

Does density-dependent individual growth simplify dynamics in age-structured populations? A general model applied to perch, *Perca fluviatilis*

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Availability of resources is a limiting factor for many populations. Diminished resource availability due to intraspecific competition is expected to decrease the annual growth increments of individuals. We study an age-structured population model for individuals with indeterminate growth and annual reproduction; parameters of the model are chosen to characterize a population with life history similar to the Eurasian perch. Different variants of this model are analyzed, all of which have a potential for exhibiting non-equilibrium population fluctuations. We demonstrate that incorporating density-dependent individual growth into these models changes the dynamics of these populations by damping or even eradicating fluctuations in abundance and biomass. This finding offers an explanation for the observed stable dynamics of unperturbed perch populations. Further, density-dependent individual growth may also be a significant factor contributing to the conspicuous empirical rarity of non-equilibrium population dynamics in general.

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Introduction

Food availability is limited in many natural systems and, thus, resource limitation is a potential regulatory factor for most species. Such limitation is especially important for species with indeterminate growth (fish, snakes, clams and others). For these, individual growth continues after maturation and fecundity tends to be closely related to body mass. Given a shortage of food, individuals will invest most of their available resources into maintaining their biomass, while allocating less resources to individual growth and, thus, lowering the annual growth increments. Higher population densities increase competition for food; therefore, annual growth increments tend to be density-dependent. Dependences of individual growth on food supply are well-documented in aquaculture (Wootton 1998). Also in oceanic populations, the availability of food is known to influence growth rates in a variety of fish species such as cod and sole (Rijnsdorp & van Beek 1991, Jørgensen 1992). Moreover, severe resource limitation has been suggested as one of the major causes of stunting in fish populations, a phenomenon observed in many freshwater systems (Eschmeyer 1937, Rask 1983, Roff 1992, Heath & Roff 1996, Ylikarjula *et al.* 1999, Claessen *et al.* 2000). In spite of its prominent role, studies on the population dynamical consequences of density-dependent individual growth are very rare. Notable exceptions are de Roos *et al.* (1990, 1992), Persson *et al.* (1998), Post *et al.* (1999) and Claessen *et al.* (2000). In particular, the studies by de Roos *et al.* (1990, 1992) investigated how changes in food supply can influence the dynamics of an age- and size-structured *Daphnia* population. Claessen *et al.* (2000) studied the influence of cannibalism on the dynamics of a perch population that was also limited by resources. In this paper, we explore the effects of density-dependent growth on oscillatory population dynamics. We study three classes of models exhibiting such fluctuations: these models are geared, respectively, to account for density-dependent newborn survival and for two forms of cannibalism. Parameters in our models are chosen to describe a fish

population similar to the Eurasian perch (*Perca fluviatilis* L.), but the results presented here are applicable to a wide range of other fish populations.

The model

In this section we introduce a discrete-time, age-structured model of fish populations that provides a platform for our subsequent analysis.

Model description

For the modeled fish population, the annual cycle of reproduction and overwintering is indexed by t and the number of individuals in age class a before reproduction during the season t is denoted by $N_a(t)$. The parameter a_m is the age at maturity and a_{\max} is the maximum age. Within each age class individuals are assumed to be ecologically identical.

Reproduction and survival

During the reproductive season t the total number of offspring born is

$$N_0(t) = \sum_{a=a_m}^{a_{\max}} f_a N_a(t), \quad (1)$$

where f_a is the number of offspring produced by an individual in age class a . Individuals in age class a survive to the next season with probability s_a ,

$$N_{a+1}(t+1) = s_a N_a(t) \quad (2)$$

for $a = 0, \dots, a_{\max} \pm 1$.

Individual growth

The growth of individual fish is modeled according to the energy allocation model by Roff (1983). It is assumed that there is a size-dependent amount of surplus energy, that is, energy in excess of maintenance requirements. Immature fish use this surplus energy for individual growth;

their annual length increments are chosen to be constant, resulting in linear growth trajectories. By contrast, mature fish invest a certain proportion of this surplus energy into reproduction instead of growth. We assume that the ratio between the weight of gonads and the somatic weight, the so-called gonadosomatic index G , is constant. This assumption applies to many fish species, including perch (Roff 1983). Then the length L_{a+1} of an individual in age class $a + 1$ is given by

$$L_{a+1} = \begin{cases} L_a + \Delta & \text{for } 0 \leq a < a_m - 1 \\ \frac{L_a + \Delta}{\sqrt[3]{1+G}} & \text{for } a_m - 1 \leq a \leq a_{\max} \end{cases}, \quad (3)$$

where Δ is the maximum annual growth increment under current growth conditions.

Size-dependent fecundity

The weight W_a of an individual fish at age a before the reproductive season is proportional to cubic length,

$$W_a = \alpha L_a^3 \quad (4)$$

where α is a constant conversion coefficient. Then the excess nutritional resources which are not used for maintenance or somatic growth are

$$\alpha \left[(L_a + \Delta)^3 - \frac{(L_a + \Delta)^3}{1+G} \right]. \quad (5)$$

These resources are used for reproduction. Assuming the weight of a single offspring individual to be given by a constant w_0 , the number of offspring produced between ages a and $a + 1$ (and released at age $a + 1$) is obtained from the expression above by dividing it by w_0 . We thus obtain

$$f_{a+1} = \frac{\alpha G}{w_0(1+G)} (L_a + \Delta)^3. \quad (6)$$

Biomass

The total biomass of the population at time

t , $W_{\text{tot}}(t)$, is the weight of the whole population excluding the newborns in age class 0.

Density-dependent growth

Density-dependent (or other biomass-dependent) growth is incorporated into the model by assuming a Maynard Smith–Slatkin-type functional response (Maynard Smith & Slatkin 1973),

$$F(b, c, W) = \frac{1}{1 + cW^b}, \quad (7)$$

where c is a constant parameter that determines the strength and b describes the type of density dependence. We assume $b = 1$ (the Beverton–Holt model), but all our results are similar for overcompensating density dependence ($b > 1$) potentially leading to chaotic dynamics. The annual length increment in year t for a total biomass $W_{\text{tot}}(t)$ is

$$\Delta(t) = \Delta_{\text{growth}} F(b_{\text{growth}}, c_{\text{growth}}, W_{\text{tot}}(t)), \quad (8)$$

where Δ_{growth} is the annual maximum growth increment in the absence of density-dependent effects on growth.

Other density- or size-dependent factors

Density dependence in newborn survival is included into the model by using a Ricker-type functional response,

$$R(d, N) = \exp(-dN), \quad (9)$$

where d is a constant parameter that (in the absence of density-dependent effects on growth) determines the carrying capacity of the fish population. The survival probability of newborns is then given by

$$s_0(t) = s_{\text{newborn}} R(d_{\text{newborn}}, N_0(t)), \quad (10)$$

where s_{newborn} is the probability of a newborn to survive to age 1 in the absence of density-dependent effects on survival. The Ricker function is also used for modeling a form of can-

nibalism where newborns are eaten by all other age classes. In this case, the survival probability of newborns is

$$s_0(t) = s_{\text{newborn}} R(d_{\text{cannibalism}}, W_{\text{tot}}(t)), \quad (11)$$

A second form of cannibalism is assumed to be dependent on the length of fish. We assume that the cannibalistic individual must be sufficiently larger than its prey, and that above the critical size difference, the survival probability of the prey decreases with increasing size difference. For modeling size-dependent survival from cannibalism, we use the following function:

$$C(p, r, L, L') = \min(\exp[p(r - L'/L)], 1). \quad (12)$$

$C(p, r, L, L')$ is the probability that during one season, a fish of size L is not eaten by a fish of size L' . The parameter r characterizes the critical value that the ratio between the lengths of the two fishes must exceed for cannibalism to occur, while the parameter p determines the steepness with which the function C decreases from 1. The probability for a fish of size L not to be eaten by fishes of size L' is $C(p, r, L, L')^{N_a}$ and, thus, the probability for a fish of size L to escape from cannibalism during one season is given by

$$s_{\text{cannibalism}}(L) = \prod_{a=0}^{a_{\text{max}}} C(p, r, L, L')^{N_a} \quad (13)$$

Environmental stochasticity

Environmental stochasticity is taken into account by multiplying juvenile and adult survival probabilities with a stochastic term that has a mean of 1 and a standard deviation σ_e and is uncorrelated between years.

Parameter values

Parameter values for the general model presented above are selected to mimic Eurasian perch populations in a general way. However, not all parameter values needed were available

in a single source, and thus, these values were collected from different sources. Moreover, in order to get a general picture we use wide ranges for some parameters, and the extreme values may not be realistic for perch.

Female perch matures at the age of 2–4 years (Alm 1959, Treasurer 1981); in our study the age at maturity is assumed to be $a_m = 4$ years. The maximum age of a perch individual is set to $a_{\text{max}} = 30$ years. A perch egg is fertilized and hatches with a very high probability, while a newly-hatched perch fry survives to age 1 with a probability between 0.0001 and 0.0015 (Nyberg 1976). These values include the effects of both density-independent and density-dependent factors. We, therefore, assume that the probability of a newborn to survive to age 1 in the absence of density dependence is higher, $s_{\text{newborn}} = 0.012$, so that increased survival is observable when density dependence is weak. Juvenile and adult survival probabilities of perch show very strong variations between different populations (Alm 1959, Craig *et al.* 1979); we use the value $s_a = 0.85$ for $a \geq 1$.

In perch, the length of newborns varies between 5.5 and 7.3 mm (Viljanen & Holopainen 1982) and in our model we assume that $L_0 = 6$ mm. The maximum annual growth increment is set to $\Delta_{\text{growth}} = 4$ cm, according to Viljanen and Holopainen (1982). The gonadosomatic index is taken as $G = 0.195$ and the conversion coefficient between length and weight of a perch individual is set to $\alpha = 0.0164 \text{ g cm}^{-3}$. Both values are calculated from the data given by Treasurer (1981). The weight of a newborn, $w_0 = 0.0035 \text{ g}$, is based on L_0 and is calculated from Eq. 4. The length ratio for the onset of cannibalism is taken as $r = 2$ (see Claessen *et al.* 2000). The standard deviation of environmental fluctuations is set to $\sigma_e = 0.2$. This is a reasonable value given the high year-to-year variations of survival probabilities observed in nature (Alm 1959, Craig *et al.* 1979); the exact value is of no importance for our results.

Results

We now study in turn three characteristic features of fish populations, each of which can lead

to strong fluctuations of population abundance and total biomass. On this basis, we explore whether and to what extent the consideration of density-dependent individual growth changes these dynamics. The three features examined are (i) density-dependent newborn survival, (ii) a form of cannibalism where newborns are consumed by all other age classes, and (iii) a form of cannibalism that is dependent on the relative length of fish. We analyze the effects of density-dependent individual growth on the coefficient of variation in total biomass. In addition, we compare the results of the deterministic models to cases where environmental stochasticity is affecting juvenile and adult survival probabilities.

Newborn survival regulation

Density dependence in the survival probability of age class 0 can result from egg diseases or from predators of newly-hatched fry. Such density dependence is incorporated into the model based on Eq. 10. This regulatory mechanism results in strongly fluctuating dynamics, as illustrated in Fig. 1a. These fluctuations are due to the emergence of a dense cohort, which almost blocks recruitment to age 1 because of density-dependent newborn survival. Once the abundance of this dense cohort has decreased, the probability of newborns to survive to older age increases again, eventually resulting in a new dense cohort. Single-cohort cycles have also previously been produced by models describing the population dynamics of Eurasian perch (Claessen *et al.* 2000).

Growth limitation has a strong impact on the population dynamics (Figs. 1b and 2). Increasing the severity of growth limitation dampens variations both in abundance and in biomass. For very strong growth limitation, the fluctuations disappear altogether and the dynamics become stable. The stable domain is depicted as the white region in Fig. 2a and b. The border between the grey and white regions in Fig. 2a and b corresponds to a bifurcation line. Below this line, dynamics are quasiperiodic, i.e., total biomass and abundance change cyclically, although not strictly periodically.

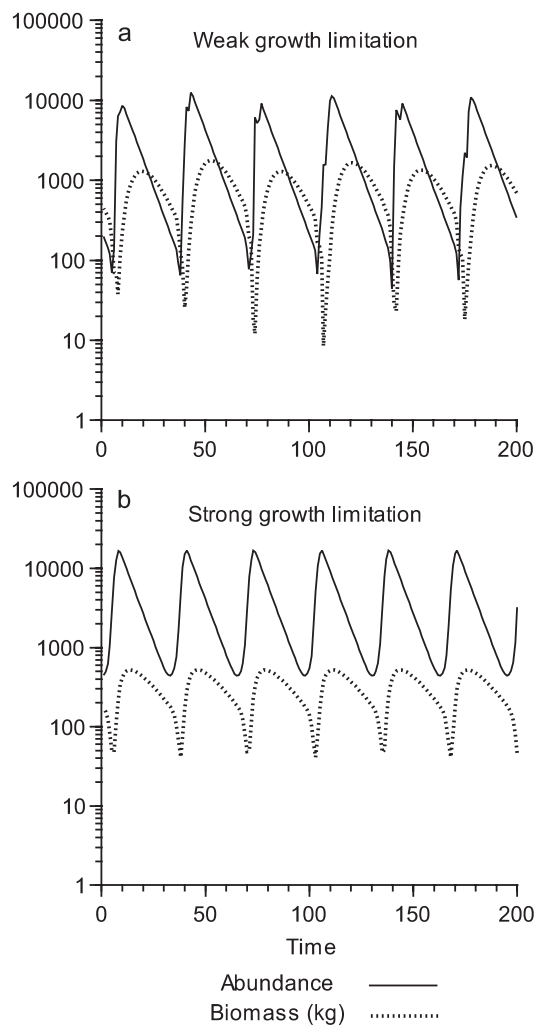


Fig. 1. — **a:** Oscillatory population dynamics resulting from newborn survival regulation ($d_{\text{newborn}} = 7 \times 10^{-7}$) and weak growth limitation ($c_{\text{growth}} = 1 \times 10^{-10}$). — **b:** Population fluctuations are dampened resulting from newborn survival regulation ($d_{\text{newborn}} = 7 \times 10^{-7}$) and strong growth limitation ($c_{\text{growth}} = 2 \times 10^{-6}$). For even stronger growth limitation fluctuations disappear altogether. Notice the logarithmic scale on the vertical axis: the reduction in the amplitude of oscillation is about tenfold.

In contrast to growth regulation, the impact of newborn survival regulation on the population dynamics is minor; the isovalue contour lines of the coefficient of variation in abundance and biomass are almost horizontal (Fig. 2a and b). Yet, as expected, the strength of newborn survival regulation has a strong influence on the

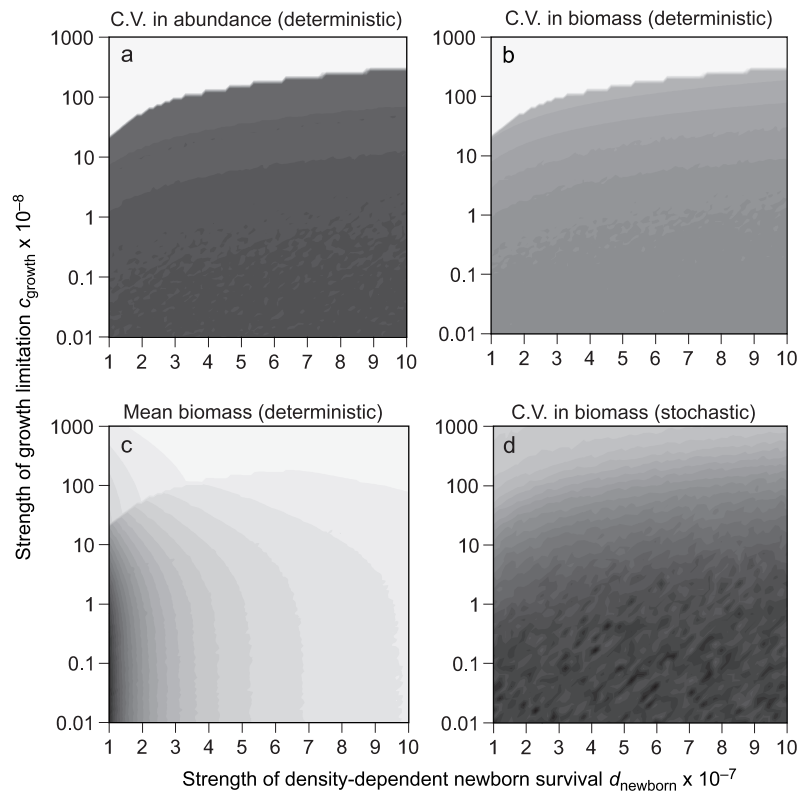


Fig. 2. Effects of newborn survival regulation and growth limitation on population dynamics. — **a**: the coefficient of variation in total biomass (range 0–1.4). — **b**: the coefficient of variation in population abundance (range 0–1.4). — **c**: mean total biomass (range 0–6000 kg). — **d**: the coefficient of variation in total biomass of the stochastic model (range 0–1.4). The coefficients are shown for variations in newborn survival regulation and growth limitation. The shading gets lighter with decreasing values of the coefficient of variation in **a**, **b** and **d** (white indicating stable dynamics) and with decreasing values of mean biomass in **c**. The border between grey and white areas in **a** and **b** shows the bifurcation between complex dynamics and a stable regime. Displayed values are based on simulation runs of 9000 generations, after removing an initial transient of 1000 generations. The horizontal axis is scaled such that population size decreases by an order of magnitude from left to right. The vertical axis is scaled such that realized growth increments range from normal ($\Delta(t) \approx \Delta_{\text{growth}}$) to severe stunting ($\Delta(t) \approx 0.2\Delta_{\text{growth}}$). The figure demonstrates that increased growth limitation dampens the fluctuations in abundance and biomass. As expected, mean biomass is largest when both regulatory factors are weak.

total biomass (Fig. 2c).

All natural populations are subject to environmental stochasticity. When environmental stochasticity is added to juvenile and adult survival probabilities, the stabilizing effect of growth limitation is still very apparent (Fig. 2d). Resulting from stochasticity, there is more variability in biomass, and the region of completely stable population dynamics has disappeared.

Cannibalism of newborns

Also cannibalism can induce non-equilibrium population dynamics. For the first form of cannibalism that we consider, we assume that newborns are consumed by all other age classes (Sanderson *et al.* 1999), *see* Eq. 11. The consequences of adding growth limitation to the resulting model (Fig. 3) are similar to those in

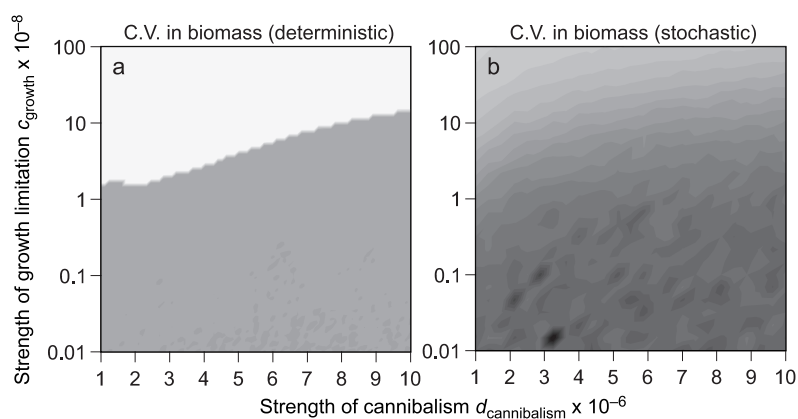


Fig. 3. Effects of newborn cannibalism and growth limitation on population dynamics. The coefficient of variation in total biomass of (a) the deterministic and (b) the stochastic model (range 0–1.5) are shown for variations in newborn cannibalism and growth limitation. Other details are as described in Fig. 2. Notice that in the deterministic model, population dynamics become completely stable if growth limitation is sufficiently severe. In contrast, with environmental stochasticity population dynamics are always fluctuating, but here growth limitation significantly reduces the coefficient of variation. The stochastic model also shows that growth limitation gradually reduces the coefficient of variation in the non-equilibrium regime, where it is almost uniform in the deterministic model.

the case of newborn survival regulation. In the quasiperiodic regime, below the white region in Fig. 3a, the coefficient of variation in total biomass is relatively insensitive to changes in the strength of the growth limitation. Above the bifurcation line, growth limitation is sufficiently strong again to force the dynamics into a stable regime. After adding environmental stochasticity, the stabilizing effect of growth limitation is very pronounced: the variability of the coefficient of variation in total biomass is actually higher than in the deterministic case (Fig. 3b).

Cannibalism dependent on relative lengths

For the second form of cannibalism analyzed here, survival from cannibalism depends on the lengths of fish involved in cannibalistic interactions: the larger the difference between their lengths, the higher the probability that the smaller fish is cannibalized (Post & Evans 1989), *see* Eqs. 12 and 13. Incorporating this regulative mechanism into the model again allows for oscillatory dynamics. However, such intrinsic

fluctuations occur only for parameter values that are not biologically feasible. We therefore consider only a stochastic model where juvenile and adult survival are influenced by environmental variations; such external perturbation results in persistent fluctuations (Fig. 4). The key observation is in agreement with the two previous cases: resource limitation of growth has a stabilizing effect on the dynamics. With increasing growth regulation variations in total biomass are reduced (Fig. 4).

Discussion

Our results demonstrate that density dependence in individual growth tends to simplify population dynamics. For the deterministic models presented, quasiperiodic oscillations of fish populations vanish when the strength of density dependence in individual growth exceeds a certain threshold. Within the quasiperiodic region, growth regulation tends to reduce the amplitude of oscillations. In the stochastic models, the amplitude of fluctuations decreases almost monotonically with growth limitation becoming stronger.

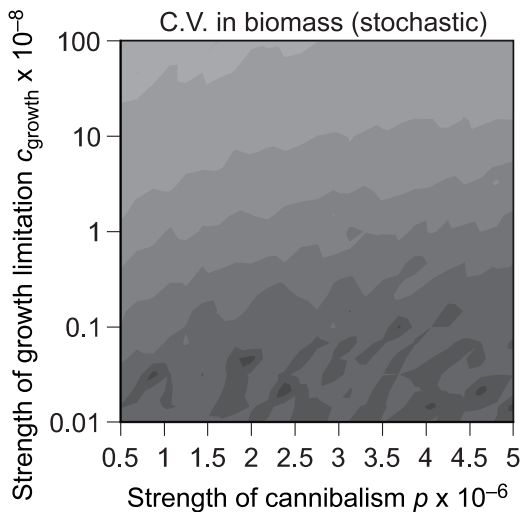


Fig. 4. Effects of size-dependent cannibalism and growth limitation on population dynamics. The coefficient of variation in total biomass is shown for the stochastic model (range 0–0.75). Other details are as described in Fig. 2. Increasing the growth limitation severity dampens variation in biomass.

We can offer two intuitive explanations for the observation that density-dependent growth tends to dampen population fluctuations. First, the effect of a year of bad growth conditions will subsequently lead to smaller size-at-age. Since growth is an additive process and decreased size reduces the reproductive potential of an individual, this will have demographic consequences during consecutive years. For this reason, the impact of variations in growth conditions extends over many years. A second explanation for the demonstrated dynamical simplification is that density-dependent individual growth spreads out the effects of density regulation over the whole population, instead of merely affecting a single age class such as newborns.

Our results give a possible explanation for a general characteristic of unperturbed freshwater fish communities: stability in biomass, with variation dampened by longevity (Treasurer *et al.* 1992). Although our results suggest that density-dependent growth can simplify dynamics, oscillating dynamics are observed for some fish populations with density-dependent indi-

vidual growth. Examples are roach (Townsend *et al.* 1990), vendace (Hamrin & Persson 1985), and yellow perch (Sanderson *et al.* 1999). In these cases, oscillatory population fluctuations are probably maintained because of phenotypically plastic maturation processes (roach), due to strong competitive asymmetries between age-classes (vendace), or as a result of particularly strong intraspecific interactions (yellow perch). Large variations in biomass are also perceived in a Eurasian perch population in an oligotrophic lake in Sweden where cannibalism is important (Claessen *et al.* 2000). Ylikarjula *et al.* (1999) have shown that age-at-maturity is expected to change in response to altered growth conditions; it remains to be investigated whether and how such adaptive responses affect the oscillatory dynamics of populations with individual growth limitation.

Resource availability and annual growth increments are tightly linked. Since food limitation has been established as the main regulatory factor for a wide variety of species — taxonomically as diverse as Arctic ground squirrels (Hubbs & Boonstra 1997), cladocerans (Barry 1997), freshwater snails (Osenberg 1989), damselflies (Fincke 1994) and fish (Rijnsdorp & van Beek 1991, Jørgensen 1992, Heath & Roff 1996, Wootton 1998) — the results presented in this paper have potentially far-reaching consequences for how ecologists will model populations with a potential for non-equilibrium dynamics. Our findings may also contribute to an understanding of why complex dynamics produced by so many simple models are seldom observed in nature.

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