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Lai Zhang · Zhigui Lin · Michael Pedersen

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Abstract The physiological-structured population models assume that a fixed fraction of energy intake is utilized for individual growth and maintenance while the remaining for adult fertility. The assumption results in two concerns: energy loss for juveniles and a reproduction dilemma for adults. The dilemma results from the possibility that adults have to breed even if metabolic costs fail to be covered. We consider a size-structured population model, where standard metabolism is given top priority for utilizing energy intake and the surplus energy, if there is any, is distributed to individual growth and reproduction. Moreover, the portion of surplus energy for reproduction is size-dependent and increases monotonically with size. Using the newly developed parameter continuation, we demonstrate their disparate effects on population dynamics. Results show that the size-dependent mechanism of energy allocation primarily exerts destabilizing effects on the system but considerably promotes species coexistence, in comparison with the size-independent mechanism. We conclude that the size-dependent mechanism is, to a large extent, a dispensable component of model ingredients when ontogeny is explicitly taken into consideration.

Keywords Characteristic equation · Dynamic energy budget theory · Life history · Parameter continuation · Size structure

L. Zhang · M. Pedersen (✉)
Department of Mathematics, Technical University of Denmark, Matematiktorvet, 303S, 2800 Kgs.
Lyngby, Denmark
e-mail: M.Pedersen@mat.dtu.dk

L. Zhang
National Institute of Aquatic Resources, Technical University of Denmark, Charlottenlund Slot,
Jægerborg Allé 1, 2910 Charlottenlund, Denmark

Z. Lin
School of Mathematical Science, Yangzhou University, Yangzhou 225002, China

1 Introduction

A pronounced scenario in aquatic ecosystems is individual ontogeny. During that course individual body size could range from the egg size of milligram up to several kilogram. The size alteration apparently affects individual life-history including feeding, growth, fertility and mortality, since body size is considered to be the most important parameter governing biological processes (Weitz and Levin 2006). Taking individual ontogenetic growth and life-history into account, structured models are usually used to describe population dynamics (Cushing 1992; de Roos 2008; Andersen and Pedersen 2010).

In general, there are three types of structured population models, that is, age-structured population models (Cushing 1992), physiological-structured population models (de Roos and Persson 2001), and trait-based size-structured population model (Hartvig et al. 2011). The fundamental difference between the first two types of models is that the transition from one stage to the next takes place automatically in the former models (which is out of our interest) but food-dependently in the latter. The trait-based structured model synthesizes the physiological-structured modeling and the community size-spectrum modeling (Andersen and Beyer 2006). It aims to provide a generic framework for size-structured food webs since species are characterized by trait (i.e. size at maturation) avoiding dealing with specific species. However, it can be reparameterised for particular ecosystems.

Built on the framework of physiological-structured population modeling, de Roos et al. (2010) studied the dynamics of *Daphnia* (de Roos et al. 1990). They developed a numerical program to continuously trace the stability boundaries where Hopf-bifurcations occur as functions of some parameters (e.g. background mortality). In this model, they assumed that a fixed proportion of energy intake is distributed to individual growth and maintenance activities while the remaining to fertility if individuals have matured. Therefore, a questions arises what happens to the remaining energy for juveniles since there is no reproduction involved. In addition, the distributed energy for growth and maintenance might be insufficient to cover metabolic costs. In case of this situation, adults have to breed even during starvation, a reproduction dilemma.

Based on those two concerns, Hartvig et al. (2011) argued that ingested energy should be firstly used for standard metabolism and secondly for growth and reproduction if there is any energy left. Moreover, the distribution of energy between growth and fertility should be dependent on individual size. Apparently, different mechanisms of energy allocation create distinct feedbacks on individual growth curve plasticity via reproduction and food intake. Therefore, our question is how differently the two strategies of energy allocation affect population dynamics.

To examine this question, we reparameterise the trait-based size-structured population model according to the *Daphnia* model (de Roos et al. 1990) and apply the newly developed numerical tool (de Roos et al. 2010). Specific model description is presented in the next section. The paper is structured as follows. In Sect. 3, a coupled delay system associated with (6)–(8) is introduced in order to trace the existence and stability boundaries of equilibrium. Section 4 is devoted to derive the characteristic equation to the delayed system. We trace the existence boundary of equilibrium and

stability boundary of positive steady states in Sect. 5. Discussion about the effects of the growth curve plasticity upon the system is carried out in the last section. The work ends up with a brief conclusion.

2 Consumer-Resource Dynamics

The model is composed of a size-structured population *Daphnia* $N(m)$ (number per unit volume) and an unstructured resource algal R (cells per unit volume). Body size m refers to individual weight (gram).

Food uptake rate of individual m , denoted by $I(m, R)$, depends on the resource density following a Holling type II function response:

$$I(m, R) = \gamma_s m^n f_r(R), \quad (1)$$

where $f_r(R) = \frac{\rho R}{1 + \rho R}$, and $\gamma_s m^n$ is the search volume. The maximum amount of energy assimilated per unit time is

$$A(m, R) = \alpha h m^n f_r(R), \quad (2)$$

where α is the assimilation efficiency, and the quotient, h/γ_s , indicates the energy content per algal cell (de Roos et al. 1990). The ingested energy is first used to pay respiration cost, $k_s m$ (West et al. 2001). The remaining surplus energy is then used for individual growth and reproduction, distributed by an allocation function (Hartvig et al. 2011):

$$\psi(m) = \left(\frac{m}{m_\infty} \right)^{0.25} \left(1 + \left(\frac{m_a}{m} \right)^\xi \right)^{-1}, \quad (3)$$

where m_∞ is the maximum body size and m_a the maturation size. $\psi(m)$ is a monotonous increasing function of body size with $0 \leq \psi(m) \leq 1$, and shows that juveniles could reproduce before reaching maturation size m_a (governed by the parameter ξ). The effect of this energy allocation is to generate biphasic growth trajectory, where juveniles grow almost linearly while adults follow the von Bertalanffy growth curves (Lester et al. 2004).

The individual growth rate and reproduction rate can be formulated as (Hartvig et al. 2011):

$$g(m, R) = \max\{A(m, R) - k_s m, 0\} (1 - \psi(m)) \quad (4)$$

and

$$\beta(m, R) = \frac{\varepsilon}{m_0} \max\{A(m, R) - k_s m, 0\} \psi(m), \quad (5)$$

where ε is the reproduction efficiency and m_0 is the size at birth (gram). Individuals suffer from the background mortality μ_b only, but die instantaneously when standard metabolism fails to be satisfied.

Table 1 Model symbols and default values

Symbol	Value	Unit	Interpretation
<i>Variable</i>			
K	–	cell·ml ^{−1}	Resource carrying capacity
μ_b	–	d(ays) ^{−1}	Background mortality
<i>Parameter</i>			
λ	9.0×10^{-6}	g·mm ^{−3}	Length-mass scaling constant ¹
ρ	7.0×10^{-6}	ml·cell ^{−1}	Shape parameter of functional response
γ_s	4.16×10^9	cell·g ^{−$\frac{2}{3}$} ·d ^{−1}	Factor of search volume
h	0.6420	g ^{$\frac{1}{3}$} ·d ^{−1}	Factor of maximum consumption rate
n	$\frac{2}{3}$	–	Exponent of maximum feeding rate
α	0.3	–	Assimilation efficiency ²
ε	0.0081	–	Reproduction efficiency
k_s	0.45	d ^{−1}	Factor of standard metabolism
m_0	4.6080	μg	Size at birth
m_a	140.6250	μg	Size at maturation
ξ	10	–	Width of allocation function ³
r_0	0.5	d ^{−1}	Resource growth rate
κ	0.5	–	Allocation efficiency ⁴
δ	1.0×10^{-9}	–	Survival threshold ⁵

¹Claessen and de Roos (2003); ²Andersen and Beyer (2006); ³Hartvig et al. (2011); ⁴Ranging from 0.3 (de Roos et al. 1990) to 0.7 (Claessen and de Roos 2003); ⁵de Roos et al. (2010). The remaining are derived from de Roos et al. (1990) based on the mass-length relation $m = \lambda L^3$, where L is body length. Varying parameter values will be specified

Finally, at population level, dynamics of $N(m)$ is described by the McKendric-von Foerster equation:

$$\frac{\partial N(m, t)}{\partial t} = -\frac{\partial(g(m, R)N(m, t))}{\partial m} - \mu(m, R)N(m, t), \quad m \in [m_0, m_\infty], \quad (6)$$

subjected to a nonlocal boundary condition reflecting the reproduction flux:

$$g(m_0, R)N(m_0, t) = \int_{m_0}^{m_\infty} \beta(m, R)N(m, t) dm. \quad (7)$$

Resource follows the logistic dynamics:

$$\frac{dR(t)}{dt} = f(R) - \int_{m_0}^{m_\infty} I(m, R)N(m) dm, \quad (8)$$

where $f(R) = r_0 R(1 - R/K)$. Initial conditions for species N and resource R are ignored since we only focus on the steady states of system (6)–(8). Relevant symbols are summarized in Table 1.

3 Delayed System

Define

$$R_t(\tau) = R(t + \tau), \quad \tau \in (-\infty, 0], \quad (9)$$

which is a resource history at time t . Define $m(a, R_t)$ to be the size that an individual has at age a and time t , given that it has experienced history R_t in the time interval $[t - a, t]$. Likewise, define $F(a, R_t)$ as the survival probability of an individual to reach age a at time t provided that it experiences the resource history in the time interval $[t - a, t]$. Then body size m and survival probability F can be determined as functions of some ordinary differential equations via those vital rates of feeding $I(m, R)$, assimilation $A(m, R)$, growth $g(m, R)$, fertility $\beta(m, R)$, and mortality $\mu(m, R)$. In addition, these rates are smooth mappings from $\mathfrak{R}_+^2$ to $\mathfrak{R}_+$.

In a similar manner to Diekmann et al. (2010), define $\tilde{m}(\zeta) = \tilde{m}(\zeta; a, \Psi)$ as the size of an individual at age ζ , given that it has experienced resource history Ψ in the time interval $[-a, 0]$ at age a , if still alive. Likewise, define $\tilde{F}(\zeta; a, \Psi)$ as the survival probability of an individual that can survive up to age ζ , given that at age a , if still alive, it has experienced resource history Ψ . $\tilde{m}(\zeta; a, R_t)$ and $\tilde{F}(\zeta; a, R_t)$ can be solved through a set of autonomous ordinary differential equations:

$$\begin{cases} \tilde{m}'(\zeta) = g(\tilde{m}(\zeta), \Psi(-a + \zeta)), & 0 \leq \zeta \leq a, \\ \tilde{m}(0) = m_0 \end{cases} \quad (10)$$

and

$$\begin{cases} \tilde{F}'(\zeta) = -\mu(\tilde{m}(\zeta), \Psi(-a + \zeta))\tilde{F}(\zeta), & 0 \leq \zeta \leq a, \\ \tilde{F}(0) = 1. \end{cases} \quad (11)$$

Then, we have

$$m(a, R_t) = \tilde{m}(a; a, R_t) \quad \text{and} \quad F(a, R_t) = \tilde{F}(a; a, R_t).$$

Denote by $b(t)$ the population birth rate (number of offspring per volume) per unit time at time t and by $a_\infty (\leq \infty)$ the maximum lifetime of an individual under unlimited food conditions. According to Diekmann et al. (2010), the population dynamics of system (6)–(8) can be described by the following system:

$$b(t) = \int_0^{a_\infty} \beta(m(a, R_t), R(t))F(a, R_t)b(t - a) da, \quad (12)$$

$$R'(t) = f(R(t)) - \int_0^{a_\infty} I(m(a, R_t), R(t))F(a, R_t)b(t - a) da. \quad (13)$$

The above system is composed of a renewal equation (12) and a delayed differential equation (13). Initial conditions are ignored since we are restricted to stationary solutions.

Clearly, a trivial equilibrium to system (12) and (13) is $(b^*, R^*) = (0, K)$. Since it is out of our interests, we disregard it here and concentrate on the interior positive

equilibria from now on. A nontrivial equilibrium can be given through the following stationary equations:

$$\Gamma(R^*) - 1 = 0, \quad (14)$$

$$f(R^*) - \Theta(R^*)b^* = 0, \quad (15)$$

$$\Gamma(R^*) := \int_0^{a_\infty} \beta(m(a, R^*), R^*) F(a, R^*) da, \quad (16)$$

$$\Theta(R^*) := \int_0^{a_\infty} I(m(a, R^*), R^*) F(a, R^*) da. \quad (17)$$

From the biological perspective, $\Gamma(R^*)$ is the expected lifetime offspring reproduction number per adult and $\Theta(R^*)$ is the expected lifetime resource consumption of a consumer individual.

Equation (14) implies that each consumer, at steady state, produces on average one offspring to replace itself during its lifetime. Recall the fertility rate (5), and we see that $\Gamma(0) < 1$ and $\Gamma(\infty) > 1$. In combination with the feeding rate (1), there is a unique solution to equation (14). Once R^* is known, the population birth rate at steady state is attainable:

$$b^*(R^*) = \frac{f(R^*)}{\Theta(R^*)}. \quad (18)$$

Therefore, the equilibrium issue to (12) and (13) boils down to find the root of equation (14). In fact, it can be calculated through the following four ordinary differential equations:

$$\frac{d}{da} m(a, R^*) = g(m(a, R^*), R^*), \quad a > 0, \quad (19)$$

$$m(0, R^*) = m_0,$$

$$\frac{d}{da} F(a, R^*) = -\mu(m(a, R^*), R^*) F(a, R^*), \quad a > 0, \quad (20)$$

$$F(0, R^*) = 1,$$

$$\frac{d}{da} \gamma(a, R^*) = \beta(m(a, R^*), R^*) F(a, R^*), \quad a > 0, \quad (21)$$

$$\gamma(0, R^*) = 0,$$

$$\frac{d}{da} \theta(a, R^*) = I(m(a, R^*), R^*) F(a, R^*), \quad a > 0, \quad (22)$$

$$\theta(0, R^*) = 0.$$

One of our targets is to trace the nontrivial equilibrium as a function of some parameters, denoted by a vector $\bar{\alpha} := (\alpha_1, \dots, \alpha_l)$. Rewrite system (14)–(15) as

$$\Gamma(\bar{\alpha}, R^*) - 1 = 0, \quad (23)$$

$$b^* = \frac{f(\bar{\alpha}, R^*)}{\Theta(\bar{\alpha}, R^*)}. \quad (24)$$

The curve induced by

$$f(\bar{\alpha}, R^*) = 0 \quad (25)$$

and (23) is called the existence boundary for the nontrivial equilibrium (b^* switches sign from negative to positive if this curve is crossed in the appropriate sense in the space defined by (23) and (25)).

We will use (19)–(22) and (23)–(24) to numerically make a track of the existence boundaries of equilibria.

4 Characteristic Equation

To obtain the characteristic equation, whose dominant eigenvalue determines the local stability of equilibrium (b^*, R^*), we linearize (12)–(13) at steady state.

4.1 Linearization of the Coupled Delay System

For convenience, define

$$\begin{aligned} \beta(a) &:= \beta(m(a, R^*), R^*), & \beta_1(a) &:= \frac{\partial}{\partial y} \beta(y, R)|_{(y, R)=(m(a, R^*), R^*)}, \\ F(a) &:= F(a, R^*), & \beta_2(a) &:= \frac{\partial}{\partial R} \beta(x, R)|_{(m, R)=(m(a, R^*), R^*)}. \end{aligned} \quad (26)$$

g_i , I_i and μ_i ($i = 1, 2$) are defined similarly. These derivatives will be specified in the next section. In addition, assume that $K(a, \lambda)$ and $L(a, \lambda)$ are solutions of the two differential equations:

$$\frac{\partial}{\partial a} K(a, \lambda) = g_1(a)K(a, \lambda) + g_2(a)e^{\lambda a}, \quad a > 0, \quad (27)$$

$$K(0, \lambda) = 0,$$

$$\frac{\partial}{\partial a} L(a, \lambda) = -\mu(a)L(a, \lambda) - \mu_1(a)K(a, \lambda)F(a) - \mu_2(a)F(a)e^{\lambda a}, \quad a > 0, \quad (28)$$

$$L(0, \lambda) = 0,$$

where λ is a complex number.

Differentiating equations (12) and (13) with respect to $b(t)$ and $R(t)$, and evaluating the resulting equations at steady state (b^*, R^*) give rise to the following two equations:

$$v(t) = \int_0^{a_\infty} \beta(a)F(a)v(t-a) da + s(t)b^* \int_0^{a_\infty} \beta_2(a)F(a) da$$

$$\begin{aligned}
 & + b^* \int_0^{a_\infty} F(a) \beta_1(a) D_2 x(a, R^*) s_t da \\
 & + b^* \int_0^{a_\infty} \beta(a) D_2 F(a, R^*) s_t da,
 \end{aligned} \tag{29}$$

and

$$\begin{aligned}
 \frac{ds(t)}{dt} &= f'(R^*) s(t) - \int_0^{a_\infty} I(a) F(a) v(t-a) da \\
 & - s(t) b^* \int_0^{a_\infty} I_2(a) F(a) da - b^* \int_0^{a_\infty} F(a) I_1(a) D_2 x(a, R^*) s_t da \\
 & - b^* \int_0^{a_\infty} I(a) D_2 F(a, R^*) s_t da,
 \end{aligned} \tag{30}$$

where the two derivatives, $D_2 x(a, R^*)$ and $D_2 F(a, R^*)$, are to be determined.

It assumes that perturbations $u(t)$ and $s(t)$ at the steady state (b^*, R^*) are of the forms $v(t) = e^{\lambda t} b^*$ and $s(t) = e^{\lambda t} R^*$. According to de Roos et al. (2010; Eqs. A.12 and A.13), we then have

$$D_2 m(a, R^*) s_t = R^* e^{\lambda(t-a)} K(a, \lambda), \tag{31}$$

$$D_2 F(a, R^*) s_t = R^* e^{\lambda(t-a)} L(a, \lambda). \tag{32}$$

4.2 Derivation of Characteristic Equation

Inserting $u(t) = e^{\lambda t} b^*$ and $s(t) = e^{\lambda t} R^*$ into (29)–(30) and dividing the resulting equations by $e^{\lambda t}$ yield that

$$\begin{aligned}
 1 &= \int_0^{a_\infty} \beta(a) F(a) e^{-\lambda a} da + R^* \int_0^{a_\infty} \beta_2(a) F(a) da \\
 & + R^* \int_0^{a_\infty} F(a) \beta_1(a) e^{-\lambda a} K(a, \lambda) da + R^* \int_0^{a_\infty} \beta(a) e^{-\lambda a} L(a, \lambda) da,
 \end{aligned} \tag{33}$$

$$\begin{aligned}
 \lambda R^* &= f'(R^*) R^* - b^* \int_0^{a_\infty} I(a) F(a) e^{-\lambda a} da \\
 & - b^* R^* \int_0^{a_\infty} I_2(a) F(a) da - b^* R^* \int_0^{a_\infty} F(a) I_1(a) e^{-\lambda a} K(a, \lambda) da \\
 & - b^* R^* \int_0^{a_\infty} I(a) e^{-\lambda a} L(a, \lambda) da.
 \end{aligned} \tag{34}$$

Set

$$\Phi_1(R^*, \lambda) = \int_0^{a_\infty} e^{-\lambda a} \beta(a) F(a) da, \tag{35}$$

$$\Phi_2(R^*, \lambda) = - \int_0^{a_\infty} e^{-\lambda a} I(a) F(a) da, \tag{36}$$

$$\begin{aligned}\Phi_3(R^*, \lambda) &= \int_0^{a_\infty} \beta_2(a) F(a) da \\ &+ \int_0^{a_\infty} e^{-\lambda a} (\beta(a) L(a, \lambda) + \beta_1(a) F(a) K(a, \lambda)) da, \quad (37)\end{aligned}$$

$$\begin{aligned}\Phi_4(R^*, \lambda) &= - \int_0^{a_\infty} I_2(a) F(a) da \\ &+ \int_0^{a_\infty} e^{-\lambda a} (I(a) L(a, \lambda) + I_1(a) F(a) K(a, \lambda)) da. \quad (38)\end{aligned}$$

Then the characteristic equation can be expressed as

$$\det \left(M(b^*, R^*, \lambda) - \begin{pmatrix} 1 & 0 \\ 0 & \lambda \end{pmatrix} \right) = 0, \quad (39)$$

where

$$M(b^*, R^*, \lambda) = \begin{pmatrix} \Phi_1(R^*, \lambda) & \Phi_2(R^*, \lambda) \\ \Phi_3(R^*, \lambda) & f'(R^*) + b^* \Phi(R^*, \lambda) \end{pmatrix}. \quad (40)$$

Recalling (24), we obtain an equivalent form of the characteristic equation as follows:

$$\begin{aligned}0 &= f(R^*) ((\Phi_1(R^*, \lambda) - 1) \Phi_4(R^*, \lambda) - \Phi_2(R^*, \lambda) \Phi_3(R^*, \lambda)) \\ &+ \Theta(R^*) (\Phi_1(R^*, \lambda) - 1) (f'(R^*) - \lambda). \quad (41)\end{aligned}$$

For any given steady state, its corresponding eigenvalue spectrum can be computed through (41), and the associated linear stability can be decided. Specifically, if all roots of the characteristic equation have negative real parts, the steady state is locally stable, otherwise, unstable if there is at least one root with positive real part.

4.3 Stability Boundary of Equilibrium

The aim of this subsection is to trace the stability boundaries of equilibria where bifurcations occur. To this end, set $\lambda = i\omega$ ($\omega > 0$) and split the entries in (40) into two real equations:

$$\Phi_j(R^*, \lambda) = \Phi_j^r(R^*, \omega) + i\Phi_j^i(R^*, \omega), \quad j = 1, \dots, 4, \quad (42)$$

where the supindices r and i refer to 'real' and 'imaginary'. Thus, we have

$$\begin{aligned}0 &= H(R^*, \omega) \\ &:= f(R^*) \left((\Phi_1^r(R^*, \omega) - 1) \begin{pmatrix} \Phi_4^r(R^*, \omega) \\ \Phi_4^i(R^*, \omega) \end{pmatrix} + \Phi_1^i(R^*, \omega) \begin{pmatrix} -\Phi_4^i(R^*, \omega) \\ \Phi_4^r(R^*, \omega) \end{pmatrix} \right) \\ &+ f(R^*) \left(-\Phi_3^r(R^*, \omega) \begin{pmatrix} \Phi_2^r(R^*, \omega) \\ \Phi_2^i(R^*, \omega) \end{pmatrix} + \Phi_3^i(R^*, \omega) \begin{pmatrix} \Phi_2^i(R^*, \omega) \\ -\Phi_2^r(R^*, \omega) \end{pmatrix} \right) \\ &+ \Theta(R^*) \left(f'(R^*) \begin{pmatrix} \Phi_1^r(R^*, \omega) - 1 \\ \Phi_1^i(R^*, \omega) \end{pmatrix} + \omega \begin{pmatrix} \Phi_1^i(R^*, \omega) \\ 1 - \Phi_1^r(R^*, \omega) \end{pmatrix} \right). \quad (43)\end{aligned}$$

Incorporating the free parameters $\bar{\alpha}$ into (43), we gain a system of three real equations (H comprises of two equations):

$$\begin{aligned} G(\bar{\alpha}, R^*) &= 0, \\ H(\bar{\alpha}, R^*, \omega) &= 0, \end{aligned} \quad (44)$$

where function $G(\bar{\alpha}, R^*) = \Gamma(\bar{\alpha}, R^*) - 1$. Equations (44) define a curve of dimension $l - 1$, the stability boundary of equilibrium.

Keep it in mind that the unknown complex functions $K(a, i\omega)$ and $L(a, i\omega)$ are involved in the characteristic equations (41). Analogously to $\Phi_j(R^*, i\omega)$, we rewrite them as

$$K(a, i\omega) = K^r(a) + iK^i(a), \quad L(a, i\omega) = L^r(a) + iL^i(a), \quad (45)$$

which lead to the following two systems (for $a > 0$):

$$\begin{aligned} \frac{dK^r(a)}{da} &= g_1(a)K^r(a) + g_2(a)\cos(\omega a), \\ \frac{dK^i(a)}{da} &= g_1(a)K^i(a) + g_2(a)\sin(\omega a), \\ K^r(0) &= 0, \quad K^i(0) = 0, \end{aligned} \quad (46)$$

and

$$\begin{aligned} \frac{dL^r(a)}{da} &= -\mu(a)L^r(a) - \mu_1(a)F(a)K^r(a) - \mu_2(a)F(a)\cos(\omega a), \\ \frac{dL^i(a)}{da} &= -\mu(a)L^i(a) - \mu_1(a)F(a)K^i(a) - \mu_2(a)F(a)\sin(\omega a), \\ L^r(0) &= 0, \quad L^i(0) = 0. \end{aligned} \quad (47)$$

With the real functions $K^r(a)$, $K^i(a)$, $L^r(a)$, and $L^i(a)$ at hand, Φ_j^r and Φ_j^i ($j = 1, \dots, 4$) can be determined via the following real ordinary differential equations:

$$\begin{aligned} \frac{d}{da}\Phi_1^r(a) &= \beta(a)F(a)\cos(\omega a), \quad a > 0, \\ \frac{d}{da}\Phi_1^i(a) &= -\beta(a)F(a)\sin(\omega a), \quad a > 0, \end{aligned} \quad (48)$$

$$\Phi_1^r(0) = \Phi_{1,0}^r, \quad \Phi_1^i(0) = \Phi_{1,0}^i,$$

$$\begin{aligned} \frac{d}{da}\Phi_2^r(a) &= \beta_2(a)F(a) + \beta(a)L_e^r(a, a) + \beta_1(a)F(a)K_e^r(a, a), \quad a > 0, \\ \frac{d}{da}\Phi_2^i(a) &= \beta(a)L_e^i(a, a) + \beta_1(a)F(a)K_e^i(a, a), \quad a > 0, \end{aligned} \quad (49)$$

$$\Phi_2^r(0) = \Phi_{2,0}^r, \quad \Phi_2^i(0) = \Phi_{2,0}^i,$$

$$\begin{aligned}\frac{d}{da}\Phi_3^r(a) &= -I(a)F(a)\cos(\omega a), \quad a > 0, \\ \frac{d}{da}\Phi_3^i(a) &= I(a)F(a)\sin(\omega a), \quad a > 0,\end{aligned}\tag{50}$$

$$\Phi_2^r(0) = \Phi_{3,0}^r, \quad \Phi_3^i(0) = \Phi_{1,0}^i,$$

$$\begin{aligned}\frac{d}{da}\Phi_4^r(a) &= -I_2(a)F(a) - I(a)L_e^r(a, a) - I_1(a)F(a)K_e^r(a, a), \quad a > 0, \\ \frac{d}{da}\Phi_4^i(a) &= -I(a)L_e^i(a, a) - I_1(a)F(a)K_e^i(a, a), \quad a > 0,\end{aligned}\tag{51}$$

$$\Phi_4^r(0) = \Phi_{4,0}^r, \quad \Phi_4^i(0) = \Phi_{4,0}^i,$$

where the initial conditions are zero since all the vital rates are continuous in age and resource concentration, and in addition

$$K_e^r(a_1, a_2) := K^r(a_2)\cos(\omega a_1) + K^i(a_2)\cos(\omega a_1),\tag{52}$$

$$K_e^i(a_1, a_2) := K^i(a_2)\cos(\omega a_1) - K^r(a_2)\cos(\omega a_1),$$

$$L_e^r(a_1, a_2) := L^r(a_2)\cos(\omega a_1) + L^i(a_2)\cos(\omega a_1),\tag{53}$$

$$L_e^i(a_1, a_2) := L^i(a_2)\cos(\omega a_1) - L^r(a_2)\cos(\omega a_1).$$

To evaluate the entries of the characteristic matrix (40) for given steady state (R^*, b^*) , we can integrate (48)–(51), (46)–(47), and (19)–(22) simultaneously. Once the characteristic equations (41) are known, the stability of the steady state is available. Varying the value of parameter $\bar{\alpha}$, the stability boundary of equilibrium can be traced. The population birth rate can be additionally computed via (41). In case of discontinuous vital rates (e.g. reproduction rate which occurs upon maturation), one can refer to de Roos et al. (2010) for detailed treatment.

5 Parameter Continuation

In this section, we shall trace the existence and stability boundaries of equilibria, using the numerical program developed by de Roos et al. (2010) to (23)–(24) and to (44), respectively. However, the numerical scheme is updated by using the Keller's method to perform continuation instead of the method introduced by de Roos et al. (2010). The Keller's parameter continuation is the most natural method for parameter continuation (Kuznetsov 1994).

The existence and stability boundaries of equilibrium are traced as functions of two free parameters, denoted by α_1 and α_2 . The resource carrying capacity K and the background mortality μ_b are used in the sequel. All boundaries are projected to the $\alpha_1 - \alpha_2$ -plane. The information involved in these figures is discussed in the next section. To decide when those integrations stop, we use the criterion introduced by Kirkilionis et al. (2001) that a_∞ is the age at which the probability of surviving up to

this age has decreased to δ . Since the mortality is constant, therefore,

$$a_{\infty} = -\frac{\log(\delta)}{\mu_b}. \quad (54)$$

5.1 Reference Model

To see the effects of the growth curve plasticity on population dynamics, we use the following model as a reference. This model is the same as ours except for the distribution of energy, which obeys the rule adopted in de Roos et al. (1990). Specifically, the growth and birth rates are

$$g_c(m, R) = \max\{\kappa A(m, R) - k_s m, 0\} \quad (55)$$

and

$$\beta_c(m, R) = \frac{\varepsilon}{m_0} (1 - \kappa) A(m, R), \quad m_a \leq m \leq m_{\infty}. \quad (56)$$

The calculations of the characteristic equations are ignored throughout this paper and only results are presented.

The maximum body size can be determined through (55) under ideal food condition, which means $f(R) = 1$. As individual approaches the maximum size, individuals stop growing. Thus, at m_{∞} we have

$$\kappa \alpha h m_{\infty}^n = k_s m_{\infty},$$

which leads to

$$m_{\infty} = \left(\frac{\kappa \alpha h}{k_s} \right)^{\frac{1}{1-n}}.$$

Here, the m_{∞} is the same as in (3). The differences in growth rate, growth trajectory and fertility rate between the two energy distributions are graphically exhibited in Fig. 1.

5.2 Tracing Existence Boundary of Equilibrium

We choose two free parameters, K and μ_b . The (14) and (18), used to trace the existence boundary of equilibrium, can be rewritten as

$$\Gamma(\alpha_1, R^*) - 1 = 0, \quad \alpha_2 = R^*. \quad (57)$$

The three-dimensional continuation reduces to be two dimensional. Hence, the boundary in α_1 – α_2 -plane is equivalent to the curve describing how the equilibrium varies with one parameter. Setting

$$G(\alpha_1, R^*) = \Gamma(\alpha_1, R^*) - 1, \quad (58)$$

then $G(\alpha_1, R^*) = 0$ defines a curve, i.e. the existence boundary of equilibrium. Applying the continuation scheme (de Roos et al. 2010) to the equations $G(\alpha_1, R^*) = 0$ and (19)–(21), the existence boundary is able to be demonstrated (dashed curve in Fig. 2).

Recall that the mortality rate is independent of body size and resource concentration. Equation (21) can be solved explicitly as

$$F(a) = e^{-\mu_b a}, \quad a > 0, \quad (59)$$

which can be used directly during parameter continuation.

5.3 Tracing Stability Boundary of Equilibrium

In contrast with the existence boundary of equilibrium, tracing the stability boundary of equilibrium is mathematically challenging. Recall the equations (44) and the two free parameters, we have

$$\begin{aligned} G(\alpha_1, \alpha_2, R^*) &= 0, \\ H(\alpha_1, \alpha_2, R^*, \omega) &= 0. \end{aligned} \quad (60)$$

The above three equations with four variables define a three dimensional surface, i.e. the stability boundary of equilibrium.

To implement the parameter continuation with (60), we have to specify the ingredients in (26) at equilibrium, which are used to evaluate the entries of the characteristic matrix. Concretely,

$$\begin{aligned} g_1(a) &= (n\alpha h f_r(R^*)m^{n-1} - k)(1 - \psi(m)) \\ &\quad - (\alpha h f_r(R^*)m^n - km) \frac{d\psi(m)}{dm}, \\ g_2(a) &= \alpha h m^n f'_r(R^*)(1 - \psi(m)), \\ \beta_1(a) &= \frac{\varepsilon}{m_0} (n\alpha h f_r(R^*)m^{n-1} - k) \psi(m) \\ &\quad + \frac{\varepsilon}{m_0} (\alpha h f_r(R^*)m^n - km) \frac{d\psi(m)}{dm}, \\ \beta_2(a) &= \frac{\varepsilon}{m_0} \alpha h m^n f'_r(R^*) \psi(m), \\ I_1(a) &= n\gamma_s m^{n-1} f_r(R^*), \quad I_2(a) = \gamma_s m^n f'_r(R^*), \\ \mu_1(a) &= 0, \quad \mu_2(a) = 0, \end{aligned} \quad (61)$$

where

$$\begin{aligned} f'_r(R^*) &= \frac{\rho}{(1 + \rho R^*)^2}, \\ \frac{d\psi(m)}{dm} &= \psi(m) \left(\frac{0.25}{m} + \frac{\xi m^{-1}}{1 + (\frac{m}{m_a})^\xi} \right). \end{aligned} \quad (62)$$

Since $\mu_1(a) = \mu_2(a) = 0$, it is easy to see from (47) that both $L^r(a)$ and $L^i(a)$ are zero. Moreover, $L_e^r(a_1, a_2)$ and $L_e^i(a_1, a_2)$ in (53) are zero as well. Then the ordinary differential equations in (49) and (51) reduce to

$$\begin{aligned} \frac{d}{da} \Phi_2^r(a) &= \beta_2(a)F(a) + \beta_1(a)F(a)K_e^r(a, a), \quad a > 0, \\ \frac{d}{da} \Phi_2^i(a) &= \beta_1(a)F(a)K_e^i(a, a) + \beta_1(a)F(a)K_e^r(a, a), \quad a > 0, \end{aligned} \quad (63)$$

$$\Phi_2^r(0) = 0, \quad \Phi_2^i(0) = 0,$$

$$\begin{aligned} \frac{d}{da} \Phi_4^r(a) &= -I_2(a)F(a) - I_1(a)F(a)K_e^r(a, a), \quad a > 0, \\ \frac{d}{da} \Phi_4^i(a) &= -I_1(a)F(a)K_e^i(a, a), \quad a > 0, \end{aligned} \quad (64)$$

$$\Phi_4^r(0) = 0, \quad \Phi_4^i(0) = 0.$$

It is now ready to carry out the parameter continuation on the stability boundary of positive equilibrium with equations (60). To evaluate (60), one has to integrate (48), (50), (63), and (64) together with (46) and (19)–(22) simultaneously. The resulting stability boundary is demonstrated and projected to the two-dimensional parameter space, i.e. $\alpha_1 - \alpha_2$ -plane (solid curve in Fig. 2).

In addition, the two distinguished stability boundaries of equilibria, corresponding to different types of energy distribution are demonstrated in Fig. 3. For convenience, the traditional distribution of energy is referred to as size-independent allocation while the other as the size-dependent allocation. As examples, some combinations of parameters are chosen to show the population dynamics via equations (6)–(8) (Fig. 4). Finally, stability boundaries for different proportions of ingest energy that is allocated to growth and maintenance, are illustrated in Fig. 5.

6 Discussion and Conclusion

The model in de Roos et al. (1990) assumes that κ percent of the total ingested energy is allocated for individual growth and maintenance. The allocation implies a loss of energy for juveniles (Fig. 1a), compared to the case of size-dependent allocation (Fig. 1c). The consequence is that juvenile growth rate is slowed down, prolonging the immature period subsequently. On the other hand, the remaining energy ($1 - \kappa$ percent) is used for adult reproduction indicating that much energy for reproduction is consumed for individuals upon maturing (Fig. 1b).

6.1 Existence and Stability Boundaries

The existence and stability boundaries are exhibited in Fig. 2. The equation (23) suggests that an interior equilibrium exists if $\Gamma(\mu_b, K) > 1$. Below the existence boundary, i.e. Region I, there is only a trivial equilibrium $(K, 0)$. Taking the background mortality μ_b and resource carrying capacity K as the bifurcation parameters,

Fig. 1 Individual growth rate (a), birth rate (b) and growth trajectory (c) under ideal food condition and default parameter values in Table 1 except for $\kappa = 0.7$. Solid and dashed curves respectively indicate the size-dependent and -independent allocation of ingested energy. Dotted lines denote the maturation size

Fig. 2 Existence (dashed) and stability (solid) boundaries of equilibria for the size-dependent allocation of ingested energy under default parameter values in Table 1. Region I indicates that interior positive equilibrium does not exist, Region II the stable equilibrium and Region III the unstable equilibrium

the branch of interior equilibrium bifurcates from the trivial steady state. The general results from bifurcation theory implies that the interior equilibrium is stable when the carrying capacity is slightly greater than the steady state (de Roos et al. 1990). Hence, the equilibria are stable in Region II but unstable in Region III. Two particular examples, i.e. $(\mu_b, K) = (0.4, 4 \times 10^5)$ and $(\mu_b, K) = (0.4, 9 \times 10^5)$, are made to demonstrate the population dynamics through integrating equations (6)–(8). The exhibition in Fig. 4 (left panels) is exactly as predicted by the stability diagram.

Fig. 3 Existence (*dashed*) and stability (*solid*) boundaries of equilibria corresponding to the size-dependent (*black*) and independent (*grey*) allocations of energy under default parameter values in Table 1. Stars $A = (0.4, 6 \times 10^5)$, $B = (0.4, 9 \times 10^5)$ and $C = (0.4, 1.2 \times 10^6)$ are chosen as examples to illustrate the dynamics of *Daphnia* and algal at population level (Fig. 4)

Fig. 4 Time-dependent *Daphnia* population biomass (*solid*) and algal concentration (*dotted*) under default parameter values in Table 1. The *left panels* correspond to the stars A and B in Fig. 3 for size-dependent allocation of energy, while the *right ones* the stars B and C in Fig. 3 for size-independent allocation of energy. Initial conditions are $N(0, m) = m^{-2.05} \times 10^{-9}$ for *Daphnia* and $R(0) = K$ for algal

Figure 2 reveals three features: (1) Increasing background mortality stabilizes population dynamics for given algal carrying capacity. It arises from that large mortality suppresses the growth of *Daphnia* population and in turn relieves the predation pressure on algal. This is identified to be the mechanism of life-history of *Daphnia* (de Roos et al. 1990). (2) Increasing resource carrying capacity destabilizes population dynamics for given background mortality. The reason behind it is as follows. Food availability of *Daphnia* individuals increases with increased resource carrying capacity, which leads to rapid growth in size, shortening the immature period and raising

Fig. 5 Comparison diagram of stability boundaries for the size-dependent allocation of energy (*solid*) and the size-independent allocation of energy under default parameter values in Table 1 except for $\kappa = 0.3$ (*dotted*), $\kappa = 0.5$ (*dashed*), and $\kappa = 0.6$ (*dot-dashed*)

adults density consequently. As population abundance rises, algal density declines dramatically. The decrease of algal population leads to the drop of fertility, growth and the total population of *Daphnia*. This induces the onset of the next cycle (Fig. 4). It is identified as the prey escape mechanism (de Roos et al. 1990). (3) The stable region increases with increasing mortality and resource capacity. It results from the interplay between the prey escape mechanism and the control of the life-history of *Daphnia*.

6.2 Comparison of Energy Distribution Mechanisms

In comparison with the size-independent energy allocation, it is easy to see the following patterns from Fig. 3. Generally, for large background mortality, the size-dependent allocation destabilizes the system but considerably favors the coexistence of *Daphnia* and algal (e.g. Fig. 4). Nevertheless, for certain combinations of resource capacity and mortality, the size-dependent allocation stabilizes population dynamics, typically for small K and μ_b .

Regarding the stability boundary, Fig. 5 demonstrates additional three patterns: (1) the size-dependent allocation of energy produces the largest unstable region while the size-independent allocation for $\kappa = 0.3$ gives rise to the smallest unstable region. (2) Stable regions shrinks with increasing κ for large values of μ_b and K but broadens for small values. (3) For the intermediate values of μ_b and K , the overlapping area between size-dependent and independent allocation increases with increased κ .

The life-history of *Daphnia* accounts for these observations. On one hand, increasing the allocation efficiency in size-independent allocation of energy leads to rapid individual growth. Two effects take place consequently. One is the shorter immature period and the other the larger mean size. The shorten juvenile stage results in the aggregation of adults, which subsequently enhances the possibility of producing more offspring. The increase in mean size suggests a higher feeding rate. Nonetheless, the energy for individual birth rate declines as κ increases. In spite of the declined birth rate, the first effect exerts a destabilizing influence on system through the prey escape mechanism. On the contrary, the second one imposes a stabilizing influence since the mean size is in exact antiphase with the oscillation of *Daphnia* density, reducing

consequently the impact of these oscillations on the algal population (de Roos et al. 1990). On the other hand, taking individual birth rate and mortality rate into consideration, the stabilizing effect is the determining factor of affecting system stability for small mortality rate but gradually replaced by the destabilizing effect as mortality increases. However, the destabilizing influence is primary in the case of size-dependent allocation of energy regardless of the background mortality rate. It is because the maturation delay is substantially reduced since all energy after paying respiration cost is fully utilized by juvenile growth.

So far, we have demonstrated the disparate effects of the two energy allocation mechanisms on the dynamics of *Daphnia* and algal. It remains unclear which mechanism operates among organisms. One the one hand, the standard dynamic energy budget (DEB) theory demonstrates that standard metabolism has priority of utilizing energy intake over all other activities (Sousa et al. 2010), even though there exists evidence showing that some organisms are still able to reproduce (e.g. Kirk 1997), or to grow (e.g. Gallardo et al. 2004), when energy intake is insufficient to cover metabolic costs.

On the other hand, the standard DEB theory assumes no competition between growth and reproduction, that is, a constant proportion of net energy (total energy minus maintenance cost) is partitioned to production. In this regard, the size-independent mechanism of energy allocation essentially follows the DEB theory. A consequence of the fixed proportion is the von Bertalanffy growth for both juveniles and adults. However, as advocated by Lester et al. (2004), juveniles grow almost linearly while adults grow in the mode of the von Bertalanffy growth curve, yielding a biphasic growth trajectory. The growth mode implies that the proportion of net energy assigned to growth decreases monotonically with size (Kooijman 2000; Nisbet et al. 2004), with which the size-dependent mechanism of energy allocation is in consistence. Moreover, from the empirical perspective, Nisbet et al. (2010) tested that size-dependent proportion of energy channeled to growth is a key requirement in order to obtain good match of model with data on *Daphnia* population dynamics, indicating the significance of size-dependent mechanism of energy allocation.

In summary, we explored the impacts on population dynamics of the growth curve plasticity determined respectively by the size-dependent and -independent mechanisms of energy allocation. Existence and stability boundaries were continuously traced using the recently developed numerical scheme. Results revealed the disparate effects between the two energy allocation strategies. The former strategy tend to destabilize population dynamics but promote species coexistence, in comparison with the other strategy. Taking individual ontogenetic growth and life history into consideration, we conclude that the size-dependent mechanism of energy allocation is, to a large extent, an important component of model ingredients.

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