Size at hatching determines population dynamics and response to harvesting in cannibalistic fish

Tobias van Kooten, Jens Andersson, Pär Byström, Lennart Persson, and André M. de Roos

Abstract: We hypothesize that size at hatching strongly affects population dynamics of cannibalistic fish species and is a crucial determinant of how populations respond to selective removal of large individuals (harvesting). We use a mechanistic mathematical model to study the relation between hatching size and response to harvesting mortality, using Eurasian perch (*Perca fluviatilis*) as a model organism. We show how hatching size determines dynamics through its effect on the relative strength of cannibalistic mortality and resource competition as mechanisms of population regulation. In populations with intermediate and large hatching size, cannibalistic mortality is an important determinant of population dynamics, and harvesting destabilizes population dynamics. When hatching size is small, population stability is less sensitive to this type of harvesting. Populations hatching at small size are regulated by competition, and harvesting large individuals affects such populations less. Harvesting can also induce the growth of very large individuals, absent in unharvested populations. Our results show that harvesting in cannibalistic lake fish populations can strongly alter population dynamics in ways that can only be anticipated on the basis of mechanistic knowledge about how populations are regulated.

Résumé : Nous avançons l'hypothèse selon laquelle la taille à l'éclosion affecte fortement la dynamique de population des espèces cannibales de poissons et qu'elle est un facteur déterminant essentiel de la réaction de la population au retrait sélectif (par récolte) des individus de grande taille. Nous utilisons un modèle mathématique mécaniste pour étudier la relation entre la taille à l'éclosion et la réaction à la mortalité due à la récolte chez la perche eurasienne (*Perca fluviatilis*) qui nous sert d'organisme modèle. Nous montrons comment la taille à l'éclosion détermine la dynamique à travers son effet sur la force relative de la mortalité due au cannibalisme et sur la compétition pour les ressources qui sont les mécanismes de régulation de la population. Chez les populations qui ont une taille moyenne ou grande à l'éclosion, la mortalité due au cannibalisme est un facteur déterminant important de la dynamique de population et la récolte déstabilise la dynamique de population. Lorsque la taille à l'éclosion est faible, la stabilité de la population est moins sensible à ce type de récolte. Les populations qui éclosent à une petite taille sont contrôlées par la compétition et la récolte de grands individus affecte moins de telles populations. La récolte peut aussi favoriser la croissance de très grands individus qui sont absents des populations non exploitées. Nos résultats montrent que la récolte faite dans des populations lacustres de poissons cannibales peut fortement modifier la dynamique de population dans des directions qui ne peuvent être prévues que d'après des connaissances mécanistes de la régulation des populations.

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Introduction

Cannibalism is a widespread phenomenon among lake fish species (Andersson et al. 2007) that can strongly affect growth patterns of individuals (Claessen et al. 2000; Persson et al. 2004), populations dynamics (Dong and DeAngelis 1998; Claessen et al. 2002; Claessen and de Roos 2003), and even community dynamics (Persson et al. 2003). Cannibalism in fish is an inherently size-based process of large individuals feeding on smaller conspecifics (Juanes 2003), and the allometric functions relating cannibalistic attack rate to victim and cannibal size determine the effects of cannibalism (Claessen et al. 2002; Persson et al. 2004). Cannibals generally have maximum and minimum victim sizes, which depend on their own body size (Polis 1981; Mittelbach and Persson 1998; Juanes 2003). The ratio of minimum victim

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size to cannibal size, i.e., the ratio below which the cannibal is too large and (or) is the victim too small for successful consumption, is the crucial parameter determining the dynamical effects of cannibalism (Claessen et al. 2002; Persson et al. 2004). Another important parameter in this respect is the size at which newborn individuals enter the population, the hatching size. Although the minimum victim-to-cannibal ratio is a relative measure, hatching size directly sets the cannibal size range to which the newborn individuals are susceptible, not relative to another quantity. We hypothesize that hatching size, which varies considerably among lake fish species (Mittelbach and Persson 1998), contributes to differences in population dynamics observed among different cannibalistic lake fish species. We study this using a mathematical model of a size-structured consumer population capable of cannibalistic feeding.

The spectrum of cannibalistic fish species includes many popular target species of both recreational and professional fisheries (Smith and Reay 1991; Juanes 2003), and it is therefore important to assess whether differences in population dynamics as a result of life history characteristics such as hatching size lead to differential responses to harvesting pressure. Harvesting often selectively targets large individuals, either as a result of harvesting regulations or because they are disproportionately more valuable to fishermen (McConnell and Strand 2000; Trondsen et al. 2003; Lawrence 2005). It has been shown that harvesting large individuals can have a strongly destabilizing impact on the dynamics of cannibalistic lake fish populations (van Kooten et al. 2007), but it is unknown how this plays out with different hatching sizes. We present results showing how the effects of harvesting large individuals differ substantially among populations with different hatching size and that these differences are induced by the effect of hatching size on cannibalism.

We study the dynamics of a cannibalistic consumer and a single resource in isolation, i.e., in the absence of other consumer and resource populations, using a generic size-structured model. Although the model is based on Eurasian perch (*Perca fluviatilis*), many aspects of perch life history and lake ecosystem characteristics are deliberately omitted, yielding a model that contains common aspects of cannibalistic lake fish life history. Despite significant simplifications, variations of this model, using the same underlying framework, correctly capture the dynamics of Eurasian perch (*Perca fluviatilis*) (Claessen et al. 2000), roach (*Rutilus rutilus*) (de Roos et al. 2003), yellow perch (*Perca flavescens*), and northern pike (*Esox lucius*) (Persson et al. 2004) living in natural ecosystems with many other species present. Our generic model allows us to connect, clearly and unambiguously, our findings to general mechanisms such as competition, cannibalistic feeding, and cannibalistic mortality. Our aim is not to validate this model further by detailed comparison with more species data, but to develop a conceptual understanding of the role of hatching size in the regulation of cannibalistic lake fish populations.

Our results show that population dynamics indeed varies strongly with hatching size and that hatching size is an important determinant of population response to harvesting. We compare our model results with a compilation of time series variability data for a number of cannibalistic species and show qualitative congruence between model results and data. Our results indicate that management strategies involving minimum size limits may have profoundly different consequences when applied to different cannibalistic target species. In this light, future studies that aim to generate such strategies for exploited populations should consider the possible effects of the complex interplay between harvesting and the cannibalistic tendency of the exploited species.

Background: size-based cannibalism and competition

Recent theoretical and empirical developments in the dynamics of cannibalistic, size-structured populations show that dynamics are determined by the relative strength of resource competition, cannibalistic mortality, and cannibalistic energy gain (Dong and DeAngelis 1998; Claessen et al. 2004; Persson et al. 2004).

Resource competition occurs both among individuals of the same size and among individuals of different sizes. Individuals of the same size are affected by resource competition in a similar way. Depending on the intensity of such competition, development can be slowed down and starvation mortality can be increased. Among individuals of different sizes, competition can be highly assymmetrical. Smaller individuals generally have lower metabolic rate (Brown et al. 2004) and hence can meet their energy requirements at lower resource densities than larger individuals. When small individuals are numerous, they can effectively control the population by reducing the resource to such low levels that all larger individuals suffer from resource shortage. The minimum resource level at which an individual can persist can be used as a proxy of (inverse) competitiveness (Tilman 1982; Persson et al. 1998). This size-based competition is strongly density-dependent and leads to convergent growth. When a population consists of many small and a few larger individuals, the small ones will determine the resource level, causing growth retardation in the larger individuals, until the small ones have “caught up” in size. Vice versa, in the presence of a large number of large individuals, a few small ones will be unable to “control” the resource level but will grow faster than the larger ones until they catch up (Persson et al. 1998). Size at hatching determines the minimum resource requirements of the most competitive individuals in the population. With equal reproductive investments (total egg mass), smaller hatching size implies more hatchlings, which means that hatching size potentially mediates the density dependence in size-based competition.

Strong resource depletion by large numbers of young of the year fish following spawning is common in freshwater fish species (Cryer et al. 1986; Hamrin and Persson 1986; Persson et al. 2003). Larger individuals will have trouble meeting their resource requirements following such a resource depletion event, but cannibalism can alleviate this food stress for larger individuals in two different ways. It either provides an alternative food source for large individuals or “eliminates the competition” (Claessen et al. 2004). The latter effect requires that the mortality inflicted on the offspring cohort is large enough that it leads to a significant recovery of the resource density and can lead to cannibals effectively controlling the resource by imposing mortality on the smaller individuals (Claessen et al. 2002). The former, cannibalism as an alternative food source, requires that consuming offspring provides the cannibal with a significant amount of energy. This typically leads to a type of population dynamics driven by resource competition among small individuals, with a few cannibals that can profit from cannibalistic feeding and reach very large sizes. The mortality imposed by these cannibals generally does not affect significantly the abundance of small individuals (Claessen et al. 2000).

When hatching size is very small, the larger individuals in the population often have trouble detecting and handling these individuals, and when they do manage to capture small individuals, they do not provide the cannibals with sufficient energy. Thus, small hatching size potentially reduces the efficiency of both the "eliminating the competition" and the "alternative resource" effects of cannibalism.

In summary, the combination of cannibalism and competition, through density-dependent feedbacks between life history and population dynamics, shapes the dynamics of cannibalistic lake fish populations (Claessen et al. 2002; Persson et al. 2004). Size at hatching is a crucial life history parameter because it simultaneously affects the relative importance of both resource competition and cannibalism in regulating lake fish populations.

Materials and methods

Model formulation

We model a cannibalistic size-structured consumer using a generic model developed in Claessen et al. (2000) on the basis of data on Eurasian perch, a common percid species throughout Europe. This model is based on an approach pioneered in Metz and Diekmann (1986) and de Roos et al. (1992), which explicitly separates the individual level (*i* state) from the population level (*p* state). The species-specific formulation of the model is restricted to the individual level, and all assumptions pertain to individual-level characteristics of perch such as foraging efficiency and energy allocation. The population level emerges from accounting for all individual dynamics and their interaction with each other and the environment. Similar models, based on the same conceptual approach, have been used successfully to model the dynamics of several lake fish species (de Roos et al. 2003; Persson et al. 2004). To study this model numerically, we use an algorithm introduced in de Roos et al. (1992), which approximates a structured population by a finite, variable number of cohorts of identical individuals. Such cohorts are added to the population when reproduction occurs and are removed when the number of individuals in the cohort falls below some threshold value (equal to 1 in this study). We assume pulsed reproduction, once per year, at the beginning of the growth season.

Following Claessen et al. (2000), we incorporate one resource population, zooplankton, parameterized to represent a population of 1 mm *Daphnia* individuals, which in the absence of consumers follow semi-chemostat dynamics. In semi-chemostat dynamics, the population growth rate is independent of population size, which can be interpreted as a description of a community of zooplankton rather than a single biological population, with zooplankton individuals growing into the size range at which they become vulnerable to fish predation. Additionally, consumers have the potential to cannibalize smaller conspecifics. Consumer feeding is limited by resource and victim availability, size-dependent attack rates, and digestive constraints. A detailed description of the model, including the population-level formulation and all equations and parameter values, is provided in Appendix A.

Hatching size and harvesting

We study the effects of changing hatching length and how populations that differ in hatching length respond differentially to harvesting mortality. Hatching length is varied by varying the allometrically related quantity hatching weight. This quantity is inversely related to the number of hatchlings, as explained in more detail below. Harvesting is modeled as a constant mortality rate, which is applied only to individuals with length greater than 100 mm. This mortality is in addition to background mortality and starvation mortality to which individuals are subjected. The size threshold was chosen to target more or less all individuals that are sexually mature, not to reflect realistic harvesting size of Eurasian perch populations. Our results are qualitatively identical for all similar harvesting size limits, but with size limits below the maturation size, harvesting easily drives populations extinct. We report results for harvesting intensities between 0.01 and $0.04 \cdot \text{day}^{-1}$, which corresponds to annual survival probabilities between 0.4 and 0.03, respectively.

The individual state

Foraging

Foraging follows a Holling type-II functional response with a size-dependent attack rate and is limited by digestion time (which is technically equivalent to handling time in the context of a type-II functional response). Digestion time per unit body mass is assumed to scale allometrically with body mass to the power of –0.8 and is hence a decreasing function of body size (Claessen et al. 2000). Zooplankton attack rate is a dome-shaped function of size (Persson et al. 1998).

A mechanistic framework to study the population dynamical consequences of size-dependent cannibalism has recently been developed (Claessen et al. 2000) that uses the body length ratio of the potential victim (the smaller individual of the pair) and of the cannibal to calculate the strength of a potential cannibalistic interaction between any pair of individuals. A cannibal of a given size is limited to a certain size range of victims, the "cannibalistic window" (Claessen et al. 2000). A cannibal of any given size has minimum and maximum victim sizes, expressed as a constant and size-independent fraction of its own body length. At the upper end, the window is constrained by the cannibal's gape size. The lower end is a combination of factors but is set mostly by the problem of detecting and handling small prey items by large cannibals. For size ratios outside the window, the cannibalistic attack rate is zero. Within the cannibalistic window, the attack rate for a cannibal of a given size increases from 0 at its minimum prey length, because the cannibal becomes less clumsy at handling and better at detecting larger food items. Similarly, going to smaller prey sizes from its maximum prey length, the attack rate increases, as smaller prey items become easier to catch and swallow. The attack rate reaches a maximum at an intermediate victim-to-cannibal length ratio where the two constraints are balanced. 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).

Energy partitioning

Our model uses the energy allocation rules described in detail in Persson et al. (1998). Here we give only a short summary. The energetic model that we use is graphically depicted in Appendix A. For a general discussion of energy allocation rules in physiologically structured models of fish populations, see Persson and de Roos (2006). All energy acquired through feeding is first used to cover a body mass dependent maintenance cost. Any leftover energy is allocated to physical growth. The energy allocated to growth is further divided between growth in structural, irreversible mass (x) such as bones, skin, and other vital organs and reversible mass (y) such as muscles and fat. We assume that the ratio of y to x is a measure of body condition. The allocation of energy to reversible and irreversible mass depends on this body condition such that the optimal condition ratios q_J (in juveniles) and q_A (in adults) are approached asymptotically. The different parameters reflect the fact that adults invest energy in reproductive tissue, which is considered reversible mass (and hence $q_A > q_J$). Starvation occurs when intake is insufficient to cover metabolic costs, in which case, growth in irreversible mass stops and reversible mass is converted to energy to cover the deficit. We assume that when adult individuals starve, they first resorb their gonad mass to cover maintenance and then turn to muscles and fat. A model study in which the reverse was assumed revealed that this assumption does not substantially affect model dynamics (van de Wolfshaar et al. 2008). When the ratio of reversible to irreversible mass falls below a threshold value (q_s), individuals suffer starvation mortality, $\mu_s(x, y)$. All adult individuals reproduce once per year, in spring. Upon reproduction, all reversible mass of all adults in excess of q_Jx is removed and converted to newborn individuals. After correcting for a non-hatchling fraction of gonad mass and male gonads (the parameter k_r, which we take to be 0.5), this removed mass is divided by the weight of a hatchling to give the number of offspring. The number of hatchlings is hence high when hatching size is small and small when newborns are large. After reproduction, all adults that spawned have reversible mass q_Jx and, given favorable food levels, start to accumulate mass such that they resume growth towards the ratio $y/x = q_A$.

Simulations

The simulations shown in Figs. 1 and 2 have been obtained by numerically integrating the size-structured population and resource population using the escalator boxcar train (EBT) algorithm (see de Roos et al. (1992) and Appendix A). We show time series for 20 years, after transients have died out. The different hatchling lengths are implemented in the model by recalculating the parameter w_0, the mass at birth, using the length–weight relationships given in Table A1 in Appendix A. We investigated a length range from 3.25 to 13 mm, which corresponds to half and double the measured mean hatching length of Eurasian perch. These lengths are within the range spanned by the different species presented (Fig. 3). We have chosen to report dynamics at harvesting intensity of 0.04·day^{-1}. At this high mortality level, the dynamical features that we report are clearly shown, but the results are qualitatively identical at lower harvesting intensity (Figs. 3, 4). The maximum lengths reported (Fig. 4) were obtained by extracting the maximum sizes found in a 200-year time series, with a hatching length step size of 0.01 mm, after time had been allowed for transients to die out. The coefficient of variation (Fig. 3) was calculated from the average and variance in abundance of individuals older than 1 year in the same simulations.

Data compilation

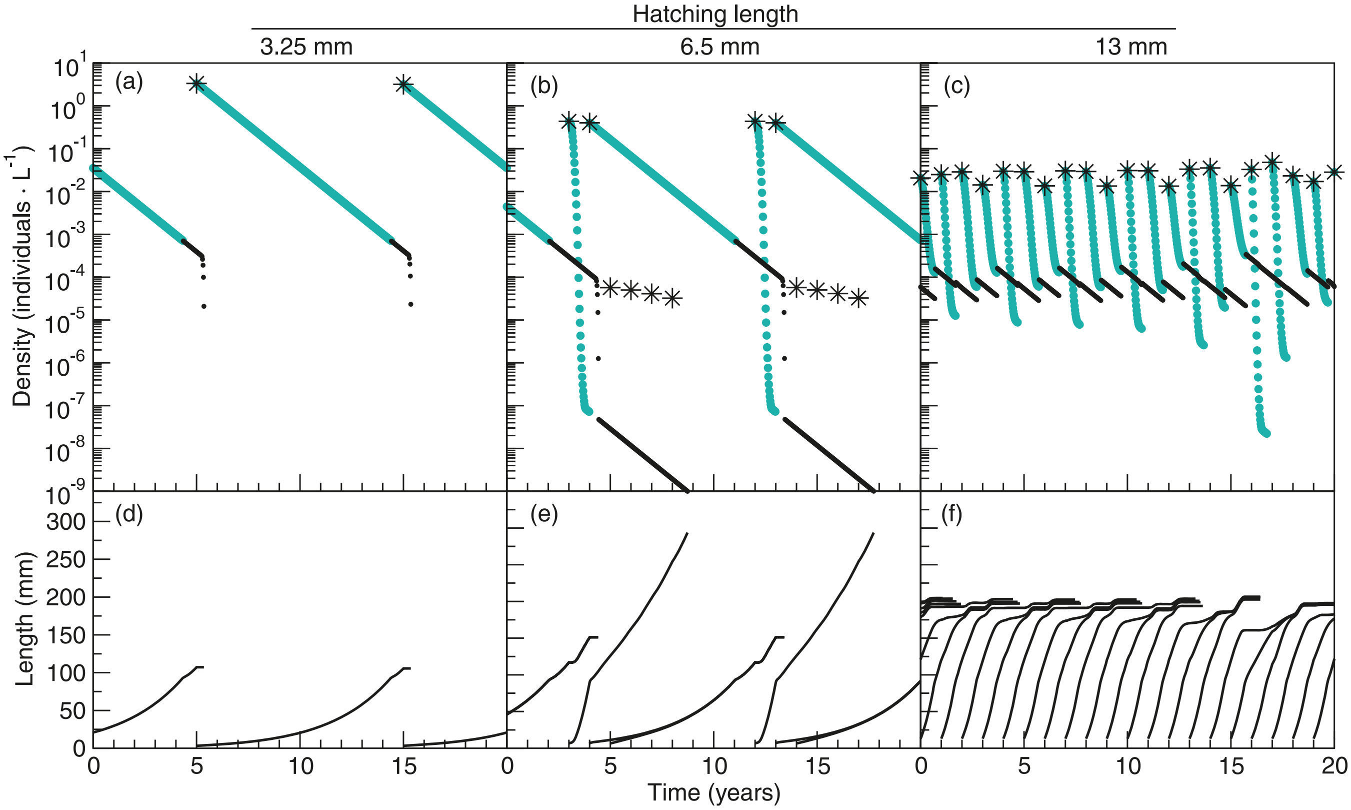
To compare results from our model with empirically observed patterns of population variability in relation to hatching size, we compiled data for as many species of commonly exploited cannibalistic lake fish as we could find. Criteria for inclusion of species were (*i*) documented cannibalism, (*ii*) availability of a time series for at least 5 years for either catch per unit effort or abundance of individuals 1 year and older, and (*iii*) a reliable estimate of mean hatchling length. For 11 species, we found data to fulfill the above requirements. To estimate population variability, we used the coefficient of variation (CV), the ratio of the population variance to the mean. All CV data come from Andersson et al. (2007), except walleye, which is calculated from data in the Global Population Dynamics Database (NERC Centre for Population Biology 1999). Data come from populations in relatively undisturbed environments. Hatching lengths come from Mittelbach and Persson (1998) or from Froese and Pauly (2007) if unavailable in the former publication. When more than one length or a hatching length range was given, we took the average value to represent that species.

Results

Population dynamics

With hatching size set to its measured value for Eurasian perch (see Appendix A, Table A2), the model exhibits so-called dwarf-and-giant cycles (Fig. 1*b*). The bulk of the individuals are born in two large pulses of offspring. A large cohort of offspring, such as those born at time (T, in years) = 3 and T = 12 (Fig. 1*b*), is rapidly cannibalized by its parents. This rapid density reduction leads to high per capita food availability, facilitating very high growth rates for the surviving individuals. During the next year (T = 4 and T = 13), another large offspring cohort is produced by the same parent cohort. These individuals are not heavily cannibalized, because the parents are so large that the newborn individuals are outside their cannibalistic window. As a consequence of high initial density and low mortality, these “dwarf” individuals grow relatively slowly (compared with Fig. 1*b*). They strongly depress the resource, causing starvation mortality in the parent cohort. The only individuals that feed on this cohort are the remaining 1-year-old individuals, but they persist in such low abundance that the mortality that they impose has no significant effects on the victim cohort. These few 1-year-old cannibals do benefit substantially from feeding on their smaller con-

Fig. 1. Model dynamics for three different hatching lengths. For small hatching size fish (*a*, *d*), the model exhibits single-generation cycles in which cannibalism is prevented by temporal segregation of cannibals and suitable victims. Intermediate hatching size (*b*, *e*) leads to dwarf-and-giant cycles, in which a few giants rely on a cohort of slow-growing dwarfs as a resource. Offspring of large hatching size populations (*c*, *f*) are born right into their parents' cannibalistic window and are hence the target of heavy cannibalism right from birth. (*a*, *b*, and *c*) The numbers of newborns (asterisks), juveniles (shaded symbols), and adults (solid symbols); (*d*, *e*, and *f*) the corresponding growth curves of all cohorts (the length of individuals in each cohort through time). The values of all other parameters are listed in Appendix A.



specifics, allowing them to attain "giant" sizes. In consecutive years, the "giant" cohort produces four additional small offspring cohorts (at T = 5–8 and T = 14–17), which are consumed almost instantaneously by the abundant "dwarfs". The "giant" cohort eventually dies out as a result of background mortality, whereas the "dwarfs" mature and reproduce twice. The individuals in the first offspring pulse become the new "giants", and the second pulse forms the new "dwarf" cohort, which drives down the resource level and causes the starvation of its parent cohort. These dynamics are driven by a mixture of cannibal-induced mortality and energy gain, which facilitate gigantism, on the one hand, and intraspecific resource competition, which causes the growth retardation leading to "dwarf" individuals, on the other hand.

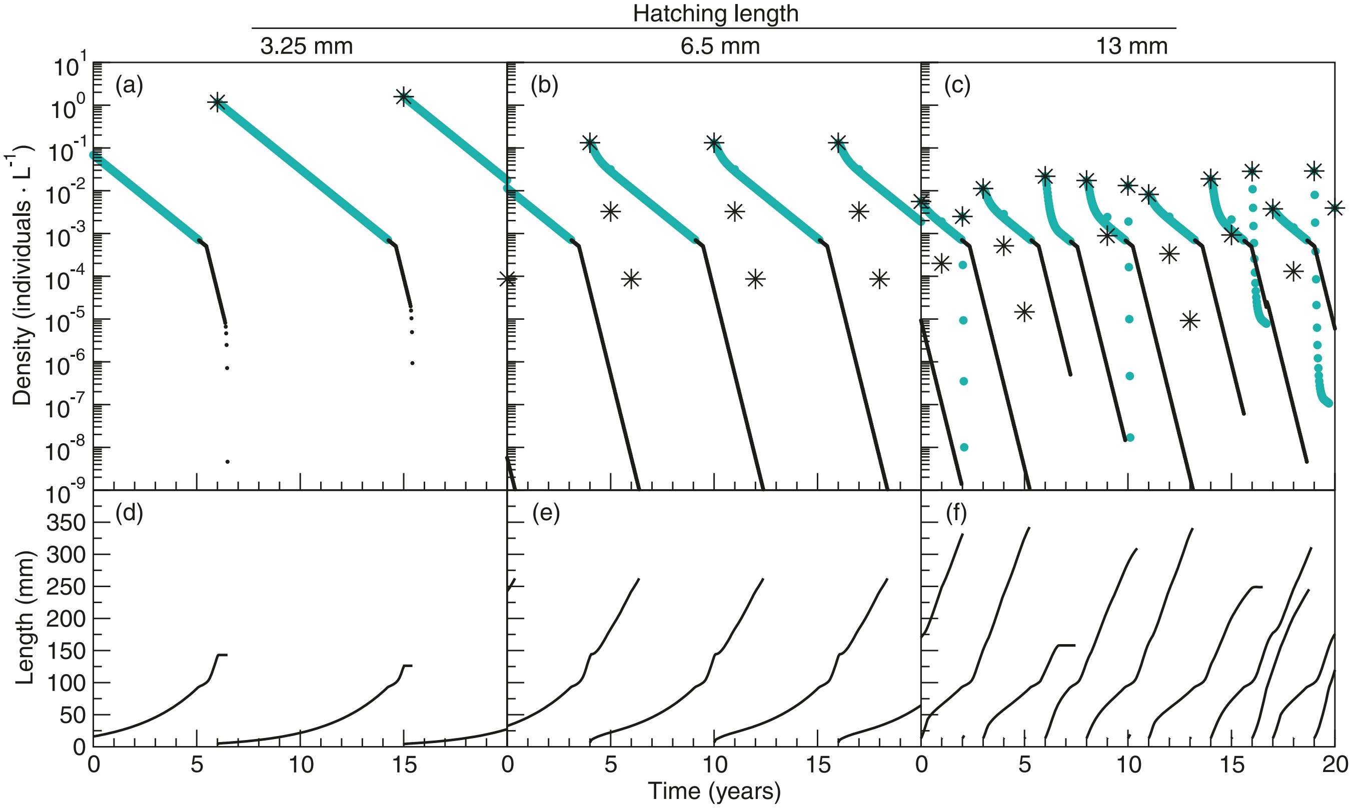
When hatching size is reduced, intraspecific competition becomes the dominant driving force in the dynamics (Fig. 1*a*). Newborn individuals are relatively safe from cannibalism, because they are outside the cannibalistic window of their parents. As a consequence of low mortality, the newborns experience strong intracohort competition, grow slowly, and strongly reduce the resource. As a consequence of the low resource density, all larger individuals that might otherwise have cannibalized the newborns in the future die of starvation. This results in high-amplitude single-generation cycles in which the population always consists of a single year class, except for a short period following reproduction. Although individuals in the population are fully capable of cannibalism, the dynamical feedback on the population level prevents the occurrence of cannibalism, because cannibals and suitable victims never co-occur in the population. Although individuals have an opportunity to reproduce each year, in most years, the population contains no adult individuals, and hence no reproduction takes place.

When the hatching size is increased (Fig. 1*c*), cannibalism becomes the dominant interaction regulating the population dynamics. Adults are constantly present in the population, and reproduction occurs each year. Newborns are large enough for the adults to cannibalize, and consequently most offspring are consumed shortly after birth. Because of the combination of the small size of the cannibalistic prey and the high number of cannibals, predation is only a marginal energy source for the cannibals, and they consequently cannot attain "giant" sizes. The surviving offspring have no shortage of resources and thus grow at their physiological maximum rate. A small fraction of each offspring cohort reaches invulnerably large sizes and matures. The population dynamics is rather stable, because the high cannibalistic mortality prevents the buildup of a large offspring cohort, which in turn prevents strong resource depletion.

Harvesting

The effect of harvesting large individuals (≥100 mm) is different for each of the three modes of population regula-

Fig. 2. Model dynamics for three different hatching lengths, harvesting large individuals (>100 mm) at harvesting intensity of 0.04·day^{-1} for a population with small (*a*, *d*), intermediate (*b*, *e*), and large (*d*, *f*) hatching size. (*a*, *b*, and *c*) The numbers of newborns (asterisks), juveniles (shaded symbols), and adults (solid symbols); (*d*, *e*, and *f*) the corresponding growth curves of all cohorts (the length of individuals in each cohort through time). The values of all other parameters are listed in Appendix A.



tion (competitive, mixed competitive–cannibalistic, and cannibalistic; shown in Fig. 1). In general, large individuals tend to be cannibals and harvesting them decreases the effect of cannibalism, pushing populations towards competition-driven regulation.

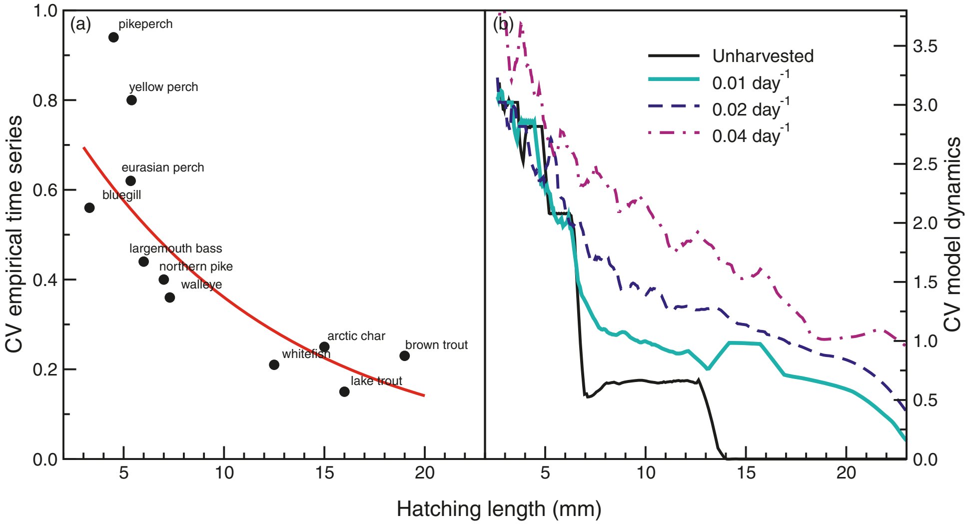
In small-hatching populations, harvesting only marginally affects dynamics (Fig. 1*a* versus Fig. 2*a*) because cannibalism does not occur in absence of harvesting, and hence it cannot be further reduced by removing large individuals. In this case, harvesting mortality simply replaces starvation mortality. Any further increase in harvesting intensity (above the 0.04·day^{-1} shown in Fig. 2) leads to a slight increase in the maximum length that the adults reach before they are starved to death by their offspring. If anything, this increased cannibal length further demotes cannibalism, because it amplifies the size difference between victims and cannibals.

The harvesting-induced shift towards more competition-driven dynamics is also apparent in populations with intermediate hatching length. The dwarf and giant dynamics present in unharvested populations become more similar to single-generation cycles when large individuals are harvested (Fig. 1*b* versus Fig. 2*b*). The population dynamics is fully dominated by a single cohort. After maturation, this cohort produces three offspring cohorts. The first and largest of these becomes the new dominant cohort, and the two consecutive offspring cohorts are completely cannibalized within days. The few adults that are not removed by harvesting can profit from the abundant cannibalistic victims and reach large size. In essence, harvesting in this type of dynamics causes a collapse of the dwarf and giant role into a single cohort of individuals.

In the other extreme case, when the population in the absence of harvesting is regulated by cannibalistic mortality (Fig. 1*c*), harvesting causes population dynamics to destabilize and the maximum size that adults attain to increase dramatically (Fig. 2*c*). In this scenario, hatching length is well within the predation window of the parent cohort, and hence newborn cohorts are fed upon from birth. Although the cannibalistic mortality numerically drives the population dynamics, the intense competition for cannibalistic prey limits the maximum size of the cannibals. Harvesting the cannibals leads to increased per capita victim availability and hence increased growth of the surviving cannibals. Eventually, at high harvesting intensity, the cannibals are so few that they can no longer control the offspring population density. Newborns may exhibit competition-induced growth retardation despite being fed upon, but only to a limited extent. The large hatching size leads to a relatively low hatchling number, which reduces their potential to depress the resource.

At very high harvesting mortality (~0.05·day^{-1} and higher), no individuals can become large, irrespective of whether the population is regulated by competition or cannibalism. Any individual that crosses the 100 mm harvesting

Fig. 3. (*a*) The relation between hatching length and the coefficient of variation (CV) for time series data of 11 commonly harvested cannibalistic lake fish species. The curve is a fit of an exponential function to emphasize the trend. (*b*) CV of model time series in relation to hatching length. Results are shown for unharvested populations and different harvesting intensities. CVs were calculated on densities of all individuals of age 1 year and older from time series of 1.8×10^4 days each at ~300 values of hatching length in the plotted range. Each line plots the running average of 10 of those points.

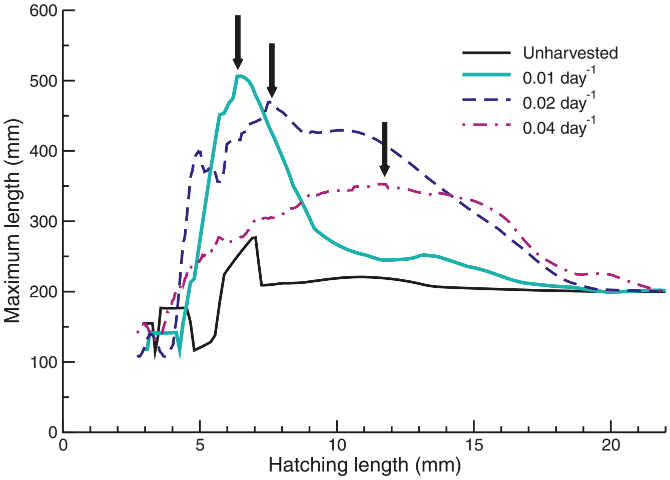


length threshold is removed from the population almost instantaneously. The period and amplitude of the cycles that occur in this parameter region are determined by the hatching size. Small-hatching populations show single-generation cycles spanning multiple years; at larger hatching size, both the period and amplitude of the cycles are decreased.

Harvesting-induced growth

Our results show that harvesting can increase the maximum size that individuals attain. At the harvesting intensity studied in Fig. 2 (0.04·day^{-1}), this effect is strongest in large-hatching populations. At lower harvesting intensity, this effect occurs for smaller-hatching species and also becomes much stronger (Fig. 4). The induction of gigantism occurs when neither competitive nor cannibalistic regulatory forces clearly dominate. To a large extent, the balance between these regulatory forces is determined by hatching length, with populations hatching at larger sizes being more regulated by cannibalistic mortality. Harvesting pushes the balance towards competitive regulation and, depending on the harvesting intensity, can push an otherwise cannibalistically regulated population into the "mixed" regulation zone, where cannibalistic giants occur. This explains why the hatching size for which the length increase is maximized shifts towards larger hatching size when harvesting intensity increases: the larger the hatching size of a population, the stronger it is regulated by cannibalistic mortality. As a result, the larger the hatching size, the higher the harvesting mortality at which the population is pushed into the intermediate regulatory regime where gigantism occurs. Furthermore, comparison of the different curves for different harvesting intensities (Fig. 4) shows that the maximum length of the cannibalistic giants is smaller at higher harvesting intensity. This is a result of the high harvesting-induced mortality, necessary for induction of the giants, that truncates the population age distribution and thereby limits the maximum size.

Fig. 4. The effect of harvesting on the maximum length of individuals found in populations across a range of hatching lengths (harvesting all individuals larger than 100 mm). Harvesting increases maximum size across a range of hatching lengths, but the maximum increase (arrows) shifts to larger hatching size at higher harvesting intensity, whereas the magnitude of the effect is reduced by the increased mortality imposed on large individuals.



Population variability

In the absence of harvesting, our model predicts that temporal variability in time series data should decrease with increasing hatching length. For model organisms with hatching length over 14 mm, cycles disappear and the model shows stable equilibrium dynamics (Fig. 3). Although age at maturation generally decreases gradually with hatching size, our results show a stepwise reduction in variability with increasing hatching size. This is a result of the assumption of discrete reproduction in our model, with each step occurring when the age at maturation crosses an integer year number. We have compiled data on temporal variability of cannibalistic lake fish species across a range of hatching sizes, which show the same pattern of decreasing variability with increasing hatching length (linear regression on data points in Fig. 3, $n = 12$, $R^2 = 0.56$, slope = –0.034, note that this is not the line drawn in the figure). The negative relationship between variability and hatching size is stronger in the model than in the data. At small hatching size, the model predicts a higher coefficient of variability than we find in the data, whereas for large-hatching populations, the model predicts complete stability, which is not found for any of the natural populations. In general, harvesting destabilizes population dynamics. In large-hatching populations, the effect is obvious already at a harvesting intensity of $0.01 \cdot \mathrm{day}^{-1}$, but at higher intensity, the destabilization occurs independent of hatching size. The reason for this destabilization is that harvesting pushes the population towards competition regulation, as it specifically targets the large, cannibalistic individuals. The overall increased CV comes about because higher harvesting intensity leads to a more strongly competition-regulated system and hence more unstable dynamics.

Discussion

We have shown that hatching size strongly affects the dynamics of cannibalistic lake fish populations. Large hatching size promotes cannibalism and prevents resource competition among small juveniles, as well as juvenile competitive effects on adults. Such populations show relatively stable dynamics controlled by cannibalistic mortality. Populations with small hatching size exhibit strong resource competition among juvenile individuals and strong competitive effects on adults, which demotes cannibalism because it creates a temporal mismatch between cannibals and suitable victims. Such populations show cyclic dynamics caused by competition among and within cohorts. Intermediate between these extremes is a type of “mixed” dynamics in which some offspring cohorts experience strong resource competition, leading to slow growth, while other cohorts show a typical “high mortality – fast growth” life history associated with cannibalistic populations. Generally, we find that population variability decreases with hatching size. We find the same relationship, though less steep, in our compilation of empirical data. The four salmonid species in this compilation clearly stand out as a group with large hatching size and relatively stable dynamics. For these hatching sizes, the model predicts a stable equilibrium. There are two likely, nonexclusive explanations for this discrepancy. First, our model populations are not exposed to any form of stochasticity, which is unlikely to be the case for natural populations. Second, it is difficult if not impossible to find a time series of unharvested salmonid populations, and as we have shown, harvesting increases population variability. For species that hatch at smaller sizes, the model overestimates the variability in population dynamics. Stochasticity would increase the variability of stable populations with large hatching size, and it has been shown that the amplitude of competition-driven cycles such as we find at small hatching size is reduced by stochasticity (van Kooten et al. 2004). Another reason for the model’s more pronounced pattern may be the presence of other species (predators, competitors, or alternative food sources). We discuss this in more detail below.

By varying the width of the cannibalistic window, Persson et al. (2004) found a similar pattern: a narrow cannibalism window led to competition-driven dynamics, whereas a very wide window induced stable cannibal-driven dynamics. They show that these types of dynamics match those of three species with corresponding life history characteristics: yellow perch has a narrow cannibalistic window and exhibits single-generation cycles (Sanderson et al. 1999); Eurasian perch has a wider cannibalistic window but still a significant size refuge, leading to dwarf and giant dynamics (Persson et al. 2004), and finally, northern pike has a very wide cannibalistic window and exhibits stable cannibal-driven dynamics. Incidentally, yellow and Eurasian perch have the smallest hatching size, whereas northern pike has the largest. Hence, our results provide an additional mechanism by which at least part of the dynamical pattern found in Persson et al. (2004) can be explained. Andersson et al. (2007) report that temporal variability among cannibalistic lake fish species is negatively correlated with several life history features related to cannibalism. We find that a substantial part of this between-species temporal variability in population density can also be explained by variations in hatching length. Our results hence provide a novel mechanism contributing to observed patterns in population variability across species.

Depending on the mode of population regulation, the effects of harvesting large individuals vary from no effects in a competition-regulated system to dramatic effects on both dynamics and individual life history in populations regulated by cannibalistic mortality. In general, harvesting large individuals reduces the strength of the cannibalistic interaction and shifts the population towards more competition-driven dynamics. We expect these results to be most pronounced in cannibalistic species with large hatching size, which exhibit relatively stable population dynamics in absence of harvesting. Early harvesting studies on Eurasian perch provide some empirical support for our findings. Alm (1951) showed that selective harvesting of adult perch from severely stunted populations induced the appearance of very large adult individuals and destabilized population dynamics. This corresponds to our model predictions for populations regulated by cannibalistic mortality.

Generality and robustness

It is often difficult to estimate the generality of simulation results obtained with parameter-rich models due to the combinatorial explosion of possible parameter settings. Any attempt at such an analysis can, at best, hope to sketch a fragmentary picture of model robustness. This, however, is where individual-based physiologically structured models such as used here really prove their worth. Every aspect of our model has a clear and unambiguous biological interpretation. We have shown how hatching size affects the result of harvesting because it mediates the relative contribution of competition and cannibalism as driving factors of population dynamics and life history patterns. This level of mechanistic understanding of our results enables us to review the effects of changes in other parameter values on the basis of logic and mechanisms rather than extensive, but not comprehensive, simulations. Hatching size is a unique parameter because it affects the strength of both cannibalism and competition, but in opposite directions. Increased hatching size facilitates cannibalism and inhibits competition, and vice versa. Other parameters can reproduce (part of) the pattern in our results by changing the relative importance of either process. Changing cannibalistic voracity (β) can shift dynamics between competitive and cannibalistic regulation, but only when the cannibalistic window is wide enough for cannibalistic regulation and the hatching size is small enough to facilitate strong resource competition. In terms of parameter values, this means a small minimum victim-to-cannibal ratio (δ), a high maximum victim-to-cannibal ratio (ε), and a small hatching mass (w_b). Increased resource productivity (rK) leads to a longer period and larger amplitude of cohort cycles but has no effect on the mode of population regulation and hence does not influence our results (Persson et al. 1998; Claessen et al. 2002). The same is true for the attack rate, handling time, and maintenance cost. Changes in the length–weight parameters can change the population regulation. Species with deep-bodied juveniles will tend to increase in length slower than more elongated species, as the former need to "put on more weight" per unit body length growth. Such deep-bodied growth forms may enhance resource competition, and we expect that such species could exhibit dynamics associated with smaller hatching sizes than they actually have. Allocating a larger fraction of energy to growth in reversible mass makes growth per unit body length more expensive and hence has similar effects.

We assume that hatching of eggs is a pulsed event occurring once per year and that all newborn individuals are exactly identical. In most fish species, there is some degree of variability in both the timing of egg hatching and the size of newborn individuals. Such relatively small initial differences can become important for population dynamics when the population is small or when there are positive feedbacks that can cause initially small variation to blow up over time (DeAngelis et al. 1993). Intracohort cannibalism is one potential positive feedback that could lead to a blow-up of variation when fast-growing, early-hatched individuals eat slow-growing, late-hatched ones. This can strongly impact size distribution of a cohort at the end of its first growth season, but the impact on long-term population dynamics is unknown (Claessen et al. 2004). Furthermore, there appears to be only limited empirical evidence for intracohort cannibalism in fish, except from aquaculture situations (Baras and Jobling (2002) but see Johnson and Post (1996)).

Further evidence for the robustness of our results comes from the fact that they are not unique to our specific model. van Kooten et al. (2007) analyze a model with a different energy allocation scheme, different parameter values, and fully continuous reproduction and find similar harvesting responses for similarly regulated populations. We hypothesized that some of our results could be caused by changes in the relative scaling between life history milestones such as maturation and optimal size for zooplankton foraging. When hatching size is increased, the size range between hatching and other life history milestones such as maturation and the optimal size for zooplankton feeding is changed. To test for such effects, we repeated our analysis using a model in which both the maturation size and the optimal size for zooplankton foraging scale with hatching size: if hatching size doubled, the other two parameters also doubled. The results from this analysis are qualitatively identical to those presented here.

The results presented here clearly show how a model parameterized for one species (Eurasian perch) can be used to generate useful qualitative insights into the dynamical consequences of harvesting across a range of species, without the need for full parameter sets for each individual species. This is a direct result of the mechanistic interpretability of our model formulation. It may be necessary, though, to use more complete, species-specific parameter sets for more in-depth, quantitative comparisons between data and model dynamics.

Our findings are based on a consumer–resource system in isolation. The ecological systems that lake fish are part of are invariably more complex. Other species in the community can act as predators, alternative prey, or competitors to our focal population. Such interactions are likely to depend on the size of the focal consumer. Like the zooplankton resource in our model, alternative resources such as, for example, benthic invertebrates are likely to benefit only a certain size range of consumers. A competitor of the small consumer individuals in our model may double as an alternative food source for the cannibals. The theoretical possibilities and the examples from real systems of such complex interactions are numerous.

The zooplankton community of any lake consists of many species, and zooplanktivores generally feed on many species, selecting for size as much as species. We use a partial work-around to solve the multispecies nature of the zooplankton community by using semi-chemostat dynamics for the resource, which uncouples population growth rate from population size, instead of the commonly used logistic resource growth. However, we still assume that all food particles are equally sized. Addition of a population of mayfly larvae (*Cloeon* sp., assumed length 6 mm) did not significantly alter our results (T. van Kooten, unpublished). Addition of multiple resources could affect our result, mostly by altering size-based competition within the consumer population. This would change the shape of the cycles that we found at small hatching size and could even stabilize the cycles in special cases. Such stabilization could alter the pattern of decreasing variability with hatching size, but it occurs only in the unlikely case that consumers of all sizes are equally competitive (de Roos and Persson 2003).

The effect of other predators depends crucially on the size specificity of such a predator and on the dynamics of the consumer population in absence of such predation. van Kooten et al. (2007) showed that the effects of size-specific mortality are greatest if the mortality targets a size range that has low mortality otherwise. In this case, predation can induce shifts in population dynamics similar to those observed when hatching size changes. It was shown recently in a whole-lake study that mass removal of Arctic char (*Salvelinus alpinus*) induced a shift from a stunted state to a much wider char size distribution (Persson et al. 2007). After the removal, brown trout (*Salmo trutta*), which feed on small Arctic char, was capable of maintaining the char population in its new state. The effects of size-specific predators that increase mortality on stages that already suffer high mortality are negligible. This means that species with small hatching size but heavy predation on small individuals will behave like populations with larger hatching size, both in terms of their dynamics and in response to harvesting of large individuals. Similarly, populations with large hatching size but heavy predation on larger individuals will tend to behave like populations with smaller hatching size. Similarly, other species competing for the same resource as the focal consumer will increase the importance of competition as a regulatory force for population dynamics, causing populations to express dynamics associated with smaller hatching size than the species actually has.

Implications

Our predictions for harvested populations are general and robust in the sense that we expect them to hold, qualitatively, for cannibalistic fish species regulated by juvenile resource competition, cannibalistic mortality, or a mixture of both. We show that population regulation may change in response to harvesting, with drastic consequences for population dynamics and life history. Our results indicate that management strategies involving minimum size limits may have profoundly different consequences when applied to different cannibalistic target species. In this light, future studies that aim to generate such strategies for exploited populations should consider the possible effects of the complex interplay between harvesting and the cannibalistic tendency of the exploited species. For successful management of lake fish populations, population-level measurements may not be enough, and detailed, mechanistic knowledge about life history and potential regulatory mechanisms is necessary.

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Appendix A

Model formulation

Physiologically structured models are based on a two-level state concept: an individual or *i* state that describes the state of an individual and a population or *p* state that is the frequency distribution over the space of possible *i* states (Metz and Diekmann 1986). A mathematical description of the behavior of a single individual (e.g., its feeding, growth, development, reproduction, and mortality) as a function of its physiological characteristics and the current environmental conditions (e.g., resource densities) constitutes the core element of any structured population model. The model that we formulate here is similar to models of size-structured consumers found in Persson et al. (1998) (see also Claessen et al. (2000) and de Roos and Persson 2001). The model used in this study is parametrized for a cannibalistic size-structured population of European perch (*Perca fluviatilis*) in central Sweden. At this latitude, the growth season for perch lasts 90 days because of low water temperatures and ice cover during the rest of the year. This consumer feeds on zooplankton and smaller conspecifics (cannibalism). We use a lake volume of 10^6 m^3. All *i*-state equations used are listed in Table A1, and all parameter values used are listed in Table A2.

i-state model

Consumers are characterized by two physiological parameters, irreversible and reversible mass (Table A2). Irreversible mass x consists of permanent structures such as skin, bones, and intestinal organs, whereas reversible mass y refers to fat reserves and other tissues such as muscles that can be resorbed. For mature individuals, reversible mass also includes gonads. All reversible mass may be used to cover metabolic costs during starvation. Total body mass of an individual consumer equals the sum of reversible and irreversible mass ($x + y$).

Relations describing the foraging rate, metabolism, and energy partitioning between growth and reproductive tissue and starvation (including starvation mortality) as a function of irreversible and reversible mass x and y, respectively, were developed in Persson et al. (1998) and are summarized in Table A1. Below we briefly describe the part of the model that relates to consumer feeding and energy channeling.

We define standardized body mass $w(x)$ of a consumer as

$$\text{(A1)} \qquad w(x) = (1 + q_J)x$$

in which q_J represents a characteristic ratio between reversible and irreversible mass for nonstarving individuals, discounting gonad mass (e.g., juveniles or adults right after spawning). The notion of standardized body mass is introduced because functional response experiments with size-structured consumers have shown a close relationship between capture rate and body length (Mittelbach 1981; Persson 1987). Hence, we assume that a consumer's condition, i.e., its reversible mass, y, does not influence its foraging rate (for a justification of this assumption, see Persson et al. 1998). The size-dependent zooplankton attack rate ($A_z(w)$) of consumers is a function of standardized body mass w. The cannibalistic attack rate depends on cannibal and victim length (denoted by l_c and l_v, respectively), which in turn are allometrically related to standardized mass w.

The attack rate of consumers on zooplankton resource is a dome-shaped function of standardized body mass (Table A1), reaching a maximum value determined by the parameter $\widehat{A}$ at a body size w_{opt}. It increases at small sizes because of increased consumer mobility and decreases at larger sizes because of reduced visibility of small-sized prey to large consumers. Zooplankton attack rate is expressed as searched volume per unit time.

All individuals in the population are both potential cannibals and potential prey, depending on their respective length. An individual with length l_c can successfully cannibalize another individual if that individual's length l_v is between δl_c and εl_c, i.e., if the victim is large enough for the cannibal to notice but small enough to fit in its mouth (Claessen et al. 2000). Cannibalistic attack rate for a cannibal with length l_c

Table A1. All *i*-state model equations.

Subject	Equation
Standardized mass	$w(x) = x(1 + q_{\mathrm{j}})$
Length–weight	$l = \lambda_1 w^{\lambda_2}$
Zooplankton attack rate	$A_{\mathrm{z}}(w) = \widehat{A}\left(\frac{w}{w_{\mathrm{opt}}}\mathrm{e}^{\left(1-\frac{w}{w_{\mathrm{opt}}}\right)}\right)^{\alpha}$
Cannibalistic attack rate	$A_{\mathrm{c}}(l_{\mathrm{c}}, l_{\mathrm{v}}) = \begin{cases} \beta(l_{\mathrm{c}})^{\sigma}\dfrac{l_{\mathrm{v}} - \delta l_{\mathrm{c}}}{(\phi - \delta)l_{\mathrm{c}}} & \text{if } \delta l_{\mathrm{c}} < l_{\mathrm{v}} \leq \phi l_{\mathrm{c}} \\ \beta(l_{\mathrm{c}})^{\sigma}\dfrac{\varepsilon l_{\mathrm{c}} - l_{\mathrm{v}}}{(\varepsilon - \phi)l_{\mathrm{c}}} & \text{if } \phi l_{\mathrm{c}} < l_{\mathrm{v}} < \varepsilon l_{\mathrm{c}} \\ 0 & \text{otherwise} \end{cases}$
Zooplankton encounter rate	$\eta_{\mathrm{z}}(x) = A_{\mathrm{z}}(w)R$
Cannibalistic encounter rate	$\eta_{\mathrm{c}}(x) = \sum_j A_{\mathrm{c}}(l, l_{\mathrm{v},j})(x_j + y_j)N_j$
Total encounter rate	$\eta(x) = \eta_{\mathrm{z}}(x) + \eta_{\mathrm{c}}(x)$
Digestion time	$H(w) = \xi_1 w^{\xi_2}$
Total intake rate	$I(x) = \frac{\eta(x)}{1+H(w)\eta(x)}$
Acquired energy	$E_{\mathrm{a}}(x) = k_{\mathrm{e}}I(x)$
Maintenance requirements	$E_{\mathrm{m}}(x, y) = \rho_1(x + y)^{\rho_2}$
Net energy	$E_{\mathrm{g}}(x, y) = E_{\mathrm{a}}(x) - E_{\mathrm{m}}(x, y)$
Fraction of energy used for growth in irreversible mass	$\kappa(x, y) = \begin{cases} \dfrac{1}{(1 + q_{\mathrm{J}})q_{\mathrm{J}}}(y/x) & \text{if } x \leq x_f \text{ and } E_{\mathrm{g}} > 0 \\ \dfrac{1}{(1 + q_{\mathrm{A}})q_{\mathrm{A}}}(y/x) & \text{if } x > x_f \text{ and } E_{\mathrm{g}} > 0 \\ 0 & \text{otherwise} \end{cases}$
Cannibalistic mortality	$\mu_{\mathrm{c}}(x) = \sum_i \frac{A_{\mathrm{c}}(l_{\mathrm{c},i}, l)N_i}{1+H(w_i)\eta(x_i)}$
Harvesting mortality	$\mu_{\mathrm{h}}(x) = \begin{cases} h & \text{if } l > l_{\mathrm{h}} \\ 0 & \text{otherwise} \end{cases}$
Starvation mortality	$\mu_{\mathrm{s}}(x, y) = \begin{cases} s(q_{\mathrm{s}}x/y - 1) & \text{if } y < q_{\mathrm{s}}x \\ 0 & \text{otherwise} \end{cases}$
Total mortality	$\mu(x, y) = \mu_{\mathrm{b}} + \mu_{\mathrm{s}}(x, y) + \mu_{\mathrm{c}}(x) + \mu_{\mathrm{h}}(x)$
Fecundity	$F(x, y) = \begin{cases} k_{\mathrm{r}}(y - q_{\mathrm{J}}x)/w_{\mathrm{b}} & \text{if } x > x_f \text{ and } y > q_{\mathrm{J}}x \\ 0 & \text{otherwise} \end{cases}$

Note: Note that for clarity, we use w as a shorthand for $w(x)$ and l instead of $l(w(x))$ whenever appropriate. The symbols l_{c} and l_{v} are used for cannibal and victim length, respectively. Subscripts i and j refer to the cohort index.

is an increasing function of victim length as long as $\delta l_{\mathrm{c}} < l_{\mathrm{v}} \leq \phi l_{\mathrm{c}}$, where ϕ is the optimum ratio between cannibal and victim length. Thereafter it is a decreasing function of victim length, which reaches zero at $l_{\mathrm{v}} = \varepsilon l_{\mathrm{c}}$. The values of δ, ϕ, and ε are based on stomach analyses and experiments in ponds and aquaria (Claessen et al. 2000, 2002; Persson et al. 2004). Combining the cannibalistic attack rates for all possible lengths of cannibals and victims yields a tent-shaped function $A_{\mathrm{c}}(l_{\mathrm{c}}, l_{\mathrm{v}})$, where l_{c} and l_{v} are allometric functions of standardized body mass w (Table A1). The attack rate at the optimum cannibal–victim ratio ϕ scales allometrically with exponent σ and cannibalistic voracity scalar β.

The digestion time $H(w)$ reflects digestive constraints related to the gut capacity of an individual with a given size (Claessen et al. 2000, 2002). It is described as an allometric function of standardized body mass.

From the size-dependent attack rates and resource abundances, the total biomass encounter rate $\eta(w)$ is calculated. This is used, together with the size-dependent digestion time, to calculate the total food intake of perch $I(w)$, which follows a Holling type-II functional response (see Table A1; Persson et al. 1998, 2004). Ingested food is assumed to be converted to energy assimilate with a constant conversion efficiency k_{e}.

An individual's energy intake $E_{\mathrm{a}}(x)$ is first used to cover metabolic requirement, which follows an allometric function $E_{\mathrm{m}}(x, y)$ of total consumer body mass $x + y$. The remaining part of the acquired energy (the net energy intake or net production $E_{\mathrm{g}}(x, y)$) is allocated to reversible and irreversible mass such that a constant ratio between the two is targeted for. This ratio for juveniles (q_{J}) differs from that for adults (q_{A}) because reversible mass in mature individuals includes gonads (hence, $q_{\mathrm{A}} > q_{\mathrm{J}}$) (Table A1; Persson et al. 1998). When energy intake does not suffice to cover the metabolic requirement, growth in irreversible mass x stops and reversible mass y is used to cover the deficit. Thus, when $E_{\mathrm{g}}(x, y) \leq 0$,

$$\text{(A2)} \qquad \frac{\mathrm{d}y}{\mathrm{d}t} = E_{\mathrm{g}}(x, y)$$

whereas irreversible mass is invariant ($\mathrm{d}x/\mathrm{d}t = 0$).

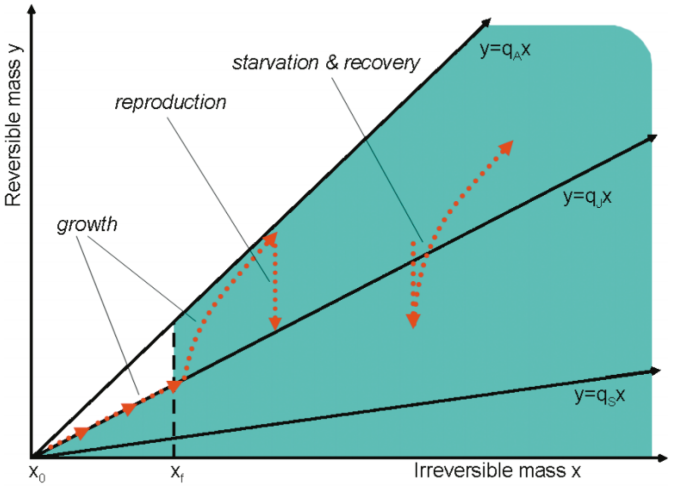
When net energy intake becomes positive again, energy is preferentially allocated to reversible mass to restore the tar-

Table A2. Model variables and parameters valid for Eurasian perch (*Perca fluviatilis*) feeding on a zooplankton resource (*Daphnia* sp., length 1 mm) and conspecifics.

Subject	Symbol	Value	Unit	Interpretation	References
i state	x		g	Irreversible mass	
	y		g	Reversible mass	
Season	Y	90	days	Length of year	
Physical dimensions	—	1.0×10^9	L	Lake volume	
Ontogeny	w_b	0.0018	g	Hatchling mass	Byström et al. 1998; P. Byström (unpublished data)
	x_f	4.6	g	Irreversible mass at maturation	Byström et al. 1998; P. Byström (unpublished data)
	q_J	0.74	—	Juvenile maximum condition	Treasurer 1981
	q_A	1.37	—	Adult maximum condition	L. Persson (unpublished data)
	k_r	0.5	—	Gonad–hatchling conversion	
Length–weight	λ_1	48.3	$\mathrm{mm{\cdot}g}^{-\lambda_2}$	Allometric scalar	Byström et al. 1998; P. Byström (unpublished data)
	λ_2	0.32	—	Allometric exponent	Byström et al. 1998; P. Byström (unpublished data)
Planktivory	α	0.62	—	Allometric exponent	Byström et al. 1998; P. Byström (unpublished data)
	$\widehat{A}$	3.0×10^4	$\mathrm{L{\cdot}day}^{-1}$	Maximum search rate	Persson 1987
	w_{opt}	8.2	g	Optimal forager size	Persson and Greenberg 1990
Piscivory	σ	0.6	—	Allometric exponent	B. Christensen (unpublished data)
	β	400.0	$\mathrm{L{\cdot}day}^{-1}{\cdot}\mathrm{mm}^{-\sigma}$	Cannibalistic voracity	B. Christensen (unpublished data)
	δ	0.05	—	Minimum no. of victims/cannibal	Buijse and van Densen 1992; Eklöv and Diehl 1994; van Densen 1994; Christensen 1996; Popova and Sytina 1977; Willemsen 1977; Lundvall et al. 1999; Persson et al. 2000
	ε	0.45	—	Maximum no. of victims/cannibal	Buijse and van Densen 1992; Eklöv and Diehl 1994; van Densen 1994; Christensen 1996; Popova and Sytina 1977; Willemsen 1977; Lundvall et al. 1999; Persson et al. 2000
	ϕ	0.16	—	Optimum no. of victims/cannibal	Lundvall et al. 1999
Handling	ξ_1	5.0	$\mathrm{days{\cdot}g}^{-(1+\xi_2)}$	Allometric scalar	Lessmark 1983; P. Byström (unpublished data)
	ξ_2	–0.8	—	Allometric exponent	Lessmark 1983; P. Byström (unpublished data)
Metabolism	ρ_1	0.033	$\mathrm{g}^{(1-\rho_2)}{\cdot}\mathrm{day}^{-1}$	Allometric scalar	Beamish 1974; Elliott 1976; Kitchell et al. 1977; Karås and Thoresson 1992
	ρ_2	0.77	—	Allometric exponent	Beamish 1974; Elliott 1976; Kitchell et al. 1977; Karås and Thoresson 1992
	k_e	0.61	—	Intake coefficient	Solomon and Brafield 1972; Beamish 1974; Elliott 1976; Rice et al. 1983; Karås and Thoresson 1992
Mortality	h	Varied	day^{-1}	Harvesting mortality rate	
	l_h	100	mm	Minimum harvesting length threshold	
	μ_b	0.01	day^{-1}	Background rate	Byström et al. 1998; P. Byström (unpublished data); B. Christensen (unpublished data)
	q_s	0.2	—	Starvation condition	
	s	0.2	—	Starvation coefficient	
Zooplankton	R		$\mathrm{g{\cdot}L}^{-1}$	Zooplankton density	
	r	0.1	day^{-1}	Zooplankton growth rate	
	K	0.003	$\mathrm{g{\cdot}L}^{-1}$	Zooplankton carrying capacity	L. Persson (unpublished data); E. Wahlström (unpublished data)

Note: All parameters except Y, r, and K refer to individual-level processes.

Fig. A1. The set of reachable individuals states, as determined by the allocation of consumed energy to irreversible (x) and reversible (y) mass. Individuals are born with an irreversible mass x_0 and a reversible mass $q_J x_0$ and grow in mass along the line $y = q_J x$ as long as no starvation occurs. When reaching maturity (at irreversible size x_f), the maximum amount of irreversible mass increases to $q_A x$. When the individuals spawn, reversible mass drops to $q_J x$, and after spawning, mass is allocated according to the overall rule for partitioning between irreversible and reversible mass (see Table A1). When starving, only reversible mass decreases, whereas during recovery after a starvation period, mass is added preferentially to reversible tissue. Below the line $y = q_s x$, starvation mortality affects individuals. Individuals can have a combination of individual state variables anywhere in the shaded area.



get y–x ratio. Hence, when energy intake exceeds basic metabolic costs ($E_g(x, y) > 0$), the changes in irreversible and reversible mass, respectively, are given by

$$\text{(A3)} \qquad \frac{dx}{dt} = \kappa(x, y)E_g(x, y)$$

$$\text{(A4)} \qquad \frac{dy}{dt} = [1 - \kappa(x, y)]E_g(x, y)$$

The process of mass change of individuals is visualized in Fig. A1. The shaded area indicates all combinations of x and y that individuals can reach. The upper straight line shows the maximum y–x ratio (which corresponds to the best body condition, $y = q_A x$) that can be reached by adults. The middle line ($y = q_J x$) is the maximum y–x ratio for juveniles. For reproductive purposes, any mass of adults above this middle line is assumed to be gonad mass. Starvation mortality occurs if individuals fall below the starvation threshold ($y = q_s x$).

It is assumed that individuals only spawn at the beginning of each growth season. When they spawn, adults allocate all reversible mass that they accumulated in excess of their standardized body mass $w(x) = (1 + q_J)x$ to the production of eggs with a constant conversion efficiency k_r, which includes compensation for non-egg gonad tissue and male gonads (Persson et al. 1998). Following a successful spawning event, an adult thus has the same reversible to irreversible mass ratio as a non-starving juvenile, whereafter the buildup of gonad mass to be released at the next reproduction event starts anew. Maturation of juvenile into adult consumers occurs on reaching a fixed threshold of irreversible mass x_f.

Background mortality (μ_b) in our model is a simple constant mortality that is equal for all individuals, independent of size. In addition to this, individuals suffer harvesting mortality μ_h, which is positive only if their length is larger than l_h, the minimum size threshold for harvesting. Additionally, individuals suffer starvation mortality (at rate μ_s) when their reversible to irreversible mass ratio y:x is below the starvation mortality limit q_s.

Population bookkeeping

The model only examines population dynamics during the growth season. The changes in consumer and resource populations during the nongrowth season are assumed to be negligible.

Resources are assumed to reproduce continuously throughout the growth season. Consumers are assumed to feed, grow (or shrink in case of starvation), and die continuously during the summer season, but reproduce only at the start of a growth season in a sharply pulsed event. The model is thus a combination of a continuous dynamical system, describing growth and survival of the consumers and production and consumption of the resource during summer, and a discrete map describing the pulsed reproduction of consumers in spring.

Analytically, the structured population model can be formulated as a system of integral equations (see Persson et al. 1998) that represent a way of bookkeeping the dynamics of all individuals making up the population. Numerically, the model can be studied using the escalator boxcar train (EBT) framework (de Roos et al. 1992; Persson et al. 1998). The EBT method is specifically designed to handle the numerical integration of the equations that occur in physiologically structured models. Below follows a short description of how the EBT method is applied to a structured population model.

The pulsed reproduction process ensures that there is a natural subdivision of the population into cohorts of individuals. Within one cohort, all individuals have the same reversible and irreversible mass. Moreover, all individuals within a cohort are assumed to grow at the same rate, i.e., individuals belonging to a given cohort do not diverge in their allocation to reversible and irreversible masses. As a result, each cohort consists of individuals that will remain identical for the duration of their life. We use a single copy of eqs. A2, A3, and A4 to describe the dynamics of the i-state variables of each cohort. When considering cohort dynamics, we use the subscripted variables x_i and y_i. During the growth season, the number of individuals N_i in a cohort i is fully determined by mortality (the number of individuals in a cohort can never increase), thus

$$\text{(A5)} \qquad \frac{dN_i}{dt} = -\mu(x_i, y_i)N_i$$

The dynamics of the entire consumer population, in terms of both its abundance and its composition, can be followed throughout the summer season by numerically integrating the system of ordinary differential equations for each cohort. In addition, changes in the zooplankton resource populations can be followed by numerical integration of the ordinary differential equation for the resource dynamics that incorporates the growth and total consumption of the resource. The latter term equals the summed foraging rate of all individuals in each consumer cohort. For a population of n cohorts, the change in resource density is given by

$$\frac{dR}{dt} = r(K - R) - R\sum_{i=1}^{n} \frac{A_z(w_i)N_i}{1 + H(w_i)\eta(w_i)} \tag{A6}$$

The resource population follows semi-chemostat dynamics. Several authors have proposed that semi-chemostat dynamics is appropriate for populations with an invulnerable small size class (Persson et al. 1998; Claessen et al. 2000; de Roos et al. 2002). The second term in eq. A6 is the total resource consumption by all consumers in the population.

At the beginning of the growth season, reproduction occurs, and a new cohort of individuals is added to the consumer population. This addition implies that the number of differential equations describing the population dynamics is increased. The total number of newborn individuals is the summed fecundity $F(x, y)$ (see Table A1) of all individuals:

$$N_{\text{tot}} = \sum_{i=1}^{n} F(x_i, y_i)N_i$$

The converted gonad mass is removed from the reproducing adults, leaving them with reversible mass $y = q_J x$. The newborn individuals are then added to the existing population in the form of a new cohort. First, the existing cohorts are renumbered:

$$\begin{cases} N_i = N_{i+1} \\ x_i = x_{i+1} \\ y_i = y_{i+1} \end{cases} \tag{A7}$$

This is a bookkeeping measure that ensures that the cohorts in the population are ordered according to age. The initial state of the newborn cohort is

$$\begin{cases} N_* = N_{\text{tot}} \\ x_* = \dfrac{1}{1 + q_J} w_b \\ y_* = \dfrac{q_J}{1 + q_J} w_b \end{cases} \tag{A8}$$

Overall, the simulation of physiologically structured populations thus involves the numerical integration of a (large) system of ordinary differential equations, which is extended in dimension at the beginning of each season with a concurrent reset of some of the variables. The dimension of the system is reduced whenever the number of individuals in a given cohort becomes negligible, at which time the differential equations for this particular cohort are removed.

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