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Effect of introducing a competitor on cyclic dominance of sockeye salmon

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HIGHLIGHTS

- A competing fish species is added to a model of sockeye salmon population dynamics.
- This enables competition for food and apparent competition mediated by a predator.
- Coexistence is not generic, apparent competition shapes the dynamics.
- Cyclic dominance or survival of competitors in large numbers may be transient.

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ABSTRACT

We study the effects of introducing a competing species into a 3-species model for the population dynamics of sockeye salmon, thereby converting a food chain into a diamond module. We find that this often leads to the disappearance of the 4-year oscillation of sockeye salmon known as cyclic dominance when parameters are chosen such that all four species can coexist. Only when the population size of the competitor is small the phenomenon of cyclic dominance can persist. There is also a large region of parameter space where either the sockeye salmon or the competitor goes extinct. We discuss how these findings can be reconciled with the prevalence of cyclic dominance in many sockeye brood lakes.

1. Introduction

Food webs usually comprise many species and interactions (Dunne, 2006). This makes it difficult to clearly identify what is causing an observed effect in an ecosystem. One way to deal with this complexity, both in experiments and in theory, is to simplify the web by selectively removing species, leaving only those with the strongest interactions. This simplification is however not without risk: weak links that complement a few strong interactions are known to stabilize food webs by dampening oscillations or by reducing their amplitude (McCann, 2000; McCann et al., 1998).

Two often studied food web structures are the three-species food chain and the four-species diamond (apparent competition) motif, which consists of two intermediate consumers that feed on a resource and are eaten by a top predator (Bascompte and Melian, 2005; Holt, 1997). The diamond motif is a particularly important food web motif, since most consumers in nature share resources and predators with other consumers (Williams and Martinez, 2000). The importance of such motifs for biological networks in general is emphasized by Milo et al. (2002), and their wide occurrence and stabilizing effect are also emphasized by Rip et al. (2010).

Already a two-species predator–prey system can show stable fixed points or exhibit persistent oscillations, depending on the strength of the coupling between the two species or the productivity of the prey (Rosenzweig and MacArthur, 1963b). A three-species food chain can therefore be interpreted as a system of two coupled oscillators, with each of the two predator–prey pairs being viewed as one (potential) oscillator (McCann et al., 1998). If both predator–prey couplings in the food chain are sufficiently strong, oscillations in the full food chain can occur. Due to the connection of two oscillating sub-systems, the dynamics of the full food chain can be more complex than that of the predator–prey

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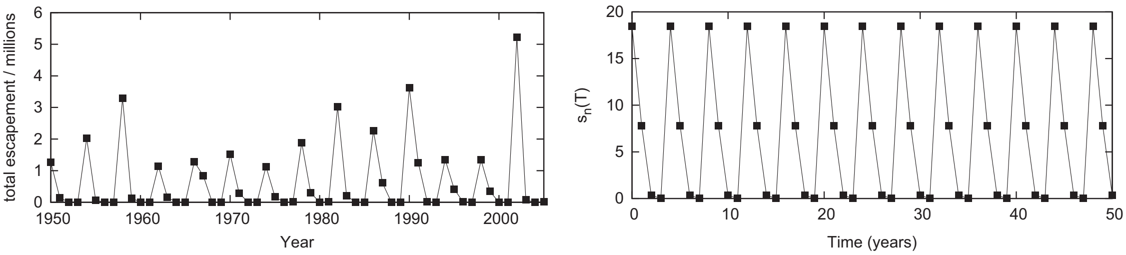

Fig. 1. Time series of measured and simulated sockeye salmon abundance. The left plot shows the number of sockeyes that was migrating to spawn in tributaries of Shuswap lake in British Columbia, Canada, and not caught by fisheries. The right plot shows simulated biomass density at the end of each year, using the 3-species food-chain model this paper builds upon. The parameters are the same as used in the extended 4-species diamond model (see Section 2), but the predator only consumes sockeye and the competitor has a biomass density of 0.

pairs in separation: aside from regular periodic oscillations, quasiperiodic oscillations and even chaos can occur (McCann and Yodzis, 1994).

Compared to the three-species chain, the diamond motif has one additional species and two additional links, which means that there are two additional potentially oscillating subsystems. Depending on the link strength, this can either stabilize or destabilize the system (McCann et al., 1998). Either way the dynamics of the diamond motif can be fundamentally different from those of a food chain.

In this paper, we study a special version of the above-mentioned two motifs by examining the effects of introducing a competitor (diamond motif) into a 3 species food chain model for sockeye salmon (*Oncorhynchus nerka*) population dynamics (Guill et al., 2011). The model is designed to reproduce the four-year oscillations observed in some of the large sockeye populations of the Fraser river basin in British Columbia, Canada (cf. Fig. 1).

The observed single generation cycles, known as cyclic dominance (Ricker, 1950; Townsend, 1989; Ricker, 1997), are remarkable because of their high regularity, the extreme amplitude (in dominant years, the abundance of sockeye spawners is usually more than a 100 times larger than in the weakest year of a cycle), and the period that is shorter than the mean generation time of the sockeye salmon. The latter characteristic is unusual for an oscillation that is driven by the interaction of a predator and a prey (Murdoch et al., 2002).

Sockeye salmon are semelparous in that they reproduce only once in their lifetime, and typically spawn in the stream or lake they hatched in. The majority of the fish spawn in late summer or autumn four years after their parents spawned, with a small fraction spawning one year later. After hatching, the sockeye fry migrate down streams to large nursery lakes where they rear for one year before migrating to the ocean. In the nursery lakes the salmon fry feed on zooplankton and are preyed upon by large piscivorous predators, e.g. rainbow trout.

The model by Guill et al. (2011) implements these life-cycle features in a three-species model for the population dynamics in the nursery lakes, resulting in a pronounced four-year oscillation over a broad range of parameter values (cf. Fig. 1). The predator grows in the dominant sockeye year, and during the weak years keeps the few sockeye fry down while losing biomass again. In the next dominant year the numerous fry find favorable growth conditions due to a weakened predator.

The basic assumptions leading to these single-generation cycles in the model are that the process responsible for the oscillation takes place in the nursery lakes and not in the ocean and that it is driven by predator–prey dynamics. These assumptions, although they cannot be proven, appear reasonable since stocks from different streams are not synchronized (which would be expected if the density-dependent process did take place in the ocean), and because a pronounced oscillation requires a strong negative coupling between different salmon lines, which can most easily be achieved via a predator.

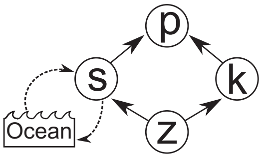

Fig. 2. Schematic representation of the diamond motif model. Solid arrows represent predator–prey relations, dashed arrows represent the salmon migration. The interactions are specified in Eqs. (1) and (3), and the letters correspond to the ones used in those equations: s = sockeye, p = predator, k = competitor, z = zooplankton.

In contrast to the model, the nursery lakes contain more species than the predator (e.g. rainbow trout) and the resource (mainly zooplankton) of sockeye fry. In particular, there exist other fish species that serve as food for the predator of sockeye fry, and that compete with sockeye fry for zooplankton food. Such a competitor might for example be kokanee salmon (a smaller, landlocked subspecies of sockeye salmon) or whitefish (Sebastian et al., 2003). By introducing the competitor we replace a 3-species food-chain motif – a zooplankton resource, sockeye fry, and their predator – with a 4-species diamond motif, depicted in Fig. 2. However, due to the discrete reproduction of the sockeye salmon and their migratory life style, they are invulnerable to the predator in the nursery lake for the majority of their life, so that the diamond motif discussed here differs in several ways from that usually discussed in the literature. We therefore focus our analysis on the question of whether or not cyclic dominance is broken down by the introduction of the competitor or if the special life cycle characteristics of sockeye salmon allow for coexistence of the competing species and persistence of the population oscillations.

2. Model

The model with a competing fish species is a straightforward extension of the previously mentioned three-species model (Guill et al., 2011). Population dynamics in the nursery lake during each year from spring to fall are modeled continuously in time with ordinary differential equations, while migration, ocean survival and spawning of the sockeye salmon are modeled by a discrete update step.

Population sizes are described by dimensionless biomass densities z_n for the zooplankton, s_n for the sockeye, p_n for the top predator and k_n for the competing fish, with n counting the years. Dynamics in the nursery lake are modeled by the following set of ordinary differential equations, which are of a form that is widely used in food web modeling (McCann et al., 1998):

$$\frac{d}{dt}z_n = rz_n \cdot \left(1-\frac{z_n}{K_n}\right) - f_{sz}(s_n, z_n) \cdot s_n - f_{kz}(k_n, z_n) \cdot k_n$$

$$\frac{d}{dt}s_n = \lambda \cdot f_{sz}(s_n, z_n) \cdot s_n - f_{ps}(p_n, s_n, k_n) \cdot p_n - d_s \cdot s_n$$