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## ONTOGENETIC NICHE SHIFTS AND FLEXIBLE BEHAVIOR IN SIZE-STRUCTURED POPULATIONS

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**Abstract.** Flexible behavior has been shown to have substantial effects on population dynamics in unstructured models. We investigate the influence of flexible behavior on the dynamics of a size-structured population using a physiologically structured modeling approach. Individuals of the size-structured population have a choice between living in a risky but profitable habitat and living in a safer but less profitable habitat. Each of the two habitats houses its own resource population on which the individuals feed. Two types of flexible behavior are considered: *discrete habitat shifts*, in which individuals instantaneously and nonreversibly shift from living in the safe habitat to the more risky/profitable habitat, and *continuous habitat choice*, in which individuals can continuously adapt their habitat choice to current resource/mortality conditions. We study the dynamics of the model as a function of the mortality risk in the risky/profitable habitat. The model formulation and parameterization are derived using data on Eurasian perch (*Perca fluviatilis*) and describe reproduction as a yearly event at the beginning of summer, while all other processes are continuous in time. The presence of two habitats per se, with unique resources that are shared among all consumers, does not change model dynamics, when compared to the one-resource situation. Flexible behavior increases the range of mortality levels for which the population can persist, because it allows individuals to hide from high mortality in the risky habitat. In contrast, flexible behavior does not significantly change the dynamics for mortality risks, where the consumer population also persists without it. Discrete habitat shifts result in model dynamics that are largely similar to the dynamics observed with continuous habitat choice, as long as individuals strongly respond to small differences in habitat profitability. In these cases, consumers spend an increasing part of their first year of life in the safe habitat, when mortality risks in the risky habitat increase. Ultimately, consumers are driven out into the risky habitat by intercohort competition from their successive year class. Therefore, major mortality and rapid growth occur among 1-yr-old individuals. Younger individuals exhibit retarded growth due to intracohort competition in the safe habitat, which may also induce large-amplitude fluctuations when the mortality risk is high in the risky habitat. With continuous habitat choice and a low responsiveness to habitat profitability, consumer persistence is increased as well, but large-amplitude fluctuations are absent. In this case, consumers always spend a significant part of their first year of life in the risky habitat, even at high mortality risks. Major mortality and rapid growth occur among individuals younger than 1 yr, while the shift to the risky habitat is mainly induced by intracohort competition for resources. The high mortality and rapid growth at younger ages lead to an increase in maximum size and fecundity of surviving individuals, as well as to larger total population biomasses. We argue that the pattern of individual habitat use is mainly determined by population feedback on resource levels.

**Key words:** cohort competition; flexible behavior; habitat use; ontogenetic niche shifts; persistence; physiologically structured population models; population feedback; size-structured populations; stability.

### INTRODUCTION

Flexible behavior in animals has been suggested to have substantial effects on population dynamics (Werner 1992, Abrams 1996, Abrams et al. 1996). In one predator–one prey systems, flexible refuge use by prey has been shown to have a stabilizing effect

on the dynamics (Ives and Dobson 1987, Mangel and Roitberg 1992, Krivan 1998). In one predator–several prey systems, optimal foraging by the predator may increase the potential for prey coexistence and also dampen oscillatory dynamics (Gleeson and Wilson 1986, Fryxell and Lundberg 1993, 1994, Krivan 1996, 1997, Van Baalen et al. 2001). Optimally foraging predators may, however, also cause the loss of stable fixed point dynamics and induce cycles. Hence, the overall effects of flexible behavior may

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be increased population persistence but decreased stability (Krivan 1996).

Theoretical studies examining the implications of flexible behavior for population dynamics have used traditional, nonstructured predator-prey models to link individual-level processes such as foraging rate to population processes (Ives and Dobson 1987, Mangel and Roitberg 1992, Werner 1992, Fryxell and Lundberg 1993, Abrams 1996, Abrams et al. 1996, Krivan 1996, 1997). In contrast, many experimental studies of flexible predator and prey behavior involve species whose populations are typically size/stage-structured, particularly fish (Werner and Hall 1977, Mittelbach 1981, Werner et al. 1983a, b, Persson 1985, Gilliam and Fraser 1987, Godin and Sproul 1988, Gilliam 1990, Persson and Greenberg 1990, Godin and Clark 1997), but also other taxa such as crustaceans and amphibians (Stein and Magnusson 1976, Jaeger and Barnard 1981, Jaeger et al. 1982, Werner and Anholt 1993). This contrast has become even more striking because of the development of a modeling framework, known as physiologically structured population models, that (1) explicitly handles the presence of size/stage-structure, and (2) in a formal and straightforward way links individual and population processes. Physiologically structured population models are based on a two-level state concept: 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 that represents the population state as a frequency distribution over the space of possible *i*-states (Metz and Diekmann 1986, de Roos 1988, 1997, Metz et al. 1988, Caswell and John 1992, DeAngelis and Gross 1992). Processes at the individual level include individual foraging, energy partitioning between growth and reproduction and mortality, all of which relate to basic state variables in animal decision making. Due to their explicit link between individual performance and population dynamics, physiologically structured models provide a natural modeling framework to study flexible behavior.

In the absence of flexible behavior, size-structured one consumer-one resource models have been shown to generate highly fluctuating population dynamics, including single-generation cycles (Persson et al. 1998). These cycles mainly result from intercohort competition between consumers of different sizes where smaller individuals are superior competitors to larger conspecifics. A question that naturally arises from the observed fluctuating dynamics is whether flexible behavior may affect the outcome of the intercohort competition and facilitate the coexistence of different size-cohorts. Such an influence of flexible behavior could thus potentially dampen oscillatory fluctuations, as found in several studies using nonstructured predator-prey models (Gleeson and Wilson 1986, Fryxell and Lundberg 1993, 1994, Krivan 1996, 1997).

To study the consequences of flexible individual be-

havior for the stability and persistence of size-structured consumer-resource systems, we analyzed an extended version of a consumer-resource model studied by Persson et al. (1998). This model was adapted to account for two resource populations, each living in its own habitat. Movements by individual consumers between the habitats were based on a decision rule taking both growth and mortality risk into account. We investigated two different scenarios for shifts between habitats. First, we considered the case when consumers shift habitat (resource) instantaneously and only once during their lifetime. Second, we considered the case when consumers continuously adapt the fraction of time they spend in each of the two habitats. The first scenario is reminiscent of a life history in which the individual goes through an ontogenetic niche shift during juvenile development. Gilliam (1982; see also Werner and Gilliam 1984, Ludwig and Rowe 1990, Houston and McNamara 1999) has determined the optimal timing for organisms to make such an ontogenetic niche shift, when individual growth and mortality are size dependent and consumer and resource populations are not changing. Here, we analyze the ontogenetic niche shift in a population dynamic context, taking into account the fact that consumer shifting itself has a feedback on resource levels in both habitats. The second scenario is reminiscent of optimal foraging behavior, as investigated by Gleeson and Wilson (1986), Fryxell and Lundberg (1993, 1994), and Krivan (1996, 1997). An important difference between the two cases is that in the second scenario the consumers can adjust their habitat use to changes in densities of the two resources caused by that same habitat shift. Thus, in this case there are population feedbacks of resource dynamics on individual habitat use. The dynamics with these scenarios of habitat use were compared with the dynamics when all consumers used only a single habitat or used both habitats in proportion to their volume.

#### MODEL FORMULATION

Physiologically structured models are based on a state concept at each of two levels of organization: an *i*-state, which represents the state of the individual (see Table 1) and a *p*-state, which is the frequency distribution over the space of possible *i*-states (Metz and Diekmann 1986, Metz et al. 1988, Caswell and John 1992, DeAngelis and Gross 1992). A mathematical description of the behavior of a single individual (e.g., its feeding, growth, development, reproduction, and mortality) as a function of its physiological characteristics and the current environmental conditions (e.g., resource densities) constitutes the core element of any structured-population model. The basic formulation of the model studied here, describing a size-structured consumer population and a nonstructured resource, is given by Persson et al. (1998, see also Claessen et al. 2000, de Roos and Persson 2001). These papers analyze the main dynamical properties of the model. We extend

TABLE 1. State variables of the standard, consumer-resource model with flexible behavior.

Symbol	Units	Interpretation
$x, x_i$	g	irreversible mass (of an individual in the $i$ th cohort)
$y, y_i$	g	reversible mass (of an individual in the $i$ th cohort)
$N_i$	...	total number of individuals in the $i$ th cohort
$z_l$	g/m <sup>2</sup>	biomass density of littoral resource
$z_p$	g/m <sup>3</sup>	biomass density of pelagic resource

the model by introducing a second (unstructured) resource population. The consumer population is considered to live in a subdivided habitat, where in each of the two habitat parts it feeds on a unique resource population. The model is parameterized for a population of Eurasian perch (*Perca fluviatilis*) as the size-structured consumer in a lake with a distinct open-water (pelagic) and vegetated (littoral) habitat. We assume that the total lake volume equals  $10^6$  m<sup>3</sup>, of which 10% is taken up by the littoral habitat. The total bottom surface area of the littoral habitat is set to  $5.0 \times 10^4$  m<sup>2</sup>, implying an average water depth in the littoral habitat of 2 m. In the pelagic habitat, zooplankton (*Daphnia* sp.) is considered the main resource, while macroinvertebrates (*Sialis* sp.) constitute the main resource in the littoral habitat.

#### The individual level

Consumers are characterized by two physiological parameters, irreversible and reversible mass, and by the fraction of time spent in the pelagic habitat. In the irreversible mass,  $x$ , compounds like bones and organs that cannot be starved away by the consumer are included, whereas reversible mass,  $y$ , includes energy reserves such as fat, muscle tissue, and also gonads for mature individuals. Reversible mass may be used to cover basic metabolism during starvation. Total body mass of an individual consumer equals the sum of reversible and irreversible mass,  $(x + y)$ . The standardized body mass  $m(x)$  of a consumer is defined as

$$m(x) = (1 + q_j)x \quad (1)$$

in which  $q_j$  represents a characteristic ratio between reversible and irreversible mass for nonstarving individuals, discounting energy reserves for reproduction (e.g., juveniles or adults right after spawning). The notion of standardized body mass is introduced, because functional response experiments with size-structured consumers have shown a close relationship between capture rate and body length independent of body condition (Mittelbach 1981, Persson 1987). To estimate attack rate and handling time parameters from such experiments, we identify the measured individual mass in the experiments with the standardized body mass  $m(x)$ .

Relations describing the foraging rate, metabolism, energy partitioning between growth and reproductive tissue, and starvation (including starvation mortality) as a function of irreversible and reversible mass,  $x$  and

$y$ , respectively, were developed in Persson et al. (1998) and are summarized in Table 2. In contrast to the consumer-resource model by Persson et al. (1998), we treat the resource populations in terms of biomass rather than number of individuals, which affects the formulations of resource growth rate, consumer attack rates, and consumer handling times. Below we briefly describe the part of the model that relates to consumer feeding and energy channeling.

The resource-specific attack rates [ $a_l(x)$  and  $a_p(x)$  for the littoral and pelagic resource, respectively] of an individual consumer are functions of its standardized body mass  $m(x)$  only. Hence, we assume that a consumer's condition, i.e., its reversible mass  $y$ , does not influence its foraging rate (see Persson et al. 1998 for a justification of this assumption). The attack rate on the pelagic resource is a hump shaped function of standardized body mass (see Fig. 1 and Table 2), reaching a maximum value determined by the parameter  $A_{\max}$  at a body mass  $m_{\text{opt}}$ . The attack rate on the littoral resource is an allometric function of standardized body mass  $m(x)$ , following data on the feeding of perch on *Sialis* (Persson and Greenberg 1990). We assume that individuals living in the littoral part of the lake feed entirely on bottom-dwelling macroinvertebrates. Therefore, the attack rate on littoral resource is expressed as the amount of bottom surface area searched per day (cf. the volume searched per day for the pelagic attack rate). Fig. 1 shows the pelagic and littoral attack rate as a function of standardized body mass.

Prey handling time is formulated in terms of digestion time per unit ingested biomass, and hence is identical for both pelagic and littoral resources. The handling time is assumed to reflect digestive constraints, related to the gut capacity of an individual with a given size (Claessen et al. 2000). It is described as an allometric function of standardized body mass  $m(x)$ .

The foraging rate of individual consumers on the littoral and pelagic resource is assumed to follow a Holling type II functional response, incorporating the resource-specific attack rate, handling time, and densities of the littoral ( $z_l$ ) or the pelagic ( $z_p$ ) resource, respectively (see Table 2 and Persson et al. 1998). The total individual foraging rate equals the sum of these littoral and pelagic foraging rates, weighted by a factor  $(1 - F)$  and  $F$ , respectively, to account for the amount of time that consumers spend in either of the two habitats. Ingested food is assumed to be converted to energy assimilate with a constant conversion efficiency.

TABLE 2. Functional relationships for the model of individual energy acquisition and use.

Function	Equation
<b>Habitat-independent functions</b>	
Standardized mass	$m(x) = (1 + q_j)x$
Handling time	$H(x) = \xi_1 m(x)^{\xi_2}$
Maintenance requirements	$E_m(x, y) = \rho_1(x + y)^{\rho_2}$
Starvation mortality	$d_s(x, y) = \begin{cases} s(q_s x/y - 1) & \text{if } y < q_s x \\ 0 & \text{otherwise} \end{cases}$
<b>Pelagic feeding and mortality</b>	
Attack rate on pelagic resource	$a_p(x) = A_{\max} \left[ \frac{m(x)}{m_{\text{opt}}} \exp \left( 1 - \frac{m(x)}{m_{\text{opt}}} \right) \right]^\alpha$
Intake rate of pelagic resource	$I_p(z_p, x) = \frac{a_p(x)z_p}{1 + H(x)a_p(x)z_p}$
Mortality in pelagic habitat	$d_p(x, y) = \mu_b + \mu_p \exp \left( -\frac{x}{x_\mu} \right) + d_s(x, y)$
Profitability of pelagic habitat	$Q_p(z_p, x, y) = \frac{k_e I_p(z_p, x) - E_m(x, y)}{d_p(x, y)}$
<b>Littoral feeding and mortality</b>	
Attack rate on littoral resource	$a_l(x) = v_1 m(x)^{\nu_2}$
Intake rate of littoral resource	$I_l(z_l, x) = \frac{a_l(x)z_l}{1 + H(x)a_l(x)z_l}$
Mortality in littoral habitat	$d_l(x, y) = \mu_b + d_s(x, y)$
Profitability of littoral habitat	$Q_l(z_l, x, y) = \frac{k_e I_l(z_l, x) - E_m(x, y)}{d_l(x, y)}$
<b>Habitat choice, total intake, total mortality</b>	
Fraction of time in pelagic habitat	$F(z_p, z_l, x, y) = \frac{V_p}{V_p + V_l \exp \{ -\sigma [Q_p(z_p, x, y) - Q_l(z_l, x, y)] \}}$
Total intake rate	$I(z_p, z_l, x, y) = F(z_p, z_l, x, y)I_p(z_p, x) + [1 - F(z_p, z_l, x, y)]I_l(z_l, x)$
Total mortality	$d(z_p, z_l, x, y) = F(z_p, z_l, x, y)d_p(x, y) + [1 - F(z_p, z_l, x, y)]d_l(x, y)$
<b>Net production, allocation, and reproduction</b>	
Net energy production	$E_g(z_p, z_l, x, y) = k_e I(z_p, z_l, x, y) - E_m(x, y)$
Fraction of net production used for growth in irreversible mass	$\kappa(x, y) = \begin{cases} \frac{1}{(1 + q_j)q_j} \frac{y}{x} & \text{if } x \leq x_f \text{ and } E_g > 0 \\ \frac{1}{(1 + q_a)q_a} \frac{y}{x} & \text{if } x > x_f \text{ and } E_g > 0 \\ 0 & \text{otherwise} \end{cases}$
Fecundity	$f(x, y) = \begin{cases} \frac{k_f(y - q_j x)}{m_b} & \text{if } x > x_f \text{ and } y > q_j x \\ 0 & \text{otherwise} \end{cases}$

Note: See *Methods* and *Results*, Persson et al. (1998), and Claessen et al. (2000) for discussion.

An individual's current energy intake is first used to cover its metabolic requirements, which follow an allometric function of total consumer body mass ( $x + y$ ). The remaining part of the ingested energy (the net energy intake or net production) is allocated to reversible and irreversible mass such that a constant ratio ( $y/x$ ) between the two is targeted for. This ratio for juveniles ( $q_j$ ) differs from that for adults ( $q_a$ ) on the grounds that reversible mass in mature individuals also includes gonads ( $q_a > q_j$ ) (Tables 2 and 3; Persson et

al. 1998). When energy intake does not suffice to cover metabolic requirements, growth in irreversible mass  $x$  stops and reversible mass  $y$  is used to cover the deficit. When net energy intake becomes positive again, energy is preferentially allocated to reversible mass in order to restore the target ratio  $y/x$ .

We have assumed that all consumers experience the same, constant background mortality in both the littoral and the pelagic habitat, which is determined by the parameter  $\mu_b$  (Tables 2 and 3). The littoral habitat is

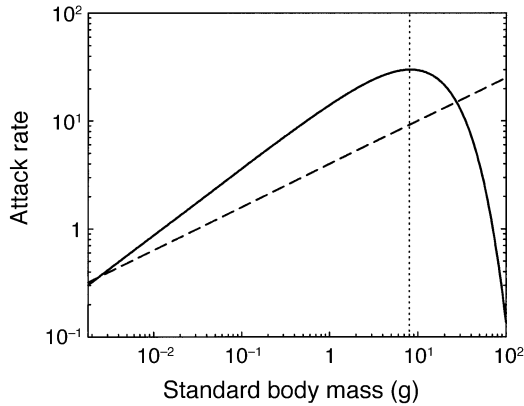


FIG. 1. Attack rate of an individual consumer on the pelagic (solid line) and littoral (dashed line) resource, as a function of its standard body mass. Pelagic and littoral attack rate are expressed in terms of the volume (in cubic meters) and area (in square meters), respectively, searched per day. The vertical dotted line represents the standard body mass at maturation.

assumed to provide a refuge from predation, especially for small fish, whereas the pelagic habitat is more risky. Therefore, in the pelagic habitat consumers experience an *additional*, size-dependent mortality rate equal to

$$\mu_p \exp\left(-\frac{x}{x_\mu}\right) \quad (2)$$

where  $x_\mu$  determines the size-scaling of this mortality

rate. We study the dynamics of the model as a function of the scaling constant  $\mu_p$ . Increasing values for  $\mu_p$  make the pelagic a more risky habitat. However, due to its large size and hence high total productivity, the pelagic is potentially a more profitable habitat. Individuals also experience starvation mortality whenever their reversible/irreversible mass ratio  $y/x$  drops below the starvation mortality limit  $q_s$  (Tables 2 and 3). The starvation mortality is modeled in such a way that death occurs with certainty when an individual's reversible mass is depleted entirely.

Pulses of reproduction occur as discrete events in time, since it is assumed that individuals only spawn at the beginning of the growing season (summer). When they spawn, adults allocate all reversible mass that they accumulated in excess of their standardized body mass  $m(x) = (1 + q_i)x$  to the production of eggs with a constant conversion efficiency. Following a successful spawning event, an adult thus has the same reversible/irreversible mass ratio  $y/x$  as a nonstarving juvenile; after that, the buildup of gonadic mass to be released at the next reproduction event starts anew. Maturation of juvenile into adult consumers occurs on reaching a fixed threshold of irreversible mass  $x_f$ .

*Modeling flexible behavior*

To incorporate flexible behavior into the structured population model, we formulate below a Markov model for the switching between habitats by a single individ-

TABLE 3. Model parameters for Eurasian perch (*Perca fluviatilis*) feeding on pelagic zooplankton (*Daphnia* sp.) and littoral macroinvertebrates (*Sialis* sp.).

Symbol	Value	Units	Interpretation
$q_j$	0.74	...	maximum juvenile condition $y/x$
$q_a$	1.37	...	maximum adult condition $y/x$
$\alpha$	0.62	...	allometric exponent in pelagic attack rate
$A_{max}$	30.0	$m^3/d$	maximum pelagic attack rate
$m_{opt}$	8.2	g	body mass with maximum pelagic attack rate
$v_1$	4.0	$m^2 \cdot d^{-1} \cdot g^{-v_2}$	allometric constant in littoral attack rate
$v_2$	0.40	...	allometric exponent in littoral attack rate
$\xi_1$	5.0	$d/g^{(1+\xi_2)}$	allometric constant in handling time function
$\xi_2$	-0.8	...	allometric exponent in handling time function
$\rho_1$	0.033	$g^{(1-\rho_2)}/d$	allometric constant in maintenance rate function
$\rho_2$	0.77	...	allometric exponent in maintenance rate function
$k_c$	0.61	...	ingestion-assimilation conversion efficiency
$m_b$	0.0018	g	total mass of an egg (newborn)
$x_f$	4.6	g	irreversible mass at maturation
$k_f$	0.5	...	gonad-offspring conversion efficiency
$q_s$	0.2	...	condition threshold $y/x$ for starvation mortality
$s$	0.2	$d^{-1}$	proportionality constant of starvation mortality rate
$\mu_b$	0.01	$d^{-1}$	constant, background mortality rate in littoral and pelagic habitat
$\mu_p$	varied	$d^{-1}$	scaling constant in additional, size-dependent mortality rate in pelagic habitat
$x_\mu$	2.0	g	characteristic size in additional, size-dependent mortality rate in pelagic habitat
$\sigma$	varied	$g^{-1}$	proportionality constant in habitat switching rate
$K_p$	3.0	$g/m^3$	resource carrying capacity in pelagic habitat
$K_l$	3.0	$g/m^2$	resource carrying capacity in littoral habitat
$r_p$	0.1	$d^{-1}$	resource regrowth rate in pelagic habitat
$r_l$	0.1	$d^{-1}$	resource regrowth rate in littoral habitat
$V_p$	$9.0 \times 10^5$	$m^3$	total volume of pelagic habitat
$V_l$	$1.0 \times 10^5$	$m^3$	total volume of littoral habitat
$A_l$	$5.0 \times 10^4$	$m^2$	total bottom surface area of littoral habitat
$Y$	90	d	duration of growing season

ual, assuming that the state of both habitats is not changing. Subsequently, we assume that this switching behavior takes place at such a rapid time scale that the distribution of individuals over both habitats is at any time in pseudo-steady-state with the current habitat conditions. This yields an expression for the fraction of time that an individual consumer of a given size spends in the pelagic zone, given the current densities of pelagic and littoral resource.

Gilliam (1982, see also Werner and Gilliam 1984) developed an individual-level theory for the timing of habitat shifts during ontogeny based on the minimization of the ratio between mortality and growth rate (the “ $\mu/g$ -rule”). We adopt the inverse of this ratio as a measure of habitat profitability to prevent problems that occur when growth rates reduce to 0. Hence, the profitabilities  $Q_l$  and  $Q_p$  of the littoral and pelagic habitat are defined as:

$$Q_l(z_l, x, y) = \frac{k_e I_l(z_l, x) - E_m(x, y)}{d_l(x, y)} \quad (3)$$

$$Q_p(z_p, x, y) = \frac{k_e I_p(z_p, x) - E_m(x, y)}{d_p(x, y)} \quad (4)$$

respectively, where  $k_e I_l(z_l, x) - E_m(x, y)$  and  $k_e I_p(z_p, x) - E_m(x, y)$  are the net energy production (assimilation minus maintenance) rates in the littoral and pelagic habitat, respectively (see Table 2);  $k_e$  is the conversion efficiency from food intake to energy assimilation rate;  $d_l(x, y)$  and  $d_p(x, y)$  are the total death rates in the two habitats. We assume that an individual consumer leaves the littoral and pelagic habitat at a rate that is proportional to

$$\exp[-\sigma Q_l(z_l, x, y)]$$

$$\exp[-\sigma Q_p(z_p, x, y)]$$

respectively. In addition, we will assume that the rate at which an individual leaves a habitat is inversely proportional to the volume of that habitat.

If  $F$  denotes the fraction of time that an individual consumer spends in the pelagic habitat, the dynamics of  $F$  on a short time scale can be described by

$$\frac{dF}{dt} = -\frac{\exp[-\sigma Q_p(z_p, x, y)]}{V_p} F + \frac{\exp[-\sigma Q_l(z_l, x, y)]}{V_l} (1 - F). \quad (5)$$

In this equation  $V_p$  and  $V_l$  refer to the volume of the pelagic and the littoral zone of the lake, respectively. Assuming that at any time the individual-level switching is in pseudo-steady-state with the current habitat conditions (i.e.,  $dF/dt \approx 0$ ) yields the following expression for  $F$ :

$$F(z_p, z_l, x, y) = \frac{V_p}{V_p + V_l \exp\{-\sigma [Q_p(z_p, x, y) - Q_l(z_l, x, y)]\}}. \quad (6)$$

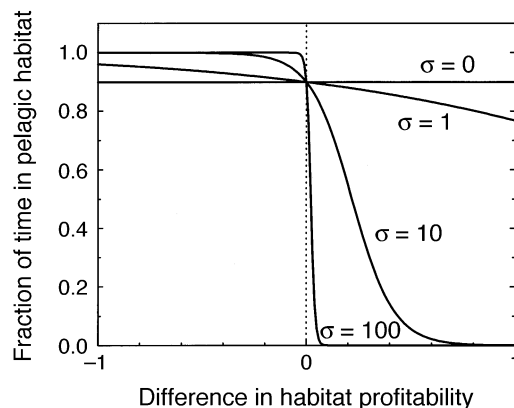


FIG. 2. Fraction of time spent in the pelagic habitat (see Eq. 6) for different values of  $\sigma$  as a function of the difference in habitat profitability between littoral and pelagic habitat,  $Q_l(z_l, x, y) - Q_p(z_p, x, y)$ .

For  $\sigma = 0$ ,  $F$  equals the ratio of the pelagic and total lake volume, which implies that individuals use both the pelagic and the littoral habitat in proportion to their volume. We will refer to this case as “proportional habitat use.” Individuals will also use both habitats proportionally if the habitats are equally profitable ( $Q_p = Q_l$ ). For positive values of  $\sigma$ , Eq. 6 represents a sigmoid function, rising from 0 when the profitability of the littoral habitat is much higher than the pelagic ( $Q_p \ll Q_l$ ), to 1 in the reverse situation ( $Q_p \gg Q_l$ ). The parameter  $\sigma$  determines the steepness of the sigmoid curve at equal habitat profitability ( $Q_p = Q_l$ ). For  $\sigma \rightarrow \infty$ , individuals will always switch instantaneously to the habitat with the highest profitability (see Fig. 2).

Given that an individual spends a fraction  $F$  of its time in the pelagic habitat, its total intake rate of resource biomass is

$$I(z_p, z_l, x, y) = F(z_p, z_l, x, y) I_p(z_p, x) + [1 - F(z_p, z_l, x, y)] I_l(z_l, x) \quad (7)$$

while its total mortality rate is an analogous, weighted average of the mortality rates experienced in either of the two habitats (see Table 2).

Newborn consumers always start life in the littoral habitat. In addition to situations in which consumers are restricted to live only in the pelagic habitat, or in which they use both the littoral and pelagic habitat proportionally, we study two scenarios of responsive behavior:

1. *Discrete habitat shift.*—With this term we refer to a situation in which individual consumers only switch habitat once during ontogeny. This switch is instantaneous and irreversible and will occur as soon as the pelagic profitability is higher than the littoral profitability (i.e., when  $Q_p(z_p, x, y) - Q_l(z_l, x, y)$  becomes positive).

2. *Continuous habitat choice.*—In this case, individual consumers continuously adapt their use of the pe-

lagic and littoral habitat to the current feeding and mortality conditions in both habitats. The fraction of time an individual of a given size and condition spends in the pelagic habitat is given by Eq. 6.

#### *The population level*

The model only examines population dynamics during the growth season, corresponding to the summer in the temperate region. The changes in consumer and resource populations during the nongrowth season (winter) are assumed to be negligible.

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

The two resources are assumed to exist in separate habitats. The population growth of both resource populations is assumed to follow semi-chemostat dynamics. Arguments for using this representation of resource population growth are given in Persson et al. (1998). Analytically the structured population model can be formulated as a system of integral equations (see Persson et al. 1998), which represents a way of bookkeeping the dynamics of all individuals making up the population. Numerically, the model can be studied using the EBT (Escalator Boxcar Train) framework (de Roos 1988, de Roos et al. 1992). The EBT method is specifically designed to handle the numerical integration of the equations that occur in physiologically structured models. Below follows a short description of how the EBT method was applied to the model studied in this paper. The Appendix presents the equations governing the within- and between-seasons dynamics of the consumer and resource populations.

The pulsed reproduction process ensures that there exists a natural subdivision of the population into cohorts of individuals. In one cohort all individuals have the same age, reversible and irreversible mass, and all spend the same fraction of their time in the pelagic habitat. All individuals within a cohort are, moreover, assumed to grow at the same rate, i.e., individuals belonging to a given cohort do not diverge in their allocation to reversible and irreversible masses. As a result, each cohort consists of individuals that will remain identical for the duration of their lives.

The dynamics of every cohort can be described by a system of ordinary differential equations, which keeps track of the number of individuals making up the cohort, their age, reversible mass, and irreversible

mass. The dynamics of the entire consumer population, both in terms of its abundance and its composition, can be followed throughout the summer season by numerically integrating the system of ordinary differential equations for each cohort separately. In addition, changes in the resource population can be followed by numerical integration of the ordinary differential equation for the resource dynamics that incorporates the semi-chemostat growth and the total resource consumption. The latter equals the summed foraging rate over all cohorts.

At the beginning of the growth season, new cohorts of individuals are added to the consumer population due to the reproductive process. This addition implies that the number of differential equations describing the population dynamics is increased. At the same time, the current value of the reversible mass in the cohorts of reproducing individuals is reset, reflecting their investment into offspring. Overall, the model simulations thus involve the numerical integration of a (large) system of ordinary differential equations, which is extended in dimension at the beginning of each season with a concurrent reset of some of the variables. The dimension of the system is reduced whenever the number of individuals in a given cohort has become negligible, at which time the differential equations for this particular cohort are removed.

#### *Parameterization of the model*

We parameterized the model based on the biology of Eurasian perch (*Perca fluviatilis*) (Table 3). Perch is a suitable model system, as it has been demonstrated that perch choose habitat in response to habitat profitability (Persson 1987, Persson and Greenberg 1990). Perch also take predation risk into account when choosing habitats, and it has been shown that the littoral habitat serves as a refuge from predation for small perch (primarily from large piscivorous perch; Persson 1993, Persson and Eklov 1995). The size at which juvenile perch switch between habitats has also been shown to depend on cannibalistic perch density (P. Byström, L. Persson, E. Wahlström, and E. Westman, *unpublished manuscript*).

Parameterization of attack rates, handling times, and metabolic demands was based on data given in Persson (1987), Persson and Greenberg (1990), and Byström and Garcia-Berthou (1999: Table 2; see also Claessen et al. 2000). The open-water prey was represented by *Daphnia*, and littoral prey was represented by *Sialis*, which both are typical and dominant prey in the pelagic and littoral habitat, respectively (Persson 1987). Parameter values were based on a temperature of 19°C.

The size-independent, background mortality rate  $\mu_b$  in the littoral and pelagic habitat was set to 0.01 per day for all individuals. The model dynamics were studied as a function of the proportionality constant in the size-dependent, pelagic mortality rate  $\mu_p$  (see Eq. 2). The length of the season was set to 90 d, corresponding



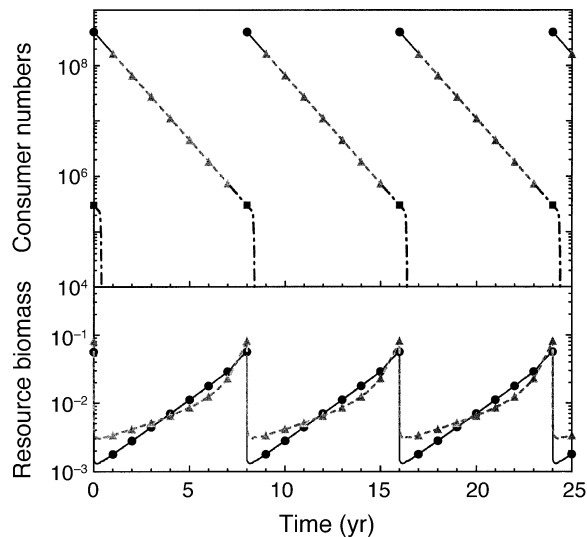


FIG. 3. Dynamics of the model when individuals use both littoral and pelagic habitat proportionally in the absence of any additional, size-dependent mortality in the pelagic habitat ( $\mu_p = 0.0$ ). Top: The solid line with circles represents individuals younger than 1 yr (YOY); the dashed line with triangles represents juvenile individuals aged 1 yr and older; and the dotted-dashed line with squares represents adult individuals. All consumer numbers are expressed as total number in the entire lake. Bottom: The solid line with circles represents the littoral resource (g biomass/m<sup>2</sup>); the dashed line with triangles represents the pelagic resource (g biomass/m<sup>2</sup>). Symbols in all curves mark the start of the season.

to the temperate region in middle Sweden. The two habitats differed in size, with the littoral habitat making up 10% and the pelagic habitat 90% of the total lake volume. We assumed an average water depth of 2 m for the littoral habitat to convert from habitat volume to total bottom area, where the individuals were assumed to feed.

## RESULTS

### *Single (pelagic) and proportional habitat use*

For the default parameters (see Table 3) and without any differences in mortality between the littoral and pelagic habitat ( $\mu_p = 0.0$ ), the model exhibits cycles with a periodicity of 8 yr, where the population is almost always made up by a single cohort of individuals. The details of these single-cohort cycles and the mechanisms bringing them about have been discussed by Persson et al. (1998). Fig. 3 shows an example of these dynamics for the case of proportional habitat use. When reproduction occurs, the large number of newborn individuals (young-of-the-year, YOY) depresses the resource levels in both the littoral and pelagic habitat to such low levels that all older individuals starve to death. The competition for food among the YOY subsequently impedes their growth. When density declines due to background mortality, resource levels can increase and individual growth speeds up. The cohort

reaches maturation size when individuals are >7 yr old. The surviving individuals have accumulated sufficient reproductive mass by the end of their 8th yr to produce a new dominant cohort. This new cohort outcompetes the remaining adults.

The occurrence of single-cohort cycles can be explained by the fact that individual competitiveness, as measured by the lowest resource levels that an individual can sustain without starving, increases with body size (Persson et al. 1998). For a given irreversible mass,  $x$ , individual growth stops at a critical resource density where net energy production is 0 (i.e., whenever  $k_c I = E_m$ ; see Table 2). Whether the individual is feeding in the pelagic or littoral habitat, this critical resource density is higher for larger individuals (results not shown; see Persson et al. 1998). The dominant cohort completely controls the resource level and exploits it to levels that are below the critical resource level of older cohorts, inducing their starvation. In the case of a single resource (habitat), Persson et al. (1998) showed that for increasing background mortality, the density of individuals in the dominant cohort declines more rapidly. As a result, resource levels increase faster, growth in size speeds up, and individuals mature earlier in the season. The dynamics change when individuals mature 1 yr earlier at an age of 6 yr old. In this case, the period of the single-cohort cycle shortens to 7 yr. With increasing mortality, the single-cohort cycles thus shorten in a stepwise manner to lower and lower periodicities, ultimately reaching a fixed-point dynamics, in which the state of the population and resource levels are identical at the beginning of each season.

Fig. 4 shows that this bifurcation pattern with stepwise transitions to single-cohort cycles of a one-year-shorter period occurs irrespective of whether consumers live only in the pelagic habitat, or use both pelagic and littoral habitat in proportion to their volume. As the size-dependent, pelagic mortality ( $\mu_p$ ) increases, the stepwise shortening of the single-cohort cycles occurs over the range of values  $0 \leq \mu_p < 0.08$ . (Here and below all thresholds in  $\mu_p$ , separating intervals with different types of dynamics, should be interpreted as approximate values.) For values of  $\mu_p$  around the points where the cycle periods shorten, some irregular dynamics may be observed. At these transitions there may also be parameter intervals where alternative attractors coexist. When consumers are restricted to live in the pelagic, the regular 2-yr cycle coexists over a significant range of  $\mu_p$  values with a stable fixed point. When consumers use both pelagic and littoral habitat proportionally, coexistence of alternative attractors occurs between a regular 2-yr cycle and a stable fixed point ( $0.05 < \mu_p < 0.08$ ) and between a regular 3-yr cycle and either a stable fixed point or irregular, small-amplitude cycles ( $0.02 < \mu_p < 0.04$ ).

From Fig. 4 we conclude that the introduction of a second resource (habitat) that is shared among all con-

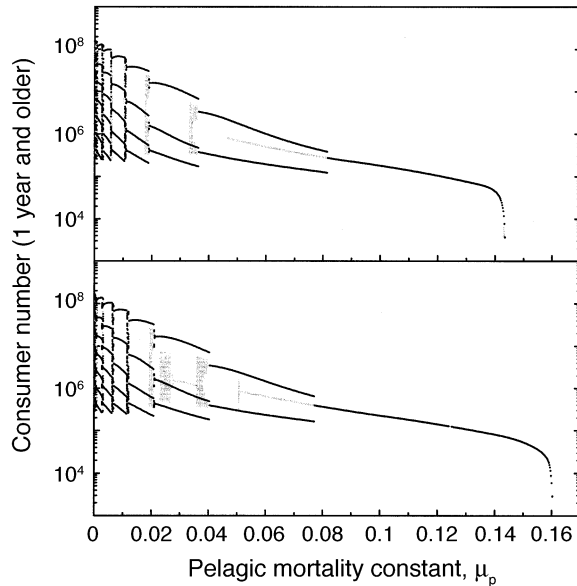


FIG. 4. Bifurcation diagram of the model when individuals are restricted to live only in the pelagic habitat (top) or to use both pelagic and littoral habitat proportionally (bottom). The total number of consumers of age 1 yr and older in the entire lake is shown as a function of the pelagic mortality constant  $\mu_p$ . Other parameters have their default value (see Table 3). For every value of the parameter, numerical simulations were carried out over a period of 400 yr (seasons). Statistics of the system at the time of reproduction (i.e., the beginning of the season) are shown for the last 50 yr of these simulations. Symbols in different shades of gray indicate the existence of alternative attractors.

sumers, only leads to marginal differences in the bifurcation pattern from the single-resource (habitat) situation. The transitions in dynamics for both cases shown in Fig. 4 occur at the same average mortality. For example, when only the pelagic is used stable equilibria occur for  $0.045 < \mu_p < 0.145$ , while they occur for  $0.05 < \mu_p < 0.16$  with proportional habitat use. Taking into account that in the latter situation an individual spends 90% of its time in the pelagic and 10% in the littoral habitat with a lower mortality probability, these ranges of  $\mu_p$  values are identical. The introduction of the second resource only leads to a higher propensity for alternative attractors over a small range of  $\mu_p$ -values ( $0.02 < \mu_p < 0.04$ ). The importance of these additional, alternative attractors (i.e., the stable fixed points and small-amplitude cycles), however, is not clear, as we did not investigate which proportion of all possible initial states of the system would converge to the different attractors.

#### *Discrete habitat shifts (littoral to pelagic)*

*Dynamics for  $0 \leq \mu_p < 0.145$ .*—When newborn individuals start their life in the littoral habitat and then switch habitats once to continue living in the pelagic, the same bifurcation sequence of single-cohort cycles is observed for low values of  $\mu_p$ , as when individuals

are restricted to live only in the pelagic. Fig. 5 shows that for  $0 \leq \mu_p < 0.145$ , habitat switching occurs at very small sizes, i.e., only a few days after the individuals are born. The littoral resource is only fed upon during these first few days of an individual's life and remains unexploited afterwards. Because we show resource densities at the beginning of the growth season, the littoral resource density in Fig. 5 equals the carrying capacity up to  $\mu_p \approx 0.175$ . For  $0 \leq \mu_p < 0.145$ , absolute densities of consumers and resources are identical, irrespective of whether individuals exhibit a discrete habitat shift (Fig. 5; top panel) or whether they are restricted to live only in the pelagic (Fig. 4; top panel). Also, the values of  $\mu_p$  at which stepwise decreases of cycle length occur are the same between the two situations. Comparing discrete habitat shifts with the situation where individuals use both habitats proportionally, the total density of consumers is slightly lower than in the proportional-use scenario, because the productivity of the littoral habitat is not exploited, while the values of  $\mu_p$  at which stepwise decreases of cycle length occur are slightly smaller for the reasons explained in the previous section. Over the entire range of  $\mu_p$  values for which the consumer population persists when individuals only use the pelagic habitat, the incorporation of a discrete habitat shift thus leads to results that are graphically indistinguishable. The robustness of the single-cohort cycles against the incorporation of a discrete habitat shift may be related to the differences in total productivity of the pelagic and littoral habitat. For the default parameter set these productivities are 270 and 15 kg prey biomass/d, respectively. This difference is primarily due to the different volumes of the two habitats, i.e., 90% and 10% of the total lake volume, respectively. As a result, consumer population feedback in the littoral habitat is always intensified compared to the feedback in the pelagic. It should be noted that the immediate switching of newborn individuals to the pelagic is entirely a population-level effect, as the foraging capacity of newborn individuals on the littoral resource is even slightly higher than on the pelagic resource.

Another consequence of the high productivity of the pelagic habitat is that the number of newborn (YOY) individuals produced is invariably large (Fig. 5). Assuming that the newborn cohort is the only one exploiting the littoral resource, the differential equation for this resource density (see Eq. A.3b in the Appendix) can be used to derive the pseudo-steady-state value imposed by the large YOY pulse. For this pseudo-steady-state resource density the right-hand side of Eq. A.3b vanishes. All our numerical studies so far have indicated that this pseudo-steady-state value is a good approximation to the actual density of resource on which the YOY is foraging at a specific time. Fig. 6 shows that the pseudo-steady-state resource density in the littoral habitat rapidly decreases when the number of YOY is  $>10^7$  and drops below their starvation

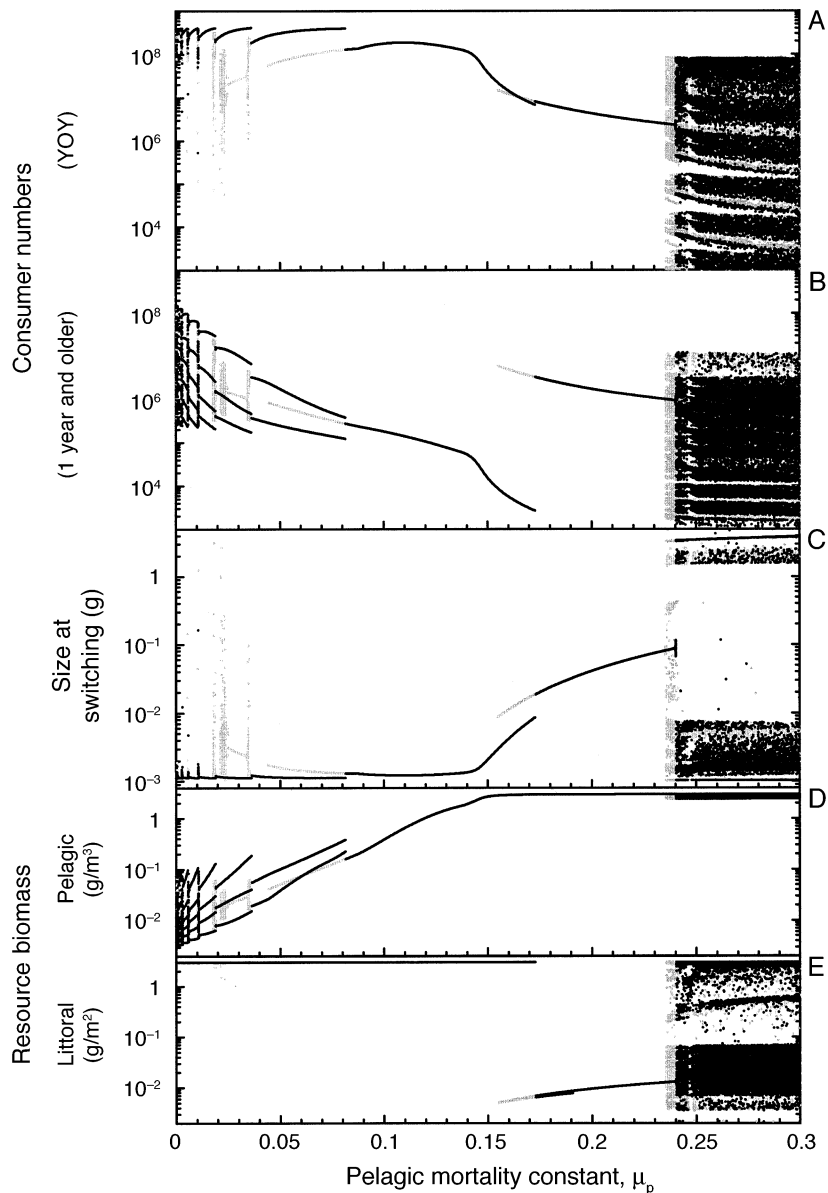


FIG. 5. Bifurcation diagram of the model when individuals move once and instantaneously during their life from littoral to pelagic habitat: (A) the total number of YOY and (B) consumers aged 1 yr and older in the entire lake; (C) their irreversible mass at habitat switching (in grams); and the resource biomass density ( $\text{g biomass}/\text{m}^3$ ) in the (D) pelagic and (E) littoral habitat are shown as a function of the mortality constant  $\mu_p$  in the open water. Other parameters have their default value (see Table 3). Symbols in different shades of gray indicate the existence of alternative attractors.

threshold if the number of YOY is  $>4 \times 10^7$ . At the time of reproduction the pelagic resource density is sufficiently large to allow adult individuals to grow and reproduce, and is at least larger than the critical resource density for a maturing individual. Under these conditions the littoral resource density at which the newborn individuals switch to the pelagic is just above their critical, starvation density (see Fig. 6). From Fig. 6 it can therefore be concluded that YOY densities  $>4 \times 10^7$  will always lead to an almost immediate niche shift to the pelagic, induced by its higher profitability.

Fig. 5 shows that this situation occurs for  $0 \leq \mu_p < 0.145$ .

The robustness of the single-cohort cycles hence results from the marginal importance of the littoral habitat for the consumer population, even though at an individual level the littoral resource is sometimes more profitable. The high total productivity of the pelagic habitat leads to the birth of large numbers of offspring in the littoral habitat. The population feedback forces these individuals out into the pelagic after a negligible time span. The niche shift is triggered by the littoral

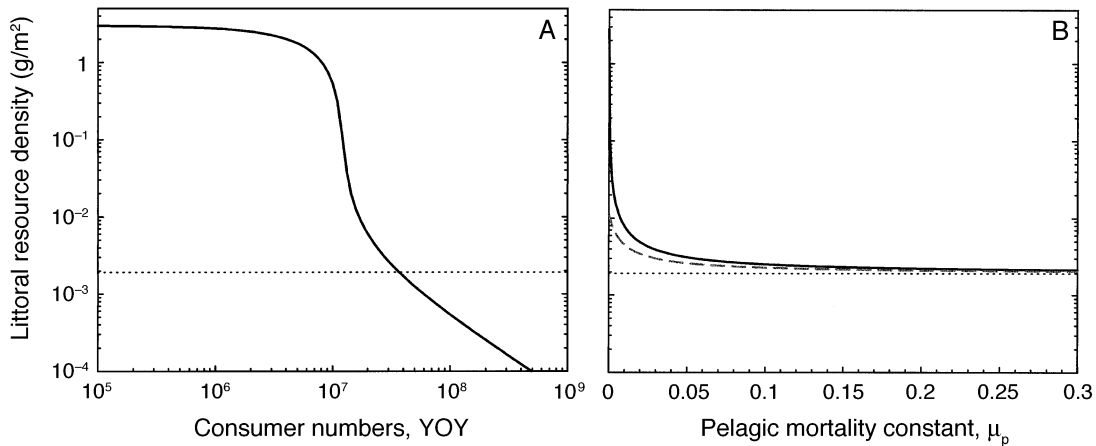


FIG. 6. (A) The pseudo-steady-state, littoral resource density (g biomass/m<sup>2</sup>) as a function of the total number of newborn individuals ( $x = x_p$ ; solid line). This pseudo-steady-state density is computed by solving the resource density at which the right-hand side of ordinary differential equation A.3b (see the Appendix) vanishes, assuming that only the newborn cohort feeds on the littoral resource. The dotted, horizontal line represents the resource density below which newborn individuals starve. (B) Littoral resource densities (g biomass/m<sup>2</sup>) at which newborn individuals switch to the pelagic habitat, when the pelagic resource density equals carrying capacity ( $z_p = K_p$ ; thick solid line) and when it equals the critical pelagic resource density for maturing individuals (thick dashed line).

resource dropping to such low levels that the current conditions in the pelagic become more profitable for the newborn individuals. Essentially, the dynamics are thus very close to the dynamics of the single resource–single consumer system studied by Persson et al. (1998).

*Dynamics for 0.145 < μ<sub>p</sub> < 0.24.*—For μ<sub>p</sub> > 0.145, the consumer population cannot persist if individuals only live in the pelagic habitat, but can do so if they go through a discrete habitat shift. For μ<sub>p</sub> increasing from 0.145, the number of YOY and consumers aged 1 yr and older sharply decreases and becomes so low that the pelagic resource density roughly equals carrying capacity (Fig. 5). This implies that there is no feedback any longer of the consumer population on the pelagic resource density and consequently also on the life history of consumers after they have passed through the habitat shift. This leads to a constant fecundity for adult individuals. Therefore, for μ<sub>p</sub> > 0.145, the consumer population is regulated by the interactions taking place within the littoral habitat, more specifically by the competition among YOY individuals and the size at which these individuals shift to the pelagic. The lower YOY density allows these individuals to start growing while living in the littoral habitat (Fig. 7A). For 0.145 < μ<sub>p</sub> < 0.175 the pelagic becomes more profitable after 10–20 d, because the attack rate on littoral resources increases less rapidly with increasing body size as compared with the attack rate on the pelagic resource (Fig. 1). The initial growth in the littoral habitat causes the increase in switch size observed over the interval 0.145 < μ<sub>p</sub> < 0.175 (Fig. 5). After switching to the pelagic, the high, size-dependent mortality decimates the density of YOY. As a consequence, they have hardly any impact on the pelagic resource

density and their growth is maximal. Within their first year of life the YOY reach the maturation size and start reproducing as 1-yr-old individuals. For mature individuals the size-dependent mortality is negligible, which allows them to reach maximum ages of 8–9 yr. Reproduction peaks at the age of 2 and declines rapidly afterwards. Individuals older than 5 yr do not reproduce any longer, as they use all assimilated food to cover their maintenance requirements.

Partly coexisting with the attractor described above in which YOY pass through the habitat shift during their first year of life, another type of dynamics is observed for 0.15 < μ<sub>p</sub> < 0.24, in which YOY switch to the pelagic almost instantaneously after reaching the age of one year (Fig. 7B). This type of dynamics occurs when the density of YOY is so low that during their first year of life they do not deplete the littoral resource to levels where the pelagic becomes more profitable. A substantial fraction of the YOY survive up to age 1, when the new YOY cohort causes a very rapid, small decrease in the littoral resource density (Fig. 7B). This small decrease is sufficient to force the 1-yr-old individuals into the pelagic. Because of the habitat shift the littoral resource density increases again considerably, which allows the new YOY cohort to stay in the littoral habitat. The high survival of YOY up to age 1 is reflected in the high densities of consumers aged 1 yr and older, shown in Fig. 5. However, this density rapidly drops after the habitat shift because of the size-dependent mortality experienced by 1-yr-old individuals (Fig. 7B). Due to the high pelagic resource density the growth of the surviving 1-yr-old individuals speeds up such that they mature in their 2nd year and reproduce for the first time as 2-yr-old individuals. Reproduction peaks at the age of 3 and declines to 0 for

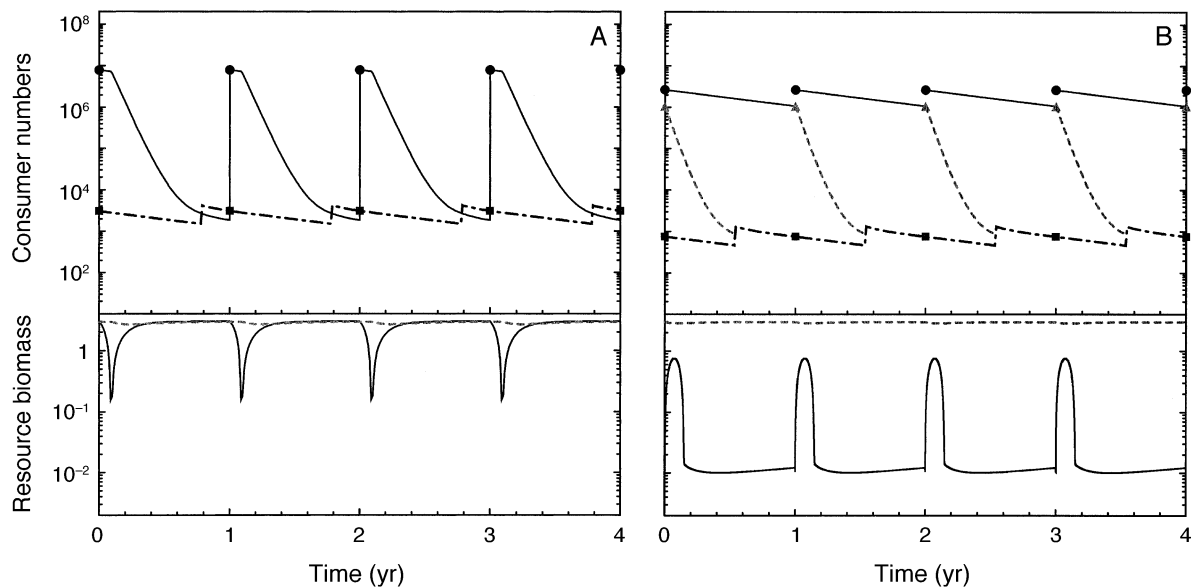


FIG. 7. Dynamics of the discrete habitat shift model for (A)  $\mu_p = 0.17$  and (B)  $\mu_p = 0.23$ . Top: The solid line with circles represents individuals younger than 1 yr (YOY); the dashed line with triangles represents juvenile individuals aged 1 yr and older; and the dotted-dashed line with squares represents adult individuals. Bottom: The solid line represents the littoral resource; the dashed line represents the pelagic resource. Symbols mark the start of the season. Units are as in Fig. 3.

individuals older than 6 yr. The maximum age is again 8–9 yr.

The two types of dynamics differ in the timing of the habitat shift (as YOY vs. as 1 yr old), the mechanism of its induction (within- vs. between-cohort competition) and the individual survival pattern (major mortality during 1st or 2nd yr of life). In addition, when individuals switch as YOY, the high mortality during their 1st yr of life induces a rapid release from intra-cohort competition, and consequently a rapid growth rate up to age 1. When switching occurs as 1-yr-old individuals, a comparable mortality, release from competition, and rapid growth only occurs after reaching age 1. As a consequence, individuals reach larger body sizes at the age of 1 yr when they switch as YOY. The survival up to the time of first reproduction and the fecundity at that and later reproduction events are, however, completely identical for the two attractors.

*Dynamics for  $\mu_p \geq 0.24$ .*—At  $\mu_p \approx 0.24$ , the fixed point at which individuals shift to the pelagic at the age of 1 yr due to the between-cohort competition with the subsequent YOY, destabilizes and gives rise to large-amplitude cycles in the number of consumers and the littoral resource density. The cycles in pelagic resource density have much smaller amplitude and remain close to the carrying capacity value at all times (see Fig. 5). For the body size at which the habitat shift occurs, values are observed that roughly separate into two ranges: individuals either switch at an irreversible mass  $x$  between their mass at birth ( $x = 0.001$ ) and 10 times that value ( $x = 0.01$ ), or they switch habitats at a size close to the maturation size.

Since the pelagic resource density is invariably close to the carrying capacity, and any feedback on consumer life history is absent after the age of 1 yr, the consumer population is only regulated through the body size at which 1-yr-old individuals shift to the pelagic. The size is completely determined by the year class strength of the YOY, which controls the littoral resource density at its pseudo-steady-state value. The fixed point destabilizes through overcompensation in this body size at habitat shift. With decreasing numbers of YOY over the range  $0.145 < \mu_p < 0.24$ , the size at habitat shift increases and the subsequent mortality from age 1 to maturation decreases. Cohorts of individuals that switch at larger body sizes produce larger pulses of offspring. If too large, these offspring cohorts themselves switch at a smaller body size, experience higher pelagic mortality, and hence produce again smaller offspring cohorts. Ultimately at  $\mu_p \approx 0.24$  this overcompensation mechanism destabilizes the fixed point. Because of the discontinuity inherent in the instantaneous and complete shift of an entire cohort of individuals, the cycle, which arises from the destabilization through overcompensation and which is initially of small amplitude (see, for example, Fig. 5, panel C), almost immediately gives way to fluctuations with very large amplitudes. The conclusion about the route to instability is corroborated by the fact that a variant of the current model, in which individuals are forced to always live in the littoral habitat up to age 1 and in the pelagic afterwards, exhibits the same destabilization at  $\mu_p \approx 0.24$ .

The model dynamics in this range of  $\mu_p$ -values is

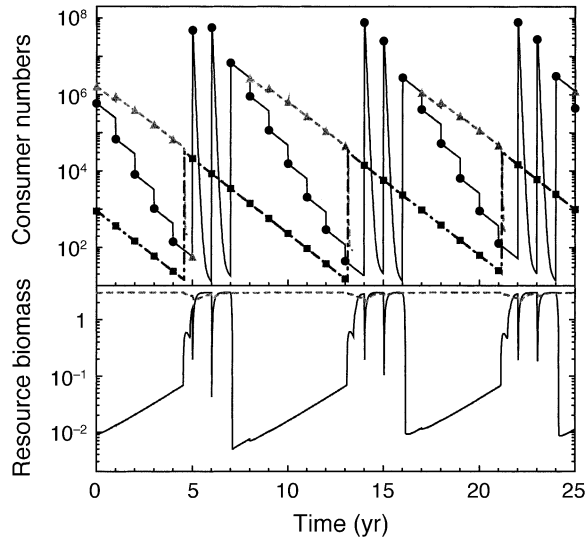


FIG. 8. Dynamics of the discrete habitat shift model for  $\mu_p = 0.28$ . Top: The solid line with circles represents individuals younger than 1 yr (YOY); the dashed line with triangles represents juvenile individuals aged 1 yr and older; and the dotted-dashed line with squares represents adult individuals. Bottom: the solid line indicates the littoral resource; the dashed line indicates the pelagic resource. Symbols mark the start of the season. Units are as in Fig. 3.

illustrated in Fig. 8 and can be described as follows: shortly before  $T = 5$  several cohorts of juvenile individuals that have been living in the littoral habitat mature almost simultaneously ( $T$  represents the time in years). The individuals switch to live in the pelagic at a size close to the maturation size and hence have not experienced the size-dependent pelagic mortality. In subsequent years these adult individuals produce two large cohorts of offspring that migrate out into the pelagic early in life at small body sizes. The few survivors of these offspring cohorts, amounting to only  $10^{-6}\%$  of their initial density, grow rapidly, mature within their first year of life, and join the cohort of adults. Because background mortality decreases the number of adult individuals in the pelagic over the years, the cohort born at  $T = 7$  is again sufficiently small to prevent depletion of the littoral resource. This and all subsequent, smaller, cohorts born up to  $T = 13$  stay for a longer time in the littoral habitat and escape the pelagic mortality. Crowding effects obviously retard their growth, since no maturation occurs until shortly before  $T = 14$  (Fig. 8), when the same simultaneous maturation pulse occurs as the one that started off the cycle. Detailed analysis of the changes in the population state over the last 6 yr of the cycle show that the cohorts that stay in the littoral habitat up to maturation strongly converge in body size. Cohorts that are born later catch up with older cohorts, whose growth is retarded due to crowding. Fig. 8 also shows that the first cohort that is small enough to prevent overexploitation of the littoral habitat is numerically dominating the entire cycle.

The dynamic pattern described above, including the pattern of "cohort stacking" in the littoral habitat and the numerical dominance of the first cohort that manages to stay in the littoral habitat, is characteristic for the entire range of dynamics between  $\mu_p \approx 0.24$  and 0.3. The dynamics may be a regular cycle with a period of 8–9 yr or may be less regular fluctuations: the height of the peaks may differ, and the period may jump between two values. By and large, however, the dynamics consist of an alternation of periods with a domination of juvenile cohorts in the littoral habitat without any significant reproduction and maturation, and periods in which the dominant cohort has matured and produces rather large pulses of YOY. These YOY individuals are destined to die off rapidly as they quickly move out into the pelagic. Only later on in life, the dominant cohort produces smaller YOY cohorts that are not too abundant to deplete the littoral resource and can hence remain in the littoral habitat.

#### Continuous habitat choice

*High responsiveness to profitability differences.*—To model continuous habitat choice, we used Eq. 6 to describe the fraction of time that individuals spend in the pelagic habitat, as a function of the difference in habitat profitability between pelagic and littoral. For high values of  $\sigma$  individuals strongly respond to small differences in habitat profitability (see Fig. 2). High values of  $\sigma$  can also be interpreted as modeling omniscient consumers. As in the case of discrete habitat shifts, consumers react almost instantaneously to differences in profitability. However, in contrast to the discrete habitat shift scenario, consumers may distribute their time over the two habitats and may also reverse their habitat choice. We first discuss the population dynamics for large  $\sigma$  values.

Similar to the case of a discrete habitat shift, the number of YOY produced during a pulse of reproduction with continuous habitat choice is high as long as  $\mu_p < 0.14$  (see Fig. 9). The high density of YOY induces an almost immediate depletion of littoral resources soon after reproduction. As a consequence, after birth YOY quickly move out into the pelagic. Their large number allows the YOY not only to control entirely the littoral, but also the pelagic resource density, depressing both to such levels that habitat profitabilities are roughly equal. Shortly after birth YOY thus tend to impose resource conditions in both littoral and pelagic that allow them to divide their time in such a way that they approximate an ideal-free distribution.

Because of the difference in productivity between the littoral and pelagic habitat, which is mainly due to their difference in volume, YOY achieve this ideal free situation only by spending most of their time (roughly 90%) in the pelagic (Fig. 9). For low values of  $\mu_p$ , the resulting dynamics are hence close to the dynamics with proportional habitat use (cf. Fig. 4). For  $0 \leq \mu_p < 0.08$  the same bifurcation pattern of single-cohort

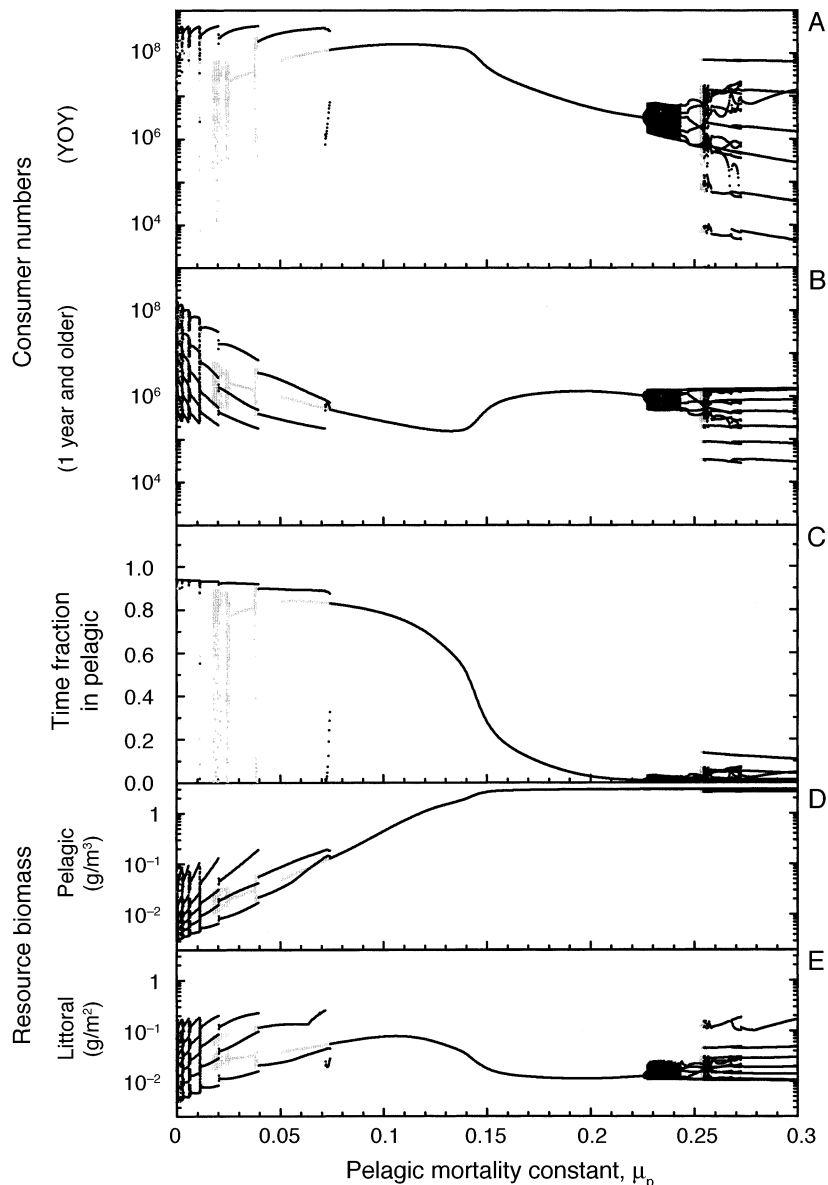


FIG. 9. Bifurcation diagram of the model when individuals continuously adapt their habitat choice to the current profitability of littoral and pelagic habitat: (A) the total number of YOY and (B) consumers of age 1 yr and older in the entire lake; (C) the fraction of time that YOY spend in the pelagic habitat; and the resource biomass density ( $\text{g biomass}/\text{m}^3$ ) in the (D) pelagic and (E) littoral habitat are shown as a function of the mortality constant  $\mu_p$  in the open water.  $\sigma = 100$ , while other parameters have their default value (see Table 3). Symbols in different shades of gray indicate the existence of alternative attractors.

cycles is observed as before with a stepwise shortening of the periodicity. These stepwise transitions occur at almost the same values of  $\mu_p$  as in the case of proportional habitat use. Obviously, single-cohort cycles are also robust against the incorporation of continuous habitat choice, for reasons that are largely similar to those discussed in the previous section on discrete habitat shifts.

With increasing values of  $\mu_p$  the density of YOY declines rapidly while they spend time in the pelagic. It is this decline in density, in conjunction with the

lower mortality in the littoral, that causes YOY to make greater use of the littoral habitat as  $\mu_p$  increases: Even though they almost immediately after birth move out into the pelagic habitat, they will do so to a lesser extent and for a shorter time. As a whole the average fraction of their first year of life spent in the pelagic habitat decreases and exhibits a sharp drop around  $\mu_p \approx 0.14$ – $0.15$  (Fig. 9). Fig. 10 shows that this sharp drop coincides with rapid changes in the survival of different year classes: Up to  $\mu_p \approx 0.13$  the average mortality rate experienced by YOY increases with increasing val-

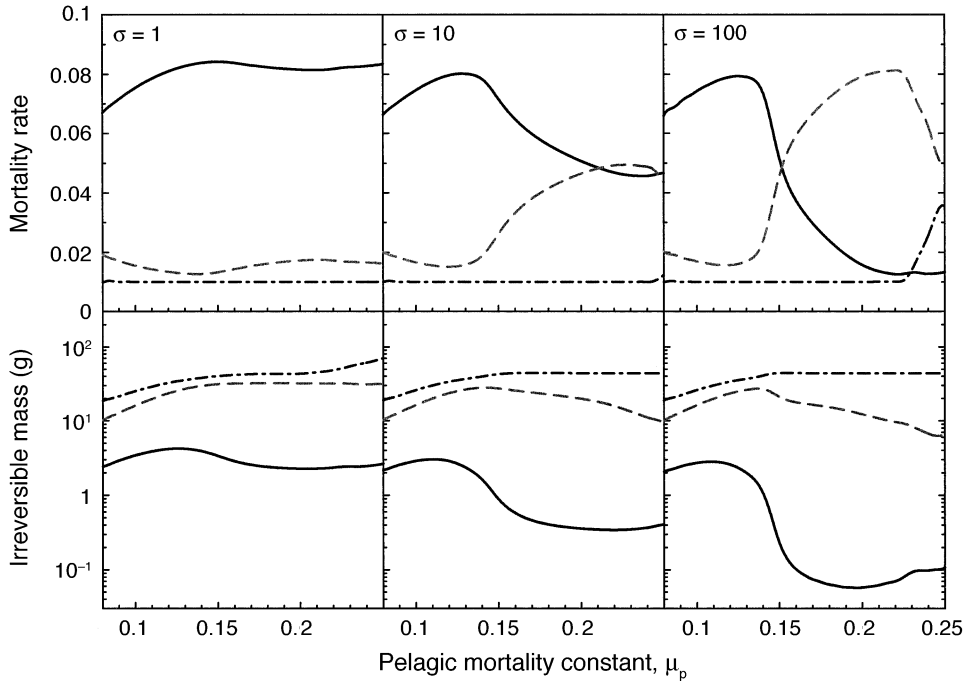


FIG. 10. Top: Average mortality rate per day over the first (solid line), second (dashed line), and third (dot-dashed line) year of life as a function of the size-dependent, pelagic mortality constant  $\mu_p$  for three different values of  $\sigma$ . Bottom: Average, irreversible body size  $x$  (g) at the age of 1 (solid line), and 2 yr (dashed line), and the average, maximum body size reached (dot-dashed line) as a function of the size-dependent, pelagic mortality constant  $\mu_p$  for three different values of  $\sigma$ . All other parameters have their default value.

ues of  $\mu_p$ , but sharply decreases over the range  $\mu_p \approx 0.13-0.15$ . Simultaneously, the average mortality rate of 1-yr-old individuals strongly increases for  $\mu_p \approx 0.13-0.15$ , while the mortality rate of older individuals equals the size-independent background mortality  $\mu_b$  (Fig. 10). Over this range of  $\mu_p$  values, the size that individuals reach at the age of 2 and, especially, 1 yr old (Fig. 10) also decreases strongly, as does the number of YOY produced in each reproduction pulse (Fig. 9).

At these  $\mu_p$  values, relatively low densities of YOY do not strongly deplete the littoral resource. Combined with the increasing riskiness of the pelagic, this keeps the YOY restricted to the littoral habitat and leads to their higher survival but retarded growth. The changes are similar to those that occur around this value of  $\mu_p$  when consumers exhibit a discrete habitat shift, although in the latter case the changes involved a discrete jump of dynamics from one attractor to the other. Here, the changes are continuous, but again involve a shift from (1) YOY spending the largest part of their time in the pelagic habitat, (2) experiencing the highest mortality, and (3) fastest growth in body size, to (1') YOY spending the largest part of their time in the littoral, (2') 1-yr-old individuals experiencing the highest mortality, and (3') fastest growth in body size. In the first case, intracohort competition is the main factor causing YOY to move into the pelagic; in the second case,

competition with the subsequent YOY forces 1 yr olds into the pelagic.

At  $\mu_p \approx 0.22$  the fixed point dynamics change to small-amplitude cycles, which at  $\mu_p \approx 0.25$ , blow up into large-amplitude fluctuations (Fig. 9). As in case of discrete habitat shifts, this destabilization arises because of overcompensation in the number of YOY produced: A large pulse of YOY reaches only small body sizes at age 1, resulting in lower subsequent survival till maturation and the production of small offspring cohorts. Vice versa, smaller pulses of YOY reach larger body sizes at age 1 and exhibit higher subsequent survival and reproduction. Fig. 11 illustrates this high (low) survival of small (large) YOY cohorts. For example, more individuals, even in absolute numbers, survive till maturation from the small cohorts born at  $T = 3$  and 8 than from the large cohorts born at  $T = 0, 5,$  and  $11$  (Fig. 11). For intermediate-sized YOY cohorts, an additional factor plays a role (for example, those born at  $T = 1, 6,$  and  $7$ ): their survival is intermediate, but their growth is retarded to such an extent that they only manage to reproduce for the first time as 3-yr-old individuals, as opposed to small and large YOY cohorts that reproduce as 2-yr-old individuals for the first time (Fig. 11).

Although different in details, the large-amplitude fluctuations that occur for  $\mu_p \geq 0.25$  show a similar pattern as observed for the model incorporating a dis-



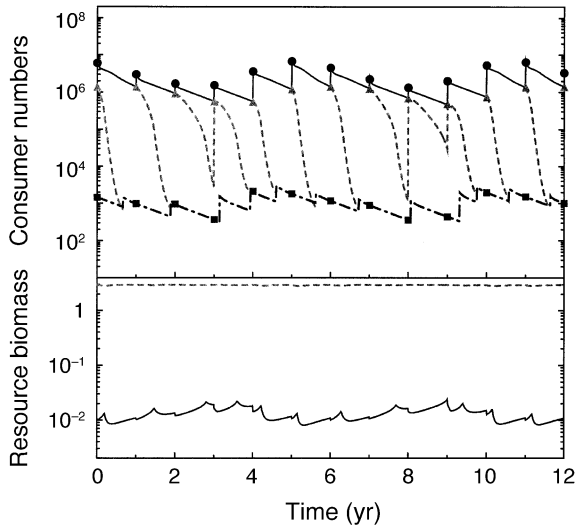


FIG. 11. Dynamics of the continuous habitat choice model for  $\mu_p = 0.23$  and  $\sigma = 100$ . Top: The solid line with circles represents individuals younger than 1 yr (YOY); the dashed line with triangles represents juvenile individuals aged 1 yr and older; and the dotted-dashed line with squares represents adult individuals. Bottom: The solid line indicates the littoral resource; the dashed line indicates the pelagic resource. Symbols mark the start of the season. Units are as in Fig. 3.

crete habitat shift (cf. Fig. 12 and Fig. 8). Shortly before  $T = 5$  several cohorts of juvenile individuals that have not suffered much from size-dependent, pelagic mortality mature almost simultaneously, forming a dominant group of adult individuals. In subsequent years these adults produce two large cohorts of offspring of which only few, if any at all, survive because of the small size these individuals reach at age 1. Their third offspring cohort (born at  $T = 7$ ; Fig. 12) is still relatively large, but does not experience competition by a large YOY cohort in the year after and can hence spend most of its juvenile period in the littoral habitat. All subsequent offspring cohorts produced by the dominant adult group are smaller and hence also spend most of their juvenile period in the littoral habitat. All these offspring cohorts converge in size and mature virtually simultaneously at  $T = 13$ , making up the new dominant group of adult individuals. As in the case of discrete habitat shifts, the dynamics are characterized by a pattern of "cohort stacking," simultaneous maturation of a number of different cohorts and numerical dominance by the first one or two YOY cohorts that are not too abundant to deplete the littoral resource, and hence manage to evade the high pelagic mortality.

*Low and intermediate responsiveness to profitability differences.*—As shown in the previous section, high responsiveness to differences in habitat profitability in case of continuous habitat choice leads to extended persistence of the consumer population and to destabilization at higher pelagic mortalities. Similar population-level consequences are observed when consum-

ers exhibit a unidirectional and instantaneous habitat shift. Both type of responses are characterized by almost stepwise dependence on the difference in profitability between the pelagic and littoral habitat (Fig. 2). For lower values of  $\sigma$  consumers respond less strongly to differences in profitability; when  $\sigma = 0$  they use both habitats proportionally to habitat volume irrespective of habitat profitability.

Fig. 13 shows that the unstable dynamics occurring at high values of  $\mu_p$  are a consequence of the rapid response to differences in habitat profitability. For  $\sigma = 10$  the small-amplitude cycles are still present for  $0.24 < \mu_p < 0.29$ , but the high-amplitude fluctuations shown in Fig. 8 no longer occur. For  $\sigma = 1$ , stable fixed point dynamics occur over the entire range of  $\mu_p$  values  $> 0.08$  (Fig. 13). The consumer population does, however, persist for all values of  $\mu_p$  investigated ( $\mu_p \leq 0.30$ ), even though with  $\sigma = 1$  the responsiveness of the consumers to profitability differences does not differ greatly from that characterizing proportional habitat use (i.e.,  $\sigma = 0$ ; see Fig. 2).

The cyclic dynamics at high  $\mu_p$  values disappear, because with lower responsiveness to profitability differences YOY will never be completely constrained to using only the littoral habitat and will therefore always experience the high pelagic mortality for part of their time. For example, with  $\sigma = 1$ , YOY spend at least 25% of their first year in the pelagic (results not shown). As a consequence, the first year of life remains the year with the highest mortality and the fastest growth in body size (Fig. 10). For  $\sigma = 1$ , regulation

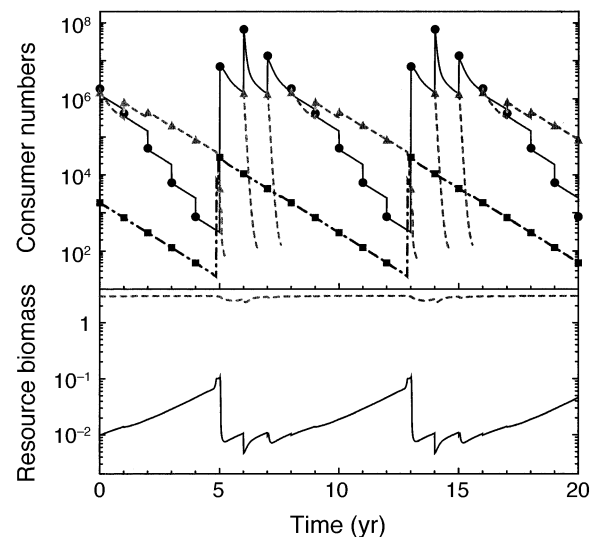


FIG. 12. Dynamics of the continuous habitat choice model for  $\mu_p = 0.28$  and  $\sigma = 100$ . Top: The solid line with circles represents individuals younger than 1 yr (YOY); the dashed line with triangles represents juvenile individuals aged 1 yr and older; and the dotted-dashed line with squares represents adult individuals. Bottom: The solid line indicates littoral resource; the dashed line indicates the pelagic resource. Symbols mark the start of the season. Units are as in Fig. 3.

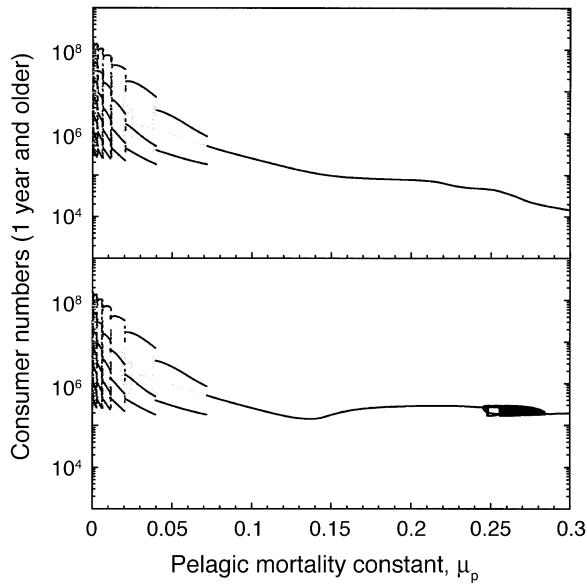


FIG. 13. Bifurcation diagram of the model when individuals continuously adapt their habitat choice to the current profitability of littoral and pelagic habitat for (top)  $\sigma = 1$  and (bottom)  $\sigma = 10$ . The total number of consumers of age 1 yr and older in the entire lake is shown as a function of the pelagic mortality constant  $\mu_p$ . Other parameters have their default value (see Table 3). Symbols in different shades of gray indicate the existence of alternative attractors.

of the consumer population is therefore mainly through the survival of YOY. Because of their substantial mortality and the concurrent rapid growth, the body size that consumers reach as 1-yr-old individuals is sufficiently large to escape high pelagic mortality afterwards. In contrast, for  $\sigma = 100$  and intermediate to large values of  $\mu_p$ , regulation of the consumer population is mainly through the body size reached by consumers at age 1, which strongly determines the subsequent survival of 1-yr-old individuals that live entirely in the pelagic habitat. Only this latter regulation incorporates an overcompensation mechanism that gives rise to unstable dynamics.

Another consequence of the high YOY mortality when  $\sigma = 1$  is that resource densities in the littoral habitat are roughly 5–10 times larger than is the case for  $\sigma = 100$  (data not shown, but see the difference in littoral resource density for  $0.08 < \mu_p < 0.14$  and  $0.15 < \mu_p < 0.22$  in Fig. 9). The surviving YOY therefore do not any longer depress littoral resource levels below the subsistence density for adults. The littoral even becomes the preferred habitat for individuals of 3 yr and older, as the attack rate on littoral resources continues to increase with body size, whereas pelagic attack rates decrease to 0 (Fig. 1). For example, for  $\sigma = 1$  and  $\mu_p = 0.30$ , YOY spend roughly 27% of their first year of life in the pelagic, shift to live entirely in the pelagic at the age of 1 year when the next YOY cohort is born, and shift back again to spend all their time in

the littoral habitat at 2–3 yr old. The increasing attack rate on littoral resources subsequently allows them to attain significantly larger body sizes than those occurring for  $\sigma = 100$  when individuals respond strongly to profitability differences (compare the left-most and right-most lower panel in Fig. 10). Concomitant with these larger body sizes, both mean individual fecundity and total population biomass of the consumers are larger for lower values of  $\sigma$  (Fig. 14).

Summarizing, when consumers only respond moderately to habitat profitability differences, the majority of newborn individuals die as YOY at small body sizes, which constitutes a smaller energy drain to the system than when major mortality occurs at the age of one year or older. Even though the survival probability till maturation is lower than in the case where individuals respond strongly to profitability differences, the survivors can reach higher body sizes and fecundities and establish a population with a larger total biomass.

DISCUSSION

*Intercohort competition, population persistence, and stability*

In size-structured consumer-resource systems, competition among and within cohorts has been shown to be an important factor shaping the population dynamics (Persson et al. 1998). In the absence of high YOY mortality, the competitive pressures exerted by small but abundant YOY may force larger and older individuals to starve, which eventually leads to the occurrence of single-cohort cycles. Persson et al. (1998) suggested that the presence of alternative resources could

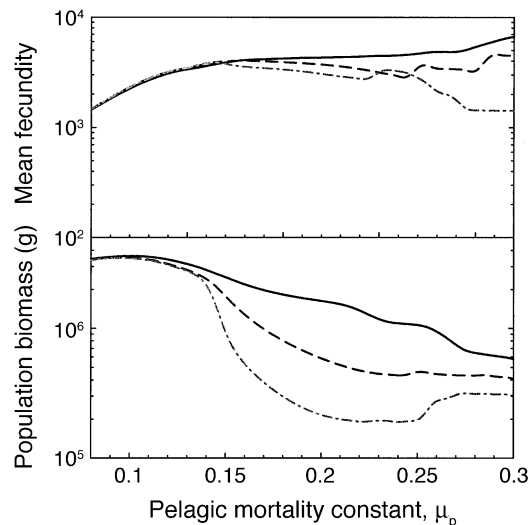


FIG. 14. Average adult fecundity (top) and total consumer biomass (bottom; g biomass in entire lake) as a function of the size-dependent, pelagic mortality constant  $\mu_p$  for  $\sigma = 1$  (solid line),  $\sigma = 10$  (dashed line), and  $\sigma = 100$  (dot-dashed line), while other parameters have their default value. Individuals continuously adapt their habitat choice to the current profitability of littoral and pelagic habitat.

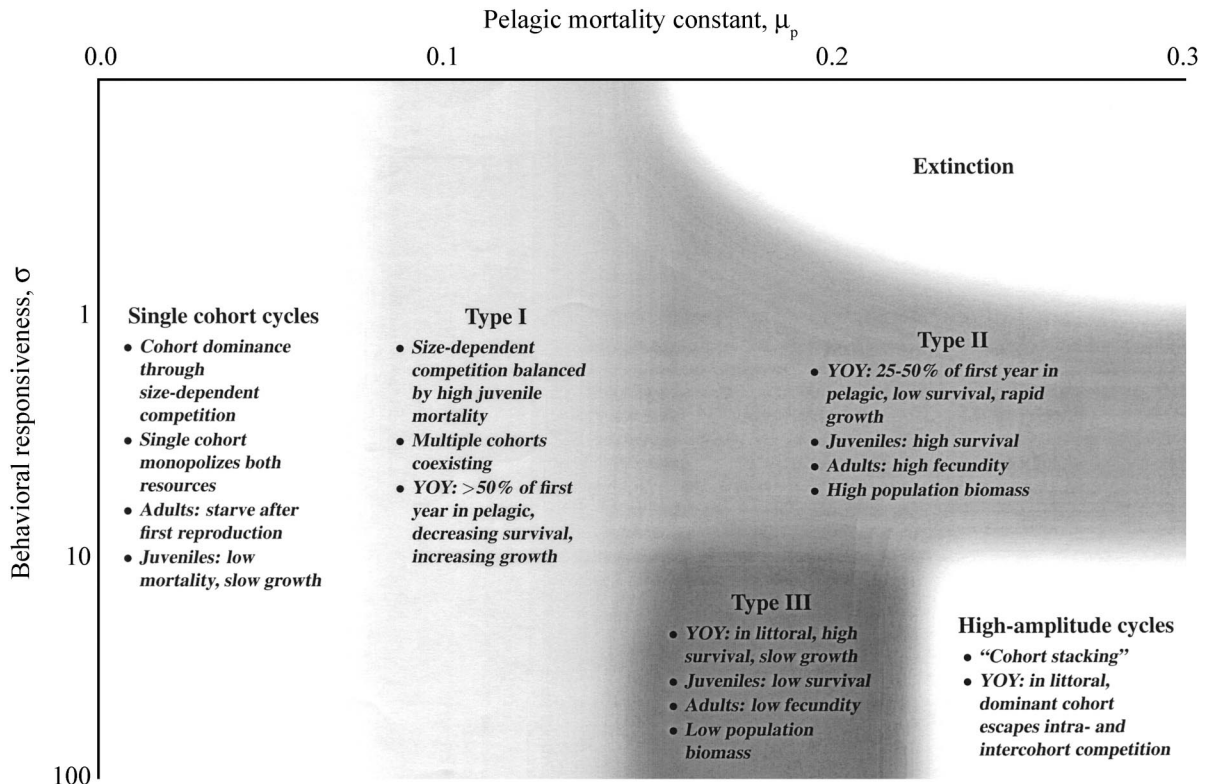


FIG. 15. Schematic overview of the types of dynamics occurring in the size-structured model with continuous habitat choice for different values of the behavioral responsiveness  $\sigma$  and the pelagic mortality constant  $\mu_p$ . The gray area indicates parameter combinations for which stable fixed points occur. Different shades of gray distinguish between fixed points with different characteristics. White areas indicate either cyclic dynamics or extinction. The designated parameter regions only qualitatively indicate where representative patterns of dynamics are to be expected, since the boundaries between them have not been located in any quantitative detail. The text presents an extensive discussion of these types of dynamics and the complex shifts between them.

potentially stabilize these single-cohort cycles. The results in this paper indicate that the addition of a second resource that is shared among all consumers does not prevent the occurrence of single-cohort cycles. Fig. 3 shows that YOY exert tight control over both pelagic and littoral resources, depleting them far below the level that adult individuals need to survive. The only way that adults can escape this intercohort competition is when they have access to a resource that is not depleted by the YOY. Because of the large YOY densities, this will only occur if the YOY attack rate on one of the resources is virtually 0. Hence, only exclusive resources will alleviate the intercohort competition between adult and newborn individuals. When the second resource is not shared among all cohorts evenly, but its exploitation is affected by ontogenetic niche shifts or flexible habitat choice, single-cohort cycles remain the dominant outcome of population dynamics at low levels of mortality. More specifically, when habitats do not differ in mortality rate (i.e., in the case of pure optimal foraging), one- and two-resource models yield the same single-cohort cycle with a period of 8 yr.

Fig. 15 summarizes the types of dynamics that we

have identified to occur in the size-structured model with continuous habitat choice for different values of the behavioral responsiveness  $\sigma$  and the pelagic mortality constant  $\mu_p$ . The characteristics of these dynamic patterns have been discussed in detail in the Results section. We did not attempt to derive precise criteria to distinguish between different types of dynamics, nor did we accurately locate the boundaries between regions of parameters that lead to different dynamics. Therefore, Fig. 15 gives only a rough overview of which type of dynamics can be expected to occur for a given combination of behavioral responsiveness and pelagic mortality, presented as a cartoon bifurcation diagram. The dynamics predicted by the model with discrete habitat shifts resemble the patterns occurring for the model with continuous habitat choice in case the behavioral responsiveness is high ( $\sigma = 100$ ).

The model results presented in this paper predict that substantial population effects of flexible behavior are only to be expected when pelagic mortality levels would cause extinction of the consumer population if the individuals did not respond to difference in habitat conditions (Fig. 15). Under these conditions, YOY

spend longer periods of time in the littoral habitat, both in case of discrete and continuous habitat shifts, before moving out into the pelagic habitat. This increased use of the littoral habitat allows the YOY to evade high pelagic mortality and ultimately leads to increased population persistence. A comparable increase in persistence has been found in unstructured population models incorporating flexible behavior (Gleeson and Wilson 1986, Fryxell and Lundberg 1993, 1994, Krivan 1996, 1997, Van Baalen et al. 2001).

Our results indicate, however, that the increased persistence occurs independent of how strongly consumers respond to differences in habitat profitability (Fig. 15). If consumer responsiveness to habitat profitability is high, as is the case when individuals exhibit a discrete habitat shift or for steep response functions with continuous habitat choice (i.e., high  $\sigma$  values; see Fig. 2), YOY spend most of their first year in the littoral habitat and are only driven out into the pelagic by competition from the subsequent YOY cohort. This may cause large-amplitude fluctuations at high levels of pelagic mortality, because the competition among the YOY themselves in the littoral habitat incorporates a potentially overcompensating mechanism: large YOY cohorts may produce small offspring cohorts as their body size at the moment of habitat shift is low through retarded growth (Fig. 15). If consumer responsiveness to habitat profitability is low (i.e., low  $\sigma$  values in case of continuous habitat choice; see Fig. 2) fixed-point dynamics occur instead. In this case, YOY always spend at least 25% of their time in the pelagic habitat. Although this causes substantial YOY mortality (the survival until maturation is significantly lower than when consumers respond more rapidly to profitability), the surviving individuals fare better. They reach larger body sizes and higher fecundities, such that the total population biomass is also significantly higher than for larger  $\sigma$  values. An increase in consumer responsiveness to differences in habitat profitability thus decreases growth and fecundity of surviving consumers, decreases total population biomass, and increases the likelihood of population fluctuations.

Depending on responsiveness, the increased consumer persistence, which results from flexible behavior, may thus be associated either with large-amplitude fluctuations or with fixed-point dynamics (Fig. 15). These results resemble the results of unstructured models incorporating optimal foraging or switching behavior of consumers. When optimal foraging by consumers follows a stepwise response to changes in resource levels, population cycles may be induced by the behavioral response per se (Gleeson and Wilson 1986, Krivan 1996, Van Baalen et al. 2001). In contrast, switching behavior of predators, representing a more gradual response to changes in resources, tends to stabilize population dynamics (Murdoch and Oaten 1975, Van Baalen et al. 2001). For an unstructured model Van Baalen et al. (2001) show that a lower responsiveness leads to

a functional response with a more convex shape, which fulfills the necessary condition for stability of the equilibrium. This route to equilibrium stability contrasts with the mechanism operating in the size-structured consumer-resource model, since in the latter the change in stability is clearly determined by the competition within and among different-sized cohorts.

#### *Patterns of habitat use and ideal free distributions*

Littoral resource densities are depleted almost instantaneously after each reproduction pulse, because of the large number of YOY produced. If individuals are capable of continuously adapting their use of both habitats, they will move out into the pelagic habitat for part of their time and distribute themselves in a way that is close to an ideal free distribution. A dynamic, ideal free distribution also occurs in unstructured models of identical consumers (Krivan 1997). The ideal free distribution of YOY allows them to control both resource densities, drive larger individuals to starvation, and hence induce single-cohort cycles. As in the size-structured, consumer-resource model studied by Persson et al. (1998), abundant YOY cohorts thus play a crucial role in the dynamics and induce single-cohort cycles at low levels of pelagic mortality. This co-occurrence of ideal free distributions and high-amplitude fluctuations contrasts with the often implicit assumption that ideal free distributions ensure population dynamic stability (Fretwell and Lucas 1970, Sutherland and Parker 1985, 1992).

While under most conditions YOY will initially distribute their time over both habitats, they will reside almost exclusively in the littoral zone when individuals respond strongly to differences in habitat profitability and pelagic mortality is high. Older and larger individuals are most often restricted to the pelagic habitat, unless responsiveness to profitability differences is low, in which case the pelagic is used by 1- and 2-yr-old individuals, with still older individuals exclusively foraging on the littoral resource. These observations resemble patterns of habitat use in, for example, bluegill sunfish (*Lepomis macrochirus*; Dimond and Storck 1985, Werner and Hall 1988) where the YOY often use both the littoral and open-water habitat during some period, while during the rest of their life they seem to be more bound to one of the habitats at a time. The usual hypothesis concerning the use of the pelagic by YOY bluegill, is that very small individuals are invulnerable to predation by larger piscivores. Mortality risks in the pelagic are hence low for a short period after hatching, which allows the YOY to exploit it. Our model predicts a similar pattern of habitat use, which is, however, entirely driven by the feedback of the YOY on littoral and pelagic resources and does not depend on an invulnerable size window early on in life. Which of these explanations is more relevant for the habitat use of YOY bluegill, can only be determined by detailed measurements of the resource dynamics during

the period in which bluegill shifts to the pelagic and back. Existing data (Mittelbach 1981) do not have sufficient resolution, but do hint at a concomitant decline in both littoral and pelagic resource during the first part of the growing season. Thus, they seem to support the idea that the population feedback of YOY on both resources may be a crucial factor in their pattern of habitat use.

#### *The effect of refuge size*

The relative sizes and productivities of the littoral and pelagic habitat parts may play an important role in determining the population dynamics. The large volume of the pelagic constitutes the basis for a high total productivity, and therefore a high total population fecundity. The feedback of the large number of YOY is significantly intensified in the littoral habitat, because it only occupies 10% of the total lake volume. This specific size of the littoral refuge as fraction of the total lake volume was chosen to reflect a typical lake morphology in northern Scandinavian lakes. Larger littoral zones, such as occur at lower latitudes, and especially lower pelagic productivities may allow for a more extensive influence of flexible behavior on the population dynamics.

To test for the influence of refuge size, we also studied the bifurcation pattern of the model with both the discrete habitat shifts and continuous habitat choice scenario, assuming that the littoral refuge part occupied 40% of the total lake volume. These results (not shown) indicate that an increase in refuge size generally increases total population biomass for all values of the pelagic mortality constant  $\mu_p$  and all values of consumer responsiveness  $\sigma$ . However, an increased refuge size does not induce qualitatively different dynamics. For low values of  $\mu_p$  single-cohort cycles occur, albeit over a slightly smaller range of parameters as compared to a 10% littoral zone fraction. Flexible behavior, both the discrete habitat shift and continuous habitat choice scenario, increases population persistence independent of the strength of consumer responsiveness to profitability differences. For high consumer responsiveness, population dynamics become unstable at a value of the pelagic mortality constant  $\mu_p$  that turns out to be virtually the same for the case with a large (40%) and a small (10%) littoral zone. Finally, also when the refuge size is larger, an increase in consumer responsiveness to habitat profitability differences decreases total population biomass and mean annual fecundity of the surviving individuals.

Thus, in contrast to intuitive expectations, the size of the refuge does not play an important role in determining the population dynamic outcome. Total population biomass, and thus the population feedback on individual life history, adjusts itself to the larger refuge size, such that the changes at the individual level are minimal. As a consequence, the larger refuge size also

induces little change to the competitive relationships within the consumer population.

#### *Different rules of individual behavior*

The results presented in this paper do not seem to depend strongly on the choice of the profitability measures (Eqs. 3 and 4) for the littoral and pelagic habitat, respectively. We have obtained roughly the same dynamic pattern when using the difference between the mass-specific growth rate and the mortality rate as profitability measure. For example, for the littoral habitat the profitability would in this case be described by

$$\frac{[k_c I_1(z_1, x) - E_m(x, y)]}{x + y} - d_1(x, y).$$

By maximizing the above quantity, a cohort of individuals would at any moment in time maximize its expected rate of change in total cohort biomass (derivation not presented). In addition, we have also obtained roughly similar results when assuming that pelagic mortality is a stepwise function of body size, adopting a constant but high value for juvenile individuals and a value equal to the background mortality in the littoral habitat after maturation. All model variants that we have studied show that ontogenetic niche shifts and flexible behavior increase consumer persistence, but that at low levels of pelagic mortality they cannot stabilize single-cohort cycles, while at high levels of pelagic mortality they may induce large-amplitude cycles in which the abundance of a YOY cohort strongly determines its subsequent fate (cf. Figs. 8 and 12). Stable fixed-point dynamics occur only for intermediate levels of pelagic mortality. This region of fixed-point dynamics is significantly larger when consumers do not strongly respond to differences in habitat profitability.

The results presented here (1) reveal that flexible behavior may play an important role in determining the outcome of competition within and between cohorts, and (2) lead to predictions about patterns of habitat use during their life history. In contrast to previous studies (Werner and Gilliam 1984) these predictions not only incorporate dependence on body size and habitat-specific resource and mortality conditions, but also take into account the feedback of consumers on both resources, as it is modulated by their flexible behavior itself. Given that different measures of habitat profitability lead to qualitatively similar results, we conclude that the precise way in which individual consumers weigh mortality risks against feeding advantages in their choice of habitat is of minor importance. Rather, it is the population feedback, especially from small, competitively superior individuals, in combination with the responsiveness to this feedback, that ultimately determines the pattern of habitat use of individual consumers during their life history.

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## APPENDIX

## POPULATION-LEVEL MODEL FORMULATION

The pulsed reproduction process ensures that there exists a natural subdivision of the consumer population into a variable number ( $c$ ) of cohorts. Every cohort is characterized by a set of variables ( $N_i, x_i, y_i$ ), representing the total number of individuals,  $N_i$ , making up the cohort, their irreversible mass,  $x_i$ , and reversible mass,  $y_i$ , respectively. The index  $i = 1, \dots, c$  refers to the cohort number, which is only used for bookkeeping purposes. The state of the resource populations in the littoral and pelagic habitat are represented by the biomass densities  $z_l$  and  $z_p$ , respectively.

*Within-season dynamics*

The dynamics of the consumer population during the growing season is described by a set of ordinary differential equations (ODEs) for the change in number of individuals in the various cohorts, their reversible and their irreversible mass. Under growing conditions, i.e.,  $E_g(z_p, z_l, x_i, y_i) > 0$ , the ODEs for  $N_i, x_i$  and  $y_i$  are given by (see also Table 2):

$$\frac{dN_i}{dt} = -d(z_p, z_l, x_i, y_i)N_i \quad (\text{A.1a})$$

$$\frac{dx_i}{dt} = \kappa(x_i, y_i)E_g(z_p, z_l, x_i, y_i) \quad (\text{A.1b})$$

$$\frac{dy_i}{dt} = [1 - \kappa(x_i, y_i)]E_g(z_p, z_l, x_i, y_i) \quad i = 1, \dots, c. \quad (\text{A.1c})$$

When food is scarce and individual maintenance requirements are higher than the current energy assimilation rate, i.e.,  $E_g(z_p, z_l, x_i, y_i) < 0$ , growth in irreversible mass stops and the energy deficit is covered from reversible mass:

$$\frac{dN_i}{dt} = -d(z_p, z_l, x_i, y_i)N_i \quad (\text{A.2a})$$

$$\frac{dx_i}{dt} = 0 \quad (\text{A.2b})$$

$$\frac{dy_i}{dt} = E_g(z_p, z_l, x_i, y_i) \quad i = 1, \dots, c. \quad (\text{A.2c})$$

The dynamics of the resource populations in both the littoral and pelagic habitat are governed by ODEs, which are coupled to the equations above by the foraging of the consumer cohorts:

$$\frac{dz_p}{dt} = r_p(K_p - z_p) - \frac{1}{V_p} \sum_{i=1}^c F(z_p, z_l, x_i, y_i)I_p(z_p, x_i)N_i \quad (\text{A.3a})$$

$$\frac{dz_l}{dt} = r_l(K_l - z_l) - \frac{1}{A_l} \sum_{i=1}^c [1 - F(z_p, z_l, x_i, y_i)]I_l(z_l, x_i)N_i. \quad (\text{A.3b})$$

Regrowth of the resource populations follows a semiche-mostat dynamics with parameters  $r_l$  and  $K_l$  or  $r_p$  and  $K_p$  for the littoral and pelagic resource, respectively (see Table 3). The factors  $1/A_l$  and  $1/V_p$  occur in these equations, because resource densities are expressed as biomass per unit bottom surface and lake volume, respectively, while the consumer population is expressed in terms of the number of individuals in the entire lake.

When individuals use both habitats proportionally,  $\sigma$  equals 0 in Eq. 6 and the value of the function,  $F(z_p, z_l, x, y)$ , is equal to 0.9 for all cohorts. In case of the discrete habitat shift scenario,  $F(z_p, z_l, x, y)$  assumes the value of 0 for newborn individuals and is set to 1, as soon as the profitability of the pelagic habitat becomes larger than the littoral profitability,  $Q_p(z_p, x, y) > Q_l(z_l, x, y)$ . For the continuous habitat choice scenario the value of  $F(z_p, z_l, x, y)$  for each cohort is specified by Eq. 6.

*Between-seasons dynamics*

For every cohort of consumer individuals a set of ODEs (A.1) (or A.2 for starving cohorts) is solved numerically from the beginning of the growing season until the beginning of the next growing season. The ODEs (A.3) for the dynamics of the resources are solved simultaneously. At the beginning of the growing season consumer reproduction takes place, which is described by a discrete map. A new consumer cohort arises with the following state:

$$N_1 = \sum_{i=1}^c f(x_i, y_i)N_i \quad (\text{A.4a})$$

$$x_1 = \frac{1}{1 + q_j} m_b \quad (\text{A.4b})$$

$$y_1 = \frac{q_j}{1 + q_j} m_b \quad (\text{A.4c})$$

while the state of all reproducing cohorts is reset such that  $y_i = q_j x_i$ . Simultaneously, the indices of all existing cohorts are renumbered for bookkeeping reasons:

$$N_{i+1} = N_i \quad (\text{A.5a})$$

$$x_{i+1} = x_i \quad (\text{A.5b})$$

$$y_{i+1} = \begin{cases} q_j x_i & \text{if } f(x_i, y_i) > 0 \\ y_i & \text{otherwise} \end{cases} \quad i = 1, \dots, c. \quad (\text{A.5c})$$

These operations increase the number of consumer cohorts by 1. The number of cohorts is kept limited by removing cohorts from the population that have become of negligible size (i.e.,  $N_i < 1$ ) due to background or starvation mortality.