Bifurcation theory, adaptive dynamics and DEB-structured populations of iteroparous species

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Revised version

Abstract

In this paper we describe a technique to evaluate the evolutionary dynamics of the timing of spawning for iteroparous species. The life cycle of the species consists of three life-stages, embryonic, juvenile and adult whereby the transitions of life-stages (gametogenesis, birth and maturation) occur at species specific sizes. The dynamics of the population is studied in a semi-chemostat environment where the inflowing food concentration is periodic (annual). A Dynamic Energy Budget (DEB) based continuous-time model is used to describe the uptake of the food, storage in reserves and allocation of the energy to growth, maintenance, development (embryo's, juveniles) and reproduction (adults). A discrete event process is used for modelling reproduction. At a fixed spawning date of the year the reproduction buffer is emptied and a new cohort is formed by eggs with a fixed size and energy content. The population consists of cohorts: for each year one consisting of individuals with the same age which die after their last reproduction event. The resulting mathematical model is a finite dimensional set of ordinary differential equations (ODE)s with fixed one-year periodic boundary conditions yielding a stroboscopic map. We will study the evolutionary development of the population using the Adaptive Dynamics (AD) approach. The trait is the timing of spawning. Pairwise and Mutual Invasibility Plots are calculated using bifurcation analysis of the stroboscopic map. The evolutionary singular strategy (ESS) value belonging to the evolutionary endpoint for the trait allows for an interpretation of the reproduction strategy of the population. In a case study, parameter values from the literature for the bivalve *Macoma balthica* are used.

1 Introduction

In temperate regions many species show a specific timing of reproduction within the seasonal cycle. In this paper we develop a technique to evaluate the evolutionary dynamics of the timing of reproduction of iteroparous species. We assume that the annual reproduction occurs at a fixed date of the year and the evolution of this life-history trait is studied Our approach combines physiologically structured population modelling to describe the dynamics at the ecological time scale with the adaptive dynamics approach which occurs at an evolutionary time scale. The developed technique can be used in a bifurcation analysis to explore how the reproduction strategy of the population depends on individual and environmental properties.

The life cycle of our model individual consists of three life-stages, embryos (no feeding, no reproduction), juveniles (no reproduction) and adults whereby the transitions of life-stages (gametogenesis, birth and maturation) occur at a fixed sizes. A DEB based model [19, 37] is used to describe the uptake of food and the allocation (following the fixed partitioning κ-rule) to either growth and maintenance or to development (in case of embryos and juveniles) and reproduction (for adults). The state of an individual is called the i-state. The three i-state variables are the volume, energy reserve density and the cumulative energy per individual allocated to development and reproduction. There is one unique state at gametogenesis (when eggs are fertilised) for at the moment of spawning all the i-state variables have a specific value. Development, growth and death are modelled by continuous time processes.

From this individual model a discrete population model [3,4,6,11,12,23] is formulated. A discrete event process is used for modelling reproduction (the production of eggs with a fixed size and energy content) at a fixed spawning date of the year forming annual cohorts. The number of eggs produced and therefore the initial number of individuals in the cohort, equals the ratio of the amount of energy allocated to reproduction by the adults and the initial energy content of eggs.

The p-state variable of the population is the number of the individuals in each cohort. Only the formation of the first year-class cohort leads to an increase in individual numbers of the population. Their number diminish due to mortality at a constant rate. Immediately after the last reproduction event the cohort dies. Hence, the maximum number of cohorts equals the maximum lifetime of an individual in years.

The dynamics of the population is studied in a semi-chemostat environment. The inflowing food concentration is periodic (annual) and models a peaked yearly algal bloom.

We will show that the state of the population-food system is described by a finite dimensional dynamical system. Due to the periodic forcing one expects that the long-term dynamics is a periodic solution of the set of ordinary differential equations (ODE)s for the i-state and p-state variables as well as the food. There are discontinuities at discrete spawning events. This periodic solution is calculated by solving a boundary value problem with cyclic boundary conditions at an arbitrary chosen time of the year. This is equivalent to the calculation of the fixed point of the associated Poincaré or stroboscopic map which allows also for the analysis of its stability. When food inflow is too low there is no positive

solution. On the other hand higher order periodic solutions can occur. The transitions between these different states can be studied by a bifurcation analysis. For an introduction in bifurcation analysis we refer the interested reader to [16, 21, 43], for the applications in ecological models to [2, 17] and for the applications in AD to [8, 18, 36].

We will study the evolutionary development of the population using the AD approach [10, 14, 24, 25]. The trait is the timing of reproduction (date of spawning). This trait is a parameter in the population model and it varies at the slow evolutionary time-scale due to rare small mutational steps while the population variables vary at the fast ecological time-scale. A time-scale argument justifies the assumption that at the fast ecological time-scale the population-food system is in the stable periodic solution before the next mutational step occurs.

Generally the invasion fitness of a mutant into a resident population is defined as its long-term exponential growth rate in a given environment set by the resident population [25]. Here, we used the dominant eigenvalue of the Jacobian matrix the stroboscopic map evaluated at the fixed point of the resident-mutant system whereby the mutant is absent. A change in the trait value can be studied by the analysis of the outcome of the competition between the resident and the mutant populations. When the invasion fitness of the mutant is positive it can invade and finally replace or coexists with the resident. In the latter case evolutionary branching can occur, whereby the population undergoes disruptive selection and with small evolutionary steps, an initially monomorphic population becomes distinctively dimorphic. A sequence of replacement steps may lead to convergence to an evolutionary singular strategy, where the resident population is not invadable by the mutant and the mutant not by the resident. An evolutionary endpoint occurs when the fitness gradient with respect to the trait becomes zero. The stability of such an endpoint can be studied by the analysis of the so-called Pairwise- and Mutual Invasibility Plots (PIP and MIP) [14, 15]. In these plots the zero invasion curves in the resident-mutant trait-plane, delimit the regions with positive and negative mutant invasion fitness. When explicit expressions for these curves exist, the PIP-plot and thereafter the MIP-plot, can be easily made. The shape of these zero invasion curves directly fix the evolutionary singular strategies (ESS) and their evolutionary stability [14].

In our case of a periodically forced population-food system we have no explicit expressions for the zero invasion curves. We can, however, use a bifurcation analysis with the resident and mutant trait being the free or bifurcation parameters, to calculate these curves numerically by continuation. In practice these curves can be calculated using computer packages such as MatCont [9] or AUTO [13]. Because of the discontinuity of the periodic solution at the time of spawning thje population model is piece-wise smooth. Therefore, it is cumbersome to use these packages directly for this study. Therefore the bifurcation curves have been computed by means of a predictor-corrector continuation method [1, 21, 27] with a full control of the numerical time integration technique of the piecewise smooth ODE system with discontinuities at spawning times.

A case study is elaborated in which the evolutionary dynamics of a bivalve *Macoma balthica* population in a periodically (annual) forced semi-chemostat environment is analysed. This bivalve feeds on algae. The annual spawning date is the single evolutionary

trait. The study of the ESSs gives insight into the reproduction strategy of the population taking ecologically and evolutionary processes as well as indirect effects via the environment (food) into account.

Our approach is remotely linked to earlier work on optimal life-history strategies [20, 22, 30], but with the difference that a well-tested model of the energy budget of the individual is used, by which means trade-offs are explicitly accounted for. Furthermore, by using AD there is no need for using optimality criteria that are always arbitrary. We therefore provide a more holistic approach, integrating physiology, ecology and evolution, than previous work has offered.

2 Ecological model formulation

2.1 Model for the individual

The three life-stages, embryo, juvenile and adult are modelled by continuous time processes for development, growth and natural mortality. The age, a, dependent DEB model [19, 37] for the changes of the structure $V(a)$, reserve density $[E](a)$ and cumulative energy allocated to development and reproduction $H(a)$ (in the sequel refered to as maturity) [33, 37] reads

$$\frac{dV}{da} = h_V(V, [E]) = \frac{\kappa(\{\dot{p}_{Am}\}/[E_m])[E]V^{2/3} - [\dot{p}_M]V}{\kappa[E] + [E_G]} \ , \tag{1a}$$

$$\frac{d[E]}{da} = h_E(t, V, [E]) = \begin{cases} -\{\dot{p}_{Am}\}V^{-1/3}[E]/[E_m] & V_0 \leq V < V_b \\ \{\dot{p}_{Am}\}V^{-1/3}(f(t) - [E]/[E_m]) & V_b \leq V \end{cases} \ , \tag{1b}$$

$$\frac{dH}{da} = h_H(V, [E]) = \begin{cases} \frac{1-\kappa}{\kappa}[E_G]\frac{dV}{da} & V_0 \leq V < V_p \\ \frac{1-\kappa}{\kappa}\left([E_G]\frac{dV}{da} + [\dot{p}_M](V - V_p)\right) & V_p \leq V \end{cases} \ , \tag{1c}$$

where the so-called functional response $f(t)$ will be defined later. The initial values for the state of the individual at gametogenesis is indicated by a subscript 0. The initial structural volume of an egg is denoted by V_0, $[E_0]$ is the reserve density. The initial maturity H_0 equals $\frac{1-\kappa}{\kappa}[E_G]V_0$. Embryos with volume $V_0 \leq V < V_b$, do neither feed nor reproduce. A juvenile is born when the size of the embryo equals V_b. The transition from a juvenile into an adult is at a fixed puberty size V_p. The juveniles with volume $V_b \leq V < V_p$ consume food but do not reproduce.

Observe that the i-state variable H of Eqn. (1c) does not occur at the right-hand side of the equations but it will appear below in the formulation of the jump conditions at the spawning date. We can directly derive for embryo's and juveniles $V_0 \leq V \leq V_p$ that

$$H(a) = \frac{1-\kappa}{\kappa}[E_G]V(a) \ . \tag{2}$$

This models the state of maturation. The relationships between the maturity H_0 and H_p

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and the structural volumes V_0 and V_p read

$$H_0 = \frac{1-\kappa}{\kappa}[E_G]V_0 \quad \text{and} \quad H_p = \frac{1-\kappa}{\kappa}[E_G]V_p \ . \tag{3}$$

We assume starvation when there is not enough reserves to pay the maintenance costs, that is when $\kappa(\{\dot{p}_{Am}\}/[E_m])[E]V^{2/3} - [\dot{p}_M]$. As a consequence $dV/da \geq 0$ and $dH/da \geq 0$. Hence for adults this means that $V \geq V_p$ and $H \geq H_p$ and the i-state variable H models the cumulative energy allocated to reproduction given by $H(t) - H_p$.

Production of eggs during spawning is modelled by a discrete process occurring (spawning) at a fixed moment of the year. The adults empty their energy reserves allocated for reproduction and the state of maturity becomes H_p again. The number of eggs produced equals the ratio of the amount of energy allocated to reproduction by the adults and the initial energy content of eggs. When the individuals have reached their maximum lifetime, denoted by $n \in \mathbb{N}$, they die directly after their last reproduction event. In the next section reproduction will be modelled at the population level.

2.2   Food–population model

Since all indivuiduals reproduce at the same time once per year it is advantageous to introduce a year-class or a cohort. A new cohort is formed at spawning events and when they have reached their maximum lifetime each cohort dies after their last reproduction event. The maximum lifetime in years is therefore also the maximum number of cohorts.

Suppose there is a single founder cohort consisting of idential individuals of the same age. When no reproduction occurs, integration of the following system

$$\frac{dV}{dt} = h_V(V, [E]) \ , \quad \frac{d[E]}{dt} = h_E(X, V, [E]) \ , \quad \frac{dH}{dt} = h_H(V, [E]) \ , \tag{4a}$$

$$\frac{dN}{dt} = -\mu N \ , \tag{4b}$$

gives the dynamic development of the individuals and the cohort as well, where $t = a + t_0$ with a the age and t_0 the time at gametogenesis of this cohort. The i-state variables, structural volume, energy reserves and maturity represent directly that of the cohort since all individuals are identical and the model is deterministic. N is the number of individuals in the cohort and this number decreases exponentially with mortality rate μ.

During integration the state dependent switches defined in Eqns. (1) are checked. The jump conditions at the spawning date due to reproduction and death after the last reproduction are derived below.

Due to the discrete reproduction at one date of the year the population always consists of n cohorts. The dynamics of the population is studied in a semi-chemostat environment. Therefore in the expression for h_E the first variable X is the time dependent food concentration in the reactor. The inflowing food concentration is periodical with a period of one

Table 1: List of symbols. The symbols in the column labelled 'dimension' stand for: t time, e energy, L length of organism, and l is the length of the reference volume of environment. This reference volume is measured in the arbitrary unit V. The parameter values for an individual life cycle of the Baltic tellin *Macoma balthica* are from [38, Table 1]. The egg energy content is $E_0 = [E_0]V_0 = 0.0059$ J, hence assuming that $V_0 = 10^{-9}$ cm^3 we have $[E_0] = 0.59\ 10^7$ J cm^{-3}.

Symbol	Dimension	Interpretation	Value	Unit
a	t	Age		d
$[E]$	$e\,L^{-3}$	Reserve density		J cm^{-3}
H	e	Energy allocated to maturity and reproduction		J
N	$\#\,l^{-3}$	Population density		V^{-1}
t	t	Time		d
V	L^3	Structural volume		cm^3
X	$\#\,l^{-3}$	Food density		V^{-1}
D	t^{-1}	Dilution rate	0.1	d^{-1}
$[E_0]$	–	Initial egg reserve density	$0.59\ 10^7$	J cm^{-3}
$[E_m]$	eL^{-3}	Maximum energy density	2085	J cm^{-3}
$[E_G]$	eL^{-3}	Costs of growth	1900	J cm^{-3}
f	–	Scaled functional response	—	—
$\{\dot{J}_{Xm}\}$	$\#\,L^{-2}\,t^{-1}$	Max. area-specific ingestion rate	1	cm^{-2}d^{-1}
H_p	e	Maturity threshold	22.8	J
n	–	Maximum lifetime	2	yr
$\{\dot{p}_{Am}\}$	$e\,L^{-2}\,t^{-1}$	Max. area-specific assimilation rate	32.9	J cm^{-2} d^{-1}
$[\dot{p}_M]$	$\#\,t^{-1}\,L^{-3}$	Volume-specific maintenance rate	24	J cm^{-3} d^{-1}
V_0	L^3	Initial egg volume	10^{-9}	cm^3
V_b	L^3	Structural volume at birth	10^{-6}	cm^3
V_p	L^3	Structural volume at maturation	0.048	cm^3
X_K	$\#\,l^{-3}$	Half-saturation coefficient	100	V^{-1}
$\overline{X}_{in}$	$\#\,l^{-3}$	Proportionality coefficient input food density	1000	V^{-1}
κ	–	Allocation coefficient	0.8	—
κ_r	–	Efficiency reproduction into eggs	$1.18\ 10^{-5}$	—
μ	t^{-1}	Mortality rate	0.001	d^{-1}
τ	t	Spawning date		d

year

$$X_{in}(t) = \overline{X}_{in}\left(0.5 + 0.5\left(1 + \cos\left(\frac{2\pi t}{365}\right)\right)^4\right). \tag{5}$$

The power 4 is used to describe a peaked yearly algal bloom. At $t = 0$ the inflow of the food supply is maximum. The time at spawning τ is measured relative to this point in time. The maximum of the forcing equals $8.5\overline{X}_{in}$ and the minimum $0.5\overline{X}_{in}$.

The periodic forcing and reproduction with the same period of one year enables us to introduce a stroboscopic map with period 365 days. Generally the time of reproduction is used as the monitoring date. Then the discrete reproduction and death after the last reproduction takes place at the boundary of the interval of one year at which the state variables are smooth function. The discontinuities occur only at the boundary conditions. However, later on with the study of the evolutionary processes we will deal with two populations spawning at different times. Therefore we place the monitoring date at the maximum food inflow rate. As a result the state variables are only piece-wise smooth with cyclic boundary conditions and jumps at the spawning date. Then the time interval of interest is t: $0 \leq t \leq 365$ with τ the spawning date as an interior point.

We introduce cohorts labelled with a subindex i, that is $i = 1, \cdots, n$. At time τ in that interval, the individuals belonging to the first cohort $i = 1$ have age $a = 0$ and for $0 \leq t \leq 365$ their age is $a = (t - \tau) \bmod 365$. At $a = 365$ the surviving individuals move to the second cohort $i = 2$. The actual age of the individuals belonging to cohort i reads $a = (t - \tau) \bmod 365 + (i - 1)365$.

The state of the system within each year is described by a finite dimensional system consisting of one ODE for the food X and for each cohort i one ODE for each of the three i-state variables: for each cohort the individual size V_i, reserves $[E_i]$ and maturity H_i, and one ODE for the p-state variable: for rach cohort the size N_i. At that event the population size changes discontinuously whereby the step-size depends on the energy stored for reproduction $H_i - H_p$, where H_p is the maturity threshold.

Then for $0 \leq t \leq 365$ we have for the system states

$$\frac{dV_i}{dt} = h_{V_i}(V_i, [E_i])\,, \quad \frac{d[E_i]}{dt} = h_{E_i}(X, V_i, [E_i])\,, \quad \frac{dH_i}{dt} = h_{H_i}(V_i, [E_i])\,, \tag{6a}$$

$$\frac{dN_i}{dt} = -\mu N_i\,, \tag{6b}$$

$$\frac{dX}{dt} = D(X_{in}(t) - X) - \{\dot{J}_{Xm}\}f(X(t))\sum_{i=1}^{n} V_i^{2/3} N_i\,. \tag{6c}$$

Here $f(X(t))$ is the Holling type II functional response:

$$f(X(t)) = \begin{cases} 0 & \text{if} \quad V \leq V_b \\ \frac{X(t)}{X_k + X(t)} & \text{if} \quad V > V_b \end{cases}, \tag{6d}$$

where X_k is the half-saturation constant and we use the fact that embryos do not feed.

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Now we formulate the interior jump conditions at the spawning dates. The number of eggs produced by the adults form the size of the new cohort

$$\lim_{t \downarrow \tau} N_1(t) = \kappa_r \sum_{i=1}^{n} \frac{\lim_{t \uparrow \tau} N_i(t)(\lim_{t \uparrow \tau} H_i(t) - H_p)}{[E_0]V_0} \ , \tag{7}$$

where $[E_0]V_0$ is the energy content of one egg and κ_r is the efficiency. The size of cohorts N_i is discontinuous at τ because at that instant for $i = 1$ a new cohort is formed by the newborns and for $i = 2, \cdots, n$ the individuals become one year older, while cohort of age-class n dies. For the transition of the other cohorts we have

$$\lim_{t \downarrow \tau} N_i(t) = \lim_{t \uparrow \tau} N_{i-1}(t) \quad \text{for} \quad i = 2, \cdots, n \ , \tag{8}$$

whereby cohort n dies at $t = \tau$.

For the i-states the structural volume and the state of maturity changes discontinuously because the energy allocated to reproduction is used for building eggs. So, we have at $t = \tau$

$$\lim_{t \downarrow \tau} V_1(t) = V_0 \ , \quad \lim_{t \downarrow \tau} V_i(t) = \lim_{t \uparrow \tau} V_{i-1}(t) \ , \tag{9a}$$

$$\lim_{t \downarrow \tau}[E_1](t) = [E_0] \ , \quad \lim_{t \downarrow \tau}[E_i](t) = \lim_{t \uparrow \tau}[E_{i-1}](t) \ , \tag{9b}$$

$$\lim_{t \downarrow \tau} H_1(t) = H_0 \ , \quad \lim_{t \downarrow \tau} H_i(t) = \min(\lim_{t \uparrow \tau} H_{i-1}(t), H_p) \ , \tag{9c}$$

for $i = 2, \cdots, n$.

For the food we have the following continuity condition

$$\lim_{t \uparrow \tau} X(t) = \lim_{t \downarrow \tau} X(t) \ . \tag{10}$$

In order to reformulate the problem in terms of the classical non-linear dynamical system theory we define the vector of state variables as follows

$$\mathbf{X} = \begin{pmatrix} V_1 \ [E_1] \ H_1 \ \cdots \ V_n \ [E_n] \ H_n \ \ N_1 \ \cdots \ N_n \ \ X \end{pmatrix}^T \tag{11}$$

The ODE equations for these variables together with the initial conditions for the new-born cohort and reproduction rules, and the cyclic boundary conditions, form a periodically forced system of ODEs. We are looking for periodic solutions of that system and its stability on the ecological times-scale. The stroboscopic map Φ is defined as

$$\mathbf{X}^{y+1} = \Phi\left(\mathbf{X}^y\right) \ , \tag{12}$$

where $y \in \mathbb{N}$ denotes the year at $t = 0$, that is at the date where the food inflow is maximum. The fixed point of this non-linear stroboscopic map Φ gives the periodic solution of the periodically forced system.

Its stability can be studied by an analysis of this stroboscopic map [21]. The eigenvalues of the Jacobian matrix of the map Φ evaluated at the fixed point give the local asymptotic behaviour. In our numerical study the Jacobian matrix is approximated by finite differences. For a stable periodic solution all eigenvalues must lie inside the unit circle in the complex plane. The periodic solution with the forcing period of one year needs not to be stable in general. To study how the stability depends on the value of a specific parameter, a numerical bifurcation analysis can be performed. Starting from the fixed point solution for the initial parameter value, the bifurcation parameter is varied. During this continuation the eigenvalues are calculated and they are used to localise critical points where eigenvalues cross the unit circle, that is where the stability changes. These critical values set the bifurcation points. A period-doubling occurs when an eigenvalue equals -1. At a transcritical bifurcation one eigenvalue equals 1. This happens for instance where the population goes extinct. Another possibility is the so called Neimark-Sacker bifurcation where the magnitude of a pair of complex conjugated eigenvalues equals one. Since we are interested in the effects of the time of spawning τ this parameter is taken as a bifurcation parameter.

2.3 Calculation of the fixed points

At a fixed point the cyclic boundary conditions read

$$\tilde{V}_i(365) = \tilde{V}_i(0) , \quad [\tilde{E}_i](365) = [\tilde{E}_i](0) , \quad \tilde{H}_i(365) = \tilde{H}_i(0) , \tag{13a}$$

$$\tilde{N}_i(365) = \tilde{N}_i(0) , \quad \tilde{X}(365) = \tilde{X}(0) , \quad i = 1, \cdots, n . \tag{13b}$$

This shows that associated with a fixed point there is a periodic solution denoted by a tilde '~'.

Observe that the ODE Eqn. (6b) is de-coupled from the other equations and can be solved directly. When the mortality rate μ is constant the result is an exponential decay of the number of individuals given by

$$\lim_{t\uparrow\tau} \tilde{N}_i(t) = \lim_{t\downarrow\tau} \tilde{N}_1(t) \exp(-365\mu i) . \tag{14}$$

Substitution into (7) gives

$$1 = R_0 := \kappa_r \sum_{i=1}^{n} \frac{\exp(-365\mu i)(\lim_{t\uparrow\tau} \tilde{H}_i(t) - H_p)}{[E_0]V_0} , \tag{15}$$

where $\lim_{t\uparrow\tau} \tilde{H}_i(t)$ is the energy allocated to maturity and reproduction at spawning date. Hence, a necessary condition for a periodic population dynamics is that each individual replaces itself during its life-time n. This means that the sum of all fertilised eggs produced by one individual at the n spawning events, denoted by R_0, equals 1.

For iteroparous species we assume that they reproduce possibly every year till the last reproduction before they die. Due to our starvation condition we have that as long as

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the individual stays alive, $H \geq H_p$, and therefore it reproduces at spawning date. Hence when there is reproduction once it occurs always on end in the consequent years till the individual dies.

2.4 Zero and positive fixed point stability analysis

We first analyse the zero fixed point, where $N_i = 0$, $i = 1, \cdots, n$, and thereafter the positive fixed point, where $N_i > 0$, $i = 1, \cdots, n$. The obtained results are relevant for the next step, which is the study of the invasion of a mutant population into a resident population. Since $\tilde{N}_i = 0$, food is not consumed and Eqn. (6c) gives the zero fixed point periodic solution for the food $\tilde{X}(t) = X_{in}(t)$.

The structure of the Jacobian matrix evaluated at this zero fixed point is indicated below where non-negative elements are denoted by a '$*$'-symbol.

$$
\begin{pmatrix} \Delta V_1(365) \\ \Delta [E_1](365) \\ \Delta H_1(365) \\ \Delta V_n(365) \\ \Delta [E_n](365) \\ \Delta H_n(365) \\ \\ \Delta N_1(365) \\ \Delta N_n(365) \\ \\ \Delta X(365) \end{pmatrix} = \begin{pmatrix} * & * & * & * & * & * & * & * & * \\ * & * & * & * & * & * & * & * & * \\ * & * & * & * & * & * & * & * & * \\ * & * & * & * & * & * & * & * & * \\ * & * & * & * & * & * & * & * & * \\ * & * & * & * & * & * & * & * & * \\ \\ 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{P}_{11} & \mathbf{P}_{1n} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{P}_{n1} & \mathbf{P}_{nn} & 0 \\ \\ * & * & * & * & * & * & * & * & * \end{pmatrix} \begin{pmatrix} \Delta V_1(0) \\ \Delta [E_1](0) \\ \Delta H_1(0) \\ \Delta V_n(0) \\ \Delta [E_n](0) \\ \Delta H_n(0) \\ \\ \Delta N_1(0) \\ \Delta N_n(0) \\ \\ \Delta X(0) \end{pmatrix} \quad (16)
$$

The Δ notation indicate that we deal with small perturbations of the state variables in the linerized form. The expressions for the elements of the N_i-block matrix are for

$$
\Delta N_1(365) = \kappa_r \exp(-365\mu) \sum_{i=1}^{i=n} \frac{\Delta N_i(0)(\lim_{t \uparrow \tau} \tilde{H}_i(t) - H_p)}{[E_0]V_0} \,,
$$

$$
\vdots
$$

$$
\Delta N_n(365) = \exp(-365\mu) \Delta N_{n-1}(0) \,.
$$

The N_i-block matrix $\mathbf{P}$ reads

$$\mathbf{P}_{11} = \kappa_r \exp(-365\mu)\frac{(\lim_{t\uparrow\tau} \tilde{H}_1(t) - H_p)}{[E_0]V_0} \ ,$$

$$\vdots$$

$$\mathbf{P}_{1n} = \kappa_r \exp(-365\mu)\frac{(\lim_{t\uparrow\tau} \tilde{H}_n(t) - H_p)}{[E_0]V_0} \ ,$$

$$\mathbf{P}_{21} = \exp(-365\mu) \ ,$$

$$\vdots$$

$$\mathbf{P}_{n(n-1)} = \exp(-365\mu) \ .$$

and all other elements are zero.

The diagonal block matrix $\mathbf{P}$ for the population number variables N_i is decoupled from the i-state variables and food variable system because of the zero elements in the matrix of the two associated rows indicated in (16). Consequently the characteristic equation is partitioned and the eigenvalues are those of the two block matrices. Calculations show that for the reference parameter values in Table 1 the eigenvalues for the remaining block matrix belonging to the i-state variables and the food variable, are inside the unit circle. Some of the eigenvalues are zero and this has to be taken into account with the calculation of the fixed point.

Hence the stability of the zero fixed point solution is determined the n eigenvalues of the diagonal block matrix $\mathbf{P}$. Observe that this matrix is precisely a clasical linear Leslie matrix (see [3, 4]). On the first row of this matrix contains the class fertilities and on the sub-diagonal the year–to–year survival probabilities. The eigenvalues and eigenvectors of this non-negative matrix are described by the Perron-Frobenius theorem [3, page 83]. Furthermore it allows for the use of net reproductive rate denoted by R_0 for the evaluation of the stability [3, page 126]: $R_0 > 0$ unstability and $R_0 < 0$ stability. Here we use the dominant eigenvalue of the block matrix $\mathbf{P}$. For the reference parameter values one real eigenvalue is inside the unit circle but the other is outside, and therefore the zero fixed point solution is unstable. This finalizes the analysis of the zero fixed point where $N_i = 0$, $i = 1, \cdots, n$.

Besides this zero fixed point there can be positive solutions where $N_i \geq 0$, $i = 1, \cdots, n$ and for a $1 \leq j \leq n$ where $N_i > 0$, $i = j, \cdots, n$. The analysis of these positive solutions is straightforward and the eigenvalues of the Jacobian matrix directly dictate the stability properties.

3 Evolutionary model formulation

We will study the evolutionary development of the population in the reactor using the adaptive dynamics approach. It is assumed that the ecological time scale (here a few years) is much faster than the evolutionary time scale (several generations). The ecological

time scale is dictated by the growth processes of the population, so the change in numbers and food dynamics. The evolution time scale is set by the rate of change of the trait parameter, the low mutation rate. The trait is the timing of the reproduction τ. Hence, the individuals from the resident and the mutant population have the same physiological parameter values except the timing of the reproduction τ. Time scale separation gives that in studying the dynamics of the trait the population dynamics is at steady state, that is at a stable fixed point of the stroboscopic map Eqn. (12).

In order to study effects of a mutational step we introduce besides the steady state resident population with trait value $\tau = \tau_r$, a mutant population with a slightly different trait value $\tau = \tau_m$. As a result the dynamics of the extended dynamical system consisting of two populations is studied. In a similar way as for the one population system a stroboscopic map can be formulated. Both populations compete for the same food X, so the ODE for the food reads

$$\frac{dX}{dt} = D(X_{in}(t) - X) - \{\dot{J}_{Xm}\}f(X(t))\Big(\sum_{i=1}^{n} V_{i,r}^{2/3} N_{i,r} + \sum_{i=1}^{n} V_{i,m}^{2/3} N_{i,m}\Big) , \qquad (17)$$

where the additional subscript denotes the resident, r, or mutant, m, population.

In summary, the governing equations for the resident and mutant population in the chemostat reactor are formed by Eqns. (12) whereby the vector of state the variables reads

$$\mathbf{X} = \begin{pmatrix} V_{i,r} & [E_{i,r}] & H_{i,r} & N_{i,r} & V_{i,m} & [E_{i,m}] & H_{i,m} & N_{i,m} & X \end{pmatrix}^T , \qquad (18)$$

where for all i-states and p-state, $v \in \{V, [E], H, N\}$, and both populations, $P \in \{r, m\}$

$$v_{i,P} = \begin{pmatrix} v_{1,P} & \cdots v_{n,P} \end{pmatrix}^T , \qquad (19)$$

Because the populations spawn at different times each year is divided into three intervals where the ODEs (4) and (17) are valid with the jump conditions such as (7), (8) and (9), at the two spawning dates for the associated population while for the fixed point furthermore the cyclic boundary conditions (13) hold true.

To study invasion of the resident population by a mutant population we consider the stability of the fixed point whereby $N_{i,r} > 0$ and the mutant is absent $N_{i,m} = 0$, $i = 1, \cdots, n$.

4 Bifurcation analysis technique

For the periodically forced system studied here, we use the bifurcation analysis approach to calculate the PIP and MIP. Regions of coexistence of the resident and the mutant populations are bounded by transcritical bifurcations of the stroboscopic map [18, 35, 36]. At these curves the system consisting of the resident and mutant populations together with the ambient food is structurally unstable with the leading eigenvalue equal to 1, whereby one population (here we assume first the mutant population) is absent while furthermore its invasion rate is zero. These curves mark regions of coexistence.

Applying bifurcation theory means that the ESS is fixed by a point $\tau_m = \tau_r$ where two transcritical bifurcation curves (one where the resident population is absent and the other where the mutant population is absent) intersect. Observe that in this point there is no unique solution because the two populations are identical and therefore only the sum of the numbers of individuals that make up the populations is fixed. The type of ESS can be found by performing a one parameter bifurcation analysis where $\tau_r = \tau_m + \varepsilon$ where ε is small.

As for the zero solution of the one-population map, it is possible to derive analytically some general results before performing a numerical bifurcation analyses whereby all parameters need to possess a value, except the free bifurcation parameter (here the trait). The situation is similar to that discussed above for the zero fixed point solution whereby the number density of the population was zero, that is $N_i = 0$ in the mutant population. The food density $X(t)$ is now different from the input function $X_{in}(t)$, but is set by the resident population. Nevertheless there is a partitioning of the Jacobian matrix, here for the mutant p-states $N_{i,m}$, $i = 1, \cdots, n$ and all the other variables. The stability charateristics of the Jacobian matrix related to the mutant p-states determines whether invasion of the mutant population occurs or not. Consequently also in this case we need to evaluate only the stability of the fixed point of the n-dimensional system for $N_{i,m}$, $i = 1, \cdots, n$. Since the fixed point of the resident population system with spawning date τ_r is stable, the invasion fitness [25] is the dominant eigenvalue of the Jacobian block matrix $\mathbf{P}$ for the mutant population with spawning date τ_m evaluated at $N_{i,m} = 0$, $i = 1, \cdots, n$. When this dominant eigenvalue is outside the unit circle the mutant can invade otherwise it cannot.

Alternatively we can using a similar expression for R_0, Eqn. (15) the following invasion fitness $s = \ln R_0$ for the mutant population with spawning date τ_m

$$s = \ln\Big(\kappa_r \sum_{i=1}^{n} \frac{\exp(-365\mu i)(\lim_{t\uparrow\tau} H_{i,m}(t) - H_p)}{[E_0]V_0}\Big) \,, \tag{20}$$

Here $H_{i,m}(t)$ is calculated using the food dynamics set by the resident population.

In this study we calculated the eigenvalues of the complete system and this guarantees that the invaded resident population is stable.

5 Case study

Many students of marine invertebrates have considered the fitness consequences of the timing of reproduction only in terms of the short-term prospects of the offspring [34]. For example, it has recently been argued that spawning by the marine bivalve *Macoma balthica*, which seems to be triggered by a temperature threshold, has shifted forward within the season as a result of global change [28]. This may have caused a temporal mismatch with the onset of the spring bloom which is believed to be of vital importance for the early larvae. Generally speaking, it is however not immediately obvious why emphasis should be put on the earliest life phase of the offspring. Adults themselves may profit from the food peak

and by these means increase total reproductive output. It might also be more profitable for the young to experience the food peak at a later stage and a larger size [31]. The debate on whether growth and development of invertebrate larvae are indeed food-limited under natural conditions has indeed not settled yet [32].

In this section we present results of our analysis for the bivalve *Macoma balthica*. Our exploration on the optimal time of spawning for this bivalve may contribute to the discussion on the importance of the food conditions during the earliest life larval phase of marine invertebrates. The parameter values of the DEB model for *M. balthica* were estimated in [38], and are given in Table 1. *M. balthica* lives in buried in sandy sea beds of the coastal zones of the Northern Atlantic. Along the European coast, *M. balthica* occurs from the White Sea at 70°N to the Gironde estuary at 45°N. In the Dutch Wadden Sea where *M. balthica* is a dominant species it can be found from the upper regions of the intertidal to the outer parts of the tidal inlets and into the coastal zone. It feeds merely on algae. In the Dutch Wadden Sea *M. balthica* spawns in April [28], while the chlorophyll levels which are indicative of algal abundance, peak in May [28].

5.1   Bifurcation analysis results

We start with the analysis of the ecological model in which case the trait, the time of spawning τ, is fixed for the resident population.

For the parameter values given in Table 1 the zero solution where $N_i = 0$ for $i = 1, 2$, is unstable. The dominant eigenvalue of the 2×2, Jacobian block matrix for the p-state variables N_i, $i = 1, 2$ is larger than 1 and the other eigenvalues are inside the unit cycle. The positive solution is stable for the parameter values given in Table 1. This stable periodic solution of the resident population is shown in Figures 1 and 2 for $\tau = 211$ d. From the analysis below we know that this trait value belongs to an ESS. Figure 1A gives the annual cycle of the inflowing food concentration $X_{in}(t)$ and the ambient food concentration $X(t)$. The food concentration increases at spawning. This is because the newly laid eggs do not feed while the adults in the second year class cohort died. In general, the difference between $X_{in}(t)$ and $X(t)$ is due to feeding of the population which causes some delay, well known for predator-prey interactions.

The number of individuals in each cohort $N_i(t)$, $i = 1, 2$ is depicted in Figure 1B. These numbers are continuously decreasing due to mortality and discontinuously due to the disappearance of the second year-class cohort after their final spawning event and only at spawning an increase due to egg production of the first year cohort. The transition from each year-class cohort to the next year-class is continuous, all individuals move to the next class.

In Figure 2 the changes of the i-state of the individuals in their first and second year class are depicted where age is related to time of the year by $a = ((t - \tau) \bmod 365) + (i - 1)365$ where i is the year-class. In Figure 2A, the size v of the eggs is small at spawning. They hedge and become juvenile at $V_i = V_b$, which become mature at $V_i = V_p$, $i = 1, 2$. Observe that there is always growth, the individuals do not shrink, even not during time periods where the food density is low. In Figure 2B the annual changes in the energy allocation to

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the reserve buffer $[E_i](t)$ together with the expression $f(t)[E_m]$ (see Eqn (1b)). In Figure 2C the energy allocation to development and the reproduction $H_i(t)$ is shown.

The PIP and MIP-plots shown in Figure 3 summarize the evolutionary results. Figure 3A is the PIP-plot. In the grey regions the mutant is able to invade the resident population, that is the mutants fitness is positive. At the interior boundaries the invasion fitness is zero. The point on the principle diagonal where the fitness gradient is zero is an ESS. The MIP-plot Figure 3B is obtained as the superposition of the PIP-plot and its mirror image along the principle diagonal [14]. On the right side of point ss^- there is a '+' below the diagonal and '−' above the diagonal. That is the local fitness gradient from above points towards ss^-. On the left side of point ss^- there is a '−' below the diagonal and '+' above the diagonal. Hence the local fitness gradient from below points also towards ss^-. This description is that of the AD-framework.

Now we give a description of the results of applying the bifurcation analysis approach. Here we only refer to the MIP-plot Figure 3B. In this diagram the transcritical bifurcation curves are drawn. There are two types of curves. At one curve the size of the mutant population is zero and at the type of curve the size of the resident population is zero. These curves mark trait values where the invasion rate of the zero size population is zero. There is an ESS at the intersection point on the diagonal where these curves meet. There are two ESSs: point ss^- at $\tau_r = 211$ d and point ss^+ at $\tau_r = 31.2$ d.

The transcritical curves close to point ss^- inclose a region where the two populations can coexist (see MIP-plot Figure 3B). However this interior point is unstable (the leading eigenvalue of the Jacobian matrix evaluated at points in this region is outside the unit cycle). Figure 4B is a one parameter diagram where population size $N_r = \sum_{i=1}^{2} N_{r,i}$ of the resident population and $N_m = \sum_{i=1}^{2} N_{m,i}$ of the mutant population as function of the trait τ_m where $\tau_r = \tau_m + 5$. This line is also drawn in Figure 4A which is a detail of Figure 3B. The interior equilibria are unstable (at the ecological time scale) and therefore branching does not occur and point ss^- is a stable ESS. The diagram shows that there is no mutual invasibility. The zero fixed point is stable below the right (catastrophic) transcritical bifurcation point indicated by an open cicle ∘ and the positive fixed point is stable above this bifurcation point.

In a similar way we find that the local fitness gradient points in both directions away from ss^+. This point forms a separatrix. Starting with a higher resident trait values mutational steps will lead to an increase of the trait towards point ss^-. On the other hand starting with a smaller trait value, mutational steps lead to a decrease towards point ss^-, where we use the fact that the MIP-plot is cyclic for $\tau = 0$ and $\tau = 365$.

For points that are more distant from the points ss^- and ss^+ in Figure 3B, the region of coexistence becomes very small and both curves are indistinguishable. Because the MIP-plot is cyclic with a period of one year, the transcritical bifurcation curves connect points ss^- and ss^+. When the two curves coincide the dynamics is the same as on the diagonal, at one side one population wins while at the other side the other wins.

We also performed a sensitivity analysis to find the impact on the ESS-value for the spawning date of a number of the parameters related to the interaction of the population with the environment while keeping all DEB-parameters for the individuals the same as in

Table 1. We studied temperature effects affecting the physiological rates of the population using the Arrhenius relationship whereby the ambient temperature (and therefore also the internal temperature of most marine organisms) fluctuates seasonally. Also the maximum and minimum values which described the periodic food forcing function given in Eqn. (5) were varied. Furthermore we increased the maximum lifetime from 2 to 5. In all cases we found only marginal effects on the results presented here based on the parameter values given in Table 1.

6   Discussion

The main aim of this paper is to study the evolutionary dynamics of the timing of spawning within the year of iteroparous species. The work here differs from Davydova's [5] dealing with semelparous species ($n = 1$) in that the population is iteroparous, that is, the individuals reproduce annually and die immediately after the last reproductive event ($n \geq 2$). However, in the model formulation, when individuals of the cohorts become adult in their last year the species is effectively semelparous.

In the AD-theory literature the PIP and MIP are constructed by calculation of the zero invasion fitness curves [14, 24]. Thereafter, the shape of these curves directly fix the ESS points and their evolutionary stability [14]. Eight different types of singular strategies are distinguished based on the second derivatives of the invasion fitness evaluated at the point. The region of invasion in the PIP Figure 3A close to point ss^- at $\tau_r = 211$ d is the same as in [14, Figure 2 case (e)]: it is ESS-stable and convergence-stable. The local fitness gradient points towards this point. For point ss^+ at $\tau_r = 31.2$ d, the region of invasion is the same as that in [14, Figure 2 case (h)]: this ESS is ESS-unstable and convergence-unstable.

In the AD-approach a mutational step is devided into two steps. First a stable resident population is invaded by the mutant population, second the mutant population replaces the resident population and this means that the new resident population is also stable. In bifurcation terms these two steps mean that starting from a stable resident population, first the resident-mutant system with zero mutant population size but with a sightly different trait value than the resident population, is unstable. Second the resident population goes extinct and the mutant population grows and reaches a stable fixed point. In our approch the stability of the new resident population is checked when the next mutational step is analysed.

In a bifurcation analysis context the zero mutant invasion fitness curve is precisely the transcritical bifurcation curve for the two-population system in the two-dimensional trait space where the trait of the resident and mutant populations are the bifurcation parameters. Generally this is done by the calculation of so called test-functions (see [21]) Or by the calquation of the eigenvlues of the Jacobian matrix. An example of the test-function is the invasion fitness defined in Eqn. (20). This simplifies the numerical calculations for there is no need to calculate the Jacobian matrix evaluated at the fixed point and its eigenvalues. However, using this invasion fitness as a test function gives no guaranty that the invaded resident population was stable and furthermore is givs no direct information about whether

invasion leads to replacement or coexistence.

The bifurcation diagram Figure 3B is an alternative for the PIP Figure 3A. The advantage of a bifurcation analysis is that it is also applicable when no simple expression for the invasion fitness is available. Furthermore because all types of bifurcations are calculated as part of the analysis of the competitive two-population system the requirements (for instance existence of a positive stably resident population) which justify the application of the adaptive dynamics approach are checked. Observe that in the bifurcation analysis approach we adhere strictly to the time-scale separation of the ecological and evolutionary time-scales. After a successful invasion of the mutant it replaces the resident population. This means that the temporal change of the trait variables at the evolutionary time scale described by the canonical equation [10], is not studied: only the calculation and evaluation of the stability of the evolutionary endpoints. In [8] the dynamics of the canonical equation is studied in great detail using bifurcation analysis technique.

In [7] a size-structured population-nutrient model is used to study evolutionary changes in fish individual life history and stock properties. In that article many elements of the AD approach are adopted. The invasion fitness is computed by two-population competition simulations. This approach is more universal and can be used for a wide range of population models and also when the ecological and evolutionary time scales are not separated (see also [35]). However, the accuracy of the simulations can be problematic and the calculations are much more time-consuming.

Although the results obtained for the bivalve *Macoma balthica* are preliminary, it is tempting to compare them with field data. From Figure 3 we learn that there are two ESS values, one is an evolutionary attractor and the other is an evolutionary repeller. At the attracting singular strategy the species spawns about 150 d before the maximum food inflow (algal bloom). This date is far away from what has been observed in the field, where spawning occurs only one month before the algal bloom [28]. At present knowledge at the level of the individual is much more extensive than what we know at the population level, including the description of food and predation dynamics. DEB parameter values, for example, are relatively well-known [38]. Hence, there is a need for more data at the population level. Nevertheless, we can already conclude that the accepted hypothesis that the seasonal timing of spawning in marine invertebrates is a response to seasonal fluctuations in food levels was not confirmed by our model analysis. It might be that besides the dynamics of the food, the seasonal fluctuations in predation pressure (see [40, 41]) are important.

In conclusion, bifurcation analysis provides an integrated approach for modelling and analysis of ecological and evolutionary processes on both individual and population level of organization. In the future the technique developed here will be used to study the evolution of reproductive strategies such as the timing of spawning of marine invertebrates or vertebrates that spawn within small time windows periodically [26, 29, 39, 40, 42].

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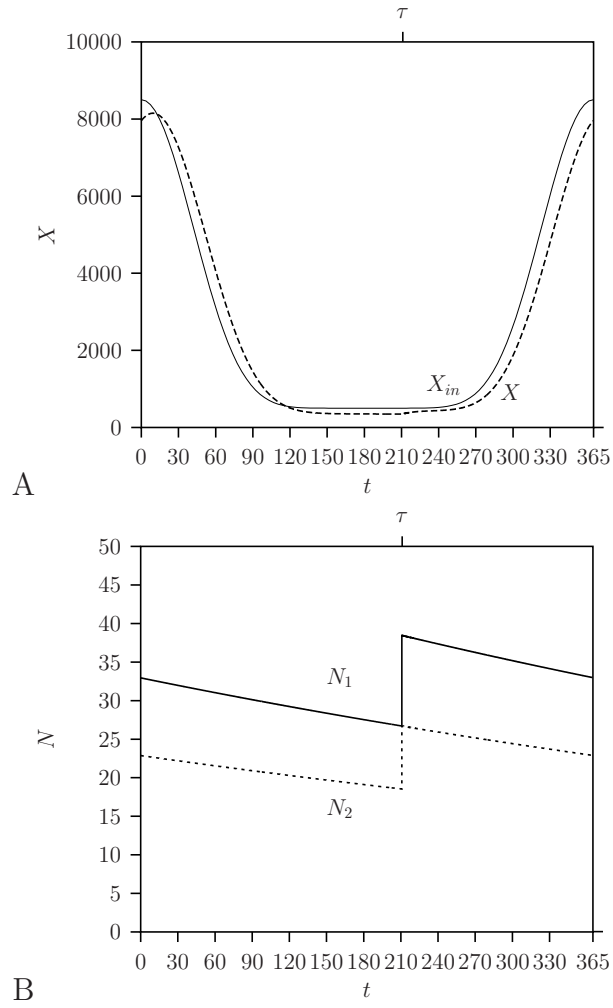
Figure 1: A: Food concentration X_{in} supplied, ambient food concentration X. B: Population densities of the cohorts N_i, $i = 1, 2$. The two p-state variables are plotted as function of the time t where $\tau = 211$ d.
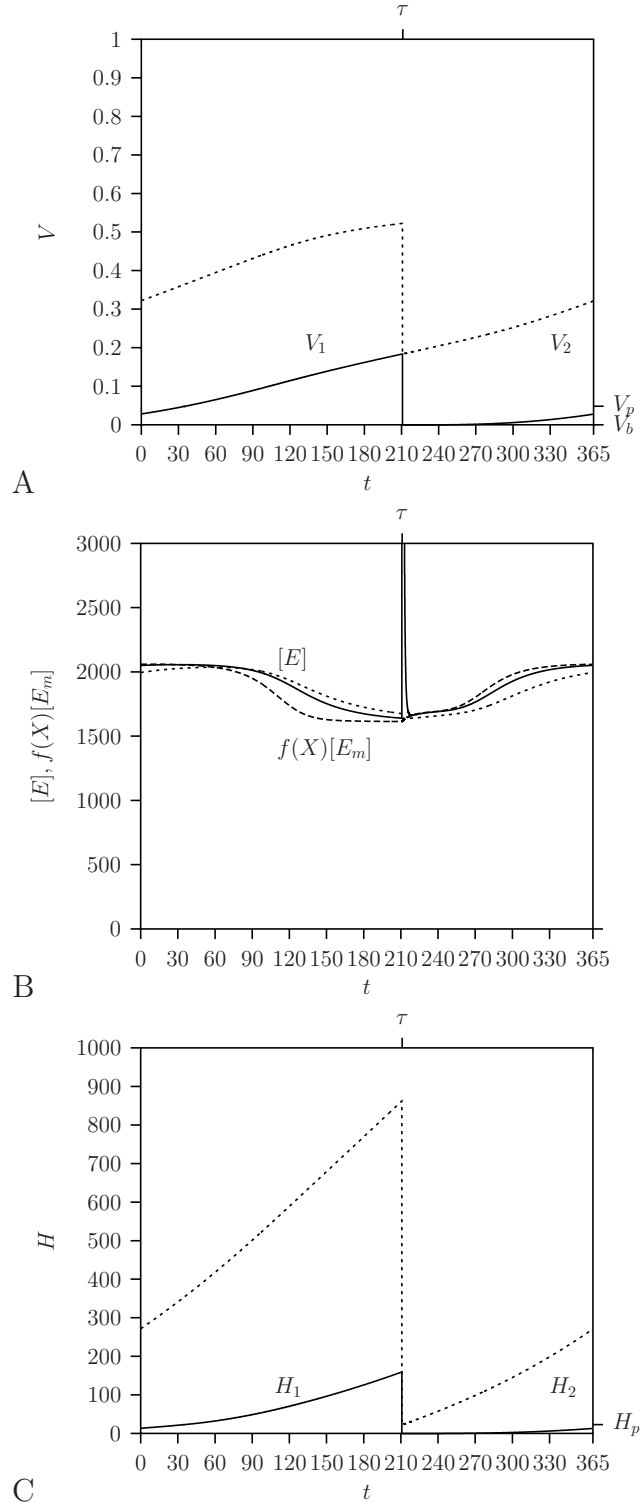
Figure 2: A: Individual biovolumes of the cohorts V_i, $i = 1, 2$. B: Energy reserves of the cohorts $[E_i]$, $i = 1, 2$ and the expression $f(t)[E_m]$. C: Maturity, cumulative energy allocated to development (embryo's and juveniles) or reproduction (adults) of the cohorts H_i, $i = 1, 2$. The three i-state variables are plotted as function of the time t where $\tau = 211$ d.
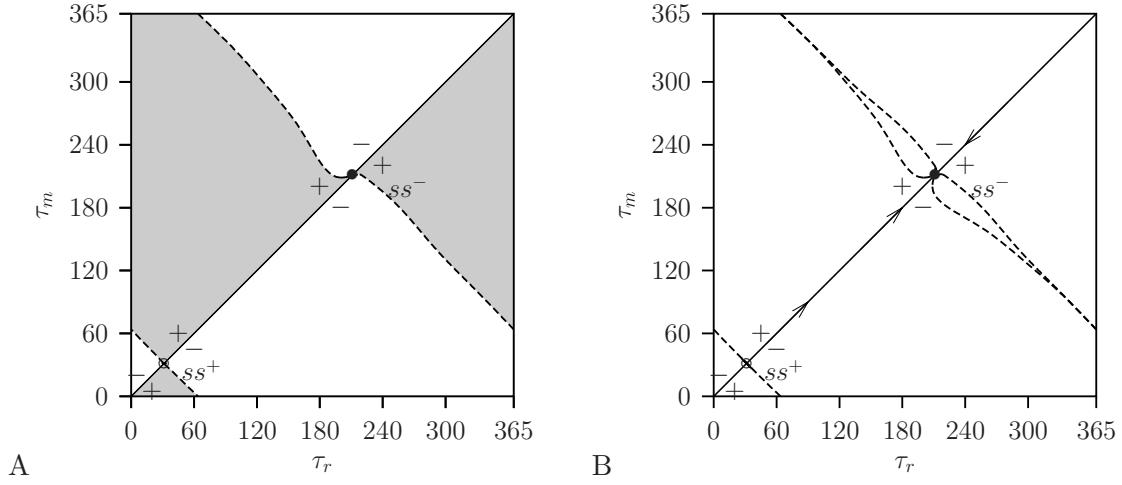
Figure 3: A: Pairwise Invasibility Plot (PIP-plot). In the grey regions the mutant may invade and replace the resident and in the white regions it cannot invade. There is a stable singular point ss^- and an unstable singular point ss^+. B: Mutual Invasibility Plot (MIP-plot). The '+'-mutant may invade and replace the resident and the '−'-mutant cannot invade. The dashed curves are the transcritical bifurcation curves. The arrows indicate the direction of the evolution.
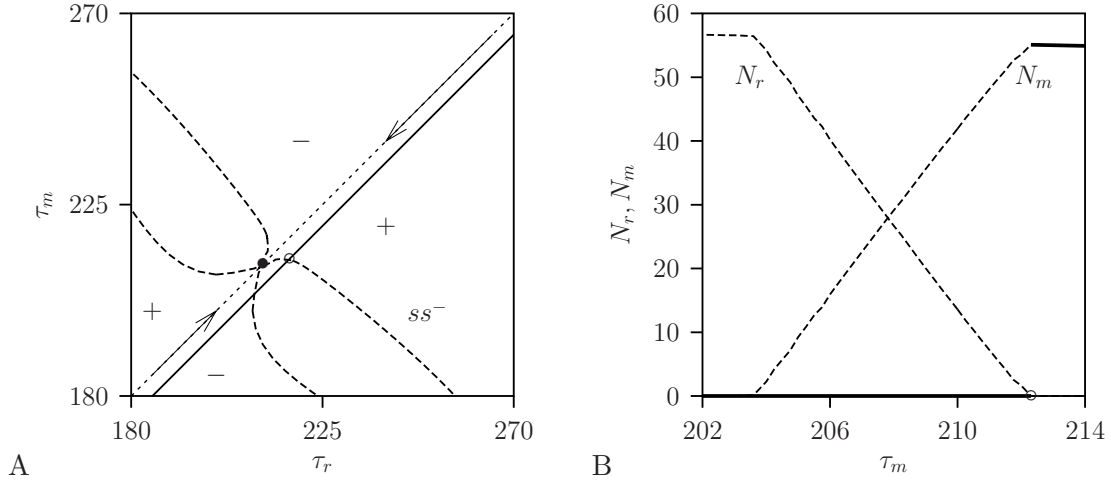

Figure 4: A: Detail of Figure 3B around point ss^-. The solid line is $\tau_r = \tau_m + 5$. B: Population densities of resident ($N_r = \sum_{i=1}^{2} N_{r,i}$) and mutant ($N_m = \sum_{i=1}^{2} N_{m,i}$) population as function of the trait τ_m where $\tau_r = \tau_m + 5$. Solid lines denote stable fixed points and dashed lines unstable fixed points. In both panels the transcritical bifurcation point is indicated by an open circle ∘.

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