NOTE AND COMMENT

Takefumi Nakazawa

The ontogenetic stoichiometric bottleneck stabilizes herbivore–autotroph dynamics

Abstract In the ecological stoichiometry theory of population dynamics, ontogenetic changes in nutrient demand have been ignored. Here, I studied a stage-structured *Daphnia*–algae herbivore–autotroph model, in which the juveniles of the herbivore had a higher nutrient (phosphorous) demand for maturation than the adults for reproduction. The model predicted that while an increase in the juvenile nutrient demand (i.e., ontogenetic stoichiometric bottleneck) affects stage-specific performances in complex ways through nutrient dynamics and resource quality, in general it has stabilizing effects on the population dynamics.

Keywords Homeostasis · P:C ratio · Phosphorous limitation · Population stability · Zooplankton–phytoplankton interaction

Introduction

Experiments have indicated that nutrient addition improves life-history traits such as reproduction, individual growth, and survival (reviewed by Sterner and Schulz 1998; Sterner and Elser 2002). It has also been acknowledged that nutrient availability has profound consequences for population and food-web dynamics (reviewed by Andersen et al. 2004; Moe et al. 2005; Hall 2009). As a consequence, in ecological stoichiometry theory, the importance of describing population growth and dynamics in terms of both energy and nutrients is emphasized to provide a better understanding of the

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community structure and material flows in ecosystems (Sterner and Elser 2002).

A common assumption in ecological stoichiometry theory is that animals have a constant body elemental composition, and consequently, a constant nutrient demand throughout their lifespan (i.e., stoichiometric homeostasis). However, this is an approximation and a simplification that has been made for model development (Grover 2003; Persson et al. 2010). One of the major causes of variable stoichiometry is associated with individual growth; that is, juveniles grow and accumulate energy, while adults use energy for reproduction. Such ontogenetic behavioral changes lead to situations in which body elemental compositions change with different life-history stages; thus, the qualities of food required vary with life-history stages (Urabe and Sterner 2001; Becker and Boersma 2003). Indeed, it is well known that in *Daphnia* juveniles have a higher phosphorous (P) content and require food that is richer in P than do adults (Hessen 1990; Hessen and Andersen 1992; Main et al. 1997; DeMott et al. 1998; Sterner and Schulz 1998; DeMott 2003). This tendency has been generally explained by the growth rate hypothesis that faster growing individuals, usually juveniles, need to synthesize relatively P-rich ribosomal RNA (Elser et al. 2000, 2003; Vrede et al. 2004).

Ecological stoichiometry theory predicts that when juveniles have higher nutrient demands than adults, population growth of such animals may be limited by the nutrient availability in the juvenile stage. Hereafter, I call this phenomenon the "ontogenetic stoichiometric bottleneck (OSB)" following Færøvig and Hessen (2003), although different terms have been used for this phenomenon (Villar-Argaiz and Sterner 2002; Andersen et al. 2004; Hall 2009). At present, little is known about the ecological consequences of OSB despite their potentially large demographic impacts (Andersen et al. 2004; Moe et al. 2005; Hall 2009). In the present study, I aim to address and answer the question of how OSB mediates population dynamics. For this purpose, I investigate a herbivore–autotroph model with a

juvenile–adult stage structure of the herbivore. In the model, I assume that the juveniles and adults have different nutrient requirements for maturation and reproduction, respectively.

Model

I study herbivore–autotroph dynamics, in which the herbivore passes through juvenile (i.e., immature) and adult (i.e., mature) stages. The juveniles and adults share a common food resource, but their performance is limited for different levels of food quality. To describe the herbivore–autotroph dynamics, I extend a simplified physiologically structured population model (De Roos et al. 2008) to include several conventional assumptions made in ecological stoichiometry theory (Sterner and Elser 2002). I use the simplified structured model as the basis for future model extensions (see arguments in De Roos et al. 2008). It is also known that the dynamics given by the simplified model closely approximate those given by the original complex structured model (De Roos et al. 2008). The model I studied is as follows:

$$\frac{dR}{dt} = r\left(1 - \frac{R}{k'}\right)R - \frac{I_{\max}R}{H + R}C_J - \frac{\alpha I_{\max}R}{H + R}C_A - dR \quad (1a)$$

$$\frac{dC_J}{dt} = \max[v_A, 0]C_A + v_J C_J - \max[\gamma, 0]C_J - \mu C_J - dC_J \quad (1b)$$

$$\frac{dC_A}{dt} = \max[\gamma, 0]C_J + \min[v_A, 0]C_A - \mu C_A - dC_A \quad (1c)$$

The model describes the changes in biomass (mg C L^{-1}), where R represents the autotroph and C_h (h = J or A) represents the juvenile or adult herbivore. The autotroph exhibits logistic growth, with an intrinsic growth rate r (day^{-1}) and a carrying capacity k' (mg C L^{-1}). The grazing rate per body mass is a Holling's type II functional response in which $I_{\max}$ (day^{-1}) and H (mg C L^{-1}) represent the maximum ingestion rate and the half saturation constant, respectively. The parameter α (dimensionless) is a simple representation of the difference between the food availability for juveniles and adults (De Roos et al. 2008). The parameters μ and d are the herbivore mortality rate and the dilution rate of the system, respectively (both in day^{-1}).

The stage-specific net biomass production rate per unit body mass (day^{-1}) is v_h (h = J or A). When it is negative, it indicates that the body mass of the herbivore decreases and the total mortality rate increases by v_h (i.e., starvation occurs). In this situation, the adults stop reproduction (i.e., only for $v_A > 0$, the adults produce offspring at the rate of v_A). Thus, it is assumed that the adults utilize all excess energy for reproduction. Meanwhile, the juveniles invest energy in their individual growth when $v_J > 0$. The maturation rate of the juveniles depends on the biomass production rate v_J, the mortality rate μ, and the birth-to-maturity body mass ratio z (dimensionless). The maturation function is described as follows (see De Roos et al. 2008 for derivation):

$$\gamma = \frac{v_J - \mu}{1 - z^{1 - v_J/\mu}} \quad (2)$$

The maturation rate should be non-negative, and hence, the juveniles mature at the rate of max $[\gamma, 0]$ (day^{-1}) (note that max $[\gamma, 0] = 0$ when $v_J < 0$ because γ has the same sign as v_J). The production rates v_J and v_A are given by the following functions:

$$v_J = \frac{\sigma I_{\max} R}{H + R}\min\left[1, \frac{Q}{q_J}\right] - T \quad (3a)$$

$$v_A = \frac{\sigma \alpha I_{\max} R}{H + R}\min\left[1, \frac{Q}{q_A}\right] - T \quad (3b)$$

where σ (dimensionless and < 1) is the assimilation efficiency and T (day^{-1}) is the mass-specific metabolic cost for maintenance.

For simplicity, I consider two limiting elements C and P. In Eq. (3a–b), it is assumed that food quality (here, the P:C ratio) can limit the stage-specific net biomass production rate v_h and thus limit reproduction or maturation (Sterner and Elser 2002). In these equations, q_J and q_A are constant P:C ratios corresponding to the juveniles and adults, respectively (both q_J and q_A have units of mg P (mg C)$^{-1}$). Although the assumption is simple, such a stepwise shift is experimentally supported for *Daphnia* (e.g., DeMott 2003). Q represents the variable P:C ratio of the autotroph (mg P (mg C)$^{-1}$). As is the convention, I assume that dead biomass is immediately remineralized and that the autotroph can absorb all available nutrients in the environment; thus, the autotroph P:C ratio is given as follows:

$$Q = \frac{N_T - q_J C_J - q_A C_A}{R} \quad (4)$$

where N_T (mg P L^{-1}) is the total P concentration in the system. The autotroph growth is limited by the availability of either C or P. Therefore, the carrying capacity of the autotroph is

$$k' = \min\left[K, \frac{N_T - q_J C_J - q_A C_A}{q_R}\right] \quad (5)$$

where K (mg C L^{-1}) is the carrying capacity determined by light intensity and q_R (mg P (mg C)$^{-1}$) is the minimum P content of the autotroph.

I perform numerical simulations to investigate the model. For the present demonstration, I use the following parameter set describing the *Daphnia*–algae system based on the model developed by Andersen (1997): $r = 1.2$, $K = 1$, $q_R = 0.0038$, $I_{\max} = 0.81$, $H = 0.2$, $\sigma = 0.8$, $T = 0.25$, $\mu = 0.02$, and $d = 0.01$. For the other parameters, I use $\alpha = 1$ and $z = 0.01$ as default values (De Roos et al. 2008). In some models (e.g., Sterner and Elser 2002; Andersen et al. 2004), the *Daphnia* P:C ratio was assumed to be 0.03 mg P (mg C)$^{-1}$. However, this value seems to correspond to the P:C ratio for juveniles

(e.g., Færøvig and Hessen 2003). The P:C ratio is generally lower for adults (see "Introduction"). Therefore, I specifically focus on how q_J affects the population dynamics along a gradient of N_T for $q_J \leq 0.03$, with q_A fixed at 0.01. All parameters will differ depending on the species identity and environmental conditions. Nevertheless, my numerical results provide useful theoretical insights into the demographic impacts of OSB. In all simulations, the initial conditions are $R(0) = \min[K, N_T/q_R]$, $C_J(0) = 0$, and $C_A(0) = 0.01$.

Results

For different levels of the juvenile nutrient demand q_J, I simulated the system along a gradient of the total nutrient concentration N_T until it reached a steady state. In general, the following pattern was observed, as in the standard consumer–resource model. The herbivore went extinct for very small values of N_T. When the herbivore persisted, the system converged to the stable equilibrium
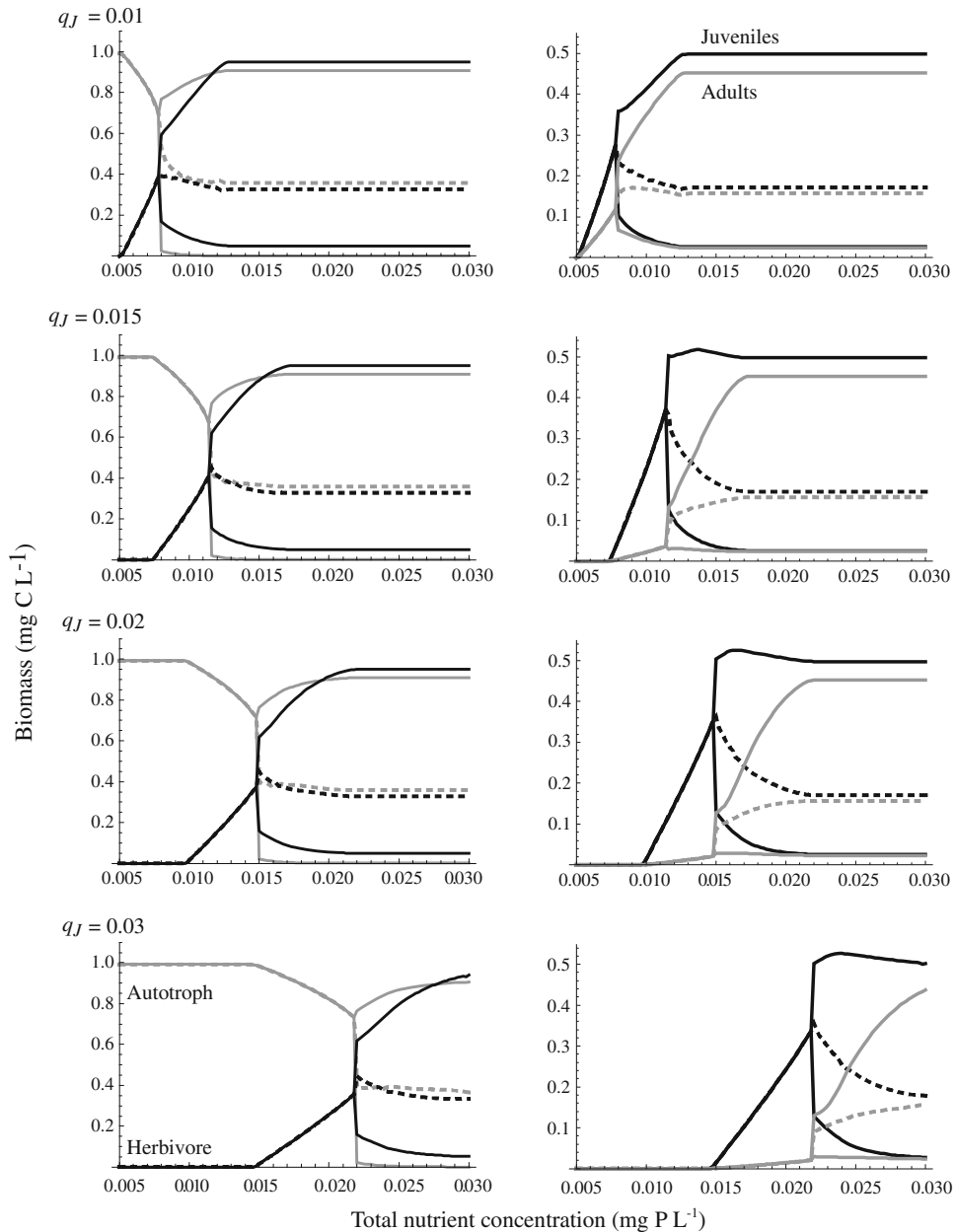

Fig. 1 Steady-state biomass along a nutrient gradient. In the *left panels*, the *black* and *gray lines* are for the autotroph R and herbivore $C_J + C_A$, respectively. In the *right panels*, the *black* and *gray lines* are for juveniles C_J and adults C_A, respectively. The *solid* and *dotted lines* represent the maximum (or minimum) and long-term average values, respectively. The q_J values corresponding to the panels, from *top* to *bottom*, are 0.01, 0.015, 0.02, and 0.03

point for intermediate values of N_T, while it exhibited fluctuations (limit-cycles) above a certain threshold (bifurcation boundary) (left panels in Fig. 1). The destabilization (i.e., increasing amplitude of population oscillations) due to enrichment was suppressed by increasing q_J, resulting in upward shifts of the bifurcation boundary; in other words, as far as the herbivore existed, an increase in q_J stabilized the system by decreasing the variability. It should be also noted that the parameter range for stable coexistence increased with an increase in q_J. The long-term average biomass of the herbivore and autotroph did not significantly change with q_J for large N_T. I also observed that the adult-to-juvenile biomass ratio varied with q_J. It seemed to decrease with an increase in q_J (right panels in Fig. 1).

I performed the above analysis for other parameter sets or initial conditions. I observed qualitatively the same results, although the results for other parameter sets were quantitatively different (see Appendix 1 for examples). In any case, I observed that an increase in q_J

significantly stabilized the system. Therefore, it seems that the stabilizing effects of OBS are robust at least within the biologically meaningful parameter space.

I also monitored the temporal dynamics at $N_T = 0.012$ by introducing a small number of adult herbivores into the autotroph population after the system reached the steady state. This numerical example showed that when q_J was high, the system reached the steady state more slowly because of the low population growth (upper panels in Fig. 2) and that the herbivore could go extinct if q_J was too high (lower panels in Fig. 2). At the steady state, the system exhibited smaller oscillation amplitudes as q_J increased (lower panels in Fig. 2). Furthermore, with an increase in q_J, the cycle period was increased (about 27 days for $q_J = 0.01$ and 33 days for $q_J = 0.015$), and the period during which $Q/q_h < 1$ (i.e., the P-limitation period) was lengthened (lower panels in Fig. 2). However, while an increase in q_J generally lengthened the P-limitation period for the juveniles (gray regions), a very large increase in q_J rather
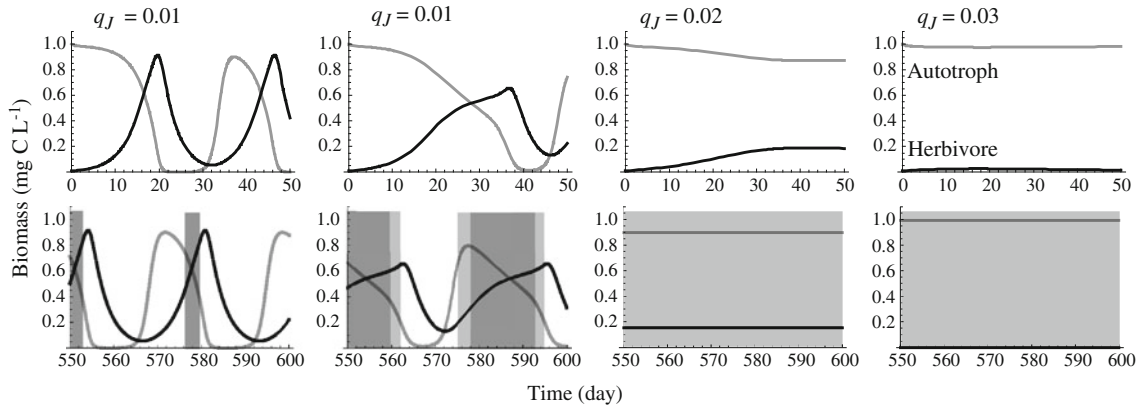

Fig. 2 Temporal dynamics in the early and steady stages after the introduction of the herbivore into the autotroph population. The *gray* and *black lines* represent the autotroph and herbivore biomass, respectively. In the *dark gray* regions of the *lower panels*, both stages are P-limited. In the *light gray* regions, only the juveniles are P-limited and the adults are C-limited. The period of P-limitation is displayed only in the *lower panels*. The q_J values corresponding to the panels, from *left* to *right*, are 0.01, 0.015, 0.02, and 0.03; $N_T = 0.012$
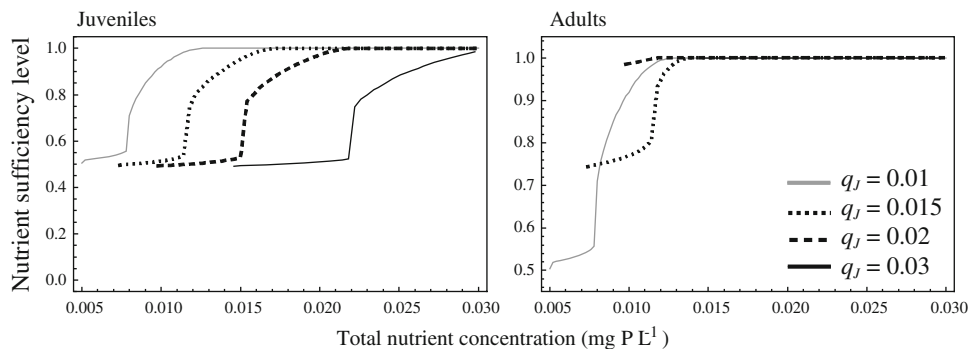

Fig. 3 Long-term averages of the nutrient sufficiency level for the juveniles (*left*) and adults (*right*); $q_J = 0.01$ (*gray*), 0.015 (*dotted*), 0.02 (*dashed*), and 0.03 (*solid*). The *lines* are shown only for the region in which the herbivore persisted

shortened the P-limitation period for the adults (dark gray regions). I also found that, along a nutrient gradient, q_J affected the long-term averages of the stage-specific nutrient sufficiency level (defined as min[1, Q/q_h]) in complex ways. An increase in q_J generally resulted in a decrease in the value for the juveniles, while the effect could be negative or positive for the adults especially for small N_T (Fig. 3).

Discussion

I theoretically showed that the ontogenetic changes in nutrient demand have considerable demographic impacts. In particular, I predicted that the stability was enhanced (i.e., the variability was reduced) by increasing the juvenile nutrient demands, although herbivore extinction became more likely at low nutrient levels (Figs. 1, 2; see also Appendix 1). In other words, this result suggests that, as far as the herbivore exists, OSB (i.e., higher nutrient demand in the juvenile stage) has stabilizing effects on the herbivore–autotroph dynamics. Intuitively, this result is explained by the degraded individual performances and population growth (Figs. 2, 3), and it is closely related to a well-known observation in consumer–resource interactions: if the population growth rate of the consumer is reduced, then the equilibrium resource density increases and the dynamics are more likely to be stable (Murdoch et al. 2003; Nakazawa et al. 2009). The observed decreases in the adult-to-juvenile biomass ratio with juvenile nutrient demands (right panels in Fig. 1) will be due to a decrease in the maturation rate (see De Roos et al. 2007 for stage-specific population regulation).

While OSB was stabilizing (Appendixes 1, 2), the consequences on stage-specific performances were complex especially in the adults (Figs. 2, 3). The predictions are explained as follows. OSB can potentially increase nutrient limitation not only for the juveniles but also for the adults, because a high nutrient demand of the juveniles may reduce the food quality (i.e., nutrient availability to the autotroph) by decreasing the nutrient excretion to the environment (see Eq. 4). The increased resource biomass due to the declined herbivore biomass (Figs. 1, 2) will also contribute to decrease the food quality. This scenario implies that OSB is stabilizing because both stages reduce their performance (see the argument above). However, the negative effect on the adults can be cancelled if the total nutrient storage of the herbivore population is reduced due to the declined herbivore biomass and the nutrient availability to the autotroph increases, which may improve adult performance. Nevertheless, because this process includes a reduction of the herbivore population growth, the improvement of adult performance may not be enough to destabilize the system. Experiments need to be carried out to investigate how different life-history stages interact with one another through nutrient dynamics and resource quality and to what extent it is related to the population stability.

I have employed a simple minimal model for a *Daphnia*-type herbivore. However, many other animals also exhibit ontogenetic changes in nutrient demands at different levels and in different patterns. For example, the decrease in P content in copepods during the copepodite stages is as drastic as or more drastic than that in *Daphnia* (Carrillo et al. 2001; Villar-Argaiz et al. 2002), suggesting the possible existence of stronger stabilizing effects than those I showed here. In vertebrates, the P:C ratio increases with growth (e.g., Pilati and Vanni 2007), because they need to build and maintain a P-rich skeleton and the relative P mass increases with the body size (Sterner and Elser 2002). My results may indicate that the stabilizing effects of OSB are qualitatively robust, regardless of the stage in which nutrient limitation is more likely to occur (see Appendix 2), because OSB will always reduce population growth in nutrient-poor environments. Even if juvenile and adult performances are limited by the availability of different elements, the stabilizing effects will be positive, although the indirect effects of the interstage interactions (see above) are absent.

Ecological stoichiometry is still incomplete, and researchers are in the initial stages of establishing a more powerful and useful framework for the study of community and ecosystem ecology. In the present study, I introduced ontogenetic changes in nutrient demand in the existing framework of the ecological stoichiometry theory of population dynamics. This is the first demonstration that OSB has important ecological consequences. The model needs to be modified in various ways (by including ontogenetic niche shifts, multiple stages, and stage-specific predators) to enhance the preliminary insights obtained from this study. More detailed information on nutrient demand during the course of individual growth is also required for various animal taxa. The present study provides important bases for such future theoretical and empirical studies aimed at integrating energy and nutrient dynamics for gaining a better understanding of the structures and dynamics of stage-structured communities in nature.

Appendix 1

In this Appendix, I present some results with different parameter settings to test the robustness of the stabilizing effects of OSB. I examined the steady state of the system along a nutrient gradient N_T for different levels of the juvenile nutrient demand q_J (as in Fig. 1) by varying one parameter value and keeping the other parameters to the default values (see text). As examples, here I varied light-induced carrying capacity K (~1.5), herbivore mortality rate μ (~0.05), dilution rate d (~0.05), stage-specific resource availability ratio α (~2) or birth-to-maturity body mass ratio z (~0.05). In any case, I found that an increase in q_J significantly stabilized the system (i.e., the bifurcation boundary shifted upward and the parameter region for stable coexistence increased). I also obtained qualitatively the same results when other parameter values were varied (results not shown). Therefore, it seems that the stabilizing effects of OSB are robust within the biologically meaningful parameter space. Notation is identical to that in Fig. 1.
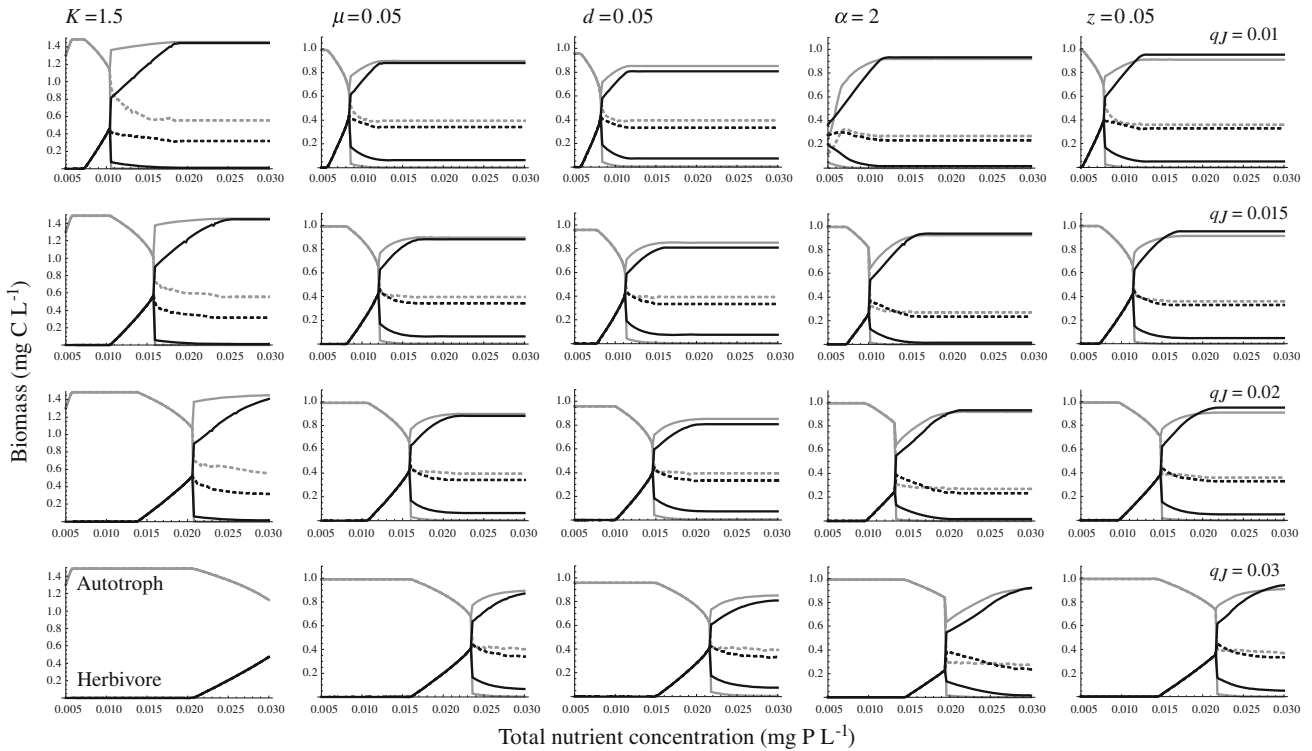
Appendix 2

Here, I show that the stabilizing effects of OSB would be qualitatively robust regardless of which stage has a higher nutrient demand. I examined the steady state of the system along a nutrient gradient N_T for different sets of (q_J, q_A) including situations where the adults had a higher P demand than the juveniles. I found that an increase in either q_J or q_A stabilized the system (i.e., the bifurcation boundary shifted upward and the parameter region for stable coexistence increased). The stabilizing effects of increasing q_J (or q_A) were larger when q_A (or q_J) was small. Panels are arranged along q_J (column) and q_A (row) (q_h = 0.01, 0.015, 0.02 or 0.03). Notation is identical to that in Fig. 1.
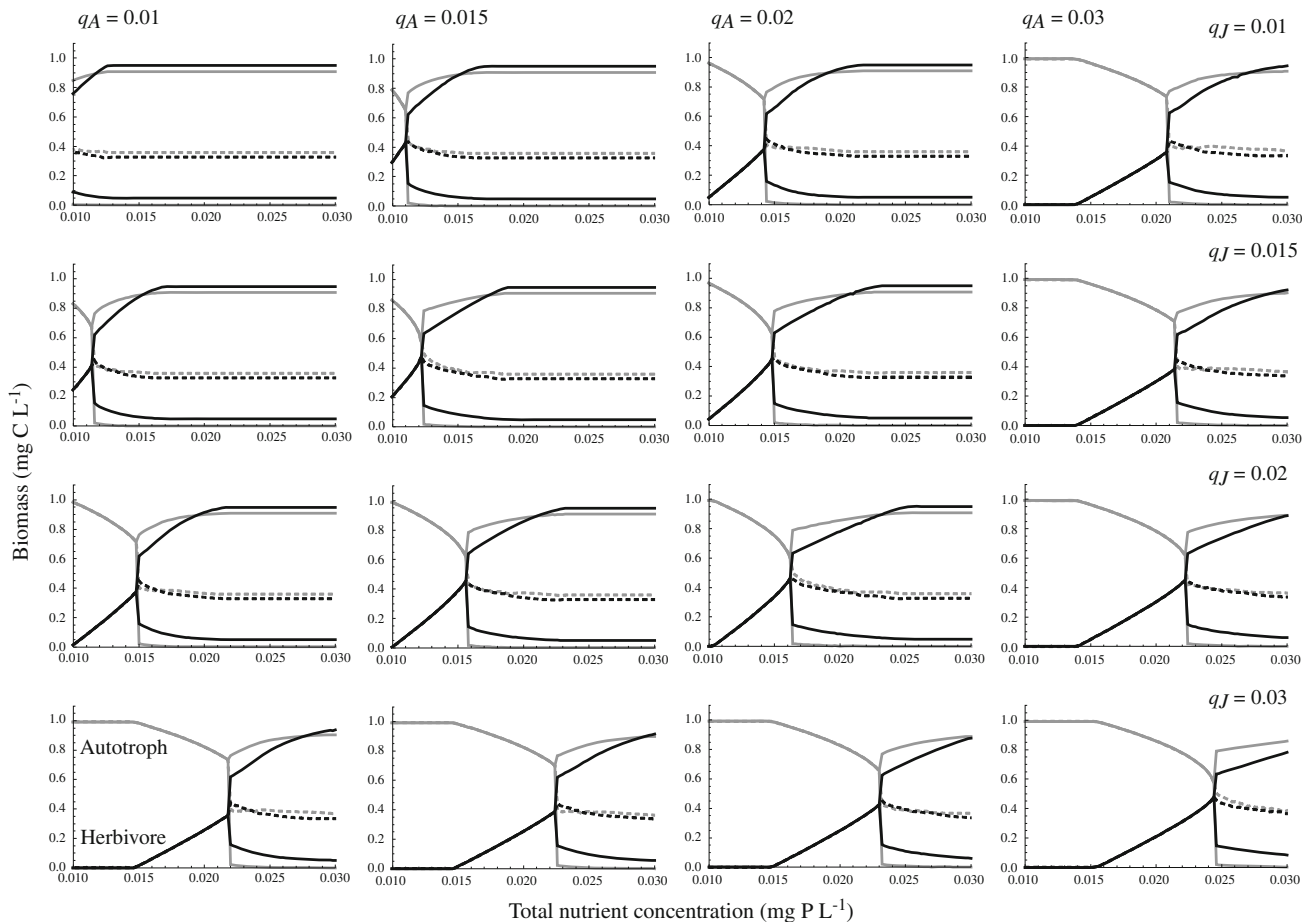
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