Physiologically structured models – from versatile technique to ecological theory

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A ubiquitous feature of natural communities is the variation in size that can be observed between organisms, a variation that to a substantial degree is intraspecific. Size variation within species by necessity implies that ecological interactions vary both in intensity and type over the life cycle of an individual. Physiologically structured population models (PSPMs) constitute a modelling approach especially designed to analyse these size-dependent interactions as they explicitly link individual level processes such as consumption and growth to population dynamics. We discuss two cases where PSPMs have been used to analyse the dynamics of size-structured populations. In the first case, a model of a size-structured consumer population feeding on a non-structured prey was successful in predicting both qualitative (mechanisms) and quantitative (individual growth, survival, cycle amplitude) aspects of the population dynamics of a planktivorous fish population. We conclude that single generation cycles as a result of intercohort competition is a general outcome of size-structured consumer–resource interactions. In the second case, involving both cohort competition and cannibalism, we show that PSPMs may predict double asymptotic growth trajectories with individuals ending up as giants. These growth trajectories, which have also been observed in field data, could not be predicted from individual level information, but are emergent properties of the population feedback on individual processes. In contrast to the size-structured consumer–resource model, the dynamics in this case cannot be reduced to simpler lumped stage-based models, but can only be analysed within the domain of PSPMs. Parameter values used in PSPMs adhere to the individual level and are derived independently from the system at focus, whereas model predictions involve both population level processes and individual level processes under conditions of population feedback. This leads to an increased ability to test model predictions but also to a larger set of variables that is predicted at both the individual and population level. The results turn out to be relatively robust to specific model assumptions and thus render a higher degree of generality than purely individual-based models. At the same time, PSPMs offer a much higher degree of realism, precision and testing ability than lumped stage-based or non-structured models. The results of our analyses so far suggest that also in more complex species configurations only a limited set of mechanisms determines the dynamics of PSPMs. We therefore conclude that there is a high potential for developing an individual-based, size-dependent community theory using PSPMs.

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One of the most pervasive features of natural communities is the variation in size that exists among organisms (Gaston and Lawton 1988, Werner 1988, Brown 1995). Body size is also the most important component affecting ecological interactions as foraging ability, metabolism, predation risk and fecundity are closely related to the size of the organism (Peters 1983, Calder 1984, Sebens 1987, Werner 1988). Many ecological

studies that have considered variation in body size have focused on variation among species and how individual body size is related to static attributes (e.g. body size-abundance pattern analyses; Gaston and Blackburn 1999; but see Yodzis and Innes 1992 for a dynamic example). At the same time, it has been increasingly recognised that a substantial part of the variation in body size relates to variation within species which has strong effects on population and community dynamics (Werner and Gilliam 1984, Neill 1988, Persson 1988, Werner 1988, Wilbur 1988, Orr et al. 1990, Olson et al. 1995, Persson et al. 1998, Claessen et al. 2000).

The importance of considering the ecological implications of intraspecific size variation is further justified by the fact that the overwhelming majority of the earth's taxa exhibit some degree of size/stage structure (Werner 1988). The rare exception is only among birds and some mammals where the size difference between a juvenile, which just becomes independent of its parents and an adult is less than an order of magnitude. Actually, a main feature of the life history of almost all species is growth and development: an estimated 80% of them metamorphose (Werner 1988), while individuals of most other animal taxa grow during a substantial part of their life cycle (Werner and Gilliam 1984, Sebens 1987, Ebenman and Persson 1988, Werner 1994). Variation in size within taxa is therefore generally a result of individuals growing during most of their life cycle (Sebens 1987, Wilbur 1988, Werner 1994). Since individual growth rates are usually affected by resource levels, an approach that explicitly considers resource-dependent individual growth may therefore form a productive framework to increase our understanding of the dynamics of populations and ultimately of biological communities in general.

In this paper, we will first address the kinds of complexities in ecological interactions at the population and community level associated with size structure using examples mainly taken from aquatic communities. We will next give a background to physiologically structured population models (PSPM) (Metz and Diekmann 1986, Metz et al. 1988, De Roos et al. 1990, 1992, De Roos 1997), which is a modelling approach especially designed to handle size-structured interactions and link individual-level performance explicitly to population dynamics. The main part of the paper discusses two cases which illustrate how physiologically structured models can be applied to study ecological issues of broad conceptual interest. These cases include (1) the effects of size-dependent competitive ability and (2) the effects of size-dependent cannibalism on population dynamics.

In the first case, we will consider how physiologically structured models may increase our ability to explain and discriminate between different mechanisms determining population dynamics. For this case we will show that the kind of population dynamics observed is predictable from individual-level capacities, i.e. size-dependent competitive ability, and can hence also be inferred from a simplified, two-life-stages (juveniles, adults) model. Murdoch et al. (1992) argued that a logical link between structured and unstructured models by means of simplifying assumptions, is a prerequisite for their effective use in ecology. We will argue that the fundamental model feature allowing such a reductionistic approach in this case is the fact that individual consumers all compete for the same one or two resources. In contrast to the detailed account of size dependence in consumer life history, the representation of resources in the PSPM is hence the same as in unstructured models.

In contrast, our example of size-dependent cannibalism can only be analysed within the domain of physiologically structured models. Neither individual nor population dynamics can a priori be predicted from the knowledge of individual level capacities, but are truly emergent results of the population feedback on resources. Nor can the model be in any way reduced to a simplified model showing the same overall results. The use of physiologically structured models is in this case absolutely necessary to gain understanding about the processes at the individual, e.g. growth trajectories, and population level. Their use is necessitated by the size-structured prey, which implies that a consumer with a particular body size faces its own, unique resource spectrum to be exploited. In a more general sense, this case suggests that most size-structured processes observed in natural communities can only be analysed within the domain of physiologically structured models.

For both cases, we also illustrate how PSPMs allow us to proceed towards a closer interaction between modelling and empirical work and how they increase our ability to quantitatively test predictions of ecological models. This increased ability results from the fact that (1) comparisons between model predictions and data have a higher discriminative power, as most parameter estimates are derived independently, and (2) that the model generates predictions about both population-level (dynamics, amplitude and period of fluctuations) and individual-level processes (growth, survival, fecundity) in a population dynamical context, which are largely independent of the assumptions that the model is based upon. Especially in our second example of size-dependent cannibalism, the model can generate a rich set of such individual-level, life-history predictions to be tested against empirical data.

Although at an early stage of development, our analysis so far suggests that the number of significant mechanisms driving the dynamics of size-structured populations, and hence the number of dominating dynamical patterns, is restricted. In addition, we show that they are largely independent of specific model assumptions and can be revealed by carefully laid-out numerical simulations in combination with some math-

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ematical analyses. The reliance on numerical solutions of PSPMs has to be contrasted to their explicit treatment of mechanisms at the individual level and their higher ability to discriminate between different mechanisms compared to non-structured or stage-based models. These considerations lead us to conclude that there is a high potential for developing a general individual-based, size-dependent community theory using PSPMs.

Size/stage-structured interactions – implications for community dynamics

In traditional population and community models, individuals are only represented at the population level by their number. Pair-wise interactions may be described by a single combination of signs (predation $+/-$, competition $-/-$, etc.) where the same strength (magnitude) of interaction pertains to each individual (Wilbur 1988, Werner 1992, Persson et al. 1997). The presence of size structure within populations undermines this typological characterisation as both the intensity and the type (sign) of specific interaction may change with the size of the interactors (Werner and Gilliam 1984, Persson 1988, Wilbur 1988, Olson et al. 1995, Persson et al. 1996a, 1999).

The intensity of interactions will vary as many individual level traits such as foraging and metabolic rates are strongly related to body size (Peters 1983, Werner 1988, 1994, Lundberg and Persson 1993, Persson et al. 1998). For example, size-dependent foraging and metabolism leads to asymmetrical competitive interactions between differently sized individuals (Persson 1985, Hamrin and Persson 1986, Werner 1994). Even without obvious changes in diet, size differences between individuals may therefore have major consequences for the interactions in communities. In addition, size-dependent shifts in diet and habitat use (ontogenetic niche shifts) tend to be the rule among size-structured populations and naturally lead to an increased potential of ecological interactions (Werner and Gilliam 1984, Werner 1986, Persson 1988).

When competing for resources, the intensity of resource limitation may vary with size in such a way that a particular stage/size class forms a bottleneck for recruitment whereas other stages/sizes may not be resource limited at all or only to a limited extent (Crowley et al. 1987, Persson 1988, Orr et al. 1990). Actually, often the critical feature of interactions between species with distinct body sizes is not how the adults interact, but how a larger species is able to recruit through juvenile stages that have body sizes (and hence size-dependent niche requirements) comparable to a smaller species. Neill (1975) demonstrated in an elegant set of experiments that a small zooplankton, *Ceriodaphnia*, could heavily reduce the food sizes used by juveniles of

much larger species and thereby outcompete and actually drive a large zooplankton like *Daphnia magna* to extinction. Adult *Daphnia* introduced into the system survived and produced many offspring, of which not a single one survived the competition by *Ceriodaphnia*. Competitive juvenile bottlenecks have been argued to be especially common in species which undergo several ontogenetic niche shifts over their life cycle, because different ontogenetic niches pose vastly different requirements on body morphology, while the adaptation to these different niches is constrained by ontogenetic trade-offs (Werner and Hall 1988, Werner and Gilliam 1984, Werner 1986, 1988, Persson 1988, Persson and Greenberg 1990a, b). They have hence been suggested to play a major role in many fish communities (Mittelbach 1983, Werner 1986, Persson 1988).

Ontogenetic niche shifts and size-dependent foraging behaviour in most cases imply that interspecific relations shift from competitive to predatory interactions over ontogeny (Neill and Peacock 1980, Neill 1988, Wilbur 1988, Polis 1988, Persson 1988, Mittelbach and Osenberg 1993, Olson et al. 1995), simultaneously changing the intensity and sign of the interaction between species. Considered over the entire life cycle, interspecific relations are thus more appropriately seen as a mixture of competitive and predator-prey interactions. A very common situation is that larger stages of the top predator are affected positively (i.e. in individual growth) by feeding on a prey species whereas small stages are affected negatively by its competition (Larkin and Smith 1954, Johannes and Larkin 1961, Lasenby et al. 1986, Persson 1988, Mittelbach and Osenberg 1993, Olson et al. 1995). This difference in response by different stages of the top predator may be related to competitive juvenile bottlenecks in that during the juvenile stage a predator species may suffer from the superior competition by a species that it later in life will prey upon, which may severely limit the rate and extent to which growing predators reach predatory stages (Mittelbach and Chesson 1987, Persson 1988, Wilbur 1988, Persson and Greenberg 1990a, b, Persson et al. 1996a). The interaction between such species will be characterised by a high degree of asymmetry.

Asymmetric interactions of a mixed type have been documented for a substantial number of fish species (Werner 1986, Persson 1988, Persson and Greenberg 1990a), anurans (Wilbur 1988), scorpions (Polis 1988, 1991), many reptiles, crustaceans, and insects (Werner and Gilliam 1984). The community consequences of these asymmetric interactions may be illustrated by the invasion of the redside shiner (*Richardsonius balteatus*) into Paul Lake (British Columbia) previously inhabited by rainbow trout (*Salmo gairdneri*) only (reviewed by Werner and Gilliam 1984). As a consequence of the invasion of redside shiner, the growth rates of large individuals increased due to the addition of a new resource of adult rainbow trout, whereas the growth

rates of small individuals decreased due to competition between small rainbow trout and redside shiner. The two stages of trout were thus affected in different ways by the redside shiner and the end result was an overall reduction in the trout population.

The niche shifts that most organisms undergo over their life cycle are a major cause of vertical heterogeneity in food webs, i.e. that the same species feeds at different trophic levels (Persson et al. 1996b, Polis and Strong 1996, Persson 1999). This phenomenon, referred to as life-history omnivory, constitutes a direct violation of the purely hierarchical feeding relations in the trophic level paradigm. A number of studies have shown that patterns in consumer–resource relationships differ from the expected relationships derived using non-structured models (Neill 1988, Persson et al. 1992, Mittelbach and Osenberg 1993, Olson et al. 1995). For example, consumer and resource densities may be positively or negatively related to each other depending on environmental conditions. Mittelbach and Osenberg 1993; see also Mittelbach and Chesson 1987, Mittelbach et al. 1988) showed that stage-dependent interactions could lead to a positive correlation between resource productivity and the density of consumers in one stage, at the same time as a negative relationship was present between the resource productivity (of another resource) and the density of another stage due to stage-dependent resource use. An overall negative relationship between predator and prey that compete with the young stages of the predator may result from that strong competition among juveniles retards their maturation and makes the adult, predatory stages fail to respond to increased levels of their resource (Neill and Peacock 1980, Neill 1988, Persson 1988, Persson et al. 1992).

A general conclusion that can be drawn from the above overview is that field and experimental studies have shown a relationship between individual level performance such as growth and community statics such as biomass and species composition (Werner 1977, Persson 1988, Olson et al. 1995). In the cases where population dynamics have been explicitly modelled, models have been based on stage (juvenile, adult) based approaches (cf. Mittelbach and Chesson 1987). Such a stage-based approach has undoubtedly proven useful in increasing our insights about size/stage-structured interactions (i.e. Mittelbach and Osenberg 1993). Still, a natural question to raise is which kind of size-dependent interactions can be efficiently handled in a stage-based modelling framework and which cannot. To deal with this question, we will first give a short introduction to a more general modelling framework to deal with size-structured interactions. We will show that this modelling approach will generate new insights into the dynamics of size-structured populations and also will allow a more critical testing of model predictions than contemporary non-structured or stage-structured mod-

els. We will also show that size-structured interactions can only be reduced to stage-based interactions under a restricted number of conditions.

Physiologically structured models: a framework to analyse size-structured population processes

Model philosophy

Physiologically structured population models offer a concise framework to explicitly and mechanistically relate population-level phenomena to individual-level processes, in cases where the former are significantly influenced by physiological (e.g. size) differences among individuals. Central to PSPMs is the clear distinction between the individual and its environment and the strict separation of the individual and population level. The model formulation process consists of the derivation of a mathematical description of how individual performance (growth, survival, reproduction) relates to the physiological characteristics of the individual and the condition of its environment. Hence, all assumptions about and parameterisation of these functional relationships in response to its current environment take place exclusively at the level of a single individual organism. The derivation of the population model is subsequently only a matter of book-keeping without making any further assumptions. Each of the three basic components, e.g. individual, environment and population, require a formal characterisation of their state, usually referred to as the i-state, E-state and p-state, respectively (Metz and Diekmann 1986, De Roos et al. 1992, 1997). For the example of a size-structured consumer population feeding on a common resource, the i-state consists of a measure of individual size, the E-state is the current food density, while the p-state consists of a listing of how many individuals of different sizes are present at a specific time. Two further assumptions underlying PSPMs state that the development in the i-state is deterministic and that the number of individuals of any type in the population is large.

Because PSPMs are based on a mathematical description of how an individual's environment influences its performance and how the individual in turn affects its environment, they explicitly account for the mechanisms of interaction between an individual and its environment. As a consequence, density dependence is also assumed to operate through an individual's environment, either by means of the effect of the total population on a common environmental factor such as food density, or by formally considering all other individuals of the population as a part of an individual's environment. For example, in our second case of size-dependent cannibalism, the cannibalistic predation

pressure and the availability of cannibalistic food is considered part of an individual's environment. This case is an example of direct density-dependent interactions, while the feeding on a common resource is an example of an indirect feedback loop. Either way, PSPMs treat density-dependent relations in a very explicit sense and are hence especially suited to elucidate how these density-dependent relations result from individual-level mechanisms.

Model formulation

For ease of presentation we will discuss the basic formulation of a PSPM for the case when reproduction occurs in a sharply pulsed event at the beginning of a growing season. All examples that are discussed below incorporate this assumption of pulsed reproduction, which for the freshwater fish communities we study, and probably numerous other systems, is biologically realistic. The points in time where reproduction occurs we will denote by T_n, where the index refers to the year number. Moreover, we will concentrate on the formulation of a simple consumer–resource model where feeding, growth, reproduction and mortality of consumers depend on body size s and on the food density F.

In case reproduction is pulsed in time and individuals are born with more or less the same body size, each reproduction event gives rise to a distinct, new cohort of individuals. In the model this cohort will be represented by a pair of values: $\{N_i(t), S_i(t)\}$, where $N_i(t)$ denotes the number of individuals in the cohort, and $S_i(t)$ the body size of these individuals. Because in PSPMs individual development (growth) is assumed to be deterministic, all individuals within the cohort will have identical body sizes throughout their life.

The modelling process in this example comes down to deriving appropriate mathematical descriptions for the individual feeding rate, $I(F, s)$, the growth rate, $g(F, s)$, the mortality rate, $d(F, s)$, and the number of offspring that is produced at a forthcoming reproduction moment, $b(F, s)$. All these elements that characterise individual life-history processes are assumed to depend on both food density and individual body size. For this modelling process, i.e. the derivation of the appropriate functional forms and their parameterisation, life-history observations on individuals with different body sizes under a range of food conditions are required. Ideally, such information should be data of experimental studies under conditions where density-dependent influences have been controlled for.

Assume that immediately after a reproduction event at $t = T_n$ the structured population consists of a collection of Q cohorts of different sizes, which have been born at the beginning of different, preceding seasons. Using the individual-level model, made up by the functions $I(F, s)$, $g(F, s)$, $d(F, s)$, and $b(F, s)$, the dynamics

of these cohorts during the following growing season ($T_n < t < T_{n+1}$) can be described by a system of two differential equations (ODEs) for each cohort (the index i in the following equations refers to different cohorts):

$$\begin{cases} \dfrac{\mathrm{d}N_i}{\mathrm{d}t} = -d(F, S_i)N_i \\ \dfrac{\mathrm{d}S_i}{\mathrm{d}t} = g(F, S_i) \end{cases} \qquad i = 0, \dots, Q-1 \qquad (1\mathrm{a})$$

The first equation describes the decrease in cohort abundance due to mortality, while the second equation describes individual growth in body size. To complete the within-season part of the population model, these Q sets of two ODEs have to be dynamically coupled to an equation for the changes in food density during the growing season. This also takes the form of a differential equation, which expresses that the change in food density at any time is a balance between autonomous growth of the resource and feeding by the size-structured consumer population:

$$\frac{\mathrm{d}F}{\mathrm{d}t} = R(F) - \sum_{i=0}^{Q-1} I(F, S_i)N_i \qquad (1\mathrm{b})$$

The function $R(F)$ models the changes in food density in the absence of any consumers, for example, a logistic growth function could be assumed. The feeding by all consumers is simply the sum of total food intake by all cohorts.

At the start of the next season (when $t = T_{n+1}$) reproduction will yield a new cohort of neonate individuals. The number of newborn individuals is the sum of the total offspring produced by each cohort separately, which equals $b(F, S_i)N_i$ (note that for juvenile sizes $b(F, S_i)$ is assumed equal to 0). The (fixed) size of the newborn individuals will be indicated with s_b. For book-keeping reasons we will use the index 0 to indicate the new cohort and increase the cohort index of all older cohorts by 1 (the cohort index i can thus be thought of as representing the cohort age). Mathematically, this reproduction process is captured by the following set of equations:

$$\begin{cases} N_0(T_{n+1}^+) = \displaystyle\sum_{i=0}^{Q-1} b(F, S_i)N_i(T_{n+1}^-) \\ S_0(T_{n+1}^+) = s_b \\ N_{i+1}(T_{n+1}^+) = N_i(T_{n+1}^-) \\ S_{i+1}(T_{n+1}^+) = S_i(T_{n+1}^-) \qquad i = 0, \dots, Q-1 \end{cases} \qquad (2)$$

The left-hand side of these equations represents the values of the cohort statistics $\{N_i(t), S_i(t)\}$ just after the reproduction event (indicated by the notation

T_{n+1}^{+}), while the right-hand side refers to their values just before the event. The first two of these equations determine the abundance and size of the newborns, while the last equations simply reflect the renumbering of all cohorts already present.

Together, the differential equations (1a) and (1b), specifying dynamics between reproduction events, and the mappings (2), specifying reproduction and renumbering of cohorts, constitute the mathematical formulation of the population model. Note that the population equations are simply derived by book-keeping the contributions of all cohorts. Model assumptions only pertain to the functions $I(F, s)$, $g(F, s)$, $d(F, s)$, and $b(F, s)$, that determine the consumer life-history and the function $R(F)$, describing the dynamics of the environment (food density) in the absence of any consumer.

The PSPM formulation presented here is highly simplified due to the assumptions that all newborn individuals have identical sizes and that reproduction occurs only at the beginning of a growing season. However, the formulation is readily extended to situations with an initial size-distribution of the newborns or situations in which pulses of reproduction are occurring at irregularly spaced moments in time. In addition, De Roos et al. (1992; see also De Roos 1988, 1997) have shown that more complicated PSPMs can be consistently approximated by a formulation along the lines given above. These include models with reproduction occurring continuously, more physiological variables determining the individual life history (De Roos et al. 1992, De Roos 1997), and even models where the physiological state of newborn individuals is related to that of the parent (De Roos 1988). This versatile technique to numerically study PSPMs has been dubbed the "*Escalator Boxcar Train*" (EBT; De Roos et al. 1992, De Roos 1988, 1997) and we thus refer to the PSPM formulation presented in this section as the EBT-formulation.

An example of an individual-level model

All examples of size-structured population dynamics we discuss below are based on a particular individual-level model, which characterises the state of an individual consumer by two measures of individual size: irreversible and reversible mass, respectively. In irreversible mass, referred to as x, compounds like bones and organs which cannot be starved away are included, whereas reversible mass, y, includes energy reserves such as fat, muscle tissue and for mature individuals also gonads. Reversible mass may be used to cover basic metabolism during starvation. 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 will only be briefly summarised here. The foraging rate of individual consumers on the resource is assumed to follow a Holling type II functional response, incorporating an attack rate, a handling time, and the resource density. Both the attack rate and handling time are functions of irreversible mass x only. Hence, a consumer's condition, i.e. its reversible mass y, does not influence its foraging rate. 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).

Fig. 1 schematically summarises the individual-level dynamics of consumers in the individual state space, spanned by the two size measures irreversible and reversible mass. This figure hence reflects all individual life-history processes. An individual's current energy intake is first used to cover its metabolic requirements, which follow an allometric function of total 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 in such manner 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 (i.e. $q_a > q_j$; 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. As soon as net energy intake becomes positive again, energy is preferentially allocated to reversible mass in order to restore the target ratio y/x. In addition to a size-independent background mortality, individuals experience starvation mortality whenever their reversible/irreversible mass ratio y/x drops below a starvation mortality threshold q_s (Fig. 1). The starvation mortality is modelled in such a way that death occurs with certainty before an individual's reversible mass is depleted entirely. Individuals are assumed to spawn only
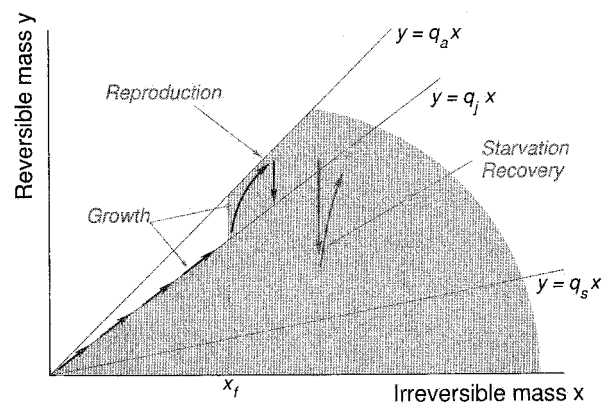

Fig. 1. The *i*-state space (reversible versus irreversible mass) of the consumer–resource model and a schematic representation of the dynamic processes affecting the individual state (see text for an explanation).

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at the beginning of the growing season (summer). When they spawn, adult individuals allocate all reversible mass that they accumulated in excess of the standard reversible mass for juveniles ($q_j x$) 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 non-starving juvenile, whereafter the build-up 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 (Fig. 1).

The population-level model is explicitly given by Persson et al. (1998), but its formulation basically follows the lines set out above. The results on population dynamics were derived using the EBT technique derived by De Roos et al. (1992; see also De Roos 1997). In the following sections we discuss two examples of interactions between individuals and their environment that result in specific population-level phenomena which have been observed in empirical systems as well.

Size-dependent competitive ability and population dynamics

Individual level aspects

The size scaling of ecological capacities in organisms has received considerable interest in the ecological literature (Peters 1983, Calder 1984, Werner 1988, Kooijman 1993, Lundberg and Persson 1993). Energy gains and energy costs (metabolism) are two basic variables which affect the individual's performance and scale with body size (Schoener 1969, Wilson 1975, Sebens 1982, Peters 1983, Calder 1984, Persson 1985, Werner 1988, Lundberg and Persson 1993). The size scaling of the foraging capacity has been suggested to vary more between species than the size scaling of metabolism depending on both the consumer type and the habitat in which the consumer search for food (two-dimensional versus three-dimensional environments) (Wilson 1975, Mittelbach 1981, Sebens 1982, Werner 1988, Lundberg and Persson 1993, Werner 1994). A consideration of size-dependent foraging and metabolism has been useful to understand habitat selection and mortality causes in very small life stages (Byström and Gàrcia-Berthóu 1999, Persson et al. 2000, Byström et al. 1998) as well as habitat distributions and growth performance of larger individuals (Mittelbach 1981, 1983, Persson 1987, Byström and Gàrcia-Berthóu 1999).

Combining the energy gained by foraging activities and the metabolic costs allows us to define the competitive ability of an organism as a function of its size. A useful measure of an individual's competitive ability at a specific size is presented by its minimum resource requirements, defined as the resource density at which
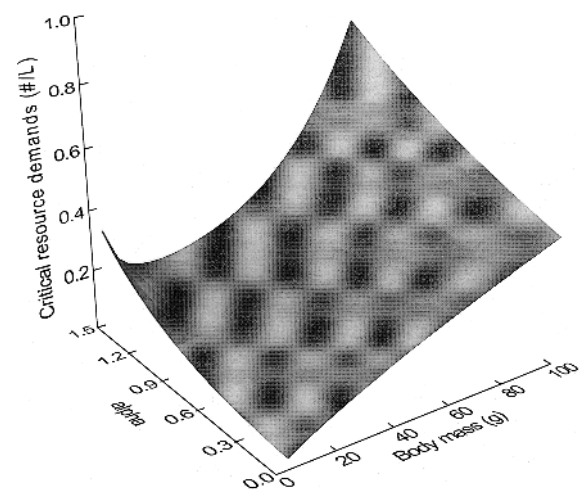

Fig. 2. Minimum resource requirements as a function of body mass and the foraging scaling parameter α (see text). Parameter values follow Table 1.

energy gained through foraging just equals maintenance requirements (Persson et al. 1998; Fig. 2). The minimum resource requirements thus represents the zero-growth food density ($dE_{growth}/dt = 0$). Depending on the size scaling of foraging rate and metabolism, the relation between minimum resource requirements and size will take different forms, which, as we will show below, have substantial impact on population dynamics.

Population level aspects

The minimum resource requirement was verbally used to explore the mechanisms behind population oscillations in vendace (*Coregonus albula*), a planktivorous fish species, (Hamrin and Persson 1986). Because of its lower metabolic demands, newborn vendace ("young-of-the-year", YOY) tolerate lower resource densities than larger vendace leading to oscillating populations driven by cohort competition between YOY and older vendace, where strong cohorts of YOY vendace suppress adult vendace reproductive output (see also Auvinen 1994 for other studies on vendace). Examples of oscillations driven by the same mechanisms are also found in another planktivorous fish, roach (*Rutilus rutilus*) (Cryer et al. 1986, Townsend and Perrow 1989, Townsend et al. 1990). Oscillations driven by a dominant juvenile cohort suppressing adult fecundity are also well known in *Daphnia* populations (Murdoch and McCauley 1985, McCauley and Murdoch 1987, 1990, De Roos et al. 1990, McCauley 1993).

Although the effects of different size scalings have been considered at the individual level, the population dynamical consequences were first formally analysed by Persson et al. (1998) using a PSPM. This model in-

cluded a mixture of discrete (reproduction) and continuous (feeding, metabolism, resource dynamics) events (see Fig. 1 and previous section). To study the effects of different size scalings of foraging rate, the following size-dependent attack rate was derived:

$$a(w) = A_{\max}\left(\frac{w}{w_o}\exp\left(1-\frac{w}{w_o}\right)\right)^{\alpha} \qquad (3)$$

where $A_{\max}$ is the maximum attack rate, w_o is the body size at which this maximum rate is achieved, and α is a size-scaling exponent (see Persson et al. 1998 for mechanistic explanations for the form of the function).

A major conclusion of the analysis was that the scaling exponent, α, was the single most important parameter affecting the dynamics (Persson et al. 1998). With a low value ($\alpha < 0.8$) of the parameter, the dynamics were characterised by large amplitude oscillations and the total dominance by one age cohort. In this case the dynamics were driven by recruiting individuals. The details of these "single-cohort" cycles (SC-cycles) and the mechanisms bringing them about, are illustrated in Fig. 3 (see also Persson et al. 1998). When reproduction occurs, the large number of newborn individuals (YOY) depresses the resource to such low levels that all older individuals starve to death. The competition for food among the YOY subsequently impedes their growth. Only while their density declines due to background mortality, resource levels can increase and individual growth speeds up. The cohort reaches the maturation size when individuals are over 3 yr old. Until the end of their 4th year they accumulate sufficient reproductive mass to produce a new dominant cohort, by which they themselves are outcompeted. The occurrence of single-cohort cycles can be explained by the fact that minimum resource requirements increase
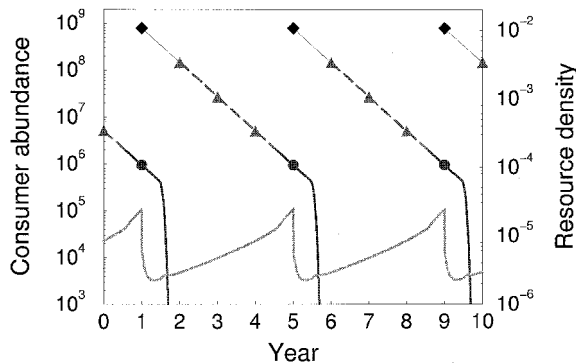

Fig. 3. Single-cohort dynamics with constant background mortality as predicted by the consumer–resource model with default parameters for roach (Persson et al. 1998). Diamonds with thin solid lines: YOY; triangles with dashed lines: juvenile individuals; circles with thick solid lines: adult individuals; solid line without symbols: resource density. Consumer densities expressed as number of individuals per lake (assumed 10^9 L); resource density as biomass (g) per litre.

monotonically with body size (cf. Fig. 2). When the size-scaling parameter α is increased, the large-amplitude dynamics collapse into stable fixed-point dynamics with many coexisting age cohorts. These stable fixed-point dynamics occur for parameter values of α that result in a relatively flat curve for the minimum resource requirement–body size relationship, indicating similar competitive abilities of differently sized individuals (Fig. 2). Increasing α further leads to the reappearance of large amplitude oscillations, but in this case, the dynamics are driven by older juveniles. Correspondingly, minimum resource requirements first decrease with size to thereafter increase (Fig. 2).

In conclusion, the analysis by Persson et al. (1998) shows that inter-cohort competition for a shared resource is a major interaction driving size-structured population dynamics. Furthermore, the kind of dynamics observed and its mechanistic underpinning can be understood on the basis of the scaling of minimum resource requirements with individual body size. The generality of the minimum resource requirements rule as a general predictor for size-structured consumer–resource dynamics, has been confirmed by the analysis of a lumped stage-based (juveniles, adults) model (De Roos and Persson unpubl.).

Empirical observations in Alderfen Broad, UK

For planktivorous fish the value of the exponent α in the scaling of attack rate with body size has been found to be $0.59-0.61$ (Mittelbach 1981, Byström and Gàrcia-Berthóu 1999, Hjelm and Persson unpubl.). For this α value, the dynamics are predicted to be recruit-driven (i.e. "single-cohort" cycles), which is broadly in agreement with empirical observations (Hamrin and Persson 1986). However, a challenging question is whether more quantitative model predictions also agree with empirical data that are independent of the data used to parameterise the model.

Cryer et al. (1986; see also Townsend and Perrow 1989, Townsend et al. 1990) report the occurrence of a 2-yr cycle in abundance of roach (*Rutilus rutilus*) in Alderfen Broad (UK; Fig. 4). Townsend and Perrow (1989) claim that the observed alternation of weak and strong year classes is due to fluctuations in adult fecundity, since individuals reproduce for the first time at the age of 3 yr. In contrast, fecundity data presented by Cryer et al. (1986) and Townsend et al. (1990) suggest that only during a growing season with strong reproduction, resource levels in the lake are suppressed to such an extent that 1-yr-old individuals fail to mature. Following a weak reproduction year 1-yr-old individuals successfully mature and manage to reproduce at an age of 2 yr, although with lower fecundity than older age classes. These older age classes are, however, present in low abundance.
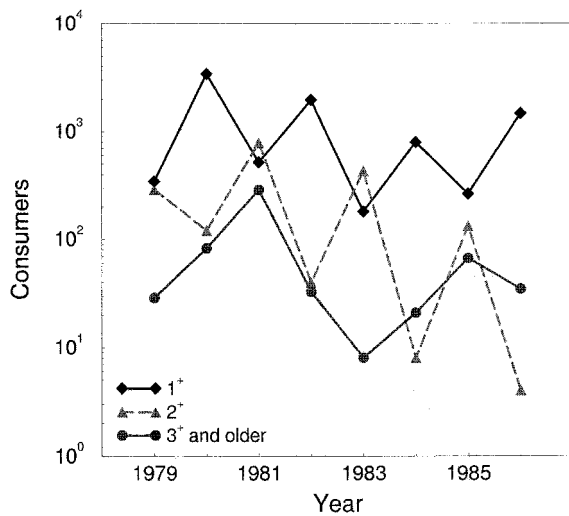
Fig. 4. Abundance estimates (total consumers in entire lake) of different age classes of roach in Alderfen Broad from 1979 to 1987. Absolute abundance estimates are derived from CPUE data in a standard perimeter electrofishing operation in October of each year (data from Table 1 in Townsend et al. 1990).

To generate quantitative predictions for the population dynamics of roach in Alderfen Broad we parameterised the model presented by Persson et al. (1998) for roach (*Rutilus rutilus*) (Table 1). Compared with its original formulation, we have changed the model structure in two respects: (1) we assume that consumer handling time is due to digestive constraints and thus follows an allometric relationship with consumer weight (see also Claessen et al. 2000), and (2) based on the observations by Townsend et al. (1990) we assume that

background mortality consists of a size-independent (as in Persson et al. 1998) and a size-dependent component. The background mortality rate $d(x)$ is therefore described by:

$$d(x) = \mu_a + \mu_j \exp(-x/x_\mu) \qquad (4)$$

where μ_a represents the size-independent background mortality rate, μ_j is a scaling constant for the size-dependent mortality rate and x_μ determines how rapidly mortality decreases with size to the constant background level μ_a. Default parameter values of the model for roach are presented in Table 1.

Fig. 5 presents the dynamics of the size-structured consumer–resource model for the default parameter set (Table 1). The population abundance of consumers is characterised by a regular 2-yr cycle with the different year classes cycling out of phase. The ratio between strong and weak year class strength, as predicted by the model at the end of a growing season, equals approximately 2.7 for the 1^+ and 2^+ individuals, while this abundance ratio of older individuals is less than 2. For the 1^+ individuals these predictions agree reasonably well with the empirical observations (Fig. 4), even though the fluctuations in the data are much more irregular and hint at a slightly larger amplitude. For the 2^+ individuals the empirical data suggest larger amplitudes and even a decrease in mean abundance over the years. These deviations may be partly explained by the fact that the abundance estimates in years with low 2^+ abundance are based on only a few individuals caught, especially in later years (cf. Table 1 in Townsend et al. 1990). The data for individuals of 3 yr and older do not show a 2-yr cycle at all, which may also be due to the very low number of individuals sampled.

Table 1. Default parameter set for the size-structured consumer–resource model presented by Persson et al. (1998), parameterised for roach (*Rutilus rutilus*) in Alderfen Broad, UK.

| Symbol	Value	Unit	Interpretation
μ_j	0.017	d^{-1}	Size-dependent mortality constant
μ_a	0.014	d^{-1}	Size-independent mortality rate
x_μ	2.0	g	Characteristic size for size-dependent mortality
ξ_1	6.0	$d/g^{(1+\xi_2)}$	Allometric constant in handling time function
ξ_2	-0.81	–	Allometric exponent in handling time function
ρ_1	0.033	$g^{(1-\rho_2)}/d$	Allometric constant in maintenance rate function
ρ_2	0.77	–	Allometric exponent in maintenance rate function
w_b	0.0014	g	Total weight of an egg (newborn)
x_f	5.0	g	Irreversible mass at maturation
q_j	0.74	–	Maximum juvenile condition y/x
q_a	1.0	–	Maximum adult condition y/x
k_e	0.61	–	Ingestion-assimilation conversion efficiency
k_r	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
T_y	120	d	Length of the growing season
V_{tot}	1.0×10^9	L	Total lake volume
α	0.6	–	Allometric exponent in attack rate
A_{max}	1.5×10^5	L/d	Maximum attack rate
w_{opt}	50	g	Optimal body size for attack rate
r_m	0.1	d^{-1}	Resource growth rate
K	0.01	g/L	Resource carrying capacity
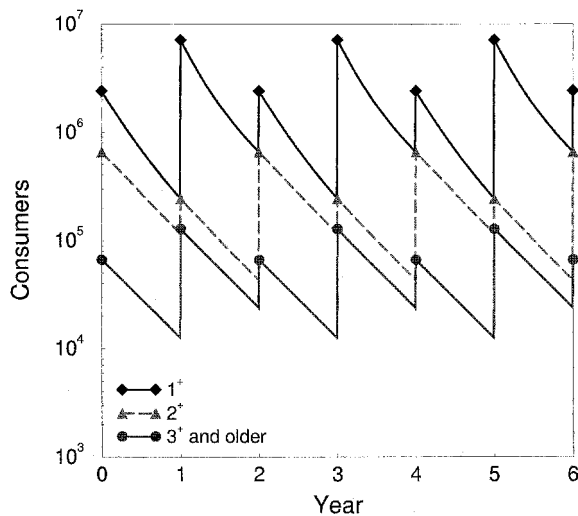
Fig. 5. Dynamics of the size-structured consumer–resource model with size-dependent background mortality and the default parameter set for roach (Table 1). Consumer densities expressed as number of individuals per 10^9 L.
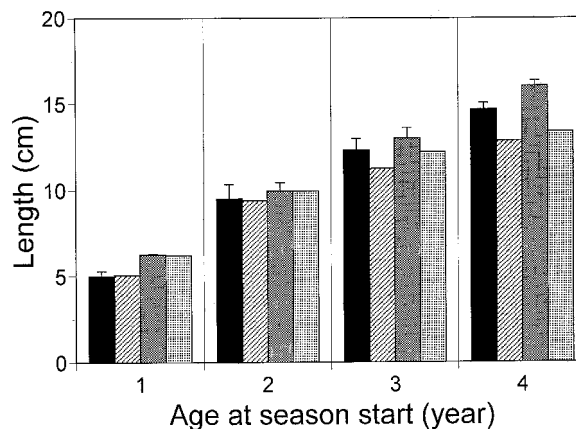

Fig. 6. Length–age relations for roach in Alderfen Broad. Black and dark grey solid bars: empirical estimates for strong and weak year classes, respectively (Townsend et al. 1990). Risers above the solid bars indicate the range in average length observed in different years. Black hatched and light grey bars: model predictions for strong and weak year classes, respectively.

It should be pointed out that the model predictions presented in Fig. 5 depend on the choice of the mortality parameters μ_a, μ_j and x_μ. The value of μ_a was chosen on the basis of the data presented by Townsend et al. (1990), while the values of μ_j and x_μ were chosen such that a 2-yr cycle in abundance resulted. Therefore, the model predictions are not strictly independent from the empirical observations, as the mortality parameters were tuned to obtain a qualitative match with the empirical population data. However, given this match at the population level, we can now consider to what extent the model correctly predicts the empirical observations at the individual level. Fig. 6 shows the relations between individual length and age for strong and weak year classes as observed by Townsend et al. (1990) and the predictions derived from the model. The model not only correctly predicts the qualitative observation that strong year classes grow more slowly than weak year classes, but also generates correct, quantitative predictions for the mean individual length at the age of 1 and 2 yr. For older individuals deviations start to occur, which again might be due to sampling errors introduced by the small number of individuals caught. Fig. 7 compares the empirical observations and model predictions for the seasonal survival of individuals as a function of their age. Because the death rate is size dependent, seasonal survival is also determined by the growth rate of individuals. Therefore, even though the parameter μ_a was estimated from Townsend et al. (1990), there is no a priori reason to expect that the predictions and observations on survival of small individuals agree. Fig. 7 reinforces the conclusion that again their is good quantitative agreement between model predictions and empirical data.

In addition to the growth and survival data, the model also correctly predicts that strong year classes start reproduction at the age of 2 yr, immediately following a season with weak recruitment (data not shown). In contrast, a weak year class faces in its second growing season the competition with the subsequent strong year class, which induces that they can only start reproducing as 3-yr-old individuals. As a consequence, a strong year class turns out to be the main contributor to the following strong year class and the weak year class after that. The reproductive contribution of weak year classes is small.

Overall the above results suggest a good correspondence between predictions and observations. Since only one mortality parameter value in the model was derived from the Alderfen Broad data, whereas all other (indi-
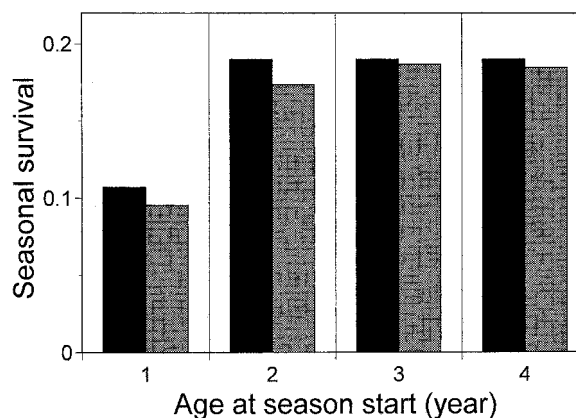

Fig. 7. Average seasonal survival as a function of age for roach in Alderfen Broad. Black bars: empirical estimates by Townsend et al. (1990); grey bars: model predictions.

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vidual-level) parameter values (i.e. those relating to size-dependent functional response, metabolism, etc.) were derived independently from a variety of studies reported in the literature, there is a high degree of independence between predictions and observations. We have shown that this one parameter set leads to a collection of model predictions at both the individual and population level that agree with empirical observations. The fact that the model simultaneously matches different predictions at different levels, leads us to conclude that the model accurately captures the essence of the dynamics as observed in Alderfen Broad. The exceptions where deviations do occur between predictions and data may be related to census error (only one or two roach captured in the years with low data points) and possibly to the fact that the model only takes a single resource into account. The major message we want to convey is that physiologically structured models extend our possibilities to quantitatively test model predictions, here exemplified by the individual survival and growth rates under conditions of population feedback, and that comparisons between model predictions and data have a higher discriminative power, as most parameter estimates are derived independently.

Multiple, shared resources

The results on the size-structured consumer–resource model discussed above (see also Persson et al. 1998) suggest that single-cohort cycles are expected to occur under a wide range of conditions. Even though several studies report data that are in line with this prediction (e.g. Hamrin and Persson 1986, Cryer et al. 1986, Shiomoto et al. 1997), the ubiquitous occurrence of SC-cycles is questionable. SC-cycles arise from competition between cohorts for a single resource through a mechanism that is akin to competitive exclusion between species. Because a number of different consumer species can stably coexist on an equal number of resources, but only by means of unstable dynamics on a smaller resource base, it is natural to ask the question whether the SC-cycles are to some extent an artefact of the model simplification to a single resource. We have studied this question by extending the model of Persson et al. (1998) in a variety of different ways with a second resource that is shared by individuals of all body sizes (De Roos et al. unpubl.) The extended model accounts for a size-structured fish population living in a lake with a distinct littoral (vegetation) and pelagic (open-water) zone, in which the individuals forage for macroinvertebrates and zooplankton, respectively. The model was parameterised for perch (*Perca fluviatilis*; see Claessen et al. 2000), using data from Persson and Greenberg (1990b) to derive relations for the foraging behaviour on macroinvertebrate prey. The dynamics of

the model were studied as a function of the juvenile mortality rate in the pelagic, μ_p, assuming that adult individuals in both the littoral and pelagic zone and juvenile individuals in the littoral zone experience a smaller, size- and stage-independent mortality rate. Higher values of μ_p imply that for a juvenile the pelagic is a more profitable, but also more risky environment.

We considered different scenarios for utilising the littoral and pelagic habitat, including a situation in which individuals use both habitats in proportion to their volume. In addition, we studied the consequences of several types of flexible habitat use. For example, the population dynamical consequences of an ontogenetic niche shift were considered by assuming that individuals start to live in the littoral habitat and decide once during ontogeny to move out into the pelagic, while the effects of an optimal-foraging type of behaviour were investigated by letting individuals continuously adapt their habitat use. In all cases of flexible behaviour, foraging decisions were based on the difference in profitability between the pelagic and littoral habitat, which was defined such that both growth advantages and mortality risks were included.

Persson et al. (1998) showed that for increasing background mortalities the SC-cycles shorten in a step-wise manner to lower and lower periodicity, ultimately reaching a fixed-point dynamics, in which the state of the population and resource levels is identical at the beginning of each season. With higher mortality rates, the more rapid decline in abundance of the cohort that dominates a SC-cycle implies that resource levels increase faster, growth in size speeds up and individuals mature earlier in the season. The dynamics change when individuals succeed to mature already before the end of the previous season, which decreases the period of the SC-cycle by 1 yr. With increasing mortality, this bifurcation pattern with stepwise transitions to SC-cycles of a period that is 1 yr shorter resulted for all types of habitat use we considered (see Fig. 8 for an example), including the cases modelling flexible behaviour. In general, the occurrence of SC-cycles is hence robust against the introduction of a second resource and flexible behaviour into the model.

When individuals used the littoral and pelagic habitat in proportion to their volume, the robustness of SC-cycles results from the fact that a newborn cohort rapidly controls and depresses both resources, again starving any older cohorts to death. In case of an ontogenetic niche shift from the littoral to the pelagic, a newborn cohort quickly decreases the profitability of the littoral zone and hence moves out into the pelagic almost right after birth. Under these conditions the dynamics are identical to a situation in which all individuals are restricted to live in the pelagic only. The strong feedback of the newborns on the littoral resource is due to their large number and to the fact that the littoral zone is relatively small, as it constitutes only 10% of the total
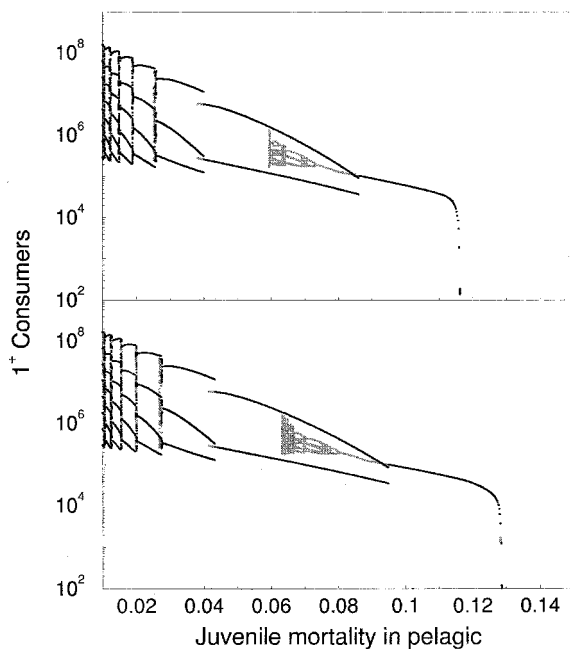
Fig. 8. Bifurcation diagram of the size-structured, consumer–resource model incorporating a zooplankton and a macroinvertebrate resource, restricted to the pelagic and littoral zone of a lake, respectively. Consumers either live in the pelagic habitat only (top) or use both habitats in proportion to their volume (bottom). The density of individuals of 1 yr and older at the start of a growing season is plotted as a function of the juvenile mortality rate in the pelagic. A regular cycle with a period of, for example, 4 yr in this diagram thus shows up as four distinct symbols at the same mortality value. Transient dynamics have been discarded. Different shades of grey represent the occurrence of alternative dynamic attractors for the same parameter value.

lake volume. Letting individuals continuously adapt their habitat use allows a newborn cohort to again gain control and depress both resources with the same consequences as if they would use the habitats proportional to their volume.

The introduction of flexible behaviour does affect dynamics in the region where otherwise stable fixed points are observed or where the consumer population would go extinct. In general, persistence is promoted by the behavioural responses, but is often associated with unstable dynamics. When individuals continuously adapt their behaviour to the habitat profitability, stable fixed points are never observed at all. In this latter case, SC-cycles result for low μ_p-values, while irregular population cycles occur at higher μ_p-values (De Roos et al. unpubl.).

Ecological implications

In summary, our studies indicate that (1) inter-cohort competition for shared resources is a major interaction driving size-structured population dynamics and (2) the type of dynamics can be inferred from a consideration of the scaling of minimum resource requirement with body size. These conclusions are to a large extent model-independent as both a size-structured model and a lumped stage-structured model confirm the minimum resource requirements rule (Persson et al. 1998, De Roos and Persson unpubl.). For exploitative consumer–resource interactions in general, the minimum resource requirement is expected to be an increasing function of consumer body size, since metabolic requirements usually scale more rapidly with body size than assimilation rates. On the basis of minimum resource requirement considerations, we therefore postulate that size-structured consumer–resource systems are primarily shaped by intraspecific competition and cohort dominance.

For the roach population in Alderfen Broad, where yearly survival was relatively low, we have shown that the observations at both the individual and the population level indeed agree with our contention. When yearly survival is high, our studies indicate that the number of YOY is so large that the feedback of their abundance on all shared resources induces the starvation of older cohorts. The large-amplitude, single-cohort cycles that result contrast strongly with the stabilising influence that is attributed to intraspecific competition in the context of traditional Lotka-Volterra competition systems. In addition, the starvation death of older individuals constitutes a strong ecological pressure favouring ontogenetic diet shifts. Although the timing of ontogenetic niche and diet shifts at an individual level has been explained on the basis of size-dependent foraging gains and mortality risks (Werner and Gilliam 1984), our studies indicate that at the population level their occurrence may make the difference between life and death from starvation under conditions of size-dependent, intraspecific competition.

Introducing size-structured prey: cannibalism

SC-cycles are analogous with the "single-generation" cycles, occurring in size- and stage-structured models with continuous reproduction (e.g. Gurney and Nisbet 1985, De Roos et al. 1990), which suggests that this type of cycles is more generally associated with population structure. As a fundamental feature of virtually all structured models that have currently been analysed, however, the environment with which individuals interact and which hence influences an individual's fate, is characterised by only one or two quantities (cf. the zooplankton and macroinvertebrate resource densities in the previous section). Most importantly, these quantities are identical for all individuals, *independent of their size*. Compared to the level of detail used to

describe the individual and its life history, the characterisation in the model of the environment with which an individual interacts is simplified and of low dimension.

This assumed low-dimensionality contrasts to the empirical fact that size-structured consumers typically prey on size-structured resources (Werner and Gilliam 1984, Wilbur 1988, Hambright 1991). In these interactions, the size range of prey that can be eaten by a predator is constrained by the predator's ability to capture and handle prey (Lundvall et al. 1999). A lower prey size boundary may be set by difficulties in detecting and retaining prey, whereas an upper boundary is set by morphological constraints of the feeding apparatus such as gape size and locomotory capacity (Breck and Gitter 1983, Persson 1987, Hambright 1991, Christensen 1996). As a result, a hump-shaped relationship is generally found between predator capture efficiency and prey size for a specific predator size with the optimum prey size increasing with predator size (Wilson 1975, Pepin et al. 1992, Fuiman and Magurran 1994, Rice et al. 1997). For example, the vulnerability of larval fish to raptorial predators have been found to first increase to a maximum and to thereafter decrease as prey fish size increases in size (Pepin et al. 1992, Fuiman and Magurran 1994, Rice et al. 1997, Lundvall et al. 1999). This pattern has been suggested to result from an increase in encounter rate between predator and prey due to increased swimming speeds and increased pigmentation of the fish prey, while capture success of predators simultaneously decreases due to better escape responsiveness of the prey fish as they grow and develop (Fuiman and Magurran 1994). Claessen et al. (2000) formalised this relation between size-structured predator (cannibal) and size-structured prey (victim) in a cannibalism model and assumed that the cannibalistic attack rate equals the product of an absolute attack rate and a size-specificity, both of which depend on individual length. The absolute cannibalistic attack rate follows an allometric function of the length of a cannibal, c. The functional form of cannibalistic size-specificity was based on observed cases of cannibalism in laboratory experiments and on data from diet analysis of field samples. Cannibalism is assumed to occur only if the ratio between victim length, v, and cannibal length, c, falls within a "cannibalistic window" formed by a lower and upper bound $v/c = \delta$ and $v/c = \varepsilon$, respectively. If the length ratio v/c falls below the lower bound δ, victims are considered too small and too translucent to be noticed by the cannibal. On the other hand, if v/c is larger than the upper bound ε, cannibalism is impossible due to gape-limitation of the cannibal or high escape capacity of the victim. Within the cannibalistic window, size-specificity is assumed to increase linearly from a value of 0 when $v/c = \delta$ to a maximum value of 1 when v/c equals an optimal victim-cannibal length ratio $v/c = \varphi$. For larger ratios the

size-specificity is assumed to decrease again linearly to reach 0 when $v/c = \varepsilon$. For any given cannibal length, c, the cannibalistic size-specificity is thus a tent function of victim length, v, reaching a maximum of 1 at $v = \varphi c$. Fig. 9 shows the overall cannibalistic attack rate, i.e. the product of the absolute attack rate and the size-specificity, as a function of both cannibal and victim length, c and v, respectively.

To the best of our knowledge, the study by Claessen et al. (2000) constitutes the first concise and detailed analysis of the population dynamics of a model with both size-structured predator and size-structured prey, in which the interaction environment is hence different for individuals of different sizes. The study extends the size-structured consumer–resource model presented by Persson et al. (1998) to account for size-dependent cannibalism in perch (*Perca fluviatilis*). In the model both the cannibalistic mortality rate, which an individual is exposed to, and the cannibalistic food spectrum that an individual can exploit, depend on the current population state (i.e. its size distribution) and therefore change dynamically. At the same time both quantities are different for individuals of different body sizes. In other words, an individual of a particular body size experiences a unique, size-specific interaction environment. In terms of the state concepts introduced in the discussion on PSPM theory, the E-state in this case is a continuous function of body size and hence infinite dimensional, while in the examples discussed previously the E-state was at most a two-dimensional vector of resource densities. As will be shown below, such a high-dimensional E-state creates the scope for entirely new dynamic phenomena that have not been found before in either structured or unstructured population models, but that at the same time closely match data on individual life histories observed in field situations.
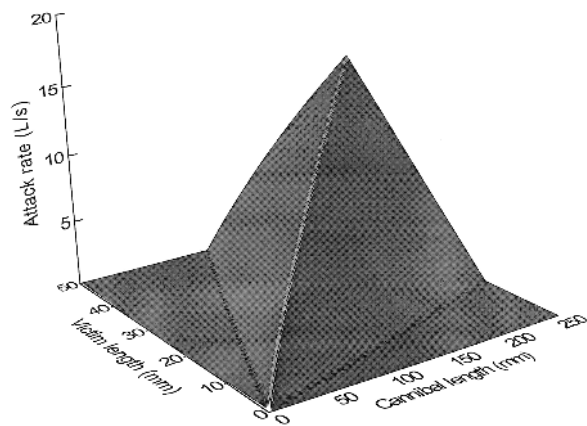
Fig. 9. Overall cannibalistic attack rate, i.e. the product of the allometric function describing the absolute cannibalistic attack rate and the tent function, describing the cannibalistic size-specificity, as a function of victim and cannibal length (Claessen et al. 2000).

Thus, these new phenomena significantly extend the scope for testing model predictions against empirical data.

Claessen et al. (2000) study the dynamics mainly as a function of a parameter β, which is the constant in the allometric scaling of absolute cannibalistic attack rate to cannibal length and hence is a measure of cannibalistic "voracity". The influences of a number of other parameters, for example, the lower and upper cannibalism bounds $v/c = \delta$ and $v/c = \varepsilon$, respectively, have been investigated as well (Claessen et al. unpubl.). For $\beta = 0$ no cannibalism occurs and the population exhibits "single-cohort" cycles driven by size-dependent competition (cf. Fig. 2). For increasing values of β the size-dependent cannibalism by larger individuals compensates more and more for their competitive disadvantages with respect to smaller individuals. The SC-cycles eventually disappear and cycles with a much reduced amplitude result, in which size-dependent competition, favouring smaller individuals, is balanced by size-dependent cannibalism, favouring larger ones. Effectively, the size-dependent mortality inflicted on the victims stabilises the dynamics without any significant effects of the energetic advantages that the cannibals experience.

For higher cannibalistic voracity (e.g. $\beta \approx 100$) the population dynamics intermittently exhibits periods with small-amplitude cycles and periods that are more like SC-cycles with a dominant cohort and reduced resource levels for a number of consecutive years (Fig. 10). In the small-amplitude cycles ($0 < T < 8$ and $14 < T < 20$ in Fig. 10) reproduction occurs every year, but a high cannibalistic mortality causes the newborn cohort to rapidly decline in density. In contrast to SC-cycles, resource levels therefore quickly improve after the reproduction pulse, which prevents older individuals from starving to death. The high resource levels lead to fast individual growth over the first 2 yr of their life to an ultimate body size that is set by the maximum zooplankton intake rate.

The end of a period with small-amplitude cycles is initiated by a newborn cohort that escapes high cannibalistic mortality early in life ($T = 8$ in Fig. 10). The escape from cannibalism comes about because the preceding cohorts that can cannibalise the newborns have suffered strongly from cannibalism themselves and are hence decimated to low densities. In addition, more abundant cohorts of still older individuals are prevented from cannibalising the newborns because of their large body sizes: their ratio of victim to cannibal size is below the threshold δ. They hence starve to death, causing a substantial drop in the density of potential cannibals. Essentially, the newborn cohort that escapes initiates a single-cohort cycle by depressing resource levels far below the critical density for adults. However, in contrast to SC-cycles not all older individuals starve to death, as the smaller ones manage to survive on a cannibalistic diet. Because of their low
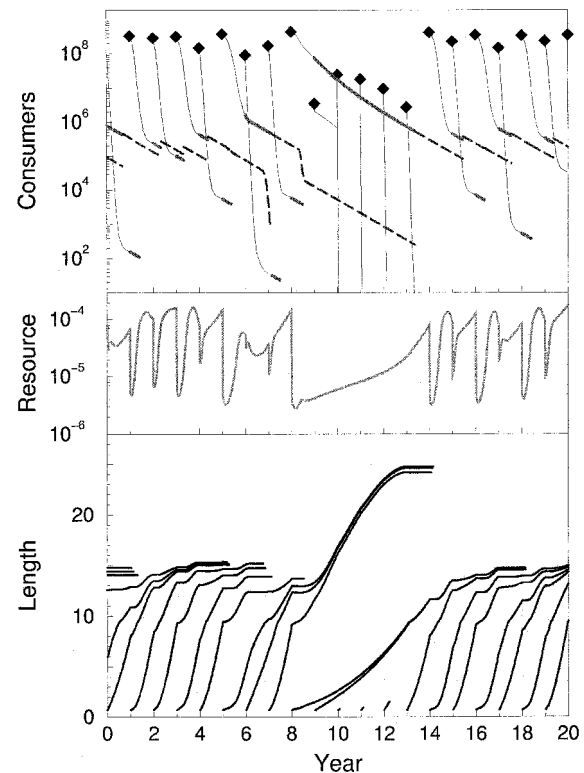

Fig. 10. Population dynamics of the size-structured, cannibalistic consumer–resource model (Claessen et al. 2000) for intermediate cannibalistic voracity ($\beta = 100$). Before $T = 8$ and after $T = 14$ the dynamics resemble small-amplitude cycles in which size-dependent cannibalism balances size-dependent competition. In between, the population is dominated by a cohort of dwarfs, which sustains a small cohort of giant individuals. Top panel: diamonds ($\blacklozenge$) indicate reproduction pulses; thin solid lines: YOY; thick solid lines: juvenile individuals older than 1 yr (termination of a line marks the maturation of all cohort members); dashed lines: adult individuals. All densities are expressed per lake (assumed 10^9 L). Middle panel: resource density as biomass (g) per litre. Bottom panel: growth trajectories (individual consumer length in cm) of all cohorts.

density, the number of individuals in the dominant cohort is hardly affected by the feeding of these cannibals. On the other hand, the cannibals themselves are confronted with abundant, cannibalistic food conditions, which allow them to enter a second growth phase, eventually reaching body sizes that are almost twice the size reached on a zooplankton diet. The combination of size-dependent competition and size-dependent cannibalism thus leads to a bimodal size distribution where the population is made up of a large group of small individuals, which as victims sustain a small group of large (giant) individuals. The competition among individuals is crucial for the dominant cohort to initiate a wave of slowly growing victims, while the cannibalism allows older cohorts to exploit this wave, "surfing" it towards high body sizes (Fig. 10).

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Even more prominently as was discussed in the section on size-dependent competition, the cannibalism model thus generates predictions about individual life histories (i.e. growth trajectories) in a population dynamic context. More specifically, the model predicts that escape from cannibalism of a particular newborn cohort during the first days of life initiates a train of events that ultimately leads to a second phase of rapid growth in the life history of a small number of older individuals (the "giants"). A recent empirical study by Persson et al. (2000) confirms the occurrence of these events in a Swedish lake in which perch is the only fish species present. Fig. 11 shows that in this particular lake in 1994 a pattern of growth acceleration occurred that is very reminiscent of the pattern exhibited by the model (Fig. 10). Comparing the model results and empirical data in more detail (Claessen et al. 2000) reveals that they show similarities, both qualitatively and quantitatively. In both cases, the transition was associated with a drop in resource density, a high survival of newborns, a drop in density of individuals older than 2 yr and a growth acceleration of the few survivors. A closer comparison of both population and individual level aspects, however, suggests significant discrepancies between model and data. First, in the model a successful recruitment is a result of a strong reproduction pulse, which is not the case in the data. Second, the growth curves of young perch during the phase with giants present differ qualitatively between model and data (cf. Figs 10 and 11). Third, in contrast to the model in which the giants subsequently have only marginal effects on population dynamics, the empirical data suggest significant dynamical consequences of this emergent phenomenon (Persson et al. 2000). These discrepancies between model and data, which we are currently investigating in more detail, illustrate the higher power of PSPMs compared to traditional population level models to discriminate between mechanisms in predicting both population level and individual level processes (i.e. growth rates) as a result of the population feedback.

For the size-structured consumer–resource model it was discussed that the results could be shown to generalize to a lumped stage-based (juveniles, adults) model (De Roos and Persson unpubl.), thereby verifying the structural robustness of the predictions. In a similar vein, the dwarf-and-giant phenomenon has been shown to generalize to a simplified model of a cannibalistic population (Claessen et al. 2000, Claessen and De Roos unpubl.). Adding a smooth cannibalistic interaction function, which is nonetheless comparable to the one discussed above, to a well-studied size-structured model with continuous reproduction (Kooijman and Metz 1984, De Roos et al. 1990, 1992, De Roos 1997) also resulted in the occurrence of a dwarf-and-giant type of dynamics, characterised by a continuous, but distinctly bimodal size-distribution. In contrast to the consumer–resource model, however, this simplified cannibalism model is still within the domain of PSPMs and cannot be reduced to a lumped stage-based formulation, due to the size-specific interaction environment. These results suggest that the occurrence of dwarfs and giants is a phenomenon which is likely to occur more generally in populations in which both size-dependent cannibalism and competition play a role.

Ecological implications

The results of the cannibalism model stress the importance of shared versus non-shared resources. Cannibalism provides an example of an ontogenetic diet shift and its consequences therefore have to be contrasted to the results of the consumer–resource model discussed previously. The form of the cannibalistic window, more specifically the lower bound $v/c = \delta$ of the prey/predator length ratio below which cannibalism is impossible, plays a crucial role. This lower bound ensures that the larger individuals have access to an exclusive resource, which can protect them from competition from smaller conspecifics. At the individual level this exclusive resource leads to the occurrence of double growth curves and thus to the subdivision of the population in dwarfs and giants. We have found that similar growth curves can also be obtained with a non-cannibalistic, exclusive resource (results not shown) that the adults can start to exploit when competition from YOY is depressing their food conditions shortly after a reproduction pulse. The double growth curves are therefore intimately linked to ontogenetic diet shifts and exclusive resources. Nonetheless, in the model these individual-level phenomena only marginally affect population dynamics because of the low relative abundance of giant individuals. At the population level the cannibalistic mortality inflicted on small individuals has the most important
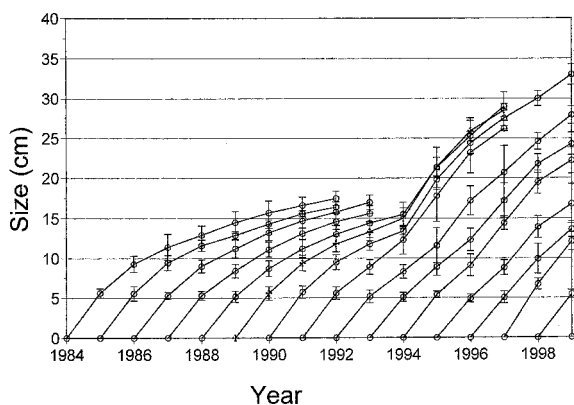

Fig. 11. Back-calculated growth trajectories of different year classes of perch in lake Abbortjärn 3 (central Sweden) from 1984 to 1998 (Persson et al. 2000 and unpubl.).

consequences as it can stabilise the large-amplitude SC-cycles and induce the occurrence of stable equilibria or small-amplitude cycles. The ensuing release from intraspecific competition leads to rapid individual growth and yearly reproduction.

The most exciting aspect of the cannibalism model is the fact that the ontogenetic diet shift to cannibalism is a truly emergent phenomenon of the population dynamics and is not at all a matter of course. Its occurrence crucially depends on the size at reproduction of the adults, the initial growth trajectory of the YOY and the presence of an initial size-refuge set by the lower bound of the cannibalism window during the first phase of life. With low δ-values adults immediately eradicate the entire YOY population without substantial energetic gains, while high δ-values cause the adults to starve before YOY reach exploitable sizes. Like in the consumer–resource case, the major mechanisms affecting the dynamics are largely model independent, since they can be shown to occur in models of vastly different lay-out that incorporate the same type of interaction function.

Discussion

A basic and seemingly unsolvable dilemma in the formulation and use of models has been to simultaneously achieve generality, realism and precision (Levins 1966). Ecologists in general have always aimed at finding universal patterns in ecological systems and tried to explain them by theories that have the virtue of generality (Persson and Diehl 1990). A high degree of precision, however, usually goes hand in hand with a loss of generality and a decrease in tractability. Our analyses of consumer–resource and cannibalistic interactions show that physiologically structured models provide a substantial degree of precision. Nonetheless, the models turn out to be tractable and lead to quite general results, despite their complexity. We have shown that one consumer–one resource interactions generally result in SC-cycles independent of specific model structure. Inclusion of a second, shared resource (one consumer–two resources) does not change this. The inclusion of flexible behaviour in the two resources case may increase the persistence beyond that present in the absence of flexible behaviour, but in the parameter space where the system persists in the absence of flexible behaviour the dynamics is the same. Including cannibalism will lead to a qualitative increase in the dimensionality of the system. Still, we have also for the cannibalism case been successful in teasing apart the different components affecting the dynamics (i.e. the cannibalistic voracity β and the lower bound of the prey/predator length ratio δ). Similar to the consumer–resource case, also here the general major mechanisms

affecting the dynamics are largely model independent. We are at present completing the first analyses of a double-structured model including a size-structured top predator where individuals, depending on size, either compete with and/or prey on a size-structured intermediate consumer feeding on a shared basic resource (Mylius et al. unpubl.). Our analyses so far suggest that the mechanisms unravelled in the consumer–resource models and the cannibalism model are of prime importance also in this more complicated model and that general conclusions also can be reached with this model configuration. Using PSPMs it thus seems feasible to obtain an understanding of the full range of dynamics of size-structured communities of three or even four species, which is comparable to the number of species in unstructured community models for which the dynamics are fully understood (cf. Holt 1997, Holt and Polis 1997, McCann et al. 1998). The decrease in generality due to the increased model complexity and the reliance on numerical solutions, which can only sometimes be broadened by analytical considerations, also has to be contrasted to, for example, the increased insights into explicit mechanisms that physiologically structured population models may provide. As discussed previously, one of the advantages of physiologically structured population models is that mechanisms are explicitly treated at the level of the individual. Parameters of Lotka-Volterra models may be possible to interpret in terms of individual level properties; for example, the competition α can be related to individual consumption capacity and carrying capacity to individual metabolic demands (Schoener 1986, Persson and Diehl 1990). However, physiologically structured models provide a much more intuitive and stringent link between individual and population processes.

Physiologically structured population models also allow for more extensive testing, both qualitatively and quantitatively, of model predictions against empirical data and make it possible to progress towards a closer interaction between modelling and empirical work. Two properties of PSPMs are responsible for the increased testing potential. First, comparisons between model predictions and empirical data have a higher discriminative power as most parameter estimates are derived independently from the empirical data set and assumptions and parameter values that are required as input exclusively pertain to individual-level processes. For example, in the roach case we used to analyse consumer–resource interactions, all individual level parameters were based on experimental work carried out in laboratory experiments with no relation to the Alderfen Broad system. Second, model predictions include both population level predictions (overall dynamics, cycle length and amplitude) as well as individual level predictions (growth, fecundity and mortality). Specifically, individual level processes are predicted in a population dynamical context, which, due to the popu-

lation feedback, are largely independent of the assumptions that the models are based upon. Moreover, these predictions generally allow more stringent tests against empirical data than predictions about the population dynamics itself. The appearance of giants and dwarfs in the cannibalism model is an example of an individual level pattern emerging in a population level context, which cannot be predicted from the knowledge of individual-level capacities. The presence of giants in both model predictions and empirical perch data represents a particularly nice illustration of how physiologically structured models can be used to critically test model predictions. To conclude, even though physiologically structured models have primarily been designed to handle size-structured processes per se, they also allow a much more critical testing of model predictions than what is possible with either non-structured, Lotka-Volterra type or lumped stage-structured models. This increased testing power is a direct result of the clear distinction between the individual and population level with their associated state concepts and the formalisation of their interrelation in terms of book-keeping and feedback.

Perspectives for an individual-based ecological theory

Community ecology aims at explaining features like species composition, relative abundances, diversity and the food web structure of biological communities. Undoubtedly, these community statics are the outcome of dynamic interactions between individual organisms that are themselves characterised by a unique set of physiological features, such as body size. Compared to traditional, unstructured models, on which most existing community theory is based, physiologically structured models have the advantage that they explicitly account for differences among individuals and are based on an individual-level model that describes how such differences affect the life history and behaviour of single organisms in interaction with their environment. The case studies in this paper illustrate how PSPMs can, in principle, be used to establish a mechanistic link between individual life histories and the dynamics of populations and communities. In addition, we have argued that PSPMs allow for a much tighter integration of modelling and experimental studies, as both model assumptions and model predictions are more clearly phrased in terms of observable biological quantities. PSPMs are formulated in terms of functions and parameters that are measurable in experiments with individuals and hence avoid making assumptions about population level quantities that are to be the outcome of the model study itself. Because of these two features we argue that PSPMs constitute an ideal framework for the development of a comprehensive theory about bio-

logical communities, which is individual-based and provides explanations for community patterns as the outcome of dynamics.

Given this potential to develop an individual-based community theory, the question arises in what aspects and to what extent it would differ from a theory based on unstructured or stage-based (juvenile/adult) models. In other words, what is actually gained by using a structured modelling approach and when is it indispensable for a mechanistic ecological theory? PSPMs will always incorporate some important features that are also captured by unstructured, Lotka-Volterra models. Under specific, restrictive assumptions about the life histories of individual organisms PSPMs can be reformulated in terms of stage-structured (juvenile/adult) models using delay-differential equations (see, for example, Gurney et al. 1983). Even reformulations in terms of unstructured, Lotka-Volterra type models are sometimes possible without violating the individual basis of the model formulation (Nisbet et al. 1996). A series of simplifying assumptions may thus allow for a logical link between structured and unstructured models (cf. Murdoch et al. 1992). Some community and population dynamical aspects will survive these simplifying assumptions and occur in all models in the link. For mechanistic explanations of these patterns and phenomena, a structured modelling approach is apparently not required. Other aspects will depend more crucially on the presence of either a discrete stage- or continuous size-structure.

Because theoretical studies that have investigated the influence of population structure on the dynamics and structure of biological communities are scarce, an accurate assessment of community aspects that sensitively depend on stage- or size-structure is, at present, impossible. However, as perhaps the most important message, our size-structured modelling efforts actually give some insight about the demarcation line for when size-structured interactions can be reduced to simpler stage-based models and when not. A reduction may be possible when all individual consumers compete for the same resources(s) whose representation does not differ from that in non-structured models (i.e. the consumer–resource model models above). Consequently, many aspects of the dynamics predicted by the consumer–resource PSPM discussed above (see also Persson et al. 1998) are also captured by a lumped stage-based (juvenile/adult) model (De Roos and Persson unpubl.). In contrast, in the case with size-dependent cannibalism, neither the individual level nor the population level dynamics can a priori be predicted from the knowledge of individual-level capacities, but are truly emergent results of population feedback. In this case, it is not possible to reduce the complexity of the model outside the domain of physiologically structured population models and a logical link between structured and non-structured models is no longer

present. The emergence of dynamical phenomena like giants also has a strong support in empirical data and can thus not be simply refuted as model artefacts (Claessen et al. 2000, Persson et al. 2000).

The fundamental feature leading to this distinction is that in the cannibalism model a consumer of a particular body size encounters its own, *unique* resource spectrum that differs from individuals of other body sizes. In other words, our analysis suggests that a structured modelling approach is especially indispensable if the interaction environment to which a particular individual is exposed and to which it responds, strongly depends on the physiological traits of the organism itself. We conjecture that some general community phenomena, such as the occurrence of competitive exclusion among consumers feeding on the same resource type and the stepwise lengthening of linear food chains along productivity gradients may be understood outside the domain of physiologically structured models, although the quantitative thresholds involved in these phenomena will most likely depend on population structure. On the other hand, for community aspects that are, for example, tied to behavioural responses of individuals or where interactions involve both size-structured consumers and size-structured prey, the use of a structured modelling approach is in our opinion absolutely necessary, as the individual-level processes involved tend to depend strongly on traits of the organism itself and responses tend to be unique for different individuals. Attempts to understand these community aspects using phenomenologically formulated, unstructured models, will have a high probability to generate results that will not generalise when the population structure is explicitly taken into account. Hence, the more unique the environment that an individual organism is exposed to and to which it responds, the more crucial a structured modelling approach will be for understanding the dynamics and structure of biological communities. Since many or perhaps most interactions involve size-structured consumers and size-structured prey, we actually expect a structured modelling approach to be essential for a large body of community theory. So far, our analyses of a PSPM including both a size-structured top predator and intermediate consumer in addition to a shared basic resource (Mylius et al. unpubl.) suggest that these modelling studies can indeed provide new insights that are of general importance to community ecology.

The role of PSPMs in bridging the gap between theory and experiments

Schmitz (this volume) convincingly argues that empirical research has been geared too much towards testing predictions of unstructured models, of which the assumptions are to a large extent based on causal rela-

tionships assumed by theoreticians and hence not sufficiently rooted in experimental and empirical data. The resolution of this problem advocated by Schmitz (this volume) is to use a purely individual-based simulation model of the study system (i.e. configuration models; Caswell and Meridith-John 1992; IBM) to summarise and integrate all available knowledge from experiments and natural history. This IBM should subsequently be used as an experimental setup to determine which of the many aspects of the system are relevant for the long-term dynamics and structure of the biological community. In other words, the IBM should be used to assess which individual-level processes exert an influence at the temporal, spatial and organisational/hierarchical scale of the biological community and which attenuate. The processes exerting an influence should subsequently be incorporated into a more analytical construct to develop a body of theory, generate predictions and test hypotheses. The key issue is that the selection and representation of individual-level mechanisms to be incorporated into the eventual analytical construct is not selected a priori or left to the theoretician, but is carried out on the basis of simulation experiments with the IBM.

We wholeheartedly agree with the view that contemporary models in ecology tend to be too phenomenological and are not sufficiently rigorous in their abstractions of individual-level mechanisms. We have argued that PSPMs resolve this problem by explicitly accounting for individual-level processes and describing the population dynamics as a pure book-keeping operation on individual life histories. Moreover, PSPMs also offer a larger scope for testing model predictions because they generate additional predictions about individual life histories in situations with population feedback. We hence consider the approach advocated by Schmitz and the one we discuss in this paper as two comparable solutions to the problem of establishing a more stringent link between the individual and population level in ecological models, thereby narrowing the gap between models and experimental/empirical data. The two approaches complement each other, as IBMs are usually designed to incorporate many more processes at the individual level in much larger detail using a set of rules to specify individual behaviour and life history. PSPMs, on the other hand, tend to account for a more restricted set of individual-level mechanisms which are represented by analytical functions that depend on the state variables characterising an individual and its environment. Because of their deterministic nature, however, PSPMs allow for more types of and more detailed (numerical) analysis than is the case with IBMs. First of all, individual-based simulations require a large number of replicates for the same parameter set to assess the ultimate dynamics, where the (deterministic) PSPMs only require a single numerical integration. But there is a general problem of resolving whether

alternative types of dynamics exist for the same parameter set. In the models presented in this paper such alternative dynamic attractors occur regularly (cf. Fig. 8; see also Persson et al. 1998, Claessen et al. 2000). Theoretically these could be found by starting numerical simulations or integrations from different initial conditions, but in practice the high degree of freedom in specifying the initial state prevents detecting alternative attractors with this approach. We have mostly detected the alternative attractors through detailed numerical studies with slowly varying parameters, but in some cases also this approach did miss the occurrence of a stable equilibrium as an alternative to population cycles for the same parameter set. For systems of differential and difference equations there exist established methods to numerically locate an entire branch of equilibria, whether they are stable or not, as a function of a parameter (Kuznetsov 1995, Kuznetsov et al. 1996). Such a numerical equilibrium and bifurcation analysis more readily detects the occurrence of alternative dynamic attractors. Kirkilionis et al. (1997) have shown that a similar approach of numerically locating an entire branch of (stable or unstable) equilibria as a function of a parameter is possible for PSPMs, as well. Although the methodology is not fully developed yet and such studies are complicated, it does offer an alternative and more powerful approach to analyse the dynamics predicted by the population model, where individual-based simulations have to rely on numerical simulations alone.

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