Journal of Theoretical Biology 389 (2016) 198–205

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Noisy predator–prey model explains oscillation patterns in sockeye salmon data

Christoph K. Schmitt*, Christian Wildner, Barbara Drossel

Institut für Festkörperphysik, TU Darmstadt, Hochschulstraße 6, 64289 Darmstadt, Germany

HIGHLIGHTS

- Model sockeye salmon population dynamics are compared to measured spawner counts.
- Consistency and amplitude of population oscillations are quantified.
- Interaction with a predator is likely to be the cause of cyclic dominance.

ARTICLE INFO

Article history:
Received 21 April 2015
Received in revised form
20 September 2015
Accepted 12 October 2015
Available online 10 November 2015

Keywords:
Oncorhynchus nerka
Cyclic dominance
Wavelet analysis
Single generation cycle

ABSTRACT

A model of sockeye salmon population dynamics that incorporates predator–prey dynamics in the nursery lakes, salmon migration and stochastic effects is compared to Fraser River sockeye salmon spawner numbers with respect to cyclic dominance. For this comparison we use a method developed by White et al. (2014) to calculate measures for the consistency and strength of cyclic dominance in the time series using its wavelet transform. We find that the model can match the oscillation patterns found in nature, both for persistently oscillating populations and for intermittent oscillations. It matches persistently oscillating populations much better than a model that does not incorporate predator–prey interaction. Persistent oscillations are more likely to occur in the model if the growth conditions for the sockeye fry are good and the coupling to the predator is strong.

1. Introduction

Several populations of sockeye salmon spawning in the Fraser River system in British Columbia, Canada, show a remarkably strong population oscillation called cyclic dominance (Ricker, 1950; Townsend, 1989; Ricker, 1997). Sockeye salmon are important ecologically, culturally and economically (Cohen, 2012). They spend much of their life in the ocean, but return to spawn where they hatched. Because sockeye salmon die after spawning, the salmon spawning runs bring large amounts of nutrients from the ocean into the rivers and lakes. Sockeye salmon are also a lucrative fishing target. Despite their importance the phenomenon of cyclic dominance is not yet fully understood.

Various causes for the oscillation have been proposed (Levy and Wood, 1992; Myers et al., 1998). One important aspect is that only a few populations are consistently oscillating, and the peaks of the oscillation occur in different years for different populations. So cyclic dominance cannot be caused by an influence that affects all sockeye populations equally. The cause affects each spawning population individually, and can therefore be expected to reside in the nursery lakes where the sockeye fry spend the first months of their life.

Guill et al. (2011) proposed that predator–prey interaction in the nursery lakes is causing cyclic dominance. A model for sockeye population dynamics was introduced, and produced time series with a striking resemblance to the spawner numbers of the persistently oscillating populations. This model was further investigated and simplified (Guill et al., 2014) or extended (Schmitt et al., 2014). Unlike these deterministic models, in nature the sockeye salmon are constantly exposed to a variety of stochastic effects. Therefore Schmitt et al. (2012) introduced random perturbations into the modelling of the sockeye life cycle.

White et al. (2014) propose a different cause for cyclic dominance. They used a model that includes the sockeye life cycle and random perturbations, but no predator–prey interaction or other forms of delayed density-dependence. In a deterministic version of this model, the spawner number would follow a dampened oscillation pattern and eventually reach a fixed point. Oscillations are sustained only due to the perturbations. This can lead to time

---

*Corresponding author. Tel.: +49 6151 16 3106; fax: +49 6151 16 3681.
E-mail addresses: christophschmitt@fkp.tu-darmstadt.de (C.K. Schmitt), drossel@fkp.tu-darmstadt.de (B. Drossel).

http://dx.doi.org/10.1016/j.jtbi.2015.10.029
0022-5193/© 2015 Elsevier Ltd. All rights reserved.

series with similar oscillation characteristics as found in nature. To quantify this similarity, White et al. (2014) introduced measures *C* for the cyclic consistency and *D* for the dominance. These are calculated using a wavelet-transform of the time series, which exposes how the frequency components in a signal vary over time. *C* quantifies how consistently the time series oscillates with a certain period, e.g. four years. *D* quantifies the amplitude of that oscillation.

While it is easy to obtain time series that oscillate weakly and intermittently from a model without predator–prey dynamics, the strong persistent oscillations observed in some natural populations are much less frequent in this model; in addition to suitable model parameters, their creation also requires a specific series of random perturbations. This suggests that it is not just the four-year life cycle combined with random perturbations that is causing cyclic dominance. In this paper, we use the measures introduced by White et al. (2014) to compare time series from our model that includes predator–prey interaction with the natural time series. We find that the model with predator–prey interaction is better able to reproduce persistent oscillations than a model without delayed density dependence. Fig. 1 shows examples of spawner counts together with the corresponding values of *C* and *D*.

In the following, we first introduce the model for sockeye salmon population dynamics and the method used to analyze the time series. Then we present our results and discuss their ecological implications.

2. Model

The model we use for sockeye salmon population dynamics was first introduced with three species in Guill et al. (2011), but in this paper we use the two-species version from Guill et al. (2014) with noise added as in Schmitt et al. (2012). It is mechanistic, containing only the ingredients we assume to be relevant to cyclic dominance. These are the sockeye life cycle and the interaction with a predator in the nursery lakes, combined with random perturbations. The predator–prey interaction is modelled continuously in time using ordinary differential equations for the biomass densities of sockeye fry and the predator from spring ($t=0$) to fall ($t=T$) of each year. The life cycle and perturbations are modelled using a discrete step that determines the spring biomasses from those at the end of earlier years. The model alternates between the continuous part and the discrete part.

The differential equations for sockeye fry biomass density F_n and predator biomass density P_n (with n denoting the current year) are

$$\frac{\mathrm{d}}{\mathrm{d}t}F_n(t) = rF_n\left(1-\frac{F_n}{K}\right) - f(F_n,P_n)P_n, \tag{1}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}P_n(t) = ef(F_n,P_n)P_n - dP_n. \tag{2}$$

The sockeye fry biomass grows logistically with maximum rate r up to a carrying capacity K. The predator loses biomass due to respiration and mortality with the rate d. The predator feeds on

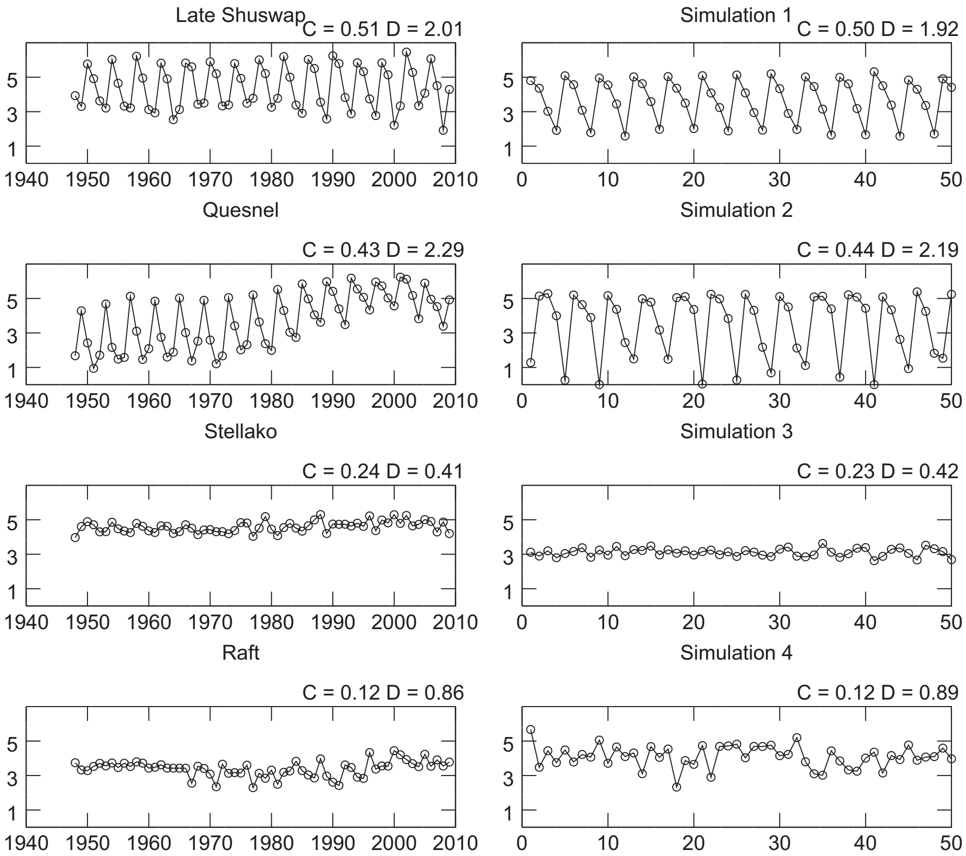

Fig. 1. Sockeye spawner abundance in four lakes in the Fraser River system (White et al., 2014), and simulation results from the model described in Section 2 with similar *C* and *D*. The simulation results have random parameters from the ranges specified in Section 4.2. They were picked randomly from the results with *C* and *D* very close to the values of the population in the left column. We plotted the base ten logarithm of the spawner abundance. The simulations give spawner densities, they were multiplied by 10^6 in order to translate this into realistic values for spawner counts. The two top rows show consistently oscillating populations, with the typical dominant–subdominant–weak–weak pattern. The populations in the bottom rows are oscillating only intermittently.