REPORTS
IN
INFORMATICS

ISSN 0333-3590

# Application of slow-fast population dynamic models

Ute Schaarschmidt, Sam Subbey and
Trond Steihaug

REPORT NO 409 July 2014

*Department of Informatics*
**UNIVERSITY OF BERGEN**
*Bergen, Norway*

This report has URL
http://www.ii.uib.no/publikasjoner/texrap/pdf/2014-409.pdf

Reports in Informatics from Department of Informatics, University of Bergen, Norway, is available at http://www.ii.uib.no/publikasjoner/texrap/.

# Application of slow-fast population dynamic models

Ute Schaarschmidt*,**, Sam Subbey*,** and Trond Steihaug**
* Department of Informatics, University of Bergen, Norway
** Institute of Marine Research, Norway

July 3, 2014

**Abstract**

The Beverton-Holt and Ricker functions are two distinct ecological descriptions of the link between a parental population size and subsequent offspring that may survive to become part of the fish stock.

This report presents a model consisting of a system of ordinary differential equations (ODEs), which couples a pre-recruit stage with several adult stages. Elements of slow-fast dynamics capture the different time-scales of the population dynamics and lead to a singular perturbation problem.

The novelty of the model presented here is its capability to replicate a broad spectrum of the stock-recruitment relationship (SRR), including the Beverton-Holt and Ricker dynamics. The results are explained using geometric singular perturbation theory and illustrated by numerical simulations.

## 1 Introduction

Ecological systems usually include different levels of organization, such as individual, population, community and ecosystem levels, see e.g., [1]. Each of these levels can be associated with a different characteristic time scale. For instance, individual processes may be described in terms of a faster time-scale than demographic events. When coupling the different levels, the distinct time-scales need to be integrated in the system.

Dynamical systems, which involve several time-scales are often referred to as slow-fast systems. Here, a subset of the set of variables is assumed to change at a faster rate then the rest of the variables. The ratio between the distinct time-scales is measured by a small parameter $\epsilon$. In this report, we focus on continuous slow-fast systems, also referred to as singularly perturbed differential equations, since they behave singularly in the limiting case $\epsilon \to 0$. It is far beyond the scope of this article to mention all literature about slow-fast systems and the reader may thus be referred to [18].

Slow-fast systems have also found some application in fisheries. For instance, slow-fast systems have been used to describe the faster movement of fishing fleets in comparison to the slower movement of fish, [3]. In [9], the migration between different patches has been assumed to happen at a faster time-scale than an epidemic process. A general theory for investigating population dynamic models involving several time-scales has also been presented, see [1] and references therein.

Recruitment is the result of spawning and survival during several early life-history stages. It is common knowledge that evolution of younger fish happens at faster rates than growth and mortality of adult fish. Therefore, dynamics of fish before and after recruitment are associated with different time-scales and can be described by slow-fast systems,

*Email: ute.schaarschmidt@ii.uib.no

see [17]. This report considers the latter application field of singularly perturbed differential equations.

### 1.1 Parametrising the stock-recruitment relationship

Recruitment is traditionally described as a function of the size of the spawning stock, as it is a result of past states of the stock. The two most popular functional representations of the relationship have been introduced by Beverton-Holt [2] and Ricker [13].

Both models assume a decrease in recruitment per spawner with stock size, but the degree of decline, often referred to as density-dependence, distinguishes the two models from each other. A Beverton-Holt function, as described by equation (1), is monotonic increasing with an asymptotic maximum. A Ricker type of SRR (see equation (2)) has a maximum and the number of recruits may decrease with increasing spawning stock (see figure 1). This phenomenon is sometimes referred to as overcompensation. Both functions can be interpreted as solutions of ordinary differential equations, which base on an assumption of linearity of the natural mortality rate in the numbers of recruits (for the Beverton-Holt model, (4)) or spawners (for the Ricker model, (5)). Herein, the initial number of eggs is assumed to be proportional to the number of spawners, $R(0) = cS(0)$. The Deriso model [4] corresponds to the Ricker model in case of $\gamma \to \infty$ and to the Beverton-Holt model in case of $\gamma = 1$, see equation (3). For a recent review about stock recruitment models, see e.g., [16].

Beverton-Holt: $$R = \frac{aS}{b+S} \quad (1) \qquad \dot{R}(t) = -\,(p + qR(t))R(t) \quad (4)$$

Ricker: $$R = aSe^{-bS} \quad (2) \qquad \dot{R}(t) = -\,(p + qS(0))R(t) \quad (5)$$

Deriso: $$R = aS(1 + \frac{b}{\gamma}S)^{-\gamma} \quad (3)$$ where $a, b, p, q \in \mathbb{R}_+, \gamma \in \mathbb{R}$

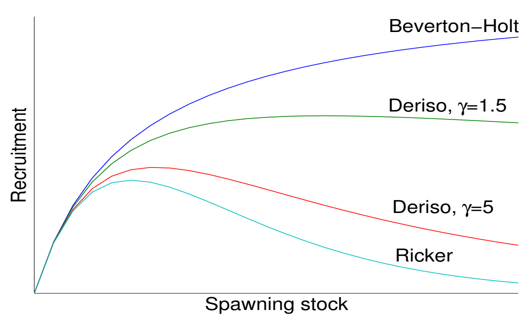



**Figure 1:** Traditional stock recruitment relationships

## 2 A SRR based on a slow-fast population dynamic model

Not only is recruitment a function of numbers of spawners, but the spawning stock consists of survivors of previous recruitments. This two-sided relationship has for example been investigated by Touzeau and Gouzé [17]. A pre-recruit stage is added to an age-structured population dynamics model. Two distinct time-scales express the fact that pre-recruit stages are often shorter than adult stages. By using continuous time, challenges of high dimensionality arising from use of smaller time-steps connected to pre-recruit development have been avoided. Further, the model adopts assumptions of the Ricker and Beverton-Holt models.

More specifically, a system of differential equations models the dynamic behaviour of numbers of pre-recruits $X_0(t)$ and adults $X_i(t)$ of some age-class $i = 1, \ldots, n$ (see equations (6)–(7)). The numbers of eggs are assumed to be proportional to the spawning stock size and the mean number $l_i$ of eggs spawned by individuals of age $i$. Adopting basic assumptions by Beverton-Holt (4) and Ricker (5), the instantaneous mortality rate of pre-recruits is assumed to be linear in $X_0$ and $X_i$, for $i = 1, \ldots, n$, respectively. The parameters $p_0$ and $p_i$ thus express the degree of the limiting effect of the density of pre-recruits and adult age-classes $i$. Density-independent mortality rates are denoted by $m_0, m_1, \ldots, m_n$. In contrast to the assumptions by Ricker and Beverton-Holt, spawning and ageing are continuous processes, with fish ageing at a constant ratio $\alpha$.

In order to cope with the fact that evolution of pre-recruits happens at faster rates than growth and mortality of adult fish, a fast time $T$ and a slow time $t = \epsilon T$ are employed. Here, the parameter $0 < \epsilon \ll 1$ describes the ratio between the two time-scales. For reasons of simplicity, let $X(t)$ denote the $(n+1)$-dimensional vector $(X_0(t), X_1(t), \ldots, X_n(t))^t$. Then, the function $A^{TG} : \mathbb{R}^{n+1} \to \mathbb{R}$ summarizes the fast events spawning, juvenile competition and cannibalism. Changes in numbers of pre-recruits consist (partly) of rapidly varying processes, while sizes of adult age-classes are slow variables.

The age-structured model also characterizes the dynamics of spawning stock and recruitment, if reproduction at any point in time is assumed to be a proportion $\alpha$ of pre-recruits and the spawning stock is the sum of fecund fish (see equation (8), where $f_i$ denotes fecundity).

$$\dot{X}_0(t) = -\alpha X_0(t) + \frac{1}{\epsilon} \underbrace{\left[ -m_0 X_0(t) + \sum_{i=1}^{n} f_i l_i X_i(t) - \sum_{i=1}^{n} p_i X_i(t) X_0(t) - p_0 X_0(t)^2 \right]}_{=A^{TG}(X(t))} \tag{6}$$

$$\dot{X}_i(t) = \alpha X_{i-1}(t) - \alpha X_i(t) - m_i X_i(t), \quad i = 1, 2, \ldots, n \tag{7}$$

$$R(t) = \alpha X_0 \quad \text{and} \quad S(t) = \sum_{i=1}^{n} f_i X_i(t) \tag{8}$$

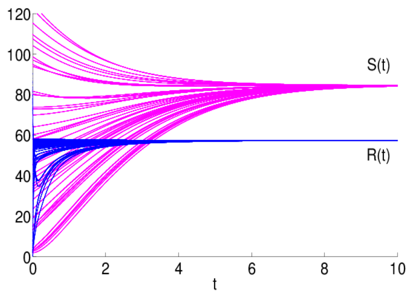
Using singular perturbation theory, [17] showed that the dynamic behaviour of the system (6)–(7) can be separated into two phases. In the first phase, fast processes are dominant, i.e. the number of pre-recruits is subject to bigger variations than numbers of adults (see figure 2(a)). Solution trajectories are attracted to a specific curve, which describes the dynamics in the second phase. This curve can be interpreted as relationship between the fast variable $X_0$ and the slow variables $X_i$ and is approximately described by the null space of function $A^{TG}$. Due to the connection between pre-recruits and recruitment, as well as adults and spawners (see equation (8)), this yields a SRR (see figure 2(b)). The dynamical system has an unstable equilibrium at 0 and a stable fixed point $X^*$ or $(R^*, S^*)$.

Assuming that all parameters are independent on age, i.e. $l_i = l$, $f_i = f$, $p_i = p$, $m_i = m$, for all $i = 1, \ldots, n$, $A^{TG}(X(t)) = 0$ yields a functional relationship between recruitment and spawning stock. If $p_0 = 0$, the approximation for the SRR corresponds to a Beverton-Holt function (9).

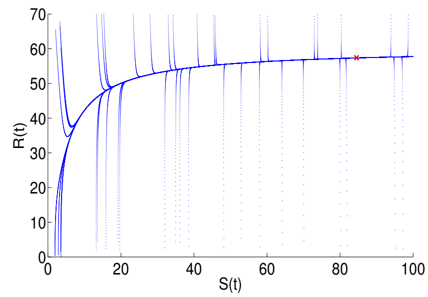
$$R(t) = \frac{\frac{\alpha l}{m_0} S(t)}{1 + \frac{p}{m_0 f} S(t)} \tag{9}$$

## 2.1 Limitations and problem description

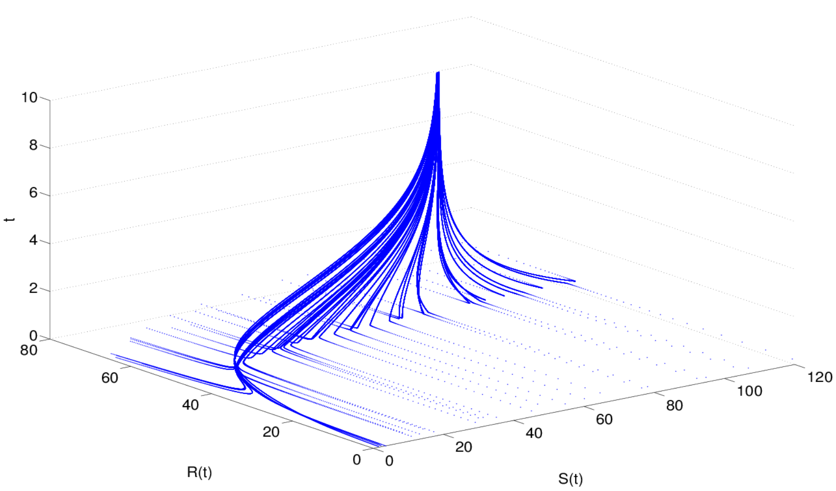
The slow-fast population dynamic model with pre-recruit stage explains a Beverton-Holt type of SRR, but a Ricker type of SRR cannot be derived from the population dynamic model. Further, it has been shown that over-compensation in the SRR cannot occur in the second phase, [17].




(a) Spawning stock size and recruitment as described by the slow-fast population dynamic model as functions of time. Recruitment converges faster to its stable equilibrium state than the spawning stock.




(b) After a short, first phase, all solution trajectories evolve similarly to a Beverton-Holt stock recruitment curve. The red cross marks the equilibrium states of recruitment and spawning stock size.




(c) Starting at random initial states, the SRR soon behaves similarly to a Beverton-Holt curve and converges to a stable equilibrium.

**Figure 2:** Numerical solution of the SRR as described by the slow-fast population dynamic model (6)–(8) at $t \in \{0, 0.0005, 0.001, \ldots, 10\}$. The following (synthetic) parameter values were used: $n = 4$, $\alpha = 0.8$, $\epsilon = 0.1$, $m_0 = 0.7$, $p_0 = 0$, $m = 0.2$, $p = 0.1$, $f = 0.5$ and $l = 15$.

A system of ordinary differential equations, which could replicate a broad spectrum of stock recruitment curves, including the Ricker and Beverton-Holt functions would be of interest for several reasons. Dynamics of several age-classes are described and the faster evolution of pre-recruits is depicted by the second time-scale. The model assumptions by Ricker explain a dome-shape of stock recruitment curves, which may arise from important mechanisms. Examples are aggregation of cannibals or predators or density-dependence of growth rates coupled with size-dependent predation [6, 13].

Therefore, the aim of the following chapter is to derive a slow-fast population dynamic system which can explain a broader spectrum of SRRs. We keep the structure of a system of differential equations with two time-scales, which describes the changes in numbers of adults and pre-recruits. But we parametrise the dynamic system in such a way that it is able to explain a set of SRRs including the Ricker model.

# 3 Addressing the limitations

This chapter starts with a short introduction to geometric singular perturbation theory. In chapter 3.2, we show that the dynamic behaviour observed by [17] is characteristic for a more general form of system of differential equations. This allows us to derive a parametrised population dynamic system, which is able to replicate the typical behaviour of recruitment as a function of the stock size in the sense of both Ricker and Beverton-Holt. Additionally, the model presented here can be interpreted as a generalization of the model introduced by [17]. This and other properties of the model presented here are summarized in chapter 3.3.

## 3.1 Introduction to Geometric Singular Perturbation Theory

Slow-fast systems are characterised by the presence of two distinct time-scales, the 'faster' time scale $T$ and the 'slower' time scale $t = \epsilon T$. Geometric singular perturbation theory provides tools for investigation of the geometric properties of slow-fast systems of the form ($F_\epsilon$). Here, vector $x \in \mathbb{R}^k$ consists of variables which change at fast rates, and vector $y \in \mathbb{R}^l$ summarizes the slow variables. Further, $f$ and $g$ denote smooth functions, $f, g \in \mathcal{C}^\infty$. The set of differential equations can be considered from two distinct, but equivalent points on view, since the system may also be expressed in terms of $t$. It is then referred to as the slow system ($S_\epsilon$).

$$\begin{aligned} x'(T) &= f(x(T), y(T), \epsilon) && (F_\epsilon) & \epsilon\dot{x}(t) &= f(x(t), y(t), \epsilon) && (S_\epsilon) \\ y'(T) &= \epsilon g(x(T), y(T), \epsilon) && & \dot{y}(t) &= g(x(t), y(t), \epsilon) && \end{aligned}$$

$$\begin{aligned} x'(T) &= f(x(T), y(T), 0) && (F_0) & 0 &= f(x(t), y(t), 0) && (S_0) \\ y'(T) &= 0 && & \dot{y}(t) &= g(x(t), y(t), 0) && \end{aligned}$$

A main idea of geometric singular perturbation is that characteristics of the reduced forms of the two systems, i.e. the case $\epsilon \to 0$, may persist in approximation for the general case $0 < \epsilon \ll 1$. More specifically, consider the limiting case $\epsilon \to 0$. Then, the fast and the slow system are reduced to lower dimensional problems ($F_0$) and ($S_0$), respectively. Central to the theory of geometric singular perturbation theory is a compact manifold included in the null-space of $f$, $M_0 \subset \{(x, y) \in \mathbb{R}^{k+l} | f(x, y, 0) = 0\}$, which is called critical manifold. Solutions of the reduced slow system are only defined for the set of zeros of function $f$. From point of view of the reduced fast system ($F_0$), the critical manifold is a set of equilibria. The first invariant manifold theorem **(1)** by Fenichel [5] states conditions sufficient for the persistence of an invariant manifold for $\epsilon > 0$ sufficiently small. The second Fenichel invariant manifold theorem **(2)** can be employed to investigate the stability of the critical manifold. The Fenichel theorems have been adapted for population dynamic models by [1]. However, we consider the slightly more general formulation of the theorems as provided by [7, 8].

**Fenichel's invariant manifold theorems.** *Assume that*

*(H1)* *$f, g$ are $C^\infty$ on a set $U \times I$, where $U \subset \mathbb{R}^{(k+l)}$ and $U$ is open and $I$ is an open interval containing 0.*

*(H2)* *There exists a manifold $M_0 \subset \{(x, y) \in \mathbb{R}^{k+l} | f(x, y, 0) = 0\}$, which is compact and normally hyperbolic relative to ($F_0$). The manifold $M_0$ is called normally hyperbolic, if the linearisation of ($F_\epsilon$) at each point in $M_0$ has exactly $l$ eigenvalues with zero real parts $\Re(\lambda) = 0$.*

*(H3)* *$M_0$ is given as the graph of a $C^\infty$ function $h^0(y)$ for any $y \in K \subset \mathbb{R}^l$, where $K$ is a compact, simply connected domain whose boundary is an $l-1$-dimensional $C^\infty$ sub-manifold.*

***(1)*** *Then, for $\epsilon > 0$ and sufficiently small, there exists a function $h^\epsilon : K \to \mathbb{R}^k$, such that the graph $M_\epsilon = \{(x, y) \in \mathbb{R}^{k+l} | x = h^\epsilon(y)\}$ is locally invariant under the flow of system ($F_\epsilon$). Further, $h^\epsilon$ is $C^r, \ \forall r < \infty$, jointly in $y$ and $\epsilon$.*

***(2)*** *Further, there exist stable and unstable manifolds of $M_\epsilon$, which are $\mathcal{O}(\epsilon)$-perturbations of and diffeomorphic to the stable and unstable manifolds of $M_0$. The stable and unstable manifolds of $M_\epsilon$ are locally invariant under the flow of ($F_\epsilon$) and $C^r, \ \forall r < \infty$.*

The condition of the manifold being normally hyperbolic means that the directions normal to the manifold correspond to eigenvalues which are not neutral. For more detailed introductions to geometric singular perturbation theory, including the theorems due to Fenichel, the reader may be referred to [8] and [7].

### 3.2 Deriving a parametrised SRR from a population dynamic model

In this chapter, we use geometric singular perturbation theory to establish a link between a population dynamic model of similar form as the model by Touzeau and Gouzé (6)–(8) and SRRs. This will allow us to derive a parametrised population dynamic model, which explains a broader spectrum of relationships between numbers of pre-recruits and adults - and thus recruitment and spawning stock size.

Consider a population dynamic model of form (10), which is a slow-fast system expressed in terms of the slow time $t$. Instead of function $A^{TG}$, we employ more generally a smooth function $A : \mathbb{R}_+^{n+1} \to \mathbb{R}_+$. Then, the functions $f(X) = -\epsilon\alpha X_0 + A(X_0, X_1, \ldots, X_n)$ and $g(X) = (g_1(X), \ldots, g_n(X))^t$, with $g_i(X) = \alpha X_{i-1} - \alpha X_i - m_i X_i$, are smooth on $\mathbb{R}_+^{k+l} \times \mathbb{R}_+$ (assumption (H1)). We restrict $A$ to a compact subspace $K \subset \mathbb{R}_+^{n+1}$, which includes all points of interest, and define the critical manifold $M_0 = \{x \in K | A(x) = 0\}$. Further, it is assumed that $A(X_0, X_1, \ldots, X_n) = 0$ may be solved for $X_0$ and thus that the critical manifold is the graph of a $C^\infty$ function $h^0(X_1, \ldots, X_n)$ (assumption (H3)).

$$\begin{aligned} \epsilon\frac{dX_0(t)}{dt} &= -\epsilon\alpha X_0(t) + A(X_0(t), X_1(t), \ldots, X_n(t)) \\ \frac{dX_i(t)}{dt} &= \alpha X_{i-1}(t) - \alpha X_i(t) - m_i X_i(t), \quad i = 1, 2, \ldots, n \end{aligned} \tag{10}$$

$$\begin{aligned} \frac{dX_0(T)}{dT} &= -\epsilon\alpha X_0(T) + A(X_0(T), X_1(T), \ldots, X_n(T)) \\ \frac{dX_i(T)}{dT} &= \epsilon\left(\alpha X_{i-1}(T) - \alpha X_i(T) - m_i X_i(T)\right), \end{aligned} \tag{11}$$

The critical manifold is normally hyperbolic, if the linearisation of ($F_\epsilon$) at each point in $M_0$ has an eigenvalue with non-zero real part, $\Re(\frac{\partial A(X_0,X_1,\ldots,X_n)}{\partial X_0}|_{M_0}) \neq 0$. We assume in the following the derivative of $A$ with respect to $X_0$ on $M_0$ to be negative, see equation (12). This is a natural assumption, since it means that the difference of spawning minus natural mortality of pre-recruits is monotonic decreasing in the number of pre-recruits. (That this assumption holds for the slow-fast population dynamic model (6)–(7) is shown in appendix B.1). A further implication of a negative partial derivative of $A$ with respect to $X_0$ on $M_0$ is that the stable manifold of $M_0$ corresponds to $\mathbb{R}_+^{k+l}$. Thus, the critical manifold $M_0$ is globally attractive.

$$\frac{\partial A(X_0, X_1, \ldots, X_n)}{\partial X_0}|_{M_0} < 0\ . \tag{12}$$

Summarizing, the conditions for Fenichel's theorems hold. Therefore, all solution trajectories (not starting in zero) of the slow-fast population dynamic model (10) are attracted to the graph of a smooth function $h^\epsilon$, which can be approximated by solving $A(X) = 0$ for $X_0$. For $t \gg \epsilon$, this yields a functional representation of numbers of pre-recruits in terms of numbers of adults, $X_0 = h^\epsilon(X_1, \ldots, X_n)$. Since spawning stock size is a weighted sum of numbers of adults $X_i(t)$ in age-classes $i = 1, \ldots, n$ and the number of pre-recruits is assumed to be proportional to recruitment, $h^\epsilon$ also describes a relationship between spawning stock size and recruitment.

Thus, parametrising $A$ will yield a population dynamic model, which explains a broader spectrum of SRRs. More specifically, we aim at defining a function $\tilde{A} : \mathbb{R}_+^{n+1} \to \mathbb{R}_+$ with the property that solving $\tilde{A}(X_0, X_1, \ldots, X_n) = 0$ for $X_0$ yields a Deriso type of relationship between adults and pre-recruits. As mentioned above, the Deriso model [4] corresponds to the Ricker model in case of $\gamma \to \infty$ and to the Beverton-Holt model in case of $\gamma = 1$ (see equation (3)). Expressing the Deriso model in terms of numbers of pre-recruits and adults yields equation (13)). Again, we used that the spawning stock is the sum of fecund adults, $S(t) = \sum_{i=1}^n f_i X_i(t)$ and the number of pre-recruits is assumed to be proportional to recruitment, $R(t) = \alpha X_0(t)$ (see equation (8)).

$\tilde{A} : \mathbb{R}_+^n \to \mathbb{R}_+$ is not uniquely defined by the property that the Deriso function (13) is solution of $\tilde{A}(X_0, X_1, \ldots, X_n) = 0$. But setting $a_i = \frac{\alpha l_i}{m_0}$, $b_i = \frac{p_i}{m_0 f_i}$ and defining function $\tilde{A}$ as described by equation (15) yields a parametrisation of function $A^{TG}$ employed in the model by Touzeau and Gouzé (6)–(8). Further, $\tilde{A}$ fulfils all conditions posed on the general function $A$. It is smooth, $\tilde{A}(X_0, X_1, \ldots, X_n) = 0$ may be solved for $X_0$ and the derivative of $\tilde{A}$ with respect to $X_0$ on $M_0$ is negative (see appendix B.1).

$$\alpha X_0(t) = (\sum_{i=1}^n a_i f_i X_i(t)) \left(1 + \frac{1}{\gamma}(\sum_{i=1}^n b_i f_i X_i(t))\right)^{-\gamma}, \quad \text{for some } a_i, b_i \in \mathbb{R}_+ \tag{13}$$

$$X_0(t) = (\sum_{i=1}^n \frac{l_i f_i}{m_0} X_i(t)) \left(1 + \frac{1}{\gamma m_0}(\sum_{i=1}^n p_i X_i(t))\right)^{-\gamma} \tag{14}$$

$$\tilde{A}(X(t)) = -m_0 X_0(t) \left(1 + \frac{1}{\gamma m_0}(\sum_{i=1}^n p_i X_i(t))\right)^{\gamma} + \sum_{i=1}^n l_i f_i X_i(t) \tag{15}$$

Thus, we derived a parametrised slow-fast population dynamic model as described by equations (16)–(18). In case of $\gamma = 1$, the dynamic system corresponds to the one by Touzeau and Gouzé in case of $p_0 = 0$. But the parametrised ODEs yield a representation of numbers of pre-recruits in terms of numbers of adults, which can be approximated by a Deriso type of relationship (14). In addition, a Deriso function describes recruitment in terms of spawning stock size, if all parameters are assumed to be age-independent (i.e. $l_i = l$, $f_i = f$, $p_i = p$, $m_i = m$, for all $i = 1, \ldots, n$). For the limiting case $\gamma \to \infty$, the dynamics of pre-recruits are described by equation (19).

$$\dot{X}_0(t) = -\alpha X_0(t) + \frac{1}{\epsilon}\underbrace{\left[-m_0 X_0(t)\left(1+\frac{1}{\gamma m_0}\sum_{i=1}^{n} p_i X_i(t)\right)^{\gamma} + \sum_{i=1}^{n} l_i f_i X_i(t)\right]}_{=\tilde{A}(X(t))} \quad (16)$$

$$\dot{X}_i(t) = \alpha X_{i-1}(t) - \alpha X_i(t) - m_i X_i(t), \quad i = 1, 2, \ldots, n \quad (17)$$

$$R(t) = \alpha X_0 \quad \text{and} \quad S(t) = \sum_{i=1}^{n} f_i X_i(t) \quad (18)$$

$$\dot{X}_0(t) = -\alpha X_0(t) + \frac{1}{\epsilon}\left[-m_0 X_0(t)\cdot\exp\left(\frac{1}{m_0}\sum_{i=1}^{n} p_i X_i(t)\right) + \sum_{i=1}^{n} l_i f_i X_i(t)\right] \quad (19)$$

### 3.3 Properties of the parametrised population dynamic model

As the parametrised population dynamic model is a special case of the dynamic system investigated in chapter 3.2, the behaviour of its solution trajectories can be explained using geometric singular perturbation theory. In a first, short phase, the spawning stock size undergoes small changes in comparison to the number of pre-recruits $X_0$. Solution trajectories are attracted to the stable critical manifold $M_\epsilon$, which can be approximated by the null space of function $\tilde{A}$. Thus, in the second phase, reproduction is a function of numbers of adults, which can be approximated by a Deriso type of relationship (20). In case of age-independent parameters ($l_i = l$, $f_i = f$, $p_i = p$ and $m_i = m$, for $i = 1, \ldots, n$), the critical manifold can be associated with a Deriso function (21), with $a = \frac{\alpha l}{m_0}$ and $b = \frac{p}{m_0 f_0}$. The SRRs corresponding to the parametrised slow-fast system are illustrated in figure 3.

$$R(t) = \frac{\alpha}{m_0}\left(\sum_{i=1}^{n} l_i f_i X_i(t)\right)\left(1+\frac{1}{m_0\gamma}\left(\sum_{i=1}^{n} p_i X_i(t)\right)\right)^{-\gamma} \quad (20)$$

$$R(t) = \frac{\alpha l}{m_0} S(t)\left(1+\frac{p}{\gamma m_0 f} S(t)\right)\right)^{-\gamma} \quad (21)$$

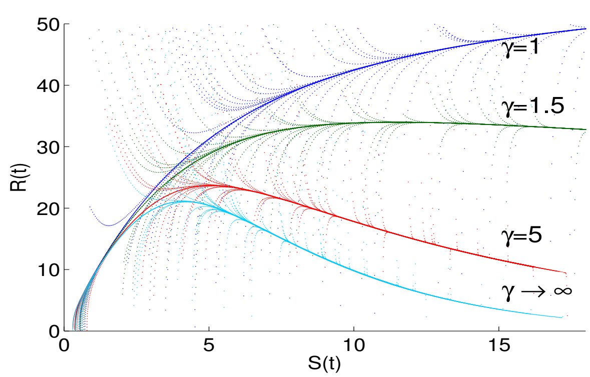
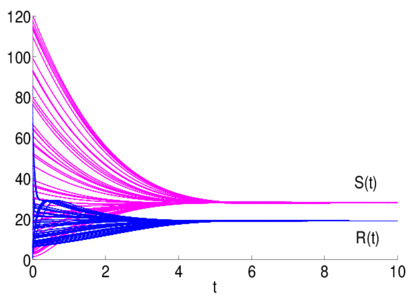
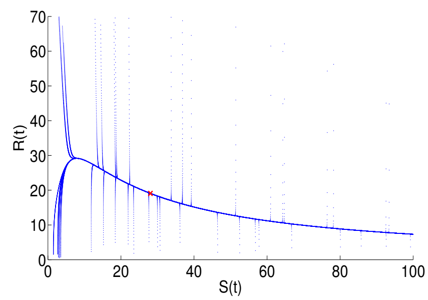



**Figure 3:** Simulation of the stock recruitment relationship corresponding to the parametrised population dynamic model at $t \in \{0, 0.005, 0.01, \ldots, 10\}$ and for four distinct values for $\gamma$. Parameter values are the same as in Figure 2.

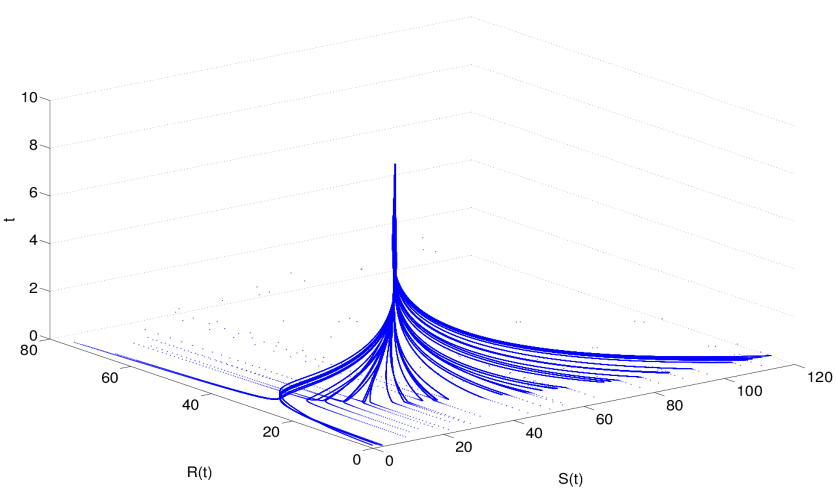
The parametrised population dynamic model has an equilibrium $X_0 = X_1 = \cdots = X_n = 0$. Further, under assumption $\alpha\epsilon < \sum_{i=1} l_i f_i \pi_i$ , a second fixed point is $(R^{**}_\gamma, S^{**}_\gamma)$ as given by equations (22)–(23)). In case of $\gamma \to \infty$, the equilibrium recruitment is given




(a) Spawning stock and recruitment converge towards a fixed point. Equilibrium recruitment $R_2^{**}$ is lower than equilibrium recruitment $R^*$ in case of $\gamma = 1$.




(b) Here, the SRR can be approximated by a Deriso function. Over-compensation occurs, but is not as strong as under Ricker assumptions.




(c) Starting at random initial states, the SRR soon behaves similarly to a Deriso function and converges then, at slower rate, to an equilibrium.

**Figure 4:** Numerical solution of the parametrised population dynamic model with $\gamma = 2$ at $t \in \{0, 0.0005, 0.001, \ldots, 10\}$. Parameter values are the same as in Figure 2.

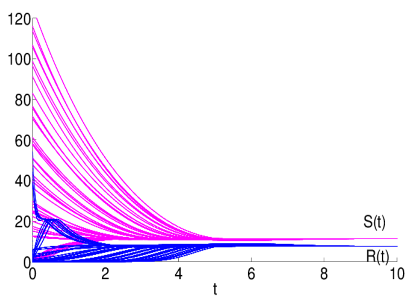
by equation (24). For a proof, see appendix B.2.

$$R_{\gamma}^{**} = \frac{\gamma m_0 \alpha}{\sum_{i=1}^{n} p_i \pi_i} \left[ \left( \frac{\sum_{i=1}^{n} l_i f_i \pi_i}{m_0} - \frac{\alpha \epsilon}{m_0} \right)^{\frac{1}{\gamma}} - 1 \right] \ , \tag{22}$$

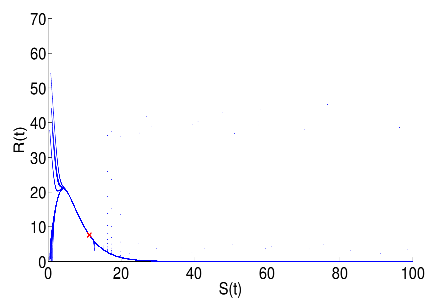
$$S^{**} = \sum_{i=1}^{n} f_i \pi_i \frac{1}{\alpha} R^{**} \quad \text{, where } \pi_i = \prod_{j=1}^{i} \frac{\alpha}{\alpha + m_j} \ , \tag{23}$$

$$R^{**} = \frac{m_0 \alpha}{\sum_{i=1}^{n} p_i \pi_i} \ln \left( \frac{\sum_{i=1}^{n} l_i f_i \pi_i}{m_0} - \frac{\alpha \epsilon}{m_0} \right) \ . \tag{24}$$

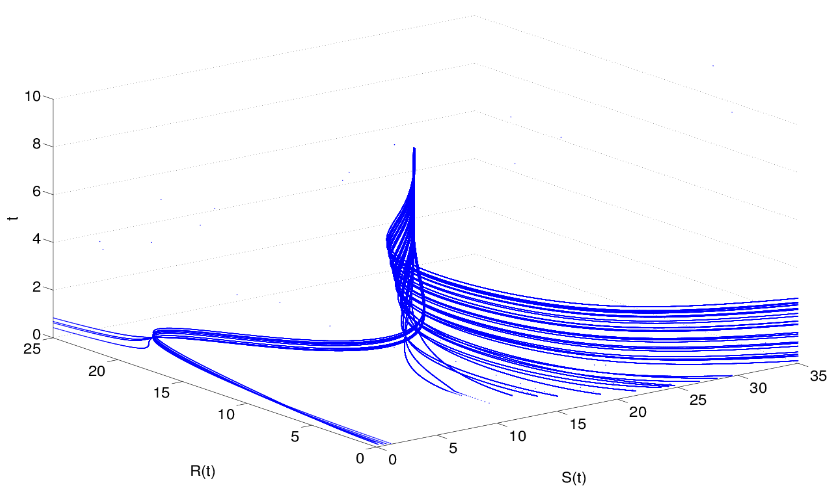
Due to the additional parameter $\gamma$, the new model can replicate a broad spectrum of the link between adult population and reproduction. Here, the instantaneous mortality rate of pre-recruits is no longer assumed to be linear in the sizes of age-classes $X_i$, $i = 1, \dots, n$, but to be polynomial of degree $\gamma$. Thus, the parameter $\gamma$ allows to assign distinct degrees of density-dependence to the stock-recruitment function.




(a) Spawning stock size and recruitment converge towards a fixed point. Equilibrium recruitment is lower than in case of $\gamma = 2$.




(b) The stock-recruitment relationship can be approximated by a Ricker function.




(c) Starting at random initial points, the SRR soon behaves similarly to a Ricker function and converges then to a fixed point.

**Figure 5:** Numerical solution of the parametrised population dynamic model with $\gamma \rightarrow \infty$ at $t \in \{0, 0.0005, 0.001, \dots, 10\}$. Parameter values are the same as in Figure 2, but note that the axis are shorter.

For $\gamma = 1$, the system corresponds to the case $p_0 = 0$ of the model by Touzeau and Gouzé (6)–(8). The trajectories of the system of differential equations approach a critical manifold, which may be approximated by a Beverton-Holt function. Further, all non-zero solutions converge to a stable equilibrium point, [17]. Recruits per spawner decrease with increasing spawning stock size, but over-compensation is not observed on the critical manifold (see Figure 2).

With increasing $\gamma$, density-dependence of the stock recruitment function increases, and overcompensation occurs for any $\gamma > 1$ (for details, see appendix B.4). Figure 4 presents the special case $\gamma = 2$. Here, it can also be observed that the equilibrium recruitment is lower in case of $\gamma = 2$ than for $\gamma = 1$. In general, it can be shown that $R^{**}_{\gamma}$ is decreasing in $\gamma$ (see appendix B.3).

For the limiting case $\gamma \to \infty$, recruitment is highly dependent on the spawning stock size, as illustrated in Figure 5. The critical manifold can be approximated by a Ricker stock recruitment function, (25). While the non-zero equilibrium was stable in case of $\gamma = 1$, Figure 5 shows an example for an asymptotic stable equilibrium.

$$R(t) = \frac{\alpha}{m_0}(\sum_{i=1}^{n} l_i f_i X_i(t)) \cdot \exp\left(-\frac{1}{m_0}(\sum_{i=1}^{n} p_i X_i(t))\right) \tag{25}$$

# 4 Summary

This report derived a parametrised version of a slow-fast and age-structured population dynamic model introduced by Touzeau and Gouzé [17]. The system couples a pre-recruit stage with several adult stages. Here, spawning and natural mortality of pre-recruits are assumed to change at a faster rate than ageing and natural mortality of adults. Geometric singular perturbation theory has been used as a tool for linking the slow-fast system to a relationship between recruitment and spawning stock. More specifically, the fast dynamics approach an equilibrium subspace, which endows the dynamic system with a functional relationship between adults and recruitment. This function can be interpreted as SRR, if all parameters (fecundity, degree of density-dependence in mortality of pre-recruits, natural mortality of adults and average number of eggs produced per fish) are assumed to be age-independent. The parametrised set of ODEs can explain the same spectrum of SRRs as the Deriso model.

# 5 Conclusions and Extensions

The parametrised population dynamic model introduced here describes a two-sided link between adult age-classes and recruitment. It reflects both the influence of age-classes on the offspring, as well as the increase of the spawning stock due to reproduction. Thus, the model allows for analysis of the SRR and its evolution over time. One reason why this is of special importance is the following.

Environmental and physical factors may alter the stock recruitment function, and affect the complete stock, including asymptotic behaviour and equilibrium states. The strength of cannibalism, predation or competition may also change, and thus affect density-dependence. Any environmental factor influencing reproduction or the spawning stock will also have an indirect impact on other life stages. The parametrised stock recruitment model presented here may thus facilitate the investigation of environmental effects on reproduction. This is exemplified by its ability to replicate a broad spectrum of SRR.

## 5.1 Possible extensions

An assumption of the population dynamic model presented here, is that spawning might immediately yield a small amount of recruits. At the same time, recruitment immediately yields a larger spawning stock. Thus, spawning would immediately yield a small addition of fish to the adult population. Therefore, discrete population dynamic models usually include a time-lag between spawning and subsequent recruitment. This means that recruitment is not a function of current spawning stock size, but of past numbers of adults. Using delay differential equations would allow to introduce this time-lag in the continuous model presented here.

The idea of using slow-fast dynamics for describing recruitment might also be extended to modelling early life history stages. That recruitment is the result of spawning and survival during several early life-history stages, has been illustrated by the use of Paulik diagrams (see e.g., [10–12]). Each of the different stages is associated with a characteristic time-scale. Thus, a possible extension of slow-fast dynamical systems is for the purpose of modelling and coupling several early life-history stages.

In this context, it has been pointed out that biological and physical influences on each of the (early) life-stages vary annually (see e.g., [14]). Therefore, a stochastic approach to slow-fast dynamic systems, which allows to define distinct types of errors for different life-stages, would also be of interest. Then, geometric singular perturbation theory may be applied for considering stochastic differential equations which include several time scales.

## A Nomenclature

| | |
|---|---|
| $t$ | slow time |
| $T$ | fast time |
| $\epsilon$ | ratio between slow and fast time $\epsilon = t/T$ |
| $R(t)$ | numbers of fish recruited to the stock at time $t$ |
| $S(t)$ | size of the spawning stock at time $t$ |
| $a$ | density-independent parameter of the classical SRR |
| $b$ | density-dependent parameter of the classical SRR |
| $i$ | age-class, $i = 1, \ldots, n$ |
| $X_i(t)$ | number of fish in age-class $i$ at time $t$ |
| $X_0(t)$ | number of pre-recruits at time $t$ |
| $\alpha$ | ratio of ageing |
| $f_i$ | fecundity of fish of age $i$ |
| $l_i$ | average number of eggs produced per fish of age $i$ |
| $p_i$ | degree of density-dependence attributed to fish of age $i$ |
| $p_0$ | degree of density-dependence attributed to juvenile competition |
| $m_i$ | natural mortality of age-class $i$ |
| $m_0$ | natural mortality of pre-recruits |
| $\gamma$ | degree of density-dependence of the SRR |

## B About some properties of the parametrised population dynamic model

Here, some properties of the parametrised population dynamic model (16)–(18) are considered in more detail. The differential equations are restated in the following.

$$\dot{X}_0(t) = -\alpha X_0(t) + \frac{1}{\epsilon}\underbrace{\left[-m_0 X_0(t)\left(1 + \frac{1}{\gamma m_0}\sum_{i=1}^{n} p_i X_i(t)\right)^{\gamma} + \sum_{i=1}^{n} l_i f_i X_i(t)\right]}_{=\tilde{A}(X(t))} \quad (26)$$

$$\dot{X}_i(t) = \alpha X_{i-1}(t) - \alpha X_i(t) - m_i X_i(t), \quad i = 1, 2, \ldots, n \quad (27)$$

$$R(t) = \alpha X_0 \quad \text{and} \quad S(t) = \sum_{i=1}^{n} f_i X_i(t) \quad (28)$$

### B.1 Normally hyperbolicity of the critical manifold

Here, we proof that the critical manifold
$M_0 = \{(X_0, X_1, \ldots, X_n) \in \mathbb{R}_+^{n+1} | A(X_0, X_1, \ldots, X_n) = 0\}$ is normally hyperbolic relative to the parametrised population dynamic model (16)–(17). The corresponding reduced fast system (with $\epsilon \to 0$) is given by,

$$\begin{aligned}\dot{X}_0(t) =& A(X_0, X_1, \ldots X_n)\\ =& -m_0 X_0(t)\left(1 + \frac{1}{\gamma m_0}\sum_{i=1}^{n} p_i X_i(t)\right)^{\gamma} + \sum_{i=1}^{n} l_i f_i X_i(t)\\ \dot{X}_i(t) =& 0\,,\ i = 1, \ldots, n\,.\end{aligned}$$

Assuming $X_1, \ldots, X_n \geq 0$, the Jacobian is

$$\frac{\partial A(X_0, X_1, \ldots, X_n)}{\partial X_0}|_{M_0} = -m_0\left(1 + \frac{1}{\gamma m_0}\sum_{i=1}^{n} p_i X_i(t)\right)^{\gamma} = \lambda < 0\,. \quad (29)$$

Thus, the real part of the eigenvalue is negative, $\Re(\lambda) < 0$ and the critical manifold normally hyperbolic for any $\gamma \in \mathbb{R}$ and in particular for $\gamma = 1$.

### B.2 Non-zero fixed point

Here, the non-zero equilibrium $X^{**}$ of the parametrised population dynamic model is derived. (Note that the existence of the equilibrium at zero is trivial.) For simplicity, we drop the dependency on time. As shown for the case $\gamma = 1$ by [17], it follows from equation (27) that $\dot{X}_i^{**} = 0$ iff $X_i^{**} = \pi_i X_0^{**}$, with $\pi_i = \prod_{j=1}^{i} \frac{\alpha}{\alpha+m_j}$ as defined above. Thus, we can substitute $X_i^{**}$ by the fractions of $X_0^{**}$. Assuming $X_0^{**} \neq 0$, the fixed point with $\dot{X}_0^{**} = 0$ is obtained as follows,

$$
\begin{aligned}
\dot{X}_0^{**} = 0 \Leftrightarrow \epsilon\alpha X_0^{**} = -m_0 X_0^{**} \left(1 + \frac{1}{\gamma m_0}\sum_{i=1}^{n} p_i X_i^{**}\right)^{\gamma} + \sum_{i=1}^{n} l_i f_i \pi_i X_0^{**} \\
\Leftrightarrow \left(1 + \frac{1}{\gamma m_0}\sum_{i=1}^{n} p_i \pi_i X_0^{**}\right)^{\gamma} = \frac{\sum_{i=1}^{n} l_i f_i \pi_i}{m_0} - \frac{\alpha\epsilon}{m_0} \\
\Leftrightarrow X_0^{**} = \frac{\gamma m_0}{\sum_{i=1}^{n} p_i \pi_i}\left[\left(\frac{\sum_{i=1}^{n} l_i f_i \pi_i}{m_0} - \frac{\alpha\epsilon}{m_0}\right)^{\frac{1}{\gamma}} - 1\right]
\end{aligned}
$$

### B.3 Influence of $\gamma$ on equilibrium recruitment

Then, we show that the equilibrium recruitment $\alpha X_0^{**}(\gamma)$ (as a function of parameter $\gamma$) is monotonic decreasing in $\gamma$.

For simplicity, substitute $\theta_1 = \frac{m_0}{\sum_{i=1}^{n} p_i \pi_i}$ and $\theta_2 = \frac{\sum_{i=1}^{n} l_i f_i \pi_i}{m_0} - \frac{\alpha\epsilon}{m_0}$. We use the property that $x\ln(x) \geq x - 1$ for any $x > 0$. Then, assuming $\sum_{i=1}^{n} l_i f_i \pi_i - \alpha\epsilon > 0$ means $\theta_2 > 0$ and assures that

$$
\begin{aligned}
X_0^{**}(\gamma) =& \theta_1 \gamma (\theta_2^{1/\gamma} - 1) \text{ is a monotonic decreasing function in } \gamma : \\
\frac{\partial X_0^{**}(\gamma)}{\partial \gamma} =& \theta_1 \left(\theta_2^{1/\gamma} - 1 - \frac{1}{\gamma}\theta_2^{1/\gamma}\ln(\theta_2)\right) \\
=& \theta_1 \left(\theta_2^{1/\gamma} - 1 - \theta_2^{1/\gamma}\ln(\theta_2^{1/\gamma})\right) \\
\leq& \theta_1 \left(\theta_2^{1/\gamma} - 1 - (\theta_2^{1/\gamma} - 1)\right) \\
=& 0
\end{aligned}
$$

### B.4 Influence of $\gamma$ on the SRR

Now, we consider the influence of $\gamma$ on the parametrised SRR, which is a Deriso type of stock recruitment function,

$$
R = \frac{\alpha l}{m_0} S \left(1 + \frac{p}{f m_0 \gamma} S\right)^{-\gamma} .
$$

That the Deriso function yields a stock recruitment curve with a non-zero maximum for any $\gamma > 1$ has been shown by [15]. Due to its importance in this report, we restate the argument for the particular Deriso function employed here. For any $\gamma > 1$, there exists a spawning stock size $\bar{S}$, such that overcompensation can be observed for any $S > \bar{S}$. Denote e.g. by

$\bar{S} = \frac{fm_0}{p(1-\frac{1}{\gamma})}$, then for any $S > \bar{S}$:

$$\begin{aligned}\frac{1}{R}\frac{\partial R}{\partial S} =& \frac{1}{R}\left(\frac{\alpha l}{m_0}\left(1+\frac{p}{fm_0\gamma}S\right)^{-\gamma} - \frac{p}{fm_0}\frac{\alpha l}{m_0}S\left(1+\frac{p}{fm_0\gamma}S\right)^{-\gamma-1}\right)\\ =& \left(1-(1-1/\gamma)\frac{p}{fm_0}S\right)\cdot\left(S(1+\frac{p}{fm_0\gamma}S)\right)^{-1} < 0\,.\end{aligned}$$

# References


[1] P. Auger, R. Bravo de la Parra, J. C. Poggiale, E. Sánchez, and L. Sanz. Aggregation methods in dynamical systems and applications in population and community dynamics. *Physics of Life Reviews*, 5:79–105, 2008. 1, 3.1

[2] R. J. H. Beverton and S. J. Holt. On the dynamics of exploited fish populations. *Fisheries Investment Series 2, Vol. 19, U.K. Ministry of Agriculture and Fisheries, London*, 1957. 1.1

[3] N. Charouki, R. Mchich, P. Auger, and N. Raissi. A management oriented competitive model with two time scales: the case of sardine fishery along the Atlantic coast between Cantin Cape and Blanc Cape. *Ecological Modelling*, 222:1253–1261, 2011. 1

[4] R. B. Deriso. Harvesting strategies and parameter estimation for an age-structured model. *Canadian Journal of Fisheries and Aquatic Sciences*, 37(2):268–282, 1980. 1.1, 3.2

[5] N. Fenichel. Geometric singular perturbation theory for ordinary differential equations. *J. Diff. Eq.*, 31:53–98, 1979. 3.1

[6] R. Hilborn, C. J. Walters, et al. Quantitative fisheries stock assessment. choice, dynamics and uncertainty. *Reviews in Fish Biology and Fisheries*, 2(2):177–178, 1992. 2.1

[7] C. K. R. T. Jones. Geometric singular perturbation theory. In *Dynamical Systems, Montecatibi Terme, 1994, Lecture Notes in Mathematics 1609, R. Johnson (ed.)*. Springer, 1995. 3.1, 3.1

[8] T. J. Kaper. An introduction to geometric methods and dynamical systems theory for singular perturbation problems. In *Analyzing multiscale phenomena using singular perturbation methods, Proceedings of Symposia in Applied Mathematics, J. Cronin and R.E. O'Malley, Jr., eds. (American Mathematical Society, Providence, RI)*, volume 56, pages 85–132, 1999. 3.1, 3.1

[9] M. Marva, R. Bravo de la Parra, and J. C. Poggiale. Approximate aggregation of a two time scales periodic multi-strain SIS epidemic model: a patchy environment with fast migrations. *Ecological Complexity*, 10:34–41, 2012. 1

[10] R. D. M. Nash. Exploring the population dynamics of Irish Sea plaice, Pleuronectes platessa L., through the use of Paulik diagrams. *J Sea Res*, 40:1–18, 1998. 5.1

[11] R. D. M. Nash and A. J. Geffen. Mortality through the early life-history of fish: What can we learn from European plaice (Pleuronectes platessa L.)? *Journal of Marine Systems*, 93:58–68, 2012. 5.1

[12] G. J. Paulik. Studies of the possible form of the stock and recruitment curve. *Rapp. P-V Reun. Cons. Perm. Int. Explor. Mer*, 164:302–315, 1973. 5.1

[13] W. E. Ricker. Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, 11(5):559–623, 1954. 1.1, 2.1

[14] B. J. Rothschild. *Dynamics of Marine Fish Populations*. Harvard University Press, Cambridge, MA, USA, 1986. 5.1

[15] J. Schnute. A general theory for analysis of catch and effort data. *Canadian Journal of Fisheries and Aquatic Science*, 42:414–429, 1985. B.4

[16] S. Subbey, J. Devine, U. Schaarschmidt, and R. D. M. Nash. Modeling and forecasting stock recruitment–current and future perspectives. *Submitted to ICES Journal of Marine Science*, 2014. 1.1

[17] S. Touzeau and J.-L. Gouzé. On the stock-recruitment relationships in fish population models. *Environmental modeling and assessment*, 3:87–93, 1998. 1, 2, 2, 2.1, 3, 3.3, 4, B.2

[18] F. Verhulst. *Methods and Applications of Singular Perturbations: Boundary Layers and Multiple Timescale Dynamics*. Springer, New York, 2005. 1