CANNIBALISM IN A SIZE-STRUCTURED POPULATION: ENERGY EXTRACTION AND CONTROL

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Abstract. Recent size-structured cannibalistic models point to the importance of the energy gain by cannibals and also show that this gain may result in the emergence of giant individuals. We use a combination of a 10-year field study of a perch (*Perca fluviatilis*) population and quantitative within-season modeling of individual and population-level dynamics to investigate which mechanisms are most likely to drive the dynamics of the studied perch population. We focused on three main aspects to explain observed discrepancies between earlier model predictions and data: (1) introduction of more than one shared resource between cannibals and victims, (2) whether or not several victim age cohorts are necessary to allow giant growth, and (3) the intensity of inter-cohort competition between young-of-the-year (YOY) perch and 1-yr-old perch.

At the start of the study period, the perch population was dominated by ''stunted'' perch individuals, and recruitment of perch to an age of 1-yr-old was negligible. Following a major death in adult perch, strong recruitments of perch to 1-yr-old were thereafter observed for a number of years. As 1-yr-olds these successful recruiters subsequently starved to death due to competition with the new YOY. The few surviving adult perch accelerated substantially in growth and became ''giants.'' At the end of the study period, the perch population moved back to the situation with stunted individuals. There was a high agreement between observed diets of cannibalistic perch and those predicted by the model for both the stunted and the giant phases. Analyses of growth rates showed that cannibalistic perch could become giants on a diet of YOY perch only, but that a supplement with the second shared resource (macroinvertebrates) was needed to reach the observed sizes. Modeling of growth and diet in the giant phase showed an exploitative competitive effect of YOY perch on 1-yr-old perch, but a restriction in habitat use of 1-yr-old perch had to be assumed to yield the observed growth rate and diet. The resource dynamics of zooplankton and macroinvertebrates were both accurately predicted by the model. Also, YOY perch mortality was accurately predicted and, furthermore, suggested that one of the trawling methods used may underestimate the number of YOY perch when they increase in size.

We conclude that the presence of a second shared resource and the restricted habitat use and absence of cannibalistic consumption by 1-yr-old perch individuals are two important mechanisms to explain the discrepancy between model predictions and data. Our results also point to the fact that that the dynamics observed may be explained by complex dynamics not involving the presence of a giant and dwarf cycle.

*Key words: cannibalism; competition; complex dynamics; energy gain from cannibalism; Eurasian perch (*Perca fluviatilis*); physiologically and size-structured population models.*

INTRODUCTION

Cannibalism, like any predator–prey interaction, involves two essential processes: the killing of prey causing prey population mortality and the extraction of

energy changing the condition of the predator. These two fundamental elements of cannibalism also form the basis for the several kinds of effects that cannibalism may have on population dynamics and persistence (Diekmann et al. 1986, Hastings and Costantino 1987, van den Bosch et al. 1988, Claessen et al. 2000, 2002, Persson et al. 2000). First, energy extracted by the cannibal may allow a population to persist under environmental conditions when a noncannibalistic population would go extinct, a phenomenon generally referred to as the ''life boat mechanism'' (Gabriel 1985, van den Bosch et al. 1988, Henson 1997). Second, increased fecundity among cannibals, as a result of increased energy intake, may lead to a destabilization of the pop-

ulation dynamics (Hastings and Costantino 1987). Third, the mortality imposed on victims may dampen population oscillations (Hastings and Costantino 1987, van den Bosch and Gabriel 1997, Claessen et al. 2000).

The intensity of cannibalistic interactions generally depends on the size relationship between cannibals and victims (Orr et al. 1990, Fagan and Odell 1996, Rice et al. 1997, Dong and DeAngelis 1998, Claessen et al. 2000, 2002, Persson et al. 2000). The cannibalistic process per se will also affect the interaction strength between cannibals and victims over time as victims consumed by the cannibals are translated into growth of the cannibals, and the mortality imposed on victims by cannibals may increase the growth of the remaining victims. As a result, the intensity of cannibalism will vary because it is strongly coupled to the growth of cannibal individuals and to the growth of victim individuals (Rice et al. 1997, Claessen et al. 2000).

Although not commonly addressed in theoretical studies (but see Dong and DeAngelis 1998, Claessen et al. 2000, 2002), cannibals often share a common resource with their victims, leading to the potential for size-dependent competition between cannibals and victims. In this context, cannibalism may have a two-fold evolutionary advantage as the cannibal benefits from both the feeding on victims and the reduced competition from victims for the shared resource (Polis 1988). Recent theoretical studies of cannibalistic systems with a shared resource suggest that, in a population-dynamical context, cannibals may either control victims and hence profit from reduced competition or profit energetically from cannibalism—but not both (Claessen et al. 2000, 2002). Claessen et al. (2000) showed that when cannibals control victims they gain most of their energy from the shared resource, and the cannibalistic population is characterized by relatively small, stunted individuals. Conversely, when cannibals profit energetically from cannibalism, most of the adult cannibal population had been outcompeted by a strong recruiting cohort, and the few surviving adults only impose a nonsignificant mortality on the recruiting cohort. These few adult individuals accelerate substantially in growth as a result of cannibalism, thereby becoming ''giants'' (Claessen et al. 2000). The mechanism by which victims outcompete cannibals is that newborn individuals are too small to be encountered by cannibals, and that these recruiting individuals depress the shared resource to a level where cannibals starve to death before they are able to start cannibalizing on the recruiting cohort. A recent paper confirms the importance of the lower size boundary for cannibalism for the occurrence of cannibal starvation death (Claessen et al. 2002).

Interestingly, data from fish populations support the prediction that individuals may accelerate in growth on successfully recruiting year classes (McCormack 1965, LeCren 1992, Persson et al. 2000). Persson et al. (2000) studied the dynamics of a Eurasian perch (*Perca fluviatilis*) population and that study includes a detailed analysis of both individual-level (growth, condition) and population-level (numbers of different cohorts, mortality patterns, resource dynamics) processes. That study also provided evidence for a major die-off of adult individuals associated with the successful recruitment of young individuals and a corresponding major decrease in abundance of the shared resource (zooplankton), as predicted by the model of Claessen et al. (2000). A closer examination, however, revealed a number of significant discrepancies between empirical data and model results (Table 1). First, the die-off of adults in the model was a result of competition with a strong cohort of young-of-the year (YOY) individuals for the common resource (zooplankton), whereas data provided no evidence that the die-off of adults was a result of competition between cannibals and victims. Second, adult individuals had to feed on several age cohorts of victims to accelerate in growth in the model of Claessen et al. (2000), whereas diet data suggested that adult individuals accelerated by cannibalizing on YOY perch only. Third, the growth rate was very low for the successfully recruiting cohort (therefore they were called ''dwarfs'') in the model, which was not the case in the data. Fourth, one successfully recruiting cohort dominated the period with giants and also formed the main resource of the giant individuals in the model, whereas data showed that a number of strong YOY year classes were recruited for a number of years. Fifth, the appearance of a strong cohort in the model was a result of a strong reproductive output, whereas this was not the case in the data. Finally, data suggested the presence of severe competition between YOY perch and 1-yr-old perch not present in the model (Claessen et al. 2000, Persson et al. 2000). The discrepancy between model predictions and data may have arisen because perch in the study lake to a large extent fed on macroinvertebrates during the stunted phase and this resource was not included in the model. Also, 1-yr-old perch restricted their habitat use to the shore region to avoid cannibalism from larger cannibals. This reduced the cannibalistic impact of 1-yr-old perch on pelagic newborn perch larvae (Persson et al. 2000, Byström et al. 2003).

One purpose of our present study is to examine more closely the basis for the discrepancies between model predictions and field data. We do this by using empirical data on population numbers and fecundities of different size classes at the start of the growth season for the periods with stunted and giant individuals, respectively, and then modeling the within-season dynamics using the population model of Claessen et al. (2000). Specifically, we focus on (1) the implications of introducing a second resource (macroinvertebrates) not present in the model of Claessen et al. (2000), (2) whether perch could accelerate in growth by cannibalizing on YOY perch only in contrast to what Claessen et al. (2000) found, and (3) the extent to which YOY perch affected 1-yr-old perch negatively through exploitative

competition. Our model predictions include the population dynamics of the two resources and perch, and the individual dynamics of growth and diets of perch ≥1-yr-old. Model predictions regarding both individual-level and population-level processes are subsequently confronted with empirical patterns. We also ask whether the dynamics of the studied perch population may be explained by mechanisms other than a dynamic based on the induction of giants and dwarfs after a period of stunted adult growth as outlined above. For example, stunted and giant periods may represent alternative attractors rather than involving the induction of giants and dwarfs (Claessen and De Roos 2003; see also Botsford 1981, Cushing 1991, 1992).

In a broader context, our approach represents a quantitative modeling framework with the purpose of developing ecology towards a more quantitative science. This framework includes a more critical test of model predictions and assumptions, and a route for a closer interaction between theoretical and empirical studies (cf. Murdoch et al. 1992, Murdoch and Nisbet 1996). The utility of the modeling approach we use—physiologically structured population models—for this purpose is due to (1) a high independence between model assumptions and empirical data against which model predictions are confronted, and (2) the modeling approach readily allows quantitative predictions at both the population and the individual level (De Roos and Persson 2001).

MATERIALS AND METHODS

Field data

The field data come from a long-term study of a perch population (*Perca fluviatilis*) in a small (9.3-ha) low-productivity lake, Abborrtjärn 3, situated in middle Sweden (64°29′ N, 19°26′ E) (Persson et al. 1996, 1999, 2000). The lake lacks surface inlets or outlets. Perch was the only fish species in the lake during 1991–1996. In late autumn 1996 and spring 1997, roach (*Rutilus rutilus*) and artificial vegetation were added to the lake as part of a whole-lake experiment. Data up to 2001 suggest that the addition of neither the roach population nor artificial structure has affected the perch dynamics to any extent—likely because the roach population still is small and only limited recruitment has been observed (L. Persson, *unpublished data*). We therefore include data up to 2001 to generate a longer time series for the perch population. Excluding data for the period 1997–2001 would, however, not have affected any of our conclusions. Methods to estimate population numbers, growth rates, and diets of different cohorts of perch are given in detail in Persson et al. (2000), and therefore here we only give a condensed summary, and similarly for methods to sample resources (zooplankton and macroinvertebrates).

Estimates of the 1991 population numbers of perch ≥2 yr old were based on gill-net catches (survey benthic gill nets, mesh sizes 9.5, 14.5, 18, 24, 29.5, 33, 38, and 46 mm, each section 7 m long) yielding a relative estimate (catch per unit effort) of population numbers and population size distribution. In all other years, population numbers and population size structures are based on absolute estimates using multiple mark–recapture methods (see Persson et al. 2000). All data on perch population censuses represent the spring situation in each year.

In spring every year, 1-yr-old perch were electrofished from a boat along the shore where they were concentrated. The entire shoreline was covered, dipping the anode of the electrofisher every 2 m. In 1995–1999 when high numbers of 1-yr-old perch were captured, population estimates were, as for older perch, based on mark–recapture methods. In years when 1-yr-old perch abundance was too low to allow population estimates based on mark–recapture (1992, 1993, 1994, 2000, 2001), estimates of 1-yr-old perch abundance based on electrofishing were transformed to absolute densities using a regression of the number of 1-yr-old perch captured during the spring electrofishing on estimates based on mark–recapture for the years 1995–1999. The abundance of 1-yr-old perch also yielded an estimate of the survival of young-of-the-year (YOY) perch from the date in the preceding year when they had moved to the shore habitat, to an age of 1-yr-old.

Estimates of the number of perch larvae are present for the period 1994–2001. Larval perch were sampled with a Bongo trawl once a week for five weeks following hatching in early June when they were distributed in the pelagic habitat. The Bongo-trawl captures yielded an absolute estimate of perch larvae abundance in terms of number of individuals per unit volume (Byström et al. 1998). Catches were corrected for gear avoidance using the equation given by Noble (1970) for Miller samplers. After YOY perch had shifted to the littoral zone in early/middle July, it was no longer possible to obtain quantitative estimates due to problems in trawling the near-shore area where the YOY perch resided and to the increased capacity of YOY perch to avoid the trawl at this date. During their littoral period YOY perch were caught by electrofishing to generate data on individual growth. Estimates of the number of YOY perch present at the end of the growth season (September) were obtained by using the frequency size distribution of YOY perch each autumn together with laboratory data on size-dependent winter mortality in perch (P. Byström, *unpublished data*). YOY perch density at the end of the growth season was obtained by dividing next spring's estimates of 1-yr old perch by the size-dependent winter survival probability.

Age and growth of individual fish were determined by calculating the size of the fish backwards in time using opercular bones (Bagenal and Tesch 1978). For YOY perch and 1-yr-old perch, growth was measured directly as these age cohorts could easily be separated

based on size. Perch start to spawn before the lake is accessible to sampling in spring, hence we could not obtain reliable estimates of fecundity based on sampled females. For the period 1992–1996 we instead calculated population fecundity based on length-specific fecundity data from Nyberg (1976) who studied perch populations with similar growth patterns and size structures. From 1997 and onwards, we directly counted the number of roe strands in the lake and the average number of eggs per strand (Persson et al. 2000).

On every sampling date, stomachs of up to 10 perch from each 20-mm size class above 100 mm were flushed for dietary analyses. During 1995–1998, stomach samples from 10–20 1-yr-old perch were taken from electrofished fish at least once a month. In 1995, additional samples were taken every week in June to study the potential presence of cannibalism by 1-yr-old perch on YOY perch. All diet data presented are based on dry mass, which, for comparisons with modeling outputs, was transformed to wet mass using a standard conversion factor. Diet data from each sampling date were grouped based on perch size classes (1-yr-old, 151–200 mm, and >200 mm perch cohorts are presented in this paper).

In every year, zooplankton was sampled 7–8 times during the growing season at three pelagic stations. Zooplankton were collected with a 100 μm-mesh net (diameter 25 cm) drawn vertically at an approximate speed of 0.5 m/s. One tow was made at each pelagic station from the thermocline (estimated with a thermistor) to the surface. In August 1992, five macroinvertebrate samples were taken with an Ekman dredge (area 630 cm²) at one littoral station at a water depth of 0.5 m. In 1993–1996 the macroinvertebrate sampling was extended to three littoral stations and in 1997 to 5 stations. For the years 1993–2001, six samples were taken in August at each station with a core sampler. Macroinvertebrates were separated into two groups. One group consisted of organisms living on macrophytes, branches, or other substrates (Hirudinea, Ephemeroptera, Trichoptera, Odonata, Coleoptera, Megaloptera) that are relatively sensitive to fish predation. The other group (mainly chironomids) consisted of organisms living in the sediment that are less sensitive to fish predation (see Persson et al. [1996] and references therein).

Modeling

Our population dynamical model of cannibalistic perch belongs to the class of physiologically structured models (Metz and Diekmann 1986, Metz et al. 1988, De Roos et al. 1990, De Roos 1997), which are specifically suited to handle the dynamics of populations involved in size-dependent interactions. These models are based on a state concept at each of two levels of organization: an *i* state that represents the state of the individual in terms of a collection of characteristic physiological traits (size, age, sex, energy reserves,

etc.) and a *p* state, which is the frequency distribution over the space of possible *i* states. The model-formulation process consists of the derivation of a mathematical description of how individual performance (growth, survival, reproduction) depends on the physiological characteristics of the individual and the condition of the environment (*i*-state description). Handling the population level (*p*-state) dynamics is subsequently just a matter of bookkeeping of all individuals in different states without making any further model assumption at this level. The core of these models is thus the individual state and its dynamics, which in our case is a description of the dynamics of the physiological state of perch individuals as a function of their current values and the condition of the environment. The environment consists of two resources (zooplankton and macroinvertebrates) and the perch population itself representing all potential cannibals and victims. The dynamics of the state variables are specified in Table 1, the equations specifying the individual-level model are in Table 2, and the parameter values derived for perch are given in Table 3. A complete derivation of model assumptions including parameterization can be found in Claessen et al. (2000). Our model differs from the model of Claessen et al. (2000) in that (1) we include two basic resources and (2) we do not consider reproduction as our analysis is focused on within-season dynamics. Thus our initial state values are based on spring values observed in the study system (see *Results*: Table 4). Furthermore, in comparison with Claessen et al. (2000) we changed the formulation of the cannibalistic attack-rate function slightly to better match empirical observations that have become available more recently (see *Materials and Methods: Cannibalism window*, and Fig. 2).

The physiological state of the individual is characterized by two *i* states, irreversible mass *x* and reversible mass *y* (Table 1, see also Persson et al. 1998). Reversible mass can be starved away when maintenance costs exceed energy intake, whereas irreversible mass cannot. Rules for how energy for growth is allocated between irreversible and reversible mass are explained in detail in Persson et al. (1998). The rules are designed such that, given a positive energy balance, the ratio y/x approaches a maximum value asymptotically, which is q_J for juveniles, and q_A for adults. We assume that $q_A > q_J$ which reflects the fact that adult individuals in addition to fat reserves also allocate energy to gonads. In our calculations, individuals below the maturation size (i.e., $x < x_f$) were assumed to start with the maximum reversible mass for that size given by $y = q_J x$, whereas individuals above the maturation size were assumed to start with the maximum reversible mass for adults, given by $y = q_A x$ (Table 2). As long as juvenile individuals have a positive energy balance, they will continue to have the same ratio of reversible to irreversible mass (q_J), but if they reach the size where

TABLE 1.　Definitions of state variables and specification of their dynamics.

A) State variables

Variable	Symbol	Unit
Individual level		
Irreversible mass	x_i	g
Reversible mass	y_i	g
Population level		
Number of cohorts	k	
Density of cohorts	$N_i,　i \in \{1, k\}$	no./L
Environment		
Resource density of zooplankton	R_z	g wet mass/L
Resource density of predator-sensitive macroinvertebrates	R_m	g wet mass/m^2
Potential cannibals/victims	$\{N_i, x_i\},　i \in \{1, k\}$	

B) Dynamics within years†

Dynamic	Equation	
Cohort mortality	$\dfrac{dN_i}{dt} = -\mu(x_i, y_i)N_i$	$i \in \{1, k\}$
Cohort per capita growth in x	$\dfrac{dx_i}{dt} = \begin{cases} f(x_i, y_i)E_{\text{growth}}(x_i, y_i) & \text{if } E_{\text{growth}} > 0 \\ 0 & \text{otherwise} \end{cases}$	$i \in \{1, k-1\}$
Cohort per capita growth in y	$\dfrac{dy_i}{dt} = \begin{cases} [1 - f(x_i, y_i)]E_{\text{growth}}(x_i, y_i) & \text{if } E_{\text{growth}} > 0 \\ E_{\text{growth}}(x_i, y_i) & \text{otherwise} \end{cases}$	$i \in \{1, k-1\}$
YOY length growth (stunted phase)	$\ell(a) = \begin{cases} 0.18 \times a + 6.2 & \text{if } a < 46.4 \\ 13.0 \times (a - 45.0)^{0.29} & \text{otherwise} \end{cases}$	
YOY length growth (giant phase)	$\ell(a) = \begin{cases} 0.0051a^2 + 0.180a + 7.5 & \text{if } a < 59.9 \\ 0.0036a^2 - 0.097a + 29.2 & \text{otherwise} \end{cases}$	
Resource dynamics	$\dfrac{dR_z}{dt} = r_z(K_z - R_z) - R_z \sum\limits_{j=1}^{k} e_{z,j} \dfrac{A_z(x_j)N_j}{1 + H(x_j)\eta(x_j)}$	
	$\dfrac{dR_m}{dt} = r_m(K_m - R_m) - R_m \sum\limits_{j=1}^{k} e_{m,j} \dfrac{A_m(x_j)N_j}{1 + H(x_j)\eta(x_j)} \dfrac{V}{S}$	

† The functions for mortality (μ), energy balance (E_{growth}), energy allocation (f), attack rates (A_z, A_m, A_c), handling time (H), and total encounter rate (η) are given in Table 2. Values for encounter efficiencies on different resources ($e_{z,i}$, $e_{m,i}$, $e_{c,i}$) were varied between 0 and 1 for different year classes (with index i; k is the index of the YOY [young-of-the-year] cohort) independently. Observe that cohort per capita growth refers to perch ≥1 yr old.

they mature, the ratio increases, approaching q_A. An individual is assumed to allocate a larger proportion of its energy intake to reversible mass if its condition (the ratio y/x) is lower (Table 2). If energy intake is smaller than metabolic costs, reversible mass will be converted to energy to cover metabolic costs. Individuals can sustain a certain mass decrease in reversible mass without an increase in starvation mortality down to a reversible-mass-to-irreversible-mass ratio given by $y = q_S x$ (Table 3). If reversible mass decreases below this ratio, the individual will start to die of starvation at a rate that increases to infinity as reversible mass decreases to zero.

All functions describing foraging intake and energy expenditure depend on size. Attack rates on zooplankton (A_z), macroinvertebrates (A_m) and conspecifics (A_c) are assumed to depend on irreversible mass only, either through a quantity $m(x) = (1 + q_j)x$, which we refer to as ''standardized mass'' or through the individual

length, which itself is an allometric function of standardized mass (see Claessen et al. 2000). The notion of standardized mass, which reflects the mass of a non-starving individual discounting its gonads, has been introduced to allow for parameter estimation from data (see Persson et al. 1998). The attack rate on zooplankton is modeled as a dome-shaped curve and the attack rate on macroinvertebrates as a power function (Table 2). The cannibalistic attack function plays an important role in the analysis and we will return to a description of this function below. The feeding rate (I) is a function of prey mass encounter and the capacity to digest prey where the prey mass encounter is the product of the consumer's attack rate, prey density, and prey individual mass. The digestion capacity (grams of prey per unit of time) is assumed to increase with standardized body mass (Table 2). For one-year-old and older perch, metabolic costs are assumed to depend on total body mass (reversible plus irreversible) following a power

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TABLE 2. Equations that specify the individual-level model.

Physiological characteristics

Standardized mass

$$m(x) = (1 + q_J)x$$

Body length

$$\ell(x) = \lambda_1 m(x)^{\lambda_2}$$

Attack rates

Zooplankton attack rate

$$A_z(x) = A\left\{\frac{m(x)}{W_{opt}}\exp\left[1 - \frac{m(x)}{W_{opt}}\right]\right\}^\alpha$$

Macroinvertebrate attack rate

$$A_m(x) = b_1 m(x)^{b_2}$$

Cannibalistic attack rate

$$A_c(c, v) = \begin{cases} \beta\left(\dfrac{v}{\phi}\right)^\sigma \dfrac{c - \dfrac{v}{\varepsilon}}{\dfrac{v}{\varepsilon} - \dfrac{v}{\delta}} & \text{if } \dfrac{v}{\varepsilon} < c < \dfrac{v}{\phi} \\[2em] \beta\left(\dfrac{v}{\phi}\right)^\sigma \dfrac{\dfrac{v}{\delta} - c}{\dfrac{v}{\delta} - \dfrac{v}{\phi}} & \text{if } \dfrac{v}{\phi} < c < \dfrac{v}{\delta} \\[2em] 0 & \text{otherwise} \end{cases}$$

Total food intake

$$I(x) = \frac{\eta(x)}{1 + H(x)\eta(x)}$$

Total digestion time

$$H(x) = \xi_1 m(x)^{\xi_2}$$

Encounter rates

Total encounter rate

$$\eta(x_i) = e_{z,i}\eta_z(x_i) + e_{m,i}\eta_m(x_i) + e_{c,i}\eta_c(x_i)$$

Zooplankton encounter rate

$$\eta_z(x) = A_z(x)R_z$$

Macroinvertebrate encounter rate

$$\eta_m(x) = A_m(x)R_m$$

Cannibalistic encounter rate

$$\eta_c(x_i) = \sum_j A_c[\ell(x_i), \ell(x_j)](x_j + y_j)N_j$$

Energy

Energy balance

$$E_{growth}(x, y) = E_{aquir.}(x) - E_{maint.}(x, y)$$

Aquired energy

$$E_{aquir.}(x) = k_e I(x)$$

Maintenance requirements

$$E_{maint.}(x, y) = \rho_1(x + y)^{\rho_2}$$

Fraction of energy allocated to growth in x

$$f(x, y) = \begin{cases} \dfrac{1}{(1 + q_J)q_J}\dfrac{y}{x} & \text{if } x < x_f \\[1.5em] \dfrac{1}{(1 + q_A)q_A}\dfrac{y}{x} & \text{otherwise} \end{cases}$$

Mortality

Total mortality

$$\mu(x, y) = \mu_0 + \mu_s(x, y) + \mu_c(x)$$

Starvation mortality

$$\mu_s(x, y) = \begin{cases} s(q_S x/y - 1) & \text{if } y < q_S x \\ 0 & \text{otherwise} \end{cases}$$

Cannibalistic mortality

$$\mu_c(x_j) = \sum_i e_{c,i}\frac{A_c[\ell(x_i), \ell(x_j)]N_i}{1 + H(x_i)\eta(x_i)}$$

Notes: The subscripts i (individual) and J (juvenile) refer to cohort indices and variables c and v to the length of a cannibal and victim, respectively, which are a function of irreversible mass. β = overall intensity of cannibalism, ϕ = optimal size ratio; e = encounter efficiency, k_e = conversion efficiency. See Table 3 for parameter symbol definitions.

function. The energy intake of the individual is the feeding rate multiplied by a conversion factor.

For YOY perch, we used empirical data on growth; hence the part of the model describing metabolic rate and growth (but *not* feeding rate) is irrelevant for YOY perch. The reason for not letting the growth of YOY perch depend on their food intake was related to the discrepancy between data and model predictions regarding YOY perch growth. Field data suggested that

perch could accelerate in growth by feeding on YOY perch only (Persson et al. 2000). Model predictions suggested that perch also need access to conspecifics older than YOY perch to gain sufficient energy for accelerating in growth (Claessen et al. 2000, 2002). By letting YOY grow in the model according to the pattern as observed in the field (Fig. 1), we could evaluate more accurately whether perch could actually accelerate through cannibalism on YOY perch only, as sug-

TABLE 3. Model parameters for perch feeding on zooplankton, macroinvertebrates, and conspecifics.

Subject	Symbol	Value	Unit	Interpretation	Source†
Lake	V	3×10^8	L	total volume	7
	S	3×10^4	m^2	benthic bottom area	4
Season		90	d	length of growth season	1
Ontogeny	x_b	0.001	g	irreversible mass at birth	1
	x_f	4.6	g	irreversible mass at maturation	1
	q_J	0.74	...	juvenile max. condition	1
	q_A	1.37	...	adult max. condition	1
Length–mass relation					
YOY < 29.2 mm	λ_1'	41.2	mm/g$^{\lambda_2}$	allometric scalar	2
	λ_2'	0.263	...	allometric exponent	2
YOY ≥ 29.2 mm	λ_1	48.0	mm/g$^{\lambda_2}$	allometric scalar	2
	λ_2	0.380	...	allometric exponent	2
Older perch	λ_1	48.3	mm/g$^{\lambda_2}$	allometric scalar	2
	λ_2	0.317	...	allometric exponent	2
Planktivory	α	0.62	...	allometric exponent	3
	$\hat{A}$	9×10^3	L/d	max. attack rate	3
	$W_{opt.}$	4.7	g	optimum consumer size	6
Benthivory	b_1	0.2	m$^2 \cdot$d$^{-1} \cdot$g^{b_2}‡	allometric scalar	4
	b_2	0.4	...	allometric exponent	4
Piscivory	σ	0.6	...	allometric exponent	4, 5
	β	400	L$\cdot$d$^{-1}\cdot$mm$^{-\sigma}$	cannibalistic voracity	4, 5
	δ	0.05	...	lower size limit§	5
	ε	0.45	...	upper size limit§	5
	ϕ	0.16	...	optimum size ratio	5
Digestion	ξ_1	5.0	d/g$^{(1+\xi_2)}$	allometric scalar	1
	ξ_2	-0.8	...	allometric exponent	1
Metabolism	ρ_1	0.033	g$^{(1-\rho_2)}$/d	allometric scalar	1
	ρ_2	0.77	...	allometric exponent	1
	k_e	0.61	...	conversion efficiency	1
Mortality	μ_0	0.005	...	background mortality rate	4
	q_S	0.2	...	starvation mortality threshold	1
	s	0.2	d^{-1}	starvation rate coefficient	1
Zooplankton semi-chemostat dynamics					
	r_z	0.05	d^{-1}	renewal rate	1
	K_z	0.001	g/L	maximum population density	6
Macroinvertebrates semi-chemosat dynamics					
	r_m	0.05	d^{-1}	renewal rate	1
	K_m	2.5	g/m^2	maximum population density	7

Note: YOY = young-of-the-year.

† References: 1, Claessen et al. (2000); 2, P. Byström, *unpublished data*; 3, Byström and Gàrcia-Berthóu (1999); 4, L. Persson, *unpublished data*; 5, Lundvall et al. (1999); 6, Wahlström (2000); 7, Persson et al. (2000).

‡ See Table 2: Macroinvertebrate attack rate.

§ Ratio of victim length to cannibal length, v/c.

gested by Persson et al. (2000) or whether the presence of the additional basal resource macroinvertebrates (absent in the model of Claessen et al. 2000) was essential. The nonlinear length–age relations fitted to the data shown in Fig. 1 are presented in Table 1. These YOY length–age relations were transformed to mass–age relations using the length–mass relations presented in Table 3.

Both resources (zooplankton and macroinvertebrates) are modeled as unstructured populations with semi-chemostat resource dynamics (i.e., amount of resource input per unit of time is independent of resource density present in the system; Persson et al. 1998, De Roos et al. 2002). The macroinvertebrate resource represents the predator-sensitive macroinvertebrates (see above field data), whose densities have been shown to be the macroinvertebrates that are more accessible to

perch and that also are affected by perch predation (Persson et al. 1996, 2000). Based on lake morphology and depth distribution of macroinvertebrates, macroinvertebrates are assumed to be present in 20% of the lake volume (at the littoral bottom) (Persson et al. 1999). The mean depth of the littoral habitat is assumed equal to 2.0 m. The zooplankton resource is assumed to consist of a homogeneously mixed population present in the whole lake volume.

Cannibalism window

We assumed that positive cannibalistic attack rates are constrained between two bounds of the ratio of victim (v) to cannibal length (c) equal to $v/c = \delta$ and ε, respectively (Tables 2 and 3). δ sets the smallest victim size as a fraction of cannibal length below which the cannibal does not encounter victims due to diffi-
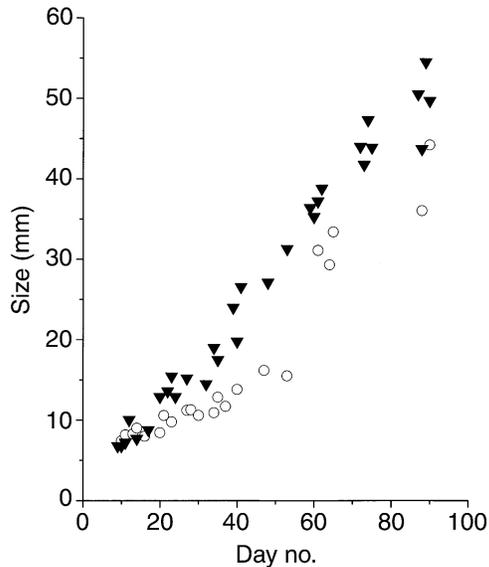
FIG. 1. Increase in size of young-of-the year perch in 1994–1997 (triangles) and in 1999–2001 (circles). Each data point is based on one sampling occasion representing the mean of ≥30 individuals.

culties in detecting them; ε sets the maximum victim size as a fraction of cannibal length above which escape ability of victims and gap constraints in the cannibal prohibit capture. Within the range of cannibal and victim sizes where cannibalistic attack rates are positive (the cannibalism window), the attack rate on differently sized victims for a specific cannibal length is assumed to increase with victim size from zero at $v = \delta c$, to an optimum at $v = \phi c$, to thereafter decrease and become zero again when victim length reaches $v = \varepsilon c$ (Table

1, Fig. 2). Our model formulation differs from that of Claessen et al. (2000, 2002) in that we, based on new experimental data, assume that the increase and the decrease in attack rate are described by nonlinear rather than linear functions of victim size (Lundvall et al. 1999) (Table 3, Fig. 2). On the ridge $v = \phi c$ representing the optimum victim length for differently sized cannibals, the attack rate is assumed to increase with victim length (and thus also cannibal length) according to the equation $\beta(v/\phi)^\sigma$ where β represents the overall intensity of cannibalism, ϕ the optimal size ratio and σ a size scaling (Claessen et al. 2000, 2002).

RESULTS

Field data

The perch population in the study lake has undergone substantial changes in numbers and size structure (Persson et al. 2000) (Fig. 3). In the years 1991–1993, the perch population was dominated by intermediately sized individuals having slow growth and reaching a maximum size of ∼180 mm (Fig. 4). Very few 1-yr-old perch were observed (individuals sized 46–61 mm in Fig. 3) despite strong reproductive outputs in all years. In the summers of 1993 and 1994 the population of perch ≥2 yr old decreased to low values. The decrease in 1994 (but not in 1993) coincided with the successful survival of a young-of-the-year (YOY) cohort reflected in a high peak in abundance of 1-yr-old perch in the spring of 1995 (Fig. 3). However, despite the co-occurrence of a decline in perch ≥2 yr old and the presence of larger numbers of YOY perch, the decrease in 1994 could not be related to competition for a shared resource (zooplankton) with YOY perch (Persson et al. 2000). High survival of YOY perch cohorts
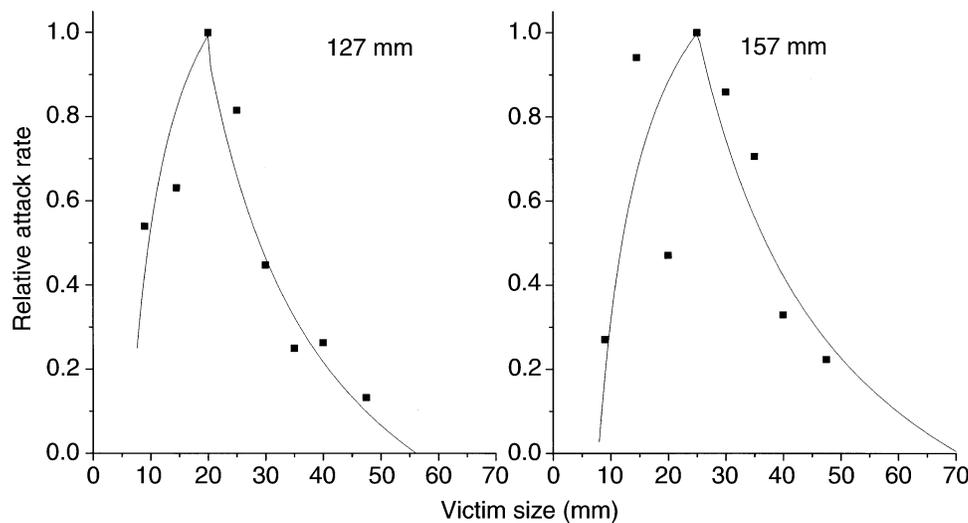

FIG. 2. Fits of the cannibalistic tent function specified in Table 3 and described in the text (see *Materials and methods: Cannibalism window*) on relative attack rates for two sizes of perch using data from Lundvall et al. (1999). The relative attack rate was set to 1 for the highest observed capture rate for each cannibal size, and the other relative attack rates were scaled in relation to these two highest capture rates.
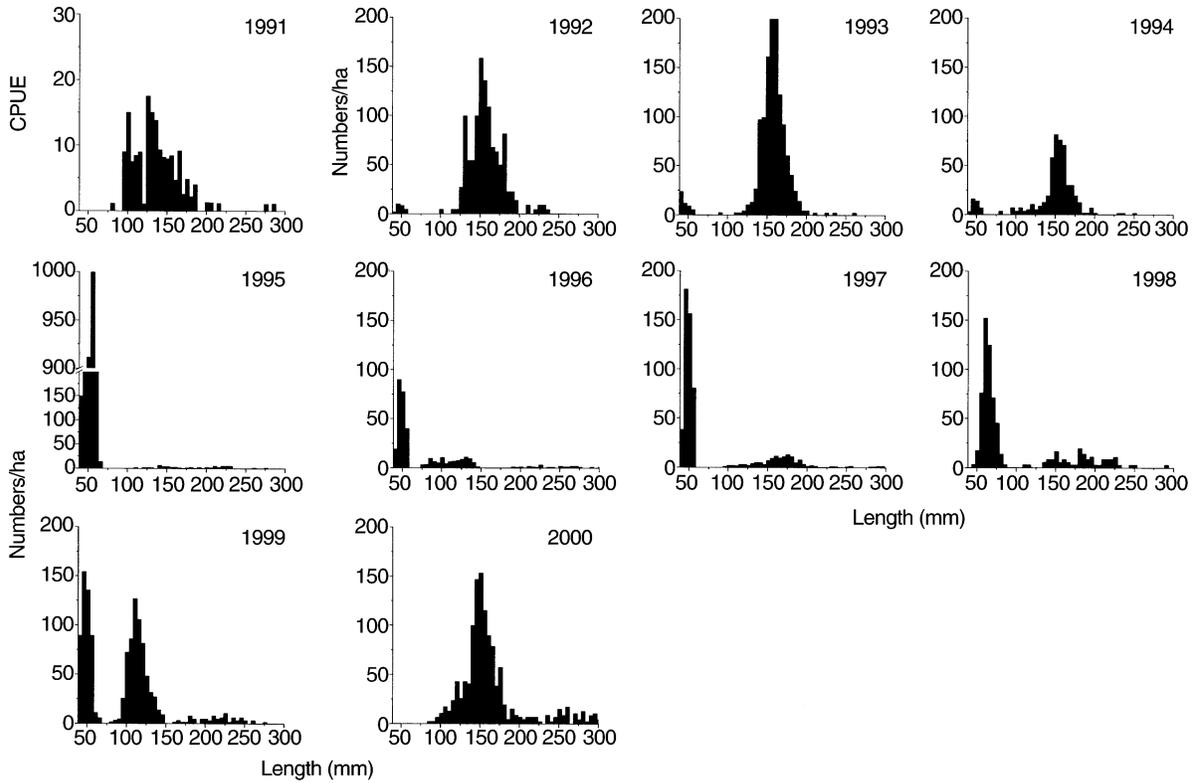
FIG. 3.   Observed size distributions of the perch population during 1991–2000. Data from 1991 were catch per unit effort (CPUE) whereas data from 1992–2000 are estimated absolute densities (number/ha).

was subsequently observed for another four years leading to high numbers of 1-yr-old perch during the years 1995–1999. In the years 1995–1997, the survival of 1-yr-old perch was very low (<5%), which was suggested to be due to inter-cohort competition with YOY perch (evidence: depression in condition of 1-yr-old perch and decreases in zooplankton resource levels associated with high numbers of YOY perch; Persson et al. 2000). Diet data showed no evidence for cannibalism

by larger perch on 1-yr-old perch. In 1998, the survival of the 1-yr-old cohort of perch to 2 yr old was high (>90%) leading to a strong cohort of 2-yr-old perch being present in 1999 (Fig. 3). Despite a high reproductive output in 1999, very few YOY survived to an age of one year and in 2000 the perch population had returned to a state similar to that in 1991–1993.

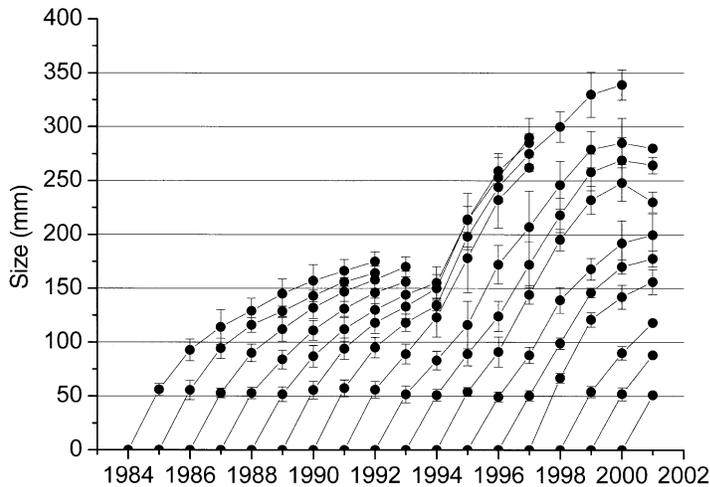The few adult perch surviving in 1994 showed strongly accelerated growth in all years with high sur-

FIG. 4.   Length–age relation for different year classes of perch during 1984–2001. Data are means ± 1 SD.
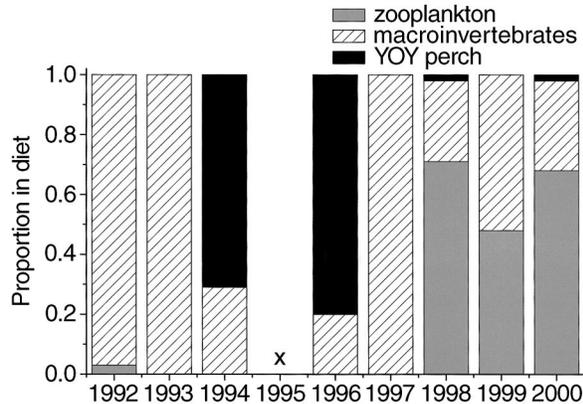
FIG. 5. Biomass proportion of zooplankton, macroinverte-brates, and young-of-the-year (YOY) perch in the diet of perch sized 161–200 mm in early August during the period 1992–2000; the "×" indicates that no fish were sampled in 1995.

vival of YOY perch. This high growth was related to a high proportion of YOY perch in the diet in July–August (Fig. 5) (Persson et al. 2000). In contrast, the diet of perch ≥2 years old during 1992–1993 and 1999–2000 was dominated by macroinvertebrates and the biomass contribution of YOY perch to the diet of perch ≥2 yr old was low (Fig. 5) (Persson et al. 2000). The diet of 1-yr-old perch in years when they were abundant enough to allow adequate sampling consisted mainly of zooplankton and macroinvertebrates (Persson et al. 2000). Cannibalism by 1-yr-old perch on YOY perch was present but was restricted to a short period in June (Byström et al. 2003).

YOY perch were not sampled in 1991–1993. The growth rate of YOY perch with high survival to 1 yr old (1994–1998) was higher than that of YOY perch in years with low survival to 1 yr old (1999–2001) (Fig. 1). This difference in growth was already present during the early larval stages. The steep increase in the size of YOY perch in early August in 1999–2001 is probably due to the fact that these individuals represented a very small, remaining number of fast-growing YOY perch sampled along the shore. Although the lower growth rate of YOY perch in 1999–2001 may have led to a lower winter survival, trap catches show that the number of YOY perch present in September was already much higher in 1994–1998 than in 1999–2001 (trap+fyke net catches September, 1994–1998: mean catch 334 individuals; 1999–2001: mean catch 19 individuals; $t_6 = 11.2$, $P < 0.0001$). Thus early cannibalism by the abundant but slow-growing perch ≥2 yr old remains the likely explanation for the low numbers of 1-yr-old perch in 1992–1994 and 2000–2001. Cannibalism as a density-dependent factor is also supported by the strong negative relationship between reproductive output and number of surviving recruits (Fig. 6).

Model results

The model was run for two phases with different perch population numbers, population structures, pop-ulation fecundity, YOY perch mortality, and resource dynamics (i.e., 1992, 1993, 1999, 2000 vs. 1994–1997) (Fig. 3). As outlined in the *Introduction*, we use the model to quantitatively scrutinize qualitative discrepancies in mechanisms suggested by the previous model formulation (Claessen et al. 200) vs. those indicated by our data—in particular, to assess the importance of adding a second shared resource, macroinvertebrates, and 1-yr-old perch habitat use for the interactions between YOY perch and 1-yr-old perch. The pathway of this analysis is given in Fig. 7. Data from 1998 were not included because that year differed from the other years with high numbers of surviving YOY perch by also having a high survival of 1-yr-old perch. One phase (1992, 1993, 1999, 2000) is characterized by many cohorts not growing beyond a size of ~180 mm and this phase will in the following be called the "stunted" phase (Fig. 4). The other phase (1994–1997) is characterized by a few adult individuals reaching lengths of up to and beyond 300 mm, and will in the following be called the "giant" phase. For each phase the estimated number (average between years) of YOY perch (number of eggs), 1-yr-old perch, and perch ≥2 yr at the onset of spring (end of May) were used as initial values (Table 4). For perch ≥2 yr, the average size distributions in 1992–1993 and 2000 (stunted phase) and 1995–1997 (giant phase) were used. Start values for resource densities were set to their maximum (Table 4). The simulations were run for 90 d, representing the growth season (June–August) in the study lake. YOY perch were assumed to hatch on day 11 (June 11), which is an average observed in the study lake (Byström et al. 2003). They were assumed to immediately move out into the pelagic habitat (Byström et al. 2003). The day at which YOY perch move back
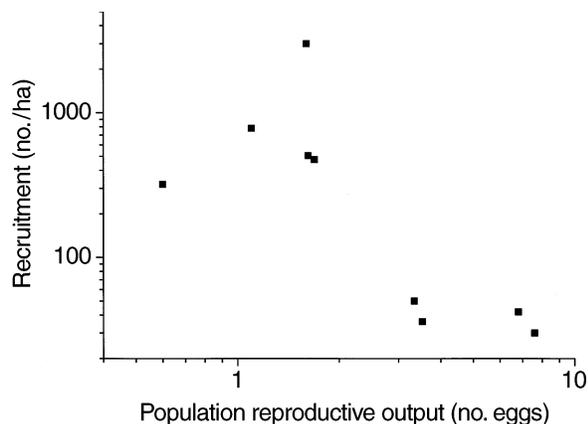

FIG. 6. The relationship between the reproductive output and the recruitment of 1-yr-old perch in the following year, during 1991–2000. Data on number of eggs before 1996 are based on regressions of fecundity on body length whereas data for 1996–2000 are based on direct counts; the data on number of eggs was multiplied by 10^6 before being graphed (so that, e.g., $1 = 10^6$ eggs). Note the logarithmic scale on both axes.
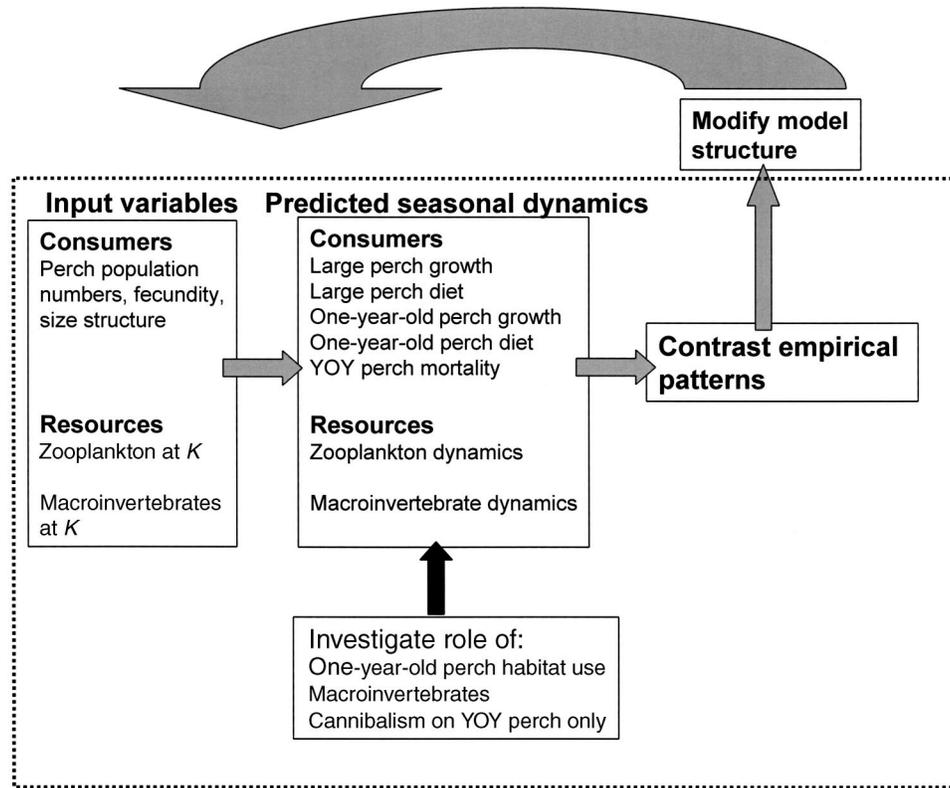
Fig. 7. Flow chart showing the logical steps in the quantitative contrast of modeling predictions with empirical data. The focus of the present study is within the dashed boundaries forming the basis for a modified multigenerational model providing a better description of the dynamics of the cannibalistic perch system (Persson 2003). Input variables were run for both the stunted and giant phases. Abbreviations: YOY = young-of-the-year; K = carrying capacity.

to the littoral area has been shown to depend on size-dependent predation risk (Byström et al. 2003). Runs varying the timing of the habitat shift within the range observed in the field showed that the time chosen at which the shift occurred did not affect the patterns observed. We therefore chose to use a fixed day (day 31) for YOY perch to shift habitat to the littoral in all runs. One-year-old perch were assumed to be restricted to the littoral habitat up to day 20 due to predation risk

from larger cannibals. After this date, 1-yr-old perch spread over the whole lake volume.

For the simulations in the stunted phase, the number of perch ≥2 yr and population reproductive output were high, whereas the number of 1-yr-old perch was low (Table 4). For the simulations in the giant phase, the opposite was the case, i.e., the number of perch ≥2 yr and population reproductive output were low and the number of 1-yr-old perch was high. Perch ≥2 yr during

TABLE 4. Initial values of the number of perch and of the resource levels used to generate model predictions for the dynamics in the two phases.

Variable	Stunted phase†	Giant phase‡
Perch ≥2 yr (numbers)	11 000	1000
One-year-old perch (numbers)	300	6000
YOY perch (number of eggs)	4×10^6	1.1×10^6
Zooplankton (g wet mass/L)	0.001	0.001
Macroinvertebrates (g wet mass/m²)	2.5	2.5

Notes: Data for the different perch cohorts are based on mean values observed (stunted phase: 1992, 1993, 1999–2000; giant phase: 1994–1998). For perch ≥2 yr old, initial size distributions (not presented) were based on mean values for the two phases. Initial size of 1-yr-old perch was the same for both phases. Values for zooplankton and macroinvertebrates assume maximum density of the resource.

† The phase characterized by many cohorts not growing beyond a size of ~180 mm.

‡ The phase characterized by a few adult individuals reaching lengths of ≥300 mm.
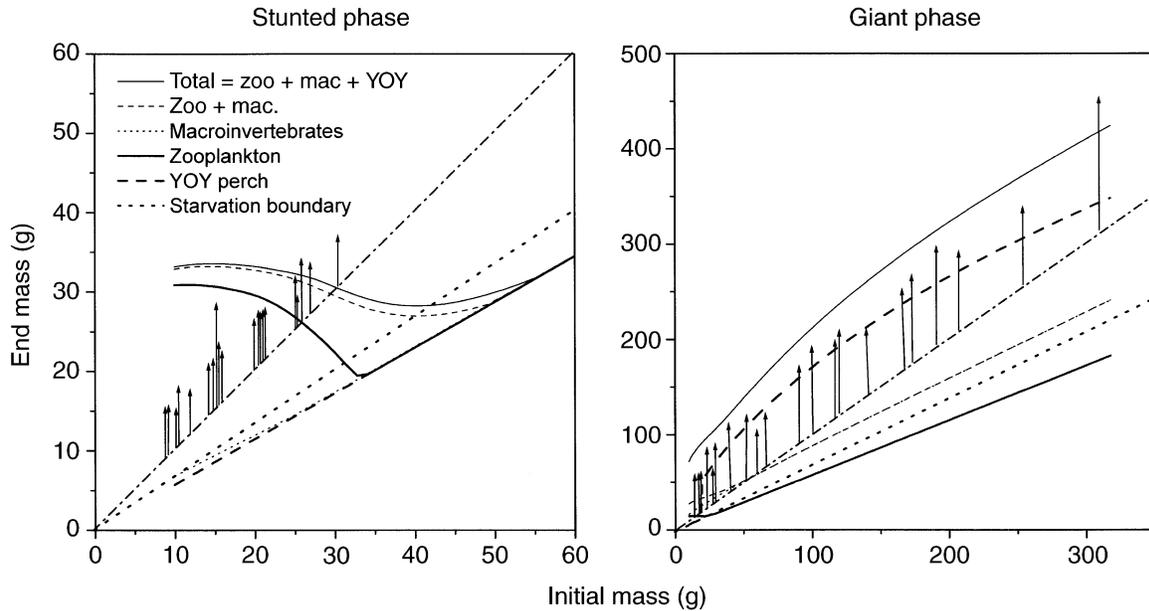
FIG. 8. Predicted changes in perch mass as a function of initial size for the stunted and giant phases. The curves represent predictions when perch were assumed to feed on macroinvertebrates only (thin dotted line), zooplankton only (thick solid line), young-of-the-year (YOY) perch only (thick dashed line), macroinvertebrates and zooplankton (thin dashed line), and macroinvertebrates, zooplankton, and YOY perch (thin solid line). The dotted–dashed line (1:1) is the total mass of an individual that just maintains its mass over the growth season ($y = q_j x$), and the dotted thick line is the total mass of an individual at the starvation level ($y = q_s x$). Inserted vectors are observed mass changes (means for each age cohort) based on Fig. 4 and mass–length relationships from Persson et al. (2000).

the stunted phase were assumed to split their time between the littoral and the open-water habitat in a ratio of 0.3:0.7, which is the estimated ratio based on trap catches (Persson et al. 2000). During the giant phase, all perch ≥2 yr were assumed to be in the littoral habitat as trap data show that these perch restricted their habitat use to the littoral habitat. To test for the effects of habitat use by YOY and perch ≥2 yr on YOY perch mortality, runs were also done altering these assumptions.

As a default situation, we assumed that 1-yr-old and older perch searched for all three prey types (macroinvertebrates, zooplankton, and YOY perch) simultaneously, whereas YOY perch only searched for zooplankton. We define the "encounter efficiency" on a prey as being 1 if perch search for that prey type simultaneously as they search for other prey types. If perch do not search for a prey type at all, the encounter efficiency for that prey type is 0. In different scenarios, we varied the encounter efficiencies on different prey types for YOY, 1-yr-old, and older perch to investigate the effects on resource dynamics and perch growth.

Growth and diets of perch ≥2 yr old

Two major focuses of our study are (1) the effects on perch performance of introducing a second (macroinvertebrate) resource, and (2) whether perch could accelerate in growth by cannibalizing on YOY perch only. To illustrate growth effects, predicted mass in-

creases are derived for an initial perch size range of 100–200 mm (8–60 g) for five different scenarios: (1) perch feeding on all three prey items, (2) perch feeding on zooplankton and macroinvertebrates, (3) perch feeding on zooplankton, (4) perch feeding on macroinvertebrates, and (5) perch feeding on YOY perch.

The predicted mass increase during the stunted phase when perch fed on all three prey items was similar to that when perch fed on zooplankton and macroinvertebrates only, showing that energy extraction from cannibalism was small (Fig. 8: left). Actually, the energy extraction from cannibalism was so small that perch feeding on YOY perch only reached reversible masses below the starvation boundary ($y = q_s x$) independent of their size. Perch feeding on macroinvertebrates only always had a negative growth but were above the starvation boundary up to a size of 9 g (Fig. 8: left). Perch feeding on zooplankton only had a predicted positive growth up to a size of 27 g. The predicted maximum size of perch when they fed on both zooplankton and macroinvertebrates amounted to 31 g. Comparing predicted growth rates with observed growth rates showed that observed perch mass increase was substantially lower than that predicted for perch feeding on zooplankton or both zooplankton and macroinvertebrates for small perch sizes. The difference between observed and predicted mass increase decreased with increasing perch size. Observed maximum sizes were, in 18 out of 21 cases, below or equal to and in only 1 case sub-
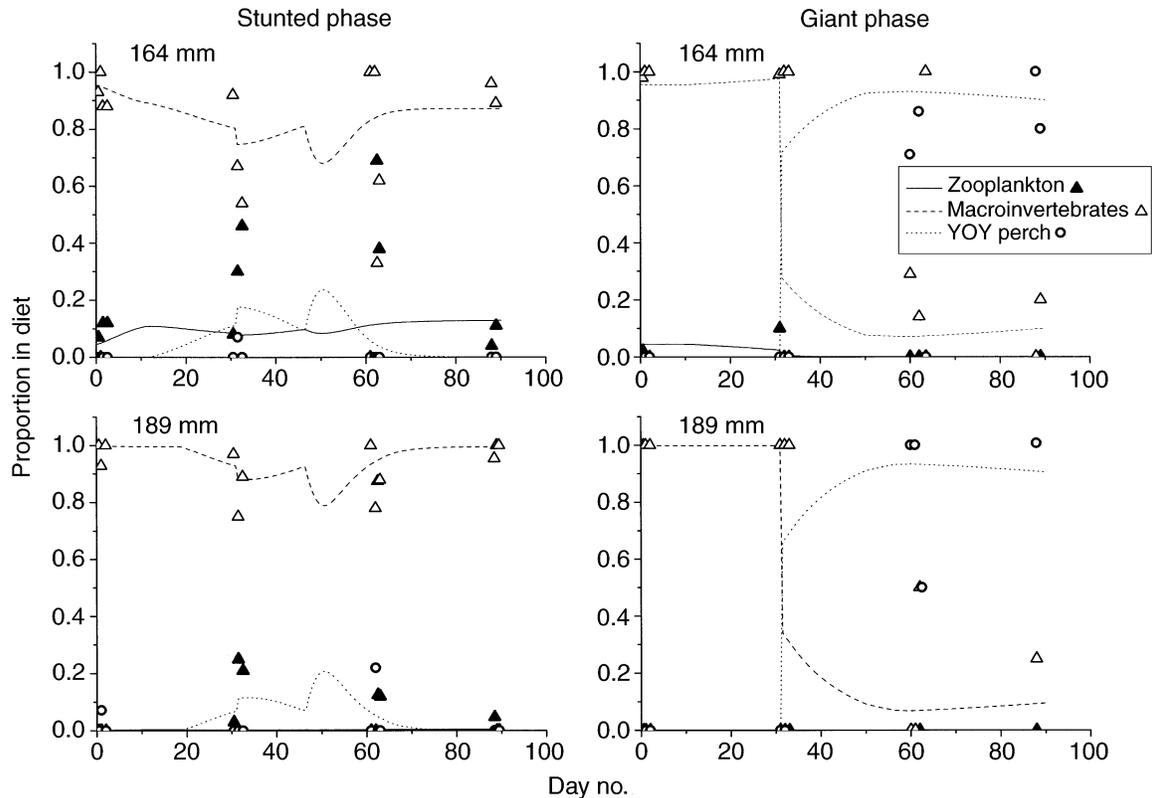
Fig. 9. Diets of two size cohorts (start size shown in panels) of perch during the stunted and giant phases. Lines represent predicted proportions of zooplankton, macroinvertebrates, and young-of-the-year (YOY) perch in the diet. The symbols represent observed diets for the two size cohorts of perch during the stunted (1992, 1993, 1999, 2000) and giant (1994–1997) phases; each symbol represents the mean of ≥10 individuals. Encounter efficiencies were assumed to be 1 for all prey types.

stantially larger than, the predicted maximum mass increase based on perch feeding on all three prey items.

Fig. 9 shows the diet predictions for two different size classes of perch ≥2 yr old. During the stunted phase macroinvertebrate prey were predicted to form the bulk of food for both size classes of perch and their importance was predicted to increase with perch size. Zooplankton was hardly predicted to be eaten at all by the largest size cohort, and this size cohort was not predicted (or observed) to have a positive growth rate. Cannibalism contributed to the diet of both size classes for a period during the middle of the growth season, but overall the predicted contribution of YOY perch to the diet of perch was small. The agreement between predicted and observed diets was generally high for the stunted phase (Fig. 9: left). For one year (2000), the observed diet of perch in summer consisted of a higher proportion of zooplankton than predicted for both size cohorts. This discrepancy between predictions and observations can be related to the fact that the zooplankton biomass in that year consisted of a higher proportion of larger (1 mm) *Daphnia* compared to other years and that our parameter estimates for the attack rate on zooplankton is based on a 0.5-mm cladoceran.

During the giant phase the predicted mass increase of perch feeding on zooplankton only was positive for size classes smaller than 14 g and ended up below the starvation boundary for most size classes (Fig. 8: right). In contrast, the predicted maximum size of perch feeding on macroinvertebrates amounted to 49 g. The predicted mass increase of perch feeding on all prey items was positive for all sizes studied and perch reached giant sizes. Restricting perch consumption to feeding on YOY perch only still allowed giant growth (Fig. 8: right). Observed growth trajectories were closest to the curve for predicted growth of perch feeding on YOY perch only, but 17 of the 21 growth trajectories were above this curve. In any case, our modeling suggests that perch may accelerate in growth and become giants even if their cannibalism is restricted to perch younger than 1-yr-old.

The predicted diets of the two size cohorts of perch during the giant phase consisted almost totally of macroinvertebrates up to the day when YOY switched to the littoral habitat (Fig. 9: right). The largest size cohort did not feed on zooplankton at all. After YOY perch had shifted to the littoral habitat, both size cohorts of perch fed mainly on YOY perch and zooplankton was
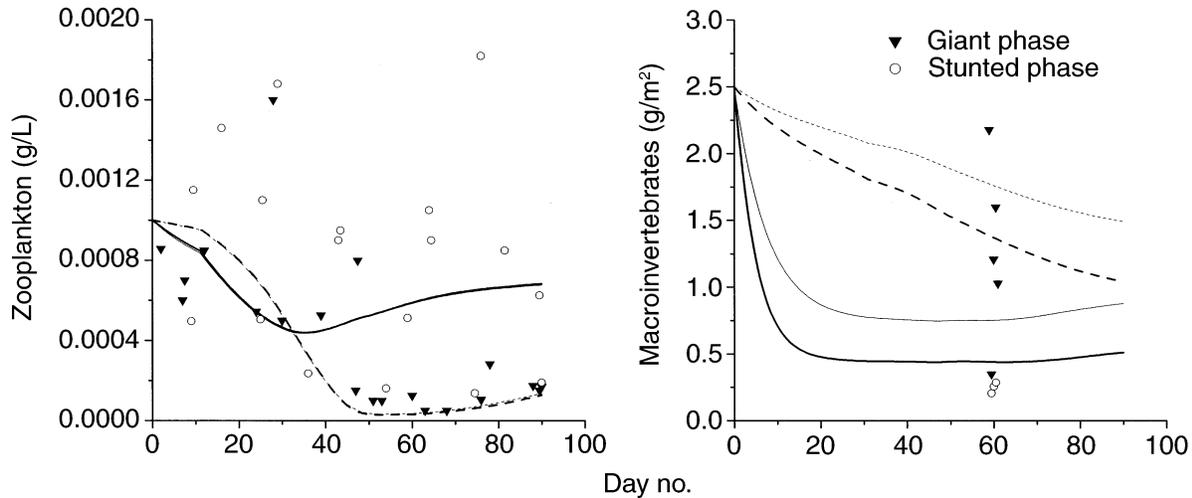
Fig. 10. Dynamics of zooplankton and macroinvertebrates during the stunted (solid lines) and giant (dashed lines) phases when young-of-the-year (YOY) perch are assumed not to feed on macroinvertebrates. Thick lines represent the situation when encounter efficiencies of perch ≥1 yr old are 1 for zooplankton, macroinvertebrates, and YOY perch; thin lines represent the situation when the encounter efficiency of perch ≥1 yr old on macroinvertebrates has been reduced to 0.5. Superimposed on model predictions are the observed zooplankton and macroinvertebrate biomasses in different years for the stunted (1992, 1993, 1999, 2000) and giant (1994–1997) phases.

totally excluded from their diets. For the giant phase, the predicted diets of both size cohorts before YOY perch moved to the shore were very close to the observed diets. There was also a high agreement between predicted and observed diets after the habitat shift of YOY perch with the exception of two data points (164 mm cohort: one observation in early August of 100% macroinvertebrates in the diet, 189 mm cohort: one observation in early August of equal amounts of YOY perch and macroinvertebrates in the diet) (Fig. 9: right).

Resource dynamics

For both phases, the predicted zooplankton biomass first decreased following the hatching of YOY perch. During the first part of the growth season, zooplankton biomass was actually lower during the stunted phase than during the giant phase (Fig. 10: left). In response to the high cannibalistic mortality of YOY perch in the stunted phase, zooplankton soon recovered to reach high levels during the second half of the growth season (Fig. 10: left). In contrast, in the giant phase the predicted zooplankton biomass was reduced to very low levels and never recovered, due to the lower YOY mortality during this phase. The fact that the predicted zooplankton resource levels were lower early on in the stunted phase than in the giant phase provides an explanation for the empirically observed lower growth rate of small YOY perch during this phase (Fig. 1, Fig. 10: left). A comparison of model predictions with observed patterns in zooplankton dynamics shows a high agreement between predictions and observations for the giant phase with respect to overall biomass and the drastic decrease in biomass over the growth season (Fig. 10: left). Similarly, the lack of this drastic de-

crease in zooplankton biomass during the stunted phase in model predictions was in correspondence with observations. Interestingly, observed zooplankton biomasses during the stunted phase were also quite variable, suggesting that factors other than perch predation were controlling zooplankton dynamics.

In the stunted phase the predicted dynamics of the macroinvertebrate resource was characterized by a strong decrease in the biomass of macroinvertebrates to <20% of its maximum density caused by consumption of perch ≥2 yr old (Fig. 10: right). In contrast, during the giant phase the macroinvertebrate biomass was predicted to be reduced to a much smaller extent as a result of the lower numbers of perch ≥2 yr old. Observed biomasses of predator sensitive macroinvertebrates in August in the giant phase were in a range similar to that predicted (Fig. 10: right). For the stunted phase, observed biomasses were lower than during the giant phase and also somewhat lower (average 0.25 g/m^2) than the predicted biomass (0.5 g/m^2) during this phase.

A reduction in macroinvertebrate encounter efficiency for perch ≥1 yr old to 0.5 only resulted in minor changes in predicted zooplankton dynamics for both phases, whereas the predicted macroinvertebrate biomass at the end of the growth season was higher with a reduced macroinvertebrate encounter efficiency (Fig. 10: right). This difference in response of resources to a changed encounter efficiency of large perch reflects the fact that macroinvertebrates are affected by consumption of larger perch, whereas the biomass of zooplankton is largely under the control of YOY perch.

Field data show that YOY perch to a certain extent include macroinvertebrates in their diet after they have
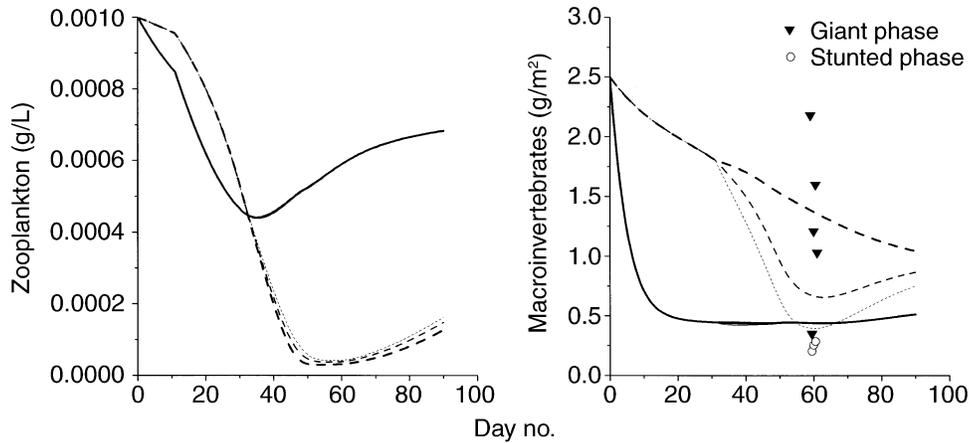
FIG. 11. Dynamics of zooplankton and macroinvertebrates during the stunted (solid lines) and giant (dashed lines) phases when young-of-the-year (YOY) perch feed on zooplankton only (thick lines), with an encounter efficiency on macroinvertebrates of 0.2 (medium thick lines) and with an encounter efficiency on macroinvertebrates of 0.5 (thin lines). Depending on macroinvertebrate encounter efficiency, YOY perch can start to feed on macroinvertebrates on day 31 after having moved to the littoral habitat. Superimposed on model predictions are the observed macroinvertebrate biomasses in different years for the stunted (1992, 1993, 1999, 2000) and giant (1994–1997) phases.

shifted to the shore habitat (Byström et al. 1998, Persson et al. 2000). Although predator-sensitive macroinvertebrates only contributed a small fraction of the YOY perch diet (Persson et al. 2000), we investigated how increasing the encounter efficiency of YOY perch on macroinvertebrates affected zooplankton dynamics. The effects of changing the YOY perch encounter efficiency on macroinvertebrates (from day 31) for the dynamics of zooplankton was only minor, and the small effect was a result of the handling (digestion) time on

the alternative prey macroinvertebrates (Fig. 11: left). During the stunted phase, the effect of increasing the macroinvertebrate encounter efficiency of YOY perch on macroinvertebrates was negligible and restricted to a time window at the middle of the growth season (Fig. 11: right). This small effect of YOY perch encounter efficiency on macroinvertebrates was due to the high mortality induced on YOY perch by cannibalism. In contrast, for the giant phase the impact of increasing the macroinvertebrate encounter efficiency of YOY perch on macroinvertebrates was substantial, leading to macroinvertebrate biomasses at the end of the season similar to those during the stunted phase (Fig. 11: right).

YOY perch mortality

The predicted mortality rate of YOY perch during the stunted phase was high, and few YOY individuals were predicted to be present at day 60 (Fig. 12). A change in assumptions about habitat uses of big and YOY perch to a situation where both YOY and ≥2-yr-old perch spend their whole time in the pelagic led to a small initial increase in YOY perch mortality, but at the middle of the season the number of surviving YOY perch was hardly distinguishable between these scenarios. Comparing the predicted mortality of YOY perch with the observed based on Bongo-trawl catches corrected for gear avoidance (Noble 1970) showed a good correspondence. The predicted mortality rate of YOY perch during the giant phase was considerably lower than that during the stunted phase especially up to day 31 (Fig. 12). The observed mortality of YOY during the giant phase was substantially higher than the predicted mortality (Fig. 12). The difference between predicted and observed mortality rate was restricted to the first 10 d after hatching. Empirical es-
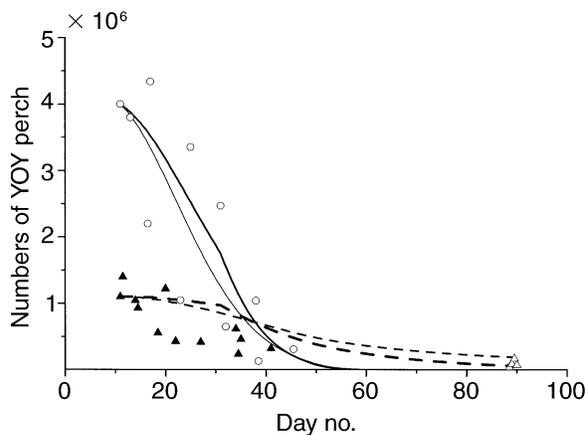

FIG. 12. Changes in the density of young-of-the-year (YOY) perch over the growth season during the stunted (solid lines) and giant (dashed lines) phases. Thick lines show predicted abundance of YOY perch for default values of habitat use of cannibals and victims. Thin lines show predicted abundance of YOY perch when both cannibals and victims spend their whole time in the pelagic habitat (observe that the total mortality of YOY perch for both habitat scenarios during the stunted phase is almost identical). Symbols are observed changes based on Bongo trawlings (○ = stunted phase, ▲ = giant phase) and mark–recapture (△ = giant phase).
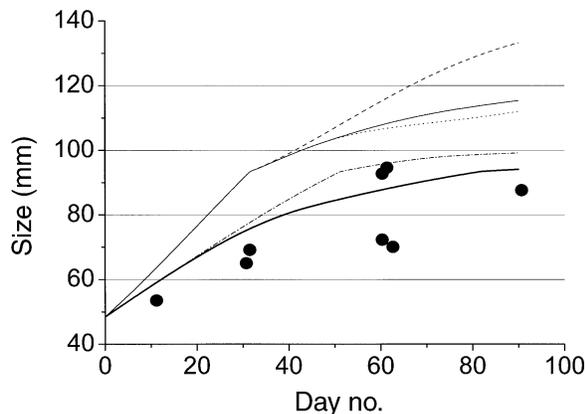
Fig. 13. Growth of 1-yr-old perch when young-of-the-year (YOY) perch are assumed to not feed at all (dashed line), feed on zooplankton only (search efficiency = 1.0; thin solid line), or feed on zooplankton and macroinvertebrates (search efficiencies = 1.0 and 0.5, respectively; dotted line). The figure also shows growth results when 1-yr-old perch can only feed on zooplankton to a limited extent (search efficiencies on zooplankton, macroinvertebrates, and YOY perch: 0.05, 1.0 and 1.0, respectively) (dashed-dotted line), and when 1-yr-old perch can only feed on zooplankton to a limited extent and do not cannibalize (search efficiencies on zooplankton, macroinvertebrates, and YOY perch: 0.05, 1.0, and 0.0, respectively) (thick solid line). Solid circles are the observed sizes of 1-yr-old perch (at day 60 a bimodal size distribution was present, and circles show the average of the upper and lower peaks).

timates of the number of YOY perch alive at the end of the growth season during the giant phase agreed closely with the predicted numbers. An assumption that all cannibalistic perch occupied the pelagic habitat during the whole growth season resulted in a higher mortality early on, but a higher number of YOY perch surviving at the end of the growth season (Fig. 12). Assumptions about habitat use during the giant phase thus affected YOY perch mortality, but the main difference in mortality of YOY perch between phases can be attributed to the difference in the number of cannibals ≥2 yr old present (Table 4, Fig. 12).

*Growth and diet of one-year-old perch
during the giant phase*

The comparison between model predictions and empirical data (Claessen et al. 2000 vs. Persson et al. 2000) pointed to a discrepancy in the extent to which competition from YOY perch affected the performance of 1-yr-old perch during the giant phase. To examine this issue, we simulated growth rates and diets of 1-yr-old perch during the giant phase. Predicted growth rates of 1-yr-old perch were estimated assuming that YOY perch did not feed at all, fed on zooplankton only, or fed on both zooplankton and macroinvertebrates (encounter efficiency 0.5). Assuming no consumption by YOY perch (i.e., no exploitative-competitive effect), the predicted size of 1-yr-old perch increased steadily over the whole growth season (Fig. 13). The predicted

growth of 1-yr-old perch when YOY perch were assumed to feed on zooplankton only was not affected by YOY perch up to day 30 (i.e., before YOY perch started to depress zooplankton) (Fig. 10: left, Fig. 13). Thereafter, the growth rate of 1-yr-old perch was lower than when YOY perch were assumed to have no effect on zooplankton, but growth was still positive during the rest of the growth season. Allowing YOY perch to also feed on macroinvertebrates (from day 31) caused only a small further growth reduction in 1-yr-old perch. A comparison of predicted and observed growth shows that the observed growth rate was considerably lower than the predicted (Fig. 13). In the data, a size bimodality developed in August, hence data points for the means of both modes are shown. The discrepancy in growth between model predictions and data developed early on in the season and may be related to a much higher proportion of zooplankton in the predicted diet of 1-yr-old perch compared to observed diets (Fig. 14: left). The predicted larger size of 1-yr-old perch also led to high levels of cannibalism of YOY perch by 1-yr-old perch over the entire period. This prediction contrasts with observations as well (Fig. 14 left). Empirical data also suggested a decline in the condition of 1-yr-old perch over time and a massive mortality of 1-yr-old perch at the end of the season (no 1-yr-old captured in late August) (Persson et al. 2000). Such a situation was not observed in the model, as 1-yr-old perch showed positive growth during the whole season.

One hypothesis to explain the discrepancy between model predictions and data with respect to growth trajectories and diets may be that predation risk from bigger perch restricted the habitat use of 1-yr-old perch to the very shore area where they had only limited access to the zooplankton resource and YOY perch. This hypothesis is supported by the fact that 1-yr-old perch were only captured at shore trap stations (Persson et al. 2000). To investigate this hypothesis, we studied the situation when 1-yr-old perch only encountered the zooplankton resource with a reduced efficiency. A reduction of the encounter efficiency on zooplankton to 0.05 resulted in a predicted growth rate and diet closer to that observed (Fig. 13, Fig. 14: middle). The predicted intensity of cannibalism was still higher (and macroinvertebrate consumption lower) than that observed, which is the main explanation for the somewhat higher predicted growth rate compared to the observed. Preventing 1-yr-old perch from cannibalizing on YOY perch resulted in a close correspondence between predictions and observations both with respect to growth and diet (Fig. 13, Fig. 14: right).

DISCUSSION

Empirical patterns

Our study provides qualitatively new empirical insights into the dynamics of the system studied. Earlier work (Persson et al. 2000) provided indirect but in-
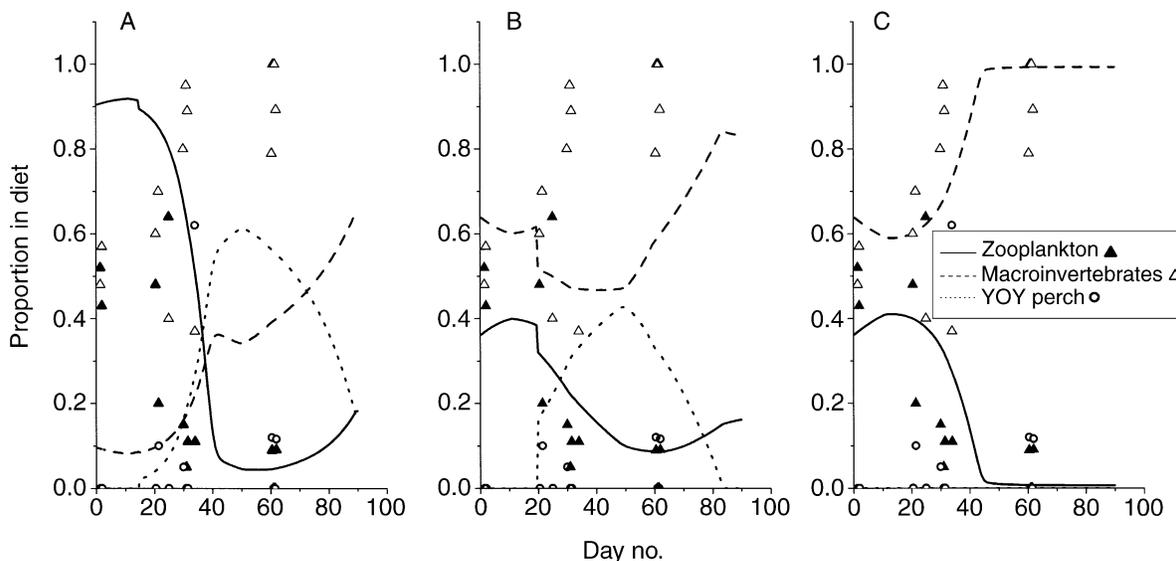
FIG. 14.　Diet of 1-yr-old perch during the giant phase. (A) The default situation; (B) the situation with restricted encounter efficiency on zooplankton; and (C) the situation with restricted encounter efficiency on zooplankton and no cannibalism (see Fig. 12). The lines represent predicted proportions of three food resources (prey) in the diet: zooplankton, macroinvertebrates, and young-of-the-year (YOY) perch. The symbols are observed diets; each symbol represents the mean of ≥10 individuals.

conclusive evidence that low population fecundity was not the cause of the low recruitment of young-of-the-year (YOY) perch during the stunted phase. Based on direct egg calculations for the period 1996–2001, we can now conclude that population fecundities are if anything higher in years with low recruitment of YOY perch to age 1 yr than in years with high recruitment of YOY perch to age 1 yr. These population fecundity data also underscore the discrepancy between the model predictions of Claessen et al. (2000) and data regarding the conditions necessary for the induction of giants: data show that the induction of giants coincides with low population fecundity, whereas the induction of giants in the model is a result of a high reproductive output. Although Claessen et al. (2002) show that giants may indeed be induced at low population fecundities, this only occurs for values of the cannibalistic voracity (β) far above that found for perch. The observed negative relationship between successful recruitment and population fecundity over the studied density region ultimately resulting in a hump-shaped Ricker stock-recruitment curve in itself also points to the fact that cannibalism is a major mechanism regulating perch recruitment (Ricker 1954). Second, the addition of growth data for YOY perch for the years 1999–2001 shows that growth in YOY perch is density dependent—a density dependence that our modeling suggests to be a result of competition for food. Finally and most importantly, the extended time series up to 2000 shows that the perch population has moved back to its previous stunted phase with high density of perch ≥2 yr old, slow individual growth rates of perch individuals, high mortality of YOY perch leading to low

recruitment to age 1 yr, cannibalism contributing only to a small extent to perch's diet and growth, and the absence of a strong depression in zooplankton biomass. A difference between the years 1991–1993 and 2000 was present in that more giant individuals were present in 2000 than in 1991–1993. The reason for this difference is not known, but may be due to the fact that the years 1991–1993 represented a later part of the stunted phase when giant individuals had died off because of lack of suitable prey items.

Conditions necessary for the developments of giants

The model predictions by Claessen et al. (2000, see also Claessen et al. 2002) showed that giant growth was a result of cannibals "surfing" on a slow-growing year class for several years. Empirical data are in conflict with this dynamical pattern as (1) diet data suggest that giant perch only cannibalize YOY perch and not older perch, and (2) the mean size of 1-yr-old perch did not differ between study years (Fig. 4) (Persson et al. 2000). Our modeling of within-season dynamics shows that perch can indeed accelerate and become giants without cannibalizing on perch older than YOY perch. Actually, our modeling suggests that perch may potentially accelerate in growth and become giants even if they do not include any other prey items than YOY perch. It should, however, be noted that (1) the observed growth rates in most cases were above those predicted from a diet of YOY perch only, and (2) the predicted growth rates are based on the assumption that perch can search for both YOY perch and macroinvertebrates simultaneously (i.e., encounter efficiencies of 1.0 for both prey). Taking both these aspects into

consideration suggests that a supplementation with macroinvertebrates is necessary to reach the observed sizes.

Our modeling of the stunted phase suggests that zooplankton is an important resource for perch up to a size of 30 g and that a combination of zooplankton and macroinvertebrates is necessary to reach observed sizes. It should be pointed out that the zooplankton size we used to simulate consumption and growth was a 0.5-mm cladoceran, which is the average size of zooplankton in the study lake (Wahlström et al. 2000), whereas Claessen et al. (2000) used a 1.0-mm cladoceran size, which will allow perch to reach a larger size feeding on zooplankton only. Still, macroinvertebrates may be important in reducing the coupling between large perch growth performance from the zooplankton dynamics as affected by YOY perch (see *Discussion: Does the perch population dynamics involve dwarf and giant cycles?*).

Resource dynamics

Our predictions (and observations) regarding the impact of perch on zooplankton dynamics show that the dynamics of this resource was affected by YOY perch (during the giant phase) but not by older perch. The small effect of larger perch (i.e., perch >150 mm) on zooplankton biomass can be related to their low attack efficiency on small zooplankton (Byström and Gàrcia Berthóu 1999, Wahlström et al. 2000). Larger perch do have an impact on the zooplankton community size structure reflected in the small average size of the zooplankton community (dominance of *Bosmina* and *Ceriodaphnia*) (Wahlström et al. 2000). However, the only perch cohort having an impact on the population *abundance* of the species dominating the zooplankton community is YOY perch. When these perch are absent during most of the growth season due to high cannibalism, the zooplankton resource remains close to its carrying capacity (see Claessen et al. [2000] for similar conclusions). Also our predictions regarding macroinvertebrate biomasses were largely in correspondence with observations. Our modeling suggests that the difference in macroinvertebrate biomass between phases (higher in the giant phase) is mainly explained by the difference in adult perch density between phases.

As described in *Materials and Methods*, above our treatment of macroinvertebrates was restricted to predator-sensitive macroinvertebrates. Diet analyses of perch show that they do consume other macroinvertebrates, particularly chironomid larvae (Persson et al. 1996), however, functional-response experiments show a very low (and prey-density-independent) attack rate on sediment-dwelling chironomids (B. Christensen and L. Persson, *unpublished data*). Furthermore, field data provide no evidence for a density-dependent relationship between perch density and macroinvertebrate biomass not sensitive to predators (Persson et al. 1999, 2000). Given these circumstances, it is likely that the

inclusion of macroinvertebrates other than predator-sensitive ones would have only added marginally to perch energy intake.

Mortality and habitat use of YOY perch

We predicted that YOY perch mortality for the giant phase should be lower than the estimated ones based on Bongo trawlings. It is well known that escape of fish larvae constitutes a major error in estimates of fish larvae abundance (Noble 1970, Wanzenböck et al. 1997). The correction we used is based on studies on the Miller sampler (Noble 1970, Rudstam et al. 2001) since estimates of size-dependent escapes are not available for Bongo trawls. The Miller sampler is a high-speed sampler (approximately double the speed of a Bongo trawl), suggesting that problems with size-dependent escape should be larger for Bongo trawls than for Miller samplers. We have several lines of evidence that the model predictions yielded more correct estimates of YOY perch abundance than the corrected Bongo-trawl estimates. First, observed growths and diets of perch and the biomass of zooplankton were correctly predicted, and this combination of correct predictions is not possible assuming that the Bongo trawlings gave correct estimates. Further more it is not possible to generate the observed growth and diet of giant perch if the estimates of YOY perch abundance based on corrected Bongo trawlings at day 31 were used, even if it is assumed that the perch totally eradicated the whole YOY perch cohort (which was not the case) (L. Persson, *simulation results not shown*). Second, independent estimates of the impact of different densities of YOY perch on zooplankton biomasses from enclosure experiments show that the densities of YOY perch predicted by the model yielded an impact on zooplankton as predicted and observed (Byström et al. 1998, Byström and Gàrcia-Berthóu 1999). Third, the independent estimates of YOY perch abundance at the end of the season were in agreement with model predictions. A size-dependent escape is also in agreement with the fact that the discrepancy between empirically estimated numbers and predicted numbers of YOY perch was larger for the giant phase when YOY perch grew faster. Our interpretation is therefore that our predicted mortality rates more closely match actual mortality rates than the mortality rates estimated from Bongo trawlings.

Our empirical data on habitat use of YOY perch and their cannibals show that the habitat use of cannibals and victims differed between the two phases. In years with high densities of cannibals, cannibals use the offshore benthic habitat to a larger extent than in years with low densities of cannibals (Persson et al. 2000). The time when YOY perch switch to the shore habitat (studied during the giant phase) also depended on the density of shore cannibals (Byström et al. 2003). This pattern led Persson et al. (2000) to suggest that habitat selection of cannibals and victims may have substantial

population dynamical consequences. In our modeling of YOY perch mortality we found that altering the assumptions about habitat use of cannibalistic and YOY perch within phases only had small effects on YOY perch mortality. Instead, the main difference in mortality rates of YOY perch between the two phases is explained by a difference in the number of cannibals. Persson et al. (2000) showed that the changes in cannibal numbers were associated with major changes in cannibal habitat use, hence the interaction between numbers and habitat use may nevertheless still be important to explain shifts in YOY perch survival between phases.

Interactions between YOY perch and 1-yr-old perch

The model predictions by Claessen et al. (2000) and the empirical results by Persson et al. (2000) differed in that the latter suggested a strong negative competitive impact of YOY perch on 1-yr-old perch to be present. Our within-season modeling supports the idea that YOY perch affect the growth of 1-yr-old perch negatively through competition. If encounter efficiency on zooplankton was not reduced, the severity of this competition was small and 1-yr-old perch were predicted to grow to a substantially larger size than observed early on in the growth season due to heavy zooplankton feeding. The larger size of 1-yr-old perch, in turn, led to the fact that YOY perch remained in the cannibalism window of 1-yr-old perch for the whole growth period (i.e., a substantial positive effect of YOY perch on 1-yr-old perch). Restricting 1-yr-old perch encounter efficiency with zooplankton and YOY perch reflecting a restricted habitat use resulted in a predicted growth and diet similar to those observed. The observed restricted habitat use of 1-yr-old perch can be related to predation risk from larger giant perch as 1-yr-old perch at the start of their growth season are susceptible to giant perch cannibalism (size ratio 50-mm perch/200-mm perch = 0.25, maximum ratio = 0.4) (Claessen et al. 2000).

Our results concerning 1-yr-old perch thus suggest that adaptive habitat use of 1-yr-old perch may have substantial effects on the long-term dynamics of this cannibalistic system. This conclusion results from the fact that the restricted habitat use of 1-yr-old perch may alter the interaction between YOY perch and 1-yr-old perch from being a mainly cannibal–victim interaction (positive effect on 1-yr-old perch) to a mainly inter-cohort competitive interaction (negative effect on 1-yr-old perch). It can be hypothesized that the die-off of 1-yr-old perch for a number of subsequent years during the giant phase is an essential element to keep the system in the giant phase characterized by repeated successful recruitment of YOY perch (see Fig. 3). In the absence of this die-off, the system would move back to the stunted phase once the first successfully recruiting perch cohort reached a size where they could ef-

ficiently deplete the YOY cohort (see sequence 1998–2000 in Fig. 3).

The importance of 1-yr-old perch habitat use for determining the interaction type points to the idea that adaptive habitat use may be of substantial importance for population dynamics. Experiments that have suggested significant effects of flexible behavior (including activity level) on population and community dynamics have generally been carried out at short-term (within-generation) and small spatial (enclosure, pond) scales (Turner and Mittelbach 1990, Werner and Anholt 1993, Persson and Eklöv 1996, Anholt and Werner 1998, Peacor and Werner 2001, Schmitz and Suttle 2001), and hence cannot address the long-term population dynamical consequences of behavior. Whether flexible adaptive behavior of perch is necessary to include or whether a fixed behavior of 1-yr-old perch is sufficient to explain the dynamics observed for the perch population also remains an issue for further analyses (see De Roos et al. [2002] for an analysis of a consumer-resource case with habitat and size-dependent habitat use).

Does the perch population dynamic involve dwarf and giant cycles?

Based on perch parameter values, Claessen et al. (2000) showed that the population dynamics of cannibals competing with their victim for a basic resource in one phase was characterized by high cannibalistic mortality on very young and small victims. This resulted in the fact that the shared resource was not strongly depressed by recruiting individuals as would have been the case in the absence of cannibalism (Persson et al. 1998). This effect represents an *indirect* positive effect of cannibalism (Polis 1988). Although cannibalism thus reduced inter-cohort competition through cannibal control of victims, the main part of the energy intake by cannibals was derived from the shared resource, and the maximum size of cannibals was small. In this phase of the cannibalistic dynamics, energy extraction is hence low and the effect of cannibalism is similar to that found in cannibalistic models that assume that cannibals do not gain energy from but only impose a mortality on victims (Diekmann et al. 1986, Hastings and Costantino 1987, Costantino et al. 1997, Van den Bosch and Gabriel 1997). The empirically observed dynamics of perch during the stunted phase in several respects resembles this dynamic as our modeling and empirical data confirm that cannibals impose a high mortality on YOY perch, and that the contribution of YOY perch to the diet and energy balance of cannibalistic perch is small in this phase. A discrepancy is that our modeling analysis shows that the addition of a second shared resource (macroinvertebrates) is essential to allow cannibalistic perch to have a positive, albeit small growth up to the maximum size that is empirically observed during the stunted phase.

While the observed dynamics during the stunted phase qualtitatively resemble that predicted by Claessen et al. (2000), the induction of giants is very different between observed data and the model. In the model by Claessen et al. (2000), recruiting individuals from a strong reproductive output depressed the resource to such a degree that most of the older individuals starved to death, leading to a low mortality of this recruiting cohort. There is no empirical evidence to support this mortality mechanism (Claessen et al. 2000, Persson et al. 2000). One explanation for the discrepancy between model predictions and data is that the macroinvertebrate resource, not included in the model, in addition to being critical for the performance of stunted cannibals also may prevent YOY perch from more or less eradicating cannibals. Even if YOY perch were assumed to affect macroinvertebrates, their impact on this resource was restricted to the time period after their shift to the shore habitat. At that time, YOY perch are highly susceptible to and energetically profitable for larger perch.

Data and predictions of the model of Claessen et al. (2000) also differ in three other major aspects. First, the shared resource (zooplankton) is expected to increase during the phase with dwarfs and giants in the model as dwarfs approach maturity. In contrast, data suggest a discrete difference in zooplankton dynamics between the two phases (Persson et al. 2003). Second, the repeated successful recruitment of YOY perch observed over a number of subsequent years (1995–1998) and the concomitant die-off of 1-yr-old perch every year in 1995–1997 is clearly in contradiction to model predictions. Third, although giants in the model fed extensively on the numerous cohort for several years, the low number of giants precluded a substantial dynamical impact (energy extraction but no control) (Claessen et al. 2000). In the data there was a 10-fold difference in number of cannibals between phases, but as a result of increased individual growth of the remaining individuals due to energy extraction from cannibalism on YOY perch, increased per capita fecundity partly compensated for the lower number of cannibals. As a result, successful recruitments of YOY perch were observed for a number of years (1995–1998). These strong YOY cohorts, in turn, exerted a substantial competitive impact on 1-yr-old perch cohorts, so energy extraction from cannibalism giants in the lake had a significant dynamical impact. Although most cannibal models ignore the energy gain of cannibalism (and hence the effects of per capita fecundity on energy intake) (Diekmann et al. 1986, Hastings and Costantino 1987, Dennis et al. 1997, Van den Bosch and Gabriel 1997), our results strongly suggest that ignoring energy extraction may lead to important elements of the interactions between cannibals and victims being neglected (Persson et al. 2003).

The fact that both zooplankton dynamics and perch recruitment differed in a discrete way between phases raises the question whether the mechanisms behind the temporal appearance of giants may be better explained by alternative attractors than by a dynamics involving a combination of dwarf and giant cycles and cannibal-driven dynamics (see Fig. 3). Recent size-structured modeling of cannibalistic dynamics using a continuous model with energy gain indeed shows that alternative equilibria may exist for intermediate values of the lower size limit (δ) of the cannibalistic window (Claessen and De Roos 2003). These two equilibria involve a stunted and a giant state, and, in accordance with observations on perch, the resource level of the shared resource (zooplankton) is lower in the giant state. The population numbers of cannibals are, however, higher in the giant state than in the stunted state in this model. The extent to which these results carry over to the perch system—which is better described by a combination of discrete (reproduction) and continuous (foraging, metabolism, mortality, resource dynamics) processes than by a purely continuous system—is also unclear (Claessen 2002). Fisher (1987) showed in a discrete model with size-dependent cannibalism and competition that bistability might be present, with the stunted state having a higher population density. However, like most other cannibal models his model lacked energy extraction. This contrasts to our study where energy extraction is shown to be dynamically important by setting up the competitive interaction between YOY and 1-yr-old perch through the recurrent production of YOY perch cohorts by giants. Our within-season modeling and empirical data suggest that (1) the second resource (macroinvertebrates) and (2) the restricted habitat use of 1-yr-old perch may be critical for the extended existence of the giant phase over several years. Indeed, an extended multigenerational analysis suggests that the inclusion of both these factors is essential to generate the dynamics observed. Furthermore, our modeling analysis suggests that a dynamics involving both stunted and giant phases does not necessarily involve alternative attractors (Persson et al. 2003).

Physiologically structured models as a framework for a quantitative ecology including a closer interaction between theory and data

A classical dilemma running through the history of ecology is the contrast between simple strategic models that offer generality but may be hard to test against empirical data from field systems especially in quantitative terms, and complex tactical models that have a high testing power but are less prone to offer generality (Levins 1966, DeAngelis and Waterhouse 1987, Murdoch et al. 1992, Murdoch and Nisbet 1996). Murdoch et al. (1992) advocated a research strategy that involved a logical linking of highly testable more complex models and more simple general models, where the essential mechanisms of the former models are preserved in the latter models, but details are removed

through a strip-off process. Physiologically structured population models (PSPMs)—which we have used in our study where distributions or cohorts rather than individuals are followed–represent models of intermediate complexity in the span from purely individual-based models to unstructured models. Despite their intermediate complexity, distribution models have proven able to successfully address general ecological issues (De Roos et al. 1990, Persson et al. 1998, Claessen et al. 2000, 2002, De Roos and Persson 2001). Following Murdoch et al. (1992), it has also been shown for some configurations that the fully structured models may be reduced to simpler stage-based models that preserve the essential mechanisms; whereas the fully structured models lend themselves to more quantitative predictions, the stage-based models allow a more complete analysis of stability properties (consumer–resource interactions: Persson et al. (1998) vs. De Roos and Persson (2003), structured tritrophic food chains: De Roos and Persson (2002) vs. De Roos et al. 2003). However, in the case of cannibalism, the strong size dependence of the cannibal–victim interactions and the feed-back effect of energy extraction on individual growth (size) and per capita fecundity makes a reduction of model complexity to stage-structured versions much more problematic (De Roos and Persson 2001). Individual-level functional formula may be simplified and the discrete reproduction assumption used in our paper relaxed, allowing, for example, the tracking of unstable equilibria (Claessen and De Roos 2003). However, in that case (and insofar as is known today) the reduction in model complexity has to take place within the domain of PSPMs.

A major advantage of the PSPM approach as illustrated by our study is that within-season modeling may fill an important role in delineating the essential mechanisms driving the dynamics, where population-level formulations would have been much less informative (Fig. 7). Through the study we have used a number of individual-level (individual growth, diet) and population-level (mortality, resource levels) analyses with the aim to uncover the basic mechanisms underlying the dynamics of the cannibalistic perch population. Conceptually, the advantage of the PSPM approach to test predictions and to develop a closer relationship between empirical and theoretical research can be related to its two-state-levels nature. In PSPMs, model assumptions adhere to the individual level, and no further assumptions are introduced at the population level—in contrast to contemporary population-level formulations (Metz et al. 1988, De Roos 1997, De Roos and Persson 2001). In our model, the individual-level assumptions are due to specifying functions for size-dependent attack rates, metabolic rates, energy channeling, etc. The derivations of these functions, including parameter estimations, are based on experiments totally independent of the cannibalistic system under study, leading to a higher independence between model assumptions and model testing of population-level dynamics than in, for example, time-series approaches where (population-level) data from the system under study are used to fit model parameters (cf. Turchin et al. 2000). Furthermore, the quantitative predictions of individual-level dynamics such as individual growth and diet has a strong independence from individual-level formulations (assumptions) since the population feedback on individual performance (i.e., the appearance of gigantic growth) cannot be predicted a priori from individual-level formulations (assumptions).

The utility of the approach that we have used also lies in the fact that individual performances (growth, diet) as a result of the population feedback are readily measurable empirically in a quantitative way. It is important to realize that the quantitative contrast between predictions and empirical observations regarding the impact of the second shared resource (macroinvertebrates) and 1-yr-old perch habitat use was essential to be able to show that a dynamics including coupled dwarf and giant cycles is highly unlikely for the system we studied. More importantly, our within-season analysis allowed us to suggest the mechanisms that were necessary to incorporate in order to yield a more correct description of the long-term dynamics of the cannibalistic system (e.g., Persson et al. 2003). This restructuring of the model represented more than a ''fine tuning'' of previous models. It meant a qualitative change in modeling perspective regarding which interactions were driving the system—for example, a shift from a focus on inter-cohort competition between YOY perch and perch ≥ 2 yr old to a focus on inter-cohort competition between YOY perch and 1-yr-old perch.

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