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PRIMARY RESEARCH PAPER

Phytoplankton food quality control of planktonic food web processes

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Abstract We developed a mechanistic model of nutrient, phytoplankton, zooplankton and fish interactions to test the effects of phytoplankton food quality for herbivorous zooplankton on planktonic food web processes. When phytoplankton food quality is high strong trophic cascades suppress phytoplankton biomass, the zooplankton can withstand intense zooplanktivory, and energy is efficiently transferred through the food web sustaining higher trophic level production. Low food quality results in trophic decoupling at the plant-animal interface, with phytoplankton biomass determined primarily by nutrient availability, zooplankton easily eliminated by fish predation, and poor energy transfer through the food web. At a given nutrient availability, food quality and zooplanktivory interact to determine zooplankton biomass which in turn determines algal biomass. High food quality resulted in intense zooplankton grazing which favored fast-growing phytoplankton taxa, whereas fish predation favored slow-growing phytoplankton. These results suggest algal food quality for herbivorous zooplankton can strongly influence the nature of aquatic food web dynamics, and can have profound effects on water quality and fisheries production.

Keywords Phytoplankton food quality · Plankton dynamics · Mechanistic models · Food web processes · Eutrophication · Lake ecosystems

Introduction

One of the greatest challenges to aquatic ecologists is untangling the natural processes and anthropogenic factors, which regulate the standing biomass of algae in pelagic ecosystems. Understanding these processes would improve our ability to control nuisance and toxic algal blooms, maintain the esthetics of surface water bodies, protect drinking water supplies, and improve fisheries production (Vollenweider, 1976; Carpenter et al., 1985; McQueen et al., 1986; Carmichael, 1994; Pauly and Christensen, 1995; Brett and Goldman, 1996, 1997; Falconer, 1999; Micheli, 1999). Despite the tremendous effort and wide variety of approaches devoted to studying this topic, the nature of food web

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variability remains controversial and arguably only partially understood (DeMelo et al., 1992; Harris, 1994; Sarnelle, 1996; Polis et al., 2000). The phytoplankton–zooplankton interface in planktonic food webs is very biochemically heterogeneous (Sterner and Hessen, 1994; Brett and Müller-Navarra, 1997), and much effort has been devoted to studying the physical and biochemical basis of algal food quality variation for herbivorous zooplankton in freshwater and marine planktonic systems (Lampert, 1981, 1987; Jónasdóttir, 1994; Sterner and Hessen, 1994; Brett and Müller-Navarra, 1997; Kleppel et al., 1998; Müller-Navarra et al., 2000). Several studies have suggested phytoplankton food quality for herbivorous zooplankton may greatly affect food web interactions in pelagic systems (Brett and Müller-Navarra, 1997; Elser et al., 2000; Müller-Navarra et al., 2004).

In order to test the potential impact of algal food quality, nutrient availability and fish predation on food web dynamics, we developed a mechanistic model of nutrient, phytoplankton, zooplankton interactions for a hypothetical temperate polymictic lake. The objective of our model was to determine how the rate at which zooplankton convert the phytoplankton they consume to zooplankton biomass (i.e., algal food quality) influences plankton dynamics and biomass distribution in pelagic ecosystems. The model was run for a matrix of nutrient availability, phytoplankton food quality, and zooplanktivory, and values for the following state variables were calculated: phytoplankton biomass, zooplankton biomass, and the phytoplankton production to biomass ratio. This approach allowed us to test the hypothesis that phytoplankton food quality plays a critical role in controlling the strength of trophic coupling in aquatic systems within the context of well established nutrient and consumer impacts on food web processes.

Several previous studies have also considered the impact of zooplankton-phytoplankton interactions on overall food web dynamics (Leibold, 1989; Grover, 1995; Loladze et al., 2000; Muller et al., 2001). The most well known of these studies are the models of Leibold (1989) and Grover (1995) which considered the impact of selective consumption of two resources of differing quality and ingestibility on food web processes. This scenario ultimately leads to dominance by the non-preferred resource (Leibold, 1989; Grover, 1995). We considered grazing by a non-selective generalist *Daphnia*-like herbivore, which we will later show favored the preferred resource type (i.e., fast growing phytoplankton). Our approach is also fundamentally different from stoichiometry based food web models (Loladze et al., 2000; Muller et al., 2001) in that it does not presume a single determinant of phytoplankton food quality. It is now well established that phytoplankton food quality for herbivorous zooplankton is dependent on multiple factors including ingestibility, digestibility, and toxicity, as well as essential fatty acid, protein, sterol and mineral content (Lampert, 1981, 1987; Jónasdóttir, 1994; Sterner and Hessen, 1994; Brett and Müller-Navarra, 1997; Kleppel et al., 1998; Müller-Navarra et al., 2000; Von Elert et al., 2003; Ravet and Brett, 2006). In this study, we do not explicitly consider the individual effects of these factors on algal food quality variation, but rather we examine how variation in quality of phytoplankton food (irrespective of what causes it) might affect biomass distribution and the strength of trophic coupling in planktonic food webs.

Methods

Our mathematical model consisted of three ordinary differential equations describing the dynamics of inorganic phosphorus (N for nutrients), phytoplankton (P), and zooplankton (Z) (see Table 1). Zooplanktivory was modeled statically, that is fish removed a fixed portion of the zooplankton each day. This model was largely based on classic oceanographic NPZ, lake algal dynamics and Lotka-Volterra predator-prey models (Oksanen et al., 1981; Fasham et al., 1990; Chapra, 1997). According to this model, phosphorus concentrations are regulated by phosphorus released by dying, sinking and respiring plankton and phosphorus taken up by growing phytoplankton. Phytoplankton community growth is a function of cell growth regulated by nutrient, light availability, and temperature, as well as

Table 1 The mathematical formulation of our NPZ model

$$\frac{dN}{dt} = (\alpha_{pc(\text{phyto})} \cdot d_{\text{phyto}} \cdot P) + \left(\alpha_{pc(\text{phyto})} \cdot \frac{W_{\text{sink}}}{h} \cdot P\right) + (\alpha_{pc(\text{zoop})} \cdot (d_{\text{zoop}} + d_{\text{fish}}) \cdot Z \cdot \Theta_{T-Z}) + \left(C_{gz} \cdot \Theta_P \cdot \Theta_{T-Z} \cdot \alpha_{pc(\text{phyto})}\left(Z - \left(\frac{\alpha_{pc(\text{zoop})}}{\alpha_{pc(\text{phyto})}} \cdot GE \cdot Z\right)\right)\right) - \left(G_{\max} \cdot \left(\frac{N}{N + K_{mm}}\right) \cdot \Theta_L \cdot (\Psi^{T-T_{\text{ref}}}) \cdot P \cdot \alpha_{pc(\text{phyto})}\right) \quad (1)$$

$$\frac{dP}{dt} = G_{\max} \cdot \left(\frac{N}{N + K_{mm}}\right) \cdot \Theta_L \cdot (\Psi^{T-T_{ref}}) \cdot P - (d_{\text{phyto}} \cdot P) - \left(\frac{W_{\text{sink}}}{h} \cdot P\right) - (Z \cdot C_{gz} \cdot \Theta_P \cdot \Theta_{T-Z}) \quad (2)$$

$$\frac{dZ}{dt} = (C_{gz} \cdot \Theta_P \cdot \Theta_{T-Z} \cdot GE \cdot Z) - (d_{\text{zoop}} \cdot Z \cdot \Theta_{T-Z}) - (d_{\text{fish}} \cdot Z) \quad (3)$$

where N is the dissolved nutrient (phosphorus) concentration (μg l^{-1}), P is the phytoplankton biomass (mg C l^{-1}), and Z is the zooplankton biomass (mg C l^{-1}). Furthermore, $\alpha_{pc(\text{phyto})}$ is the phytoplankton elemental phosphorus to carbon ratio, d_{phyto} is the phytoplankton death rate, W_{sink} is the phytoplankton sinking rate, h is the depth of the mixed layer, $\alpha_{pc(\text{zoop})}$ is the zooplankton phosphorus to carbon ratio, d_{zoop} is the zooplankton death rate as a function of senescence and starvation, d_{fish} is the rate of zooplanktivory, Θ_{T-z} is the effect of temperature on zooplankton metabolism, C_{gz} is the maximum zooplankton biomass specific grazing rate, Θ_P is the effect of phytoplankton biomass on grazing, GE is zooplankton growth efficiency (i.e., growth in carbon/consumption in carbon), $G_{\max}$ is the maximum growth rate of the phytoplankton, K_{mm} is the Michaelis–Menten half saturation constant for phytoplankton growth, Θ_L is the effect of light intensity on phytoplankton growth, Ψ is a temperature coefficient for phytoplankton growth, T is the lake's temperature, and T_{ref} is the reference temperature for which the $G_{\max}$ value was obtained.

$$\text{If } P \leq 0.04 \text{ mg C l}^{-1}, \text{ then } d_{\text{zoop}} = \frac{0.09 \cdot \varphi - \varphi \cdot P}{100}. \qquad \text{If } P > 0.04 \text{ mg C l}^{-1}, \text{ then } d_{\text{zoop}} = \frac{0.044 + 0.05 \cdot \varphi - 1.1 \cdot P}{100}. \quad (4)$$

Where φ is zooplankton mortality due to senescence (Boersma and Vijverberg 1994).

$$\Theta_{T-Z} = 0.1113 \cdot e^{0.1093 \cdot T}. \qquad \text{If } P < 0.255 \text{ mg C l}^{-1}, \text{ then } \Theta_P = 3.92 \cdot P \qquad \text{If } P \geq 0.255 \text{ mg C l}^{-1}, \text{ then } \Theta_P = 1. \quad (5).$$

We used a Type I functional response for feeding because this type of response was reported by Lampert and Sommer (1997) for *Daphnia*.

$$\Theta_L = \left(\frac{2.718 \cdot f_p}{\gamma \cdot h} \cdot \left(e^{\frac{-I_0}{I_s} \cdot e^{-\gamma \cdot h}} - e^{\frac{-I_0}{I_s}}\right)\right) \quad (6)$$

where f_p is the photoperiod, γ is the light extinction coefficient, I_0 is the average light intensity at the surface during the day, and I_S is the optimum light intensity.

$$\gamma = \frac{-\ln(0.1)}{SD} + 0.4 \cdot P \quad (7)$$

where SD is the secchi disk depth without phytoplankton.

losses due to senescence, sinking and grazing. Zooplankton community growth is a function of the rate at which algae is consumed (corrected for temperature and food concentration), zooplankton energetic efficiency and losses due to zooplankton senescence, starvation and zooplanktivory. This model was modified to account for the bioenergetics of freshwater phytoplankton and zooplankton growth and nutrition. Our model is at the simple end of the NPZ-aquatic biogeochemical cycling spectrum of models (Arhonditsis and Brett, 2004).

Nutrient availability was varied across a gradient spanning very low to very high total phosphorus (TP) concentrations (i.e., 5, 10, 20, 40, 80, and 160 μg TP L^{-1}). Variation in algal food quality for herbivorous zooplankton was simulated by varying the rate at which zooplankton converted phytoplankton consumed to their own biomass, i.e., zooplankton gross growth efficiency (GE) which is defined as the ratio of zooplankton growth to zooplankton consumption (both in carbon units). GE was varied across a gradient spanning very low to very high energetic efficiency (Straile, 1997) (i.e., 4, 8, 16, 32, and 64%). The intensity of zooplanktivory (or d_{fish}) used in these simulations was varied from 0.0 to 0.5 day^{-1}, by 0.1 day^{-1} increments and was in addition to any mortality already caused by starvation or senescence.

We applied this model to a hypothetical 6 m deep polymictic lake, with solar radiation intensity and photoperiod corresponding to the 45th degree latitude. Water temperature was characterized as a sine wave with a maximum of 20°C in mid summer and a minimum of 7°C in mid winter. The (hypothetical) lake was modeled as a completely mixed reactor (Chapra, 1997); it did not stratify and phosphorus, phytoplankton and zooplankton were uniformly distributed throughout the water column. This model only considered processes occurring in the pelagic system (i.e., it was necessary to draw boundaries around the system modeled), and thus did not consider nutrient losses to outflows or from the pelagic zone to the sediments (via settling phytoplankton). This model also did not consider nutrient loading from the watershed or nutrient gains from the sediments via internal loading. For this reason, we assumed that as plankton died or sank out of the water column they instantaneously released all of their phosphorus to the water mass. Overall phosphorus mass balance was maintained at all times. That is, total nutrients (i.e., TP concentration) = inorganic phosphorus (N) + phosphorus in phytoplankton (N_P) + phosphorus in zooplankton (N_Z) = a constant value. In contrast to our model, in natural lakes nutrients are lost to and gained from the sediments on a seasonal basis dependent on the redox state and other conditions in the upper sediment layer. In addition, over the long-term phosphorus inputs to the lake are offset by equal losses of phosphorus to the outflow and a long term net loss to the sediments (Welch, 1992).

In this study, a subset of the input vector remained fixed during our numerical experiments. Several of these parameters (e.g., maximum phytoplankton growth rate, settling velocity, half-saturation growth constant, maximum zooplankton grazing rate) can be very influential on the model outputs (Arhonditsis and Brett, 2005). For these parameters, we used the geometric mean of all published values, reflecting a broad spectrum of models and a variety of conditions (Table 2). Specifically, the parameters used to represent phytoplankton dynamics were for a wide variety of freshwater taxa, whereas the parameters used to represent the zooplankton were primarily for *Daphnia* spp. In addition, implicit in the NPZ configuration of our model is that phytoplankton are the sole food type and have uniform food quality (instead of more than one resources of different ingestibility, see Leibold, 1989; Grover, 1995), which makes the zooplankton non-selective (daphnid-like) feeders (Lampert and Sommer, 1997). To prevent the complete "die-off" of the phytoplankton and zooplankton in the model, we pre-specified minimum community sizes of 0.03 and 0.01 mg C l^{-1}, respectively. These minimum specified levels are approximately equivalent to 0.6 μg chlorophyll *a* and one adult crustacean zooplankter per liter. Conceptually, this assumption reflects the fact that new phytoplankton and zooplankton is continuously recruited from the sediments in natural systems (Hansson, 1996; Brendonck et al., 1998).

The model was run for seven years with 4 h time-steps, and the model was assumed to have stabilized when the phytoplankton and zooplankton seasonal patterns were repeated each year (i.e., an "equilibrium" was reached). In most cases, this occurred in the fourth or fifth year, the results presented are annual averages for the sixth and seventh years. Phytoplankton biomass, zooplankton biomass and the phytoplankton gross production to biomass ratio (an indicator of phytoplankton community species composition) were calculated as response variables. We used a three-way ANOVA with TP, GE and d_{fish} to assess their main effects and interactions on zooplankton biomass, phytoplankton biomass and the phytoplankton P/B ratio. Response data were log transformed for these analyses to meet the assumptions of normality/homoscedasticity

Table 2 The terms, coefficients and sources used during model development

Symbol	Term	Unit	Value	Source
TP	Total Phosphorus	$\mu g^{*}l^{-1}$	5, 10, 20, 40, 80, 160	1
$a_{pc(phyto)}$	Phytoplankton elemental P:C ratio	molar	0.00389	2
d_{phyto}	Phytoplankton ambient death rate	day^{-1}	0.021	3, 4, 5
W_{sink}	The phytoplankton settling velocity	$m^{*}day^{-1}$	0.24	3, 5
h	The depth of the lake	m	6	
$a_{pc(zoop)}$	Zooplankton elemental P:C ratio	molar	0.01075	2
d_{zoop}	Zooplankton mortality due to senescence and starvation	day^{-1}	See equation	6
d_{fish}	Zooplankton mortality due to zooplanktivory	day^{-1}	0.0, 0.1, 0.2, 0.3, 0.4, 0.5	7
Θ_{T-z}	Temperature affect on zoplankton metabolism	unitless	see equation	8
C_{gz}	maximum zooplankton biomass specific grazing rate	%C day^{-1}	49%	8
Θ_p	The effect of phytoplankton biomass on zooplankton grazing	unitless	see equation	8
GE	Zooplankton growth efficiency	%C	4, 8, 16, 32, 64	9
G_{max}	Maximum phytoplankton growth rate	day^{-1}	1.3	4, 10, 11, 12
K_{mm}	The Michaelis–Menten half saturation growth constant	$\mu g^{*}l^{-1}$	2.9	3, 5, 10, 11, 12, 13
Θ_L	The effect of light intensity on phytoplankton growth	unitless	see equation	
ψ	Temperature adjustment coefficient for phytoplankton growth	unitless	1.11	5
T	The lake temperature	°C	Sine wave (min = 7, max = 20)	
T_{ref}	Reference temperature for which G_{max} was obtained	°C	20	4, 10, 11, 12
φ	Zooplankton mortality due to senescence	unitless	–188	6
f_p	Photoperiod (fraction of the day)	unitless	Sine wave (min = 0.31, max = 0.69)	
γ	The light extinction coefficient	m^{-1}	see equation	
I_0	The average light intensity at the surface during the day	Ly/day	Sine wave (min = 93, max = 362)	
I_s	The optimum light intensity for phytoplankton growth.	Ly/day	165	3, 14
SD	Secchi disk depth without phytoplankton	m	10	

1. Welch (1992); 2. Brett et al. (2000); 3. Zison et al. (1978); 4. Tilman (1982); 5. Reynolds (1984); 6. Boersma and Vijverberg (1994); 7. Brett et al. (1992); 8. Lampert and Sommer (1997): 9. Straile (1997): 10. Ahlgren (1987); 11. Grover (1989); 12. Grover (1991); 13. Jorgensen et al. (1991); 14. Kirk (1994), Arhonditsis and Brett (2005)

(Zar, 1999). The proportion of the overall variability explained by the different factors was used to assess their relative importance as drivers of the plankton biomass and phytoplankton community species composition (Arhonditsis et al., 2003).

Results and discussion

Zooplankton were eliminated in many of the simulations, a phenomenon commonly observed for large zooplankton taxa in response to fish predation (Brooks and Dodson, 1965). The relationship between zooplankton growth efficiency (GE), total phosphorus availability (TP) and the zooplanktivory level above which the zooplankton was eliminated (critical d_{fish}) is shown in Fig. 1a. The critical zooplanktivory level was strongly dependent on GE, weakly dependent on TP concentrations at levels below 20 μg l^{-1}, and independent of nutrient supplies at TP concentrations above 30 μg l^{-1}. If GE was low and zooplanktivory high zooplankton were eliminated, however, if food quality was high zooplankton persisted even when zooplanktivory was intense.

Phytoplankton biomass responded to increasing nutrient availability, with the slope of this response strongly dependent on GE (Fig. 1b). When GE was low (i.e., 4–16%) the increase in algal biomass with nutrient supply was steep, however when GE was high algal biomass was suppressed by zooplankton grazing even at high nutrient concentrations. Figure 1c shows phytoplankton biomass plotted against zooplankton biomass for the full range of GE, d_{fish}, and TP

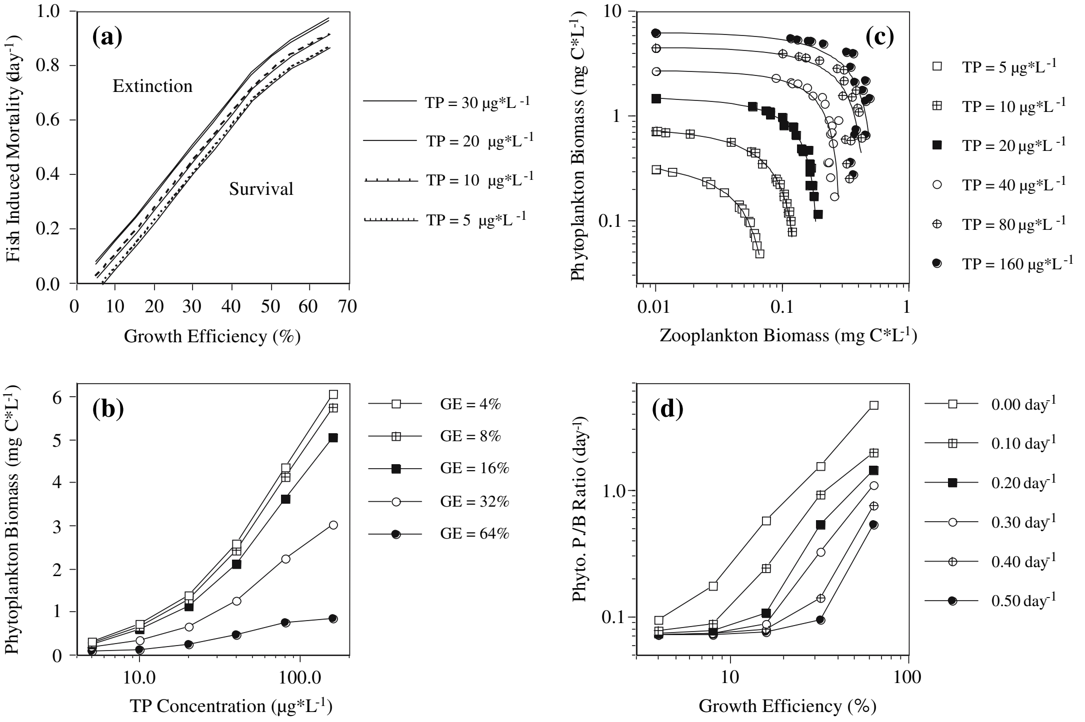

Fig. 1 (**a**) The elimination threshold for zooplankton biomass as a function of food quality, zooplanktivory and nutrient availability; (**b**) phytoplankton biomass as a function of nutrient availability and food quality; (**c**) phytoplankton biomass as a function zooplankton biomass and nutrient availability; and (**d**) the phytoplankton production to biomass ratio as a function of food quality and zooplanktivory

concentrations used in these simulations. These results show a clear negative relationship between phytoplankton and zooplankton biomass, especially at TP concentrations of 40 μg l^{-1} and below. At nutrient concentrations of 80 μg TP l^{-1} and above the phytoplankton and zooplankton biomass relationship became increasingly unstable, with a wide range of phytoplankton biomass values observed when zooplankton biomass was high. Because of this, at high nutrient concentrations zooplankton biomass alone was not sufficient to predict phytoplankton biomass. For example, at 160 μg TP l^{-1} zooplankton biomass alone explained 86.5% of the variability in phytoplankton biomass, whereas a multiple (stepwise) regression model which also included GE and d_{fish} explained 95.4% of the phytoplankton variability. Similar results were obtained when analyzing the 80 μg TP l^{-1} data. Furthermore, the transition from low to high zooplankton biomass, and resultant depression of phytoplankton biomass was relatively sharper at higher nutrient concentrations. The results depicted in Fig. 1c also show that as nutrient concentrations increased a given phytoplankton biomass was able to support a larger zooplankton biomass and that at a specific zooplankton biomass a larger phytoplankton biomass could persist.

The phytoplankton production to biomass (P/B) ratio increased as GE increased and as d_{fish} decreased (Fig. 1d). This suggests the high zooplankton biomass and intense herbivory associated with high phytoplankton food quality tend to drive phytoplankton communities towards rapidly growing species, whereas low phytoplankton food quality and high zooplanktivory tend to drive the phytoplankton towards slower growing taxa. If we also consider that faster growing phytoplankton (e.g. diatoms and cryptophytes) tend to be high food quality (Brett and Müller-Navarra, 1997; Brett et al., 2000), then these results suggest that the food web conditions set up by high food quality phytoplankton may be self-reinforcing. On the other hand, slower growing low food

Table 3 Variance partitioning results for an ANOVA of the model outputs

Source	df	Zooplankton Biomass	Phytoplankton Biomass	Phytoplankton Prod./Biom.
TP	5	11.8%	59.7%	25.9%
GE	4	47.4%	28.5%	53.0%
TP*GE	20	2.5%	0.7%	1.5%
d_{fish}	5	18.4%	7.5%	13.4%
TP*d_{fish}	25	1.7%	0.2%	0.6%
GE*d_{fish}	20	13.0%	3.2%	5.3%
TP*GE*d_{fish}	100	5.2%	0.2%	0.3%

The values presented are the percent sum of squares for the three state variables squares for the three state variables and their interactions

quality phytoplankton like cyanobacteria cannot persist when exposed to intense herbivory due to their slow growth rates. Thus, *Daphnia* will be unable to control cyanobacteria blooms once fully developed, but intense herbivory by *Daphnia* could prevent cyanobacteria blooms from initiating (Schoenberg and Carlson, 1984).

The results of a three-way ANOVA (see Table 3) with TP, GE and d_{fish} show the zooplankton biomass observed in these simulations was most strongly regulated by GE, followed by d_{fish} and TP, with a strong interaction between GE and d_{fish}. Phytoplankton biomass was most strongly regulated by TP concentrations, followed by GE and then somewhat distantly by d_{fish}. The phytoplankton P/B ratio was most strongly regulated by GE, followed by TP and d_{fish}.

We also used our model to generate a surface contour plot of zooplankton and phytoplankton biomass responses to phytoplankton food quality (GE) and zooplanktivory (d_{fish}) at a nutrient concentration of 30 µg TP l^{-1} (Fig. 2). This plot shows that at combinations of high fish predation and low food quality zooplankton were eliminated which allowed phytoplankton to achieve their maximum biomass at that nutrient level. However, once the zooplankton elimination threshold was overcome (due to reduced zooplanktivory and/or improved food quality), the zooplankton community rapidly built up a large biomass which suppressed the phytoplankton (Fig. 2). At a specific nutrient level phytoplankton biomass was strongly related to zooplankton biomass in a negative curvilinear fashion, see also Fig. 1c. The rough surface on the upper plateau of zooplankton biomass was caused by predator-prey oscillations.

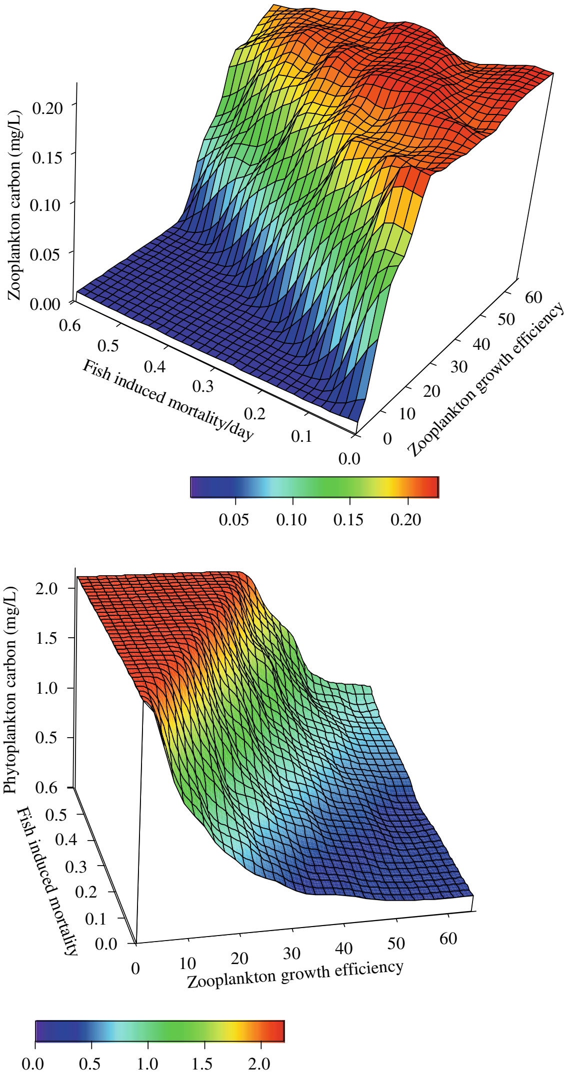

Fig. 2 Predicted phytoplankton and zooplankton biomass as a function of phytoplankton food quality and zooplanktivory for a TP concentration of 30 µg l^{-1}

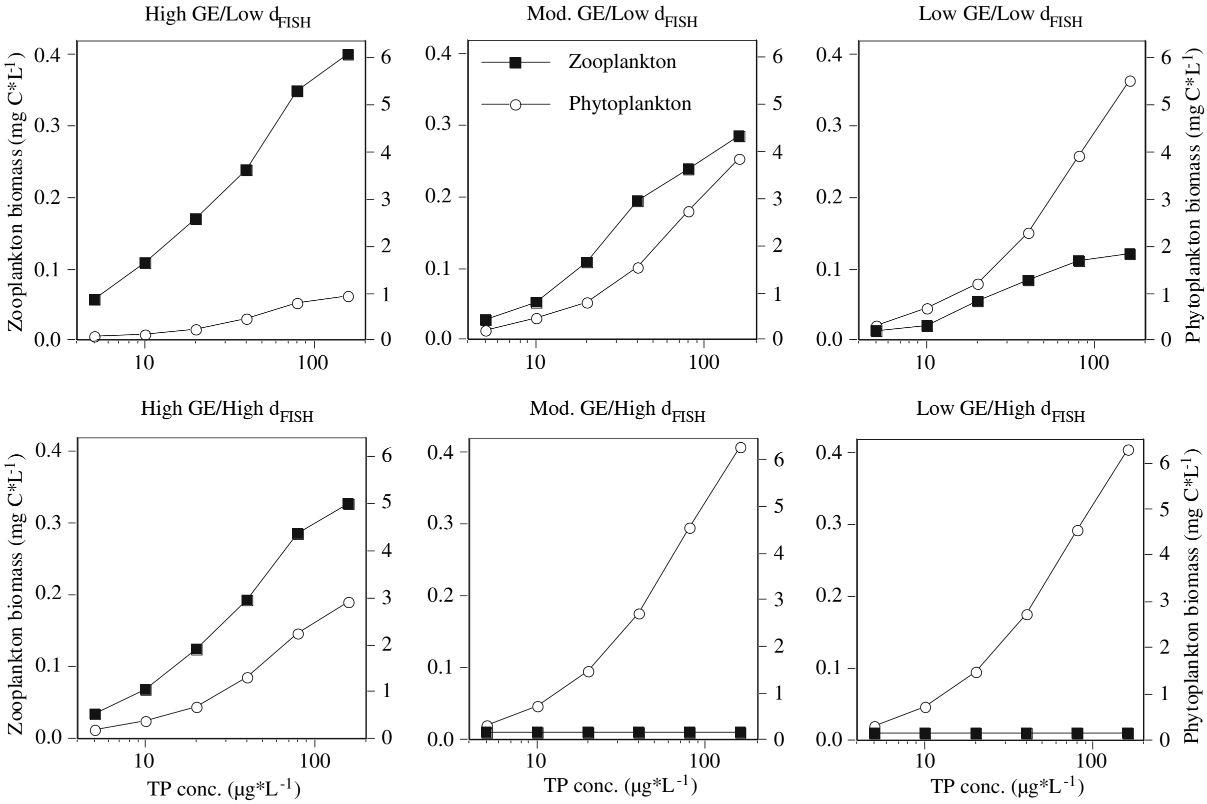

Fig. 3 Predicted phytoplankton and zooplankton biomass across a gradient of TP concentrations for a matrix of high, moderate and low food quality and high and low zooplanktivory. In the matrix of high GE conditions were represented by averaging the simulation results obtained for GE = 32 and 64%; moderate GE was represented using the results for GE = 16%; low GE was represented by averaging the results obtained for GE = 4 and 8%; high d_{fish} was represented by averaging the results for 0.3, 0.4, and 0.5 day^{-1}; and low d_{fish} was represented by averaging the results for 0.0, 0.1, and 0.2 day^{-1}

To examine how zooplankton and phytoplankton biomass simultaneously responded to increasing nutrient supplies in these simulations, we plotted zooplankton and phytoplankton biomass for a matrix of food quality and fish predation (Fig. 3). These comparisons show a very wide range of zooplankton and phytoplankton biomass responses to increasing TP concentrations (Fig. 3). When GE was high and d_{fish} low, zooplankton responded strongly and phytoplankton weakly to increasing nutrient supplies. When GE and d_{fish} were high, the zooplankton withstood intense zooplanktivory and still suppressed phytoplankton biomass. When GE was moderate and d_{fish} low, both zooplankton and phytoplankton biomass increased as nutrient supplies increased. When GE was low or moderate and d_{fish} high, phytoplankton biomass responded strongly to increasing nutrients and zooplankton was eliminated at all nutrient levels.

Our model differs from classic theoretical food web models (Oksanen et al., 1981) in that all of the coefficients used in our simulations were representative of values observed in freshwater planktonic food webs, and especially *Daphnia* dominated systems. *Daphnia* spp. play a critical role on the food webs of temperate freshwater planktonic systems because they are large, fast growing and efficient herbivores, and they are also the preferred prey for zooplanktivorous fish because of their size and slow swimming speed (Lampert and Sommer, 1997). *Daphnia* are also the first group of zooplankton eliminated when zooplanktivory increases (Brooks and Dodson, 1965). Our results show that the ultimate ability of zooplankton to suppress algal communities was very strongly tied to the food quality of the phytoplankton. High energetic efficiency at the plant-animal interface is a prerequisite for having high rates of energy transfer throughout the food web, strong food web interactions and especially strong algal biomass suppression. This is consistent with Vollenweider's (1976) prediction that *"the phytoplankton-zooplankton interrelationship appears to be particularly dependent on the species composition of the phytoplankton. If the phytoplankton is composed primarily of species edible for zooplankton, one may find a relatively low phytoplankton standing crop*". Algal food quality for *Daphnia* spp. may also be of paramount importance in determining whether populations of these zooplankters are able to withstand fish predation and still suppress phytoplankton biomass.

When phytoplankton food quality was high our model gave results which were essentially identical to those of the classic Oksanen model (Oksanen et al., 1981), which predicts that in two trophic level systems (plants/herbivores), increased primary production will result in increased herbivore biomass but constant plant biomass because herbivores will simply crop-off the increased algal production (see high GE/low d_{fish} scenario in Fig. 3). The Oksanen model also predicts that in systems of three trophic levels (plants/herbivores/carnivores), increased nutrient availability will result in increased algal biomass and constant zooplankton biomass because fish predation will crop-off the increased zooplankton production, releasing the phytoplankton from herbivory. Our model gave results consistent with this prediction when algal food quality was moderate or low and zooplanktivory high (see Fig. 3). When algal food quality was high, the zooplankton withstood intense zooplanktivory, while still maintaining a high biomass and suppressing algal production. In fact, at high algal food quality these systems shifted towards inverted biomass distributions a phenomenon commonly observed in upwelling regions of the world's oceans (Gasol et al., 1997). This model also showed that when algal food quality is high and zooplanktivory weak the system oscillated between frequent "clear water phases" (not presented here). Clear water phases were less frequent and less pronounced when zooplanktivory was intense because the fish predation on zooplankton ameliorated the boom/bust zooplankton cycles characteristic of spring clear water phases in productive temperate lakes (Lampert et al., 1986; Sommer et al., 1986). Dependence of *Daphnia* population oscillations on algal food quality has previously been noted in natural systems (Kerfoot et al., 1988). From a water quality and fisheries production perspective, the high GE/high d_{fish} scenario depicted in Fig. 3 is optimal, because it results in a food web which can sustain high rates of upper trophic level production without accumulating excessive algal biomass.

Several authors have noted that the responses of phytoplankton and zooplankton biomass to fish predation and nutrient additions are often "decoupled" (McQueen et al., 1986; Brett and Goldman, 1996, 1997; Micheli, 1999). Our model predicted trophic decoupling at the plant-animal interface when phytoplankton food quality for herbivorous zooplankton was low, which may generally be the case in cyanobacteria dominated hypereutrophic systems (Müller-Navarra et al., 2004). Interestingly, trophic cascades at the phytoplankton trophic level were weak when food quality was low despite the fact that at low food quality fish predation completely eliminated zooplankton. Relieving intense zooplanktivory when algal food quality was low had little impact on the phytoplankton, because under these conditions herbivory by zooplankton had little impact on algal biomass even in the absence of fish predation (compare phytoplankton biomass in the low GE/high d_{fish} and low GE/low d_{fish} scenarios in Fig. 3). Conversely, fish predation had its strongest impact on zooplankton biomass when phytoplankton food quality was low because under these conditions the zooplankton was easily eliminated by fish predation. Thus, low phytoplankton food quality resulted in weak trophic cascades at the phytoplankton level and strong cascades at the zooplankton level. This is the least desirable scenario for lake managers because it results in algal biomass accumulation, and associated water quality problems such as poor water clarity, taste and odor problems in drinking water supplies, and in extreme cases toxic cyanobacteria blooms. This scenario also does not support high rates of upper trophic level production, even though the energy available at the base of the food web to support fisheries production appears to be high.

Despite the fact that the mathematical structure of our model was quite different, when phytoplankton food quality was intermediate our model provided predictions very similar to those of the controversial ratio-dependent model (Arditi and Ginzburg, 1989). Under these conditions algal and zooplankton biomass increased with nutrient availability in a nearly linear fashion, as shown by the moderate GE/low d_{fish} scenario in Fig. 3. Ratio-dependent type responses were also observed when both food quality and zooplanktivory were high, see high GE/high d_{fish} scenario in Fig. 3.

Comparisons with other models

As previously mentioned other studies have also considered the impact of variation in phytoplankton food quality (for herbivorous zooplankton) on planktonic food web interactions. Liebold (1989) considered the case were a consumer has two types of resources which differ in their ingestibility. In general, Liebold's model predicts systems with higher carrying capacities (i.e., nutrients) will have higher zooplankton biomass and zooplankton biomass will decline as the intensity of fish predation increases. This model also predicts the proportion of edible (i.e., ingestible) phytoplankton will increase with increasing fish predation, and the proportion of resources resistant to herbivory should increase with nutrients. In contrast to these predictions, our model suggests that when phytoplankton food quality is low zooplankton will respond very weakly (and phytoplankton will respond strongly) to increasing nutrient availability irrespective of fish predation. When phytoplankton food quality is high, our model predicts zooplankton can maintain a large biomass even when zooplanktivory is intense. Furthermore, when food quality is high our model predicts zooplankton will respond strongly and simultaneously suppress phytoplankton biomass as nutrient availability increases. Our model also predicts increasing zooplanktivory will shift the community towards taxa with lower P/B ratios; zooplanktivory depresses zooplankton biomass (when the phytoplankton is low to moderate food quality) and releases the phytoplankton from herbivory thus favoring slower growing taxa.

Recent stoichiometric food quality/trophic coupling models (e.g., Loladze et al., 2000; Muller et al., 2001) have adopted a different approach for study growth efficiency effects. Loladze et al. (2000) used the Rosenzweig-MacArthur variation of Lotka-Volterra equations to include a term that accounts explicitly for nutrient limitation. Hence, the zooplankton production efficiency of their model includes two terms: (a) the maximum growth efficiency that is achieved if optimal food quality is being grazed, and (b) phosphorus limitation. The first term is a constant and resembles our GE term, and it could be used to represent any food quality constraint. The second (nutrient limitation) term assumes that overall growth efficiency decreases by a factor directly proportional to the imbalance between the C:P ratios of the zooplankton and the phytoplankton/seston they consumed. These assumptions in combination with the absence of a simulated free nutrient pool, transformed the two biotic compartments (prey and predator) into potential competitors for phosphorus. In order to facilitate comparisons between our models, we ran the Loladze et al. (2000) model while varying zooplankton mortality from 0.05 to 0.50 day^{-1}, TP from 5 to 40 μg l^{-1}, GE from 5 to 80%, and setting the light determined phytoplankton carrying capacity (K) to 0.75 or 1.5 mg C l^{-1}, while holding all other model parameters the same as reported in their Table 1 (Loladze et al., 2000).

These results show that specifying a low zooplankton mortality rate in the Loladze model almost always resulted in high zooplankton biomass, despite the fact that some of the highest phytoplankton C:P ratios were observed in these scenarios (Fig. 4). Paradoxically, it was commonplace for large *Daphnia* populations (i.e., 10–30 individuals l^{-1}) to persist for several weeks with phytoplankton biomass below 0.01 mg l^{-1}. This occurred because the Loladze model did not include a term to describe zooplankton mortality

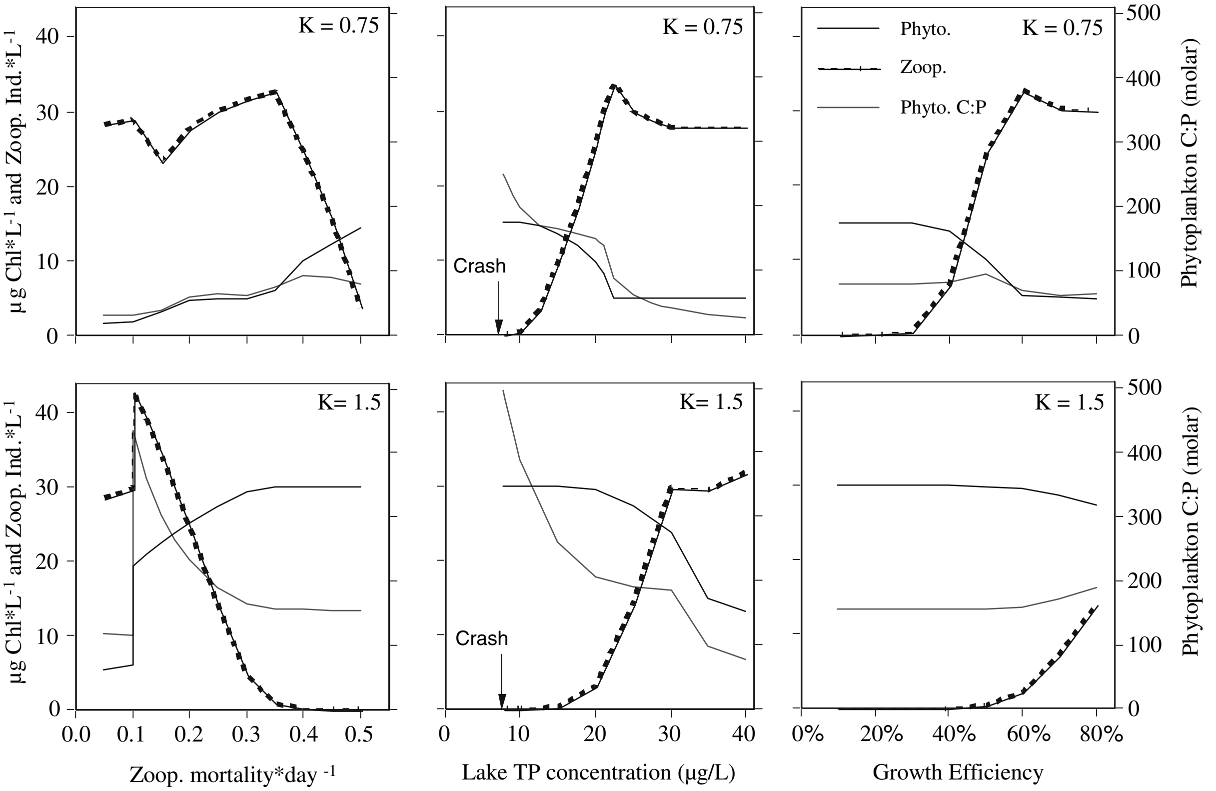

Fig. 4 Model predictions for the Loladze et al. (2000) stoichiometric based food quality/trophic coupling model for a range of zooplankton mortality, total phosphorus concentrations and the zooplankton growth efficiencies (C: Chl *a* = 50; 1 zooplankton individual = 15 µg C). These results correspond to phytoplankton carrying capacities of 0.75 and 1.5 mg C l^{-1}, while varying zooplankton mortality, TP availability and zooplankton growth efficiency individually. All other parameter values are as reported in Table 1 of Loladze et al. (2000)

due to starvation and when phytoplankton concentrations were ≈0 mg l^{-1} zooplankton dynamics were governed solely by the pre-specified background mortality rate. The Loladze et al. (2000) model also predicted an inverse relation between phytoplankton biomass and TP concentrations (Fig. 4). This occurred because the pre-specified maximum phytoplankton biomass (e.g., the carrying capacity term) was not dependent on nutrient concentrations and the overall supply of TP influenced the C:P ratio of the phytoplankton. When TP concentrations were high, phytoplankton C:P ratios were lower and the zooplankton were more able to over-exploit the phytoplankton. The predictions reported in Loladze et al. (2000), i.e., food quality control of zooplankton biomass when phytoplankton biomass was high, only occurred when extremely high GE values (i.e. ≥60%) were used (Fig. 4). Much weaker, or no, zooplankton, phytoplankton, and phytoplankton C:P ratio responses occurred when a GE of 43%, the 75th percentile reported by Straile (1997), was used in these simulations.

Conclusions

Our model suggests algal food quality and zooplanktivory interact to determine whether zooplankton will be eliminated by predation. When combinations of low food quality and high fish predation cause zooplankton elimination, nutrients solely control algal biomass. Low food quality makes the zooplankton susceptible to over-exploitation, results in weak trophic cascades, and leads to nutrient control of algal biomass. In contrast, high algal food-quality allows the zooplankton community to sustain relatively high biomass and to depress phytoplankton biomass to low levels even when zooplanktivory is intense. The phytoplankton community shifts towards r-selected species with increasing food quality and towards K-selected species with increasing fish predation and nutrient supply. For the range of parameter values considered, the present model provides a more plausible description of phytoplankton food quality impacts on trophic coupling and phytoplankton-zooplankton interactions than does an alternative stoichiometric-based food web interaction model.

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