Available online at www.sciencedirect.com
ScienceDirect

ELSEVIER

Mathematics and Computers in Simulation xx (xxxx) xxx–xxx

MATHEMATICS AND COMPUTERS IN SIMULATION
www.elsevier.com/locate/matcom

Original articles

A parametrized stock-recruitment relationship derived from a slow-fast population dynamic model

Ute Schaarschmidt[a],*, Trond Steihaug[a], Sam Subbey[b]

[a] *Department of Informatics, University of Bergen, Pb 7803, N-5020 Bergen, Norway*
[b] *Institute of Marine Research, Pb 1870, N-5817 Bergen, Norway*

Received 15 August 2014; received in revised form 12 October 2017; accepted 12 October 2017
Available online xxxxx

Abstract

The Beverton–Holt, Ricker and Deriso functions are three distinct descriptions of the link between a parental population size and subsequent offspring that may survive to become part of the fish population.

This paper presents a model consisting of a system of ordinary differential equations, which couples a stage of young fish with several adult stages. The slow-fast dynamics captures the different time scales of the dynamics of the population and leads to a singular perturbation problem.

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

Keywords: Slow-fast; Population dynamic; Stock-recruitment relationship; Geometric singular perturbation theory; Stage-structured model

1. Introduction

Fish populations decrease due to (natural and fishing) mortality and increase when new generations of fish resulting from egg production are added to the existing population. In the literature, the spawning stock refers to the part of the stock that is matured enough (called spawners) to contribute to the reproduction process, while stock-recruitment means the relationship between the spawning stock and number of young fish resulting from egg production.

Recruitment is traditionally described as a function of the number of spawners (spawning stock size). The two most popular representations of the relationship have been introduced by Beverton–Holt [2] and Ricker [15]. Both models assume a decrease in recruitment per spawner with stock size, but the degree of decline, often referred to as

* Corresponding author.
E-mail addresses: ute.schaarschmidt@ii.uib.no (U. Schaarschmidt), Trond.Steihaug@ii.uib.no (T. Steihaug), samuel.subbey@imr.no (S. Subbey).

https://doi.org/10.1016/j.matcom.2017.10.008
0378-4754/

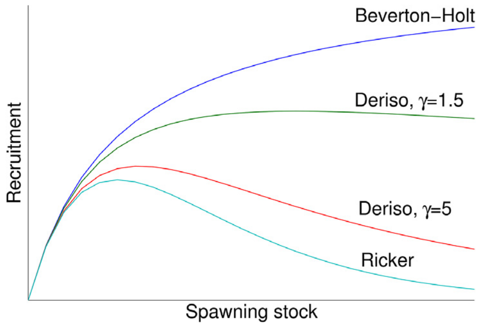

Fig. 1. Traditional stock-recruitment relationships.

Table 1
Processes described by the age-structured model (4)–(5).

$\sum_{i=1}^{n} l_i f_i X_i(t)$	Rate of egg production
$-m_i X_i(t)$	Rate of mortality of individuals in age-class $i = 0, \dots, n$
$-\sum_{i=1}^{n} p_i X_i(t) X_0(t)$	Rate of mortality as function of numbers of adults
$-p_0 X_0(t)^2$	Rate of mortality as function of the number of prerecruits
$\pm \alpha X_i(t)$	Rate of ageing of individuals in age-class $i = 0, \dots, n$

density-dependence, distinguishes the two models from each other. A Beverton–Holt function, as described by Eq. (1), is strictly increasing with an asymptotic maximum. A Ricker type of stock-recruitment relationship (SRR) given by Eq. (2) has a maximum and is dome-shaped, i.e., recruitment may decrease with increasing spawning stock size (as illustrated in Fig. 1). The Deriso model [4] corresponds to the Ricker model for $\gamma \to \infty$ and to the Beverton–Holt model for $\gamma = 1$, see Eq. (3). Here, R denotes recruitment and S the number of spawners. In the following, we let $a, b, \gamma \in \mathbb{R}_+ \setminus \{0\}$, with $\mathbb{R}_+$ the set of non-negative real numbers.

$$\text{Beverton–Holt:} \quad R = \frac{aS}{1 + bS} \tag{1}$$

$$\text{Ricker:} \quad R = aSe^{-bS} \tag{2}$$

$$\text{Deriso:} \quad R = aS(1 + \frac{b}{\gamma} S)^{-\gamma}. \tag{3}$$

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 [21]. A prerecruit stage (including eggs, larvae and juveniles) is added to a continuous time population dynamic model with discrete age structures. For further discussion about age-structured models, see e.g. [13]. Dynamic processes at the prerecruit stage evolve on shorter time scales than at other stages and in [21], two distinct time scales are used.

More specifically, a system of differential equations describes the dynamic behaviour of numbers of prerecruits $X_0(t)$ and adults $X_i(t)$ of age-class $i = 1, \dots, n$ at time $t \geq 0$, with positive natural number n. The processes described by Eqs. (4)–(5) are listed in Table 1. Initial conditions of the form $X_i(0) \geq 0$ for $i = 0, \dots, n$ ensure that $X_i(t) \geq 0$ for all $t > 0$ and $i = 0, \dots, n$, [21]. The rate (of change in numbers of individuals with time) of egg production is assumed to be proportional to the numbers of adults and the average rate $l_i > 0$ of eggs spawned per individual of age i. The rate of mortality per prerecruit is assumed to be linear in X_0 and X_i, for $i = 1, \dots, n$. The parameters $p_0 \geq 0$ and $p_i \geq 0$ express the degree of the limiting effect of the numbers of prerecruits and adult age-class i, respectively. Rates of mortality per individual of age i, which are independent of X_j, $j = 0, \dots, n$, are called density-independent and are denoted by m_i, for $i = 0, \dots, n$. The rate of ageing per individual is $\alpha > 0$. A nomenclature including parameters and their units is given in Table A.2. In the following, we let parameters be chosen as described in Table A.2. We remark that the parameters may in practice vary with time, but the assumption of time-independent model parameters is standard practice in fisheries science, [14].

In order to cope with the fact that evolution of prerecruits happens at faster rates than ageing and mortality of adult fish, a fast time T and a slow time $t = \epsilon T$ are used. The parameter $0 < \epsilon \ll 1$ describes the ratio between the two

Please cite this article in press as: U. Schaarschmidt, et al., A parametrized stock-recruitment relationship derived from a slow-fast population dynamic model, Mathematics and Computers in Simulation (2017), https://doi.org/10.1016/j.matcom.2017.10.008.