



Contents lists available at ScienceDirect

## Journal of Theoretical Biology

journal homepage: [www.elsevier.com/locate/yjtbi](http://www.elsevier.com/locate/yjtbi)

## Four types of interference competition and their impacts on the ecology and evolution of size-structured populations and communities

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### HIGHLIGHTS

- Interference competition can positively affect abundance of adult individuals and the population's reproduction rate.
- The evolutionary response to foraging interference and metabolic interference is smaller maturation size at low to intermediate interference intensity and larger maturation size at high interference intensity. The evolutionary response to survival interference and reproductive interference is always larger maturation size.
- All four types of interference competition can induce disruptive selection and thus promote initial diversification.
- Foraging interference and reproductive interference catalyze the formation of diverse communities with complex trophic structure only at high levels of interference intensity, while survival interference does so already at intermediate levels. Reproductive interference can only support relatively smaller communities with simpler trophic structure.

### ARTICLE INFO

#### Article history:

Received 8 August 2014

Received in revised form

5 May 2015

Accepted 15 May 2015

#### Keywords:

Adaptive dynamics

Biodiversity

Evolutionary branching

Food webs

Size structured populations

### ABSTRACT

We investigate how four types of interference competition – which alternatively affect foraging, metabolism, survival, and reproduction – impact the ecology and evolution of size-structured populations. Even though all four types of interference competition reduce population biomass, interference competition at intermediate intensity sometimes significantly increases the abundance of adult individuals and the population's reproduction rate. We find that foraging and metabolic interference evolutionarily favor smaller maturation size when interference is weak and larger maturation size when interference is strong. The evolutionary response to survival interference and reproductive interference is always larger maturation size. We also investigate how the four types of interference competition impact the evolutionary dynamics and resultant diversity and trophic structure of size-structured communities. Like other types of trait-mediated competition, all four types of interference competition can induce disruptive selection and thus promote initial diversification. Even though foraging interference and reproductive interference are more potent in promoting initial diversification, they catalyze the formation of diverse communities with complex trophic structure only at high levels of interference intensity. By contrast, survival interference does so already at intermediate levels, while reproductive interference can only support relatively smaller communities with simpler trophic structure. Taken together, our results show how the type and intensity of interference competition jointly affect coexistence patterns in structured population models.

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<http://dx.doi.org/10.1016/j.jtbi.2015.05.023>

0022-5193/© 2015 Published by Elsevier Ltd.

## 1. Introduction

An important aspect of individual life history that has received comparatively little attention is the interference that takes place between individuals when they compete for resources. Interference competition is hypothesized to be a major force driving natural selection (Rosenzweig, 1978; Dieckmann et al., 2004; Bolnick, 2004). This belief is reinforced by recent theoretical studies on the evolutionary emergence of food webs (e.g., Caldarelli et al., 1998; Drossel et al., 2001; McKane, 2004; Loeuille and Loreau, 2005; Rossberg et al., 2008; Brännström et al., 2011, 2012), which demonstrate that interference competition can promote species diversity. These studies canonically assume that interference competition elevates individual mortality, but elevated mortality is in fact only one of several possible outcomes.

Interference competition in general exerts negative effects on individuals (Miller, 1967; Goss-Custard, 1980; Smallegange et al., 2006), through injury (Briffa and Sneddon, 2007), loss of energy, foraging time (Briffa and Sneddon, 2007; Stillman et al., 1997), a reduction in food intake rate or in effective fecundity (Vahl et al., 2005). The outcome of interference competition may be any combination of (i) reduced foraging rate (e.g., due to reduced searching time), (ii) increased metabolic requirements (e.g., by interference activities), (iii) reduced survival rate (e.g., through fierce contests), and (iv) reduced reproduction rate (e.g., predation on egg or larvae). Foraging interference and metabolic interference directly affects individual physiology while survival and reproduction interference directly affect population demographic quantities.

The four different types of interference competition are indistinguishable in unstructured population models, such as those used in several recent studies on food-web evolution (e.g., Loeuille and Loreau, 2005; Rossberg et al., 2008; Brännström et al., 2011). This is because interference competition in unstructured population models can essentially only be incorporated as a reduction of the per-capita growth rate which mathematically is equivalent to an increase in mortality. Any inherent differences between the four different types of interference competition considered here can thus only become apparent in physiologically structured population models that incorporate ontogenetic development of individuals from juvenile to adult (de Roos and Persson, 2013). As the widespread use and legacy of unstructured population models have favored a tradition in which interference competition is represented as increased mortality, little is currently known about how interference competition acting on other ecological processes impacts the ecology and evolution of size-structured populations and communities.

In this paper, we investigate how the aforementioned four types of interference competition affect the ecological and evolutionary dynamics of size-structured populations and communities. We base our investigation on a recently developed modeling framework for fish populations. First, we introduce the size-structured population model that we use in our investigation and phenomenologically model the four types of interference competition at the individual level. We then explore the effects of interference competition on the demography and evolution of a single population. After we have elucidated the effects on a single population, we consider the impact of interference competition on the diversity and trophic structure of evolved communities. Finally, we conclude with a discussion in which we recapitulate our main findings, aim to place them in a broader context, and identify promising directions for future research.

## 2. Methods

The size-structured population model used in this paper builds on the framework for aquatic food webs of fish populations by

Hartvig et al. (2011) in which well-mixed individuals share a common habitat (Section 2.1 and Appendix A). Individuals can interfere with each in any of four qualitatively different ways, with the strength of interference in each case depending on the individuals' body size and maturation size (Section 2.2 and Appendix A). While the body size changes through the life time of an individual, the maturation size is assumed to be an evolving trait which is faithfully inherited from parents to offspring except for rare and small mutations at birth (Section 2.3). As our model is not concerned with reproductive isolation, we use the term ecotype rather than species for a population of individuals with the same maturation size. We characterize the ecotype by maturation size which is generally recognized as one of the most important life history characteristics in fish populations (Charnov et al., 2012), because it determines how energy is allocated between growth and reproduction. More specifically, the allocation to reproduction per unit body-mass after maturation is (for constant food abundance) approximately proportional to maturation size raised to the power  $-1/4$ .

### 2.1. Size-structured population model

We briefly outline the size-structured population model below and refer to Appendix A for a more detailed description including model equations (Table A1) and parameters (Table A2). We consider a large number of individuals characterized by their body size  $w$  which each belong to any of several ecotypes. An ecotype  $i$  is characterized by the maturation size  $m_i$ . Individuals grow in size, reproduce, and die at rates that depend on their size, availability of resources, and antagonistic interference with other individuals. The growth rate ( $g(w, m_i)$ , Eq. M8 in Table A1) is food dependent and determined from size-based predation on both resource and consumer individuals, following the principle of "big-eat-small" (Ursin, 1973). This principle allows for within-population predation (cannibalism) which is a ubiquitous phenomenon in fish populations (Fox, 1975; Polis, 1981; Smith and Reay, 1991; Elgar and Crespi, 1992). The rate at which predators encounter prey depends on the volume that the predator can search in one unit of time. Following an established allometric relationship, this volume scales with predator body size (Appendix A). Individuals can die as a result of predation by larger individuals (Eq. M10 in Table A1), background mortality, or starvation mortality (Eq. M11 in Table A1), which together combine to give an individual mortality rate  $\mu(w, m_i)$ . Finally, mature individuals produce offspring at a food- and size-dependent rate  $b(w, m_i)$  (Eq. M9 in Table A1).

Building on the individual-level processes described above, the demographic dynamics of ecotype  $i$  are described by the following equations (McKendrick, 1926; von Foerster, 1959; de Roos, 1997),

$$\frac{\partial}{\partial t} N_i(w, t) + \frac{\partial}{\partial w} (g(w, m_i) N_i(w, t)) = \mu(w, m_i) N_i(w, t), \quad (1a)$$

$$g(w_0, m_i) N_i(w_0, t) = \frac{\epsilon}{2w_0} \int_{w_0}^{M_i} b(w, m_i) N_i(w, t) dw. \quad (1b)$$

Here,  $N_i(w, t)$  is the size spectrum of ecotype  $i$  at time  $t$ , and  $M_i = m_i/\eta$  is the maximally attainable size of ecotype  $i$ , where  $\eta$  is the ratio of maturation size to maximum size. Eq. (1a) describes how the size spectrums of the ecotype changes over time as a consequence of individual growth and mortality. Newborn individuals enter the populations through the boundary condition, Eq. (1b), in which the constituent elements can be understood as follows: Offspring of size  $w_0$  are produced by adults at a size-dependent birth rate  $b(w, m_i)$  and survive the larvae stage with probability  $\epsilon$ . The fraction  $1/2$  reflects an assumed equal sex ratio.

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