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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.

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.

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 (Mailleret and Lemesle, 2009), which combines continuous dynamics for most of the time with sharp changes at some predefined 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

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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 $s_b \le s < s_m$ 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 $R_{\max,i}$:

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

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 $\nu_j(R_1)$ and $\nu_a(R_1, R_2)$, then equals the balance between ingestion and maintenance requirement:

$$\nu_j\left(R_1\right) = \sigma I_{\max} R_1 - Q, \tag{2}$$

$$\nu_a\left(R_1, R_2\right) = \sigma I_{\max}\left(\eta R_1 + (1-\eta) R_2\right) - Q. \tag{3}$$

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