

REVIEW

The influence of size-dependent life-history traits on the structure and dynamics of populations and communities

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Abstract

Individual organisms often show pronounced changes in body size throughout life with concomitant changes in ecological performance. We synthesize recent insight into the relationship between size dependence in individual life history and population dynamics. Most studies have focused on size-dependent life-history traits and population size-structure in the highest trophic level, which generally leads to population cycles with a period equal to the juvenile delay. These cycles are driven by differences in competitiveness of differently sized individuals. In multi-trophic systems, size dependence in life-history traits at lower trophic levels may have consequences for both the dynamics and structure of communities, as size-selective predation may lead to the occurrence of emergent Allee effects and the stabilization of predator–prey cycles. These consequences are linked to that individual development is density dependent. We conjecture that especially this population feedback on individual development may lead to new theoretical insight compared to theory based on unstructured or age-dependent models. Density-dependent individual development may also cause individuals to realize radically different life histories, dependent on the state and dynamics of the population during their life and may therefore have consequences for individual behaviour or the evolution of life-history traits as well.

Keywords

Allee effects, community structure, density-dependent individual development, generation cycles, life history, population dynamics, size-structure, size-structured models.

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INTRODUCTION

In many species, body size is one of the most important traits of an individual organism. It determines to a large extent the type and strength of ecological interactions that the individual is subjected to and influences most, if not all, key life-history processes, including food choice, foraging capacity, growth, development, reproduction and mortality (Peters 1983; Calder 1984; Sebens 1987; Werner 1988; Werner & Gilliam 1984). For example, larger individuals generally forage at larger rates on larger prey and run smaller risks to fall victim to predators (Paradis *et al.* 1996). At an individual level, the influence of body size on ecological performance (estimated via vital rates such as growth, reproduction, or mortality, or interaction rates, mainly through foraging and being preyed upon) has been the subject of many experimental and theoretical studies. For

example, the size-dependent foraging capacity of *Daphnia* and the subsequent allocation of assimilated energy to growth, reproduction and metabolism have been measured in detail under a variety of conditions (e.g. Lampert 1977; Gurney *et al.* 1990; McCauley *et al.* 1990; Kooijman 1993, 2000). Similarly, the foraging behaviour and individual energetics of many fish species have been well documented (e.g. Elliott 1976; Mittelbach 1981; Fuijman 1994; Hjelm & Persson 2001). These experimental findings have been used to develop generic, individual-level models of foraging, growth and development that do not strongly focus on a particular biological species (e.g. Kooijman 1993, 2000; Nisbet *et al.* 2000; West *et al.* 2001). Kooijman (1993, 2000) presents the most elaborate and at the same time most concise theoretical framework (the ‘dynamic energy budget’ theory) describing the uptake and use of both energy and nutrients by individual organisms.

In contrast, species-specific models of individual feeding, growth and life history have been developed for *Daphnia* (e.g. Gurney *et al.* 1990; McCauley *et al.* 1990) and for a number of fish species (e.g. Persson *et al.* 1998).

The ontogenetic scaling of ecological performance with body size has also been used to explain patterns at the population and community levels (Werner 1988, 1994). For example, many predatory species grow during their juvenile period through size ranges that are similar to their future prey (Werner 1988; Wilbur 1988; Polis 1991). Since they are adapted to a predatory life style later on, the juvenile predators generally suffer from superior competition by individuals of their future prey species (Werner & Gilliam 1984; Werner 1986, 1988; Persson 1988). These so-called 'juvenile bottlenecks' have been argued to play a major role in many fish communities (Mittelbach 1983; Werner 1986; Persson 1985, 1987, 1988). Recruitment bottlenecks have also been suggested to have major influences in other aquatic communities (Neill 1988). Size-dependent, intraspecific interactions where large numbers of juvenile individuals suppress their own growth as well as adult fecundity have been argued to drive the population dynamics in *Daphnia* (McCauley & Murdoch 1987). In many fish species, population dynamics are shaped by either competitive or even predatory (cannibalistic) interactions between different age cohorts (Cryer *et al.* 1986; Hamrin & Persson 1986; Persson 1988).

Surprisingly, our theoretical understanding about the relationship between size-dependent ecological performance and population and community processes is rather limited. Understanding this interplay requires assessing how size-dependent changes during ontogeny in, for example, feeding ecology, mortality risks and reproduction rates influence the population age-, stage- or size-structure, how this population structure in turn influences the interaction with other species and eventually the structure and dynamics of biological communities. The development of ecological theory about these issues has been hampered by the lack of an appropriate modelling framework and appropriate (numerical) techniques for mathematical analysis. The earliest models of age-structured populations (Kermack & McKendrick 1927) are almost as old as the basic competition and predator-prey models of Lotka and Volterra, while the first size-structured models were formulated some 40 years ago (VonFoerster 1959; Sinko & Streifer 1967). Matrix models have also been used extensively to model dynamics of size-structured populations (Caswell 2001). None of these models, however, explicitly accounts for interactions of individuals with food resources and predators. Given the dependence of ecological performance on individual body size, these interactions are the key to understanding how size-dependent life-history components influence the dynamics and structure of populations and communities.

The development of stage-structured population models (Gurney *et al.* 1983; Nisbet & Gurney 1983) and physiologically structured population models (PSPMs) (Metz & Diekmann 1986; De Roos *et al.* 1992; De Roos 1997) has facilitated more rigorous studies of the relationship between individual life-history components and population dynamics. Stage-structured models are especially suited for modelling life histories where there are big differences in feeding, growth, reproduction and mortality among individuals in different stages, but little difference among individuals within the same stage. These models have been applied primarily to insect and invertebrate populations with distinct metamorphosis events (Gurney *et al.* 1980, 1983; Nisbet & Gurney 1983; Nisbet *et al.* 1989; McCauley *et al.* 1996). PSPMs do not require subdivision of the life history into distinct stages, and can account for life histories in which physiological traits and ecological interaction rates vary continuously. Size-structured population models constitute a subclass of PSPMs and have been developed and analysed to study the dynamics of *Daphnia* (De Roos *et al.* 1990, 1992, 1997) and various fish populations (Persson *et al.* 1998; Claessen *et al.* 2000, 2002; De Roos & Persson 2001, 2002; De Roos *et al.* 2002), but they have been used to a lesser extent than stage-structured models owing to their inherent complexity.

In this review, we discuss the theoretical insight that has emerged from recent studies on populations that are engaged in size-dependent, ecological interactions. We address the following three major issues:

- 1 In consumer-resource systems, size-dependent life-history components of consumers lead to population cycles that are driven by differences in competitiveness of differently sized individuals. The characteristics of these cycles depend on whether juvenile or adult individuals are competitively dominant.
- 2 In multi-trophic systems, size-dependent life-history components and interaction rates have consequences for both the dynamics and the structure of the biological community. An important new phenomenon is that consumers with size-selective foraging habits may exert a feedback on their own performance, which is operating and filtered through the life history of their prey. As one of the consequences of this new type of density dependence, consumers may exhibit an emergent Allee effect (De Roos & Persson 2002; De Roos *et al.* 2003), even though their foraging is completely exploitative.
- 3 In addition to these influences of the individual life history on population and community processes, the realized life history of individual organisms may, in turn, be strongly influenced by population and community dynamics. Individuals of similar age, but born at different times may, for example, either reach giant sizes or remain

dwarfs throughout their life (Claessen *et al.* 2000). This subtle population feedback on life history could have important evolutionary consequences and calls for new evolutionary analyses that explicitly account for population size-structure and its effect on individual life history.

A central question addressed in our review is how the individual life history affects population dynamics and, in turn, how population-level processes affect the life history of individual organisms. We focus on (modelling) studies that deal with the individual life history explicitly, while touching only briefly on studies that phenomenologically incorporate life-history effects as (delayed) density-dependent population processes (see recent work and reviews by Benton *et al.* 2001; Beckerman *et al.* 2002). In contrast to most studies that primarily focus on the consequences of life history for population dynamics, we draw attention to the fact that population feedback or density-dependence acting on the individual life history may have substantial consequences for community structure, as well as for the evolution of the life history itself. These consequences may be far-reaching and non-trivial and have up to now not been rigorously revealed.

AGE-, STAGE- AND SIZE-STRUCTURE

The property that sets structured population models apart from other models is that it is really the individual life history that is modelled instead of the behaviour (e.g. feeding, reproduction, mortality) of the entire population (De Roos *et al.* 1990; De Roos 1997). Appropriate state variables for the individual organism (e.g. size) are chosen to form the individual or *i*-state. Next, all life-history processes, like feeding, growth, reproduction and mortality, are modelled as a function of this individual state and variables that characterize the environment, such as ambient food density or density of predators. Together, the resulting formulations represent a mathematical description of an individual life history. The population is represented by a distribution, which specifies how many individuals of a particular *i*-state are present. This distribution, also referred to as the population or *p*-state, may be a density function over the entire physiologically relevant size range that individuals can attain. On the basis of the individual-level model, a set of equations describing the dynamics of the population state can be derived without further assumptions. Thus, all model assumptions pertain to the individual level as opposed to the population level, which allows structured models to be more easily based on experimental and empirical data (McCauley *et al.* 1996; De Roos & Persson 2001). Both stage-structured models (Gurney *et al.* 1983; Nisbet & Gurney 1983) and PSPMs (Metz & Diekmann 1986; De Roos *et al.* 1992; De Roos 1997) are

characterized by the above description. In contrast, although size-structured matrix models (Caswell 2001) may include density-dependent transition probabilities from one size class to another and are extremely valuable in assessing the dynamic consequences of these transitions (e.g. Fujiwara & Caswell 2001), the link with individual life history is substantially weaker. Given our focus on the interplay between life history and population or community dynamics, we highlight the insight that has emerged from studying stage-structured and physiologically structured models.

Simply accounting for age-, stage- or size-structure in population models in itself has no effect whatsoever, unless the vital rates and the interaction rates of individual organisms with their environment (e.g. food, predators) depend on their age, stage or body size. (For ease of presentation we will collectively refer to such age, stage or size dependence as 'life-history dependence'.) Three different aspects of life-history dependence can be distinguished:

- 1 The delay encompassing the juvenile period, between the time of birth of an individual and when reproduction begins represents the most prominent life-history dependence in vital rates. Such a delay generally works as a destabilizing factor in that the system is more likely to exhibit cycles (Gurney *et al.* 1980).
- 2 A second feature of life-history dependence pertains to the nature of the size scaling of ecological performance with body size. For example, the scaling relations of foraging and mortality rates with body size have been argued to depend on the type of habitat (Wilson 1975; Werner 1988; Persson *et al.* 1998). In essence, the juvenile delay discussed above also falls into this category of effects, since the reproduction rate is only non-zero for individuals in the adult stage.
- 3 A last and rather fundamental aspect of life-history dependence in ecological performance is whether the life history itself is fixed or is influenced by some kind of population feedback. In strictly age-dependent cases (continuous age-distribution or discrete age-classes), individual progress through its life history is predetermined. In contrast, in purely size-dependent cases, individual growth in size, and hence progression through various life stages, generally depends on food intake. The feedback of population foraging on ambient food density implies that individuals will differ in the time to grow to particular body sizes, which will depend on the food densities experienced since birth. In other words, the life-history trajectory followed by different individuals may be different due to population feedback on the environmental conditions. If maturation occurs on reaching a particular size-threshold, the duration of the juvenile period will vary over time as well.

These three distinct aspects of life-history dependence (the juvenile delay, the size scaling of ecological performance and the population feedback on realized life history) are accounted for to a different extent in age-, stage- and continuously size-structured models. All model types can account for the juvenile delay. Stage- and size-structured models can account for size-dependencies in rates to differing degrees. However, the most important distinction is whether population feedback on realized life-history traits occurs. This aspect of life-history dependence only occurs in models that account for a continuous size-distribution (e.g. De Roos *et al.* 1990, 1992, 2002; Persson *et al.* 1998) and stage-structured models with variable stage duration (Nisbet & Gurney 1983; Gurney & Nisbet 1985). Models without a population feedback on individual development are essentially age-structured and we use the terms age- and size-structured models in accordance with this distinction.

Many of the phenomena induced by life-history dependence in models with continuous distributions can also be found to a greater or lesser extent in analogous models that only recognize distinct stages. For example, the introduction of a juvenile delay induces cyclic dynamics, irrespective of whether population age-, stage- or size-structure is accounted for. Also, an invulnerable age class has been found to stabilize dynamics in a stage-structured model of host–parasitoid interactions (Murdoch *et al.* 1987), while a comparable stabilizing effect occurs in a continuous size-structured model incorporating an invulnerable size class (see below). In contrast, the phenomena that result from population feedback on life history, in particular, the population feedback operating through the life history of prey individuals (see section ‘Consequences of size-structure for community structure’) and the life-history differences arising from this feedback (see section ‘On the interplay between life history and population dynamics’) will not occur in age-structured population models. These phenomena may also be difficult to find in models with discrete stages only. We expect future studies to reveal that this population feedback on realized individual life history is one of the most crucial aspects of the interplay between individual and population-level processes.

CONSEQUENCES OF SIZE-STRUCTURE FOR POPULATION DYNAMICS

The earliest and simplest stage-structured models considered single insect populations (Gurney *et al.* 1980, 1983; Lawton & Hassell 1981; Nisbet & Gurney 1983; Gurney & Nisbet 1985; Bellows & Hassell 1988). The studies were inspired by observations that many natural or laboratory populations of insects would exhibit fluctuating dynamics even in rather constant environments (Nicholson 1954; Gurney *et al.* 1983; Ebenmann 1988, Godfray & Hassell

1989 and references therein). A major characteristic of these fluctuations pointed to successive generations being segregated in time, even though the individual life history, in principle, would allow for overlapping generations. In general, the modelling studies did not explicitly account for the interaction of the insects with resources (but see Nisbet & Gurney 1983) and modelled competition for resources as a form of density dependence. These studies focused on the stability properties of the equilibrium and on the fluctuation period of the population cycles that emerged.

In general, these single-population models predict that cycles with a periodicity related to the generation time of the individual organism will occur under a wide range of parameter combinations. Two types of cycles are distinguished: cycles in which the fluctuation periodicity is slightly larger than the generation time of the individual, but smaller than twice this value. These cycles are referred to as ‘single-generation cycles’. In the other type of cycles, referred to as ‘delayed-feedback cycles’, the fluctuation periodicity is two to four times the generation time. The mechanism driving these cycles is the expression of competition among larval (Gurney *et al.* 1983; Gurney & Nisbet 1985) or adult individuals (Gurney *et al.* 1980) as a density-dependent change in vital rates. In an elegant and revealing study, Gurney & Nisbet (1985) showed that if an increase in larval competition was immediately expressed as either an increase in larval death rate or a slowing down of larval development, single-generation cycles resulted. In contrast, if the expression was delayed and resulted in a decreased survival through the pupal stages or a reduced fecundity when adult, delayed-feedback cycles resulted.

Single-generation and delayed-feedback cycles are two of the most important advancements in the theory about the life history–population dynamic interplay. These concepts are not specifically tied to size-dependence in individual life history, as many of the single-population stage-structured models just discussed are essentially age-structured. Nisbet & Gurney (1983) even show that a size-structured model with variable stage duration is less likely to show sustained single-generation cycles than an analogous, age-structured model with fixed stage durations (but see De Roos *et al.* 1990, and below for the opposite claim). Single-generation and delayed-feedback cycles have also been subject of experimental and empirical studies. McCauley & Murdoch (1987) pointed to the potential of generation cycles in natural consumer–resource systems in their synthesis of *Daphnia*–algal dynamics from lakes throughout the world. Recent analyses (Murdoch *et al.* 2002) highlight the importance of single-generation and delayed-feedback cycles in natural systems for more than 100 different species (including marine and freshwater fish, birds, mammals, invertebrates and insects) displaying cyclic dynamics. These

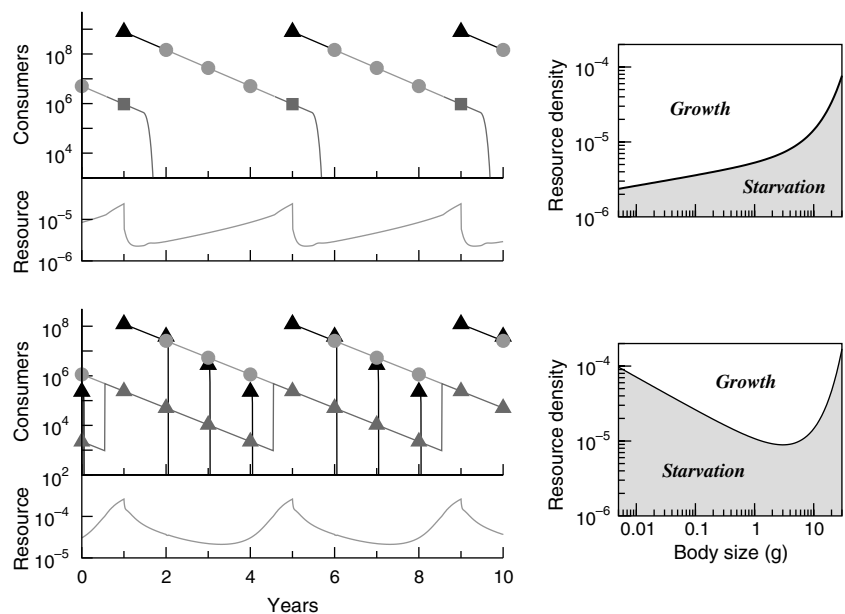
authors hypothesized that generalist predators, who are weakly coupled to particular prey species, should display single-species-like dynamics. When the cycle periods were scaled to the generation time of the consumer, the predictions from the hypothesis were very well supported. This suggests that an important class of population dynamic phenomena is indeed tightly linked to aspects of individual life history and the developmental delay in particular.

The occurrence of single-generation and delayed-feedback cycles is closely tied to the presence of a juvenile delay and bears little relation with the other two aspects of size-dependent life histories: the size-scaling of vital rates and the population feedback on realized life history. These issues have been addressed in later studies, mainly using PSPMs. De Roos *et al.* (1990, 1997) study the interaction of a size-structured *Daphnia* consumer population feeding on an unstructured algae resource. With self-renewing food, i.e. an algal population that follows logistic growth in the absence of the consumer, the model exhibits for most combinations of parameters classical predator-prey cycles. Effects of the size-structure on population dynamics leading to single-generation cycles are only observed for a restricted set of parameter values, for which an analogous, unstructured model approaches a stable equilibrium. Without self-renewing food dynamics (i.e. when the algal population follows semi-chemostat dynamics in the absence of consumers), De Roos *et al.* (1990) show that only single-generation cycles occur. Since growth in body size is food dependent, the size-age relationship changes with an increase or decrease in equilibrium food density and is hence influenced by a population feedback that operates via the feeding pressure of the consumer population on

ambient food densities. An increase in food density translates into three effects: (i) individuals grow more rapidly and hence mature at a younger age; (ii) individuals reach larger sizes and hence at every age have a higher foraging capacity; and (iii) a higher fecundity. De Roos *et al.* (1990) show that the food-dependent juvenile delay (i) is a major destabilizing factor compared to an analogous model with a fixed juvenile delay. The influence of the changing size-age relation on foraging (ii) is a stabilizing factor, since it allows the consumer population to counter fluctuations in food density not only via its functional response, but also through a change in individual foraging capacity following the change in length-age relation. The last effect of the changing size-age relation on reproduction (iii) is shown to have only minor consequences.

Persson *et al.* (1998) analysed the influence of the size scaling of life-history components on population dynamics using a physiologically structured model for the population dynamics of roach (*Rutilus rutilus*). This model differs from other size-structured models in that reproduction was assumed only to occur during a peaked event at the start of the growing season (summer), whereas feeding, growth, metabolism and mortality were modelled as continuous-time processes. The type of population dynamics exhibited by the model was reliably predicted by the scaling of the 'minimum resource requirement' (MRR) with body size (see Fig. 1). This MRR is defined as the food density at which the individual food intake, which was modelled using a size-dependent attack rate and handling time, exactly suffices to cover the size-dependent maintenance requirements. For food densities above the MRR the individual can grow, for lower densities it will starve and possibly die of starvation.

Figure 1 Representative examples of the juvenile- (*top*) and adult-driven (*bottom*) cycles, as predicted by the model of Persson *et al.* (1998). The model represents a size-structured consumer population feeding on an unstructured resource. Reproduction occurs as a pulsed event at the beginning of summer, giving rise to new cohorts of individuals. Feeding, growth, mortality and resource production are continuous-time processes. Left panels: dynamics of newborn (age between 0 and 1; *black triangles*), juveniles (*light-grey circles*) and adult (*dark-grey squares*) consumer individuals and resource density. Right panels: zero-growth isocline (*solid lines*), defined as the food density at which assimilation rate exactly equals metabolic requirements, for individual consumers as a function of their body size.



With the MRR being a strictly increasing function of body size, population cycles occurred in which the population almost always consisted of a single cohort of individuals, i.e. a group of individuals born at exactly the same time (Fig. 1; top panel). In these so-called 'single-cohort' cycles the large number of newborn individuals that are produced during a reproduction event suppress the food density until just above their MRR, such that all larger individuals starve to death. The single cohort reaches its maturation size threshold after its numbers have decreased due to background mortality. The survivors build up gonad mass and release it in a strong reproduction event at the beginning of the following summer, starting the cycle anew. The competitive dominance of small individuals, in the sense that they have a lower MRR, enforces a cycle in which individuals are essentially semelparous. These cycles can be seen as an extreme type of single-generation cycles in which the short period of reproduction that characterizes adult life in single-generation cycles is compressed into a single reproduction event. De Roos & Persson (2001) showed that these cycles correctly describe the fluctuations in a natural population of roach with a periodicity of only 2 years including the quantitative predictions of individual growth rates of strong and weak cohorts. With this short period both the model and the natural population show an alternation of strong and weak year classes, in which the strength of the year class strongly affects the growth and survival during the first and second year of life.

Persson *et al.* (1998) found that a stable equilibrium only occurred if the MRR was relatively independent of body size. In contrast, a second type of population cycle occurred when larger individuals were competitively dominant, in the sense that the MRR decreases, at least initially, with body size (Fig. 1; bottom panel). In these cycles, adults are continuously present in the population and reproduce every year. However, the first offspring that adults produce reach in their first year of life a range of body sizes that makes them competitively dominant (i.e. possess the lowest MRR). These first offspring suppress food densities to such low levels that all offspring produced by their parents in later reproduction pulses starve to death. The dominant juveniles retard their own growth and development, until their density has dropped due to background mortality and food density has recovered. This allows the dominant juveniles to mature and replace their parent cohort. As in the single-cohort cycles, a single cohort of individuals dominates the population throughout its juvenile period. After maturation these individuals immediately produce the next dominant cohort, but the adults do not die of starvation and remain reproductively active until they die of background mortality. Furthermore, growth retardation of juvenile individuals occurs late in the juvenile period, as opposed to early on in the juvenile period during single-cohort cycles. Thus, even

though the periodicity of these cycles is close to the generation time of the dominant cohort, they have several distinctive features that set them apart from the single-cohort or single-generation cycles. The same mechanism as described here, i.e. the asymmetric competition between large and small juveniles, has been argued to induce sustained population oscillations in a simulation model of laboratory populations of *Callosobruchus chinensis* and *C. maculatus* (Bellows 1982).

The relationship between size-dependent competitiveness of different life stages and the resulting type of population dynamics has been analysed further by De Roos & Persson (2003) using a two-stage, juvenile–adult model in which maturation was governed by reaching a particular size threshold and the competitiveness of juvenile versus adult individuals was represented by the ratio of their respective feeding rates. Corroborating the findings by Persson *et al.* (1998), stable equilibria were only found to occur when juveniles and adults were competitively similar. Furthermore, population cycles occurred when either the juvenile feeding capacity was roughly twice as large as that of adults (juvenile-driven cycles) or vice versa (adult-driven cycles). Many of the cycle characteristics identified by Persson *et al.* (1998) also characterize the juvenile-driven and adult-driven cycles found in the two-stage, juvenile–adult model of De Roos & Persson (2003). Table 1 summarizes the main properties of these two types of cycles.

The simplicity of the two-stage model allowed for a deeper understanding of the relevant mechanisms giving rise to juvenile-driven and adult-driven cycles. Variation in juvenile delay (and hence also juvenile survival) due to fluctuations in food density was a necessary requirement for adult-driven cycles to occur. In contrast, juvenile-driven cycles also occurred in an age-structured version of the model. Even though reproduction was modelled as a continuous time process, in juvenile-driven cycles discrete

Table 1 Qualitative characteristics of juvenile- and adult-driven population cycles, occurring when either juveniles or adults are more competitive, respectively. Characteristics in italics are essential for the occurrence of the cycles

Aspect	Juvenile driven	Adult driven
Amplitude	Large	Small
Period-delay ratio	<i>c.</i> 1	>1.2
Size distribution	One dominant cohort	Constant
Fecundity – adults	<i>In phase</i>	Out of phase
Juvenile delay	Short/variable	Long/ <i>very variable</i>
Juvenile survival	High/variable	Low/ <i>very variable</i>
Food density	High	Low
Juvenile–adult ratio	Low	High
Adult fecundity	Low	High
Adult lifespan	Short	Long

cohorts developed and adults were only present in the population during short periods of time. The main mechanism driving these cycles is the covariation in adult density and adult fecundity, which arises because the total feeding pressure exerted by a juvenile cohort decreases during its development due to background mortality. As a consequence, food densities and hence fecundity reaches a maximum at the same time as the dominant cohort matures. In a model variant, in which this covariation could not occur, the juvenile-driven cycles disappeared.

The above discussion makes clear that in single-population models or structured consumer–unstructured resource models, population cycles with a periodicity between one and two times the generation time of the individuals predominate. However, these ‘single-generation’ cycles do not form a uniform class, as different types of these cycles occur, depending on which life stages are competitively dominant (see Table 1). Delayed-feedback cycles are up to now only found in stage-structured models, in which a delayed expression of within-stage competition on ecological performance is explicitly assumed (but see Briggs *et al.* 1999 for a mechanistic origin of delayed-feedback cycles). In continuous size-structured models they have not been found, most probably because the models of individual life history that the models are based upon do not incorporate a mechanism for the required delayed expression of competition. When a structured population model incorporates the classical combination of a logistic prey growth and a saturating predator functional response, classical predator–prey or prey–escape cycles are expected to predominate with single-generation cycles occurring only under limited sets of conditions (Nisbet *et al.* 1989; De Roos *et al.* 1990). This theoretical prediction for *Daphnia* populations is in strong contrast with the experimental data, where single-generation cycles are the most frequently occurring dynamic pattern (McCauley & Murdoch 1990; McCauley *et al.* 1999) and predator–prey cycles can only be generated through very specific experimental manipulation (McCauley *et al.* 1999). To reconcile this discrepancy between model predictions and empirically observed dominating dynamics remains an issue for further research.

Single-generation and delayed-feedback cycles generically occur in a wide range of structured population models. On the other hand, specific models may exhibit more complex, but less generic population dynamic patterns. For example, modelling studies of the effect of inter-stage cannibalism in *Tribolium* have revealed a wide range of dynamics patterns, ranging from equilibrium dynamics, periodic and aperiodic fluctuations to chaos (Costantino *et al.* 1997; Dennis *et al.* 1997). These studies primarily aimed at testing the congruence between model predictions and experimental observations, and they did not explicitly address the interplay between life history and population dynamics. Hence, we do

not elaborate on them here. Recently, it has been advocated that population models should account for the consequences of delayed life-history effects (Benton *et al.* 2001; Beckerman *et al.* 2002). Such effects are argued to result, for example, when conditions during early development of an individual influence its performance later in life or when maternal effects significantly influence offspring performance (Benton *et al.* 2001; LaMontagne & McCauley 2001). Modelling studies on these delayed life-history effects have, however, not yet explicitly linked the individual life-history processes to the dynamics of the population and have represented the delayed life-history effect phenomenologically as a delayed, density-dependent population process. Since many of the mechanisms that give rise to single-generation or delayed-feedback cycles are also classified as a delayed life-history effect (Beckerman *et al.* 2002), further studies, which explicitly account for the individual life history, are needed to understand the significance of these effects for the population dynamics.

CONSEQUENCES OF SIZE-STRUCTURE FOR COMMUNITY STRUCTURE

Most studies involving structured population models have focused on the consequences of population age-, stage- or size-structure for dynamics. One area in which stage-structured models have been used extensively relates to the interaction between hosts and parasitoids (see, among others, Murdoch *et al.* 1987; Briggs *et al.* 1993; Godfray & Briggs 1995; Murdoch & Briggs 1996). These studies often concern an insect pest population that is to be biologically controlled at a low overall density by parasitoids. Because violent outbreaks of the pest population are to be prevented, stability of the equilibrium is a natural focal point (Murdoch & Briggs 1996). In contrast, the consequences of population structure for community composition have been studied to a much lesser extent (but see McCann 1998).

One of the earliest examples showing that population size-structure may be crucial for population persistence and hence community structure concerns the ‘life-boat mechanism’ in cannibalistic populations (Van den Bosch *et al.* 1988). This mechanism allows a cannibalistic population to persist under food conditions, which would cause its extinction in the absence of cannibalism. Polis (1981) discusses a number of examples from natural populations, primarily zooplankton and fish, in which this mechanism may operate. Under conditions that food is abundant for juvenile individuals, but absent or very low for adults, the latter can gain indirect access to the juvenile food source by cannibalism. In the absence of cannibalism, adults would not reproduce and the population goes extinct. Van den Bosch *et al.* (1988) identified under which conditions this phenomenon is effective, resulting in a ‘mean-yield

criterion': if on average an adult can produce more than a single newborn offspring from cannibalizing one juvenile individual, the 'life-boat mechanism' can prevent population extinction. Naturally, the mean-yield criterion can only hold if the juveniles grow in body size in between their time of birth and the time they are on average cannibalized by the adults. This mass increase makes that the net balance of cannibalism in energetic terms can be positive. The life-boat mechanism also implies that the cannibalistic population exhibits an Allee effect: for a range of adult food densities a small initial population would not succeed in reaching a positive equilibrium density, as in the initial phase the density of cannibalistic food is too low. The small initial population is destined to go extinct. With larger initial densities, however, the adults would have sufficient access to cannibalistic food to establish an equilibrium population. The life-boat mechanism has been the subject of a number of theoretical studies (e.g. Cushing 1992; Diekmann *et al.* 2003), but, to our knowledge, has only once been investigated experimentally (Van den Bosch & Santer 1993).

Given a prey population with a distinct age-, stage-, or size-structure, it may be argued that predators specializing on different life stages occupy different niches, even though they share the same prey population. As an obvious consequence, multiple predators may be expected to coexist on a single prey. For a host–two parasitoid system, Briggs *et al.* (1993) showed, however, that this niche segregation between an egg-stage parasitoid and a larval-stage parasitoid only leads to coexistence, when there is substantial variability in the time that host individuals spend in the vulnerable stages. When this duration is exponentially distributed some hosts mature out of the vulnerable egg stage into the vulnerable larval stage almost immediately, while others mature after very long time

periods. This essentially implies that part of the hosts can be exclusively attacked by only the egg-stage predator, while the larval-stage predator has virtually exclusive access to another part of the host population. If the duration of egg and larval stage are more resembling fixed time delays, coexistence of both parasitoids is not possible (Briggs 1993).

A novel consequence of size- or stage-specific predation on community structure was recently reported by De Roos & Persson (2002) using a linear food-chain model consisting of an unstructured resource, a size-structured consumer and an unstructured predator population. Both the consumer and predator forage exploitatively on resource and consumers, respectively, but predators only attack small consumer individuals. Figure 2 compares the predictions of this size-structured food-chain model with an unstructured, analogous model. The unstructured model predicts the characteristic, step-wise lengthening of the food chain and, once present, the positive correlation between predator and resource density with increasing productivity of the environment (Oksanen *et al.* 1981). The size-structured model, however, predicts that the curve relating the three-species equilibrium to productivity is folded. The upper part of this branch represents stable, the lower part unstable equilibria. Over the range of productivities for which the curve is folded, both equilibrium without predators (only resource and consumers) and equilibrium with predators is stable.

The bistability between equilibria with and without predators over a substantial range of productivities comes about because of the changes that the predators induce in the size-structure of their prey population. Since the predators forage size-selectively these changes exert a *positive* feedback on their own performance. In both the unstructured and the size-structured model, predators increase the

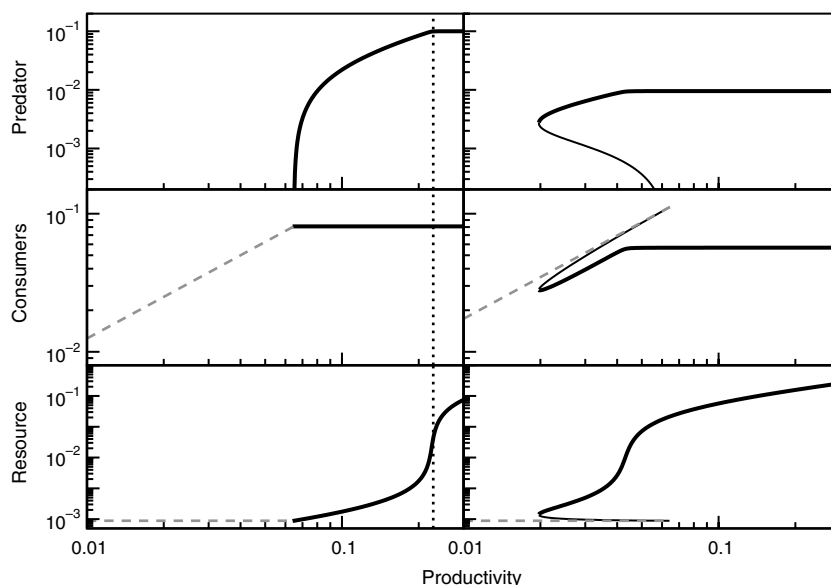


Figure 2 Representative pattern of variation in predator (*top*), consumer (*middle*) and resource (*bottom*) densities as a function of productivity for the size-structured food-chain model (*right*) of De Roos & Persson (2002) and its unstructured analogue (*left*). The average predator attack rate in the unstructured food-chain model is chosen such that the intersection points between the curves representing the predator–consumer–resource equilibrium (solid lines) and the consumer–resource equilibrium (dashed lines) is located at the same value of productivity. Thick and thin solid lines indicate stable and unstable predator–consumer–resource equilibria, respectively. The unstructured model exhibits limit cycle dynamics for productivity values to the right of the vertical dotted line.

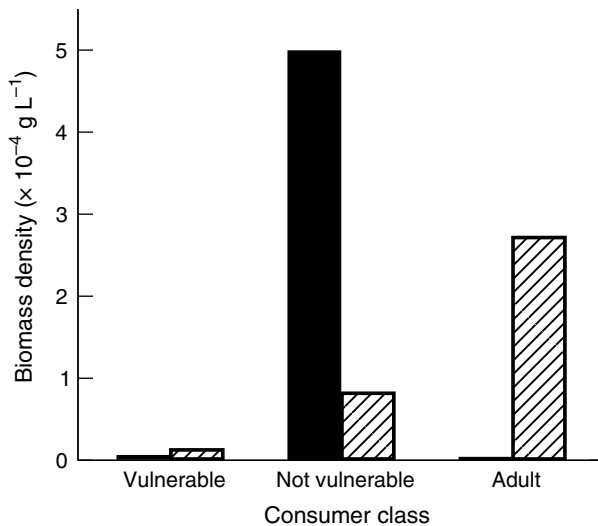


Figure 3 Biomass distribution over the vulnerable, non-vulnerable juvenile and adult consumer size-class in the absence (solid bars) and presence (hatched bars) of predators, as predicted by the size-structured food-chain model of De Roos & Persson (2002) for the same value of environmental productivity.

mortality rate of the consumers. However, in the size-structured food-chain model this predation mortality causes a thinning among juvenile consumer individuals, which reduces intraspecific competition among consumers and accelerates consumer growth. Thus, owing to predation the biomass-size distribution of the consumer population changes (Fig. 3), such that the biomass-density of intermediately sized, non-vulnerable juvenile consumers is significantly reduced and the biomass-density of adult individuals substantially increases. The increase in the density and body size of adults results in a higher total population reproduction, which in turn leads to an increase in the biomass density of small consumers that are vulnerable to predation. Therefore, even though predators reduce the *total* consumer biomass in both the unstructured and the size-structured model (cf. Fig. 2), in the size-structured model the *vulnerable* consumer biomass is predicted to be higher when predators are present (Fig. 3). The feedback of predators on their own food availability thus operates via the life history of the consumer. The relaxation of intraspecific competition can be viewed as a filter that modifies the essentially negative effect of a decrease in consumer biomass due to predation into a positive feedback on predator food availability. These effects only come about because there is a population feedback on the life history (i.e. the size-age relation, of individual consumers: a reduction in the density of consumers leads to an increase in resource densities and thus to an increase in the body size at any given age) and this phenomenon cannot occur in an age-structured version of the model (De Roos & Persson 2002).

As a consequence of the bistability, predators exhibit an ‘emergent’ Allee effect even though they possess none of the commonly invoked mechanisms for this effect, such as sexual reproduction or group foraging (Courchamp *et al.* 1999; Stephens & Sutherland 1999). Instead, their foraging is completely exploitative. In the bistable range of productivities, small initial populations of predators cannot successfully establish themselves in a system with consumers and resource, because they are too few in number to produce the changes in consumer size-distribution that are necessary for their own persistence. In contrast, larger initial populations of predators do succeed to approach an equilibrium population. More recently, De Roos *et al.* (2003) have shown that the emergent Allee effect can only occur if the consumer population, in the absence of predators, is regulated through density-dependent retardation of the growth and development of juveniles. In contrast, if this regulation occurs through density-dependent fecundity or mortality emergent Allee effects cannot occur. If the consumer population in the absence of predators is regulated through density dependence in juvenile development, emergent Allee effects will occur whenever there is overcompensation in this regulation, such that a decrease in juvenile density actually increases the total maturation rate of the juveniles. In other words, the relationship between total maturation rate out of the juvenile stage and juvenile density should be hump-shaped. De Roos *et al.* (2003) also show that under these conditions, predators that prey exclusively on very small consumer individuals, as well as predators that prey on adult consumers, will exhibit an emergent Allee effect. Both positive and negative size-selective predation will thus give rise to an emergent Allee effect.

These results predict that Allee effects and bistability of equilibria are more common characteristics of biological communities than expected till now and may provide alternative explanations for phenomena previously ascribed to stoichiometric effects or food web influences (Worm *et al.* 2002). Especially, zooplankton species like *Daphnia* have a high reproductive capacity in the absence of predators and are hence likely to be regulated by juvenile growth retardation. For *Daphnia*, in particular, growth retardation has been claimed to be an important regulating factor (McCauley & Mudroch 1987). Similarly, many fish species can produce a very large number of eggs given sufficient food conditions. In the absence of predation these populations are likely to exhibit regulation through juvenile growth retardation as well. As can be seen in Fig. 3, one expression of juvenile growth retardation is that populations become dominated by intermediately sized individuals and lack a substantial density of large adults. Indeed, such a ‘stunted’ composition has been frequently observed for fish populations and has been attributed to a lack of (predation)

mortality (Langeland & Jonsson 1990; Ridgway & Chapleau 1994).

A phenomenon that is associated with the emergent Allee effect is that the predator population may exhibit a catastrophic collapse: for values of the productivity close to the folding point (Fig. 2), a small reduction in productivity may cause a dramatic drop in predator density leading to its extinction. Resurrection of the population is subsequently only possible if the productivity is increased substantially until beyond its invasion threshold, which is the level of productivity shown in Fig. 2 (top panel; right column) where the folded predator equilibrium curve meets the x -axis. De Roos & Persson (2002) argue that this mechanism may explain the collapse and lack of recovery that is observed in exploited marine fish species, since the model predicts the same catastrophic collapse to occur when mortality rates of the predator are varied. Indeed, model predictions with respect to the change in biomass–size distribution of the consumer (Fig. 3) do agree with the changes in the community of capelin (*Mallotus mallotus*) and zooplankton that have been observed after the over-exploitation and collapse of the Atlantic cod (*Gadus morhua*) stocks in the Northwest Atlantic (Carscadden *et al.* 2001). This mechanism also provides a contrasting explanation for the slow recovery of freshwater sports fisheries that have collapsed because of overexploitation (Post *et al.* 2002).

In traditional models of biological food webs, which ignore population structure altogether, the effect of consumption is always negative, as it will decrease food density and subsequently reduce the fecundity. Intuitively, this type of negative feedback is also the first thing that springs to mind when considering the effects of consumption. The results discussed above show, however, that due to the life-history dependence of ecological performance, the feedback of individuals on their own performance may be far subtler. We consider this type of feedback, which is filtered through life history, as an important new aspect in community ecology, which may give rise to new and unexpected phenomena.

ON THE INTERPLAY BETWEEN LIFE HISTORY AND POPULATION DYNAMICS

In the context of the consumer–resource or tritrophic interactions discussed above, the effect of population feedback on individual life history is limited to a change in growth rates, leading to a change in body size at each age and hence to a change in the duration of the juvenile period. With more complex ecological interactions, where both the intensity and nature of interactions vary, the effects on the individual life history may be much more dramatic. Claessen *et al.* (2000, 2002) provide a compelling example based on

the interplay of size-dependent competition for a shared resource and size-dependent cannibalism. The population model is based on the consumer–resource model developed by Persson *et al.* (1998), in which all individual-level processes depend on individual body size and the resource density in the environment. Feeding, growth, metabolism and mortality of consumers as well as the production of new resource are modelled as continuous-time processes. Reproduction, on the other hand, only occurs at the beginning of the growing season (summer). The cannibalistic interactions are added to this basic consumer–resource model and described as a function of both cannibal and victim length. More specifically, it is assumed that a cannibal of a given size can capture victims, whose size is within a particular range. This range is referred to as the ‘cannibalism window’. Cannibalism is only possible if the ratio of victim-to-cannibal length exceeds a lower threshold value, referred to with a parameter δ , and is also below an upper threshold value. The assumptions about the lower and upper thresholds are based on experimental and empirical observations of realized cannibalistic events (Claessen *et al.* 2000).

Figure 4 summarizes some results of this size-structured cannibalism model, parameterized for European perch (*Perca fluviatilis*) feeding on *Daphnia*, for three different values of the minimum ratio between victim-to-cannibal length, δ . With a high value of this minimum ratio (Fig. 4, left panel; $\delta = 0.08$) the cannibalism model exhibits exactly the same type of single-cohort cycles as the consumer–resource model of Persson *et al.* (1998) (see also Fig. 1). After production of a new offspring cohort, a parent cohort starves to death, because the newborn individuals suppress the resource density below the minimum resource requirement of the adults. Because the newborns grow slowly, they never enter the cannibalism window of their parents. Hence, the adults die out before they can start cannibalizing the newborns. Under these conditions, the length–age relation of the individuals has a convex shape, indicating extreme growth retardation due to the intraspecific competition for the alternative resource.

In contrast, with a very low value of the minimum ratio between victim-to-cannibal length (Fig. 4, right panel; $\delta = 0$), the newborn individuals are vulnerable to cannibalism by adults from their birth onwards and adults start cannibalizing them immediately. The density of newborn individuals is quickly reduced, which allows the density of the alternative resource to recover. Adult individuals do not suffer any starvation. They essentially counter the size-dependent competition, in which the newborns have the advantage with their size-dependent cannibalism. Nonetheless, since adults kill newborns early on they do not gain substantial amounts of energy from doing so and their diet mainly consists of the alternative resource. Cannibalism

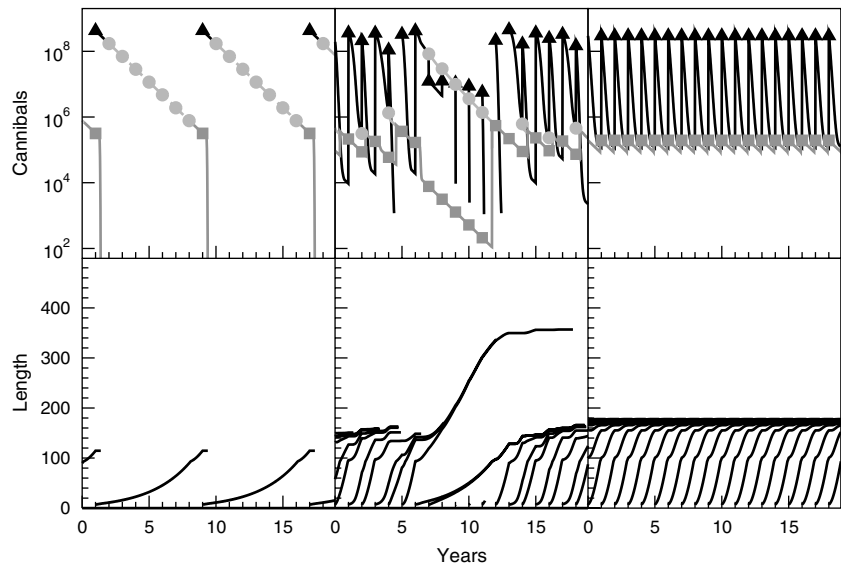


Figure 4 Representative dynamics of the cannibalistic model analysed by Claessen *et al.* (2000, 2002) for different values of δ (left: $\delta = 0.08$; middle: $\delta = 0.056$; right: $\delta = 0.0$), the minimum ratio between victim and cannibal length at which cannibalism can occur. Top row shows the dynamics of newborn (age between 0 and 1; black triangles), juvenile (light-grey circles) and adult (dark-grey squares) cannibals. Bottom row: length–age relations for cannibals born at different times.

under these conditions thus turns out to be more like infanticide. The model exhibits very stable dynamics with fluctuations in newborn and adult densities within any single growing season, but invariant dynamics between years. On a year-to-year basis the model thus exhibits fixed-point dynamics. Claessen *et al.* (2000, 2002) refer to this type of dynamics as ‘cannibal-driven’. The length–age relation of the individuals has a concave shape with rapid juvenile growth, such that they reach reproductive sizes already at the end of their first year. The maximum individual size they reach is however low, which signifies the lack of energetic gain from cannibalism. The observed dynamics in this case resemble the dynamics exhibited by models of the inter-stage cannibalism in *Tribolium* (Costantino *et al.* 1997; Dennis *et al.* 1997), which ignore energetic gains of cannibalism altogether and are hence more appropriately interpreted as infanticide models.

For intermediate values of the minimum ratio between victim-to-cannibal length (Fig. 4, middle panel; $\delta = 0.06$), the population dynamics consists of an alternation between the ‘cannibal-driven’ dynamics and single-cohort cycles that are representative for low and high values of δ , respectively. During the periods with cannibal-driven dynamics adult individuals impose significant cannibalistic mortality on newborn individuals, which results in a rapid decline in their density, a recovery of the density of alternative resource and a rapid juvenile growth. The maximum individual size during these periods is however low. During a single-cohort phase of dynamics, one juvenile cohort dominates the population throughout and substantially retards its own growth in body size. A drop in the number of adult individuals due to starvation initiates the transition between these two types of periods. But, a small number of adult individuals survive this period of low resources. These

survivors subsequently start cannibalizing the dominant juvenile cohort. Because of their low density, the inflicted cannibalistic mortality is small. Because of the relatively high value of δ the adults cannibalize their victims when the latter already have reached rather large body sizes. Hence, at the individual level the energetic gain of cannibalism is substantial and induces an increase in the adult growth rate. The surviving adults thus follow a life history in which they experience two periods of accelerating growth, one right after birth and the other shortly after their first offspring production. In the end, these ‘giant’ adults reach lengths that are more than twice the maximum size that is reached during the cannibal-driven phases. Claessen *et al.* (2000, 2002) refer to this type of dynamics as ‘dwarf-and-giant’ cycles.

The most intriguing aspect of these results is that the realized individual life history may be strikingly different for two individuals that are born at slightly different times (compare the fates of the individuals born at $T = 5$ and $T = 6$ in Fig. 4, middle panel, respectively). The state of the population at the time of birth and the subsequent developments in population density and structure may cause individuals either to follow a length–age trajectory with two periods of rapid growth or a growth trajectory with severe growth retardation during the juvenile period and a maximum size only slightly larger than the maturation size. This difference in realized life history is entirely due to the influence of the various mechanisms of population feedback and the subtle interplay between them: intraspecific competition retarding individual development, cannibalistic mortality relaxing these competitive constraints and cannibalistic energy gain inducing gigantic growth. It is to be expected that this interplay will also have consequences outside the domain of population ecology, for example, for

behavioural ecology or the evolution of life-history characteristics. In contrast, up to now there are hardly any evolutionary studies that take into account this population feedback on realized life history (but see Claessen & Dieckmann 2002).

PERSPECTIVE

The main body of ecological theory about population dynamics and community structure is based on rather simple models that represent populations either by the number of individuals or by the total biomass. These models have brought forward concepts like predator–prey cycles and the stepwise lengthening of food chains with productivity (Oksanen *et al.* 1981), which have become cornerstones in the analysis of natural ecosystems. What additional value is there in taking into account population age- or size-structure? Or differently phrased: do size-dependent individual life histories merely lead to extensions and variations on a core of ecological theory that is based on unstructured models or should we view the unstructured theory as a limiting case?

Over the last two decades there have been an increasing number of studies of structured population models with a major focus on the influence on (single) population or consumer–resource dynamics. This has firmly established two new concepts, single-generation and delayed-feedback cycles, which have subsequently proven their value in analysing the dynamics of natural populations (e.g. Murdoch *et al.* 2002). The results suggest that accounting for population structure simply extends the existing body of ecological theory, which is based on unstructured models. De Roos *et al.* (1990) argue this point most explicitly with respect to the occurrence of predator–prey and single-generation cycles in size-structured consumer–resource models.

In contrast, little attention has been paid to situations in which size-structure is accounted for at a lower trophic level, nor have the implications of population size-structure for community composition been investigated in much detail. The occurrence of emergent Allee effects shows that community predictions may change drastically if size-structure is introduced at an intermediate level and somewhat more realistic interactions between species, i.e. that predation is often size-selective, are considered. Also, in such models classical predator–prey cycles, which should occur whenever predators control their prey at low densities, may not be as common as expected, if part of the prey population is invulnerable (Murdoch *et al.* 1987). Figure 5 illustrates this fact for the size-structured food-chain model analysed by De Roos & Persson (2002). The graph shows how the width of the window in which consumers are vulnerable to predation affects either the consumer biomass density in stable equilibrium or the minimum and maximum

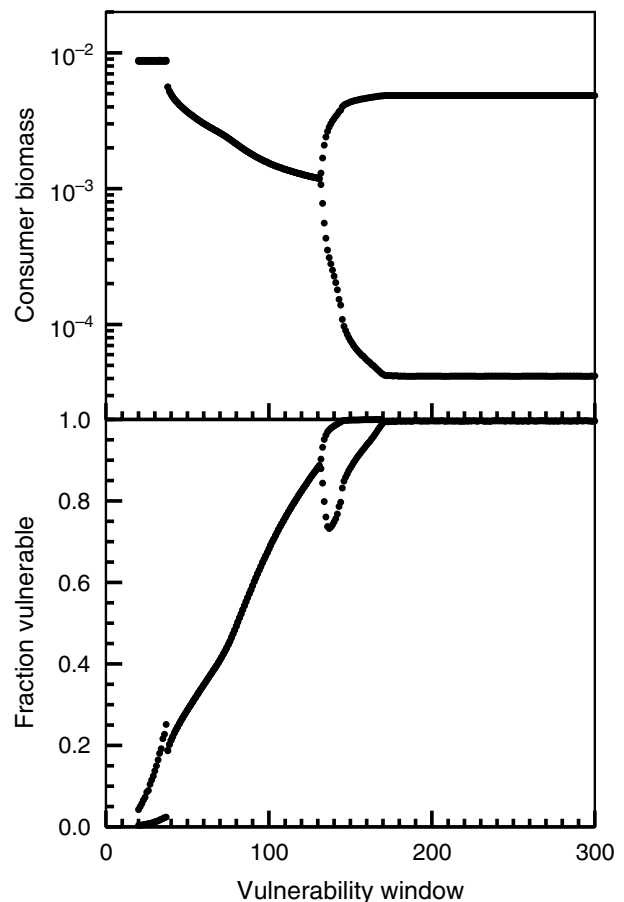


Figure 5 Long-term dynamics of the size-structured food-chain model of De Roos & Persson (2002) for different values of the vulnerability window (in mm) of the consumer. The graph shows the maximum and minimum consumer biomass (*top*) and the fraction of the consumer biomass that is vulnerable to predation (*bottom*), as observed during time integration of the model. Consumers are assumed to be born at a length of 7 mm and start reproducing at a length of 110 mm.

consumer biomass density observed during the population cycle, if present. The graph clearly indicates that predator–prey cycles will only occur when in terms of biomass more than 90% of the consumer population is totally vulnerable to predation. In other words, only a small part of the adult population needs to be invulnerable to prevent these cycles to occur. These results shed doubt on the relevance of established concepts like predator–prey cycles and the stepwise lengthening of food chains with productivity, when population structure is accounted for. They support the view that insights based on unstructured population models merely represent limiting cases of a larger, more realistic body of ecological theory.

This theory is expanding rapidly. Many of the interesting dynamical features of life histories can be investigated in the

deterministic frameworks discussed above. Alternative frameworks involving individual-by-individual simulation models that account for each individual organism as a distinct entity and describe its dynamics by means of rules (*i*-state configuration models; Caswell & John 1992) are available and have been used to study stochastic effects. New questions can be addressed using chains of models with differing levels of complexity (Murdoch *et al.* 1992; Murdoch & Nisbet 1996) and we have demonstrated that much can be gained in understanding mechanisms from comparisons of models with differing levels of complexity (e.g. Persson *et al.* 1998 vs. De Roos & Persson 2003 or De Roos & Persson 2002 vs. De Roos *et al.* 2003). Finally, there have been major advances in mathematical methodology that assist greatly in obtaining qualitative and quantitative results for PSPMs. These include reliable numerical integration methods (De Roos *et al.* 1992; De Roos 1997) and techniques to compute equilibria of PSPMs numerically without any analytical manipulation (Kirkilionis *et al.* 2001; Diekmann *et al.* 2003; see also Claessen & De Roos 2003). As a consequence, PSPMs may be more suited to yield general ecological and evolutionary theory about the interplay of individual life history and population or community dynamics. In short, a solid conceptual foundation is in place to understand the dynamical implications of feedbacks between life history and population and community-level interactions.

In our opinion, the insight summarized in this review calls for more serious and elaborate studies on the relationship between individual life history and population or community dynamics. The consequences of this interplay may be far-reaching and non-trivial and have up to now not been rigorously revealed. The fact that individual development may be density-dependent and influenced by changes in the environmental conditions that individuals experience is likely to be of prime importance. Many existing ecological and evolutionary models represent the individual biology in an almost ridiculously simple manner that their conclusions can be rightfully questioned. The mathematical and numerical tools to forge a link between the individual and the population level are now available. Using the mathematically daunting, structured population models and the tools for their analysis may not be half as easy as analysing a small set of ordinary differential equations representing an unstructured model, but it may be the only way to seriously account for the apparent complexity that characterizes the life history of individual organisms.

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