

## POPULATION FEEDBACK AFTER SUCCESSFUL INVASION LEADS TO ECOLOGICAL SUICIDE IN SEASONAL ENVIRONMENTS

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**Abstract.** For most consumer species, winter represents a period of harsh food conditions in addition to the physiological strain that results from the low ambient temperatures. In size-structured populations, larger-bodied individuals do better during winter as they have larger energy reserves to buffer starvation periods. In contrast, smaller-bodied individuals do better under growing conditions, as they have lower maintenance costs. We study how the interplay between size-dependent life-history processes and seasonal changes in temperature and food availability shape the long-term dynamics of a size-structured consumer population and its unstructured resource. We show that the size dependence of maintenance requirements translates into a minimum body size that is needed for surviving starvation when consumers can adapt only to a limited extent to the low food densities in winter. This size threshold can lead to population extinction because adult individuals suffer only a little during winter and hence produce large numbers of offspring. Due to population feedback on the resource and intense intra-cohort competition, newborn consumers then fail to reach the size threshold for survival. Under these conditions, small numbers of individuals can survive, increase in density, and build up a population, which will subsequently go extinct due to its feedback on the resource. High juvenile mortality may prevent this ecological suicide from occurring, as it releases resource competition among newborns and speeds up their growth. In size-structured populations, annual fluctuations in temperature and food availability may thus lead to a conflict between individual fitness and population persistence.

*Key words:* consumer–resource interaction; extinction; population dynamics; seasonality; size-structure.

### INTRODUCTION

For most species, winter represents a period of limited food availability as low ambient temperatures reduce the productivity of their resource. At the same time, low temperatures increase metabolic requirements for homeothermic species due to increased heat loss. Adaptations to conserve energy and reduce heat loss vary and can come about through behavioral and physiological changes such as huddling in a community nest, increased fur thickness, or torpor (Hales and Able 2001, Jackson et al. 2001, Humphries et al. 2003). Poikilothermic species exhibit a passive and direct response to temperature, and become less active when ambient temperatures decrease. Reducing physiological rates by spending less energy on maintenance or locomotion is beneficial when resources are not abundant, but reduced activity can have a disadvantage when foraging activity is reduced while food is still available to some extent. Foraging activity and maintenance requirements are the most important determinants of the individual energy budget. Besides their scaling with temperature, these physiological rates both depend on individual body size, but their scaling with size differs. This allows smaller

individuals to persist without starving at lower resource levels than larger ones (Yodzis and Innes 1992, Persson et al. 1998). On the other hand, larger individuals have been shown to lose proportionally less weight and withstand starvation better than small ones during winter (Post and Evans 1989).

Several studies on winter mortality of young fish, including both marine (Schwalme and Chouinard 1999, Beamish and Mahnken 2001, Hales and Able 2001) and freshwater species (Oliver and Holeton 1979, Shuter et al. 1980, Post and Evans 1989, DeAngelis et al. 1991), show that mortality during winter can be high for small individuals. Most commonly, overwinter survival and individual length follow an increasing sigmoid relationship, with no survival of individuals in small size ranges (Shuter et al. 1980, Post et al. 1998). Similarly, models focused on temperature effects and winter mortality of fish also predict that individuals have to reach a minimum size threshold in order to survive winter (Shuter et al. 1980, DeAngelis et al. 1991). These studies, however, only follow the fate of a single cohort of individuals and hence do not account for the feedback of the entire population on the resource, nor do they reveal the role that seasonality plays throughout the entire life history. Hamrin and Persson (1986) studied several generations of a vendace population (*Coregonus albula*) which exhibited cyclic behavior with a periodicity of two

years. During the summer period, individual mortality was found to be positively correlated with body size, as a consequence of the competitive dominance of small individuals over larger ones. In winter, this relationship showed a negative correlation, with small individuals experiencing a higher mortality rate than large ones (Hamrin and Persson 1986).

Seasonal fluctuations in temperature may thus result in small individuals having a competitive advantage over larger ones under growing conditions, while being worse off when facing starvation. The benefits of a particular body size, therefore, change over time, depending on food conditions and seasonal temperature fluctuations. It is, however, unclear how size-dependent competition among conspecifics interacts with seasonality in temperature in shaping the long-term population dynamics. With the use of a size-structured population model, we address this question by studying the effect of seasonality on a consumer species and its resource. This type of model allows us to model explicitly the size and temperature dependence of life-history processes (feeding, growth, mortality, reproduction) at the individual level. The model describes the population dynamics as a change in frequency distribution of differently sized individuals over time, and allows for feedback of the consumer population on its resource (Persson et al. 1998). We study how seasonal changes in consumer activity and resource productivity influence the persistence of the size-structured consumer population. The annual change in temperature is modeled as a distinct growth and non-growth season, while resource productivity and consumer activity track these changes in temperature.

#### MODEL

The consumer–resource system is modeled using a physiologically structured population model (PSPM), which describes the population dynamics in terms of physiological processes at the individual level. In a PSPM, an individual state or *i*-state is defined, which represents the physiological state of an individual. In addition, a population or *p*-state is recognized, which represents the frequency distribution over all *i*-states. Finally, the environment in which the consumers live is represented by an *e*-state (environment state), which in our model incorporates the ambient resource density and temperature (Claessen et al. 2000, de Roos and Persson 2001). We assume that the consumer population is size-structured and feeds on an unstructured resource, which follows semi-chemostat dynamics in absence of consumers (Persson et al. 1998). Parameter values are listed in the Appendix (Table A1) and reflect the interaction of Eurasian perch (*Perca fluviatilis*) and its resource *Daphnia* spp. (1.0 mm).

##### *Consumer physiology, the i-state*

Here we present only a brief outline of the individual life-history model, for a more detailed description we

refer to Claessen et al. (2000), de Roos et al. (2002), Persson et al. (1998), and de Roos and Persson (2001). The body mass of an individual is divided into irreversible ( $x$ ) and reversible ( $y$ ) mass. Irreversible mass consists of material that cannot be used to prevent starvation, such as bones and vital organs. Reversible mass can be used to prevent starvation and includes fat, muscle tissue, and gonad mass. The ratio between reversible and irreversible mass ( $y/x$ ), also referred to as fat ratio, is a measure of the condition of the individual. Ingestion, maturation, and background mortality are assumed to be independent of the individual condition, depending on irreversible mass only. In contrast, the individual condition does influence maintenance, energy allocation to growth vs. reproduction and starvation mortality, which hence depend on both reversible and irreversible mass.

Individual consumers forage on the unstructured resource following a Holling type II functional response. Both attack rate and handling time are assumed to be size dependent (Persson et al. 1998). The attack rate is modeled using a hump-shaped function (Appendix: Table A2), based on the assumption that with increasing size locomotion and visual abilities increase. Attack rate decreases at larger consumer body sizes due to a decrease in rod density, which affects the ability to discern small prey, and an increase in the escape probability of small prey (e.g., through the gills of larger fish [Persson et al. 1998, Claessen et al. 2000]). The handling time decreases with size due to increasing gape and gut size (Persson et al. 1998, Claessen et al. 2000, de Roos et al. 2002).

Consumed food is assimilated with a constant conversion efficiency. Assimilated energy is used first to cover maintenance costs. If assimilated energy exceeds maintenance costs, net energy production is invested into growth of irreversible and reversible mass according to an allocation function (see Appendix: Table A2), which targets for a constant ratio between reversible and irreversible mass equal to  $q_j$  or  $q_a$ , for juveniles and adults, respectively. Consumer energetics hence follow a net production model (Lika and Nisbet 2000).

We assume that individuals mature when a certain size threshold  $x_m$  is reached (Claessen et al. 2000). After maturation, an individual starts to invest more energy into reversible mass, which is modeled by using a larger maximum fat ratio  $q_a$  for adults than the fat ratio  $q_j$  for juveniles ( $q_a > q_j$ ; Appendix: Table A2). The amount of reversible mass exceeding  $y = q_j x$  is considered gonad mass, which is accumulated during the growth period. At the start of the non-growth period gonad mass is fixed for egg production and stored until reproduction the following spring. Only if starvation is imminent, egg mass is reabsorbed to cover maintenance. This priority of using reversible mass before gonad mass is supported by data on Atlantic cod (*Gadus morhua*), which show that gonad mass actually increased during winter while

carcass and liver dry mass decreased to satisfy maintenance requirements and prevent starvation (Schwalme and Chouinard 1999). Reproduction occurs at the beginning of a growth period in a pulsed event. If a mature individual survives the winter period, it will reproduce the egg mass that was allocated at the start of winter or whatever remains of it in case gonad mass has been used to cover maintenance costs. Any reversible mass that is left after egg production is considered somatic reserve. Together the newborn, young of the year (YOY) individuals form a new cohort.

When energy intake is smaller than the maintenance requirements, reversible mass is used to cover the deficit. If this causes the fat ratio  $y/x$  to drop below a threshold starvation value  $q_s$ , the individual starts to suffer from starvation mortality with a rate  $\mu_s$ . The rate of starvation increases with decreasing reversible mass and is modeled such, that death is imminent when there is no reversible mass left (Appendix: Table A2). Besides the possibility of starvation mortality, all individuals suffer from background mortality. This background mortality,  $\mu_0$ , represents dying from other causes than starvation. Juveniles ( $x < x_m$ ) in addition are assumed to suffer an extra mortality on top of the background mortality, as their small size may make them more vulnerable to predation, e.g., by insect larvae. For simplicity, we take this additional juvenile mortality to be the same and equal to  $\mu_j$  for juveniles of all sizes. We verified that a dependence on body size of this juvenile mortality does not qualitatively change our results (not shown). The total per capita mortality rate is the sum of starvation, background, and juvenile mortality (Persson et al. 1998, Claessen et al. 2000).

*Consumer environment (e-state) and consumer and resource response to temperature changes*

The resource follows semi-chemostat dynamics, with turnover rate  $r$  and maximum abundance  $K$ , in absence of consumption. Hence, maximum resource productivity equals  $rK$  (in  $\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ ). Semi-chemostat resource growth has been argued to describe more realistically the growth of a prey population with invulnerable, but mature, size classes (Persson et al. 1998, Claessen et al. 2000). Both the resource and the consumer experience the same annual temperature regime.

Temperature is assumed to change in a stepwise manner from a minimum of  $4^\circ\text{C}$  in winter to a maximum of  $20^\circ\text{C}$  in summer. If  $\tau$  ( $0 \leq \tau \leq 365$  days) indicates the time since the beginning of the year and  $T(\tau)$  represents the temperature at a particular time of the year, this representation is hence described by the following step function:

$$T(\tau) = \begin{cases} 20.0 & \text{if } 0 \leq \tau < S \\ 4.0 & \text{if } S \leq \tau < Y. \end{cases} \quad (1)$$

The parameters  $Y$  ( $=365$  days) and  $S$  represent the length of the year and the duration of the summer period, respectively. We assume  $S = 90$  days in

accordance with the growth period in temperate regions (Persson et al. 1998, Claessen et al. 2000). Notice that the time point  $\tau = 0$  corresponds to the start of the growth period. We study this step-function representation of the annual temperature fluctuations, because it allows for a detailed mathematical analysis of the individual-level response to varying temperature and facilitates comparisons with earlier studies of size-structured consumer–resource interactions, which considered the winter period to be a period of complete stasis (Persson et al. 1998, Claessen et al. 2000). We have also studied model dynamics using a sinusoidal function for the change in temperature during the year and an Arrhenius function to describe the temperature dependence of the physiological rates and the resource productivity. Because the two representations of annual temperature fluctuations yield qualitatively similar results, we restrict ourselves here to the model with a stepwise temperature regime. For a detailed description of the sinusoidal function and the corresponding results, we refer to Van de Wolfshaar (2006: Chapter 5).

All parameter values for the individual-level physiological processes of the consumer and the productivity of the resource are presented in the Appendix (Table A1) and represent estimates for summer conditions, i.e., when  $T = 20^\circ\text{C}$ . For reasons of simplicity, we assume that the low water temperatures in winter reduce all physiological rates of the consumer (mortality, maintenance, and foraging rate) with the same scaling factor,  $\gamma_c$ , whereas they reduce resource productivity with a factor  $\chi_r$ .

*Population size distribution, the p-state*

Because of the pulsed reproduction of consumers at the start of the growing season the population is naturally subdivided into distinct cohorts (indexed by  $i$ ). These cohorts are characterized by their abundance,  $N_i$ , and the irreversible ( $x_i$ ) and reversible mass ( $y_i$ ) of the individuals making up the cohort. The number of cohorts making up the size-structured consumer population may vary and will increase whenever reproduction occurs and decrease when all individuals in the cohort have died. Dynamics of these cohort statistics are described in terms of ordinary differential equations, as given by Persson et al. (1998) and de Roos and Persson (2001). These dynamics we studied numerically with the use of a numerical method for integration of physiologically structured models (de Roos et al. 1992).

RESULTS

Since the parameters  $\gamma_c$  and  $\chi_r$  represent the extent to which winter temperatures reduce consumer physiology and resource productivity, respectively, their ratio is a measure of the extent to which changes in consumer physiological rates keep pace with the changing resource availability in winter. If  $\gamma_c$  and  $\chi_r$  are equal, the ratio between consumer rates and resource productivity does not change throughout the year. The decreasing

temperature during winter in this case only implies an identical slowing down of both consumer and resource dynamics. Temperature variation then represents a scaling of time. The population changes during the winter period with slow dynamics will be the same as the changes that would occur in a much shorter period at the faster, summer rates. Therefore, for  $\gamma_c = \chi_r$ , incorporating a winter period in the size-structured model will lead to the same dynamics as observed in the models that consider winter to be a period of complete stasis (Persson et al. 1998) and have a slightly longer growing season between consumer reproduction pulses.

#### Individual-level starvation dynamics

Individuals with a reversible mass above the threshold value  $q_s x$  do not suffer from starvation mortality. On the other hand, the starvation mortality function (Appendix: Table A2) is such that an individual will die with certainty if it fully depletes all its reversible mass, i.e.,  $y = 0$ . Hence, an individual will have a decreasing probability to survive the winter period the more its fat ratio  $y/x$  drops below  $q_s$ . Assuming that food intake during winter equals zero, the reversible mass of an individual only decreases, as it is used to cover maintenance requirements. These dynamics are described by the following differential equation:

$$\frac{dy}{dt} = -\gamma_c \rho_1 (x + y)^{p_2} \quad (2)$$

where  $\rho_1$  is the maintenance allometric constant. The factor  $\gamma_c$  reduces the maintenance requirements during winter and affects the rate at which reversible mass is depleted. Hence, with a lower value of  $\gamma_c$ , individuals can endure longer periods before the onset of starvation mortality. Note that, by assumption, irreversible mass  $x$  does not change during this period.

Solving Eq. 2 leads to the following expression for the time  $\tau_s$  it takes an individual with irreversible mass  $x$  to deplete all its fat reserves at the start of the starvation period,  $y(0)$ , down to the starvation threshold, such that  $y(\tau_s) = q_s x$ :

$$\tau_s = \frac{[x + y(0)]^{(1-p_2)} - (x + q_s x)^{(1-p_2)}}{\gamma_c \rho_1 (1 - p_2)}$$

where  $p_2$  is the maintenance allometric exponent.

Assuming that an individual has the maximum amount of somatic reserves but no gonad mass at the beginning of the winter, i.e., that  $y = q_j x$ , and taking  $\tau_s$  equal to the duration of the winter ( $W$ ), this equation can be solved for the minimum irreversible mass  $x_s$  that a growing juvenile consumer should have in order to survive the winter without experiencing any starvation mortality at all:

$$x_s = \left[ \frac{\gamma_c \rho_1 (1 - p_2) W}{(1 + q_j)^{1-p_2} - (1 + q_s)^{1-p_2}} \right]^{\frac{1}{1-p_2}} \quad (3)$$

An analogous derivation for the case that  $y(W) = 0$  leads to an expression for the minimum irreversible mass  $x_0$  that an individual should have in order to have any chance at all to survive the winter:

$$x_0 = \left[ \frac{\gamma_c \rho_1 (1 - p_2) W}{(1 + q_j)^{1-p_2} - 1} \right]^{\frac{1}{1-p_2}} \quad (4)$$

For values below  $x_0$ , a well-fed, juvenile consumer will deplete its fat reserves ( $y = q_j x$ ) with which it enters the winter period down to zero before the end of winter, and will hence die with certainty. For successful recruitment to the second year, a young of the year (YOY) consumer hence has to reach at least this lower size threshold  $x_0$  during its first growth period.

For individuals with an irreversible mass  $x_0 < x < x_s$  at the onset of winter, the probability to survive starvation,  $P_s$ , ranges between 0 and 1, and is larger for larger values of  $x$ .  $P_s$  can be computed by numerical integration of differential Eq. 2 together with the differential equation describing the dynamics of  $P_s$ :

$$\frac{dP_s}{dt} = -\mu_s(x, y) P_s \quad (5)$$

Note that this equation only considers dying from starvation (see Appendix: Table A2), and hence assumes that  $P_s$  equals 1 at the start of winter. Fig. 1A shows the survival probability  $P_s$  as a function of the irreversible mass  $x$  for individuals that have the maximum amount of somatic reserves ( $y(0) = q_j x$ ) at the start of winter.  $P_s$  is a sigmoidal function of individual size, rising rapidly from 0 at  $x = x_0$  to 1 at  $x = x_s$  with increasing body size. From Eqs. 3 and 4, we infer that  $x_0$  and  $x_s$  increase with the product  $\gamma_c \rho_1 W$ . Fig. 1B (dotted lines) shows  $x_0$  and  $x_s$  as a function of the reduction factor  $\gamma_c$ . In addition,  $x_s$  is larger for larger values of  $q_s$  ( $0 < q_s \leq 1$ ). The starvation mortality coefficient  $s$  determines the steepness of the curve of  $P_s$  as a function of  $x$  between the two size thresholds  $x_0$  and  $x_s$ .

#### Population-level dynamics

With a growth period equal to 90 days and winter a period of complete stasis, the consumer–resource model shows a recruitment-driven single-cohort cycle with a cycle period of eight years in the absence of the additional juvenile mortality (Persson et al. 1998, Claessen et al. 2000). The recruitment-driven cycles begin with a strong reproductive pulse of a newly matured age class. The numerical dominance of YOY causes a strong reduction of the resource level immediately after the reproductive pulse. Since the maintenance requirements scale faster with body size than intake rates, the low resource values will cause adults to die from starvation but not the YOY. The YOY grow and become mature at an age of somewhat more than seven years. After maturation, they produce a large number of offspring and, like their parents, they are subsequently

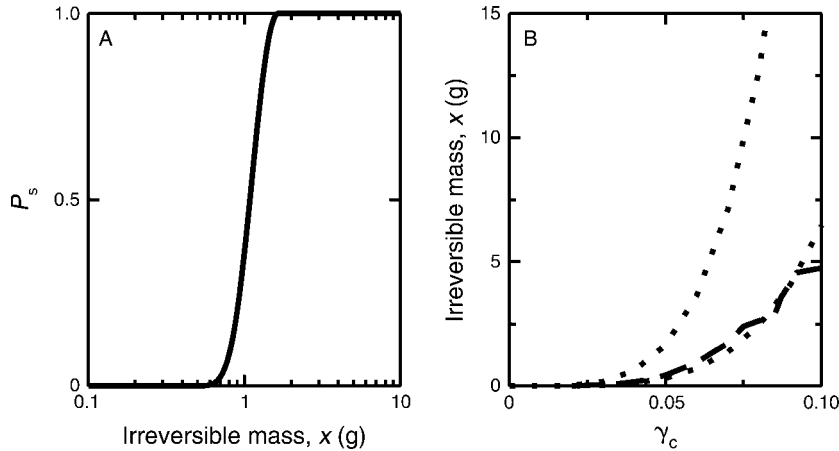


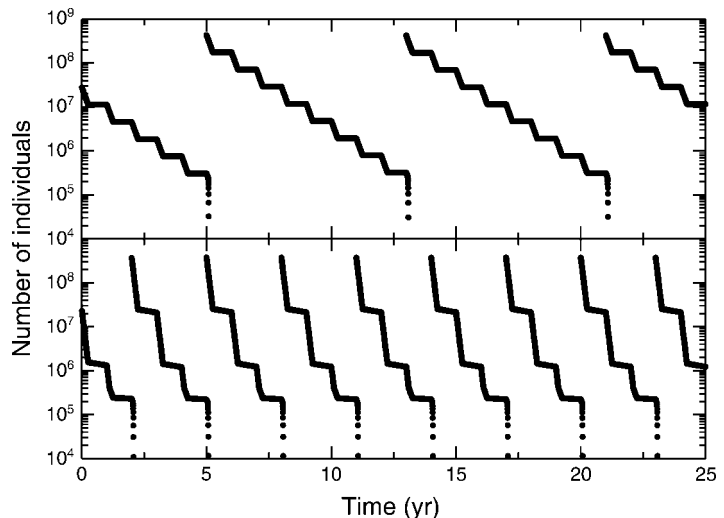
FIG. 1. (A) Survival probability ( $P_s$ ) of consumers during a period without any food intake as a function of their irreversible mass  $x$  (on a log scale). Irreversible mass consists of material that cannot be used to prevent starvation, such as bones and vital organs.  $P_s$  only represents surviving starvation mortality: background mortality is not included. The curve relates to a starvation period of 275 days with  $\gamma_c = 0.05$  ( $\gamma_c$  is a parameter representing the extent to which winter temperatures reduce consumer physiology). (B) Minimum irreversible mass as a function of  $\gamma_c$  that is needed for a nonzero chance to survive a starvation period of 275 days ( $x_0$ , lower dotted line) and to survive this period without suffering any starvation mortality at all ( $x_s$ , upper dotted line). Also shown is the minimum individual size of YOY (young of the year) consumers that survive the winter. This dashed line is obtained from the bifurcation analysis of the model with varying juvenile mortality and pertains to the lowest value of juvenile mortality for which the consumer population can persist. For both panels, it is assumed that at the start of the starvation period individuals have the maximum amount of somatic reserves  $y = q_j x$ , where  $y$  is reversible mass (mass that can be used to prevent starvation, such as fat, muscle tissue, and gonad mass), and  $q_j$  is the ratio between reversible and irreversible mass for juveniles.

outcompeted by their offspring, which starts the cycle anew (Fig. 2, top panel; Persson et al. 1998).

Fig. 3 shows the bifurcation diagram of the population dynamics as a function of juvenile mortality  $\mu_j$ . The figure shows the number of YOY and juvenile consumers, recorded at the beginning of the year ( $\tau = 0$ ), and the size that YOY have reached at the end of their first growth season. The three columns of panels in the figure show these relationships for different values of  $\gamma_c$ , the factor by which winter temperature reduce consumer physiological rates, and  $\chi_r$  equal to  $10^{-9}$ . For  $\gamma_c = 10^{-9}$

(left-hand panels), the winter period is virtually a period of complete stasis. For low juvenile mortality, the population exhibits an eight-year single-cohort cycle as described above (Persson et al. 1998). When juvenile mortality increases, juveniles die more rapidly, which relaxes resource competition. As a consequence, resource density increases faster after a reproduction pulse, individuals grow more quickly, and reach the size of maturity earlier. The period of the cycles shortens if individuals manage to grow so quickly that they can advance their first reproduction event one full year. With

FIG. 2. Model dynamics for two different values of  $\mu_j$  (juvenile mortality in addition to background mortality) and  $\gamma_c$  (a parameter representing the extent to which winter temperatures reduce consumer physiology), with population size on a log scale. The top panel shows a regular eight-year single-cohort cycle in the number of consumer individuals for  $\mu_j = 0.0$  and  $\gamma_c = 0.0$ . The lower panel shows a three-year single-cohort cycle that occurs for  $\mu_j = 0.02$  and  $\gamma_c = 0.02$ , with  $\chi_r = 10^{-9}$  (the factor by which low water temperatures in winter reduce resource productivity; see also Fig. 3).



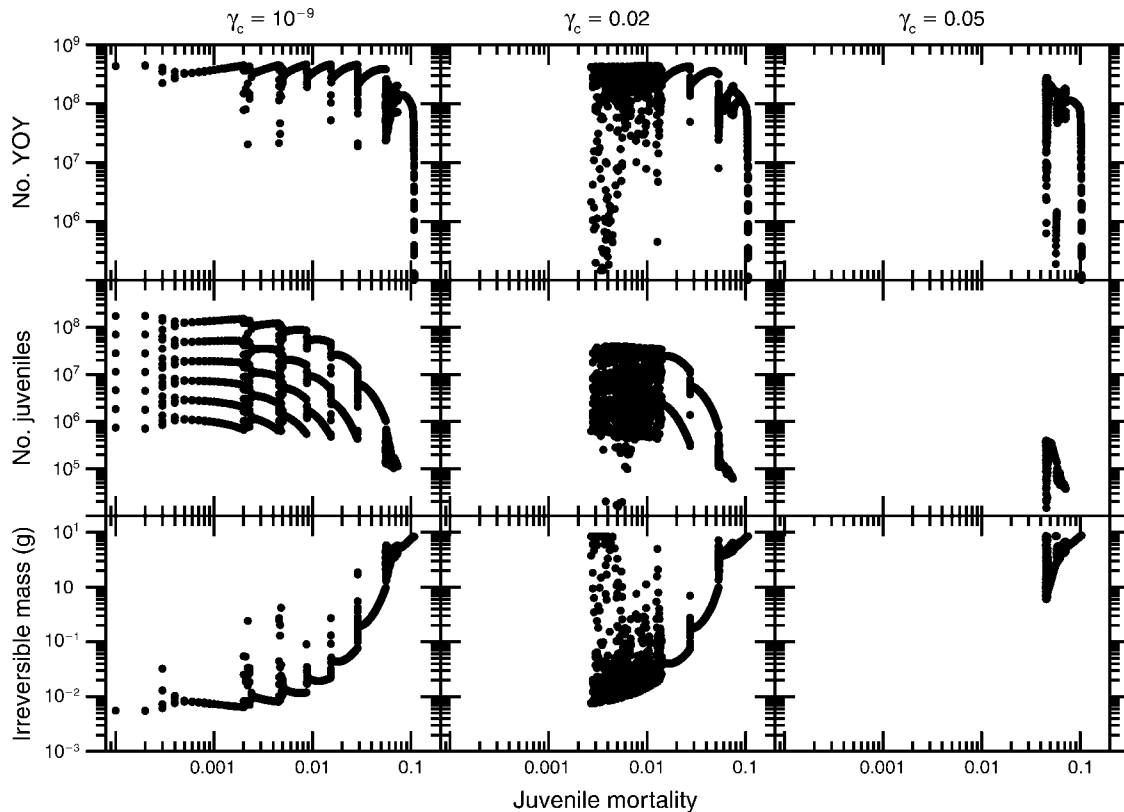


FIG. 3. Bifurcation diagram of the consumer population with  $\mu_j$  (juvenile mortality in addition to background mortality) as the bifurcation parameter for different values of  $\gamma_c$ , the factor by which consumers can reduce their physiological rates in winter (with  $\chi_r = 10^{-9}$  [the factor by which low water temperatures in winter reduce resource productivity]). Top and middle panels show the number of young of the year (YOY) and juveniles, respectively, at the beginning of each year (day 0). The bottom panels show the size of YOY after their first growth period, i.e., the size they reach at the age of 1 year. All axes are log scale.

increasing juvenile mortality the duration of the single-cohort cycle therefore reduces in a stepwise manner.

The size that YOY attain at the end of their first growth period increases with increasing juvenile mortality, as the latter leads to reduced resource competition. The surviving individuals have a higher per capita food intake and attain larger sizes. The maximum size a YOY can reach at the end of its first growth season is bounded by the length of this period and by its maximum rate of resource ingestion.

The middle and right-hand panels of Fig. 3 show the bifurcation diagram for  $\gamma_c = 0.02$  and  $\gamma_c = 0.05$ , respectively. For  $\gamma_c = 0.02$  (i.e., all physiological rates, including mortality, of the consumer proceed in winter at a rate equal to 2% of its summer equivalent), persistence of the population is not possible for values of  $\mu_j$  below 0.0027 (Fig. 3, middle panels). For  $0.0027 < \mu_j < 0.015$ , irregular dynamics are observed, where regular single-cohort cycles occurred for  $\gamma_c = 10^{-9}$ . Although irregular, these dynamics do consist of recruitment-driven single-cohort cycles only with a cycle period that varies over time (results not shown). For both  $\gamma_c = 0.02$  and  $\gamma_c = 10^{-9}$ , regular single-cohort cycles with a period of two or three years as well as fixed-point

dynamics occur for comparable values of the juvenile mortality if  $\mu_j > 0.0015$ . Fig. 2 (lower panel) shows the three-year single-cohort cycle to illustrate the reduction in cycle length with increasing values of  $\mu_j$ . Note that, for  $\mu_j = 0.02$  and  $\gamma_c = 0.02$ , the number of individuals decreases quickly during summer and slowly during winter (lower panel), while for  $\mu_j = 0.0$  and  $\gamma_c = 0.0$ , the number of individuals decreases during summer but does not change during winter (top panel). With an increase of  $\gamma_c$ , winter is no longer a period of complete stasis and all physiological rates are reduced to a lesser extent. The difference in the extent to which individual consumer physiological rates are reduced hence leads to (1) a lack of persistence for very low values of juvenile mortality and (2) a perturbation of the regular single-cohort cycles leading to irregular dynamics for intermediate values of juvenile mortality. Although irregular, the dynamics of the population remain nonetheless recruitment driven. The lack of consumer persistence is very pronounced for larger values of the winter rate reduction,  $\gamma_c = 0.05$ , as persistence is only possible for  $\mu_j > 0.045$  (Fig. 3, right panels). Irregular dynamics are observed as well, but only over a small range of values of juvenile mortality.

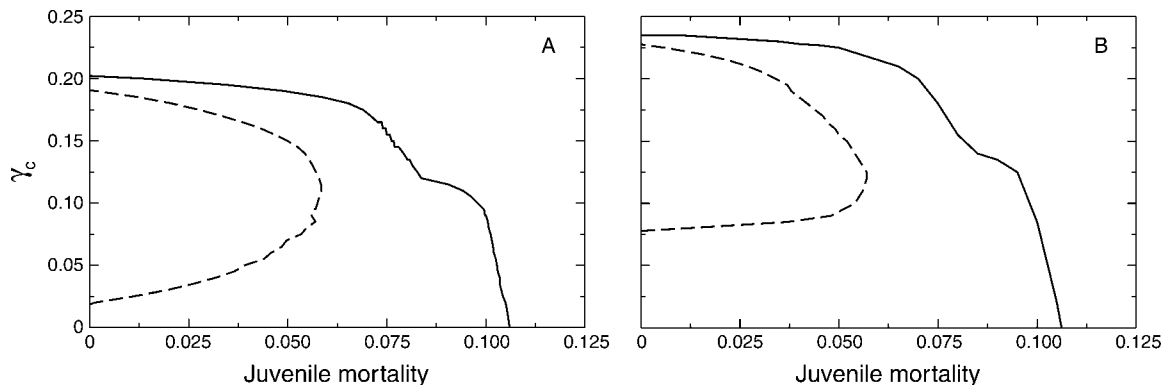


FIG. 4. Invasion (solid line) and persistence boundary (dashed line) of the consumer population as a function of  $\mu_j$  (juvenile mortality in addition to background mortality) and  $\gamma_c$  (a parameter representing the extent to which winter temperatures reduce consumer physiology). All parameter combinations to the left and below the invasion boundary allow for consumer invasion into a system. Of those parameter sets, the combinations of  $\mu_j$  and  $\gamma_c$  to the left of the persistence boundary lead to consumer extinction after invasion. Consumer persistence is hence only feasible for those parameter values between the invasion and the persistence boundary. (A)  $\chi_r = 10^{-9}$ ; (B)  $\chi_r = 10^{-3}$ ; where  $\chi_r$  is the factor by which low water temperatures in winter reduce resource productivity.

From the bifurcation diagrams (Fig. 3), we can infer for a given value of  $\gamma_c$  both the lowest and the highest value of  $\mu_j$  for which the consumer population can persist. The highest of these two values of  $\mu_j$  we will refer to as the “invasion threshold,” as it indicates the level of juvenile mortality below which a low number of consumers is able to increase in numbers and build up a population. The lowest of  $\mu_j$  values will be referred to as the “persistence threshold,” as below this level of juvenile mortality the population will go extinct. We repeated the bifurcation studies for a large range of different values of  $\gamma_c$  and thus constructed the invasion and persistence boundary, respectively, that bound the parameter combinations of  $\gamma_c$  and  $\mu_j$  for which the population can persist (Fig. 4A). The invasion threshold (solid lines in Fig. 4) occurs at lower  $\mu_j$  values when  $\gamma_c$  increases. With higher values of  $\gamma_c$ , the maintenance requirements of consumers are reduced to a lesser extent during winter, and hence their fat ratio  $y/x$  is more likely to drop below the threshold  $q_s$ . They are therefore more likely to experience bouts of starvation, such that lower levels of  $\mu_j$  are already sufficient to prevent the buildup of a consumer population. The persistence boundary (dashed lines in Fig. 4) follows a non-monotonic relationship between  $\gamma_c$  and  $\mu_j$ . For  $\gamma_c < 0.1$  an increase of  $\gamma_c$  implies that the persistence boundary shifts to higher values of  $\mu_j$ , as was already clear from Fig. 3. With higher values of  $\gamma_c$ , the YOY have to attain large sizes at the end of the first growth period to have a chance at surviving the winter (Fig. 1B). These large sizes can only be achieved when competition for resources among the YOY is reduced, i.e., at higher levels of juvenile mortality when their numbers decrease more rapidly. For  $\gamma_c > 0.1$ , however, the persistence boundary bends back to lower values of  $\mu_j$  with increasing values of  $\gamma_c$ . Here, an increase in  $\gamma_c$  results in older individuals suffering from their decreased ability

to adjust maintenance requirements and hence depleting their energy reserves to a larger extent during winter. As a result, the total population fecundity declines and fewer YOY are produced. With less competition the YOY grow more quickly, such that with lower juvenile mortality they manage to reach sufficiently large body sizes at the end of the growth period to survive winter.

The range of mortality conditions for which persistence is possible hence narrows substantially with increasing values of consumer reduction factor  $\gamma_c$ . Consumer invasion is possible for a larger range of parameter values, but the population will nonetheless go extinct eventually (to the left and below the persistence boundary; Fig. 4A). In this parameter region, low densities of consumers do well and build up a population, but eventually the feedback of high population densities on the resource density leads to reduced growth rates of YOY and their starvation during winter. Fig. 1B compares the minimum irreversible mass  $x$  of YOY reached at the end of their first growth period, which we observed in population dynamic simulations at the minimum value of  $\mu_j$  that allows for persistence, with the analytically derived thresholds  $x_s$  and  $x_0$  (Eqs. 3 and 4). This ultimate size of YOY observed in the simulations is close to the analytically derived minimum size threshold  $x_0$  that allows for any survival during winter at all. Hence, consumer persistence is possible as long as a small fraction of YOY manage to survive the winter period.

If resource productivity is reduced to a lesser extent (higher values of  $\chi_r$ ), some resource may still be available for consumers to forage on during winter. Fig. 4B also shows the persistence–invasion plot for  $\chi_r = 10^{-3}$ . For higher values of  $\chi_r$ , the population can invade for higher values of  $\gamma_c$  due to the increased resource productivity in winter, but not for higher values of  $\mu_j$ . Invasion is impossible for  $\mu_j$  larger than a threshold

value, which leads to the death of all newborn individuals within one year, irrespective of the resource productivity. Feedback of high population densities on resources again limits population persistence, even though resource productivity is reduced to a lesser extent. Compared to the situation when resource productivity is almost zero in winter ( $\chi_r = 10^{-9}$ ; Fig. 4A), the lower part of the persistence boundary has shifted toward higher values of  $\gamma_c$ . For low values of  $\gamma_c$ , food intake is no longer limited by resource availability but by the slowing down of the consumer's physiological rates, including foraging rate. For higher values of  $\gamma_c$ , resource availability becomes again the limiting factor ( $\gamma_c > 0.075$ ), resulting in a lack of persistence. Hence, despite increased resource productivity in winter, the feedback from the population on resource density is strong and still causing population extinction for a large range of parameter values.

#### DISCUSSION

In agreement with earlier studies (DeAngelis et al. 1991, Post et al. 1998) our results indicate the importance of reaching a minimum body size at the start of winter for individuals to survive the ensuing period of starvation. Because growth is food dependent and hence influenced by intraspecific competition, the minimum size threshold may lead to population extinction as a consequence of population feedback on resources. For substantial ranges of low juvenile mortality, small numbers of consumers may do well and increase in abundance, whereas starvation of newborn individuals during winter will drive the population extinct when reaching high densities. We refer to this type of extinction as ecological suicide because of the critical role of the consumer population feedback on its resource. Since low mortality rates are beneficial for individual fitness, extinctions under these circumstances represent a conflict of interest between a single individual and the population as a whole. Population persistence may thus be more related to interactions among individuals and their environment than individual-level performance itself. The maximum resource density, determined by the (abiotic) environment, and the individual capacity to reduce physiological rates are not prohibiting population persistence, as at low densities individuals are able to invade. Instead, the resource density is not sufficient for population persistence as soon as it gets depressed by large numbers of individuals resulting in an ecological suicide of the population.

For reasons of simplicity, we assumed ingestion, maintenance, and mortality to follow similar scaling relationships with temperature. Consumers may, however, be more flexible in reducing the energetic costs of ingestion during winter by optimally adjusting their foraging behavior to the current feeding opportunities. Similarly, we assumed that mortality during winter was lower on the grounds that less active consumers stand a

lower chance of detection by predators, which are possibly less active as well. On the other hand, during winter, individuals have a poorer condition and may hence be more vulnerable for predation. We argue that different scalings of ingestion and mortality with temperature during winter will only lead to small quantitative but not qualitative changes in our results. Fig. 1B shows that, at the persistence threshold where ecological suicide occurs, the minimum irreversible mass  $x$ , which YOY reach at the end of their first growing season, is very close to the size  $x_0$ . The latter we derived by considering how quickly an individual consumer depletes its reversible mass during winter to cover maintenance in the absence of any food. This suggests that the extinction of the population is primarily driven by maintenance requirements and the extent to which these can be reduced during winter, irrespective of ingestion and mortality during winter.

In addition to its temperature dependence, the scaling of maintenance with body size to a power less than 1 plays a crucial role in the ecological suicide. While deriving the individual energy budget model, Persson et al. (1998) assumed net energy production to be allocated to reversible and irreversible mass in such a way that a constant fat ratio is targeted for, based on observations of such ratios in fish. This assumption implies that energy reserves scale proportional to body size. The unequal scaling of energy reserves and maintenance requirements with body size results in the S-shaped survival probability function  $P_s$  (Fig. 1A) as a function of body size, which closely agrees with observations on survival under field conditions (Post et al. 1998). The minimum body size for survival  $x_0$  that is part of this S-shaped survival probability function ultimately leads to the ecological suicide (see Fig. 1B). However, the scaling of maintenance with body size to a power less than 1 is also responsible for the fact that the parameter domain, for which population invasion and build up is possible, is significantly larger than the parameter domain, for which the population persists. It implies that adults suffer much less starvation during winter than juveniles and are hence capable of investing considerable energy into reproduction and production of offspring under conditions that allow hardly any growth in body size of the smaller juveniles. The large densities of offspring result in the feedback on resource density that ultimately drives the offspring cohort to extinction during winter.

The dynamics of reindeer (*Rangifer tarandus*), introduced to St. Matthew Island in 1944, may provide an example of a small population of consumers that can expand, but which eventually goes extinct due to winter starvation when reaching high population densities (Klein 1968). Reindeer were introduced to the island in 1944 and increased in abundance from 29 animals to 6000 in 1963. In 1957, the weight of the reindeer were significantly higher than the individual weight in domestic herds of reindeer, but body weight declined with roughly 40% over the following years as a



consequence of high population densities. In the winter of 1963–1964 the entire population of 6000 reindeer died of starvation due to extreme snow conditions. This pattern of reindeer population growth and die-off on St. Matthew Island was claimed to reflect similar dynamics on other island situations with introduced animals. It was believed to be a product of the limited development of ecosystems as well as the deficiency of potential population-regulation factors, such as predation (Klein 1968). Like our modeling results, these data highlight the important role that population feedback might play in the persistence of populations. For invading species one has to consider the possibility that successful establishment of a few individuals does not necessarily mean successful persistence of an entire population. With increasing population abundance also the impact on the environment grows, which may eventually lead to severe deterioration of that environment, poorer individual body conditions and hence to ecological suicide of the total population.

Even though at an individual level growth in body size is the crucial process for survival, at a population level, persistence is largely determined by individual mortality and intraspecific competition. Intense competition among newborns and high survival at low levels of juvenile mortality may lead to recruitment failure, such that YOY stand little chance to survive their first winter. In our model, the consumer population exhibits single-cohort cycles in which adults are being outcompeted by their own offspring and YOY form the only cohort in the population. We have shown that the introduction of seasonality may lead to irregular dynamics, but even these irregular dynamics are driven by the competitive impact of newborn individuals on their parents. In addition, the model is deterministic in the sense that all individuals that are born in a particular year remain identical in size throughout their life. In this setting, recruitment failure in a single year obviously leads to immediate extinction. When relaxing these conditions, that is, in case of dynamics other than single-cohort cycles and with more variability in life history of similarly aged individuals, the effect of recruitment failure may be less extreme. However, Persson et al. (1998) studied the dynamics of the size-structured consumer–resource population in the absence of seasonality, but including variability in the size at birth of neonate consumers. This type of within-year-class variability led to dynamic patterns that are indistinguishable from the patterns obtained without such variability. As another type of within-year-class variability van Kooten et al. (2004) investigated the influence of variation in individual growth in body size induced by heterogeneous spatial distributions of resources. Despite considerable divergence among individuals of the same year class, recruitment-driven, single-cohort cycles remained the dominant type of population dynamics for most parameter combinations. Under all conditions, periods of highly cyclic dynamics,

in which the population was dominated by competition within a single newborn cohort, were regularly observed, irrespective of the extent of individual growth variation. Such intense competition within a single newborn cohort is also the driving force behind the ecological suicide we report in this paper. We therefore expect that variability within year classes will also have limited effect on our results and that the combination of large densities of offspring and low mortality will result in a low recruitment success and therefore pose an increased risk of extinction.

The use of more than a single resource can influence the risk of extinction of the consumer population. When adults forage on more resources they are likely to suffer less from intraspecific competition and to produce even more offspring, which could increase the risk of the ecological suicide. In contrast, ecological suicide may be prevented if variability in resource use by YOY results in sufficient life-history variation for some to escape starvation. This variability in YOY life history should then, however, persist despite population feedback, within-cohort competition and possibly optimal foraging behavior of YOY, processes which all tend to equalize their per-capita intake rates. Therefore, we again expect that the combination of large densities of offspring and low mortality will result in a low recruitment success and pose an increased risk of extinction.

If a certain body size or body mass is needed to overcome a (yearly) environmental event such as winter, the presence of predators can facilitate persistence by reducing intra-specific competition. In a variety of natural systems this beneficial role of predation on population persistence has been revealed. For example, tadpoles in temporary ponds have to reach a certain size to metamorphose before the pond dries out. Data show an increased number of metamorphs when, in a pond with high tadpoles density, predators are present (Wilbur 1988). Without the predators, most tadpoles were too small to metamorphose and survive due to the high competition pressure. Byström et al. (1998) showed, for YOY perch, that high resource competition during summer resulted in smaller individuals with a poorer condition in autumn. These smaller individuals suffered from higher winter mortality compared to the larger individuals from the control experiment with low competition. In a field experiment with isopods and amphipods, amphipod size increased with predator presence (Sparrevik and Leonardsson 1999). In this respect, cannibalistic populations are of special interest, as adult cannibals may impose the necessary mortality on their own offspring for the latter to grow fast enough to survive the winter. Cannibalistic populations can hence be hypothesized to have a higher chance to persist under more severe winter conditions, when individuals have to survive on energy reserves for a longer time. In agreement with this, Post et al. (1998) note that the average length of individuals entering winter was

indirectly affected by cannibalism through reduced competition. Claessen et al. (2002) discusses that populations with permanent cannibalism occur for short growth seasons and population with occasional cannibalism for long growth seasons on a gradient of season length. In addition, for Arctic charr (*Salvelinus alpinus*) it has been shown that the frequency of cannibalism increases with latitude and altitude (Griffiths 1994). These results all lead to the proposition that in seasonal environments the presence of predators may actually promote the persistence of species at lower trophic levels, in which case predator extinction can give rise to a cascade of extinctions among its prey species due to increased intraspecific competition. Predators can thus be viewed as shaping an optimal environment for their prey species to persist.

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#### APPENDIX

Tables with parameter values and equations used for the physiologically structured population model of perch (*Perca fluviatilis*) and its resource (*Ecological Archives* E089-015-A1).