



# 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.

© 2015 Elsevier Ltd. All rights reserved.

## 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 damped 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](mailto:christophschmitt@fkp.tu-darmstadt.de) (C.K. Schmitt), [drossel@fkp.tu-darmstadt.de](mailto:drossel@fkp.tu-darmstadt.de) (B. Drossel).

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

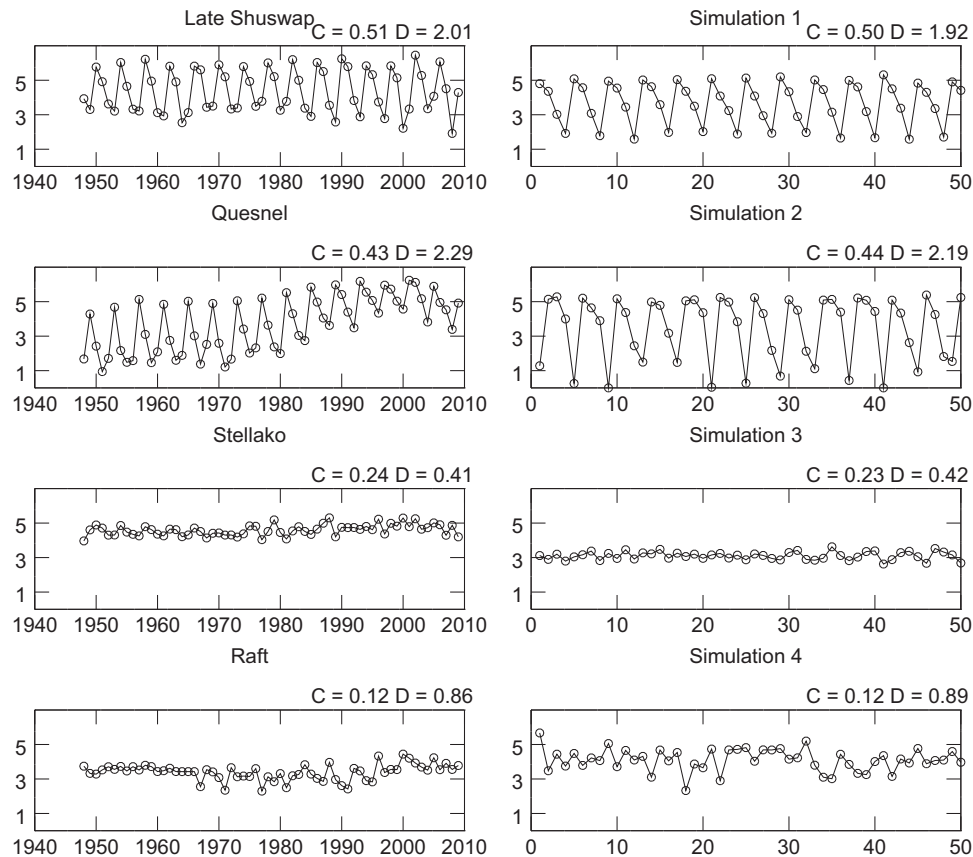
The model we use for sockeye salmon population dynamics was first introduced with three species in Guill et al. (2011), but in this paper we use the two-species version from Guill et al. (2014) with noise added as in Schmitt et al. (2012). It is mechanistic, containing only the ingredients we assume 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

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

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

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.

the sockeye fry with a biomass conversion efficiency  $e$  and a Beddington–De Angelis functional response

$$f(F_n, P_n) = \frac{IF_n}{B_0 + F_n + cP_n} \quad (3)$$

Here,  $I$  denotes the maximum feeding rate,  $B_0$  is the half-saturation prey density (at infinitesimal predator density), and  $c$  is a predator interference parameter.

Several assumptions and simplifications are made: using biomass densities implies that the number of individuals is so large that the actions of single individuals are not important. We also assume that the effects of inhomogeneous biomass distribution in space can be neglected in this context. Furthermore all parameters are constant in time, and all species parameters are set to a single value for the whole population. This means that the body mass changes of sockeye fry during their time in the lake and possible depletion of their food supply are neglected, and that the species and size distributions of predators are ignored. These simplifications are legitimate because in this model the most important effect of the nursery lake dynamics is the delayed density dependence of the total biomass growth over the whole season, which is caused by the coupling to a predator. As long as the differential equations incorporate this, their details are not important. The differential equations could be even further simplified by neglecting density dependence in prey growth and predation, but this would make the dynamics too unrealistic.

One of the most important assumptions inherent in this model is the existence of a specialist predator of sockeye fry. Both the absence of additional species in the model foodweb and the shape of the functional response are based on this. We have shown that strong oscillations with a period of four years can also be obtained in a model containing an additional prey species, but the parameter range is smaller than with a specialist predator (Schmitt et al., 2014). Models with two prey species and adaptive feeding dynamics (slow prey switching) also reproduce cyclic dominance over a wide parameter range (unpublished). In two lakes with strongly oscillating sockeye populations, sockeye fry are known to be an integral part of the diet of rainbow trout (Ward et al., 1964; Sebastian et al., 2003).

The sockeye life cycle and migration are also simplified. Sockeye salmon usually spawn at age 3+, some at 4+, and generally die after spawning (Pauley et al., 1989; Cohen, 2012). This means that the number of spawners can be calculated from previous fall fry densities as follows:

$$S_{n+1} = a((1 - \epsilon)F_{n-3}(T) + \epsilon F_{n-4}(T)). \quad (4)$$

We assume that the number of spawners depends linearly on the fall fry biomass density with a conversion factor  $a$ . A fraction  $\epsilon$  of sockeye salmon spawns at age 4+, the rest at age 3+. The fry starting biomass density is then calculated using a Beverton–Holt recruitment function:

$$F_{n+1}(0) = \frac{bS_{n+1}}{1 + \frac{bS_{n+1}}{K_S}} \quad (5)$$

$K_S$  denotes the capacity of the spawning grounds,  $b$  is the fry biomass per spawner for small spawner numbers.

The predator starting biomass density depends linearly on the biomass density at the end of the previous year:

$$P_{n+1}(0) = s_w P_n(T). \quad (6)$$

The dynamics of the (so far) deterministic model have been analyzed by Guill et al. (2014). After long times, the salmon abundance either becomes constant or shows an oscillation with a period of four years, depending on the parameter values. The conditions for oscillation are strong interaction of the sockeye fry

with the predator and the ability for the sockeye fry to reach large biomass densities. This means for example that the maximum feeding rate  $I$  and the maximum spring and fall fry densities  $K_S$  and  $K$  need to be high.

During their life cycle (hatching, rearing in a lake, downstream migration, feeding near the shore, time in open waters, upstream migration, spawning) the sockeye salmon are subjected to varying environmental conditions, e.g. water temperature during migration and survival conditions at sea, that are so far not included in this model. We incorporate these by applying noise to the sockeye survival rate in the discrete step. A random number  $x_n$  is drawn every year according to the lognormal distribution with width  $\sigma$  and an implied mean of 1:

$$p_\sigma(x_n) = \frac{1}{\sqrt{2\pi}\sigma x_n} \exp\left(-\frac{(\ln x_n)^2}{2\sigma^2}\right), \quad x_n > 0. \quad (7)$$

The number of spawners is then multiplied by that number:

$$S_{n+1} = ax_n[(1 - \epsilon)F_{n-3}(T) + \epsilon F_{n-4}(T)]. \quad (8)$$

The only parameter here is the width  $\sigma$  of the distribution, which corresponds to the strength of environmental perturbations. With weak noise the dynamics stay close to the unperturbed attractor and fluctuate around it. Usually, these oscillations clearly show the period four because of the sockeye life cycle, especially but not only if the unperturbed attractor is cyclic. Strong noise can cause phase jumps in an otherwise cyclic system (Schmitt et al., 2012).

The model parameter values are listed in Table 2. They were estimated based on biological data and allometric scaling relations (Guill et al., 2014). The predator parameters are based on rainbow trout, which are known to feed on sockeye fry in some lakes (Ward et al., 1964; Sebastian et al., 2003). However, the values are only estimates, and almost all of them most likely vary considerably between different sockeye populations. The growth conditions for sockeye fry are not the same in different lakes, and neither are the size and kind of predators. Furthermore the length of the migration route through the river differs between the spawning lakes. Because of these differences, below we will vary the model parameters around their estimated mean values.

The model was implemented using the C programming language and the GNU Scientific Library.

**Table 1**

Consistency  $C$  and dominance  $D$  of the Fraser River sockeye populations (White et al., 2014). The numbers in the left column are used to identify the populations in other figures.

#	Name	$C$	$D$
1	Weaver	0.02	0.22
2	Pitt	0.02	0.31
3	Birkenhead	0.08	0.42
4	Stellako	0.24	0.45
5	Fennell	0.13	0.57
6	Chilko	0.18	0.59
7	Portage	0.26	0.60
8	Gates	0.22	0.64
9	Harrison	0.12	0.67
10	Early Stuart	0.13	0.70
11	Seymour	0.34	0.73
12	Cultus	0.29	0.74
13	Raft	0.12	0.87
14	Bowron	0.18	0.88
15	Nadina	0.19	1.00
16	Late Stuart	0.28	1.57
17	Late Shuswap	0.51	1.91
18	Quesnel	0.43	2.18

**Table 2**

Overview of the parameter standard values used in this paper. The biological reasons for choosing these values are given by [Guill et al. \(2014\)](#). The parameters from that article were slightly adapted to better fit the natural data.

Symbol	Parameter	Value
$T$	Length of growth season	140 d
$r$	Sockeye fry maximum growth rate	$0.026 \text{ d}^{-1}$
$K$	Sockeye fry carrying capacity of the lake	$2 \text{ g m}^{-2}$
$e$	Ecological efficiency of predators	0.85
$d$	Predator respiration rate	$0.0048 \text{ d}^{-1}$
$I$	Predator maximum feeding rate	$0.0192 \text{ d}^{-1}$
$B_0$	Predator feeding rate half-saturation density	$0.021 \text{ g m}^{-2}$
$c$	Predator competition strength	0.52
$s_W$	Predator overwinter survival	0.85
$\epsilon$	Proportion of sockeye spawning at age 4+	0.1
$a$	Spawner density per biomass density	$0.01 \text{ g}^{-1}$
$b$	Maximum fry biomass per spawner	12.8 g
$K_S$	Spawning grounds capacity	$0.1 \text{ g m}^{-2}$

### 3. Methods

To analyze the noisy time series from the model we use a method developed by [White et al. \(2014\)](#). A wavelet power spectrum is calculated, which gives information about the oscillation frequencies present in the time series. It is similar to a Fourier spectrum in this regard, but is time dependent. It shows the frequency composition of a signal around each point in time, taking neighbouring points into account. In order to determine the presence of longer period oscillations, the variations in a larger interval have to be examined. From the wavelet power spectrum we can calculate measures for the consistency  $C$  and dominance  $D$  of the period four oscillation. We then use these measures to compare 50-year time series from our model to ones from nature, while varying the model parameters. Because of the noise in the model two time series obtained from the same parameter set can vary considerably, and so can their consistency and dominance values.

Our analysis proceeds as follows: first, the model is initialized with random starting values and the simulation runs for 2000 timesteps (years). For the last 50 of those the sockeye spawner density is recorded. We chose the duration of 50 years because it is similar to the available spawner data and for consistency with [White et al. \(2014\)](#). The resulting timeseries is then log10-transformed. A wavelet power spectrum is obtained using the methods described by [Torrence and Compo \(1998\)](#). We use the Morlet-Wavelet with  $\omega_0 = 6$ :

$$\Psi_0(\eta) = \pi^{-1/4} \exp(i\omega_0\eta) \exp\left(-\frac{\eta^2}{2}\right). \quad (9)$$

This is a plane wave modulated by a Gaussian. The discrete wavelet transform at period  $s$  and time  $n$  is given by

$$w_{s,n} = \sum_{n'=0}^{N-1} f_{n'} \Psi^*\left(\frac{(n'-n)\delta t}{s}\right). \quad (10)$$

$\delta t$  is the time step between two points, in this case one year.  $\Psi$  is the wavelet function, which is obtained by normalizing the base wavelet  $\Psi_0$ , taking into account the change of the argument.  $\Psi^*$  is the complex conjugate of the function. To obtain a spectrum for every point in time, the transformation needs to be calculated for all times  $n$  and all relevant periods  $s$ . Here we use

$$s_k = 2^{1+(1/4)k}, \quad k = 0, \dots, 9. \quad (11)$$

The power of period  $s_k$  at time  $n$  is  $|w_{s_k,n}|^2$ . We now calculate the relative power in a period  $s$ :

$$W'_{s,n} = \frac{|w_{s,n}|^2}{\sum_{k=1}^{k_{\max}} |w_{s_k,n}|^2}. \quad (12)$$

From this the consistency of period  $s$  is calculated using the following formula:

$$C = \frac{\overline{W'_{s,n}}}{1 + \sqrt{\text{var}(W'_{s,n})}}, \quad (13)$$

where  $\overline{W'_{s,n}}$  denotes the temporal arithmetic mean, and var is the temporal variance.

Note that to avoid boundary effects only those values that are at least ten years from the borders of the time series are considered.  $C$  is between 0 and 1, it is high if the average relative power of period  $s$  is high and there is little variance in the power. We only look at  $s = 4$  in this paper, because the generation length of the Fraser River stocks is close to four. In the spawner numbers of Fraser River sockeye  $C$  is about 0.1–0.5, depending on the population (see [Table 1](#)).

The consistency  $C$  thus tells us whether the time series is persistently oscillating with period four. Since  $C$  is calculated based on the relative power, it contains no information about the actual strength of the oscillation. This information is contained in the dominance  $D$ . In order to calculate  $D$ , all data points for which period four is not the one with the highest power in the wavelet spectrum are first removed from the time series. In this reduced time series, all windows of four points (one period) are considered, and in each of them the mean difference between the highest point and the other three is calculated,

$$D_i = \frac{4}{3} \max_{j=i, \dots, i+3} (x_j) - \frac{1}{3} \sum_{j=i}^{i+3} x_j, \quad i = 1, \dots, N-3. \quad (14)$$

Finally the average over all windows is taken:

$$D = \overline{D_i}. \quad (15)$$

$D$  can be considered an average logarithmic distance between the highest point in each cycle and the lower ones. The values calculated for natural time series range roughly from 0.4 to 2.2.

Several example time series, both real and simulated, are shown in [Fig. 1](#) with their corresponding  $C$  and  $D$ . Further examples of empirical data and simulation data from a model without predator–prey dynamics together with their corresponding wavelet power spectrum can be found in [White et al. \(2014\)](#).

The analysis was carried out using MATLAB code provided by [White et al. \(2014\)](#) as a supplement to their article. The code was adapted to run in octave.

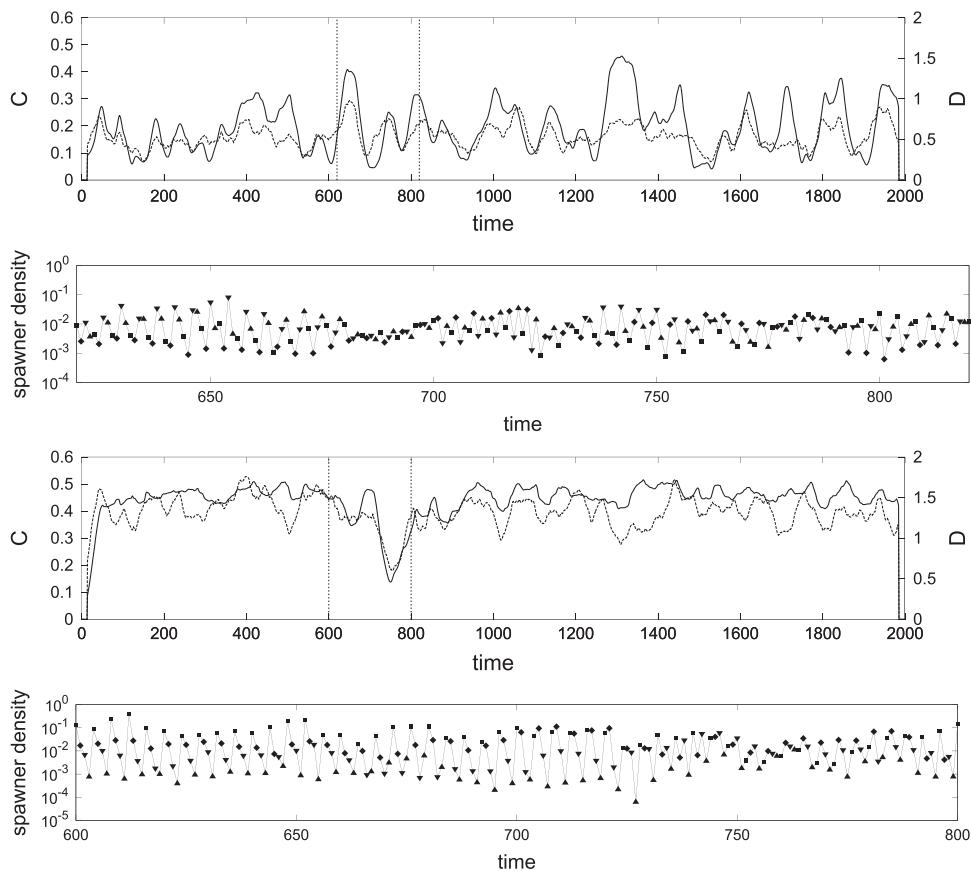
### 4. Results

We first investigate to what extent time series obtained from the same set of parameter values can vary. Then we draw the model parameters randomly from realistic intervals and evaluate the resulting range of  $C$  and  $D$  values. Next we determine for each lake of [Table 1](#) the parameter intervals that can generate time series whose  $C$  and  $D$  are similar to those of the lake, and discuss how the differences in the parameters relate to different types of oscillation patterns in the lakes.

#### 4.1. Variation of $C$ and $D$ for fixed parameter values

In order to show how much  $C$  and  $D$  can vary for one set of model parameters, we evaluated  $C$  and  $D$  for all 50-year windows of the 2000 year time series instead of only using the tail. [Fig. 2](#)





**Fig. 2.** Values of consistency  $C$  and dominance  $D$  over the course of 2000 year simulation (odd rows) and parts of the corresponding time series (even rows). In the top two rows the attractor without noise would be a fixed point ( $K = 0.3 \text{ g m}^{-2}$ ), for the bottom two rows a limit cycle ( $K = 2 \text{ g m}^{-2}$ ). The noise strength  $\sigma$  is 0.5 for both, all other parameters are at the standard values listed in Table 2. The development of  $C$  and  $D$  over time is calculated via a sliding window of 50 years over the whole time series. The vertical bars mark the beginning and end of the part shown on the right.  $C$  is plotted as a solid line using the axis on the left,  $D$  as a dashed line using the axis on the right.

shows the  $C$  and  $D$  values obtained as the window slides over the long time interval of the simulation, once for a time series where the attractor would be a fixed point in the absence of noise, and once for a cyclic attractor. Both time series frequently show oscillations resembling the cyclic dominance pattern observed in nature, but the pattern is a lot more stable if the attractor is cyclic.

For the time series with the fixed point attractor,  $C$  fluctuates wildly from 0.05 to 0.45, while  $D$  ranges from 0.2 to 1.5. With the cyclic attractor  $C$  and  $D$  are fairly consistently high:  $C$  is mostly 0.35–0.55, but can sometimes dip to values as low as 0.15.  $D$  is usually between 1.2 and 1.5, but can drop as low as 0.7. In natural data  $C$  is about 0.1–0.5,  $D$  between 0.4 and 2.2.

The dips in the values calculated from simulations can be understood by looking at the time series. The oscillation switches to a period of two for approximately 10 years, so four is not the dominant period in this part of the time series. Even though during most of the 50 years period four is still the dominant one, those few years with different dynamics cause a strong drop of  $C$ . So cyclic consistency is a fitting name for this metric, it is very high only if the period four oscillation is consistent. The increase in  $D$  for the cyclic attractor is mostly due to the increased carrying capacity. It makes higher sockeye densities viable, while pushing down the lowest densities, increasing the spread of values.

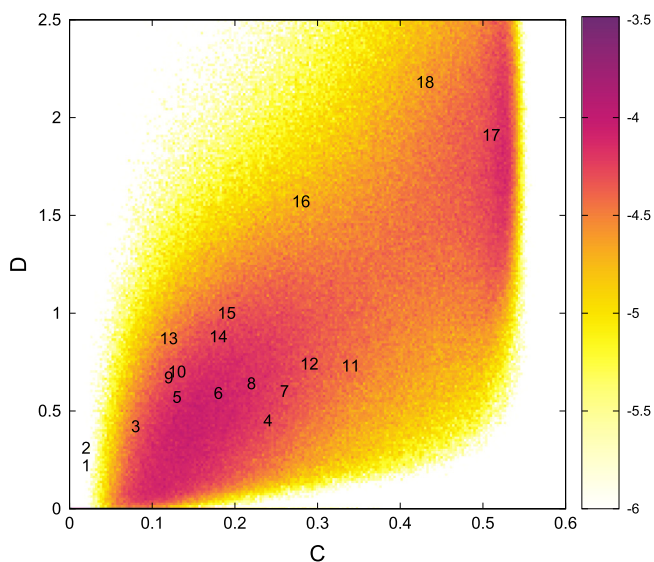
#### 4.2. Distribution of $C$ and $D$ for varying parameter values

As shown in the previous section, the values of  $C$  and  $D$  vary a lot for constant parameter values, but the range of values that can randomly come up depends in turn on the model parameters. To find out what range of values of  $C$  and  $D$  is contained in the model

and to determine the systematic influence of the parameter values, we varied almost all model parameters randomly, simulated the population dynamics, and calculated the  $C$  and  $D$  from the last 50 years of the time series. This was done for two million parameter combinations. Most parameters were drawn uniformly from 50% to 150% of their standard value. This should cover a wide spectrum of possible situations.

There are several exceptions. The ecological efficiency  $e$  was kept constant because the estimates for it are very well established. The noise strength was varied between 0.2 and 1.4 to cover a wide range of imaginable situations. The minimal value is above zero because there is always some noise in nature. The maximum value was chosen because time series generated with even higher values do not resemble natural dynamics. The growth season length  $T$  was varied only between two thirds and four thirds of its standard value because it is naturally limited at the top end: the sockeye fry spawn in spring and the lake freezes over in winter. We assume the overwinter survival rate of the predator  $s_w$  to be smaller than one, so it was varied only between 0.7 and 1.

The resulting density plot of  $C$ – $D$  pairs is shown in Fig. 3. Most of the pairs found in nature are hit by the distribution to some extent. The only two natural pairs that are obviously outside the distribution due to their extremely low  $C$  refer to Pitt lake and Weaver lake, which are both near the coast. To assess how well the model is able to reproduce the characteristics of naturally occurring time series we introduce two simple definitions: a model result is “very close” to a natural time series if their values of  $C$  differ by less than 0.0125, and those of  $D$  by less than 0.0625. The resulting rectangle around each natural data point covers about 5% of the observed value range in each direction. We take “close” to



**Fig. 3.** Density plot showing the distribution of  $C$  and  $D$  when many parameters are varied. The parameter ranges are given in Section 4.2. Note that the density scale is logarithmic (the numbers on the colourbar are the  $\log_{10}$  of the relative frequency), so a time series with random parameters is far more likely to have  $C$  and  $D$  in a dark area than in a light one. The  $C$  and  $D$  values for many Fraser River sockeye populations are shown as numbers inside the plot, the corresponding names are found in Table 1.

mean being up to two times as far away as for very close points. 7.3% of pairs are very close to ones found in nature, 23% are close.

$C$  and  $D$  were set to 0 if the sockeye went extinct in the time series. This happened in about 9.2% of cases, either because of unfortunate starting values, a series of disadvantageous perturbations, or random parameter combinations making survival impossible. Finally there is a small portion (2.9%) of pairs where  $D$  is zero, but  $C$  is nonzero. This happens if the period four component of the wavelet power spectrum is never the largest one.

#### 4.3. Realistic parameter intervals for Fraser River lakes

To find out more about the systematic effects of specific parameters, all time series for which  $C$  and  $D$  are in very close proximity to one of the pairs from a natural time series by the above definition were grouped and analysed more closely. Fig. 4 shows box plots of the distribution of each parameter for each of these groups. Because noise has a very strong effect on the time series, various parameter combinations can lead to time series resembling a natural one. The median of the parameter distribution that led to time series similar to the natural ones is usually close to the standard value of the parameter. The parameter distribution is generally quite broad, and for most parameters there is little dependence on which lake the parameter set belongs to.

For most parameters, significant differences only exist between lakes with persistent oscillation and ones with only intermittent oscillation. The independence of the specific form of the time series from exact parameter values shows that not only the parameters influence the result: noise has a similarly large or even larger influence. Depending on the specific sequence of random numbers, there may be more or less oscillation, and the amplitude may be larger or smaller.

The only major exception is the noise strength  $\sigma$ . The median of the distribution of  $\sigma$  differs quite strongly between populations. Also the range of noise strengths that is likely to reproduce the values of each time series is much smaller than for other parameters. The median noise strength clearly corresponds to the dominance  $D$  of the population. Stronger noise causes stronger

oscillations. An exception to this are the very consistently oscillating populations in Quesnel and Shuswap lake, which have a far lower noise strength than needed to reproduce similarly strong but less persistent oscillations. Their time series are very similar to strongly oscillating ones in the deterministic model, so their features can be reproduced with weak noise despite the strong oscillation.

As previously mentioned, other parameter values also differ between persistently and intermittently oscillating populations. Comparing the parameters leading to time series resembling strongly cyclic populations – Late Stuart (14), Quesnel (17) and Shuswap (18) – to the ones leading to time series with weak intermittent cycles might give some clues to the causes of cyclic dominance.

Three groups of parameters can be identified. One is formed by the parameters pertaining to the sockeye fry living conditions in the lake: the carrying capacity  $K$ , maximum growth rate  $r$ , the capacity of the spawning grounds  $K_s$ , and the length of the growth season  $T$ . On average, all of these parameters are significantly higher for time series resembling strongly cyclic ones. So according to the model, lakes where the sockeye fry thrive are more likely to contain strongly cyclic populations.

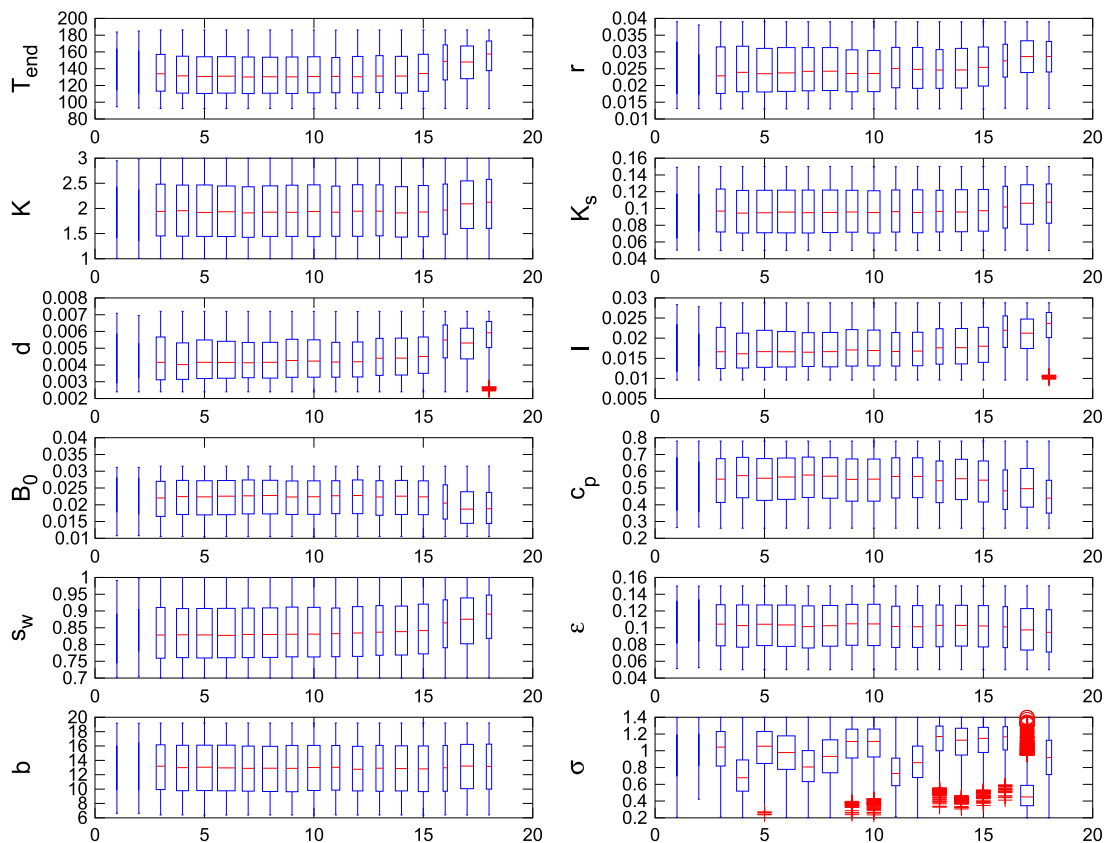
The second group of parameters consists of those dealing with the predator and the predator–sockeye interaction: the maximum feeding rate  $I$  (and the predator respiration rate  $d$  which is coupled to it), the saturation parameters of the functional response  $B_0$  and  $c_p$ , and the predator overwinter survival rate  $s_w$ . For strongly cyclic time series the predator–prey interaction is much stronger on average, with both a higher maximum and slower saturation, and the overwinter survival rate of the predator is higher. So cyclic dominance seems to require strong coupling to a predator, and the better growth conditions for sockeye fry allow them to survive the high predation pressure.

This confirms the results from all deterministic versions of this model (Guill et al., 2011, 2014; Schmitt et al., 2014) and the previous analysis of a stochastic version (Schmitt et al., 2012). In all of these cyclic dominance requires good growth conditions and strong coupling to a predator.

Finally there are parameters dealing with the time the salmon do not spend in the nursery lake: the noise strength  $\sigma$ , the proportion of age 4+ spawners  $\epsilon$ , and the fry biomass per spawner  $b$ . While the noise strength  $\sigma$  is fairly low for the Quesnel and Shuswap populations, the Late Stuart population shows similarly strong oscillations but has extremely high noise strength. So there is no clear relation between the strength of random perturbations and cyclic dominance. The survival of a population during migration and in the ocean and the quality of the spawning grounds are all collected in the fry biomass per spawner  $b$ . It is slightly higher for populations with cyclic dominance, just like the parameters from the first group. The proportion of age 4+ spawners  $\epsilon$  is slightly lower in the strongly cyclic populations, bringing their average generation length closer to the oscillation period of four years. This seems to facilitate strong persistent oscillations.

## 5. Discussion

The comparison between cyclic consistency and dominance values obtained from the model with naturally occurring combinations leads to two main conclusions: First, noise is necessary to obtain time series similar to ones found in nature, incorporating it into models is vital to understanding empirical time series. Second, strong predator–prey interaction combined with good growth conditions for sockeye fry makes persistent oscillations more likely.



**Fig. 4.** Overview of what parameter values best reflect the situation in the various sockeye populations. The populations are on the x-axis, ordered by their corresponding value of  $D$  (see Table 1). Numbers 16 (Stuart), 17 (Shuswap) and 18 (Quesnel) show strong cyclic dominance. The parameter distribution is visualized as a box plot. The horizontal line in the middle of the box marks the median, the box around it contains the second and third quartile of data points. The width of the box corresponds to the number of data points in the distribution. The vertical lines end at the minimum and maximum value of the distribution. However, points which are further from the borders of the box than 1.5 times its height are considered outliers and are marked separately as crosses (or circles for extreme outliers).

As shown in several different models, noise can excite a period four oscillation in sockeye salmon populations (Myers et al., 1998; Worden et al., 2010; White et al., 2014). The cause of this is obvious: four years is close to the generation length of Fraser River sockeyes, so if a lot of salmon spawn in one year, four years later their numerous offspring will spawn. The oscillations are dampened in these models, but sometimes noise can sustain oscillations for longer times. It is therefore possible to obtain time series similar to the ones from persistently oscillating populations like the late Shuswap run from the model in White et al. (2014). It treats the sockeye life cycle in a similar manner to the model used in this paper, but instead of the predator–prey interaction in the lakes it uses a Beverton–Holt stock recruitment function. In that model the oscillation usually only persists for a limited time. Also, the phase of the oscillation changes frequently. This is different from the strongly oscillating natural populations, where consistent oscillations have been observed for decades (see Fig. 1 for modern counts, and Ward et al. (1964) for an overview of older data). This consistency points to something enhancing and stabilizing the oscillation, therefore it seems to us unlikely that cyclic dominance is caused solely by random perturbations.

In contrast, our model can produce such consistent oscillations because it includes a predator–prey interaction. Such an interaction introduces a delayed density dependence, which is required for population oscillations in the absence of noise. In the absence of noise, the biomass densities either go to a fixed point or oscillate with an exactly repeating pattern of period four, depending on the parameters. By including noise, both types of empirical data, those with only intermittent oscillations, as e.g. in the Raft and Stellako stocks, and those with persistent oscillations, as in the Quesnel

and Shuswap stocks, are generated by the model. This means that only when both noise and predator–prey interaction are taken into account, the full spectrum of sockeye dynamics observed in nature is recovered. The only two lakes that are not well captured by our analysis are the Pitt and Weaver lakes. The assumptions of our model do apparently not apply to them. Indeed, in Pitt lake predation is not relevant to sockeye fry survival (Diewert and Henderson, 1992), and adults frequently spend an extra year in the ocean (Henderson et al., 1991). Additionally egg to fry survival is boosted by a salmon hatchery. A model that does not incorporate predation, such as the one by (White et al., 2014), is thus better suited to the situation in Pitt lake, and it produces time series with  $C$  values as low as in Pitt and Weaver lake.

We have shown that strong predator–prey interaction combined with good growth conditions for sockeye fry supports persistent oscillations also in our stochastic model. White et al. (2014) found that oscillations especially occur in populations with a close to linear stock–recruitment relationship. This means the population is far from its maximum capacity, and thus possibly at higher risk of extinction. At first glance this seems to contradict our finding that oscillations are more likely in lakes with especially good conditions for the sockeye fry. However, single generation cycles are characterized by their population numbers repeating themselves after one generation. If a larger than usual number of spawners is unable to produce a larger than usual amount of offspring, such an oscillation will be quickly dampened (unless other driving factors are present). So the observation that stocks which exhibit cyclic dominance are far from saturation is to be expected. It also does not contradict the presence of good growth conditions enabling oscillations: those can be present independently of the

actual number of spawners. The fact that the strongly oscillating Quesnel and Shuswap populations are also two of the most productive ones supports this thesis.

We thus agree that a close to linear stock–recruitment relationship is required for cyclic dominance, which means that the potential for oscillation is concurrent with a larger susceptibility of the population to changes in spawner number. In a saturated population, strongly reducing the number of spawners will have a far smaller long-term effect than in a population that strongly responds to changes in spawner number. But a close to linear stock–recruitment relationship does not necessarily imply a high risk of extinction, it implies just that something other than the spawner–recruit relationship is limiting the population. It also implies that reduced spawner numbers will lead to reduced recruitment. On the other hand, eliminating the external factors limiting such oscillating populations may lead to rapid growth.

It is known that in Quesnel and Shuswap lake sockeye fry and eggs are an important part of the diet of rainbow trout (Ward et al., 1964; Sebastian et al., 2003). So these lakes fulfill both of the conditions for cyclic dominance found in this paper and in previous studies of deterministic models with predator–prey interaction (Guill et al., 2011, 2014; Schmitt et al., 2014). In Pitt lake on the other hand predation is not important to the survival of sockeye fry, and the sockeye population does not exhibit cyclic dominance (Diewert and Henderson, 1992). Unfortunately the interaction of predators with sockeye fry in most other lakes in the Fraser river system is not as well studied. Also it is difficult to compare the strength of predator–prey interactions between different lakes because they have different species distributions. It is generally very difficult to measure the strength of these interactions, especially in the field. However, such a comparison between different lakes would be very useful for validating our theory and could open up new options in salmon management. Investigating possible other causes of delayed density dependence in the sockeye nursery lakes may also be a valuable avenue of investigation. The importance of the coupling to a predator could in principle be measured since predator populations change in dependence of the sockeye population if they are responsible for the sockeye oscillation. Our model predicts an oscillation of the predator biomass which is considerably weaker than that of the sockeye salmon, but far from negligible. Since the prey preference of rainbow trout in Quesnel lake is known to change with body size (Sebastian et al., 2003), different age classes of the predator will be affected differently by changing sockeye biomass, and the actual amount of predation on sockeye fry may be difficult to evaluate. Nevertheless, if a predator is indeed responsible for cyclic dominance, the biomass of at least some age classes must be affected quite strongly by the amount of available sockeye fry, and it should be possible to measure this effect.

Another way to distinguish between oscillations driven by stochasticity and oscillations driven by predator–prey dynamics may be looking at the strength of random influences on different sockeye populations. White et al. (2014) require strong driving noise to obtain model time series resembling cyclic dominance,

while we see fairly weak noise in the time series resembling the most consistently oscillating populations. However, the strength of random influences acting on different sockeye population would be difficult to define properly outside of a model. Only if one easily measurable type of random influence (for instance spawning stream temperature) did dominate the overall noise, would an evaluation of the strength of randomness be feasible.

## Acknowledgements

This work was supported by the DFG under contract number Dr300/9-1. We thank Christian Guill for valuable discussions and Will White for his helpful review.

## References

- Cohen, B., 2012. The uncertain future of Fraser River sockeye. Public Works and Government Services Canada.
- Diewert, R., Henderson, M., 1992. The effect of competition and predation on production of juvenile sockeye salmon (*Oncorhynchus nerka*) in Pitt Lake. Technical Report, Canadian Technical Report of Fisheries and Aquatic Sciences 1797.
- Guill, C., Carmack, E., Drossel, B., 2014. Exploring cyclic dominance of sockeye salmon with a predator–prey model. *Can. J. Fish. Aquat. Sci.* 71 (7), 959–972.
- Guill, C., Drossel, B., Just, W., Carmack, E., 2011. A three-species model explaining cyclic dominance of Pacific salmon. *J. Theor. Biol.* 276, 16–21.
- Henderson, M., Diewert, R., Hume, J., Shortreed, K., Levy, D., Morton, K., 1991. The carrying capacity of Pitt Lake for juvenile sockeye salmon (*Oncorhynchus nerka*). Technical Report, Canadian Technical Report of Fisheries and Aquatic Sciences 1797.
- Levy, D.A., Wood, C.C., 1992. Review of proposed mechanisms for sockeye salmon population cycles in the Fraser River. *Bull. Math. Biol.* 54, 241–261.
- Myers, R.A., Mertz, G., Bridson, J.M., Bradford, M.J., 1998. Simple dynamics underlie sockeye salmon (*Oncorhynchus nerka*) cycles. *Can. J. Fish. Aquat. Sci.* 55, 2355–2364.
- Pauley, G., Risher, R., Thomas, G., 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific northwest)—sockeye salmon. U.S. Fish Wildl. Serv. Biol. Rep. 82 (11.116). U.S. Army Corps of Engineers, TR EL-82-4. 22 pp.
- Ricker, W.E., 1950. Cycle dominance among the Fraser sockeye. *Ecology* 31, 6–26.
- Ricker, W.E., 1997. Cycles of abundance among Fraser River sockeye salmon (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.* 54, 950–968.
- Schmitt, C.K., Guill, C., Carmack, E., Drossel, B., 2014. Effect of introducing a competitor on cyclic dominance of sockeye salmon. *J. Theor. Biol.* 360, 13–20.
- Schmitt, C.K., Guill, C., Drossel, B., 2012. The robustness of cyclic dominance under random fluctuations. *J. Theor. Biol.* 308, 79–87.
- Sebastian, D., Dolighan, R., Andrusak, H., Hume, J., Woodruff, P., Scholten, G., 2003. Summary of Quesnel Lake kokanee and rainbow trout biology with reference to sockeye salmon. Stock Management Report No. 17, Ministry of Water, Land, and Air Protection, Province of British Columbia.
- Torrence, C., Compo, G.P., 1998. A practical guide to wavelet analysis. *Bull. Am. Meteorol. Soc.* 79, 61–78.
- Townsend, C.R., 1989. Population cycles in freshwater fish. *J. Fish Biol.* 35 (Supplement A), 125–131.
- Ward, F.J., Larkin, P.A., 1964. Cyclic dominance in Adams River sockeye salmon. International Pacific Salmon Fisheries Commission.
- White, J.W., Botsford, L.W., Hastings, A., Holland, M.D., 2014. Stochastic models reveal conditions for cyclic dominance in sockeye salmon populations. *Ecol. Monogr.* 84, 69–90.
- Worden, L., Botsford, L.W., Hastings, A., Holland, M.D., 2010. Frequency responses of age-structured populations: pacific salmon as an example. *Theor. Popul. Biol.* 78, 239–249.