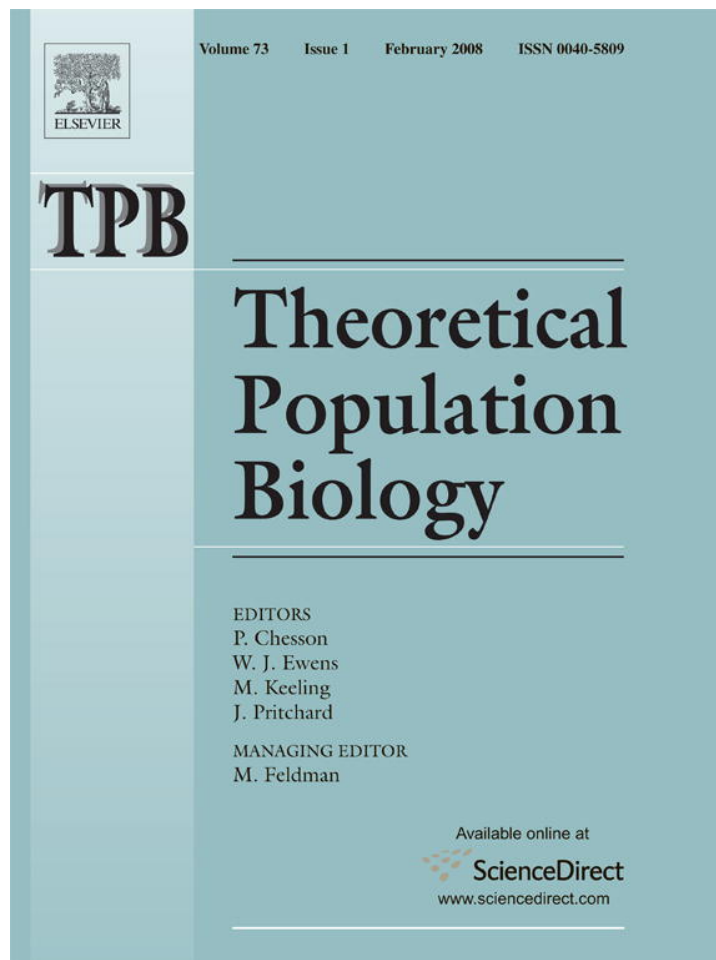


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Simplifying a physiologically structured population model to a stage-structured biomass model

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Abstract

We formulate and analyze an archetypal consumer–resource model in terms of ordinary differential equations that consistently translates individual life history processes, in particular food-dependent growth in body size and stage-specific differences between juveniles and adults in resource use and mortality, to the population level. This stage-structured model is derived as an approximation to a physiologically structured population model, which accounts for a complete size-distribution of the consumer population and which is based on assumptions about the energy budget and size-dependent life history of individual consumers. The approximation ensures that under equilibrium conditions predictions of both models are completely identical. In addition we find that under non-equilibrium conditions the stage-structured model gives rise to dynamics that closely approximate the dynamics exhibited by the size-structured model, as long as adult consumers are superior foragers than juveniles with a higher mass-specific ingestion rate. When the mass-specific intake rate of juvenile consumers is higher, the size-structured model exhibits single-generation cycles, in which a single cohort of consumers dominates population dynamics throughout its life time and the population composition varies over time between a dominance by juveniles and adults, respectively. The stage-structured model does not capture these dynamics because it incorporates a distributed time delay between the birth and maturation of an individual organism in contrast to the size-structured model, in which maturation is a discrete event in individual life history. We investigate model dynamics with both semi-chemostat and logistic resource growth.

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1. Introduction

Physiologically structured population models (PSPM; Metz and Diekmann, 1986; De Roos, 1997) are a class of models which explicitly link individual life history and population dynamics. PSPM are based on a core model of all relevant individual-level processes, in particular feeding, development, reproduction and mortality. These processes are dependent on the state of the individual organism itself and the environment in which it lives. Body size has often been used as the representative variable determining the

individual or *i*-state, whereas food density has been most frequently used to characterize its environment. Given a model of the individual life history and the interaction of the individual with its environment (e.g. its food source) bookkeeping operations suffice to arrive at the specification of the dynamics of the population or *p*-state. This population-level model can either be formulated in terms of partial differential (Metz and Diekmann, 1986; De Roos, 1997) or integral equations (Diekmann et al., 1994). PSPM can be analyzed using a number of different techniques. Apart from investigating them analytically, their dynamics can be studied with a numerical integration method (De Roos, 1988; De Roos et al., 1992; De Roos, 1997), which has proved its robustness in a variety of cases

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(e.g. De Roos et al., 1990; Claessen et al., 2000). More recently, numerical bifurcation methods have been developed (Kirkilionis et al., 2001; Diekmann et al., 2003), which allow to compute branches of equilibria of the models as a function of one of the model parameters (e.g. Claessen and De Roos, 2003).

Individual-level models that form the core of PSPM, for example those describing population dynamics of fish (e.g. Persson et al., 1998; Claessen et al., 2000) or zooplankton (e.g. De Roos et al., 1990), are usually based on a consistent set of assumptions about the acquisition and use of food and energy for covering maintenance requirements, growth in body size and reproduction. Non-trivial and parameter-rich functions of body size and food are often used to model the life history processes, since they are as much as possible based on experimental data under a range of laboratory conditions. Hence, the core model of a PSPM generally is a detailed, mechanistic mathematical description of individual life. On the one hand, this mechanistic rooting in individual life history allows for disentangling in detail the causal relationships between the individual-level processes and the generated population dynamics (for illustrative examples, see Claessen et al., 2000; Persson et al., 2003, 2004). On the other hand, the resulting complexity of the PSPM makes model analysis a daunting task despite the continuation techniques recently developed by Kirkilionis et al. (2001). Studies of PSPM with more than a single species are therefore rare (Van De Wolfshaar et al., 2006).

Studies of PSPM with individual body size as structuring i -state variable have contributed significantly to our understanding about the consequences of size-dependent individual life history processes for population dynamics. In systems of a size-structured consumer feeding on an unstructured resource population intraspecific competition among differently sized consumer individuals may give rise to population cycles with a period equal to the generation time of the consumer (Persson et al., 1998; De Roos and Persson, 2003; De Roos et al., 2003). These population dynamic effects are the most prominent consequences of size-dependent individual life history processes when the size-structured population occupies the highest trophic level in the modeled community. In contrast, if species at lower trophic levels are size-structured, size-dependent life history processes may also influence the structure and possible equilibria of the ecological community. De Roos and Persson (2002) have shown that an unstructured predator population foraging size-selectively on small prey individuals may suffer from an emergent Allee effect, which results from food-dependence in the prey life history. They found that for a range of parameter values a predator–prey and a predator-free community state could coexist, which are both locally stable. A similar bistability occurs when predators forage size-selectively on large consumers (De Roos and Persson, 2005a). Furthermore, Van Kooten et al. (2005) show that bistability may also occur between two different community equilibria in which both

predators and consumers coexist, but at different densities and with different equilibrium population structures. Van De Wolfshaar et al. (2006) study the interaction between two size-structured populations in an intraguild-predation system with top predators and intermediate consumers. In this setting, the size-dependent interaction strongly limits the possibilities of coexistence and as a rule bistability occurs between a predator-dominated and a prey-dominated equilibrium. All these community consequences have been shown to arise primarily because individual growth is food-dependent and hence varies with population density (De Roos and Persson, 2002, 2005a). This makes food-dependent growth in body size the key life history process that sets size-structured models apart from unstructured as well as age-structured models.

In few-species systems size-dependent life history processes and in particular food-dependent growth thus promote the occurrence of multiple community equilibria under the same conditions. These equilibria may differ in three important aspects: the species composition of the community, the numerical abundances and the structure (i.e. size distribution) of the constituting populations. The results inspire the question to what extent such effects also occur in larger communities involving more than two size-structured populations and to what extent they influence the dynamics and structure of such communities. It is, however, infeasible to address this question using models that are composed of elements as complex as the size-structured population models, which have for example been used to investigate the emergent Allee effect (De Roos and Persson, 2002). A simpler, more aggregated model is required as a core building block to formulate and successfully analyze models of larger species ensembles. Unstructured models of the Lotka–Volterra type, however, only account for reproduction and death as life history processes that are important for population dynamics. These models ignore individual growth in body size despite that it is an important process in the life history of most species (Werner, 1988), leading to major changes in their ecology during ontogeny. There is hence a clear need for an archetypal, population dynamic model, which realistically accounts for food- and size-dependent growth in body size, but which is nonetheless more amenable to analysis than the PSPMs that account for a complete population size distribution. In this paper we derive and investigate the properties of such an archetypal, population dynamic model. The model, which we refer to as the *stage-structured biomass model*, is formulated in terms of a set of ordinary differential equations. Nonetheless, under equilibrium conditions the model predictions are identical to those of a PSPM accounting for a continuous size-distribution, from which the stage-structured biomass model is derived. Under these conditions the model therefore consistently translates individual life history processes, in particular food-dependent growth in body size, to the population level. In the following sections we derive the structured biomass community model from its underlying PSPM and

compare the dynamics of both models under a range of conditions.

2. Model derivation

2.1. Size-structured population model

We start the derivation of the stage-structured biomass model by formulating a size-structured population model, which is rigorously based on individual life history. The model incorporates in a simple manner the three most basic aspects of size-dependent life histories: (1) both foraging rate and metabolic requirements increase with body size; (2) growth in body size depends on food availability; and (3) small, juvenile individuals do not reproduce but use their energy for growth and development, while larger, adult individuals use their energy for reproduction. All dynamic energy budget models that have been formulated to describe individual acquisition and use of food for growth and reproduction incorporate these basic assumptions in one way or another (see for example Gurney et al., 1990; Persson et al., 1998; Kooijman, 2000).

As individual- or *i*-state we characterize individuals with their size s , which we interpret as body weight or mass. Individuals are assumed to be born with size s_b and mature on reaching size s_m . All individuals are assumed to forage on the shared resource, the density of which is denoted by R , following a Holling type-II functional response with half-saturation constant H . Their maximum ingestion rate is assumed to scale linearly with body size s . For juvenile individuals ($s_b < s < s_m$) we assume that the proportionality constant of this scaling relation equals I_{max} , while for adults we assume it to equal qI_{max} (De Roos and Persson, 2003). The factor q phenomenologically captures stage-specific differences in resource availability and resource use between juveniles and adults. It is introduced to avoid the complexity of modeling such stage-specific feeding differences in a more mechanistic manner with separate resources for juveniles and adults. Ingested resource is assimilated with efficiency σ and first used to cover maintenance requirements. These are also assumed to scale linearly with body size s with proportionality constant T . The remaining net energy production is converted into new consumer biomass. Juvenile individuals ($s_b < s < s_m$) produce new biomass through growth in body size, while adults are assumed to convert all their net biomass production into new offspring. Adults hence do not grow and have the identical size $s = s_m$. Overhead costs associated with growth in body size or the production of offspring are assumed to be subsumed in the maintenance requirements (Yodzis and Innes, 1992). Producing offspring therefore requires a biomass investment per newborn individual equal to the size at birth s_b .

These assumptions lead to the following expressions for the net biomass production *per unit body mass* as a function

of resource density R :

$$v_j(R) = \sigma I_{max} \frac{R}{H + R} - T \quad (1)$$

and

$$v_a(R) = \sigma q I_{max} \frac{R}{H + R} - T, \quad (2)$$

for juveniles and adults, respectively. The expressions closely follow the bioenergetics approach introduced by Yodzis and Innes (1992) except for the fact that we distinguish between juveniles and adults, which may differ in their resource use as well as their mortality.

At low resource densities ingestion may be insufficient to cover maintenance requirements, leading to a negative net biomass production for juveniles, adults or both of them. We will assume that juvenile growth equals 0 when juvenile net biomass production is negative and that similarly reproduction equals 0 when adult net biomass production is negative. We introduce the notation $v_j^+(R)$ and $v_a^+(R)$ to indicate the net biomass production by a juvenile and an adult, respectively, restricted to non-negative values:

$$v_j^+(R) = \begin{cases} \sigma I_{max} \frac{R}{H + R} - T & \text{if } R > \frac{H}{\sigma I_{max}/T - 1}, \\ 0 & \text{otherwise,} \end{cases} \quad (3)$$

$$v_a^+(R) = \begin{cases} \sigma q I_{max} \frac{R}{H + R} - T & \text{if } R > \frac{H}{\sigma q I_{max}/T - 1}, \\ 0 & \text{otherwise.} \end{cases} \quad (4)$$

The above assumptions on individual life history imply that the juvenile growth rate in body mass, denoted by $g(R, s)$, follows:

$$g(R, s) = v_j^+(R)s = \begin{cases} \left(\sigma I_{max} \frac{R}{H + R} - T \right) s & \text{if } R > \frac{H}{\sigma I_{max}/T - 1}, \\ 0 & \text{otherwise} \end{cases} \quad (5)$$

while the rate $b(R, s_m)$ at which adults reproduce offspring of size s_b is given by

$$b(R, s_m) = v_a^+(R) \frac{s_m}{s_b} = \begin{cases} \left(\sigma q I_{max} \frac{R}{H + R} - T \right) \frac{s_m}{s_b} & \text{if } R > \frac{H}{\sigma q I_{max}/T - 1}, \\ 0 & \text{otherwise.} \end{cases} \quad (6)$$

Note that adults do not grow in body size any more after reaching the size at maturation s_m . We assume that juvenile and adult individuals are exposed to a constant background mortality rate μ_j and μ_a , respectively. On top of that, we assume that all juvenile consumers irrespective of their body size experience an additional starvation mortality equal to $-v_j(R)$ when food intake is insufficient to cover their maintenance requirements and hence $v_j(R) < 0$. Similarly, we assume adult consumers to experience an

additional starvation mortality equal to $-v_a(R)$ on top of their background mortality, if adult ingestion is smaller than maintenance ($v_a(R) < 0$). Total juvenile and adult mortality, which we indicate with $d_j(R)$ and $d_a(R)$, respectively, hence equal:

$$d_j(R) = \begin{cases} \mu_j & \text{if } R > \frac{H}{\sigma I_{max}/T - 1}, \\ \mu_j - v_j(R) & \text{otherwise} \end{cases} \quad (7)$$

and

$$d_a(R) = \begin{cases} \mu_a & \text{if } R > \frac{H}{\sigma q I_{max}/T - 1}, \\ \mu_a - v_a(R) & \text{otherwise,} \end{cases} \quad (8)$$

respectively. When the food intake of individuals is smaller than their maintenance, these assumptions about mortality ensure for every value of body size s that the decrease in biomass of the cohort of consumers with that body size exactly equals the balance between total food assimilation and total maintenance rate of that cohort. Hence, the assumptions guarantee conservation of energy and biomass at the level of consumer size cohorts under both growing and starvation conditions.

Finally, we will study model predictions with two different types of resource dynamics in the absence of consumers. We either assume that in the absence of consumers the resource density follows semi-chemostat dynamics (Persson et al., 1998):

$$G(R) = \delta(R_{max} - R). \quad (9)$$

Alternatively, we assume that resource dynamics follows a logistic growth process:

$$G(R) = \delta R \left(1 - \frac{R}{R_{max}} \right). \quad (10)$$

For both types of dynamics R_{max} equals the resource density in the absence of consumers. The parameter δ represents the resource turn-over and per capita growth rate in case of semi-chemostat and logistic resource dynamics, respectively. The resource density decreases due to the consorted foraging of all consumers on it.

Let $c(t, s)$ represent the size distribution of juvenile consumers with $s_b \leq s < s_m$ and $C(t)$ the total number of adult consumers with $s = s_m$. The dynamics of the consumer–resource system can then be described by the following set of differential equations:

$$\frac{\partial c(t, s)}{\partial t} + \frac{\partial g(R, s)c(t, s)}{\partial s} = -d_j(R)c(t, s) \quad \text{for } s_b \leq s < s_m, \quad (11a)$$

$$g(R, s_b)c(t, s_b) = b(R, s_m)C, \quad (11b)$$

$$\frac{dC}{dt} = g(R, s_m)c(t, s_m) - d_a(R)C, \quad (11c)$$

$$\frac{dR}{dt} = G(R) - \frac{R}{H + R} \left(I_{max} \int_{s_b}^{s_m} s c(t, s) ds + q I_{max} s_m C \right) \quad (11d)$$

(see Metz and Diekmann, 1986; De Roos, 1997). The partial differential equation (11a) describes the change in the juvenile size distribution $c(t, s)$ due to growth and mortality, whereas the boundary condition (11b) accounts for its change due to reproduction of offspring. The ODE (11c) describes the dynamics of the number of adult consumers as a balance between a maturation term ($g(R, s_m)c(t, s_m)$) and mortality ($d_a(R)C$). In a similar way the ODE (11d) describes the change in resource density due to resource production and resource foraging by consumers.

2.2. Stage-structured biomass model

In this section we aggregate the size-structured model (11) into a biomass-based consumer–resource model in terms of ordinary differential equations. We use two differential equations to describe the dynamics of the total biomass in the juvenile and adult stage, defined as

$$J = \int_{s_b}^{s_m} s c(t, s) ds \quad (12)$$

and

$$A = s_m C, \quad (13)$$

respectively, and a third equation for the dynamics of the resource density R . The latter is identical to the ODE (11d), but rewritten in terms of R , J and A . For the following derivation we first assume that ingestion is sufficiently high for both juveniles and adults to cover maintenance requirements, such that juvenile and adult net-production, $v_j(R)$ and $v_a(R)$, respectively, are positive. Consequently, the expressions for the juvenile growth and adult reproduction rate simplify to $g(R, s) = v_j(R)s$ (see Eq. (5)) and $b(R, s_m) = v_a(R)s_m/s_b$ (see Eq. (6)), respectively. Furthermore, under these conditions starvation mortality can be neglected, such that the juvenile and adult mortality rates, $d_j(R)$ and $d_a(R)$, can be replaced by the background values μ_j and μ_a , respectively. In the second part of this section we will extend the model to cover also starvation conditions.

The ODE for A can be derived in a straightforward manner by multiplying the left- and right-hand side of the ODE for C (11c) with the adult size s_m

$$\frac{dA}{dt} = s_m g(R, s_m)c(t, s_m) - \mu_a A. \quad (14)$$

The ODE for J can be derived by first differentiating the integral in the right-hand side of the definition for J (Eq. (12)) with respect to time and subsequently using the partial differential equation (11a) to substitute the

time derivative:

$$\begin{aligned} \frac{dJ}{dt} &= \int_{s_b}^{s_m} s \frac{\partial c(t, s)}{\partial t} ds \\ &= - \int_{s_b}^{s_m} s \frac{\partial g(R, s) c(t, s)}{\partial s} ds - \int_{s_b}^{s_m} s \mu_j c(t, s) ds \\ &= -s g(R, s) c(t, s) \Big|_{s_b}^{s_m} + \int_{s_b}^{s_m} g(R, s) c(t, s) ds - \mu_j J. \end{aligned}$$

Using the boundary condition (11b) and the expressions $g(R, s) = v_j(R)s$ (Eq. (5)) and $b(R, s_m) = v_a(R)s_m/s_b$ (Eq. (6)) for the juvenile growth rate and the adult fecundity, respectively, this ODE can be written as

$$\frac{dJ}{dt} = v_a(R)A - s_m g(R, s_m) c(t, s_m) + v_j(R)J - \mu_j J.$$

To arrive at a closed system of ODEs the maturation term

$$s_m g(R, s_m) c(t, s_m) = v_j(R) s_m^2 c(t, s_m) \quad (15)$$

has to be expressed in terms of J and A . This reformulation will be carried out in such a way that the equilibria of the closed system of ODEs are identical to the equilibria of the basic size-structured model (11). In an equilibrium of the size-structured model the following equality relates the value of the stable size-distribution, which we denote by $\tilde{c}(s)$, at any size s to its value at s_b :

$$g(R, s) \tilde{c}(s) = g(R, s_b) \tilde{c}(s_b) \exp\left(- \int_{s_b}^s \frac{\mu_j}{g(R, \xi)} d\xi\right).$$

In this expression the exponential term represents the individual survival probability up to size s . Using Eq. (5) for the juvenile growth rate in size the integral in the exponential term can be evaluated, leading to

$$\tilde{c}(s) = \frac{g(R, s_b) \tilde{c}(s_b)}{v_j s} \left(\frac{s}{s_b}\right)^{-\mu_j/v_j}. \quad (16)$$

Here and in the following derivation we suppress the argument of the resource-dependent function $v_j(R)$ to shorten the notation. Using the stationary size distribution the equilibrium juvenile biomass density \tilde{J} can be written as

$$\begin{aligned} \tilde{J} &= \int_{s_b}^{s_m} s \tilde{c}(s) ds \\ &= \frac{g(R, s_b) \tilde{c}(s_b)}{v_j} s_b^{\mu_j/v_j} \int_{s_b}^{s_m} s^{-\mu_j/v_j} ds \\ &= \frac{g(R, s_b) \tilde{c}(s_b)}{v_j - \mu_j} s_b^{\mu_j/v_j} (s_m^{1-\mu_j/v_j} - s_b^{1-\mu_j/v_j}). \end{aligned}$$

From this equality the product $g(R, s_b) \tilde{c}(s_b) s_b^{\mu_j/v_j}$ can be expressed in terms of \tilde{J} :

$$g(R, s_b) \tilde{c}(s_b) s_b^{\mu_j/v_j} = \frac{v_j - \mu_j}{s_m^{1-\mu_j/v_j} - s_b^{1-\mu_j/v_j}} \tilde{J}. \quad (17)$$

Given expression (16) for the equilibrium size distribution the maturation term (15) can be rewritten as

$$v_j s_m^2 \tilde{c}(s_m) = g(R, s_b) \tilde{c}(s_b) s_b^{\mu_j/v_j} s_m^{1-\mu_j/v_j}$$

which can be expressed using Eq. (17) in terms of \tilde{J} :

$$v_j s_m^2 \tilde{c}(s_m) = \frac{v_j - \mu_j}{1 - \left(\frac{s_b}{s_m}\right)^{1-\mu_j/v_j}} \tilde{J}. \quad (18)$$

Now define the function $\gamma(v)$ as

$$\gamma(v) = \frac{v - \mu_j}{1 - z^{1-\mu_j/v}} \quad (19)$$

with $z = s_b/s_m$, the ratio of newborn and maturation body size. Notice that the function $\gamma(v)$ has the same sign as v , has a regular limit equal to $-\mu_j/\ln(z)$ for $v \rightarrow \mu_j$ and approaches 0 for $v \downarrow 0$. Re-introducing the food-dependence of the juvenile net-biomass production rate $v_j(R)$ the dynamics of the resource, juvenile and adult consumer densities can now be described by the following system of ODEs:

$$\frac{dJ}{dt} = v_a(R)A + v_j(R)J - \gamma(v_j(R))J - \mu_j J, \quad (20a)$$

$$\frac{dA}{dt} = \gamma(v_j(R))J - \mu_a A, \quad (20b)$$

$$\frac{dR}{dt} = G(R) - \frac{R}{H + R} (I_{max} J + q I_{max} A). \quad (20c)$$

It should be noted that in the absence of differences in resource use between juveniles and adults (i.e. when $q = 1$) $v_j(R)$ always equals $v_a(R)$. If in addition juveniles and adults both experience the same background mortality ($\mu_j = \mu_a$) the above system of equations can be simplified into the following system of two equations for the total consumer biomass, $B = J + A$, and the resource density R

$$\frac{dB}{dt} = v(R)B - \mu B, \quad (21a)$$

$$\frac{dR}{dt} = G(R) - I_{max} \frac{R}{H + R} B \quad (21b)$$

in which $v(R) = v_j(R) = v_a(R)$ and $\mu = \mu_j = \mu_a$. Ignoring background mortality altogether (i.e. setting $\mu = 0$) Yodzis and Innes (1992) formulated the above system of equations as a bio-energetic model for consumer–resource dynamics. Hence, the stage-structured biomass model is related to the Yodzis and Innes-model, but accounts in addition for separate consumer life stages that differ in their use of resources and their exposure to predators.

The derivation of the stage-structured consumer–resource model (20) is based on the assumption that the net biomass production is positive for individuals of all sizes. More specifically for

$$v_j(R) > 0 \quad \text{and} \quad v_a(R) > 0. \quad (22)$$

In equilibrium situations these two size-independent conditions necessarily hold and by argument of continuity it can also be reasoned that the conditions hold in the neighborhood of any equilibrium state. However, when resource density is so low that juvenile and adult biomass production turn negative ($v_j(R) < 0$ and $v_a(R) < 0$,

respectively) juvenile growth in body size and adult fecundity reduce to 0. Under these conditions the juvenile size distribution $c(t, s)$ and the adult consumer density C only change due to background and starvation mortality and dynamics are described by

$$\frac{\partial c(t, s)}{\partial t} = -d_j(R)c(t, s) \quad \text{for } s_b \leq s < s_m,$$

$$\frac{dC}{dt} = -d_a(R)C,$$

$$\frac{dR}{dt} = G(R) - \frac{R}{H + R} \left(I_{max} \int_{s_b}^{s_m} sc(t, s) ds + qI_{max}s_m C \right).$$

As before we can straightforwardly derive an ODE for adult biomass A from the above system of equations by multiplying the left- and right-hand side of dC/dt with the adult size s_m . The ODE for juvenile biomass J is again derived by differentiating the integral expression for J (Eq. (12)) and substitution of the partial differential equation for $c(t, s)$. This derivation is, however, simplified because reproduction and growth in body size do not occur under starvation conditions. The dynamics of the stage-structured biomass model under starvation conditions is hence described by the following system of ODEs:

$$\frac{dJ}{dt} = -(\mu_j - v_j(R))J, \tag{23a}$$

$$\frac{dA}{dt} = -(\mu_a - v_a(R))A, \tag{23b}$$

$$\frac{dR}{dt} = G(R) - \frac{R}{H + R} (I_{max}J + qI_{max}A) \tag{23c}$$

in which we have substituted the expressions for the juvenile and adult death rate, $d_j(R)$ (Eq. (7)) and $d_a(R)$ (Eq. (8)), respectively, that hold under conditions of negative net biomass production rates.

Combining Eqs. (20) and (23) describing dynamics under growing and starvation conditions, respectively, the general form of the stage-structured biomass model is given by the following system of ODEs:

$$\frac{dJ}{dt} = v_a^+(R)A + v_j(R)J - \gamma(v_j^+(R))J - \mu_j J, \tag{24a}$$

$$\frac{dA}{dt} = \gamma(v_j^+(R))J + v_a(R)A - v_a^+(R)A - \mu_a A, \tag{24b}$$

$$\frac{dR}{dt} = G(R) - \frac{R}{H + R} (I_{max}J + qI_{max}A). \tag{24c}$$

In comparison to the model equations (20) the second ODE contains two additional terms $v_a(R)A$ and $v_a^+(R)A$, which cancel as long as $v_a(R)$ is positive and amount to $v_a(R)A$ otherwise, reflecting the starvation mortality of adults under conditions of negative net-biomass production (see Eq. (23b)). Furthermore, under these conditions the reproduction rate equals 0, as indicated by $v_a^+(R)$ in the first term of the first ODE. The second term in the ODE for

J reflects that juvenile net production rate $v_j(R)$ increases juvenile biomass when juvenile ingestion is larger than maintenance and that juvenile biomass decreases otherwise as a consequence of starvation mortality. The assumptions on the individual mortality rate $d_j(R)$ (Eq. (7)) guarantee that the latter biomass loss rate exactly equals the negative biomass balance between ingestion and maintenance (see Eq. (23a)). The final difference between Eqs. (20) and (24) is the restriction of the maturation term $\gamma(v_j^+(R))J$ to non-negative values, reflecting the assumption that juvenile growth stops when juvenile net-production turns negative.

2.3. Scaling and parameterization

We will only briefly describe how we have non-dimensionalized both the size-structured and the stage-structured biomass model without presenting the scaled model equations themselves. The half-saturation constant H represents a resource biomass density, expressed in terms of gram biomass per unit volume. Changing its value can be considered to reflect changes in the unit volume, in which we express the densities R , J and A . Without loss of generality we can therefore choose the value of H equal to 1, bearing in mind that this fixes the environmental volume in which the consumer population is assumed to live and thus scales the biomass densities R , J and A . The time variable t we scale with the mass-specific metabolic rate parameter T . To this end we define a new time variable $t' = tT$ and express the dynamics of resource and consumers as a function of t' . Note that in the following units of time hence refer to the inverse of the metabolic rate parameter T . The resulting set of equations for the stage-structured biomass model is largely identical to the set (24) except for that the values of H and T are set equal to 1 and the rate parameters δ , I_{max} , μ_j and μ_a are expressed as multiples of the mass-specific metabolic rate parameter T . In the size-structured model (11) time and the densities of resource R and adult consumers C are scaled as in the stage-structured model, i.e. with the metabolic rate parameter T and the half-saturation constant H , respectively. However, in addition we scale the body size variable s by the maturation size s_m , rephrasing the model in terms of the scaled size variable $s' = s/s_m$. This scaling necessitates that the juvenile consumer size distribution $c(t, s)$ is in addition scaled by the factor s_m , defining the scaled juvenile consumer density as $c'(t, s') = c(t, s' \cdot s_m)s_m/H$. The scaled size at birth now equals $z = s_b/s_m$, which variable also governs the maturation rate (19) in the stage-structured biomass model.

After scaling the model dynamics are governed by two parameters governing resource growth in the absence of consumers and six parameters describing growth, development, reproduction and death of consumers. In case of semi-chemostat resource dynamics we adopt the default value $R_{max} = 2$ and $\delta = 1$ for the maximum resource density in the absence of consumers and the resource turn-over

rate, respectively. The latter value implies that resource turn-over rate is approximately equal to the turn-over rate of consumer biomass through maintenance. In case of logistic resource growth we study model dynamics as a function of R_{max} , as its value tends to significantly affect dynamics predicted by consumer–resource models with so-called paradox-of-enrichment cycles (Rosenzweig, 1971) occurring at high values of R_{max} . For the resource per capita growth rate we choose as default value $\delta = 1$.

Across differently sized consumer, species mass-specific metabolic rate, mass-specific maximum ingestion rate and mortality rate all tend to be proportional to the quarter power of adult body size of the species (Peters, 1983; Yodzis and Innes, 1992; Brown et al., 2004). For the mass-specific maximum ingestion rate an estimate of 0.1 for the proportionality constant in this quarter-power scaling relation can be derived from data on zooplankton grazing rates presented by Hansen et al. (1997). Peters (1983) estimates the proportionality constant for the mass-specific metabolic rate scaling to equal 0.01, which is in line with estimates provided by Yodzis and Innes (1992) and Brown et al. (2004). These two estimates lead to a default value $I_{max} = 10$ for the ratio between the mass-specific maximum ingestion rate and the mass-specific metabolic rate. Gillooly et al. (2001) provide an estimate for the proportionality constant in the quarter-power scaling law of mortality rate equal to 0.001. We therefore assume that the ratio between background mortality rate and metabolic rate equals 0.1 for both juvenile and adult consumers, i.e. $\mu_j = \mu_a = 0.1$. The ratio between newborn and maturation size we estimated from data on egg and adult weight for a large number of marine copepod species presented by Huntley and Lopez (1992). These data show the ratio to range between 0.001 and 0.02 with a median value of 0.01. As default value we therefore adopt $z = 0.01$.

For assimilation efficiency we assume as default value $\sigma = 0.5$ on the basis of data provided by Peters (1983) and Yodzis and Innes (1992). Finally, we will investigate model dynamics while varying the value of q representing the ratio between juvenile and adult maximum ingestion rate. An estimate for this parameter can hardly be derived from experimental data as it is only a phenomenological representation of stage-specific differences in resource availability and resource use between juveniles and adults.

3. Results

3.1. Semi-chemostat resource dynamics

Fig. 1 illustrates the dynamics of both the size-structured model (11) and the stage-structured biomass model (24) with semi-chemostat resource dynamics when starting from the same initial conditions. Both models predict exactly the same dynamics for the resource density, which rapidly and smoothly approaches its equilibrium value. Predictions for the dynamics of juvenile and adult consumer biomass, however, differ between the two models. Most prominently, in the size-structured model juvenile and adult biomass follow damped oscillations and adult biomass initially decreases, whereas in the stage-structured model both juvenile and adult biomass smoothly approach the stable equilibrium with adult biomass increasing immediately from $t = 0$. The stage-structured model is derived from the size-structured one by relating the (equilibrium) maturation rate to the (equilibrium) juvenile density. Essentially, this relationship translates into the assumption that at any point in time the size-distribution of juvenile consumers equals the equilibrium size distribution that would result given the prevailing resource density and

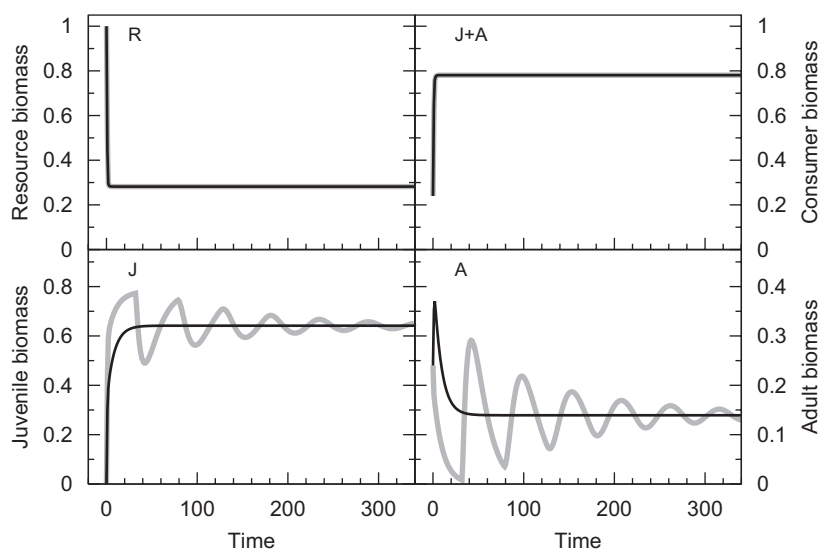


Fig. 1. Dynamics of resource (left, top panel), total (right, top panel), juvenile (left, bottom panel) and adult consumer biomass (right, bottom panel) as predicted by the size-structured model (11) (gray lines) and the stage-structured biomass model (24) (black lines) with semi-chemostat resource dynamics, starting from the same initial conditions: $R(0) = 1.0$, $C(0) = A(0) = 0.2$ and $c(0, s) = 0$. $q = 1.0$, all other parameters have default values.

consumer population birth rate. As a consequence, the birth of new consumers immediately translates into a simultaneous increase in maturation rate and is smeared out over time. In contrast, in the size-structured model individual birth events lead to distinct maturation events at a later point in time, which is determined by the time that the newborn consumers need to grow from the size at birth s_b to the maturation size s_m . This difference explains why the increase in juvenile biomass in the stage-structured model translates into an immediate increase in adult biomass due to maturation, whereas adult biomass in the size-structured model only increases after $t = 15$.

The transient dynamics shown in Fig. 1 ultimately lead to an equilibrium, which in both models is locally stable for the particular value of $q = 1$. In the size-structured model stable equilibria are only expected to occur when juvenile and adult consumers are roughly equivalent competitors, i.e. for values of q close to 1 (De Roos and Persson, 2003). Sustained population cycles are expected to arise when either juvenile or adult consumers have a distinct competitive advantage (q significantly smaller or larger than 1, respectively). Although the size-structured model differs in some aspects from the model studied by De Roos and Persson (2003) these predictions hold true as is shown in Fig. 2. This figure illustrates the long-term dynamics predicted by both models as a function of q by plotting equilibrium densities of resource, juvenile, adult and total consumer biomass in case the model equilibrium is stable and the maximum and minimum values of these biomass densities in case the long-term dynamics are oscillatory. For $q < 1$ there is a large range of parameters for which the size-structured model exhibits regular population cycles, in

which especially juvenile and adult consumer biomass exhibit large-amplitude oscillations. Oscillations in resource and total consumer biomass (Fig. 2, top panels) are smaller. These cycles are so-called single-generation cycles (Nisbet and Gurney, 1983), in which a single cohort of consumers dominates the population dynamics throughout its entire life and the cycle period is slightly larger than the juvenile delay between birth and maturation. Juvenile and adult consumers hence do not occur simultaneously in the population, but mostly alternate in time (De Roos and Persson, 2003). De Roos and Persson (2003) refer to these cycles as *juvenile-driven* cycles as they arise through a competitive dominance of juvenile consumers. Also for q significantly larger than 1 regular population cycles with a period slightly larger than the juvenile delay are observed in the size-structured model, but these are of much smaller amplitude. Again, the oscillations in juvenile and adult biomass are larger than the oscillations in total consumer biomass, as well as resource biomass, but the differences are minimal. Juvenile and adult consumers coexist continuously in the population, distinguishing these cycles from the single-generation cycles occurring for $q < 1$. De Roos and Persson (2003) provide a detailed analysis of the characteristics and mechanisms giving rise to both types of population cycles and we will hence not discuss them here any further.

The stage-structured model predicts the equilibrium to be stable throughout the entire range of q -values for which an internal equilibrium occurs (Fig. 2). Hence, it does not exhibit any of the oscillatory dynamics displayed by the size-structured model. The two models yield identical predictions for q between approximately 0.9 and 1.6 (see Fig. 2). Even though population cycles occur for both $q < 1$

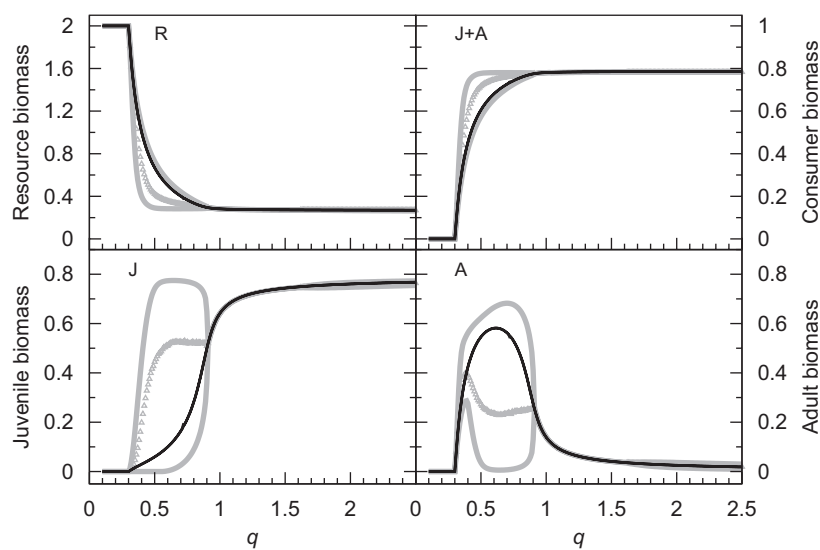


Fig. 2. Maximum and minimum (during one cycle) resource density (left, top panel), total (right, top panel), juvenile (left, bottom panel) and adult consumer biomass (right, bottom panel) as predicted by the size-structured model (11) (gray lines) and the stage-structured biomass model (24) (black lines) with semi-chemostat resource dynamics for different values of q . Gray triangles indicate the time-averaged biomass densities of resource, juvenile, adult and total consumers in the size-structured model in case of population oscillations. These results were obtained using long numerical simulations of model dynamics with regular, stepwise increases as well as decreases in q . $R_{max} = 2.0$, all other parameters have default values.

and $q > 1$, we argue that for $q > 1$ the differences between the stage-structured and size-structured model are in fact minor, because (1) average biomass densities of resource, juvenile, adult and total consumers measured over long time periods in the size-structured model are always approximately equal to the equilibrium values predicted by the stage-structured model and (2) both models predict juveniles and adults to coexist continuously in the population, even in case the size-structured model exhibits sustained oscillations. In contrast, for $q < 1$ the equilibrium densities of resource, juvenile, adult and total consumer biomass predicted by the stage-structured model are significantly different from the time-averaged values of these densities in the population cycles predicted by the size-structured model (Fig. 2), during which the stage-structured model moreover fails to capture the alternating occurrence of juveniles and adults in the population.

The stage-structured biomass model hence poorly approximates the predictions of the size-structured model in case the latter exhibits juvenile-driven, single-generation cycles. Otherwise, the predictions of both models are completely identical whenever they approach a stable equilibrium and similar when oscillations occur that are driven by competitive dominance of adult consumers ($q > 1$). We have found these conclusions to be largely independent of the values of R_{max} and δ that govern the semi-chemostat dynamics. Both parameters change the resource productivity, which equals δR_{max} , in the same way. Increases in these parameters translate into almost proportional increases in both juvenile and adult consumer biomass, but generally do not change model dynamics in a relative sense.

3.2. Logistic resource dynamics

Similar to the results obtained with semi-chemostat resource growth, dynamics with logistic resource growth predicted by the stage-structured biomass model for q close to or larger than 1 closely resemble the dynamics of the size-structured model. Fig. 3 illustrates the long-term dynamics predicted by both models for $q = 1$ by plotting the densities of resource, juvenile, adult and total consumer biomass as a function of the maximum resource density R_{max} . The figure shows the equilibrium biomass densities in case of a stable equilibrium and the observed maximum and minimum values of these biomass densities in case the long-term dynamics are fluctuating. For low values of R_{max} both models predict the equilibrium to be stable, while for larger values of R_{max} large-amplitude cycles occur. These cycles are equivalent to the predator–prey cycles that generally occur in models with logistic resource growth and a non-linear consumer functional response (so called “paradox-of-enrichment” cycles, Rosenzweig, 1971; or “prey-escape” cycles, De Roos et al., 1990). The Hopf bifurcation point separating the parameter ranges with stable equilibria and limit cycles, respectively, occurs in both models at the same parameter value. In addition, both models make identical predictions about most aspects of the population cycles, in particular the maximum and minimum values of resource and total consumer biomass as well as the period of the oscillations. The stage-structured biomass model predicts only a more adult-biased stage-distribution of the consumer population during the cycles: in the stage-structured model adult biomass is up to twice as high and juvenile biomass only 60% of the densities in the size-structured model.

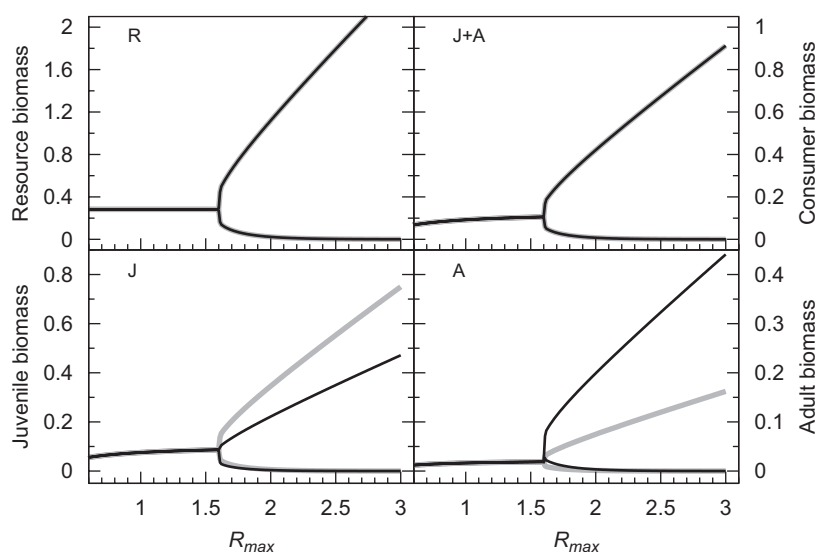


Fig. 3. Maximum and minimum resource density (left, top panel), total (right, top panel), juvenile (left, bottom panel) and adult consumer biomass (right, bottom panel) as predicted by the size-structured model (11) (gray lines) and the stage-structured biomass model (24) (black lines) with logistic resource dynamics for different values of R_{max} . These results were obtained using long numerical simulations of model dynamics with regular, stepwise increases as well as decreases in R_{max} . $q = 1.0$, all other parameters have default values.

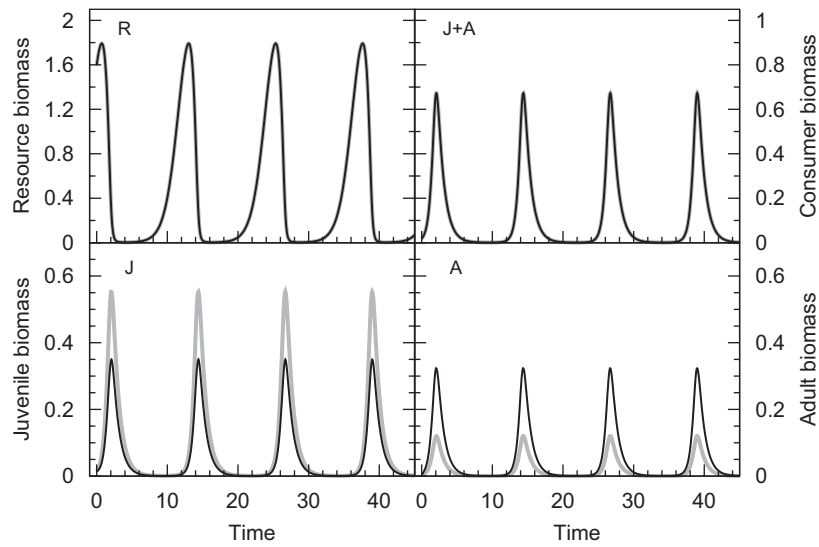


Fig. 4. Large-amplitude cycles as predicted by the size-structured model (11) (gray lines) and the stage-structured biomass model (24) (black lines) with logistic resource dynamics for $q = 1.0$ and $R_{max} = 2.5$, all other parameters having default values. Transient dynamics of resource (left, top panel), total (right, top panel), juvenile (left, bottom panel) and adult consumer biomass (right, bottom panel) has been discarded.

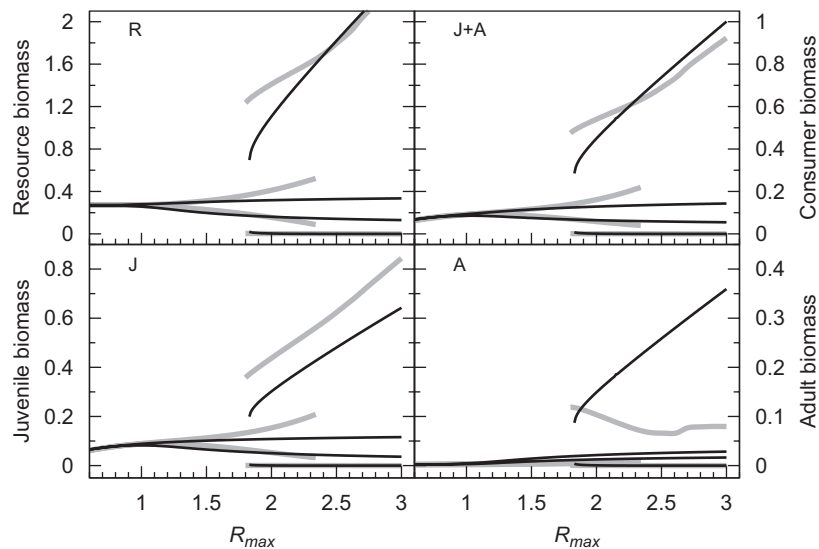


Fig. 5. As Fig. 3, but for $q = 2.0$.

Fig. 4 shows the large-amplitude cycles that occur for $q = 1.0$ and $R_{max} = 2.5$. The figure illustrates that both the size-structured and stage-structured model make identical predictions for the resource biomass density and the cycle period, as well as for total consumer biomass, while the stage-structured model predicts higher adult consumer biomass densities. The cycles are characterized by highly correlated, in-phase oscillations in both juvenile and adult biomass density. A rapid increase in resource density at the beginning of a cycle quickly leads to an increase in population birth rate. These newborn individuals rapidly mature (in 2–3 time units), which leads to the almost simultaneous increase in adult density. High population birth rates and rapid maturation will sustain as long as resource densities are high, while both reproduction and

maturation stop when resource densities decline to very low levels. Hence, whenever reproduction occurs, the newborn individuals will rapidly mature. As a consequence, population size-structure plays hardly any role in these cycles.

For $q = 2.0$ the stage-structured and size-structured model predict two types of regular population cycles (Fig. 5) to occur. Both models predict that for $R_{max} > 1.8$ the large-amplitude cycles occur that were also found for $q = 1.0$. With $q = 2.0$ the period of these cycles as observed in the stage-structured model is slightly larger than the cycle period in the size-structured model. Otherwise, the similarities and differences in predictions of both models regarding these cycles are like those discussed above for $q = 1.0$. Both models predict the occurrence of a second type of regular

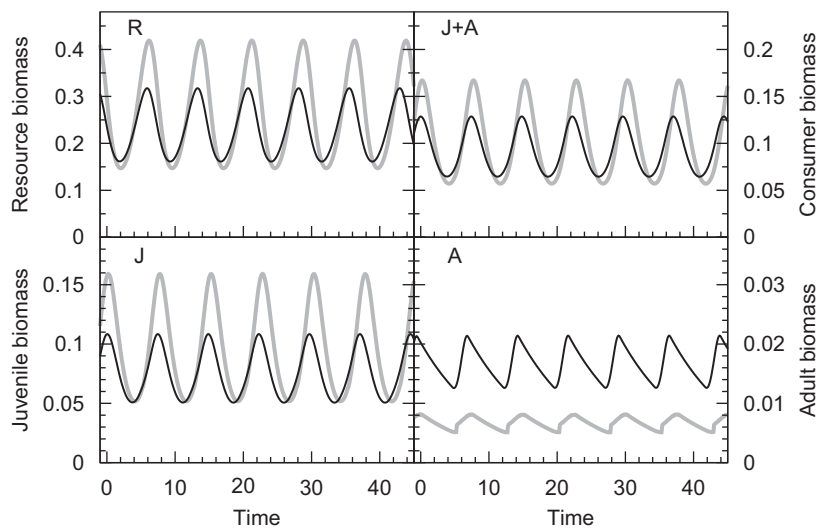


Fig. 6. Small-amplitude cycles as predicted by the size-structured model (11) (gray lines) and the stage-structured biomass model (24) (black lines) with logistic resource dynamics for $q = 2.0$ and $R_{max} = 2.0$, all other parameters having default values. Transient dynamics of resource (left, top panel), total (right, top panel), juvenile (left, bottom panel) and adult consumer biomass (right, bottom panel) has been discarded.

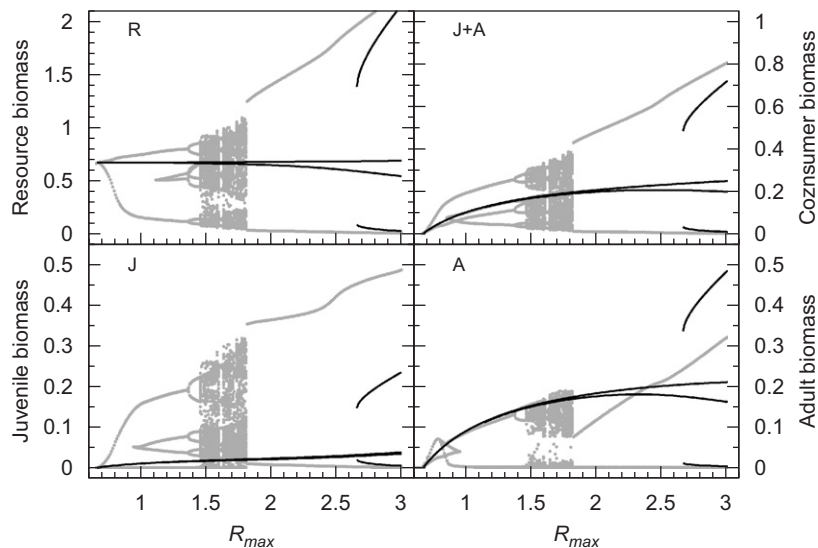


Fig. 7. As Fig. 3, but for $q = 0.5$. For $R_{max} < 1.8$ dynamics are irregular. Hence, multiple maximum and minimum densities of resource, total, juvenile and adult consumer biomass occur for the same parameter value. These are indicated with gray dots to distinguish these irregular dynamics from the regular population cycles occurring for $R_{max} > 1.8$.

population cycles with a much smaller amplitude for $R_{max} > 0.9$. The stage-structured model predicts these cycles to occur for all values of $R_{max} > 0.9$ with only a limited increase in cycle amplitude with increasing R_{max} . For low values of R_{max} both models make similar predictions about the amplitude of these cycles, but the size-structured model predicts it to increase at higher values of R_{max} and shows a loss of stability of these cycles for $R_{max} > 2.4$. In both models the two types of cycles hence occur as alternative attractors for intermediate values of R_{max} .

Fig. 6 shows that both models make comparable predictions about the period of the small-amplitude cycles. The cycle period is much shorter than the juvenile stage

duration (30–35 time units for the cycles shown in Fig. 6). The fluctuations in resource density cause both reproduction and juvenile growth to stop during phases of low resource densities, but juvenile growth is more affected because of the foraging superiority of adults ($q = 2.0$). All juveniles experience several bouts of retarded growth during their development, as the juvenile stage duration is considerably longer than the cycle period. Juvenile and adult consumers are present during all phases of the population cycle and oscillate roughly in phase. The stage-structured model again predicts a more adult-biased population composition, like for the large-amplitude cycles.

Dynamics of the stage-structured model for $q = 0.5$ are qualitatively similar to its dynamics with $q = 2.0$ (Fig. 7): at larger values of R_{max} the population exhibits either a small- or a large-amplitude cycle with the same characteristics as discussed above for $q = 2.0$. For our default parameter values the small-amplitude cycles occur for $R_{max} > 1.2$, while the large-amplitude cycles occur as an alternative attractor for $R_{max} > 2.6$. In the size-structured model large-amplitude cycles also occur when $q = 0.5$ for values of $R_{max} > 1.8$ (Fig. 7), but small-amplitude cycles do not. For $R_{max} > 1.8$ the size-structured model thus exhibits only one of the types of dynamics that are found in the stage-structured model. Similarities and differences between predictions of both models regarding the large-amplitude cycles are like discussed above for larger values of q .

For $R_{max} < 1.8$ the size-structured model exhibits dynamics related to the single-generation oscillations found with semi-chemostat resource growth for $q < 1$ (De Roos and Persson, 2003).

Fig. 8 illustrates these dynamics for $q = 0.5$ and $R_{max} = 1.2$. Notice that the stage-structured model predicts equilibrium dynamics for these parameter values, which has been omitted from the figure for clarity. In contrast to all other types of population cycles described above, in which juvenile and adult biomass exhibited highly correlated, in-phase oscillations, the population cycles shown in Fig. 8 are characterized by an alternation in time of juvenile and adult consumers. The period of the cycles (roughly 15 time units in Fig. 8) is slightly larger than the juvenile stage duration (roughly 12 time units). Resource densities are once during an entire population cycle and then for short periods only sufficiently high for reproduction to occur (at $t = 12, 27$ and 42 in Fig. 8; note the adult

starvation threshold). The newborn cohort of individuals dominates the population dynamics throughout its lifetime and gives rise to the next dominant cohort. The increase in juvenile biomass following a reproduction pulse induces a rapid decline in resource biomass leading to starvation mortality among adults. Juvenile biomass shows a bimodal dynamics during the cycle. In the first half of the cycle juvenile biomass decreases due to background and starvation mortality, whereas growth in body size of juveniles leads to an increase in their total biomass shortly before they mature. After maturation, the adults at first experience still some starvation mortality, until resource densities have recovered sufficiently to give rise to the next generation cycle.

Resource, juvenile and adult consumer biomass densities may hence exhibit more than a single (local) maximum during a population cycle, as a consequence of the interplay between food-dependent reproduction, mortality and growth in body size. With increasing R_{max} the cycles become more and more irregular due to the interplay between the oscillatory propensity embodied in the logistic resource growth and the single-generation characteristic of the consumer dynamics. For R_{max} between 1.45 and 1.8 dynamics of the size-structured model are so irregular that they appear chaotic. Nonetheless, the single-generation characteristic of the population cycles is preserved with an alternation in time of juveniles and adult consumers (results not shown). In contrast, the stage-structured model does not exhibit any irregular dynamics, presumably because it misses the mechanism for single-generation dynamics in the consumer population. For $q = 0.5$ and low values of R_{max} the size-structured and stage-structured model therefore differ in their predictions, mainly due to the single-generation type cycles that do occur for $q < 1$ in the size-structured, but not in the stage-structured model with its distributed time delay between the birth and maturation of an individual organism.

4. Discussion

We derived the stage-structured biomass model from a size-structured population model, which is individual based and accounts for a continuous size distribution of consumers. The derivation ensures that every equilibrium we find in the stage-structured model has an identical counterpart in the full size-structured model. Most importantly, however, the derivation from a size-structured population model implies that the stage-structured biomass model consistently translates assumptions about consumption, growth and bioenergetics of individual consumers into a resource-dependent, population-level maturation rate, rather than the more intuitive approach of assuming an ad-hoc, phenomenological dependence of maturation on resource density. We therefore argue that under equilibrium conditions the stage-structured biomass model is rigorously individual based. We have shown that the size-structured and stage-structured model even make

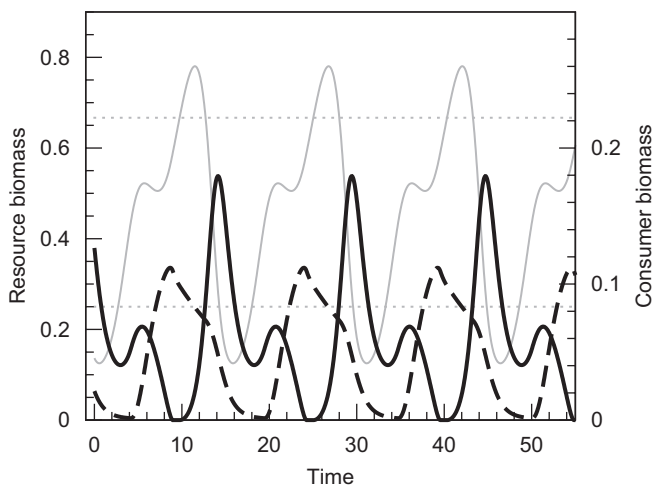


Fig. 8. Size-structured model dynamics, showing resource (gray lines), juvenile (black, solid lines) and adult (black, dashed lines) consumer biomass, with logistic resource dynamics for $q = 0.5$ and $R_{max} = 1.2$, all other parameters having default values. Transient dynamics has been discarded. Horizontal, dotted lines indicate the resource levels at which juvenile (lower line) and adult (upper line) net biomass production equals 0 (see the conditions in Eqs. (3) and (4)). For lower resource densities starvation mortality occurs.

similar predictions under non-equilibrium conditions, as long as q is close to or larger than 1. As the main difference between the models, the stage-structured model fails to capture the single-generation cycles predicted by the size-structured model when juvenile consumers are competitively superior to adults.

To allow simplification of the size-structured population model into a stage-structured biomass model in terms of two ODEs, we followed Yodzis and Innes (1992) in their assumption that within species consumer ingestion and maintenance are proportional to consumer body size (Yodzis and Innes, 1992, p. 1154) (Note that this assumption is distinct from but easily confused with their assumption that among different species the mass-specific rates of ingestion and maintenance scale with a power -0.25 of the species body mass, Yodzis and Innes, 1992, p. 1155–1156). For both ingestion and maintenance rate intraspecific size-scaling exponents different from 1 have been reported (Peters, 1983; Brown et al., 2004). Yodzis and Innes (1992) argue that this discrepancy will not lead to greatly different values for the ingestion and maintenance rate of the population as a whole, given that the intraspecific size-scaling exponents tend to have values around 0.75. These authors hence consider the assumption that ingestion and maintenance scale proportional to body size justifiable on the grounds that it leads to a tractable, parameter-sparse model. In the context of the stage-structured biomass model the consequences of the assumption are not immediately clear. The model results suggest that dynamics are to a considerable extent shaped by the competitive balance between juvenile and adult consumers (see also De Roos and Persson, 2003). A size-scaling exponent smaller than unity for ingestion rate would imply that juveniles are more competitive than adults while gathering food. This would make the type of dynamics reported for $q < 1$ more likely to occur. In contrast, a smaller-than-unity, size-scaling exponent for maintenance requirements would give adult consumers an energetic advantage over juveniles, making the types of dynamics as reported for $q > 1$ more likely to occur. The net effect of different size-scaling exponents for ingestion and maintenance will therefore be hard to predict in general and will depend on the detailed values of both exponents.

We derived the stage-structured model because of the need for an archetypal, population dynamic model that consistently accounts for food- and size-dependent growth in body size, in addition to the two life history processes, i.e. reproduction and mortality, that are normally incorporated in Lotka–Volterra type population models. In contrast to PSPM that account for an entire population size distribution, the model is simple enough to be used in multi-species community models, in which individual body size plays an important role. The stage-structured model can in addition be used to assess the generality of conclusions derived from PSPMs. Because of their complexity, it has been questioned whether individual-based and physiologically structured population models can lead

to broad conclusions, applying to a variety of systems, or yield system-specific insights only (Bolker et al., 2003). Murdoch and Nisbet (1996; see also Murdoch et al., 1992) have proposed that the generality of individual-based models can be assessed by investigating a chain of related models of increasing simplicity that nonetheless embody the mechanisms, which are considered relevant for the population dynamics observed. In this spirit the stage-structured model can be used to assess the robustness and generality of the claim that many of the community effects observed in size-structured community models are induced by food-dependent individual growth in body size (De Roos and Persson, 2005a). Similar to Murdoch and Nisbet (1996), De Roos and Persson (2005b) also advocate a hierarchical approach to individual-based model analysis, but stressed in addition the importance of an individual-level basis for both model development and simplification. The stage-structured biomass model also fits in with the latter perspective, as it is formally derived from and hence based on a strictly individual-based model accounting for an entire population size distribution.

We formulated the stage-structured model while only distinguishing between juvenile and adult consumers. The model is, however, readily extended to account for more consumer stages, both juvenile and adult. Consider a situation in which a total of $N + 1$ stages is distinguished, which are indexed by $i = 0, \dots, N$, and let the biomass in these stages be represented by C_i . The dynamics of the entire consumer population is then described by:

$$\frac{dC_0}{dt} = \sum_{i=1}^N (1 - \kappa_i) v_i^+(R) C_i + v_0(R) C_0 - \gamma_0(v_0^+(R)) C_0 - \mu_0 C_0 \quad (25a)$$

$$\frac{dC_i}{dt} = \gamma_{i-1}(\kappa_{i-1} v_{i-1}^+(R)) C_{i-1} + v_i(R) C_i - (1 - \kappa_i) v_i^+(R) C_i - \gamma_i(\kappa_i v_i^+(R)) C_i - \mu_i C_i \quad \text{for } i = 1, \dots, N. \quad (25b)$$

In these equations the parameters κ_i represent the fraction of biomass production that the individuals in a particular stage invest in somatic growth, while the remainder is invested into reproduction. Their weight-specific somatic growth and reproduction rates hence equal $\kappa_i v_i(R)$ and $(1 - \kappa_i) v_i(R)$, respectively. For mathematical reasons it has to be assumed that the smallest juveniles do not reproduce ($\kappa_0 = 1$), while the largest adults do not grow ($\kappa_N = 0$). For the youngest juvenile stage recruitment of biomass to the stage is through reproduction, which is described by the summation term in the right-hand side of equation (25a). Otherwise the equations describing the dynamics of the various stages are similar. The terms $-(1 - \kappa_i) v_i^+(R) C_i$ only take effect under starvation conditions and ensure mass balance under these conditions. Analogous to Eq. (19) the maturation functions are defined as

$$\gamma_i v = \frac{v - \mu_i}{1 - z_i^{1 - \mu_i/v}} \quad (26)$$

In which the parameter z_i represents the ratio of the initial and final mass in stage i . Like the two-stage model that we analyzed, this multi-stage extension predicts the same equilibria as a size-structured model in terms of partial differential equations (Metz and Diekmann, 1986; De Roos, 1997), in which individuals in the different stages experience different mortality rates μ_i and/or have different biomass production rates $v_i(R)$ through differences in their intake rate or in their resource base.

Iwasa et al. (1987, 1989) pioneered the simplification of ecosystem models with large numbers of state variables into aggregated models of lower dimension phrased in terms of a smaller set of composite state variables. This simplification can either be exact, in which case the dynamics of the composite state variables is identical in both the original, high-dimensional model and its aggregated analogue. Iwasa et al. (1987) refer to this procedure as “perfect aggregation”. Alternatively, the aggregation of the original ecosystem model may be approximate, in which case the difference in dynamics of the composite state variables as described by both models is in one way or the other minimized. Aggregation has been applied to models of varying complexity, ranging from food chain models of moderate dimension (Kooi et al., 1998, 2002) to detailed models of an entire ecosystem (Raïck et al., 2006). For spatially structured population dynamic models a number of aggregation approaches have been developed in recent years (see Dieckmann et al., 2002, for an overview). The necessary conditions that allow perfect aggregation of PSPM were derived by Metz and Diekmann (1991), while Arino et al. (2000) and Bravo de la Parra et al. (2000) provide examples of approximate aggregation of age-structured population models. One approach to carry out approximate model aggregation exploits differences in time or spatial scale of various sub-processes for model simplification (Auger and Poggiale, 1998; Auger et al., 2000; Auger and Lett, 2003). Processes taking place on a fast time scale are then assumed to have reached equilibrium when considering dynamics of processes at the slower time scale. Our simplification of a size-structured model into a stage-structured analogue is based on such a distinction of time scales. Essentially, we assume that dynamics of the size distribution within the juvenile stage are taking place on a fast time scale compared to the demographic processes of reproduction, maturation and mortality. Hence, we assume that on the population dynamic time scale the juvenile size-distribution is continuously in the equilibrium state that corresponds to the current population birth rate and resource density.

The assumption clearly breaks down in case of the single-generation cycles, which occur in the size-structured model for $q < 1$ and during which the population consists of a cohort of individuals of approximately the same age and size. In the size-structured model this entire cohort of individuals will mature at roughly the same time. In contrast, in the stage-structured model the assumption of a persistent equilibrium size-distribution within the juvenile

stage implies that maturation of these individuals is distributed over time, hence occurs continuously with some individuals maturing immediately after they are born. This explains the deviations we find between the size-structured and stage-structured model for $q < 1$. The juvenile period can also be modeled with multiple juvenile stages using the model extension presented in Eq. (25). Increasing the number of juvenile stages will progressively reduce the possibility that individuals mature shortly after they are born and will hence lead to a better approximation of the discreteness of the maturation process in the size-structured model. Indeed, the same stage-structured model as derived in this paper, but with two instead of a single juvenile stage predicts the occurrence of cycles for some q -values smaller than 1 and semi-chemostat resource dynamics (results not shown). The cycles found are, however, characterized by a small amplitude and continuous coexistence of juveniles and adults in the population. The representation of the juvenile period as two stages hence leads to predictions that are qualitatively more similar to the predictions of the size-structured model, but a good approximation of the discreteness of maturation during the single-generation cycles requires a larger number of juvenile stages. These results also make clear that synchronized maturation of consumers that are born at the same time promotes the occurrence of population oscillations in size-structured consumer–resource systems, which arise because of size-dependent competition among cohorts (De Roos and Persson, 2003). Any increase in variability in the timing of maturation among consumers that are born at the same time will decrease this propensity.

Even though body size has been recognized to play an important role in ecological communities (Woodward et al., 2005) current community models only take it into account to a limited extent. The cascade model (Cohen et al., 1990) is based on Lotka–Volterra type interactions between species and ignores body size of species. The niche model (Williams and Martinez, 2000) has been combined with population dynamic equations based on the bio-energetic approach developed by Yodzis and Innes (1992), but the food web is constructed by ordering species on the basis of their niche value, which is not related to body size (Williams and Martinez, 2004; Brose et al., 2005). As a consequence, in this model changes in body size are synonymous to changes in the interaction strength between species. As of yet, Loeuille and Loreau (2005) present the only community model that is consistently based on body size considerations. In this model the body size of a particular species determines on which other species it can forage, with which species it competes through interference competition as well as its loss rate through maintenance and mortality. The model is, however, an unstructured model and ignores within-species size variation. The stage-structured community model we derived provides a useful approach to investigate the influence of within-species size variation on community dynamics. In particular, it can be used to address the question whether food-dependent

growth and size-specific predation promote the occurrence of multiple community equilibria under the same conditions as well as the diversity of ecological communities, as recently hypothesized by De Roos and Persson (2005a).

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