Stabilization of population dynamics via threshold harvesting strategies

Daniel Franco[a,b], Juan Perán[a]

[a] *Departamento de Matemática Aplicada, E.T.S.I. Industriales, Universidad Nacional de Educación a Distancia (UNED), c/ Juan del Rosal 12, 28040, Madrid, Spain.*
[b] *Centre for Mathematical Biology, Department of Mathematical Sciences, University of Bath, Bath BA2 7AY, UK.*

Abstract

We study two different harvesting/thinning control strategies in the framework of one dimensional discrete time population models. They have the common feature of considering a threshold population size, commonly called Biomass at the limit, under which the population is not altered, and they differ in how the harvesting/thinning is applied when that threshold is surpassed: one uses the well known proportional feedback control, whereas the other employs the recently proposed target oriented control. We focus on the possibility of applying these strategies to control the chaotic behaviour predicted by some one dimensional discrete time population models. We discuss the basic properties of both strategies and compare them with other simpler control methods. Particularly, we show that increasing the threshold does not affect, or almost does not affect, a stable exploited population as long as the threshold is lower than the carrying capacity of the system.

Keywords: Discrete time population models, Harvesting/thinning, Control of chaos, Stabilization strategies, Unimodal maps, Threshold strategies.

1. Introduction

Very simple mathematical models of single species population dynamics with intraspecific competition can have a very rich and complex behaviour (May, 1976). Although there is still a lack of experimental evidence of this behaviour for one dimensional systems, it has been observed in laboratory,

Email address: dfranco@ind.uned.es (Daniel Franco)

for example, for a three dimensional model of a predator-prey system consisting of a bacterivorous ciliate and two bacterial prey species (Becks et al., 2005).

In this paper, we investigate the possibility of controlling chaos in discrete time population models by employing two harvesting control methods based on threshold management policies (see Quinn and Deriso, 1999, chapter 11). These policies consider a population size under which there is an increasing risk of stock collapse. This population size is commonly called *Biomass at the limit* and denoted by B_{lim}, as defined by ICES (2011, section 1.2) following the recommendations of FAO (1995). Essentially, B_{lim} acts as a threshold under which harvesting/thinning is banned and, depending on how the harvesting is done when this threshold is surpassed, we have different types of management policies.

Using the concept of variable structure systems and virtual equilibrium points, Costa and Faria (2011) have recently shown that a certain post-reproductive threshold policy (we include its definition in equation (9) at the end of section 3) can induce cyclic behaviour in an otherwise stable population as a consequence of the combination of harvest pressure and excessively protective threshold densities, even when the biomass at the limit B_{lim} is lower than the carrying capacity of the system. Here, we show that such undesirable dynamics, from a management point of view, are not a general characteristic of the threshold policies. We rigorously prove that increasing the threshold B_{lim} does not affect or almost does not affect a stable exploited population as long as B_{lim} remains under the carrying capacity for the considered controls. Quite to the contrary, this increase in the protection of the species can induce a stable behaviour in an otherwise cyclic exploited population in some cases. The reason for the difference between our results and those of Costa and Faria (2011) are the different time when the population is measured to decide whether or not to harvest.

There is some evidence of the potential for increasing the mortality to lead to a higher variability in population abundance of different species (Zipkin et al., 2009). This phenomenon has been found in higher dimensional discrete models (Dennis et al., 1997; Zipkin et al., 2009). In one-dimensional discrete models this higher variability was recently reported adding a sort of age-structure in two different ways. In Anderson et al. (2008), which dealt with fisheries, it is argued that this higher variability could be related to an age truncation effect caused by the harvesting when it focuses on adult individuals because of their bigger sizes. In Liz and Ruiz-Herrera (2012), this higher variability appeared in a model that included density-independent survivorship of adults. Here, we show that an increase of the mortality, due to an increase of the harvesting effort, can lead to a higher variability in one-dimensional discrete systems (without considering any sort of age-structure) when employing threshold policies.

The rest of the paper is structured as follows. In section 2 we describe two piecewise smooth control of chaos methods, which model threshold policies (Quinn and Deriso, 1999). After interpreting them and showing how they are related to other control methods mentioned in this introduction, we prove that these threshold control methods are able to stabilize a wide range of one-dimensional systems defined by certain unimodal maps. In section 3 we make some numeric simulations to illustrate, among other things, how the stabilization predicted by our results is attained. We observe new phenomena (for example the existence of Farey trees, bistability, hysteresis and border collision bifurcations) in comparison with the behaviour of other control methods. Finally, section 4 is destined to a discussion of the results obtained.

2. Control of chaos: Threshold Methods.

2.1. Control of chaos

Chaos control theory focuses on attaining the stabilization of an unstable orbit of a chaotic system and many strategies have been proposed for obtaining such an objective (Schöll and Schuster, 2008). From an ecological point of view, it is natural to consider strategies of control of chaos that introduce new parameters in the model which are easy to modify and change the state variable in a desirable way.

Essentially, applying one of these chaos control strategies to a discrete time population model can be done after or before reproduction, see Seno (2008) and (Hilker and Liz , 2013, (this issue)) for some considerations about this aspect. Along the paper, if it is not explicitly established in another way, we suppose that the control is applied before reproduction. In such a case, many of these control strategies, change the uncontrolled population model given by a map f into the following controlled one

$$x_{n+1} = f(g(C, x_n)), \quad n \in \mathbb{N},$$

where C is a vector of control parameters and the map g determines the harvesting/stocking amount removed/added in each generation by the expression

$$D_n := x_n - g(C, x_n), \quad n \in \mathbb{N}. \tag{1}$$

The control methods can be classified in three groups according to the sign of the sequence D_n defined in (1): if $D_n \geq 0$ for $n \geq 0$, i.e. if they stabilize the population without having to add individuals during the intervention, then we call them *harvesting control methods*; if $D_n \leq 0$, then we call them *stocking control methods*; and if D_n changes sign, we call them *harvesting/stocking control methods*.

An example of harvesting control method is the Limiter Control (LC) (Hilker and Westerhoff, 2006), modelling a fixed escapement harvesting strategy (Sinclair et al., 2006). Some methods are harvesting control methods or stocking control methods depending on the values of the control parameters. An examples of such a method is Proportional Feedback (PF) control (Carmona and Franco, 2011; Güémez and Matías, 1993; Liz, 2010b), modelling a fixed proportion harvesting (stocking) strategy (Sinclair et al., 2006). Whereas, for example, the Target Oriented Control (TOC) (Dattani et al., 2011; Franco and Liz, 2013) is a harvesting/stocking control method given by

$$g(T, c, x) = x - c(x - T), \tag{2}$$

where roughly speaking the parameter T is used to establish a *target population size* and the parameter $c \in [0, 1]$ is used to stabilize the system. The threshold methods we are going to discuss next are related to LC, PF, and TOC.

2.2. Threshold methods

For each $B_{lim} \geq 0$ and $0 \leq c \leq 1$ we consider the controlled maps

$$f(g_1(B_{lim}, c, x)) \quad \text{and} \quad f(g_2(B_{lim}, c, x)),$$

where g_1 and g_2 are

$$g_1(B_{lim}, c, x) := \begin{cases} x, & x \leq B_{lim}, \\ (1-c)x, & x > B_{lim}; \end{cases} \tag{3}$$

and

$$g_2(B_{lim}, c, x) := \begin{cases} x, & x \leq B_{lim}, \\ x - c(x - B_{lim}), & x > B_{lim}. \end{cases} \tag{4}$$

We note that if $c \neq 0$, then both maps are piecewise linear. The map g_1 has a discontinuity at $x = B_{lim}$ and it is monotone increasing in any interval not containing B_{lim}. Whereas map g_2 is continuous, monotone increasing and piecewise smooth with one singular point at $x = B_{lim}$.

From an ecological point of view both maps define the same *subsistence interval* $[0, B_{lim}]$, where no harvesting is allowed when the population belongs to it. However, each map describes a different harvesting method if the population size is greater than the threshold value B_{lim}.

- The strategy g_1 applies to population sizes greater than B_{lim} a proportional harvesting, which removes a proportion c of the population and therefore generates population sizes below the Biomass at the limit in certain circumstances. It is easy to implement, since one only needs to monitor the population to know if it is above or below the threshold population size B_{lim}, and then, either do nothing or apply a proportional harvesting. From an environment management perspective, going below the Biomass at the limit when applying the control could be controversial. However, for many deterministic models, as for example the Ricker model, this strategy guarantees the persistence of the species since the controlled map takes positive values for positive population sizes and the origin maintains its repulsive character.

- The strategy g_2 applies to population sizes greater than B_{lim} a TOC control given by map (2) with target $T = B_{lim}$, that is, a harvesting following the strategy presented in Dattani et al. (2011), which removes $c\times$(population$-B_{lim}$). Contrary to g_1, this strategy guarantees that once the population size is above B_{lim}, it remains so, under the effect of the control, and only the intraspecific competition could generate population sizes below the threshold B_{lim}.

Motivated by the above description, hereinafter, we refer to the control methods defined by g_1 and g_2 as *Proportional Threshold Control* (PTC) and *Target Oriented Threshold Control* (TOTC) respectively. We note that following Costa and Faria (2011), we could have named them Threshold Control and Proportional Threshold Control, respectively. However, given the context, our choice appears clearer and to transmit more information with the chosen terminology.

Not having access to a source of individuals, as it happens with some wild populations, makes impossible the application of stocking or harvesting/stocking control methods. Therefore, in the management of natural resources the harvesting control methods are of high interest. Both PTC and TOTC are harvesting control methods. This is clear for PTC, since it uses the harvesting control method PF outside the subsistence interval. For TOTC, where we use the harvesting/stocking TOC method outside $[0, B_{lim}]$, we note that choosing a target size T for TOC smaller or equal than the threshold value B_{lim} renders TOC to be a strict harvesting strategy and we are taking $T = B_{lim}$. Since we are going to show next that both methods are able to stabilize a positive equilibrium for a wide range of population models, it is very important to note that such a stabilization is performed by just removing individuals in a certain way.

We remark that having $c = 0$, with independence of the value of B_{lim}, means that we are switching off the control by doing no harvest. When the control is switched on, roughly speaking, TOTC lies in between LC and PF and PTC generalizes PF for the following reasons. On the one hand, it is not difficult to see that removing the subsistence interval, that is taking $B_{lim} = 0$, reduces both control methods to the PF method. On the other hand, in the case of $B_{lim} > 0$, if we take the maximum harvesting effort $c = 1$, then we obtain that the control strategy TOTC coincides with LC.

3. Results

In this section we present two results which show that PTC and TOTC are able to stabilize certain chaotic systems towards a positive equilibrium. The proofs of both results can be found in the Appendix.

We assume that the map f, which defines the uncontrolled system, satisfies the following hypotheses:

(A1) $f\colon [0,b] \to [0,b]$ ($b = \infty$ is allowed) is continuously differentiable and such that $f(0) = 0$, and $f(x) > 0$ for all $x \in (0,b)$.

(A2) f has only two nonnegative fixed points $x = 0$ and $x = K > 0$, $f(x) > x$ for $0 < x < K$, and $f(x) < x$ for $x > K$.

(A3) f has a unique critical point $d < K$ in such a way that $f'(x) > 0$ for all $x \in (0,d)$, $f'(x) < 0$ for all $x > d$, and $f'(0^+), f'(b^-) \in \mathbb{R}$.

Condition (A1) imposes the offspring to be positive for any positive population size in the interval considered, i.e. $[0,b]$, to take the zero value in the absence of a population, and to change smoothly as the population varies. Hypothesis (A2) essentially asserts that overpopulation, *i.e.* going above the carrying capacity K, leads to a smaller population size at the next generation. Whereas (A3) assumes that there exists a population size d leading to the maximum offspring. Conditions (A1)-(A3) are standard for a population in which density dependence occurs through *scramble* competition (see Britton, 2003). A well known example of a map satisfying conditions (A1)-(A3) is given by

$$f(x) = xe^{r(1-x)}, \quad r > 0. \tag{5}$$

The former map was introduced by Ricker (1954) in the context of stock and recruitment in fisheries and we use it here to illustrate our results.

3.1. Target Oriented Threshold Control

Our first result deals with TOTC defined by (4).

Proposition 1. *Assume f satisfies (A1)-(A3). Then the controlled system*

$$x_{n+1} = f(g_2(B_{lim}, c, x_n))$$

has at least one positive equilibrium for each $B_{lim} \in [0, \max_{x\in[0,b]} f(x)]$ and $c \in [0, 1)$.

Moreover, if B_{lim} is lower than the carrying capacity K, then there is a positive equilibrium in $(B_{lim}, f(d)]$, which is asymptotically stable if the harvesting effort c belongs to the interval

$$\max\left\{0, 1 - \frac{1}{\sup_{x\in(B_{lim},f(d))} |f'(x)|}\right\}. \tag{6}$$

Proposition 1 establishes that if a certain harvesting effort controls a population towards an asymptotically stable equilibrium with $B_{lim} = 0$, then increasing B_{lim} in the interval $[0, K]$ does not affect the existence of that asymptotically stable fixed point. Instead, increasing B_{lim} in $[0, K]$ can have a stabilizing effect for an equilibrium since expression (6) decreases as B_{lim} increases.

We can appreciate the mentioned stabilizing effect of increasing B_{lim} in Figure 1. This figure illustrates the long-term dynamics of the controlled system for each combination of control parameters, c and B_{lim}, for a fixed initial population. Note, for example, how for a harvesting effort of $c = 0.6$ and the chosen initial condition the system tends to a cycle of period two if no subsistence interval is considered, there is not an attracting equilibrium. However, the population tends to a fixed point if we increase B_{lim} and we take it between approximately 0.5 and 1.

It is important to point out that Proposition 1 is also valid if we apply the control after reproduction because g_2 is continuous and strictly increasing in the third variable x, making both systems (pre-reproductive and post-reproductive) topologically equivalent.

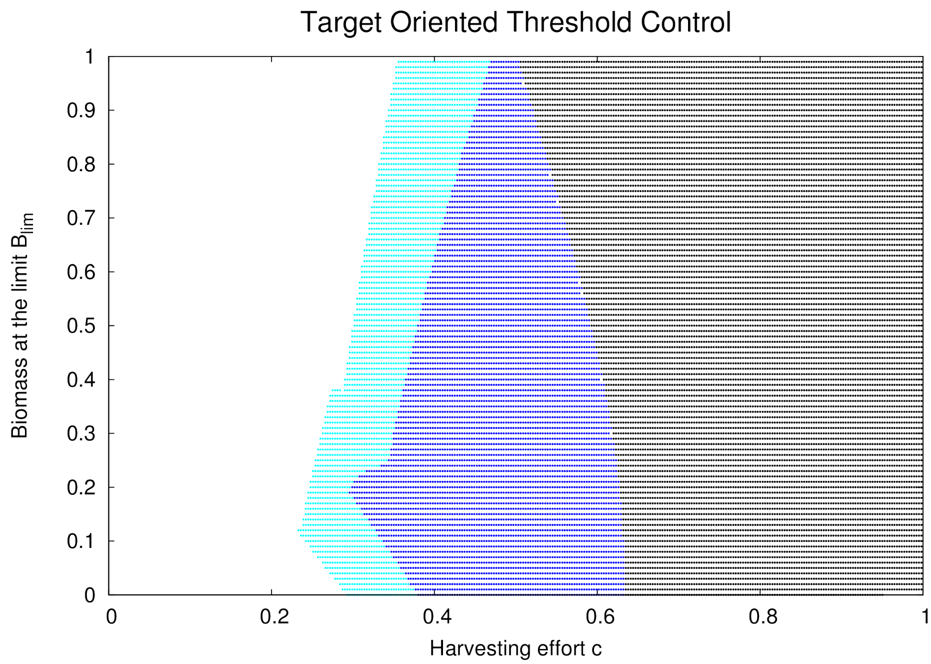

Figure 1: Long-term dynamics of the controlled system depending on the control parameters c and B_{lim} obtained by numerical simulations. The uncontrolled system is given by the Ricker map with $r = 3$, so the carrying capacity is $K = 1$. In the black region on the right the system tends to an asymptotically stable equilibrium. Note how this region becomes wider as B_{lim} increases showing that, as Proposition 1 asserts, more protective threshold densities help in the stabilization of an equilibrium as long as $B_{lim} < K$. The other coloured regions correspond to pairs of control parameters for which the system tends to an asymptotically stable cycle of period two (dark blue/dark grey) and or four (light blue/light grey), respectively. The asymptotic dynamics for the control parameters in the white region have periods different from 1, 2, or 4. The initial condition has been chosen as $x_0 = 0.99$ (see the Discussion for another plot generated with a pseudo-random initial condition).

3.2. Proportional Threshold Control

Our second result deals with PTC defined in (3). We add the following condition on the second derivative of f with the aim of being able to use a result of Liz (2010b) in the proof:

(A4) $f''(x) < 0$ on $(0, d)$.

As a reward of assuming (A4), we get the uniqueness of the nontrivial fixed point for the controlled system. We remark that the same uniqueness can be obtained for TOTC if we assume (A1)-(A4) in Proposition 1.

Proposition 2. *Assume f satisfies (A1)-(A4). Then, for $B_{lim} < K$, the controlled system*

$$x_{n+1} = f(g_1(B_{lim}, c, x_n))$$

has a unique positive equilibrium if and only if

$$0 \leq c < 1 - \frac{\min f^{-1}(B_{lim})}{B_{lim}}. \tag{7}$$

Moreover, there exists $c^* \in \left[0, 1 - \frac{d}{f(d)}\right]$, independent of B_{lim}, such that the above positive equilibrium is asymptotically stable for c belonging to

$$\left(c^*, 1 - \frac{\min f^{-1}(B_{lim})}{B_{lim}}\right).$$

Although, we can not use the same argument as in Proposition 1, it is easy to prove that Proposition 2 is also valid if we apply the control after reproduction. We point out that applying PTC after reproduction gives the controlled map

$$g_1(B_{lim}, c, f(x)) = \begin{cases} f(x), & f(x) \leq B_{lim}, \\ (1-c)f(x), & f(x) > B_{lim}; \end{cases} \tag{8}$$

and not the map studied in Costa and Faria (2011)

$$g(B_{lim}, c, f(x), x) = \begin{cases} f(x), & x \leq B_{lim}, \\ (1-c)f(x), & x > B_{lim}. \end{cases} \tag{9}$$

Notice that the map (9) does not guarantee that the harvesting takes place when the population size is greater than B_{lim} since the model assumes a difference in the timing of the measurement of the population and the timing of the harvesting. During such a period of time the population could have dropped towards a smaller size because of the intraspecific competition. This difference in the timing is the source of the destabilization described in Costa and Faria (2011) when increasing B_{lim} in the interval $[0, K]$. In our case, the fact that the asymptotic stability is independent of B_{lim} guarantees that choosing a harvesting effort in the interval $\left(c^*, 1 - \frac{\min f^{-1}(K)}{K}\right)$ allows to increase B_{lim} in $[0, K]$ maintaining an asymptotically stable equilibrium (see Figure 2). Note how the length of the intervals of harvesting efforts able to stabilize a positive equilibrium almost does not change when using PTC in Figure 2. The difference in the length of those intervals for $B_{lim} = 0$ and $B_{lim} = 1$ is approximately 0.01. However, for the control defined by (9) the interval decreases as B_{lim} increases and disappears if B_{lim} is greater than approximately 0.55.

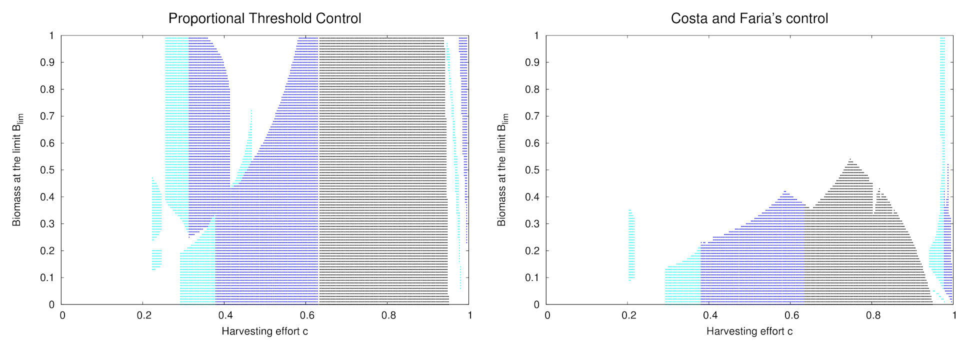

Figure 2: Long-term dynamics of the controlled systems depending on c and B_{lim} and obtained by numerical simulations. On the left using the controlled map (8) and on the right using (9), i.e., a post-reproductive PTC. The uncontrolled system is given by the Ricker map with $r = 3$, so the carrying capacity is $K = 1$. In the black regions the controlled system tends to an asymptotically stable positive equilibrium. Both dark blue regions coincide when $B_{lim} = 0$, that is, in the interval for which an exploited population is stabilized towards an equilibrium without a threshold policy, approximately $(0.63, 0.95)$. But as B_{lim} increases the asymptotic dynamics of the control studied by Costa and Faria (2011) suddenly changes to a highly oscillatory behaviour, whereas PTC almost maintains the same interval of stabilizing harvesting efforts. The other coloured regions correspond to pairs of control parameters for which the system tends to an asymptotically stable cycle of period two (dark blue/dark grey) or four (light blue/light grey). The asymptotic dynamics for the control parameters in the white region have periods different from 1, 2, or 4. The initial condition has been chosen as $x_0 = 0.99$ (see the Discussion for another plot generated with a pseudo-random initial condition).

It is also important to notice that, by the monotonicity properties of the map P defined in the proof of Proposition 2 in the Appendix, the asymptotically stable population size increases as the harvesting effort c increases in the interval $\left(c^*, 1 - \frac{d}{f(d)}\right)$. This means that PTC inherits the known hydra effect (Abrams, 2009) of PF in the same interval of parameters for the harvesting effort c. We recall that a hydra effect occurs when the mean population size increases as a consequence of increasing the harvesting effort. From a management perspective, choosing a harvesting effort in the interval $\left(c^*, 1 - \frac{d}{f(d)}\right)$ seems to be a good choice since a small overexploitation produces theoretically an increase in the population size. Since $\left(c^*, 1 - \frac{d}{f(d)}\right) \subset \left(c^*, 1 - \frac{\min f^{-1}(K)}{K}\right)$, in such a harvesting effort interval, an augmentation of B_{lim} in $[0, K]$ does not affect the stability of the equilibrium.

4. Dynamics of the controlled populations

In the previous section we have proved that it is possible to use both PTC and TOTC to stabilize a positive equilibrium provided that the threshold subsistence population size B_{lim} is below the carrying capacity K. This section is devoted to numerically analyse how the dynamics of the controlled systems vary with the control parameters: harvesting effort c and the threshold B_{lim}.

We consider several cases when the Proposition 1 and Proposition 2 guarantee the stabilization of an equilibrium, that is when $B_{lim} < K$. We have plotted the orbit diagrams (frequently called bifurcation diagrams too) for different values of B_{lim} in this situation. For the sake of completeness, at the end of the section we briefly address what occurs if B_{lim} is above the carrying capacity K. All the numerical simulations have been done taking as uncontrolled system the one given by the Ricker map with $r = 3$. The harvesting effort c (horizontal axis) varies with step size 0.005. For each fixed c the initial condition is chosen as a pseudo-random number belonging to the interval $[0, 2.463]$. The first 900 population values are ignored, then the next 100 are plotted against the control parameter c.

We have remarked that PTC and TOTC use harvesting/thinning procedures from PF and TOC respectively. In consequence one could expect not to find many differences in the way the stabilization is achieved from those of PF and TOC. However, as we are going to see next, the piecewise-linear controls PTC and TOTC have many properties not observable in PF and TOC. For comparison, we present in Figure 3 the orbit diagrams of PF and TOC.

These new phenomena are intrinsically related to the piecewise-smooth character of the controlled maps and to the additional type of bifurcations (called *border collision* bifurcations) that such maps can generate. Border collision bifurcations are characterized by abrupt jumps in the multipliers of periodic orbits and can cause different types of behaviour, from changes of stability to a sudden transition from a stable fixed point to a fully developed chaotic attractor (Di Bernardo et al., 2008). These types of bifurcations occur, for example, when a fixed point reaches the discontinuity boundary of the map or of the derivative of the map. We point out that our objective is not doing a complete characterization of all the possible bifurcations presented for the range of parameters considered and we will restrict ourselves to some selected cases.

4.1. Target Oriented Threshold Control

Let us consider first the control TOTC when B_{lim} is small in relation to the carrying capacity. In Figure 4 (left) we see an orbit diagram similar to those for the PF and TOC methods in Figure 3. Increasing the harvesting effort, the stabilization of a positive equilibrium takes place after some period halving bifurcations. Moveover, a hydra effect is clearly present, and the positive equilibrium seems to be a global attractor as soon as it is asymptotically stable. But now, contrary to what happens for PF, increasing the harvesting effort c does not provoke the extinction of the population, even with a small Biomass at the limit as, for example, the one given by $B_{lim} = 0.1$. This feature is shared with TOC. However, we recall that TOC needs to add individuals to achieve the stabilization of the system, that is, it is a harvesting/stocking control method, whereas TOTC is a harvesting control method.

For $c = 1$ the positive equilibrium takes the value $f(B_{lim})$. Selecting the Biomass at the limit as the population in which the maximum offspring is attained, that is $B_{lim} = d$, we would observe a hydra effect in which the population size increases when increasing the harvesting effort until the maximum of the harvesting effort ($c = 1$) is attained. This type of hydra effect is related to TOC for the specific target $T = d$ and does not appear in PF, where there is an initial increasing response of the population size to harvesting/thinning, but when the harvesting pressure is high this effect reverses (see Figure 3 (right) where we have selected $T = d = 1/3$ to show this type of hydra effect in the TOC orbit diagram). Taking everything into account we can say that TOTC, when B_{lim} is small in relation to the carrying capacity, gets advantages of TOC without having to add population.

Next, let us fix B_{lim} closer to the carrying capacity. In Figure 4 (right) we observe two phenomena with important ecological consequences. The

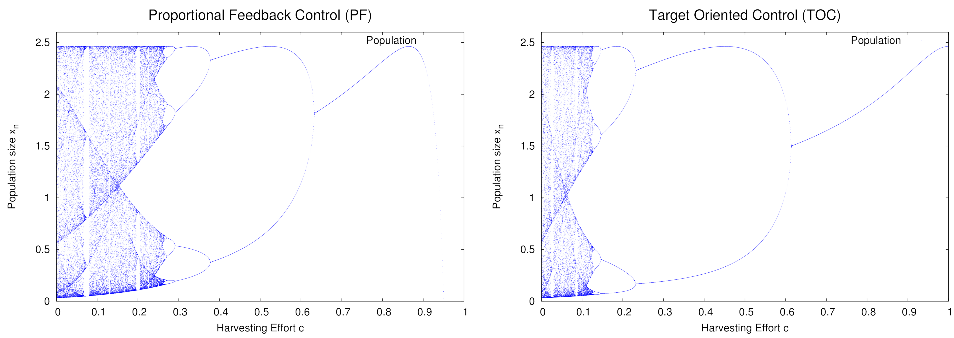

Figure 3: Orbit diagrams of the PF and TOC methods applied before reproduction to the Ricker map (5) with $r = 3$. The control parameter varies in $[0, 1]$ for PF and TOC. For TOC we have fixed the target size as $1/3$.

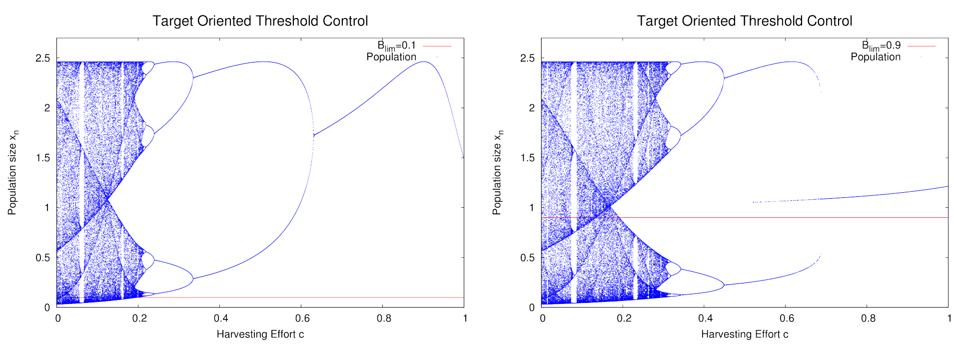

Figure 4: Orbit diagrams of TOTC as the harvesting effort varies for $B_{lim} = 0.1$ (left) and $B_{lim} = 0.9$ (right). Increasing the harvesting effort a fixed point is stabilized in both cases. This stabilization takes place for a much smaller harvesting effort in the case $B_{lim} = 0.9$ than when $B_{lim} = 0.1$. In case $B_{lim} = 0.9$ the fixed point gains stability after a border collision bifurcation and not after a period halving bifurcation (case $B_{lim} = 0.1$). Additionally, for $B_{lim} = 0.9$, there is bistability. In a considerable range of harvesting efforts the fixed point coexists with a different attractor. Whereas for $B_{lim} = 0.1$ the fixed points seems to be a global attractor.

first one is *bistability*: after its stabilization the positive equilibrium coexists with an asymptotically stable cycle which disappears in a saddle node bifurcation generating *hysteresis* (see Strogatz, 1994, and the discussion for more details about the consequences of hysteresis). The second new phenomenon is how the stabilization of the positive equilibrium is attained. Instead of the commonly present smooth period halving bifurcation, in the case $B_{lim} = 0.9$ this stabilization seems to take place by means of a border collision bifurcation (Di Bernardo et al., 2008) and the positive equilibrium suddenly gains stability.

We note that the bistability causes a strong variability in the frequency (calculated as the number of times that the population is above B_{lim} during a fixed number of generations divided by that number of generations) and curtailment (calculated as the total population harvested during a fixed number of generations) depending on the initial population size (results not shown).

It is convenient to remark the following with respect to the bistability. We have chosen $c \in [0, 1]$ in TOTC to guarantee that the control does not send the population below the Biomass at the limit. The control method TOC was considered in just that situation by Franco and Liz (2013). But Dattani et al. (2011) introduced TOC for $c \geq 0$, and they show that bistability is present for TOC if $c \geq 1$. This last bistability is not the source of the one reported here.

4.2. Proportional Threshold Control

Now, let us consider PTC. In Figure 5 we have plotted the orbit diagrams for $B_{lim} = 0.3$.

In contrast to what happens for PF and TOT, we observe that an increase in the harvesting effort in certain intervals can augment the population variability. For example, when increasing the harvesting effort from $c = 0.225$ to $c = 0.4$, the attractor changes from a period four cycle to a period two one, but passing through what seems to be a chaotic attractor and cycles of different periods (Figure 5 below left). We have noticed that some of the asymptotically stable period two and four cycles appear for smaller harvesting effort c than if we take for example $B_{lim} = 0.1$, suggesting that a greater Biomass at the limit could help to stabilize certain periodic solutions with less harvesting effort.

We have proved that there is no positive equilibrium if the harvesting effort surpasses a critical value given by expression (7). When crossing that value we observe the existence of cycles with periods equal to the sum of the periods of the two neighboring cycles. This phenomenon is called *Farey*

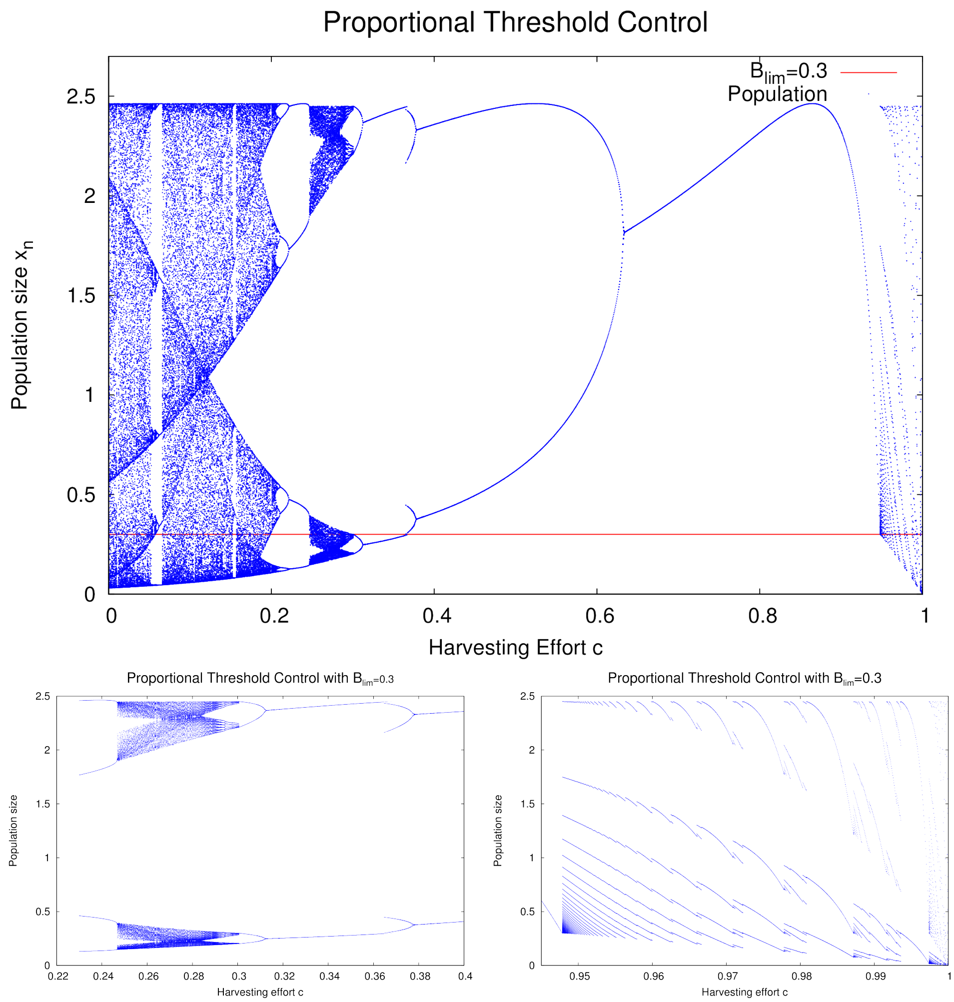

Figure 5: Orbit diagrams of PTC as the harvesting effort varies for $B_{lim} = 0.3$. Above for the whole range of control parameter c and below for two selected subintervals of harvesting efforts. Observe how the population variability increases as the harvesting effort increases from $c = 0.225$ to $c = 0.4$ (below left): the attractor changes from a period four cycle to a period two one, but passing through chaotic and periodic attractors. Also observe that, for very high harvesting efforts (below right), PTC generates a Farey tree instead of the extinction of the population that PF produces (see Figure 3).

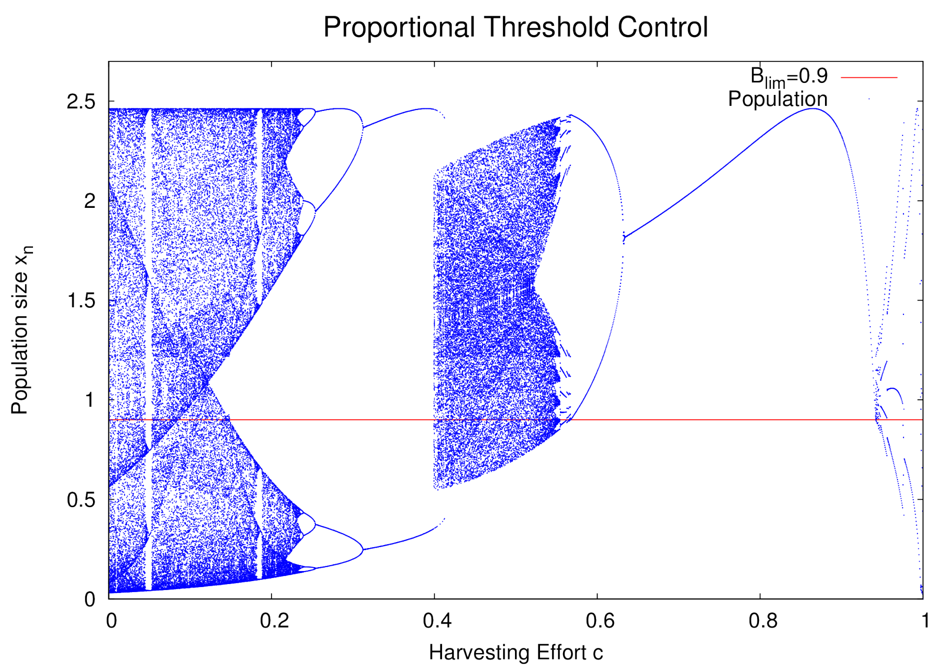

Figure 6: Orbits diagrams of PTC for $B_{lim} = 0.9$. Increasing the harvesting effort can augment the population variability. For $c \approx 0.35$ there is an attracting cycle of period two; whereas for $c \approx 0.41$ the diagram suggests the coexistence of two attractors: a cycle and a chaotic attractor created in a border collision.

tree. See Di Bernardo et al. (2008) for more details on this type of behaviour and Figure 5 (below right) for a detailed region of the orbit diagram where the described phenomenon is easier to observe. We note that these cycles only take values in the interval $(\epsilon_c, f(B_{lim})]$, with $\epsilon_c > 0$ for each parameter $c < 1$. Therefore, we could add some level of stochasticity in the model and the risk of extinction will be avoided even if the critical value given by expression (7) is surpassed by a certain amount which increases with B_{lim}.

Figure 6 shows the orbit diagrams of PTC for $B_{lim} = 0.9$. We observe as in the case $B_{lim} = 0.3$ that increasing the harvesting effort can augment the population variability. For example, for $c \approx 0.35$ there is numerical evidence of an attracting cycle of period two; for $c \approx 0.41$ the diagram suggests the coexistence of two attractors: a cycle and a chaotic attractor created in a border collision. That chaotic attractor is present until it disappears in another border collision and the controlled system has again only an attracting period two cycle. Further increasing the harvesting effort, such a cycle collapses in a positive asymptotically stable equilibrium after a period halving bifurcation.

In contrast to TOTC the stabilization of the fixed point occurs at the same harvesting effort than for $B_{lim} = 0.3$. This is in accordance with Proposition 2, which states that the stabilization occurs for $c = c^*$ independently of $B_{lim} \in [0, K]$.

4.3. Biomass at the limit greater than the carrying capacity

To finish this section, let us suppose that $B_{lim} > K$. We recall that setting B_{lim} is a precautionary measure. Therefore, considering $B_{lim} > K$ seems to be not realistic and we include it here only for the completeness of our theoretical study.

The Proportional Threshold Control PTC is still able to stabilize a positive equilibrium if $B_{lim} > K$ (see Figure 7 left). However, as B_{lim} increases, the interval of values for the harvesting effort c which stabilizes the system towards an equilibrium, shrinks around the value $1 - \frac{d}{f(d)}$ (where the superstability of the equilibrium is guaranteed) and chaotic behaviour is near by. Therefore, there is a high risk that a small perturbation provokes undesirable effects. We remark that it is possible to calculate the exact size of the above mentioned shrinking interval of harvesting effort. Indeed, following the ideas in the proof of Proposition 2 and noting that in this situation the set $f^{-1}(B_{lim})$ has exactly two values, it is not difficult to see that the controlled map has an asymptotically stable positive equilibrium for each

$$c \in \left(\max\left\{ c^*, 1 - \frac{\max f^{-1}(B_{lim})}{B_{lim}} \right\}, 1 - \frac{\min f^{-1}(B_{lim})}{B_{lim}} \right),$$

where c^* is defined in Proposition 2.

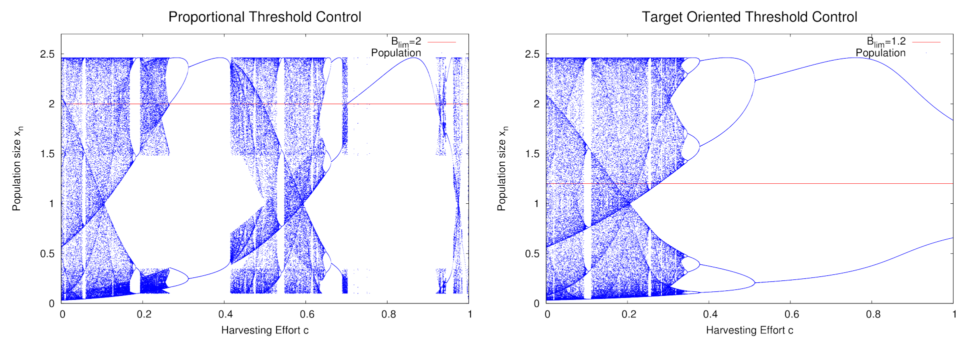

Figure 7: Carrying capacity K inside the subsistence interval $[0, B_{lim})$. On the left PTC with $B_{lim} = 2$ and on the right TOTC with $B_{lim} = 1.2$. PTC still stabilizes an equilibrium, but oscillatory behaviour is near by. TOTC is not longer able to create an attracting fixed point, but increasing the harvesting effort TOTC still stabilizes cycles.

Contrary to PTC, assuming $B_{lim} > K$ obstructs the existence of an asymptotically stable positive equilibrium for TOTC. Nevertheless, the harvesting effort maintains its stabilizing effect and the population is driven towards asymptotically stable cycles as the harvesting effort increases. We observe that for $B_{lim} = 1.2$ the stabilization of a period two cycle is attained (Figure 7 right). If B_{lim} is larger, then the stabilized cycle has a bigger period, for example, we have observed that for $B_{lim} = 2.0$ it has period four.

We note that in this situation the carrying capacity $K = 1$ of the uncontrolled system is an unstable equilibrium for the controlled system for any $c \in [0, 1)$.

5. Discussion

We have investigated the effects of two different harvesting threshold control methods on the dynamics of one-dimensional discrete time population models. Although we have mainly dealt with the situation in which the control is performed before reproduction, our results are valid in the post-reproductive case as well.

In Proposition 1 and Proposition 2, under certain general conditions for population models and if B_{lim} is smaller than the carrying capacity, we have proved that PTC and TOTC are able to stabilize a positive equilibrium. Besides, we have shown that increasing the threshold B_{lim} does not affect (TOTC) or almost does not affect (PTC) a stable exploited population as long as B_{lim} remains under the carrying capacity. We note that having $B_{lim} < K$ seems a natural assumption from a management perspective.

Our results contradict the conclusion in Costa and Faria (2011) that excessively protective threshold densities induce cyclic behaviour in an otherwise stable exploited population. The reason for this difference lies in the definition of the control (9) considered in Costa and Faria (2011), which introduces a delay between the moment in which the population is measured to know if it is greater than the threshold and the moment in which the harvesting takes place.

Furthermore, our results show that, independently of the size of B_{lim}, for a low harvesting pressure c the analysed system is unstable under the proposed controls. This suggests that the harvesting pressure plays a more important role in the stabilization of the chaotic system than the threshold size. Nevertheless, in the case of TOTC we could see that increasing B_{lim} helps to create an asymptotically stable population for wider intervals of harvesting efforts. This last comment must not be misunderstood. As we will discuss soon, such an asymptotically stable population could have a small basin of attraction, coexisting with another attractor.

There exists a substantial relationship between PTC and TOTC and PF and TOC. This relationship is not an obstacle for important differences in their behaviour. For example, while the harvesting control method PF verifies that an increase in the harvesting effort simplifies the dynamics of the system (Liz, 2010b), for PTC such an increase can lead to a higher variability. This type of behaviour was reported in systems (see Dennis et al., 1997; Zipkin et al., 2009) and recently in one-dimensional maps by either considering external noise and changes in the demographic structure (Anderson et al., 2008), or by using a model that includes density-independent survivability of adults, i.e. a sort of age-structure (Liz and Ruiz-Herrera, 2012). We want to highlight that our numerical simulations show that this higher variability can also be produced by harvesting/thinning in nonoverlapping populations without age-structure but where a subsistence interval is established. This could be considered an unexpected effect, because considering a Biomass at the limit models a preventive measure. However, we believe that it is a natural effect when the behaviour of the population is complex since leaving an uncontrolled interval of population sizes preserves the potential variability of the species.

Another difference with respect to PF and TOC is that the stabilization of the positive fixed point can be achieved without a cascade of period halving bifurcations. We have observed *border collision* bifurcations (see Di Bernardo et al., 2008), linked to the piecewise-smooth character of the controlled maps, in which an unstable fixed point changes to an asymptotically stable one (see Figure 4 right).

For PF and TOC, the stabilized positive equilibrium is unique if f satisfies certain conditions. This uniqueness elicits the following key question: Under which additional conditions on f does the local stability of the positive equilibrium guarantee its global stability for the controlled map? Of course, this issue has relevant consequences from a practical point of view and has been considered in several control methods (Franco and Liz, 2013; Liz, 2010b; Schreiber, 2001). Having a negative Schwartzian derivative was enough for PF and TOC because the results of Singer (1978) can be employed, since those controls do not affect the sign of the Schwartzian derivative. However, the presence of bistability in our numerical simulations shows that this condition is not enough for PTC and TOTC.

In our opinion the appearance of bistability is the main drawback of TOTC when compared with TOC. We have shown the existence of bistability between a cycle of period two and the stabilized positive fixed point (see Figure 4 right). This means that the population, depending on its initial size, can be driven towards different states. The coexistence of these two different attractors generates a phenomenon called hysteresis, in which a small decrease in the harvesting effort can, for example, move the population from an attracting fixed point to a large amplitude period two cycle, and increasing the harvesting effort again will not reverse the situation (see Strogatz, 1994). Moreover, this coexistence also produces that the frequency and amount of harvest vary notably depending on the initial population size. Bistability is also possible for PTC, for example between cycles and chaotic attractors (see Figure 6). Notice that this bistability of TOTC and PTC does not appear in Figures 1 and 2 because we chose there the same fixed initial condition. If instead we choose a random initial population for each pair of parameters (c, B_{lim}), we obtain the graphs in Figure 8, clearly showing areas of bistability.

In addition to the previously discussed global stability issue, our study suggest some research directions to follow. First, stopping the harvest completely when the population size is lower than the threshold can be considered an extreme measure. Instead, a less intensive harvest may be tolerable. It would be interesting to know what characteristics of PTF and TOTC would be inherited for such policies. Second, as we have pointed out, bistability is the main drawback of TOTC and PTC and we have not dealt with the key issue of the sizes and properties of the basins of attraction of the coexisting attractors, which would be certainly useful from a management point of view. Third, we have focused on models with overcompensation and without Allee effect, so a natural question is which (if any) of the properties can be extended to models with undercompensation and/or Allee effect. And fourth, the analysed strategies could be implemented, in principle, in experimental microcosms (see Fryxel et al., 2005) to try observe the behaviours we have found here.

Summarizing, our research points out that normal protective threshold densities do not induce cyclic behaviour in an otherwise stable exploited population and are valid control of chaos methods under certain conditions. However, the appearance of bistability, among other new phenomena, suggests to take cautionary measures when employing these harvesting strategies to stabilize the population.

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Appendix

In this appendix we prove the stability results presented in Section 3. We begin with the proof of Proposition 1 about TOTC. As we have remarked, this control does not modify the continuous character of the uncontrolled map and we can take advantage of that property.

Proof of Proposition 1

If $B_{lim} \geq K$, then the existence of at least one positive equilibrium is trivial since the carrying capacity K of the uncontrolled map is also a positive equilibrium for the controlled map.

If $B_{lim} < K$, then we have by (A2)

$$f(g_2(B_{lim}, c, B_{lim})) = f(B_{lim}) > B_{lim},$$

and by (A3)

$$f(g_2(B_{lim}, c, f(d))) - f(d) < 0.$$

Therefore, we can apply Bolzano's Theorem to guarantee the existence of at least one fixed point of the controlled map in the bounded interval $(B_{lim}, f(d))$.

In the interval $(B_{lim}, f(d))$, the derivative of the controlled map satisfies

$$(f \circ g_2)' = (1-c)(f' \circ g_2).$$

Thus, since $g_2(B_{lim}, c, x) \in (B_{lim}, f(d))$ for $x \in (B_{lim}, f(d))$, taking c greater than

$$\max\left\{0, 1 - \frac{1}{\sup_{x\in(B_{lim},f(d))} |f'(x)|}\right\}$$

is enough to guarantee that any fixed point in the interval $(B_{lim}, f(d))$ is asymptotically stable. □

Next, we prove the stability result related to PTC.

Proof of Proposition 2 Following the proof of (Liz, 2010b, Theorem 1) we obtain that, for the assumed conditions, there exists a unique positive fixed point K_c for the map

$$f((1-c)x) \tag{10}$$

for each c between $c = 0$ and $c_1 = 1 - 1/f'(0)$. The value of K_c coincides with the ordinate of the intersection between the graph of f and the line $(1-c)y = x$. Moreover, the map

$$\begin{array}{rcc} P\colon [0, c_1) & \to & (0, f(d)] \\ c & \to & K_c, \end{array}$$

is increasing in $(0, 1 - \frac{d}{f(d)})$; decreasing in $(1 - \frac{d}{f(d)}, c_1)$; and satisfies $P(0) = K$, $P(1 - \frac{d}{f(d)}) = f(d)$, and $\lim_{c\to c_1} P(c) = 0$.

Now, since $B_{lim} < K$, the controlled map $f(g_1(B_{lim}, c, x))$ has no fixed points on $[0, B_{lim}]$ for any $c \in [0, 1]$. Besides, K_c is a fixed point of $f(g_1(B_{lim}, c, x))$ if and only if K_c is a fixed point of (10) and satisfies the additional condition $B_{lim} < K_c$.

By (A1)-(A4) the set $f^{-1}(B_{lim})$ has at most two values and the minimum of them satisfies $\min f^{-1}(B_{lim}) < d$ and $1 - \frac{\min f^{-1}(B_{lim})}{B_{lim}} \in \left(1 - \frac{d}{f(d)}, c_1\right)$. Moreover, it is not difficult to verify that

$$P\left(1 - \frac{\min f^{-1}(B_{lim})}{B_{lim}}\right) = B_{lim}.$$

Therefore, by the monotonicity properties we have recalled for P, we have

$$P(c) > B_{lim} \quad \Leftrightarrow \quad 0 \le c < 1 - \frac{\min f^{-1}(B_{lim})}{B_{lim}},$$

and we have proved the first affirmation of the result.

Proving the last affirmation of the result is just following the reasoning for the asymptotic stability in the proof of Liz (2010b, Theorem 1), so we omit it. □

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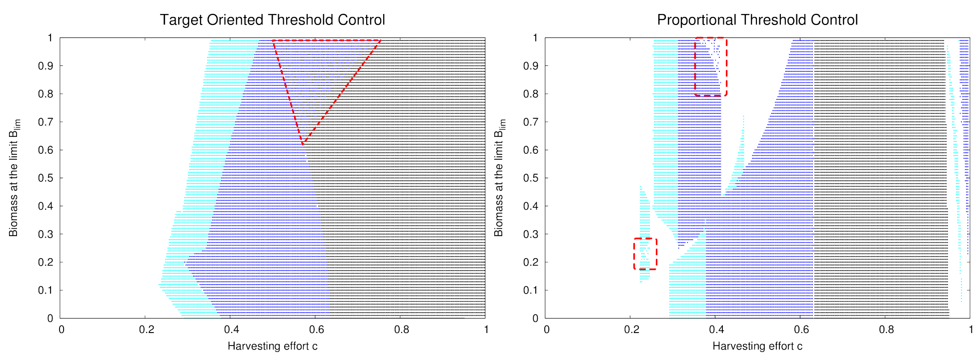

Figure 8: Asymptotic dynamics of the controlled system obtained as in Figure 1 and 2, but choosing a different pseudo-random initial condition for each pair (c, B_{lim}). See Figure 1 for an explanation of the meaning of the different colours. The triangle indicates an area of bistability between a fixed point and a period two cycle for TOTC. For PTC there also exists bistability in some areas, for example the ones enclosed with rectangles, but it seems that it never occurs between an attracting fixed point and whatever other attractor.