

# A general approach for analysis of physiologically structured population models: the R package ‘PSPManalysis’

André M. de Roos

Institute for Biodiversity and Ecosystem Dynamics  
University of Amsterdam, Amsterdam, The Netherlands

and

Santa Fe Institute, Santa Fe, New Mexico 87501, USA

Email: [A.M.deRoos@uva.nl](mailto:A.M.deRoos@uva.nl)

ORCID ID: <https://orcid.org/0000-0002-6944-2048>

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**Running head:** Steady state analysis of PSPMs

## Summary

1. How environmental conditions affect the life history of individual organisms and how these effects translate into dynamics of population and communities on ecological and evolutionary time scales is a central question in many eco-evolutionary studies.
2. Physiologically structured population models (PSPMs) offer a theoretical approach to address such questions as they are built upon a function-based model of the life history, which explicitly describes how life history depends on individual traits as well as on environmental factors. PSPMs furthermore explicitly account for population feedback on these environmental factors, which translates into density-dependent effects on the life history. PSPMs can thus capture life histories in quite some detail but lead to population-level formulations in terms of partial differential equations that are generally hard to analyse.
3. Here I present a general methodology and a R software package for computing how the ecological steady states of PSPMs depend on model parameters and to detect bifurcation points in the computed curves where dynamics change drastically. The package makes specifying the population model unnecessary and only requires a relatively straightforward implementation of the life history functions as input. It furthermore allows for analysing the evolutionary dynamics and evolutionary singular states of the PSPMs based on Adaptive Dynamics theory.
4. Given the central role of the individual life history in many studies, there is substantial scope for using the presented methodology in fields as diverse as ecology, ecotoxicology, conservation biology and evolutionary biology, where it has already been applied to problems like the evolution of cannibalism, niche shifts and metamorphosis.

## Keywords

Steady state computations, bifurcation analysis, life history, demography, environmental feedback, evolutionary analysis, adaptive dynamics

## Introduction

1 The life history of individual organisms plays a central role in ecology and evolution, determining the  
2 demography of populations and thereby their persistence and existence. Together with the interactions  
3 with other species it shapes the dynamics of interacting populations and communities and through mu-  
4 tation and selection it leads to evolutionary change in species traits. Methodologies to assess how life  
5 history characteristics translate into consequences at the population level, such as population growth  
6 rate, are hence a core part of many ecological and evolutionary studies.

7 Modelling approaches that describe population and community dynamics explicitly on the basis of in-  
8 dividual life histories are referred to as structured-population models (Tuljapurkar & Caswell, 1997).  
9 Matrix models (Caswell, 2001) are the most common type of structured-population models. Matrix  
10 models describe the population dynamics in discrete time, as do integral projection models (IPMs, Ell-  
11 ner, Childs, & Rees, 2016). Structured-population models describing dynamics in continuous time  
12 include stage- (Nisbet & Gurney, 1983) and size-structured population models (Sinko & Streifer, 1969;  
13 de Roos, Metz, Evers, & Leipoldt, 1990), which both belong to the more general class of physiolog-  
14 ically structured population models (PSPMs, Metz & Diekmann, 1986; de Roos, 1997). Although all  
15 structured-population models explicitly include a modeled representation of individual life history, they  
16 differ in the way they account for this life history (de Roos, 2020). Matrix models and IPMs are primar-  
17 ily data driven. IPMs, for example, are formulated using (non-)linear relationships that result from fitting  
18 observational data on the scaling of somatic growth rate and fecundity with individual body size (Rees,  
19 Childs, & Ellner, 2014). In contrast, PSPMs (Metz & Diekmann, 1986; de Roos, 1997) are formulated  
20 using a function-based model of the individual life history, which also accounts for the effect of envi-  
21 ronmental variables, such as food availability and predator density, on this life history (de Roos, 2020).  
22 For example, individual foraging, growth and reproduction are in many PSPMs described by a dynamic  
23 energy budget model for individual energetics (Kooijman, 2010). In turn, PSPMs account for how these  
24 environmental variables are impacted by the population as a whole. PSPMs hence capture with more  
25 mechanistic detail how individual-level processes, like energetics, together with the interactions of the  
26 individual with its environment shape the life history and how the feedback of the entire population on  
27 this environment has a density-dependent impact on that life history. PSPMs are therefore especially

28 suited to analyse how particular mechanisms or aspects of the life history or ecology of an individual  
29 would affect the population and community dynamics.

30 The downside of the increased mechanistic detail of PSPMs is their mathematical tractability (de Roos,  
31 2020). Where linear algebra offers a rich tool set to analyse matrix models and IPMs, simple PSPMs  
32 are formulated in terms of the more daunting partial differential equations (Metz & Diekmann, 1986;  
33 de Roos, 1997). Fortunately, though, a collection of numerical techniques is now available that allows  
34 for analysing the ecological and evolutionary dynamics of even fairly complicated PSPMs (Hin & de  
35 Roos, 2019a; ten Brink, de Roos, & Dieckmann, 2019; Chaparro Pedraza & de Roos, 2020). The aim  
36 of this paper is to provide an introduction to these techniques and to the R package ‘PSPManalysis’  
37 implementing them. This toolbox includes techniques for the demographic and steady-state analysis  
38 (Diekmann, Gyllenberg, & Metz, 2003; de Roos, 2008) of PSPMs, which also allow for the analysis  
39 of evolutionary dynamics of PSPMs, based on the framework of ‘Adaptive Dynamics’ (Dieckmann  
40 & Law, 1996; Metz, Geritz, Mesz ena, Jacobs, & van Heerwaarden, 1996; Geritz, Kisdi, Mesz ena, &  
41 Metz, 1998). In addition, the ‘PSPManalysis’ package includes the ‘Escalator Boxcar Train’ (de Roos,  
42 Diekmann, & Metz, 1992), a numerical integration technique specifically developed for PSPMs.

43 To use the ‘PSPManalysis’ package it is not necessary to bother with the population-level representation  
44 of the model in terms of partial differential equations or the like. The user can concentrate on the life  
45 history and the ecology of the individual organisms. The necessary ingredients of the model specification  
46 are conceptually straightforward as they include (i) the individual state variables (traits), such as age or  
47 body size, that determine the life history; (ii) the environmental variables, such as food availability or  
48 predation pressure, that impinge on and shape the life history; (iii) the rates of development, reproduction  
49 and mortality dependent on these individual state and environmental variables; (iv) how an individual  
50 impacts its environment; and (v) the conditions determining that the environment of the individuals is in  
51 steady-state. The routines implemented in the ‘PSPManalysis’ package take these individual life history  
52 ingredients as input and numerically analyse their population-level consequences, both in ecological and  
53 evolutionary time.

## 54 **Materials and methods**

### 55 **The individual life history model**

56 To illustrate the analysis of ecological steady states and the evolutionary analysis of PSPMs with the  
57 ‘PSPManalysis’ package I use the life-history model described in Chaparro Pedraza and de Roos (2020)  
58 as an example. This model is loosely based on the life history of salmon with individuals starting their  
59 life in a safe nursery habitat, in which they are protected from predation but suffer from competition for  
60 resources. At some point during their life the individuals switch to a more risky growing habitat, where  
61 competition for resources is absent, but individuals are exposed to predation mortality. All equations  
62 occurring in the model are presented in Table 1, while Table S1 in the supporting information lists all  
63 parameters with their default values.

64 Individuals are in the model characterised by their length  $\ell$  and their population, to which I will refer  
65 to as the ‘consumer’ population, is hence length-structured. Migration to the growing habitat and mat-  
66 uration occur on reaching threshold body sizes, at length  $\ell = \ell_s$  and  $\ell = \ell_m$ , respectively. Feeding on  
67 resources, growth in body size and reproduction are in the model described by the dynamic energy bud-  
68 get (DEB) model developed by Jager, Martin, and Zimmer (2013). In the nursery habitat the consumers  
69 compete for a shared resource  $X$  at a rate that is proportional to their squared length and to the scaled  
70 functional response value  $X/(K + X)$  (Table 1). In the growth habitat competition is assumed negligi-  
71 ble and individuals have *ad-libitum* food. The DEB model predicts individuals under constant resource  
72 densities to grow in length following a vonBertalanffy growth curve with ultimate body length equal to  
73  $\ell_{inf} X/(K + X)$  and  $\ell_{inf}$  in the nursery and growth habitat, respectively (Table 1). Reproduction only  
74 occurs after individuals have migrated to the growth habitat since  $\ell_s < \ell_m$ . Following the DEB model  
75 adult fecundity is proportional to squared individual length.

76 Consumer mortality in the nursery habitat is assumed constant, while in the growth habitat mortality is  
77 negatively size-dependent, proportional to  $\ell^{-d}$  (Table 1). In Chaparro Pedraza and de Roos (2020) size-  
78 dependent mortality in the growth habitat is assumed non-dynamic. Here I assume it to be proportional  
79 to the density of a dynamic, unstructured predator population that forages on consumers of different  
80 length following a linear functional response and that experiences a constant mortality rate  $\mu_p$ . In the

81 model this predator population is represented with its scaled density, which incorporates the (constant)  
82 conversion efficiency between ingested biomass of consumers and the predator's numerical response,  
83 indicated with  $B$  (Table 1). The contribution of individual consumers to predator intake equals the  
84 product of their vulnerability to predation and their biomass  $\ell^3$ . Finally, following Chaparro Pedraza  
85 and de Roos (2020) turn-over of the resource in nursery habitat in the absence of consumers is described  
86 by a semi-chemostat growth equation.

87 This tritrophic interaction between a resource and a size-structured consumer population in a nursery  
88 habitat, which goes through a habitat shift during its life history and subsequently supports a specialist  
89 predator population in the growth habitat, is fully determined by 3 life history functions, describing  
90 development, reproduction and mortality ( $\gamma(\ell, X)$ ,  $\beta(\ell)$ , and  $\mu(\ell, P)$  in Table 1, respectively), 2 functions  
91 describing the impact of differently sized consumer individuals on their environment through foraging on  
92 the resource and contribution to predator food intake ( $\alpha(\ell, X)$  and  $\varepsilon(\ell)$ , respectively), and by 2 functions  
93 that determine the dynamics of the shared resource in the nursery habitat and the predator in the growth  
94 habitat ( $g(R)$  and  $h(B)$ , respectively; Table 1).

## 95 **General methodology**

96 In the context of PSPMs Metz and Diekmann (1986) introduced the fundamental distinction between the  
97 individual and its environment with accompanying state concepts. The crucial aspect of this distinction  
98 is that the individual life history is fully determined by the state of the individual in combination with the  
99 state of its environment. Given a constant environment all individuals are therefore independent, which  
100 implies that in PSPMs all forms of density dependence operate through the environment. As a further  
101 consequence, the individual life history functions are the only necessary ingredients for the computation  
102 of population equilibrium states. I will shortly present the general methodology for computation of  
103 equilibria in PSPMs here using the tritrophic model introduced above, but it should be stressed that it is  
104 straightforward to generalise the methodology to far more complex PSPMs (see Diekmann et al., 2003,  
105 for a detailed discussion).

Given a constant, equilibrium resource density  $\tilde{X}$  in the nursery habitat the individual length in equilibrium  $\tilde{\ell}(a, \tilde{X})$  as a function of age  $a$  and resource density  $\tilde{X}$  is the solution of the ordinary differential

equation (ODE):

$$\frac{d\tilde{\ell}}{da} = \gamma(\tilde{\ell}(a, \tilde{X}), \tilde{X}) \quad (1)$$

with initial condition  $\tilde{\ell}(0, \tilde{X}) = \ell_0$ . Similarly, denoting the equilibrium predator density in the growth habitat as  $\tilde{P}$ , the probability for an individual to survive up to age  $a$ , which I indicate with  $\mathcal{F}(a, \tilde{X}, \tilde{P})$ , is the solution of the ODE:

$$\frac{d\mathcal{F}}{da} = -\mu(\tilde{\ell}(a, \tilde{X}), \tilde{P}) \mathcal{F}(a, \tilde{X}, \tilde{P}) \quad (2)$$

106 with initial condition  $\mathcal{F}(0, \tilde{X}, \tilde{P}) = 1$ . Notice that survival depends on both resource and predator density  
107 in equilibrium, as the resource density determines how quickly individual consumers grow and hence  
108 how long they experience low mortality in the nursery habitat and the predator density influences their  
109 survival in the growth habitat.

The expected reproduction rate by a consumer individual at a particular age equals its fecundity times the probability it survives up to that age. Accumulating these reproductive contributions by integration over all possible ages that individuals can reach results in the following expression for the expected number of offspring produced by a single consumer individual throughout its lifetime, indicated with  $R_0$ , as a function of resource density  $\tilde{X}$  and predator density  $\tilde{P}$ :

$$R_0(\tilde{X}, \tilde{P}) = \int_0^{\infty} \beta(\tilde{\ell}(a, \tilde{X})) \mathcal{F}(a, \tilde{X}, \tilde{P}) da \quad (3)$$

110 Obviously, the equilibrium state of the size-structured consumer population is determined by the con-  
111 dition  $R_0(\tilde{X}, \tilde{P}) = 1$ , implying that every newborn consumer is expected to just replace itself during  
112 life.

For the resource density in the nursery habitat to be in equilibrium the resource turn-over should balance total resource consumption by all consumers in the nursery habitat. The latter equals the product of the amount of resources that an individual consumer is expected to consume during its life time and the consumer population birth rate, which I will indicate with  $\tilde{b}$ . The expected lifetime consumption by an individual is an integral similar to the expression above for  $R_0$  but involving the foraging rate  $\alpha(\ell, X)$  as opposed to the fecundity  $\beta(\ell)$ . The steady-state condition for the resource is hence given by the

condition:

$$G(\tilde{b}, \tilde{X}, \tilde{P}) = g(\tilde{X}) - \tilde{b} \int_0^{\infty} \alpha(\tilde{\ell}(a, \tilde{X}), \tilde{X}) \mathcal{F}(a, \tilde{X}, \tilde{P}) da = 0 \quad (4)$$

113 in which the integral represents the expected lifetime resource intake by a single consumer.

Lastly, the predator population in the growth habitat is in steady state when its numerical response  $B$  equals its per-capita mortality rate  $\mu_p$ . Given the scaling of the predator population density such that its numerical response equals its functional response, the quantity  $B$  equals the product of the consumer population birth rate  $\tilde{b}$  and the expected amount of biomass that a consumer individual during its lifetime contributes to the per-capita food intake rate of the predator. The latter is given by an integral similar to the expression for  $R_0$  in equation (3) but involving the function  $\varepsilon(\ell)$  as opposed to the fecundity  $\beta(\ell)$ . The steady-state condition for the predator is given by the condition:

$$H(\tilde{b}, \tilde{X}, \tilde{P}) = \tilde{b} \int_0^{\infty} \varepsilon(\tilde{\ell}(a, \tilde{X})) \mathcal{F}(a, \tilde{X}, \tilde{P}) da - \mu_p = 0 \quad (5)$$

114 The integral in the above expression represents the expected lifetime contribution by a consumer to the  
115 food intake of a single predator.

116 Even though the ODE (1) for the growth in length is in the current model sufficiently simple to allow for  
117 an explicit expression for the length at age  $\ell(a, \tilde{X})$  in equilibrium, analytical evaluation of the integrals  
118 in the expressions for  $R_0(\tilde{X}, \tilde{P})$ ,  $G(\tilde{b}, \tilde{X}, \tilde{P})$  and  $H(\tilde{b}, \tilde{X}, \tilde{P})$  is not possible because of the dependence of  
119 consumer mortality on length. Hence, steady states of the PSPM can only be computed by solving the  
120 equilibrium conditions (eqs. (3), (4) and (5)) numerically and iteratively for the unknown variables  $\tilde{b}$ ,  
121  $\tilde{X}$  and  $\tilde{P}$ . Solving such a system of (non-linear) equations can be achieved by standard methods, such  
122 as the Newton-Raphson method (Press, Flannery, Teukolsky, & Vetterling, 1988), but for the fact that  
123 it is impossible to derive explicit expressions for the integrals in the functions  $R_0(\tilde{X}, \tilde{P})$ ,  $G(\tilde{b}, \tilde{X}, \tilde{P})$  and  
124  $H(\tilde{b}, \tilde{X}, \tilde{P})$  even in a model as simple as the one discussed here. Definitely, the same holds for more  
125 complex PSPMs as well.

The key idea to address this issue, originally proposed by Kirkilionis et al. (2001), is to consider the integrals occurring in the equilibrium conditions as a function of the upper limit of the integration and



define the following functions:

$$\begin{aligned}
 R_0(a, \tilde{X}, \tilde{P}) &= \int_0^a \beta(\tilde{\ell}(\zeta, \tilde{X})) \mathcal{F}(\zeta, \tilde{X}, \tilde{P}) d\zeta \\
 I_1(a, \tilde{X}, \tilde{P}) &= \int_0^a \alpha(\tilde{\ell}(\zeta, \tilde{X}), \tilde{X}) \mathcal{F}(\zeta, \tilde{X}, \tilde{P}) d\zeta \\
 I_2(a, \tilde{X}, \tilde{P}) &= \int_0^a \varepsilon(\tilde{\ell}(\zeta, \tilde{X})) \mathcal{F}(\zeta, \tilde{X}, \tilde{P}) d\zeta
 \end{aligned}$$

The value of these integrals can then be computed by numerically integrating the system of ODEs:

$$\left\{ \begin{array}{ll}
 \frac{d\tilde{\ell}}{da} = \gamma(\tilde{\ell}(a, \tilde{X}), \tilde{X}) & \tilde{\ell}(0, \tilde{X}) = \ell_0 \\
 \frac{d\mathcal{F}}{da} = -\mu(\tilde{\ell}(a, \tilde{X}), \tilde{P}) \mathcal{F}(a, \tilde{X}, \tilde{P}) & \mathcal{F}(0, \tilde{X}, \tilde{P}) = 1 \\
 \frac{dR_0}{da} = \beta(\tilde{\ell}(a, \tilde{X})) \mathcal{F}(a, \tilde{X}, \tilde{P}) & R_0(0, \tilde{X}, \tilde{P}) = 0 \\
 \frac{dI_1}{da} = \alpha(\tilde{\ell}(a, \tilde{X}), \tilde{X}) \mathcal{F}(a, \tilde{X}, \tilde{P}) & I_1(0, \tilde{X}, \tilde{P}) = 0 \\
 \frac{dI_2}{da} = \varepsilon(\tilde{\ell}(a, \tilde{X})) \mathcal{F}(a, \tilde{X}, \tilde{P}) & I_2(0, \tilde{X}, \tilde{P}) = 0
 \end{array} \right. \quad (6)$$

for the length  $\tilde{\ell}(a, \tilde{X})$  at age  $a$ , survival  $\mathcal{F}(a, \tilde{X}, \tilde{P})$ , expected cumulative reproduction  $R_0(a, \tilde{X}, \tilde{P})$ , expected cumulative resource ingestion  $I_1(0, \tilde{X}, \tilde{P})$  and expected biomass contribution to the predator food intake  $I_2(0, \tilde{X}, \tilde{P})$  of a consumer individual up to age  $a$  (The ODEs for these last 3 quantities are derived by differentiating their integral expressions with respect to  $a$ ). Using these quantities the steady-state conditions of the PSPM can be expressed as:

$$\left\{ \begin{array}{l}
 R_0(\infty, \tilde{X}, \tilde{P}) = 1 \\
 \tilde{b} I_1(\infty, \tilde{X}, \tilde{P}) = g(\tilde{X}) \\
 \tilde{b} I_2(\infty, \tilde{X}, \tilde{P}) = \mu_p
 \end{array} \right. \quad (7)$$

126 The Newton-Raphson method can be used to solve this system of equations iteratively for the unknown  
 127 variables  $\tilde{b}$ ,  $\tilde{X}$  and  $\tilde{P}$ , but for every evaluation of these equations the ODEs (6) have to be integrated  
 128 numerically. This integration in theory has to proceed until infinite age but in practice integration is  
 129 stopped when the probability to survive  $\mathcal{F}(a, \tilde{X}, \tilde{P})$  has dropped below some very low value (e.g.  $1.0 \cdot$

130  $10^{-9}$ ).

131 The methodology discussed above is sufficiently general that it can be applied to a wide range of PSPMs,  
132 including those with finitely many individual and environmental state variables and with individuals that  
133 are born with finitely many different states at birth (Diekmann et al., 2003). The R package ‘PSP-  
134 Manalysis’ uses this methodology to compute steady states of PSPMs but also implements pseudo-  
135 arclength continuation techniques to compute steady state curves as a function of 1 or 2 model param-  
136 eters (Kuznetsov, 1998, Chapter 10). The results section illustrates how to use this curve continuation  
137 approach for model analysis. While computing such curves the ‘PSPManalysis’ package furthermore  
138 detects certain bifurcation points, which are points along a curve where the nature of the computed equi-  
139 librium undergoes a qualitative change. As illustrated in the results section, such a qualitative change  
140 could refer to whether or not a particular equilibrium state can or can not be invaded by a population.  
141 For the detection of these bifurcation points the ‘PSPManalysis’ package again uses the techniques and  
142 tests presented in Kuznetsov (1998, Chapter 10).

Diekmann et al. (2003) discuss that the approach to compute steady states of PSPMs can also be used  
to analyse evolutionary dynamics using the theory of Adaptive Dynamics (Dieckmann & Law, 1996;  
Metz et al., 1996; Geritz et al., 1998). Adaptive dynamics theory explicitly relates evolution by natural  
selection to population dynamics by considering whether rare mutant phenotypes can invade and take  
over a resident population. The invasion fitness of such rare mutants is determined by their population  
growth rate under the environmental conditions imposed by the population with resident phenotype.  
Because the quantity  $R_0(\infty, \tilde{X}, \tilde{P}) - 1$  has the same sign as this mutant invasion fitness, it can be used  
as fitness proxy (Diekmann et al., 2003; Durinx, Metz, & Meszéna, 2007). Therefore, the sign of the  
selection gradient is determined by the derivative of  $R_0(\infty, \tilde{X}, \tilde{P})$  with respect to a model parameter  
representing a life history trait. I will focus below on the length to switch to the growth habitat  $\ell_s$ .  
Endpoints of evolution in  $\ell_s$ , also referred to as *evolutionarily singular strategies* or ESSs then satisfy  
the condition

$$\frac{dR_0(\infty, \tilde{X}, \tilde{P})}{d\ell_s} = 0$$

143 which implies that the invasion fitness reaches a maximum or minimum and the selection gradient van-  
144 ishes for the given set of environmental conditions  $\tilde{X}$  and  $\tilde{P}$ . The characteristics of the ESS can be

145 determined on the basis of second-order derivatives of  $R_0(\infty, \tilde{X}, \tilde{P})$  with respect to the life history pa-  
146 rameter as explained in detail by Geritz et al. (1998). Furthermore, the fitness gradient  $dR_0(\infty, \tilde{X}, \tilde{P})/d\ell_s$   
147 also determines the rate at which the life history trait  $\ell_s$  changes over evolutionary time following the  
148 ‘canonical equation of Adaptive Dynamics’ derived by Dieckmann and Law (1996).  
149 Detailed introductions to the theory of adaptive dynamics are found in Dieckmann and Law (1996), Metz  
150 et al. (1996), Geritz et al. (1998), Durinx et al. (2007), and Lion (2018). The ‘PSPManalysis’ package  
151 implements the techniques and conditions from adaptive dynamics discussed in these publications to  
152 locate ESSs and to identify their properties; for example, by classifying them as a ‘continuously stable  
153 strategy’, which refers to an ESS to which the life history trait evolves and is furthermore evolutionary  
154 stable, or as ‘branching point’, where evolutionary branching or diversification can occur (see Geritz et  
155 al., 1998, for details). For this purpose the ‘PSPManalysis’ package computes the first and second-order  
156 derivatives of  $R_0(\infty, \tilde{X}, \tilde{P})$  with respect to a life history parameter through numerical differentiation.

### 157 **Model implementation for ‘PSPManalysis’**

158 The life history model presented in Table 1 has to be implemented in an R script to be analysed with  
159 the ‘PSPManalysis’ package. The implementation requires the specification of 3 vectors and 4 functions  
160 (see Table 2). The vectors define the model dimensions, the environmental state variables and the model  
161 parameters, whereas the functions define the right-hand side of the ODEs (6), their starting values and  
162 the boundaries of the different stages in the life history as well as the last two of the conditions (7)  
163 that determine the steady states of the environmental variables. In the Supporting Information this  
164 implementation of the example model in R is discussed in more detail.

165 Although the life-history model to be analysed can be specified in R, the entire ‘PSPManalysis’ package  
166 is written in the C language. The package is designed in such a way that implementation of the life  
167 history model in C is also possible and in fact preferable. The implementation of the example model  
168 used in this paper in the C language is included in the Supporting Information to this paper as a C header  
169 file (with extension .h). The implementation in C has a similar, self-explanatory layout as the model  
170 implementation in R shown in Table 2 and adaptation of the implementation for another PSPM should  
171 only require basic knowledge of the C language. Specifying the model definition in R may be more

172 straightforward, but comes at a substantial computational cost: Using the model implementation in C  
173 rather than the R implementation decreases the computational time for the results presented in the next  
174 section with a factor 40-50.

## 175 **Results**

### 176 **Bifurcation analysis of ecological steady states**

177 The main purpose of the ‘PSPManalysis’ package is to compute the steady states of a PSPM as a func-  
178 tion of one of the model parameters, which I from here on refer to as the bifurcation parameter. This not  
179 only requires the ‘PSPManalysis’ package implementing the methodology, but also a strategy to execute  
180 the computations in a comprehensive manner. Figure 1 shows the equilibrium bifurcation curves of the  
181 example model as a function of  $X_{max}$ . The figure itself was produced using basic plotting commands  
182 in R on the basis of data computed with the main function called `PSPMequi` provided by the ‘PSPM-  
183 analysis’ package. A total of 3 computational steps were needed to generate the data for Figure 1 with  
184 the ‘PSPManalysis’ package. Here I discuss these computational steps in broad terms, focussing on the  
185 computational strategy rather than on the relevant R commands, which are discussed in more detail in  
186 the supporting information.

187 Key to the computation of steady state curves as a function of model parameters is a good starting point.  
188 For the example model we can start the computations at the trivial steady state  $(\tilde{b}, \tilde{X}, \tilde{P}) = (0, X_{max}, 0)$ ,  
189 which will be the only steady state for maximum resource densities close to 0, because consumers then  
190 do not encounter sufficient resources to reach the length at maturation (note the maximum length equal  
191 to  $\ell_{inf} X / (K + X)$ ). As a first step to generating the data for Figure 1 this resource-only equilibrium with  
192 zero density of both the length-structured consumer and predator was computed for increasing values of  
193 the bifurcation parameter  $X_{max}$ , starting from  $X_{max} = 0.1$ . The result is the curve section with increasing  
194 equilibrium densities  $\tilde{X}$  at low values of  $X_{max}$  in Figure 1. This computational step would be superfluous  
195 as the value of this steady state is known exactly as  $(\tilde{b}, \tilde{X}, \tilde{P}) = (0, X_{max}, 0)$ , but for the fact that the  
196 function `PSPMequi` in the ‘PSPManalysis’ package with which this computational step is carried out,  
197 locates a bifurcation point along the curve. It labels this bifurcation point with the string "BP #0",

198 indicating that this bifurcation point represents a branching point (also called transcritical bifurcation  
199 point (Kuznetsov, 1998)) for the structured population with index 0 (the consumer population; because  
200 the ‘PSPManalysis’ package is written in C, indices conform to the C convention, in which the first  
201 element of a vector has index 0 rather than index 1 such as in R). From the output of the function  
202 `PSPMequi` it can be inferred that for  $X_{max}$  values to the left of this branching point consumers can not  
203 establish themselves in the computed, resource-only equilibrium, because their lifetime reproductive  
204 output  $R_0$  is below 1, whereas they can for values to the right of it. These steady states to the left and  
205 right of the bifurcation point are therefore stable and unstable (saddle points), respectively.

206 Step 2 of the computations uses the bifurcation point located in the first computational step as starting  
207 point to compute the curve of consumer-resource steady states as a function of  $X_{max}$ . The resulting curve  
208 corresponds to the part of the equilibrium curves shown in Figure 1 with constant resource density,  
209 linearly increasing densities of consumer biomass in the nursery and growth habitat and zero density for  
210 the unstructured predator. In this curve the `PSPMequi` function detects a branching point (or transcritical  
211 bifurcation point) for the environment variable with index 1 (the unstructured predator population),  
212 which it labels as "BPE #1" (see Figure 1). The consumer-resource steady states to the right of this  
213 branching point can be invaded by the unstructured predator population, as indicated by the positive  
214 per-capita growth rate that the function `PSPMequi` produces as output. Predators can hence increase in  
215 abundance from low densities for higher  $X_{max}$ -values. In contrast, predators have a negative per-capita  
216 growth rate and can thus not invade the consumer-resource steady state for  $X_{max}$ -values to the left of  
217 the branching point labeled "BPE #1" in Figure 1, which may therefore represent a stable equilibrium.  
218 Whether or not these steady states are indeed stable or, alternatively, cycles in consumer and resource  
219 abundance occur can only be investigated using numerical studies of the dynamics, because appropriate  
220 test functions that detect transitions from stable equilibrium states to limit cycles (occurring at so-called  
221 Hopf bifurcation points (Kuznetsov, 1998)) are currently not available for PSPMs.

222 The last step of the analysis uses the detected branching point for the unstructured predator population  
223 to start a computation of the steady states with positive predator density as a function of  $X_{max}$ . The  
224 result of this computation is a folded curve of steady state values which extends to a minimum just be-  
225 low  $X_{max} = 4$ . This point at which the equilibrium curve doubles back on itself is another bifurcation

226 point called limit point (or saddle-node bifurcation point Kuznetsov, 1998) and labeled by the func-  
227 tion  $PSPMequi$  with "LP" (see Figure 1). Ecologically, this minimum value of  $X_{max}$  represents the  
228 persistence boundary of the unstructured predator population whereas the branching point detected in  
229 step 2 and labeled "BPE #1" represents the predator's invasion boundary. In between the persistence  
230 and invasion boundary two steady states are possible: a consumer-resource steady state that can not be  
231 invaded by the predator and a predator-consumer-resource equilibrium. On the basis of the general bi-  
232 furcation theory presented in Kuznetsov (1998) it can be inferred that the part of the predator-consumer-  
233 resource equilibrium curve between the two bifurcation points represents unstable equilibrium states  
234 (saddle points).

235 Because they represent the invasion and persistence boundary of the predator, it may be ecologically  
236 relevant to assess how the location of the bifurcation points labeled "BPE #1" and "LP" depends on  
237 other model parameters. The  $PSPMequi$  function therefore also allows for the computation of these  
238 bifurcation points as a function of a second model parameter. Figure 2 shows the location of these two  
239 bifurcation points as a function of the maximum resource density  $X_{max}$  and the predator mortality rate  
240  $\mu_p$ . For values in the region of parameter space between the two lines in Figure 2 two steady states  
241 occur that are potentially stable, a tritrophic steady steady state with predators and a consumer-resource  
242 steady state that predators can not invade. This region of bistability is larger at higher rates of predator  
243 mortality.

## 244 **Evolutionary analysis**

245 A particular strength of the 'PSPManalysis' package is that it can also be used to calculate evolutionary  
246 singular strategies (ESSs) using the framework of Adaptive Dynamics (Dieckmann & Law, 1996; Metz  
247 et al., 1996; Geritz et al., 1998). The package therefore allows studying questions about the evolution of  
248 life history traits in a context with population and community feedback on the environment in which the  
249 evolutionary process takes place. Figure 3 provides as an example the equilibrium bifurcation curves of  
250 the example model as a function of the individual length at the habitat switch  $\ell_s$ . Because it influences  
251 the extent of resource competition and predator vulnerability an individual experiences throughout life,  
252 this trait can be expected to be under strong selection. The data shown in Figure 3 have been computed

253 as before with the function `PSPMequi`, which can also produce as output the value of the selection  
254 gradient, that is, the derivative  $dR_0(\infty, \tilde{X}, \tilde{P})/d\ell_s$  of the lifetime reproductive output  $R_0$  with respect to  
255 the life-history parameter  $\ell_s$  (see bottom panel of Figure 3). In the absence of the predator selection  
256 for a smaller size at habitat shift occurs, but in the presence of the predator the function `PSPMequi`  
257 detects an evolutionary singular state (ESS), which it labels as "CSS #0" on the basis of the second-  
258 order derivatives of  $R_0$  with respect to  $\ell_s$ . The label indicates that the ESS is convergent stable, such  
259 that the value of  $\ell_s$  will evolve toward the  $\ell_s$  value of this CSS, while after fixation mutants with slightly  
260 different values of  $\ell_s$  will not be able to invade (see Geritz et al., 1998, for further details about the ESS  
261 classification).

262 Once an evolutionary singular strategy has been detected the function `PSPMequi` can be used to con-  
263 struct a pairwise invasibility plot (PIP; Van Tienderen & de Jong, 1986; Geritz et al., 1998), that is, a  
264 graph of the sign of a mutant's invasion fitness as a function of the life-history trait value of both the  
265 resident and the mutant (Figure 4, left panel). Starting from the CSS detected in Figure 3 the function  
266 `PSPMequi` was used to compute a boundary with zero mutant fitness as a function of the resident and  
267 mutant life-history trait value. This boundary corresponds to the curve separating regions with positive  
268 and negative mutant fitness in the PIP shown in Figure 4 (left panel).

269 Finally, the 'PSPMAnalysis' package also includes a function `PSPMevodyn`, which can be used to sim-  
270 ulate the dynamics of evolving life-history parameters over evolutionary time (Figure 4, right panel).  
271 These evolutionary dynamics are described by the canonical equation of Adaptive Dynamics (Dieck-  
272 mann & Law, 1996). The trajectory of  $\ell_s$  over evolutionary time shown in Figure 4 (right panel) con-  
273 firms that the individual length at the habitat switch evolves to the value of the convergent stable ESS  
274 shown in Figure 3, but since the function `PSPMevodyn` can not simulate combined mutant and resident  
275 dynamics, it is not possible to verify whether or not evolutionary branching is possible at this ESS.

276 The results shown in Figure 3 and 4 were on purpose computed with a low value of  $X_{max} = 0.5$ , as the  
277 default value of  $X_{max} = 5.0$  results in a more complicated, and hence also more intriguing evolutionary  
278 outcome of the selection process in  $\ell_s$  (Figure 5). For this value of  $X_{max}$  the range of  $\ell_s$  over which both  
279 a consumer-resource equilibrium and a predator-consumer-resource equilibrium occur is more extensive  
280 and the evolutionary singular state (classified by the `PSPMequi` function as an evolutionary repeller and

281 labeled "ERP #0") now occurs on the part of the curve representing saddle-node steady states of the  
282 predator, consumer and resource. This state is hence ecologically unstable and thus unreachable. As  
283 before smaller values of  $\ell_s$  are selected for in the absence of the predator, as this reduces competition  
284 for resources among consumers. In the presence of the predator, however, larger values of  $\ell_s$  confer  
285 a selective advantage. As a consequence, with predators present evolution will result in larger values  
286 of  $\ell_s$  until the limit point is reached around  $\ell_s = 22.5$ , at which point the predator goes extinct and the  
287 community collapses to a consumer-resource equilibrium. After predator extinction, the direction of  
288 evolution reverses and smaller values of  $\ell_s$  are selected for until the value of this life-history parameter  
289 reaches the bifurcation point labeled "BPE #1" in Figure 5, below which the predator can once again  
290 invade the consumer-resource equilibrium. From Figure 5 it can hence be inferred that over evolutionary  
291 time cycling will occur between a consumer-resource steady state and a steady state with predator, driven  
292 by the selection process in  $\ell_s$ . Simulating the evolutionary dynamics with the `PSPMevoDyn` function  
293 following the canonical equation of Adaptive Dynamics would, however, not reveal such evolutionary  
294 cycling as this function can not switch between the two ecological steady states.

## 295 **Discussion**

296 This paper outlines a general methodology for the analysis of PSPMs, presents a strategy how to apply  
297 this methodology to ecological and evolutionary questions and introduces a R package that implements  
298 the numerical tools required by this methodology. This methodology has been used to gain insight about  
299 how individual development affects the ecological dynamics of size-structured populations and commu-  
300 nities (de Roos & Persson, 2013). More recently, it was applied to a variety of evolutionary problems,  
301 ranging from the evolution of ontogenetic niche shifts (ten Brink & de Roos, 2017), metamorphosis  
302 (ten Brink et al., 2019), cannibalism (Hin & de Roos, 2019a), ontogenetic size-scaling (Hin & de Roos,  
303 2019b) and the timing of habitat shifts (Chaparro Pedraza & de Roos, 2020). Given the importance  
304 of the individual life history for many eco-evolutionary questions and the importance of environmental  
305 feedback on this life history (Lion, 2018), however, there is scope to apply the methodology to a wide  
306 range of eco-evolutionary problems.

307 Physiological structured population models are key to the presented methodology. In contrast to for



308 example integral projection models (Ellner et al., 2016) PSPMs are not directly based on observational  
309 life history data. Such data, however, are often collected under at most a few different sets of environ-  
310 mental or density-dependent conditions and hence offer limited information about how the individual  
311 life history changes under environmental feedback. In contrast, PSPMs are based on a functional model  
312 of the individual life history that mechanistically accounts for the interplay between the life history and  
313 the environment (de Roos, 2020). PSPMs therefore often address the question how the individual life  
314 history is shaped by both individual traits and environmental, density-dependent impacts. The current  
315 paper shows that to address such questions it suffices to specify only the model of the individual life  
316 history model dependent on individual traits and environmental variables. Formulating a population-  
317 level model is not required as the translation to the population level is sufficiently generic that it can be  
318 abstracted into a software approach.

319 The capabilities of the ‘PSPManalysis’ package are more extensive than highlighted in this paper. Next  
320 to the routines for the bifurcation analysis of ecological steady states, the package includes routines  
321 for the demographic analysis of PSPMs (following de Roos, 2008), the simulation of the ecological  
322 dynamics of structured populations (de Roos et al., 1992), the computation of evolutionary singular  
323 states as a function of parameters and the computation of the individual life history under different  
324 environmental conditions. All procedures use the same specification of the individual life history, such  
325 as the one shown in Table 2, which moreover has a generic structure that is readily adapted to many  
326 different life history models. Other methods for the bifurcation analysis of PSPMs do exist (Breda,  
327 Diekmann, Gyllenberg, Scarabel, & Vermiglio, 2015; Gyllenberg, Scarabel, & Vermiglio, 2018) and  
328 can handle more complex bifurcations, such as Hopf bifurcation points, that can not be detected and  
329 analysed with the ‘PSPManalysis’ package, but these methods always have to be specifically tailored  
330 to the particular PSPM. The generic and easy-to-adapt implementation of the life history model is the  
331 key aspect of the ‘PSPManalysis’ package that makes it useful for a wide range of eco-evolutionary  
332 problems.

333 Theoretical studies in ecology and evolutionary biology often aim for deriving analytical insight, as such  
334 insight is considered to apply more generally to a wide range of systems. The complexity of models that  
335 can be investigated analytically is, however, severely limited. For example, conditions determining

336 the equilibrium of a size-structured consumer-resource system and its stability can be derived analytically only if mortality is size-independent and an explicit expression for the size-at-age relationship is available (de Roos et al., 1990). The derived conditions are themselves, however, not transparent and nevertheless have to be solved numerically. To facilitate mathematical analysis structured models are then often simplified, for example by replacing size-dependent life history functions with far easier age-dependent ones. Size-dependent and age-dependent life histories (and hence size-structured and age-structured population models) are however fundamentally different from each other, if growth in body size and hence the progression through ontogeny depends on environmental factors like food availability (de Roos & Persson, 2013). Often the choice is hence between a simple model for which analytical results are possible or a model with a more faithful representation of the complexity of real life histories that can only be investigated numerically. In this context the power of numerical bifurcation analysis (Kuznetsov, 1998) has received too little attention. It offers a more powerful approach than brute-force numerical simulations of dynamics, as it provides more comprehensive insight about the different types of stable dynamic patterns that can occur for given combinations of model parameters. The very essence of bifurcation theory furthermore guarantees that these dynamic patterns occur over at least a range of parameter values, lending the results some measure of generality. Methodology and software for the numerical bifurcation analysis of models in terms of ODEs have been available for a while (Dhooge, Govaerts, & Kuznetsov, 2003), the ‘PSPManalysis’ package is intended to provide some of the same capabilities for the general class of PSPMs and thereby facilitate investigating questions about the relationship between complex individual life histories and the dynamics of populations and communities on both ecological and evolutionary time scales.

## 357 **Acknowledgements**

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## 360 **Data accessibility**

361 No experimental or empirical data are used or collected in this study. The ‘PSPAnalysis’ package can  
362 be installed from CRAN using the command:

```
363 install.packages("PSPAnalysis")
```

364 The most recent version can always be installed using the command:

```
365 devtools::install_bitbucket("amderoos/PSPAnalysis", subdir = "R/",  
366                               build_vignettes = TRUE)
```

367 The Supplementary Information contains:

- 368 1. Table S1 with model parameters and their default values.
- 369 2. A discussion of the implementation of the life history model of Chaparro Pedraza and de Roos  
370 (2020) in the R script called "Salmon.R" (also shown in Table 2).
- 371 3. A discussion of the R commands used to generate the data for the figures in this paper.
- 372 4. The R script called "EcoFigures.R" with the R code to generate Figures 1 and 2.
- 373 5. The R script called "EvoFigures.R" with the R code to generate Figures 3, 4 and 5.
- 374 6. The C header file called "Salmon.h" with the C implementation of the life history model of  
375 Chaparro Pedraza and de Roos (2020).

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449 **Tables**

**Table 1:** Model functions of the individual life history model of Chaparro Pedraza and de Roos (2020).

Function		Description
<i>Life history functions</i>		
$\gamma(\ell, X) = \begin{cases} \xi \left( \ell_{inf} \frac{X}{K+X} - \ell \right) & \ell < \ell_s \\ \xi (\ell_{inf} - \ell) & \text{otherwise} \end{cases}$		Growth rate in length
$\beta(\ell) = \begin{cases} B_{max} \ell^2 & \ell > \ell_m \\ 0 & \text{otherwise} \end{cases}$		Fecundity
$\mu(\ell, P) = \begin{cases} \mu_1 & \ell < \ell_s \\ \mu_2 + \phi \ell^{-d} P & \text{otherwise} \end{cases}$		Mortality
<i>Impacts on the environment</i>		
$\alpha(\ell, X) = \begin{cases} I_{max} \frac{X}{K+X} \ell^2 & \ell < \ell_s \\ 0 & \text{otherwise} \end{cases}$		Foraging on resource in nursery habitat
$\varepsilon(\ell) = \begin{cases} \phi \ell^{3-d} & \ell > \ell_s \\ 0 & \text{otherwise} \end{cases}$		Contribution to predator numerical response
<i>Functions related to the environment</i>		
$g(X) = \rho (X_{max} - X)$		Resource turn-over rate
$h(B) = B - \mu_p$		Predator per-capita growth rate as a function of the numerical response $B$

**Table 2:** The implementation in R of the individual life history model of Chaparro Pedraza and de Roos (2020) for the analysis with the ‘PSPManalysis’ package.

---

```
PSPMdimensions <- c(PopulationNr = 1, IStateDimension = 2,
                    LifeHistoryStages = 3, ImpactDimension = 5)

EnvironmentState <- c(X = "GENERALODE", P = "PERCAPITARATE")

DefaultParameters <- c(Rho = 0.01, Xmax = 5.0,
                       K = 1.0, Imax = 0.0025, Bmax = 0.002725,
                       L0 = 2.0, Ls = 20.0, Lm = 30.0, Linf = 115.0,
                       Xi = 0.00051, Mu1 = 0.002, Mu2 = 0.006,
                       D = 0.75, Phi = 0.001, Mup = 0.006)

StateAtBirth <- function(E, pars) {
  with(as.list(c(E, pars)),{
    c(Age = 0.0, Length = L0)
  })
}

LifeStageEndings <- function(lifestage, istate, birthstate, BirthStateNr, E, pars) {
  with(as.list(c(E, pars, istate)),{
    maturation = switch(lifestage, Length - Ls, Length - Lm, -1)
  })
}

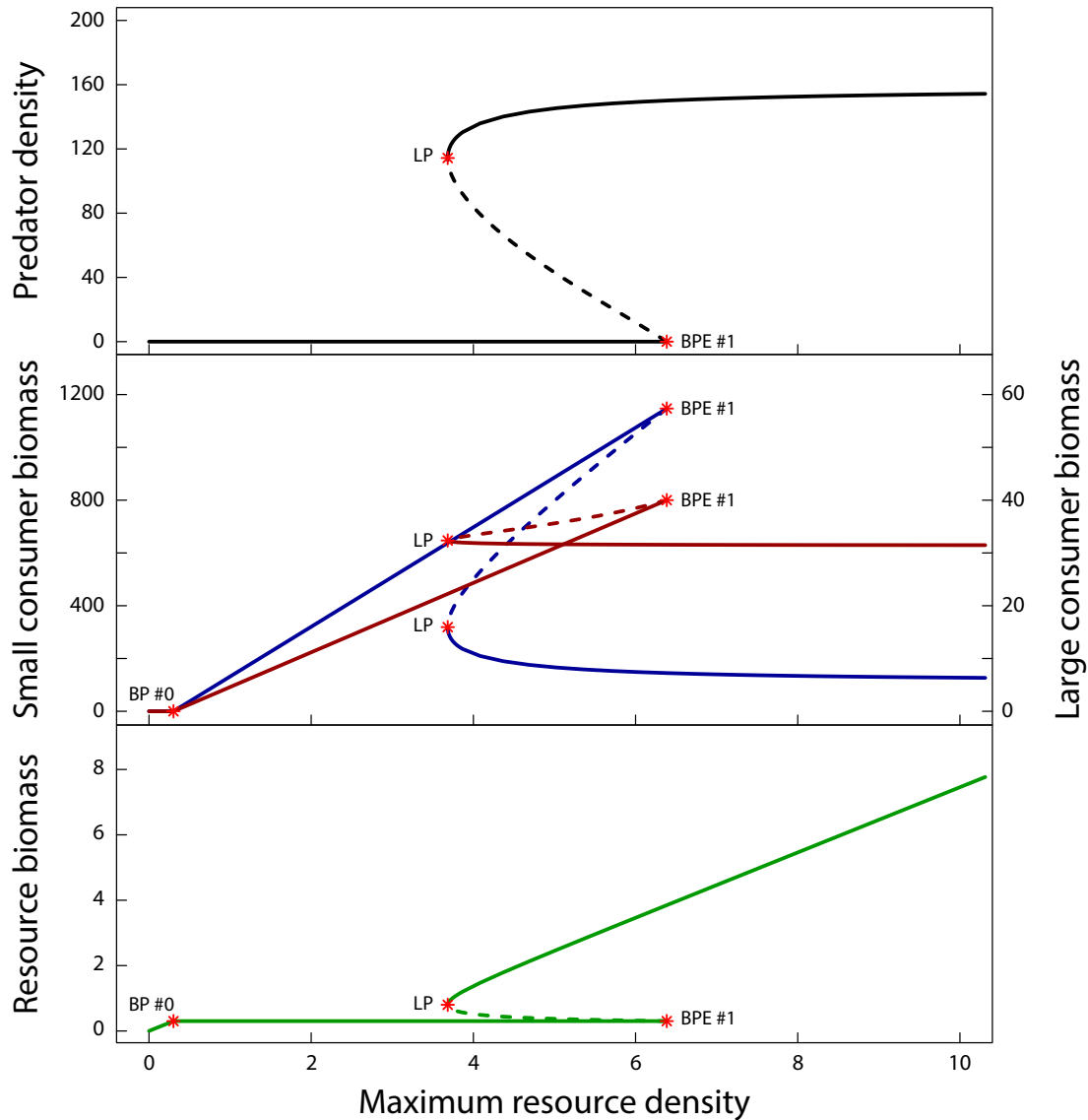
LifeHistoryRates <- function(lifestage, istate, birthstate, BirthStateNr, E, pars) {
  with(as.list(c(E, pars, istate)),{
    list(
      development = c(1.0,
                     switch(lifestage, Xi*(Linf*X/(K+X) - Length),
                             Xi*(Linf - Length), Xi*(Linf - Length))),
      fecundity = switch(lifestage, 0, 0, Bmax*Length^2),
      mortality = switch(lifestage, Mu1, Mu2 + Phi*P*Length^(-D),
                        Mu2 + Phi*P*Length^(-D)),
      impact = switch(lifestage,
                      c(Imax*X/(K+X)*Length^2, 0, Length^3, 0, 0),
                      c(Imax*X/(K+X)*Length^2, Phi*Length^(3-D), 0, Length^3, 0),
                      c(Imax*X/(K+X)*Length^2, Phi*Length^(3-D), 0, 0, Length^3))
    )
  })
}

EnvEqui <- function(I, E, pars) {
  with(as.list(c(E, pars)),{
    c(Rho*(Xmax - X) - I[1], I[2] - Mup)
  })
}
```

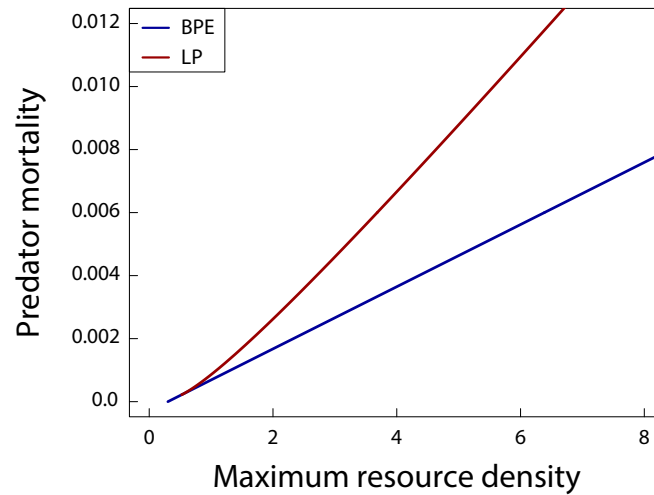
---



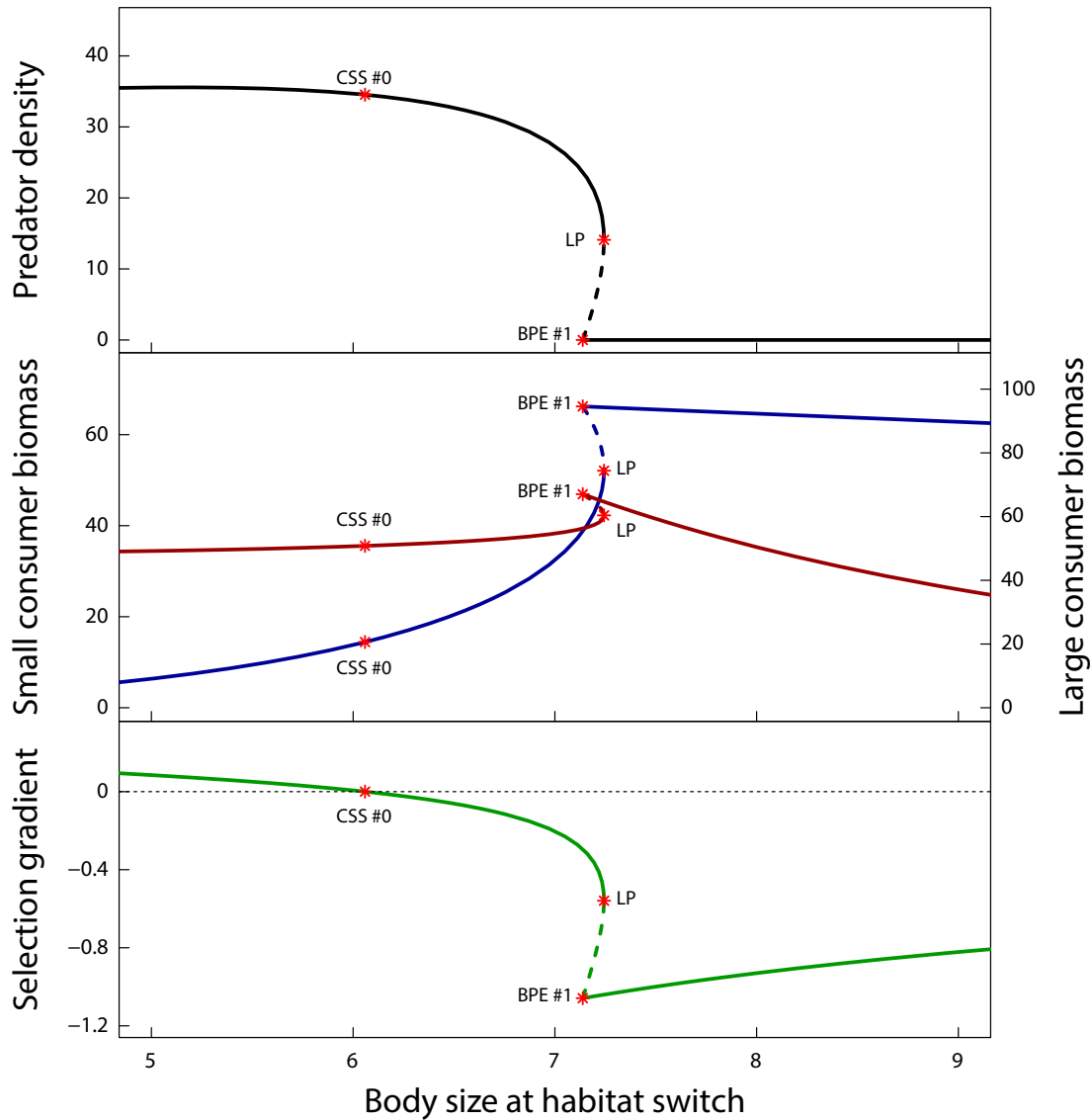
450 **Figures**



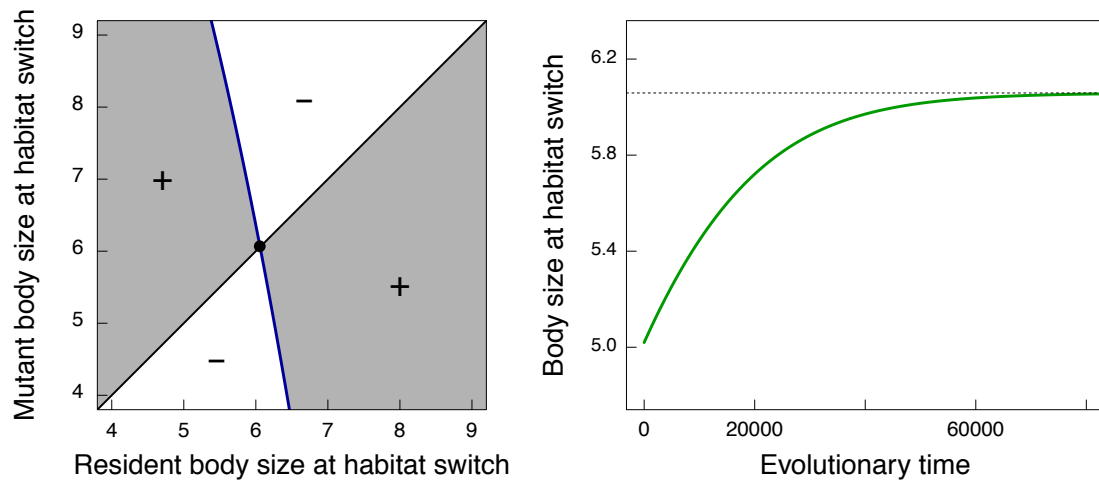
**Figure 1:** Steady state densities of the unstructured predator population (*top panel*), the length-structured consumer population in the nursery and growth habitat (*middle panel*) and the basic resource (*lower panel*) in the example model (see Table 1) as a function of the maximum resource density  $X_{max}$ . All other parameters have default values (Table S1 in the supporting information). See the main text for details about the bifurcation points labeled "BP #0" (branching point for structured population with index 0), "BPE #1" (branching point for the environmental variable with index 1) and "LP" (limit point). Solid lines represent possibly stable equilibria, dashed lines represent saddle points. The curve sections with unstable resource-only and consumer-resource steady states that can be invaded by the structured consumer and unstructured predator, respectively, have been omitted for clarity.



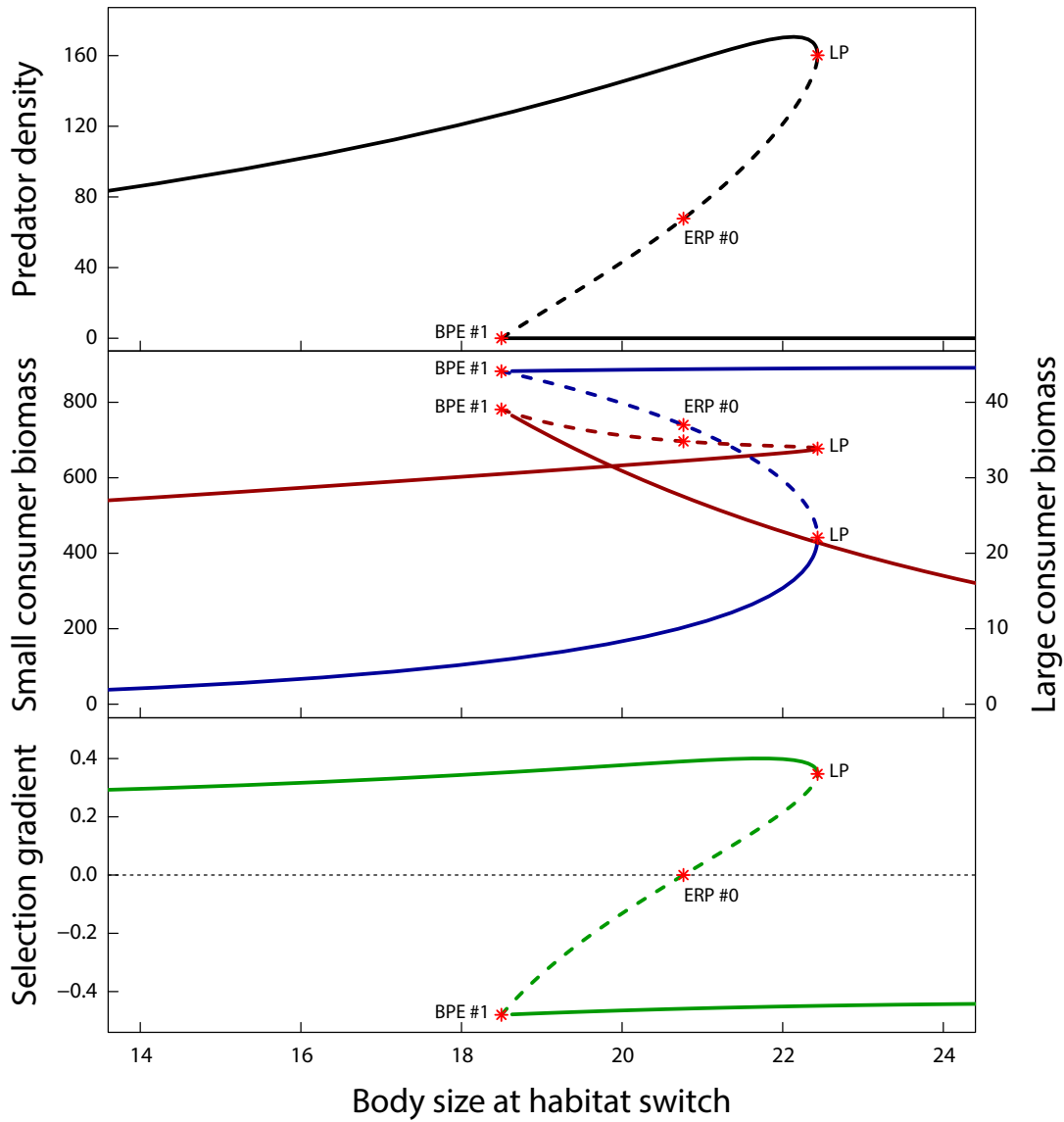
**Figure 2:** Location of the bifurcation points shown in Figure 1 as a function of the maximum resource density  $X_{max}$  and the predator mortality rate  $\mu_p$ . Only the location of the bifurcation points labeled "BPE #1" (branching point for the environmental variable with index 1) and "LP" (limit point) are shown, as the location of the bifurcation point labeled "BP #0" (branching point for structured population with index 0) is independent of the predator mortality rate  $\mu_p$ . All other parameters have their default values (Table S1 in the supporting information).



**Figure 3:** Steady state densities of the unstructured predator population (*top panel*) and the length-structured consumer population in the nursery and growth habitat (*middle panel*), as well as the selection gradient on the individual length at habitat switch  $\ell_s$  in the example model (see Table 1) as a function of this length at habitat switch  $\ell_s$ . Maximum resource density  $X_{max} = 0.5$ , all other parameters have their default values (Table S1 in the supporting information). See the main text for details about the bifurcation points labeled "BPE #1" (branching point for the environmental variable with index 1) and "LP" (limit point) and the evolutionary steady state labeled "CSS #0" (convergent stable evolutionary state for structured population with index 0). Solid lines represent possibly stable equilibria, dashed lines represent saddle points. The curve sections with unstable resource-only and consumer-resource steady states that can be invaded by the structured consumer and unstructured predator, respectively, have been omitted for clarity.



**Figure 4:** *Left:* Pairwise invasibility plot showing combinations of the resident and mutant value of the length at habitat switch  $\ell_s$  with positive and negative invasion fitness of the mutant. *Right:* Simulation of the dynamics of the evolving value of the length at habitat switch  $\ell_s$  over evolutionary time as predicted by the canonical equation of Adaptive Dynamics (Dieckmann & Law, 1996).



**Figure 5:** As Figure 3 but for  $X_{max} = 5.0$ . The point labeled "ERP #0" refers to an evolutionary repellor for the structured population with index 0 (see main text for details). Notice the opposing signs of the selection gradient in the consumer-resource and predator-consumer-resource equilibrium, which predicts that evolutionary cycling will occur for the body length at habitat switch  $\ell_s$  between the bifurcation points labeled "BPE #1" and "LP" resulting in repeated invasion and extinction of the predator population.