# THE EFFECT OF HARVESTING ON THE SPATIAL SYNCHRONY OF POPULATION FLUCTUATIONS

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# ABSTRACT

Harvesting in space affects, in general, the spatial scale of the synchrony in the population fluctuations, which determines the size of the areas subjected to simultaneous quasi-extinction risk. Here we show that harvesting reduces the population synchrony scale if it depends more strongly on population fluctuations than the density dependence of the growth rate in the absence of harvesting. We show that constant and proportional harvesting always increases the spatial scale, using a theta-logistic model for density regulation. We also provide exact scaling results under harvesting for the Beverton-Holt and the Ricker stock-recruitment models that are commonly applied, e.g. in fisheries. Our results indicate that harvest in areas with large abundances should be encouraged to avoid increase of the spatial scale of synchrony in the population fluctuations that can lead to unexpected quasi-extinction of populations over large areas. Our results quantify this harvesting impact giving the resulting scales of spatial synchrony of population synchrony. This emphasizes the importance of estimating the form of density dependence as well as the dependency of harvest upon population density of exploited populations, in order to get reliable predictions of the size of areas that can undergo simultaneous quasi-extinction.

*Key words*: *spatial dynamics, harvest theory, stochastic dynamics, density dependence, environmental stochasticity*.

## 1. Introduction

One of the greatest contributions of harvest theory has been to provide general principles for how populations of exploited species should be managed. For example, the concept of Maximum Sustainable Yield denotes the maximum equilibrium harvest rate (Reed, 1978; Quinn and Deriso, 1999), which in a stable environment is obtained by keeping the population at the size that maximizes the population growth rate. For a logistic model of density regulation this population size is half the carrying capacity $K$. Another example of such a general principle is threshold harvesting, providing the optimal strategy for reduced risk of extinction or the probability of reduction in population size to an unacceptable low level in a stochastic environment (Lande et al., 1995, 1997). Although these principles have been difficult to implement in practice, they still provide important guidelines for identification of overall goals for the management strategy of exploited species.

Traditionally harvesting theory has focused on modelling the dynamics of a single population over time. This ignores that many intensively harvested species are spread out in space and migrate over large areas. Accordingly, a central aim in obtaining a sustainable management strategy is therefore to consider the effects of harvesting at relative small geographical scales and then distribute the total quotas among sub-areas within the distributional range of the species according to some set of predetermined criteria (Lavsund et al, 2003; Cadgan et al., 2017). An additional complication introduced by space is that fishermen and hunters are often selective in their choice of areas to harvest. This may occur because of logistic constraints to access areas, management regulations (e.g. formation of reserves) or may be based on some kind of spatial harvesting strategy (e.g. by specifically visiting areas with high yields) (Ling and Milner-Gulland, 2008).  Over the last decades there has therefore been increased focus on how harvest will affect interactions among subpopulations localized in different areas (McCullough, 1996; Jonzén et al., 2001; Fogarty and Botsford, 2007; Ling and Milner-Gulland, 2008; Kerr et al., 2010; Williams and Hastings, 2013; Burgess et al., 2014; Benson et al., 2015; Takashina and Mougi, 2015). This implies that the dynamics at a single location cannot be understood without including spatial aspects of the dynamics. A nice illustration has been the recent attention to formation of marine reserves as a management option (Tuck and Possingham, 2000; Gell and Roberts, 2003). General management principles for exploited species should therefore include a spatial dimension (Hilborn et al., 2003; Schindler et al., 2010; Hilborn, 2012; Benson et al., 2015).

Spatial synchrony is a concept usually referring to the temporal covariance or correlation between two quantities, for example population densities, measured at different spatial distances (Ranta et al., 1998; Lande et al., 2003; Liebhold et al., 2004). Ignoring sampling variances the correlations are by definition one at distance zero, and in a large homogeneous area they often decrease monotonically towards zero at large distances where fluctuations are independent (Liebhold et al., 2004; Sæther et al. 2007) . The spatial scale of the synchrony is a distance where correlations typically are considered to be large below that value and small at larger distances. In an isotropic model a circle with radius equal to the scale then typically is an area with rather similar population densities. Such scales can be defined in many different ways, for example where the correlation passes 0.5, $e^{-1} \simeq 0.37$ or 0.10 (Bjørnstad and Falck, 2001), but can also be expressed through the shape of the whole autocorrelation function (Engen et al., 2005). Lande et al. (1999) scaled the correlation (or covariance) function by a constant factor to produce a distribution and used the standard deviation of this distribution as a measure of spatial scale. If the correlation has an exponential form, this scale is then where the correlation equals $e^{-1} \simeq 0.37$ , whereas for a Gaussian form it equals $e^{-0.5} \simeq 0.61$.

The spatial scale of the synchrony in population fluctuations is an important characteristic with important ecological ramifications to describe how population dynamics covary in space. For instance, synchronous populations tend to be more vulnerable to extinction or quasi-extinctions than populations that show spatially asynchronous population fluctuations (Heino et al., 1997; Heino, 1998; Palmqvist and Lundberg, 1998), and if the spatial scale is large, extinctions may occur surprisingly fast over large areas (Engen 2007). Importantly, the degree of spatial scaling of the population dynamics can also be understood from basic processes affecting fluctuations in population size. This is illustrated by the model of Lande et al. (1999), who analyzed a spatial population model with spatially correlated noise, local density regulation and dispersal. Using the scale defined as standard deviation their main result is expressed by the equation

$$l_N^2 = l_e^2 + \frac{m l_f^2}{\gamma} \ . \qquad (1)$$

Here, $l_N$ is the spatial scale of the spatial autocovariance function for population densities, $l_e$ is the corresponding scale for the spatial correlation of the environmental noise, $m$ is the dispersal rate and $l_f$ is the standard deviation of dispersal distance, while $\gamma$ is the strength of local density regulation. In models with no spatial dimension $1/\gamma$ is the mean return time to equilibrium (May, 1974). An important conclusion from this analysis is that even the effect of small and moderate dispersal over small distances may be very large if the strength of local density dependence is small. A small $\gamma$ makes effects of local migration spread out in space through generations, creating large areas with similar densities. If there is no dispersal then $l_N = l_e$, which is Moran's (1953) classical result.

The purpose of the present paper is to analyze how different harvesting strategies affect the spatial scale of population fluctuations. We show that harvesting may either increase or decrease the spatial scale, depending on spatial characteristics of the harvesting strategy, that is, the harvest at different locations with different population densities.

## 2. Dynamic population model in time and space

A general class of population models in continuous time with no spatial structure has the form

$$dN = [r - g(N)]Ndt + \sigma_e NdB(t), \tag{2}$$

where $g(N)$ is an increasing function of population size $N$, expressing density regulation through how it reduces the growth rate $r$-$g(N)$ as population size increases. The parameter $\sigma_e^2$ is the environmental noise and $dB(t)$ is the infinitesimal increment of a standard Brownian motion during time $dt$ so that the expectation E $[dB(t)]=0$ and var $[dB(t)]=dt$. The temporal variance of the noise term $N\sigma_e dB$ is accordingly $N^2\sigma_e^2 dt$. The carrying capacity $K$ is defined as the equilibrium population size of the corresponding deterministic model so that $r$ - $g(K)=0$. A harvesting strategy can be defined through a harvesting rate $h(N)$, meaning that $h(N)dt$ individuals are harvested during $dt$. The dynamics then change to

$$dN = [r - g(N)]Ndt - h(N)dt + \sigma_e NdB. \tag{3}$$

A central focus for the harvest theory is to find choices of harvesting rates $h(N)$ that produce large mean annual yields while maintaining long-term sustainability of the harvest (Hilborn and Walters, 1992; Quinn and Deriso; 1999). A general conclusion is that constant harvesting in a fluctuating environment leads to unstable dynamics with large risk of extinction (Beddington and May, 1977). As another extreme, thresholds harvesting reduces the risk of unexpected severe reductions in population size and hence represents the most sustainable approach when the population size is known (Reed, 1978, 1979; Lande et al.

1995, 1997), although temporal fluctuations in the yield will be large (Lande et al., 1997; Sæther et al., 2001).

In absence of harvesting, Lande et al. (1999) analyzed the spatial dynamics of $N(x, t)$, the population density at location $x=(x_1,x_2)$ in the plane at time $t$, using the linearization at the carrying capacity which at any location and time replaces $[r-g(N)]N$ by $-Kg'(K)(N-K)=-\gamma(N-K)$, where $\gamma$ is the strength of density regulation. A logistic model is defined by $g(N)=rN/K$ giving $\gamma=r$. Adding density independent dispersal at rate $m$ to this model and writing $f(y)$ for the two-dimensional distribution of dispersal distance $y$ for dispersing individuals, the spatio-temporal model in the neighborhood of $K$ takes the simple linear form

$$dN(x,t)=-\gamma[N(x,t)-K]dt+m\,dt\int[N(x-y,t)-N(x,t)]f(y)dy+\sigma_e K dB(x,t), \quad (4)$$

where the integration is performed over the entire two-dimensional plane and the noise is approximated by the noise at $N=K$. The noise terms are here spatially correlated with spatial autocorrelation $\rho_e(y)=\mathrm{E}[dB(x,t)dB(x+y,t)]/dt$. This model yields stationary fluctuations of population densities with a spatial correlation $\rho_N(y)=\mathrm{corr}[N(x,t),N(x+y,t)]$.

Using this model, Lande et al. (1999) derived their simple result for the spatial scale of fluctuations in densities given by Eq. 1. Defining the scale along a given direction in space, which without loss of generality may be chosen as the first axis $y_1$, as the standard deviation of the scaled autocorrelation function, so that the squared scale is $l_N^2=\int y_1^2\rho_N(y_1,y_2)dy_1dy_2/\int\rho_N(y_1,y_2)dy_1dy_2$, they derived Eq. 1, where all scales refer to the same direction in space.

## 3. The effect of harvesting

### *3.1 Theta-logistic dynamics*

Adding harvesting as in Eq. 3 at each point in space now yields exactly the same kind of linearized model as in Eq. 4, but with a smaller deterministic equilibrium $K_h$ and a different strength of density regulation $\gamma_h$, because harvesting by itself is a density regulating process (Fig. 1). The spatial scale under harvesting is accordingly found simply by replacing $\gamma$ by $\gamma_h$ in Eq. 1. Harvesting increases the spatial scale if $\gamma_h < \gamma$, and will otherwise reduce it. The new parameters under harvesting may in general be calculated numerically for any choice of harvesting strategy characterized by a new deterministic equilibrium $K_h$.

A wide array of models has been proposed to describe the form of density regulation in natural populations. Here we will apply the theta-logistic model $g(N) = r(N/K)^{\theta}$ (Gilpin and Ayala, 1973), which defines a general class of models by varying just one parameter $\theta$. Large values of $\theta$ indicate strong density regulation around *K*, whereas for small $\theta$ density regulation starts to act at small population sizes (Lande et al., 2003). Another advantage of the theta-logistic model is that it provides for specific values of $\theta$ commonly used models for the form of the density-regulation such as the logistic ($\theta$=1) as in Fig. 1, the loglinear ($\theta$=0) model using appropriate scaling of the growth rate, as well as the ceiling model ($\theta$= infinite). In Appendix A we derive a simple analytic solution for $\gamma_h$ under theta-logistic dynamics for a given choice of $K_h$, and harvesting rates expressed as power functions $h(N) = cN^{\Psi+1}$. This represents constant harvest for $\psi$ = -1 and proportional harvesting for $\psi$ = 0. Choosing $\psi = \theta$ the density dependence generated by harvesting has the same form as the density regulation under no harvesting (Fig. 1). A large positive value of $\psi$ corresponds to threshold harvesting with no harvesting below $K_h$ and strong harvesting as soon as the density exceeds $K_h$. For this model it is shown in Appendix A that

$$\gamma_h = \gamma + r(\psi - \theta)[1 - (K_h / K)^{\theta}]. \quad (5)$$

In combination with Eq. 1 this shows that the spatial scale of population fluctuations increases by harvesting if the strategy is given by the parameter $\psi$ smaller than $\theta$. This conclusion is general in the sense that it holds for any values of the parameter $r$, $K$ and $\theta$ describing the dynamics under no harvesting.

Many types of density regulation can be approximated by a theta-logistic model using the first order expansion of $\ln g(N)$ at $N$=$K$ writing in general $\theta = d \ln g(N) / d \ln N$ evaluated at $N$=$K$. A range of harvesting strategies with small reduction of the carrying capacity can be expressed by first order expansions of $\ln[h(N)/N]$ writing $d \ln[h(N)/N] / d \ln N = \psi$ at $N$=$K$, so that Eq. 5 then can serve as an approximation (see Appendix A for details).

A general conclusion emerging from Eq. 5 is that $\gamma_h$ is smaller than $\gamma$ if $\psi < \theta$. Accordingly, if the harvesting is done so that it by itself represents a weaker density regulation then that given by $\theta$ in the absence of harvesting, then from Eq. 1 the spatial scale of density fluctuations increases by harvesting (Fig. 1). In the opposite case for stronger harvest than the density-regulation, the spatial scale decreases and approaches the scaling of the spatial autocorrelation in the environment $l_e$ producing the Moran (1953) -effect (Fig. 2).

Threshold harvesting corresponds to the limit obtained as $\psi$ approaches infinity. Let us keep $K_h$ constant, meaning that one always harvest down to the threshold $K_h$ at any location if the density is larger than $K_h$ and otherwise do not harvest at those locations. From Eq. 5 it appears that $\gamma_h$ takes large values when $\psi$ increases giving approximately $l_N = l_e$. However, for very large values of $\psi$ the approximation obtained by linearization at $K_h$ will not be accurate. Nevertheless, the effect of dispersal will disappear approximately with spatial scale corresponding approximately to Moran's (1953) result for strategies close to threshold harvesting.

We use these general results for the theta-logistic model to make a simple illustration depicted in Fig. 1 of the effects of constant and proportional harvesting in the logistic model choosing $K_h$ = 0.75*K*. The spatial scale under harvesting is given by Eq. 1 replacing $\gamma$ with minus the slope $\gamma_h$ at $N = K_h$. From Eq. 5 constant harvesting gives $\gamma_h / \gamma$ = 1/2 and proportional harvesting $\gamma_h / \gamma$ = 0.75. Thus, constant and proportional harvesting make $\gamma_h < \gamma$ and hence increases the spatial scale of the synchrony in the population fluctuations. In contrast, harvesting proportional to $N^2$ gives $\gamma_h / \gamma$ =1. Hence, the spatial scaling remains unchanged if the harvesting has the same form as the original density regulation, that is, proportional to $N^2$ for the logistic model. Finally, stronger dependence on *N* (here exemplified by $N^3$ that gives $\gamma_h / \gamma$ =5/4) reduces the spatial scale of the population dynamics.

*4.2 Special cases: the Beverton-Holt and the Ricker stock recruitment models*

The two most commonly used models in fishery biology are the stock-recruitment models of Ricker (1954) and Beverton and Holt (1957). Assume that the fecundity at small densities is *f* and that adult survival *s* is unaffected by density. The Beverton-Holt and Ricker models then describe the fecundity (recruitment) at density *N* by the relations $f/(1+\alpha N)$ and $fe^{-\beta N}$, respectively, where $\alpha$ and $\beta$ are positive parameters expressing the strength of the density regulation. The corresponding population growth *dN* in continuous time is accordingly $N[f/(1+\alpha N)+s-1]dt$ and $N[fe^{-\beta N}+s-1]dt$. We show in Appendix B that $\theta$ equals $1/(1+\alpha K)$ and $\beta K/(e^{\beta K}-1)$, which always take values between 0 and 1 for both models. Hence, using the theta-logistic approximation constant and proportional harvesting provide $\gamma_h < \gamma$ for both models, and these harvesting strategies result in increased spatial scale of population fluctuation. On the other hand, harvesting rate proportional to $N^2$ ($\psi$ = 1) will always decrease the spatial scale.

In Appendix B we also compute $\gamma_h$ exactly for the two stock-recruitment models. This enables us to compare how the effect of a given harvest (e.g. from $K$ to $K/2$) on the spatial scaling depends on variation in vital rates (Fig. 3). For both the Beverton-Holt (Fig. 3a) and the Ricker (Fig. 3b) model the spatial scale in the population dynamics increases with decreasing adult fecundity rate. However, the scaling effects of increasing adult survival rate differed between the two models. In the Ricker-model the scaling effect of the harvest was relatively unaffected or decreased with increasing adult survival (Fig. 3a) , whereas the increase in spatial scaling of a given harvest was particularly large among long-lived species subject to a Beverton-Holt model of density regulation (Fig. 3b). The accuracy of the theta-logistic approximation for the two models (Appendix B) was good as long as the carrying capacity under harvesting was larger than about 90 % of $K$ (Fig. A1). The approximation is seen to be conservative in the sense that is overestimates the value of $1/\gamma_h$ and hence the effects of harvest on the spatial scaling of the population dynamics.

## 5. Discussion

Here we propose that management of spatially structured exploited populations living in a fluctuating environment should encourage harvesting representing a stronger type of density regulation than that in the absence of harvesting (Fig. 1) to avoid that harvesting increases the spatial synchrony in the population fluctuations (Fig. 2). For the theta-logistic model of density regulation (Gilpin and Ayala, 1973) we provide an analytical result (Eq. 5) for the critical strength of density regulation from harvesting that must be exceeded to prevent an increase in the synchrony of the population dynamics over larger areas. Such an increase of the scale should be avoided to reduce the risk of extinction or reduction in population size to a low level in large areas (Foley, 1997; Heino et al., 1997; Heino, 1998; Palmqvist and Lundberg, 1998; Ciannelli et al., 2013). This extends previous conclusions from temporal models of optimal harvesting in stochastic environments (Lande et al., 1995, 1997; Sæther et al., 2001) indicating that sustainability requires a strong dependency of harvest on population size, being small for small population sizes and large when the population density exceed some threshold. Thus, the general results obtained here can be used as foundation for developing more specific harvest strategies that include spatial variation in harvest rates, which has been identified as a general problem in management of exploited species (Hilborn et al., 2003; Schindler et al., 2010; Hilborn 2012).

Here we have analyzed the effects of harvesting on the spatial dynamics by assuming harvesting at a rate $cN^{\psi+1}$ at location $x$ and time $t$. For a closed population with appropriate choice of $c$ this covers a wide array of harvesting strategies, including constant ($\psi$ = -1) and proportional ($\psi$ = 0) harvesting, as well as approaching pure threshold harvesting in the limit as $\psi$ approaches infinity. For the theta-logistic model of density regulation (Gilpin and Ayala, 1973; Lande et al., 2003) our results show that harvesting will increase the spatial scale if performed in a way corresponding to choosing $\psi < \theta$. In practice, $\theta$ varies among species but in many taxa it often is located between 0 and 1 (Sæther and Engen, 2002; Sæther et al., 2002). For example, Lillegård et al. (2005) estimated $\theta$ for Norwegian spring spawning herring *Clupea harengus* to be about 0.57. Furthermore, the commonly applied stock-recruitment models in fisheries, the Beverton-Holt and Ricker models, has parameters $\theta = d\ln g(N)/\ln N|_{N=K}$ between zero and 1 when approximated by a theta-logistic model. However, in many populations of terrestrial vertebrates $\theta$ may be larger than 1 (Sæther and

Engen, 2002; Sæther et al., 2002, 2008) so that proportional harvesting is always expected to increase the spatial scale and harvesting strategies with stronger dependence on population size (larger values of $\psi$ ) should be encouraged.

We have derived a general result for the effects of harvesting on the spatial synchrony of the population fluctuations for the theta-logistic model expressed by $\gamma_h$ given by Eq. 5 in combination with equation Eq. 1 (Fig. 2). For more general types of models, such as the one obtained by replacing $N^{\theta}$ with a general form of density regulation $g(N)$ , it is difficult to find transparent analytical results. However, the theta-logistic is a very general type of model that covers a large number of different forms of density regulation (Lande et al, 2003) and for conservative harvesting only down to about 90% of $K$ (Lande et al., 1997), it works well as an approximation (see Appendix A). Furthermore, for the commonly applied Beverton-Holt and Ricker types of density regulation we have provided exact results for the effects of harvesting expressed by power functions (Appendix B). These results are, however, not as general as those for the theta-logistic model because an increase or decrease in spatial scale by harvesting depend on all parameters in the model (and not only $\theta$ as in the theta-logistic model).

These analyses are based on several simplifying assumptions that may restrict their practical applicability. Firstly, we assume that the parameters characterizing the population dynamics are exactly known and that there is no biases in the population estimates. For instance, in non-spatial models uncertainty in estimates of population sizes should imply cautious harvest strategy by increasing the threshold based on the estimated population size as an insurance against overestimation of population size that can lead to too aggressive and non-sustainable harvesting (Engen et al., 1997). Secondly, the analyses are based on a spatially homogeneous model. This means that this model is inappropriate for examining the effects of refuges, e.g. caused by establishment of non-harvest reserves (Gell and Roberts,

2003) or the presence of logistically inaccessible areas (Ling and Milner-Gulland, 2008). Thirdly, we assume no effects of fluctuations in the age-structure, which often strongly affect temporal variation in population size of many species subject to harvest (Quinn and Deriso, 1999; Solberg et al., 1999).

Although these simplifying assumptions mean that it may be difficult to apply our proposed strategies in practice, the analysis may still serve as a general guideline for harvesting spatially distributed populations. For instance, our results imply that one should encourage searching for high density areas for harvesting and avoid harvesting in areas with small densities as this not only gives larger mean annual yield, but also decreases the spatial scale of population fluctuations. Following such guidelines will tend to break down the synchrony so that unexpected severe reductions of population size or even quasi-extinctions over large areas can be avoided.  In practice is not possible to perform harvesting proportional to a given $h(N)$ at any location in space, but our results can still be applied to give general suggestions for managers determining quotas. To utilize the theory it is important to have good knowledge about the form of density regulation as well as estimates of densities in space at each discrete time when quotas are determined, which requires extensive sampling (Benson et al., 2015; Cadigan et al., 2017) as well as spatial statistical methods for smoothing (Cressie and Wikle, 2011). From a given estimated spatial field of densities  one can locate areas with for example large, medium and small densities (or some finer class division), and give large quotas relative to total population in the large density areas, much smaller in the medium, and no harvesting in the small density area, with details depending on the form of density dependence. The density dependence, estimate of $K$ as well as mean densities in the three areas may suggest harvesting efforts ensuring no increase in spatial scale of population synchrony.

In this paper we are not addressing the problem of optimal harvesting in terms of mean annual yield. Based on analyses of non-spatial models it is known that the optimal solution is threshold harvesting provided known population sizes (Lande et al., 1997), and strategies close to that when population sizes are estimated with some uncertainty (Engen et al., 1997). How to deal with threshold harvesting in space is, however, an extremely complex mathematical challenge. For proportional harvesting the problem was analyzed analytically for small and moderate noise by Engen (2017) and some promising results were obtained. This will without any doubt be an important area for further research.

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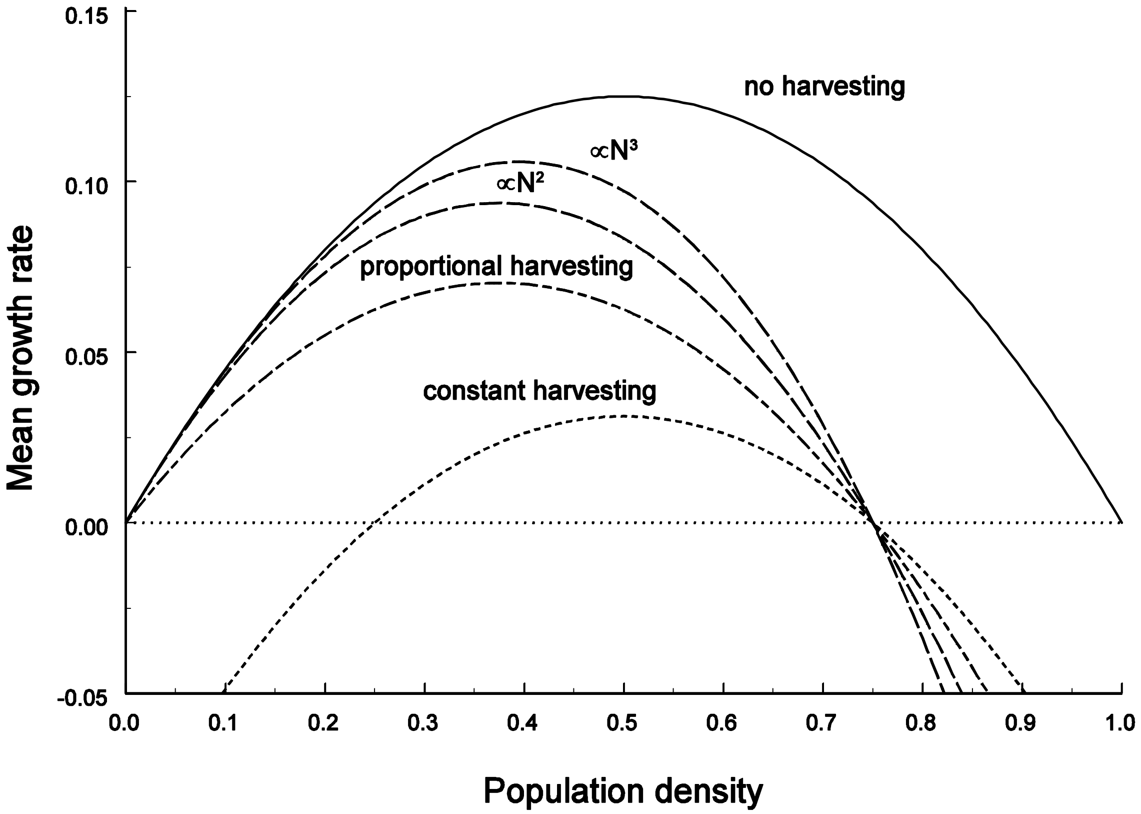
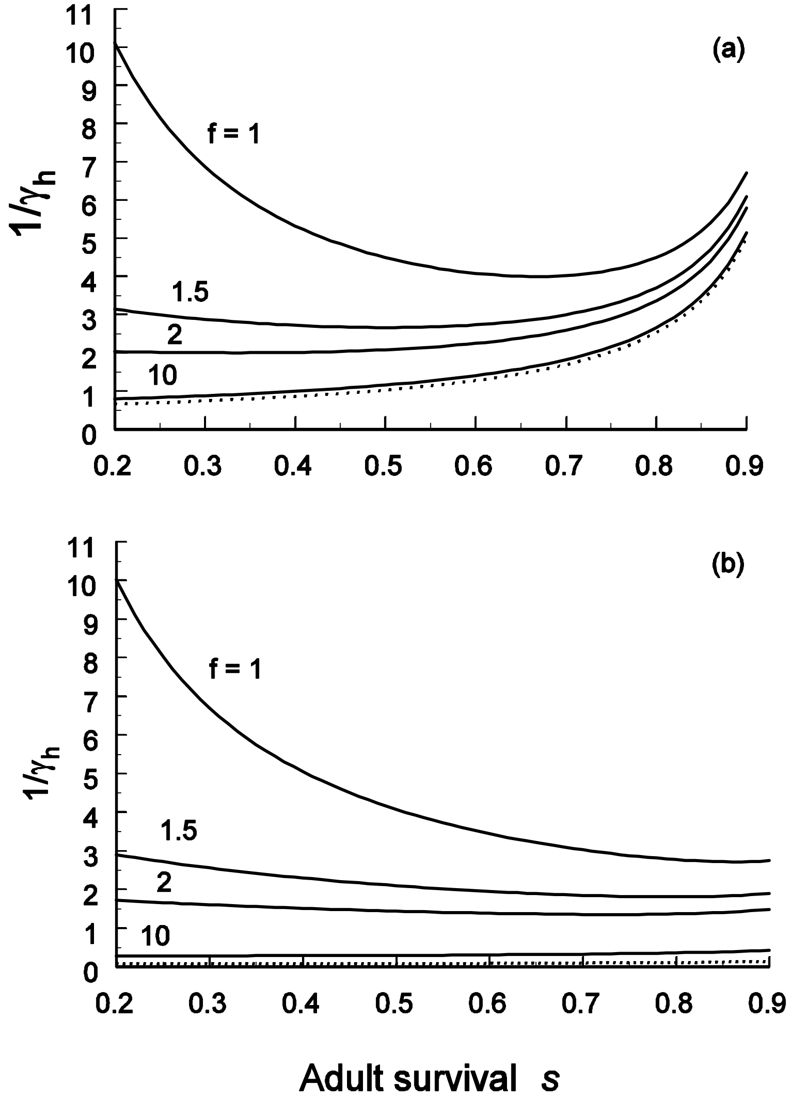
## Legend to figures

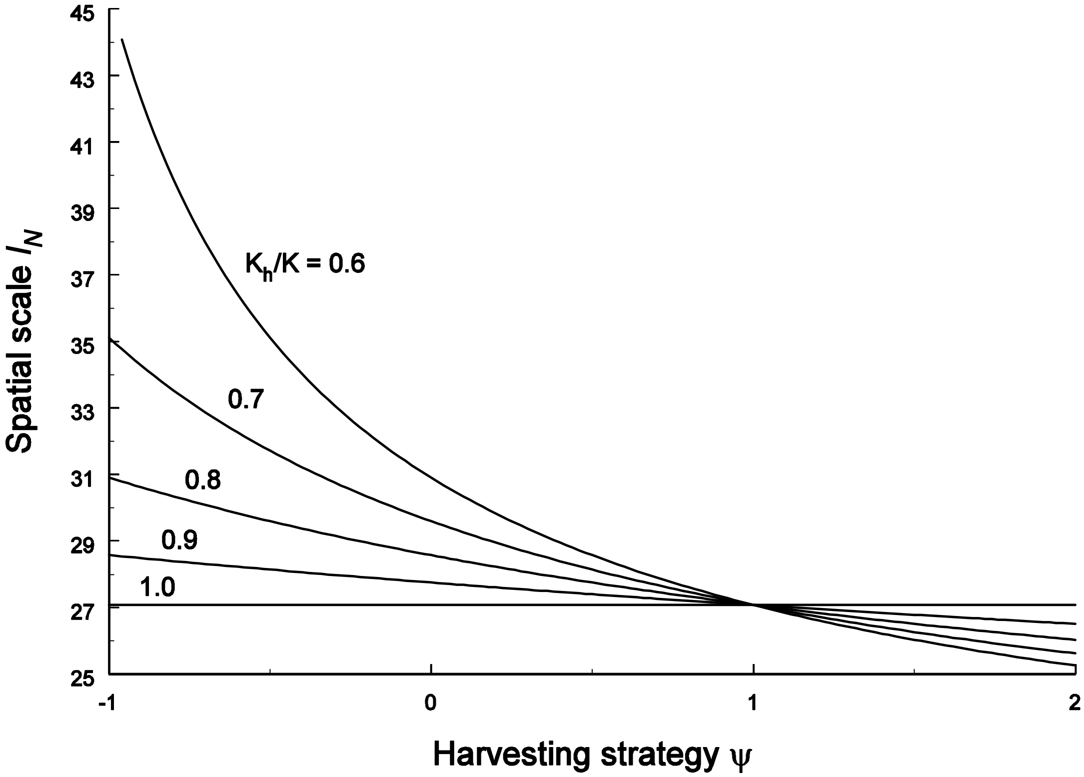
**Fig. 1**. The mean growth rate $\mathrm{E}\,(dN/dt)$ for the logistic model of density regulation as a function of population density *N* in the case of no harvesting (solid line) as well as for four different harvest strategies (constant and proportional harvesting as well as harvest proportional to $N^2$ and $N^3$) (dashed lines). The mean growth rate at small densities under no harvesting is $r$ =0.5 and the carrying capacity without harvesting is $K$ = 1. The strength of density regulation without harvesting is $\gamma = r = 0.5$. All 4 harvesting strategies are scaled by a factor so that the deterministic equilibrium under harvesting is $K_h = 0.75K$.

**Fig. 2**. The spatial scale of the synchrony in population size $l_N = \sqrt{l_e^2 + ml_f^2/\gamma_h}$ , where $l_e$ is the spatial scale for the spatial correlation of the environment noise, *m* is the dispersal rate, $l_f$ is the standard deviation of dispersal distance and $\gamma_h$ is the strength of local density regulation under harvesting, as function of the harvesting strategy $\psi$. The harvesting rate is $cN^{\psi+1}$ with *c* chosen to give carrying capacity $K_h$ under harvesting. $\psi$ = -1 and $\psi$ = 0 express constant and proportional harvesting, respectively. The dynamics is logistic ($\theta$ = 1) and results are shown for 5 different values of $K_h/K$. The parameter $\gamma_h$ is found by Eq. 5. Parameter values are $r$ = 0.3, m = 1, $l_f$ = 10, and $l_e$ =20, while *K* is arbitrary.

**Fig. 3**. The factor $1/\gamma_h$ (see Eq. 1) determining the spatial scaling of the population dynamics for the Beverton-Holt (a) and Ricker (b) model as function of adult survival for different fecundities *f* at small densities by proportional harvesting ($\psi$ = 0) down to half of the initial carrying capacity, that is $K_h = K/2$. The other parameters are *f* = 5 and *s* = 0.8.


0.15
0.10
0.05
0.00
-0.05
Mean growth rate
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Population density
no harvesting
$\propto N^3$
$\propto N^2$
proportional harvesting
constant harvesting


(a)
$1/\gamma_h$
f = 1
1.5
2
10
0
1
2
3
4
5
6
7
8
9
10
11
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
(b)
$1/\gamma_h$
f = 1
1.5
2
10
0
1
2
3
4
5
6
7
8
9
10
11
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Adult survival $s$


45
43
41
39
37
35
33
31
29
27
25
-1
0
1
2
Spatial scale $l_N$
Harvesting strategy ψ
$K_h/K$ = 0.6
0.7
0.8
0.9
1.0