

Size-Dependent Mortality Induces Life-History Changes Mediated through Population Dynamical Feedbacks

Tobias van Kooten,^{1,*} Lennart Persson,^{1,†} and André M. de Roos^{2,‡}

1. Department of Ecology and Environmental Science, Umeå University, S-901 87 Umeå, Sweden;

2. Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94084, 1090 GB Amsterdam, The Netherlands

Submitted September 4, 2006; Accepted March 1, 2007;
Electronically published June 11, 2007

Online enhancement: appendix.

ABSTRACT: The majority of taxa grow significantly during life history, which often leads to individuals of the same species having different ecological roles, depending on their size or life stage. One aspect of life history that changes during ontogeny is mortality. When individual growth and development are resource dependent, changes in mortality can affect the outcome of size-dependent intraspecific resource competition, in turn affecting both life history and population dynamics. We study the outcome of varying size-dependent mortality on two life-history types, one that feeds on the same resource throughout life history and another that can alternatively cannibalize smaller conspecifics. Compensatory responses in the life history dampen the effect of certain types of size-dependent mortality, while other types of mortality lead to dramatic changes in life history and population dynamics, including population (de-)stabilization, and the growth of cannibalistic giants. These responses differ strongly among the two life-history types. Our analysis provides a mechanistic understanding of the population-level effects that come about through the interaction between individual growth and size-dependent mortality, mediated by resource dependence in individual vital rates.

Keywords: size-structured population, dynamics, cohort cycles, cannibalism, resource competition, resource-dependent growth, size-dependent mortality.

* Corresponding author; e-mail: tobias.v.kooten@emg.umu.se.

† E-mail: lennart.persson@emg.umu.se.

‡ E-mail: aroos@science.uva.nl.

The majority of organisms grow significantly during a substantial portion of their life, and for many species, growth is so large that their ecological role changes dramatically during their ontogeny (Peters 1983; Calder 1984; Polis 1984; Werner 1988). Different life stages of the same species may have different environmental requirements, engage in different competitive interactions, and use different resources. An estimated 85% of all taxa undergo some form of metamorphosis, leading to large changes in body morphology (Werner 1988). This is in part due to the numerical dominance of insect taxa, but even among vertebrates, 75% of all taxa show substantial growth during most of their life. Only in birds and mammals are juvenile and adult body size generally within an order of magnitude of each other.

Among other ecological traits, mortality risk has been found to be strongly dependent on body size in many different taxa (Paine 1976; Keller and Ribi 1993; Wilbur 1997; Boulton and Polis 1999; de Roos and Persson 2002; Craig et al. 2006). Changes in the magnitude of such size- or stage-dependent mortality can affect population dynamics in dramatic and unexpected ways. For example, in a combination of modeling and experiments, Dennis et al. (1995, 1997) showed that manipulation of adult mortality rates in laboratory populations of the cannibalistic flour beetle *Tribolium* sp. can both stabilize population dynamics and induce complex population dynamics, depending on its intensity. These models developed for *Tribolium* assume that food is available in unlimited quantities. While appropriate for the laboratory populations for which these models are developed, this assumption may not be valid for many organisms in the wild. In nature, food limitation seems to be the norm rather than the exception. Even in the most determinately growing species, growth is to some degree dependent on energetic gain, and in the majority of taxa, this food dependence is rather strong (Sebens 1987; Werner 1988; Wilbur 1988; Karkach 2006).

Several experiments have incorporated the effects of food limitation and food-dependent growth in the context of size-dependent mortality. Short-term experiments have

generally shown that size-dependent mortality increases growth of the surviving individuals through thinning (Wilbur et al. 1983; Vonesh 2005; Craig et al. 2006), although these effects can be obscured by indirect effects of predator presence (Brodin and Johansson 2002; Werner and Peacor 2003). Experiments covering multiple generations have shown a multitude of effects of this compensatory growth in response to size-dependent mortality. In his classical blowfly experiments, Nicholson (1954a, 1957) reported that experimentally increased mortality of adults led to reduced larval density but did not affect adult density. Increased mortality on small juveniles led to strongly increased adult density. Such an overcompensatory effect in another life stage was also observed in experimental manipulation of soil mite populations (Cameron and Benton 2004). Increased egg mortality led to increased adult density, presumably because such mortality promotes maturation through reduced competition in earlier life stages. Increased mortality of other life stages did not result in such strong compensatory responses. Recent theoretical studies have confirmed that in populations regulated by resource competition, an increase in size-dependent mortality can lead to increased density in other life stages or even in the stage that is affected by the mortality (de Roos and Persson 2002; de Roos et al. 2003; van Kooten et al. 2005). A general understanding of these direct and indirect effects of size-dependent mortality and food-dependent growth on both population dynamics and individual life history is, however, lacking.

Here we study the effects of size-dependent, density-independent mortality on a consumer species with resource-dependent individual development. In this system, changes in mortality rate potentially lead to changes in per capita resource availability, which in turn affects the life history of individuals. We investigate the effects of such mortality applied to different life stages for two archetype species with markedly different life-history strategies: one pure consumer archetype that feeds on the same resource throughout its ontogeny and one with a more complex life history that undergoes an ontogenetic niche shift from resource feeding to cannibalistic feeding. For the pure consumer archetype, resource-dependent growth is the major density-dependent process regulating the population. The cannibalistic case is more complex, since in addition to food-dependent growth, mortality of potential victims depends on the density of cannibals, and cannibal growth depends on the density of suitable victims. The population dynamics of both these archetype species is well understood in the absence of additional size-dependent mortality. The population of pure consumers generally shows cohort cycles driven by intraspecific size-dependent competition (Nisbet and Gurney 1982; Persson et al. 1998; Murdoch et al. 2003). For the parameters we use, the

cannibalistic population shows stable dynamics driven by high cannibalistic mortality of juvenile individuals, although variation in parameters may lead to high-amplitude dynamics (Claessen et al. 2002; Claessen and de Roos 2003).

We show that the response to size-dependent mortality depends crucially on the affected life stage and that it is dramatically different for the different consumer archetypes. By careful consideration of the regulatory mechanisms, we develop an integrative understanding of the effects of size-dependent and density-independent mortality across life-history types.

Methods

Model Formulation

Our model is a physiologically structured population model, based on a framework developed by Metz and Diekmann (1986) and using the numerical algorithms set forth by de Roos et al. (1992). This approach uses a separate formulation for the individual and population level. All assumptions pertain to the individual level, while the population level is essentially the sum of all individual states plus the state of the environment. The model used here is identical to that used by Claessen and de Roos (2003), which is a simplified version of more species-specific models used by Claessen et al. (2000, 2002) and Persson et al. (2003, 2004a). Strong qualitative congruence of the model we use with more complex, species-specific models was shown by Claessen et al. (2000). An example highlighting the similarity between the simplified model used here and its more complex analogue is presented in figures A5 and A6 in the appendix in the online edition of the *American Naturalist*. The simplified model uses body length as a structuring variable on which all individual-level processes depend. The model describes the dynamics of a population of length-structured consumers feeding on an unstructured resource population. A great advantage of the model approach that we use compared with simpler alternatives lies in the fact that our model formulation allows us to distinguish between individuals born at different times. This allows us to draw growth trajectories such as at the bottom of figures 1 and 5, which increase the level of mechanistic understanding that is gained from our results.

In this study, we are primarily interested in single-species dynamics of a size-structured species with food-dependent growth. For this reason, we chose to model resources with semichemostat dynamics. The constant resource growth rate is strongly stabilizing, since it acts to partially decouple the resource population from the consumer dynamics. This stabilizing effect prevents the oc-

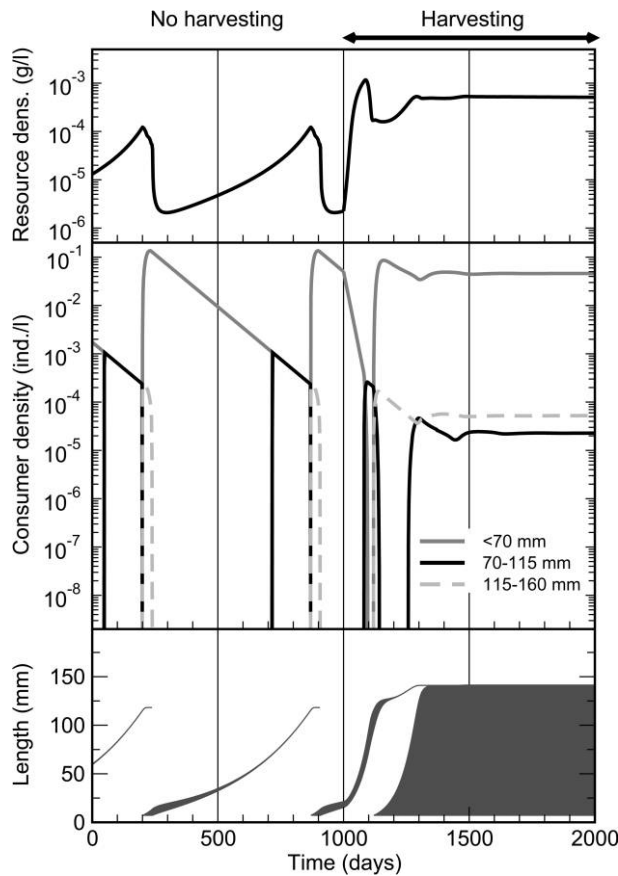


Figure 1: Shift from single-generation cycles to a stable population size distribution induced by harvesting small juvenile individuals (7–70 mm; from $t = 1,000$ onward, with intensity $\mu_{H1} = 0.05$) in a consumer population that shows single-generation cycles in the absence of harvesting (up to $t = 1,000$).

currence of consumer-resource cycles, which would occur with the commonly used logistic resource growth (Murdoch et al. 2003). Murdoch et al. (2002) show that population dynamics of many species, despite being part of larger and highly complex food webs, can be adequately described using single-species models. Another advantage of semichemostat resource dynamics is that it better approximates feeding regimes in published experiments dealing with size-dependent mortality. In such experiments, food input rate is usually independent of feeding rate (Nicholson 1957; Cameron and Benton 2004).

The population-level formulation is listed in table 1, the individual-level equations of our model are listed in table 2, and the default parameter values are listed in table 3. Below we briefly discuss only the model formulation. An in-depth discussion of assumptions and derivation of the individual-level model can be found in the studies by Persson et al. (1998), Claessen et al. (2000, 2002), and Claessen

and de Roos (2003). The parameter set we use is largely identical to the one used by Claessen and de Roos (2003), which is based on the life-history of Eurasian perch (*Perca fluviatilis*), a common piscivorous lake fish. We have modified the parameters for cannibalism such that all individuals are potential cannibalistic victims from birth. The density-independent, size-dependent mortality, which we extensively vary, will henceforth be referred to as “harvesting.”

Individual Level. Consumers foraging on resource follow a Holling Type II functional response with a length-dependent attack rate and are limited by digestion time (which is technically equivalent to handling time in the context of a Type II functional response). Digestion time is a decreasing function of length. Attack rate on zooplankton is a bell-shaped function of length. Biological arguments for selecting the forms of these functions are given by Persson et al. (1998) and Claessen et al. (2000). When zooplankton intake exactly suffices to cover maintenance, individuals neither grow nor reproduce. This length-dependent “critical resource demand” (CRD) is obtained by equating the resource intake rate $\gamma_a(x)$ to the maintenance requirement $m(x)$ (see table 2). The resulting function describes the CRD for all possible consumer lengths, which determines the size-based intraspecific resource competition and, to a large extent, also the exhibited population dynamics. Parameter changes result only in quantitative changes in population dynamics as long as they do not qualitatively alter the shape of the CRD function (Persson et al. 1998; de Roos and Persson 2003). For our functions and parameters, CRD strictly increases with length, implying that smaller consumers can survive on lower resource density. The maximum attainable length of consumers can be found by finding the length for which the CRD is equal to the resource carrying capacity, which is at approximately 153 mm in our model.

All consumer individuals are both potential cannibals and potential cannibalistic victims. The strength of the

Table 1: Specification of the dynamics of model state variables

Variable	Equation
Partial differential equation	$\frac{\partial n}{\partial t} + \frac{\partial gn}{\partial x} = -\mu(x)n(x)$
Boundary condition	$g(x_b)n(x_b) = \int_{x_f}^{x_{\max}} b(x)n(x)dx$
Resource dynamics	$\frac{dR}{dt} = r(K - R) - \int_{x_b}^{x_{\max}} \frac{A(x)R}{1 + H(x)\gamma(x)} n(x)dx$

Note: Individual-level functions are listed in table 2. Parameters are listed in table 3. Note that in the case of a cannibalistic consumer, the functions $g(x)$, $b(x)$, $\mu(x)$, and $\gamma(x)$ depend on $n(x)$, the population size distribution. This has been left out for simplicity. For the same reason, the time argument has been dropped from variables and functions.

Table 2: Individual-level functions

Variable	Equation
Body mass	$w(x) = \lambda x^3$
Zooplankton attack rate	$A(x) = \begin{cases} \alpha x^2 (x - x_p)^2 & \text{if } x \leq x_p \\ 0 & \text{otherwise} \end{cases}$
Cannibalistic attack rate ^a	$T(x_c, x_v) = \begin{cases} \frac{x_v - \delta x_c}{(\phi - \delta)x_c} & \text{if } \delta x_c < x_v \leq \phi x_c \\ \frac{\epsilon x_c - x_v}{(\epsilon - \phi)x_c} & \text{if } \phi x_c < x_v < \epsilon x_c \\ 0 & \text{otherwise} \end{cases}$
Cannibalistic maximum attack rate	$\nu(x) = \beta x^2$
Total encounter rate	$\gamma(x) = \gamma_a(x) + \gamma_c(x)$
Zooplankton encounter	$\gamma_a(x) = A(x)R$
Cannibalistic encounter	$\gamma_c(x) = \int_{\delta x}^{\epsilon x} \beta x^2 T(x, y) w(y) n(y) dy$
Food assimilation rate	$F(x) = c_a \frac{\gamma(x)}{1 + H(x)\gamma(x)}$
Digestion time	$H(x) = \xi x^{-3}$
Maintenance requirements	$M(x) = \rho x^3$
Growth rate in length	$g(x) = \begin{cases} 0 & \text{if } \kappa F(x) < M(x) \\ \frac{1}{3\lambda x^2} (\kappa F(x) - M(x)) & \text{otherwise} \end{cases}$
Reproductive rate	$b(x) = \begin{cases} \frac{c_r (1 - \kappa) F(x)}{w(x_b)} & \text{if } x > x_r \\ 0 & \text{otherwise} \end{cases}$
Total mortality	$\mu(x) = \mu_0 + \mu_s(x) + \mu_c(x) + \mu_H$
Cannibalistic mortality	$\mu_c(x) = \int_{x/\epsilon}^{x/\delta} \frac{\beta x_c^2 T(x_c, x)}{1 + H(x_c)\gamma(x_c)} n(x_c) dx_c$
Starvation mortality	$\mu_s(x) = \begin{cases} 0 & \text{if } \kappa F(x) > M(x) \\ s(M(x) - \kappa F(x)) & \text{otherwise} \end{cases}$

^a We use the notation x_c and x_v to indicate the length of cannibal and victim, respectively.

cannibalistic interaction (the attack rate) depends on the ratio of victim to cannibal length and is determined by physiological constraints of the cannibal. The cannibalistic attack rate increases with victim length up to an optimum and then decreases until it reaches 0 at the maximum victim length. This results in a tent-shaped function that describes the cannibalistic attack rate of all possible cannibal sizes on all possible victim sizes (Claessen et al. 2000, 2002).

Following the model proposed by Kooijman and Metz (1984), consumers allocate a fraction κ of all assimilated energy to growth and metabolism and the rest to reproduction. Metabolic requirements are assumed to scale linearly with body volume, that is, length cubed. Maintenance takes precedence over growth, and if maintenance cost exceeds the fraction of intake rate allocated to growth, individuals stop growing altogether and experience starvation mortality proportional to the energetic deficit. The

remainder of the acquired energy is used for reproductive tissue. For juveniles, this energy is assumed to be invested in the development of reproductive organs (Kooijman 2000). Adults produce offspring at a rate equal to the investment in reproduction divided by the mass of an offspring.

Population Level. The population dynamics of the consumers described above can analytically be formulated as a partial differential equation and a boundary condition describing the time evolution of a distribution of individuals over all possible lengths and the reproduction process, respectively (Metz and Diekmann 1986; see table 1). To simulate such a population, we use the escalator boxcar train method, an algorithm specifically designed to handle the mathematical difficulties associated with structured populations (de Roos et al. 1992; de Roos 1997). The approach involves discretizing the population length dis-

Table 3: State variables and parameters

Symbol	Default value	Unit	Interpretation
x	...	mm	Individual length
$n(x)$...	L^{-1}	Population size distribution
R	...	$g L^{-1}$	Resource density
x_b	7	mm	Length at birth
x_r	115	mm	Length at maturation
λ	9×10^{-6}	$g mm^{-3}$	Length-weight scaling constant
α	7.0×10^{-4}	$L day^{-1} mm^{-4}$	Planktivory attack rate scaling constant
x_p	160.0	mm	Maximum length of planktivory
β	.4 ^a	$L day^{-1} mm^{-2}$	Cannibalistic voracity
δ	.0	...	Lower limit of predation window
ϵ	.7	...	Upper limit of predation window
ϕ	.2	...	Optimum of predation window
c_a	.6	...	Assimilation efficiency
c_c	.5	...	Efficiency of offspring production
ξ	1.7×10^{-6}	$day g^{-1} mm^3$	Digestion time scaling constant
ρ	2.5×10^{-7}	$g day^{-1} mm^{-3}$	Metabolic rate scaling constant
κ	.7	...	Allocation coefficient
μ_0	.01	day^{-1}	Background mortality rate
μ_H	Varied	day^{-1}	Harvesting mortality rate
s	1	g^{-1}	Starvation mortality coefficient
r	.1	day^{-1}	Zooplankton population growth rate
K	3×10^{-3}	$g L^{-1}$	Zooplankton carrying capacity

Note: Parameterization (for references, see Claessen et al. 2000) for Eurasian perch (*Perca fluviatilis*) feeding on a zooplankton resource (*Daphnia* sp., length 1 mm) and conspecifics. All parameters except r and K refer to individual-level processes. The time argument has been left out from notation of variables.

^a Set to 0.0 for the pure consumer archetype.

tribution into a finite but variable number of cohorts of individuals born at approximately the same time. The properties of individuals change over time, but all individuals in a cohort remain identical for the duration of their lives. The number of cohorts in the population increases when reproduction takes place or decreases when the density of individuals in a cohort becomes negligible (10^{-13} individuals L^{-1} in our study).

Harvesting

Harvesting mortality is implemented as a constant, continuous, density-independent mortality rate μ_H for all individuals in the relevant size range, in addition to the background mortality rate (μ_0). This mortality is, in accordance with other rate parameters in our model, expressed as a daily rate. A more intuitive understanding of the harvesting mortality rate can be gained by calculating the reduced life expectancy and survival of susceptible individuals over a longer period. In the absence of starvation, cannibalism, and harvesting and with a background mortality rate of 0.01 day^{-1} , the life expectancy of a just matured individual is $1/\mu_0$, or 100 days. A daily adult harvesting rate of 0.01 halves this period, while a rate of 0.05 reduces it to <17 days.

Survival decreases exponentially with increasing harvesting rate according to $S_s = e^{-(\mu_0 + \mu_H)t}$, where t is the time period in days. A harvesting rate of 0.05 for 20 days hence leads to a 30% survival.

Analysis

In the consumer-resource formulation of our model, without cannibalism, we distinguish between three types of individuals: small juveniles (7–70 mm), larger juveniles (70–115 mm), and adult individuals (>115 mm). In the absence of cannibalism, we study the effects of harvesting mortality targeting each of these size classes. With cannibalism, individuals in our model undergo an ontogenetic niche shift, changing from obligate feeding on basic resources early in life to an obligately piscivorous stage as large adults. In between they consume a mixed diet, the exact composition of which depends on the individual's size and the availability of the resources. We can discriminate four functionally different types of individuals in the model population: (1) small juvenile resource feeders (7–70 mm), (2) larger juveniles with a mixed diet (70–115 mm), (3) relatively small adults with a mixed diet (115–160 mm), and (4) large, exclusively cannibalistic adults

(>160 mm). We study the effects of selective mortality on size classes 1–3. The large, obligately cannibalistic individuals are not present in the absence of harvesting as a result of population feedbacks (see “Results”). In addition, we study the effects of harvesting all adult individuals (>115 mm).

Results

No Cannibalism

In the absence of any additional mortality, the maximum length that consumer individuals reach is slightly more than 115 mm, the maturation length threshold (figs. 1, 2). The population exhibits single-generation cycles driven by competitive superiority of smaller individuals. Cohort formation occurs because smaller individuals grow in length faster than larger ones, resulting in convergent growth. This convergent growth in turn leads to synchronized maturation and hence pulsed reproduction. This large pulse of newborns depletes the resource to such an extent that they deny food to their parents, which starve to death shortly after. The population dynamics is driven by a negative density-dependent effect of smaller individuals on larger conspecifics. This type of dynamics has been found in a number of models with different structures (continuous time, discrete time, and intermediate types; Nisbet and Gurney 1982; Persson et al. 1998; de Roos and Persson 2003; Murdoch et al. 2003).

Harvesting Small Juveniles. Increased harvesting mortality of small juvenile consumers stabilizes population dynamics. An example of this stabilizing effect is shown in figure 1. During the first 1,000 days, the population is unharvested and exhibits single-generation cycles. From $t = 1,000$ onward, the small juvenile individuals (with length between 7 and 70 mm) are subjected to harvesting mortality with intensity 0.05 day^{-1} . The effects of varying harvesting intensity on small juveniles is shown in more detail in figure 2. The harvesting mortality causes a reduction in the density of small juveniles, which results in higher resource availability and hence accelerated growth for those individuals that survive the harvesting. This increases average consumer length (fig. 2) and shortens the cycle period, because it results in maturation at an earlier age. The stabilizing effect of harvesting mortality is clearly reflected by the reduced amplitude of the fluctuations in resource density. Although the average adult density increases with increased harvesting intensity (fig. 2), it reduces the number of simultaneously maturing adults, which leads to a more gradual offspring production. This, combined with the quick reduction in offspring numbers due to harvesting mortality, decreases the newborn co-

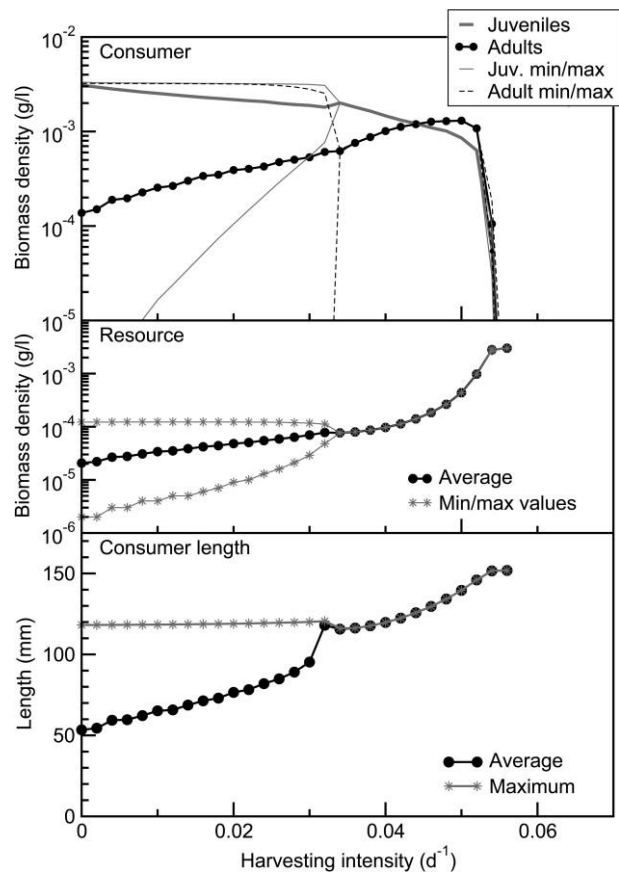


Figure 2: Stabilizing effect of harvesting small juvenile consumers (7–70 mm) in a consumer–resource interaction. *Top*, average, minimum, and maximum densities of juvenile and adult consumers. For a stable population (above $\mu_{H1} = 0.033$), these coincide. *Middle*, average, minimum, and maximum resource density. *Bottom*, average and maximum length of the largest individuals in the population. Single-generation cycles persist up to $\mu_{H1} = 0.033$; at higher harvesting mortality rates, the population dynamics is stable. At $\mu_{H1} = 0.056$, the consumer population goes extinct. Average, minimum, and maximum values are calculated for each harvesting intensity value from a 4,000-day period, starting after transient dynamics has disappeared.

hort’s capacity to reduce the resource, as indicated by an increase in the resource minimum with increasing harvesting intensity (fig. 2). This minimum, which succeeds each reproduction pulse, causes the starvation of all parent individuals in single-generation cycles (such as after $t = 200$ and $t = 970$ in fig. 1). The maximum resource density, which occurs just before reproduction (at $t = 200$ and $t = 970$ in fig. 1), is largely independent of harvesting intensity. At $\mu_{H1} \approx 0.032$, the density-dependent effect of the newborn pulse is so strongly reduced that it no longer causes significant adult starvation, and population dynamics stabilizes. After the stabilization, the consumer population density is controlled by the imposed mortality rather

than by life-history constraints and resource competition among generations, because it is this mortality that determines the number of individuals that reach maturity. Furthermore, the low juvenile biomass induced by high harvesting mortality results in higher resource density (fig. 2), which facilitates increased maximum consumer size with higher harvesting intensity. Around $\mu_H = 0.05$, mortality is so high that resource competition no longer slows growth, and all individuals grow at their maximum physiological rate. Any further mortality cannot be compensated for through faster development and hence causes a decreased abundance in all size classes. Reflecting the low consumer density, the resource density approaches its carrying capacity ($3.0 \times 10^{-3} \text{ g L}^{-1}$; fig. 2). At $\mu_H \approx 0.056$, the population goes extinct.

Harvesting Larger Individuals. Qualitatively, the effects of increased mortality on other size classes are highly similar to the results presented above for small juvenile individuals. The major difference is that the thresholds at which the single-generation cycles collapse and the population goes extinct shift to higher harvesting intensity. When large juveniles are harvested (between 70 and 115 mm), both thresholds still occur but lie close together (see fig. A1 in the appendix in the online edition of the *American Naturalist*). Stabilization occurs at $\mu_H \approx 0.22$, and the population goes extinct at $\mu_H \approx 0.24$. When larger individuals are targeted, population extinction occurs at higher and higher harvesting intensity. When adults 115 mm and larger are targeted, the population can no longer be driven extinct by harvesting mortality (see fig. A2 in the appendix in the online edition of the *American Naturalist*). This occurs because a harvesting threshold equal to the maturation length, 115 mm, ensures that all maturing individuals can reproduce, if only for a very short time interval, before being killed. Stabilization of the single-generation cycle is not possible either when only adult individuals are harvested. On the contrary, adult mortality reinforces the mechanism driving the single-generation cycles. It replaces the starvation mortality that would otherwise be the result of the newborn-induced resource depletion. It is the imposed harvesting mortality itself, which is stabilizing when juvenile individuals are targeted, that causes the cyclic dynamics to persist even at very high harvest mortality rates when adults are targeted.

Cannibalism

The individual- and population-level consequences of size-dependent cannibalism have been extensively studied in a series of recent articles (Claessen et al. 2000, 2002, 2004; Claessen and de Roos 2003; Persson et al. 2003, 2004a, 2004b). In the absence of harvesting mortality, our can-

nibalistic population exhibits “cannibal-driven” dynamics, which is typical for species that are strongly cannibalistic (Claessen et al. 2002; Persson et al. 2004b). This type of dynamics is characterized by the presence of a constant and numerous contingent of cannibals, which consumes the bulk of all offspring before those offspring can themselves become cannibals. The high mortality of newborns results in stable population dynamics (fig. 5). The large number of cannibals paired with the relatively low energetic gain of eating very small victims implies that only a small fraction of the energy gain of cannibals comes from eating conspecifics; the majority comes from resource feeding. Despite the limited direct energetic gain from cannibalism, the imposed mortality provides a very efficient way to eliminate competition for resources from smaller conspecifics. The cannibalistic population is hence regulated by a negative density-dependent effect of large individuals on smaller conspecifics. The “direction” of regulation is hence to some extent opposite of what we observe in a pure consumer population, where it is the small individuals that limit the persistence of their larger conspecifics.

Harvesting Juveniles. The only effect on population dynamics when the smallest individuals (length range 7–70 mm) are targeted by harvesting mortality is a steady decrease in density in all size classes in the population (see fig. A3 in the appendix in the online edition of the *American Naturalist*). The population density remains stable, and the life history of individuals is unaltered. The mortality on small juveniles imposed through harvesting is compensated for by reduced cannibalistic mortality. Because the energetic gain of cannibalism is negligible (as outlined above), there is no effect on population dynamics or life history. At a certain harvesting intensity threshold ($\mu_H \approx 0.05$ for our parameter values), the imposed mortality exceeds the mortality that would otherwise be inflicted by cannibals, and a further increase in harvesting intensity leads to a sharp decrease in the abundance of all size classes in the population. At $\mu_H \approx 0.055$, the population goes extinct.

Targeting larger juveniles (70–115 mm; see fig. A4 in the appendix in the online edition of the *American Naturalist*) does not affect the population dynamics up to a threshold level of harvesting mortality ($\mu_H \approx 0.035$), where a positive feedback mechanism is triggered and the maximum size that individuals can attain increases sharply from approximately 160 to more than 300 mm. The abundance of juvenile individuals (7–115 mm) is higher after the shift, while the density of adults is smaller (fig. 3). Increasing harvesting mortality from 0 reduces the number of individuals that reach the adult stage. This increases the per capita availability of resource and cannibalistic prey

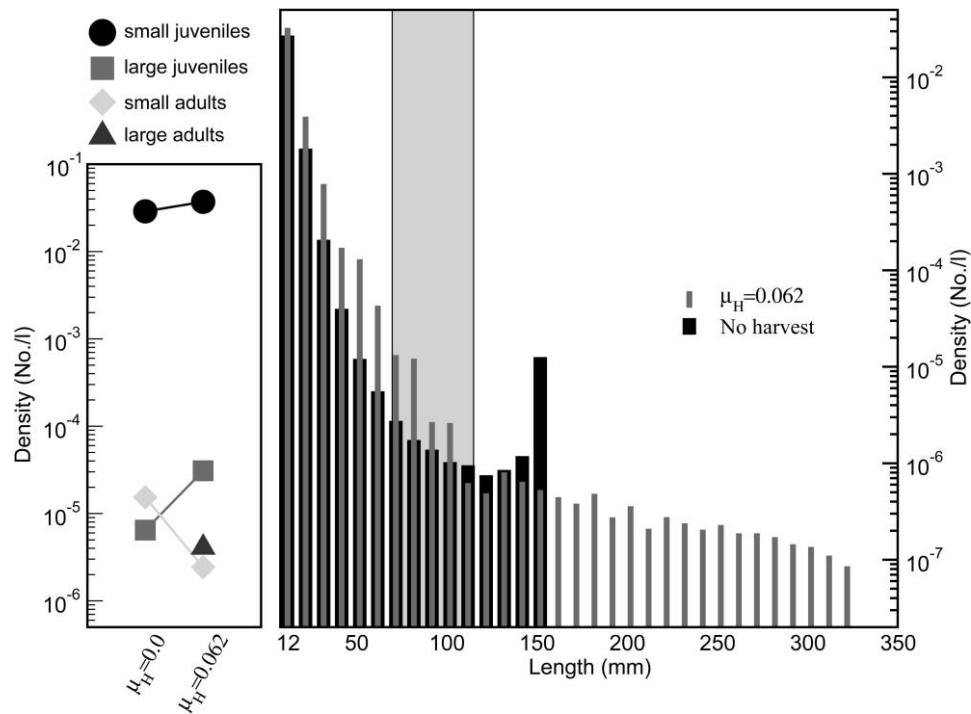


Figure 3: Harvesting large juvenile individuals (70–115 mm; squares on left, gray area on right) induces a clear shift in the length distribution of a population regulated by cannibalistic mortality. *Left*, density of four different length classes (squares, small juveniles, 7–70 mm; circles, large juveniles, 70–115 mm; diamonds, small adults, 115–160 mm; triangles, large adults, >160 mm). *Right*, population length distribution. Each bar represents the density of individuals in a 10-mm-length interval, plotted at the center of each interval.

for the remaining adults, allowing them to reach larger body sizes, where they have access to larger, more profitable prey, which in turn allows them to grow even more. The combination of larger body size and more profitable prey leads to a disproportionately higher per capita fecundity of these individuals, which further increases cannibalistic prey availabilities. This positive feedback induces the dramatic shift in population size distribution illustrated in figure 3. For population stability, it is necessary that the combined effect of harvesting and cannibalism keeps the density in the large juvenile stage (70–115 mm) low to prevent overexploitation of prey. However, the increased inflow into the large juvenile stage (70–115 mm) induced by harvesting (fig. 3) is so strong that it eventually allows the large juveniles to escape the control through harvesting and cannibalism, which leads to destabilization of the population dynamics (at $\mu_H \approx 0.075$). Ultimately, the harvesting mortality becomes so strong that, despite any compensatory mechanisms, it strongly reduces the numbers of newborns produced, driving the population to extinction (at $\mu_H \approx 0.3$).

Harvesting Adults. Increased mortality on adult individ-

uals larger than 115 mm in length is strongly destabilizing even at very low harvesting intensity. This is because such mortality reduces the cannibalistic mortality inflicted on small individuals that stabilizes population dynamics. The emerging cyclic population dynamics is characterized by the occurrence of very large “cannibalistic giants” that can reach lengths in excess of 750 mm (figs. 4, 5).

The reduced density of adult individuals reduces the influence of cannibalism on population dynamics and increases the influence of resource competition. The harvested adults lose their ability to numerically control the juveniles (with length ≤ 115 mm), leading to higher juvenile density and consequent resource monopolization, resource competition within the juvenile cohort, convergent growth, and hence destabilization of population dynamics (fig. 4). These population dynamical processes are identical to those that shape population dynamics in the absence of cannibalism. However, single-generation cycles do not emerge here, because cannibalism offers an alternative resource for those adults that survive the harvesting. Instead, a more complex population dynamical cycle appears (fig. 5). Numerically, the population dynamics is driven by a dominant cohort that monopolizes the re-

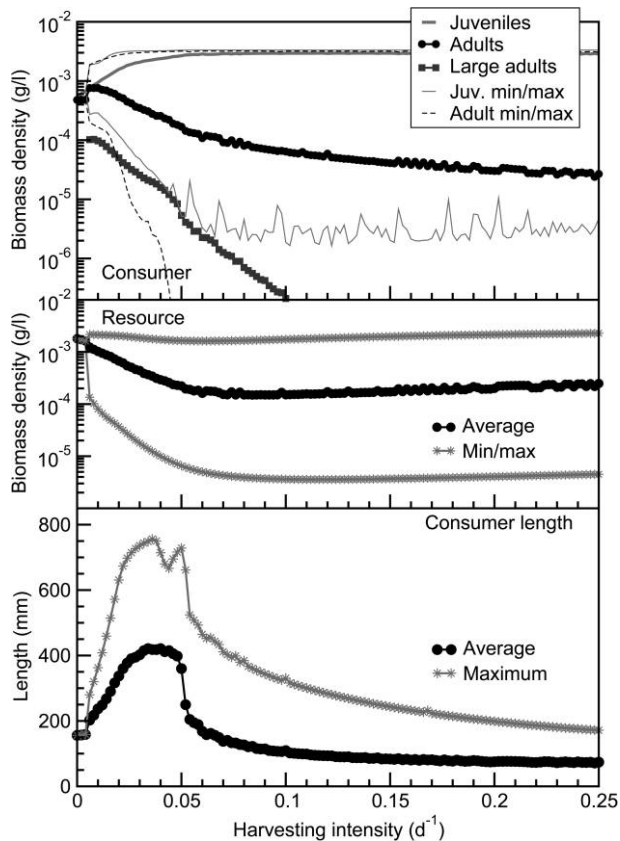


Figure 4: Destabilizing effect of harvesting adults (≥ 115 mm) in a population regulated by cannibalistic mortality. *Top*, average, minimum, and maximum biomass density of juvenile and adult consumers (≥ 115 mm) and average density of large adults (≥ 160 mm). *Middle*, average, minimum, and maximum resource densities. Convergence of minimum and maximum on the average in the top two panels indicates population stability. *Bottom*, average and maximum length of the largest individuals in the population. After the destabilization at low harvesting intensity, cannibalistic giants appear. Further increased harvesting intensity reduces the ultimate size that these giants reach. Average, minimum, and maximum values are calculated for each harvesting intensity value from a 4,000-day period, starting after transient dynamics has disappeared.

source and induces strong competition among small individuals, such as in single-generation cycles (cf. the high-amplitude resource dynamics and strongly pulsed reproduction in the middle of fig. 5 and that of fig. 1). After the production of a dominant cohort, the life-history trajectories of similar-sized cohorts converge toward it, while individuals that are large enough to feed on it show strongly accelerated growth. These fast growers are very few in number, and although they reach very large sizes, they have no significant effect on population dynamics. This type of dynamics has been coined “dwarf and giant dynamics” (Claessen et al. 2000, 2002). In previous work, these dynamics have been found for specific parametri-

zation of the cannibalistic interactions; we find here that they can also be induced by increased density-independent adult mortality. At higher harvesting mortality ($\mu_H \geq 0.037$), the maximum attainable size starts to decrease, because harvesting mortality kills individuals before they can reach their potential maximum size set by the availability of cannibalistic victims. Eventually, this leads to the formation of “single-generation cycles,” where the death of adult individuals is the result of harvesting mortality rather than starvation through intercohort competition (from $\mu_H \approx 0.1$; fig. 4). Once the population exhibits this type of dynamics, the effects of harvesting are minimal, and it is impossible to drive the population to extinction.

Harvesting only small adults with a mixed diet (115–160 mm) leads, at low intensity, to results similar to the scenario where only large juveniles (70–115 mm) are targeted by harvesting mortality; the maximum size that individuals can attain gradually increases up to a maximum length of more than 300 mm at $\mu_H \approx 0.04$. When harvesting intensity is increased further, the population destabilizes, and dynamics is similar to that shown in figure 5 (*middle, right*). However, because of the size refuge from harvesting for individuals larger than 160 mm, the cannibals can reach even larger sizes up to 800 mm. These cannibalistic giants also occur at higher harvesting intensity; the maximum size remains very high up to $\mu_H \approx 0.225$. Eventually, harvesting mortality is so high that no individuals survive to reach invulnerable size, leading to single-generation dynamics.

Comparison of Life-History Types

For both cannibalistic and pure consumer archetypes, population dynamics is stable when mortality of small juvenile individuals is high and unstable when such mortality is low. In the absence of harvesting mortality, this size-dependent mortality is low for the pure consumer archetype, resulting in unstable population dynamics. Contrastingly, the cannibalistic archetype shows stable population dynamics in the absence of harvesting, because large individuals impose very high cannibalistic mortality on small juveniles. In the pure consumer population, increased harvesting mortality on small juvenile individuals stabilizes population dynamics; in the cannibalistic population, such harvesting mortality has no effect, because it merely replaces mortality that would otherwise be inflicted by cannibalism. Similarly, harvesting adult individuals has no effect in the pure consumer population because it replaces mortality that would otherwise occur through starvation. In contrast, in the cannibalistic population, harvesting adults strongly decreases cannibalistic mortality on juveniles, and hence it has a strongly destabilizing effect on population dynamics. The stabilization of a population of

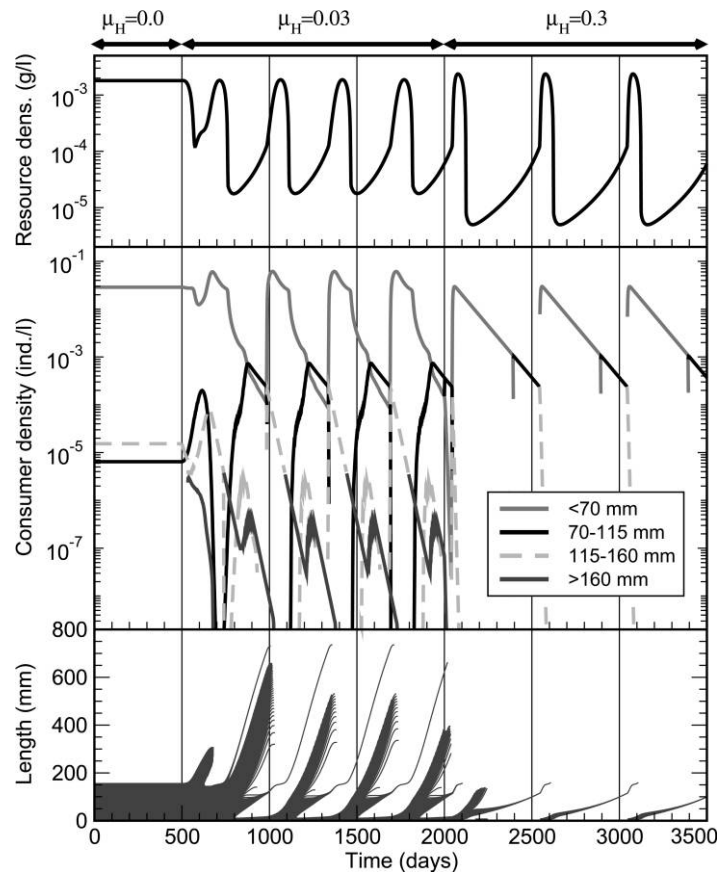


Figure 5: Shift from stable cannibal-driven dynamics to complex dynamics, with cannibalistic giants to single-generation cycles induced by adult mortality when harvesting intensity is increased from 0.0 (up to $t = 500$) to 0.03 (up to $t = 2,000$) to 0.3 (from $t = 2,000$ onward), targeting all adult individuals (length ≥ 115 mm). The harvesting intensity becomes so high that all individuals are killed before reaching “giant” length, and the population dynamics turns into a type of degenerate single-generation cycle where the adult mortality is caused by harvesting instead of starvation.

pure consumers leads to a somewhat increased maximum body length of consumers, while the destabilization of a cannibalistic population can induce the growth of “cannibalistic giants.”

Discussion

We have analyzed the effects of size-selective mortality on a consumer with resource-dependent growth. As a general result, we find that for both the pure and the cannibalistic consumer archetype, selective mortality on smaller individuals can more easily drive a population to extinction than can selective mortality on adults. In addition, both archetypes show a large compensatory capacity through food-dependent individual growth. Other effects of varying mortality depend on both the size range it is applied to and the life history of the consumer.

As a test of robustness, we have repeated our study using a species-specific model for Eurasian perch (*Perca fluvia-*

tilis) from Claessen et al. (2002). This model assumes different energy allocation rules, resource attack rate, and handling time functions and a discrete reproduction event once per year instead of continuous reproduction. Under these substantially different model assumptions, the results of size-selective harvesting are highly similar (see figs. A5, A6). For the pure consumer population, we find the same stabilization of dynamics with increasing harvesting intensity targeting small juvenile individuals (cf. figs. 2, A5). This similarity shows that our results also extend to cohort cycles with overlapping generations (i.e., where adults do not starve to death after reproduction), which are present in the alternative model. Such cycles appear more common in natural systems than the strict cohort switching found in our fully continuous model. The similarity between the continuous and the discrete-continuous models is not surprising, given that also in this model, smaller individuals can persist at lower resource densities than larger ones (they have a lower “critical resource density,” where intake

exactly equals maintenance). Persson et al. (1998) and de Roos and Persson (2003) show that this property determines the type of cycles that emerges. We conclude that our result that density-independent mortality targeting juveniles stabilizes cohort cycles holds as long as juveniles have a lower critical resource density than adults.

As for the pure consumer population, our results for the cannibalistic consumer completely carry over to the alternative model. Increasing adult mortality induces the same switch from stable, cannibal-driven dynamics to large-amplitude fluctuations and the growth of cannibalistic giants that we find in the current study (cf. figs. 4, A6). The relevant parameters determining the dynamics of populations regulated by cannibalism are the cannibalistic voracity and the minimum victim to cannibal size ratio (β and δ , respectively; Claessen et al. 2002). At very low cannibalistic voracity and a very large minimum size ratio, the population is regulated by size-dependent competition and hence exhibits cohort cycles. Populations with intermediate minimum victim to cannibal ratios can exhibit dwarf and giant dynamics. In such populations, harvesting adult individuals reduces the size of the cannibalistic giants, eventually leading to cohort cycles. Our results hence hold for cannibalistic populations with significant cannibalistic voracity and intermediate and low minimum victim to cannibal ratio. For populations exhibiting cohort cycles due to a high victim to cannibal ratio, harvesting can increase co-occurrence of cannibals and suitable victims in the population, and for such populations, the results may differ from ours.

Both species archetypes that we model use an energy budget model, where acquired energy is always partitioned between somatic and gonadic tissue, which results in significant body growth potential after maturation. Such "mixed" energy allocation is found in a large number of invertebrate taxa, including clams, cladocerans, crayfish, mollusks, insect species, and echinoderms. It is the general rule among fish, amphibians, and reptiles, which dominate vertebrates taxonomically (Sebens 1987; Karkach 2006). Mammals, birds, and most insect species have a more extreme allocation, where growth stops on maturation, and all energy is channeled to reproduction (Karkach 2006). As long as adults are competitively inferior, our results for the pure consumer archetype species still hold, and the exact size of the adults is irrelevant. Our results for the pure consumer archetype are hence valid for both allocation types. For the cannibalistic archetype, the size of adults determines their potential prey size range. Halted somatic growth at a fixed size may reduce the cannibalistic mortality risk and impose a refuge from cannibalism at a large size, which is to some extent similar to reducing the maximum victim to cannibal size ratio (ϵ). The effect of such a reduction is small in populations regulated by can-

nibalistic mortality, only strengthening the dominance of large juveniles and small adults (Claessen et al. 2002). Such an alternative allocation model would not alter the mechanism that regulates the population in the absence of harvesting and hence does not change the shift from cannibal-driven dynamics to cohort cycles with increased adult harvesting intensity, but it may have a quantitative effect on the population size distribution.

Changes in resource productivity do not qualitatively alter population dynamics for the pure consumer archetype. Because we assume semichemostat resource dynamics, no paradox of enrichment-like phenomena occurs (Murdoch et al. 2003). Below a threshold resource productivity, the consumer cannot persist; above it, the population shows cohort cycles, the period and amplitude of which increase with increasing productivity (Persson et al. 1998). The same holds for a population regulated by cannibalistic mortality. As a rule, with semichemostat resource dynamics, changes in productivity cannot change the mechanism that regulates a population driven by cannibalistic mortality (Claessen et al. 2002). Our results hence hold for any resource productivity high enough to support a consumer population, given that cannibalistic mortality regulates the population. One exception should be noted for populations where the cannibalistic control is very weak; for example, because of a fairly high value of the lower limit of the cannibalistic window (δ), increased productivity can change the mode of population regulation from cannibal-driven to dwarf and giant cycles.

We are far from the first to report the potential stabilizing effect of size-dependent mortality (Mech 1966; Murdoch and Oaten 1975; McNair 1987; Murdoch et al. 2003). However, all these studies show the stabilization of multigenerational consumer-resource cycles by a third species that imposes density-independent, size-dependent mortality. The effects of size-dependent mortality on cycles induced by intraspecific mechanisms are much less studied, although these cycles appear to be the more common type (Murdoch et al. 2002). Similarly, Dennis et al. (1995, 1997) reported destabilization of a cannibalistic population in response to adult mortality. However, these results come from a laboratory system where food is present in unlimited quantity, and cannibals are assumed to gain no energy through feeding on conspecifics. These conditions, which strongly constrain the dynamical richness of the system (Claessen et al. 2004), may be less relevant outside the laboratory (Sebens 1987; Werner 1988; Wilbur 1988).

In the pure consumer, we find a strong increase in adult biomass density with increasing harvesting of small juveniles, while increased adult mortality invariably leads to decreased average biomass density of adults. Correspondingly, a recent experimental study showed that in a soil mite population that is regulated by resource limitation,

increased mortality on the adult stage decreased adult abundance, while increased egg mortality led to increased adult density (Cameron and Benton 2004). The positive effect of egg mortality on adult abundance was suggested to come about through released resource competition in the juvenile stage, leading to an increase in the number of emerging adults. In line with both our findings and those of Cameron and Benton (2004), Nicholson (1957) reported that when 50% of young blowfly larvae were destroyed each day, the adult population more than doubled. Furthermore, destruction of 50% of the adult population every second day led to a decrease in the density of both immature and mature individuals (Nicholson 1954*b*, 1957). The increase in adult biomass density that we find in response to increased mortality for small juvenile individuals was first found by de Roos and Persson (2002). It occurs when the mortality of one juvenile consumer relaxes the food-dependent growth of the remaining individuals to such an extent that more than one new juvenile is produced. Such “overcompensatory” responses have important consequences for ecological communities (de Roos and Persson 2002; de Roos et al. 2003; van Kooten et al. 2005).

Our results indicate a sort of trade-off in the response of cannibalistic populations to size-dependent mortality. Through the intricate interplay of dynamical feedback mechanisms, size-selective mortality on adult individuals can induce a greater than fourfold increase in maximum body length. However, such increased growth can occur only during unstable, cyclic population dynamics. This finding is in line with earlier studies of cannibalistic population dynamics, which argue that the occurrence of cannibalistic giants and population stability are mutually exclusive phenomena (Claessen et al. 2000; Persson et al. 2004*a*). In contrast, we have shown that when mortality is increased selectively for large juvenile individuals, induction of strongly enlarged cannibals is possible without destabilizing population dynamics. This result is a novel addition to the developing theory of size-dependent cannibalism, as reviewed by Claessen et al. (2004).

Stunting (the occurrence of a narrow population size distribution dominated by slow-growing small individuals) is a common phenomenon as a result of overstocking and/or underharvesting of fish species. Reducing the density of small individuals has been shown to increase the growth of the remaining population (Schneider and Lockwood 2002). Our results support the efficiency of this method for consumer species. In contrast, for cannibalistic species, our model predicts that removal of small individuals has no effect. In accordance with this prediction, selective removal of small individuals to break the stuntedness and increase the production of large individuals in populations of northern pike (*Esox lucius*), a notoriously

cannibalistic fish species, appears to be highly inefficient (Goeman and Spencer 1992; Margenau 1995). Further empirical support for our results regarding cannibalistic species comes from early harvesting studies on Eurasian perch (*P. fluviatilis*) in small lakes (Alm 1951). In agreement with our predictions, selective harvesting of adult perch led to a clear and almost immediate increase in recruitment and induced the appearance of large adult individuals. Preharvesting, the size distributions of the perch populations were strongly stunted, which is typical for populations under cannibalistic control.

Acknowledgments

We thank W. Wilson and three anonymous reviewers for comments on earlier versions of the manuscript. L.P. and T.v.K. are financially supported by grants from the Swedish Research Council and the Swedish Research Council for Environment, Agricultural Sciences, and Spatial Planning. A.M.d.R. is supported by the Netherlands Organization for Scientific Research.

Literature Cited

- Alm, G. 1951. Year class fluctuations and span of life of perch. Institute of Freshwater Research Drottningholm Report 33:17–38.
- Boulton, A. M., and G. A. Polis. 1999. Phenology and life history of the desert spider, *Diguetia mojavea* (Araneae, Diguetidae). *Journal of Arachnology* 27:513–521.
- Brodin, T., and F. Johansson. 2002. Effects of predator-induced thinning and activity changes on life history in a damselfly. *Oecologia* (Berlin) 132:316–322.
- Calder, W. A. I. 1984. *Size, function and life history*. Harvard University Press, Cambridge, MA.
- Cameron, T. C., and T. G. Benton. 2004. Stage-structured harvesting and its effects: an empirical investigation using soil mites. *Journal of Animal Ecology* 73:996–1006.
- Claessen, D., and A. M. de Roos. 2003. Bistability in a size-structured population model of cannibalistic fish: a continuation study. *Theoretical Population Biology* 64:49–65.
- Claessen, D., A. M. de Roos, and L. Persson. 2000. Dwarfs and giants: cannibalism and competition in size-structured populations. *American Naturalist* 155:219–237.
- Claessen, D., C. Van Oss, A. M. de Roos, and L. Persson. 2002. The impact of size-dependent predation on population dynamics and individual life history. *Ecology* 83:1660–1675.
- Claessen, D., A. M. de Roos, and L. Persson. 2004. Population dynamic theory of size-cannibalism. *Proceedings of the Royal Society B: Biological Sciences* 271:333–340.
- Craig, J. K., B. J. Burke, L. B. Crowder, and J. A. Rice. 2006. Prey growth and size-dependent predation in juvenile estuarine fishes: experimental and model analyses. *Ecology* 87:2366–2377.
- Dennis, B., R. A. Desharnais, J. M. Cushing, and R. F. Costantino. 1995. *Nonlinear demographic dynamics: mathematical models, statistical methods, and biological experiments*. *Ecological Monographs* 65:261–281.
- . 1997. Transitions in population dynamics: equilibria to pe-

- riodic cycles to aperiodic cycles. *Journal of Animal Ecology* 66: 704–729.
- de Roos, A. M. 1997. A gentle introduction to physiologically structured population models. Pages 119–204 in H. Caswell and S. Tuljapurkar, eds. *Structured-population models in marine, terrestrial, and freshwater systems*. Chapman & Hall, New York.
- de Roos, A. M., and L. Persson. 2002. Size-dependent life-history traits promote catastrophic collapses of top predators. *Proceedings of the National Academy of Sciences of the USA* 99:12907–12912.
- . 2003. Competition in size-structured populations: mechanisms inducing cohort formation and population cycles. *Theoretical Population Biology* 63:1–16.
- de Roos, A. M., O. Diekmann, and J. Metz. 1992. Studying the dynamics of structured population models: a versatile technique and its application to *Daphnia*. *American Naturalist* 139:123–147.
- de Roos, A. M., L. Persson, and H. Thieme. 2003. Emergent Allee effects in top predators feeding on structured prey populations. *Proceedings of the Royal Society B: Biological Sciences* 270:611–618.
- Goeman, T., and P. Spencer. 1992. Fish community responds to manipulation of northern pike and yellow perch densities in a Minnesota centrarchid lake. Minnesota Department of Natural Resources Investigational Report 416. St. Paul, MN.
- Karkach, A. S. 2006. Trajectories and models of individual growth. *Demographic Research* 15:348–400.
- Keller, G., and G. Ribi. 1993. Fish predation and offspring survival in the prosobranch snail *Viviparus ater*. *Oecologia (Berlin)* 93:493–500.
- Kooijman, S. A. L. M. 2000. *Dynamic energy and mass budgets in biological systems*. 2nd ed. Cambridge University Press, Cambridge.
- Kooijman, S. A. L. M., and J. Metz. 1984. On the dynamics of chemically stressed populations: the deduction of population consequences from effects on individuals. *Ecotoxicology and Environmental Safety* 8:254–274.
- Margenau, T. A. 1995. Stunted northern pike: a case history of community manipulations and field transfer. Wisconsin Department of Natural Resources Research Report 169. Madison, WI.
- McNair, J. N. 1987. A reconciliation of simple and complex models of age-dependent predation. *Theoretical Population Biology* 32: 383–392.
- Mech, L. D. 1966. *The wolves of Isle Royale*. U.S. National Park Service Fauna Series no. 7.
- Metz, J., and O. Diekmann. 1986. *The dynamics of physiologically structured populations*. Springer, Berlin.
- Murdoch, W. W., and A. Oaten. 1975. Predation and population stability. *Advances in Ecological Research* 9:1–131.
- Murdoch, W. W., B. E. Kendall, R. M. Nisbet, C. J. Briggs, E. McCauley, and R. Bolser. 2002. Single-species models for many-species food webs. *Nature* 417:541–543.
- Murdoch, W. W., C. J. Briggs, and R. M. Nisbet. 2003. *Consumer-resource dynamics*. Monographs in population biology. Princeton University Press, Princeton, NJ.
- Nicholson, A. J. 1954a. Compensatory reactions of populations to stresses, and their evolutionary significance. *Australian Journal of Zoology* 2:1–8.
- . 1954b. An outline of the dynamics of animal populations. *Australian Journal of Zoology* 2:9–65.
- . 1957. The self-adjustment of populations to change. *Cold Spring Harbor Symposia on Quantitative Biology* 22:153–173.
- Nisbet, R. M., and W. S. C. Gurney. 1982. *Modelling fluctuating populations*. Wiley, Chichester.
- Paine, R. T. 1976. Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology* 57:858–873.
- Persson, L., K. Leonardsson, A. M. de Roos, M. Gyllenberg, and B. Christensen. 1998. Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. *Theoretical Population Biology* 54:270–293.
- Persson, L., A. M. de Roos, D. Claessen, P. Byström, J. Lövgren, S. Sjögren, R. Svanbäck, E. Wahlström, and E. Westman. 2003. Gigantic cannibals driving a whole-lake trophic cascade. *Proceedings of the National Academy of Sciences of the USA* 100:4035–4039.
- Persson, L., D. Claessen, A. M. de Roos, P. Byström, S. Sjögren, R. Svanbäck, E. Wahlström, and E. Westman. 2004a. Cannibalism in a size-structured population: energy extraction and control. *Ecological Monographs* 74:135–157.
- Persson, L., A. M. de Roos, and A. Bertolo. 2004b. Predicting shifts in dynamics of cannibalistic field populations using individual-based models. *Proceedings of the Royal Society B: Biological Sciences* 271:2489–2493.
- Peters, R. H. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge, MA.
- Polis, G. A. 1984. Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? *American Naturalist* 123:541–564.
- Schneider, J. C., and R. N. Lockwood. 2002. Use of walleye stocking, antimycin treatments, and catch-and-release angling regulations to increase growth and length of stunted bluegill populations in Michigan lakes. *North American Journal of Fisheries Management* 22:1041–1052.
- Sebens, K. P. 1987. The ecology of indeterminate growth in animals. *Annual Review of Ecology and Systematics* 18:371–407.
- van Kooten, T., A. M. de Roos, and L. Persson. 2005. Bistability and an Allee effect as emergent properties of stage-specific predation. *Journal of Theoretical Biology* 237:67–74.
- Vonesh, J. R. 2005. Sequential predator effects across three life stages of the African tree frog, *Hyperolius spinigularis*. *Oecologia (Berlin)* 143:280–290.
- Werner, E. 1988. Size, scaling, and the evolution of complex life cycles. Pages 60–81 in B. Ebenman and L. Persson, eds. *Size-structured populations: ecology and evolution*. Springer, Berlin.
- Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84:1083–1100.
- Wilbur, H. M. 1988. Interactions between growing predators and growing prey. Pages 3–9 in B. Ebenman and L. Persson, eds. *Size-structured populations: ecology and evolution*. Springer, Berlin.
- . 1997. Experimental ecology of food webs: complex systems in temporary ponds. *Ecology* 78:2279–2302.
- Wilbur, H. M., P. J. Morin, and R. N. Harris. 1983. Salamander predation and the structure of experimental communities: anuran responses. *Ecology* 64:1423–1429.