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Alternative stable states in a stage-structured consumer–resource biomass model with niche shift and seasonal reproduction

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ABSTRACT

We formulate and analyze a stage-structured consumer–resource biomass model, in which consumers reproduce in a pulsed event at the beginning of a growing season and furthermore go through a niche shift during their life history. We show that the resulting semi-discrete model can exhibit two stable states that can be characterized as a development-controlled state and a reproduction-controlled state. Varying resource availabilities and varying the extent of the niche shift determines whether juveniles or adults are more limited by their resource(s) and can lead to switches between the alternative stable states. Furthermore, we quantify the persistence of the consumer population and the occurrence of the two alternative stable states as a function of resource availabilities and extent of the niche shift. All the results show that irrespective of the type of reproduction of the consumers (continuous or seasonal), the stage-structured model will exhibit alternative stable states as long as development of the juvenile stage and reproduction of the adult stage are both resource-dependent.

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1. Introduction

In general, population growth is not only determined by mortality and the reproduction by adults but also by the development and maturation of juveniles. Nonetheless, in classical Lotka–Volterra type consumer–resource models only reproduction is accounted for and assumed to be resource-dependent. Resource availability also affects the growth of juveniles and determines whether and when juveniles mature. When juveniles experience a high resource availability relative to adults, they will mature fast and the juvenile stage duration will be short. Consequently, adult density will be high and reproduction will be limited by the more restricted availability of adult resource. A population that is regulated mainly by limited reproduction has been referred to as governed by “reproduction control” (De Roos and Persson, 2013). On the other hand, when juvenile resource availability is low compared to adult resource availability juveniles will grow slowly, the juvenile stage lasts for a long time and many juveniles die before maturation. As a consequence, few juveniles mature to the adult stage. Such a population state is referred to as governed by “development control” (De Roos and Persson, 2013). These two cases would lead to either a bottleneck in the juvenile or in the adult stage with direct consequences for the growth of the consumer population as a whole.

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Unlike the development and maturation of juveniles, which is generally a continuous process, the reproduction by adults can be either continuous or discrete (Bronson, 2009). Many animal species in particular in temperate regions are characterized by “seasonal reproduction” and produce offspring only within a limited time period of the year, while their foraging on resources and their decline in abundance through mortality continues throughout the year. To model population dynamics that result from both continuous and discrete processes, we can use semi-discrete modeling (Maillet and Lemesle, 2009), which combines continuous dynamics for most of the time with sharp changes at some pre-defined time instants. Pachepsky et al. (2008) analyzed a consumer–resource model with seasonal reproduction and showed that this resulted not only in the consumer–resource cycles that also occur in continuous models, but also in overcompensation cycles induced by the seasonal reproduction. Zhou et al. (2013) compared several models of predator–prey interactions and suggested that the use of semi-discrete modeling would give us a better insight into the link between theoretical results and empirical data.

Growth in body size makes individuals change during their life history in more aspects than just their size. Individuals may, for example, occupy different ecological niches, live in different habitats and forage on different resources with little or no resource overlap during different stages of their life history (De Roos and Persson, 2013). These shifts in resource use during life history are referred to as ontogenetic niche shifts. Forseth et al. (1994), for example, showed that in different age-groups of Arctic charr the

individuals feed to a different extent on zooplankton and zoobenthos. Rudolf and Lafferty (2011) suggested that in the large majority of species individuals change their diets during development with little resource overlap even in non-metamorphosing species. Furthermore, these authors argued that niche shifts may have considerable consequences for biodiversity loss, because they introduce an essential dependence of consumer species on multiple resources. Schreiber and Rudolf (2008) showed that in a consumer–resource model a niche shift between the juvenile and adult stage results in the occurrence of two stable equilibria under the same conditions of resource productivities. These alternative stable states (ASS) differ from each other in the process that limits population growth most; either the development of juveniles is limited or adult reproduction is suppressed. Guill (2009) and De Roos and Persson (2013) have observed the same bistability between an equilibrium governed by development control and another governed by reproduction control in slightly different types of consumer–resource models, suggesting that this bistability induced by ontogenetic niche shift is a generic phenomenon in consumer–resource systems.

These consumer–resource models, however, all assume that reproduction occurs continuously in time, in contrast to the seasonal reproduction that characterizes many species. Since a pulse of offspring production represents a major perturbation to the consumer–resource interaction, the question arises whether the bistability observed in continuous-time models will also occur in the presence of seasonal reproduction and whether different equilibrium states occur that are governed by the same controlling mechanisms as in continuous models. Previous studies of size-structured population models that model reproduction as a seasonally pulsed event in the year (e.g. Persson et al., 1998; Claessen et al., 2000; Van De Wolfshaar et al., 2008 and Van Leeuwen et al., 2014) invariably show that pulsed reproduction leads to stage-driven, so-called single-cohort cycles, in which the population dynamics is dominated by a single cohort throughout its life, outcompeting and driving to extinction all differently sized individuals. Bistability has up to now never been shown to occur in these models. These models assume, however, that all individuals born in the same year mature at exactly the same age and hence do not diverge in their development. This contrast with experimental evidence (Huss et al., 2008) that considerable divergence in body size arises among individuals of the same year class. In this paper, we therefore formulate a simple model that represents reproduction as a pulsed event, but allows individuals of the same year class to mature at different times, and investigate the robustness of the occurrence of ASS as a result of ontogenetic niche shift by analyzing the dynamics of a stage-structured biomass model with pulsed reproduction of consumers. As our main result we show that alternative stable states also occur over a substantial range of resource availabilities, as in the case with continuous reproduction, and for different degrees of niche overlap between juvenile and adult consumers.

2. Model formulation

We base our model formulation on the stage-structured consumer–resource biomass model formulated by De Roos et al. (2008) as a simplification of a fully size-structured model, in which consumers forage on a shared resource following a Holling type II functional response. De Roos et al. (2008) studied how resource availability affects model dynamics and showed that the stage-structured biomass model is an exact approximation of the fully size-structured model under equilibrium conditions. The non-equilibrium dynamics of the stage-structured and size-structured model are not identical, but closely resemble each other. Guill (2009) used a variant of the consumer–resource model formulated

by De Roos et al. (2008), in which he assumed consumers forage following linear functional responses and replaced the explicit dependence on resource availability by a within-stage, direct density dependence of consumers, to study the occurrence of alternative stable states when juveniles and adults feed on separate resources. Our stage-structured consumer–resource biomass model follows these two earlier models, but explicitly accounts for separate juvenile and adult resources, on which consumers feed following linear functional responses. As the major difference, however, we reformulate the model to account for seasonal reproduction. Following Persson et al. (1998), the year is divided into two parts: a growing season and a non-growing season. The growing season corresponds to the summer in the temperate region while the non-growing season corresponds to the winter. In the present paper, we only model the dynamics during the growing season, assuming the non-growing season adds nothing but only a scaling down of all rates.

In the model formulated by De Roos et al. (2008) consumer individuals are distinguished from each other by their body size, denoted by s . All consumer individuals are born with the same size s_b and mature when they reach the size s_m . Following maturation consumers are assumed not to grow any more but to invest their entire net-biomass production into reproduction. The consumer population can thus be divided into two stages: juveniles with body size $s_b \leq s < s_m$ and adults with body size s_m and only adults can reproduce. The total biomass of juveniles and adults are denoted with J and A , respectively. In contrast to the model of De Roos et al. (2008) we account for a single consumer population that feeds on two resources R_1 and R_2 .

Both resources follow semi-chemostat growth in the absence of consumers with turn-over rates ρ_i and maximum densities $R_{\max,i}$:

$$G_i(R_i) = \rho_i (R_{\max,i} - R_i), \quad i = 1, 2. \quad (1)$$

We analyze the influence of the type of resource growth in Section 5, in which both resources are assumed to follow more familiar logistic growth.

The resource densities decrease through foraging by consumers. Resource 1 is shared by juveniles and adults while resource 2 is only foraged on by adults. Individuals hence exhibit an “ontogenetic niche shift”, a change in ecological niche during their life history (De Roos and Persson, 2013). The extent of the niche shift is modeled with the parameter η , such that the foraging preference of adults for resource 1 and 2 equals η and $1 - \eta$, respectively. The resources are consumed by juveniles and adults following a linear functional response (the form of the functional response does not affect the results qualitatively, we also studied the case for a Holling type II functional response, see Appendix A for details). The attack rate per unit body mass for both juveniles and adults are denoted by $I_{\max}$.

Ingested resources are converted to consumer biomass with an efficiency σ and the maintenance requirements per unit biomass of juveniles and adults are the same, denoted by Q . The net biomass productivity per unit biomass for juveniles and adults, denoted as $v_j(R_1)$ and $v_a(R_1, R_2)$, then equals the balance between ingestion and maintenance requirement:

$$v_j(R_1) = \sigma I_{\max} R_1 - Q, \quad (2)$$

$$v_a(R_1, R_2) = \sigma I_{\max} (\eta R_1 + (1 - \eta) R_2) - Q. \quad (3)$$

At low densities of resources the ingestion may not cover the maintenance requirements of consumer individuals, in which case it is assumed that individuals experience starvation mortality. Following De Roos et al. (2008) we assume that development and maturation of juveniles as well as reproduction by adults halt when ingestion is not sufficient to cover the maintenance. We therefore

Table 1

Within-season dynamics of the model. Turn-over and consumption of resources, maturation of juveniles, allocation to energy storage for reproduction and mortality of consumer individuals are assumed to be continuous-time processes. Mortality includes both background and starvation mortality, which occurs when the ingestion is not sufficient to cover the maintenance (when $v_j(R_{1,n}) < 0$ or $v_a(R_{1,n}, R_{2,n}) < 0$). Maturation and allocation to energy storage for reproduction cease when starvation of juvenile or adult consumers, respectively, occurs.

Variable	Description	Dynamical equation
$R_{1,n}$	Density of resource 1	$\frac{dR_{1,n}}{dt} = G_1(R_{1,n}) - I_{\max} R_{1,n} (J_n + \eta A_n)$
$R_{2,n}$	Density of resource 2	$\frac{dR_{2,n}}{dt} = G_2(R_{2,n}) - I_{\max} (1 - \eta) R_{2,n} A_n$
J_n	Juvenile biomass	$\frac{dJ_n}{dt} = v_j^+(R_{1,n}) J_n - \gamma(v_j^+(R_{1,n}), \mu) J_n - d_j(R_{1,n}) J_n$
A_n	Adult biomass	$\frac{dA_n}{dt} = \gamma(v_j^+(R_{1,n}), \mu) J_n - d_a(R_{1,n}, R_{2,n}) A_n$
B_n	Energy storage	$\frac{dB_n}{dt} = v_a^+(R_{1,n}, R_{2,n}) A_n - d_a(R_{1,n}, R_{2,n}) B_n$

introduce the notations $v_j^+(R_1)$ and $v_a^+(R_1, R_2)$ to restrict the net-biomass production per unit body mass of juveniles and adults to non-negative values:

$$v_j^+(R_1) = \max\{v_j(R_1), 0\}, \quad (4)$$

$$v_a^+(R_1, R_2) = \max\{v_a(R_1, R_2), 0\}. \quad (5)$$

Background mortality, indicated by μ , we assume to be equal for both juveniles and adults. The sum of background and starvation mortality for juveniles and adults is given by:

$$d_j(R_1) = \mu + (v_j^+(R_1) - v_j(R_1)) \quad (6)$$

$$d_a(R_1, R_2) = \mu + (v_a^+(R_1, R_2) - v_a(R_1, R_2)). \quad (7)$$

Notice that the last terms within parentheses in these expressions equal 0 when $v_j(R_1)$ and $v_a(R_1, R_2)$ are positive, respectively. Furthermore, as shown in De Roos et al. (2008) these expressions for mortality of juvenile and adult consumers ensure mass conservation in the stage-structured biomass model.

Throughout the growing season juvenile biomass increases through somatic growth in body size of juveniles, given by $v_j^+(R_1)J$, and decreases through mortality, $d_j(R_1)J$, and maturation. The maturation of juveniles is modeled using the expression for mass-specific maturation rate derived in De Roos et al. (2008):

$$\gamma(v_j^+(R_1), \mu) = \frac{v_j^+(R_1) - \mu}{1 - z^{1 - \mu/v_j^+(R_1)}}. \quad (8)$$

Here μ is the background mortality rate of the consumer and $z = s_b/s_m$ is the ratio of consumer body size at birth to that at maturation. The maturation rate ensures that juveniles can only grow in body size when they have positive net biomass productivity, that is $v_j(R_1) > 0$, and also takes into account that high mortality decreases the likelihood that juveniles survive until their body size reaches the maturation threshold. As shown by De Roos et al. (2008) the functional form of the maturation rate is a crucial element for the stage-structured biomass model to be an approximation to its fully size-structured analogue, as it consistently translates the assumptions on individual life history to the population level. The maturation rate of juvenile to adult biomass, given by $\gamma(v_j^+(R_1), \mu)J$, increases adult biomass, which decreases throughout the growing season due to mortality, $d_a(R_1, R_2)A$.

Unlike the continuous-time consumer–resource biomass models, we consider reproduction to be a discrete event. We assume that adults consume resources, die of background and possibly starvation mortality and store energy for reproduction in their bodies continuously throughout the growing season and only reproduce by releasing a pulse of offspring in a very short time period at the beginning of each growing season. We use a constant T to indicate the duration of one growing season, which is also the interval between two reproduction events. We assume that the

investments in reproduction that in the continuous-time model of De Roos et al. (2008) are immediately released as offspring are accumulated as reproductive energy storage by adults in their body. These investments equal $v_a^+(R_1, R_2)$ per unit adult body mass, which translates into an allocation to reproductive storage by all adults equal to $v_a^+(R_1, R_2)A$. As discussed before, adults only store energy for reproduction when their ingestion is sufficient to cover the maintenance, that is when $v_a(R_1, R_2)$ is positive. We will denote the amount of mass or energy stored by all adults during the season between one reproduction and the next with the variable B . Because the energy storage of an adult perishes when the individual dies, the energy storage B experiences the same mortality rate as adults. Assuming $t \in (0, T)$ is the time within a growing season, we define $R_{1,n}(t)$ and $R_{2,n}(t)$ to be the densities of two resources and $J_n(t)$ and $A_n(t)$ to be the biomass of juveniles and adults at time t within the n th season. The dynamics during the n th growing season are described by a system of ordinary differential equations (ODEs), shown in Table 1.

At the beginning of the next growing season a discrete change occurs in the consumer, but not the resource biomass, as adults are assumed to release all the energy stored for reproduction as new juvenile biomass. The discrete changes in biomass at the beginning of the $(n + 1)$ th growing season are hence described by:

$$R_{i,n+1}(0) = R_{i,n}(T), \quad i = 1, 2, \quad (9)$$

$$J_{n+1}(0) = J_n(T) + B_n(T), \quad (10)$$

$$A_{n+1}(0) = A_n(T), \quad B_{n+1}(0) = 0. \quad (11)$$

Here $R_{i,n}(T)$, $J_n(T)$, $A_n(T)$ and $B_n(T)$ represent the resource densities, juvenile biomass, adult biomass and energy storage, respectively, at the end of the n th season just before the pulse of reproduction occurs. The full model dynamics, including both the within-season dynamics and the discrete mapping describing the pulses of reproduction, are described by the ODEs presented in Table 1 in combination with the recurrence relations (9)–(11).

3. Model scaling

To simplify our discussion we can set the period parameter T equal to 1, without loss of generality. The five parameters in the model that represent rates and hence have a dimension per unit time, ρ_i , $I_{\max}$, Q and μ , are consequently scaled by the reproduction period T to $\rho_i T$, $I_{\max} T$, QT and μT . The other parameters, z , σ , η and $R_{\max,i}$, which are not dependent on time, are unaffected by this scaling. In this paper we will mainly discuss how the parameters $R_{\max,i}$ and η affect model dynamics, while the other parameters are set to default values that are inferred from De Roos and Persson (2013), see Table 2.

Table 2
The parameters and their default values.

Parameter	Default value	Definition
$\rho_1 T$	10.0	Turn-over rate of resource 1
$\rho_2 T$	10.0	Turn-over rate of resource 2
$R_{\max,1}$	Varying	Maximum density of resource 1
$R_{\max,2}$	Varying	Maximum density of resource 2
$I_{\max} T$	100.0	Attack rate of consumer per unit body mass
QT	10.0	Maintenance cost of consumer per unit body mass
σ	0.5	Conversion efficiency of consumer
η	Varying	Adult preference on resource 1
μT	1.0	Stage-independent background mortality rate of consumer
z	0.1	Ratio of consumer body size at birth to that at maturation

4. Semi-chemostat resource dynamics

We calculated stable and unstable fixed points of the model using standard root-finding procedures implemented in C to locate the equilibria of the equations: $R_{1,n+1}(0) = R_{1,n}(T) = R_{1,n}(0)$, $R_{2,n+1}(0) = R_{2,n}(T) = R_{2,n}(0)$, $J_{n+1}(0) = J_n(T) + B_n(T) = J_n(0)$ and $A_{n+1}(0) = A_n(T) = A_n(0)$, where $R_{1,n}(T)$, $R_{2,n}(T)$, $J_n(T)$, $A_n(T)$ and $B_n(T)$ are calculated from $R_{1,n}(0)$, $R_{2,n}(0)$, $J_n(0)$, $A_n(0)$ and $B_n(0) = 0$ by numerical integration of the within-season dynamics. Programs used for the analysis are available from the authors on request. We will study how the parameters $R_{\max,i}$ and η affect equilibrium consumer biomass. As a key feature of our model, however, it should be noted that due to the pulsed reproduction resources densities, juvenile and adult biomass are always varying during a growing season as opposed to the constant equilibrium densities in continuous models. Because of this, we focus on the average biomass of juvenile and adult consumers. These average densities were calculated by numerical integration of the ODEs $d\bar{J}/dt = \bar{J}(t)$ and $d\bar{A}/dt = \bar{A}(t)$ within each growing season with initial states $\bar{J} = \bar{A} = 0$. As discussed in the introduction, the model can potentially exhibit two different types of equilibria, either an equilibrium regulated by development control or an equilibrium regulated by reproduction control. We study the occurrence of these two potential states as a function of one and two parameters.

4.1. Varying resource productivities

In this subsection we assume that resource 1 is only consumed by juveniles, while adults only consume resource 2, i.e. η is set equal to 0. Consumers hence exhibit a complete niche shift at the moment they mature, which is the same scenario as analyzed by Guill (2009), but now with the explicit resource dependence instead of direct density dependence. A partial niche shifts (i.e. $\eta \neq 0$), which would lead to competition between juvenile and adult consumers, will be discussed in Section 4.2.

Fig. 1 presents a bifurcation diagram, showing the average juvenile and adult consumer biomass at equilibrium as a function of the maximum density of resource 1, $R_{\max,1}$, when the maximum density of resource 2 is fixed at $R_{\max,2} = 0.4$. At low values of $R_{\max,1}$ ($R_{\max,1} \lesssim 0.21$) consumers cannot persist, as resource densities are too low for juveniles to cover their maintenance costs and grow in body size and they will hence die of starvation. At values of $R_{\max,1}$ slightly larger than the persistence threshold at $R_{\max,1} \approx 0.21$ a single equilibrium occurs, in which juvenile biomass makes up the largest part of the population. At this equilibrium juveniles do not have sufficient resource, leading to severe competition among juvenile individuals and very slow maturation. Meanwhile, adults have ample resource and hence a high net-biomass production. They store substantial energy for reproduction and thus produce many offspring at each reproduction event, which intensifies the competition among juveniles. As a consequence, in this equilibrium the population dynamics are development-controlled (De

Fig. 1. Average juvenile and adult consumer biomass at equilibrium as a function of the maximum density of resource 1, $R_{\max,1}$, when $R_{\max,2} = 0.4$ and $\eta = 0.0$. The solid curves indicate the (potentially) stable equilibrium while the dashed curves indicate the unstable equilibrium (saddle points). All other parameters have default values.

Roos and Persson, 2013), that is, mostly governed by limited maturation.

The case is reversed when $R_{\max,1}$ is large compared to $R_{\max,2}$ ($R_{\max,1} \gtrsim 0.47$). Population dynamics are then mostly controlled by limited reproduction, because juveniles now grow and mature fast. Adult biomass makes up the largest part of the consumer population, but competition among adults is intense and adults spend most of their energy intake on maintenance. Adults store little energy for reproduction and produce only limited numbers of offspring that subsequently experience little resource competition.

For intermediate values of $R_{\max,1}$ ($0.35 \lesssim R_{\max,1} \lesssim 0.47$) model dynamics are characterized by bistability as the development-controlled and reproduction controlled equilibrium co-occur (Fig. 1).

An analogous change in possible equilibrium densities occurs for varying $R_{\max,2}$ when the maximum density of resource 1 is fixed at $R_{\max,1} = 0.4$, see Fig. 2. Persistence of the consumer population is not possible when $R_{\max,2}$ is very low, because adults do not have sufficient resources to cover their maintenance costs and store energy for reproduction. As $R_{\max,2}$ increases model dynamics will first converge to a reproduction-controlled equilibrium state. At this equilibrium adults produce only limited numbers of offspring at each reproduction event. The low densities of juveniles experience, however, very little resource competition in this state and hence mature fast. For increasing values of $R_{\max,2}$ bistability occurs between the reproduction-controlled equilibrium and an equilibrium controlled by limited development. In the latter the bottleneck in dynamics occurs in the juvenile as opposed to the adult stage. At even higher values of $R_{\max,2}$ the development-controlled equilibrium is the unique attractor of model dynamics. In other words, competition among consumers for resources leads to a bottleneck in one of the two stages, either in the juvenile stage,

Fig. 2. Average juvenile and adult consumer biomass at equilibrium as a function of the maximum density of Resource 2, $R_{\max,2}$, when $R_{\max,1} = 0.4$ and $\eta = 0.0$. The solid curves indicate the (potentially) stable equilibrium while the dashed curves indicate the unstable equilibrium (saddle points). All other parameters have default values.

Fig. 3. Combinations of maximum resource densities for juvenile and adult consumers, for which consumer persistence is possible (the region between the dark curves) and for which bistability occurs (the region between the gray curves). Here $\eta = 0.0$ and all other parameters have default values.

which results in a development-controlled equilibrium, or in the adult stage leading to a reproduction-controlled equilibrium.

The combinations of maximum densities of the two resources for which the consumer population can persist are shown in Fig. 3. Within the region of persistence consumers occur in a reproduction-controlled equilibrium when $R_{\max,1}$ is high compared to $R_{\max,2}$. In particular, the consumer equilibrium is always governed by limited reproduction when $R_{\max,1} \geq R_{\max,2}$. For low values of $R_{\max,1}$ the consumer equilibrium is development-controlled, whereas bistability occurs when $R_{\max,2}$ is not too much higher than $R_{\max,1}$. Compared to the version of the model analyzed by De Roos and Persson (2013), in which consumer reproduction is continuous in time rather than a pulsed event, the bistability of equilibria occurs over smaller ranges of maximum resource densities and in particular is not observed for $R_{\max,1} \geq R_{\max,2}$.

4.2. Varying the extent of the niche shift

In Section 4.1 η is set to 0 in order to show how varying resource availabilities affects the model dynamics; in this subsection we discuss the case for $0 < \eta \leq 1$. As defined in Section 3, η represents the adult preference for foraging on resource 1. A positive value of η implies that adults begin to exploit resource 1 and hence that competition occurs between adults and juveniles for resource 1. Larger values of η result in more severe competition between

Fig. 4. Average juvenile and adult consumer biomass (top panel) and resource availability for juvenile and adult consumers (lower panel) at equilibrium as a function of the adult preference on resource 1, η , when $R_{\max,1} = 0.4$ and $R_{\max,2} = 0.3$. The solid curves indicate the (potentially) stable equilibrium while the dashed curves indicate unstable saddle points. All other parameters have default values. The average resource availabilities for juvenile and adult consumers are defined as $\bar{R}_j = \bar{R}_1$ and $\bar{R}_a = \eta \bar{R}_1 + (1 - \eta) \bar{R}_2$, respectively, with $\bar{R}_1 = \int_0^1 R_1(t) dt$ and $\bar{R}_2 = \int_0^1 R_2(t) dt$ the average biomass density of resource 1 and 2, respectively, during the interval between two reproduction pulses.

adults and juveniles, while $\eta = 1$ implies that juveniles and adults share resource 1 as their only food source.

A bifurcation diagram of the average consumer biomass as a function of η with constant maximum resource densities is shown in Fig. 4. Since both maximum resource densities are sufficiently large to guarantee persistence, changing η will not affect consumer persistence. The choice of η does, however, affect the bistability of equilibria in the model. When η is close to 0, a unique equilibrium occurs, in which the maturation rate of juveniles is higher than the net-biomass production of adults as a result of the higher resource availability for juveniles (Fig. 4, lower panel). This equilibrium is therefore reproduction controlled, which corresponds to our earlier observation concerning Fig. 3 that for all maximum resource densities $R_{\max,1} \geq R_{\max,2}$ only an equilibrium governed by limited reproduction occurs. Increasing values of η lead to a relaxation of the competition among adult consumers, which results in the occurrence of a region of bistability between the equilibrium governed by reproduction control and an equilibrium governed by development control. For $R_{\max,1} \geq R_{\max,2}$ bistability can hence occur, but only when consumer individuals partially change their ecological niche on maturation. In the development-controlled equilibrium adults are experiencing a better resource availability than juveniles (Fig. 4, lower panel). As a consequence, adult net-biomass production and hence fecundity is high and juveniles constitute the largest part of the population biomass. For $\eta \gtrsim 0.27$, however, only the development-controlled equilibrium occurs.

For $\eta = 1$ juveniles and adults feed on and compete with each other for resource 1 only. Because all energetic parameters of juveniles and adults are chosen to be the same, this implies that juveniles and adults are limited by resource availability to the same extent. This condition is referred to as “ontogenetic symmetry in energetics” (De Roos et al., 2013; Persson and De Roos, 2013). In this case a unique equilibrium occurs, which is dominated by juvenile biomass.

Fig. 5 shows the combinations of $R_{\max,2}$ and η for which the consumer population persists and for which bistability between

Fig. 5. Combinations of adult preference on resource 1, η , and maximum density of resource 2, $R_{\max,2}$, for which consumers can persist (the region above the dark curve) and for which bistability between a reproduction- and a development-controlled equilibrium occurs (the region between the gray curves). Here $R_{\max,1} = 0.4$ and all other parameters have default values.

the two alternative stable states occurs. When $\eta = 0.0$, the consumer persistence requires a positive availability of resource 2, since it is the only resource adults feed on. As η increases, the adults forage more and more on resource 1, and hence are less dependent on the presence of resource 2. For this reason the persistence boundary, expressed as the minimum value of $R_{\max,2}$ below which extinction occurs, is a decreasing curve of η . When η is approximately larger than 0.51, adults do not need resource 2 any longer for persistence because they can forage sufficiently on resource 1.

The parameter regions for which persistence is possible are divided into three different parts, similar to Fig. 3: a parameter region with a unique, development-controlled equilibrium, a region with a unique reproduction-controlled equilibrium and a region with bistability. It is easy to understand this: for a particular, constant $R_{\max,1}$ increasing values of η would imply that juveniles are more resource-limited as they have to compete more with adults. As a consequence, the region with a development-controlled equilibrium increases when η increases, until finally the region with two stable states disappears (at $\eta \approx 0.34$, where a cusp point occurs). On the other hand, for a constant η , it is more likely that a reproduction-controlled equilibrium occurs when the availability of resource 2 is smaller, as it implies more severe competition among adult individuals.

Based on the results discussed above we conclude that the alternative stable states that occur for different combinations of resource availabilities and extent of the niche shift are caused by the model feature that both development and maturation of juveniles and reproduction (energy storage) of adults are resource-dependent. $R_{\max,1}$ and η determine how much resource is available for juveniles while $R_{\max,1}$, $R_{\max,2}$ and η determine how much resource is available for adults. As a result, a bottleneck may occur in either the juvenile or the adult life stage of the consumer.

4.3. Maintenance of energy storage

In the basic model formulation we have assumed that the stored reproductive energy B does not require any maintenance costs. Therefore, all reproductive energy built up by adults during the season is completely released as juvenile offspring when reproduction occurs. The validity of this assumption is unclear, although it has been argued that storage of lipids and fat tissue should not cost any energy (Kooijman, 2000).

Because energy storage B may at times be larger than adult biomass A and maintenance requirements of storage could then

Fig. 6. Combinations of the maximum densities of the two resources for which bistability occurs for three different values of ϵ : $\epsilon = 0.0$ (the region between the gray curves, same results as in Fig. 3), $\epsilon = 0.5$ (the region between the dark solid curves) and $\epsilon = 1.0$ (the region between the dark dashed curves). Here $\eta = 0.0$ and all other parameters have default values.

Fig. 7. Combinations of the adult preference on resource 1, η , and the maximum density of resource 2, $R_{\max,2}$, for which bistability occurs with three different values of ϵ : $\epsilon = 0.0$ (the region between the gray curve, same results as in Fig. 5), $\epsilon = 0.5$ (the region between the dark solid curve) and $\epsilon = 1.0$ (the region between the dark dashed curve). Here $R_{\max,1} = 0.4$ and all other parameters have default values.

significantly reduce consumer biomass, we will consider a model variant that accounts for maintenance requirements of stored energy. To this end we revise Eq. (3) as follows:

$$v_a(R_1, R_2) = \sigma I_{\max} (\eta R_1 + (1 - \eta) R_2) - Q \left(1 + \epsilon \frac{B}{A}\right), \quad (12)$$

where ϵ is the ratio of maintenance requirements for energy storage B to that of somatic adult biomass.

Obviously, a larger value of ϵ has the potential to decrease consumer biomass as more energy will be lost during the season. However, the analysis of the model variant with positive ϵ values reveals that ϵ does not qualitatively affect the occurrence of alternative stable states in the model and only leads to quantitative differences in model predictions, as shown in Figs. 6 and 7. Because we are mainly studying the occurrence of bistability here, the persistence boundaries are not presented in Figs. 6 and 7 so that the bistability boundaries can be more clearly contrasted. Instead, we show the persistence boundaries for different values of ϵ in Appendix B, see Fig. B.

From Figs. 6 and 7 it can be deduced that the alternative stable states never disappear regardless of the value of ϵ . Furthermore, larger ϵ lead to smaller parameter regions with a development-controlled equilibrium and with bistability, while the parameter region with a reproduction-controlled equilibrium becomes larger. The reason is that when ϵ increases the average maintenance cost during one growing season for adults increases relative to

Fig. 8. Consumer biomass, averaged over one growing season, at equilibrium (gray curves) and the maximum and minimum value of consumer biomass during numerical simulations of model dynamics (dark curves) as a function of $R_{\max,1}$ (Fig. 8(a) and (d)), $R_{\max,2}$ (Fig. 8(b) and (e)) and η (Fig. 8(c) and (f)) for logistic resource growth (left panels) and semi-chemostat resource dynamics (right panels). All the panels indicate the total consumer biomass which is the sum of average juvenile and adult biomass and energy storage. In Fig. 8(a) and (d), $R_{\max,2} = 0.4$ and $\eta = 0.0$; in Fig. 8(b) and (e), $R_{\max,1} = 0.4$ and $\eta = 0.0$; in Fig. 8(c) and (f), $R_{\max,1} = 0.4$ and $R_{\max,2} = 0.3$. All other parameters have default values.

the requirement of juveniles, which implies adults need more resource to cover their maintenance requirements. Consequently for larger ϵ adults are more limited by their resources, increasing the likelihood that an equilibrium is controlled mostly by limited reproduction.

5. Logistic resource dynamics

De Roos et al. (2008) compare the dynamics of a fully size-structured population model and a simplified stage-structured biomass model with both logistic growth and semi-chemostat growth of the resource. To investigate the influence of the type of resource growth on the current results we revise the resource growth function, given by Eq. (1), as follows:

$$G_i(R_i) = \rho_i R_i \left(1 - \frac{R_i}{R_{\max,i}} \right), \quad i = 1, 2. \quad (13)$$

Here ρ_i and $R_{\max,i}$ are the intrinsic growth rates and the carrying capacities of the resources, respectively. We study the long-term dynamics as well as the average consumer biomass at equilibrium of the model as a function of $R_{\max,1}$, $R_{\max,2}$ and η using numerical simulations. Fig. 8 shows the results of these numerical simulations for both logistic resource dynamics (three left panels) and semi-chemostat resource dynamics (three right panels). As in Section 4 we focus on the mean biomasses during one season, which were calculated by numerical integration of the ODEs $d\bar{J}/dt = J(t)$, $d\bar{A}/dt = A(t)$ and $d\bar{B}/dt = B(t)$ within each growing season with initial states $\bar{J} = \bar{A} = \bar{B} = 0$. Fig. 8 shows the long-term

average of total consumer biomass, the sum of average juvenile and adult biomass and energy storage $\bar{J} + \bar{A} + \bar{B}$, as well as its minimum and maximum value (dark curves). The maximum and minimum average biomasses were obtained using long-term numerical simulations of model dynamics with regular, stepwise increases as well as decreases in the parameter of interest and the average equilibrium biomasses were calculated using the same method as Section 4.

As shown in Fig. 8(a) and (d), the model exhibits stable fixed-point dynamics with both logistic and semi-chemostat resource growth for smaller values of $R_{\max,1}$. As discussed in Section 4 the consumer population in this fixed-point dynamics is controlled by limited maturation. When $R_{\max,1}$ increases both models exhibit alternative dynamic attractors over a range of $R_{\max,1}$ values, of which one attractor is the development-controlled fixed point, whereas the other attractor represent cyclic dynamics. These cycles result from the high maturation rate of juveniles that characterizes a reproduction-controlled consumer population. In one season juveniles have sufficient resource and mature into adult stage rapidly after they are born. These adults, however, are limited by their resource and store little reproductive energy and reproduce very few offspring. This small number of newborn juveniles in the following season results in fewer adult individuals and increasing adult resource. As a consequence, adults store more reproductive energy and therefore the total production of newborns is higher during the next reproduction event. Two such seasons alternate, resulting in regular, large-amplitude cycles for larger $R_{\max,1}$. The model with semi-chemostat resource dynamics exhibits these cycles for all values of $R_{\max,1}$, for which a

reproduction-controlled model equilibrium exists, whereas these cycles disappear in the model with logistic resource growth for $R_{\max,1} > 0.52$, where stable fixed point dynamics occur (Fig. 8(a)). The reason is that when $R_{\max,1}$ is larger than $R_{\max,2}$, the juvenile biomass is lower than adult biomass and resource 1 is at very high density. In the case of logistic resource dynamics the productivity of resource 1 is lower than in the case of semi-chemostat resource dynamics, which is always a constant $\rho_1 R_{\max,1}$. Consequently, with semi-chemostat growth total consumer biomass is higher than with logistic resource growth, and in the latter case adults are less limited and the amplitude of fluctuation in density of resource 1 is smaller. The fluctuation in availability of resource 1 is therefore too small to result in cycles in the model with logistic resource growth.

The case is reversed when $R_{\max,1}$ is fixed but $R_{\max,2}$ is varied. Both models exhibit a reproduction-controlled state when $R_{\max,2}$ is just above the threshold of consumer extinction. When $R_{\max,2}$ increases both models exhibit alternative stable states first and then switch to a development-controlled state (Fig. 8(b) and (e)). Similar to the case shown by Fig. 8(a) and (d), when the consumer population is reproduction-controlled both models exhibit small-amplitude cycles. However, as a main difference, with semi-chemostat resource dynamics at large $R_{\max,2}$ the model exhibits fixed-point dynamics and a development-controlled consumer state (Fig. 8(e)), whereas large-amplitude cycles occur with logistic resource growth when $R_{\max,2} > 1.63$ (Fig. 8(e)). When $R_{\max,2}$ is much larger than $R_{\max,1}$ the consumer population is governed by development-control. Juveniles consequently have very poor resource conditions and grow very slowly in body size. As discussed above, the productivity and therefore recovery of resource 1 in the logistic growth model is smaller than in the semi-chemostat model, leading to juveniles experiencing a high starvation mortality rate during multiple seasons. Very few juveniles therefore mature into adult stage and adult biomass keeps decreasing in the seasons during which juveniles are starving. Such starvation in juvenile stage lasts for a long time and disappears only when the density of resource 1 recovers to a level higher than starvation threshold of juveniles. This switching on and off of juvenile starvation leads to the fluctuations in consumer biomass observed in Fig. 8(b) when $R_{\max,2}$ is quite large.

The case for fixed resource productivities but varying niche shift extent η is simpler. As shown in Fig. 8(c) and (f) when η is small both models exhibit small-amplitude cycles and for large η both models approach the stable (development-controlled) equilibrium. In both models when η is small the consumer population is controlled by limited reproduction, while juveniles grow and mature fast to adult stage. Population cycles occur in this case due to the same mechanisms as discussed above in relation to Fig. 8(a) and (d).

Summarizing, although logistic resource growth sometimes leads to different model dynamics compared to semi-chemostat resource growth, it does not qualitatively change the occurrence of alternative stable types of dynamics that originate because of the energetic asymmetry between the two consumer stages. In fact, for the same parameter values, the bistability regions in case of logistic resource growth tend to be larger than with semi-chemostat resource dynamics (see Fig. 8 as well as Appendix A), because resource productivities are smaller for logistic resource growth and consumer individuals are hence more likely to be energetically limited than in case of semi-chemostat resource dynamics.

6. Discussion

In classical, continuous-time consumer–resource models only the reproduction of adults is assumed to be resource-dependent while the maturation rate of juveniles is either ignored altogether, when different life stages are not accounted for at all, or in

case of stage-structured models considered to be constant. As a consequence, only reproduction of adults can be limited by resource and can thus be affected by the population feedback that operates through population foraging and resource depletion. In contrast, when resource-dependent maturation is taken into account an asymmetry in energetics between juveniles and adults may arise, potentially leading to two different modes of population regulation: either (1) juveniles mature fast while adults only reproduce very little, or the reversed case, (2) adults reproduce at a high rate but juveniles mature very slowly. In the case juveniles and adults differ in their diet and hence forage to an extent on different resources these two modes of population regulation may lead to a third scenario, in which two types of equilibria occur under the same conditions as alternative stable states.

Schreiber and Rudolf (2008) and Guill (2009) showed in two different continuous, stage-structured consumer–resource models that a complete niche shift during consumer life history, corresponding to the case with $\eta = 0.0$ in our model, can lead to alternative stable states over substantial ranges of productivities of the two resources. De Roos and Persson (2013) presented similar results and in addition consider the case that consumers only exhibit a partial niche shift in resource use. These authors show that the likelihood of bistability is smaller when the extent of the niche shift decreases. In agreement with these earlier results we show that conditions with two potential, stable states also predominate in a semi-discrete model, in which consumers reproduce in a pulsed event, and that the extent of the niche shift, as parameterized by the niche shift parameter η , affects the parameter domain with bistability in the same way as found for completely continuous-time models. This bistability between equilibria that are either controlled by limited reproduction or by limited juvenile development has been shown to have consequences for community structure. For example, De Roos and Persson (2013) showed that a stage-specific predator specializing on juvenile consumers may only be able to invade a consumer population at equilibrium that is controlled by limited development. As a consequence, increasing resource availability for juvenile consumers, which results in the consumer population becoming controlled by limited reproduction, will drive this predator to extinction. This so-called emergent predator-exclusion will also occur for a stage-specific predator on adult consumers with increasing resource availability for these adults.

The extent of the niche shift in our model determines the resource availability for juveniles and adults. As a consequence, the persistence boundary and the bistability boundary are both affected by parameter η , see Fig. 5. Comparing these results with the results presented by De Roos and Persson (2013) reveals that they largely correspond with each other and that hence the pulsed reproduction we consider only changes model behavior quantitatively, but not qualitatively. The distinguishing feature of our model is that juveniles cannot feed on resource 2 and hence resource 1 is always required for consumer persistence, whereas resource 2 is not essential when $\eta R_{\max,1}$ is sufficiently large.

The phenomenon of seasonal reproduction that we consider in our model is a common phenomenon among most species in temperate regions. Although a pulse of offspring production represents a major perturbation to the system state, we find that the bistability between alternative stable states as reported from fully continuous models also occurs in our model. As discussed in Section 4 there is a periodic perturbation due to the pulsed release of reproductive energy by adult individuals. Hence, a stable state in our model corresponds to fixed point dynamics, in which juvenile biomass, adult biomass and resources densities cycle throughout the growing season, but always have the same values at a fixed time within the growing season, for example, just after reproduction has occurred. These cycles in biomass densities may

be significant and be so large that, for example, adults experience substantial starvation mortality right after reproduction due to competition by the abundant juveniles, but still gather sufficient energy in the remainder of the season to reach high fecundities at the next reproduction event. The extent to which population dynamics is more limited by juvenile development and maturation or by adult reproduction is therefore poorly reflected by the instantaneous biomass densities and can only be revealed by considering the average biomass densities of juveniles and adults, which are the integrations of $J(t)$ and $A(t)$ over the growing season.

The analysis of the seasonal reproduction in combination with a niche shift in our stage-structured consumer–resource biomass model provides insights into the dynamics of consumer species with direct implications for the transfer of energy between different trophic levels in ecosystems. In particular, we find that seasonal reproduction decreases the likelihood of an equilibrium state, in which the consumer population is controlled by limited development and maturation of juveniles, compared to a continuous model (Guill, 2009) (Fig. 3). The reason is that seasonal reproduction can more or less release the bottleneck as juvenile biomass keeps decreasing during the season and can only increase when reproduction occurs. In other words, in the case of continuous reproduction juveniles are more likely to be limited by their resource availability than in the case of seasonal reproduction. Nonetheless, our results show that the bottleneck can never be released completely by seasonal reproduction such that there are always conditions for which either an equilibrium controlled by limited development or an equilibrium controlled by limited reproduction occur in our model. The fact that consumer populations with seasonal reproduction are less likely to experience a bottleneck in juvenile development and maturation implies that the biomass distribution of these populations is less likely to be skewed toward juveniles (De Roos and Persson, 2013) and hence provide fewer foraging opportunities for predator species that specialize on these juvenile stages. The consequences of these effects for the persistence of species at higher trophic levels, we will discuss in future studies.

We have shown the robustness of the occurrence of bistability in the present stage-structured biomass model by studying three variants of the initial model. It can be concluded that the maintenance of reproductive energy (Section 4.3), as well as the types of resource dynamics (Section 5) and consumer functional response (Appendix A), do not qualitatively affect the occurrence of alternative stable states. These model variants exhibit some quantitative differences in the results due to differences in the energetics at the individual level. However, none of them can change the energetic asymmetry between two consumer stages, which lead to the different types of consumer dynamics and regulation.

7. Conclusion

A consumer–resource model with two stages, seasonal reproduction and a niche shift in consumer life history is studied. We find that the model can exhibit alternative stable states dependent on the availabilities of juvenile and adult resources and the extent of the niche shift that consumers experience. The two stable states are mainly regulated by limited maturation from the juvenile stage when juveniles experience a low resource availability and limited adult fecundity when adult resource(s) are low, respectively. Our results show that seasonal reproduction can to some extent release a potential bottleneck in juvenile development, leading to a much smaller parameter region with a development-controlled equilibrium state than in the case of continuous reproduction. However,

these differences are quantitative as seasonal reproduction does not qualitatively affect the occurrence of alternative stable states in the model.

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Appendix A. Analysis of the model with Holling type II functional response

In the main text the consumers are assumed to forage on the resources following a linear functional response, where earlier articles about the continuous-time models, such as De Roos et al. (2008) assumed consumer foraging following a Holling type II functional response. However, as we show in this appendix in our present semi-discrete model the form of the functional response does not affect the occurrence of bistability qualitatively. To verify the effect of the functional response, we revise the net-biomass biomass production per unit body mass for juveniles and adults, denoted by Eqs. (2) and (3) as follows:

$$v_j(R_1) = \sigma I_{\max} \frac{R_1}{H + R_1} - Q, \quad (\text{A.1})$$

$$v_a(R_1, R_2) = \sigma I_{\max} \frac{\eta R_1 + (1 - \eta) R_2}{H + (\eta R_1 + (1 - \eta) R_2)} - Q. \quad (\text{A.2})$$

Here H is the half saturation constant. Similar to the case discussed in Section 4 we calculate the bistability boundary as a function of two parameters to show the occurrence of alternative stable states, see Fig. A. Note that we will not discuss any more details about the two types of stable states and the mechanisms at the individual level giving rise because they are the same as discussed in the main text. Instead, we mainly compare the bistability regions in the models with two different types of functional responses.

From Fig. A it can be found that the bistability does not disappear in the case of a Holling type II functional response. However, some quantitative differences are observed: with both types of resource dynamics the bistability regions shrink when a Holling type II functional response is introduced. These quantitative differences arise because the population energetics change at the individual level: given the same amount of resource(s), in the case of a Holling type II functional response the net-biomass productivity of consumer individuals is lower than that in the case of linear functional response. As a consequence, more resources are ingested in the latter case. This change increases the likelihood that consumer individuals are limited by their resource.

Appendix B. Persistence boundaries for different values of ϵ

For clarity and to highlight the bistability regions the persistence boundaries for different values of ϵ were omitted from Figs. 6 and 7 in the main text. In this appendix, we reproduce for completeness these two figures including the persistence boundaries, see Fig. B. For larger ϵ values the persistence boundary always occurs at higher maximum resource densities than for smaller ϵ , which implies at a larger ϵ consumers require more resource to persist. The reason is that if ϵ is larger the maintenance costs of adults is higher and hence more energy is lost during the season.

Fig. A. The bistability boundaries of the model as a function of $R_{\max,1}$ and $R_{\max,2}$ (A1 and A3), and η and $R_{\max,2}$ (A2 and A4). The two left panels show the results of the model with semi-chemostat resource dynamics while the two right ones show the results of the model with logistic resource dynamics. The dark curves indicate the boundaries for the case of linear functional response which is studied in the main text while the gray curves indicate the case of Holling type II functional response with $H = 1$. The parameter settings are the same as the main text: in A1 and A3 η is set to 0; in A2 and A4, $R_{\max,1} = 0.4$; all other parameters have default values.

Fig. B. The persistence and bistability boundaries of the model as a function of $R_{\max,1}$ and $R_{\max,2}$ (B1), and η and $R_{\max,2}$ (B2) for three different values of ϵ . The bistability boundaries are the same shown by Figs. 6 and 7. Here the persistence boundaries, below which the consumer cannot persist, are shown. In Figure B1 all the parameters have the same values as Fig. 6 and in Figure B2 they have the same values as Fig. 7.

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