

CHAPTER TWELVE

Interplay between individual growth and population feedbacks shapes body-size distributions

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Body size in contemporary ecology

Body size and variation in body size have formed the focus of many studies in ecology, ranging from the study of individual performance to large-scale communities and ecosystems (Werner & Gilliam, 1984, Gaston & Lawton, 1988, Werner, 1988, Cohen, Johnson & Carpenter, 2003, Brown *et al.*, 2004, Loeuille & Loreau, 2005). This focus is well-founded given the large variation in body size that exists among organisms from micro-organisms to large mammals (Gaston & Lawton, 1988; Werner, 1988). Body size is also the most important trait that affects the performance of individuals. Basic ecological capacities such as foraging rate and metabolic requirements are close functions of body size (Peters, 1983; Kooijmann, 2000; Brown, *et al.*, 2004) affecting, for example, competitive abilities of differently sized organisms (Wilson, 1975; Persson, 1985; Werner, 1994). Body size strongly influences the diet of consumers with mean prey size, but also the variation in the size of prey eaten, increasing with predator size (Wilson, 1975; Werner & Gilliam, 1984; Cohen *et al.*, 2005; Woodward & Warren, this volume; Humphries, this volume). Furthermore, the risk for an organism being preyed upon is heavily influenced by its own body size as well as the body size of its potential predator (Polis, 1988; Werner, 1988; Claessen, De Roos & Persson, 2000).

Given its influence on basic individual ecological processes, body size has been an important variable in the investigation of larger ecological entities including communities, food webs and ecosystems. For example, predator-prey size ratios have formed the basis for food-web models such as the cascade model (Chen & Cohen, 2001), and for estimating interaction strengths in food webs (Emmerson & Raffaelli, 2004). Body size has also been the key variable in the analysis of food-web patterns with regard to numerical and biomass abundance at different trophic positions (Cohen *et al.*, 2003; Cohen, this

volume). Another example where body size is a key variable is in size spectra analyses of the organization of trophic dynamics among populations of organisms (Kerr & Dickie, 2001; Shin *et al.*, 2005). Finally, during the last decade the 'metabolic theory of ecology' (West, Brown & Enquist, 1997; Brown *et al.*, 2004) has become very popular and is heavily founded on body-size variation. This theory has been advanced by its proponents to form a conceptual basis for ecology comparable to that of genetic theory for evolution and to 'link the performance of individual organisms to the ecology of populations, communities, and ecosystems' (Brown *et al.*, 2004; Brown, Allen & Gillooly, this volume).

Neglected aspects of body size in contemporary ecology

Although body size plays a central role in ecology, an important aspect of body size in many ecological communities has been largely neglected in the theoretical and empirical research mentioned above. In fact, the ecological entities upon which patterns have been analyzed are based on 'average individuals' (of different body sizes), an approach that basically is in conflict with a Darwinian view stressing variation among the individual organisms (see De Roos & Persson, 2005a). A major part of observed body-size variation is related to within-species variation, as individuals grow over a substantial part of their life cycle, whereas most contemporary ecological studies restrict their attention to between-species variation. To consider ontogenetic variation among individuals seems essential for any conceptual synthesis, given that the overwhelming majority of the Earth's taxa exhibit some degree of size/stage structure (Werner, 1988) and the ecological effects of intraspecific variation in body size are well represented in the other chapters of this volume (e.g. Woodward & Warren, this volume; Warwick, this volume). Actually a whole body of theory on ontogenetic development and food-dependent growth of individuals was developed during the 1980s (Sebens, 1982; Werner & Gilliam, 1984; Sebens, 1987; Sauer & Slade, 1987; Ebenman & Persson, 1988), a literature that has been largely neglected by more recent ecological studies on body size.

The purpose of this chapter is to give first a short historical overview of studies considering patterns of development and growth in organisms and to link size-dependent individual performance to community patterns. Second, we give an overview of how to progress towards an explicit and rigorous link between individual body size and population and community processes. Our focus will be on how size-dependent interactions shape the dynamics and structure of ecological communities including body-size distributions.

Development and growth – a retrospective overview

As already mentioned, considering individual growth and development is important, because the majority of animals exhibit substantial changes in size and/or morphology over their ontogeny (Werner, 1988). Further, for most plant

species growth and development is a major aspect of their life history. An overview of different animal taxa shows that major changes in body morphology as a result of metamorphosis are present in more than 85% of all taxa (25 of 33 phyla) (Werner, 1988). This pattern largely results because of the very many species of insects. Nevertheless, even if only vertebrates are considered, individuals of 75% of all taxa show substantial growth for much of their lives, which is due to the taxonomic dominance of fish, amphibians and reptiles. Actually, it is only among altricial birds and some mammals where the young are close to the adult body size when they become independent of the parents (Werner, 1988).

Scaling constraints and growth patterns

It has been suggested that large changes in body size due to ontogenetic development and growth impose a number of constraints on the body morphology of organisms related to physical, chemical and biological processes (Peters, 1983; Calder, 1984; Werner, 1988; Stearns, 1992; Humphries, this volume). When increasing in size, scaling properties – depending on both physical and ecological constraints – will set limits over which size range a particular lifestyle can be exploited (Calder, 1984; Werner, 1988). For example, physical parameters acting on small and large organisms are very different exemplified/illustrated by the effects of different Reynolds numbers on small and large aquatic organisms, respectively (Humphries, this volume). For small organisms, the low Reynolds number means that they swim with friction as the propulsive mode. In contrast, large organisms use the inertia of the water to propel themselves (Werner, 1988). Within the broader limits set on morphology by physical constraints, ecological constraints are also present related to, for example, which prey types an organism with a specific body morphology and size can efficiently utilize (Werner, 1988; Woodward & Warren, this volume). In particular, the morphologies that can evolve to efficiently handle different prey sizes during different parts of ontogenesis are constrained by genetic additive covariance in the genotype (Werner, 1988; Ebenman, 1992).

Werner (1988) argued that allometric growth in organisms is only partly sufficient to cope with the different demands on body morphology made during different parts of the life cycle. These constraints imposed by allometric growth therefore result in an ‘allometric scaling problem’ for performance over the life cycle. He argued that, if scaling imposes a problem during the ontogeny, there should be patterns among the variety of life-history strategies by which animals cope with this problem (Cohen, 1985; Werner, 1988). Four particular tactics were discussed by Cohen (1985) and Werner (1988). The first represents organisms that largely avoid the problem of substantial size change by specializing as a very small adult (for example protozoans). The second tactic represents organisms in which the basic (small) trophic apparatus

remains intact but is multiplied (e.g. coral polyps). The third tactic represents the situation where the adults extensively provide the egg and juvenile with transformable mass (e.g. yolk, maternal fluids, bodies of prey) until the young has reached a size where it can take up the parental lifestyle (birds and mammals). Fourth, the organism may adopt a succession of complex life histories that accommodate the increase in size (insects, amphibians, fish). Here, complex life cycles in the form of metamorphosis represent a way to break up genetic covariances between sizes/stages (Werner, 1988; Ebenman, 1992).

One common trait among the two groups (birds and mammals) where the parents provide the egg and juvenile with transformable mass until it can take up the parental lifestyle is endothermy, including a high body temperature (Case, 1979; Stearns, 1992). This observation suggests that the rapid development from juvenile to adult in these groups not only requires the ability to provide eggs/juveniles with extensive amounts of energy, but also the ability to transform that energy rapidly into growth. This leads to the hypothesis that there is a relationship between endothermy and individual growth rate, an assumption that is supported by empirical data, because mammals and birds have a growth rate that is an order of magnitude higher than that of ectotherms such as reptiles and fishes (Ricklefs, 1973; Case, 1979).

In summary, species for which individual growth and development plays a smaller role are primarily found among unicellular organisms and endotherms. In other organisms, substantial growth and development after the juvenile becomes independent of its parents is the rule. The different growth patterns observed among different organisms have formed the basis for different classifications of growth types (see Sebens, 1987). Without giving a more detailed description of these classification schemes, they have focused on two aspects of ontogenetic growth: the extent to which growth and development is plastic/indeterminate and hence food dependent, and the extent to which the asymptotic size is fixed or food dependent. In several instances these two aspects of growth have been mixed. For example, Stearns (1992) defined determinate growth as the situation where individuals do not grow in size after maturation. This definition of determinate growth is in our opinion not satisfactory, as it totally neglects whether growth up to maturation is food dependent or not. As considered above, ontogenetic growth and development take very different forms in different groups of taxa. Food-dependent growth over ontogeny can be continuous, as in fish and plants, or discrete where the development time between stages is food dependent, as in many invertebrates. We argue that it is food-dependent development per se that forms one dividing line for how ontogenetic development will affect individual performance, population and community processes and the biomass structures.

Individual-level formulations for how individuals grow - linkage to community patterns

The main message to be drawn from the above overview is that ontogenetic growth and development are characteristic of many organisms on Earth and that individual performance over ontogeny is constrained by both physical and ecological factors. At a broad scale, organisms showing substantial growth after becoming independent of their parents and those that do not can be separated along the endothermy-ectothermy gradient. At the same time, the different growth patterns described above are limited to broad categories, and a more quantitative link between individual performance and growth, with its consequences for community attributes such as body-size patterns, is therefore needed. A number of attempts were also undertaken during the 1980s to link individual body-size dependent performance and the dynamics of ecological communities.

First, the scaling of foraging rate and metabolism with body size was used to determine the competitive ability of differently sized organisms and to predict niche shifts over ontogeny based on energy maximization (Mittelbach, 1981; Werner & Gilliam, 1984; Werner, 1988). Second, as the risk of being eaten is also a function of body size, the literature on individual size-dependent performance also came to include the effects of predation using optimal control theory (Werner & Gilliam, 1984). This individual-based framework using explicit body-size scalings of different rates was quite successfully applied to predict and understand the distribution of species and size classes within and between systems, primarily in freshwater fish communities (Mittelbach, 1981; Werner, 1986; Persson, 1988). Implicitly this approach assumed that community patterns could be predicted from individual-level traits ignoring population-level dynamics and feedbacks. An exception is the study by Hamrin and Persson (1986) on population cycles in cisco (*Coregonus albula*) where the population dynamics were explained from size-dependent foraging and metabolic rate including feedbacks on the resource. Modelling methods to address the dynamics of size-structured dynamics (Sinko & Streifer, 1967) were already being discussed at this time (Werner & Gilliam, 1984). However, more complete modelling formulations to address size-structured dynamics were first developed during the second half of the 1980s (Metz & Diekmann, 1986; De Roos *et al.*, 1990) and their efficient use in ecological theory started first in the 1990s, which is the focus of the rest of this chapter (De Roos *et al.*, 1990; Persson *et al.*, 1998; Claessen, De Roos & Persson, 2000).

Developments of an explicit link from individual body size to population dynamics

Brown *et al.* (2004) envisage metabolic theory to link the performance of individual organisms to the ecology of populations, communities and ecosystems.

This might be true for some elements of the hierarchy from individuals to ecosystems, but a number of key elements, especially at the level of populations, are inadequately considered. Although we agree that there are constraints on ecological performance, such as individual metabolic rate, population maximum growth rate and ecosystem turnover as a function of body size (Brown *et al.*, 2004), this theory addresses how ecological interactions shape body-size distributions in ecological communities only to a limited extent. Moreover, given that ontogenetic development is a major feature in most organisms, the effect of ontogeny on the development of body-size distributions is also a major aspect to take into account. In the following, we briefly describe a modelling framework that (i) explicitly links individual-level processes, including body-size scaling, to population-size distributions and, (ii) considers ontogenetic development. We will subsequently discuss how food-dependent development rate gives rise to both dynamical and structural patterns not present in unstructured theory and how this shapes body-size distributions. It will become evident that body size in different ecological configurations is both an input to (by determining individual performance) and outcome of (as a result of population feedbacks) ecological interactions.

Modelling framework

The modelling approach we consider are physiologically structured population models (PSPMs) (Metz & Diekmann, 1986; De Roos *et al.*, 1990) referred to as *i*-state distribution models. They are based on two different state concepts, the individual or *i*-state and the population or *p*-state. The *i*-state represents the state of the individual in terms of a collection of characteristic physiological traits, such as size, age and energy reserves, while the *p*-state is the frequency distribution over space of all possible *i*-states. The model formulation process consists of deriving a mathematical description of how individual performance (growth, survival, reproduction) depends on the physiological characteristics of the individual and the condition of the environment (*i*-state description). Handling the population-level (*p*-state) dynamics is subsequently just a matter of bookkeeping of all individuals in different states without making any further model assumption at this level (Fig. 12.1). The core of PSPMs is thus the individual state and the modelling of the individual life history. The derivation of the PSPM proceeds by writing down the equations describing the *i*-state dependent processes of energy gathering (attack rate, digestive capacity), metabolism, energy channeling between somatic and gonad growth and survival (generally a function of energy status and size-dependent mortality from predators) (see De Roos *et al.*, 1990 and Persson *et al.*, 1998 for examples). Energy allocated into gonad tissue may be spent continuously or discretely constrained by, for example, season.

Bookkeeping provides the link from the individual to the population level, which also includes calculations of the impact of the total population on its

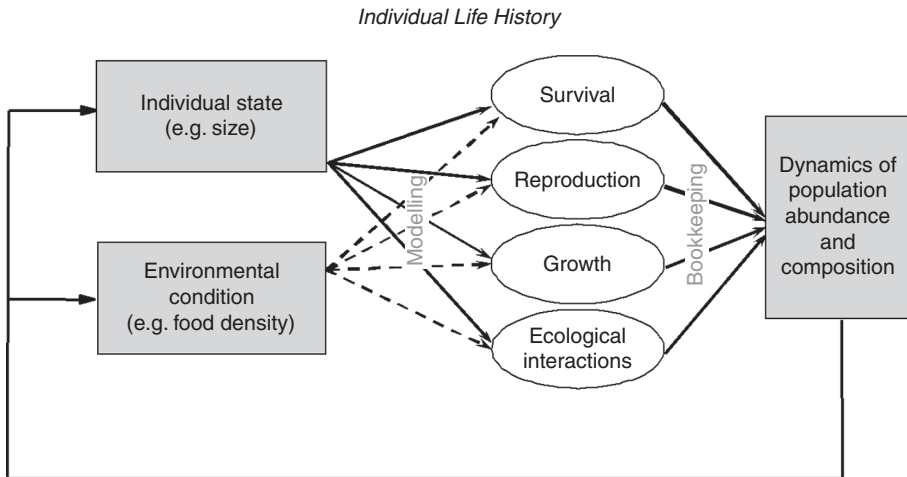


Figure 12.1 Schematic representation of the philosophy behind the framework of physiologically structured population models. Based on the state of the individual and the environmental condition, we can model foraging rate, growth, survival and reproduction of the individual, while the population state is merely a bookkeeping of all individuals in all i -states.

environment. The change in the environment resulting from this impact represents the population feedback on individual life history and/or behaviour (Fig. 12.1). In a consumer-resource system, for example, the population influence on consumer life history operates through an increased or decreased density of resource, which affects individual growth, mortality and reproduction. In addition to i - and p -states, an environmental (E) state is defined, which in the consumer-resource system is the resource. In a system including predators of the consumer, the E -state also includes all potential predators on a consumer of a specific i -state.

Ontogenetic development - dynamical aspects

As discussed above, the size scalings of foraging and metabolic rate were recognized as basic variables to determine the competitive ability of differently sized individuals (Mittelbach, 1981; Lundberg & Persson, 1993; Werner, 1994). We extend this individual-level argumentation to analyze its population-level consequences using two case studies, a size-structured consumer-resource and a cannibalistic system, with the purpose of showing how size-structured dynamics may induce temporal variation in body-size distributions. For a consumer-resource model, the body-size scalings of foraging rate (attack rate, digestive capacity) and metabolism have been shown to have major effects on the population dynamics observed (Persson *et al.*, 1998). Combining the size scaling of attack rate, digestive rate and metabolic rate allows us to calculate

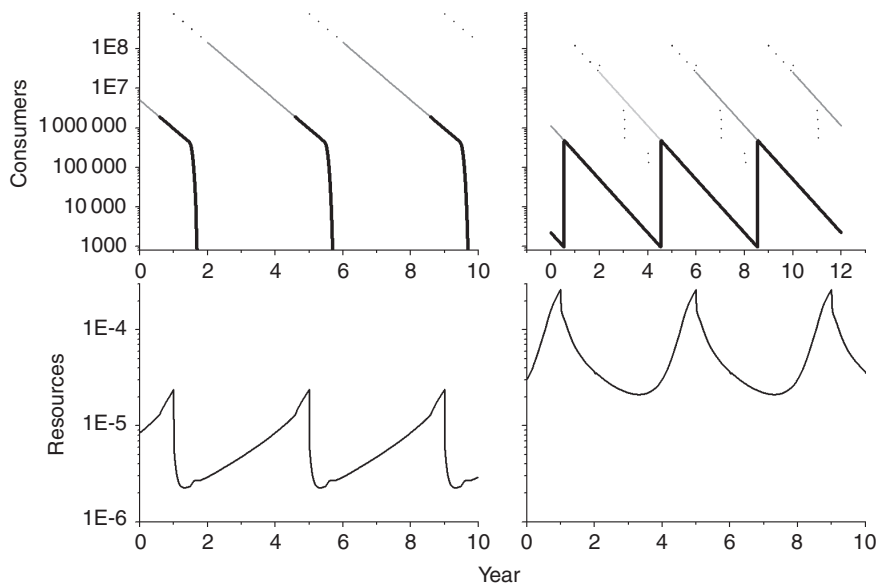


Figure 12.2 Changes in the numbers of young-of-the-year (dotted black lines), juveniles from an age of one year (solid grey lines) and adult (black solid thick lines) consumers and resource levels in the two types of cohort cycles discussed in the text. Left panels: cohort cycle driven by recruiting individuals. When a strong cohort is born, it almost immediately depresses the resource to low levels and out-competes older cohorts. The pattern repeats itself when the dominating recruiting cohort matures and gives rise to a new strong reproductive pulse. Right panels: cohort cycle driven by larger juveniles. When a strong cohort is born it causes a decrease in the resource for several years driving new cohorts to starvation death (vertical dotted grey lines) despite that adult reproduction is present for several years (years 2–4).

the resource level that differently sized individuals need to just meet maintenance (critical resource density, Persson *et al.*, 1998). If the critical resource density increases monotonically with body size, cohort cycles driven by competitively superior recruiting cohorts will prevail (Fig. 12.2). In contrast, when critical resource density at first decreases with body size but increases thereafter, cohort cycles driven by larger individuals will occur (Fig. 12.2). Finally, in a narrow parameter range where critical resource density is relatively independent of body size, equilibrium conditions with many coexisting size cohorts will prevail (Persson *et al.*, 1998). The different dynamics observed can thus be predicted from the form of the critical resource-density function.

The cycle length of the resulting cohort cycles, which are driven by cohort interactions is, in contrast to predator–prey cycles, set by the time it takes individuals to reach maturation (generation time \approx cycle length). A literature review shows that single generation cycles (37% of all cycling populations) are as

common as traditional predator-prey cycles (38% of all cycling populations) among fluctuating populations (Murdoch *et al.*, 2002). Together with another type of stage-based dynamics, delayed-feedback cycles (25% of all cycling populations), size/stage-based cycles thus are the dominant type of cycle observed in populations. Moreover, predator-prey cycles are found almost exclusively in specialist predators. Two further things can be stated about size-dependent consumer-resource dynamics. First, the observed size scalings of foraging rate and metabolism (that determine the competitive ability of differently sized individuals) suggest that cyclic dynamics should dominate over equilibrium dynamics, with the consequence that the body-size distributions of consumer populations will vary over time. Second, cohort ('single species') cycles are common in many species systems (Murdoch *et al.*, 2002), suggesting that intra-specifically driven cycles cannot be ignored in many species systems. Typical examples of cohort-dominated cycles include population oscillations in *Daphnia* and planktivorous fish (McCauley *et al.*, 1999; Persson *et al.*, 1998). For planktivorous fish, estimated critical-resource demands show that these cycles are recruit-driven with an observed cycle length of 2–5 years. For shorter cycles (2–3 years), age cohorts may coexist and a cycling in growth rates of the different age cohorts is observed (Hamrin & Persson, 1986; Cryer, Peirson & Townsend, 1986; Townsend, Sutherland & Perrow, 1990). For longer cycles, strong age cohorts become more dominant and major shifts in size distributions can be observed over the years due to growth of dominant age cohorts (Fig. 12.3) (Sanderson *et al.*, 1999).

Cannibalism represents an extension of consumer-resource interactions to include predation among consumers. Because many cannibals share a common resource with their victims, the latter may subject the cannibals to severe exploitative competition for this shared resource (Polis, 1988; Persson, 1988; Polis, Myers & Holt, 1989). Experiments and field data, particularly on cannibalistic fish, show that a positive cannibalistic attack rate is constrained between a lower boundary below which the cannibal does not encounter a victim because of difficulties in seeing it, and an upper boundary above which the escape ability of victims and gape-size constraints prevents cannibalism (Claessen *et al.*, 2000, Juanes, 2003). Analyses of the dynamics of cannibalistic systems show that three aspects of the size scaling of the cannibalistic attack function are important in determining population dynamics and cannibal-size distributions. The maximum victim/cannibal size ratio has less effect on population dynamics, but a strong effect on the ultimate size that an individual reaches and thereby the size distribution of the cannibal population (Claessen *et al.*, 2002). In contrast, the overall rate by which the cannibalistic attack rate increases with cannibal size and the lower victim/cannibal size ratio have major effects on population dynamics and therefore on the degree of temporal variation in size distributions of cannibalistic populations (Claessen *et al.*, 2000, 2002).

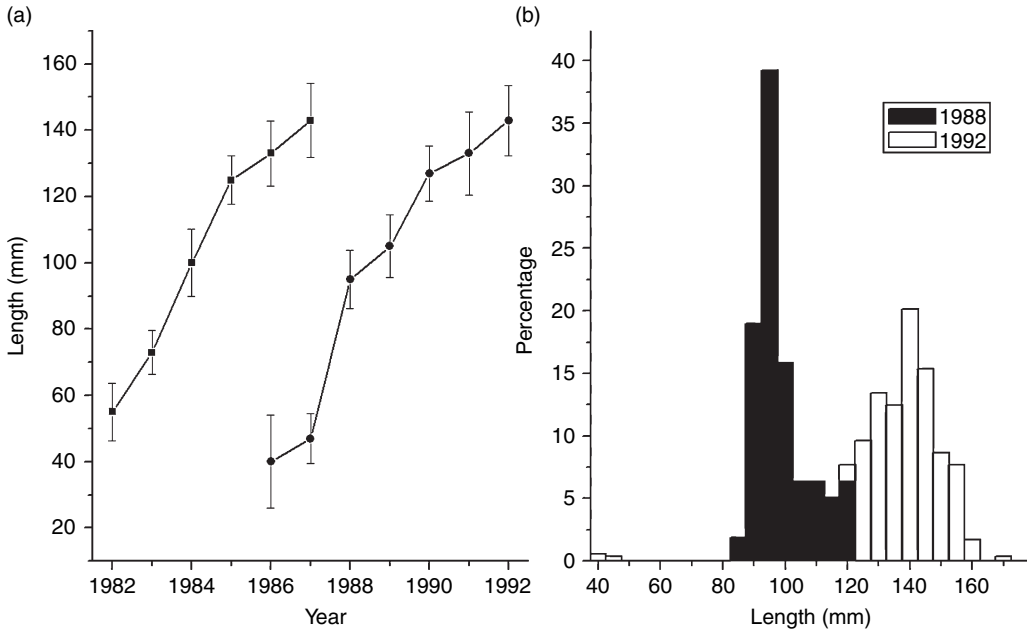


Figure 12.3 (a) Growth (mean \pm 1 SD) of two dominating cohorts of yellow perch (*Perca flavescens*) born in 1980 and 1985, respectively. (b) Shift in the size distribution of yellow perch from 1988 to 1992 as a result of growth of the dominating cohort born in 1985 (data from Sanderson *et al.*, 1999).

Three different dynamical outcomes can be found: (i) low-amplitude/fixed-point dynamics, where cannibals control victims by inducing a high mortality on them, (ii) high-amplitude cohort cycles of the kind discussed above, in which victims outcompete cannibals before the latter can start cannibalizing, and (iii) a dynamics involving a mix of the previous two. Studies of cannibalistic perch (*Perca fluviatilis*) populations show that this species with a relatively high minimum victim-cannibal size ratio agrees with theoretical expectations and undergoes shifts in dynamics between a ‘stunted’ cannibal-driven phase and a phase driven by inter-cohort competition resulting in dramatic shifts in size distributions (Fig. 12.4b). The phases are also characterized by very different life-history trajectories with a periodic appearance of giant individuals (Fig. 12.4a).

In conclusion, the two examples (consumer-resource and cannibalistic interactions) used here to illustrate the implications of size-structured interactions on dynamics show that different size scalings of individual rates have strong influences on distribution of body sizes over time. As the dynamics of species such as fish, feeding near the top of food web, feed back on lower trophic components, the changes in size distribution at these higher trophic positions will also cascade down to cause shifts in overall size distribution of the food web (Cryer *et al.*, 1986; Shiimoto *et al.*, 1997; Persson *et al.*, 2003).

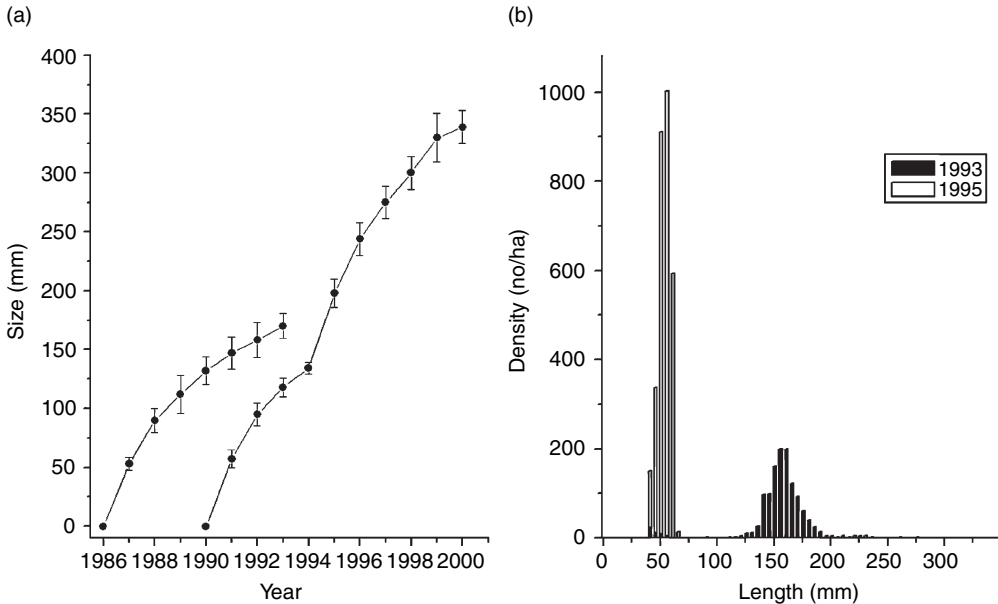


Figure 12.4 (a) Examples of growth curves (mean \pm 1 SD) of perch becoming stunted (born in 1986) and becoming giants (born in 1990) in Lake Abborrtjärn 3. (b) Shift in perch size distributions between stunted (1993) and giant phases (1995). The main part of the size distribution in 1993 consisted of stunted mature perch with a median size of 156 mm. The main part of the size distribution in 1995 consisted of small immature perch on which a few large mature perch are feeding (data from Persson *et al.*, 2003).

Ontogenetic development and community structure

Analyses of the dynamics of consumer-resource and cannibalistic systems show how different body-size scalings impact population dynamics and temporal changes in body-size distributions. Size-structured dynamics in these systems also have the potential to result in alternative states, which, particularly in cannibalistic systems, may result in very different size distributions (Claessen & De Roos, 2003). An extension of physiologically structured population models to more complex trophic configurations will further increase the likelihood of alternative states. In the following, we discuss alternative states and body-size distributions of populations exemplified by tritrophic food chains and tritrophic configurations with life-history omnivory.

Since the classical paper by Brooks and Dodson (1965) it is generally accepted that size-dependent predation by top predators has a strong structuring impact on prey size distributions. Size-dependent predation in combination with food-dependent development in prey has the potential to lead to alternative stable states with vastly different size distributions of the prey (De Roos & Persson, 2002). In the tritrophic food chain studied by De Roos and Persson (2002), two

alternative states were found under otherwise identical conditions, one consumer-resource, the other a predator-consumer-resource state. It is noteworthy that the invasion boundary of the predator occurred at a higher productivity level than its persistence boundary and, similarly, the harvesting persistence boundary for the predator was positioned at higher harvesting levels than the invasion boundary, making these systems prone to catastrophic collapses. The mechanistic explanation behind this catastrophic behaviour of the system is that a predator selecting small size classes of the consumer will increase the development rate of the remaining consumers into larger adult size classes, leading to increased population fecundity of the consumer and, therefore, counter-intuitively to an increased number in individuals of the size class that the predator feeds on (Fig. 12.5a) (De Roos & Persson, 2002). This overcompensatory effect has been termed an *emergent Allee effect* as it, in contrast to other mechanisms accounting for Allee effects, is purely based on exploitation of resources. The emergent Allee effect is also present if the predators select the largest size classes in the consumer population (De Roos, Persson & Thieme, 2003b; De Roos & Persson, 2005b). Size-structured dynamics in tritrophic food chains have also been shown to lead to the possibility of predator facilitation, where one predator may allow

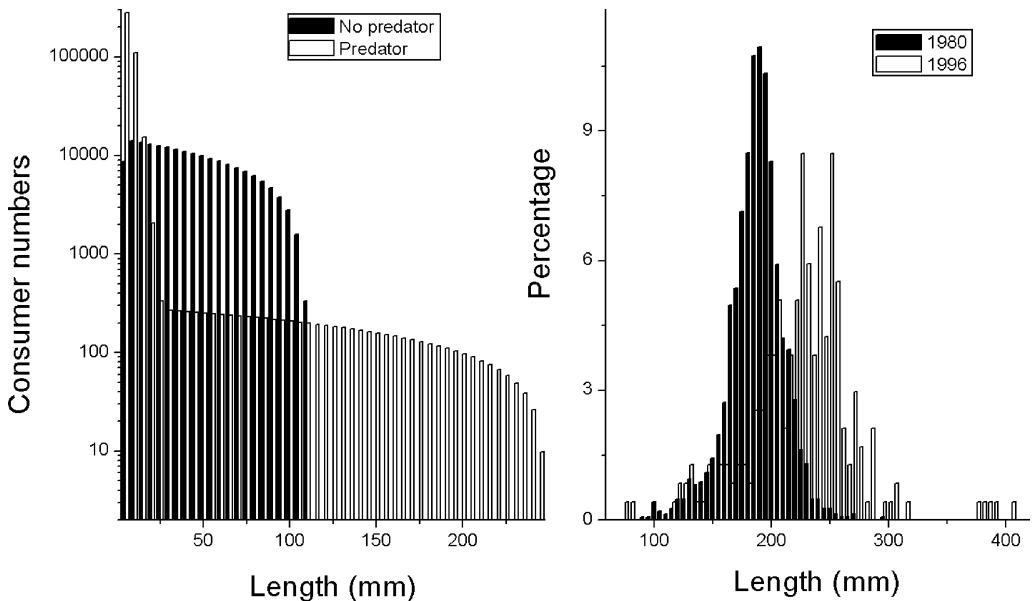


Figure 12.5 (a) Size distributions of the consumer species in the absence (black bars) and presence (white bars) of size-selective predators in the tritrophic model with size structure in the consumer population. (b) Size structure of the char population in Takvatnet in 1985 and 1998 (data from Klemetsen *et al.*, 2002).

the invasion of another predator by altering the size structure of the consumer (De Roos & Persson, 2005b).

The emergent Allee effect may be one explanation for the collapse and lack of recovery that has been observed in stocks of marine top predators (Carscadden, Frank & Leggett, 2001; De Roos & Persson, 2002). In agreement with model predictions, capelin, the main prey fish of cod, has been observed to show decreased per capita fecundity and mean size following the collapse of the North Atlantic cod (Carscadden *et al.*, 2001). A large-scale removal of a fish stock in the Norwegian Lake Takvatn provides another example suggesting alternative states induced by the emergent Allee effect. At the beginning of the study, the population of the numerically dominant fish species (Arctic char) was stunted, with very few individuals growing larger than 25 cm (Fig. 12.5b) (Klemetsen *et al.*, 2002). Following the removal of more than 70% of the Arctic char during the late 1980s, individual growth rate increased drastically, leading to a shift towards larger individuals in the size distribution that still persists (Fig. 12.5b). Despite the reduction of the Arctic char population, population fecundity increased substantially to more than six times the original population fecundity, thus showing strong elements of an overcompensatory effect. Following the reduction in char numbers, its main predator, brown trout, which was very rare at the start of the experiment, has increased in numbers by 30 times. Thus, the data for both predator and prey all support the contention that the dynamics of this system may involve an emergent Allee effect.

The trait that individuals grow over their life cycle will affect the dominant interaction they experience between competitive and predatory interactions resulting in life-history omnivory (Werner & Gilliam, 1984; Lasenby, Northcote & Fürst, 1986; Persson, 1988; Wilbur, 1988). For size-structured omnivorous (intraguild predation) systems, food-dependent development has been shown to reduce the scope for coexistence between top predator and intermediate consumer compared to unstructured models or structured models where transitions between stages is not food (or density) dependent (van de Wolfshaar, 2006). In systems with life-history omnivory where the top predator competes with the intermediate consumer at small sizes ($-,-$ effect) but preys on it at larger sizes ($+,-$ effect), model results and field data suggest that very different size distributions of the predator and prey will develop depending on environmental conditions (for example, productivity). Modelling results suggest that the growth of young (young-of-the-year) top predators will generally be slower in the presence of the intermediate consumer than in its absence, showing an interspecific competitive effect of the intermediate consumer on juvenile predators (Figs. 12.6a, b). In contrast, the effects on the growth of larger size classes of the top predator can be qualitatively different, with both an increase as well as a decrease in the maximum size of the top predator in the presence of the intermediate consumer compared with in its

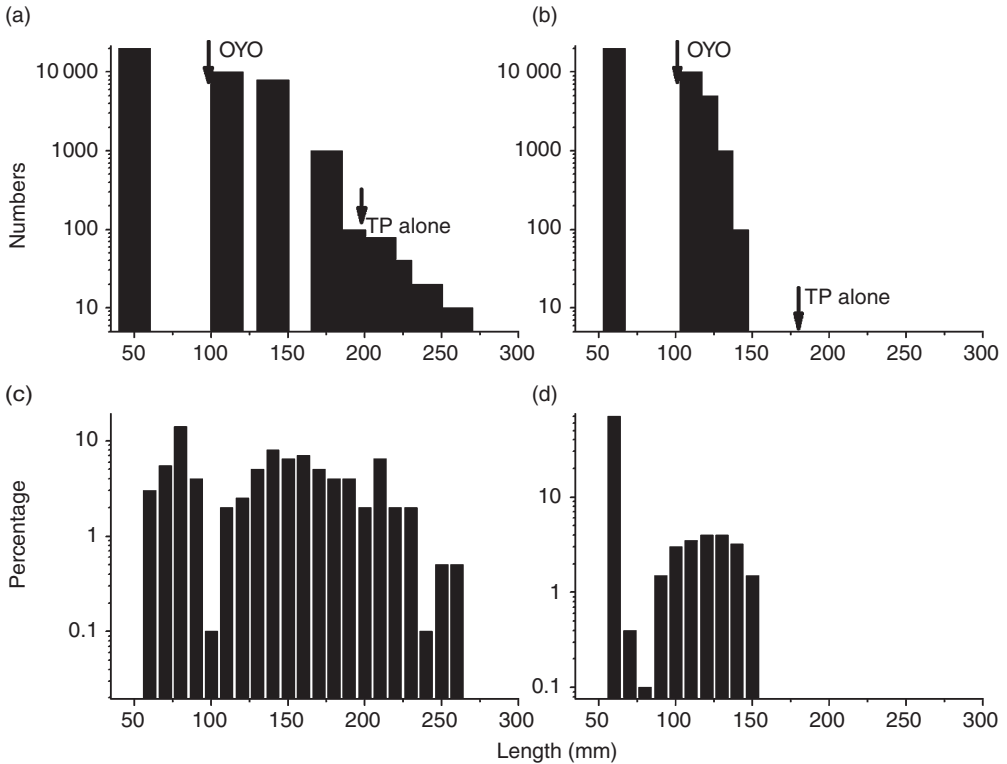


Figure 12.6 Above: model predictions of size distributions of top predator (TP) where the maximum size achieved is increased (a) or decreased (b) in the presence of the intermediate consumer compared with when the intermediate consumer is absent (arrows TP alone). In both cases the sizes of one-year-old (OYO) top predators are smaller in the presence of the intermediate consumer than in its absence (arrows OYO) (from van de Wolfshaar, 2006). Below: different size distributions of perch in moderately productive Lake N. Bolmen (c) and highly productive Lake Sövdeborg (d) (data from Persson, 1983).

absence (Figs. 12.6a, b) (van de Wolfshaar, 2006). Varying size distributions of perch (top predator) populations coexisting with roach (*Rutilus rutilus*) (intermediate consumer) have also been observed and attributed to the relative strength of predatory and competitive interactions, respectively (Figs. 12.6c, d) (Persson, 1983; Byström, Persson & Wahlström, 1998). The empirical relationship between intermediate consumer abundance and size distribution and top predator abundance and size distribution is presently under investigation.

To summarize, size-dependent multispecies interactions exemplified in the tritrophic food chain and in systems with life-history omnivory potentially cause substantially different body-size distributions of communities. Furthermore, size-dependent dynamics clearly affect the stability properties of ecological communities and promote the presence of alternative states. This

suggests that an explicit consideration of the dynamics of size-dependent interactions may be essential to understand and predict body-size distributions in many systems.

Extensions to more complex configurations

The results presented above show that size-dependent processes have important implications for the dynamics and structure of ecological communities. Size-structured interactions may promote the likelihood of alternative states in terms of both species composition (presence/absence) as well as size distributions of coexisting species. Still, the model complexity and parameter richness of the consumer-resource model considered above that forms the basis for many of the results discussed here, will limit the extent to which these models can be expanded to multispecies configurations. Since many of the questions raised in the body-size literature deal with multi-species systems, there is a need for simpler modules that can handle more speciose systems but still incorporate essential aspects of the individual's life history, especially food-dependent growth.

Recently, a model-building block based on stages, termed a 'structured biomass community module' has been developed that accounts for food-dependent development and maturation (De Roos *et al.*, unpublished). This modelling approach parallels the bioenergetics population models developed by Yodzis and Innes (1992) for non-structured populations. Compared with the consumer-resource model considered above, the dimensionality of the system is heavily reduced to a two-stage (juveniles, adults) model. Both juvenile and adult consumption is assumed to follow a Type II functional response with a maximum ingestion rate I_{\max} and a half saturation constant H . The net production per unit of biomass for adult (v_a) and juveniles (v_j), respectively, is given by:

$$\begin{aligned} v_a &= q\sigma I_{\max} \frac{R}{H+R} - T \\ v_j &= \sigma I_{\max} \frac{R}{H+R} - T \end{aligned} \tag{12.1}$$

q represents the difference between adults and juveniles in time spent foraging on the resource. It is assumed that ingestion and metabolic rate scale linearly with body mass. Ingested energy is assimilated with an efficiency σ , and assimilated energy is first used to cover maintenance T . The net energy left is transformed into consumer biomass.

For a system with juveniles (J) investing all their net energy into growth and adults (A) investing all their net energy into reproduction, the dynamics of the system takes the following form:

$$\begin{aligned}
\frac{dJ}{dt} &= \nu_a^+ A + \nu_j J - \gamma \nu_j^+ J - \mu_j J \\
\frac{dA}{dt} &= \nu_a A - \nu_a^+ A + \gamma \nu_j^+ J - \mu_A A \\
\frac{dR}{dt} &= \rho - \delta R - \frac{R}{H + R} (I_{\max} J + q I_{\max} A)
\end{aligned}
\tag{12.2}$$

Juvenile biomass increases through recruitment ($\nu_a^+ A$) and growth in biomass ($\nu_j J$) and decreases due to maturation to the adult stage ($\gamma \nu_j^+ J$) and mortality ($\mu_j J$). Adult biomass increases through maturation of juveniles ($\gamma \nu_j^+ J$) and decreases due to mortality ($\mu_A A$). $\nu_a^+ A$ can only take positive values and ensures that no reproduction in adults takes place if resource levels are too low to sustain maintenance. Similarly, $\gamma \nu_j^+ J$ ensures that no maturation takes place if resource levels are too low. ρ is resource productivity and δ resource turn-over rate. The maturation function γ is dependent on juvenile mortality, newborn and adult size, and the net production per unit body mass of juveniles, ν_j .

The structured biomass community model is derived through the formulation of a physiologically structured population model and also yields the same equilibrium results as the latter. Analyses show that the multiple equilibria resulting from the emergent Allee effect, emergent facilitation and ontogenetic niche shifts are also present in this more aggregated biomass community model (De Roos *et al.*, unpublished). With a body-size perspective, this more aggregated module thus has the potential to allow an investigation of size-structured induced shifts in body-size distributions in many species systems.

Conclusions

As evident in our retrospective overview, growth and development is a major feature of many organisms on Earth, hence the implications of this for individual, population, community and ecosystem processes can hardly be neglected. This circumstance has also been recognized in the most recent body-size literature (Woodward *et al.*, 2005; Woodward & Warren, this volume). As discussed in this chapter, growth and development take different forms in different organisms, but one dividing line can be seen along the ectothermy–endothermy gradient. Theoretical studies suggest that a critical element giving rise to the various size-dependent patterns is food-dependent development per se and not whether organisms continue to grow in somatic size over their whole life period (De Roos *et al.*, 2003b; De Roos *et al.*, unpublished). That is, whether individuals continue to grow in somatic tissue or allocate all their net energy into reproduction after maturation is not a factor affecting the presence of, for example, the emergent Allee effect.

The recent body-size literature has emphasized the need to document size-dependent interactions at the level of individuals, with the main purpose of reducing biases in estimates of predator/prey (parasitoid/host) ratios (Cohen

et al., 2005). The investigation of individual size scaling of foraging rates in particular, was a significant area of research 20 years ago including the development of individual level models (Werner & Gilliam, 1984). The development of the framework of physiologically structured population models with its two-level (individual, population) representation has made it possible formally to connect size-dependent individual-level processes to the population level, which, in turn, has allowed us to start to answer questions about the effects of body-size scaling for population and community dynamics and its feedbacks on body-size distributions. The insights gained so far from these analyses concern both dynamical aspects and equilibrium properties. As an example of the former, studies of size-structured consumer-resource systems show that cohort cycles are the most common outcome of consumer-resource interactions (Persson *et al.*, 1998). Furthermore, these cohort cycles are not restricted to systems with few species but are also present in many-species systems; hence the non-equilibrium dynamics resulting from cohort dynamics cannot be ignored in a food-web context (Murdoch *et al.*, 2002). Correspondingly, the presence of temporal variation in body-size distribution is increasingly recognized in the body-size literature (Stead *et al.*, 2005; Woodward *et al.*, 2005).

Studies of multitrophic systems show that size-dependent processes will give rise to alternative equilibrium states with major ramifications for overall body-size distributions (De Roos & Persson, 2002; De Roos *et al.*, 2003a). Given the common observation of food-dependent development in organisms, we argue that approaches not incorporating food-dependent development may have a limited capacity to yield both understanding of, and useful predictions, about the dynamics and structure of ecological communities.

A major challenge for the future is to develop approaches that allow the analyses of more complex configurations in terms of the number of species present, but still encompass major processes resulting from ontogenetic development (De Roos *et al.*, unpublished). Such approaches should also make it possible to provide new insights about the community dynamics based on a relatively limited number of intraspecific size-scaling parameters along the lines of the body-size based trophic dynamic models developed for interspecific interactions by Yodzis and Innes (1992).

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