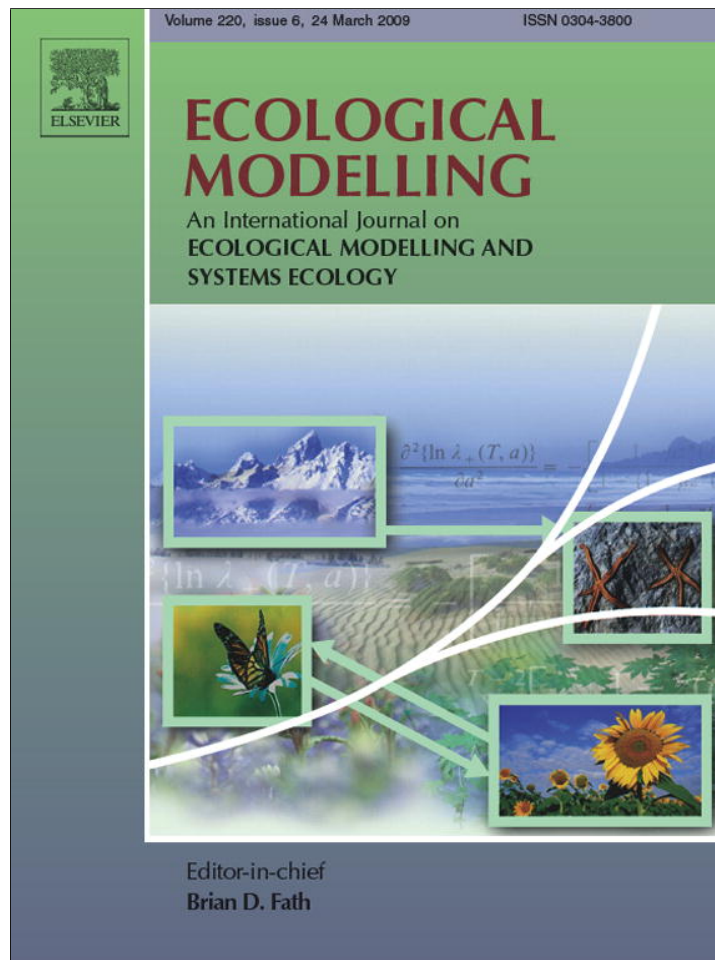


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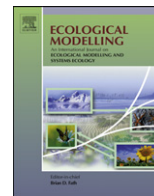
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The effects of seston food quality on planktonic food web patterns

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ABSTRACT

In planktonic food webs, the conversion rate of plant material to herbivore biomass is determined by a variety of factors such as seston biochemical/elemental composition, phytoplankton cell morphology, and colony architecture. Despite the overwhelming heterogeneity characterizing the plant–animal interface, plankton population models usually misrepresent the food quality constraints imposed on zooplankton growth. In this study, we reformulate the zooplankton grazing term to include seston food quality effects on zooplankton assimilation efficiency and examine its ramifications on system stability. Using different phytoplankton parameterizations with regards to growth strategies, light requirements, sinking rates, and food quality, we examined the dynamics induced in planktonic systems under varying zooplankton mortality/fish predation, light conditions, nutrient availability, and detritus food quality levels. In general, our analysis suggests that high food quality tends to stabilize the planktonic systems, whereas unforced oscillations (limit cycles) emerge with lower seston food quality. For a given phytoplankton specification and resource availability, the amplitude of the plankton oscillations is primarily modulated from zooplankton mortality and secondarily from the nutritional quality of the alternative food source (i.e., detritus). When the phytoplankton community is parameterized as a cyanobacterium-like species, conditions of high nutrient availability combined with high zooplankton mortality led to phytoplankton biomass accumulation, whereas a diatom-like parameterization resulted in relatively low phytoplankton to zooplankton biomass ratios highlighting the notion that high phytoplankton food quality allows the zooplankton community to sustain relatively high biomass and to suppress phytoplankton biomass to low levels. During nutrient and light enrichment conditions, both phytoplankton and detritus food quality determine the extent of the limit cycle region, whereas high algal food quality increases system resilience by shifting the oscillatory region towards lower light attenuation levels. Detritus food quality seems to regulate the amplitude of the dynamic oscillations following enrichment, when algal food quality is low. These results highlight the profitability of the alternative food sources for the grazer as an important predictor for the dynamic behavior of primary producer–grazer interactions in nature.

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1. Introduction

The elucidation of the energy flow and element cycling patterns at the primary producer–grazer interface has received considerable attention in aquatic ecology (Sterner and Hessen, 1994; Gulati and Demott, 1997; DeMott et al., 2001; Brett et al., 2006; Zhao et al., 2008a). Despite the large number of studies conducted, the mechanisms underlying the strength of the trophic coupling in planktonic food webs remain controversial and arguably only partially understood. Generally, the control of zooplankton abundance and the conversion rate of plant material to herbivore biomass are determined by food quantity as well as food quality such as seston biochemical/elemental composition, phytoplankton cell morphology, and colony architecture (Brett and Müller-Navarra, 1997). In

this context, one of the most debatable issues is the relative role of the deficiencies in essential elements (e.g., nitrogen and phosphorus) and biochemical compounds [e.g., essential fatty acids (EFAs)] on zooplankton growth and reproduction. There are studies suggesting that the algal taxonomic differences in food quality due to differences in their fatty acid (FA), protein, amino acid content, and digestion resistance determine the trophic transfer efficiency in aquatic pelagic food webs, e.g., FA limitation hypothesis (Müller-Navarra et al., 2004). Others pinpoint the critical role of the discrepancy between the prey and predator elemental somatic ratios underscoring the importance of phosphorus-insufficient algal diets on food web structure and pelagic ecosystem functioning, e.g., mineral phosphorus limitation hypothesis (Sterner and Schulz, 1998; Elser and Urabe, 1999).

The phosphorus limitation hypothesis mainly stems from the imbalance between the nearly constant carbon (C) to phosphorus (P) ratios in herbivorous zooplankton and the highly variable C:P ratios of the grazed seston (Elser and Urabe, 1999; DeMott

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et al., 1998; DeMott and Pape, 2005). One of the predictions of the stoichiometric theory involves the relationship between the consumer's P content to maximal growth through RNA and protein synthesis (Acharya et al., 2004). Grazers with high P somatic content are predicted to have high RNA concentrations and high maximal growth rates when feeding on P-rich diets and the rationale for this causal link is that the fast growth requires a high cellular concentration of ribosomal RNA to meet the protein synthesis demands (Elser et al., 1996). Vrede et al. (2002) demonstrated that the RNA:DNA ratio in *Daphnia galeata* was positively correlated with the somatic growth rate and increased as the seston C:P molar ratio was decreasing below a critical value of approximately 200. The stoichiometric theory also predicts a trade-off between maximal growth rate and sensitivity to P-limiting conditions, i.e., consumers with high P requirements/maximal growth rates should be strongly limited when seston is P deficient (DeMott and Pape, 2005). Empirical evidence suggests that for P-rich zooplankton such as *Daphnia*, the phosphorus limitation threshold occurs when seston C:P is greater than 150–375 with a most possible value of 300 (Brett et al., 2000). Furthermore, several recent studies highlight the effects of indirect P limitation on zooplankton growth and reproduction, e.g., P-limited algae can undergo structural and morphological changes (thicker cell walls) that reduce their digestibility (Van Donk and Hessen, 1993; Ravet and Brett, 2006).

FAs are nutritionally critical molecules that determine the trophic transfer efficiency, the secondary production, and the functional integrity of aquatic food webs (Brett and Müller-Navarra, 1997). In animals, the physiologically EFAs are the $\omega 3$ FAs eicosapentaenoic acid (EPA, 20:5 $\omega 3$) and docosahexaenoic acid (DHA, 22:6 $\omega 3$) and the $\omega 6$ FA arachidonic acid (ARA, 20:4 $\omega 6$) (Brett et al., 2006). There is a great deal of literature emphasizing the important role of these FAs on the zooplankton growth, fecundity, lipid composition, osmotic stress tolerance, molting, and survival (Brett and Müller-Navarra, 1997; DeMott et al., 2001). For example, empirical models developed across a wide range of lake trophic states show that zooplankton growth and egg production are strongly related to the seston 20:5 $\omega 3$ concentrations (Müller-Navarra, 1995; Müller-Navarra et al., 2000; Persson et al., 2007). Recently, Danielsdottir et al. (2007) presented modeling results suggesting planktonic food webs with high phytoplankton food quality at their base can attain inverted biomass distributions with primary producers being suppressed by intense herbivory, rapidly growing zooplankton able to withstand moderately intense predation from planktivorous fish, and an efficient energy transfer from primary producers to upper trophic levels. The FA composition of phytoplankton varies considerably amongst taxa, with cryptophytes and diatoms having high food quality, green algae intermediate quality, and cyanobacteria poor food quality (Brett and Müller-Navarra, 1997; Demott and Müller-Navarra, 1997; Brett et al., 2000).

As the empirical evidence for the regulatory role of three distinct and not mutually exclusive factors (P limitation, FA limitation, and food quantity) on the strength of the primary producer–grazer coupling has grown, several models have been developed to advance our theoretical understanding of where and when their individual and/or synergistic effects become important (Mulder and Bowden, 2007). Considerable insights into the potential implications of the ecological stoichiometry have been gained by a series of homeostatic consumer models that explicitly account for the effects of P-deficient food on zooplankton growth rate as well as on consumer-driven P recycling (e.g., Andersen, 1997; Andersen et al., 2004). For example, Sterner (1997) modeled the effects of food quantity (C) and quality (P) on the growth of homeostatic heterotrophic consumers, indicating that consumer growth differs between high and low P food concentrations only when food quantity is above a critical level. Hence, two diets might give identical consumer growth rates at low food quantity but can also give dif-

ferent consumer growth at high food quantity. A recent modeling study, however, showed that the metabolic cost for maintaining zooplankton homeostasis can be significant, such that food quality is important even when the food quantity is low (Anderson, 2005). Quite intriguing results were also presented by Loladze et al. (2000), who modified the Rosenzweig–MacArthur variation of the Lotka–Volterra equations and demonstrated that the chemical heterogeneity in the first two trophic levels can transform the prey and the predator into competitors for phosphorus. On the other hand, there is a surprising gap in the literature of predictive frameworks for the FA limitation, i.e., modeling studies that explicitly consider the constraints on zooplankton growth pertinent to the biochemical heterogeneity of the lake seston (Gulati and Demott, 1997; Arhonditsis and Brett, 2005a,b; Zhao et al., 2008b).

In this study, we use a five-compartment plankton population model to examine the role of bottom-up vis-à-vis top-down control mechanisms on planktonic food webs by explicitly considering recent advances in stoichiometric theory and seston biochemical food quality effects on zooplankton assimilation efficiency. Using different phytoplankton characterizations with regards to growth strategies, light requirements, sinking rates, and food quality, we test the stability of planktonic systems under varying zooplankton mortality/fish predation, light conditions, nutrient availability, and detritus food quality levels. We also attempt to elucidate the patterns of energy flow in the plant–animal interface induced from quantitative and qualitative changes of allochthonous particulate matter loading. Our analysis concludes by underscoring the need of representing the primary producer–herbivore interactions in stoichiometrically/biochemically realistic terms, thereby gaining insights into the factors that affect biomass distribution and the strength of trophic coupling in planktonic food webs.

2. Methods

2.1. Model description

The model simulates a seasonally unforced, spatially homogeneous pelagic system that exchanges mass with the hypolimnion.

Table 1
The specific functional forms of the plankton model.

$$\begin{aligned} \frac{dPO_4}{dt} &= -\frac{PO_4}{e+PO_4} \frac{a}{b+cPHYT} PHYT P/C_{phyt} + \gamma d \frac{ZOO P^3}{pred^2+ZOO P^2} P/C_{ZOO P} + \phi DET_P \\ &+ k(PO_{4(hypo)} - PO_4) \\ \frac{dPHYT}{dt} &= \frac{PO_4}{e+PO_4} \frac{a}{b+cPHYT} PHYT - rPHYT - \frac{\lambda PHYT^2}{\mu^2+PHYT^2+\omega DET_C^2} ZOO P - (s+k) PHYT \\ \frac{dZOO P}{dt} &= \frac{\alpha_C \lambda (PHYT^2+\omega DET_C^2)}{\mu^2+PHYT^2+\omega DET_C^2} ZOO P - d \frac{ZOO P^3}{pred^2+ZOO P^2} \\ \alpha_C &= \frac{C/P_{ZOO P} \alpha_P (PHYT^2 P/C_{phyt} + \omega DET_C DET_P)}{PHYT^2 + \omega DET_C^2} \\ \alpha_P &= \frac{\alpha_{P1} FQ}{\alpha_{P2} + FQ} \\ FQ &= \left(FQ_1^2 \sqrt{PHYT} + FQ_2^2 \sqrt{DET_C} \right) ZOO P_{C/PLIM} \\ ZOO P_{C/PLIM} &= \begin{cases} 1 & \text{if } Graz_{C/P} \leq C : P_0 \\ \frac{C : P_0}{Graz_{C/P}} & \text{if } Graz_{C/P} > C : P_0 \end{cases} \\ Graz_{C/P} &= \frac{(PHYT^2 + \omega DET_C^2)}{(PHYT^2 P/C_{phyt} + \omega DET_C DET_P)} \\ \frac{dDET_C}{dt} &= rPHYT + \frac{[PHYT^2 - C/P_{ZOO P} \alpha_P (PHYT^2 P/C_{phyt} + \omega DET_C DET_P)] \lambda}{\mu^2 + PHYT^2 + \omega DET_C^2} ZOO P \\ &- (k + \phi + \psi) DET_C + DET_{C(EXOG)} * \\ \frac{dDET_P}{dt} &= rPHYT P/C_{phyt} + \frac{[(1-\alpha_P) PHYT^2 P/C_{phyt} - \alpha_P \omega DET_C DET_P] \lambda}{\mu^2 + PHYT^2 + \omega DET_C^2} ZOO P - (k + \phi + \psi) \\ &DET_P + DET_{P(EXOG)} * \end{aligned}$$

*The constant terms $DET_{C(EXOG)}$ and $DET_{P(EXOG)}$ were introduced to examine plankton response to varying exogenous P:C ratios (see Fig. 9).

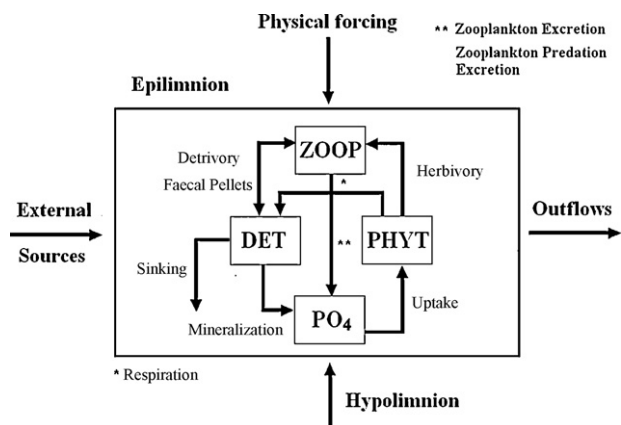


Fig. 1. The phosphate–detritus–phytoplankton–zooplankton model.

The model consists of five ordinary differential equations representing the flow of energy and elemental cycling among the model compartments: phosphate (PO₄), phytoplankton (PHYT), zooplankton (ZOOP), detritus carbon (DET_C), and detritus phosphorus (DET_P) (Table 1 and Fig. 1). Here, we briefly describe the model structure along with the modifications introduced to explicitly represent the producer–grazer interactions in stoichiometrical/biochemical terms, while the definitions of the model parameters are provided in Table 2.

Phytoplankton: The equation for phytoplankton biomass considers phytoplankton production and losses due to basal metabolism, settling, and herbivorous zooplankton grazing. Phosphorus limitation on phytoplankton growth follows Michaelis–Menten kinetics, while light extinction in the water column stems from background light attenuation and self-shading effects. Phytoplankton sinks out of the mixed layer at a constant rate. The basal metabolism includes all internal processes that decrease algal biomass (respiration and excretion) as well as natural mortality.

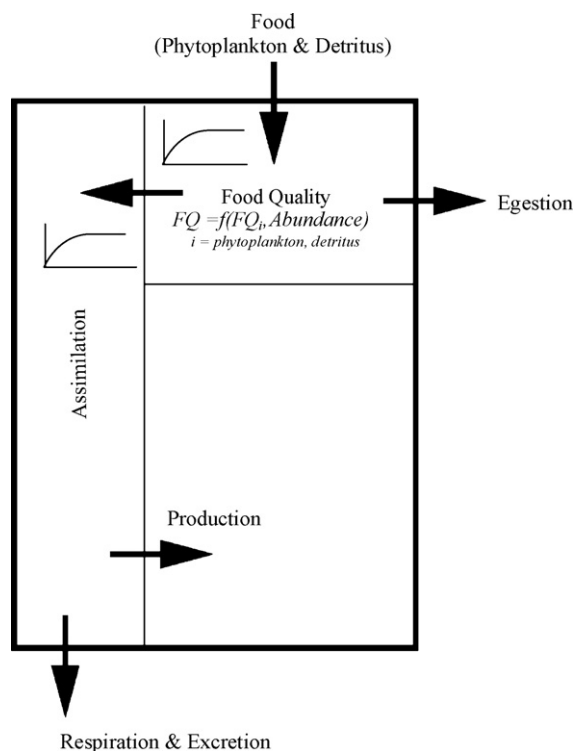


Fig. 2. Schematic representation of the homeostatic consumer in the plankton model. The available food is in the form of phytoplankton and detritus. The grazed seston is either assimilated or egested as determined by the food quality. Assimilated food is used for maintenance/production, and then exported via respiration and excretion. The latter processes along with zooplankton mortality are implicitly accounted for by the closure term.

Table 2
Parameter definitions of the plankton model.

| Variable | Symbol | Initial | Units |
|--|-----------------------|---------|---------------------------------------|
| Phosphorus | PO ₄ | 0.5 | g P m ⁻³ |
| Phytoplankton biomass | PHYT | 0.1 | g C m ⁻³ |
| Zooplankton biomass | ZOOP | 0.05 | g C m ⁻³ |
| Detritus Carbon | DET _C | 0.08 | g C m ⁻³ |
| Detritus Phosphorus | DET _P | 0.01 | g P m ⁻³ |
| Parameter | Symbol | Default | Units |
| Maximum phytoplankton (PHYT) growth rate | <i>a</i> | * | m ⁻¹ day ⁻¹ |
| Light attenuation by water | <i>b</i> | * | m ⁻¹ |
| Phytoplankton self-shading coefficient | <i>c</i> | * | m ² (g C) ⁻¹ |
| Higher predation on zooplankton (ZOOP) | <i>d</i> | * | day ⁻¹ |
| Half-saturation constant for predation | <i>pred</i> | 0.03 | g C m ⁻³ |
| Half-saturation constant for PO ₄ uptake | <i>e</i> | * | g P m ⁻³ |
| Cross-thermocline exchange rate | <i>k</i> | 0.05 | day ⁻¹ |
| Phytoplankton respiration rate | <i>r</i> | * | day ⁻¹ |
| Phytoplankton sinking loss rate | <i>s</i> | * | day ⁻¹ |
| Phosphorus to carbon ratio for phytoplankton | P/C _{phyt} | 0.015 | g P (g C) ⁻¹ |
| Phosphorus to carbon ratio for zooplankton | P/C _{zoop} | 0.029 | g P (g C) ⁻¹ |
| Zooplankton growth efficiency for phosphorus | α _{P1} | 0.9 | unitless |
| Half saturation constant for zooplankton growth efficiency | α _{P2} | 0.03 | (g C m ⁻³) ^{1/2} |
| Food quality of phytoplankton | FQ ₁ | * | unitless |
| Food quality of detritus | FQ ₂ | * | unitless |
| Critical threshold for mineral P limitation | C:P ₀ | 35 | g C (g P) ⁻¹ |
| Regeneration of zooplankton predation excretion | γ | 0.6 | unitless |
| Maximum zooplankton grazing rate | λ | 0.6 | day ⁻¹ |
| Zooplankton grazing half-saturation coefficient | μ | 0.035 | g C m ⁻³ |
| Relative zooplankton preference for detritus compared to phytoplankton | ω | 1 | unitless |
| Hypolimnetic phosphate input | PO _{4(hypo)} | * | g P m ⁻³ |
| Detritus (DET) remineralization rate | φ | 0.17 | day ⁻¹ |
| Detritus sinking rate | ψ | 0.3 | day ⁻¹ |

*See Appendix for the specific values used in our numerical experiments.

Table 3
Equilibrium values and oscillatory ranges of the diatom-like species (r-strategist, high sinking rate, high light requirement, and high food quality) under varying light conditions, nutrient availability, zooplankton mortality, and three detritus food quality levels.

| Light <i>b</i> | Hypolimnetic phosphate PO _{4(hypo)} | Zooplankton mortality <i>d</i> | Detritus food quality FQ ₂ | Phytoplankton PHYT | Zooplankton ZOOPT | Carbon assimilation α_C | Phosphorous assimilation α_P | Oscillatory range |
|-------------------|---|-----------------------------------|--|-----------------------|----------------------|-----------------------------------|--|-------------------|
| High | High | High | 0.2 | 1.070 | 0.049 | 0.427 | 0.830 | – |
| | | | 0.5 | 1.068 | 0.051 | 0.432 | 0.841 | |
| | | | 0.7 | 1.066 | 0.052 | 0.436 | 0.850 | |
| High | High | Low | 0.2 | 0.124 | 1.076 | 0.136 | 0.590 | – |
| | | | 0.5 | 0.115 | 1.065 | 0.136 | 0.634 | |
| | | | 0.7 | 0.110 | 1.055 | 0.137 | 0.670 | |
| High | Low | High | 0.2 | 0.392 | 0.044 | 0.402 | 0.790 | – |
| | | | 0.5 | 0.391 | 0.046 | 0.410 | 0.806 | |
| | | | 0.7 | 0.390 | 0.047 | 0.416 | 0.820 | |
| High | Low | Low | 0.2 | 0.072 | 0.561 | 0.142 | 0.555 | – |
| | | | 0.5 | 0.067 | 0.555 | 0.143 | 0.599 | |
| | | | 0.7 | 0.063 | 0.549 | 0.144 | 0.637 | |
| Low | High | High | 0.2 | 0.697 | 0.047 | 0.417 | 0.815 | – |
| | | | 0.5 | 0.694 | 0.049 | 0.424 | 0.828 | |
| | | | 0.7 | 0.691 | 0.050 | 0.429 | 0.838 | |
| Low | High | Low | 0.2 | 0.027 | 0.092 | 0.222 | 0.546 | – |
| | | | 0.5 | 0.026 | 0.091 | 0.236 | 0.592 | |
| | | | 0.7 | 0.025 | 0.091 | 0.249 | 0.630 | |
| Low | Low | High | 0.2 | 0.255 | 0.041 | 0.387 | 0.767 | – |
| | | | 0.5 | 0.251 | 0.043 | 0.396 | 0.786 | |
| | | | 0.7 | 0.249 | 0.044 | 0.403 | 0.802 | |
| Low | Low | Low | 0.2 | 0.024 | 0.061 | 0.244 | 0.550 | – |
| | | | 0.5 | 0.023 | 0.062 | 0.261 | 0.594 | |
| | | | 0.7 | 0.022 | 0.062 | 0.275 | 0.632 | |

Phosphate: The phosphate equation considers the phytoplankton uptake, the proportion of the zooplankton mortality/higher predation that is recycled in the system as dissolved P. Epilimnetic phosphate levels are also fuelled by the bacteria-mediated mineralization of detritus, and are subject to diffusive mixing with the hypolimnion.

Zooplankton: Zooplankton grazing and losses due to natural mortality/consumption by higher predators are the main two terms in the zooplankton biomass equation. Zooplankton has two alternative food sources (phytoplankton and detritus) of equal palatability ($\omega = 1$). A fraction of zooplankton grazing is assimilated and fuels growth, while both herbivory and detritivory were formulated using

Table 4
Equilibrium values and oscillatory ranges of the cyanobacterium-like species (K-strategist, low sinking rate, low light requirement, and low food quality) under varying light conditions, nutrient availability, zooplankton mortality, and three detritus food quality levels.

| Light <i>b</i> | Hypolimnetic phosphate PO _{4(hypo)} | Zooplankton mortality <i>d</i> | Detritus food quality FQ ₂ | Phytoplankton PHYT | Zooplankton ZOOPT | Carbon assimilation α_C | Phosphorous assimilation α_P | Oscillatory range |
|-------------------|---|-----------------------------------|--|-----------------------|----------------------|-----------------------------------|--|-------------------|
| High | High | High | 0.2 | 17.56 | 0.039 | 0.370 | 0.714 | – |
| | | | 0.5 | 17.51 | 0.048 | 0.417 | 0.807 | |
| | | | 0.7 | 17.48 | 0.051 | 0.435 | 0.841 | |
| High | High | Low | 0.2 | 5.216 | 2.862 | 0.176 | 0.352 | 0–1 |
| | | | 0.5 | 3.731 | 2.995 | 0.202 | 0.420 | |
| | | | 0.7 | 2.947 | 2.832 | 0.211 | 0.449 | |
| High | Low | High | 0.2 | 1.615 | 0.026 | 0.252 | 0.488 | – |
| | | | 0.5 | 1.584 | 0.035 | 0.340 | 0.659 | |
| | | | 0.7 | 1.567 | 0.041 | 0.380 | 0.736 | |
| High | Low | Low | 0.2 | 0.895 | 0.255 | 0.144 | 0.292 | <0.72 |
| | | | 0.5 | 0.585 | 0.419 | 0.181 | 0.405 | |
| | | | 0.7 | 0.038 | 0.114 | 0.197 | 0.497 | |
| Low | High | High | 0.2 | 14.13 | 0.038 | 0.361 | 0.698 | – |
| | | | 0.5 | 14.06 | 0.047 | 0.412 | 0.797 | |
| | | | 0.7 | 14.03 | 0.051 | 0.431 | 0.834 | |
| Low | High | Low | 0.2 | 3.916 | 1.653 | 0.170 | 0.335 | <0.39 |
| | | | 0.5 | 0.030 | 0.038 | 0.173 | 0.351 | |
| | | | 0.7 | 0.025 | 0.039 | 0.220 | 0.450 | |
| Low | Low | High | 0.2 | 1.233 | 0.025 | 0.237 | 0.459 | – |
| | | | 0.5 | 1.173 | 0.034 | 0.328 | 0.634 | |
| | | | 0.7 | 1.136 | 0.039 | 0.370 | 0.717 | |
| Low | Low | Low | 0.2 | 0.031 | 0.018 | 0.075 | 0.146 | – |
| | | | 0.5 | 0.021 | 0.020 | 0.145 | 0.283 | |
| | | | 0.7 | 0.018 | 0.021 | 0.194 | 0.381 | |

Numbers in italics correspond to the averages of the limit cycles for FQ₂ = 0.2, 0.5, and 0.7.

the Holling type III function. Phosphorus assimilation efficiency is directly related to the “food quality” (FQ) concentration, a variable that encompasses the effects of both food quantity and quality on the energy flow across food webs (Arhonditsis and Brett, 2005a). Food quality is dynamically characterized on the basis of two factors: (i) the imbalance between the C:P ratio of the grazed seston and a critical C:P₀ ratio above which zooplankton growth is limited by P availability and (ii) the variability in food quality due to differences in highly unsaturated FA, amino acid, protein content, and/or digestibility. We used a hyperbolic formula to relate the P assimilation efficiency with the variable food quality concentration (Fig. 2). Homeostasis is attained by assuming a C to P assimilation efficiency ratio similar to the C:P zooplankton somatic ratio. Finally, a sigmoidal closure term was selected to represent a “switchable” type of predator behavior controlled by a threshold prey concentration (Edwards and Yool, 2000).

Detritus: The detritus pool is expressed in units of both C (DET_C) and P (DET_P). Detritus sinks out of the epilimnion at a constant rate and is transformed to phosphate by the mineralization processes. Phytoplankton respiration and a fraction of the zooplankton growth that represents the faecal pellets/egested material also contribute to the detritus stock.

2.2. Numerical experiments

We examined the response of planktonic food webs to an assortment of ambient conditions, that is, the parameters controlling light

availability, hypolimnetic nutrient inputs, and zooplankton mortality were each given a specific high or low value (see Appendix A). Our numerical experiments analyzed plankton patterns to the resulting eight (2³) permutations of ambient conditions. In the first two sets of numerical experiments, phytoplankton was characterized as a diatom- and cyanobacterium-like species, respectively. The diatom-like species is modeled as a r-strategist with high maximum growth rate and higher metabolic losses, superior phosphorus kinetics, high light requirement (approximated by a higher self-shading coefficient), and high sinking velocity. It should also be noted that the absence of a term that explicitly accounts for silica limitation on phytoplankton growth implies that the requirements of the diatom-like species are met. By contrast, the cyanobacterium-like species is modeled as K-strategist with low maximum growth and metabolic rates, weak P competitor, higher tolerance to low light availability, and low settling velocity. Simulations were run for each species under each of the eight conditions with varying detrital food quality. In the third set of numerical experiments, phytoplankton was modeled as an intermediate species (parameterized between the diatom- and cyanobacterium-like extremes). The scenario of the intermediate species was divided into three trial sets, modeled with low, moderate, and high detritus food quality. Simulations of the three trials, under each of the eight conditions, were run with varying phytoplankton food quality. The numerical study of our dynamical system is based on MATCONT, a graphical MATLAB software package that implements a prediction-

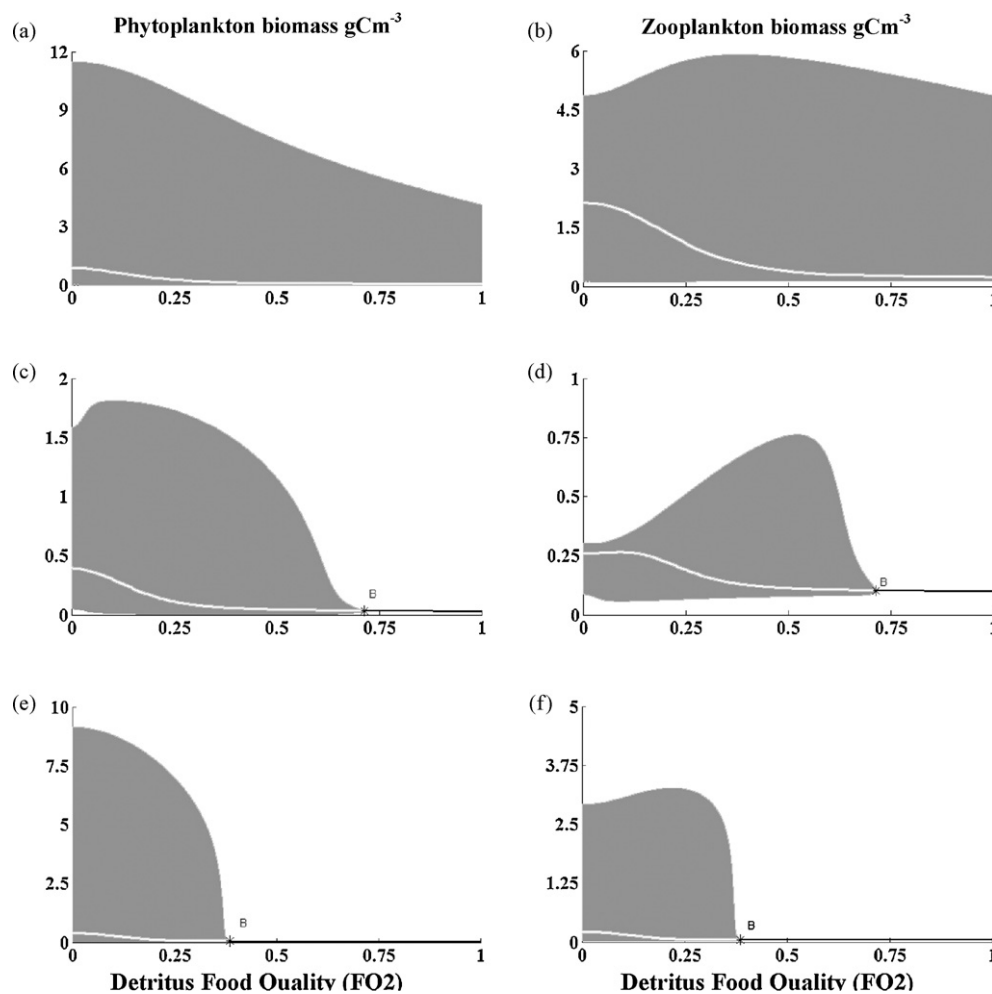


Fig. 3. Parameterization of the phytoplankton compartment as a cyanobacterium-like species: variation of the plankton levels with varying detritus food quality under conditions of: (a and b) high light availability, high hypolimnetic phosphate fluxes, and low zooplankton mortality; (c and d) high light availability, low hypolimnetic phosphate fluxes, and low zooplankton mortality; (e and f) low light availability, high hypolimnetic phosphate fluxes, and low zooplankton mortality. Stable steady states are represented by a solid black line, unsteady steady states by a solid white line, oscillatory regions are colored grey, and asterisks denote Hopf bifurcation points.

correction continuation algorithm, based on the Moore–Penrose matrix pseudo-inverse, to compute curves of equilibria, limit cycles, and fold bifurcation points of limit cycles (Dhooge et al., 2003).

3. Results

The same initial conditions (PO_4 , PHYT, ZOOP, DET_C , and DET_P) = (0.5, 0.1, 0.05, 0.08, and 0.01) were used for all the numerical experiments examined. Table 3 shows equilibrium values and oscillatory ranges of the diatom-like phytoplankton parameterization under varying zooplankton mortality, light conditions, nutrient availability, and detritus food quality levels. Our model showed robust stability and none of the eight scenarios triggered oscillatory behavior. The relatively similar assimilation rates and plankton biomass levels among the three detritus food quality (FQ_2) values are indicative of its minor role with the diatom-like species. Conditions of high zooplankton mortality, especially when combined with high nutrient and/or light availability, resulted in the highest phytoplankton biomass levels. The same scenarios were also characterized by the highest carbon (a_C) and phosphorus (a_P) assimilation efficiency values highlighting the weight placed on food availability by the mathematical formulation used in our analysis.

The configuration of the phytoplankton compartment with cyanobacterium-like attributes provided a greater range of plank-

ton biomass values. In many of the cases parameterized with low zooplankton mortality, the state variables were not attracted to steady-state values but rather underwent unforced oscillations over a wide range of detritus food quality values (Table 4). On the other hand, high zooplankton mortality/fish predation stabilized the system, and when combined with high nutrient availability resulted in extremely high phytoplankton biomass accumulation ($14\text{--}18\text{ g C m}^{-3}$). Cyanobacteria biomass decreased in response to increasing detritus food quality, whereas zooplankton carbon and phosphorus assimilation efficiency showed a positive relationship with the FQ_2 values. The bifurcation diagram of the cyanobacterium-like species along with the zooplankton biomass against the detritus food quality, under high light availability, high hypolimnetic phosphate, and low zooplankton mortality are illustrated in Fig. 3a and b. Oscillatory behavior (grey color) is manifested over the entire FQ_2 range, while the solid white line indicates the existence of unsteady steady states, i.e., states that repel rather than attract nearby trajectories. The planktonic dynamics under conditions of high light availability, low hypolimnetic phosphate fluxes, and low zooplankton mortality are characterized by limit cycles at each value of FQ_2 between 0 and 0.72 (Fig. 3c and d). The amplitude of the oscillations is decreasing with increasing detritus food quality and the point $FQ_2 = 0.72$, where the limit cycle collapses onto steady state, is called Hopf bifurcation. The oscillatory range becomes narrower ($FQ_2 < 0.39$) when low light and high

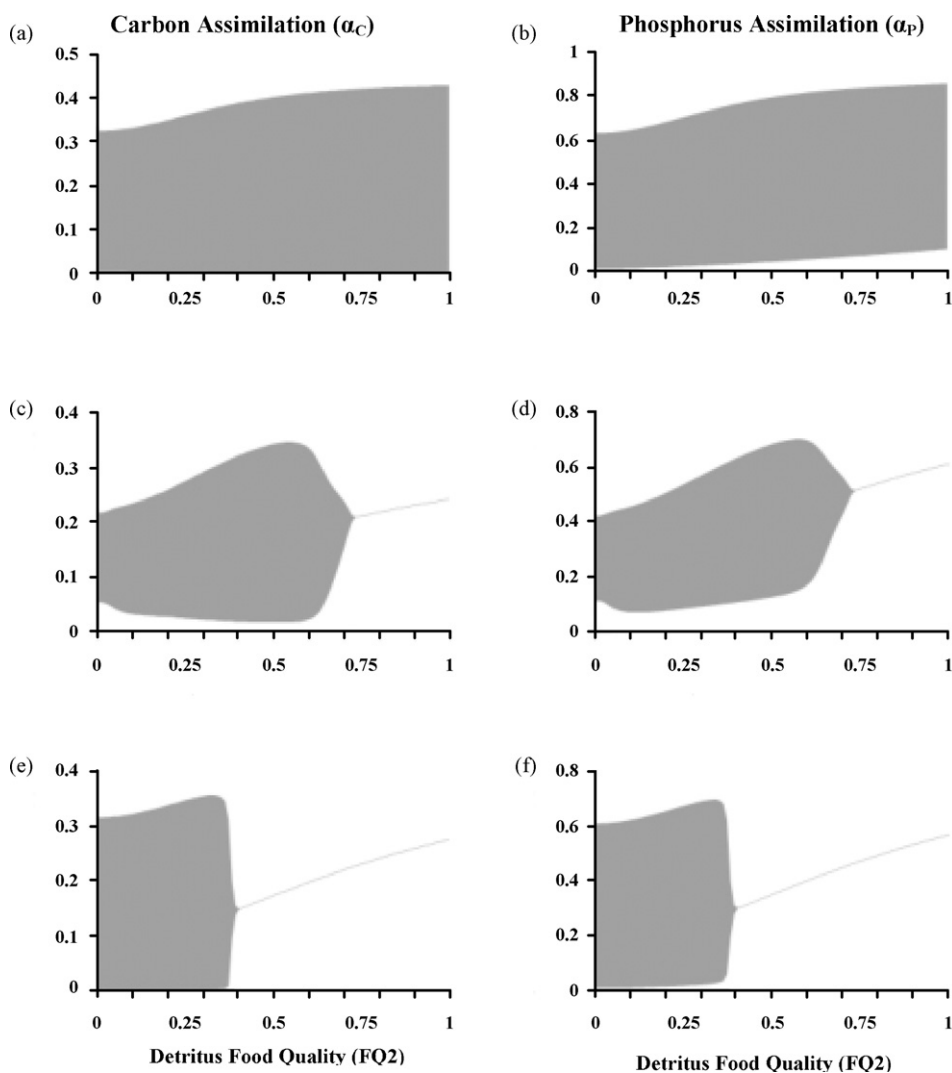


Fig. 4. Parameterization of the phytoplankton compartment as a cyanobacterium-like species: variation of carbon and phosphorus zooplankton assimilation efficiency with varying detritus food quality under the three scenarios presented in Fig. 3.

Table 5

Equilibrium values and oscillatory ranges of the intermediate species under varying light conditions, nutrient availability, zooplankton mortality, and low detritus food quality levels ($FQ_2 = 0.2$).

| Light <i>b</i> | Hypolimnetic phosphate $PO_{4(hypo)}$ | Zooplankton mortality <i>d</i> | Phytoplankton food quality FQ_1 | Phytoplankton PHYT | Zooplankton ZOOPT | Carbon assimilation α_C | Phosphorous assimilation α_P | Oscillatory range |
|-------------------|--|-----------------------------------|--------------------------------------|-----------------------|----------------------|-----------------------------------|--|-------------------|
| High | High | High | 0.2 | 1.802 | 0.028 | 0.274 | 0.531 | – |
| | | | 0.5 | 1.764 | 0.044 | 0.401 | 0.777 | |
| | | | 0.7 | 1.752 | 0.050 | 0.428 | 0.830 | |
| High | High | Low | 0.2 | 0.300 | 1.052 | 0.134 | 0.343 | – |
| | | | 0.5 | 0.154 | 1.060 | 0.135 | 0.477 | |
| | | | 0.7 | 0.123 | 1.000 | 0.136 | 0.552 | |
| High | Low | High | 0.2 | 0.540 | 0.022 | 0.206 | 0.399 | – |
| | | | 0.5 | 0.519 | 0.037 | 0.357 | 0.696 | |
| | | | 0.7 | 0.511 | 0.044 | 0.398 | 0.777 | |
| High | Low | Low | 0.2 | 0.171 | 0.325 | 0.135 | 0.302 | 0.63 –0.89 |
| | | | 0.5 | 0.072 | 0.374 | 0.143 | 0.427 | |
| | | | 0.7 | 0.057 | 0.347 | 0.152 | 0.504 | |
| Low | High | High | 0.2 | 1.298 | 0.026 | 0.256 | 0.495 | – |
| | | | 0.5 | 1.245 | 0.043 | 0.390 | 0.757 | |
| | | | 0.7 | 1.226 | 0.048 | 0.421 | 0.817 | |
| Low | High | Low | 0.2 | 0.450 | 0.226 | 0.134 | 0.273 | 0.08 –0.52 |
| | | | 0.5 | 0.043 | 0.093 | 0.176 | 0.402 | |
| | | | 0.7 | 0.028 | 0.076 | 0.219 | 0.507 | |
| Low | Low | High | 0.2 | 0.365 | 0.020 | 0.184 | 0.357 | – |
| | | | 0.5 | 0.317 | 0.034 | 0.334 | 0.654 | |
| | | | 0.7 | 0.294 | 0.040 | 0.379 | 0.745 | |
| Low | Low | Low | 0.2 | 0.132 | 0.059 | 0.115 | 0.226 | 0.12 –0.29 |
| | | | 0.5 | 0.027 | 0.041 | 0.188 | 0.388 | |
| | | | 0.7 | 0.023 | 0.042 | 0.239 | 0.502 | |

Numbers in italics correspond to the averages of the limit cycles for $FQ_1 = 0.2, 0.5,$ and 0.7 .

nutrient availability is combined with low zooplankton mortality (Fig. 3e and f). Interestingly, the assimilation efficiency for P did not exceed the 60% level in the majority of the numerical experiments examined (Fig. 4b, d, and f), while the contemporaneous

carbon assimilation efficiency values were consistently lower than 40% (Fig. 4a, c, and e).

Tables 5–7 provide the equilibrium values and the oscillatory ranges when phytoplankton is parameterized as an intermediate

Table 6

Equilibrium values and oscillatory ranges of the intermediate species under varying light conditions, nutrient availability, zooplankton mortality, and intermediate detritus food quality levels ($FQ_2 = 0.5$).

| Light <i>b</i> | Hypolimnetic phosphate $PO_{4(hypo)}$ | Zooplankton mortality <i>d</i> | Phytoplankton food quality FQ_1 | Phytoplankton PHYT | Zooplankton ZOOPT | Carbon assimilation α_C | Phosphorous assimilation α_P | Oscillatory range |
|-------------------|--|-----------------------------------|--------------------------------------|-----------------------|----------------------|-----------------------------------|--|-------------------|
| High | High | High | 0.2 | 1.775 | 0.040 | 0.372 | 0.721 | – |
| | | | 0.5 | 1.757 | 0.047 | 0.417 | 0.809 | |
| | | | 0.7 | 1.749 | 0.051 | 0.434 | 0.841 | |
| High | High | Low | 0.2 | 0.144 | 1.045 | 0.136 | 0.497 | – |
| | | | 0.5 | 0.122 | 0.995 | 0.136 | 0.558 | |
| | | | 0.7 | 0.109 | 0.958 | 0.137 | 0.605 | |
| High | Low | High | 0.2 | 0.525 | 0.033 | 0.321 | 0.624 | – |
| | | | 0.5 | 0.514 | 0.041 | 0.382 | 0.746 | |
| | | | 0.7 | 0.509 | 0.045 | 0.408 | 0.798 | |
| High | Low | Low | 0.2 | 0.080 | 0.366 | 0.151 | 0.442 | <0.85 |
| | | | 0.5 | 0.063 | 0.349 | 0.155 | 0.505 | |
| | | | 0.7 | 0.051 | 0.333 | 0.157 | 0.556 | |
| Low | High | High | 0.2 | 1.260 | 0.038 | 0.359 | 0.696 | – |
| | | | 0.5 | 1.234 | 0.046 | 0.409 | 0.793 | |
| | | | 0.7 | 1.221 | 0.050 | 0.428 | 0.831 | |
| Low | High | Low | 0.2 | 0.073 | 0.133 | 0.167 | 0.399 | <0.31 |
| | | | 0.5 | 0.029 | 0.076 | 0.213 | 0.491 | |
| | | | 0.7 | 0.026 | 0.075 | 0.239 | 0.562 | |
| Low | Low | High | 0.2 | 0.331 | 0.030 | 0.299 | 0.583 | – |
| | | | 0.5 | 0.303 | 0.038 | 0.362 | 0.711 | |
| | | | 0.7 | 0.286 | 0.042 | 0.390 | 0.769 | |
| Low | Low | Low | 0.2 | 0.028 | 0.040 | 0.177 | 0.364 | – |
| | | | 0.5 | 0.023 | 0.042 | 0.226 | 0.474 | |
| | | | 0.7 | 0.021 | 0.043 | 0.262 | 0.555 | |

Numbers in italics correspond to the averages of the limit cycles for $FQ_1 = 0.2, 0.5,$ and 0.7 .

Table 7
Equilibrium values and oscillatory ranges of the intermediate species under light conditions, nutrient availability, zooplankton mortality, and high detritus food quality levels ($FQ_2 = 0.7$).

| Light <i>b</i> | Hypolimnetic phosphate $PO_{4(hypo)}$ | Zooplankton mortality <i>d</i> | Phytoplankton food quality FQ_1 | Phytoplankton PHYT | Zooplankton ZOOPT | Carbon assimilation α_C | Phosphorous assimilation α_P | Oscillatory range |
|-------------------|--|-----------------------------------|--------------------------------------|-----------------------|----------------------|-----------------------------------|--|-------------------|
| High | High | High | 0.2 | 1.762 | 0.045 | 0.406 | 0.787 | – |
| | | | 0.5 | 1.752 | 0.050 | 0.428 | 0.830 | |
| | | | 0.7 | 1.746 | 0.052 | 0.438 | 0.851 | |
| High | High | Low | 0.2 | 0.116 | 0.978 | 0.137 | 0.578 | – |
| | | | 0.5 | 0.107 | 0.949 | 0.137 | 0.615 | |
| | | | 0.7 | 0.100 | 0.926 | 0.138 | 0.646 | |
| High | Low | High | 0.2 | 0.517 | 0.039 | 0.368 | 0.718 | – |
| | | | 0.5 | 0.511 | 0.044 | 0.399 | 0.780 | |
| | | | 0.7 | 0.507 | 0.047 | 0.416 | 0.814 | |
| High | Low | Low | 0.2 | <i>0.064</i> | <i>0.348</i> | <i>0.159</i> | <i>0.522</i> | <0.75 |
| | | | 0.5 | <i>0.052</i> | <i>0.333</i> | <i>0.159</i> | <i>0.564</i> | |
| | | | 0.7 | <i>0.045</i> | <i>0.321</i> | <i>0.161</i> | <i>0.602</i> | |
| Low | High | High | 0.2 | 1.241 | 0.044 | 0.397 | 0.770 | – |
| | | | 0.5 | 1.226 | 0.048 | 0.421 | 0.818 | |
| | | | 0.7 | 1.217 | 0.051 | 0.433 | 0.842 | |
| Low | High | Low | 0.2 | 0.029 | 0.076 | 0.214 | 0.496 | – |
| | | | 0.5 | 0.026 | 0.075 | 0.237 | 0.557 | |
| | | | 0.7 | 0.024 | 0.075 | 0.256 | 0.608 | |
| Low | Low | High | 0.2 | 0.311 | 0.036 | 0.348 | 0.683 | – |
| | | | 0.5 | 0.292 | 0.040 | 0.381 | 0.750 | |
| | | | 0.7 | 0.279 | 0.043 | 0.399 | 0.789 | |
| Low | Low | Low | 0.2 | 0.024 | 0.042 | 0.223 | 0.467 | – |
| | | | 0.5 | 0.022 | 0.043 | 0.256 | 0.541 | |
| | | | 0.7 | 0.020 | 0.043 | 0.281 | 0.599 | |

Numbers in italics correspond to the averages of the limit cycles for $FQ_1 = 0.2, 0.5,$ and 0.7 .

species between the diatom- and cyanobacterium-like extremes. Our results show that the role of the phytoplankton food quality (FQ_1) on plankton dynamics can vary significantly depending on the assigned food quality values to detritus. Namely, low detritus food quality ($FQ_2 = 0.2$) combined with low zooplankton mortality results in oscillatory behavior over a fairly wide range of phytoplankton food quality levels (Table 5). In contrast with the cyanobacterium-like configuration, it is also interesting to note that the scenario of high light and nutrient availability along with low zooplankton mortality did not produce limit cycles. The same phytoplankton parameterization was also characterized by relatively low C (<0.4) and P (<0.8) assimilation efficiencies, aside from the scenario in which conditions of high nutrient availability and high zooplankton mortality/fish predation are combined with higher phytoplankton food quality levels (>0.7). Intermediate detritus food quality value ($FQ_2 = 0.5$) tends to stabilize the system, and limit cycles are only manifested when low zooplankton mortality is combined with nutrient- or light-limiting conditions (Table 6). Our model demonstrated robust stability with high detritus food quality ($FQ_2 = 0.7$), and only one scenario (high light, low hypolimnetic phosphate, and low zooplankton mortality) triggered oscillatory behavior (Table 7). The relatively similar plankton biomass levels and assimilation rates among the three FQ_1 values indicate that phytoplankton food quality becomes less important, when the quality of the alternative food sources (e.g., detritus) is high.

Fig. 5 shows the Hopf bifurcation points A and B that separate FQ_1 values for which trajectories are attracted to limit cycles or to steady states, when the intermediate phytoplankton species is combined with low detritus food quality ($FQ_2 = 0.2$). The scenario of light-limiting conditions, high phosphate availability, and low zooplankton mortality results in wide amplitude oscillations over a broad range of phytoplankton food quality values (Fig. 5c, d). These planktonic patterns dissipate as the hypolimnetic phosphate fluxes decrease regardless of the light availability, i.e., small

amplitude oscillations occur over a relatively narrow phytoplankton food quality range (Fig. 5a, b, e, and f). Interestingly, the same model parameterization (low hypolimnetic phosphate and low zooplankton mortality) produces similar small to moderate amplitude limit cycles over a broader phytoplankton food quality band (0–0.8), when detritus food quality is higher ($FQ_2 \geq 0.5$) and the light is not a limiting factor for phytoplankton growth (Fig. 6a, b, e, and f). On the other hand, light-limiting conditions combined with moderate detritus food quality ($FQ_2 = 0.5$) and high nutrient abundance result in oscillatory behavior when phytoplankton food quality is low, $FQ_1 < 0.3$ (Fig. 6c and d).

In Fig. 7, we plot two-parameter bifurcation diagrams, which show how the qualitative nature of the previous patterns changes as detritus food quality and zooplankton mortality/fish predation vary under light-limiting conditions and high hypolimnetic nutrient inputs. Using phytoplankton specifications with low food quality attributes, the range and the levels of zooplankton mortality where plankton demonstrates oscillatory behavior covary with detritus food quality (Fig. 7a and b). On the other hand, plankton limit cycle response to different zooplankton mortality is fairly independent from the detritus food quality levels, when phytoplankton food quality is high (Fig. 7c and d). It should be noted that the latter scenario (intermediate species with $FQ_1 = 0.7$) produces limit cycles within a zooplankton mortality range (0.10–0.23 day⁻¹) that is not examined in Table 7.

We also examined the relative role of light and nutrient availability on the manifestation and persistence of oscillatory behavior associated with resource enrichment. Fig. 8 shows that the phytoplankton response to increasing light availability varies among the different phytoplankton characterizations and detritus food quality levels. When phytoplankton is parameterized as a diatom-like species, oscillations occur in a relatively narrow range of the background light attenuation b (0.1–0.17 m⁻¹) regardless of the detritus food quality (Fig. 8a, b). On the other hand, the cyanobacterium-

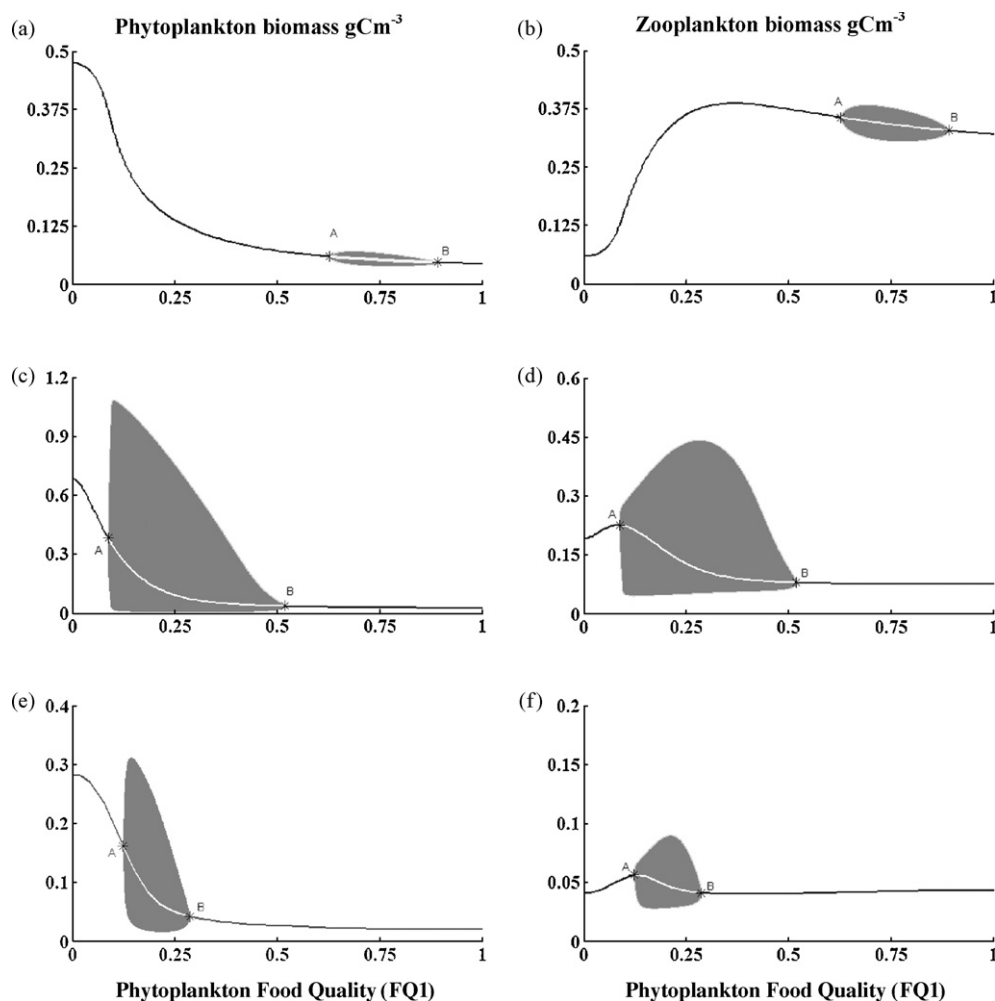


Fig. 5. Parameterization of the phytoplankton compartment as an intermediate species: variation of the plankton levels with varying phytoplankton and low detritus food quality ($\text{FQ}_2 = 0.2$) under conditions of: (a and b) high light availability, low hypolimnetic phosphate fluxes, and low zooplankton mortality; (c and d) low light availability, high hypolimnetic phosphate fluxes, and low zooplankton mortality; (e and f) low light availability, low hypolimnetic phosphate fluxes, and low zooplankton mortality.

like species undergoes limit cycles over a broad range of light and nutrient availability when the detritus food quality is low (Fig. 8c). Interestingly, the amplitude of the oscillations along with region where the system is destabilized significantly reduces ($b < 0.17$) when higher food quality value is assigned to detritus (Fig. 8d). Further insights into the role of the phytoplankton food quality are gained from the comparison between the two intermediate species of low and high food quality (Fig. 8e–h). Namely, higher phytoplankton food quality not only narrows down the limit cycle area but also shifts the oscillatory region towards lower light attenuation values.

Finally, we introduced allochthonous particulate matter loading into the system to examine the planktonic patterns induced from the pertinent quantitative and qualitative changes. Specifically, the exogenous particulate C was set equal to the median, the first and third quartile of the frequency distribution presented by Persson et al. (2007), while particulate P was varied to obtain the range of exogenous P:C ratios reported in the same study. We examined two scenarios of the cyanobacterium-like parameterization that resulted in oscillatory behavior over a wide range of detritus food quality, i.e., high light availability, high/low hypolimnetic phosphate inputs, and low zooplankton mortality (Fig. 9). The inclusion of the exogenous particulate matter terms stabilized the system and the limit cycles disappeared throughout the P:C ratios examined. The phytoplankton steady-state values show a nearly exponential increase after the exceedance of a critical seston C:P ratio of approximately $150\text{--}160 \text{ gC}(\text{gP})^{-1}$ (Fig. 9a and b), where

zooplankton decreases to a minimum biomass value (Fig. 9c) or gets eliminated (Fig. 9d). Notably, the decrease of the exogenous P:C ratio from 0.03 to $0.001 \text{ gP}(\text{gC})^{-1}$ resulted in a curvilinear increase of the seston C:P ratio from 120 to $180 \text{ gC}(\text{gP})^{-1}$ (Fig. 9e and f).

4. Discussion

Theoretical analyses of the impact of food quality on the flow of energy/matter at the plant–animal interface are usually based on two assumptions: (i) the food quality is solely specified in terms of the element:carbon ratios (e.g., P:C or N:C ratio) of the grazed seston and (ii) the production efficiency of the limiting nutrient is constant. Nonetheless, there is overwhelming evidence that factors other than the zooplankton somatic nutrient content are important in determining the variability in maximal growth rate, egg production, and sensitivity to resource-limited growth (Müller-Navarra et al., 2004; DeMott and Pape, 2005). Recently, empirical models developed across trophic gradients suggest that food availability imposes the greatest limitation on *Daphnia* growth in oligotrophic lakes, P limitation comes into play only when total P concentration is low ($\approx \text{TP} \leq 4 \mu\text{g L}^{-1}$), and EPA limitation becomes an important factor in both oligotrophic and eutrophic systems (Persson et al., 2007). In this study, we attempted to integrate all the potentially limiting factors by using a dynamic approach that accounts for the effects of both ingested food quantity and quality on zooplankton P production efficiency (Arhonditsis and Brett, 2005a; Zhao et al.,

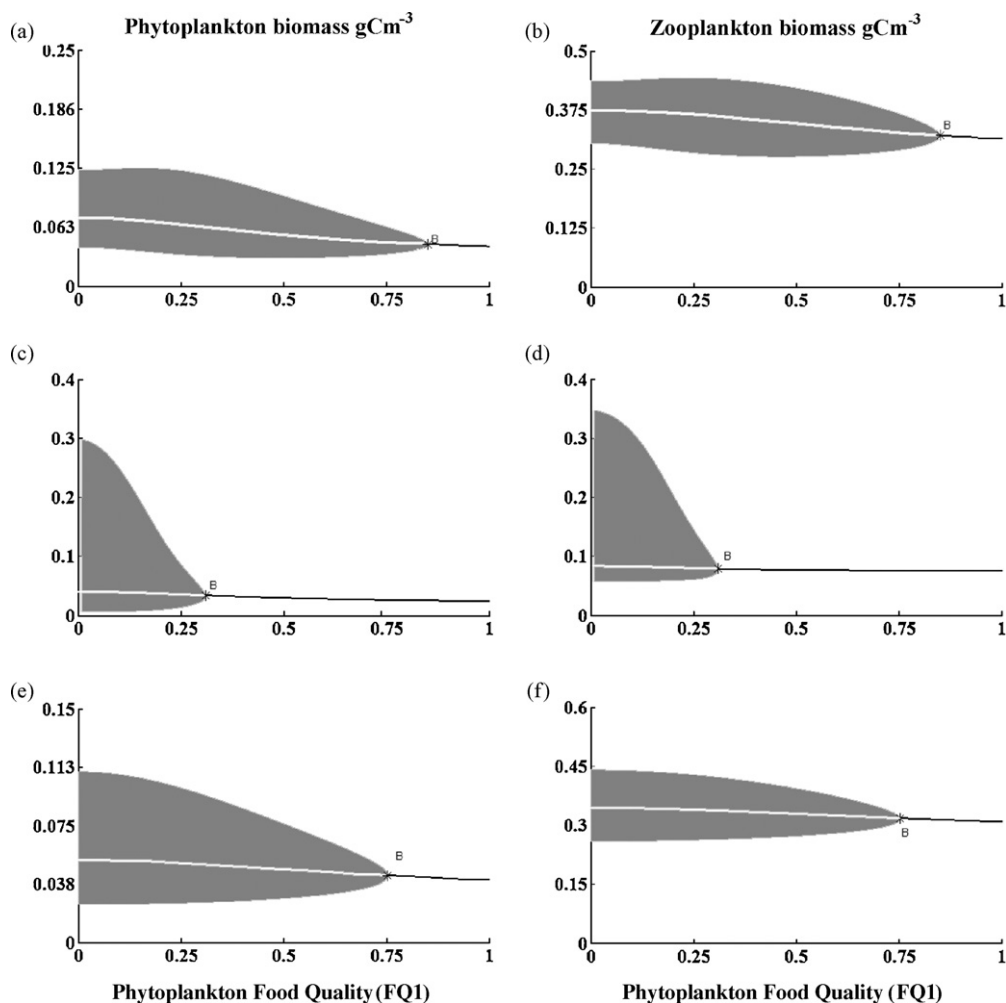


Fig. 6. Parameterization of the phytoplankton compartment as an intermediate species: variation of the plankton levels with varying phytoplankton food quality under conditions of: (a and b) high light availability, low hypolimnetic phosphate fluxes, low zooplankton mortality, and moderate detritus food quality ($FQ_2 = 0.5$); (c and d) low light availability, high hypolimnetic phosphate fluxes, low zooplankton mortality, and moderate detritus food quality ($FQ_2 = 0.5$); (e and f) high light availability, low hypolimnetic phosphate fluxes, low zooplankton mortality, and high detritus food quality ($FQ_2 = 0.7$).

2008b). Aside from the typically considered mismatch between the zooplankton somatic and seston C:P ratio (Olsen et al., 1986; Loladze et al., 2000; Mulder and Bowden, 2007), the food quality term also introduces a scheme in which each food type concentration is weighted by the respective quality, i.e., a surrogate of the FA content and/or digestibility resistance. Under the assumption of homeostatically regulated internal nutrient ratios, our model postulated a moderately strong saturation-type relationship between C assimilation efficiency and food quantity (Fig. 10a), whereas the resulting a_C values were consistently lying within the second and third quartiles of the major zooplankton taxa values reported by Straile (1997). Importantly, the a_C -seston C:P ratio (Fig. 10b) and a_C -overall food quality (Fig. 10c) relationships in our numerical experiments were relatively similar to those commonly reported in the literature (Brett and Müller-Navarra, 1997; Vrede et al., 2002; DeMott et al., 2004).

Trophic coupling in plankton communities is considered one of the most variable and least predictable links among all levels of the food webs (McQueen et al., 1989; Brett and Goldman, 1997; Müller-Navarra et al., 2000). The repercussions of the strength variability of the phytoplankton-zooplankton interactions on ecosystem functioning can vary from the ideal condition of the inverted food web pyramid of the Peruvian upwelling zone or the clear-water phase of many temperate lakes, where relatively low phytoplankton biomass can sustain high zooplankton and fish production,

to the least desirable scenario of hypereutrophic systems, where high primary producer biomass coexists with low production at the higher trophic levels (Brett and Müller-Navarra, 1997). In this analysis, the parameterization of phytoplankton as a diatom-like species resulted in relatively low phytoplankton to zooplankton biomass ratios (0.10–21.83 with an average of 6.34), whereas the cyanobacterium-like specification showed significant accumulation of phytoplankton biomass (0.33–450.25 with an average of 99.13). Thus, our results reiterate the notion that high phytoplankton food quality allows the zooplankton community to sustain relatively high biomass and/or to suppress phytoplankton biomass to low levels, while low algal food quality results in weak trophic cascades and leads to nutrient control of algal biomass (Grover, 1995; Danielsdottir et al., 2007). In contrast with the majority of the recent modeling studies, however, our analysis also considers the role of an alternative food source, i.e., detritus, which appears to shape the food web architecture, especially when phytoplankton food quality is low. In particular, when phytoplankton is parameterized as an intermediate species, our model shows that the detritus food quality levels can modulate the phytoplankton to zooplankton biomass ratio and significantly alter the planktonic dynamics (see also following discussion).

Several studies have demonstrated that the selection of the closure term can strongly influence the dynamics of plankton population models (Steele and Henderson, 1992; Edwards and Yool,

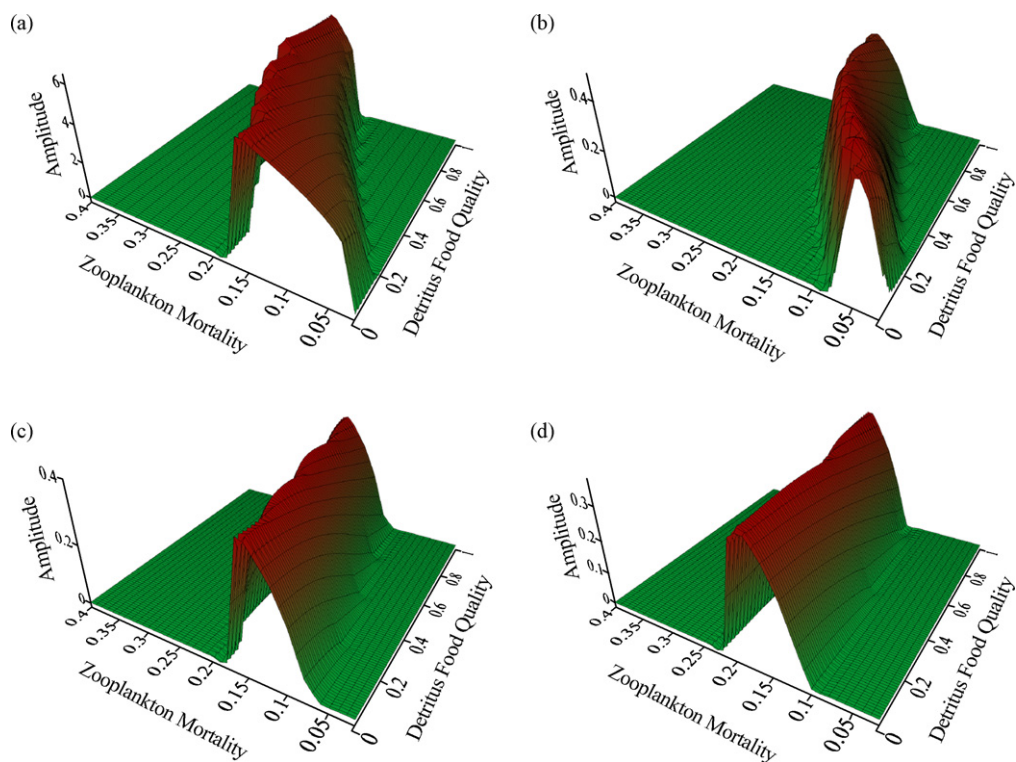


Fig. 7. Phytoplankton limit cycle response to different zooplankton mortality and detritus food quality levels under limiting light conditions and high hypolimnetic nutrient input: (a) cyanobacterium-like species, (b) intermediate species ($FQ_1 = 0.2$), (c) intermediate species ($FQ_1 = 0.5$), and (d) intermediate species ($FQ_1 = 0.7$).

2000). Edwards (2001) pointed out that the selection of the zooplankton mortality term can be more influential on the dynamic behavior of a planktonic system than adding the detritus compartment to a limiting nutrient–phytoplankton–zooplankton model. In this model, the zooplankton mortality/higher predation term was formulated as being dependent on the zooplankton density, i.e., we assume a “switchable” type of predation from planktivorous fish, while the natural mortality is implicitly included in the closure term. Gatto (1991) showed that the introduction of such a density-dependent mortality term in a simple predator–prey model counteracts oscillatory behavior stemming from resource enrichment. Similarly, the results presented here suggest that the occurrence of oscillations is largely determined from the zooplankton mortality values, although its importance varies with the seston food quality. When algal food quality is low, the range and the levels of zooplankton mortality, which produce plankton limit cycles, are determined from the detritus food quality levels. Namely, low detritus food quality broadens the range and decreases the levels of zooplankton mortality where limit cycles occur, while high detritus food quality tends to stabilize the system and oscillatory behavior is manifested at higher zooplankton mortality rates. On the other hand, high algal food quality strengthens the phytoplankton–zooplankton coupling, thereby increasing the direct impact of zooplankton mortality as well as minimizing the control exerted from the detritus food quality levels on plankton limit cycle response.

The stability properties of the stoichiometrically explicit autotroph–herbivore models have received considerable attention in the modeling literature (Andersen, 1997; Loladze et al., 2000; Andersen et al., 2004). Loladze et al. (2000) presented a two dimensional bifurcation diagram with respect to total P and light intensity to distinguish among the effects of different types of enrichment: energy, nutrient, or combined energy–nutrient enrichment. It was shown that both light energy and nutrient enrichment can destabilize the system, but ultimately only energy enrichment leads

to the deterministic extinction of zooplankton. The same analysis provided evidence that some combinations of nutrient and light levels result in bistability patterns suggesting that in such systems externally caused perturbations may significantly change system behavior, population density, and producer/grazer ratio. In this study, although we did not provide evidence for the latter assertion, we did find that the paradox of enrichment holds in a rather wide light–nutrient availability range. The results also suggest that both phytoplankton and detritus food quality determine the extent of the limit cycle region, whereas high algal food quality increases system resilience by shifting the oscillatory region towards lower light attenuation levels. On the other hand, when algal food quality is low, the amplitude of the dynamic oscillations following enrichment seems to be regulated by the detritus food quality. The latter result implies that the presence of high detritus food quality can prevent the minimum abundance of species from falling below certain levels, and thus increases the robustness of stability of the primary producer–grazer systems even if the light and nutrient availability conditions along with the phytoplankton food quality are not favourable. In this regard, our results are qualitatively similar to those reported by Genkai-Kato and Yamamura (1999) highlighting the profitability of the alternative food sources (e.g., unpalatable algal species and detritus) for the grazer as an important predictor for the dynamic behavior of phytoplankton–zooplankton relationships.

The question arising from the previous results is what do we know from the literature with regards to the detritus food quality and its ability to meet the consumer nutritional requirements in aquatic food webs? Based on the pathways in which the detrital particulate organic matter is formed, it can be classified into two categories: (i) decomposing algal cell or plant fragments, which contain remnant lignin and cellulose and are encapsulated in different types of exopolymer secretions (Decho and Lopez, 1993; Lemke et al., 2007) and (ii) organic aggregates, originally derived from dissolved organic matter, which are colonized by microbes

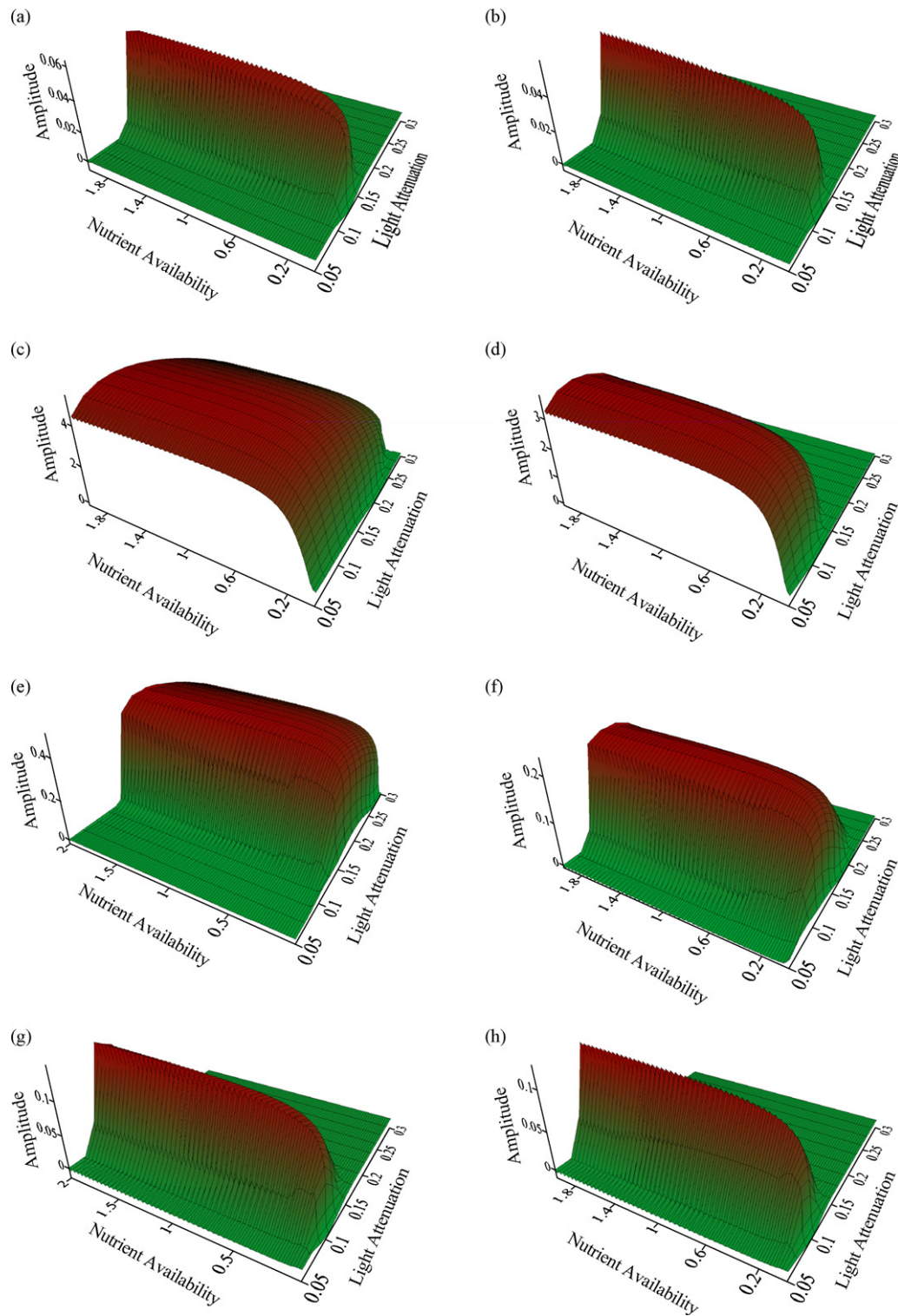


Fig. 8. Phytoplankton limit cycle response to different nutrient availability ($PO_4(\text{hypo})$, hypolimnetic phosphate input) and light limitation (b , background light attenuation) levels under low zooplankton mortality. The left hand panels correspond to a (a) diatom-, (c) cyanobacterium-like species, and two intermediate species with food quality (e) $FQ_1 = 0.2$ and (g) 0.7 combined with detritus food quality $FQ_2 = 0.2$. The right hand panels (b, d, f, and h) correspond to the same species with detritus food quality $FQ_2 = 0.5$.

(bacteria, algae, and fungi) and are usually encased in a mixture of exopolymers (Alber and Valiela, 1994; Lemke et al., 2007). These complex forms of detritus and their associated labile components have been reported to be major food resources for the secondary production (Vos et al., 2002; Lemke et al., 2007), although their nutritional value is usually inferior to the planktonic seston quality (e.g., Ahlgren et al., 1997; Cavaletto and Gardner, 1999). The

abundance, nutrient content, biochemical quality, and state of decomposition of detritus also show significant spatiotemporal variability determined by factors such as the phytoplankton community composition as well as the chemical oxidation, bacterial decomposition, and cell leaching during settling onto the sediments (Vos et al., 2002). For example, Ahlgren et al. (1997) found distinct differences in chemical composition between particulate

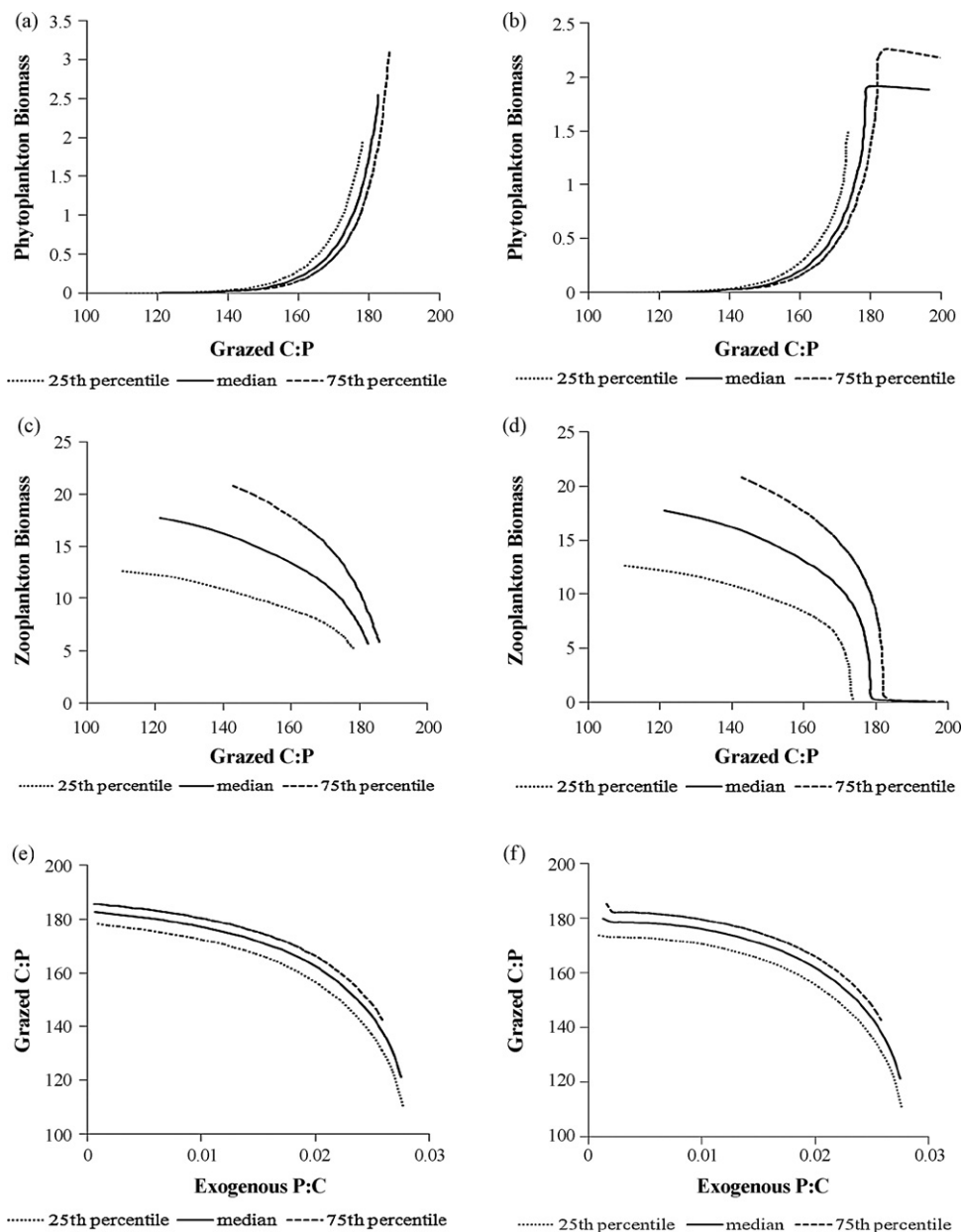


Fig. 9. Plankton and seston C:P response to varying exogenous P:C ratios under high light availability, low zooplankton mortality, low (a–c) and high (d–f) hypolimnetic nutrient inputs. The phytoplankton compartment has cyanobacterium-like attributes and the detritus food quality was set equal to 0.5.

matter in the photic and aphotic zones, especially with regards to the polyunsaturated FA content, whereas other studies highlight the discrepancy between the detritus-consumer elemental ratios as the primary growth constraint when detritivory accounts for a substantial proportion of zooplankton feeding (Enríquez et al., 1993; Cross et al., 2003). Thus, irrespective of the primary limiting factor (biochemical quality versus stoichiometry), evidence from the literature suggests that some of the numerical experiments examined in which detritus food quality was assumed higher than algal food quality ($FQ_1 < FQ_2$) are probably unrealistic, and solely intended to demonstrate the range of dynamics produced from our plankton model.

The importance of particle feeding on zooplankton growth is further complicated when considering the exogenous particulate organic material inputs. The quantification of relative support of consumers by autochthonous and allochthonous resources has received considerable attention, and several recent studies have shown that the impact of terrestrial subsidies depends on character-

istics of the exogenous material, the pathway of entry into the food web, the zooplankton community structure, and the system productivity (Carpenter et al., 2005; Cole et al., 2006; Pace et al., 2007). Generally, allochthony seems to be low in both eutrophic lakes and oligotrophic, clear-water lakes, whereas the terrestrial subsidy to consumers is considered significant in relatively small systems with greater humic content, i.e., higher color and DOC (Pace et al., 2007). Earlier studies pointed out that cladocerans are less dependent relative to copepods on autochthonous sources, and can obtain their carbon through direct feeding on terrestrially derived POC (Cole et al., 2006). Nonetheless, this hypothesis was not verified from Pace et al. (2007), who suggested that cladocerans are mainly supported from autochthonous C (even if they have to vertically migrate below the mixed layer) and selectively from some allochthonous sources such as Gram-negative bacteria. In this context, interesting scenarios for examination with the present model are the ecological implications of the quality differences between exogenous and endogenous particles ($FQ_{2(\text{endogenous})} \neq FQ_{2(\text{exogenous})}$) or the

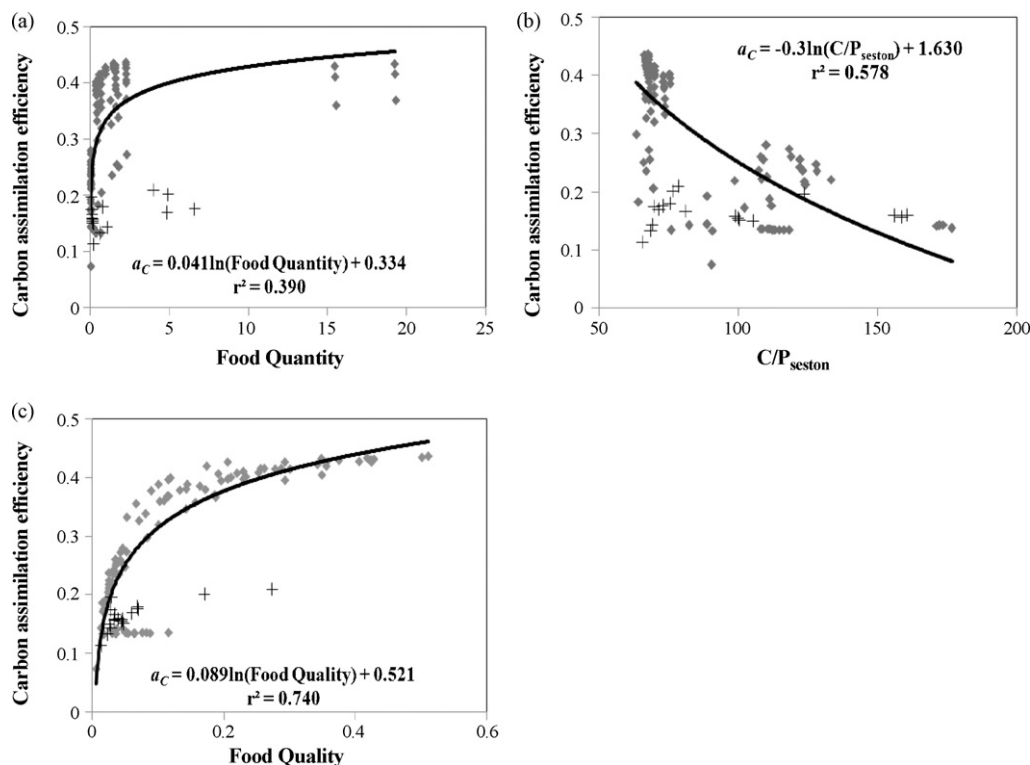


Fig. 10. The relationship between carbon assimilation efficiency and (a) food quantity (g Cm^{-3}), (b) C:P ratio (g C (g P)^{-1}), and (c) food quality $\text{FQ} ((\text{g Cm}^{-3})^{1/2})$ in the numerical experiments presented in Tables 3–7. Scenarios that resulted in limit cycles (crosses) were not used to fit the lines.

preferential zooplankton grazing between planktonic and detrital seston ($\omega \neq 1$).

The introduction of allochthonous particulate matter into the system allowed insights into the planktonic patterns induced from some of our model assumptions. That is, the current model structure assumes that the excess nutrients during zooplankton feeding replenish the detritus pool; an assumption reflecting the notion that zooplankton homeostasis is maintained during the digestion and assimilation process by removing elements in closer proportion to zooplankton somatic ratios than to the seston elemental ratio (DeMott et al., 1998; Elser and Foster, 1998). In support of this hypothesis, Arhonditsis and Brett (2005b) found that the assignment of higher values to the particulate fraction of the egested material more closely reproduced the observed Lake Washington dynamics, whereas the assumption that homeostasis is maintained via post-assimilation processing and differential respiration/excretion of nutrients in dissolved form resulted in unrealistic hypolimnetic accumulation of the non-limiting nutrients. On the other hand, Anderson (2005) formulated a model with an explicit representation of the consumer metabolic processes, which rendered support to the alternative hypothesis that multi-nutrient balancing is regulated by post-absorptive mechanisms. Similar empirical evidence was provided by Darchambeau et al. (2003) who indicated that zooplankton stoichiometry when feeding on unbalanced diets (high C:P) is mainly attained by disposing the excess dietary C via respiration and excretion of DOC. Our results here indicate that the homeostatic regulations based on physiological solutions operating before food absorption in the gut can significantly increase the seston C:P ratios in P-limiting conditions (Fig. 9e and f), thereby accentuating the likelihood of elemental imbalance and growth constraints both in the pelagic zone and the detritus-based benthic communities (Cross et al., 2003).

In conclusion, our analysis underscores the critical role of seston food quality on the patterns of energy and nutrient flow at the primary producer–herbivore interface. Seston food quality can

regulate the manifestation of unforced oscillations and thus the stability of planktonic food webs. Using different phytoplankton parameterizations, we showed that high phytoplankton food quality allows the zooplankton community to obtain relatively high biomass and to exert control on phytoplankton biomass, while low algal food quality results in weak trophic cascades and leads to nutrient-driven algal biomass variability. Both phytoplankton and detritus food quality determine the extent of the limit cycle region during resource (e.g., nutrients and light) enrichment conditions, whereas algal food quality primarily regulates system resilience by determining the resource availability levels in which oscillations occur. Detritus food quality seems to modulate the amplitude of the dynamic oscillations following enrichment, when algal food quality is low. Thus, the profitability of the alternative food sources for herbivorous grazers can be important predictors for the dynamic behavior of autotroph–herbivore interactions in nature. Recent empirical and modeling studies provide evidence that the assumption of strict element homeostasis does not always explain zooplankton dynamics in P-deficient environments (DeMott et al., 2004; DeMott and Pape, 2005; Mulder and Bowden, 2007; Ferrão-Filho et al., 2007). For example, Ferrão-Filho et al. (2007) showed significant interspecific variability in cladoceran somatic P content in response to food C:P ratio variation, although the sensitivity to P limitation is also dependent on food concentration. The same study proposed the dynamic energy budget theory as an alternative strategy to describe the interplay between organisms and environment with regards to energy/element acquisition and utilization (Kooijman, 1995). According to this framework, the distinction between structural components and internal reserves of the animal body can explain how organisms meet their nutritional requirements and cope with the variability of environmental conditions (Kooijman, 2001). Future modeling efforts should focus on refining the mathematical representation of the zooplankton adaptive strategies to different quantity and quality food conditions as well as on elucidating their implications on trophic

transfer and ecosystem functioning (recycling rates and feedback loops).

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Appendix A. Parameter specifications for Tables 3–7

| Diatom-like species | | Value |
|---|-----------------|---------------|
| Maximum phytoplankton (PHYT) growth rate | <i>a</i> | 0.25 |
| Phytoplankton respiration rate | <i>r</i> | 0.18 |
| Phytoplankton sinking loss rate | <i>s</i> | 0.15 |
| Phytoplankton food quality | FQ ₁ | 0.8 |
| Half-saturation constant for PO ₄ uptake | <i>e</i> | 0.01 |
| Phytoplankton self-shading coefficient | <i>c</i> | 0.5 |
| Cyanobacteria-like species | | Value |
| Maximum phytoplankton (PHYT) growth rate | <i>a</i> | 0.1 |
| Phytoplankton respiration rate | <i>r</i> | 0.05 |
| Phytoplankton sinking loss rate | <i>s</i> | 0.001 |
| Phytoplankton food quality | FQ ₁ | 0.2 |
| Half-saturation constant for PO ₄ uptake | <i>e</i> | 0.03 |
| Phytoplankton self-shading coefficient | <i>c</i> | 0.05 |
| Intermediate species | | Value |
| Maximum phytoplankton (PHYT) growth rate | <i>a</i> | 0.2 |
| Phytoplankton respiration rate | <i>r</i> | 0.14 |
| Phytoplankton sinking loss rate | <i>s</i> | 0.08 |
| Detritus Food Quality | FQ ₂ | 0.2, 0.5, 0.7 |
| Half-saturation constant for PO ₄ uptake | <i>e</i> | 0.018 |
| Phytoplankton self-shading coefficient | <i>c</i> | 0.35 |
| Scenarios parameter ranges | | |
| | Low | High |
| Light availability (<i>b</i>) | 0.25 | 0.08 |
| Hypolimnetic phosphate input (PO ₄ (_{hyp})) | 0.05 | 1.95 |
| Zooplankton mortality (<i>d</i>) | 0.08 | 0.35 |

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