



A three-species model explaining cyclic dominance of Pacific salmon

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ABSTRACT

The four-year oscillations of the number of spawning sockeye salmon (*Oncorhynchus nerka*) that return to their native stream within the Fraser River basin in Canada are a striking example of population oscillations. The period of the oscillation corresponds to the dominant generation time of these fish. Various—not fully convincing—explanations for these oscillations have been proposed, including stochastic influences, depensatory fishing, or genetic effects. Here, we show that the oscillations can be explained as an attractor of the population dynamics, resulting from a strong resonance near a Neimark Sacker bifurcation. This explains not only the long-term persistence of these oscillations, but also reproduces correctly the empirical sequence of salmon abundance within one period of the oscillations. Furthermore, it explains the observation that these oscillations occur only in sockeye stocks originating from large oligotrophic lakes, and that they are usually not observed in salmon species that have a longer generation time.

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1. Introduction

In many ecological systems distinct population oscillations are known, with their specific dynamical characteristics often captured by simple generic models. Among these are the spatial synchronisation of the lynx-hare oscillations in Canada (Elton and Nicholson, 1942; Odum, 1953; Blasius et al., 1999), the chaotic oscillations of boreal rodents in Fennoscandia (Hanski et al., 1993), or the cyclic outbreak dynamics of the spruce budworm (Ludwig et al., 1978; Royama, 1984). The four-year oscillations of sockeye salmon (*Oncorhynchus nerka*) in the Fraser River basin in Canada are another well-documented example of such large-scale population oscillations (Ricker, 1950; Townsend, 1989; Ricker, 1997). They are a typical example of single-generation cycles (Gurney and Nisbet, 1985; Murdoch et al., 2002). Every fourth year (which is the dominant generation time) the abundance of these fish is at very high levels, reaching several million fish in some spawning populations, but drops to numbers between several hundred and a few 10,000 individuals in the following years (hence the term *cyclic dominance*). Different stocks can have their population maximum in different years (Fig. 1 and Appendix). The oscillations were reported as early as the 19th century and are evident for instance in the extremely high catches by

fisheries every fourth year (Rounsefell and Kelez, 1938). This both economically and conservationally important phenomenon has been ascribed either to transient effects or to stochastic influences (Myers et al., 1998), to depensatory predation (Larkin, 1971), to fishing (Walters and Staley, 1987), or to genetic effects (Levy and Wood, 1992; Walters and Woodey, 1992), but all of these explanations are still not fully convincing (Levy and Wood, 1992; Ricker, 1997).

The sockeye salmon return to spawn in their native stream or lake in late summer and then die, which means that the salmon generations do not overlap. The hatched fry migrate downstream in the following spring and feed for one season in large freshwater lakes, before they migrate to the ocean, where they spend the next two and a half years. The carcasses of the adult salmon are decomposed and provide an important phosphorus input into the rearing lakes of the fry. Since the oscillations of sockeye salmon originating from different lakes are not in phase, we have clear evidence that the relevant processes causing the phenomenon of cyclic dominance take place in the rearing lakes rather than in the ocean.

2. Model and results of computer simulations

It is our aim to develop a generic model capturing only the essential mechanisms required for the occurrence of cyclic dominance. As such, the model is kept very simple and is not designed to quantitatively predict the population dynamics of all species in the corresponding lake ecosystems.

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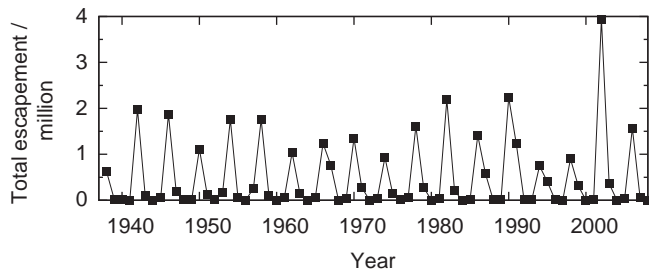


Fig. 1. Empirical time series of sockeye salmon abundance. Total escapement (number of male and female adults that escape the fisheries) of the late Shuswap Lake run. Shuswap lake is one of the most important rearing lakes of juvenile sockeye salmon. Data for five other lakes are provided in the Appendix.

The model uses standard continuous population dynamics equations for sockeye fry, $s_n(t)$, their predator (e.g. rainbow trout), $p_n(t)$, and their zooplankton food (mainly daphnia), $z_n(t)$, during the growth season from spring ($t=0$) to fall ($t=T$) in year n , combined with a rule for calculating the three population sizes at the beginning of the next season as a function of the population sizes at the end of the previous season(s). The sockeye fry population at the end of a season gives rise to the number of spawning adults three years later, which in turn determines the number of sockeye fry in the following spring, and represents a nutrient input that affects the carrying capacity of the zooplankton. A small fraction of the salmon stays in the ocean for one more year and mature at age 5, thus causing a mixing between the four brood lines of a spawning population. An even smaller fraction matures at age 3, but since these fish are predominantly small-sized males (Ricker, 1997) that do not influence the number of fertilised eggs, they are neglected in this study.

The general structure of the model, which combines continuous population dynamics during the growth season with a discrete update scheme capturing the seasonally driven migration and reproduction of the species of interest, has also been applied in a modelling study of the dynamics of fish preying on zooplankton (Persson et al., 1998). Here, however, we have chosen a much simpler form of the continuous dynamics which is sufficient to generate cyclic dominance. It is given by the following equations of motion:

$$\begin{aligned} \frac{d}{dt} s_n(t) &= \lambda \cdot a_{sz} \frac{z_n(t) \cdot s_n(t)}{1 + c_s \cdot s_n(t) + z_n(t)} - a_{ps} \frac{s_n(t) \cdot p_n(t)}{1 + c_p \cdot p_n(t) + s_n(t)} - d_s \cdot s_n(t) \\ \frac{d}{dt} z_n(t) &= z_n(t) \cdot \left(1 - \frac{z_n(t)}{K_n} \right) - a_{sz} \frac{z_n(t) \cdot s_n(t)}{1 + c_s \cdot s_n(t) + z_n(t)} \\ \frac{d}{dt} p_n(t) &= \lambda \cdot a_{ps} \frac{s_n(t) \cdot p_n(t)}{1 + c_p \cdot p_n(t) + s_n(t)} - d_p \cdot p_n(t) \end{aligned} \quad (1)$$

The variables s_n , z_n , and p_n are biomass densities that are made dimensionless. The parameters in these equations and their numerical values used in the computer simulations are as follows. $\lambda=0.85$ denotes the assimilation efficiency of ingested prey biomass of carnivores (Yodzis and Innes, 1992). The maximal per unit mass ingestion rates of salmon, $a_{sz}=10$, and predators, $a_{ps}=1.6$, scale allometrically with bodymass according to a power law with exponent $-1/4$ (Brown et al., 2004). We assume the predators to be approximately 1500 times heavier than the sockeye fry, which fixes the ratio a_{sz}/a_{ps} . The parameters $d_s=1$ and $d_p=0.16$ represent biomass loss due to respiration and mortality; they also scale allometrically with body mass. The feeding terms include saturation at high prey densities, and a predator interference term in the denominator with interference strengths set to $c_s=1$ and $c_p=0.2$. This Beddington (1975) functional response has been chosen since it describes

consumer–resource interactions more accurately than the more frequently used Holling type II form (Skalski and Gilliam, 2001). Similar predator interference terms are also used by other modellers (Walters and Christensen, 2007).

The matching conditions used to determine the biomasses of the species at the beginning of the next season from their values at the end of the previous season(s) are given by

$$s_{n+1}(0) = \gamma((1-\varepsilon)s_{n-3}(T) + \varepsilon s_{n-4}(T))$$

$$z_{n+1}(0) = K_{n+1}$$

$$p_{n+1}(0) = p_n(T) \quad (2)$$

with ε the proportion of surviving sockeye that return to their native lakes at the age of 5 to spawn and die. The parameter γ summarises survival from smolt to adult fish (including ocean survivability and loss to fisheries), spawning success, and egg to fry survival. The various factors are estimated from empirical data (Walters and Staley, 1987; Hume et al., 1996; Pauley et al., 1989) and yield $\gamma=0.4$.

According to empirical observations (Levy and Wood, 1992), the zooplankton level at the end of one year has no effect on the following year. However, its carrying capacity K_{n+1} is a function of the nutrients provided by the adult salmon and thus a function of the initial fry biomass of that year (Hume et al., 2005):

$$K_{n+1} = K_0 + \left(\kappa \frac{s_{n+1}(0)}{\kappa_0 + s_{n+1}(0)} \right) \quad (3)$$

(For a review on the importance of salmon-derived nutrients for freshwater ecosystems, see Gende et al., 2002 and citations therein.) Consumer dependent resource productivity is certainly a rather uncommon phenomenon. In the lake ecosystems under consideration, it provides an important positive feedback to the system, but it does not seem to be crucial for the mathematical mechanism underlying the oscillations (Guill et al., in press). The three parameters determining the carrying capacity K_n of the zooplankton in year n are set to $K_0=15$, $\kappa=10$, and $\kappa_0=2$. The numerical values of these parameters are difficult to determine from empirical data. However, since the nutrient concentration in the brood lakes nearly doubles in years following dominant sockeye returns compared to years following non-dominant sockeye returns (Hume et al., 2005), it seems reasonable that the constant fraction of the carrying capacity, K_0 , and the maximum of the variable fraction, κ , are of the same order of magnitude.

Fig. 2a shows a time series of the biomass of the sockeye fry at the end of the growth season. The first 300 years are cut off to show only the stable periodic oscillation with one strong year followed by one intermediate year and two weak years, just as in the empirical data of most sockeye stocks showing cyclic dominance (Fig. 1 and Appendix). When the simulation parameters are chosen differently (e.g., $c_s=0.2$), the difference between the strong and the intermediate year may become less pronounced. By additionally increasing K_0 and c_p , their order may even become reversed. This is also observed in the empirical data of some stocks.

When a parameter is varied, for instance the constant fraction of the zooplankton carrying capacity, K_0 , the dynamical pattern may change. Fig. 3 shows the biomass $s_n(T)$ of the sockeye fry at the end of the season for different values of K_0 , from year $t=5000$ to year 5200. For small K_0 , all sockeye lines are equally strong (only one point is visible for each value of K_0). This means that the dynamics reaches a fixed point and that there is no cyclic dominance. With increasing K_0 , the fixed point eventually becomes unstable. First a bifurcation to quasiperiodic behaviour occurs (the attractor contains infinitely many points for each

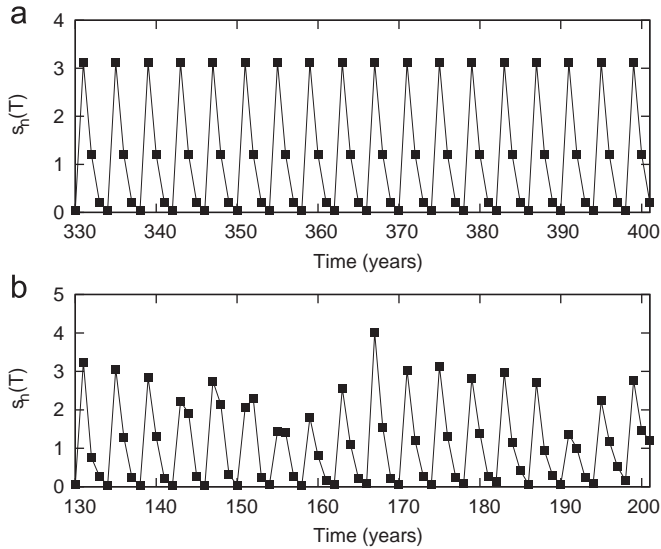


Fig. 2. Simulated time series. Attractor of sockeye salmon dynamics generated by computation of the time-continuous model, showing oscillations with period 4 and the same pattern in the sequence of salmon abundance as in the empirical data. Only the biomasses at the end of each growth season are shown. (a) Deterministic model, (b) dynamics with up to 50 percent fluctuations in the survivability of the sockeye salmon in the ocean (proportional to γ), see Discussion. Parameter values for these simulations are as explained in Section 2.

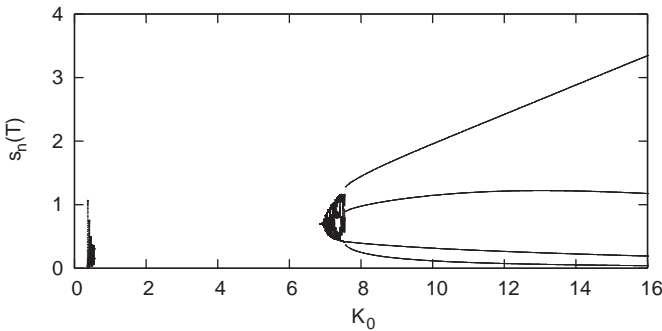


Fig. 3. Bifurcation diagram of the biomass of the sockeye fry at the end of the season. The bifurcation parameter is the constant fraction of the zooplankton carrying capacity K_0 . For each value of K_0 , 200 consecutive data points are plotted.

value of K_0), and then the frequency of the oscillation becomes locked at 4. Now only four points are visible for each value of the bifurcation parameter, indicating periodic oscillations.

3. Bifurcation analysis

In order to understand and interpret these observations, we first note that the continuous population dynamics during the season, together with the matching conditions applied between two seasons, can be viewed as a discrete map (a so-called Poincaré map), giving the sockeye and predator biomasses at the end of one year as a function of the biomasses at the end of the previous years.

To obtain this map, one first has to integrate the dynamical equations over one season, giving $s_n(T)$ and $p_n(T)$ as a function of $s_n(0)$ and $p_n(0)$. The zooplankton can be eliminated since the initial condition of the zooplankton depends on $s_n(0)$ only. Next, one expresses $s_{n+1}(0)$ and $p_{n+1}(0)$ as a function of $s_{n-3}(T)$, $s_{n-4}(T)$ and $p_n(T)$, using the matching conditions.

The mechanism which generates the population oscillation is based on the nature of the instability of the stationary state

$s_n(T)=s^*(T)$, $p_n(T)=p^*(T)$ of our system. The corresponding bifurcation can be investigated in terms of a linear stability analysis. Close to the fixed point, the dynamics can be approximated by linear terms. Denoting the distance of the biomasses from their fixed point value by $\delta s_n = s_n(T) - s^*(T)$, etc., the linear approximation of this map has the form

$$\begin{pmatrix} \delta s_{n+1} \\ \delta s_n \\ \delta s_{n-1} \\ \delta s_{n-2} \\ \delta s_{n-3} \\ \delta p_{n+1} \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & m_s & \varepsilon_1 & -a \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & b & c & m_p \end{pmatrix} \begin{pmatrix} \delta s_n \\ \delta s_{n-1} \\ \delta s_{n-2} \\ \delta s_{n-3} \\ \delta s_{n-4} \\ \delta p_n \end{pmatrix} \quad (4)$$

with positive parameters $m_s, m_p, a, b, c, \varepsilon_1$. The general structure of the matrix in Eq. (4) is determined only by the matching conditions and is valid for any time-continuous model applied during the seasons. The equations of motion of the latter only determine the numerical values of the parameters in Eq. (4).

The first line of the matrix describes the influence on the sockeye fry of year $n+1$ of the sockeye fry of year $(n-3)$ and $(n-4)$ (which are the parents of the fry in year $(n+1)$), and of the predator population. m_s and ε_1 are positive, since more parents imply more offspring. $-a$ is negative, since more predators imply less fry. The other nontrivial line of this matrix, the last line, describes the influence on the predators of year $(n+1)$ of the sockeye fry of year $(n-3)$ and $(n-4)$ (which are the parents of the predator's food), and of the predator population in the previous year. All three parameters are positive, since more food implies more predator growth and since more predators in one year give rise to more predators in the next year.

The eigenvalues of this matrix determine the nature of the dynamics near the bifurcation. When all eigenvalues have an absolute value smaller than 1, the fixed point is stable, and the dynamics converges to this fixed point. When the absolute value of one or more eigenvalues is larger than 1, the fixed point is unstable, and the dynamics approaches a different attractor.

In order to understand the dynamics resulting from this matrix, we first consider the case that the matrix elements ε_1 , b , and c vanish. This means that all salmon return at age 4, and that the trout have a good choice of other food so that their dynamics is independent of that of the salmon fry. In this case the eigenvalues of the matrix are m_p , 0, and the four fourth roots of m_s . Since the four salmon lines are independent from each other in this case, the sequence δs_n has trivially the period 4 and simply iterates the initial four values, with an amplitude decreasing for $m_s < 1$ and increasing otherwise (and with the trout being independent of the salmon). When m_s is increased from a value smaller than 1 to a value larger than 1, all four eigenvalues $m_s^{1/4}$ cross the unit circle simultaneously, and the fixed point becomes unstable. This degeneracy is lifted when the parameters ε_1 , b , and c are made nonzero. As long as these parameters are not large, one can expect the four main eigenvalues to remain close to the real and imaginary axis, respectively, implying a (possibly damped) oscillation with a period close to 4.

The type of bifurcation that occurs when the fixed point becomes unstable depends on which eigenvalue crosses first the unit circle as a control parameter is increased. In order to determine the type of the bifurcation, we evaluated the parameters of the matrix numerically from our computer simulations of the time continuous model when going through the bifurcation (i.e., when K_0 increases from 6.4 to 7.5), and we calculated the eigenvalues λ of the matrix. Fig. 4 shows that the bifurcation is caused by a pair of complex conjugate eigenvalues crossing the unit circle, indicating a Neimark Sacker bifurcation (the discrete version of the Hopf bifurcation). Since the dominant eigenvalues

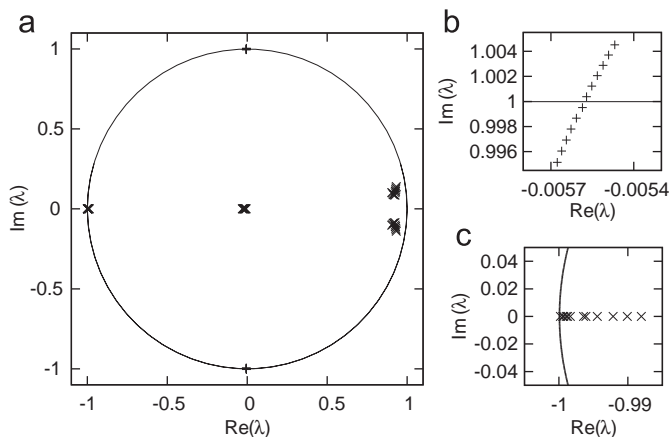


Fig. 4. Eigenvalues of the matrix from Eq. (4), as obtained from a linear stability analysis of the time-continuous model. K_0 increases from 6.4 to 7.5 as the eigenvalues move outwards. The zoom shows that the eigenvalues close to the imaginary axis (+) are the first ones to cross the unit cycle.

(depicted with the symbol +) are close to $\pm i$, the period of the resulting oscillation is close to 4. In the linear, time discrete model (Eq. (4)), the bifurcation is mainly driven by the parameters m_s and, to a minor extent, a , which correspond to reproduction of the four-year old sockeyes and predation by the rainbow trouts, respectively. The fixed point becomes unstable when either of these parameters increases.

Now, it is known from the theory of bifurcations that if the period at such a bifurcation is close to 4, there occurs a strong resonance, which means that the period becomes locked exactly at the value 4 not far beyond the bifurcation point. In contrast to conventional mode locking that gives rise to Arnold tongues, a strong resonance is due to nonlinearities that are of the same order as the leading nonlinearity (which ensures the stability of the quasiperiodic orbit in the first place), and frequency locking therefore occurs over a much wider range of parameters (Kuznetsov, 2004).

The two complex conjugate eigenvalues are the first ones to cross the unit circle when a and ε_1 are small non-negative numbers and when m_p is well below 1. Since ε_1 , b , and c are small compared to m_s , the period of the resulting oscillation remains close to 4, and the locking at period 4 therefore occurs not far beyond the bifurcation. When these conditions are not met, the unit circle is typically first crossed at -1 , and a period-doubling (or *flip*) bifurcation occurs.

4. Discussion

The four-year oscillations of sockeye salmon in the Fraser River are a typical example of single-generation cycles (as opposed to predator–prey cycles, Gurney and Nisbet, 1985), a phenomenon that has also been extensively studied in the context of, e.g., host–parasitoid (Godfray and Hassell, 1989) or daphnia–zooplankton (de Roos et al., 1990) systems. In the latter case, individuals of different age or size of a consumer species directly compete with each other for a resource, while the biological situation in the present study is somewhat different: The salmon fry of different brood lines do not compete with one another directly, since they populate the rearing lakes at distinct, non-overlapping times. The interaction between the brood lines is mediated by the long-living predators, which have a net effect on the salmon that is similar to competition (apparent competition). In contrast to other models that produce single-generation cycles, the cycle

period 4 observed in our system is not identical to the mean generation time, which is larger than four years, and not all salmon mature and reproduce at the same age. The locking of the period at 4 is due to a strong resonance, a phenomenon which plays no role in the cited models.

The three-species model analysed in this study is in principle also capable of showing conventional predator–prey cycles. If the parameters were chosen such that the complex conjugate pair of eigenvalues of the matrix in Eq. (4) that is close to the real axis at $+1$ is the first to cross the unit circle, oscillations with a period much larger than four years occur and the year-to-year variation between brood lines is rather small (results not shown). However, this type of oscillations is not seen in the sockeye populations rearing in the Fraser River basin.

The considerations in the previous section lead to two basic conditions under which strong resonance and thus period-four generation cycles can be observed: First, an increase in the number of spawning salmon must lead to a sufficiently strong increase in this number four years later (i.e. m_s must be large enough). If the number of fry migrating to the ocean is dominated by other factors, such as a strongly limited carrying capacity for the fry, the population will be at a fixed point rather than on the oscillating side of the bifurcation. Second, the four salmon lines must be coupled in order for the Neimark Sacker bifurcation to occur, rather than a period doubling bifurcation. In our model, this coupling is due to a fraction of sockeye returning at age 5 instead of age 4, and, more importantly, due to the predator being sufficiently strongly coupled to sockeye dynamics.

Previous studies of salmon dynamics, used in salmon management, are based on the Ricker model (Ricker, 1950; Hume et al., 1996) or the Larkin model (Larkin, 1971; Martell et al., 2008; Marsden et al., 2009). Because both models have a strongly limited carrying capacity for the fry, and because they do not include explicitly the predator dynamics, the only bifurcation occurring in those models is the flip bifurcation. Building on both modelling approaches, Myers et al. (1998) have demonstrated that an unstable (decaying) period-4 oscillation can be excited by stochastic driving. However, it remains unclear over how long the oscillations can be maintained in that study without a change in the phase. Furthermore, that stochastic model produces only episodically the typical sequence of a dominant, a subdominant and two weak years described in Section 2 and seen in our simulations, Fig. 2).

In principle, the coupling between the four salmon lines can also occur through the food of the sockeye fry. However, there is no empirical evidence that there is a negative effect of a strong sockeye year on the daphnia population in the following year that limits the growth of the sockeye fry in that year (Levy and Wood, 1992).

The two conditions for a strong resonance of period 4 fit together with the empirical observation that it occurs only in large oligotrophic lakes, such as those of the Fraser River basin. The smaller and ultra-oligotrophic lakes in the outer coast regions of British Columbia do not show these oscillations. Their nutrient content is neither large enough to raise large fry numbers, nor to allow for salmon predators to become strong. On the other hand, cyclic dominance cannot be expected in nutrient-rich lakes, because the spawning adults would not be an important nutrient input, and because the coupling to the predator would not be strong enough in a situation where there were more predator species and more prey species for these predators.

Since there are large fluctuations in the proportion of fry that survive to return to their nursery lake, we included noise in the matching condition for the sockeyes, Eq. (2), in order to determine with how much noise superimposed on the deterministic dynamics the period-4 oscillation can persist. Fig. 2b shows a

data series generated with 50 percent noise in ocean survivability superimposed to the deterministic dynamics. The oscillation is still clearly visible, although the system has a phase shift every 300 years on average. With less noise, the phase shift occurs less often, and with 100 percent noise, the cyclic dominance vanishes in our simulations. When a large perturbation acts only for a limited time, the oscillation quickly recovers afterwards. In fact, the recovery following the blocking of the Fraser River migration routes early in the last century, can be seen in the non-dominant brood lines of the Shuswap stock in Fig. 1 and in the data of some of the stocks presented in the Appendix. Unfortunately, the year 2009 has seen another large perturbation, with most Fraser sockeye expected to return that year not surviving in the ocean, so that the expected strong escapement did not occur.

The age composition of sockeye stocks was also found to strongly influence the potential of the system to show a strong resonance. The fraction of adult sockeyes that returns at the age of five years instead of four years, ε , was set to 0.1 in the simulations and we could show that the resonance appears for $0 < \varepsilon \leq 0.3$, but for very small values of ε (< 0.02) the non-dominant lines disappear completely with increasing K_0 . The resonance condition was best met at $\varepsilon \approx 0.2$, where the resonance occurred nearly directly after the Neimark Sacker bifurcation. The parameter ε is also measured in the real populations (Healey, 1987). For the sockeye salmon populations of the Fraser River it is approximately 0.08, while for the less productive outer coast lakes of British Columbia (where cyclic dominance is not observed) it is between 0.56 and 0.76.

Some of the sockeye populations of the Bristol Bay area (Alaska), most notably the Kvichak River stocks, also exhibit strong oscillations (Fair, 2003; Rogers and Schindler, 2008) despite a broader distribution of the age at spawning than in

the Fraser River stocks (West and Fair, 2006; West et al., 2009). However, the oscillations are not as regular, with maxima of the populations occurring every fourth or fifth year. This is consistent with our model, as it indicates a quasiperiodic oscillation rather than a fixed oscillation period associated with a strong resonance.

Our results do not rule out additional mechanisms such as compensatory fishing (Walters and Staley, 1987) or genetic effects (Walters and Woodey, 1992), which would reduce the population sizes of weak lines to values smaller than those resulting from our model. However, these additional assumptions are not needed to explain the occurrence of cyclic dominance in the first place.

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Appendix A. Escapement data for sockeye stocks showing cyclic dominance

Many spawning stocks of sockeye salmon in the upper Fraser River basin are not stationary but have been dramatically increasing in size over the last decades (e.g. Fig. A1a, b, and d), following

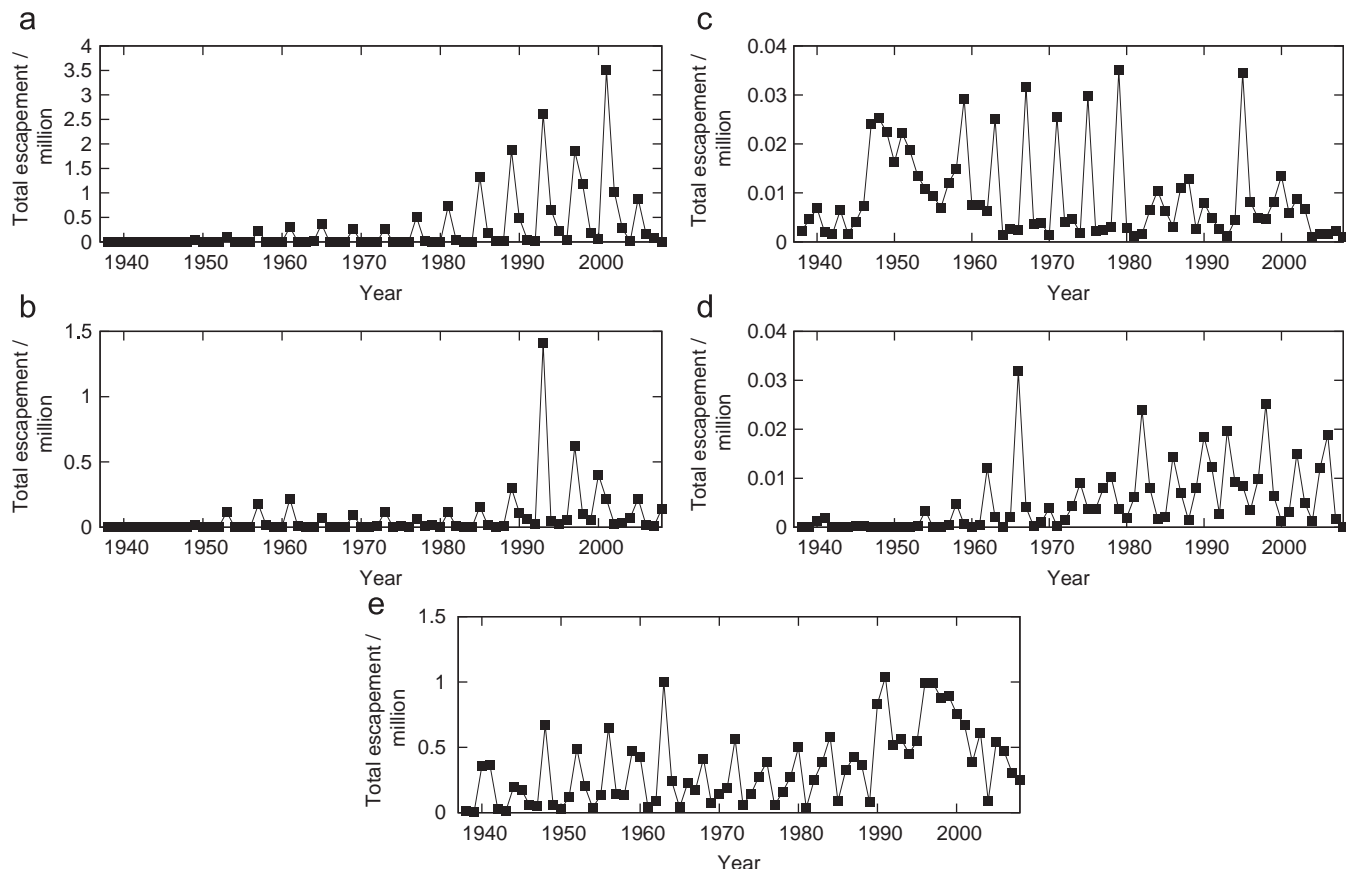


Fig. A1. Escapement data of for sockeye spawning stocks in the Fraser River basin. (a) Quesnel Lake, (b) Stuart Lake, (c) Bowron Lake, (d) Seton Lake, (e) Chilko Lake.

a massive disturbance of the stocks at the beginning of the 20th century. Nevertheless, the oscillatory pattern has clearly emerged again.

In some stocks (most notably the Bowron Lake stock, Fig. A1c), cyclic dominance is observed only episodically. This dynamical pattern may appear when the system is close to the bifurcation point.

The sockeye salmon stock of Seton Lake (Fig. A1e) also displayed cyclic dominance, but for nearly two decades (five cycles), the dominant line is followed by the weakest line instead of the sub-dominant line. In this stock, cyclic dominance broke down in the early 1990s.

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