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PSPManalysis: Steady-state and bifurcation analysis of physiologically structured population models

André M. de Roos^{1,2} 

¹Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands

²Santa Fe Institute, Santa Fe, NM, USA

Correspondence

André M. de Roos

Email: a.m.deeroos@uva.nl

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Abstract

1. How environmental conditions affect the life history of individuals and how these effects shape population and community dynamics on ecological and evolutionary time-scales is a central question in many eco-evolutionary studies.
2. Physiologically structured population models (PSPMs) allow to address this question theoretically as PSPMs are built on a function-based life-history model, which explicitly describes how life history depends on individual traits and environmental factors. PSPMs furthermore explicitly account for population feedback on these environmental factors, which translates into density-dependent effects on life history.
3. PSPManalysis is an R package that allows to simulate ecological dynamics of PSPMs, compute their ecological steady states as a function of model parameters and detect bifurcation points in the computed curves where dynamics change drastically. It furthermore allows for analysing evolutionary dynamics and evolutionary singular states of PSPMs based on Adaptive Dynamics theory. The package only requires a relatively straightforward specification of the life-history functions as input.
4. Compared to dynamic simulations alone, PSPManalysis uses methods from bifurcation analysis to gain a more complete and comprehensive understanding of model behaviour which is much less dependent on particular parameter values or initial model conditions. Given the central role of the individual life history in many studies, there is substantial scope for using PSPManalysis in fields as diverse as ecology, ecotoxicology, conservation biology and evolutionary biology.

KEYWORDS

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

1 | INTRODUCTION

The individual life history plays a central role in ecology and evolution, determining demography and persistence of populations and, together with interactions with other species, shaping the dynamics

of interacting populations and communities. An individual's life history furthermore influences its fitness and thereby governs the evolutionary change in species traits. Methodologies to assess how life-history characteristics translate into consequences at the population level are hence a core part of many eco-evolutionary studies.

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Physiologically structured population models (PSPMs, de Roos, 1997; Metz & Diekmann, 1986) provide a theoretical approach to analyse links between individual life history and population dynamics, as PSPMs describe population dynamics on the basis of a function-based model of the life history, which also accounts for effects of environmental variables, such as food availability and predator density (de Roos, 2020). PSPMs furthermore account for how these environmental variables are impacted by the population as a whole. While matrix (Caswell, 2001) and integral projection models (Ellner et al., 2016) are better suited to analyse life-history observations and infer their population dynamical consequences (de Roos, 2020), PSPMs capture with considerable mechanistic detail how individual-level processes, like energetics, together with interactions of the individual with its environment shape its life history and how feedback of the entire population on this environment has density-dependent impacts on that life history. PSPMs are therefore particularly useful to analyse how particular mechanisms or aspects of the life history or ecology of an individual would affect the population and community dynamics. The downside of PSPMs, however, is their mathematical tractability. The most simple PSPMs that only account for population size-structure can be formulated using partial differential equations (de Roos, 1997; Metz & Diekmann, 1986), but in general PSPMs are more appropriately couched in terms of coupled systems of nonlinear renewal equations and differential delay equations (Diekmann et al., 2007). Recently, numerical methodology (Kirkilionis et al., 2001; Sánchez-Sanz & Getto, 2016) was developed that allows for analysing ecological and evolutionary dynamics of even fairly complicated PSPMs (ten Brink et al., 2019; Chaparro-Pedraza & de Roos, 2020; Hin & de Roos, 2019) without bothering about these complicated population-level model formulations. This paper introduces the package PSPMAnalysis implementing this methodology.

2 | OVERVIEW OF SOFTWARE

As input, PSPMAnalysis only requires specification of the following aspects of the life history of individual organisms and how they interact with their environment: (a) the individual state variables, such as body size, that determine the individual life history; (b) the environmental variables, such as food availability or predation pressure, that impact the individual life history; (c) the vital rates, in particular the rates of development, rates of change in individual state variables, rates of reproduction and mortality, and how these depend on the individual state and environmental variables; (d) how individuals impact their environment; and (e) the conditions determining steady states of the environment. With these ingredients as input, PSPMAnalysis numerically analyses their population-level consequences, both in ecological and evolutionary time.

Because of their formulation in terms of partial differential equations PSPMs are often analysed using numerical simulations of the dynamics at particular parameter values for specific initial conditions. PSPMAnalysis implements functions for such simulations of ecological dynamics using the Escalator Boxcar Train (EBT) method

(de Roos, 1997; de Roos et al., 1992). More importantly, however, PSPMAnalysis uses the theory on bifurcations in nonlinear dynamical systems (Kuznetsov, 1998) for model analysis. Bifurcation analysis provides more complete and comprehensive understanding of model dynamics because the results are much less dependent on particular parameter values or initial conditions (Kuznetsov, 1998). For that purpose, PSPMAnalysis includes functions to compute demographic quantities, such as population growth and stable population states (de Roos, 2008), as well as equilibrium population states (Diekmann et al., 2003) of PSPMs. These models can be of arbitrary complexity with individuals characterized by multiple variables (traits) and multiple environmental variables, such as resource and predator densities, influencing their life history. PSPMAnalysis also uses curve continuation techniques (Sánchez-Sanz & Getto, 2016) to compute these equilibrium states over ranges of model parameters and detects the so-called bifurcation points, at which a qualitative change in model dynamics occurs (Kuznetsov, 1998). In addition, PSPMAnalysis allows for an evolutionary analysis of the computed ecological steady states based on the framework of 'Adaptive Dynamics' (Dieckmann & Law, 1996; Metz et al., 1996).

PSPMAnalysis thus allows for more extensive analysis of a substantially larger class of PSPMs than other packages geared at structured population models such as Mizer (Scott et al., 2014) and plant (Falster et al., 2015) for dynamic simulations of size-spectrum models and size-structured plant populations, respectively, or IPMpack (Metcalf et al., 2013) for demographic analysis of integral projection models.

The main computational routines of the PSPMAnalysis package are implemented in C for performance reasons with R functions (R Core Team, 2020) providing the interface to these routines. Finally, the package includes a very detailed manual, which discusses the full functionality of the package and illustrates its use with step-by-step instructions.

3 | ANALYSIS OF AN EXAMPLE MODEL

The life-history model described in Chaparro-Pedraza and de Roos (2020) is used here to illustrate the functionality of the PSPMAnalysis package. This model is based on the life history of salmon with individuals starting life in a nursery habitat, where they are protected from predation but compete for a shared resource X . Individuals subsequently shift to a growing habitat with negligible and ad libitum food but where they experience predation mortality. All model equations are presented in Table 1, while Table S1 lists default parameters values.

Individuals are characterized by their age a as well as their length l and the focal population (from here on called the 'consumer') is therefore age- and length-structured. Migration to the growing habitat and maturation occur on reaching length $l = l_s$ and $l = l_m$ respectively. Resource feeding, growth in body size and reproduction are linked through a dynamic energy budget (DEB) model (Chaparro-Pedraza & de Roos, 2020). The DEB model predicts individuals to

TABLE 1 Life-history functions^a of the model of Chaparro-Pedraza and de Roos (2020)

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

^aSymbols used: l (cm): length; X (g/m^3): resource biomass; P ($\text{no.}/\text{m}^3$): (scaled) predator density; B (day^{-1}): predator numerical response; ξ (day^{-1}): von Bertalanffy growth rate; I_s and I_m (cm): body size at habitat shift and maturation; I_{∞} (cm): maximum body size at maximum feeding; K (g/m^3): half-saturation resource density; B_{\max} ($\text{cm}^{-2}/\text{day}$) and I_{\max} ($\text{g cm}^{-2} \text{day}^{-1}$): fecundity and ingestion proportionality constants; μ_1 and μ_2 (day^{-1}): mortality rate in habitats 1 and 2; d (-): exponent in size-dependent predation; ϕ ($\text{cm}^d \text{m}^3/\text{day}$) and μ_p (day^{-1}): predator attack and mortality rate; ρ (day^{-1}) and X_{\max} (g/m^3): turnover rate and maximum density of resource; See Table S1 for full details.

grow following a von Bertalanffy growth curve with ultimate body length equal to $I_{\infty}X/(K+X)$ and I_{∞} in the nursery and growth habitat respectively (Table 1). Reproduction occurs after migration to the growth habitat since $I_s < I_m$, while fecundity is proportional to squared individual length.

Mortality in the nursery habitat is constant, but in the growth habitat decreases with body size (Table 1). In contrast to Chaparro-Pedraza and de Roos (2020), size-dependent mortality is assumed proportional to the density of predators that prey on consumers following a linear functional response and experience a mortality rate μ_p . The scaled predator density P incorporates the conversion efficiency between ingested consumer biomass and the predator's numerical response B (Table 1). The contribution of consumer individuals to predator intake equals the product of their vulnerability to predation (l^{-d}) and their biomass (l^3). Resource turnover in the nursery habitat follows semi-chemostat growth dynamics.

The interaction between resource, structured consumer and predator is fully determined by seven functions (Table 1): three life-history functions, describing development, reproduction and mortality, two functions describing consumers' impact on their environment through resource foraging and contribution to predator intake and two functions determining resource and predator dynamics in the nursery and growth habitat respectively. The Supporting

Information (Section 2) shows how to implement these functions in an R script for analysis with PSPManalysis (implementation in C is possible and in fact preferable as it speeds up computations by a factor 40–50).

The function PSPMequi, which is the main R function in the PSPManalysis package, uses the methodology of Kirkilionis et al. (2001) and Sánchez-Sanz and Getto (2016) (Supporting Information, Section 5) to compute steady states of PSPMs as a function of a model parameter, called the bifurcation parameter. Figure 1, which was produced from output of PSPMequi using basic plotting commands in R, shows the results of such computations as a function of maximum resource density X_{\max} for the example model in Table 1. Three computational steps generated the data for Figure 1. The R commands for these computational steps are discussed below (see Supporting Information, Section 3, for a more detailed presentation). After installing and loading the PSPManalysis package (see Data availability statement below) running the command:

```
demo("Salmon", package = "PSPManalysis", echo = FALSE)
```

illustrates the generation of all figures in a step-by-step manner and thus supports the following presentation.

For low maximum resource densities, the example model only allows a steady state with zero consumer and predator density and the resource equal to its maximum density ($\bar{X} = X_{\max}$), because consumers do not encounter sufficient food to mature (maturation length equals $I_{\infty}X/(K+X)$). Starting in this resource-only equilibrium for $X_{\max} = 0.1$, the following call to PSPMequi was used to compute resource-only equilibria for increasing values of X_{\max} :

```
EqR <- PSPMequi(modelName = "Salmon.R", biftype = "EQ",
  startpoint = c(0.1, 0.1), stepsize = 0.5, parbnds =
  c(1, 0.01, 10), options = c("popZE", "0", "envZE", "1"))
```

This call resulted in the thin curve section with increasing densities \bar{X} at low values of X_{\max} in Figure 1. The function PSPMequi takes as first argument the name of the file with the model implementation (see Supporting Information, Sections 2 and 4), while the argument biftype = "EQ" determines the type of computation to be performed, here indicating that an equilibrium curve should be computed as a function of a single model parameter. The argument stepsize indicates whether the curve continuation should start towards higher or lower values of the model parameter and the relative size of these steps. The first element of the argument parbnds indicates which model parameter to vary by specifying the index of this parameter in the vector of parameters, while the second and third element of the argument parbnds specify the minimum and maximum value of this parameter at which to halt the computations. The model parameter that is varied during the computation is from here on referred to as the bifurcation parameter.

The two elements "popZE" and "0" in the options argument of the first command instruct the function to assume a zero equilibrium density for the structured population with index 0

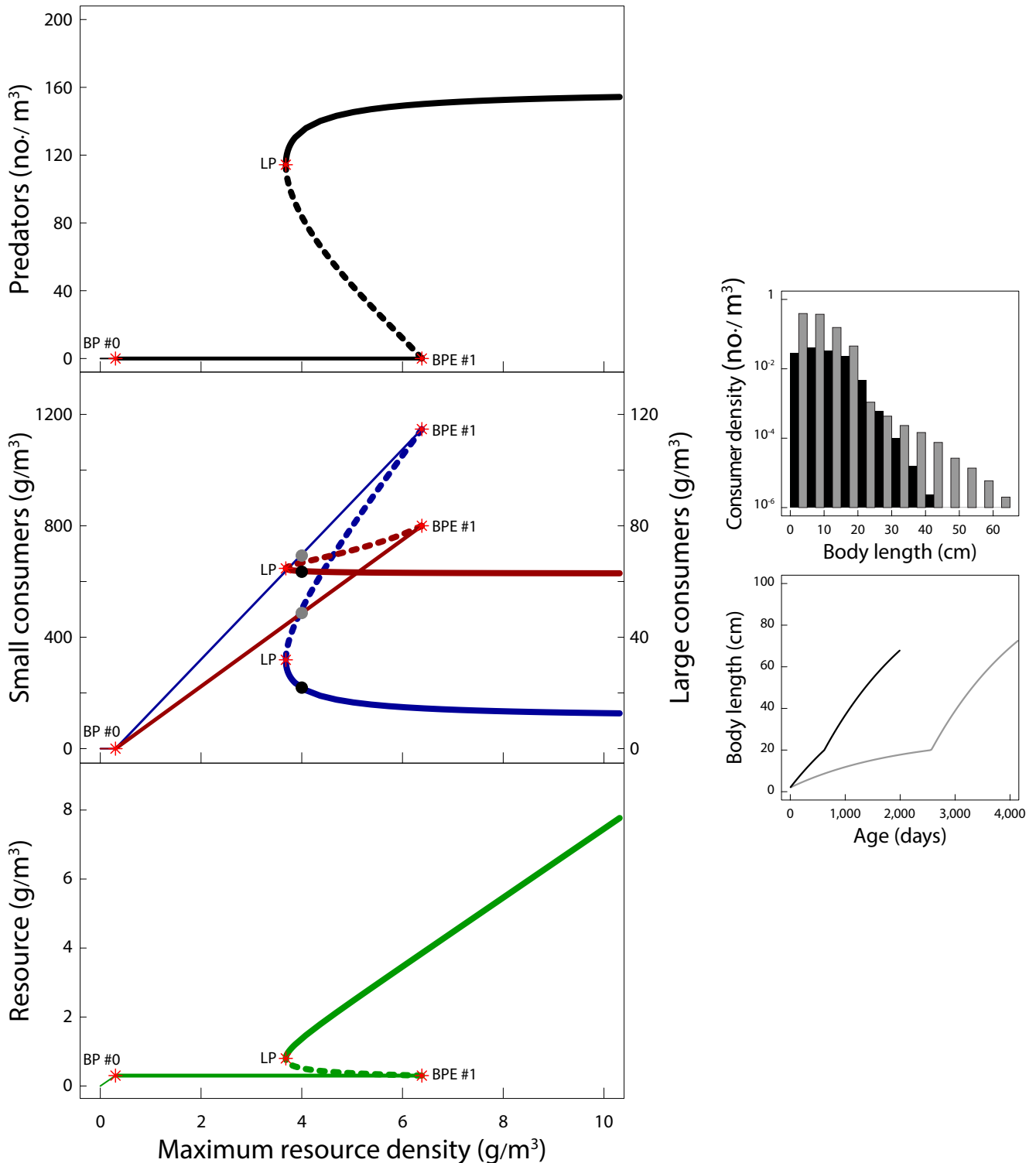


FIGURE 1 Left: Equilibrium densities of predator (top), consumers (middle) in the nursery (blue) and growth habitat (red) and resource (bottom) dependent on maximum resource density X_{\max} . Solid and dashed lines represent possibly stable equilibria and saddle points respectively. Curve sections representing resource-only and consumer-resource equilibria that can be invaded by the consumer and predator, respectively, are omitted for clarity. Curve sections with increasing line width are computed in three consecutive computational steps, starting from zero maximum resource density (thin) and bifurcation points labelled 'BP #0' (medium) and 'BPE #1' (thick) respectively. See text for details about these steps and the bifurcation points labelled 'BP #0', 'BPE #1' and 'LP'. Right: Length distribution (top) and length-age relationship (bottom) of the consumer population in the consumer-resource equilibrium (grey bars and grey curve in top and bottom panel respectively) and the predator-consumer-resource equilibrium (black bars and black curve in top and bottom panel respectively) for maximum resource density $X_{\max} = 4.0$ (corresponding to equilibria indicated with grey and black dots in middle panel on the left). Otherwise default parameter values (Table S1)

(the consumer; because PSPAnalysis is written in C, the first vector element has index 0 rather than 1) and the two elements "envZE" and "1" do the same for the environmental variable with index 1 (= 2nd vector element, the unstructured predator). Indicating that these two populations have zero equilibrium density simplifies and speeds up computations. Because these two populations have zero density, the argument startpoint contains only two values: the value of the bifurcation parameter X_{\max} at which to start the computations and an estimate for the equilibrium resource density in this state. This computational step is only useful because PSPMequi detects a bifurcation point along the curve, labelling it with the string 'BP #0' (Figure 1) to indicate it represents a branching (or transcritical bifurcation) point (Kuznetsov, 1998) for the structured population with index 0 (= 1st vector element, the consumer). The output of PSPMequi indicates that for X_{\max} values below this branching point consumers cannot persist, because their lifetime reproductive output R_0 is below 1, whereas they can for higher X_{\max} values. The steady states to the left and right of the bifurcation point are therefore stable and unstable (saddle points) respectively.

The coordinates of the detected branching point 'BP #0' (Figure 1) are returned in the element bifpoints of the list EqR that PSPMequi produces as output. In the following call to PSPMequi a value of 0 for the birth rate of the structured consumer population is added to the first two elements of the vector EqR\$bifpoints (representing the value of the bifurcation parameter and the equilibrium resource density) to compute the curve of consumer-resource steady states dependent on X_{\max} :

```
EqCR <- PSPMequi(modelname = "Salmon.R", biftype = "EQ",
  startpoint = c(EqR$bifpoints[1,1:2], 0),
  stepsize = 0.5, parbnds = c(1, 0.0, 10), options =
  c("envZE", "1"))
```

resulting in the medium-thick curve sections in Figure 1 with constant resource density, increasing consumer densities in nursery and growth habitat and zero predator density. In addition to the change in startpoint the pair "popZE" and "0" is dropped from the options argument as a zero equilibrium density will no longer be enforced for the structured consumer population. In the computed curve, PSPMequi detects another branching (transcritical bifurcation) point, now for the environment variable with index 1 (= 2nd vector element, the predator), labelling it as 'BPE #1' (Figure 1). The output of PSPMequi indicates a negative (positive) predator growth rate for X_{\max} values to the left (right) of this branching point, implying that predators can invade the consumer-resource equilibrium for higher X_{\max} values. To assess whether consumer-resource steady states for X_{\max} values left of the branching point are stable or, alternatively, consumer-resource cycles occur requires numerical simulations of model dynamics, as test functions are currently lacking to detect transitions from stable equilibrium states to limit cycles for PSPMs.

A final invocation of PSPMequi uses the branching point labelled 'BPE #1' (Figure 1), which is returned in the output list

element EqCR\$bifpoints of the previous step, as starting point to compute steady states with positive predator density as a function of X_{\max} :

```
EqPCR <- PSPMequi(modelname = "Salmon.R", biftype = "EQ",
  startpoint = EqCR$bifpoints[1,1:4], stepsize =
  -0.5, parbnds = c(1, 0.0, 10))
```

The computation of this curve starts off to lower values of X_{\max} (notice the negative stepsize argument) as otherwise negative predator densities would result. The result of this computation is a folded curve that extends to a minimum at $X_{\max} \approx 4$. The function PSPMequi labels this minimum as 'LP' (Figure 1), thus classifying it as a limit (or saddle-node bifurcation) point (Kuznetsov, 1998).

Ecologically, this minimum X_{\max} value represents the persistence boundary of the predator, whereas the branching point labelled 'BPE #1' represents its invasion boundary. General bifurcation theory (Kuznetsov, 1998) stipulates that the curve section connecting these two bifurcation points represents unstable steady states or saddle points. PSPMequi also allows for computing the location of the predator's invasion and persistence boundary (labelled 'BPE #1' and 'LP', respectively, in Figure 1) dependent on a second model parameter. Figure 2 illustrates this for the maximum resource density X_{\max} and predator mortality rate μ_p . For parameter combinations between the invasion ('BPE #1') and persistence boundary ('LP') in Figure 2, two potentially stable steady states occur, a tritrophic steady state with predators and a consumer-resource steady state that predators cannot invade.

The PSPAnalysis package also allows for calculating evolutionary singular strategies using the framework of Adaptive Dynamics (Dieckmann & Law, 1996; Metz et al., 1996) and thus permits studying the evolution of life-history traits in a population and community context. While computing equilibrium curves

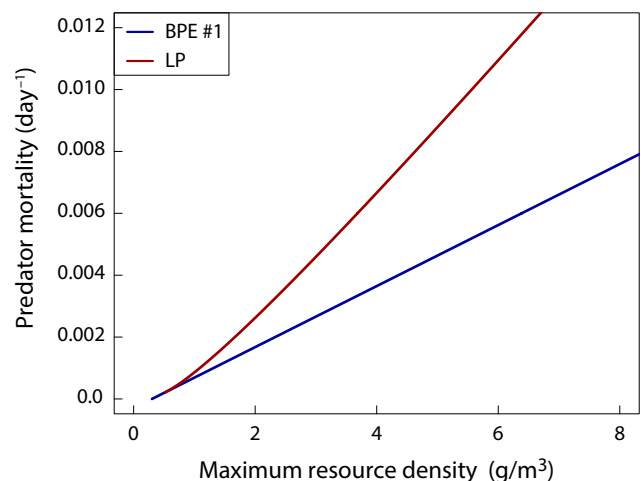


FIGURE 2 Location of the bifurcation points labelled 'BPE #1' and 'LP' in Figure 1 dependent on maximum resource density X_{\max} and predator mortality rate μ_p . Otherwise default parameter values (Table S1). See Supporting Information (Section 3) for a detailed discussion of the R commands to compute the data for this figure

as function of a life-history parameter the function `PSPMequi` can produce as output the selection gradient on this parameter, which equals the derivative of the lifetime reproductive output R_0 with respect to the life-history parameter (Diekmann et al., 2003). Figure 3 shows the equilibrium curves of the example model dependent on the length at habitat shift l_s , including its selection gradient (see Supporting Information, Section 3, for details about the R commands for these computations). In the absence of predators, smaller sizes at habitat shift are selected, but with predators present `PSPMequi` detects an evolutionarily singular state (Brännström et al., 2013), which it labels as ‘CSS #0’ on the basis of second-order derivatives of R_0 with respect to the length at habitat shift l_s (Geritz et al., 1998). The label indicates that this singular state is

convergent stable, such that the value of l_s will evolve towards this CSS value, while after fixation mutants with slightly different values of l_s cannot invade. Starting from this CSS, the function `PSPMequi` can also compute the curve with zero mutant fitness dependent on both resident and mutant life-history trait value, which corresponds to the boundary separating regions with positive and negative mutant fitness in the pairwise invasibility plot (or PIP, van Tienderen & de Jong, 1986) shown in Figure 4 (left).

Finally, the evolutionary dynamics of life-history parameters, as described by the canonical equation of Adaptive Dynamics (Dieckmann & Law, 1996), can be simulated with the function `PSPMevodyn` in the `PSPAnalysis` package (Figure 4, right). The trajectory of the length at habitat shift l_s over evolutionary time shown

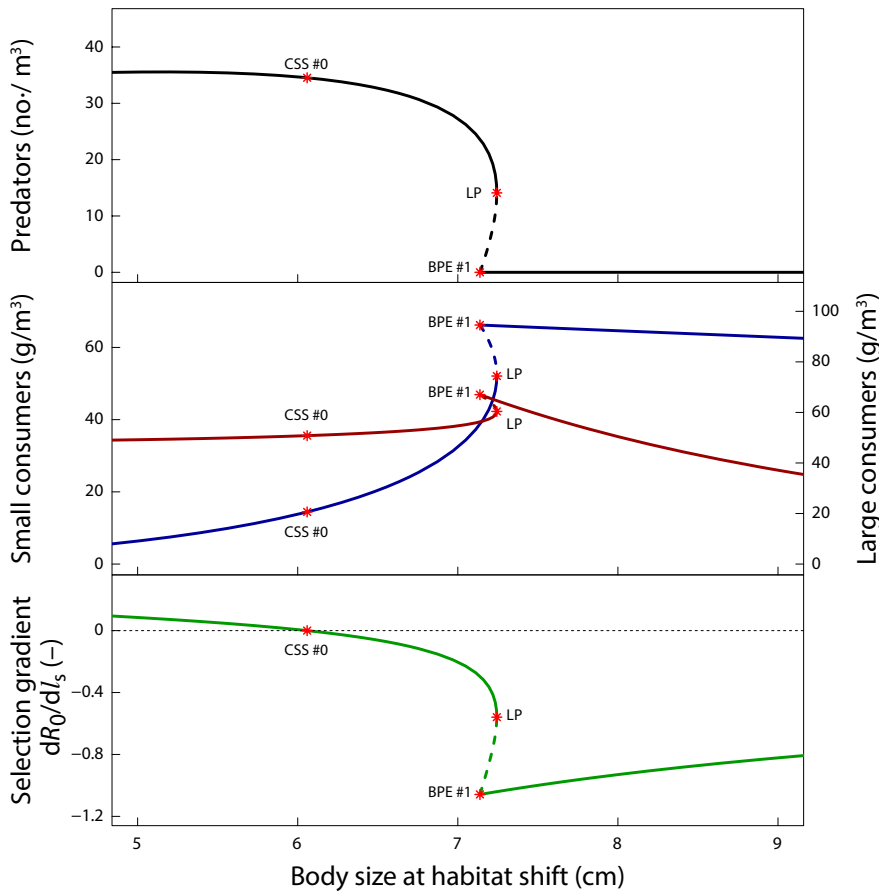


FIGURE 3 Equilibrium densities of predator (top) and consumers (middle) in the nursery (blue) and growth habitat (red) dependent on the length at habitat shift, plus the selection gradient (bottom) on this parameter. Solid and dashed lines represent possibly stable equilibria and saddle points respectively. Curve sections representing consumer-resource steady states that can be invaded by predators are omitted for clarity. See text for details about the bifurcation points labelled ‘BPE #1’, ‘LP’ and ‘CSS #0’. Otherwise default parameter values (Table S1). See Supporting Information (Section 3) for a detailed discussion of the R commands to compute the data for this figure

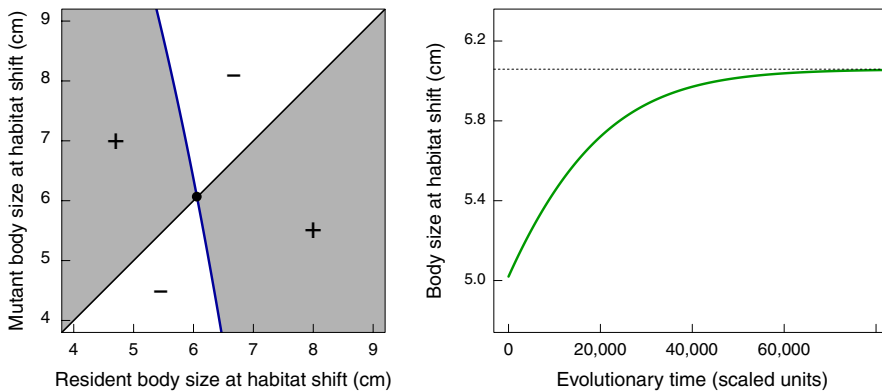


FIGURE 4 Left: Pairwise invasibility plot showing combinations of resident and mutant value of the length at habitat shift with positive and negative mutant invasion fitness. Right: Simulation of the value of the length at habitat shift over evolutionary time as predicted by the canonical equation of Adaptive Dynamics (Dieckmann & Law, 1996). See Supporting Information (Section 3) for a detailed discussion of the R commands to compute the data for this figure

in Figure 4 (right) confirms that length at habitat shift evolves to its CSS value, but since the function `PSPMeodyn` cannot simulate combined mutant and resident dynamics, it cannot verify whether evolutionary branching occurs at this evolutionary singular state.

4 | DISCUSSION

The methodology for analysing PSPMs provided by `PSPManalysis` has previously been used to investigate how ontogeny affects ecological dynamics of size-structured communities (de Roos & Persson, 2013) and, more recently, to study evolution of metamorphosis (ten Brink et al., 2019), cannibalism (Hin & de Roos, 2019) and timing of habitat shifts (Chaparro-Pedraza & de Roos, 2020). Given the importance of individual life history for eco-evolutionary dynamics and of environmental feedback on this life history, the methodology is, however, applicable to a wide range of eco-evolutionary questions. This includes questions in ecotoxicology and conservation biology, as `PSPManalysis` is especially suited to investigate links between the dynamic energy budget (DEB) of individuals and its population consequences (de Roos & Persson, 2013) and DEB models are widely used to assess the consequences of toxicants and changing temperature (Nisbet et al., 2000).

The function `PSPMequi` is the main component of `PSPManalysis` and its functionality is more extensive than discussed here. Next to `PSPMequi` and `PSPMeodyn`, the `PSPManalysis` package also includes functions for demographic analysis (`PSPMdemo`; de Roos, 2008), simulating ecological dynamics (`PSPMecodyn`; de Roos et al., 1992) and calculating individual life histories for given environmental conditions (`PSPMind`). All functions are described in the extensive manual included with the `PSPManalysis` package and use the same implementation of the individual life history with a generic structure that is readily adapted to many different life-history models.

To answer questions about how individual life history shapes population and community dynamics and in turn is shaped by both individual traits and environmental, density-dependent impacts, it is therefore not required to formulate and painstakingly analyse complicated, population-level equations. Instead, the `PSPManalysis` package only requires the specification of the life-history model dependent on individual traits and environmental variables and provides a generic software approach to translate its consequences to the population level. The package therefore shifts the focus to the process that is at the core of all ecological and evolutionary dynamics: how an individual organism develops throughout its life in the particular environment it lives in.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

The `PSPManalysis` package is available on CRAN (<https://CRAN.R-project.org/package=PSPManalysis>) and can be installed and subsequently loaded using the commands:

```
install.packages("PSPManalysis")
library(PSPManalysis)
```

After loading the package, all computations necessary to reproduce the figures presented in this paper can be executed step-by-step by executing the following `demo()` command:

```
demo("Salmon", package = "PSPManalysis", echo = FALSE)
```

No data have been used in this paper, other than the contents of the `PSPManalysis` package available on CRAN.

ORCID

André M. de Roos  <https://orcid.org/0000-0002-6944-2048>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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