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Predator harvesting in stage dependent predation models: Insights from a threshold management policy

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ABSTRACT

Stage dependent predation may give rise to the hydra effect – the increase of predator density at equilibrium as its mortality rate is raised. Management strategies that adjust predator harvest rates or quotas based on responses of populations to past changes in capture rates may eventually lead to a catastrophic collapse of predator species. A proposed threshold management policy avoids the hydra effect and its subsequent danger of predator extinction. Suggestions to extend the application of threshold policies in areas such as intermediate disturbance hypothesis, density-trait mediated interactions and non-optimal anti-predatory behavior are put forward.

1. Introduction

Consumer–resource models with stage structure have been employed to investigate issues such as trophic cascades and trophic level concept [29], response of trophic levels to nutrient enrichment [28], size refuge [6], stability [24], ontogenetic shifts [27], emergence of predator Allee effects [35]. These analyzes can encompass variation of mortality rates lending themselves to the investigation of harvesting effects in structured settings.

In this light [2] analyzed the effect of predator mortality on the dynamics of some stage-structured predator–prey models. An important feature that emerges from the studied structures is the hydra effect – the increase of predator density at equilibrium as its mortality rate is raised. As regards this effect, a major implication concerns management actions such as fisheries. For instance, adaptive management adjusts harvest rates or quotas based on responses of populations to past changes in harvest rates. Since predator density increases with the combined forces of natural mortality and harvesting, this result reflects a situation where, for example, fixed proportional predator harvesting may be safely increased. However, it is demonstrated that such adjustments will eventually lead to a catastrophic collapse of predator species [2].

Along with management schedules such as constant harvest rate, fixed proportional harvest and fixed escapement level, threshold policy is an alternative strategy to exploit consumer–resource systems. Its application can be seen in areas such as fishery [30,31,8], terrestrial harvesting [20], conflict uses of aquatic vegetation [36] and control of non-native predators [32].

Because of the undesirable effects of a continuous disturbance in a structured predator–prey system, namely, fixed proportional predator harvesting, a threshold management policy is proposed in order to avoid predator collapse in two stage dependent predation models analyzed by Abrams and Quince [2]. A threshold management policy, as presented here, consists of curtailing harvesting (removal, culling, grazing) to promote species rebuilding when a population drops below a threshold level. In these cases, even with harvesting intensities beyond critical values (i.e., those which provoke predator extinction), it is shown that the proposed threshold strategy still precludes predator extinction.

2. The mathematical structure of the threshold policy

A threshold policy (hereinafter called TP) can be defined as the function $\phi(\tau)$,

$$\phi(\tau) = \begin{cases} 1 & \text{if } \tau > 0 \\ 0 & \text{if } \tau \leqslant 0, \end{cases} \tag{1}$$

where τ is the chosen threshold.

Given a species N with a particular population dynamics, its behavior under the proposed TP, ϕ, will be described by

$$\frac{dN}{dt} = f(N) - \phi(\tau)g(N) \tag{2}$$

where $\phi(\tau)$ is defined as in (1) and

$\tau = N - N_{th}$.

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$f(N)$ is the species growth rate, $g(N)$ is a density dependent function describing any species removal rate, and N_{th} a chosen threshold level. The control action is enacted whenever the N level is above N_{th}. This policy creates two systems – namely, a system of ordinary differential equations with discontinuous right-hand sides [17,3] – with their own equilibrium points, separated by the threshold curve. Accordingly, if the equilibrium points are located in their opposite regions, they are named virtual equilibrium points. Otherwise, they are called real equilibrium points (see Fig. 1). In case the locally stable equilibrium points are virtual, they will never be attained since the dynamics switches as soon as the trajectories cross the threshold N_{th}. In this setup a *sliding mode* [34] along N_{th} may occur, if in some of its vicinity the vector fields of both structures are directed toward each other. This sliding dynamics may tend to a pseudo-equilibrium – a new steady state located on the switching surface. However, it is worth mentioning that the existence of virtual equilibria is not a necessary condition for the occurrence of a sliding regime (see [14,15]). This dynamical behavior consists of rapidly alternating control activation and suppression. The next examples will confirm that this strategy can avoid predator collapse in stage dependent predation dynamics by means, in part, of the creation of virtual equilibrium points [9,25].

3. Harvesting in stage dependent predation models

3.1. Stage dependent predation model I

The model to be considered in this section reflects density-dependence operating via adult birth rate, density dependent juvenile growth and predation only on juvenile prey. It takes on the following form [2]:

$$\frac{dN_1}{dt} = \beta_2 N_2(1-\alpha_2 N_2) - d_1 N_1 - GN_1(1-\alpha_1 N_1) - \frac{sN_1}{1+sh_1N_1}P$$
$$\frac{dN_2}{dt} = GN_1(1-\alpha_1 N_1) - d_2 N_2$$
$$\frac{dP}{dt} = \left(\frac{e_1 sN_1}{1+sh_1N_1} - D\right)P \tag{3}$$

N_1 and N_2 are the young and the adult prey populations, respectively; P is the predator population; β_2 is the maximum per capita birth rate of adult prey, which is a linear decreasing function of adult prey dictated by α_2; d_1 and d_2 are parameters giving the per capita death rates of juvenile and adult prey; D is the per capita death rate of the predator. $GN_1(1-\alpha_1 N_1)$ is the density dependent transition rate from young to adults in the prey population and α_1 is the proportional rate of decrease in this transition with increased density of young prey. This density dependent maturation is a reasonable assumption for a population in which the maturation age of young individuals is not fixed, but depends on, e.g., the availability of food or suitable habitat (components of intra-specific competition). s_1 is the per capita capture rate of young prey by a searching predator, while h_1 is the predator's handling time of a young prey item; e_1 is the conversion efficiency of ingested young prey into new predators individuals.

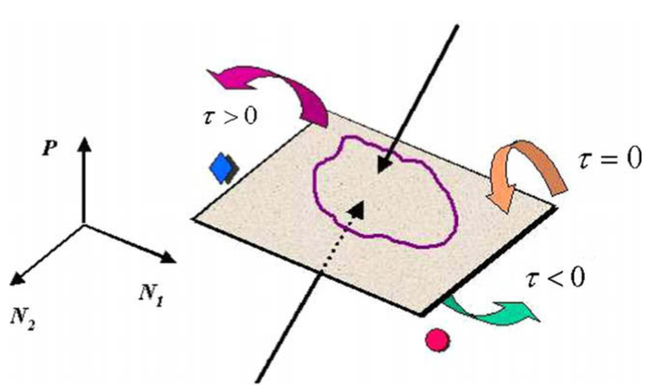

Fig. 1. A schematic figure of a sliding mode in a hypothetical phase space $N_1 \times N_2 \times P \cdot \tau = 0$ is the threshold surface. ◆ – equilibrium point of region $\tau < 0$ (below $\tau = 0$); • – equilibrium point of region $\tau > 0$ (above $\tau = 0$). These points are lying in opposite regions, hence they are virtual equilibrium points. The region delimited by the smooth curve on the surface $\tau = 0$ represents a sliding mode region. Throughout the sliding mode region the vector fields of each structure (solid arrow, $\tau > 0$; dashed arrow, $\tau < 0$) are directed toward each other.

Applying the TP (1) to the predator harvesting in (3), yields

$$\frac{dN_1}{dt} = \beta_2 N_2(1-\alpha_2 N_2) - d_1 N_1 - GN_1(1-\alpha_1 N_1) - \frac{s_1N_1}{1+s_1h_1N_1}P$$
$$\frac{dN_2}{dt} = GN_1(1-\alpha_1 N_1) - d_2 N_2$$
$$\frac{dP}{dt} = \left(\frac{e_1 sN_1}{1+s_1h_1N_1} - D\right)P - \varepsilon\phi(\tau)P \tag{4}$$

where $\phi(\tau)$ is defined as in (1) and

$\tau = P - P_{th}$.

P_{th} is the chosen predator threshold, ε is the harvesting intensity applied to the predator and $\varepsilon\phi(\tau)$ is the harvesting rate.

System (4) consists of two structures: (i) no predator harvesting (i.e., $\phi(\tau) = 0$ when $\tau < 0$) which generates an asymptotically stable behavior towards the point ($N_1 = 1.4999; N_2 = 2.7750; P = 2.8604$) with the given parameter values (Fig. 2(a)). When $D = 0.6$, a relatively high predator population is present compared with the respective predator equilibrium values for lower D values; (ii) predator harvesting intensity $\varepsilon = 0.3$ (i.e., $\phi(\tau) = 1$ when $\tau > 0$) which brings about predator extinction, tending to the point ($N_1 = 6.4802; N_2 = 8.7604; P = 0$). Hence, increasing D to 0.9 through the combined effect of predator natural mortality and predator harvesting, predator population experiences a collapse towards extinction (Fig. 2(b)). These two structures correspond to two distinct models which are separated in the phase space $N_1 \times N_2 \times P$ by the switching plane $P = P_{th}$ (the TP graph). Accordingly, phase space $N_1 \times N_2 \times P$ is split into two regions – one for $\phi = 0$ (below P_{th}) and one for $\phi > 0$ (above P_{th}). P_{th} was chosen so that the equilibrium points of each structure be virtual (located in opposite regions as in Fig. 1). Besides, the position of the threshold P_{th} creates opposed vector fields in some region of its vicinity. This setting engenders a sliding mode which corresponds to a rapid alternation of no harvesting ($\phi = 0$) and harvesting ($\phi > 0$) along the predator threshold (Fig. 2(c)). The numerical results show that applying the proposed TP, the achieved stabilization along the threshold ($P_{th} = 2.7$) lies near the pre-harvesting regime (i.e., $P = 2.8604$ when $D = 0.6$).

Since the sliding mode evolves on the threshold $\tau = 0$, its dynamics is given by the time derivative of (3) in model (4), i.e.,

$$\frac{d\tau}{dt} = \frac{dP}{dt} = 0. \tag{5}$$

From expression (5) and the equation of P in (4), the average harvesting of the threshold policy for the stage-specific predation model (4), $\varepsilon\phi_{equiv}P_{th}$ (also denoted as the *equivalent harvesting rate*), can be calculated according to

$$\frac{dP}{dt} = \left(\frac{e_1 sN_1}{1+s_1h_1N_1} - D\right)P_{th} - (\varepsilon\phi_{equiv}(\tau)P_{th}) = 0. \tag{6}$$

Hence, the equivalent yield Y_{equiv} is given by