The regulating effect of growth plasticity on the dynamics of structured populations

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Availability of data and material

Not applicable

Code availability

The findcurve software for analysing the equilibrium dynamics can be downloaded from <https://bitbucket.org/amderoos/findcurve/>. The EBT software for simulation of timeseries can be downloaded from <https://staff.fnwi.uva.nl/a.m.deroos/EBT/>.

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JCC and AMdR contributed to the conception of this study. JCC formulated and analysed the model and wrote the first version of the manuscript. JCC and AMdR contributed to the writing of later versions of the manuscript. Both authors read and approved the final version of the manuscript.

Abstract Plasticity is the extent to which life history processes such as growth and reproduction depend on the environment. Plasticity in individual growth varies widely between taxa. Nonetheless, little is known about the effect of plasticity in individual growth on the ecological dynamics of populations. In this article we analyse a physiologically structured population model of a consumer population in which the individual growth rate can be varied between entirely plastic to entirely non-plastic. We derive this population level model from a dynamic energy budget model to ensure an accurate energetic coupling between ingestion, somatic maintenance, growth, and reproduction within an individual. We show that the consumer population is either limited by adult fecundity or juvenile survival up to maturation, depending on the level of growth plasticity and the non-plastic individual growth rate. Under these two regimes we also find two different types of population cycles which again arise due to fluctuation in respectively juvenile growth rate or adult fecundity. In the end our model not only provides insight into the effects of growth plasticity on population dynamics, but also provides a link between the dynamics found in age- and size-structured models.

Keywords somatic growth rate · size structure · trade-off · single cohort cycles · population dynamics

1 Introduction

Phenotypic plasticity is the difference in individual phenotypes due to the influence of the environment (Sultan and Stearns, 2005; Miner et al., 2005). It can arise if individual behaviour or individual life history processes such as growth, reproduction and mortality depend on the environment. As population dynamics arises from the accumulation of individual life histories (Miller and Rudolf, 2011), it is evident that plasticity in life history processes can strongly influence the dynamics of populations. Although plasticity is widely explored in the context of evolutionary dynamics, the effect of plasticity of life history traits on population dynamics is less well understood (Schmitz et al., 2003; Miner et al., 2005).

The population dynamic effects of plasticity in different life history processes cannot be considered separately, as many life history processes are linked through energy allocation schemes within an individual. It is therefore important to know the rules of within-individual energy allocation, when considering plasticity in life history processes (Nisbet et al., 2000; Brown et al., 2004). Different frameworks have been formulated to understand individual energy allocation (Kooijman, 2000; West et al., 2001; Hou et al., 2008; Sousa et al., 2008). In general, assimilated energy is divided over maintenance, growth and reproduction, while a deficit in assimilated energy can lead to additional mortality due to starvation. If a life history process is entirely non-plastic, it does not depend on the environment and requires a predetermined amount of energy. The

energy requirements of such a demand-driven process could be met through changes in behaviour to adapt the energy intake or by changes in the energy flow to other processes (Kooijman, 2010). In contrast, a purely supply-driven process is by definition plastic, because it depends entirely on the amount of assimilated energy and therefore on the food conditions of the environment. Models for individual energy allocation mainly differ in the priority of different processes (Lika and Nisbet, 2000; Kooijman, 2000; Zhang et al., 2011; Jager et al., 2013), but commonly maintenance costs are considered as a non-plastic (demand-driven) process while both growth and reproduction are considered as a plastic (supply-driven) process (but see De Roos et al. (2009) for an example of a model in which growth is incorporated as a demand-driven process).

A life history process for which plasticity strongly differs between taxa is the individual growth in body size. Environment-dependent changes in individual growth rate are observed in a wide range of ectothermic species ranging from *Daphnia* (McCauley et al., 1990) and fish (Lorenzen and Enberg, 2002; Zimmermann et al., 2018) to amphibians and reptiles (Halliday and Verrel, 1988) but it is even suggested that the growth rate of some large fossil mammals was flexible (Köhler and Moyà-Solà, 2009). This suggests that the growth rate in most ectotherms and early endotherms is plastic. In contrast, the growth rate of most modern endotherms (e.g. birds and mammals) is relatively independent of environmental influences. To maintain a constant growth rate in a fluctuating environment, it is necessary to regulate the amount of energy acquired and allocated to somatic growth. This can partly be achieved by the ability to maintain a constant homeostasis and adaptive behaviour (Kooijman, 2010). Meanwhile, the resting metabolic expenditure of endotherms exceeds that of ectotherms by an order of magnitude, even when corrected for expenditure for thermoregulation or under conditions with limited energy demand such as during torpor or hibernation (Bennett and Ruben, 1979). The additional resting metabolic expenditure in endotherms is likely used to maintain a constant energy flow to growth in order to maintain a constant somatic growth rate. This latter idea is supported by field observations of ungulates which experience delayed reproduction and decreased fecundity with low food abundance (Skogland, 1986; Clutton-Brock et al., 1987; Festa-Bianchet et al., 1995; Coulson et al., 2000; Albon et al., 2000) and laboratory observations on house mice, which stopped ovulating while maintaining growth under reduced food conditions (Perrigo, 1990). Altogether this suggests that the growth rate of endotherms is largely predetermined and non-plastic rather than supply driven.

Whereas the plasticity of life history characteristics can be considered as a continuous trait ranging from non-plastic to highly plastic (Sultan and Stearns, 2005), the individual growth rate in structured population models is generally assumed to be either non-plastic or entirely plastic. This results in two categories of structured models with different dynamics. For example, age-based models, such as used in fisheries management

(Schnute and Richards, 1998), assume that individuals of the same age are of similar size. The growth rate of individuals is thus implicitly assumed to be independent of the environment, suggesting that individual growth is a non-plastic process (De Roos et al., 2003). In these models, the population structure is entirely determined by the individual reproduction and mortality rate. Population dynamic cycles in these models arise due to the delay between birth and maturation and the competition between different life stages (Gurney et al., 1983; Gurney and Nisbet, 1985; De Roos et al., 2003; Pfaff et al., 2014). In contrast, most size-structured models are based on a dynamic energy budget model in which individual growth is modelled as a supply-driven process. As a consequence, the individual growth rate depends on the resource density and is therefore entirely plastic (De Roos et al., 1990; De Roos and Persson, 2001). Due to the highly plastic individual growth rate, the size-structured models can show a range of population structures and different types of population dynamic cycles which mainly depend on the competitive strength of different life stages (De Roos et al., 2003; de Roos and Persson, 2003). Due to the discrete differences between these two classes of structured models, it is largely unclear how predictions from (age-structured) models with non-plastic growth relate to (size-structured) models with entirely plastic growth.

Although we know most about the ecological dynamics when individual growth is either entirely plastic or non-plastic, it is more likely that for most species the actual level of plasticity in individual growth lies between these extremes. This raises the question how population dynamics changes when the plasticity in individual growth is at intermediate levels. Here we present a size-structured model in which we vary the individual growth rate from non-plastic to entirely plastic. We base this model on a simple Dynamic Energy Budget (DEB) model (Jager et al., 2013) to ensure a plausible scheme for energy allocation within an individual. Herewith we restrict ourselves to the simplest case in which the environment only consists of a single dynamic resource. Therefore, non-plastic growth in our model indicates that the individual growth rate is entirely independent of the resource density and requires a predetermined amount of energy. In contrast, entirely plastic growth indicates that the individual growth rate depends on the resource density, is completely supply driven and fluctuates accordingly. We will explore how the population dynamics in this model changes with respect to the level of growth plasticity as well as the maximum density of the resource, as an increase in the latter is generally known to destabilise the dynamics from structured population models, resulting in population dynamic cycles (De Roos et al., 1990).

2 Model formulation

2.1 Individual energy dynamics

As a basis for the individual energy dynamics, we use a simplified DEB model described by Jager et al. (2013). This model describes energy intake, somatic growth and reproduction in terms of energy stored in lean mass (E_m). In the DEB theory framework, it is generally assumed that individuals of all sizes and ages have the same shape and body composition and therefore both the mass and size of an individual scale with the energy stored in lean mass. Energy ingestion (I) is assumed to scale with the resource density (R) following a Holling type II functional response ($f(R) = \frac{R}{R_h + R}$, with R_h the half saturation constant), the individual surface area ($E_m^{2/3}$) and the maximum ingestion rate per unit surface area (I_R):

$$I = I_R f(R) E_m^{2/3} = I_R \frac{R}{R_h + R} E_m^{2/3} \quad (1)$$

We assume assimilation efficiency in the gut is constant and the surface specific maximum ingestion rate times the assimilation rate is represented by α . The original energetic model by Jager et al. (2013) assumes growth is plastic and follows a κ -rule in which a fraction κ of the assimilated energy is used for somatic growth and somatic maintenance costs. The somatic maintenance costs are assumed to be nonplastic and scale with the energy stored in lean mass through the energy specific maintenance costs (b). Covering somatic maintenance costs has priority over somatic growth. This yields the following differential equation for plastic somatic growth:

$$\frac{dE_m}{dt} = \gamma_m (\kappa \alpha f(R) E_m^{2/3} - b E_m) \quad (2)$$

With γ_m the conversion efficiency of assimilated energy to lean mass. These assumptions imply that individuals follow a Von Bertalanffy type of growth curve when the resource density is constant. The maximum lean mass reached by an individual is proportional to $f(R)^3$, whereas the growth rate is independent of resource density (Jager et al. 2013).

We assume individuals mature when reaching a predetermined amount of energy stored in lean mass (E_J). In adult individuals, a fraction $1 - \kappa$ of the assimilated energy is channelled to reproduction, while this fraction is used for maturation in juvenile individuals. This results in the following differential equation for the total amount of energy (E_r) invested by adults into the production of juveniles:

$$\frac{dE_r}{dt} = \gamma_r (1 - \kappa) \alpha f(R) E_m^{2/3} \quad (3)$$

With γ_r the conversion efficiency of assimilated energy to energy in newborn lean mass.

To formulate a version of the model with nonplastic growth, the somatic growth rate has to be decoupled from the resource density. In other words, a constant amount of energy is used for somatic growth and somatic maintenance, independent of the current resource density. To stay close to the original model with plastic growth, nonplastic somatic growth is assumed to follow a Von Bertalanffy growth trajectory as well. This results in the following differential equation for nonplastic somatic growth:

$$\frac{dE_m}{dt} = \gamma_m \left(\kappa \alpha \zeta E_m^{2/3} - b E_m \right) \quad (4)$$

Here we introduce a parameter ζ as a scalar modulating the nonplastic growth rate to replace the scaled functional response ($f(R)$) in the plastic growth rate. Individuals following the nonplastic growth dynamics (eq. (4)) will therefore grow at the same rate as individuals that follow the plastic growth dynamics (eq. (2)) with a scaled functional response ($f(R)$) equal to ζ . To capture the entire spectrum from nonplastic growth to entirely plastic growth, we introduce the parameter ϕ , which represents the extent to which growth is plastic. This results in our general formula for somatic growth:

$$\frac{dE_m}{dt} = \gamma_m \left(\phi \kappa \alpha f(R) E_m^{2/3} + (1 - \phi) \kappa \alpha \zeta E_m^{2/3} - b E_m \right) \quad (5)$$

We assume all energy not used for somatic processes is used by juveniles for maturation and by adults for reproduction, resulting in the following expression for the investment in reproductive energy:

$$\frac{dE_r}{dt} = \begin{cases} 0 & \text{if } E_m < E_J \\ \gamma_r \left(\alpha f(R) E_m^{2/3} - \left(\phi \kappa \alpha f(R) E_m^{2/3} + (1 - \phi) \kappa \alpha \zeta E_m^{2/3} \right) \right) & \text{if } E_m > E_J \end{cases} \quad (6)$$

With E_J the energy in lean mass corresponding to the size at which individuals mature.

Equations 5 and 6 simplify to the model described by Jager et al. (2013) if growth is entirely plastic ($\phi = 1$). In addition, notice that the investment in growth in our model is higher compared to the κ -rule model with entirely plastic growth if $f(R) < \zeta$, while investment in reproduction is higher if $f(R) > \zeta$.

By comparing the equation for the assimilated energy ($\alpha f(R) E_m^{2/3}$) with the energy used for growth (eq. 5), it is clear that the rate of energy supply may become insufficient to maintain the outlined energy allocation scheme. If energy supply becomes insufficient, we assume starvation and rechanneling of energy occur. An individual could encounter three types of starvation conditions (Fig. 1).

Under the most severe starvation condition, ingested energy is insufficient to cover somatic maintenance costs (red area in figure 1). This regime occurs when:

$$b E_m > \alpha f(R) E_m^{2/3} \quad (7)$$

Fig. 1 In addition to growth dynamics, individuals can encounter three types of starvation conditions, depending on the energy in lean mass and the scaled functional response of the resource density. The boundaries of these dynamics shift when growth shifts from non-plastic ($\phi = 0$) to entirely plastic ($\phi = 1$). Under severe starvation conditions (red area) assimilated energy is insufficient to cover maintenance costs. Under supply-driven starvation conditions (green area), the energy allocated to somatic processes is insufficient to cover maintenance costs. Under demand-driven starvation conditions (blue area), assimilated energy is insufficient to cover the costs for maintenance and demand-driven growth.

We will refer to this condition as *severe starvation* following De Roos et al. (1990) and we will assume individuals starve instantaneously when it occurs.

Under less severe starvation conditions, ingested energy is sufficient to cover somatic maintenance costs but the energy allocated to somatic processes is not (green area in figure 1):

$$\alpha f(R) E_m^{2/3} > b E_m > \phi \kappa \alpha f(R) E_m^{2/3} + (1 - \phi) \kappa \alpha \zeta E_m^{2/3} \quad (8)$$

De Roos et al. (1990) refers to this starvation condition as *mild starvation* but we will use the term *supply-driven starvation*, because the supply of energy to somatic processes is insufficient to cover maintenance costs.

The last type of starvation occurs if the assimilated energy is insufficient to cover all energy requirements for somatic growth and maintenance:

$$\phi \kappa \alpha f(R) E_m^{2/3} + (1 - \phi) \kappa \alpha \zeta E_m^{2/3} > \alpha f(R) E_m^{2/3} > b E_m \quad (9)$$

We will refer to this type of starvation as *demand-driven starvation*, because the energy demand for growth is too high for the energy supplied by assimilation. From inequality (9), it is clear that the boundary between growth conditions and demand-driven starvation is dependent on resource density, but not on individual size (Fig. 1, boundary of the blue area).

Comparison of the three starvation conditions shows that all three starvation boundaries intersect at a single point ($E_m = \frac{\alpha \kappa}{b} \frac{1-\phi}{1-\phi \kappa} \zeta$, Fig. 1). If we do not take into account the conditions in which severe starvation occurs, individuals can only suffer demand-driven starvation if the energy stored in lean mass is below this

critical value ($E_m < \frac{\alpha\kappa}{b} \frac{1-\phi}{1-\phi\kappa} \zeta$), while individuals can only suffer from supply-driven starvation if the energy stored in lean mass is above this critical value ($E_m > \frac{\alpha\kappa}{b} \frac{1-\phi}{1-\phi\kappa} \zeta$). In other words, small and large individuals are vulnerable to demand-driven and supply-driven starvation, respectively.

In general we assume energy is rechanneled under starvation conditions from the energy flow with sufficient energy to the energy flow with the deficit (e.q. from maturation and reproduction to growth and somatic maintenance or vice versa). More specifically, this means that under supply-driven starvation, growth stops and reproduction is reduced:

$$\frac{dE_m}{dt} = 0 \quad (10a)$$

$$\frac{dE_r}{dt} = \begin{cases} 0 & \text{if } E_m < E_J \\ \gamma_r (\alpha f(R) E_m^{2/3} - b E_m) & \text{if } E_m > E_J \end{cases} \quad (10b)$$

While under demand-driven starvation, reproduction stops and growth is reduced:

$$\frac{dE_m}{dt} = \gamma_m (\alpha f(R) E_m^{2/3} - b E_m) \quad (11a)$$

$$\frac{dE_r}{dt} = 0 \quad (11b)$$

These rechanneling rules imply that relatively small individuals prioritise growth if experiencing (demand-driven) starvation conditions, while relatively large individuals prioritise reproduction if experiencing (supply-driven) starvation conditions (Fig. 1b).

It is likely that the re-channelling of energy will bring additional costs such as starvation mortality. We assume starvation mortality scales with the energy deficit and is zero at the supply-driven starvation boundary and the demand-driven starvation boundary. In addition we assume starvation mortality approaches infinity if individual energetics approaches the severe starvation boundary. As a consequence, individuals will starve with certainty before entering severe starvation conditions. The starvation-induced mortality rate (μ_s) under supply-driven starvation we therefore assume to follow:

$$\mu_s = q_s \max \left(\frac{b E_m - (\phi \kappa \alpha f(R) E_m^{2/3} + (1 - \phi) \kappa \alpha \zeta E_m^{2/3})}{\alpha f(R) E_m^{2/3} - b E_m}, 0 \right) \quad (12)$$

And under demand-driven starvation conditions:

$$\mu_s = q_s \max \left(\frac{(\phi \kappa \alpha f(R) E_m^{2/3} + (1 - \phi) \kappa \alpha \zeta E_m^{2/3}) - \alpha f(R) E_m^{2/3}}{\alpha f(R) E_m^{2/3} - b E_m}, 0 \right) \quad (13)$$

2.2 Growth dynamics

According to DEB theory (Kooijman, 2010), the individual body mass can be expressed in terms of energy stored in lean mass by using the mass specific energy density (d_v). In the same way the volume can be related to the mass with the volume specific mass (δ_v) and the length can be related to the volume with a shape scaling constant (δ_m).

$$W = \frac{E_m}{d_m} = d_v V = d_v (\delta_m \ell)^3 \quad (14a)$$

$$\ell = \frac{V^{1/3}}{\delta_m} = \frac{W^{1/3}}{d_v^{1/3} \delta_m} = \frac{E_m^{1/3}}{d_m^{1/3} d_v^{1/3} \delta_m} \quad (14b)$$

Using these equalities, the individual dynamics can be expressed in terms of individual length instead of energy stored in lean mass (Table 1, see also the supplementary materials)(Murphy, 1983; De Roos et al., 1990). To do so, we use expressions for the investments into somatic growth ($F_g(R, \ell)$), reproduction ($F_r(R)$) and growth and reproduction together ($F_t(R, \ell) = F_g(R, \ell) + F_r(R)$), which depend on the resource density, the ultimate size under unlimited food conditions (ℓ_∞) and possibly the actual length (ℓ). Note that these investments are proportional to the energy allocation to growth and reproduction. In addition, these quantities are expressed per unit surface area and could therefore be interpreted as the (area specific) growth rate, fecundity and biomass production as well. The dynamics of the length-age relationship ($\ell(t, a)$) is defined in terms of the Von Bertalanffy growth rate (r_B) times the investments into growth ($F_g(R, \ell)$ or $F_t(R, \ell)$) in combination with the size at birth (ℓ_b). Individuals mature when reaching the size at maturation (ℓ_J). The individual fecundity ($\beta(R, \ell)$) is defined in terms of the reproduction rate (r_F) times the investments into reproduction ($F_r(R)$ or $F_t(R, \ell)$). Lastly, the dynamics of the population age-distribution ($n(t, a)$) depends on the individual background mortality (μ_b) and the individual starvation mortality ($\mu_s(R, \ell)$) in combination with the population birth rate ($n(t, 0)$) calculated as the total reproductive output of the population at a given time.

For simplicity we will assume the resource to be unstructured and the dynamics of the resource without consumption to be described by semi-chemostat dynamics, with a turn-over rate ν and a maximum resource density K :

$$\frac{dR}{dt} = \nu(K - R) - \int_0^{a_{max}} I_{max} f(R) \ell(t, a)^2 n(t, a) da \quad (15)$$

The parameter I_{max} is a scaled version of I_R , representing the ingestion rate per unit surface area in terms of length instead of energy stored in lean mass.

Table 1 Equations describing the population dynamics under growth conditions and supply-driven ($F_g(R, \ell) < 0$), demand-driven ($F_r(R) < 0$) and severe ($F_t(R, \ell) < 0$) starvation conditions. Notice that as long as extreme starvation does not occur ($F_t(R, \ell) > 0$) supply- and demand-driven starvation are mutually exclusive, such that $F_r(R) \leq 0$ implies $F_g(R, \ell) > 0$ and $F_g(R, \ell) \leq 0$ implies $F_r(R) > 0$.

Population age-distribution dynamics	
$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} =$	$-(\mu_b + \mu_s(R, \ell)) n(t, a)$
$n(t, 0) =$	$\int_0^{a_{max}} \beta(R, \ell(t, a)) n(t, a) da$
Energetic surpluses/deficits	
$F_g(R, \ell) =$	$(\phi f(R) + (1 - \phi)\zeta) \ell_\infty - \ell$
$F_r(R) =$	$\left(\phi \frac{(1-\kappa)f(R)}{\kappa} + (1 - \phi) \left(\frac{f(R)}{\kappa} - \zeta \right) \right) \ell_\infty$
$F_t(R, \ell) =$	$F_g(R, \ell) + F_r(R) = \frac{f(R)}{\kappa} \ell_\infty - \ell$
Length-age dynamics	
$\frac{\partial \ell}{\partial t} + \frac{\partial \ell}{\partial a} =$	$\begin{cases} r_B F_g(R, \ell) & \text{if } F_g(R, \ell) > 0 \text{ and } F_r(R) > 0 \\ r_B F_t(R, \ell) & \text{if } F_r(R) \leq 0 \text{ and } F_t(R, \ell) > 0 \\ 0 & \text{otherwise} \end{cases}$
$\ell(t, 0) =$	ℓ_b
Individual fecundity	
$\beta(R, \ell) =$	$\begin{cases} r_F F_r(R) \ell^2 & \text{if } \ell_J < \ell, F_g(R, \ell) > 0 \text{ and } F_r(R) > 0 \\ r_F F_t(R, \ell) \ell^2 & \text{if } \ell_J < \ell, F_g(R, \ell) \leq 0 \text{ and } F_t(R, \ell) > 0 \\ 0 & \text{otherwise} \end{cases}$
Starvation mortality	
$\mu_s(R, \ell) =$	$\begin{cases} 0 & \text{if } F_g(R, \ell) > 0 \text{ and } F_r(R) > 0 \\ -q_s \frac{F_g(R, \ell)}{F_t(R, \ell)} & \text{if } F_g(R, \ell) \leq 0 \text{ and } F_t(R, \ell) > 0 \\ -q_s \frac{F_r(R)}{F_t(R, \ell)} & \text{if } F_r(R) \leq 0 \text{ and } F_t(R, \ell) > 0 \\ \infty & \text{if } F_t(R, \ell) \leq 0 \end{cases}$

3 Mathematical analysis

Model equilibria can be calculated following the procedure described by De Roos et al. (1990). At a constant resource density $R = \bar{R}$ and hence a constant value of the functional response ($f(\bar{R})$) the consumer population can only persist if the functional response is sufficiently high for extreme and demand-driven starvation not to occur ($F_t(\bar{R}, \ell), F_r(\bar{R}) > 0$), because otherwise consumers would die instantaneously or never reproduce. With a constant functional response, investment in growth and the individual size can be solved explicitly as

a function of age, which results in a Von Bertalanffy growth curve:

$$F_g(\bar{R}, \ell) = ((\phi f(\bar{R}) + (1 - \phi)\zeta) \ell_\infty - \ell_b) e^{-r_B a} = F_{g\infty}(\bar{R}) e^{-r_B a} \quad (16a)$$

$$\ell(\bar{R}, a) = \ell_b + (1 - e^{-r_B a}) F_{g\infty}(\bar{R}) = \ell_b e^{-r_B a} + (\phi f(\bar{R}) + (1 - \phi)\zeta) (1 - e^{-r_B a}) \ell_\infty \quad (16b)$$

Herein we introduce $F_{g\infty}(\bar{R})$ as the lifetime investment in growth at the constant resource density $\bar{R}$ given an individual survives, which we will use as an age independent quantity for energy investment in growth (Note that $F_{g\infty}(\bar{R})$ equals the integral of the product $r_B F_g(\bar{R}, \ell(\bar{R}, a))$ over the entire lifetime for an individual living at resource density $\bar{R}$). From comparing the growth curve with the supply-driven starvation condition, it is clear that individuals do not experience supply-driven starvation when living at a constant resource density $\bar{R}$ ($F_g(\bar{R}, \ell) > 0$). The Von Bertalanffy growth curve also defines the age at maturation at the constant food density ($\bar{a}_J$), which is the age at which individuals reach the size at maturation ($\ell(\bar{R}, \bar{a}_J) = \ell_J$). For individuals to reach this maturation size at the constant resource density $\bar{R}$ individuals of length ℓ_J should not experience supply-driven starvation ($F_g(\bar{R}, \ell_J) > 0$). When individuals do not experience starvation conditions, the dynamics of the population age-distribution can be simplified and solved explicitly, resulting in an expression for the density of individuals at a given age:

$$\bar{n}(a) = \bar{n}(0) e^{-\mu_b a} \quad (17)$$

By substituting the Von Bertalanffy growth curve (eq. (16)) and the age distribution in equilibrium (eq. (17)) in the expression for the population birth rate, we arrive at an expression for the lifetime reproductive output (LRO):

$$LRO = r_F F_r(\bar{R}) \int_{\bar{a}_J}^{a_{max}} \ell(\bar{R}, a)^2 e^{-\mu a} da = r_F F_r(\bar{R}) \int_{\bar{a}_J}^{a_{max}} \left(\ell_b + (1 - e^{-r_B a}) F_{g\infty}(\bar{R}) \right)^2 e^{-\mu a} da \quad (18)$$

The lifetime reproductive output represents the average number of offspring an individual is expected to produce during its lifetime. A population is in equilibrium if every individual on average replaces itself and therefore the lifetime reproductive output in equilibrium equals one. By setting the lifetime reproductive output to one, we can solve for the functional response in equilibrium, which we indicate with $f(\tilde{R})$, because this is the only unknown in the lifetime reproductive output. The functional response and the resource density in equilibrium $\tilde{R}$ are therefore completely determined by the growth, reproduction and mortality traits of the consumer population and hence independent of resource growth conditions.

The last step is to derive the population birth rate in equilibrium ($\tilde{n}(0)$) from the dynamics of the resource (eq. (15)), which together with the resource density defines the complete equilibrium:

$$\tilde{n}(0) = \frac{\nu (K - \tilde{R})}{I_{max} f(\tilde{R}) \int_0^{a_{max}} \ell(\tilde{R}, a)^2 e^{-\mu a} da} \quad (19)$$

From equation (19) it follows that the resource density in equilibrium equals the maximum resource density ($\tilde{R} = K$) at the persistence boundary of the consumer population ($\tilde{n}(0) = 0$). Therefore the persistence boundary is calculated by setting the lifetime reproductive output equal to one and substituting the resource density with the maximum resource density (eq. (33)).

The stability boundary of the model can be calculated through linearisation of the dynamic equations around the equilibrium state as outlined by (De Roos et al., 1990). The derivation of the conditions determining the stability boundary is explained in detail in the supplementary materials (eq. (39) - (47)).

3.1 Energetic tradeoff

At a given, constant resource density $\bar{R}$ both the investments into growth ($F_{g\infty}(\bar{R})$) and the investments into reproduction ($F_r(\bar{R})$) change with the growth plasticity (ϕ). This change can be expressed as the derivative of these investments with respect to the level of growth plasticity:

$$\frac{\partial F_{g\infty}}{\partial \phi} = (f(\bar{R}) - \zeta) \ell_{\infty} \quad (20a)$$

$$\frac{\partial F_r}{\partial \phi} = -(f(\bar{R}) - \zeta) \ell_{\infty} \quad (20b)$$

The direction of a change in energy allocation due to growth plasticity is determined by the non-plastic asymptotic size ($\zeta \ell_{\infty}$) compared to the plastic asymptotic size ($f(\bar{R}) \ell_{\infty}$). An increase in growth plasticity will lead to an increase in growth investments and a decrease in reproductive investments if the plastic asymptotic size exceeds the non-plastic asymptotic size ($f(\bar{R}) \ell_{\infty} > \zeta \ell_{\infty}$). In contrast, an increase in growth plasticity will lead to a decrease in growth investments and an increase in reproductive investments if the non-plastic asymptotic size exceeds the plastic asymptotic size ($f(\bar{R}) \ell_{\infty} < \zeta \ell_{\infty}$). It is also clear that the effect of the growth plasticity on the growth investments is always opposite to the effect on reproductive investments. This reveals a tradeoff in which an increase in investment in growth will always lead to a decrease in investment in reproduction and vice versa.

A change in growth plasticity affects the lifetime reproductive output through both the growth investments and the reproductive investments:

$$\frac{dLRO}{d\phi} = \frac{\partial LRO}{\partial F_{g\infty}} \frac{\partial F_{g\infty}}{\partial \phi} + \frac{\partial LRO}{\partial F_r} \frac{\partial F_r}{\partial \phi} = \left(\frac{\partial LRO}{\partial F_{g\infty}} - \frac{\partial LRO}{\partial F_r} \right) (f(\bar{R}) - \zeta) \ell_{\infty} \quad (21)$$

Explicit expressions for the partial derivatives $\frac{\partial LRO}{\partial F_{g\infty}}$ and $\frac{\partial LRO}{\partial F_r}$ are derived in the supplementary information. From equation (21) it is clear that the lifetime reproductive output of an individual is completely independent of the growth plasticity (ϕ) if the plastic asymptotic size equals the non-plastic asymptotic size ($f(\bar{R}) \ell_{\infty} = \zeta \ell_{\infty}$).

From equations (16) and (18) we can furthermore infer that the lifetime reproductive output increases with both an increase in energy allocation to growth and energy allocation to reproduction ($\frac{\partial LRO}{\partial F_{g\infty}} > 0$ and $\frac{\partial LRO}{\partial F_r} > 0$). We therefore can distinguish a parameter region in which an increase in growth investments has a larger effect on lifetime reproductive output than a similar increase in reproductive investments ($\frac{\partial LRO}{\partial F_{g\infty}} > \frac{\partial LRO}{\partial F_r}$) and a parameter region in which an increase in reproductive investments has a larger effect on lifetime reproductive output than a similar increase in growth investments ($\frac{\partial LRO}{\partial F_{g\infty}} < \frac{\partial LRO}{\partial F_r}$). We will refer to the dynamics in these regions as growth-limited and reproduction-limited dynamics respectively. Whether or not the lifetime reproductive output increases with an increase in growth plasticity depends on whether the dynamics are growth- or reproduction-limited in combination with whether the plastic growth asymptotic size ($f(\bar{R})\ell_\infty$) is larger or smaller than the non-plastic asymptotic size ($\zeta\ell_\infty$). Furthermore, an increase in growth plasticity (ϕ) results in a change from an increase to a decrease in lifetime reproductive output when the dynamics changes from growth to reproduction limited, assuming that the plastic asymptotic size is larger than the non-plastic asymptotic size ($f(\bar{R})\ell_\infty > \zeta\ell_\infty$). Alternatively, when the plastic asymptotic size is smaller than the non-plastic asymptotic size ($f(\bar{R})\ell_\infty < \zeta\ell_\infty$) an increase in growth plasticity ϕ results in a change from an increase to a decrease in lifetime reproductive output when the dynamics changes from reproduction to growth limited. The value of the growth plasticity (ϕ) at which the boundary between these two areas occurs, strongly depends on the plastic energy allocation constant (κ) but is also influenced by other parameters (equations (34) - (37)).

4 Numerical analysis

The persistence boundary and the stability boundary have been studied numerically as a function of model parameters using general root finding and curve continuation procedures implemented in C (Findcurve software by De Roos (2019)). Time dynamics of the model have been computed using the Escalator Boxcar Train (EBT) method, especially designed for the numerical integration of physiologically structured population models (De Roos, 1988; De Roos et al., 1992). For the numerical analysis of the model and corresponding figures we use a parameter set representing *Daphnia magna* feeding on algae, comparable to the parameter values used by De Roos et al. (1990) (table 2). We use slightly different definitions of the half saturation constant of the functional response (R_h) and the reproduction rate (r_F). Therefore, we recalculated the values of these parameters to ensure our model is numerically equivalent to the model analysed by De Roos et al. (1990)

Table 2 Parameters used in the structured population model for *Daphnia magna* feeding on algae derived from De Roos et al. (1990)

Parameters of the structured population model				
ϕ	Plasticity in somatic growth	varied	-	
ζ	Scalar of the non-plastic growth rate	0.1 or 1	-	
κ	Plastic growth energy allocation constant	0.3 or 0.9	-	
ℓ_b	Length at birth	0.8	mm	
ℓ_J	Length at maturation	2.5	mm	
ℓ_∞	Asymptotic length under unlimited food conditions	20κ	mm	
a_{max}	Maximum age	70	d	
r_B	time constant of growth	0.15	d ⁻¹	
r_F	time constant of reproduction	0.00714	mm ⁻³ d ⁻¹	
μ_b	background mortality rate	0.03	d ⁻¹	
q_s	starvation mortality scaling constant	0.2	d ⁻¹	
I_{max}	Maximum feeding rate per unit surface area	1.8	10 ⁶ cells mm ⁻² ml ⁻¹ d ⁻¹	
R_h	Half saturation constant of functional response	0.14	cells	
ν	semi-chemostat renewal rate	0.5	d ⁻¹	
K	maximum resource density	varied	10 ⁶ cells ml ⁻¹	

if growth is entirely plastic ($\phi = 1$). From here on we will refer to the structured *Daphnia* populations as consumers, while the unstructured algae community is referred to as the resource.

4.1 Equilibrium dynamics

In general, four different configurations of the regions with growth-limited and reproduction-limited dynamics are possible (Derivation in supplementary materials 34 - 37). (1) If the growth energy allocation constant κ is below a specific threshold value ($\kappa \approx 0.857$ with our parameter set) and the plastic asymptotic size exceeds the non-plastic asymptotic size ($f(\tilde{R})\ell_\infty > \zeta\ell_\infty$, Fig. 2A) the dynamics is always growth-limited. (2) If the plastic growth energy allocation constant κ is below the threshold value and the non-plastic asymptotic size exceeds the plastic asymptotic size, ($\kappa < 0.857$, $f(\tilde{R})\ell_\infty < \zeta\ell_\infty$, Fig. 2B), the dynamics is growth limited at high growth plasticity (high ϕ) and reproduction limited at low growth plasticity (low ϕ). (3) In contrast, if the plastic growth energy allocation constant κ is above the threshold value and the plastic asymptotic size exceeds the non-plastic asymptotic size ($\kappa > 0.857$, $f(\tilde{R})\ell_\infty > \zeta\ell_\infty$, Fig. 2C), the dynamics is growth limited at low growth plasticity (low ϕ) and reproduction limited at high growth plasticity (high ϕ). (4) Lastly, the

Fig. 2 Persistence boundary (red line, numerically solved from eq. (33)) and stability boundary (green, numerically solved from (49)) and the boundary between dynamics (yellow dashed, numerically solved from equation (35c)) as a function of the growth plasticity (ϕ) and the maximum resource density (K) when the plastic asymptotic size exceeds the non-plastic asymptotic size ($f(\tilde{R})\ell_\infty > \zeta\ell_\infty$) (left panels) and when the non-plastic asymptotic size exceeds the plastic asymptotic size ($\zeta\ell_\infty > f(\tilde{R})\ell_\infty$) (right panels). At the persistence boundaries (red lines), the Maximum resource density is equal to the resource density in equilibrium.

dynamics is always reproduction limited if the plastic energy allocation constant κ exceeds the threshold value and the nonplastic asymptotic size exceeds the plastic asymptotic size ($\kappa > 0.857$, $f(\tilde{R})\ell_\infty < \zeta\ell_\infty$, Fig. 2D).

With an increase or decrease of ϕ the average lifetime reproductive output increases if the growth plasticity (ϕ) approaches the boundary between growth-limited dynamics and reproduction-limited dynamics (Fig. 2B and C, yellow line). An increase in lifetime reproductive output with a change in ϕ implies that the lifetime reproductive output will equal 1 at a lower resource density, which hence decreases in equilibrium, while equilibrium consumer population density increases. The maximum resource density (K) needed for the

consumer population to persist decreases accordingly if the growth plasticity (ϕ) approaches the boundary between the two regions (Fig. 2B and C, red line). In contrast, the lifetime reproductive output always increases with an increase in growth plasticity if the dynamics does not change between growth-limited dynamics and reproduction-limited dynamics. This leads to a decrease in resource density and an increase in population density at equilibrium with increasing growth plasticity. Again, the maximum resource density (K) needed for the consumer population to persist decreases accordingly (Fig. 2A and D, red line).

4.2 Population dynamic cycles

The bifurcation analysis revealed three parameter regions with cyclic dynamics (Fig. 2A and B, green lines). One of these regions occurred when the dynamics is limited by reproduction (Fig. 2B, low ϕ). In these cycles (Fig. 3a), the area specific investment in growth ($F_{g\infty}$) and therewith the maturation rate is relatively high and constant due to the high and largely non-plastic growth rate. As a result, individuals mature at a young age and the population consists of a low number of juveniles and a high number of adults. A peak in the number of juveniles occurs simultaneously with a peak in investment in reproduction (F_r). The high density of juveniles results in a depletion of the resource, which is directly followed by a decrease in fecundity. Although individuals mature at a young age, a new large reproductive event only occurs after the consumer density has sufficiently decreased by mortality for the resource density to recover. In other words, a new cycle starts of competition between adults is reduced. As a result, the resource density and the investment in reproduction fluctuate in phase with the juvenile density but out of phase with the adult density, with a period of several times the juvenile delay. It is clear that these cycles occur due to the fluctuations in fecundity. We therefore refer to these cycles as fecundity-driven cycles.

The two other regions with cyclic dynamics occur when the dynamics is growth-limited (Fig. 2A and Fig. 2B for high ϕ). During these cycles (Fig. 3b and c) the area specific investment in growth ($F_{g\infty}$) and therewith the maturation rate is very low and shows periodic increases with a large amplitude. The investment in reproduction reaches a maximum simultaneously with the maturation rate. The occurrence of the high fecundity simultaneous with the high adult density results in the production of a large cohort of juveniles. This cohort decreases the resource density, which is followed by a decrease in the fecundity and maturation rate. The juvenile cohort matures and reproduces after the consumer density has sufficiently decreased by mortality for the resource density to recover. In other words, a new cycle starts as soon as competition between juveniles is sufficiently reduced. This results in cycles dominated by a single cohort from which all

Fig. 3 Population dynamic cycles for three combinations of ζ and ϕ with $K = 0.5$ and $\kappa = 0.3$. The surface specific total investment in growth if individuals would not die ($F_{g\infty}$) and the surface specific investment in reproduction are displaced as a measure of growth and fecundity. Note the different vertical axes for the consumer densities. The red vertical lines mark the occurrence of a peak in adult density to ease comparison between graphs.

individuals mature simultaneously and directly produce a new dominant cohort. Consequently, the period of the cycles is approximately equal to the juvenile delay. This type of cycles also occurs when the individual fecundity is assumed to be independent of the resource density (Fig. S1), which shows that these cycles are caused by the fluctuations in maturation rate rather than fluctuation in the fecundity. We therefore refer to this type of cycles as maturation-driven cycles.

5 Discussion

We analysed a model in which the individual growth rate could be varied between entirely non-plastic ($\phi = 0$) to entirely plastic ($\phi = 1$). Although the model was formulated at an individual level to ensure closed individual energy dynamics, the model was analysed at the population level. In the extreme case in which growth is entirely plastic ($\phi = 1$) the model simplified to a classic size-structured model as analysed by De Roos et al. (1990). Because in this case the individual growth rate is coupled to the resource density, the age-size relationship varies per cohort if the resource density fluctuates, for example during population dynamic cycles

(Fig. S2b). In contrast, if growth is completely non-plastic ($\phi = 0$), the model is equivalent to an age-structured model given that there is a unique relationship between age and body size. Under this extreme condition, the individual growth rate in our model only changes if the demand-driven starvation condition ($F_r < 0$) occurs, but the analysis of the model did not reveal any dynamic regimes in which individuals experienced demand-driven starvation. The growth rate is thus completely fixed if growth is non-plastic ($\phi = 0$), which results in a fixed age-size relationship even during population dynamic cycles (Fig. S2a). With the fixed age-size relationship, the model can be converted to an age-based model resembling our model with non-plastic growth. Besides linking energetic models with plastic and non-plastic growth, our model thus also connects classic age-structured models with classic size-structured models.

Our analysis divided the parameter space in a region with growth-limited and a region with reproduction-limited dynamics. In the region with growth-limited dynamics, changes in the area-specific investments in growth have a larger effect on the lifetime reproductive output than changes in the area-specific investments in reproduction. In contrast, in the region with reproduction-limited dynamics, changes in the area-specific investments in reproduction have a larger effect on lifetime reproductive output than changes in the area-specific investments in growth. At the boundary of the regions with different limiting mechanisms the consumer population exploits the resource most efficiently and can persist on the lowest resource density (Fig. 2). In other words, on this boundary the energy allocation to growth and reproduction is most optimal. The location of this optimum is closely related to the classic tradeoff regarding energy allocation to growth and reproduction (Stearns, 1992), in which an optimal strategy arises through avoidance of severe limitation in growth or reproduction. Although this is an very intuitive tradeoff, we tied it to the specific energy budget of individuals. Namely, an optimal energy allocation strategy can only occur if the plastic energy allocation constant is low (low κ) and the non-plastic asymptotic size exceeds the plastic asymptotic size in equilibrium ($f(\tilde{R})\ell_\infty < \zeta\ell_\infty$) or if the plastic energy allocation constant is high (high κ) and the plastic asymptotic size exceeds the non-plastic asymptotic size in equilibrium ($f(\tilde{R})\ell_\infty > \zeta\ell_\infty$). Hence, an optimal energy allocation can only occur when energy is relatively evenly distributed between growth and reproduction to avoid severe limitation through growth and reproduction. As a consequence evolution cannot always reach an optimal energy allocation scheme if evolution only acts on growth plasticity.

The parameter regions in which the dynamics is limited by growth or reproduction show different kind of population dynamics cycles. In the region with growth-limited dynamics, the cycles are caused by fluctuations in maturation, which is caused by fluctuations in growth rate. These maturation-driven cycles occur because a cohort of newborn individuals outcompetes the adult individuals. This results in single cohort cycles, which are

characterised by the synchronisation of a high resource density with the maturation of the dominant cohort. The oscillation period of these cycles is approximately equal to the juvenile delay (De Roos et al., 2003). Single cohort cycles generally occur in models incorporating a juvenile delay and, based on the oscillation period, are mainly observed in generalist species (Murdoch et al., 2002). The type of single cohort cycles found in our model are described in more detail by De Roos et al. (2003) as juvenile-driven cycles, which occur if juvenile individuals outcompete adults because they can survive on a lower resource density. The mechanism for these juvenile-driven cohort cycles is observed in various fish species (Townsend et al., 1990; Hamrin and Persson, 1986; Townsend and Perrow, 1989) and experimental *Daphnia* populations (Murdoch and McCauley, 1985; McCauley, 1993).

In the parameter region with reproduction-limited dynamics the cycles are caused by fluctuations in average fecundity. These fecundity-driven cycles are characterised by low amplitude oscillations with a period of more than four times the juvenile delay of the consumer. In addition, the total consumer density lags behind the resource density. These characteristics occur because a dominant cohort of newborn individuals depletes the resource, which causes fecundity to decrease. The dominant cohort of juveniles matures before the resource density is recovered, which delays their main reproductive event until the resource density is recovered, which is far beyond the age at maturation. The fecundity-driven cycles thus differ from the reproduction driven cycles in that competition relaxes after instead of before the maturation of a dominant cohort.

The fecundity-driven cycles in our model show resemblances with various previously described types of cycles. The oscillation period of the fecundity-driven cycles is more than four times the juvenile delay of the consumer plus two times the juvenile delay of the resource, which is generally considered indicative of consumer-resource cycles (Murdoch et al., 2002). The fecundity-driven cycles indeed show an increase in resource density leading to an increase in consumer reproduction as is found in classic non-structured models with consumer-resource cycles (Rosenzweig and MacArthur, 1963). In classic consumer-resource cycles this occurs because the resource periodically escapes the control of the consumer, which, however, cannot occur in our model, because in our model the resource follows semi-chemostat dynamics (De Roos et al., 1990). Instead, the increase in resource density in the fecundity-driven cycles is due to a relaxation of competition between consumers and are therefore different from classic consumer-resource cycles. The fecundity-driven cycles also show some resemblances with delayed-feedback cycles. One could argue that the depletion of the resource by a dominant cohort has a delayed effect, because it only affects the dominant cohort after maturation. Pfaff et al. (2014) suggested that delayed-feedback cycles can have a period of more than 4 times the juvenile delay and arise if the juvenile delay is decoupled from the resource density, which exactly occurs in the fecundity-

driven cycles we found. Nonetheless, the fecundity-driven cycles do not correspond to the original description of delayed-feedback cycles from Gurney et al. (1983), because the depletion of the resource in the fecundity-driven cycles also has a direct effect on the consumer population, while Gurney et al. (1983) describe a complete separation of time between the moment of competition and the effect of competition. These resemblances between the fecundity-driven cycles, consumer-resource cycles and delayed feedback cycles at least show that very detailed knowledge is needed to disentangle different types of cycles in structured populations Hastings (2020).

In this article we presented a model in which we varied the plasticity in individual growth. More plastic growth is generally expected in ectotherms because the growth rate in these individuals is highly dependent on the environment, while less plastic growth is generally expected in endotherms because in these individuals growth is generally independent of the environment. Including a non-plastic growth-rate results in an additional demand-driven process in the energy allocation scheme of individuals. We assumed that a potential deficit or surplus of energy from demand-driven growth is compensated by a change in energy allocation to reproduction. Another strategy to cover a deficit in ingested energy could be to increase energy ingestion by adaptive behaviour (Kooijman, 2010). Although this strategy might weaken the tradeoff between growth and reproduction, it is unlikely that adaptive behaviour could account for the entire deficit when individuals live in a natural ecosystem, as sufficient resource should be available to increase the consumption by adaptive behaviour. In our model, the resource density is regulated by competition between consumers. Therefore, an increase in consumption due to adaptive behaviour would lead to an increase in competition and a decrease in resource density which also could enlarge the energy deficit. Even if sufficient resource is available, ingested energy is limited by physiological and time constraints which are implemented in our model by using a type II functional response to model energy ingestion. It is therefore unlikely that adaptive behaviour can account for the full energy deficit caused by non-plastic growth and a tradeoff between energy allocation to growth and reproduction occurs.

We showed that the tradeoff between energy investment in growth and reproduction results in population dynamics regulated by respectively maturation or fecundity. Populations limited by maturation and the corresponding cohort cycles are widely explored in the context of ecological communities (De Roos et al., 2007, 2008; Persson et al., 2007; Van Leeuwen et al., 2008; van Kooten et al., 2007), while the dynamics of populations limited by fecundity are less studied in structured populations (see De Roos et al. (2009) for an example) and is an open topic. In any case our model analysis revealed how life history strategies of species in terms of energy allocation and plasticity affect the mechanisms which limit the population and determine the type of

population dynamic cycles. In this way we provide a new step in linking distinct ecological phenomena such as non-plastic growth and plastic growth, age and stage structure and populations limitation by individual growth and fecundity.

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6 Appendices

6.1 From energy flow to growth dynamics

Here we outline the calculations to transform the model in terms of individual energy dynamics into a size based population model. We define the composite parameters ℓ_∞ , r_B and r_F representing the asymptotic length of an individual, the Von Bertalanffy growth rate in length and the reproduction rate proportionally constant of an individual.

$$\ell_\infty = \frac{\kappa\alpha}{bd_m^{1/3}d_v^{1/3}\delta_m} \quad (22a)$$

$$r_B = \frac{by_m}{3} \quad (22b)$$

$$r_F = \frac{by_r}{\ell_b^3} \quad (22c)$$

6.1.1 Starvation boundaries

We start with reformulating the starvation boundaries (eq. (7) - (9)), which also results in the area-specific energy surplus (or deficit) available for growth (F_g), reproduction (F_r) and total biomass production (F_t). This is done by replacing the energy in lean mass (E_m) with the equivalent in terms of size ($d_md_v(\delta_m\ell)^3$, eq. (14)) after which we simplify the equation and substitute the composite parameters. For severe starvation conditions (eq. (7)) this results in:

$$bE_m > \alpha f(R)E_m^{2/3} \quad (23)$$

$$bd_md_v(\delta_m\ell)^3 > \alpha f(R)d_m^{2/3}d_v^{2/3}(\delta_m\ell)^2$$

$$\ell > \frac{f(R)}{\kappa} \frac{\kappa\alpha}{bd_m^{1/3}d_v^{1/3}\delta_m} \Rightarrow$$

$$0 > \frac{f(R)}{\kappa} \ell_\infty - \ell = F_t(R, \ell)$$

We can do the same for the supply-driven starvation condition (eq. (8)):

$$bE_m > \phi\kappa\alpha f(R)E_m^{2/3} + (1-\phi)\kappa\alpha\zeta E_m^{2/3} \quad (24)$$

$$bd_md_v(\delta_m\ell)^3 > \phi\kappa\alpha f(R)d_m^{2/3}d_v^{2/3}(\delta_m\ell)^2 + (1-\phi)\kappa\alpha\zeta d_m^{2/3}d_v^{2/3}(\delta_m\ell)^2$$

$$\ell > (\phi f(R) + (1-\phi)\zeta) \frac{\kappa\alpha}{bd_m^{1/3}d_v^{1/3}\delta_m} \Rightarrow$$

$$0 > (\phi f(R) + (1-\phi)\zeta) \ell_\infty - \ell = F_g(R, \ell)$$

The demand-driven starvation condition (eq. (9)) is not dependent on the energy stored in lean mass, so we only have to simplify this condition:

$$\phi\kappa\alpha f(R)E_m^{2/3} + (1-\phi)\kappa\zeta E_m^{2/3} > \alpha f(R)E_m^{2/3} \quad (25)$$

$$\phi\kappa f(R) + (1-\phi)\kappa\zeta > f(R) \Rightarrow$$

$$0 > \phi \frac{(1-\kappa)}{\kappa} f(R) + (1-\phi) \left(\frac{f(R)}{\kappa} - \zeta \right) = F_r(R)$$

6.1.2 Growth rate

To derive the differential equation for the length of an individual, we have to rewrite the differential equation for the energy stored in lean mass, in terms of length.

$$\frac{d\ell}{dt} = \frac{d}{dt} \frac{E_m^{1/3}}{d_m^{1/3} d_v^{1/3} \delta_m} = \frac{1}{3d_m^{1/3} d_v^{1/3} \delta_m E_m^{2/3}} \frac{dE_m}{dt} \quad (26)$$

We now can substitute the differential equation for the energy in lean mass under normal growth conditions (eq. (5)), to derive the differential equation for growth in length under growth conditions:

$$\begin{aligned} \frac{d\ell}{dt} &= \frac{\gamma_m}{3d_m^{1/3} d_v^{1/3} \delta_m E_m^{2/3}} \left(\phi\kappa\alpha f(R)E_m^{2/3} + (1-\phi)\kappa\alpha\zeta E_m^{2/3} - bE_m \right) \\ &= \frac{b\gamma_m}{3} \left((\phi f(R) + (1-\phi)\zeta) \frac{\kappa\alpha}{bd_m^{1/3} d_v^{1/3} \delta_m} - \frac{E_m^{1/3}}{d_m^{1/3} d_v^{1/3} \delta_m} \right) \\ &= r_B ((\phi f(R) + (1-\phi)\zeta) \ell_\infty - \ell) \\ &= r_B F_g(R, \ell) \end{aligned} \quad (27)$$

In the same way we can rewrite the differential equation for energy in lean mass (eq. (11)) under demand-driven starvation conditions:

$$\begin{aligned} \frac{d\ell}{dt} &= \frac{\gamma_m}{3d_m^{1/3} d_v^{1/3} \delta_m E_m^{2/3}} \left(\alpha f(R)E_m^{2/3} - bE_m \right) \\ &= \frac{b\gamma_m}{3} \left(\frac{\kappa\alpha}{\kappa b d_m^{1/3} d_v^{1/3} \delta_m} f(R) - \frac{E_m^{1/3}}{d_m^{1/3} d_v^{1/3} \delta_m} \right) \\ &= r_B \left(\frac{f(R)}{\kappa} \ell_\infty - \ell \right) \\ &= r_B F_t(R, \ell) \end{aligned} \quad (28)$$

6.1.3 Fecundity

To derive the fecundity in terms of number of individuals ($\beta(R, \ell)$), we have to divide the energy investment in reproduction ($\frac{dE_r}{dt}$) by the energy in lean mass of a newborn individual ($E_b = d_m d_v (\delta_m \ell_b)^3$). Under normal

growth conditions (eq. (6)), this results in:

$$\begin{aligned}
 \beta(R, \ell) &= \frac{1}{E_b} \gamma_r \left(\alpha f(R) E_m^{2/3} - \left(\phi \kappa \alpha f(R) E_m^{2/3} + (1 - \phi) \kappa \alpha \zeta E_m^{2/3} \right) \right) \\
 &= \frac{1}{d_m d_v (\delta_m \ell_b)^3} \gamma_r \left(\alpha f(R) d_m^{2/3} d_v^{2/3} (\delta_m \ell)^2 - \left(\phi \kappa \alpha f(R) d_m^{2/3} d_v^{2/3} (\delta_m \ell)^2 + (1 - \phi) \kappa \alpha \zeta d_m^{2/3} d_v^{2/3} (\delta_m \ell)^2 \right) \right) \\
 &= \frac{b \gamma_r}{\kappa \ell_b^3} (f(R) - (\phi \kappa f(R) + (1 - \phi) \kappa \zeta)) \frac{\kappa \alpha}{b d_m^{1/3} d_v^{1/3} \delta_m} \ell^2 \\
 &= \frac{r_F}{\kappa} (\phi(1 - \kappa) f(R) + (1 - \phi) (f(R) - \kappa \zeta)) \ell_\infty \ell^2 \\
 &= r_F F_r(R) \ell^2
 \end{aligned} \tag{29}$$

We can use the same steps to derive the fecundity under supply-driven starvation conditions from equation (10).

$$\begin{aligned}
 \beta(R, \ell) &= \frac{\gamma_r}{E_b} \left(\alpha f(R) E_m^{2/3} - b E_m \right) \\
 &= \frac{\gamma_r}{d_m d_v (\delta_m \ell_b)^3} \left(\alpha f(R) d_m^{2/3} d_v^{2/3} (\delta_m \ell)^2 - b d_m d_v (\delta_m \ell)^3 \right) \\
 &= \frac{b \gamma_r}{\ell_b^3} \left(\frac{f(R)}{\kappa} \frac{\kappa \alpha}{b d_m^{1/3} d_v^{1/3} \delta_m} - \ell \right) \ell^2 \\
 &= r_F \left(\frac{f(R)}{\kappa} \ell_\infty - \ell \right) \ell^2 \\
 &= r_F F_t(R, \ell) \ell^2
 \end{aligned} \tag{30}$$

6.1.4 Starvation mortality

Lastly we reformulate the equations for the starvation mortality in terms of length instead of energy stored in lean mass. For the supply-driven starvation mortality (eq. (12)) this becomes:

$$\begin{aligned}
 \mu_s(R, \ell) &= q_s \frac{b E_m - \left(\phi \kappa \alpha f(R) E_m^{2/3} + (1 - \phi) \kappa \alpha \zeta E_m^{2/3} \right)}{\alpha f(R) E_m^{2/3} - b E_m} \\
 &= q_s \frac{b d_m d_v (\delta_m \ell)^3 - \left(\phi \kappa \alpha f(R) d_m^{2/3} d_v^{2/3} (\delta_m \ell)^2 + (1 - \phi) \kappa \alpha \zeta d_m^{2/3} d_v^{2/3} (\delta_m \ell)^2 \right)}{\alpha f(R) d_m^{2/3} d_v^{2/3} (\delta_m \ell)^2 - b d_m d_v (\delta_m \ell)^3} \\
 &= q_s \frac{\ell - (\phi f(R) + (1 - \phi) \zeta) \frac{\kappa \alpha}{b d_m^{1/3} d_v^{1/3} \delta_m}}{\frac{f(R)}{\kappa} \frac{\kappa \alpha}{b d_m^{1/3} d_v^{1/3} \delta_m} - \ell} \\
 &= -q_s \kappa \frac{(\phi f(R) + (1 - \phi) \zeta) \ell_\infty - \ell}{f(R) \ell_\infty - \kappa \ell} \\
 &= -q_s \frac{F_g(R, \ell)}{F_t(R, \ell)}
 \end{aligned} \tag{31}$$

We can do the same for the demand-driven starvation mortality (eq. (13)):

$$\begin{aligned}
 \mu_s(R, \ell) &= q_s \frac{\left(\phi \kappa \alpha f(R) E_m^{2/3} + (1 - \phi) \alpha \kappa \zeta E_m^{2/3} - \alpha f(R) E_m^{2/3} \right)}{\alpha f(R) E_m^{2/3} - b E_m} \\
 &= q_s \frac{\left(\phi \kappa \alpha f(R) d_m^{2/3} d_v^{2/3} (\delta_m \ell)^2 + (1 - \phi) \alpha \kappa \zeta d_m^{2/3} d_v^{2/3} (\delta_m \ell)^2 - \alpha f(R) d_m^{2/3} d_v^{2/3} (\delta_m \ell)^2 \right)}{\alpha f(R) d_m^{2/3} d_v^{2/3} (\delta_m \ell)^2 - b b d_m d_v (\delta_m \ell)^3} \\
 &= q_s \frac{\left(\phi f(R) + (1 - \phi) \zeta - \frac{f(R)}{\kappa} \right) \frac{\kappa \alpha}{b d_m^{1/3} d_v^{1/3} \delta_m} \ell^2}{\frac{f(R)}{\kappa} \frac{\kappa \alpha}{b d_m^{1/3} d_v^{1/3} \delta_m} \ell^2 - \ell^3} \\
 &= -q_s \frac{(\phi(1 - \kappa) f(R) + (1 - \phi)(f(R) - \kappa \zeta)) \ell_\infty}{f(R) \ell_\infty - \kappa \ell} \\
 &= -q_s \frac{F_r(R)}{F_t(R, \ell)}
 \end{aligned} \tag{32}$$

6.2 Mathematical analysis

Persistence boundary

From equation (19) it follows that the resource density at the extinction boundary of the population ($\tilde{n}(0) = 0$) is equal to the maximum resource density ($\tilde{R} = K$). The existence boundary can therefore be found by setting the lifetime reproductive output (eq. 18) equal to one with $\tilde{R} = K$:

$$\frac{r_F}{\kappa} (\phi(1 - \kappa) f(K) + (1 - \phi)(f(K) - \zeta \kappa)) \ell_\infty \int_{\tilde{a}_J}^{a_{max}} \ell(K, a)^2 e^{-\mu a} da = 1 \tag{33}$$

6.2.1 Boundary between growth- and reproduction-limited dynamics

In the main text we distinguished growth-limited dynamics in which the effects through energy investments in growth exceed the effects through energy investments in reproduction ($\frac{\partial LRO}{\partial F_{g\infty}} > \frac{\partial LRO}{\partial F_r}$) and reproduction-limited dynamics in which the effects through energy investments in reproduction exceed the effects through energy investments in growth ($\frac{\partial LRO}{\partial F_{g\infty}} < \frac{\partial LRO}{\partial F_r}$). Given a constant resource density $\bar{R}$ we can obtain an explicit expression for the derivative of the lifetime reproductive output with respect to the lifetime energy investments in growth and the energy investments in reproduction:

$$\frac{\partial LRO}{\partial F_r} = r_F \int_{a_J}^{a_{max}} \ell(\bar{R}, a)^2 e^{-\mu a} da \tag{34a}$$

$$\frac{\partial LRO}{\partial F_{g\infty}} = r_F F_r(\bar{R}) \left(\int_{a_J}^{a_{max}} 2\ell(\bar{R}, a) \left(1 - e^{-r_B a} \right) e^{-\mu a} da - \frac{\partial a_J}{\partial F_{g\infty}} \ell_J^2 e^{-\mu a_J} \right) \tag{34b}$$

$$\frac{\partial a_J}{\partial F_{g\infty}} = - \frac{(\ell_J - \ell_b)}{r_B ((\phi f(\bar{R}) + (1 - \phi) \zeta) \ell_\infty - \ell_b) ((\phi f(\bar{R}) + (1 - \phi) \zeta) \ell_\infty - \ell_J)}$$

The boundary between the regions with growth- and reproduction-limited dynamics occurs if the derivative of the lifetime reproductive output with respect to the energy investment in growth equals the derivative of

the energy in vestment in reproduction.

$$0 = \frac{\partial LRO}{\partial F_{g\infty}} - \frac{\partial LRO}{\partial F_r} \quad (35a)$$

$$= F_r(\bar{R}) \int_{a_J}^{a_{max}} 2\ell(\bar{R}, a) (1 - e^{-r_B a}) e^{-\mu a} da - F_r(\bar{R}) \frac{\partial a_J}{\partial F_{g\infty}} \ell_J^2 e^{-\mu a_J} - \int_{a_J}^{a_{max}} \ell(\bar{R}, a)^2 e^{-\mu a} da \quad (35b)$$

$$= \int_{a_J}^{a_{max}} [2F_r(\bar{R}) (1 - e^{-r_B a}) \ell_\infty - \ell(\bar{R}, a)] \ell(\bar{R}, a) e^{-\mu a} da - F_r(\bar{R}) \frac{\partial a_J}{\partial F_{g\infty}} \ell_J^2 e^{-\mu a_J} \quad (35c)$$

In the extreme case in which the size at birth is zero and individuals mature directly at birth ($\ell_J = \ell_b = 0$), the age at maturation does not affect the lifetime reproductive output and equation (36) becomes zero if the term between squared brackets becomes zero. We can rewrite this term as:

$$[2F_r(\bar{R}) (1 - e^{-r_B a}) \ell_\infty - \ell(\bar{R}, a)] = \left(2\frac{f(\bar{R})}{\kappa} - 3\zeta - 3(f(\bar{R}) - \zeta)\phi \right) (1 - e^{-r_B a}) \ell_\infty - \ell_b e^{-r_B a} \quad (36)$$

If we then simplify the equation further and assume that the size at birth equals zero ($\ell_b = 0$), we can obtain the following solution:

$$2\frac{f(\bar{R})}{\kappa} - 3\zeta - 3(f(\bar{R}) - \zeta)\phi = 0 \quad (37)$$

or

$$\kappa = \frac{2f(\bar{R})}{3(\phi f(\bar{R}) + (1 - \phi)\zeta)} \quad (38)$$

If all growth is plastic ($\phi = 1$) this equality is satisfied if the plastic energy allocation constant (κ) equals two-thirds. If the functional response exceeds the non-plastic growth scalar ($f(\bar{R}) > \zeta$), the plastic energy allocation constant (κ) at which equality (37) is satisfied, increases with decreasing growth plasticity (ϕ). In contrast, if the non-plastic growth scalar exceeds the functional response ($f(\bar{R}) < \zeta$), the plastic energy allocation constant (κ) at which (37) is satisfied decreases with decreasing growth plasticity (ϕ). In other words, $\kappa = 2/3$ represents a threshold value. If the plastic energy allocation constant (κ) is below this threshold value, the boundary between the growth-limited dynamics and the reproduction-limited dynamics occurs if the non-plastic growth scalar exceeds the functional response ($f(\bar{R}) > \zeta$). If the plastic energy allocation constant (κ) is above the threshold value, the boundary between the growth-limited dynamics and the reproduction-limited dynamics occurs if the functional response exceeds the non-plastic growth scalar ($f(\bar{R}) > \zeta$).

From equation (36) it is clear that a positive size at birth ($\ell_J = \ell_b > 0$) introduces an additional negative term. The introduction of this negative term decreases the threshold value of κ . From equation (35c) it is clear that the introduction of a size at maturation above the size at birth ($\ell_J > \ell_b > 0$) includes an additional positive term. The introduction of this positive term would increase the threshold value of κ .

6.2.2 Stability analysis

The stability boundaries can be found by linearisation and substitution of exponential trial solutions, following De Roos et al. (1990). We first define a small perturbation in the equilibrium state of the resource, the age distribution and the individual size ($\epsilon_R, \epsilon_m, \epsilon_\ell$):

$$\epsilon_R(t) = R(t) - \tilde{R} \quad (39a)$$

$$\epsilon_n(t, a) = n(t, a) - \tilde{n}(a) \quad (39b)$$

$$\epsilon_\ell(t, a) = \ell(t, a) - \ell(\tilde{R}, a) \quad (39c)$$

As long as these perturbations are sufficiently small, starvation conditions will not occur and the system can be described by equations which are differentiable within their domain of definition.

$$I(R, \ell) = I_{max} f(R) \ell^2 \quad \text{for } \ell_b \leq \ell \leq (\phi f(R) + (1 - \phi)\zeta) \ell_\infty \quad (40a)$$

$$g(R, \ell) = r_B ((\phi f(R) + (1 - \phi)\zeta) \ell_\infty - \ell) \quad \text{for } \ell_b \leq \ell \leq (\phi f(R) + (1 - \phi)\zeta) \ell_\infty \quad (40b)$$

$$b(R, \ell) = \frac{r_F}{\kappa} (\phi(1 - \kappa)f(R) + (1 - \phi)(f(R) - \kappa\zeta)) \ell_\infty \ell^2 \quad \text{for } \ell_b \leq \ell \leq (\phi f(R) + (1 - \phi)\zeta) \ell_\infty \quad (40c)$$

$$d(R, \ell) = \mu_b \quad \text{for } 0 \leq a \leq a_{max} \quad (40d)$$

The perturbation in the age at maturation (ϵ_a), can be expressed in terms of the perturbation in length as shown by De Roos et al. (1990).

$$\epsilon_a(t) = \frac{-\epsilon_\ell(t, \tilde{a}_J)}{g(\tilde{R}, \ell_J)} \quad (41)$$

We can substitute the perturbations in the partial differential equations to formulate a linearised system of equations in which we neglect all second and higher order terms:

$$\frac{\delta \epsilon_n}{\delta t} + \frac{\delta \epsilon_n}{\delta t} = -\mu_b \epsilon_n \quad (42a)$$

$$\begin{aligned} \epsilon_n(t, 0) = & \int_{\tilde{a}_J}^{a_{max}} b(\tilde{R}, \ell(\tilde{R}, a)) \epsilon_n(t, a) + b_R(\tilde{R}, \ell(\tilde{R}, a)) \tilde{n}(a) \epsilon_R(t) + b_\ell(\tilde{R}, \ell(\tilde{R}, a)) \tilde{n}(a) \epsilon_\ell(t, a) da \\ & - b(\tilde{R}, \ell_J) \tilde{n}(\tilde{a}_J) \epsilon_a(t) \end{aligned} \quad (42b)$$

$$\frac{\delta \epsilon_\ell}{\delta t} + \frac{\delta \epsilon_\ell}{\delta t} = g_R(\tilde{R}, \ell(\tilde{R}, a)) \epsilon_R + g_\ell(\tilde{R}, \ell(\tilde{R}, a)) \epsilon_\ell \quad (42c)$$

$$\epsilon_\ell(t, 0) = 0 \quad (42d)$$

$$\begin{aligned} \frac{d \epsilon_R}{dt} = & -\nu \epsilon_R \\ & - \int_0^{a_{max}} I(\tilde{R}, \ell(\tilde{R}, a)) \epsilon_n(t, a) + I_R(\tilde{R}, \ell(\tilde{R}, a)) \tilde{n}(a) \epsilon_R(t) + I_\ell(\tilde{R}, \ell(\tilde{R}, a)) \tilde{n}(a) \epsilon_\ell(t, a) da \end{aligned} \quad (42e)$$

In which the functions $g_R, g_\ell, b_R, b_\ell, I_R$ and I_ℓ indicate the partial derivatives of the functions $g(R, \ell), b(R, \ell)$ and $I(R, \ell)$, with respect to R and ℓ respectively.

The following step is to substitute exponential trial solutions:

$$\epsilon_R(t) = \Delta_R e^{\lambda t} \quad (43a)$$

$$\epsilon_n(t, a) = \Delta_n(a) e^{\lambda t} \quad (43b)$$

$$\epsilon_\ell(t, a) = \Delta_\ell(a) e^{\lambda t} \quad (43c)$$

$$\epsilon_a = \Delta_a e^{\lambda t} \quad (43d)$$

into the linearised system, leading to

$$\frac{\partial \Delta_n}{\partial a} = -(\mu_b + \lambda) \Delta_n \quad (44a)$$

$$\begin{aligned} \Delta_n(0) = & \int_{\tilde{a}_J}^{a_{max}} b(\tilde{R}, \ell(\tilde{R}, a)) \Delta_n(a) + b_R(\tilde{R}, \ell(\tilde{R}, a)) \tilde{n}(a) \Delta_R + b_\ell(\tilde{R}, \ell(\tilde{R}, a)) \tilde{n}(a) \Delta_\ell(a) da \\ & - b(\tilde{R}, \ell_J) \tilde{n}(\tilde{a}_J) \Delta_a \end{aligned} \quad (44b)$$

$$\frac{\partial \Delta_\ell}{\partial a} = g_R(\tilde{R}, \ell(\tilde{R}, a)) \Delta_R + g_\ell(\tilde{R}, \ell(\tilde{R}, a)) \Delta_\ell - \lambda \Delta_\ell \quad (44c)$$

$$\Delta_\ell(0) = 0 \quad (44d)$$

$$\lambda \Delta_R = -\nu \Delta_R - \int_0^{a_{max}} I(\tilde{R}, \ell(\tilde{R}, a)) \Delta_n + I_R(\tilde{R}, \ell(\tilde{R}, a)) \tilde{n}(a) \Delta_R + I_\ell(\tilde{R}, \ell(\tilde{R}, a)) \tilde{n}(a) \Delta_\ell(a) da \quad (44e)$$

We now need to derive the the explicit derivatives of the ingestion, growth and reproduction functions with respect to the resource and the size:

$$I_R(R, \ell) = I_{max} f'(R) \ell^2 \quad (45a)$$

$$g_R(R, \ell) = r_B \phi f'(R) \ell_\infty \quad (45b)$$

$$b_R(R, \ell) = r_F (1 - \kappa \phi) \frac{f'(R)}{\kappa} \ell_\infty \ell^2 \quad (45c)$$

$$I_\ell(R, \ell) = 2 I_{max} f(R) \ell \quad (45d)$$

$$g_\ell(R, \ell) = -r_B \quad (45e)$$

$$b_\ell(R, \ell) = 2r_F \left(\phi \frac{1 - \kappa}{\kappa} f(R) + (1 - \phi) \frac{f(R) - \kappa \zeta}{\kappa} \right) \ell_\infty \ell \quad (45f)$$

In which $f'(R)$ is the derivative of the functional response with respect to the resource density R .

We can solve for $\Delta_n(a)$ and $\Delta_\ell(a)$ explicitly and all quantities can be expressed in terms of Δ_R and Δ_b which we write in stead of $\Delta_n(0)$.

$$\Delta_n(a) = \Delta_b e^{-\mu_b a} e^{-\lambda a} \quad (46a)$$

$$\Delta_\ell(a) = \frac{r_B \phi f'(\tilde{R}) \ell_\infty}{r_B + \lambda} \left(1 - e^{-(r_B + \lambda)a} \right) \Delta_R \quad (46b)$$

$$\Delta_a = \frac{-\Delta_\ell(t, \tilde{a}_J)}{g(\tilde{R}, \ell_J)} = - \frac{\phi f'(\tilde{R}) \ell_\infty}{\left(\phi f(\tilde{R}) + (1 - \phi) \zeta \right) \ell_\infty - \ell_J} \frac{1 - e^{-(r_B + \lambda) \tilde{a}_J}}{r_B + \lambda} \Delta_R \quad (46c)$$

From this we directly arrive at the stability matrix:

$$S(\lambda)\Delta = \begin{pmatrix} s_{11} & s_{s12} \\ s_{21} & s_{22} \end{pmatrix} \begin{pmatrix} \Delta_b \\ \Delta_R \end{pmatrix} \quad (47)$$

With elements:

$$\begin{aligned} s_{11} &= b_c(\tilde{R}) \frac{\bar{A}_s(\lambda, \tilde{a}_J)}{\tilde{n}(0)} - 1 \\ s_{12} &= \frac{r_F}{\kappa} (1 - \kappa\phi) f'(\tilde{R}) \ell_\infty \bar{A}_s(0, \tilde{a}_J) \\ &\quad + b_c(\tilde{R}) \frac{\phi}{r_B + \lambda} f'(\tilde{R}) \ell_\infty \left(\frac{(1 - e^{-(r_B + \lambda)\tilde{a}_J}) \ell_J^2 e^{-\mu_b \tilde{a}_J}}{((\phi f(\tilde{R}) + (1 - \phi)\zeta) \ell_\infty - \ell_J)} + 2r_B \bar{A}_\ell(\tilde{a}_J) \right) \\ s_{21} &= -I_R f(\tilde{R}) \frac{\bar{A}_s(\lambda, 0)}{\tilde{n}(0)} \\ s_{22} &= -\nu - \lambda - I_R f'(\tilde{R}) \left(\bar{A}_s(0, 0) + 2 \frac{r_B \phi}{r_B + \lambda} f(R) \ell_\infty \bar{A}_\ell(0) \right) \end{aligned} \quad (48)$$

with:

$$\begin{aligned} b_c(\tilde{R}) &= \frac{r_F}{\kappa} \left(\phi(1 - \kappa) f(\tilde{R}) + (1 - \phi) (f(\tilde{R}) - \kappa\zeta) \right) \ell_\infty, \\ \bar{A}_s(s, a_{min}) &= \int_{a_{min}}^{a_{max}} \tilde{n}(0) \ell(\tilde{R}, a)^2 e^{-(\mu_b + s)a} da, \\ \bar{A}_\ell(a_{min}) &= \int_{a_{min}}^{a_{max}} \tilde{n}(0) (1 - e^{-(r_B + \lambda)a}) \ell(\tilde{R}, a) e^{-\mu_b a} da \end{aligned}$$

In which $f'(\tilde{R})$ represents the derivative of the type II functional response with respect to the resource density in equilibrium. The eigenvalues of the system are now the roots of

$$\det(S(\lambda)) = 0 \quad (49)$$

7 Supplementary figures

Fig. S1 Population dynamic cycles with a resource independent fecundity. The fecundity is made independent by substituting the resource density in the function of the individual fecundity with the equilibrium resource density ($\beta(\bar{R}, \ell(t, a))$). The cycles are the same as the cycles represented in figure 3b and c. This shows that this type of cycles is not caused by a fluctuations in the individual fecundity. The maturation rate is calculated as the inverse of the prospective age at maturation if the current resource density remained constant (a_J^{-1}). The fecundity is calculated as the population birth rate divided by the number of adults ($\frac{n(t,0)}{\int_{a_J}^{a_{max}} n(t,a)da}$). Note the different vertical axis for the consumer densities.

Fig. S2 Age-size relationships at different times during population cycles if growth is non-plastic (a) or entirely plastic (b).

The graphs are constructed with $K = 0.5$, $\zeta = 1$ and $\kappa = 0.3$. Different coloured lines indicate different moments during the simulation. All age-size curves for non-plastic growth (a) do overlap. Also note the different scaling of the vertical axes.