Bubbles, chaos, and the Hydra effect in delayed population models

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We study the effects of increasing harvesting in a population model whose dynamics is governed by the delay-differential equation with negative feedback

$$x'(t) = -\delta x(t) + f(x(t-\tau)), \tag{1}$$

were $x(t)$ is the number of adult members of the population at time t, δ is the natural mortality rate, and f is the so-called *stock-recruitment* relationship. It is assumed that there is a constant maturation period τ, and a constant probability of survival to adulthood.

The most famous population model of this type was suggested by Gurney, Blythe and Nisbet [1] , and it is known as the *Nicholson's blowflies equation*:

$$x'(t) = -\delta x(t) + px(t-\tau)e^{-\beta x(t-\tau)},\ \delta, p, \beta, \tau > 0. \tag{2}$$

Assuming a strategy of constant effort harvesting prior to reproduction, we consider the following modification of equation (1):

$$x'(t) = -(\delta+\gamma)x(t) + f((1-\gamma)x(t-\tau)), \tag{3}$$

where $\gamma \in (0,1)$ is the rate of harvesting effort.

We analyze the changes in the dynamics of the solutions of (3) when γ is increased from 0 to 1, taking as a case of study the Nicholson's blowflies equation (2). The most interesting phenomena that we report are:

- The existence of *bubbles* in the bifurcation diagram, which are characterized by two consecutive Hopf-bifurcation points,
- a route of period-doubling bifurcations to chaos, and
- the *Hydra effect*, that means that a population can increase its abundance in response to an increase in its per-capita mortality rate (see [2]).

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References

[1] W. S. C. Gurney, S. P. Blythe and R. M. Nisbet, *Nicholson's blowflies revisited*, Nature **287** (1980), 17–21.

[2] P. A. Abrams, *When does greater mortality increase population size? The long story and diverse mechanisms underlying the hydra effect*, Ecol. Lett. **12** (2009), 462–474.