ADAPTIVE HABITAT USE IN SIZE-STRUCTURED POPULATIONS: LINKING INDIVIDUAL BEHAVIOR TO POPULATION PROCESSES

Lennart Persson[1,3] and André M. De Roos[2]

[1]*Department of Ecology and Environmental Science, Umeå University, SE-901 87 Umeå, Sweden*
[2]*Institute of Biodiversity and Ecosystem Dynamics, University of Amsterdam, POB 94084, NL-1090 GB Amsterdam, The Netherlands*

Abstract. The inclusion of flexible behavior in population models can be viewed as part of the development of a mechanistic population/community framework based on individual-level concepts. Based on short-term experiments and analyses of the dynamics of nonstructured models, trait-mediated indirect effects resulting from flexible behavior have been suggested to have major effects on population and community dynamics. We use physiologically structured population models (PSPMs) to account for and assess the importance of flexible behavior in population models where individuals differ substantially in size. We investigate a consumer–resource system in which a size-structured consumer feeds on two resources that are present in two habitats differing in predation risk (pelagic open water vs. littoral vegetation). We compare two flexible rules that individuals might use to trade off foraging gains and size-dependent mortality risks in the two habitats. One rule maximizes the ratio of growth over mortality, and the other optimizes the expected instantaneous biomass increase.

As a result of strong population feedback, the dynamics and habitat use are qualitatively the same for both rules when open-water mortalities are low, and indeed differ little from a case in which individuals use the two habitats in a fixed proportion. At higher open-water mortalities, the consumers using the two flexible rules show high-amplitude population cycles, whereas consumers using a fixed rule cannot persist. Overall, our results suggest that the behavioral rule used by individuals may be of minor importance, whereas the population feedback is of major importance. In nonstructured models, increased persistence induced by flexible behavior co-occurs with destabilization, as we find here, but the mechanisms behind this pattern are different, driven by cohort cycles rather than by the paradox of enrichment. We argue that extrapolating from experimental data which describe short-term experiments may overemphasize or misrepresent the long-term, population-level effects of flexible behavior. The inclusion of behavior as a proper individual state in physiologically structured population models remains a fundamental issue to solve.

Key words: adaptive habitat use; cohort dynamics; flexible behavior; foraging; individual state; Markov process; mechanistic theory; optimality; population dynamics; population state; predation risk; size structure.

INTRODUCTION

Pioneer papers on flexible behavior focused on optimal foraging or, as stated by MacArthur (1972), on the economics of consumer choice (MacArthur and Pianka 1966, Schoener 1969, Charnov 1976, Pyke et al. 1977). One of the motivations for developing foraging theory at that time was to progress toward a deeper understanding of consumer–resource interactions, including the habitat and diet choices of consumers (Schoener 1986, Tilman 1987, Persson and Diehl 1990). Furthermore, behaviorally oriented ecologists argued that flexible behavior should have major effects on population and community dynamics (Dill 1987, Lima and Dill 1990). In a broader context, the whole endeavor of including flexible behavior in pop-

ulation and community ecology can be viewed as part of an attempt to develop a more mechanistic, individual-based approach to ecology in which individual-level concepts form the basis for a conceptual framework upon which to develop an understanding of population- and community-level processes (Schoener 1986, Tilman 1987, DeAngelis and Gross 1992). Schoener (1986) suggested that there was no formal impediment to extending the domain of mechanistic models to include behaviorally flexible individuals. At the same time, he recognized practical impediments, in the form of increased model complexity, as obstacles (Schoener 1986, Persson and Diehl 1990, Werner 1998; see also Inchausti [1994] for a general treatment of reductionism in ecology).

In support of early claims about the importance of behavior for population and community processes, population models accounting for adaptive or flexible behavior show that it has a number of dynamical con-

sequences. For example, adaptive behavior in prey in one-predator–one-prey situations may stabilize predator–prey interactions (Ives and Dobson 1987, Mangel and Roitberg 1992). Flexible behavior may dampen oscillations in optimally foraging one-predator–two-prey situations, but also may cause the loss of stable equilibria (Gleeson and Wilson 1986, Fryxell and Lundberg 1994, Křivan 1996, 1997, Křivan and Sikder 1999). Studies of community modules including three feeding levels predict that, along productivity gradients, correlations in abundance of species at adjacent feeding levels may result from adaptive behavior at one or several levels. Models excluding adaptive behavior show no such correlations between feeding levels (Abrams 1996, Abrams et al. 1996).

All of these population models accounting for flexible behavior have in common the assumption that there is no variation in traits among individuals. This ignores the fact that many of the species, which have been experimentally studied to investigate the effects of adaptive behavior, are typically characterized by a high degree of size variation among individuals within populations. Examples include insects, fish, and amphibians (Mittelbach 1981, Werner et al. 1983*a*, *b*, Persson and Greenberg 1990, Werner and Anholt 1993, Beckerman et al. 1997, Schmitz et al. 1997, Peacor and Werner 2001). Furthermore, decision rules derived at the individual level to predict the habitat use of individuals as a function of habitat-dependent foraging gains and predations risks, in many cases, have been set in a size-dependent context. This concerns models in which a time horizon is either absent (Gilliam 1992, Werner and Gilliam 1984) or present (Clark and Levy 1988, Ludwig and Rowe 1990, Crowley and Hopper 1994).

Where population models with flexible behavior have ignored individual (size) variation, the experimental studies on flexible behavior considering size variation have not assessed its importance in a full population dynamical context. Rather, they have commonly been restricted to time spans shorter than one generation, too short for any population feedback to have a significant influence (Persson and Eklöv 1995, Schmitz et al. 1997, Peacor and Werner 2001). Both types of studies thus give only a partial answer to the question of how flexible behavior affects population and community processes in size-structured systems. Furthermore, in unstructured consumer–resource models, flexible behavior of consumers generally modifies the strength of their interaction with the resource population(s). In such systems, flexible behavior directly influences the interaction that may stabilize or destabilize dynamics. In size-structured consumer–resource models, however, dynamics are primarily determined by size-dependent resource competition between different consumer cohorts (Persson et al. 1998). These interactions are at most indirectly affected by any (size-dependent) foraging behavior of the consumers. Mod-

els of unstructured populations incorporating flexible behavior may therefore have little to say about the effects of flexible behavior in size-structured systems, and a direct relationship between the effects of flexible behavior in structured and unstructured settings cannot be expected a priori.

In this paper, we discuss the influence of flexible behavior and population feedback on the long-term dynamics of a population in which individuals differ in body size and the behavioral response is size dependent. Using physiologically structured population models (PSPMs) (Metz et al. 1988, De Roos et al. 1992), we show how to link individual behavior to population dynamics in populations exhibiting size variation. In a previous paper, we studied the dynamics of a size-structured consumer population feeding on two resource populations in two habitats where one habitat was more risky (De Roos et al. 2002). We analyzed the effects of variation in mortality rate in the more risky habitat for scenarios in which individuals have (1) fixed behavior, (2) change habitat once and instantaneously during their life, and (3) continuously adapt the proportion of time that they spend in each habitat. We discuss the results of this analysis in relation to the impact of trait-mediated indirect effects. Second, we use the third scenario as a case to explore the effects of two different decision rules by which individuals trade off foraging gains vs. mortality risk between two habitats in a size-specific way. Our general finding is that the population dynamics and patterns of habitat use observed are largely independent of which decision rule was used and, instead, are largely determined by the population feedback. We furthermore contrast the results from our modeling of long-term population dynamics, which underline the importance of population feedback brought about by size-dependent competition among different consumer cohorts, with the results from short-term experiments lacking complete population dynamics and showing strong effects of flexible behavior.

Finally, we address the important problem of mechanistically introducing behavior in population models based on optimality arguments. This problem is related to defining (1) an appropriate individual state (sensu Metz et al. 1988), and (2) an optimality criterion that an organism can use on a short time scale for behavioral decisions and that also determines the outcome of selection under population feedback (Mylius and Diekmann 1995). Our conclusion is that the incorporation of flexible behavior as part of the individual's state in a population dynamical framework beyond a phenomenological description remains a fundamental problem that becomes increasingly apparent in the modeling of size-structured interactions.

MODELING FRAMEWORK

Individual state

Studying the effects of flexible behavior on population and community dynamics in a mechanistic way

entails, at the basic level, the process of finding a stringent relationship between individual- and population-level processes. In physiologically structured models, this relationship is explicitly handled by using a state concept at each of the two levels of organization: an *i* state that represents the state of the individual in terms of a collection of characteristic physiological traits (size, age, sex, energy reserves, etc.), and a *p* (population) state that is the frequency distribution over the space of possible *i* (individual) states (Metz and Diekmann 1986, Metz et al. 1988, Caswell and John 1992, DeAngelis and Gross 1992, De Roos 1997). The model formulation process consists of deriving a mathematical description of how individual performance such as feeding, growth, and mortality is related to the characteristics of the individual and the condition of its environment, whereas the derivation of the *p* (population) state dynamics is subsequently only a matter of bookkeeping. Therefore an important characteristic is that all model assumptions apply to the individual level. Compared to traditional models, physiologically structured models offer a more straightforward way to explicitly and mechanistically link individual-level processes to population-level phenomena. Generally, it can be said that a collection of variables qualifies as the *i* state of the system if (1) the behavior of the system at time *t* is fully determined by the values of these variables plus the condition of the environment, and (2) the values of these variables at $t + \tau$ are fully determined by their values at *t* plus the intervening environmental history (Metz et al. 1988). The *i* state and its dynamics thus fulfill the criteria of a Markov process. We will consider this issue in more detail in the discussion when dealing with the question of how flexible behavior can be incorporated as part of the individual-level dynamics.

We use as an example a size-structured consumer population feeding on two resource populations that are not size structured, each of which is found in one of two habitats (the pelagic open water or the littoral vegetation habitat). Feeding, metabolism, growth, and mortality of the consumer are continuous processes, whereas reproduction in the consumer takes place discretely once every year. Our model is deterministic and belongs to the class of physiologically structured models called distribution models, meaning that distributions, rather than separate individuals, are followed over time (Caswell and John 1992). We will first give a description of the individual-level formulations, and thereafter a short description of how the population level is handled. For a full description of the model formulations and parameter values, we refer to Persson et al. (1998) and De Roos et al. (2002).

Individual level descriptions.—The core part of the structured population model is a description of the dynamics of individual consumers, which includes processes such as individual feeding, growth, development, reproduction, and mortality, as a function of the current state of the individual and the condition of the environment (here, the resource levels and mortality rates in the two habitats). We assume that the consumer's foraging, metabolism, growth, survival, and reproduction at each given resource density can be described as functions of two physiological variables, irreversible and reversible mass. In irreversible mass, *x*, we include compounds such as bones and organs that cannot be starved away by the consumer. In reversible mass, *y*, we include energy reserves such as fat, muscle tissue, and gonads. These reserves can be used to cover basic metabolism during starvation. Hence, the total mass of the individual equals $x + y$. The individual can tolerate a decrease in reversible mass to a threshold value $(q_s x)$ below which it starts to die of starvation (starvation mortality, μ_s). Functions describing the relationships between energy intake and growth, metabolism, partitioning into reproductive tissue, and starvation are given in Persson et al. (1998). Here we only discuss the functions pertaining to foraging on the two resources and the mortality in the two different habitats.

The resource-dependent attack rates, $a_v(x)$ and $a_p(x)$, for the littoral resource and pelagic resource, respectively, are functions of the consumer's irreversible mass only. For both attack rates, we thus assume that the condition of the individual (represented by *y*) does not affect its foraging rate. The attack rate on the pelagic resource is a hump-shaped function (Persson et al. 1998), whereas we use an allometric form for the attack rate on the littoral resource function of irreversible mass (De Roos et al. 2002). Generally, the attack rate on a specific prey size as a function of consumer size is expected to be hump shaped (Persson et al. 1998). However, the hump is displaced to the right for the larger littoral macroinvertebrate prey compared to the smaller zooplankton prey. Consumer sizes observed in the simulations are all to the left of the hump of the size-dependent attack rate for the macroinvertebrate prey, which allows the use of a simpler power function for this prey type. Handling of prey is given as an allometric function of consumer size (Claessen et al. 2000) in terms of digestion time per unit mass of prey. It is identical for the pelagic and littoral resources. The foraging rate of individual consumers on the two resources is assumed to follow a Holling Type II functional response (see Persson and Greenberg [1990] for experimental evidence).

We assume that all individuals experience the same constant background mortality in the vegetation (refuge) habitat, independent of size. The pelagic habitat is riskier and individuals here, in addition to this constant background mortality, will also experience a size-dependent mortality given by

$$\mu_p \exp\left(-\frac{x}{x_p}\right) \qquad (1)$$

where μ_p is a constant and x_p sets the size scaling of

this additional pelagic mortality rate. The total mortality that an individual experiences thus equals the sum of background mortality, starvation mortality, and the explicit size- and habitat-dependent predation mortality. The higher mortality in the pelagic habitat results because predators are more efficient in unstructured environments (Werner et al. 1983*a*, Person and Eklöv 1995). No population dynamics or dynamics in habitat use of predators are assumed.

Decision rules.—Charnov's (1976) foraging model for prey selection has been used in several studies to predict habitat shifts in size-structured populations (Mittelbach 1981, Werner et al. 1983*b*, Persson and Greenberg 1990). Because of its threshold behavior, in which a prey or habitat either is not used at all ($p = 0$) or is used as encountered ($p = 1$), it is not at all straightforward to link this individual foraging model to population-level formulations (Křivan 1996, 1997). De Roos et al. (2002) derived for a size-structured situation a formulation that avoids the step function by letting the tendency of an individual to leave the pelagic habitat be proportional to $\exp(-\sigma Q_p(z_p, x, y))$, and letting p the tendency to leave the littoral be proportional to $\exp(-\sigma Q_v(z_v, x, y))$. Here Q_p and Q_v are the profitabilities of the pelagic and the littoral habitats, respectively; z_p and z_v are the resource levels in the pelagic and littoral habitats, respectively; and σ is a proportionality constant that determines how fast an individual responds to a change in resource levels.

We assume that individuals split their time between the littoral and the pelagic habitats, where F represents the fraction of time that they spend in the pelagic habitat and $(1 - F)$ is the fraction that they spend in the littoral habitat. In addition to assuming that the rate at which the individual leaves a habitat is inversely proportional to the exponential of that habitat's profitability, as previously discussed, we will also assume that this rate is inversely proportional to the volume of the habitat (V_p for pelagic habitat, V_v for littoral habitat). On a short time scale, the dynamics of the time fraction F that an individual of a specific size spends in the pelagic habitat can hence be described by

$$\frac{dF}{dt} = -\frac{\exp[-\sigma Q_p(z_p, x, y)]}{V_p} F$$
$$+ \frac{\exp[-\sigma Q_v(z_v, x, y)]}{V_v}(1 - F). \quad (2)$$

The total intake of an individual that splits time between the two habitats is given by

$$I(z_p, z_v, x, y) = F(z_p, z_v, x, y)I_p(z_p, x)$$
$$+ [1 - F(z_p, z_v, x, y)]I_v(z_v, x) \quad (3)$$

where I_p is the food intake in the open-water habitat and I_v is the food intake in the vegetation habitat.

We use two different measures of habitat profitability, both of which take foraging gains and mortality

risks into account. The main reason for using two different measures is to investigate the extent to which the choice of a specific rule affects the population dynamics observed. The first rule has been investigated in detail with respect to the effects of size-dependent pelagic mortality rate on the size-dependent habitat use of individuals and population dynamics (De Roos et al. 2002). In this case, individuals are assumed to maximize the ratio of growth rate (g) over mortality (μ): (g/μ). This formula is the inverse of the μ/g ratio that was derived by Gilliam (1982) to predict habitat choice of juveniles in a stable population without a time horizon. The former formula avoids the problem of the latter formula when individuals are not growing ($g = 0$).

In the second case, we assume that individuals optimize their expected, instantaneous rate of biomass increase, given that next to growing at a rate $g(t)$ they have a probability $\mu(t)$ per unit time of dying. An individual with mass $(x + y)$ should, in this case, optimize the quantity $g(t)/(x + y) - \mu(t)$ (per day, derivation not shown). In both cases, growth depends on the resource densities in the vegetation (z_v) and the pelagic (z_p) habitat and on the irreversible and reversible mass, x and y, respectively. Growth is the summation of energy intake (which, as previously stated, only depends on x) and the maintenance expenditure (which depends on both x and y). Mortality is specified by the function $\mu(x, y)$, which depends on both x and y because of the possibility of starvation mortality. For the first rule, the profitabilities of the pelagic (Q_p) and the littoral (Q_v) habitats are given by

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

$$Q_v(z_v, x, y) = \frac{k_e I_v(z_v, x) - E_m(x, y)}{\mu_v(x, y)}. \quad (5)$$

Here k_e is a conversion efficiency constant translating food intake rate to energy assimilation rate; the function E_m represents the metabolic demands; and μ_p and μ_v are the mortality rates in the pelagic and littoral habitats, respectively. For the second rule, the profitabilities of the pelagic (Q_p) and the littoral (Q_v) habitats are

$$Q_p(z_p, x, y) = \frac{k_e I_p(z_p, x) - E_m(x, y)}{(x + y)} - \mu_p(x, y) \quad (6)$$

$$Q_v(z_v, x, y) = \frac{k_e I_v(z_v, x) - E_m(x, y)}{(x + y)} - \mu_v(x, y). \quad (7)$$

It should be noted that both rules are derived on the basis of optimality arguments, which is a questionable assumption that we will return to in the *Discussion*.

Population state

At the population level, the model describes the consumer–resource dynamics during the growth season

corresponding to summer in the temperate region. It is assumed that changes in consumer and resource populations during the nongrowth (winter) season are negligible (or accounted for simply by an overall scaling down of processes; see Persson et al. [1998]). As previously described, consumer consumption, metabolism, growth or starvation and mortality, and resource dynamics are continuous processes, whereas reproduction of the consumer population is a discrete event taking place once every year. The model is thus a combination of a continuous dynamical system describing the growth and mortality of consumers and resource dynamics, and a discrete map handling the discrete reproductive event every spring.

Analytically, one can formulate physiologically structured population models as a system of integral equations, which is a way of tracking the dynamics of all individuals that constitute the population (see Persson et al. 1998). Numerically, the models can be studied using the EBT (Escalator Boxcar Train) method (De Roos 1988, De Roos et al. 1992; see also De Roos 1997 for an extensive introduction to physiologically structured models including the EBT). This method has been designed specifically for the numerical integration of the equations that occur in physiologically structured models. The EBT method was also used to carry out the numerical studies reported in this paper.

The pulsed-reproduction process ensures that there exists a natural subdivision of the population into cohorts of individuals that all have the same age and reversible and irreversible mass. All individuals within a cohort are assumed to grow at the same rate, i.e., individuals belonging to a given cohort do not diverge in their allocation to reversible and irreversible masses. The dynamics of every cohort can therefore be described by a system of three ordinary differential equations, which keep track of the number of individuals making up the cohort, their reversible mass, and their irreversible mass. The dynamics of the entire consumer population, both in terms of its abundance and its state, can then be followed throughout the growth season by numerically integrating the system of ordinary differential equations for each cohort separately.

At the beginning of the season, new cohorts of individuals are added to the consumer population through reproduction. This addition implies that the number of differential equations describing the population dynamics increases. At the same time, the current value of the reversible mass in the cohorts of reproducing individuals is reset because of their investment into offspring. Overall, the model simulations thus involve the numerical integration of a 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 (see De Roos et al. 1992). 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.

The two resources are assumed to occur in two separate habitats, the open-water and vegetation habitats. The population growth of the two resources is continuous and is described by semi-chemostat dynamics; hence, the inflow rate of the resources is independent of consumer ingestion (cf. De Roos et al. 2002). Changes in the two resource populations are followed by the numerical integration of two ordinary differential equations for the resource dynamics that incorporate the semi-chemostat growth and the total resource consumption. The latter equals the summed foraging rate over all cohorts and represents the population feedback on the resources and, in turn, through the resulting changes in resource levels, on the life history of individual consumers themselves. Semi-chemostat dynamics may be more realistic than the commonly used logistic growth dynamics when (1) the resource has a physical refuge or (2) the resource includes invulnerable (smaller), albeit mature, size classes that grow into a vulnerable size range (Persson et al. 1998).

Parameterization of the model

The model was parameterized based on experimental data for Eurasian perch (*Perca fluviatilis*). Parameter values for attack rates, handling times, and metabolic demands have been estimated experimentally for perch (Persson and Greenberg 1990, Byström and Garcià-Berthoú 1999). These parameter values are given in De Roos et al. (2002). Habitat use that depends on resources and predation risk has also been shown to occur in perch (Persson 1993, Diehl and Eklöv 1995, Persson and Eklöv 1995), even during its early life stages (Byström et al., *in press*). In our model, the cladoceran *Daphnia* and the megalopteran *Sialis* represented the open water and littoral prey, respectively (for details, see De Roos et al. 2002). The two habitats differed in size, with the pelagic habitat making up 90% of the total lake volume and the littoral habitat the remaining 10%.

The size-independent background mortality, μ_b, was set to 0.01 in both habitats for all individuals. We analyzed the dynamics of the model as a function of the proportionality constant μ_p in the size-dependent pelagic mortality (Eq. 1). Because the profitability measures used in the two flexible-behavior rules quantitatively measure profitability in units that are of different orders of magnitude, different σ values were used when comparing the two rules. For the g/μ rule, we used a σ value of 100 and for the $g/(x + y) - \mu$ rule, a σ value of 1000. Both values represent a high responsiveness to environmental changes (De Roos et al. 2002). The choices of σ values were thus chosen to not let the degree of responsiveness affect the dynamics (see De Roos et al. [2002] for an analysis), but rather to study the different optimization criteria in the two decision rules.

RESULTS

Comparing the population-level consequences of the two decision rules

Our previous studies have shown that, given the size-scaling relationships of foraging and metabolic rates documented for perch, as well as for other fish species that feed as planktivores or benthivores, large-amplitude dynamics driven by dominating recruiting (young-of-the-year, YOY) cohorts prevail. These so-called single-cohort cycles occur because the smallest individuals have the highest competitive ability (lowest minimum resource requirements; Persson et al. 1998). De Roos et al. (2002) showed that the dynamics are unaffected by the introduction of a second shared resource if the two resources are used indiscriminately. The dynamics do not change because the dominating cohort controls both the vegetation and pelagic resource, keeping them both at levels that are too low for other cohorts to survive. An increase in the pelagic mortality constant μ_p results in a decrease in cycle length, because the more rapid decline in abundance of the dominant cohort allows the resources to recover faster, leading to increased growth rate and earlier maturation of individuals. Increasing the pelagic mortality constant (μ_p) above 0.08 in the one-consumer–two-resources system with proportional habitat use results in the collapse of the cohort cycles into stable fixed-point dynamics (De Roos et al. 2002).

Introducing flexible behavior using the g/μ rule does not change the dynamics in the region of cohort cycles to any extent (Fig. 1). The dynamics strongly resemble the dynamics observed without flexible behavior, because a dominating YOY cohort depletes the vegetation resource early on in its life and therefore soon starts to exploit the pelagic resource to the same extent as for fixed habitat use, i.e., proportional to the habitat's volume (90% of the time in the pelagic; Fig. 1C). Individuals of the dominant cohort split their time between habitats in approximately an ideal free distribution. Using the $g/(x + y) - \mu$ rule instead of the g/μ rule does not have an effect on the dynamics either, in terms of both the observed fluctuations in abundance and the pelagic habitat use of the YOY (i.e., the time fraction spent there; Figs. 1 and 2). In the parameter region with a pelagic mortality constant up to 0.08, the single-cohort cycles described in Persson et al. (1998) are thus insensitive to (1) the addition of a second resource, (2) the addition of flexible habitat use, and (3) which of the two rules was used for flexible habitat use. This insensitivity to assumptions about habitat use is the result of the strong feedback that a dominant cohort exerts on the resources: even though consumers can respond to differences in habitat profitability, the flexible behavior does not change the dominance relationships between different cohorts in either of the two habitats. Within this parameter region, alternative types of dynamics are possible, but also the alternative
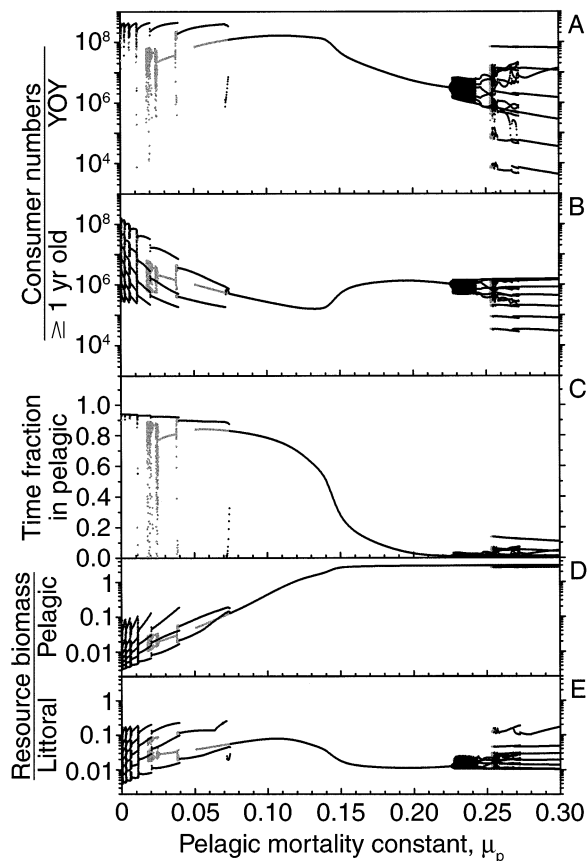

FIG. 1. Bifurcation diagram of the model when habitat profitability is determined by the g/μ rule. (A) Number of young-of-the-year (YOY) individuals, (B) number of individuals ≥ 1 yr old, (C) the proportion of time that YOY fish spend in the pelagic habitat, (D) biomass (g/m^3) of the pelagic resource, and (E) biomass (g/m^2) of the littoral resource are shown as a function of the pelagic mortality constant, μ_p. Data refer to the system at the time of reproduction. Symbols in different shades of gray indicate the presence of alternative attractors. Observe that μ_p runs between 0 and 0.3. Note the y-axis log scale in all panels except (C).

dynamics is insensitive to whether flexible behavior is present or not and which of the two flexible rules is used (Figs. 1 and 2; De Roos et al. 2002). Interestingly, empirical examples in which cohort-driven cycles have been documented and mortality rates have been estimated (Hamrin and Persson 1986, Townsend et al. 1990) fall within this parameter region, where flexible behavior is expected to have no effect on population dynamics or habitat use.

For μ_p values from 0.08 to 0.16 (for alternative dynamics, μ_p values above ≈ 0.045), proportional habitat use results in stable equilibria, with the consumer going extinct at a μ_p value around 0.16 (De Roos et al. 2002). Because individuals spend a fixed proportion (0.9) of their time in the pelagic habitat, consumer density decreases monotonically with increasing μ_p. Stable equilibria are also present for both flexible-behavior rules
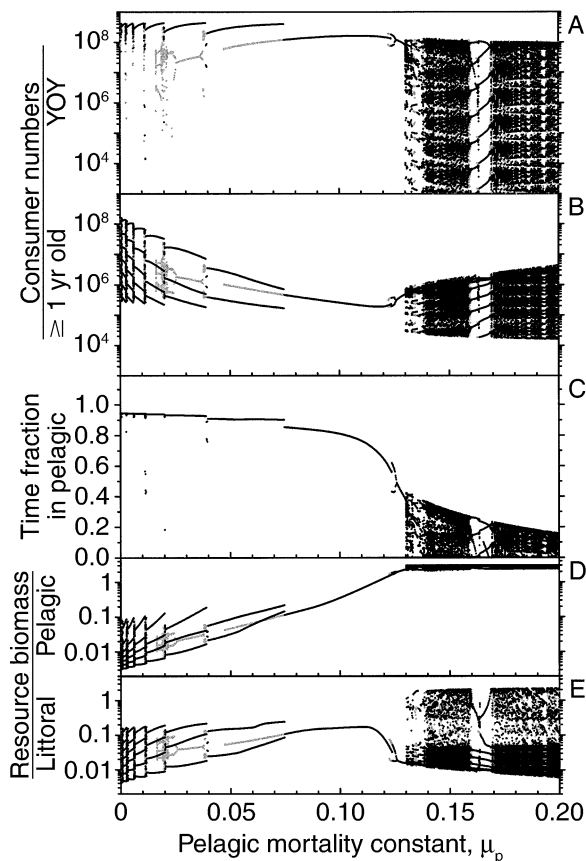
Fig. 2. Bifurcation diagram of the model when habitat profitability is determined by the $g/(x + y) - \mu$ rule. (A) Number of YOY individuals, (B) number of individuals ≥ 1 yr old, (C) the proportion of time that YOY fish spend in the pelagic habitat, (D) biomass (g/m^3) of the pelagic resource, and (E) biomass (g/m^2) of the littoral resource are shown as a function of the pelagic mortality constant, μ_p. Data refer to the system at the time of reproduction. Observe that μ_p runs between 0 and 0.2.

in this parameter region (Figs. 1 and 2). However, flexible behavior in consumers here results in a habitat use that may differ from that when consumers spend a fixed proportion of their time in each habitat. In turn, this difference in habitat use leads to differences in the mortality pattern as compared to the situation with proportional habitat use. Using the g/μ rule, the density of YOY fish rapidly declines while they spend time in the pelagic habitat, because of its high mortality risk. This decline in abundance, in combination with the lower mortality in the vegetation habitat, causes YOY fish to increase their use of the vegetation habitat as μ_p increases (Fig. 1C). A rapid decrease in the use of the pelagic by YOY fish is especially seen at $\mu_p \approx$ 0.13–0.15. Compared to the parameter region with cohort cycles in which intracohort competition among YOY fish forces them out into the pelagic habitat, it is competition in the vegetation with next year's YOY cohort that forces 1-yr-old fish out into the pelagic

habitat. Flexible behavior in the region with stable equilibria thus has an effect on the pattern of habitat use and size-specific mortality, but not on population dynamics.

With the g/μ rule, the fixed-point dynamics is destabilized for μ_p values >0.22. For a μ_p value >0.25, this dynamics blows up into irregular, large-amplitude cycles once again. These cycles occur because of an overcompensation in the number of YOY fish produced by adults flourishing in the pelagic habitat (Figs. 1 and 2). Dominant cohorts are in this parameter region caused by very different mechanisms from those of the cohort cycles at lower μ_p values. Here, a large YOY cohort results in slow growth during the first year of life and, hence, a small size at age 1. As a consequence, when forced out into the pelagic by next year's YOY cohort, these individuals experience low survival to maturity. In contrast, a small YOY cohort may have high growth during its first year of life and, hence, high survival to maturity (De Roos et al. 2002).

The $g/(x + y) - \mu$ rule yields the same qualitative pattern as the g/μ rule with respect to dynamics and habitat use of YOY fish, but the dynamics is destabilized at a lower μ_p value (≈ 0.13) for this rule; i.e., the parameter region with fixed-point dynamics is compressed (Fig. 2). It should, however, be noted that any quantitative comparisons are to be made with caution in this region because of the influence of σ on the μ_p value at which the fixed-point dynamics is destabilized (observe that the transition from cohort cycles to fixed-point dynamics at a μ_p value of 0.08 is unaffected by the value of σ; De Roos et al. 2002). Although the two behavioral rules lead to different amplitude and regularity of the large-amplitude dynamics at μ_p high values, the dynamics resulting from both rules is characterized by the dominance by one cohort over a long time period.

In conclusion, our results show that for μ_p values up to 0.08, flexible habitat use by consumers results in the same population dynamics, the same YOY fish habitat use, and the same mortalities as compared to proportional habitat use. For these low μ_p values, flexible behavior does not affect the size-dependent competition relationships that are the main determinant of population dynamics in this parameter region. At intermediate μ_p values, fixed-point dynamics is observed for all types of habitat use, but YOY fish use the pelagic habitat to a smaller extent with flexible behavior. Overall, an effect of flexible behavior is mainly seen in an increased persistence at high μ_p values, although the g/μ rule results in fixed-point dynamics for μ_p values between 0.14 and 0.22. The two different behavioral rules lead to highly similar population dynamics and habitat use of consumers, with dynamics changing from single-cohort cycles, to fixed-point dynamics, to irregular, large-amplitude cycles with increasing μ_p.

DISCUSSION

Short-term experiments and long-term dynamics

More than a decade ago, behaviorally oriented ecologists suggested that flexible behavior should have a significant influence on population and community dynamics (Dill 1987, Lima and Dill 1990). Since then, vast numbers of short-term (within-generation) and usually small-scale experiments have been carried out to support this view (Werner et al. 1983*a*, *b*, Turner and Mittelbach 1990, Persson and Eklöv 1995, Diehl and Eklöv 1996, Beckerman et al. 1997, Schmitz et al. 1997, Peacor and Werner 2001). In particular, Peacor and Werner (2001) argued for the importance of trait-mediated indirect effects relative to density-mediated indirect effects. Many of these experimental studies have involved organisms that exhibit some type of size or stage structure, and experimental tests, in many cases, also have considered behavioral responses as a function of size (e.g., Turner and Mittelbach 1990, Diehl and Eklöv 1995, Peacor and Werner 2001). Considering the short-term, within-generation scale of these studies, support for the thesis that the observed community responses in the experiments also have consequences for long-term dynamics has been based on projections from theoretical models neglecting size variation among individuals (i.e., Gleeson and Wilson 1986, Fryxell and Lundberg 1994, Křivan 1996, 1997, Křivan and Sikder 1999). To assess the implications of flexible behavior for long-term population and community dynamics, we thus largely lack (1) empirical studies over longer time periods, and (2) a theoretical analysis of the effects of flexible behavior in size-structured populations (for the latter, see De Roos et al. 2002).

In the region with cohort-driven cycles, we found that the population dynamics and the habitat use of YOY fish were unaffected by either the flexible behavior per se or which of the two behavioral rules was used. Cohort-driven population dynamics within the expected mortality range has been documented in planktivorous fish, i.e., roach, *Rutilus rutilus*, and vendace, *Coregonus albula* (Hamrin and Persson 1986, Townsend et al. 1990, De Roos and Persson 2001). Short-term pond experiments with roach have demonstrated behavioral responses to predators, as well as indirect effects on zooplankton resource levels (Persson and Eklöv 1995). Still, our modeling results suggest that on a longer time scale, roach populations should exhibit cohort-driven cycles and that, due to roach's strong impact on their resource, the behavior expressed by roach in this case should lead to an almost proportional use of habitats, indistinguishable from fixed behavior.

This example with cohort-driven cycles illustrates a situation in which short-term within-generation experiments show community-wide effects of behavior, whereas the strong multigeneration feedbacks in the system make any effect of flexible behavior on the long-term dynamics unlikely, leading to a total dominance of density-mediated indirect effects. Studies of comparative systems in North American lakes have shown that the size at habitat shift from the vegetation to the open-water habitat in bluegill sunfish (*Lepomis macrochirus*) varies with predation risk (predator density; Werner and Hall 1988). Thus, the extended persistence that results from flexible behavior potentially may be important for this system. However, without time series data on bluegill and resource densities over a longer time period, it cannot be decided whether this pattern represents a consumer–resource system with higher pelagic mortality, for which our modeling results predict that habitat shifts of YOY fish should depend on μ_p (Figs. 1C and 2C), or is a result of interactions in a different community configuration than the consumer–resource system.

Results from the consumer–resource system that we studied suggest that effects of flexible behavior occur only at high μ_p values beyond the domain of cohort cycles driven by recruiting individuals. For these parameters, flexible behavior increases the persistence of the system. Theoretical analyses of size-structured community configurations including flexible behavior, other than the consumer–resource system just discussed, are absent. However, theoretical and empirical analyses for perch show that size-dependent cannibalism potentially may induce very high predation risks (Claessen et al. 2000, Persson et al. 2000). Empirical studies using perch also show that niche shifts in young stages are strongly affected by predation risk, and density-dependent habitat use has been empirically demonstrated in perch cannibals (Persson et al. 2000, Byström et al., *in press*). Although it is premature to draw any further conclusions in the absence of a complete population dynamical analysis, it is possible that trait-mediated indirect effects will turn out to play a larger role in more complex interaction configurations than the one that we have studied here. What can be concluded, based on our modeling and empirical population studies, is first of all that the population feedbacks between consumers and resources and between consumer cohorts of different sizes are of major importance, a circumstance often neglected in the behavioral literature. Second, although our comparison was restricted to two behavioral rules, our results point out that the specific behavioral rule may have only minor, nonqualitative, effects when flexible behavior does affect population persistence.

Our model is essentially a tritrophic-level model, with the top predator fixed and only present as a size- and habitat-dependent mortality rate. We have increased the complexity of the two other levels by having two resources and, most importantly, by adding size structure to the intermediate level. A natural question to ask is: what is the relationship between our results and those of similar nonstructured models? One interesting result that we obtained was that flexible behavior

increased persistence toward higher μ_p values, but this co-occurred with a destabilization of the system. Interestingly, a similar relationship has been found in nonstructured models (see Křivan 1996, Křivan and Sikder 1998). A closer look at the mechanisms behind this relationship shows, however, that the mechanisms are very different in nonstructured and size-structured models. In nonstructured models, the destabilization is a result of a paradox-of-enrichment phenomenon (see Křivan 1996, Křivan and Sikder 1999). In contrast, in size-structured consumer–resource interactions, the destabilization is entirely due to cohort interactions. This shift from a prey-escape mechanism to an inter-cohort interaction mechanism, when adding to size structure, points out that we only to a limited extent expect results of nonstructured models to carry over to size-structured models.

Optimality and population dynamics

The decision rules used in our analysis of the effects of flexible behavior on population dynamics were based on optimality arguments. Optimality forms a corner stone in behavioral ecology and also in the study of the effects of flexible behavior on population dynamics (Gleeson and Wilson 1986, Fryxell and Lundberg 1994, Křivan 1996, 1997, Křivan and Sikder 1999). However, in a population dynamical context, the assumption of optimality is a tricky one. In general, the framework of population dynamics, on both ecological and evolutionary time scales, is based on the assumption that the dynamics is entirely Markovian; i.e., given the state of the system and the external input at time t, the dynamics of the system is completely determined. This may hold in both a deterministic sense, such that only one trajectory is possible from time t onward, and a stochastic sense, i.e., that an entire family of trajectories is possible from time t onward, but that the probability of occurrence of each trajectory is fixed. This Markovian perspective is very explicit in the derivation of an appropriate i state in physiologically structured population models, because in PSPMs, a collection of variables only qualifies as an i state if the i state, together with the environmental input or E condition exerted on the individual, completely determines its future development and, hence, life history (Metz et al. 1988). Simultaneously, the i state and the E condition determine the impact that the individual will have on its environment, i.e., the feedback that we have shown has a strong influence on individual habitat use.

If we now consider how to deal with behavior in PSPMs, we have to go through three crucial steps: (1) identify one or more variables to represent the behavior of the individual and incorporate this as part of the i state; (2) define how the behavior of the individual changes as a function of its current i state and the current environmental condition, and (3) specify how the behavior of the individual affects its impact on the environment. For comparison, we can consider the problem of accounting for size in PSPMs. First, a measure of body size has to be included as part of the i state. Second, we need to do experiments to derive functions for how body size changes as a function of the i state (i.e., size) itself and the current environmental condition (for example, food levels). In other words, we have to determine the growth rate of the individual as a function of size and resources. Finally, we need to estimate how different-sized individuals affect the environment by, for example, feeding (see Byström and Garcìa-Berthóu [1999], Hjelm and Persson [2001] for experimental examples of estimates in fish). In the case of behavior, we directly run into problems with both steps 1 and 2. In analyses of the effects of flexible behavior on population dynamics, the individual's decision is generally based on optimality arguments; step 1, the issue of identifying the variables to characterize the behavior (such as hunger level or sense of predation risk), is never explicitly addressed. Instead, it is assumed that natural selection favors individuals that behave ''optimally'' given the constraint set. Step 2 is also problematic, in that rules are derived based on a long-term (life history) target. For example, the μ/g rule (or the g/μ rule used in this paper) is based on the maximization of survival to maturity, which is assumed to take place at a fixed size in a constant environment (Gilliam 1982). The use of these rules and their assumptions illustrates two basic weaknesses of the decision rules derived in behavioral ecology: (1) a long-term target is assumed, and (2) the impact of individuals on the environment is not handled. It should be pointed out that, although dynamic optimization models may include a feed back of individual behavior on resources (Houston and McNamara 1999), this feedback is restricted to the within-generation time scale.

Thus, a critical issue is to identify the mechanistic basis of individual decision making. Generally, this issue has been outside the domain of optimal foraging theory, but at the same time, the issue is essential in the derivation of an appropriate representation of the behavior of the individual. A Markovian perspective means that we have to derive rules for individual behavior that only use the present state of the individual plus the present environmental input, and we cannot use rules that imply a long-term target on an evolutionary time scale, such as optimality models. The discrepancy between time scale of assessment and time scale of effects becomes crucial in a population dynamical context over many generations, where the long-term feedback of individuals on their environment is considered. Even worse, theoretical analyses suggest that only in very special cases can an optimality criterion be defined that is both measurable at a short time scale and determines the outcome of evolution (Mylius and Diekmann 1995).

In conclusion, the problem of incorporating behavior as part of a proper i state is, at present, a major obstacle for realistically incorporating flexible behavior into

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PSPMs. This problem is not restricted to PSPMs, as it is also relevant for nonstructured models. The problem with incorporating behavior only shows up much more prominently in PSPMs than in classical population dynamical models, because in PSPMs, the individual-level processes are explicitly represented. At present, this circumstance severely limits the extent to which we may develop a mechanistic population ecology theory based on individual, behavioral concepts. To end on a more positive note, our results suggest that the specific type of decision rule used may have only minor effects on the dynamics. Hence, existing decision rules may, at least as a start, suffice to investigate the effects of behavior on population and community dynamics.

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