Long time dynamics of a three-species food chain model with Allee effect in the top predator

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ABSTRACT

The Allee effect is an important phenomenon in population biology characterized by positive density dependence, that is a positive correlation between population density and individual fitness. However, the effect is not well studied in multi-level trophic food chains. We consider a ratio dependent spatially explicit three species food chain model, where the top predator is subjected to a strong Allee effect. We show the existence of a global attractor for the model, that is upper semicontinuous in the Allee threshold parameter m. Next, we numerically investigate the decay rate to a target attractor, that is when $m = 0$, in terms of m. We find decay estimates that are $\mathcal{O}(m^\gamma)$, where γ is found explicitly. Furthermore, we prove various overexploitation theorems for the food chain model, showing that overexploitation has to be driven by the middle predator. In particular overexploitation is not possible without an Allee effect in place. We also uncover a rich class of Turing patterns in the model which depend significantly on the Allee threshold parameter m. Our results have potential applications to trophic cascade control, conservation efforts in food chains, as well as Allee mediated biological control.

1. Introduction

Interactions of predator and prey species are ubiquitous in spatial ecology. Therein a predator or a "hunting" organism, hunts down and attempts to kill a prey, in order to feed. Three species food chains are inherently more complex. They model situations where say two predators are competing for a single prey [1,2]. Spatially explicit models of such ecological interactions have been very well studied [3,1,4–6]. In most of these models, the prey is regulated or "inhibited" from growing to carrying capacity due to predation by the predator. Whereas loss in the predator is due to death or intraspecific competition. However, there are various other natural self regulating mechanisms in a population of predators (or prey). For instance, much research in two species models, has focused on one such mechanism: the so called Allee effect. However, less attention has been paid to this mechanism in the three species case. This effect, named after the ecologist Walter Clyde Allee, can occur whenever fitness of an individual in a small or sparse population, decreases as the population size or density does [7]. Since the pioneering work of Allee [8,9], Allee dynamics has been regarded as one of the central issues in the population and community ecology, and in conservation biology, and many works on the subject have appeared [10–14,10,15–17].

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The effect can be best understood by the following equation for a single species u,

$$\frac{du}{dt} = u(u - m)(1 - u/K), \tag{1}$$

essentially a modification to the logistic equation. Here $u(t)$ the state variable, represents the numbers of a certain species at a given time t, K is the carrying capacity of the environment that u resides in, and m is the Allee threshold, with $m < K$. A strong Allee effect occurs if $m > 0$, [18]. This essentially means that if u falls below the threshold population m, its growth rate is negative, and the species will go extinct [19]. Note, $u^* = 0$, K are stable fixed points for (1), and $u^* = m$ is unstable. Thus dynamically speaking the global attractor, which is the repository of all the long time dynamics of (1) is $[0, K]$. An interesting question can now be posed: what happens to this attractor as $m \to 0$? Ecologically speaking, this is asking: what happens to the species u as the Allee threshold m is decreased? When $m = 0$ the only stable fixed point is $u^* = K$, with $u^* = 0$ being half stable. Thus the global attractor is now reduced to a single point K. What we observe is that the difference between having a slight Allee effect (say $0 < m \ll 1$) and having no Allee effect ($m = 0$), can *change completely* what the global attractor of (1) is. That is to say, the global attractor changes from an entire set $[0, K]$, to a single fixed point K. From an ecological point of view, this says as long as there is a slight Allee effect there is an extinction risk for u, but without one *there is none*, and u will always grow to carrying capacity. If one can prove that an attractor $\mathcal{A}_m$ approaches a target attractor $\mathcal{A}_0$, in a continuous sense, in the case of spatially explicit/PDE model, the attractor $\mathcal{A}_m$ is said to be *robust* at $m = 0$ [20]. The PDE literature is rich with robustness results [21,20,22,23]. To the best of our knowledge there are not many robustness results in three species food chain models, where the parameter of interest is the Allee threshold m. However robustness results on various related two, three and even four species reaction–diffusion models have appeared [24–26]. Note, unless a systems dynamics are robust, there is no possibility to capture the same in a laboratory experiment or natural setting.

On the same lines, a phenomenon that occurs in large food chains, is the excessive harvesting/predation of certain species in the chain, via the predators in the trophic level above them. In many aquatic food chains, this can lead to trophic cascades [27]. Formally, overexploitation refers to the phenomenon where excessive harvesting of a species can result in its extinction. Mathematically, for a two species predator–prey system, one can prove an overexploitation type theorem, if one shows for a large enough initial density of the predator, the prey will be depredated on till extinction. In this case, if the predator does not have an alternate food source, it will also subsequently go extinct. Although there is a fair amount of literature on this in two species models [28], it is less studied in three species models. In particular, the Allee effect itself on overexploitation, in multi-trophic level food chains, has not been sufficiently explored.

Our primary goal in the current manuscript is to propose and analyze a reaction–diffusion three species food chain model, with an Allee effect in the top predator. In particular, we aim to investigate the link between the Allee threshold parameter m, and the longtime dynamics of the three species food chain, in terms of

- Robustness of global attractors in terms of the Allee threshold parameter m.
- Overexploitation phenomenon in the food chain model, as it is effected by the Allee threshold parameter m.
- Pattern formation and the effect on patterns that form in the food chain model due to the Allee threshold parameter m.

Our hope is that this model could be used as a feasible toy model, to better understand overexploitation phenomenon in multi level food chains, Trophic cascades, Conservation efforts in food webs and Biological control, all of which are mediated via an Allee effect. To this end we consider a situation where a prey species u serves as the only food for a specialist predator v which is itself predated by a generalist top predator r.

This is a typical situation often seen in nature in various food chains [29]. The governing equations for populations u and v follow ratio dependent functional responses, and are modeled by the Volterra scheme i.e., the middle predator population dies out exponentially in the absence of its prey. There is recently much debate about functional responses used in ecology, and the ratio dependent response is considered to be more realistic than its Holling type counterparts [30]. The above situation is described via the following system of PDE. This is nondimensionalized. The nondimensionalisation is standard [1].

$$\frac{\partial u}{\partial t} = d_1 \Delta u + u - u^2 - w_1 \frac{uv}{u + v}, \tag{2}$$

$$\frac{\partial v}{\partial t} = d_2 \Delta v - a_2 v + w_2 \frac{uv}{u + v} - w_3 \left(\frac{vr}{v + r} \right), \tag{3}$$

$$\frac{\partial r}{\partial t} = d_3 \Delta r + r(r - m)\left(c - \frac{w_4 r}{v + D_3} \right), \tag{4}$$

the spatial domain for the above is $\Omega \subset \mathbb{R}^n$, $n = 1, 2, 3$. Ω is assumed bounded, and we prescribe Neumann boundary conditions $\nabla u \cdot \mathbf{n} = \nabla v \cdot \mathbf{n} = \nabla r \cdot \mathbf{n} = 0$. Neumann boundary conditions are very natural in spatial ecology, as they describe a situation where there is no net flux of species through the boundary. Thus they are best suited for our current application. They are also more physical in a greater number of applications, than say Dirichlet boundary conditions [1]. However, the physical relevance, depends on the specific application at hand. For example, it is the Dirichlet boundary condition that is used, when there is actual death of species on the boundary, (implying a "hostile boundary"). For example, it could