Large-amplitude consumer-resource cycles allow for the evolution of ontogenetic niche shifts in consumer life history

Hanna ten Brink[1,2,*], André M. de Roos[2]

Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, 1090 GB Amsterdam, P.O. Box 94248, the Netherlands

ABSTRACT

In many size-structured populations individuals change resources during the course of their ontogenetic development. Different resources often require different adaptations to be effectively exploited. This leads to a trade-off between small and large individuals in direct developing species. Specialization on the resource used later in life turns out to be hardly possible in case of equilibrium dynamics. However, size-structured populations often exhibit population cycles. Non-equilibrium dynamics can change evolutionary behavior when compared with equilibrium dynamics. Here, we study the evolution of specialization on a secondary resource that is available only to large individuals, using the framework of adaptive dynamics. We show that in case of small-amplitude cycles, specialization on a secondary resource is hardly possible. Specialization will either decrease the resource intake of large individuals or severely increase competition among small individuals such that they cannot mature. Specialization on a secondary resource is often possible in case the population exhibits large-amplitude cycles. Specialization in that case increases the resource intake of large individuals and therefore prevents starvation. While specialization on a secondary resource increases competition among small individuals, maturation is still possible in case of large-amplitude cycles. We furthermore show that there is ecological bistability where small- and large-amplitude cycles coexist, giving rise to evolutionary bistability.

1. Introduction

Bream (*Abramis brama*) switches from feeding on zooplankton to benthic invertebrates as it increases in size (Persson and Brönmark, 2002). The iguanine lizard *Ctenosaura pectinata* preys upon insects when small but becomes vegetarian when large (Durtsche, 2004). Not only fish or lizards switch their diet during ontogeny. In fact, the majority of all free-living animal species change their niche during their life (Werner and Gilliam, 1984). Most research has focused on the optimal timing of these ontogenetic niche shifts (Claessen and Dieckmann, 2002; Werner, 1988; Werner and Gilliam, 1984), whereas it is not well understood why they evolved in the first place. Although it may be beneficial for individuals to change resource use over ontogeny (Werner and Gilliam, 1984), there is also a cost connected to shifting diets. A morphology that allows individuals to feed on a certain food type is not necessarily efficient when feeding on a different food type (e.g., Andersson, 2003; Hjelm et al., 2003; Meyer, 1989). In direct developing species this leads to a trade-off between early and late foraging success; individuals can either specialize in feeding on the resource they use early in life or in feeding on the resource they use later in life.

It has been shown with a discrete, age-structured population model that the relative amount of resources in the different niches determines on which resource individuals with an ontogenetic niche shift specialize (Ebenman, 1992). In case the resource that newborn individuals feed on is plentiful, evolution favors a morphology where individuals are specialized in feeding on the resource used later in life. Vice versa, evolution favors a morphology specialized in feeding on the resource used early in life in case this resource is limited (Ebenman, 1992). In the study of Ebenman (1992) it was assumed that individuals have a fixed juvenile period. However, in most species growth is determined by food intake rather than age (de Roos and Persson, 2013). Changing feeding efficiencies over ontogeny will affect resource densities and thereby the growth of individuals. This will in turn change the

* Corresponding author.
  E-mail addresses: johanna.tenbrink@ieu.uzh.ch (H. ten Brink), A.M.deroos@uva.nl (A.M. de Roos).
[1] Current address: Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland.
[2] Declarations of interest: none.

optimal feeding strategy. Therefore, when studying the evolution of ontogenetic niche shifts one should take into account the feedback between the resource environment and the different strategies of individuals.

In a study that did take into account the aforementioned feedback loop it was found that the trade-off between early and late foraging success limits the evolution of ontogenetic niche shifts (ten Brink and de Roos, 2017). While individuals are able to broaden their diet during ontogeny, individuals adopt a morphology specialized in feeding on the primary resource. Individuals are therefore not very efficient in utilizing the resource used later in life (ten Brink and de Roos, 2017). However, some species (e.g., many piscivorous fish; Byström et al., 2013; Mittelbach and Persson, 1998) have a morphology specialized in feeding on the resource used later in life. How did such life-history strategies evolve? The aim of this article is to gain insight into how specialization on a secondary resource can evolve, taking into account the feedback between the resource environment and the individuals.

Most theoretical studies on the evolution of life-history traits, including studies on the evolution of ontogenetic niche shifts (e.g., Claessen and Dieckmann, 2002; ten Brink and de Roos, 2017) assume equilibrium population dynamics, despite the fact that ecological systems can show different types of dynamics, such as limit cycles or chaos. Ecological dynamics affect evolutionary dynamics and vice versa, it is therefore no surprise that the evolutionary behavior of a system can be affected by the type of population-dynamical attractor (Dercole et al., 2002; Hoyle et al., 2011; Nurmi and Parvinen, 2013; Parvinen, 1999; White et al., 2006).

Taking into account the effect of the type of population dynamics on the evolutionary behavior is potentially important in studying ontogenetic niche shifts. Ontogenetic niche shifts occur by definition at some point during an individual's development. The timing of such switches is largely determined by the size of an individual (Werner and Gilliam, 1984). It is therefore appropriate to study the evolution of ontogenetic niche shift with the use of size-structured population models. Size-structured populations often exhibit population cycles and the type of population fluctuation is determined by the competitive ability of individuals (de Roos and Persson, 2003, 2013; Persson et al., 1998). Population cycles cause fluctuations in resources as well, which in turn will determine whether feeding and specialization on a certain diet is beneficial or not. It is therefore expected that the type of population cycles can affect the evolution of ontogenetic niche shifts.

In this paper we study the effect of the type of population dynamics on the evolution of ontogenetic niche shifts. We use a size-structured consumer-resource model and the adaptive dynamics approach (Durinx et al., 2008; Geritz et al., 1998). We assume a single consumer population utilizing two alternative resources. One resource is available for all individuals while the other resource is available only for large individuals. A trade-off between foraging abilities is assumed; the more efficient an individual uses one resource, the less efficient it can use the other. Previous works showed that under equilibrium conditions specialization on the resource available only for large individuals is not possible when this negatively affects offspring performance (ten Brink and de Roos, 2017). In this work we investigate if this result holds under non-equilibrium conditions as well.

2. Model and methods

2.1. Model description

We use a simple dynamic energy budget model for individual consumers of different sizes. Our model extends the Kooijman-Metz model (de Roos et al., 1990; Kooijman and Metz, 1984) by introducing a second resource population and starvation mortality.

The derivations of the functions of this model with one resource have been described before (de Roos et al., 1990; Kooijman and Metz, 1984). We therefore only shortly outline the model below. The set of equations and functions describing the model in more detail are listed in Tables 1 and 2 respectively.

Consumers are born with size ℓ_b, get access to the secondary resource at size ℓ_v and subsequently mature into adults at a length ℓ_j. We divide the consumer population in three size-classes; small juveniles, large juveniles, and adults. We define small juveniles as all individuals with a body length smaller than ℓ_v. Immature individuals with a body size equal to or larger than ℓ_v but smaller than ℓ_j are regarded as large juveniles. All individuals with a body size equal to or larger than ℓ_j are defined as adults.

The growth of both resources follows semi-chemostat dynamics with a turnover rate of δ and supply rates P_1 and P_2, respectively. In the absence of consumers the dynamics of the primary and secondary resource hence follow:

$$\frac{dX_1}{dt} = P_1 - \delta X_1,$$
$$\frac{dX_2}{dt} = P_2 - \delta X_2. \tag{1}$$

The maximum densities that the primary and the secondary resource can reach in the absence of the consumers thus equals $X_{1,\max} = P_1/\delta$ and $X_{2,\max} = P_2/\delta$, respectively. We assume that the two resources occur in the same habitat and that only large juveniles and adults can feed on both resources. To ease the extension to a secondary resource, we will reformulate the original model description. This will allow us to use a trade-off between the two attack rates, which is in line with previous work (ten Brink and de Roos, 2017). Resource ingestion follows a Holling-type-2 functional response and is proportional to the squared length of an individual with proportionality constant I_m. In the original model description (de Roos et al., 1990; Kooijman and Metz, 1984), the size-dependent resource ingestion for consumers foraging only on the primary resource is hence formulated as

$$I_1(X_1, \ell) = \frac{I_m \xi X_1}{1 + \xi X_1} \ell^2. \tag{2}$$

In this equation ξ is the shape parameter of the functional response. Ingested food is assimilated with a conversion efficiency σ, of which a fixed fraction κ is used for maintenance and growth in body mass. Body mass is proportional to cubed individual length with proportionality constant β. The remainder of the assimilated food is invested in maturation (juveniles) or reproduction (adults). Maintenance takes precedence over growth and is also proportional to the cubed length of an individual with proportionality constant χ. Growth in mass $(= \beta \ell^3)$ hence equals $\kappa \sigma I_1(X_1, \ell) - \chi \ell^3$, which leads after some rewriting (see de Roos et al., 1990) to the following expression for the growth rate in length of small individuals $(\ell < \ell_v)$ feeding solely on the primary resource:

$$g(X_1, \ell) = \gamma \left(\frac{\ell_m \xi X_1}{1 + \xi X_1} - \ell \right), \tag{3}$$

where γ $(= \chi/(3\beta))$ represents the growth rate constant. Parameter ℓ_m $(= \kappa \sigma I_m/\chi)$ is the maximum size individuals can reach under very high food conditions. This parameter is a composite parameter that among others depends on the proportionality constant I_m relating food intake at ad-libitum food supply to the squared length of an individual (de Roos et al., 1990; Kooijman and Metz, 1984).

In our reformulated model Holling's disc equation is used to model the consumer's functional response such that

$$I_1(X_1, \ell) = \frac{a_1 X_1}{1 + h a_1 X_1} \ell^2, \tag{4}$$

Table 1
Model equations.

Equation	Description
$\dfrac{dX_1}{dt} = P_1 - \delta X_1 - \displaystyle\int_{\ell_b}^{\ell_m} I_1(X_1, X_2, \ell)c(t,\ell)\,d\ell$	Dynamics resource 1
$\dfrac{dX_2}{dt} = P_2 - \delta X_2 - \displaystyle\int_{\ell_v}^{\ell_m} I_2(X_1, X_2, \ell)c(t,\ell)\,d\ell$	Dynamics resource 2
$\dfrac{\partial c(t,\ell)}{\partial t} + \dfrac{\partial g(X_1, X_2, \ell)c(t,\ell)}{\partial \ell} = -(\mu + S(X_1, X_2, \ell))c(t,\ell)$	Consumer size distribution dynamics
$g(X_1, X_2, \ell_b)c(t,\ell_b) = \displaystyle\int_{\ell_b}^{\ell_m} b(X_1, X_2, \ell)c(t,\ell)\,d\ell$	Population birth rate

Table 2
Functions of the model.

Function	Expression	Description
$I_1(X_1, X_2, \ell)$	$\begin{cases} \dfrac{a_1 X_1}{1 + h a_1 X_1}\ell^2 & \text{if } \ell < \ell_v \\[2mm] \dfrac{a_1 X_1}{1 + h(a_1 X_1 + a_2 X_2)}\ell^2 & \text{otherwise} \end{cases}$	Ingestion of resource 1
$I_2(X_1, X_2, \ell)$	$\begin{cases} 0 & \text{if } \ell < \ell_v \\[2mm] \dfrac{a_2 X_2}{1 + h(a_1 X_1 + a_2 X_2)}\ell^2 & \text{otherwise} \end{cases}$	Ingestion of resource 2
$\ell_\infty(X_1, X_2, \ell)$	$\begin{cases} \ell_m h \dfrac{a_1 X_1}{1 + h a_1 X_1} & \text{if } \ell < \ell_v \\[2mm] \ell_m h \dfrac{a_1 X_1 + a_2 X_2}{1 + h(a_1 X_1 + a_2 X_2)} & \text{otherwise} \end{cases}$	The length at which somatic growth stops given the current food conditions
$\ell_s(X_1, X_2, \ell)$	ℓ_∞ / κ	Length of instantaneous death
$\ell_{crit}(X_1, X_2, \ell)$	$\ell_s - q_s(\ell_s - \ell_\infty)$	Length at which starvation occurs
$g(X_1, X_2, \ell)$	$\begin{cases} \gamma\left(\ell_m h \dfrac{a_1 X_1}{1 + h a_1 X_1} - \ell\right) & \text{if } \ell < \ell_v \le \ell_\infty \\[2mm] \gamma\left(\ell_m h \dfrac{a_1 X_1 + a_2 X_2}{1 + h(a_1 X_1 + a_2 X_2)} - \ell\right) & \text{if } \ell_v \le \ell \le \ell_\infty \\[2mm] 0 & \text{otherwise} \end{cases}$	Growth rate
$b(X_1, X_2, \ell)$	$\begin{cases} 0 & \text{if } \ell < \ell_j \\[2mm] r_m h \dfrac{a_1 X_1 + a_2 X_2}{1 + h(a_1 X_1 + a_2 X_2)}\ell^2 & \text{if } \ell_j \le \ell \le \ell_\infty \\[2mm] \dfrac{r_m}{1-\kappa}\left(h \dfrac{a_1 X_1 + a_2 X_2}{1 + h(a_1 X_1 + a_2 X_2)} - \kappa\dfrac{\ell}{\ell_m}\right)\ell^2 & \text{if } \ell_j \le \ell > \ell_\infty \end{cases}$	Reproduction rate
$S(X_1, X_2, \ell)$	$\begin{cases} 0 & \text{if } \ell \le \ell_{crit}(X_1, X_2, \ell) \\ \mu_s(\ell - \ell_{crit}) & \text{if } \ell_{crit} < \ell < \ell_s \\ \infty & \text{if } \ell \ge \ell_s \end{cases}$	Starvation mortality

For brevity of notation function arguments have been omitted where possible.

where $a_1 = I_m \xi$ and $h = 1/I_m$. The growth of an individual feeding only on the primary resource (Eq. (3)) is now reformulated as

$$g(X_1, \ell) = \gamma\left(\frac{\ell_m h a_1 X_1}{1 + h a_1 X_1} - \ell\right). \qquad (5)$$

In the new model formulation, food intake of large individuals ($\ell \ge \ell_v$) feeding on two resources equals

$$I_2(X_1, X_2, \ell) = \frac{a_1 X_1 + a_2 X_2}{1 + h(a_1 X_1 + a_2 X_2)}\ell^2. \qquad (6)$$

Using the same assumptions as before, growth of large individuals then follows

$$g(X_1, X_2, \ell) = \gamma\left(\frac{\ell_m h(a_1 X_1 + a_2 X_2)}{1 + h(a_1 X_1 + a_2 X_2)} - \ell\right). \qquad (7)$$

Under sufficient food conditions adults ($\ell \ge \ell_j$) produce offspring at a rate

$$b(X_1, X_2, \ell) = r_m h \frac{a_1 X_1 + a_2 X_2}{1 + h(a_1 X_1 + a_2 X_2)}\ell^2. \qquad (8)$$

In this equation parameter r_m ($= (1-\kappa)\sigma I_m/(\beta \ell_b^3)$) represents the proportionality constant relating fecundity at ad-libitum food availability to squared individual length (de Roos et al., 1990; Kooijman and Metz, 1984).

When the fraction κ of assimilated energy is not sufficient to cover maintenance costs, growth ceases and energy allocated to reproduction is reduced (Table 2). When the total amount of ingested food is not enough to pay maintenance costs, individuals die instantaneously. When the size of individuals is close to the size at which this instantaneous death occurs, consumers suffer already from increased starvation mortality $S(X_1, X_2, \ell)$ (Table 2). Note that because large individuals have access to two resources while small individuals have access only to a single resource, the size at which starvation occurs is different depending on the size class of a consumer (Table 2).

The density function $c(t, \ell)$ represents the size distribution of the consumer population at time t. Since individual consumer biomass is assumed proportional to cubed length with proportionality constant β, the integral

$$\int_{\ell_1}^{\ell_2} \beta \ell^3 c(t, \ell)\,d\ell \qquad (9)$$

gives the total biomass of the consumers with a length between ℓ_1 and ℓ_2 at time t. Eq. (9) is used to calculate the biomass densities of the three different consumer size-classes.

We assume that the two resources require different morphological adaptations to be effectively utilized. We therefore use a

simple linear trade-off between the attack rate on the primary and the secondary resource

$$a_1 = (1 - \psi)A_{\max},$$
$$a_2 = \psi A_{\max}. \tag{10}$$

In this equation parameter ψ is the relative degree of specialization on the secondary resource. Such a trade-off between a_1 and a_2 directly affects resource intake, growth, birth, and death but does not change the composite parameters ℓ_m and r_m. Note that the diet of large individuals is determined by the two resource densities and the degree of specialization. When the resource densities fluctuate over time, the diet of large individuals changes on an ecological timescale. To characterize the diet composition of large individuals we will present the fraction of the secondary resource in their diet. This fraction is calculated as

$$\frac{a_2 X_2}{a_1 X_1 + a_2 X_2}. \tag{11}$$

The parameterization of the model is based on a planktivorous fish foraging on two unstructured resources (de Roos and Persson, 2002). Default parameters can be found in Table 3. We will study the evolution of specialization parameter ψ for different supply rates of the secondary resource (P_2).

2.2. Model analysis

We use the framework of adaptive dynamics (Durinx et al., 2008; Geritz et al., 1998) to study the evolution of specialization on a secondary resource. Since the model lacks an analytical solution we use the EBT-method (de Roos, 1997; de Roos et al., 1992) to study both the ecological dynamics and the evolutionary behavior of the model numerically. The ecological dynamics are studied by integrating the model over long time periods while varying specialization parameter ψ with small steps (see box 3.5 in de Roos and Persson, 2013 for an explanation of this procedure).

To calculate if a mutant can invade we start with a single, resident consumer population with a certain trait value ψ_{res}, that is settled at its ecological attractor. We then introduce two mutant populations. One real mutant with a trait value of ψ_{mut} and as a control one control mutant population with exactly the same trait value ψ_{res} as the resident population. Since we are interested only if these mutants can invade in the environment set by the residents, the mutants themselves do not affect the resources. We introduce these two mutant populations by assuming that for a 1000 days a few newborn mutants are produced at the same time that the resident population reproduces. Because the resident population is at its ecological attractor, the control mutant population that has exactly the same degree of specialization as the resident population will in the long run not change in size after these 1000 days. To check if the other, real, mutant population grows or shrinks we compare after 2,000,000 days the size of this population with the size of the control population. If the mutant population is larger than this control population this mutant can invade, if it is smaller it cannot. This step is repeated for many trait combinations of ψ_{res} and ψ_{mut} to construct the pairwise invasibility plots (PIPs).

In addition to studying the evolution of specialization ψ for the different types of population cycles, we also studied this in case of equilibrium dynamics using the PSPManalysis software package (de Roos, 2016). The PSPManalysis packages automatically detects and classifies evolutionary singular strategies according to the classification of Geritz et al. (1998). The package can compute where the mutant has a positive and negative growth rate and can in this way construct a PIP (see de Roos, 2016 for details). Even though the steady state of the size-structured model is unstable and hence

not an ecological attractor, we nonetheless analyze the evolutionary dynamics in this steady state because the resource fluctuations in case of small-amplitude population cycles (see below) are close to the constant resource densities in the (unstable) equilibrium state. The analysis thereby provides insights into the mechanisms that prevent the evolution of specialization in case of small-amplitude cycles.

3. Results

We will first show the different types of ecological dynamics that can be found in the model. Secondly, we discuss the costs and benefits of specialization on a resource that is available only for large individuals. Thirdly, we will show that the type of population dynamics determines whether or not specialization on the secondary resource can evolve. In the fourth section we explain the mechanisms that prevent the evolution of specialization in case of equilibrium, intermediate- and small-amplitude cycles. In the last section we show why specialization on a secondary resource can evolve in case of large-amplitude cycles.

3.1. Ecological dynamics

The consumer population displays, in the absence of an ontogenetic niche shift ($\psi = 0$), three different types of cycles. One large-amplitude single-cohort cycle, in which the population is dominated by a single cohort throughout its lifetime, and two types of intermediate- and small-amplitude cycles where there are multiple cohorts present at the same time (Fig. 1). The different types of cycles do sometimes co-occur. Fig. 2 shows, for two different values of the supply rate of the primary resource P_1, where the different type of cycles occur as a function of the supply rate of the secondary resource P_2 and the degree of specialization ψ. The two smaller-amplitude cycles disappear in case individuals are more specialized on the secondary resource. Stable equilibrium dynamics do not occur for the chosen parameter values.

Fig. 2B shows that for low and intermediate supply rates of the secondary resource, the three different types of population cycles co-occur for most values of specialization parameter ψ. By choosing $P_1 = 0.009\,\text{mg}\,\text{l}^{-1}\text{day}^{-1}$ we can study if the type of population dynamics lead to different evolutionary outcomes.

3.2. Costs and benefits of specialization on a secondary resource

A mutant may invade a resident population when its long-term average per capita growth rate is positive in the environment set by the resident population (Metz et al., 1992). A mutant's per capita growth rate is determined by the number of offspring it produces, which in our model depends on the time until maturation and the survival and reproduction rates. The trade-off between specialization on the primary and secondary resource (Eq. (10)) implies that individuals that are more specialized on the secondary resource, as small juveniles grow slower compared to small juveniles that are less specialized on the secondary resource. Small juveniles do not have access to the secondary resource and do therefore not benefit from a morphology specialized in feeding on this resource. In the first part of the life cycle specialization on the secondary resource is always disadvantageous since it slows down growth. Specialization on the secondary resource can therefore evolve only if this initial disadvantage is compensated for later in life. Specialization on the secondary resource is for large individuals advantageous only when this will increase their growth and reproduction rates. Since growth and reproduction depend on the resource intake, $X_2 > X_1$ is a necessary, but not sufficient, condition for specialization to be advantageous.
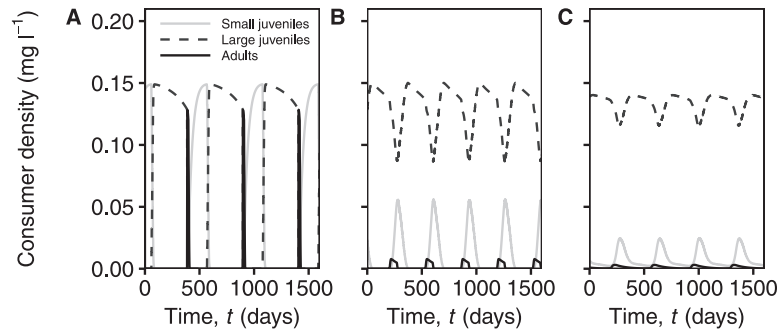
Fig. 1. Three different types of oscillatory dynamics can be found in the Kooijman–Metz model. Depending on the initial conditions, the population fluctuations have a large-(A), intermediate- (B), or small-amplitude (C). Biomass densities (mg l^{-1}) of small juveniles (grey, solid line), large juveniles (dark-grey, dashed line), and adults (black, solid line) over time (days). The secondary resource is not exploited ($\psi = 0$), other parameters have default values (Table 3).

Table 3
Standard parameters of the model.

| Parameter	Description	Default value	Unit
δ	Resource turnover rate	0.1	day^{-1}
P_1	Supply rate of resource 1	0.009	mg l^{-1}day^{-1}
P_2	Supply rate of resource 2	variable	mg l^{-1}day^{-1}
ℓ_b	Length at birth	7	mm
ℓ_v	Length at which secondary resource becomes available	40	mm
ℓ_j	Length at maturation	110	mm
ℓ_m	Maximum length	300	mm
h	Handling time	10	day mm^{2}mg^{-1}
A_{max}	Maximum value of the attack rate	6.667	day^{-1}mm^{-2}l
κ	Proportion of energy invested in maintenance and growth	0.7	-
γ	Von Bertalanffy growth rate	0.006	day^{-1}
r_m	Proportionality constant of reproduction	0.003	day^{-1}mm^{-2}
μ	Background mortality	0.01	day^{-1}
μ_s	Scaling constant of starvation mortality	0.2	day^{-1}
q_s	Threshold fraction for onset starvation mortality	0.3	-
β	Length to weight proportionality constant	$9 \cdot 10^{-3}$	mg mm^{-3}
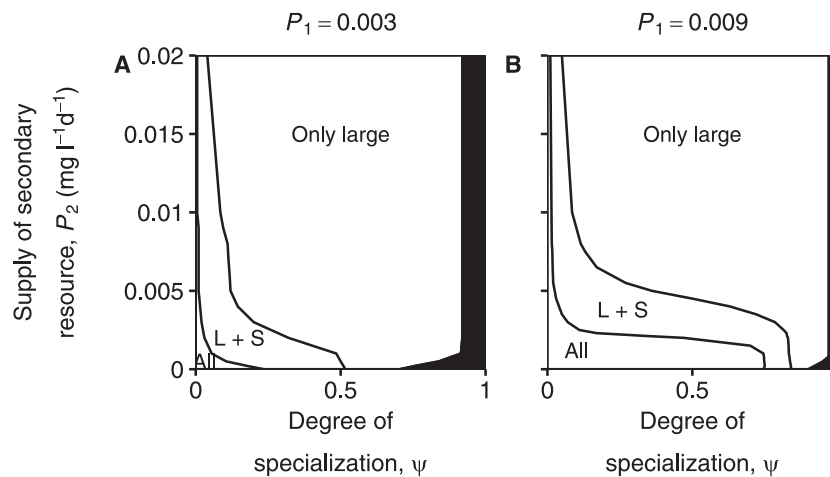
Fig. 2. Occurrence of the three types of population cycles (large (L), small (S) and intermediate) as a function of the degree of specialization on the secondary resource (ψ) and the supply rate of this resource (mg l^{-1}day^{-1}) for two values of P_1, the supply rate of the primary resource (mg l^{-1}day^{-1}). The dark areas indicate the parameter range where there is no viable population. Parameter values as in Table 3.

3.3. The type of population dynamics affects the evolutionary outcome

Fig. 3 shows PIPs for three different supply rates of the secondary resource (results for other supply rates are shown in Appendix A). This figure shows that the evolution of the specialization parameter ψ is highly affected by the type of population dynamics.

In case of large-amplitude cycles, the specialization parameter ψ can evolve to very high values, meaning that individuals specialize in feeding on the secondary resource (upper row in Fig. 3). While the evolutionarily stable strategies (ESSs) are for all supply rates convergence and evolutionary stable (continuously stable strategy, CSS), the PIPs show that a mutant that is substantially different from the resident strategy can invade, the CSS is therefore only locally evolutionary stable.
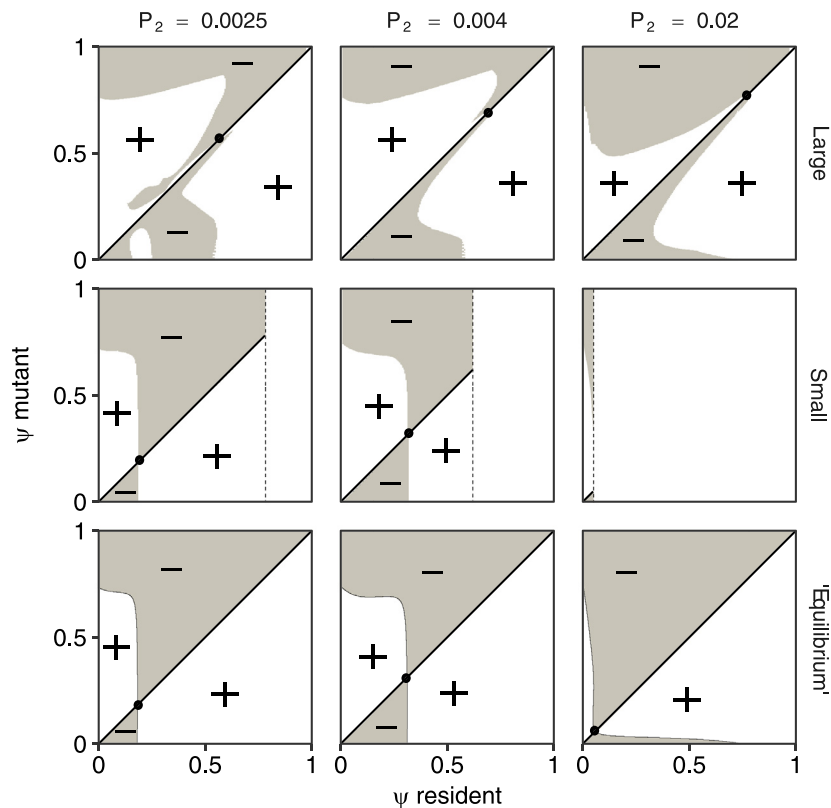
Fig. 3. Pairwise invasibility plots for different types of population dynamics and different values of the supply rate of the secondary resource (mg $l^{-1} day^{-1}$). The grey areas indicate negative invasion fitness, the white areas indicate positive invasion fitness. The black dots indicate the locations of the CSSs. The dashed lines in the PIPs for small-amplitude cycles indicate where this type of cycles disappears. Parameter values as in Table 3.

When the population displays small-amplitude cycles, the specialization parameter ψ evolves to low values for most supply rates of the secondary resource (Fig. A.1 and middle row in Fig. 3). This implies that individuals have a morphology that is efficient in feeding on the primary resource, but not very efficient in feeding on the secondary resource. Interestingly, the evolutionary result is the same for intermediate-amplitude cycles (Fig. A.1 in Appendix A) and when equilibrium dynamics are assumed (bottom row in Fig. 3). The ESSs in these cases are all convergence stable strategies.

Note that for high supply rates of the secondary resource, both the small- and intermediate-amplitude cycles occur only for low values of the specialization parameter ψ (Fig. 2B). For low values of specialization parameter ψ the selection gradient is positive (Fig. 3). Evolution therefore takes the specialization parameter ψ to the boundary of existence of the small- or intermediate-amplitude dynamics, at which point attractor switching to the large-amplitude cycles occurs (Geritz et al., 2002). Evolution will subsequently drive parameter ψ to the CSS value of these large-amplitude cycles.

We will first analyse in more detail the mechanisms that prevent the specialization parameter ψ to evolve to high values in case of small- and intermediate-amplitude cycles or when equilibrium dynamics are assumed. Secondly, we will show why consumers evolve a morphology highly specialized in feeding on the secondary resource in case of large-amplitude cycles.

Because the evolutionary dynamics are qualitatively the same for small- and intermediate-amplitude cycles and when equilibrium dynamics are assumed (Figs. 3 and A.1), we will, for convenience, analyze evolution in the context of such equilibrium dynamics, even for high values of the supply rate of the secondary resource, for which the small- and intermediate-amplitude cycles

disappear (Fig. A.1). This approach will allow us to better unravel the mechanisms that prevent the specialization parameter ψ to evolve to high values.

3.4. Evolution of specialization under equilibrium conditions and in case of intermediate- and small-amplitude cycles

Figs. 3 and A.1 show that under equilibrium population dynamics, the CSS of the specialization parameter ψ would initially increase with increasing supply rates of the secondary resource, but would ultimately decrease again to low values. Only for a small range of supply rates of the secondary resource, the specialization parameter ψ would be able to evolve to relatively high values (Fig. A.1).

Fig. 4A shows the equilibrium densities of the two resources as a function of the degree of specialization ψ of the resident population in case of a low supply rate of the secondary resource. This figure shows that the density of the secondary resource is higher than the density of the primary resource in case the resident population is not or only slightly specialized in feeding on the secondary resource. Therefore, a mutant that specializes more on the secondary resource than the resident would increase its resource intake and could therefore invade. Vice versa, the primary resource is more abundant than the secondary resource in case the resident population has a morphology highly specialized on the secondary resource (Fig. 4A). In this case a mutant that is less specialized would have a higher resource intake than the resident and could therefore invade. The specialization parameter ψ would therefore evolve to a value such that the density of the primary resource, X_1, almost equals the density of the secondary resource, X_2 (Fig. 4A). Since individuals would have a morphology specialized in feeding
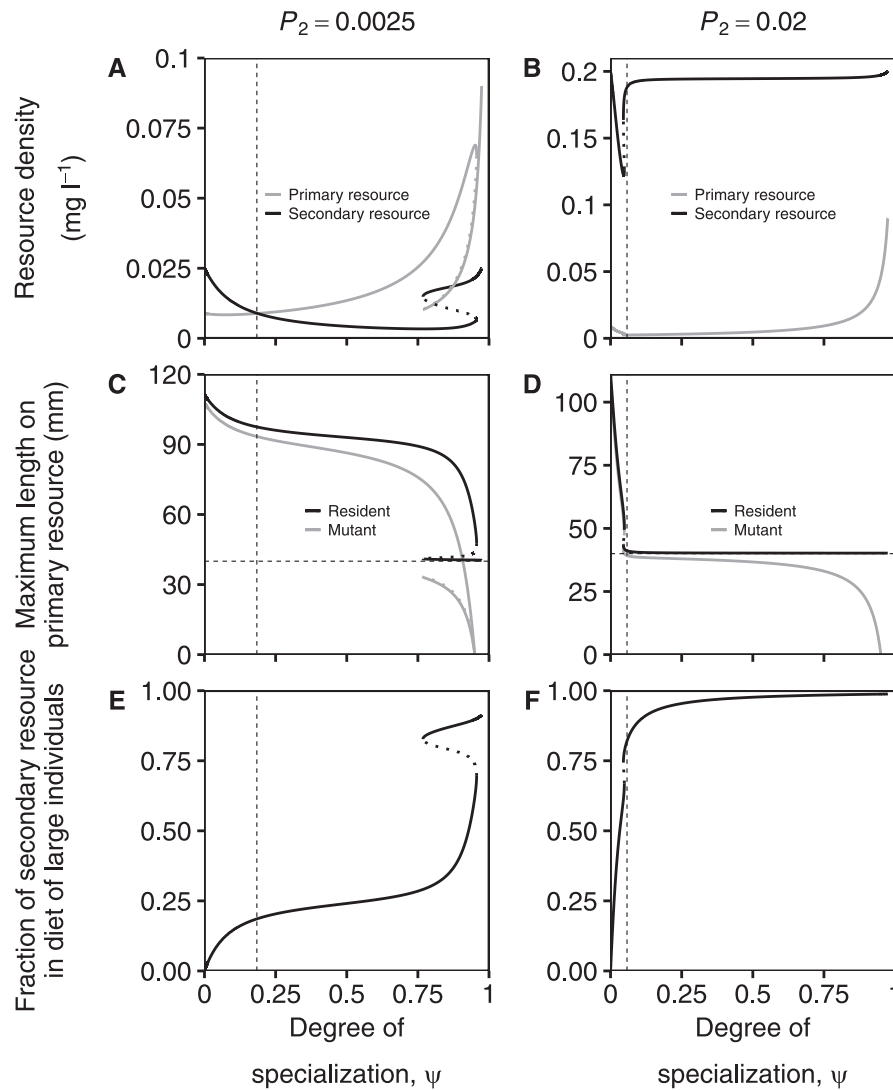
Fig. 4. Steady-state values predicted by the model as a function of the degree of specialization of the resident population. Solid and dashed lines refer to steady states that are unstable foci and saddle points, respectively. Upper panels A and B: Densities of the primary (grey line) and secondary (black line) resource (mg l^{-1}). Middle panels C and D: The maximum size (mm) individuals can reach when feeding only on the primary resource as a function of the degree of specialization (black line). The grey line indicates the maximum size that mutant individuals that are slightly more specialized in feeding on the secondary resource ($\psi_{\mathrm{mut}} = \psi_{\mathrm{res}} + 0.01$) can reach in the environment set by the resident strategy. The horizontal dashed line indicates a length of 40 mm, the size at which the second resource becomes available. Bottom panels E and F: The fraction of the secondary resource (calculated as Eq. (11)) in the diets of large individuals ($\ell \geq \ell_{\mathrm{v}}$). The vertical dashed lines indicate the location of the CSS if the resident population would be in the steady state (unstable). Other parameter values as in Table 3.

on the primary resource, the diet of large individuals would mainly consist of this resource in the CSS (Fig. 4E).

Increasing the supply rate of the secondary resource increases the value of ψ where the densities of both resources are equal. Therefore, the specialization parameter ψ would initially evolve to higher values with increasing supply rates (Figs. 3 and A.1). For high supply rates specialization on a secondary resource is, however, impeded by the trade-off between small and large individuals.

Fig. 4B shows that for high supply rates, the density of the secondary resource is always higher than the density of the primary resource, independent of the level of specialization. Large individuals almost exclusively forage on the secondary resource as soon as the specialization parameter $\psi > 0$ (Fig. 4F). It would for large individuals therefore be beneficial to specialize on the secondary resource. Nonetheless, the specialization parameter ψ does not evolve to high values (Fig. 3).

Because large individuals have a lot of food available as soon as $\psi > 0$, adults of the resident population produce many offspring that depress the density of the primary resource. The competition for this primary resource is then so intense, that the maximum size that small juveniles can reach while feeding on this resource, is barely above the threshold value for switching to the secondary resource (horizontal dashed line in Fig. 4D). Mutant individuals with a slightly larger value of specialization parameter ψ than the resident would be less effective in feeding on the primary resource (Eq. (10)). They would therefore not be able to reach the threshold size needed to switch to the secondary resource. These mutant individuals will never mature and cannot invade the resident population.

To summarize, for low supply rates the specialization parameter ψ evolves to low values since further specialization on a secondary resource would decrease the resource intake of large individuals (Fig. 4A). While large individuals do include the secondary resource in their diet, they mainly feed upon the primary resource
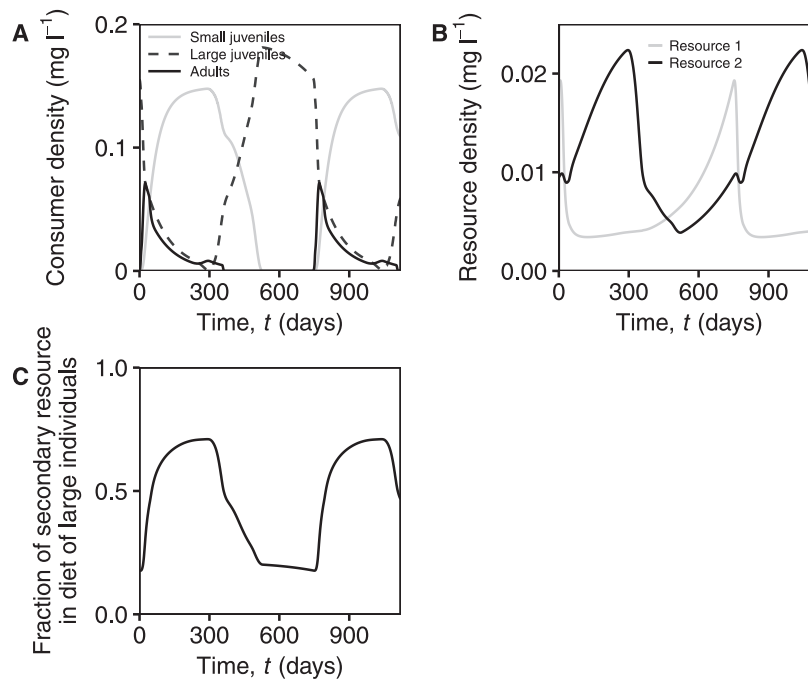
Fig. 5. Large-amplitude cycles in case of low supply rates of the secondary resource. Panel A: Density (mg l^{-1}) of small juveniles (grey, solid line), large juveniles (dark-grey, dashed line) and adults (black, solid line) over time (days). Panel B: Densities (mg l^{-1}) of the primary (grey) and secondary (black) resource over time. Panel C: Fraction of the secondary resource (calculated as Eq. (11)) in the diet of large individuals ($\ell \geq \ell_v$). $P_2 = 0.0025$ (mg l^{-1}day^{-1}), $\psi = 0.3$, other parameters as in Table 3.

(Fig. 4E). For high supply rates, large individuals mainly feed upon the secondary resource (Fig. 4F). It would therefore for large individuals be beneficial to evolve a morphology specialized in feeding on this abundant resource. However, competition among the abundant small individuals prevents the specialization parameter ψ to evolve to high values. Only for intermediate values of the supply rate, some specialization evolves (Figs. 3 and A.1). In that case increasing the specialization parameter ψ is beneficial for large individuals while at the same time competition among the smallest individuals is not severe enough to prevent specialization on the secondary resource.

3.5. Evolution of specialization in case of large-amplitude cycles

When the population exhibits large-amplitude cycles, the specialization parameter ψ can evolve to high values for most supply rates of the secondary resource (Figs. 3 and A.1). To explain why the degree of specialization ψ evolves to high values we will first discuss in detail the ecological dynamics (Figs. 5 and 7). We show in these figures a resident population with a strategy of $\psi = 0.3$. The ecological dynamics are, however, qualitatively the same for different values of ψ. In Figs. 6 and 8 we show the growth, survival probability and reproductive output of a resident individual ($\psi = 0.3$) and a mutant that is slightly more specialized on the secondary resource ($\psi = 0.31$). We will first explain how the degree of specialization evolves in case of low supply rates (Figs. 5 and 6), secondly we explain how the degree of specialization evolves for high supply rates (Figs. 7 and 8).

Fig. 5A shows that at day 0 a cohort of large juveniles matures and starts to reproduce at a high rate. Shortly afterward, the population mainly consists of small juveniles. Since these juveniles feed only on the primary resource, the density of this resource is low, while that of the secondary resource is high (Fig. 5B). Around day 300, small juveniles recruit to the large juvenile size class (Fig. 5A) and include the secondary resource in their diet (Fig. 5C). Therefore, the density of the secondary resource decreases while the

density of the primary resource increases (Fig. 5B). Around day 750, large juveniles mature into adults (Figs. 5A and 6A) that reproduce a new, abundant cohort of offspring (Fig. 5A). These offspring subsequently decrease the primary resource to very low levels (Fig. 5B), causing a high starvation mortality among their parents, which in turn leads to an increase in the secondary resource. Because the density of the secondary resource is higher than the density of the primary resource, a mutant that is slightly more specialized on the secondary resource has more food available than the residents, starves less (grey line Fig. 6B), and therefore produces more offspring (Fig. 6C). Because mutants are less effective on the primary resource they grow slightly slower (Fig. 6A), start reproducing later, and initially have a lower reproductive output than residents (first part of Fig. 6C). However, since the survival probability of the mutant is higher than that of the resident (Fig. 6B), the mutant reproductive output catches up with the resident around day 850 (Fig. 6C). Since the reproductive output of a mutant individual is ultimately higher than that of an individual of the resident population, it can invade in the population and the specialization parameter ψ will evolve to high values.

When the supply rate of the secondary resource is higher, the specialization parameter ψ evolves to high values as well (Figs. 3 and A.1). However, the mechanism behind the evolution of specialization is in this case different. As with low supply rates, the cycle starts off at day 0 with a cohort of large juveniles maturing and starting to reproduce (Fig. 7A). Because the supply rate of the secondary resource is high, many more offspring are produced compared to the case where the supply rate was low. Competition among the smallest individuals is therefore very high and growth is slow (Fig. 8A). Initially, the density of the primary resource is for both resident and mutant individuals too low to reach the threshold size where the secondary resource becomes available (Fig. 7B). Over time the density of small individuals decreases because of background mortality (Fig. 7A). This leads to an increase in the density of the primary resource such that recruitment to the next size class is possible (Fig. 7B). Around day 930 the first
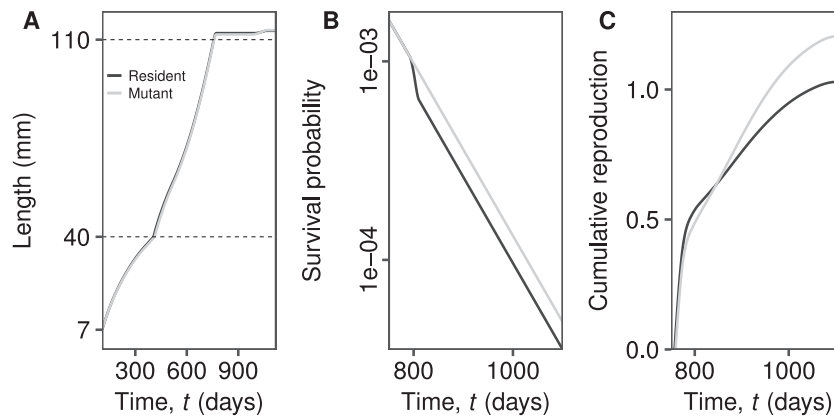
Fig. 6. Differences in growth (A), survival (B) and reproduction (C) of an individual of the resident population (black lines) and a mutant individual (grey lines) in the environment set by the resident population when the supply rate of the secondary resource is low (see Fig. 5 for the corresponding population dynamics). Panel A: Growth of a resident individual and a mutant born at day 107. The dashed lines indicate when the secondary resource becomes available (at a size of 40 mm) and when the individual matures (at a size of 110 mm). Panel B: Resident adults starve because of a lack of food while mutant adults stay alive in the environment set by the resident population and continue to reproduce. Panel C: Cumulative reproduction of a resident adult and a mutant adult over time in the environment set by the resident. $P_2 = 0.0025$ (mg l^{-1}day^{-1}), $\psi_{res} = 0.3$, $\psi_{mut} = 0.31$, other parameters as in Table 3.
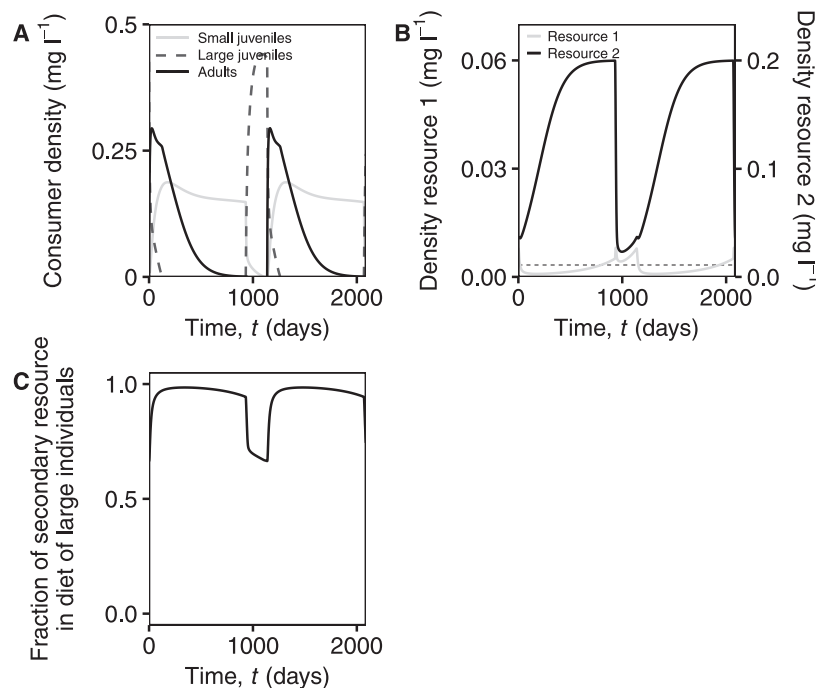

Fig. 7. Large-amplitude cycles in case of high supply rates of the secondary resource. Panel A: Density (mg l^{-1}) of small juveniles (grey solid line), large juveniles (dark-grey, dashed line) and adults (black, solid line) over time (days). Panel B: Densities (mg l^{-1}) of the primary (grey) and secondary (black) resource over time. The dotted line indicates the density of the primary resource that is necessary for resident individuals to reach a size of 40 mm. Panel C: Fraction of the secondary resource (calculated as Eq. (11)) in the diet of large individuals ($\ell \geq \ell_v$). $P_2 = 0.02$ (mg l^{-1}day^{-1}), $\psi = 0.3$, other parameters as in Table 3.

individuals recruit to the large juvenile size class. The secondary resource is now available and since it is very abundant (Fig. 7B), growth is accelerated (Fig. 8A). Around day 1100 the first large juveniles mature into adults (Figs. 7A and 8A). These adults can continue to grow since there is lots of the secondary resource available (Fig. 8A). The reproduction rate is therefore very high, leading to a large number of offspring (Fig. 7A). Even though these offspring decrease the density of the primary resource to very low levels (Fig. 7B), starvation among adults does not occur (Fig. 8B) since large individuals feed almost exclusively on the very abundant secondary resource (Fig. 7C).

Mutant individuals that are more specialized on the secondary resource initially grow slower. However, as soon as these mutants have access to the secondary resource, they grow faster and can re-produce more (Fig. 8C), since the density of the secondary resource is always higher than the density of the primary resource. Under equilibrium conditions, the specialization parameter ψ could not evolve to high values when the supply rate was high since this increased competition among the smallest individuals such that they could not grow to the next size class (Fig. 4D). When the population exhibits large-amplitude cycles, the primary resource increases as soon as the small juveniles of the resident population grow into the large juvenile size-class and start to forage on the secondary resource. This allows some mutant individuals to reach the threshold size for feeding on the secondary resource somewhat later. Since the secondary resource is very abundant, mutants can make up for the delay in the first part of their life and ultimately produce more offspring (Fig. 8C).
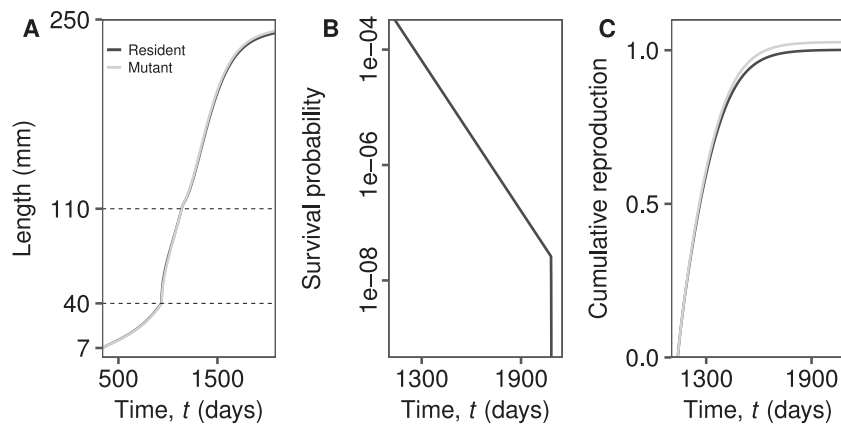
Fig. 8. Differences in growth (A), survival (B) and reproduction (C) of an individual of the resident population (black lines) and a mutant individual (grey lines) in the environment set by the resident population when the supply rate of the secondary resource is high (see Fig. 7 for the corresponding population dynamics). Panel A: Growth of a resident individual and a mutant born at day 335. The dashed lines indicate when the secondary resource becomes available (at a size of 40 mm) and when the individual matures (at a size of 110 mm). Panel B: The survival probability of resident adults and mutant adults is equal. Adults do not starve when a new cohort arrives because they can feed on the secondary resource. Panel C: Cumulative reproduction of a resident adult and a mutant adult over time in the environment set by the resident. $P_2 = 0.02$ (mg l^{-1}day^{-1}), $\psi_{res} = 0.3$, $\psi_{mut} = 0.31$, other parameter values as in Table 3.

4. Discussion

In this paper we studied the evolution of ontogenetic niche shifts under non-equilibrium dynamics. We showed that specialization on a resource that is available only for large individuals is hardly possible in case of small- or intermediate-amplitude cycles. Surprisingly, specialization on such a resource does evolve in case of large-amplitude cycles. To understand why specialization on a secondary resource does not evolve in case of small- or intermediate-amplitude cycles, we also analyzed the evolutionary dynamics assuming equilibrium dynamics, even though the steady state of the model analyzed here is ecologically unstable. While it was shown before that specialization on a secondary resource is hardly possible under equilibrium conditions (ten Brink and de Roos, 2017), we here reveal the mechanisms that prevent this.

Our results show that different ecological dynamics lead to different selection pressures and therefore to very different evolutionary outcomes. These differences occur because of the different ecological conditions that individuals experience depending on the type of population cycles. Notably, these different types of population cycles are all internally generated and co-occur for the same parameter set. In case of large-amplitude cycles and low supply rates of the secondary resource, adults experience high juvenile-driven starvation mortality, which makes it advantageous to specialize on a secondary resource. These starvation conditions do not occur in case of small- and intermediate-amplitude cycles or when we assume equilibrium conditions. In case of equilibrium conditions and high supply rates of the secondary resource, the constant presence of small individuals would suppress the primary resource to such low levels that less efficient individuals would not be able to grow sufficiently to reach the second feeding niche. While competition for the primary resource is still severe in case of large-amplitude cycles, the recruitment of the dominant cohort to the next size class releases competition for the primary resource during a short time-interval, allowing less efficient individuals to mature.

The large-amplitude single cohort cycles that allow for the evolution of specialization on a secondary resource occur because small individuals can, in the absence of an ontogenetic niche shift, outcompete their parents (de Roos et al., 1990). Due to the differences in scaling between intake (with a power of 2/3) and metabolic demands (with a power of 1) with body weight, smaller individuals can withstand lower resource levels than larger in-

dividuals. Large-amplitude cycles where adults quickly die after reproducing because of juvenile-induced starvation mortality, are common predictions of size-structured consumer-resource models (de Roos and Persson, 2003, 2013; Persson et al., 1998). We therefore expect that our result is not specific for the chosen model formulation, but can be found in many size-structured models.

Our results suggest that the type of population dynamics plays an important role in the evolution of ontogenetic niche shifts. We predict that specialization on a resource used later in life is only possible in case the population exhibit large-amplitude cohort cycles. Such cycles where newborn individuals outcompete their parents have been reported for several freshwater fish species (Hamrin and Persson, 1986; Persson and De Roos, 2006; Townsend et al., 1990). It is expected that intercohort competition of small individuals on large individuals mainly occurs in small habitats, such as lakes, where all life stages of the population occupy the same area (Andersen et al., 2017). Large-amplitude cohort cycles are less likely to occur in fish species occupying large habitats, such as marine fish population (Andersen et al., 2017). It would be interesting to compare the occurrence of ontogenetic niche shifts in fish in freshwater and marine systems to test our prediction that niche shifts can be driven by population dynamics. One complication of such a study is that it is rather difficult to empirically show if a species is specialized on the resource used later in life and not efficient in feeding on the resource used early in life. Such a test requires the comparison of diets, feeding efficiencies, and morphologies of different populations or closely related species.

Even though individuals specialize on the secondary resource in case of large-amplitude cycles, it would still be beneficial for them to be effective on the primary resource as well. Small individuals depend on this resource for their growth and they can therefore reproduce earlier on in their life when they are more effective in feeding. Metamorphosis allows for the independent evolution of stage-specific traits, such that small juveniles can specialize on the primary resource while large juveniles and adults specialize on the secondary resource (Moran, 1994). It has been shown that, under equilibrium conditions, metamorphosis can evolve to increase the level of specialization of small individuals on the primary resource, even though metamorphosis is very costly for larger individuals (unpublished results). While there is probably selection to increase juvenile performance, it is still an open question if the benefits of better specialized juveniles outweigh the costs of metamorphosis in case of large-amplitude cycles.
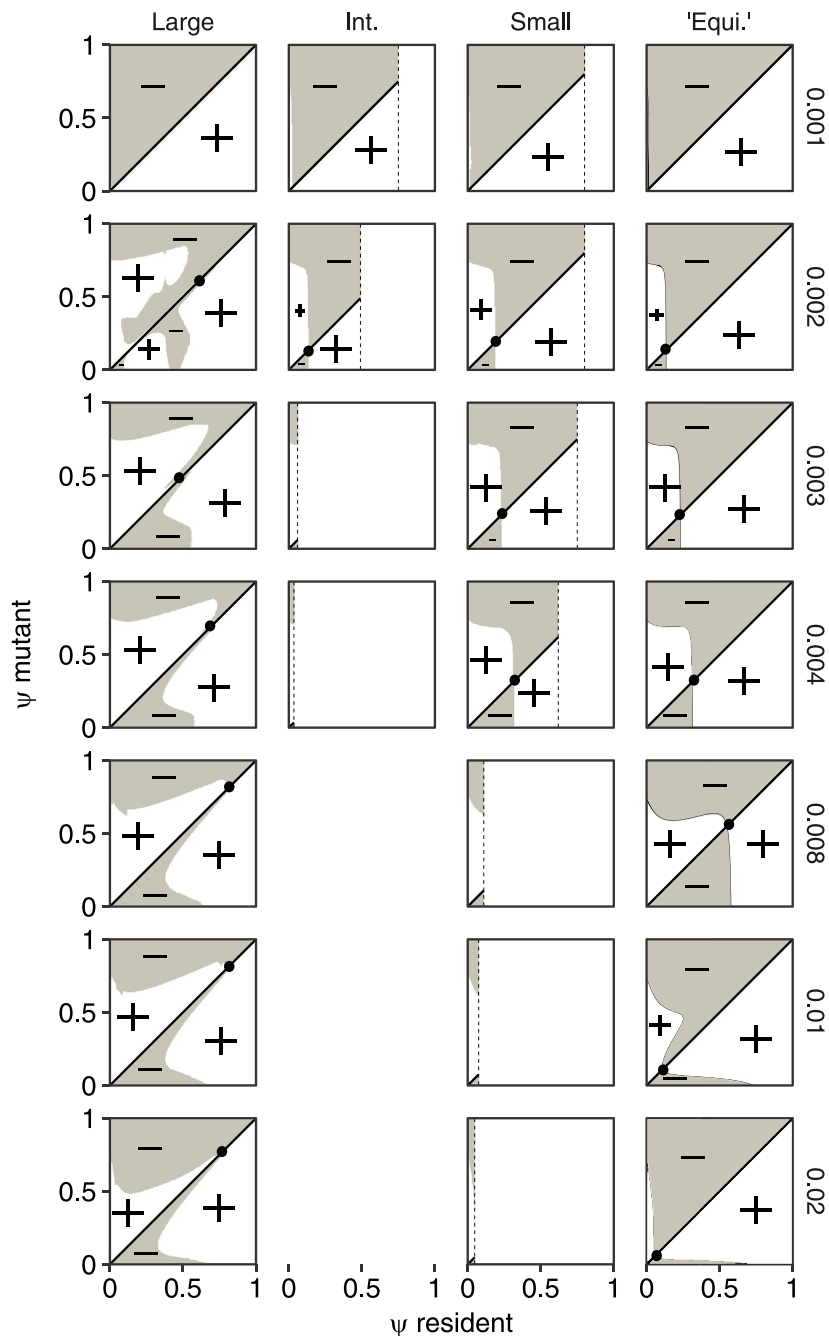
Fig. A.1. Pairwise invasibility plots for different types of population dynamics and different values of the supply rate of the secondary resource (mg l^{-1}day^{-1}). The grey areas indicate negative invasion fitness, the white areas positive. The black dots indicate the locations of the CSSs. The dashed line in the PIPs for intermediate- and small-amplitude cycles indicates where these types of cycles disappear. For clarity we have omitted the PIPS for intermediate-amplitude cycles in case of high supply rates. These type of cycles disappear as soon as specialization parameter $\psi > 0$. Parameter values as in Table 3.

It has been shown before that non-equilibrium dynamics can lead to different evolutionary outcomes compared to equilibrium conditions (Hoyle et al., 2011; Nurmi and Parvinen, 2013; Parvinen, 1999; White et al., 2006). Parvinen (1999) showed that migration is beneficial in case the population is in a two-cyclic orbit, but not in case of equilibrium conditions. White et al. (2006) and Hoyle et al. (2011) showed with the use of a discrete-time model that under non-equilibrium conditions and with certain trade-offs, evolutionary branching is possible in ecological scenarios that do not allow for branching under equilibrium conditions. Nurmi and Parvinen (2013) looked into the evolution of resource specialization and identified evolutionary scenarios, such as evolutionary suicide, that were found only under non-equilibrium conditions.

Our work differs in three main aspects from these results. First, in our model different types of ecological dynamics are possible for the same set of parameters. Dependent on the initial conditions, the consumer population can exhibit three types of population cycles which lead to two different evolutionary outcomes. This is in contrast with the studies mentioned above (except Parvinen, 1999), that all showed a change in population dynamics (and therefore evolutionary dynamics) as a function of a change in a parameter value. A second difference is that independent of the type of population dynamics, we always find continiously stable strategies (CSSs). The type of population dynamics only affects the location of these CSSs. This is in contrast with the work of Parvinen (1999), White et al. (2006), Hoyle et al. (2011), and

Nurmi and Parvinen (2013) who all find that non-equilibrium dynamics change the type of evolutionary attractor, e.g., from an evolutionary repeller to an evolutionary branching point. Lastly, most of these studies find changes in the type of evolutionary attractor in case of non-linear trade-offs but not for linear trade-offs (Hoyle et al., 2011; Nurmi and Parvinen, 2013; White et al., 2006). We found different evolutionary outcomes depending on the type of dynamics, even though we assumed a linear trade-off between the attack rates on the primary and secondary resource. It is likely that different trade-offs lead to even more distinct evolutionary outcomes, dependent on the type of population dynamics. The boundary in the PIPs between mutant types that can and can not invade the resident population in case of small- and intermediate-amplitude cycles intersects the diagonal almost vertically. A slight change in the trade-off function could therefore already change the ESS to an evolutionary branching point. However, the effect of different trade-off functions on the evolution of ontogenetic niche shifts is beyond the scope of this study.

In summary, we showed that population cycles have a striking effect on the evolution of ontogenetic niche shifts. The evolutionary outcome can be completely reversed when the type of population dynamics change. These results have important consequences, since population cycles resulting from size-dependent interactions are a common observation in natural systems (Murdoch et al., 2002). It is therefore essential to consider the effect of the type of population cycles when studying the evolution of life-history traits.

Acknowledgments

Appendix A

In this appendix we show pairwise invasibility plots (PIPs) for many different supply rates of the secondary resource.

Fig. A.1 shows that the PIPs for small- and intermediate-amplitude cycles are similar to the PIPs where equilibrium dynamics are assumed. The specialization parameter ψ initially evolves to higher values with increasing supply rates. Because the secondary resource is available at high density, it is beneficial for individuals to specialize in feeding on that resource. However, for high values of the supply rate, parameter ψ will evolve to very low values. This implies that consumers are very efficient in feeding on the primary resource and not on the secondary resource. Competition among the smallest individuals hinders specialization on the resource used later in life.

The specialization parameter ψ evolves to high values in case of large-amplitude cycles (Fig. A.1). Only when the supply rate is very low ($0.001\ \mathrm{mg\ l^{-1}day^{-1}}$), individuals will specialize in feeding on the primary resource.

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