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Modelling the role of highly unsaturated fatty acids in planktonic food web processes: Sensitivity analysis and examination of contemporary hypotheses

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ABSTRACT

Aquatic food web models typically treat the constituent trophic levels as static elements interacting with one another and the environment. Dynamic biological stoichiometry has relaxed this assumption and considers evolutionary responses in said elements. The incorporation of organismal response in food web models holds promise for a more realistic portrayal of ecosystem dynamics. Recent advances in aquatic ecology pinpoint the importance of highly unsaturated fatty acids (HUFAs) on food web interactions and ecosystem resilience. In this study, we utilized a HUFA explicit submodel in conjunction with a limiting nutrient–phytoplankton–zooplankton–detritus (NPZD) mathematical system to incorporate elements of the physiology of individual animals into the context of plankton dynamics. Our HUFA-augmented plankton model provided a realistic platform to examine functional properties and physiological strategies that modulate resource procurement in different trophic environments and to effectively link variability at the organismal level with ecosystem-scale patterns. First, we were able to illustrate the implications of the filling-cup hypothesis, in which species' fitness stems from dynamic HUFA turnover rates in response to bottom-up stresses. We then examined an evolutionary hypothesis of consumer fitness dependence on HUFA quota management strategies, whereby adaptive individuals with low HUFA minimum and optimum requirements gain competitive advantage. Several studies have reported higher HUFA concentrations in consumers than producers, and our results suggest that this pattern could be driven by a combination of conservative turnover and elevated bioconversion rates. Oligotrophic settings showed strong reliance upon exogenous phosphorus subsidies and frequently yielded inverted food web biomass distributions. With the prevalence of eutrophic conditions, consumer growth is primarily controlled by HUFA availability, and the associated biochemical limitation can ultimately result in patterns of algal accumulation. Finally, our study discusses directions to improve the representation of the producer–grazer interactions and thus advance our understanding of the factors that determine the flow of nutrients and energy to the higher trophic levels.

1. Introduction

Colloquially described as the most dynamic, yet least understood link in aquatic food webs, the plant–animal interface is unique in its degree of heterogeneity. The disparity between phytoplankton cellular construct and zooplankton somatic makeup is substantial in terms of biochemical and elemental composition (Brett, 1993; Brett and Müller-Navarra, 1997; Hastings and Conrad, 1979; Sterner and Hessen, 1994). Structures at various scales – ranging from molecules to organelles, cells to organs – vary markedly in elemental composition. These differences may be linked to specific physiological functions (Elser et al., 1996), but are also shaped by the competition with other species and interactions with the environment (Elser and Urabe, 1999). Nutrient stoichiometry considers the constraints and consequences of mass balance of multiple chemical elements in ecological interactions (Elser and Urabe, 1999; Elser et al., 1996; Hessen, 1997; Sterner et al., 1995). This theory began after the realization of the fundamental problems arising when describing ecosystems in only one currency (Elser et al., 1996; Mansson and McGlade, 1993). For example, the inability to capture trophic biomass accumulation in energy-based system conceptualizations prompted modelers to consider multi-currency strategies to further understand ecological/evolutionary processes (Krebs and Houston, 1989). Elemental (nitrogen or phosphorus) disparities between producers and grazers may be more important than available energy in determining reproductive success. As such, zooplankton production may be limited by algal mineral phosphorus, as grazer stoichiometry remains reasonably constant while grazed seston nutrient content can be quite variable (Brett et al., 2000).

Recently, however, an alternative hypothesis has emerged, challenging the role of ecological stoichiometry as the primary regulatory factor of mass and energy flow across the food web. Many researchers now believe additional factors may play a role in producer–grazer dynamics, such as the biochemical food quality. Highly unsaturated fatty

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acids (HUFAs) are nutritionally critical molecules transferred across the plant–animal interface (Dalsgaard et al., 2003; Graeve et al., 1994), many of which cannot be synthesized by animals. Empirical findings suggest HUFAs may be strongly correlated with lake trophic status (Müller-Navarra et al., 2004). Müller-Navarra et al. (2004) reported a decrease in algal HUFA concentrations as lakes became increasingly eutrophic. While few experimental studies have followed up, preliminary modeling work on biochemical food quality suggest food webs with high (biochemical) quality primary producers may yield inverted distributions, i.e., large grazer biomass supported by a comparatively low autotrophic biomass (Danielsdottir et al., 2007; Perhar and Arhonditsis, 2009). The physiologically active essential fatty acids in animals are eicosapentaenoic acid (EPA 20:5ω3), docosahexaenoic acid (DHA 22:6ω3) and arachidonic acid (ARA 20:4ω6) (Sargent et al., 1999). These HUFAs have been linked to species growth, reproductive success, and neural development in both zooplankton and fish (Brett et al., 2006; Ravet et al., 2003; Sargent et al., 1999). The HUFA 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; Brett et al., 2000; DeMott and Müller-Navarra, 1997).

The assumption of a rigid ecological stoichiometry was first relaxed in the mathematical depictions of phytoplankton dynamics (Zhao et al., 2008a). Referred to in the contemporary literature as phytoplankton cell quotas or intracellular storage, internal nutrient reserves provide a more vivid look into the cell structure and functioning relative to the ambient conditions (Droop, 1968). The premise of quota flexibility assumes species with rigid resource requirements (i.e., low quota flexibility) suffer decreases in growth rate when experiencing low nutrient levels, while organisms with high quota flexibility can alter cellular requirements to offset decreased nutrient availability and minimize the effects on growth rate (Goldman and McCarthy, 1978). Algae may adapt to low nutrient availability through changes in form, structure, and function to enhance procurement, storage, and utilization of resources. For an algal species to become dominant in a resource-limited environment, it is critical to maintain a positive net growth (Turpin, 1988). Empirical studies have shown maximum specific uptake rates increase under severe limitation (Gotham and Rhee, 1981; Perry, 1976; Riegman and Mur, 1984), while others argued against the idea of transport adaptation in favor of quota adjustment (Turpin, 1988). Namely, low quota flexibility species lead to a tight link between uptake and growth, whereas growth can be more independent of uptake if quota flexibility is high. When resource-limiting conditions are experienced, an organism with low minimum nutrient requirements is expected to be more competitive than one with higher basal metabolic losses. Organisms with high optimal nutrient values may not achieve maximum growth until ambient conditions are favorable and could be outcompeted by individuals with lower optimal requirements.

Attempts to revisit the concept of rigid zooplankton stoichiometry began with Andersen's (1997) homeostatic *Daphnia* model. Later work by Anderson et al. (2005) modeled the nutrient content of consumers as a function of several biological processes, such as assimilation of ingested substrates, respiration, protein turnover, additional basal costs (e.g., osmoregulation), and biomass production. The authors underscored the importance of food quality even when intake is quantitatively low, due to the considerable maintenance costs of non-carbon substrates. Mulder and Bowden (2007) modeled grazer carbon production efficiency as a function of both phytoplankton and zooplankton stoichiometries. A regulatory coefficient that depicted the degree of homeostasis in an organism was also used to establish quasi-dynamic zooplankton stoichiometries (Sterner and Elser, 2002). The consideration of physiological limits to resource storage indicated that zooplankton minimum and optimum quotas (and their respective flexibilities) may govern the capacity of an individual to remain competitive under resource-limiting conditions. Mulder and Bowden's (2007) dynamic stoichiometry model matched the empirical data used reasonably well (DeMott et al., 1998, 2004), thereby offering insights into the ecological implications of dynamic producer and consumer stoichiometries.

In the present study, we take a HUFA explicit look into the predictive statements made by a NPZD mathematical system (Perhar and Arhonditsis, 2012; Perhar et al., 2012). Our first objective is to conduct a detailed sensitivity analysis of the plankton model after the addition of the HUFA submodel. We then examine the ecological implications of several contemporary HUFA-related hypotheses and address critical questions regarding the evolutionary impacts of different internal resource management strategies in zooplankton. What are the ramifications of relaxing intra-organism homeostatic rigidity at the population-level? Which are the primary factors that control congener bioconversion rates and resource quota flexibility? We also attempt to elucidate the primary drivers of planktonic processes under different nutrient loading regimes by focusing on the causal association between seston biochemical quality and lake trophic status. Finally, we draw parallels between our model predictions and empirical findings from the planktonic food web literature, while underscoring the interplay between intra-organism level processes and macro-ecological parameterization.

2. Model description

Substantial emphasis has been placed into modeling the physical and biochemical basis of algal food quality to herbivorous zooplankton (Danielsdottir et al., 2007; Loladze et al., 2000; Perhar and Arhonditsis, 2009, 2012; Perhar et al., 2012, Sterner and Hessen, 1994; Zhao et al., 2008b). To explicitly test the HUFA-related aspects of food quality, we have considered a planktonic food web model with an enhanced zooplankton compartment that accounts for intra-organism processes governing the fate of ingested resources. Mathematical descriptions of the HUFA explicit submodel and host plankton model are listed in Tables 1 and 2, respectively. The host model, into which we are plugging our submodel, is a zero dimensional, seasonally unforced nutrient–phytoplankton–zooplankton–detritus (NPZD) model approximating pelagic conditions (see Perhar and Arhonditsis, 2009). Mitra and Flynn (2007) argue that interactions take place at the particle/individual level, yet most models track biomass. In an attempt to bridge the gap between the two modeling strategies, our approach combines aspects of the individual animals into a population model (see Fig. 1 for model layout). Our zooplankton growth is dependent upon a series of internal processes, such as the biomass and moult turnover, hormone production, stoichiometrically regulated nutrient release, and substrate bioconversion (Perhar et al., 2012). Population-level parameter information was readily available in the literature, but physiological parameters proved to be more difficult, especially those directly related to the handling of HUFAs. As a result, we established educated guesses for threshold quantities (e.g., minimum and optimal HUFA quota) and physiological processes (e.g., turnover rate, bioconversion rate and efficiency).

In tracking food particles through a zooplankter's gut, a fraction of grazed seston is assimilated based on its morphological characteristics (see also Table 1). The ingested material is then separated into three distinct internal pools (phosphorus, EPA, DHA). These pools are first used to address maintenance requirements in the forms of biomass and moult turnover. The fate of dissolved organic turnover release depends on substrate type. That is, phosphorus may be subjected to recycling, bacterial mineralization and eventual uptake by phytoplankton (Table 2), whereas HUFA release is assumed to be permanently lost from the system (Fig. 1). The remaining quantities in the assimilated pools are incorporated into the internal reservoirs. We have accounted for the interplay among the various resource pools, namely, bioconversion of shorter-chained polyunsaturated fatty acids (PUFAs) into EPA, and bioconversion of EPA into DHA

Table 1
Zooplankton submodel with explicit biochemical considerations on somatic growth.

- Zooplankton growth as a function of *P*, *EPA*, *DHA* somatic content

$$Growth = \pi \cdot \min(g_{LIM1}, g_{LIM2}, g_{LIM3}),\quad 0 \le g_{LIM1}, g_{LIM2}, g_{LIM3} \le 1$$

- Zooplankton *P* limitation

$$g_{LIM1} = \frac{P_{INT} - P_{\min}}{P_{opt} - P_{\min}}$$

- Zooplankton *EPA* limitation

$$g_{LIM2} = \frac{EPA_{INT} - EPA_{\min}}{EPA_{opt} - EPA_{\min}}$$

- Zooplankton *DHA* limitation

$$g_{LIM3} = \frac{DHA_{INT} - DHA_{\min}}{DHA_{\mathrm{opt}} - DHA_{\min}}$$

- Zooplankton assimilation rate

$$As_C = \frac{\lambda \alpha_C \left(\omega_{PHYT} PHYT^2 + \omega_{DET} DET^2\right)}{\mu^2 + \omega_{PHYT} PHYT^2 + \omega_{DET} DET^2}$$

- Carbon assimilation efficiency

$$\alpha_C = \frac{\alpha_{C1} FQ_{TOT}}{\alpha_{C2} + FQ_{TOT}}$$

- Seston food quality as a function of its *P* content

$$\text{If } \mathrm{GRAZ_P} \le P_{\min},\quad Z_{PLIM} = \frac{GRAZ_P}{P_{\min}}$$
$$\text{If } \mathrm{GRAZ_P} > P_{\min},\quad Z_{PLIM} = 1$$

- Food quality concentration as a function of seston abundance and nutritional quality

$$FQ_{TOT} = \left[\left(FQ_i{}^2 \sqrt{PHYT_i}\right) + \left(FQ_{DET}{}^2 \sqrt{DET}\right)\right] Z_{PLIM}$$

- Grazed *P* per unit of carbon

$$GRAZ_P = \frac{\omega_{PHYT} PHYT^2 PC_{PHYT} + \omega_{DET} DET_C DET_P}{\omega_{PHYT} PHYT^2 + \omega_{DET} DET_C{}^2}$$

- Grazed EPA per unit of carbon

$$GRAZ_{EPA} = \frac{\omega_{PHYT} PHYT^2 f_{EPA:C} + \omega_{DET} DET_C{}^2 s_{EPA:C}}{\omega_{PHYT} PHYT^2 + \omega_{DET} DET_C{}^2}$$

- Grazed DHA per unit of carbon

$$GRAZ_{DHA} = \frac{\omega_{PHYT} PHYT^2 f_{DHA:C} + \omega_{DET} DET_C{}^2 s_{DHA:C}}{\omega_{PHYT} PHYT^2 + \omega_{DET} DET_C{}^2}$$

- Selective-feeder preference of phytoplankton; see Table 3 for filter-feeder specification.

$$\omega_{PHYT} = \frac{pref_p PHYT}{pref_p PHYT + pref_d DET_C}$$

- Selective-feeder preference of detritus; see Table 3 for filter-feeder specification

$$\omega_{DET} = \frac{pref_d DET_C}{pref_p PHYT + pref_d DET_C}$$

- Post-maintenance *P*, *EPA*, *DHA* internal pool
- *P*, *EPA*, *DHA* mass balance in the zooplankton body

$$P_{PM} = As_C GRAZ_P - P_{INT}(\tau_P(1-m) - m\tau_m)$$

$$\text{If } EPA_{PM} \le thresh,\ \frac{dP_{INT}}{dt} = P_{PM} - \mathrm{P_{INT}}\ \mathrm{Growth} - P_{INT}\chi$$

$$EPA_{PM} = As_C \cdot f_{EPA:Ci} - EPA_{INT}\ [\tau_{epa}(1-m) - m\tau_{\mathrm{m}}] - \varepsilon J_{PUFA}\rho + (1-\varepsilon) J_{\mathrm{PUFA}}\rho \quad \frac{dEPA_{INT}}{dt} = EPA_{PM} - EPA_{\mathrm{INT}} Growth - EPA_{INT} h$$

$$DHA_{PM} = As_C \cdot f_{DHA:Ci} - DHA_{INT}\ [\tau_{dha}(1-m) - m\tau_{\mathrm{m}}] + \varepsilon J_{\mathrm{PUFA}}\rho\nu \quad \frac{dDHA_{INT}}{dt} = DHA_{PM} - DHA_{INT} Growth - DHA_{INT} h.$$

Else,

$$EPA_{PM} = (1-e_1)[As_C GRAZ_{EPA} - EPA_{INT}(\tau_{EPA}(1-m) - m\tau_m)]$$
$$DHA_{PM} = As_C GRAZ_{DHA} - DHA_{INT}(\tau_{DHA}(1-m) - m\tau_m) + \nu e_1[As_C GRAZ_{EPA} - EPA_{INT}(\tau_{EPA}(1-m) - m\tau_m)].$$

(an energetically expensive, yet not uncommon process; Persson and Vrede, 2006). Internal quotas control the animal's realized growth rate, in a fashion similar to algal growth modeled by Grover (1991) in his variable internal stores (VIS) model. Before growth, however, internal resources are taxed for hormonal and reproductive requirements from the EPA and DHA pools, and stoichiometrically regulated release of phosphorus. The logic governing the aforementioned processes determines the fitness level of the individual zooplankter (Fig. 2).

Zooplankton species can potentially assess seston food quality and dynamically allocate substrate between somatic and reproductive requirements (Wacker and Martin-Creuzburg, 2007). We consider animal growth limitations imparted by internal phosphorus, EPA, and DHA levels. These limitations are controlled by actual, optimal, and minimum somatic quotas. Critical thresholds (parameter thresh) were created to delineate a series of decisions made by a zooplankter and determine its response to the prevailing trophic conditions (Fig. 2 and Table 3). The default model setting is to consider a zooplankter that operates under favourable environmental conditions, such that ingested food is adequate across all nutritional factors considered (i.e., EPA, DHA, phosphorus), thus allowing the animal to perform maintenance and somatic growth without switching off regulatory release and hormone production or requiring to elongate PUFAs. In the logic sequence determining when to shut off somatic processes, somatic phosphorus quota is first addressed; if the saturation fraction is below a prespecified threshold (threshold values were set to 0.05 for each congener across both zooplankton species due to lack of data), then stoichiometrically regulated release/excretion is reduced. The first HUFA quota to be examined is DHA; if the internal content exceeds the optimal quota, elongation from EPA is turned off and no further reactions/regulations are applied. In a similar manner, if the DHA saturation fraction is less than the defined threshold value, DHA contribution to hormone production and reproduction is reduced. Next the animal considers EPA; if internal EPA quota exceeds the optimal, elongation from PUFAs to EPA is turned off, and a fraction of EPA is elongated to DHA. If the internal EPA quota is low (i.e., the EPA saturation fraction is lower than the threshold value assigned), EPA sinks in the forms of hormone production and DHA bioconversion are reduced and turned off, respectively. Thus, depending on the path chosen, EPA elongation into DHA may or may not occur, and molecules converted into DHA may have origins as PUFAs or EPA (Fig. 2).

Table 2
Specification of host NPZD model.

$$\frac{dZOOP}{dt} = ZOOPGrowth - d\frac{ZOOP^3}{pred^2 + ZOOP^2}$$

$$\frac{dPHYT}{dt} = \frac{PO_4}{e + PO_4}\ \frac{a}{b + cPHYT} PHYT - rPHYT - \frac{\lambda \omega_{PHYT} PHYT^2}{\mu^2 + \omega_{PHYT} PHYT^2 + \omega_{DET} DET_C{}^2} ZOOP - (s+k)PHYT$$

$$\frac{dDET_C}{dt} = rPHYT + \frac{\left[(1-\alpha_C)\omega_{PHYT} PHYT^2 - \alpha_C \omega_{DET} DET_C^2\right]\lambda}{\mu^2 + \omega_{PHYT} PHYT^2 + \omega_{DET} DET_C{}^2} ZOOP - (k + \varphi + \psi) DET_C$$

$$\frac{dDET_P}{dt} = rPHYT\ PC_{PHYT} + \frac{\left[(1-\alpha_C)\omega_{PHYT} PHYT^2 PC_{PHYT} - \alpha_C \omega_{DET} DET_C DET_P\right]\lambda}{\mu^2 + \omega_{PHYT} PHYT^2 + \omega_{DET} DET_C{}^2} ZOOP\ \ - (k + \varphi + \psi) DET_P$$

$$\frac{dPO_4}{dt} = -\frac{PO_4}{e + PO_4}\ \frac{a}{b + cPHYT} PC_{PHYT} PHYT + \gamma d \frac{ZOOP^3}{pred^2 + ZOOP^2} P_{INT} + \phi DET_P + k(PO_{4(hypo)} - PO_4) + DOP_{RECYCLE} DOP_{RELEASE}$$

$$DOP_{RELEASE} = [P_{INT}(\tau_P(1-m) - m\tau_m) + P_{INT}\chi] ZOOP$$

3. Mathematical procedure and analysis

We used the fourth-order Runge–Kutta solver in Matlab's ordinary differential equation toolbox, with a time step of 0.1 days; we deduced experimentally that a step size of 0.1 days presented an ideal tradeoff between resolution and computational time. We ran the model for 5000 days (time units), to ensure the system had settled to equilibrium (steady state or oscillatory) by the last 500 days, which were then used to derive three summary statistics

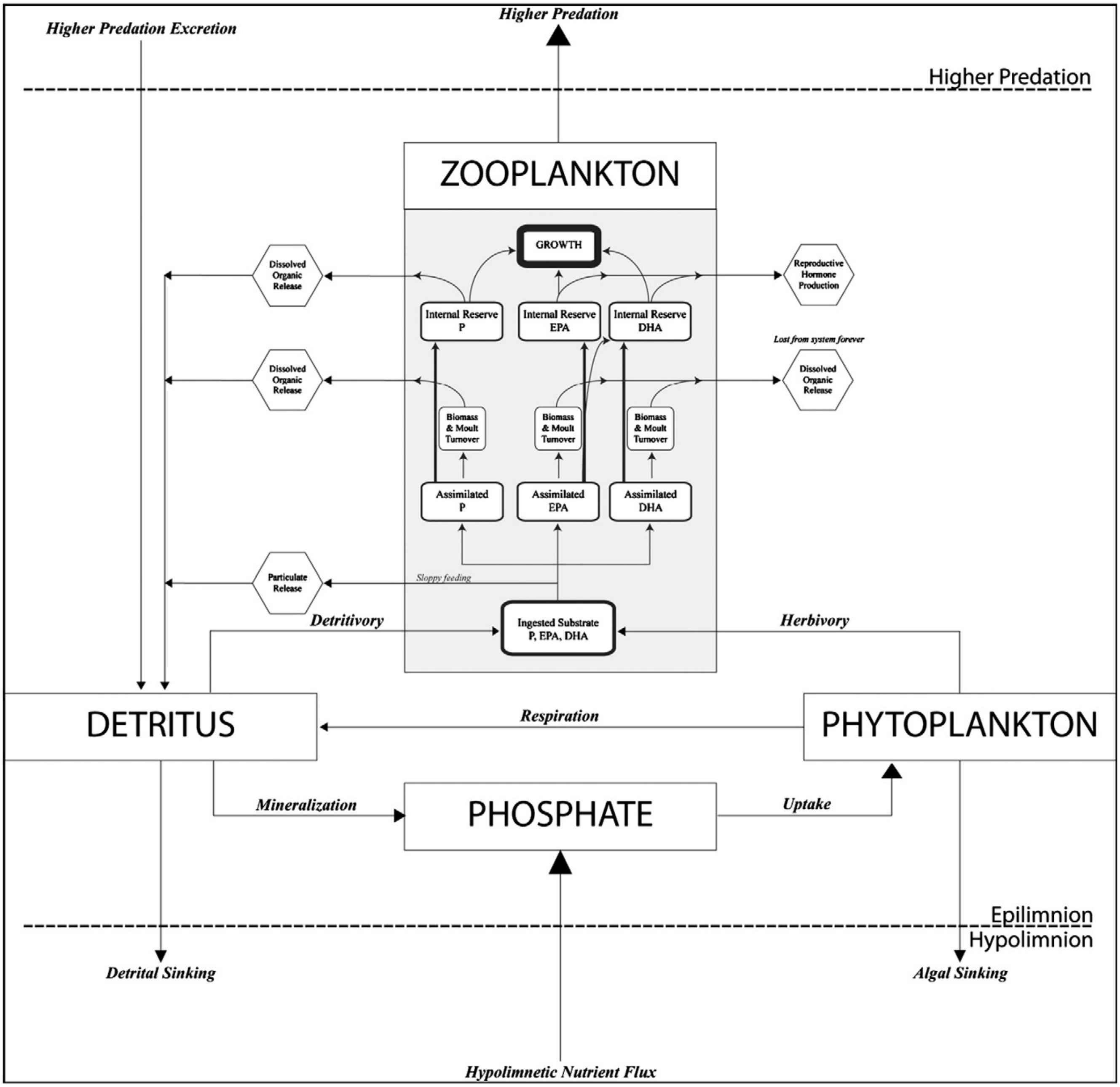


Fig. 1. Model flow diagram illustrating the mass fluxes within a limiting nutrient–phytoplankton–zooplankton–detritus system. Intra-organism processes are illustrated in the zooplankton compartment and determine the grazer interactions with the rest compartments.

(i.e., mean, minimum, and maximum values) for each state variable. In cases of oscillatory behaviour, we used the minimum and maximum values to characterize the oscillation limits.

Similar to Perhar and Arhonditsis (2009), we defined three phytoplankton characterizations: diatom-like, cyanobacteria-like, and an intermediate species. The diatom-like species are modelled after r-selected algae, with high growth, respiration, and sinking rates, superior phosphorus uptake kinetics and large HUFA concentrations. Conversely, we model cyanobacteria as K-selected species, with slower growth, respiration and sinking rates, inferior phosphorus uptake kinetics and virtually barren of HUFAs. The intermediate species are considered to bridge the transitional gap between diatoms and cyanobacteria, and we set their HUFA characteristics as chlorophyte-like (see Table 4 for phytoplankton parameterizations). Zooplankton species are classified as either filter or selective feeders, loosely resembling cladocerans and copepods, respectively. Filter feeders are assumed to have non-discriminate food preference, high grazing and fecundity rates, and high somatic EPA and phosphorus requirements. We model food selectivity as a combined effect of abundance and relative preference for food items of higher nutritional quality. Our selective feeders are modeled to exhibit a preference for high food quality, have low grazing and fecundity rates, and high somatic DHA requirements (see Table 3 for zooplankton parameterizations). In this model, detritus can be thought of as dead or dying organic matter of autochthonous origin with good or poor food quality. Detrital nutritional quality is determined by the EPA and DHA content, and the morphological properties that shape the detritus ingestibility and digestibility (Table 5).

We examined the ecological patterns associated with continuums that depicted different planktonic food web configurations (three phytoplankton, two zooplankton, and two detritus food quality parameterizations). A continuum is defined as a continuous shift in parameters from one species to another, over the course of 100 intervals.

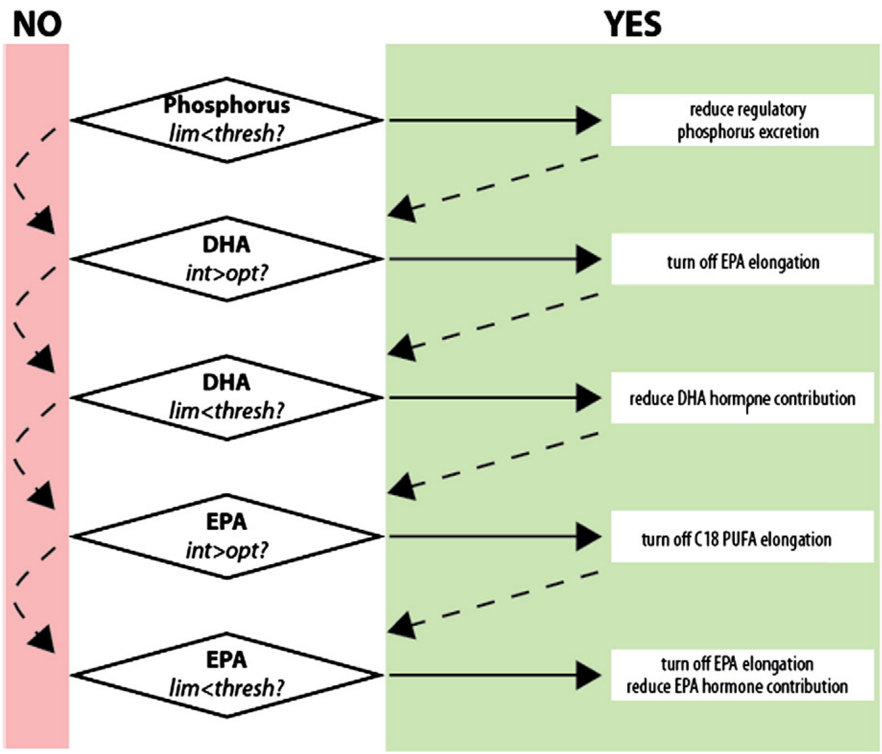


Fig. 2. Decision diagram governing the somatic structure of our grazer. Somatic processes such as bioconversion, hormone production and regulatory excretion are triggered by somatic resource availability. Physiological responses are determined by comparing resource quota (int) to optimal quota (opt), and/or comparing growth limitation by a particular resource (e.g., g_{LIMi}) to a prespecified threshold value (thresh).

Algae are defined by 11 parameters shifted linearly during our experiments (see Table 4). At one end of the algal continuum (=1), phytoplankton species are defined as diatom-like, the middle point (=50) refers to intermediate species, and the other end (=100) corresponds to the cyanobacteria-like characterization. For example, point 25 on the algal continuum represents a species with parameters set exactly half-way between the diatom-like and intermediate phytoplankton characterizations. Similarly, the zooplankton continuum accounts for shifts from filter feeders (1) to selective feeders (100), and the detritus continuum from poor (1) to good (100) food quality. While our species continuums admittedly have inherent drawbacks, we believe that this approach allows exploring the parameter space in a continuous fashion and could conceivably pinpoint critical threshold conditions at which system dynamics rapidly shift. Static parameters not used in continuums or examined in our experiments are reported in Table 6.

In this study, we first present unidimensional sensitivity analyses that stretch one parameter at a time across mathematically possible

Table 3
Zooplankton parameterization for a filter-feeder and a selective feeder.

Parameter	Symbol	Filter feeder[a]	Selective feeder[b]	Units
Minimum somatic phosphate quota	P_{min}	0.009	0.003	mg P (mg C)$^{-1}$
Optimal somatic phosphate quota	P_{opt}	0.05	0.03	mg P (mg C)$^{-1}$
Minimum somatic EPA quota	EPA_{min}	0.0007	0.0008	mg EPA (mg C)$^{-1}$
Optimal somatic EPA quota	EPA_{opt}	0.0082	0.008	mg EPA (mg C)$^{-1}$
Minimum somatic DHA quota	DHA_{min}	0.0001	0.0017	mg DHA (mg C)$^{-1}$
Optimal somatic DHA quota	DHA_{opt}	0.0014	0.0166	mg DHA (mg C)$^{-1}$
Phosphate turnover rate	τ_p	0.1	0.3	day^{-1}
EPA turnover rate	τ_{epa}	0.1	0.1	day^{-1}
DHA turnover rate	τ_{dha}	0.1	0.0184	day^{-1}
Somatic moult fraction	m	0.05	0.05	dimensionless
Somatic moult rate	τ_m	0.05	0.05	day^{-1}
Fraction of EPA elongated	e_1	0.05	0.9	dimensionless
Efficiency of EPA elongation	v	0.5	0.9	mg DHA (mg EPA)$^{-1}$
Efficiency of PUFA elongation	ρ	0.5	0.5	dimensionless
HUFA hormone production rate	h	0.8	0.4	day^{-1}
Excretion rate	x	0.25	0.25	day^{-1}
Maximum grazing rate	λ	0.6	0.4	day^{-1}
Zooplankton grazing half saturation constant	μ	0.035	0.035	mg CL^{-1}
Regeneration rate of predation excretion	γ	0.6	0.6	day^{-1}
Maximum growth rate	π	0.9	0.6	day^{-1}
Zooplankton growth efficiency	α_{C1}	0.9	0.9	dimensionless
Zooplankton growth half saturation constant	α_{C2}	0.03	0.03	$\sqrt{\text{mg CL}^{-1}}$
Congener limitation threshold	$thresh$	0.05	0.05	dimensionless

[a] Cladoceran-like grazer with non-discriminate food preference; high grazing and fecundity rates; high somatic EPA and phosphorus requirements.
[b] Copepod-like grazer with intelligent food preference for higher quality prey; low grazing and fecundity rates; high somatic DHA requirement.

Table 4
Phytoplankton parameterization for a diatom-like, intermediate, and cyanobacteria-like species.

Parameter	Symbol	Diatom*	Chlorophyte**	Cyanobacteria***	Units
Maximum growth rate	a	0.25	0.2	0.1	day^{-1}
Respiration rate	r	0.18	0.14	0.05	day^{-1}
Sinking loss rate	s	0.15	0.08	0.001	day^{-1}
Algal food quality	FQ_i	0.8	0.5	0.2	Dimensionless
Phosphate uptake 1/2 saturation constant	e	0.01	0.018	0.03	$mg\ P\ L^{-1}$
Self-shading coefficient	c	0.5	0.35	0.05	$m^2(mg\ C)^{-1}$
Algal EPA content	$f_{EPA:C}$	0.05	0.002	0.015	$mg\ EPA\ (mg\ C)^{-1}$
Algal DHA content	$f_{DHA:C}$	0.02	0.001	0	$mg\ DHA(mg\ C)^{-1}$
Algal P content	PC_{PHYT}	0.015	0.015	0.015	$mg\ P\ (mg\ C)^{-1}$
Algal C18 PUFA content	f_{PUFA}	0.0029	0.0255	0.007	$mg\ C18(mg\ C)^{-1}$
Cladoceran grazing preference (algae)	$pref_p$	0.5	0.5	0.5	Dimensionless
Cladoceran grazing preference (detritus)	$pref_d$	0.5	0.5	0.5	Dimensionless
Cladoceran grazing preference (algae)	$pref_p$	0.9	0.75	0.3	Dimensionless
Cladoceran grazing preference (detritus)	$pref_d$	0.1	0.25	0.7	Dimensionless

*r-strategist; high food quality, easily ingestible, HUFA-rich algae.
**Intermediate algal parameterization specified with chlorophyte HUFA concentrations.
***K-strategist; low food quality, low ingestibility, HUFA poor algae.

(but not always ecologically/physiologically plausible) ranges, while keeping everything else constant. [Literature ranges for all the parameters introduced by the zooplankton growth mechanistic model are provided in the Electronic Supplementary Material.] Resultant dynamics are therefore entirely attributed to the parameter being analyzed. Dynamics from one-dimensional sensitivity scans using a continuum are attributed to the changing characteristics of a group of parameters, classifying phytoplankton, zooplankton or detritus. In two-dimensional settings, we tested two parameters as well as two continuums against one another. The latter experiments were more useful to test system response to hypothetical ecological scenarios (e.g., a degrading algal base against a shifting grazer community). All figures are plotted using summary data from time series analyses. One-dimensional plots illustrate steady state equilibrium using one solid line, and oscillations with two solid lines (representing minimum and maximum limits of oscillations taken from time series analyses). In two-dimensional plots, the mean values are represented with a colour map; oscillatory regions are bound in a white contour, and colour map values contained within bound regions represent mean values of oscillatory behaviour.

4. Results and discussion

4.1. Sensitivity analysis

Model sensitivity to the new parameters introduced with the HUFA submodel was examined with the "one parameter at a time" approach, i.e., one parameter was tested at a time and the rest of the parameter vector was kept constant at default values (Tables 2–4). While a pragmatic approach to analyze the impact of the additional complexity associated with the HUFA component, we caution that this strategy fails to capture the interactive effects among the different parameters and thus the inference drawn about the role of individual parameters is conditional upon the values assigned to the rest of the vector. We employed combinations of a generic filter feeding zooplankter with different phytoplankton characterizations (see Tables 2 and 3 for zooplankton and phytoplankton parameter specifications, respectively). Our parameterization of a filter feeder resembles to a cladoceran-like grazer, i.e., one that has a non-discriminate food preference, high grazing and fecundity rates, high EPA and low DHA somatic concentration. The high fecundity rate also carries a high somatic phosphorus requirement (Elser et al., 1996; Sterner et al., 1995). We spanned the entire range of mathematically possible – though not necessarily ecologically plausible – parameter values to gauge system response to the availability of both biochemical molecules and nutrients. We conducted several numerical experiments that assessed an assortment of physiological processes, i.e., zooplankton somatic turnover rates vs. algal substrate concentration (Fig. 3a–r), EPA–DHA bioconversion fraction vs. bioconversion efficiency (Fig. 3s–x), and hormone production rate vs. stoichiometrically regulated release rates (Fig. 3y–ad).

4.1.1. Resource availability and somatic turnover

Interactions between animals and their environment may be influenced by consumer-driven nutrient recycling (Elser et al., 1996). One form of nutrient recycling is somatic turnover. In a physiological context, turnover reflects the loss of substrate as a consequence of respiration or the release of old material as new matter is assimilated (Lee et al., 1971). Release of HUFAs could also coincide with organic phosphorus release in the form of damaged membrane particles (i.e., phospholipids). Life history characteristics may shed light on zooplankton physiological requirements and substrate handling. Cladocerans, for example, can be generalized as fast growing, fast maturing individuals with multiple generations per growing season (Dodson and Frey, 2001). Conversely, copepods are slower growing, metamorphic animals which complete only one or two generations per growing season (Williamson and Reid, 2001). Cladocerans require more phosphorus than copepods (Andersen and Hessen, 1991), and the increased demands are linked to protein synthesis in ribosomes which in turn is closely associated with their capacity to achieve faster growth rates (Main et al., 1997). Both EPA and DHA have important roles in phospholipids (Smyntek et al., 2008), but while EPA can be mobilized liberally for eicosanoid and hormone production (Gurr et al., 2002), DHA is retained in membranes and spared conservatively (Stillwell and Wassall, 2003). Daphnia tend to accumulate EPA, possibly due to EPA's role in organism growth and reproduction (Becker and Boersma, 2003; Müller-Navarra

Table 5
Detritus parameterization defining good and poor quality.

Parameter	Symbol	Good	Poor	Units
Food quality	FQ_{DET}	0.8	0.2	Dimensionless
Seston EPA content	$S_{EPA:C}$	0.01	0.00001	$mg\ EPA(mg\ C)^{-1}$
Seston DHA content	$S_{DHA:C}$	0.01	0.00001	$mg\ DHA(mg\ C)^{-1}$

Table 6
Default parameter values of the plankton model.

Parameter	Symbol	Default	Units
Background light attenuation	b	0.05	m^{-1}
Higher predation rate on zooplankton	d	0.05	day^{-1}
Hypolimnion phosphate loading	$PO_{4(hypo)}$	0.2	$mg\ P\ L^{-1}$
Half saturation constant zooplankton predation	pred	0.03	$mg\ C\ L^{-1}$
Detritus remineralization rate	φ	0.17	day^{-1}
Detritus sinking rate	ψ	0.3	day^{-1}
Cross thermocline exchange rate	k	0.05	day^{-1}
Mineralization rate of DOP release	$DOP_{RECYCLE}$	0.5	Dimensionless

et al., 2000). Freshwater copepods overwinter actively and tend to accumulate DHA, suggestive of DHA's role as an anti-freeze agent that ensures membrane fluidity in cold climates (Farkas, 1979; Stillwell and Wassall, 2003).

Our model treats HUFAs and nutrients as interacting essential resources. Zooplankton parameterization governs the extent to which each substrate is important, and therefore which food source is the most valuable (Table 4). Diatoms are rich in EPA and DHA, and are generally considered an excellent food source for zooplankton (Brett and Müller-Navarra, 1997). Our system was largely insensitive to EPA turnover rate and EPA concentration in diatoms (Fig. 3a and b), exhibiting small amplitude oscillations in response to extremely high values of EPA turnover. The lack of response to the variability in EPA somatic content may be partly driven by our univariate sensitivity analysis. That is, the repercussions of extremely low algal EPA:C on the prey–predator dynamics could have been moderated by the default values assigned to PUFA somatic content. The system also showed no quantitative response to the variations of DHA turnover rate or DHA concentration in diatoms (Fig. 3g and h). Unlike EPA and DHA, the absence of internal mechanisms to replenish the somatic P pool resulted in markedly different responses. In particular, our model exhibited an inverted food web biomass distribution at low P turnover rates and producer accumulation at higher levels of P turnover (Fig. 3m). Our planktonic system was also tightly linked to the variability of the algal phosphorus content (Fig. 3n). Zooplankton production was limited at low P:C levels and was stimulated by the algal phosphorus increase shortly after a transitional zone of oscillatory behavior.

Chlorophytes contain significantly less EPA and DHA than diatoms do, but are extremely rich in PUFAs (Brett and Müller-Navarra, 1997; Wacker and Martin-Creuzburg, 2007). Zooplankton with enhanced capacity to convert PUFAs to HUFAs may benefit from a chlorophyte-rich diet. Yet, the zooplankton parameterization used for this simple unidimensional exercise apparently minimized the interplay between the internal EPA and DHA pools through a low bioconversion rate. Consequently, increased EPA:C had little impact on the internal DHA pool, thus imparting little to no impact on grazer biomass (Fig. 3d). Our model's inability to retro-convert DHA to EPA rendered a higher somatic DHA:C also ineffective in enhancing the grazer biomass (Fig. 3j). The variability of the somatic EPA and DHA turnover rates with a chlorophyte-based diet induced a wide range of plankton responses (Fig. 3c and i). In particular, we note the somewhat counterintuitive pattern associated with the variations of the EPA turnover rate, which was characterized by shifts between oscillatory regions, steady equilibria, and back to oscillations. Generally, zooplankton response to the variability of the phosphorus content of a chlorophyte-rich diet was qualitatively similar to that of a diatom-rich diet (Fig. 3o and p).

Cyanophytes contain trace EPA amounts and are reasonably stocked with PUFAs, but contain virtually no DHA—problematic for grazers with high somatic DHA requirements (Brett et al., 2006). The system showed little (if any) response to substrate turnover, always exhibiting biomass accumulation in the first trophic level (Fig. 3e, k, and q). Likewise, algal biochemical content had little impact on zooplankton when feeding on cyanophytes (Fig. 3f, l, and r). Most notably, cyanophytes with a high EPA:carbon ratio destabilized the system into limit cycle oscillations (Fig. 3f). While somatic turnover rates and algal resource concentration parameters alone impart little effect on overall system functioning, our results suggest that even with our univariate strategy, subtle changes in animal physiology or prey resource content are least effective under extreme scenarios (i.e., high quality diatoms and low quality cyanophytes), and have greatest impact with intermediate quality prey (i.e., chlorophytes). In other words, our results suggest algal food bases commonly associated with oligotrophic and hyper-eutrophic conditions may be the most resilient against changes of the plankton characterization associated with the parameters tested. Diatoms were postulated to be a rich food source, and thus subtle shifts in their resource content (or the somatic handling of said resources) had little effect. In a similar manner, cyanophytes were such a poor food choice that variations in the properties tested were unable to strengthen the algal–grazer coupling. Chlorophytes were an intermediate food source and may render a food web that more faithfully depicts the physiological adaptations of the plankton communities.

4.1.2. HUFA bioconversion

Studies have shown that DHA-accumulating zooplankton, such as freshwater copepods, exhibit DHA enrichment even when fed upon EPA-rich food sources, and this pattern was interpreted as evidence of EPA elongation into DHA (Persson and Vrede, 2006; Ravet et al., 2010). Our HUFA submodel accounts for this one-way conversion via two parameters: fraction of EPA elongated to DHA (e_1) and elongation efficiency (v). As previously mentioned, the former parameter is controlled by a series of logic rules (see Fig. 2), and represents the fraction of remaining EPA converted to DHA after maintenance requirements are met. Several studies have also suggested the energetic costs of such conversion may be high (DeMott and Müller-Navarra, 1997; Kainz et al., 2004; von Elert, 2002). To accommodate this notion, we have included an efficiency term to tax the bioconverted substrate via respiration, i.e., substrate subject to elongation that is not converted to DHA is assumed to be lost via respiration. A diatom-rich diet represents a source of EPA and DHA for the grazer, and thus somatic elongation to DHA may not be as essential as in a diet lacking DHA (e.g., chlorophytes). Consequently, zooplankton response to the variations of the corresponding parameters was fairly minimal with a diatom-rich diet (Fig. 3s and t), but was more sensitive when assuming a chlorophyte-based diet (Fig. 3u and v). As the fraction of EPA elongated to DHA was increased, the chlorophyte-dominated system became more stable. Zooplankton feeding on a cyanophyte-rich diet exhibited a drastic and erratic response to the EPA fraction elongated (Fig. 3w). In each instance, the efficiency of elongation was either uninfluential (Fig. 3t and x) or the impact was very minute (Fig. 3v), making the elongation fraction the primary (and perhaps only) influential bioconversion parameter considered (see also the Bioconversion hypothesis section for further analysis).

4.1.3. Hormone production and nutrient regulation

In our model, two more processes that determine the fate of phosphorus and fatty acids in the animal body are the allocation of HUFAs for eicosanoid and hormone production, and the stoichiometrically regulated release of internal phosphorus. Studies have shown individuals allocate HUFAs for somatic functioning or reproductive processes (Wacker and Martin-Creuzburg, 2007), and that Daphnia egg composition is affected by maternal diet (Guisande and Harris, 1995; Guisande et al., 1999; Laabir et al., 1999). Clutch and mean egg size are also dependent on maternal diet (Guisande et al., 1996). Daphnia were shown to produce larger eggs when facing a food shortage, possibly in an attempt to produce fewer yet fitter offspring (Guisande and Gliwicz, 1992; Martin-Creuzburg et al., 2005). Higher food abundance yields larger clutches and smaller eggs (Wacker and Martin-Creuzburg, 2007), but egg-hatching success has been reported as being proportional to egg size (Hutchinson, 1967). Eggs represent a very large sink for EPA in mature female cladocerans, and may contain two to three times more than the somatic tissue (Wacker and Martin-Creuzburg, 2007).

While our model does not account explicitly for reproductive processes such as egg production, hatching and parthenogenesis, we do employ a proxy to reproduction via a HUFA requirement for hormone production. This first-order loss rate provides insight into somatic growth rather than reproduction, as it removes HUFAs from the internal pool governing growth. We tested model sensitivity to hormone production rates (Fig. 3y, aa, and ac), and found that zooplankton feeding on diatom and chlorophyte diets showed virtually no variation in response to differing hormonal production rates, maintaining inverted food web biomass distributions throughout the tested range. Zooplankton feeding on a cyanophyte-rich diet also showed no qualitative response to changing hormone production requirements, and consistently exhibited primary producer accumulation. Hormone production rate is a parameter heavily influenced by other physiological parameters (see logic diagram in Fig. 2), possibly explaining the lack of a system response. That is, the logic rules may have turned hormone production on (or off) based on somatic concentrations, regardless of the actual parameter value specified. Stoichiometric phosphorus release rate (Fig. 3z, ab, and ad) is also governed by a series of logic rules, and can be seen as a pressure release valve, whose only objective is to ensure somatic phosphorus remains between the minimum and optimal values as defined by the species characterization. A diatom-rich diet may act as a destabilization force of the planktonic food web, if the phosphorus release rate is high (Fig. 3z). Chlorophyte and cyanophyte diets showed little to no qualitative variation (Fig. 3ab and ad). Under the scenario of a diatom-rich diet, the zooplankton sensitivity to phosphorus excretion is consistent with the system response to the diatom phosphorus content (Fig. 3n). Founded upon the premise that phosphorus and fatty acids are interactively essential resources, our model predicts that diatoms may also be a sub-standard diet (or destabilization force), if their phosphorus content is low. Likewise, if the phosphorus internal management of the grazers is poor, they may not be able to fully capitalize on a nutritionally balanced diet.

4.2. Quota limit hypothesis

While modeling studies on phytoplankton internal nutrient management were first published over 4 decades ago (Droop, 1968), little effort has been made to unravel the impact of intra-organism resource management at the plant–animal interface. According to Brett et al. (2009), one of the outstanding questions related to zooplankton physiology focuses on the upper and lower bounds of internal HUFA storage, and how these limits impact individual performance and fitness. Shifting from a static consumer to a dynamic one poses several challenges that may be distinctly different from those encountered when conceptualizing a dynamic producer. Yet, we believe that certain lessons from phytoplankton ecology may be applicable. For example, Bold and Wynne (1978) report algae to be very diverse in cellular, molecular and genetic architectures, resulting in different nutrient requirements and quota bounds. In the same context, Grover's (1991) VIS model illustrated the link between nutrient quota flexibility and uptake in determining an individual's competitive capacity; we hypothesize the same may hold true between zooplankton somatic quotas and growth. Extrapolating this argument to zooplankton and organic compounds (i.e., HUFAs), we once again coupled a generic filter feeder with diatoms (Fig. 4a), chlorophytes (Fig. 4b), and cyanophytes (Fig. 4c). We ran two-dimensional phase space explorations, scanning minimum and optimal somatic EPA:carbon ratios, and then tracked changes in zooplankton biomass.

When feeding on EPA-rich prey (i.e., diatoms; Fig. 4a), the response of zooplankton to variations in minimum somatic EPA was fairly minimal, while optimal somatic EPA was more influential and delineated the region in which the grazer was satisfied. If the grazer is subjected to lesser food quality (i.e., chlorophytes and cyanophytes), our study suggests a stronger interplay between minimum and optimal somatic EPA concentrations (Fig. 4b and c). Generally, combinations of low minimum and optimum EPA resulted in high zooplankton abundance. According to our model specification, a low minimum internal quota is indicative of a species able to survive in substrate poor conditions by effectively allotting the available resources to growth and basal metabolism, while a low optimum quota allows an individual to achieve its maximum growth potential faster. These factors could also be associated with the organism size (an aspect not explored in this study), as larger individuals may also have higher absolute EPA requirements, e.g., when sexually mature females begin amassing HUFAs into eggs. Lower absolute EPA requirements could give smaller individuals (e.g., juvenile cladocerans) a competitive edge, assuming nearly equal growth rates (Dodson and Frey, 2001). In the latter case though, there is contradictory evidence suggesting that the opposite may also hold true, as juvenile zooplankters may require a higher HUFA:carbon ratio than their mature counterparts for proper development (Brett et al., 2009; Dodson and Frey, 2001). Cyanophyte-fed grazers showed an equal tradeoff between minimum and optimum somatic EPA (Fig. 4c, bottom left corner), until the minimum quota exceeds a certain threshold and subsequently becomes the primary regulatory factor of zooplankton abundance (i.e., see increased steepness of the isopleths in top right corner). A chlorophyte diet did not show this shift and exhibited a zooplankton population codependent on both optimum and lower bounds. Yet, we also note that the scenario of chlorophyte-based diet demonstrated a discontinuity pattern within the parameter space explored, with an abrupt shift from a fairly constant steady state equilibrium to unforced oscillations, when combinations of high minimum and optimum EPA were considered (Fig. 4b, top right corner).

The general pattern observed under the scenarios examined was the advantage of a low minimum quota, or an easily satisfied EPA demand. This competitive advantage coupled with a low optimal EPA quota achieved the best results, but this outcome may not always be the case in nature, as organisms with the lowest resource requirements often have traits that could potentially impede their dominance (Sommer, 1985, 1989). To put our results into perspective, we hypothesize that zooplankton seasonal succession may be driven by the interplay among the ambient conditions, food availability, and biochemical food quality combined with species' internal management strategies. For example, a large portion of the available food during the spring bloom (in north-temperate lakes) is rich in HUFAs (e.g., diatoms), thereby allowing consumers such as cladocerans to reach their growth potential. While cladoceran dominance in the spring is primarily controlled by favourable temperature conditions and high growth rates (Sommer, 1986), we also believe that biochemical quotas and kinetics may also shape the zooplankton community structure. Lower limits may become more important in early or mid-summer, when diatoms are gradually being replaced by the markedly lower in HUFA content chlorophytes. The focus now shifts from optimal to minimum resource (e.g., fatty acids and phosphorus) quotas, as high quality food becomes scarce, and is

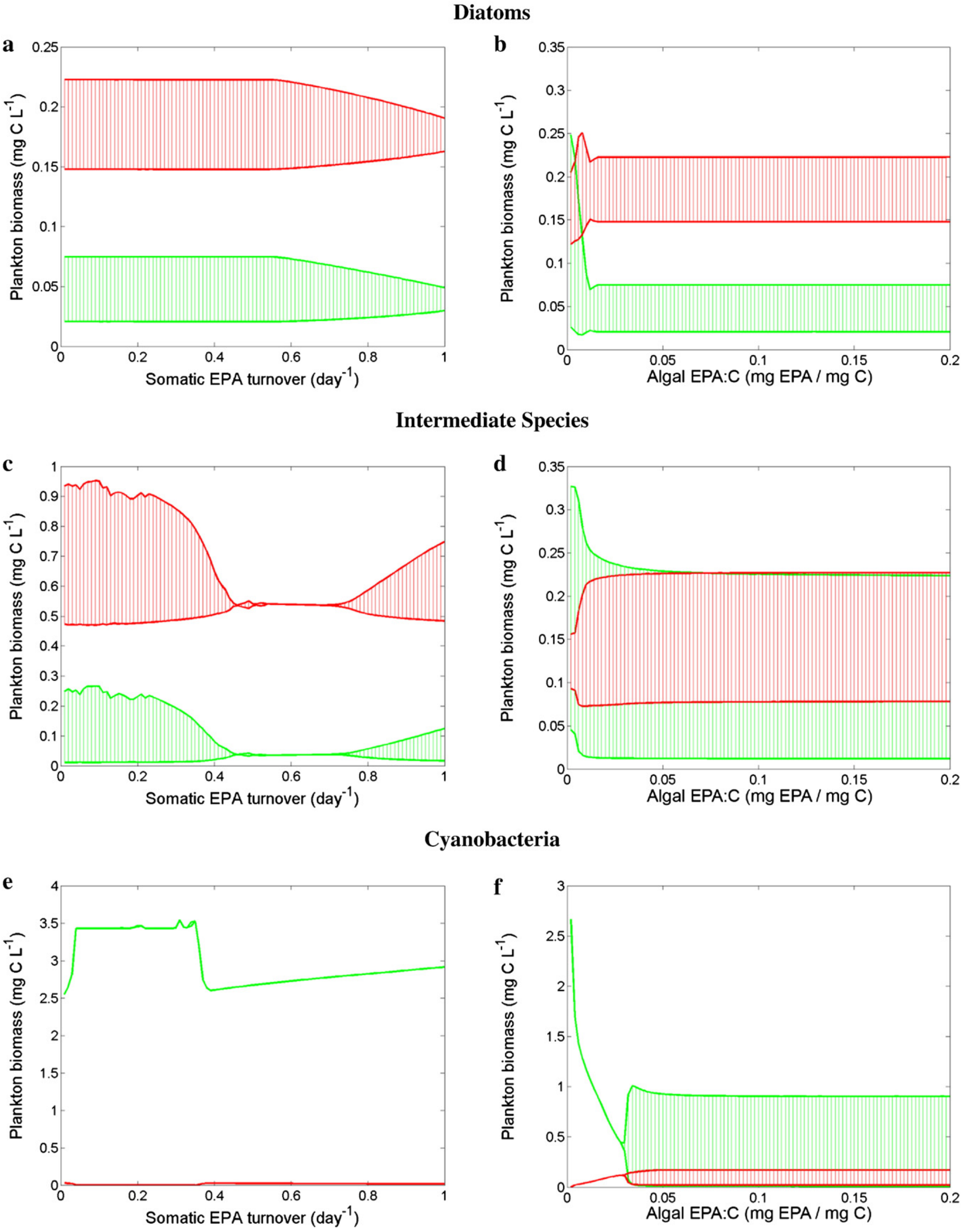
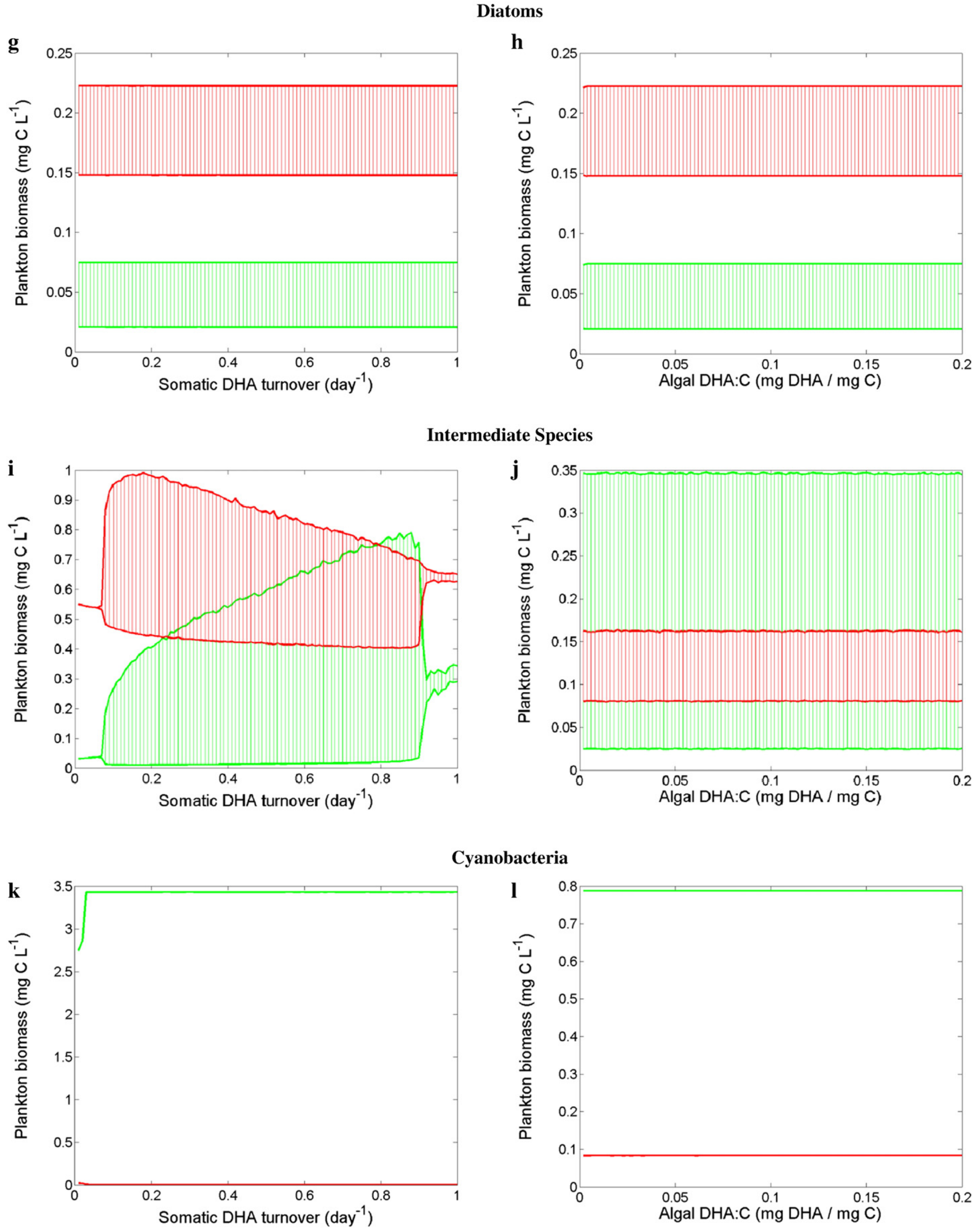


Fig. 3. Sensitivity analysis of phytoplankton (green) and zooplankton (red) biomass to intra-organism parameters. Grazer parameterization was held constant as a generic filter feeder (i.e., fast grazing, fast growing, EPA-accumulating animal with high phosphorus requirements; see Table 3). Multiple algae parameterizations were considered: diatoms (a, b, g, h, m, n, s, t, y, z), chlorophytes (c, d, i, j, o, p, u, v, aa, ab), and cyanophytes (e, f, k, l, q, r, w, x, ac, ad); see Table 4 for parameter specifications. Parameters controlling somatic turnover rates (EPA: a, c, e; DHA: g, i, k; P: m, o, q), algal resource concentrations (EPA: b, d, f; DHA: h, j, l; P: n, p, r), EPA–DHA elongation fraction (s, u, w), EPA–DHA elongation efficiency (t, v, x), hormone production fraction (y, aa, ac), and stoichiometrically regulated release fraction (z, ab, ad) were tested.



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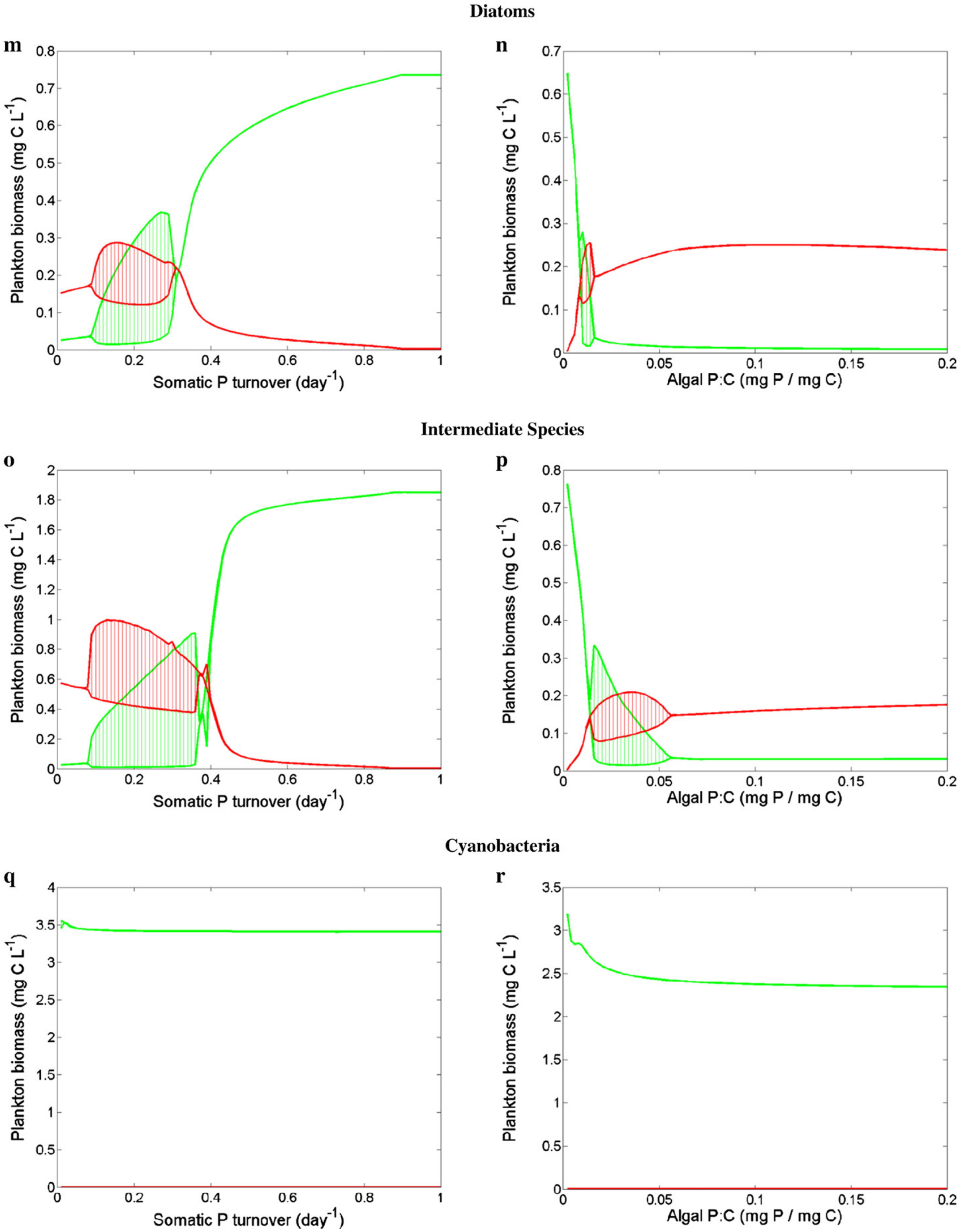


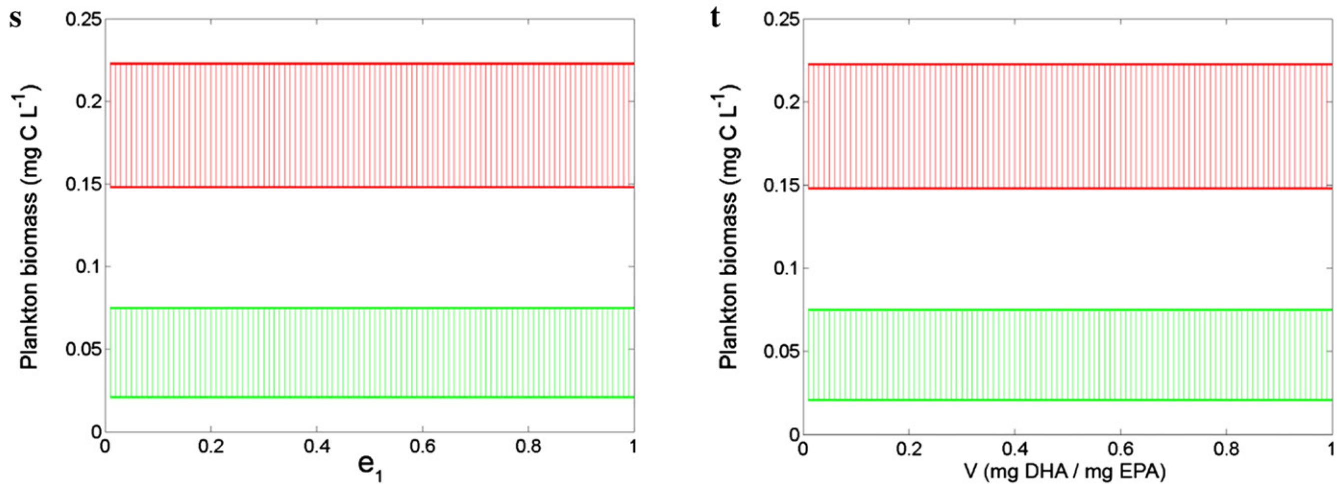
Diatoms

Intermediate Species

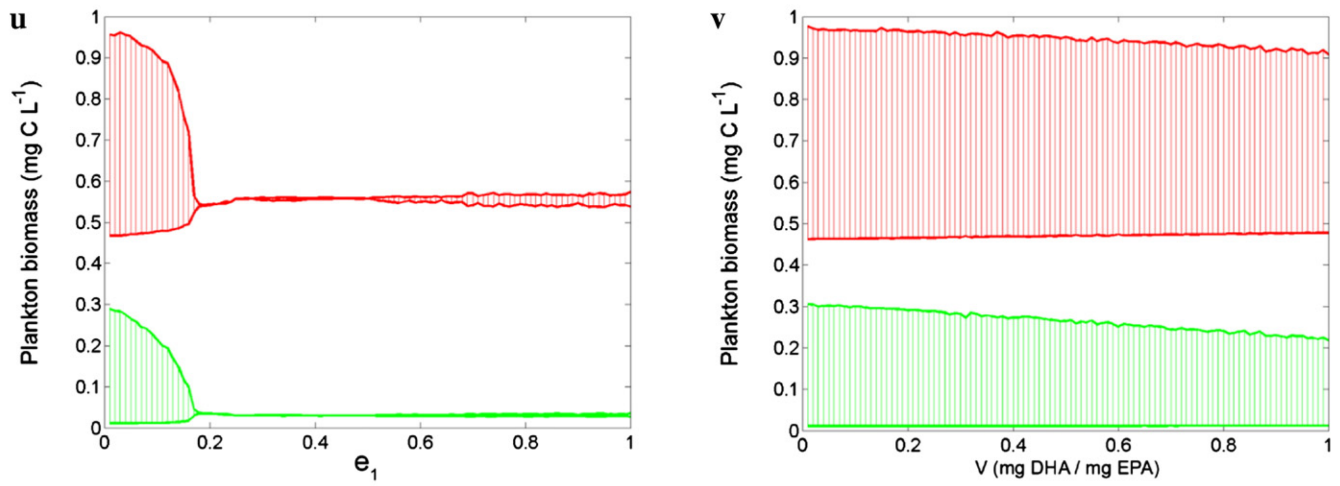
Cyanobacteria

Fig. 3 (*continued*).

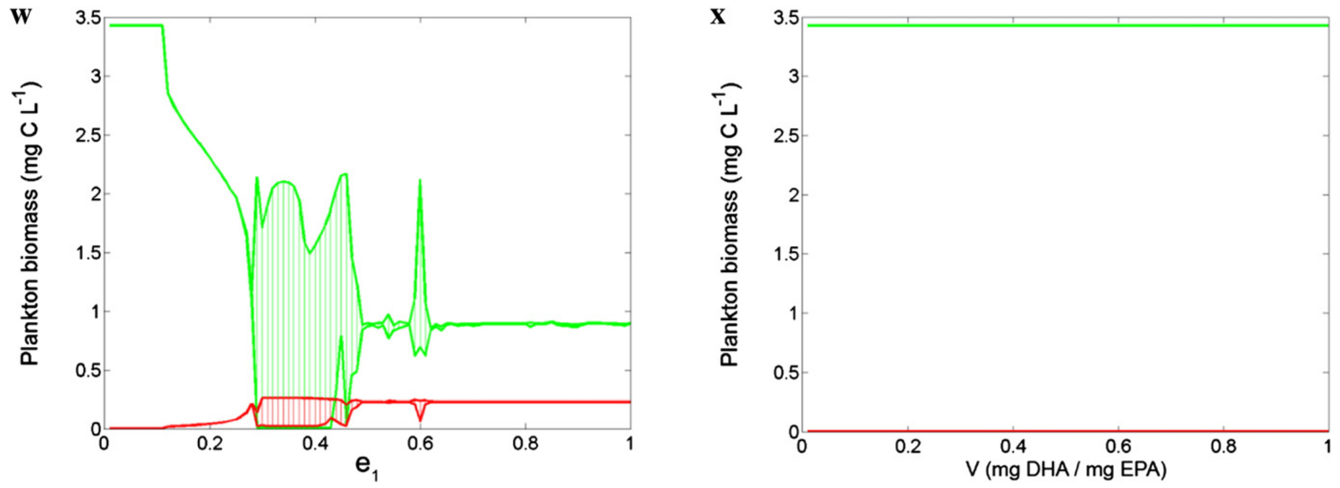
Diatoms



Intermediate Species



Cyanobacteria



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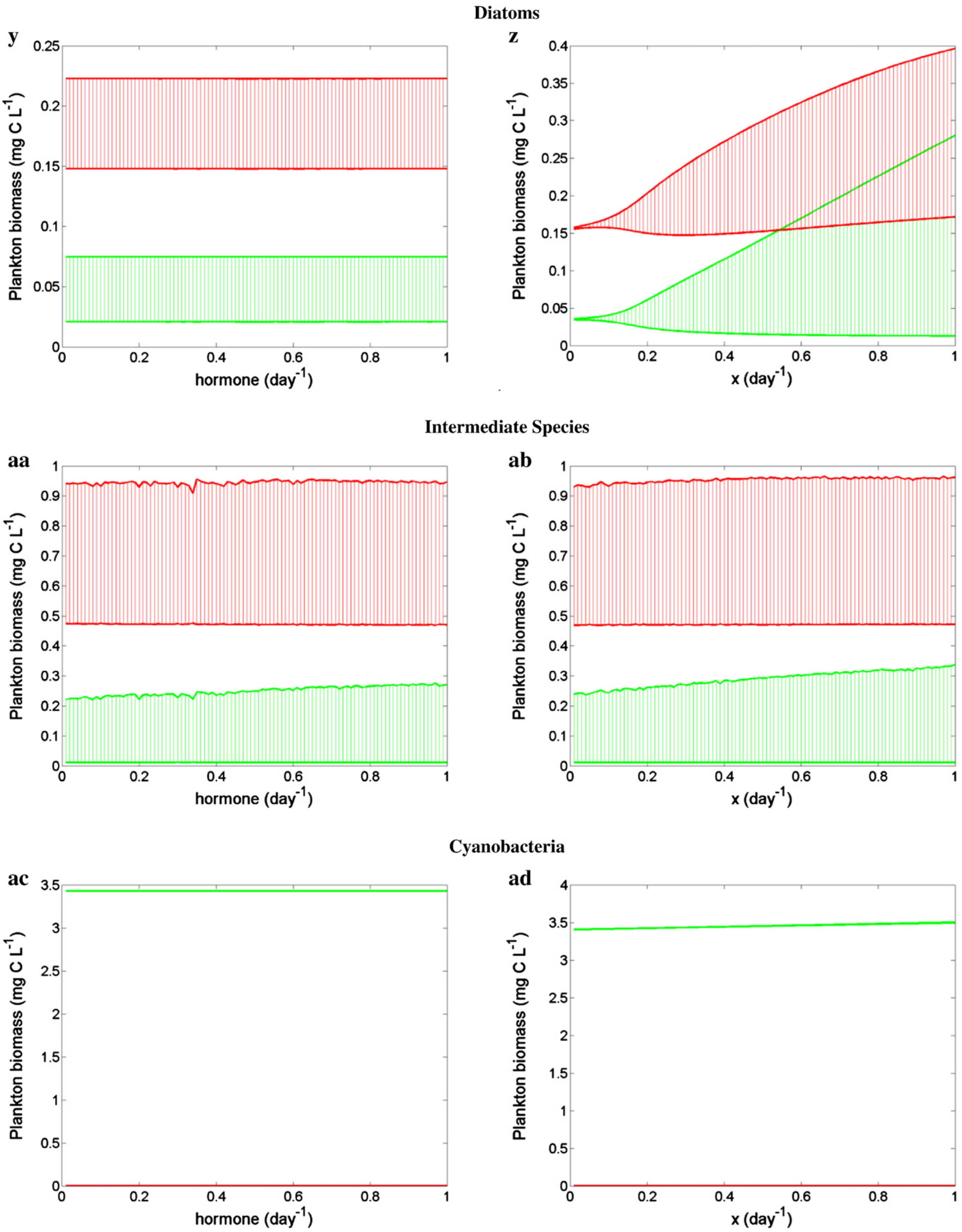

Fig. 3 (*continued*).

further accentuated towards the end of the growing season when cyanophytes become dominant.

Lessons learned from phytoplankton modeling studies are helpful in forming a new zooplankton paradigm. In particular, Sommer (1985, 1989) delineated primary producers into affinity, velocity, and storage specialists, while Grover (1991) argued that nutrient limited phytoplankton cells have the ability to uptake more substrate than immediate growth calls for. In a similar manner, we can hypothesize that the same food procurement strategies hold true for zooplankton and HUFA-starved animals are capable of storing excess lipids in the forms of glycerides, sterols, and cholesterol (Lee et al., 1971). However, the complexity of zooplankton imposes barriers that prevent us from directly applying concepts used to characterize algal competition patterns.

- There are distinguishing morphological/physiological features and behavioral strategies amongst different taxonomic groups that could also shed light on their HUFA accrual patterns and competitive performance in varying trophic settings. For example, copepods have a more developed nervous system and tend to reproduce sexually (Elofsson, 1971; Hosfeld, 1996; Strickler and Bal, 1973). Cladocerans typically reproduce via parthenogenesis, but sexual reproduction is possible and can be triggered by external factors (Dodson and Frey, 2001). Moulting in cladocerans allows increases in body size, although the energetic costs of moulting may be a major constraint on the maximum body size achieved (Dodson and Frey, 2001). Copepod development is much more complex than cladocerans' life history, but allometric growth of certain body parts is still not well understood (Williamson and Reid, 2001).
- Additional complexity is being added when accounting for spatial and interactive dynamics that are not directly applicable to phytoplankton, e.g., zooplankton prey preference and mobility. Studies have shown certain zooplankton species can learn to avoid harmful/unpalatable food (Teegarden, 1999). DeMott and Moxter (1991) reported the freshwater copepod *Diaptomus birgei's* preference for ingesting specific cyanophyte species while avoiding others that were toxic. Turiff et al. (1995) reported the copepod *Calanus finmarchicus* selectively grazed on small diatom species, in the presence of lesser quality (but non-toxic) algae. Many zooplankton species are negatively buoyant, i.e., prone to passive sinking (Haury and Weihs, 1976; Hutchinson, 1967; Lowndes, 1942), and may have to expend energy to maintain a constant depth in the water column. Bainbridge (1952) reported hop and sink behavior in *Calanus finmarchicus*, whereby an individual swims vertically upward in short bursts, followed by passive sinking to maintain a desirable depth. Similarly, *Daphnia magna* also uses hop and sink motion, during and after feeding periods, whereas hungry individuals utilize horizontal motion in search of food (Stearns, 1975). Another critical question involves the capacity of these adjustments to impair an individual's ability to distinguish good quality food.

Our modeling experiment illustrates the benefits of a flexible quota, where food quantity and quality shortages can solely be accommodated with quota adjustments. Phosphorus and HUFA availability in producers may act as selective forces on grazers, and while we stress that zooplankton quota strategy is a contributing factor to overall fitness, it is more likely one component of a larger and more complex framework.

4.3. Filling-cup hypothesis

The HUFA content varies widely among algal species (Brett and Müller-Navarra, 1997), and thus zooplankton must be facing greater challenges to achieve balanced nutrition when experiencing unfavourable algal diets. Robin et al. (2003) introduced the fatty acid dilution model to link changes in fish fatty acid profiles with their diet variability. Processes considered included input through predation, dilution through growth, and the assumption of direct incorporation into somatic tissues (Bell et al., 2001; Castledine and Buckley, 1980; Torstensen et al., 2000). The sequence in which our HUFA submodel processes grazed substrates is consistent with the dilution model, thereby allowing further investigation of Jobling's (2004) filling-cup hypothesis. The latter hypothesis uses the analogy of a cup being filled to describe an individual's capacity to manage resource accumulation: at first, there is negligible turnover, followed by overflow (i.e., turnover) as the optimal quota is met.

Individual zooplankters are known to dynamically allocate substrate between somatic growth and reproductive processes (Wacker and Martin-Creuzburg, 2007). We paired an intermediate food quality producer (i.e., chlorophyte) with a generic filter feeder, and subsequently evaluated the effects of algal EPA concentration and somatic EPA turnover rate on zooplankton biomass (Fig. 5). Tracing different trajectories along this two-dimensional space, we found an interesting interplay between algal biochemical content and somatic turnover rates. In particular, a constant algal EPA concentration along a trajectory of increasing somatic EPA turnover rate resulted in a decreasing zooplankton biomass. When nearly all assimilated substrate is subject to turnover, there is little room for growth and the zooplankton population declines. Conversely, a fixed turnover rate coupled with an increasing algal EPA concentration yielded an increased zooplankton population. According to the predictions of the filling-cup hypothesis, the zooplankter is faced with the challenge to maintain homeostatic equilibrium through an adjustment of the turnover rates to the biochemical/nutritional content of its diet. In nature, however, the relation between resource management and species abundance may not be that straightforward, as the homeostatic strategy could only apply to congeners vital to physiological structure. Finally, we note that the previous univariate sensitivity analysis demonstrated the emergence of destabilization patterns in response to the increase of chlorophyte EPA content (Fig. 3c and d), but the current analysis did not. The latter pattern suggests that the dynamic internal handling of substrates and physiological processes in our zooplankter can be one of the factors that negate (or mitigate) the extreme effects of resource enrichment, as manifested in classical prey–predator models (Rosenweig, 1971).

4.4. Phytoplankton community composition and zooplankton dynamics

Müller-Navarra et al. (2004) offered empirical evidence that zooplankton growth may be limited by food quantity in oligotrophic environments and food quality in eutrophic settings. In this study, we attempted to understand the underlying factors of these empirical findings by considering a filter feeder that grazes upon an algal continuum. The premise of the algal continuum was to capture the transition from high quality algae (diatoms) to low quality algae (cyanophytes), while chlorophytes represented the intermediate phytoplankton characterization (see Procedure). Primary producer vectors consist of nine parameters: maximum growth rate (a), respiration rate (r), sinking loss rate (s), morphological food quality (FQ_i), self-shading coefficient (c), nutrient uptake half saturation constant (e), internal EPA content ($f_{EPA:C}$), internal DHA content ($f_{DHA:C}$), and PUFA flux (J_{PUFA}) (see Table 4). The algal gradient is a continuous shift from high, to intermediate, to low quality algae. In addition to the changing prey landscape, the hypolimnetic phosphate concentration was modulated to reproduce different levels of phosphorus availability in the system, i.e., hypolimnetic phosphate was used as a surrogate to mimic the impact of the nutrient loading (Perhar and Arhonditsis, 2009). In brief, we scanned a trophic gradient from a low nutrient loading and high food quality region ($x=0$), to a high nutrient loading and low food quality region ($x=100$).

The associated phytoplankton and zooplankton biomass maps illustrate a region of instability as the algal community shifts towards cyanophytes (Fig. 6a and b). In Fig. 6c, we show the phosphorus

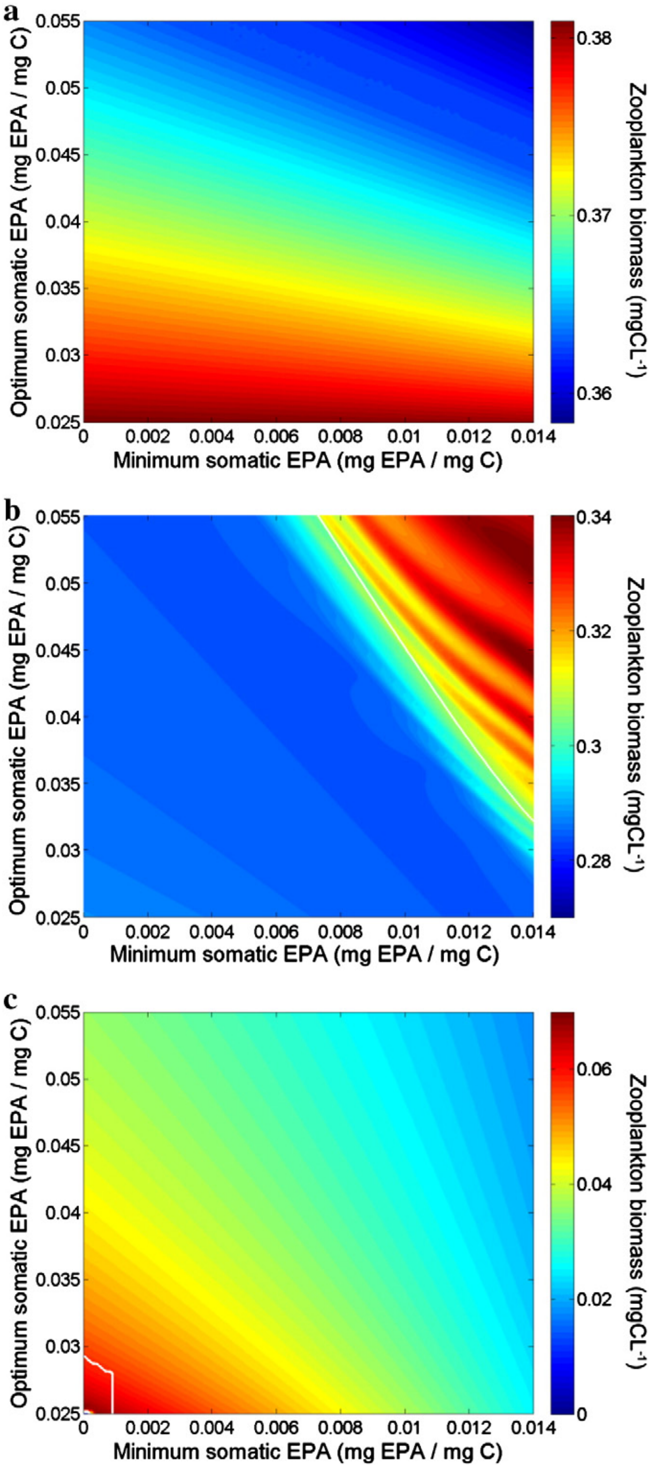

Fig. 4. Sensitivity analysis testing consumer (generic filter feeder; see Table 3 for specifications) biomass against internal EPA requirements (minimum vs. optimal), while feeding on a (a) diatom-like, (b) chlorophyte-like, and (c) cyanophyte-like species (see Table 4 for phytoplankton parameterizations). Regions of instability (i.e., limit cycles) are delineated by a white contour.

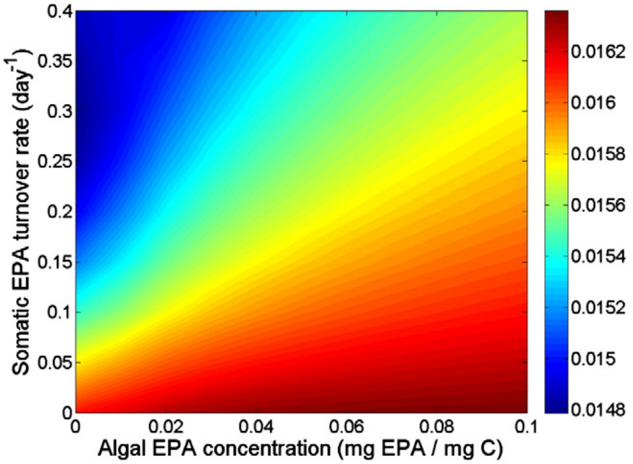

Fig. 5. Sensitivity analysis testing the filling-cup hypothesis. The flexibility of an organism's turnover rate is tested against resource availability in algae, by pairing a generic filter feeder with a chlorophyte-based diet. Zooplankton biomass (mg C L^{-1}) is shown in response to somatic EPA turnover rate (day^{-1}) and algal EPA concentration (mg EPA mg C^{-1}). In this experiment, modified EPA$_{opt}$ (0.003 mg EPA mg C^{-1}) and e_1 (0.03) parameters were used in conjunction with the default filter feeder parameterization (see Table 3).

saturation of phytoplankton against the algal continuum and also traced a trajectory (white line) that represents an algal phosphorus saturation level around 65%. The latter condition was used in our subsequent analysis as it allows studying the phytoplankton–zooplankton interactions, while avoiding both algal nutrient starvation and complete saturation. In Fig. 6d, we show that phytoplankton is characterized by a suppressed population ($0<x<60$), followed by limit cycle oscillations ($60<x<90$), and finally rapid growth/accumulation ($x>90$). The zooplankton response correspondingly illustrates a steady biomass decline, limit cycle oscillations, and ultimately population extinction (Fig. 6e). Our results suggest that oligotrophic settings can be characterized by inverted food web distributions, whereby a small pool of producers is able to sustain a large pool of grazers. By contrast, hyper-eutrophic conditions resulted in producer biomass accumulation, limited grazer presence, and eventual grazer extinction. Similar results were reported in less explicit modeling studies utilizing a combined food quality term as a proxy for seston biochemical and morphological properties (Arhonditsis and Brett, 2005a,b; Danielsdottir et al., 2007; Perhar and Arhonditsis, 2009; Zhao et al., 2008b).

Even though the efficiency with which consumers assimilate autotrophic biomass into somatic tissue depends heavily on food quality, existing empirical evidence suggests that there is no single definition of algal food quality (Müller-Navarra, 2008). For example, the underlying causes of the poor nutritional value of cyanophytes for zooplankton have been an amalgamation of cellular stoichiometry, cellular morphology, colonial formations, toxicity, and HUFA concentrations (Ravet et al., 2010). Our HUFA explicit submodel allowed us to examine the relative importance of nutrient stoichiometry (phosphorus quota), HUFA content (EPA and DHA quota), and morphological limitations on carbon assimilation efficiency (Fig. 6f). Under oligotrophic conditions, zooplankton is relatively satisfied with available HUFAs, but phosphorus-starved and thus growth is only limited by available phosphorus. As nutrient loading increases, phosphorus limitation becomes less of an issue, but HUFA availability begins to wane. Under hyper-eutrophic conditions ($x>90$), carbon assimilation efficiency remains high, ruling out morphological interference as the reason behind zooplankton extinction in our modeling experiments. Phosphorus quota is also near optimal, ruling out nutrient availability in prey. Of the two HUFA substrates, somatic EPA depletes completely, halting zooplankton growth and resulting in a population crash. Puzzlingly, it was EPA (rather than DHA) that caused the population to crash, despite the fact that cyanophytes contain trace amounts of EPA but virtually no DHA (see Table 4). We attribute this anomaly to a confused animal due to malfunctioning logic in our model (namely, incorrect specification of the thresh parameters). According to our results, zooplankton seemed to be bioconverting all available EPA into DHA in order to satisfy somatic DHA requirements, which ultimately results in depletion of the somatic EPA. We believe that this pattern is unlikely to hold true in the

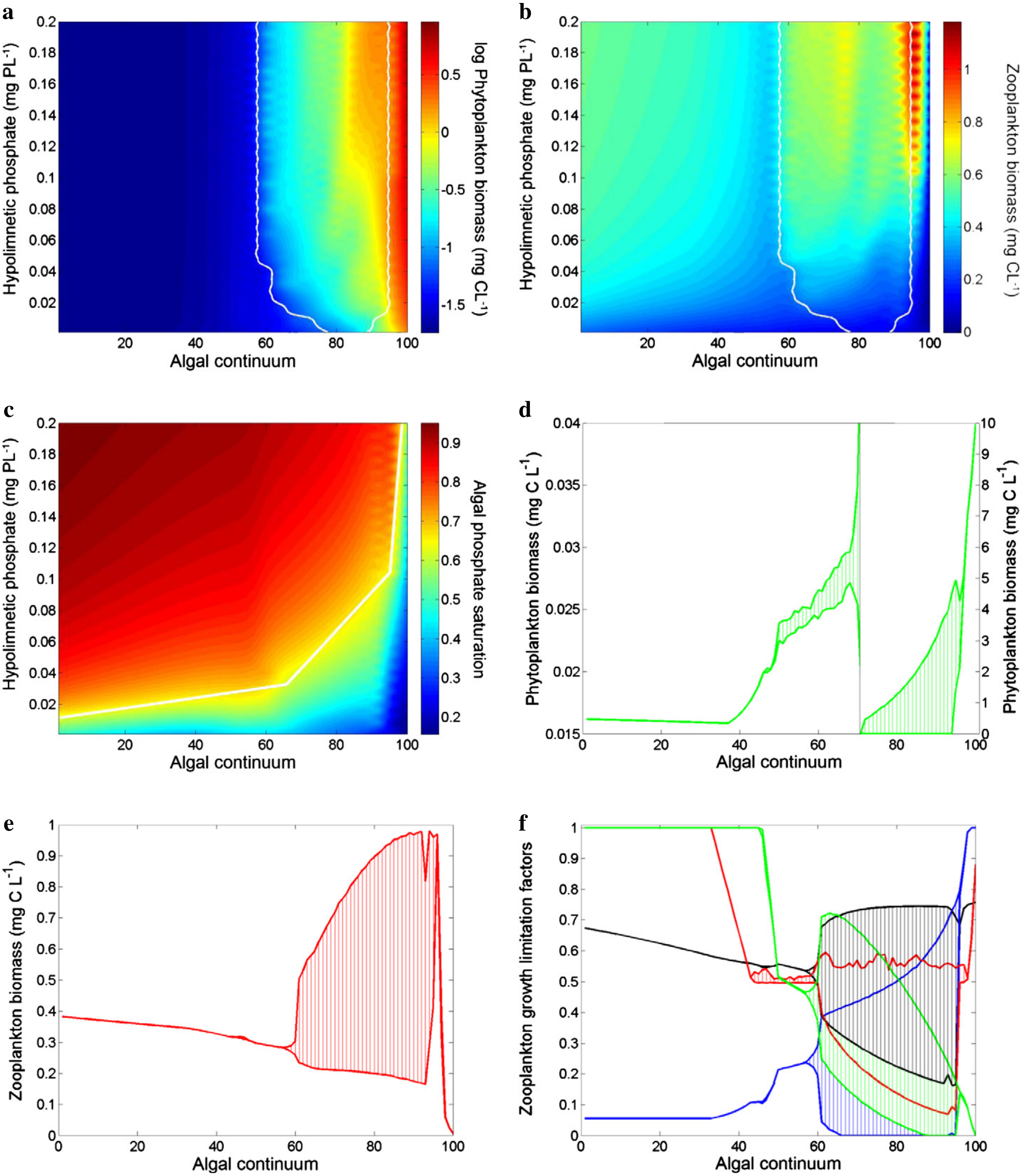

Fig. 6. Plankton dynamics induced by an algal species gradient vs. nutrient fluxes from the hypolimnion (a and b). In panel (c), the trajectory (white line) delineated represents algal phosphorus saturation between 60 and 70%, thereby avoiding nutrient starvation and complete saturation. The subsequent one-dimensional analyses (panels d, e) depict the corresponding phytoplankton and zooplankton biomass along the phosphorus limitation trajectory outlined in panel (a). In panel (f), the corresponding resource limitations to zooplankton growth are also shown (blue = phosphorus limitation, red = DHA limitation, green = EPA limitation, black = carbon assimilation efficiency).

real world, which in turn raises fundamental questions regarding the nature of bioconversion from one resource pool to another as well as the critical thresholds at which different types of bioconversion occur. Importantly, this experiment suggests an important tradeoff between zooplankton nutrient and biochemical limitation across different trophic states, and thus operational models intended to address environmental management problems may fail to depict plankton dynamics, if they consider only one contributing factor (i.e., phosphorus) to algal food quality and zooplankton growth limitation.

4.5. Bioconversion hypothesis

Omega-3 and omega-6 HUFAs are labeled essential, as animals lack the enzymes needed to synthesize these molecules (Brett and Müller-Navarra, 1997). The most physiologically active essential fatty acids in fish are EPA, DHA, and ARA, and fish fatty acid profiles can reflect their dietary intake (Bell, 1998; Henderson and Tocher, 1987; Higgs and Dong, 2000; Jobling, 2001; Sargent et al., 1989, 2002). The latter likelihood underpins the use of essential fatty acids as biomarkers. Yet, skeptical views argue that the faithfulness of such depiction is modulated by the bioconversion potential (or molecular modification) within the animal body (Kirsch et al., 1998). For example, herbivorous zooplankton taxa show distinct fatty acid accumulation patterns, although they frequently appear to be disconnected from their diet (Brett et al., 2009; Farkas, 1979). Experimental evidence has shown DHA-accumulating copepods to amass DHA even when consuming an EPA-rich diet (Ravet et al., 2010). Persson and Vrede (2006) discuss that “it is also possible that the enrichment of DHA in copepods may be explained either as an effect of selective feeding on DHA-rich food particles, and/or metabolization of other fatty acids. However, the similarity among cladoceran and copepod taxa in their overall PUFA content, as well as the presence of 22:5 omega-6, suggests that bioconversion is a likely explanation.” Daphnia feeding on EPA-depleted diets have also exhibited EPA amassing, through three possible bioconversion mechanisms: direct EPA assimilation (Wacker and Martin-Creuzburg, 2007), synthesis from shorter-chained PUFAs (e.g., ALA, see Müller-Navarra, 2006; Ravet et al., 2010; Schlechtriem et al., 2006), and finally retro-conversion from DHA (Taipale et al., 2011; von Elert, 2002; Weers et al., 1997).

Our modeling approach to bioconversion is a one-way flow from EPA to DHA. We considered a complex logic path to determine the sequence of internal regulatory switches (see Fig. 2), and bioconversion was ultimately controlled by two parameters: fraction of post-maintenance somatic EPA upgraded to DHA (e_1), and efficiency of bioconversion (v). Testing the algal continuum against EPA to DHA elongation fraction underscored an important relationship between food quality and zooplankton physiology (Fig. 7a). A zooplankter with substantial DHA requirements fared well when feeding on DHA-rich food such as diatoms ($x<50$), and elongation fraction had no significant impact on biomass. As algal DHA concentrations fell, however, with the succession from diatoms to chlorophytes, and eventually cyanophytes, zooplankton biomass fell to zero unless a substantial fraction of EPA was being elongated to DHA. Additional dynamics between fraction of EPA elongated to DHA and bioconversion efficiency are shown for diatoms, chlorophytes and cyanophytes (Fig. 7b–d). Our analysis of EPA to DHA conversion fraction against conversion efficiency with high quality algae (i.e., diatom) suggests a disconnect between the two bioconversion factors. Somatic DHA accumulation was entirely dependent on elongation fraction, most likely resultant of a very rich food source and somatic DHA near saturation. The underlying logic may have reduced the importance of bioconversion as both EPA and DHA quotas were being met with a diatom-rich diet. A diet consisting of chlorophytes yielded a somatic DHA content codependent on both elongation fraction and efficiency (Fig. 7c), but only after exceeding a critical elongation fraction threshold (e_1) of approximately 0.5. Below this threshold, somatic DHA was nearly zero, indicating that the fraction of EPA molecules elongated to be the primary regulatory factor before efficiency could play a role. Chlorophytes are a rich source of PUFAs (see Table 4), and grazers feeding on chlorophyte-rich diets may be able to efficiently elongate shorter-chained PUFAs into HUFAs. A high EPA–DHA elongation fraction could permit chlorophyte-fed grazers to bioconvert twice and amass DHA, i.e., PUFA to EPA and then EPA to DHA. Qualitatively similar results were produced for cyanophytes, although a few orders of magnitude lower (Fig. 7d).

Our examination of mathematically possible, yet not always physiologically plausible, combinations of the fraction of EPA elongated to DHA and the efficiency of EPA–DHA elongation, aimed to identify possible thresholds beyond which physiological parameterizations could explain the ability of certain organisms to survive in unfavorable trophic conditions. While our results show that zooplankton survival even in a cyanobacteria-dominated environment is conceivable, we caution the thermodynamic requirements for such a feat may not be. Our results highlight the interplay between the two controlling parameters (in our interpretation of the elongation mechanism) and the environment, but it is important to note that we cannot validate some of our predictions in “real world” conditions as these parameters are very difficult to measure. Tagged EPA molecules, for example, can be used to quantify the bulk of DHA derived from EPA in an individual, but measuring the associated energetic cost remains challenging.

4.6. Alternative parameterizations of the plankton model

Thus far, our experiments have considered a filter feeding, cladoceran-like zooplankter. To test the importance of zooplankton parameterization based on physiological processes and empirical data, we constructed a zooplankton species continuum in a fashion similar to the algal continuum constructed previously, transitioning from a filter feeder to a selective feeder that grazes intelligently, considering food abundance and quality (see Table 4 for zooplankton grazing parameterizations for corresponding algal groups). In conjunction with the algal continuum, we ran simulations with a dynamic plant–animal interface, i.e., continuous shifts in both producers and grazers (see Procedure; Fig. 8). Certain physiological processes (i.e., moulting fraction and moulting rate) were held constant due to lack of empirical evidence to associate them with specific zooplankton characterizations. The filter feeder was parameterized to exhibit cladoceran-like traits, i.e., a fast grazing, fast growing animal with high phosphorus requirements and a tendency to accumulate EPA. The select feeder resembled a copepod-like animal, with a lower grazing rate, slower growth, selective grazing strategy to seek high quality algae over detritus (and detritus over low quality algae), and a high DHA requirement coupled with the increased ability to convert EPA to DHA.

High quality algae (i.e., diatoms; $x\sim0$) yielded a somewhat higher zooplankton population under selective feeding as compared to filter feeding, a pattern fairly consistent with lesser quality algae (i.e., chlorophytes; $x\sim50$). Notably, the predominance of select feeders was manifested with both low (Fig. 8a) and high quality detritus (Fig. 8b). Transitioning to cyanophytes ($x\sim100$), as the main algal food source, the diminishing food quality yielded low zooplankton biomass and destabilization of the plant–animal interface. Interestingly, the onset of oscillations was experienced earlier and was more prolonged with the select feeders than the filter feeders; in the presence of high quality algae only select feeders experienced destabilization and eventual extinction (Fig. 8b). That is, the selective feeding strategy (or the stronger affinity for phytoplankton-dominated diet) was less resilient, and therefore more susceptible to system equilibrium loss. Copepods can utilize their chemoreceptors to track down high food quality, but cladocerans cannot control their diet composition (Bundy and Paffenhöfer, 1997). Instead, they decide to ingest or reject particles at the time of ingestion, and thus increased food abundance may require additional grooming by cladocerans to clean their filter and feeding apparatus, which in turn results in higher respiration rates (Dodson and

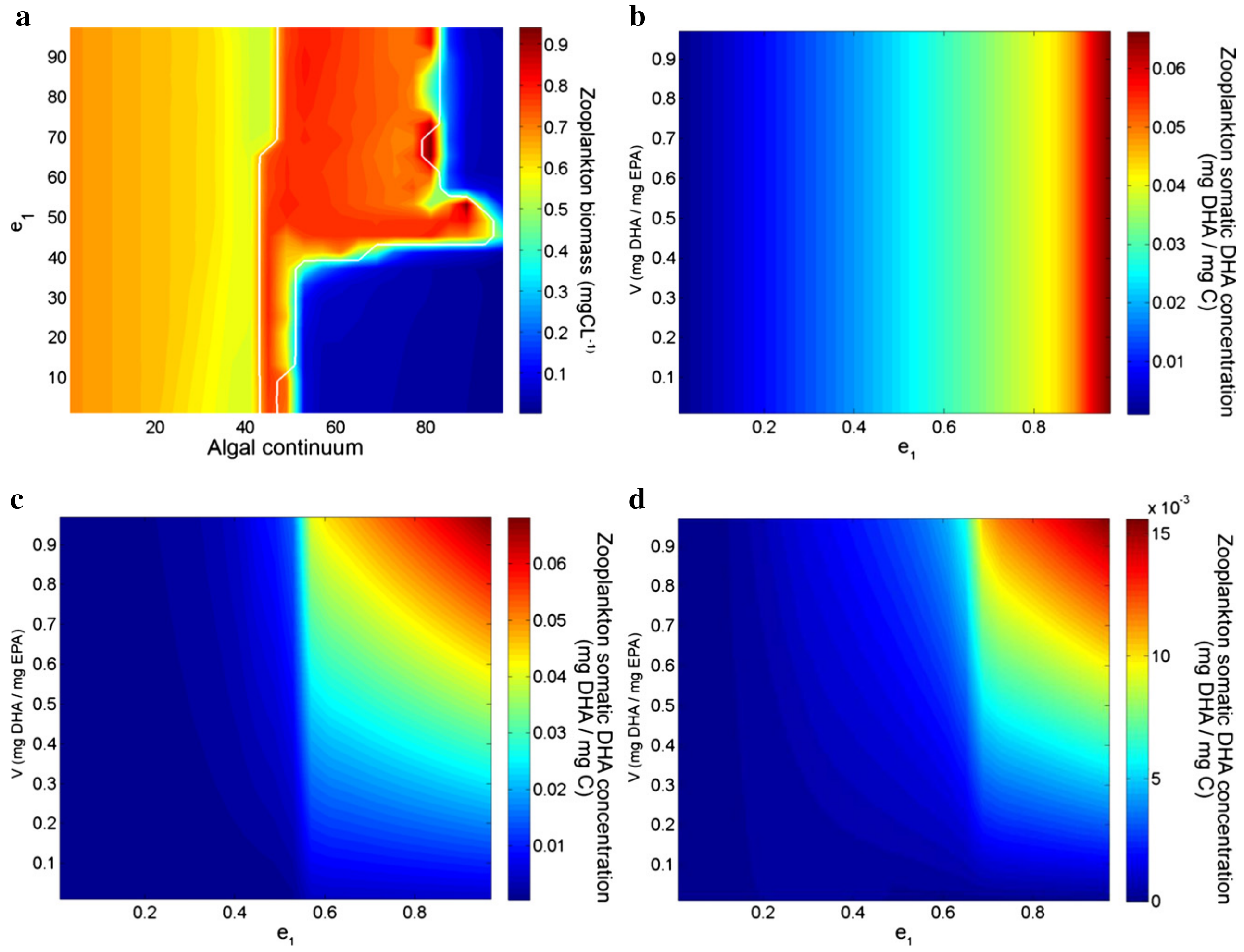

Fig. 7. Sensitivity analysis illustrating the interplay between factors controlling zooplankton DHA accumulation. Zooplankton biomass (mg C L^{-1}) is shown as a response to varying e_1 (fraction of EPA elongated to DHA) and v (efficiency of EPA–DHA elongation), while feeding on a (a) diatom-, (b) chlorophyte-, and (c) cyanophyte-like species.

Frey, 2001). It may be possible for the respiration rate to surpass the assimilation rate under enrichment scenarios, possibly explaining the cyanobacteria accumulation and cladoceran population crash commonly associated with hyper-eutrophic conditions (Dodson and Frey, 2001). Counter to our expectations though, the filter feeder does not go extinct and perseveres much further along the algal continuum due to its superior feeding kinetics assigned relative to the select feeder (Fig. 8a and b). One-dimensional trajectory scans also show cladoceran and copepod response to a shifting algal base under low (Fig. 8c and e) and high (Fig. 8d and f) detritus food quality.

Detritus is classified as either decomposing algal and plant fragments, or organic aggregates derived from dissolved organic matter colonized by bacteria (Perhar and Arhonditsis, 2009). Nutritional value of detritus is generally lower than algae (Cavaletto and Gardner, 1999), although this may be reversed in conditions of predominance of extremely poor quality algae. Perhar and Arhonditsis (2009) showed that the detritus food quality seems to regulate the amplitude of the dynamic oscillations following enrichment, when algal food quality is low. This finding highlights 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. Our analysis considers detritus, but thus far, the parameterization has remained constant. Utilizing the zooplankton continuum from previous experiments, we constructed a detritus continuum shifting from low to high quality (Fig. 9). Parameters controlling detritus food quality were limited to detritus EPA:C, detritus DHA:C, and morphological food quality (FQ_{DET}); detritus phosphorus content was computed dynamically as part of the model (see detritus parameterization in Table 5).

A diet based on diatoms proved once again to be very nutritious and not significantly affected by the quality of the alternate food source (Fig. 9a). Filter feeders overshadowed the opportunistic select feeders utilizing their superior grazing kinetics to take advantage of the HUFA-rich algae. Detritus food quality played a minor role in determining zooplankton biomass in the presence of high quality algae. Strongest response to a viable secondary food source was observed with a chlorophyte diet, although the plankton patterns observed were somewhat paradoxical. Namely, a diet based on DHA-poor chlorophytes yielded somewhat higher abundance for select feeders, who require large amounts of DHA relative to filter feeders (Fig. 9b). The patterns observed with the chlorophyte-based diet were more responsive to detritus food quality, in that increased quality led to a decrease in zooplankton biomass under a selective grazing strategy, and a minute increase under a non-selective strategy. This perplexing outcome may be due to the extremely high PUFA content in chlorophytes (see Table 4), and selective feeders' enhanced ability to bioconvert EPA into DHA (see also our Bioconversion hypothesis section). Both strategists were elongating PUFAs into EPA, but selective feeders were then able to rapidly and efficiently elongate the new EPA molecules into DHA. This may have induced EPA limitation in our selective-feeders. On the other hand, a cyanophyte-dominated algal community yielded localized pockets of system instability and oscillations around the region of a hybrid zooplankter *(y ~ 50)* (Fig. 9c). Aside from this sudden emergence of limit cycle oscillations, the scenario of

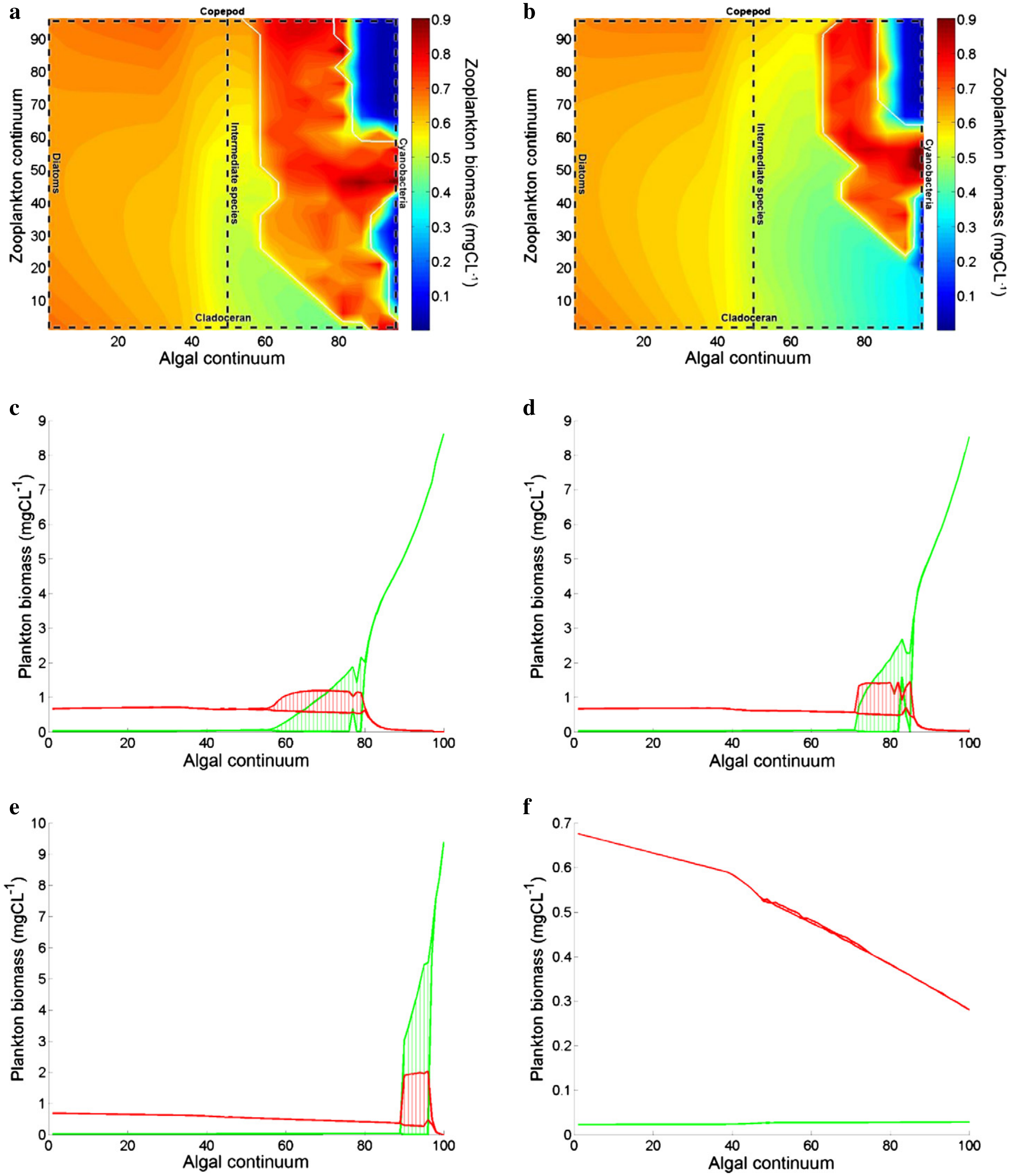

Fig. 8. Sensitivity analysis of a changing grazer parameterization in response to a changing food base and detritus food quality. The algal continuum along the *x*-axis represents a shift from a diatom-like ($x=0$), to a chlorophyte-like ($x=50$), and to a cyanophyte-like species ($x=100$). The zooplankton continuum along the *y*-axis represents a shift from a filter feeder ($y=0$) to a select feeder ($y=100$). Zooplankton biomass response to the producer and grazer parameterization are shown under scenarios of (a) poor and (b) good detritus food quality. One-dimensional plots illustrating producer (green) and grazer (red) biomass for selective (c and d) and filter feeders (e and f) are shown under scenarios of poor (c and e) and good (d and f) detritus food quality.

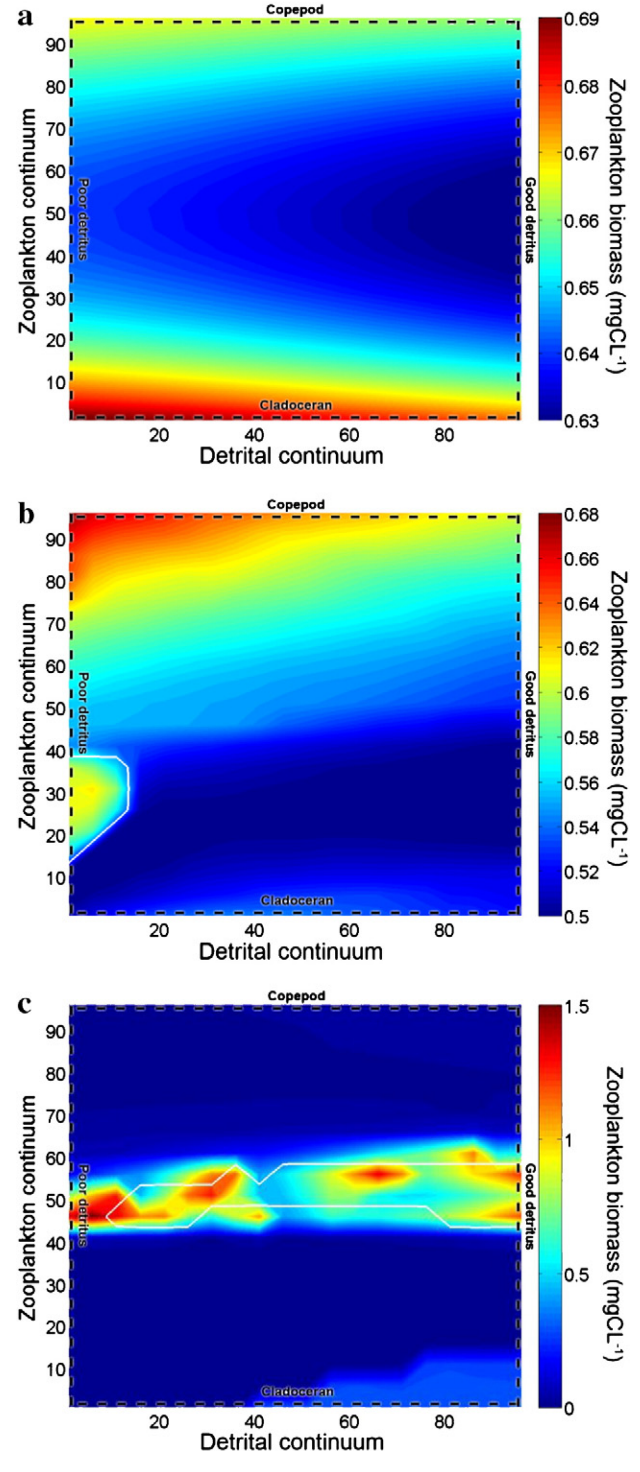

Fig. 9. Detritus tested against consumers in a continuous fashion. The detrital continuum along the x-axis represents a shift from poor ($x = 0$) to high ($x = 100$) quality. The consumer continuum along the y-axis represents a shift from a cladoceran-like ($y = 0$) to a copepod-like grazer ($y = 100$). Our experiments depict zooplankton biomass (mg C L^{-1}) and were conducted using a (a) diatom-like, (b) intermediate, and (c) cyanobacteria-like species.

cyanophyte dominance exhibited little response to the detritus food quality variability. In our previous work (Perhar and Arhonditsis, 2009), we stressed the importance of a viable secondary food source for zooplankton, and underscored its ability to significantly modulate grazer population dynamics. In the present study, detritus food quality exhibits control on zooplankton biomass, but is overshadowed by algal food quality. We assume detritus food quality (biochemical and morphological) to be significantly inferior to phytoplankton food quality in the present study; this was not strictly the case in our previous work (Perhar and Arhonditsis, 2009). It is plausible, however, that detritus food quality may surpass algal food quality via subsidies from benthic and allochthonous sources, and the microbial loop, but these factors are outside the scope of the current study.

5. Conclusions and future perspectives

In this study, we attempted to reproduce the biochemical control of zooplankton growth with a plankton model typically used in the study of aquatic ecosystem dynamics (Arhonditsis and Brett, 2004). Our sensitivity analysis offered insights into the role of seston food quality and homeostatic regulatory zooplankton parameters, although the results presented herein are conditional upon the plankton characterizations postulated. One assumption of the present analysis is related to the fate of fatty acid turnover, in that this organic release is assumed to be permanently lost from the system. The plankton dynamics induced if we relax this assumption may need to be examined and subsequently validated in a “real-world” context. The microbial loop can be a source of certain biochemicals that are essential in meeting the nutritional requirements of zooplankton and thus enhancing the trophic transfer efficiency (Klein-Breteler et al., 1999). Bacteria rapidly uptake dissolved organic carbon, which in turn may be consumed by ciliates and heterotrophic nanoflagellates (HNF). The latter constituents of the microbial loop usually exert minimal control on the fatty acid composition (Harvey et al., 1997), or convert PUFAs to HUFAs at a very low rate (Sul et al., 2000). Controlled experiments could further elucidate the implications of this feedback loop to the biochemical quality of alternative food sources. For example, one critical question arising involves the capacity of the microbial loop to offer a reliable bypass pathway that allows sustaining a healthy consumer population in systems dominated by inferior food quality algae. If the microbial loop is to be viewed as a dissolved HUFA to particulate HUFA mechanism, the yield will be dependent on alternate HUFA subsidies and covary with algal species. The existence of such a mechanism, however, suggests the possibility of a balanced diet for zooplankton under adverse conditions, comprised of substrates from multiple food sources.

Identifying critical thresholds at which population dynamics rapidly change (the so-called regime shifts) is of paramount importance when designing nutrient loading management strategies, e.g., delineation of the nutritional value of the major food sources associated with a plant–animal interface that shifts from inverted distribution to producer accumulation. Becker and Boersma (2005) examined the mineral and biochemical limitations on *Daphnia magna* growth, and reported significantly lower EPA growth requirements relative to phosphorus. The authors concluded that the EPA saturation levels for zooplankton growth are much lower than previously considered, and thus challenged the notion of biochemical limitation on zooplankton. Brett (2010), however, pinpointed several methodological (limit of detection), experimental (replication), and statistical (inconsistent statistical reporting) flaws in the Becker and Boersma (2005) study that call into question the conclusions drawn. Robust experiments for quantifying feeding rates and thresholds of nutritional/biochemical limitation are of utmost importance to mechanistic modeling. Another interesting angle for future examination is related to the intra-specific competition between juvenile and mature individuals; the juveniles are expected to have lower absolute requirements due to their size, but significantly higher minimum quotas for rapid growth. Our modeling results suggest that larger individuals would have an advantage in food quality limiting conditions, but further investigation is required.

One of the shortcomings of the present analysis is the assumption of a unidirectional bioconversion from EPA to DHA. Several studies (Brett and Müller-Navarra, 1997; Müller-Navarra, 1995; Persson and Vrede, 2006; Von Elert, 2002) discuss zooplankton ability to bioconvert fatty acids from one form to another, but more detailed analyses explicitly tracking multiple fatty acids may shed light on the likelihood (and relative magnitudes) of bidirectional conversions. We hope that our findings and assumptions have a recursive impact on empirical and laboratory research, but also serve as a stepping stone for HUFA integration into an operational modeling context. For example, the structural shifts in zooplankton communities induced from external nutrient loading may partly be attributed to the changes in phytoplankton HUFA content. In this context, a natural next step of the present analysis is the incorporation of the HUFA explicit submodel into a management-oriented model. Understanding the fundamental attributes of seston food quality should not be seen as an entirely academic pursuit, but rather as an application that could potentially yield more efficient water quality management practices.

In conclusion, we have integrated intra-organism level aspects into a simple plankton model. We examined multiple contemporary hypotheses and our findings can be summarized as follows:

- optimal HUFA and phosphorus somatic quotas are critical for zooplankton growth when high quality seston is abundant, while poor quality food conditions put emphasis on minimum zooplankton quotas;
- combinations of low minimum and optimal resource quotas are advantageous for zooplankton growth;
- the capacity of consumer species to modulate turnover in response to resource availability can be critical in maintaining the resilience of the zooplankton community;
- modulation of the somatic turnover may counteract Rosenweig's (1971) paradox of prey enrichment leading to predator–prey destabilization;
- bioconversion (e.g., EPA elongation) can alleviate the growth limitations imposed by poor seston quality;
- grazers are primarily phosphorus-limited under oligotrophic conditions, whereas HUFA limitations becomes critical in eutrophic settings;
- dynamic handling of internal resource pools and efficient allocation between growth and basal metabolism may control consumer survival in declining trophic environments;
- select feeding strategies render competitive advantage under intermediate characterizations of the phytoplankton community, but growth strategies and feeding kinetics become more important under both ideal and severely adverse trophic conditions;
- viable alternative autochthonous or allochthonous food sources can offer minimum relief to feeding stresses imposed by low quality algae.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.ecoinf.2012.10.005.

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MODELLING THE ROLE OF HIGHLY UNSATURATED FATTY ACIDS IN PLANKTONIC FOOD WEB PROCESSES: SENSITIVITY ANALYSIS AND EXAMINATION OF CONTEMPORARY HYPOTHESES

ELECTRONIC SUPPLEMENTARY MATERIAL

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Table 1. Tabulation of modeled and measured parameter values relevant to our proposed mechanistic zooplankton growth sub model

Parameter	*Symbol*	*Units*	*Reported Values*
Maximum growth rate	π	day^{-1}	0.05-0.3 day^{-1}(b), 0.3-0.58 day^{-1} (c), 0.15-0.9 day^{-1}(g), 0.05-0.55 day^{-1}(k), 0.15-0.58 day^{-1}(p), 0.8 day^{-1}(s)
Minimum zooplankton somatic phosphorus	P_{min}	mg P (mg C)$^{-1}$	0.004$_{\text{mg/mg}}$(s)
Optimal zooplankton somatic phosphorus	P_{opt}	mg P (mg C)$^{-1}$	0.0115$_{\text{molP:molC}}$(r), 0.024$_{\text{mg/mg}}$(s)
Minimum zooplankton somatic nitrogen	N_{min}	mg N (mg C)$^{-1}$	
Optimal zooplankton somatic nitrogen	N_{opt}	mg N (mg C)$^{-1}$	0.1695 $_{\text{molN:molC}}$ (r)
Minimum zooplankton somatic EPA	EPA_{min}	mg EPA (mg C)$^{-1}$	
Optimal copepod somatic EPA	EPA_{opt}	mg EPA (mg C)$^{-1}$	12.9-23$_{\%\text{TFA}}$(d), 0-1.7$_{\%\text{TFA}}$(e), 8$_{\text{mg/gDW}}$(t)
Optimal cladoceran somatic EPA	EPA_{opt}	mg EPA (mg C)$^{-1}$	9.2$_{\%\text{TFA}}$(a), 7.7-15.8$_{\%\text{TFA}}$(d), 6.76-6.76$_{\mu\text{mol/mgDW}}$(j), 12.4$_{\%\text{TFA}}$(m), 11.8$_{\%\text{TFA}}$(q), 8.2$_{\text{mg/gDW}}$(t)
Minimum zooplankton somatic DHA	DHA_{min}	mg DHA (mg C)$^{-1}$	
Optimal copepod somatic DHA	DHA_{opt}	mg DHA (mg C)$^{-1}$	13.5-35.9$_{\%\text{TFA}}$(d), 6.3-9.2$_{\%\text{TFA}}$(e), 16.1$_{\text{mg/gDW}}$(t)
Optimal cladoceran somatic DHA	DHA_{opt}	mg DHA (mg C)$^{-1}$	1.5$_{\%\text{FA}}$(a), 4.9-12.3$_{\%\text{TFA}}$(d), 0.38-0.61 $_{\mu\text{mol/mgDW}}$ (j), 0.1$_{\%\text{TFA}}$(m), 0.9$_{\%\text{TFA}}$(q), 1.4$_{\text{mg/gDW}}$(t)
Seston EPA to carbon ratio	$s_{EPA:C}$	mg EPA (mg C)$^{-1}$	0.71 $_{\mu\text{mol/mgDW}}$ (j), 1.2-4.5$_{\text{mg/gDW}}$(l), 3.0%TFA(q), 1.2-2.3$_{\text{mg/gDW}}$(t)
Seston DHA to carbon ratio	$s_{DHA:C}$	mg DHA (mg C)$^{-1}$	0.50 $_{\mu\text{mol/mgDW}}$ (j), 0.3-2.9$_{\text{mg/gDW}}$(l), 2.1$_{\%\text{TFA}}$(q), 2.7-5.8$_{\text{mg/gDW}}$(t)
Phytoplankton phosphorus to carbon ratio	$f_{P:Ci}$	mg P (mg C)$^{-1}$	0.0039 $_{\text{molP:molC}}$ (r), 2.5-10$_{\text{mg/mg}}$(s)
Phytoplankton nitrogen to carbon ratio	$f_{N:Ci}$	mg N (mg C)$^{-1}$	0.1042 $_{\text{molN:molC}}$ (r)
Diatom EPA to carbon ratio	$f_{EPA:Ci}$	mg EPA (mg C)$^{-1}$	12.8$_{\%\text{TFA}}$(e), 4.6-11.1$_{\%\text{TFA}}$(n), 0.6-12.5$_{\%\text{TFA}}$(o), 16.9$_{\%\text{TFA}}$(u)
Diatom DHA to carbon ratio	$f_{DHA:Ci}$	mg DHA (mg C)$^{-1}$	4.5$_{\%\text{TFA}}$(e), 0.1-1.9$_{\%\text{TFA}}$(o), 2.5$_{\%\text{TFA}}$(u)
Chlorophyte EPA to carbon ratio	$f_{EPA:Ci}$	mg EPA (mg C)$^{-1}$	0.1$_{\%\text{TFA}}$(c), 0-0.3$_{\mu\text{g/gDW}}$(p), 0$_{\%\text{TFA}}$(u)
Chlorophyte DHA to carbon ratio	$f_{DHA:Ci}$	mg DHA (mg C)$^{-1}$	0$_{\%\text{TFA}}$(c), 0-0.1$_{\mu\text{g/gDW}}$(p), 0$_{\%\text{TFA}}$(u)
Cyanophyte EPA to carbon ratio	$f_{EPA:Ci}$	mg EPA (mg C)$^{-1}$	1.5$_{\%\text{TFA}}$(c), 1.8-2.2$_{\mu\text{g/gDW}}$(p), 0.7$_{\%\text{TFA}}$(u)
Cyanophyte DHA to carbon ratio	$f_{DHA:Ci}$	mg DHA (mg C)$^{-1}$	0$_{\%\text{TFA}}$(c), 0$_{\mu\text{g/gDW}}$(p), 0.6$_{\%\text{TFA}}$(u)
Zooplankton biomass phosphorus turnover rate	τ_p	day^{-1}	0.094 day^{-1}(r)
Zooplankton biomass nitrogen turnover rate	τ_n	day^{-1}	0.094 day^{-1}(r)
Zooplankton biomass EPA turnover rate	τ_{epa}	day^{-1}	0.051-0.31 day^{-1}(i)
Zooplankton biomass DHA turnover rate	τ_{dha}	day^{-1}	0.051-0.31 day^{-1}(i)

Zooplankton moult P turnover rate	τ_m	day^{-1}	0.4 day^{-1}(r)
Moult as a fraction of zooplankton biomass	m	dimensionless	0.05(r)
Maximum zooplankton grazing rate	λ	day^{-1}	0.6 day^{-1}(h)
Zooplankton carbon assimilation efficiency	α_{c1}	Dimensionless	0.9(h)
Half saturation constant for zooplankton growth efficiency	α_{c2}	(mg C L^{-1})$^{1/2}$	0.03 (mg C L^{-1})$^{1/2}$ (h)
Phytoplankton food preference	ω_{PHYT}	Dimensionless	1(h)
Detritus food preference	ω_{DET}	Dimensionless	1(h)
Diatom food quality	FQ_{DIA}	Dimensionless	0.8(h)
Chlorophyte food quality	FQ_{CHL}	Dimensionless	0.5(h)
Cyanophyte food quality	FQ_{CYAN}	Dimensionless	0.2(h)
Excretion rate	χ	day^{-1}	
Flux of C18 PUFA, precursor to EPA (from diatoms)	J_{PUFA}	mg PUFA (mg C)$^{-1}$ day^{-1}	$0.25_{\%DW}$(b), $8.5_{\%TFA}$(e), $0.8\text{-}13.2_{mg/gDW}$(l), $2.5\text{-}7.2_{\%TFA}$(n), $0.2\text{-}5.9_{\%TFA}$(o), $11.7_{\%TFA}$(q), $2.9_{\%TFA}$(u)
Flux of C18 PUFA, precursor to EPA (from chlorophytes)	J_{PUFA}	mg PUFA (mg C)$^{-1}$ day^{-1}	$3_{\%DW}$(b), 0.8-13.2 (l), $2.5\text{-}7.2_{\%TFA}$(n), $10.1\text{-}26.9_{\mu g/gDW}$(p), $11.7_{\%TFA}$(q), $25.5_{\%TFA}$(u)
Flux of C18 PUFA, precursor to EPA (from cyanophytes)	J_{PUFA}	mg PUFA (mg C)$^{-1}$ day^{-1}	$0.25_{\%DW}$(b), 0.8-13.2 (l), $2.5\text{-}7.2_{\%TFA}$(n), $0.8\text{-}3.2_{\mu g/gDW}$(p), $11.7_{\%TFA}$(q), $7_{\%TFA}$(u)
Conversion efficiency of ALA to EPA	ρ	mg EPA (mg ALA)$^{-1}$	
Fraction of EPA to DHA conversion via elongation	ε	dimensionless	
Conversion efficiency of EPA to DHA	ν	mg DHA (mg EPA)$^{-1}$	
Hormone production rate	h	day^{-1}	

(a) Ballantyne et al., (2003); **(b)** Brett and Müller-Navarra, (1997); **(c)** Brett et al., (2006); **(d)** Farkas and Herodek, (1964); **(e)** Graeve et al., (2005); **(f)** Fraser et al., (1989); **(g)** Ferrão-Filho et al., (2003); **(h)** Perhar and Arhonditsis, 2009; **(i)** Shin et al., (2000); **(j)** Müller-Navarra, (2006); **(k)** Müller-Navarra et al., (2000); **(l)** Kainz et al., (2004); **(m)** Weers et al., (1997); **(n)** Wacker and Martin-Creuzburg, (2007); **(o)** Viso and Marty, (1993); **(p)** Ravet and Brett, (2006); **(q)** Persson and Vrede, (2007); **(r)** Anderson et al., (2005); **(s)** Mulder and Bowden, (2007); **(t)** Kainz et al., (2009); **(u)** Ravet et al., 2010).

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