_5	Phytoplankton loss constant (m mol N m^{-3})	0.20			0.01	0.01
k_6	Zooplankton loss constant (m mol N m^{-3})	0.14				
NC_{abs}	Absolute maximum phytoplankton N:C ($\text{mol N} [\text{mol C}]^{-1}$)	0.17				
NC_m	Maximum phytoplankton N:C affecting growth rate ($\text{mol N} [\text{mol C}]^{-1}$)	0.15				
NC_0	Minimum phytoplankton N:C ($\text{mol N} [\text{mol C}]^{-1}$)	0.04				
PdH	Hill constant for death function (dimensionless)				0.5	0.5
μ_{max}	Phytoplankton maximum growth rate (d^{-1})	1.21				
V_b	Bacteria maximum growth rate (d^{-1})	1.00				
α	Slope of photosynthesis–irradiance curve ($[\text{W m}^{-2}]^{-1} \text{d}^{-1}$)	0.05				
β	Assimilation efficiency for N (AE_N) (dimensionless)	0.60				
δ	Fraction of zooplankton loss as DON (dimensionless)	0.19				
ϵ	Fraction of zooplankton loss to NH_4^+ (dimensionless)	0.67				
μ_1	Maximum phytoplankton death rate (d^{-1})	0.05			0.25	0.25
μ_2	Maximum zooplankton death rate (d^{-1})	0.50				
μ_3	Maximum bacteria death rate (d^{-1})	0.25				
μ_4	Rate of detritus remineralization (d^{-1})	0.10				

Table 2. Summary of NPZBD model configurations. Panels in Fig. 1, as indicated, portray the behavior of the zooplankton configurations for SMP at ingestion (SMP_{Ing}) and at assimilation (SMP_{AE}). Descriptions in the text and in figures indicated as “+qd” are for models in which the nongrazing loss of phytoplankton was enhanced at low nutrient status (quality-linked death) by application of Eq. 7 instead of by the original density-dependent function (Eq. 5).

Model configuration	SMP_{Ing}	SMP_{AE}	Fig. 1	Phytoplankton nongrazing loss (death) equation
Original	+ve	0	Panel B	Eq. 5 (density dependent)
Default	0	0	Panel A	Eq. 5 (density dependent)
Test 1	0	-ve	Panel E	Eq. 5 (density dependent)
Test 2	+ve	-ve	Panel F	Eq. 5 (density dependent)
Default +qd	0	0	Panel A	Eq. 7 (quality dependent)
Test 1 +qd	0	-ve	Panel E	Eq. 7 (quality dependent)

prey effectively limits capture of all prey types via feedback from the level of how replete is the gut or feeding vacuole. The actual rate of grazing on the individual prey type (G_i) is the minimum of the two activities, as enacted via the minimum function in Eq. 2. K_I is the half-saturation constant for the feedback function; it is not (as is K_{pred} in Eq. 1) a constant affecting prey capture per se. The IS function contains no more constants than does RS:

$$G_i = MIN \left(G_{max} \cdot \frac{\sum (Cr_i \cdot F_i)}{(\sum (Cr_i \cdot F_i) + K_I)}, \sum (Cr_i \cdot F_i) \right) \cdot \frac{Cr_i \cdot F_i}{\sum (Cr_i \cdot F_i)} \quad (2)$$

Model fits to data—The NPZBD model was tuned using an evolutionary algorithm as supported by Powersim Solver (Isdalstø, Norway) against the BioTrans data set for 47°N, 20°W, in the Atlantic (as used by Fasham and Evans 2000; a detailed description of this data set is given by Lochte et al. 1993) with a common set of constants for all but the zooplankton grazing terms. Table 1 gives these zooplankton-specific constants, plus other biological constants for the simulation that differ from those given in Fasham (1993). The NPZBD model was then configured to account for SMP at the levels of ingestion and assimilation in order to consider the effects of changes in zooplankton behavior on system dynamics.

Consideration of SMP at ingestion and assimilation of phytoplankton—The traditional NPZBD models inadvertently display an inherent + SMP_{Ing} along with 0 SMP_{AE} (original in Table 2; Fig. 1B). As argued in the Introduction, the default expectation must be neutral SMP (i.e., 0 SMP_{Ing} and 0 SMP_{AE} ; default in Table 2; Fig. 1A). In order to correct for the implicit +ve SMP_{Ing} inadvertently displayed in the traditional N-based NPZBD models, the operational value of the phytoplankton capture rate parameter, $Cr_{phyto}^{operational}$, used to compute the N-specific grazing rate of phytoplankton (G_{phyto} using Eq. 2), was changed from its original value (Cr_{phyto} ; Table 1) by reference to phytoplankton N:C, according to Eq. 3.

$$Cr_{phyto}^{operational} = Cr_{phyto} \cdot \frac{NC}{NC_m} \quad (3)$$

This modification alters the grazing on phytoplankton N biomass as a linear function of its N:C. Equation 3 accounts for the decrease in N ingestion with a decline in phytoplankton N:C (NC) relative to its maximum N:C

(NC_m). This equation thus changes the relationship between phytoplankton prey quality, ingestion, and predator growth from that shown in Fig. 1B (+ve SMP_{Ing}) to the default expectation shown in Fig. 1A (i.e., to 0 SMP_{Ing}).

Traditional NPZ-type models display no SMP at the point of assimilation (i.e., 0 SMP_{AE} ; the value of AE_N remains fixed, as in Fig. 1B and in Fig. 1A). In order to consider the effect of decreased assimilation efficiency during consumption of poor-quality phytoplankton (i.e., -ve SMP_{AE}), AE_N for phytoplankton was configured as a function of phytoplankton N:C by application of Eq. 4. This allows AE_N for phytoplankton to range as a linear function of N:C (between its minimum, NC_0 , and maximum, NC_m) between 100% and 50% of its normal value (i.e., of the tuned value for β ; Table 1). This range was used in reflection of the experimental results obtained by Jones et al. (2002). The value of β for consumption of other prey items (bacteria and detritus) was held unchanged:

$$\beta_{phyto}^{operational} = \beta_{phyto} \cdot \left(0.5 + 0.5 \cdot \left(\frac{NC - NC_0}{NC_m - NC_0} \right) \right) \quad (4)$$

Different combinations of SMP at ingestion (Eq. 3) and/or assimilation (Eq. 4) of phytoplankton were tested. Table 2 shows the combinations of SMP_{Ing} and SMP_{AE} employed and how these relate to the pictorial representations in Fig. 1.

Neutral SMP was assumed at ingestion and assimilation for bacteria and detritus.

Loss of phytoplankton through nongrazing events—There are various nongrazing loss terms for phytoplankton employed by different workers in NPZ-type of models (e.g., Fasham et al. 1990; Evans and Garçon 1997); these relate loss to phytoplankton N-biomass concentration rather than to their nutrient status. In reality, the decline in nutrient status (i.e., N:C) of phytoplankton may be associated with alterations in various physiological factors, such as enhanced aggregation, sinking, and/or lysis of nutrient-stressed cells (Smayda 1970; Brussaard 2004). In order to consider the effects of alternative nongrazing losses, we employed two methods of enhancing nongrazing phytoplankton death (Pd , d^{-1}). One of these (Eq. 6) replaced the original hyperbolic mortality function in

Fasham (1993) (Eq. 5) with a sigmoidal term that would enhance death with biomass density more sharply than does the original. Here, μ_l is the maximum loss rate, k_5 is the half-saturation constant for loss of phytoplankton N biomass, and PdH is the Hill constant defining the shape of the sigmoidal response curve. The alternate function (Eq. 7) related the loss term to the nutrient status of the algae (described by the quotient, NCu ; see phytoplankton component discussed previously) rather than to the biomass concentration. As NCu declines, so phytoplankton death rate (Pd) increases. The sigmoidal functions in Eqs. 6 and 7 default to rectangular hyperbolic descriptions when $PdH = 1$:

$$Pd = \frac{\mu_l \cdot P}{k_5 + P} \quad (5)$$

$$Pd = \frac{\mu_l \cdot P^{PdH}}{k_5^{PdH} + P^{PdH}} \quad (6)$$

$$Pd = \frac{\mu_l \cdot (1 + k_5^{PdH}) \cdot (1 - NCu)^{PdH}}{k_5^{PdH} + (1 - NCu)^{PdH}} \quad (7)$$

Table 2 lists the different combinations of SMP at ingestion and assimilation coupled with different phytoplankton loss functions as used in the simulations.

Results and discussion

Model fits to data—Before proceeding to consider the implications of SMP, it is necessary to demonstrate that a model equipped with the new prey selectivity function (IS) can give a fit to the data that is not dissimilar to an otherwise identical model equipped with ratio-based (RS) selectivity function. The two NPZBD models, with the N:C quota-style description of phytoplankton growth and with either the RS or the IS grazing functions, were fitted to the BioTrans data. These produced similar outputs (Fig. 3), with the most notable difference being that the grazing on detritus was greater using the IS version (Fig. 3H). Figure 3 thus displays the capability of an IS-equipped NPZBD model with +ve SMP_{Ing} and fixed AE ($\equiv 0$ SMP_{AE}) to produce a similar output to that of the traditional RS-equipped NPZ-type model (original configuration in Table 2; behavior pattern in Fig. 1B).

We conclude from Fig. 3 that the IS function itself does not introduce changes in system behavior; all subsequent simulations used the IS-based model so as to avoid the problems inherent with the use of RS.

Effect of SMP—Correcting for the inherent +ve SMP_{Ing} in the traditional NPZ (original configuration in Table 2; behavior pattern in Fig. 1B) to the default expectation of 0 SMP_{Ing} (default configuration in Table 2; behavior pattern in Fig. 1A) has a major effect on the simulation output (Fig. 4). The fit for zooplankton is improved (Fig. 4B), while that for phytoplankton is much worse during summer (Fig. 4A); there are relatively minor changes for bacteria and detritus (Fig. 4C,D). Further

manipulations, by invoking $-ve$ SMP_{AE} with or without correcting for +ve to 0 SMP_{Ing} (tests 1 and 2 in Table 2), also have major effects on the simulations. Figure 5A shows changes in the phytoplankton N:C that in the default and test 1 configurations (Table 2) affect their rate of capture ($Cr_{phyto}^{operational}$; Eq. 3, Fig. 5B) and hence the grazing rates (Fig. 4E,G,H; cf. Fig. 3E,G,H). The minimum N:C using the original configuration is ~ 0.07 (C:N = 14.3). Figure 5B shows changes in AE_N for phytoplankton consumption that occur through the use of Eq. 4 in test 1 and test 2.

The best fits to the zooplankton dataset are achieved when the model configurations employed $-ve$ SMP_{AE} (i.e., tests 1 and 2; Fig. 4B). However, the test 1 configuration (employing 0 SMP_{Ing}) produced the worst description for the phytoplankton summer bloom data (Fig. 4A) because of the decrease in zooplankton grazing on phytoplankton during this period (Fig. 4E,F). This event is related to the decline in phytoplankton N:C (Fig. 5A) affecting phytoplankton capture rate (Fig. 5B). In contrast, the test 2 configuration retaining the +ve SMP_{Ing} (as present in the original configuration) but now in conjunction with $-ve$ SMP_{AE} (Fig. 1F vs. Fig. 1B) provided relatively better fits to the phytoplankton data (Fig. 4A); this reflects the enhanced predation on poor-quality phytoplankton using this configuration (Fig. 4F,B), while the zooplankton growth rate was still lower than described by the original configuration (see Figs. 1F vs. 1E vs. 1B).

There are two reasons why the phytoplankton description is best with the original configuration (Fig. 4A). First, this configuration enhanced predation of poor-quality phytoplankton; this exhibition of +ve SMP_{Ing} maintains constant N-specific ingestion kinetics (Cr_{phyto} constant in Fig. 5B). Second, the zooplankton retain a fixed (constant) assimilation efficiency for the limiting nutrient showing 0 SMP_{AE} (AE_N constant; Fig. 5B) regardless of any decline in food quality (Fig. 5A). However, as described in the Introduction, there is no evidence at all that zooplankton display such behavior; they cannot continue to grow at the same rate regardless of their N:C. It is also worth noting that good model fits to experimental data for zooplankton behavior cannot be obtained using a combination of +ve SMP_{Ing} coupled with 0 SMP_{AE} (Mitra 2006).

There is cause to expect a combination of high ingestion rate coupled with depressed assimilation efficiency (i.e., +ve SMP_{Ing} and $-ve$ SMP_{AE} ; Fig. 1F) in zooplankton such as copepods. Copepods presented with high densities of phytoplankton, which are often likely to be nutrient deprived, can engage in messy feeding (Møller 2005), consuming more prey while displaying shorter gut transit times (Besiktepe and Dam 2002; Tirelli and Mayzaud 2005) and hence lower trophic transfer efficiencies (akin to a lower β in the NPZBD model, i.e., lower AE_N). In nature, the phytoplankton dominating spring and summer are very different; for example, diatoms typical of spring blooms may constitute poorer prey for copepods (Ceballos and Ianora 2003), especially when nutrient deprived (Jones and Flynn 2005). Under such conditions, copepods display low AE. However, output from this configuration (test 2), which displayed +ve SMP_{Ing} , was little better than test 1

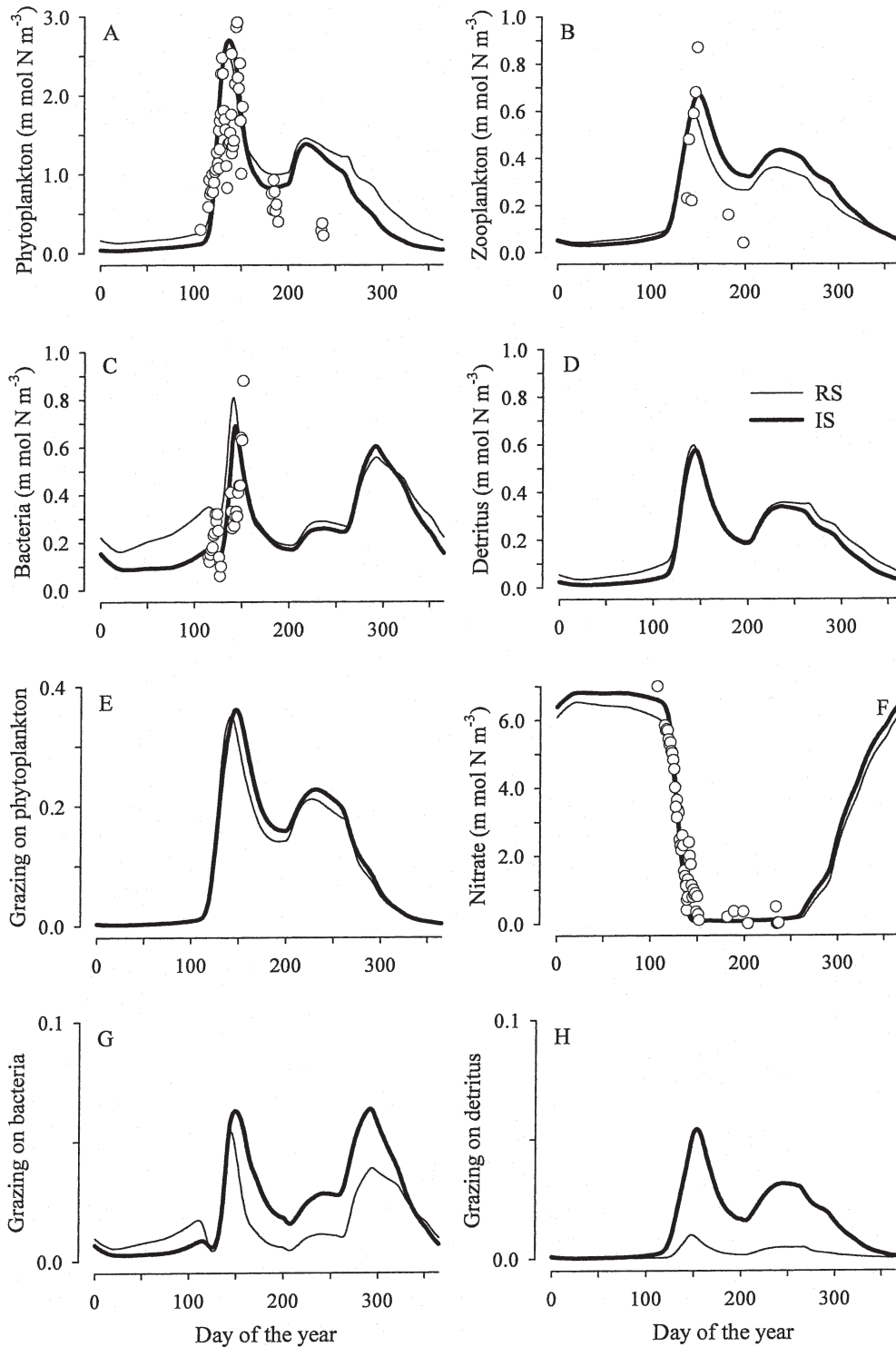


Fig. 3. Fits of phytoplankton, zooplankton, bacteria, and nitrate data to NPZBD models using different prey selection descriptions (RS or IS) and the original model configuration (Tables 1, 2). Also shown are the outputs for detritus and zooplankton grazing rates ($\text{m mol N m}^{-3} \text{d}^{-1}$) on phytoplankton, bacteria, and detritus. Circles denote data.

(Fig. 4), with the establishment of a large, poorly grazed summer phytoplankton bloom.

Another feature that is affected by changes in the configuration of the zooplankton component is nutrient

regeneration. A decreased rate of grazing on phytoplankton of poor nutritional status in summer (see Figs. 4E, 5A,B) inevitably leads to lower ammonium regeneration rates and hence to positive feedback maintaining nutrient

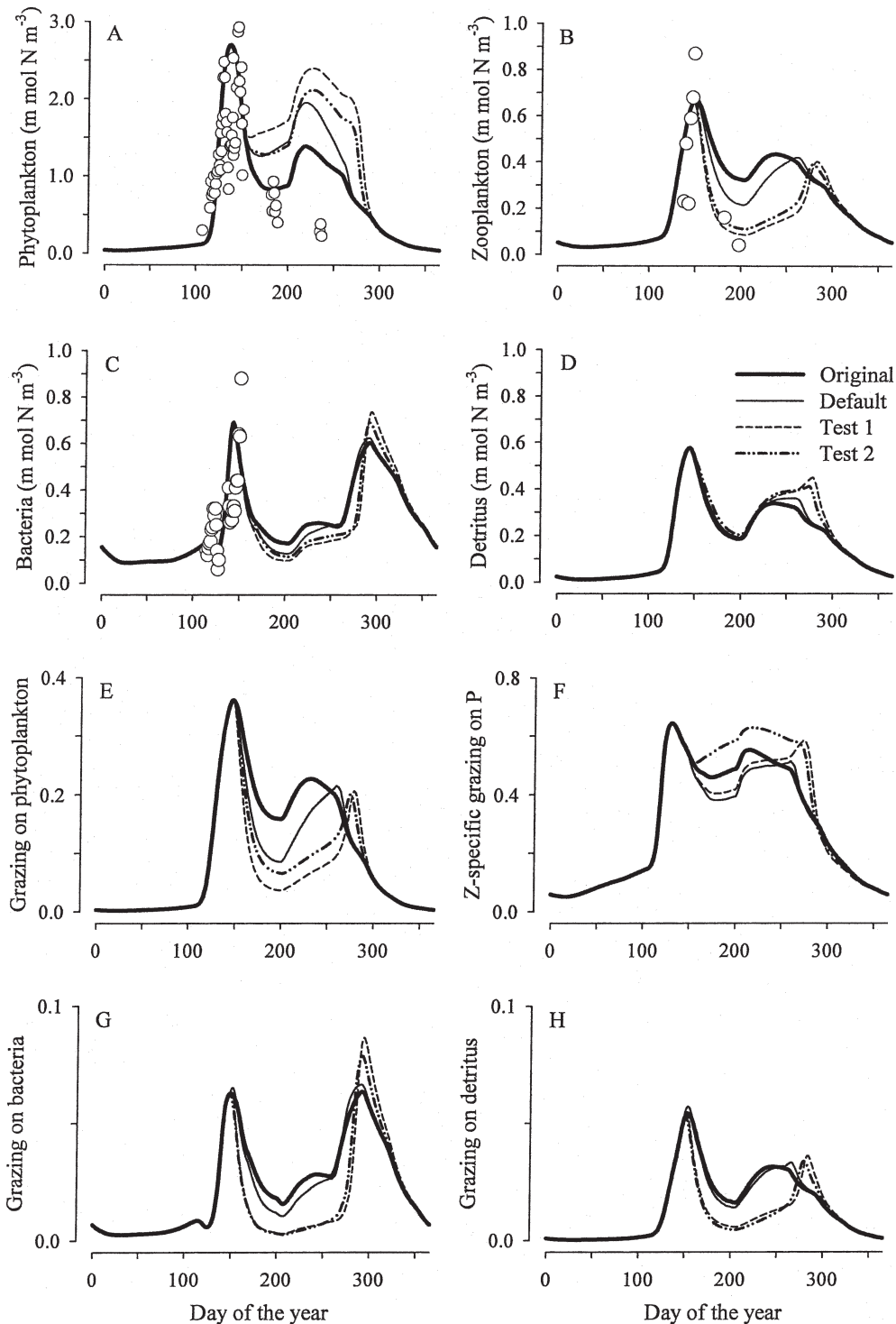
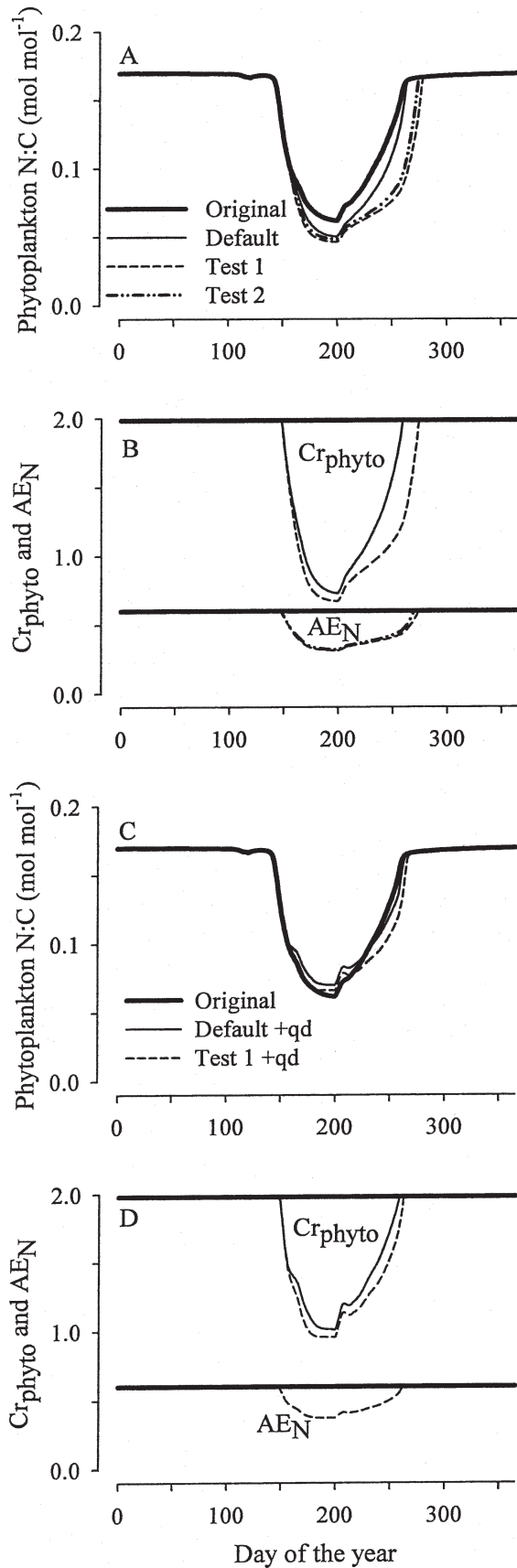


Fig. 4. Effects on model output of changing the description of zooplankton grazing behavior on phytoplankton. The original configuration (thick line) is the same as in Fig. 3 for the IS model. See Table 2 for definition of configurations. Circles denote data.

stress in the phytoplankton. This feeds back through decreasing zooplankton activity and growth, further decreasing regeneration. Although not simulated here, any decrease in the ingestion of poor-quality phytoplankton ($-ve SMP_{Ingr}$) that may develop in response to decline in phytoplankton N:C would exacerbate this situation even

further. Microzooplankton may be more likely than mesozooplankton to decrease ingestion of poor-quality prey (Mitra and Flynn 2005). Mitra and Flynn (2006a) demonstrate the powerful effect of such changes in zooplankton behavior on food web dynamics, while Irigoien et al. (2005) discuss the role of antipredator



mechanisms (which would invoke $-ve SMP_{Ing}$) in the formation of midocean blooms.

The invocation of $-ve SMP_{AE}$, resulting in a decrease in assimilation efficiency with ingestion of poor-quality food, will affect the nature of material voided by the zooplankton. Thus, with the consumption of low-quality (low N:C) phytoplankton, per unit of nitrogen ingested, more nitrogen is now voided in particulate form. In nature, this particulate material is more likely either to be lost from the euphotic zone (depending on the organisms releasing it; Tseitlin 1999) or to drive bacterial production and the associated microbial loop.

From the previous discussion, we are confronted with the paradox that the best description of biomass levels from the NPZBD model, and especially of phytoplankton (Fig. 4A), is given when employing an unsupportable description of zooplankton behavior. It is, therefore, necessary to seek an explanation for this state of affairs. An obvious candidate is the nongrazing phytoplankton loss term, which one may suspect to be underrepresented in the original model description.

The role of nongrazing phytoplankton losses—The effect of changing nongrazing losses was first considered by replacing the original simple hyperbolic phytoplankton death rate term (Eq. 5) with a sigmoidal density-dependent description (Eq. 6). However, this did not improve model output; while it lowered the size of the N-limited summer phytoplankton bloom, it also adversely affected the size of the N-sufficient spring bloom (not shown). However, linking the loss of phytoplankton to nutrient status (using Eq. 7, quality-linked nongrazing mortality, hereafter termed +qd) does improve the fit. By inclusion of this quality-linked nongrazing loss function, the model now describes a peak spring bloom followed by a low summer biomass, in keeping with the data (Fig. 6A vs. Fig. 4A). The zooplankton output remains relatively unchanged, with a lower biomass in summer than did the original configuration (Fig. 6B vs. Fig. 4B); the outputs for test 2 +qd are similar to test 1 +qd (and hence are not plotted).

Zooplankton-specific grazing rates on phytoplankton are altered markedly (Fig. 6F vs. Fig. 4F) because there are less phytoplankton available. In consequence of this lowered availability of prey for zooplankton consumption, plus a greater contribution of nongrazing phytoplankton losses to an increased level of detritus (Fig. 6D), the consumption dynamics of detritus also change (Fig. 6H vs. Fig. 4H). In more complex models, with explicit description of micro- and mesozooplankton, one may expect

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Fig. 5. Changes in phytoplankton N:C (A and C), Cr_{phyto} and AE_N for phytoplankton (B and D). Panels (A) and (B) are for simulations shown in Fig. 4; panels (C) and (D) are for simulations shown in Fig. 6. In panel (B), Cr_{phyto} for original and test 2 are identical, and AE_N for original and default are identical. See Table 2 for definition of configurations. Cr_{phyto} has units of $[\text{mol N} (\text{mol N})^{-1} \text{d}^{-1}] [\text{m mol N m}^{-3}]^{-1}$; AE_N is dimensionless.

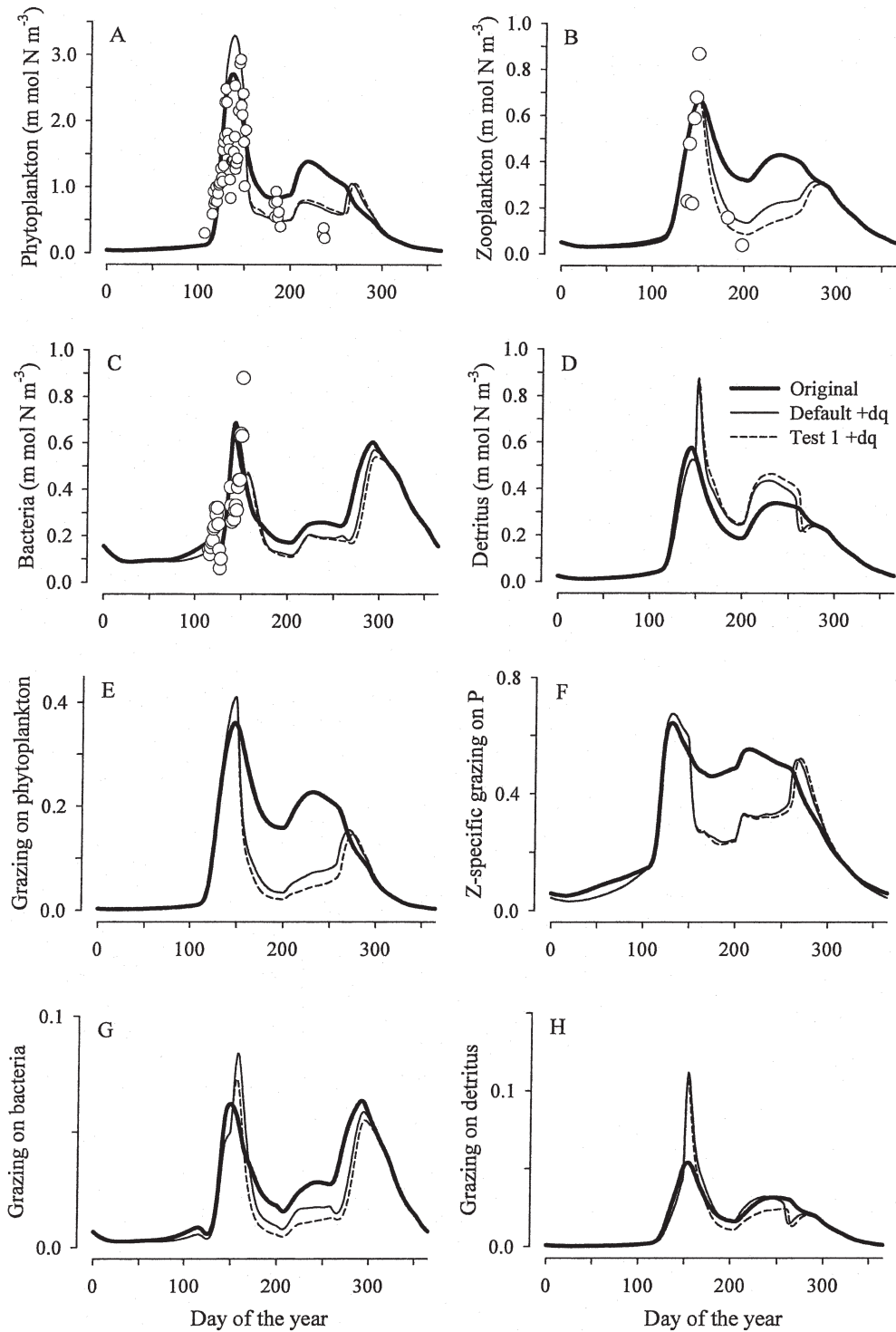


Fig. 6. Effects on model output of changing the description of zooplankton grazing behavior on phytoplankton and phytoplankton nongrazing losses. For definition of configurations, see Table 2; see also Fig. 5. The original configuration (thick line) is the same as in Fig. 3 for IS model. Circles denote data.

a changed role for the microbial loop driven by the transfer of primary production through nongrazing losses.

The absence of a large nutrient-limited phytoplankton biomass in the summer results in the lessening of nutrient

stress on those remaining phytoplankton consuming regenerated ammonium. Thus, the depression in phytoplankton N:C is not as great or so prolonged as in the simulations without quality-linked nongrazing losses

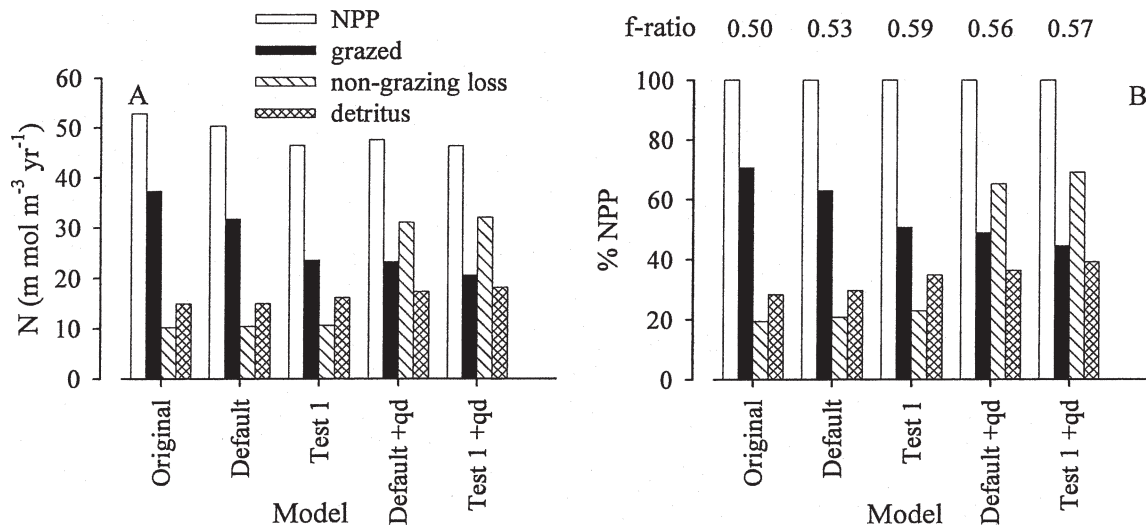


Fig. 7. Fate of primary production. Net N-specific primary production (NPP); NPP channeled to grazing (Pg); NPP which is lost through nongrazing activities (Pd); annual loss of detritus from the system (D). Panel (A) shows absolute fluxes; panel (B) shows the results as a percentage of NPP, together with the annual *f*-ratio [nitrate assimilation/(ammonium assimilated + nitrate assimilated)]. See Table 2 for definition of configurations. See also Figs. 4, 5, and 6.

(Fig. 5C vs. Fig. 5A). Accordingly, the change in zooplankton behavior as indicated by changes in Cr_{phyto} and AE_N (Fig. 5D vs. Fig. 5B) is not as pronounced.

Fate of primary production—In comparison with the original configuration, the default and test 1 configurations have less primary production consumed by zooplankton (Fig. 7; test 2 is similar to default). This is because in these configurations the large summer bloom of poor-quality phytoplankton (Figs. 4A, 5A) blocks the activity of zooplankton (Figs. 4B,E, 5B; Irigoien et al. 2005). Because nutrient regeneration is lowered, there is a subsequent decreased annual primary production with these configurations in comparison to the original (Fig. 7A). With the inclusion of enhanced phytoplankton nongrazing loss linked to poor nutrient status (Eq. 7), giving default +qd and test 1 +qd in Figs. 6 and 7, the shunting of primary production through the detrital route is enhanced (Fig. 7). Given that this description is in terms of N and that the N:C of the phytoplankton is halved during this event, changes in the loss of algal carbon are greater than would appear from the plots. However, the model takes no account of differences in sinking rates of detritus from different sources; this would affect the overall dynamics (Tseitlin 1999). These alternative configurations also display different *f*-ratio values (Fig. 7B). The original configuration has the lowest *f*-ratio (lowest proportion of primary production supported by nitrate assimilation), associated with the greater role of zooplankton grazing in controlling phytoplankton growth and hence in regenerating ammonium. The structure of the model thus has important implications for the description of primary production in general terms.

The detrimental effect of phytoplankton of poor nutritional quality on the predator-prey interaction can be a sensitive regime-switching mechanism (Mitra and Flynn 2006a). The effect can be much greater than that suggested

by changes in N:C (Mitra 2006), in part because of the synergistic effects of nutrient stress on secondary metabolite (toxin) synthesis (John and Flynn 2002; Cembella 2003). However, it is apparent that changes in nongrazing phytoplankton losses associated with deterioration in nutritional status may be just as powerful as changes in zooplankton behavior in altering trophic dynamics.

In this work we identify a series of biologically erroneous assumptions within the description of the traditional NPZ-type models. There is no biological justification for the original description of zooplankton grazing term in NPZ-type models, with its implicit display of enhanced ingestion of poor-quality prey (+ve SMP_{Ing}) coupled with constant assimilation efficiency (0 SMP_{AE}), as portrayed in Fig. 1B. Further, we demonstrate that it is important to describe not only the grazing losses but also the nongrazing losses of phytoplankton that occur concurrent with changes in phytoplankton nutritional status. Model configurations with 0 SMP_{Ing} (Fig. 1A) or +ve SMP_{Ing} coupled with -ve SMP_{AE} have descriptions of zooplankton behavior in closer accordance with evidence from biology. Indeed, -ve SMP_{Ing} may be more likely for microzooplankton (Mitra 2006). Further, enhanced phytoplankton loss with poor nutrient status (incorporated using Eq. 7) is also on much firmer grounds (Smayda 1970). This is especially so since there is no physiological argument for the simple density link to phytoplankton death (see also Kiørboe et al. 1996), as used in the traditional NPZ-type models.

That the output of traditional NPZ-type models gives a fit that is in reasonable accord with the data is an example where two wrongs (grazing and nongrazing descriptions) appear to make a right. There is a real risk that errors within model structure can be countered by misrepresentations elsewhere in the system. This is especially likely for parts of the system that are poorly constrained by data. Zooplankton are often poorly described, and sometimes data are not available at all (e.g., the Kerfix station; Jeandel et al. 1998),

while phytoplankton loss processes (especially associated with sedimentation, lysis, and dissolved organic matter release) are also poorly parameterized. Other models, of greater complexity than NPZ models, also do not account for changes in zooplankton growth dynamics with food quality, although they may relate non-grazing phytoplankton loss to their nutritional status (e.g., European Regional Seas Ecosystem Model (ERSEM); Blackford et al. 2004). Grazing dynamics, the loss of material at phytoplankton death, and the route it follows will also depend on the type of algae (e.g., diatoms vs. *Phaeocystis*). Martin et al. (2006), from an analysis of field data, also conclude that models of oceanic carbon flux need to be reexamined and that sedimentation rates may be underestimated.

As models develop in complexity, with the use of multiple plankton functional group models (Anderson 2005), it is all the more important that critical biological processes are simulated correctly or at the least that they are not simulated incorrectly. This requires not only that modelers pay adequate attention to the description of those processes but also that biologists design experiments that can properly test model predictions (Flynn 2005a).

References

- ANDERSON, T. R. 2005. Plankton functional type modelling: Running before we can walk? *J. Plankton Res.* **27**: 1073–1081.
- , D. O. HESSEN, J. J. ELSER, AND J. URABE. 2005. Metabolic stoichiometry and the fate of excess carbon and nutrients in consumers. *Am. Nat.* **165**: 1–15.
- BESIKTEPE, S., AND H. G. DAM. 2002. Coupling of ingestion and defecation as a function of diet in the calanoid copepod *Acartia tonsa*. *Mar. Ecol. Prog. Ser.* **229**: 151–164.
- BLACKFORD, J. C., J. I. ALLEN, AND F. J. GILBERT. 2004. Ecosystem dynamics at six contrasting sites: A generic modeling study. *J. Mar. Syst.* **52**: 191–215.
- BRUSSAARD, C. P. D. 2004. Viral control of phytoplankton populations—a review. *J. Eukaryot. Microbiol.* **51**: 125–138.
- CEBALLOS, S., AND A. IANORA. 2003. Different diatoms induce contrasting effects on the reproductive success of the copepod *Temora stylifera*. *J. Exp. Mar. Biol. Ecol.* **294**: 189–202.
- CEMBELLA, A. D. 2003. Chemical ecology of eukaryotic microalgae in marine ecosystems. *Phycologia* **42**: 420–447.
- DARCHAMBEAU, F. 2005. Filtration and digestion responses of an elementally homeostatic consumer to changes in food quality: A predictive model. *Oikos* **111**: 322–336.
- DAVIDSON, K., K. J. FLYNN, AND A. CUNNINGHAM. 1992. Non-steady state ammonium-limited growth of the marine phytoflagellate, *Isochrysis galbana* Parke. *New Phytol.* **122**: 433–438.
- EVANS, G. T., AND V. C. GARÇON. 1997. One-dimensional models of water column biogeochemistry. p. JGOFS report 23/97. JGOFS Bergen, Norway.
- FASHAM, M. J. R. 1993. Modelling the marine biota, p. 457–504. *In* M. Heimann [ed.], *The global cycle*. Springer-Verlag, gNATO ASI Series Vol I 15.
- , H. W. DUCKLOW, AND S. M. MCKELVIE. 1990. A nitrogen-based model of plankton dynamics in the oceanic mixed layer. *J. Mar. Res.* **48**: 591–639.
- , AND G. T. EVANS. 2000. Advances in ecosystem modelling within JGOFS, p. 417–446. *In* R. G. Hanson, H. W. Ducklow and J. G. Field [eds.], *The changing ocean carbon cycle: A midterm synthesis of the Joint Global Flux Study*. Cambridge University Press.
- , K. J. FLYNN, P. PONDIVEN, T. R. ANDERSON, AND P. W. BOYD. 2006. Development of a robust ecosystem model to predict the role of iron on biogeochemical cycles: A comparison of results for iron-replete and iron-limited areas, and the SOIREE iron-enrichment experiment. *Deep-Sea Res. I* **53**: 333–366.
- FLYNN, K. J. 2003. Modelling multi-nutrient interactions in phytoplankton: Balancing simplicity and realism. *Prog. Oceanogr.* **56**: 249–279.
- . 2005a. Castles built on sand: Dysfunctionality in plankton models and the inadequacy of dialogue between biologists and modellers. *J. Plankton Res.* **12**: 1205–1210.
- . 2005b. Modelling marine phytoplankton growth under eutrophic conditions. *J. Sea Res.* **54**: 92–103.
- , AND K. DAVIDSON. 1993. Predator-prey interactions between *Isochrysis galbana* and *Oxyrrhis marina*. II. Release of non-protein amines and faeces during predation of *Isochrysis*. *J. Plankton Res.* **15**: 893–905.
- , ———, AND J. W. LEFTLEY. 1993. Carbon-nitrogen relations during the batch growth of *Nannochloropsis oculata* (Eustigmatophyceae) under alternating light and dark. *J. Appl. Phycol.* **5**: 465–475.
- FRANKS, P. J. S. 2002. NPZ models of plankton dynamics: Their construction, coupling to physics and application. *J. Oceanogr.* **58**: 379–387.
- GENTLEMAN, W., A. LEISING, B. FROST, S. STROM, AND J. MURRAY. 2003. Functional responses for zooplankton feeding on multiple resources: A review of assumptions and biological dynamics. *Deep Sea Res. II* **50**: 2847–2875.
- HESSEN, D. O., AND T. ANDERSEN. 1992. The algae-grazer interface: Feedback mechanisms linked to elemental ratios and nutrient cycling. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* **35**: 111–120.
- IRIGOIEN, X., K. J. FLYNN, AND R. P. HARRIS. 2005. Phytoplankton blooms: A “loophole” in microzooplankton grazing impact? *J. Plankton Res.* **27**: 313–321.
- JEANDEL, C., AND OTHERS. 1998. KERFIX, a timeseries station in the Southern Ocean: A presentation. *J. Mar. Syst.* **17**: 555–569.
- JOHN, E. H., AND K. J. FLYNN. 2002. Modelling changes in paralytic shellfish toxin content of dinoflagellates in response to nitrogen and phosphorus supply. *Mar. Ecol. Prog. Ser.* **225**: 147–160.
- JÓNASDÓTTIR, S. H. 1994. Effects of food quality on the reproductive success of *Acartia tonsa* and *Acartia hudsonica*—laboratory observations. *Mar. Biol.* **121**: 67–81.
- JONES, R. H., AND K. J. FLYNN. 2005. Nutritional status and diet composition affect the value of diatoms as copepod prey. *Science* **307**: 1457–1459.
- , ———, AND T. R. ANDERSON. 2002. The effect of food quality on carbon and nitrogen growth efficiency in *Acartia tonsa*. *Mar. Ecol. Prog. Ser.* **235**: 147–156.
- KIØRBOE, T., AND OTHERS. 1996. Sedimentation of phytoplankton during a diatom bloom: Rates and mechanisms. *J. Mar. Res.* **54**: 1123–1148.
- KOSKI, M., W. KLEIN BRETELER, N. SCHOGT, S. GONZALEZ, AND H. H. JAKOBSEN. 2006. Life-stage specific differences in exploitation of food mixtures: diet mixing enhances copepod egg production but not juvenile development. *J. Plankton Res.* **28**: 919–936.
- LOCHE, K., H. W. DUCKLOW, M. J. R. FASHAM, AND C. STIENEN. 1993. Plankton succession and carbon cycling at 47°N 20°W during the JGOFS North Atlantic Bloom Experiment. *Deep Sea Res. II* **40**: 91–114.
- MARTIN, E. S., X. IRIGOIEN, R. P. HARRIS, A. LÓPEZ-URRUTIA, M. V. ZUBKOV, AND J. L. HEYWOOD. 2006. Variation in the transfer of energy in marine plankton along a productivity

- gradient in the Atlantic Ocean. *Limnol. Oceanogr.* **51**: 2084–2091.
- MITRA, A. 2006. A multi-nutrient model for the description of stoichiometric modulation of predation in micro- and mesozooplankton. *J. Plankton Res.* **28**: 597–611.
- , AND K. J. FLYNN. 2005. Predator-prey interactions: Is “ecological stoichiometry” sufficient when good food goes bad? *J. Plankton Res.* **27**: 393–399.
- , AND ———. 2006a. Promotion of harmful algal blooms by zooplankton predatory activity. *Biol. Lett.* **2**: 194–197.
- , AND ———. 2006b. Accounting for variation in prey selectivity by zooplankton. *Ecol. Model.* **199**: 82–92.
- MØLLER, E. F. 2005. Sloppy feeding in marine copepods: Prey-size-dependent production of dissolved organic carbon. *J. Plankton Res.* **27**: 341–356.
- POSTEL, L., H. FOCK, AND W. HAGEN. 2000. Biomass and abundance, p. 83–192. *In* R. Harris, P. Wiebe, J. Lenz, H. R. Skjoldal and M. Huntley [eds.], ICES zooplankton methodology manual. Elsevier Academic Press.
- SMAYDA, T. J. 1970. The suspension and sinking of phytoplankton in the sea. *Oceanogr. Mar. Biol. Annu. Rev.* **8**: 353–414.
- STEELE, J. H. 1976. The role of predation in ecosystem models. *Mar. Biol.* **35**: 9–11.
- , AND E. W. HENDERSON. 1992. The role of predation in plankton models. *J. Plankton Res.* **14**: 157–172.
- STERNER, R. W., AND J. J. ELSER. 2002. *Ecological stoichiometry: The biology of elements from molecules to the biosphere.* Princeton University Press.
- STROM, S. L., AND H. LOUKOS. 1998. Selective feeding by protozoa: Model and experimental behaviors and their consequences for population stability. *J. Plankton Res.* **20**: 831–846.
- TANG, K. W., AND H. G. DAM. 1999. Limitation of zooplankton production: Beyond stoichiometry. *Oikos* **84**: 537–542.
- TIRELLI, V., AND P. MAYZAUD. 2005. Relationship between functional response and gut transit time in the calanoid copepod *Acartia clausi*: Role of food quantity and quality. *J. Plankton Res.* **27**: 557–568.
- TSEITLIN, V. B. 1999. The influence of faecal pellets sinking rate and the distribution of planktonic animals on organic carbon flux from the upper layer of the ocean. *Okeanologiya* **39**: 248–252.

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