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The coevolution of two phytoplankton species on a single resource: Allelopathy as a pseudo-mixotrophy

Shovonlal Roy

School of Mathematics, The University of Manchester, Alan Turing Building, Manchester M13 9PL, United Kingdom

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A B S T R A C T

Without the top-down effects and the external/physical forcing, a stable coexistence of two phytoplankton species under a single resource is impossible — a result well known from the principle of competitive exclusion. Here I demonstrate by analysis of a mathematical model that such a stable coexistence in a homogeneous media without any external factor would be possible, at least theoretically, provided (i) one of the two species is toxin producing thereby has an allelopathic effect on the other, and (ii) the allelopathic effect exceeds a critical level. The threshold level of allelopathy required for the coexistence has been derived analytically in terms of the parameters associated with the resource competition and the nutrient recycling. That the extra mortality of a competitor driven by allelopathy of a toxic species gives a positive feed back to the algal growth process through the recycling is explained. And that this positive feed back plays a pivotal role in reducing competition pressures and helping species succession in the two-species model is demonstrated. Based on these specific coexistence results, I introduce and explain theoretically the allelopathic effect of a toxic species as a 'pseudo-mixotrophy'—a mechanism of 'if you cannot beat them or eat them, just kill them by chemical weapons'. The impact of this mechanism of species succession by pseudo-mixotrophy in the form of alleopathy is discussed in the context of current understanding on straight mixotrophy and resource-species relationship among phytoplankton species.

1. Introduction

In aquatic systems the phytoplankton community evolves under the influence of numerous top-down and bottom-up effects, as well as that due to environmental fluctuations. The resultant of all these effects leads to an extreme diversity of phytoplankton species under a limited variety of resources (Hutchinson, 1961; review by Scheffer et al., 2003). It is generally accepted from the principle of competitive exclusion, that the number of species coexisting at equilibrium cannot exceed the number of limiting 'factors' (Hardin, 1960). In theoretical ecology, several mechanisms, based on resource partitioning, different forms of predation, biomass fluctuations and environmental factors, have been found for the coexistence of species (Chesson, 2000). In particular, for the phytoplankton community, since the resource-competition theories do not support a stable coexistence (Tilman, 1982), the extreme diversity of the species is generally understood through a non-equilibrium dynamics. Top down effects, resource fluctuation, complexity of species interaction and influence of physical forcing (such as mixing, advection) provide mechanisms for driving this non equilibrium—a detailed account of these mechanisms can be found in the reviews by Scheffer et al. (2003) and by Roy and Chattopadhyay (2007a). It is important to note that, without the top-down effects and the physical forces, none of the existing simple resource-competition models demonstrates a stable coexistence of two phytoplankton species under a single limiting resource.

In the context of functioning of aquatic systems, the release of chemical substances by the individuals of a species affecting the members of another species – known as allelopathy – has a significant role. Allelopathy has been reported in phytoplankton communities at least before three decades (e.g., Maestrini and Bonin, 1981; Mason et al., 1982). Since then there exists an accumulating evidence for the potential significance of allelopathy in phytoplankton interaction (Cembella, 2003; Hulot and Huisman, 2004; Solé et al., 2005). A number of laboratory experiments (Arzul et al., 1999; Graneli and Johansson, 2003; Fistarol et al., 2004; Schatz et al., 2005) as well as field studies (Rengefors and Legrand, 2001; Schagerl et al., 2002) have established that the toxic chemicals released by the group of toxin-producing phytoplankton (TPP) potentially act as allelopathic agents in the phytoplankton community. de Freitas and Fredrickson (1978) and Levin (1988) have introduced the effect of allelopathy in resource competition through mechanistic models. Moreover, several mechanistic models have been analyzed to understand

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E-mail address: shovonlal_roy@yahoo.com.

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the effect of inhibition, either from external or from internal sources (review, Hsu and Waltman, 2004). It has been shown mechanistically that toxin production might be helpful in some cases for coexistence: e.g., when the toxin production is a plasmid-encoded trait (Hsu and Waltman, 2004), or when toxin production is regulated in relation to competitor density, as might happen through quorum sensing mechanisms (Braselton and Waltman, 2001). Recent results suggest that, by modulating the top-down effects of grazer zooplankton, the inhibitory effects of TPP can drive the planktonic non-equilibrium (Roy et al., 2006). Further, the effects of such 'toxin-allelopathy' of a TPP, present as a third species, can successfully overturn the competitive exclusion of two non-toxic phytoplankton undergoing a Lotka–Volterra interaction (Roy and Chattopadhyay, 2007b). However, concentrating on purely resource-competition models, it is fair to say that the works so far have suggested that some 'particular' properties are required to make coexistence possible, and that even the simplest mechanistic models of allelopathy have a strong tendency to exclusion.

In microbial ecology, the mixotrophic species are known to have a complicated role in competitive interaction as well as in food-web interaction (Davidson, 1996). The species of mixotrophic algae are an important component of phytoplankton communities in natural waters (e.g., Wiedner and Nixdorf, 1998). By switching to phagotrophy these species can sustain their growth when they are mixed out of euphotic zone (Bird and Kalff, 1989). In conditions of low radiation, temperature, salinity, pH, and situations when algal species are unlikely to meet their carbon requirement for photosynthesis, the species are known to survive through mixotrophy (Hammer, 2003; Hammer and Pitchford, 2006). Thus, mixotrophy contributes to the coexistence algal species under limiting-resource conditions. However, recent studies have suggested that some algal species (e.g., *Prymnesium*) can be toxin producer as well as mixotrophic, and in such scenario they show a 'kill and eat' behavior (Tilmann, 2003). Although, toxin production has been recognized as a distinctive feature of many algal species, not many species has yet been identified as a two-in-one package of mixotrophy and allelopathy.

Based on the growing body of evidences on plankton allelopathy, and the increasing interest on the mixotrophic interaction, here I address the question as to whether the allelopathy alone can act a potential factor for the competitive coevolution of two phytoplankton under a single resource. If so, is there any theoretical connection between the effect of a pure allelopathy and the well known effect of mixotrophy on the survival or coexistence of microbial species. Further, is the coexistence dynamics driven by allelopathy is stable? And under this context, how does allelopathy of toxin producers contribute to the resource-species relationship, at least in an ideal situation where the top-down effects do not come into play? To address these issues, I developed and analyze a mathematical model describing the competition for a single nutrient between a non-toxic phytoplankton and a toxin-producing phytoplankton. The results are discussed in the contexts of understanding the key roles of allelopathy and their similarity with mixotrophy on competitive exclusion and phytoplankton diversity.

2. Nutrient competition model under allelopathy

Nutrient competition models of phytoplankton are well studied in several contexts. Starting from a well-known resource-competition model, I construct a mathematical model for describing the interaction between a non-toxic (species 1 with biomass $P_1(t)$) and a toxic phytoplankton (species 2 with biomass $P_2(t)$) under a single nutrient (with concentration $N(t)$). The structure of the model without the effect of allelopathy is similar to that of a standard resource competition model used by many authors (such as Huisman and Weissing, 1999). Species 2 being toxic, the competitive interaction of the two species is affected significantly by its allelopathic ability.

The characteristic and the mode of action of the allelopathic chemicals in marine ecosystems is generally poorly understood and is still under investigation (Cembella, 2003). In general the presence of external and internal inhibition has been explored in a number of mathematical models, and the representations of the inhibitory effects have been taken both explicitly and implicitly (review, Hsu and Waltman, 2004). Based on the studies conducted previously, it is fair to say that there is no universally accepted formulation of the functional form for describing the allelopathic effect of one algae on another (Solé et al., 2005; Hammer and Pitchford, 2006). The complexity of allelopathic effect is generally studied using some nonlinear function, either directly affecting the growth rate or generating an extra mortality to the target species (e.g., Grover, 1997; Hsu and Waltman, 2004; Hammer and Pitchford, 2006). Maynard-Smith (1974) has proposed theoretically an implicit representation of the allelopathic effect by introducing a nonlinear term in a two species competition model. The non-linear allelopathic term is proportional to the product of the concentration of the toxic species and the square of the concentration of the target species (Maynard-Smith, 1974). However, only very few studies (e.g., Uchida et al., 1999) have directly implemented the theoretical representations of plankton allelopathy to either an experimental or a field data. The experimental data of several phytoplankton species conducted by Schmidt and Hansen (2001) has been used by Solé et al. (2005) to validate the allelopathic function proposed by Maynard-Smith (1974). In general this function gives a reasonable qualitative agreement with the experimental data, expect for low concentration of toxic species during the pre-proliferation states (Solé et al., 2005). This limitation of the Maynard-Smith (1974) function has been overcome by introducing a quadratic term for the concentration of both toxic and non-toxic species (Solé et al., 2005). Following these studies, for developing the present model I employ an implicit allelopathic effect (such as Hammer and Pitchford, 2006), and describe it by the modified Maynard-Smith (1974) function developed by Solé et al. (2005).

Therefore, the time evolution of the biomass of a non-toxic and a toxic phytoplankton competing for a single nutrient can be represented as follows:

$$\begin{aligned}\frac{dN}{dt} &= \text{net nutrient input} - \text{uptake by species 1}\\ &\quad - \text{uptake by species 2}\\ &= d\,(N_0 - N) - \frac{\mu_1 P_1 N}{K_1 + N} - \frac{\mu_2 P_2 N}{K_2 + N}\\ &\equiv \phi_0\,(N(t), P_1(t), P_2(t))\,, \end{aligned} \tag{1}$$

$$\begin{aligned}\frac{dP_1}{dt} &= \text{growth} - \text{loss} - \text{loss due to toxin-allelopathy},\\ &= \frac{\mu_1 P_1 N}{K_1 + N} - m_1 P_1 - \gamma P_1^2 P_2^2\\ &\equiv \phi_1\,(N(t), P_1(t), P_2(t))\,, \end{aligned} \tag{2}$$

$$\begin{aligned}\frac{dP_2}{dt} &= \text{growth} - \text{loss}\\ &= \frac{\mu_2 P_2 N}{K_2 + N} - m_2 P_2\\ &\equiv \phi_2\,(N(t), P_1(t), P_2(t))\,. \end{aligned} \tag{3}$$

A description of the model parameters with their units and a possible range of magnitudes considered for the analysis is given in Table 1.