Theoretical Population Biology 92 (2014) 55–61

Contents lists available at ScienceDirect

Theoretical Population Biology

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

Facilitation of intraguild prey by its intraguild predator in a three-species Lotka–Volterra model

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ARTICLE INFO

Article history:
Received 9 April 2012
Available online 8 December 2013

Keywords:
Intraguild predation
Immobilization
Multiple resource phenotypes
Stable coexistence
Marine microzooplankton

ABSTRACT

Explaining the coexistence of multiple species in the competition and predation theatre has proven a great challenge. Traditional intraguild predation (IGP) models have only relatively small regions of stable coexistence of all species. Here, we investigate potential additional mechanisms that extend these regions of stable coexistence. We used a 3-species Lotka–Volterra system to which we added an interaction term to model a unidirectional facilitative relationship between the two predators in the IGP. In this modelling study the IG predator was able to precondition a part of the common resource by an instantaneous manipulation, which resulted in the immobilization of the resource species. This mechanism of immobilization facilitated the resource uptake by the IG prey and thus increased its growth rates even in the presence of the common predator. The facilitative relationship of the IG prey by the IG predator produced a stable coexistence of both predators even though the IG prey was an inferior competitor for a common resource, which cannot be attained with the traditional IGP models. Furthermore, our model predicted a 3-species stable coexistence even at high enrichment where no coexistence was found in the basic IGP model. Thus, we showed that diversity of resource traits could significantly alter emergent community patterns via shifts in exploitative competition of IGP-related predators. The described mechanism could potentially lead to a higher efficiency in exploitation of common resources and thus promote higher diversity in a real community.

1. Introduction

One of the large dilemmas in population and community ecology is the seemingly stable coexistence of many more species than predicted by theoretical studies. In particular, systems with intraguild predation have attracted a lot of attention (Polis and Holt, 1992; Rosenheim et al., 1993; Křivan, 1996; Křivan and Diehl, 2005; Finke and Denno, 2002; Woodward et al., 2005; Janssen et al., 2007; Amarasekare, 2007; Namba et al., 2008), with a main focus on those regions in the parameter space that allow the coexistence of two predators involved in intraguild predation (IGP). In short, in a food web with IGP, one player (IG predator) is both predator and competitor of another player (IG prey), both of which predate on a common prey (resource) (Polis et al., 1989).

In general, the mathematical theory of 3-species IGP systems (Polis and Holt, 1992; Holt and Polis, 1997; Abrams and Roth, 1994a,b; Abrams and Fung, 2010) has clearly shown the exclusion of intermediate trophic levels at high resource levels (and hence high carrying capacities) (Diehl and Feißel, 2001) whereas coexistence is possible only at lower resource levels combined with superior competitive abilities of the IG prey for the communal resource (Stoecker and Evans, 1985; Holt and Polis, 1997; Diehl and Feißel, 2001). Even though some experimental and observational evidence exists supporting the theoretical premises for coexistence, the wealth of empirical data suggests a widely spread persistence of IGP systems in both terrestrial (Brodeur and Rosenheim, 2000; Arim and Marquet, 2004) and aquatic communities (Polis et al., 1989; Mylius et al., 2001; Borer et al., 2003; Denno and Fagan, 2003), and hence a more robust theoretical framework is needed to explain this coexistence.

To include the effect of increasing diversity of the common resource on population dynamics in IGP systems recently the 3-species IGP model (Holt and Polis, 1997) was modified by Holt and Huxel (2007). The authors extended the basic 3-species model with omnivory (Holt and Polis, 1997) to a so-called "partial IGP" model in which "partial" overlap between competitors for a single resource existed, but both predators had exclusive other resources. In this model an alternative resource enhanced the tolerance of the IG prey against attacks from IG predators and also relaxed

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http://dx.doi.org/10.1016/j.tpb.2013.11.005

the competitive relationship among the IGP species. Independent of competitive ability of the IG prey in the exploitation of the shared resource the IG prey could persist by using the alternative resource. Likewise, in a modelling exercise Daugherty et al. (2007) extended the IGP model with trophic supplementation investigating three forms of a supplementary feeding outside of the basic IGP module. Not surprisingly, they postulated a higher potential for the persistence of the IG prey due to exploitation of external resources.

Furthermore, it has been argued that the destabilizing effect of enrichment on population persistence (Rosenzweig, 1971; May, 1987; Gilpin, 1972) could result from the specific model assumptions rather than from true behaviour observed in natural system (Gross et al., 2004). In theoretical deliberations this effect could be avoided by a different choice of functional response for the IG predator (Gross et al., 2004).

In many natural systems where IGP occurs the IG prey seems to have a mutualistic or at least facilitative relationship with the IG predator (Crowley and Cox, 2011). Contrary to the competitive exclusion principle in systems with competitors for a single resource, stability in IGP systems often stems from this commensalism (Hosack et al., 2009). Hereby one consumer alters the common resource and thus benefits the other. Theoretical studies on mutualistic positive interactions among competing species with a single limiting resource showed that these interactions could support multispecies coexistence (Gross, 2008). Recently, an IGP relation with facilitation between IG predator and IG prey was observed in experiments on a microzooplankton community (Löder et al., 2013). The authors showed that the IG predator preconditioned a substantial part of the common resource during its feeding attacks by immobilizing it without ingestion. Such preconditioned individuals were more vulnerable to predation by the IG prey than mobile individuals of the same resource species. Moreover it was observed that in the presence of IG predator the growth rate of IG prey was significantly higher than in the IG prey and resource treatment (Löder et al., 2013).

Here, we attempt to combine previous amendments to the classical IGP models, by, on the one hand, increasing the functional diversity of the common resource and, on the other hand improving on the interaction term in the model. We focused our modelling study on the IGP-related facilitative relationship that could be a part of naturally developed behaviour of micro-grazers. In particular, such a mechanism could facilitate microzooplanktons avoidance of predation pressure from higher trophic levels. To investigate the remarkable mutualistic relationship observed in the experiment of Löder et al. (2013) and also other possible interaction patterns in the system here we propose an extension of a basic IGP model (Holt and Polis, 1997; Diehl and Feißel, 2000). We show that the mutualistic relationship could be produced in the theoretical model by using the interaction term that depends on densities of IG predator and resource. Our main interest was to analyze whether the facilitative effect due to the immobilization mechanism (Löder et al., 2013) was sufficient to reduce the degree of competition between both consumer species thus potentially increasing the probability of coexistence of all three species.

This paper is organized as follows. In the first section we describe the experimental background (Löder et al., 2013) of the IGP system with immobilization. We then introduce the theoretical formulation of the IGP immobilization model. We provide a numerical stability analysis of the equilibrium densities for various food web configurations including cases with exclusion and coexistence of IG predator and IG prey, and examine the ranges of immobilization rates and enrichment at which permanent coexistence can be found.

2. Description of experimental system

The experimental background of the model was a three species microzooplankton IGP system (Löder et al., 2013). Two microzooplankton predators, a large heterotrophic ciliate and a small heterotrophic dinoflagellate, and their communal phototrophic dinoflagellate prey *Scrippsiella trochoidea* (∼20 μm length) were used. The smaller dinoflagellate predator *Gyrodinium dominans* (∼30 μm length) was also a potential prey item (IG prey) for the larger predator (IG predator), *Favella ehrenbergii* (∼160 μm length). All three species are typically found coexisting in the North Sea.

Using intensive live observations Löder et al. (2013) observed that F rejected a significant proportion $\sim 26 \pm 3\%$ of its S catch after initial contact. The rejected resource items were incapable of active movement. This caused a higher uptake of the common resource by the IG prey, allowing a higher growth rate of the IG prey in treatments with all three species present. Moreover, *G. dominans* demonstrated a strong selective behaviour towards immobilized species when offered in a mixture including mobile cells S_m. The selectivity behaviour was due to the high speed of escape shown by the mobile items as compared to the measured mean speed of IG prey. In fact, the ingestion rates of IG prey measured in the immobilized prey treatment were larger by a factor of 20 than the rates in the control treatment.

The main conclusion of the study by Löder et al. (2013) was that through the high selectivity of IG prey for immobile prey combined with the immobilization activity of the IG predator there should be scope for coexistence of these organisms in a much wider parameter space than previously believed according to the simple IGP models.

3. The IGP model with immobilization

To provide the theoretical background for the observed commensalistic relationship we introduced an omnivory model with an IGP unit derived from a simple non-spatial Lotka–Volterra system with the linear functional responses adapted from Holt and Polis (1997). We reformulated the 3-species IGP model proposed in Polis and Holt (1992), Holt and Polis (1997) and Diehl and Feißel (2000, 2001) by adding an immobilization term and thus creating two pools of resources.

The set of equations for the population densities is as follows:

$$\begin{aligned}
\frac{dS_m}{dt} &= [r(1 - S_m K^{-1}) - aG]S_m - fFS_m, \\
\frac{dS_i}{dt} &= cfFS_m - [bG + fF]S_i - m_{S_i}S_i, \\
\frac{dG}{dt} &= [a'aS_m + a'bS_i - gF - m_g]G, \\
\frac{dF}{dt} &= [f'fS_i + (1-c)f'fS_m + g'gG - m_f]F,
\end{aligned} \tag{1}$$

where the state variables S_m and S_i are the densities of mobile and immobilized species. The parameters of the model and populations are described in Table 1. The numerical values for the attack rates were chosen to be similar to the experimentally observed ones (Löder et al., 2013). Here r is the maximum specific growth rate of the resource population S_m, K is the carrying capacity of the resource defined as enrichment factor in the previous models (Diehl and Feißel, 2000, 2001). The density-independent mortality rates for G and F are defined as m_g and m_f correspondingly. They