UNIVERSITÄT OSNABRÜCK

Beiträge des Instituts für Umweltsystemforschung
der Universität Osnabrück

Herausgeber: Prof. Dr. Michael Matthies

Beitrag Nr. 32

# Control of chaotic population dynamics: Ecological and economic considerations

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November 2005

Institut für
Umweltsystemforschung
Universität Osnabrück

ISSN-Nr. 1433-3805

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**ISSN 1433-3805**

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# Contents

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# Control of chaotic population dynamics: Ecological and economic considerations

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**Abstract**

The increasingly acknowledged role of chaos in population dynamics involves severe implications for the management of species. So-called violent oscillations may lead to small densities making possible population extinction as well as to high densities making the population susceptible for disease outbreaks or over-crowding. This contribution provides an astonishingly simple approach to deal with both mentioned cases. It is based on effectively controlling irregularly fluctuating populations with threshold mechanisms, which can also be used to model basic ecological processes such as immigration or refuges. Its application is investigated with respect to the required effort, robustness against noise and planning reliability (variance reduction). Limiter control proves to be a powerful tool in controlling populations, but decision-makers have to be aware that well-intended management measures can have the exactly opposite effect in certain situations. The results also indicate that chaos may be difficult to detect in real populations due to limitations by environmental conditions.

**Keywords:** Population dynamics, chaos control, limiter, threshold, difference equation.

# 1. Introduction

The control and the management of population dynamics is one of the main objectives of mathematical modelling in ecology. The prediction of optimal harvesting rates, for

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instance in fishery or forestry, is intended to guarantee a sustainable development and optimal yields. Other examples include the control of pest species, e.g. in agriculture, epidemics, invasions of exotic species or genetically modified organisms – each of them causing possibly catastrophic ecosystem-breakdowns, severe economic damage or enormous threats on health (Shigesada and Kawasaki, 1997; Kot, 2001; Murray, 2002; Edelstein-Keshet, 2005, and references therein).

Mathematical models have been used to estimate the effects of different management scenarios such as harvesting, culling, hunting, poisoning, vaccination, quarantine, immunocontraception, barrier zones, release of sterile individuals, predators or competitors (e.g. Holling, 1978; Lewis and van den Driessche, 1993; Sharov and Liebhold, 1998; Courchamp and Cornell, 2000; Murray, 2002). In the context of conservation biology, management conversely aims at stabilizing endangered populations. Possible measures include habitat management, e.g. the construction of corridors or stepping-stone population patches, or the introduction of additional individuals to support the focal population.

Since the seminal work of May in the mid-1970s (May, 1974; May and Leonard, 1975; May, 1976; May and Oster, 1976), it has been recognized that even simple deterministic population models have the potential for erratic fluctuations. This has made chaos an ongoing topic among theoretical ecologists (Hassell et al., 1976; Gilpin, 1979; Takeuchi and Adachi, 1983; Hastings and Powell, 1991; Allen et al., 1993; Hanski et al., 1993; Ellner and Turchin, 1995; Vayenas and Pavlou, 1999; Perry et al., 2000; Cushing et al., 2003; Kooi and Boer, 2003; Turchin, 2003). Mathematical models do suggest that aperiodic oscillations are ubiquitous in time and space, and play an important as well as contructive role in stabilization and self-organization. At the same time, the occurence of chaos in real-world populations remains controversial. Sceptic arguments include that irregular oscillations may be induced by superimposed noise or that the "violent" chaotic oscillations leading to partially small densities are prone to population extinction, and species thus evolve towards a more stable dynamic behaviour. However, there is increasing experimental evidence in favour of chaotic population dynamics (Costantino et al., 1995, 1997; Becks et al., 2005).

McCallum (1992) found that chaotic population dynamics change to simple cyclical behaviour in a wide parameter range if a simple constant of external recruitment is added. This recognition was picked up by Stone (1993), who showed that a small perturbation is enough to break down the period-doubling route to chaos. Parthasarathy and Sinha (1995) introduced this approach into the physics literature as the constant feedback control. Doebeli (1993) applied certain adjustments to the growth rate, thus driving the population to a stable state. Doebeli and Ruxton (1997) and Solé et al. (1999) next investigated the proportional feedback method by Güémez and Matías (1993), the former in the context of metapopulations and the latter in the context of population dynamics as well as continuous-time and individual-based models. Various control schemes have been explored by Gamarra et al. (2001) and applied to a tritrophic time-continuous model. Gamarra and Solé (2000) had already shown that varying trapping effort in this model can explain the sudden shifts in the amplitudes of the lynx oscillations which are observed in the Hudson Bay Company records – one of the most popular data sets in ecology. Their system presumes a minimum bound for the lynx, which is modelled by an additive constant and may be biologically explained by the possible existence of alternative prey. Schwartz et al. (2004) derive vaccine strategies in a stochastic model of measles, in order to suppress epidemic outbreaks before they occur. Hudson et al. (1998) present very interesting data from field experiments in which the parasitic nematode *Trichostrongylus tenuis* has been removed from individual red grouses (*Lagopus lagopus scoticus*). By treating estimatedly 15-50% of a population, cyclic population crashes as well as the variance in population density have been clearly reduced. Desharnais et al. (2001) made further progress by studying the outbreak control of the flour beetle *Tribolium castaneum*. They did not only simulate a three-dimensional system describing the different insect stages, but they also experimentally demonstrated that the introduction of a few adult individuals in a laboratory population results in a dampening of the fluctuations.

In this contribution, we shall propose the application of a very simple control scheme to population models with non-overlapping generations, which can be described by a single nonlinear difference equation. The idea is based on a threshold mechanism: In each time the population density exceeds a certain threshold density $h$, it is simply reset to $h$, e.g. by way of hunting or some other method appropriate for the given situation. The threshold can be determined as a critical density above which infectious diseases may spread or there are losses due to competition or overcrowding. There may be also environmental restrictions which prevent the population from reaching its intrinsic carrying capacity. Alternatively, the threshold can also be applied as a lower threshold. This reflects the introduction of additional individuals or the existence of a refuge within the population. Immigration could also be modelled in this way, especially if the population experiences a strong rescue effect (Brown and Kodric-Brown, 1977) and is recolonized from other patches in a source-sink or meta-population (e.g. Allen et al., 1993).

This simple control mechanism was explored theoretically in a physics context with the aim to control chaotic dynamics. Ott et al. (1990) had shown that asymptotically small perturbations can stabilize natural states of the uncontrolled chaotic system. But this requires much knowledge of the system's state. Corron et al. (2000) were the first who experimentally stabilized unstable periodic orbits using simple limiters, with the goal to use the least possible effort. They introduced the term *limiter control*. We will use this term throughout this contribution, though we will consider a fixed threshold which corresponds, to be precise, to a hard limiter (Wagner and Stoop, 2001; Stoop and Wagner, 2003). The dynamics of limited (flat-topped) maps had already been analyzed by Glass and Zeng (1994), and Sinha (1994) studied limiters in the sense of external, applied control.

This contribution is outlined as follows. In the next section, limiter control is applied to the well-known logistic map (e.g. Collet and Eckmann, 1980; Kaplan and Glass, 1995). As it turns out, a limiter from above results in a higher mean population density. At least at first sight, this paradoxic result seems to be somehow counterintuitive. As will be demonstrated, this paradoxon is due to a simple restriction of the phase space. The usage of limiter control is studied with respect to (i) noise, (ii) reduction of variance and (iii) the required effort. The next section deals with another chaotic population model, namely that of Ricker (1954). Since the Ricker model has some other specific features than the logistic model, different results can be observed. In section 4., the point of view is shifted from control from above (e.g. in the sense of optimal harvesting) to control from below (e.g. in the sense of supporting threatened species). Finally, the usage of limiter control in population modelling and its pitfalls are discussed and related to similar work.

# 2. Limiter control of the logistic map

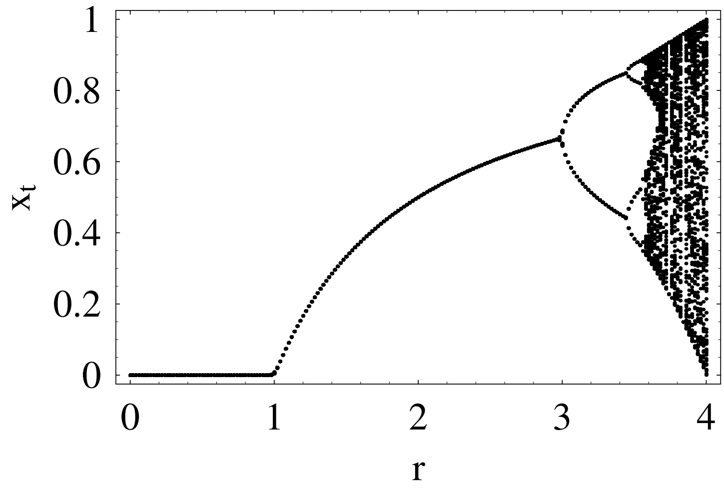


Figure 2.1: Bifurcation diagram of the logistic map (2.2).

Let $x_t$ be the density (or abundance) of a population in year (or generation) $t, t \in \mathbb{N}$. Then the time series of the population densities is given by the difference equation

$$x_{t+1} = f(x_t) \tag{2.1}$$

and an initial value $x_0 > 0$, where $f(x_t)$ is for density-dependent models a nonlinear function of $x_t$. The logistic map is a well-known model of density-dependent growth. It can be described by the quadratic function

$$f(x_t) = r(1 - x_t)x_t \ . \tag{2.2}$$

This is the scaled version where the interval $0 \leq x_t \leq 1$ is invariant for $0 \leq r \leq 4$. The parameter $r > 0$ is the intrinsic growth rate. Fig. 2.1 shows the bifurcation diagram of the logistic model, i.e. all the asymptotically occuring densities are plotted for each value of the parameter $r$. Note that in this and in all other Figures, the asymptotic densities have been restricted for computational reasons to 128 values after an initial time of 100 generations. It is well-known, that there may be up to two fixed points of the logistic map. The trivial solution $x^{*_0} = 0$ is stable for $r < 1$ and becomes unstable for $r > 1$, where the nontrivial solution

$$x^{*_1} = \frac{r}{r-1} \tag{2.3}$$

emerges. This fixed point is stable for $1 < r < 3$. For $r > 3$, a cascade of period-doubling flip bifurcations takes place. For $r_\infty = 3.5699...$, chaotic dynamics interwoven with periodic windows can be observed. A chaotic time series is shown in Fig. 2.2a for $r = 4$.

## 2.1 Hard limiter control and its paradoxic effect

Let us now apply limiter control from above to the logistic map. Then eq. (2.2) becomes

$$f_h(x_t) = \min\{r(1 - x_t)x_t, \ h\} \tag{2.4}$$

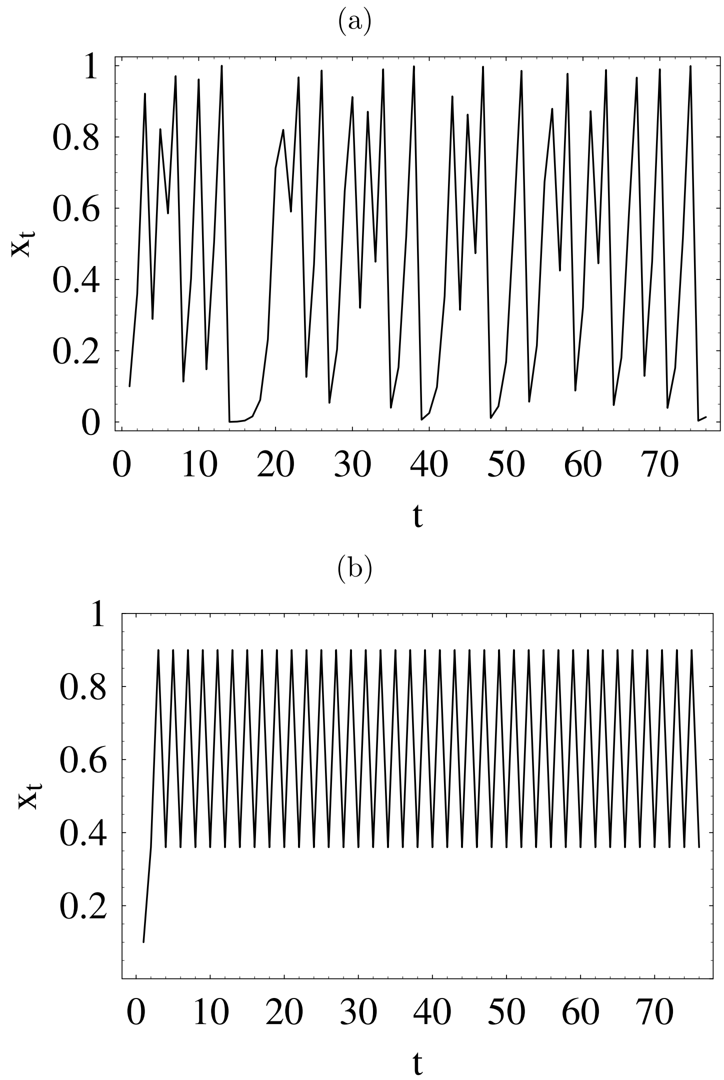


Figure 2.2: Time series of the logistic map (2.2) in the chaotic regime (a) and with hard limiter control (b). Parameter values: $r = 4, x_0 = 0.1, h = 0.9$.

with the limiter $h \in (0, 1)$. The resulting time series for $r = 4$ and $h = 0.9$ is shown in Fig. 2.2 b. The formerly chaotic dynamics has been forced to a periodic oscillation. This aspect will be addressed again below. Now, however, it should be noticed that the mean density $\bar{x}$ has increased to 0.612... (compared to 0.511... in model (2.2) without limiter; 1000 generations each, $x_0 = 0.1$). Fig. 2.3 depicts the asymptotic dynamics of the controlled model depending on the limiter $h$. For $h = 1$, the dynamics is still chaotic, but already for a slightly smaller $h$ the oscillations become periodic. At around $h = 0.9$ there appears a two-cycle, which amplitudes decrease with $h$ and vanish at $h = 0.75$, where the fixed point $x^{*1}$ is met. For $h < 0.75$, the dynamics are simply forced to the limiter. The mean densities are over a wide range of limiters clearly larger than the mean density of the logistic map without limiter control. This is a counterintuitive result, since the density has been limited from above, and one would expect a decreasing mean.

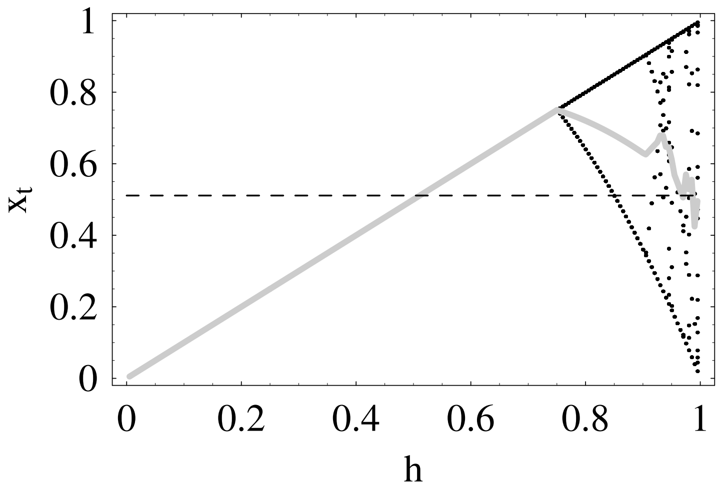


Figure 2.3: Bifurcation diagram of the limiter-controlled logistic map (2.4) with $r = 4$. The grey line represents the mean of the asymptotic densities. The dashed line corresponds to the mean density of the logistic model without limiter control.

Note that limiter control has already been applied by Wagner and Stoop (2001) to the logistic map. Here, we provide to our knowledge the first study in population biology context and therefore want to highlight the paradoxic effect, that the limiter control aimed at reducing the population density results in the probably non-intended increase in mean density, which shall be referred to as paradox of simple limiters.

An intuitive explanation of this paradox is given in Fig. 2.4. The well-known cobwebbing algorithm is applied both to the logistic map and its limiter-controlled variant. The algorithm starts at $x_0 = 0.5$, because from there the maximum of the logistic map is reached. This allows the dynamics to be mapped back to the descending branch intersecting the abscissa. Hence, in the chaotic regime the ergodic orbit fills out the whole interval $[0, 1]$. Conversely, in the limiter-controlled model the mapping cannot explore the whole descending branch, because the top is cut off. The dynamics is thus restricted to a much smaller interval. The differences in possible densities are highlightened in thick grey. One can easily see that the missing lower interval is a larger one than the missing upper interval. This means that the state interval is "shifted up", which explains the larger mean density.

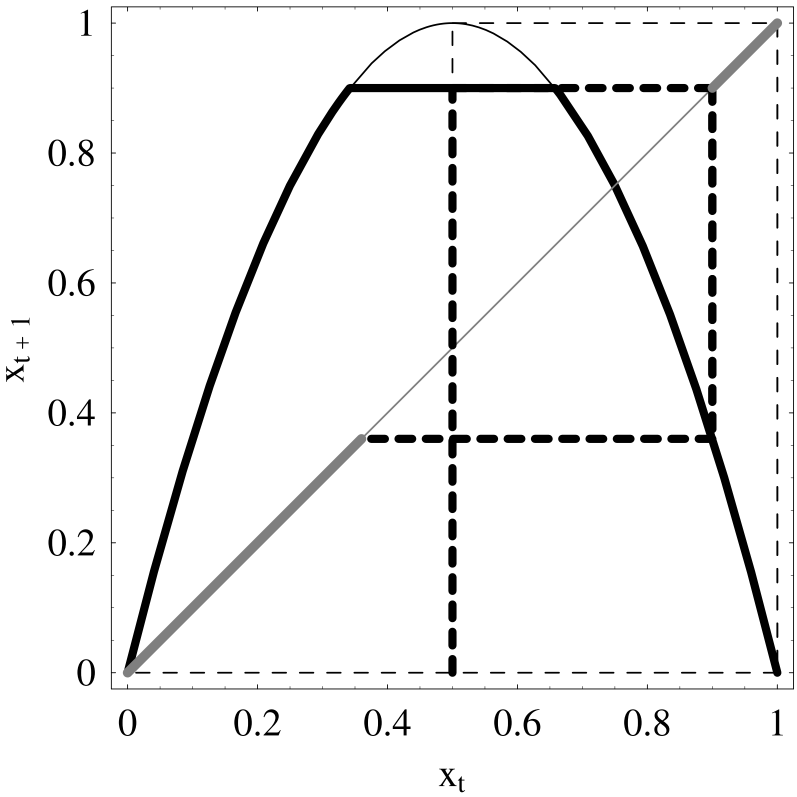


Figure 2.4: The quadratic mapping (thin line) and its flat-topped limiter control variant (thick line). The cobwebbing is displayed in respective dashed lines. The diagonal is shown in a grey line, and the difference in the intervalls pronounced in thick grey lines. Parameters: $r = 4, h = 0.9, x_0 = 0.5$.

The flat-topped mapping also explains why the limiter-controlled dynamics becomes forced to periodic oscillations or stable fixed points (Glass and Zeng, 1994; Sinha, 1994; Wagner and Stoop, 2002). Once an orbit reaches the cut-off region (and due to the ergodicity it will), the image will always be the same. Hence, the system is trapped in a superstable cycle (Glass and Zeng, 1994). The length of this cycle can easily be determined (Sinha, 1994). If the $k$-th iterate of $f(x_t)$ exceeds the limiter $h$, then a period $k$ is obtained. Thus one could principally compute the mean density. Generally, flat-topped unimodal maps cannot exhibit chaotic motion. Although they undergo a course of period-doubling, they show an exponential convergence towards the period-doubling accumulation point (Wagner and Stoop, 2002). For the chaotic regime the mean density can be calculated as well. This is demonstrated in Peitgen et al. (2004), pp. 485, for $r = 4$.

## 2.2 Noise

The simplicity of the limiter control is based on the application of a constant threshold, which is independent of the current system state. In real-world situations, however, the deterministic threshold value is very probably not matched exactly or superimposed by noise. In this subsection, the impact of a stochastic limiter on the resulting dynamics shall be investigated. The model (2.4) is extended to a version with multiplicative noise in the limiter

$$f_{h,\omega}(x_t) = \min\{r(1-x_t)x_t,\ h(1+\omega\xi_t)\}\ , \tag{2.5}$$

where $\omega > 0$ is the noise intensity and $\xi_t$ a Gaussian random variable with mean zero and variance one. Naturally, the dynamics itself is affected by environmental or demographic stochasticity and could be randomized. But since we are primarily interested in the consequences of a noisy limiter, we restrict ourselves to this latter case.

The resulting bifurcation diagrams are shown in Fig. 2.5 for various noise intensities. Since the dynamics is affected by noise, the deterministic orbits are blurred. For larger limiters, this effect is naturally stronger in absolute values. The general shape of the mean density remains qualitatively the same as in the deterministic model. Though the noise has some bluring effect on the mean density as well, the paradox of the simple limiters can still be observed even for a noise intensity as large as $\omega = 0.2$.

## 2.3 Variance

Since limiter control turns the dynamics from chaos to periodicity or stable fixed points, it automatically enables predictability. This might be of special interest from a management point of view, because it guarantees knowledge of the system's future development.

For a reliable exploitability of the system, one might additionally wish variances in the densities as small as possible. In Fig. 2.6, the variances are plotted against the applied limiters. Compared to the variance of the model without limiter, the application of thresholds rapidly reduces the deviations in the system dynamics. With the limiter approaching the nontrivial solution $x^{*_1}$, the variance nearly vanishes. This also holds true for noisy limiters. Only in the extreme case with $\omega = 0.2$, the variance does not disappear immediately, but is still much smaller than in the non-controlled situation.

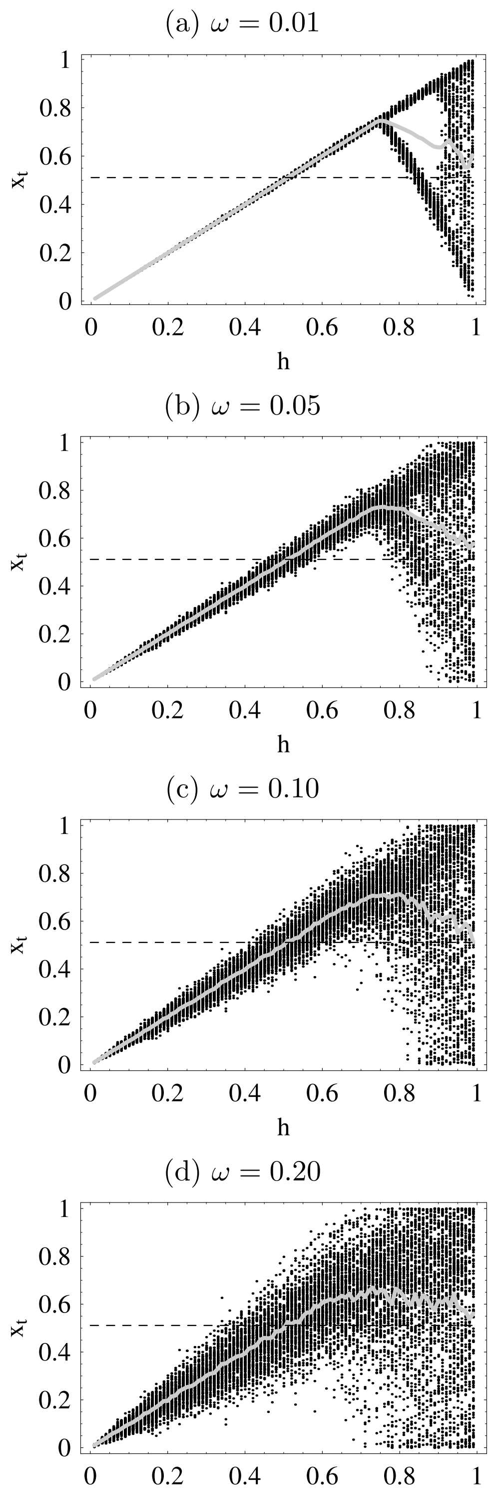


Figure 2.5: Bifurcation diagram of the noisy limiter-controlled logistic map (2.5). Parameters as in Fig. 2.3

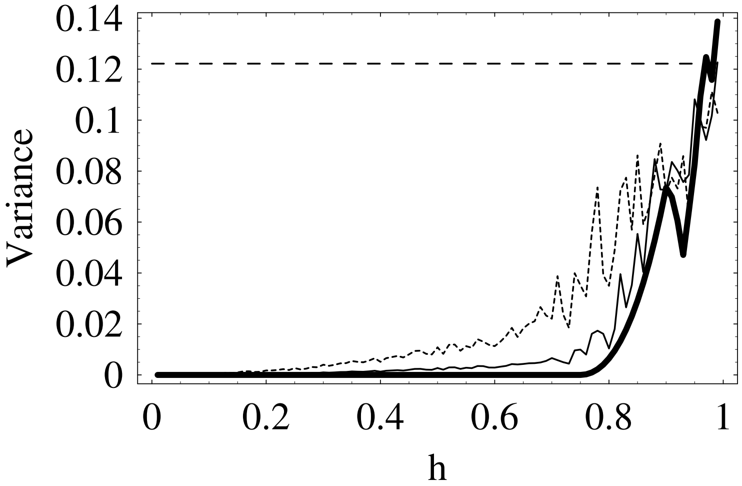


Figure 2.6: Variances in the densities of the limiter-controlled logistic map (2.5) with noise intensities $\omega = 0.0$ (thick line), $\omega = 0.1$ (solid line) and $\omega = 0.2$ (dotted line). The dashed line corresponds to the variance in model (2.2) without limiter control. Other parameters as in Fig. 2.3.

## 2.4 Effort

When applying limiters, one has to follow a single rule, namely to reduce the density to a threshold in the case this threshold is exceeded. How much effort does it cost on average to apply the limiter? Let us first define the effort in a single time step as the absolute difference between the limiter and the image of the mapping if limiter control would not be applied. For example, in the logistic model this is the difference between the thick and the thin dashed lines starting at $x_t = 0.5$ in Fig. 2.4. The effort is only accounted for if the limiter is applied. Averaging over time, one thus obtains the mean effort $E$

$$E = \frac{1}{T} \sum_{t=t_0}^{t_0+T} |f(x_t) - f_{h,\omega}(x_t)| \ . \tag{2.6}$$

Throughout this contribution, the parameters $t_0$ and $T$ are the same as in the bifurcation diagram for determining the asymptotic dynamics, i.e. $t_0 = 100, T = 128$.

The effort is plotted in Fig. 2.7 against the limiter for various noise intensities. In the deterministic case (thick line), one can observe that there is only little effort for a limiter close to unity. Around $h = 0.85$, there is a small hump, but at $h = 0.75$ the effort vanishes. This can be explained as follows. The limiter control induces the orbit to map exactly on the fixed point. In the deterministic model, the system will remain in this state, whereas in the stochastic models each small perturbation will be reinforced, because the fixed point is unstable. As a consequence, there is a minimum of effort if the limiter matches the fixed point $x^{*1}$ as long as there is no or only small noise. For larger noise intensities, the minimum simply vanishes.

For limiters smaller than the fixed point, there is a large maximum of effort around $h = 0.4$. This can be made clear by performing the cobwebbing algorithm. An application of limiter control with such small limiters thus is unreasonable in real-world situations.

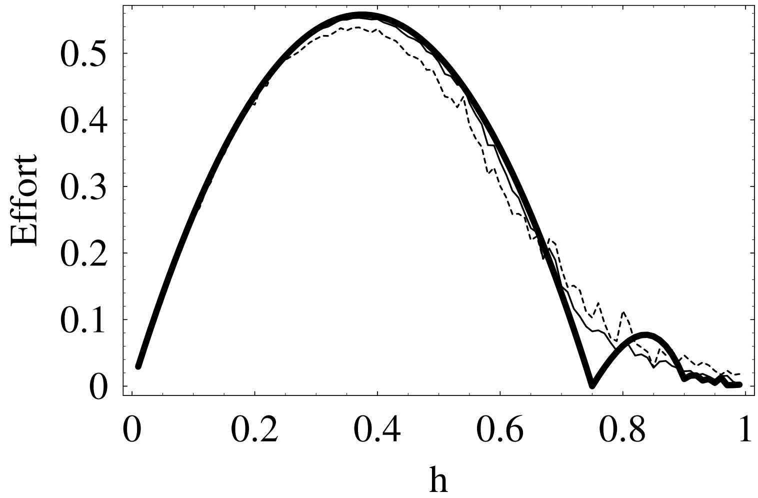


Figure 2.7: Effort as defined in (2.6) of applying limiter control in the logistic map (2.5) with noise intensities $\omega = 0.0$ (thick line), $\omega = 0.1$ (solid line) and $\omega = 0.2$ (dotted line). Other parameters as in Fig. 2.3.

# 3. Limiter control of the Ricker model

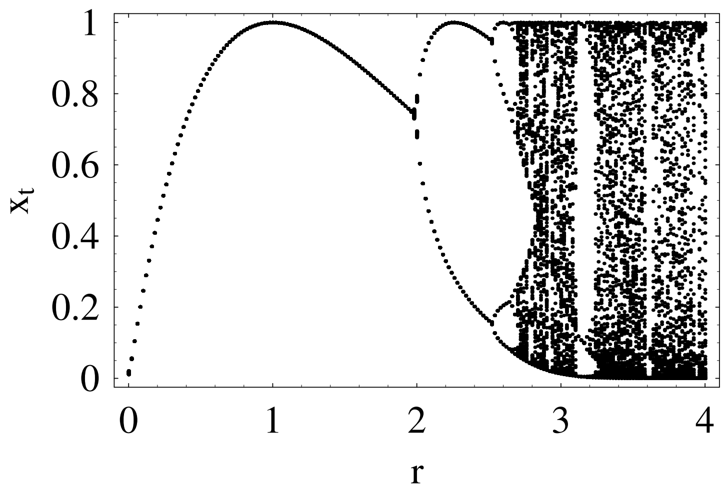


Figure 3.8: Bifurcation diagram of the ricker model (3.8).

In this section, the Ricker model (1954) shall be considered as another example exhibiting overcompensatory behaviour, too, but also some other distinguished characteristics. The Ricker model reads

$$f(x_t) = x_t \exp(r(1 - \frac{x_t}{K})) \tag{3.7}$$

with parameters $r, K > 0$. For the sake of comparability with the logistic map, the above mapping is transformed to obey images within the unit interval just. Therefore, introducing the variable $\tilde{x}_t = rx_t/(K \exp(r(1 - 1/r)))$ and then omitting the tilde for notational simplicity, the above equation can be transformed into

$$f(x_t) = x_t \exp(r - \exp(r-1)x_t) \ . \tag{3.8}$$

The bifurcation diagram with varying parameter $r$ is shown in Fig. 3.8. The trivial fixed point $x^{*0} = 0$ is always unstable. The nontrivial solution

$$x^{*1} = r \exp(1 - r) \tag{3.9}$$

is stable for $r < 2$ and unstable otherwise. From $r = 2$ on, a cascade of period-doubling bifurcation drives the dynamics to chaotic oscillations with some interwoven periodic windows.

## 3.1 Hard limiter control

The limiter-controlled model of (3.8) reads in its stochastic version

$$f_{h,\omega}(x_t) = \min\{f(x_t),\ h(1 + \omega\xi_t)\}\ . \tag{3.10}$$

The bifurcation diagram of the deterministic model with varying limiter $h$ is shown in Fig. 3.9a. As can be expected, the chaotic regime of the non-controlled model is forced to periodic cycles or, in the case that the limiter is at least as small as the nontrivial solution, to a stable fixed point. The mean densities roughly remain at the same level as in the model without limiter control. This holds for basically the whole range of reasonable limiters. Hence, limiter control is a practical tool for guaranteeing that population dynamics do not swap over predetermined limiter thresholds, while at the same time the mean density is nearly conserved. Only for a small interval of limiters, say $0.35 < h < 0.5$, limiter control slightly reduces the mean population density (and, of course, for $h < x^{*1}$). The effect of a noisy limiter is qualitatively the same as for the logistic model. The corresponding figures are omitted for the sake of brevity.
The paradox of simple limiter control as seen for the logistic model cannot be observed for the Ricker model. This is due to the special form of the mapping $f(x_t)$, cf. the sketched cobwebbing algorithm in Fig. 3.10. For large values of $x_t$ $f(x_t)$ decreases, but in such a way that it remains positive. Due to the sharp decline of this convex branch the image $x_{t+1}$ can be mapped back again also to the center of the mapping's top. Though the extent of the possible state space is reduced, as highlighted by the thick grey line, the simulations indicate that the mean of the periodic motion does not differ much from the mean of the chaotic motion.

## 3.2 Variance and effort

Considering the variance in Fig. 3.9b, one can observe that the variations are at about the same level for a large limiter (roughly $h > 0.85$ in the deterministic case and $h > 0.75$ in the cases with stochasticity). But then the variance decreases with decreasing limiter towards (nearly) zero for $h < x^{*1}$, where the orbit is stabilized at the fixed point or the limiter value.
The effort is plotted against the limiter in Fig. 3.9c. There is a minimum at $h = x^{*1}$ for the same reason as explained for the logistic model. There are, however, some more humps. They are due to the cycles with short periodicity as can be seen in Fig. 3.9a. Because the limiting procedure with much "removal" of density has to be performed more frequently, the mean effort is increased. The effect of noise blurs these deterministic extrema.

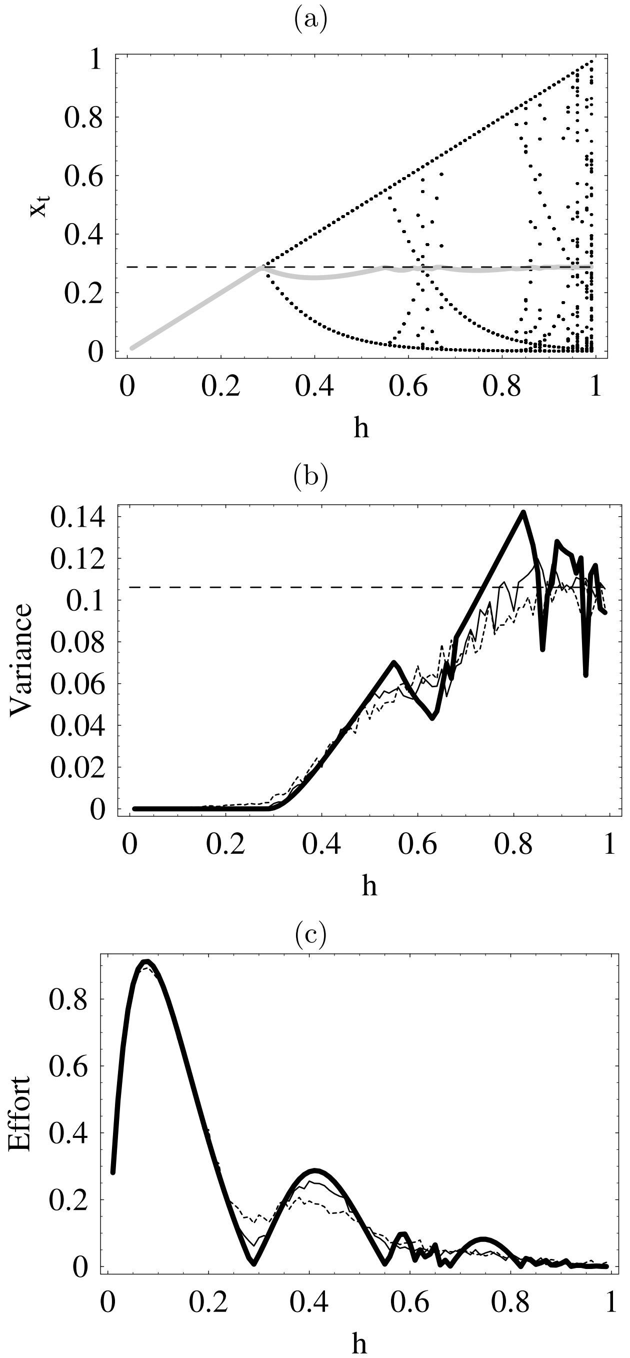


Figure 3.9: Limiter-controlled Ricker model (3.10). (a) Bifurcation diagram and mean densities of the determinsitic model, (b) variances and (c) efforts depending on the limiter $h$. Other parameters as in Fig. 3.8. Parameters: $r = 3.5$, and the noise intensities in (b) and (c) are chosen as $\omega = 0.0$ (thick line), $\omega = 0.1$ (solid line) and $\omega = 0.2$ (dotted line).

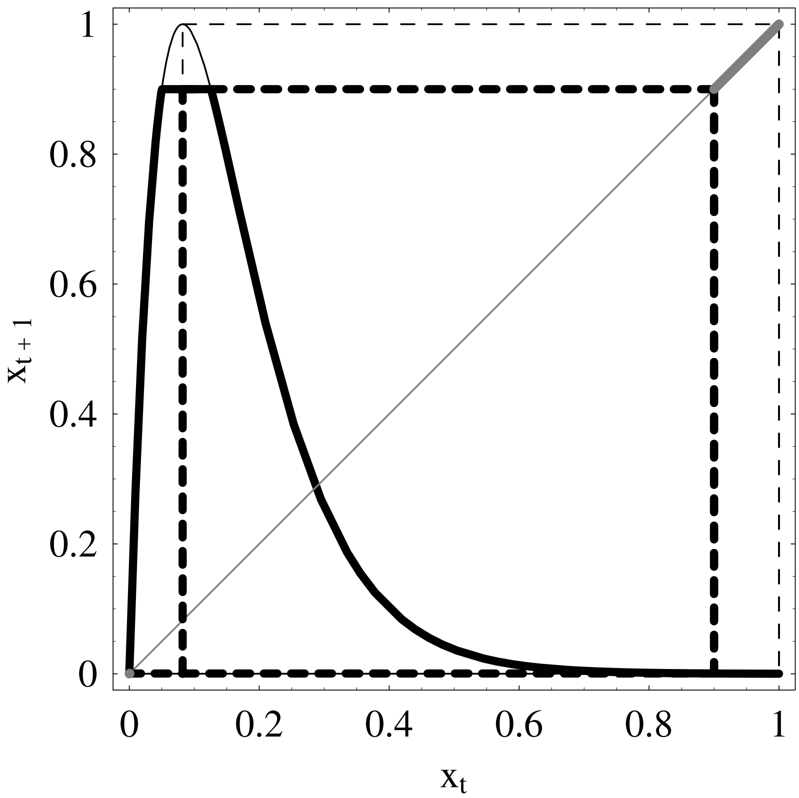


Figure 3.10: The mapping of the Ricker model (thin line) and its flat-topped limiter control variant (thick line). The cobwebbing is displayed in respective dashed lines. The diagonal is shown in a grey line, and the difference in the intervalls pronounced in thick grey lines. Parameters: $r = 3.5, h = 0.9, x_0 = \exp(1 - r)$.

# 4. Limiter control "from below": Population support

So far the limiter has been applied from above, i.e. a maximum operator has been used to pose an upper threshold. This section, in contrast, aims at supporting a population to maintain densities above a certain threshold. Restocking programs are common practice especially in commercially managed populations with the primary aim of incrementing the yield. The rehabilitation of populations is another example of stocking activities. If the densitiy would become too small, the population is prone to extinction because of demographic stochasticity or inbreeding. The (re-)introduction of additional individuals can be a tool to guarantee population persistence at a super-critical level. This situation, which typically arises in conservation biology or in upholding endangered stocks, can be dealt with very easily by applying the limiter control "from below":

$$f_{h,\omega}(x_t) = \max\{f(x_t),\ h(1+\omega\xi_t)\}\ . \tag{4.11}$$

The notations are the same as before. The results are shown in Fig. 4.11 for the logistic map (left column) and the Ricker model (right column). The modified mappings and the corresponding cobwebbing can be seen in the first row (Fig. 4.11a and e, respectively). Analogously to the previous case with a limiter from above, a region of the phase plane is cut off and thus forces the dynamics either on a periodic orbit or, if $h \geq x^{*_1}$, on a fixed point. This is illustrated in the plots of the asymptotic densities against the limiter value $h$ in the second row. For very small limiter values, the mean density in the logistic model decreases (Fig. 4.11b). Anyway, such a small choice of the minimum population density probably would not prevent a possible extinction as a consequence of demographic stochasticity. Because of this, a small, but substantial limiter value can be supposed. If this is set to at least $h = 0.05$, the mean density is in this case significantly increased over a wide range. In the Ricker model, the reduction in the mean density cannot be observed (Fig. 4.11f). Instead, the limiter control immediately enriches the mean density. In the deterministic case with $\omega = 0$, the limiter control does not have an effect at exactly $h = x^{*_1}$, but already for small noise intensities the curve is blurred. Since the effect of noise is qualitatively the same as in the preceding sections, the corresponding plots are not shown for the sake of brevity.
The third and the fourth row of Fig. 4.11 show the variance and the effort of the limiter control, respectively. The variance of the limiter-controlled logistic map is effectively reduced in the regions around $0.05 < h < 0.1$ and $h > 0.15$ (Fig. 4.11c). In the Ricker model, in contrast, the variance increases and is nearly doubled for the limiter value (Fig. 4.11g) for which the population enrichment is maximal. But already for slightly larger limiters, the variance soon vanishes. In the reasonable parameter range for $h$, the effort for the limiter control does not exceed approximately 0.3 in the logistic model and 0.1 in the Ricker model (Fig. 4.11d,h). Again, noise blurs the resulting curves and especially polishes the effort around $h = x^{*_1}$.

# 5. Discussion and conclusions

The aim of this contribution was to study the effect of limiter control in the field of population biology. Two standard discrete-time models describing the density-dependent growth of populations, namely the logistic map and the Ricker model, have been controlled

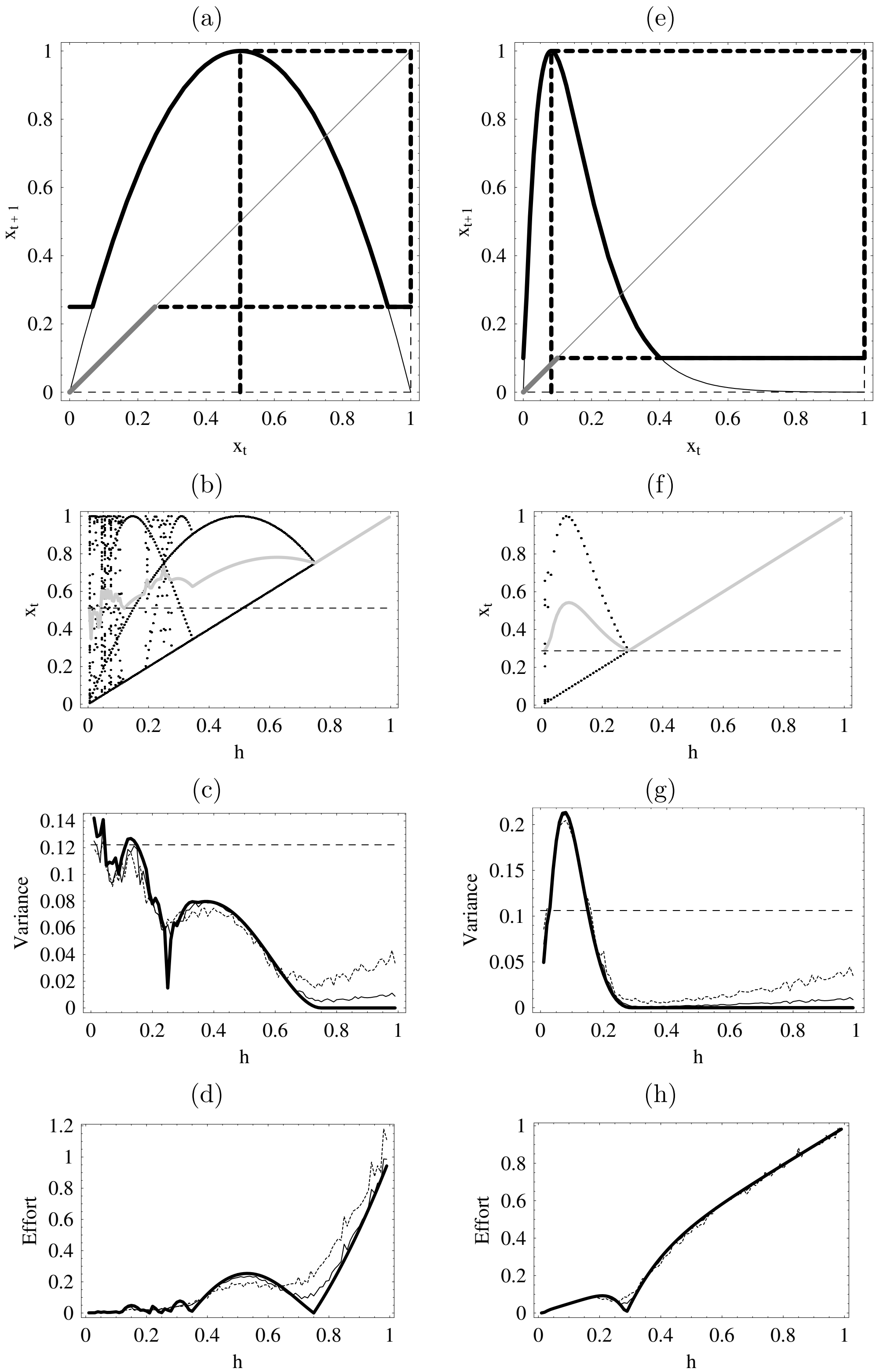


Figure 4.11: Limiter control "from below" for the logistic (left) and the Ricker model (right). First row: Asymptotic densities (average in grey), second row: variance, third row: effort, always against the imiter, and fourth row: cobweb diagram with limiter $h = 0.25$ (logistic) and $h = 0.1$ (Ricker). Paramerer values: $r = 4.0$ (logistic model), $r = 3.5$ (Ricker model). The noise intensities in the third and fourth row are chosen as $\omega = 0.0$ (thick line), $\omega = 0.1$ (solid line) and $\omega = 0.2$ (dotted line).

with simple limiters. This control method has been investigated from two points of view: On the one hand, applying an upper threshold the population densities are restricted not to exceed levels which may be deleterious with respect to a sustainable development (e.g. overcrowding or disease transmission). On the other hand, a lower threshold (restocking) with the aim to maintain populations can have important implications for conservation biology or ensuring reliable yields.

Constant limiters and even their randomized variants force the dynamics on periodic orbits or stable fixed points. Note that limiters are not restricted to be interpreted as a control method. They are also capable of modelling environmental restrictions, external ceilings against reaching the carrying capacity, predation pressure, immigration or refuges as outlined in the introduction. Hence, chaotic attractors are unlikely to be observed in systems with continually hard perturbations. The results presented in this contribution thus coincide with previous suggestions that chaos in real populations may be a "fragile process" (Stone, 1993). The application of a lower threshold is closely related to the control approach studied by McCallum (1992). Actually, the constant feedback control also yields the stabilization of chaos, but it should be noted that there still remain parameter ranges in which irregular fluctuations are possible. Furthermore, despite its simplicity, limiter control supports the experimental finding by Desharnais et al. (2001) that the introduction of individuals significantly reduces the mean density.

There is a pecularity of limiter control in the logistic map which has important consequences for the management of populations and may be understood as a general warning against the naive application of unreflected measurement programs. An upper threshold induces what we have termed the paradox of simple limiter control: The mean density increases instead of an intuitively expected reduction. There is a similar caveat for the lower threshold, when the limiter is chosen too small. Management decisions, which may be well-intended, can thus have strongly opposite impacts. Similar counter-intuitive dynamics are known in the literature. E.g., an increase of the carrying capacity destabilizes the population towards densities prone to extinction (paradox of enrichment, Rosenzweig, 1971), a predator mediates the coexistence of competing prey species which otherwise would go extinct (Takeuchi and Adachi, 1983), the eradication of invaders that were threatening endemic species causes a much greater harm to the latter (mesopredator release, Courchamp et al., 1999).

The Ricker model does not exhibit this paradoxic effect. This can be attributed to the concavity of the Ricker mapping. The mean population density practically remains constant for a large range of minimum-limiters. For maximum-limiters, the mean density mainly increases. Preliminary studies show that similar mappings such as the Hassell model in the chaotic regime obey the same characteristics.

Since the application of sharp limiters may be a bit "brutal", noise has additionally been considered, in order to model the cases in which the limiter is subject to fluctuations. The results turn out to be robust. In many instances, however, a hard limiter control will be impossible, because one does not have access to the full system or can only cull a portion of the population. Therefore, future work might take into account *soft* limiters (Wagner and Stoop, 2001; Stoop and Wagner, 2003). Overall, limiter control can be a very effective and at the same time simple tool to control the population, while either maintaining or enriching its mean density. Numerical investigations, moreover, show that there is only little effort required in certain, realistic parameter ranges. Furthermore, the limiter control can contribute to reducing the variance. The decision whether to use limiter control thus depends on the specific aim in mind. Each control measure naturally has to be very carefully assessed.

## Acknowledgements

The authors thank Ned J. Corron for his suggestion to consider the effort of limiter control and comments on the manuscript. Horst Malchow and Hiromi Seno are acknowledged for comments and discussion during earlier stages of this contribution.

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ISSN 1433-3805