POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	54	4	621–632	2006

State-of-the-art review

Lennart PERSSON[1], André M. De ROOS[2]

[1]Department of Ecology and Environmental Science, Umeå University, S-901 87 Umeå, Sweden,
e-mail: lennart.persson@emg.umu.se
[2] Institute of Biodiversity and Ecosystems, University of Amsterdam, P.O.B. 94084,
NL-1090 GB Amsterdam, Netherlands, e-mail: aroos@science.uva.nl

SIZE-STRUCTURED INTERACTIONS AND THE DYNAMICS OF AQUATIC SYSTEMS

ABSTRACT: Size variation within species as a result of individual growth and development over the life cycle is a ubiquitous feature of many aquatic organisms. We review the implications of this size variation for the dynamics of aquatic systems. Ontogenetic development results in differences in size dependent competitive abilities between differently sized individuals giving rise to cohort cycles that are qualitatively different from traditional predator prey cycles. Size-dependent interactions also mean that the type of interaction – competitive or predatory – changes over the life cycle as a result of an increase in size. At the intraspecific level, cannibalistic interactions may, depending on the life history characteristics of the cannibal, give rise to either equilibrium or cycles driven by a mixture of inter-cohort cannibalism and competition. In multispecies contexts, size variation and particularly food dependent growth lead to the presence of alternative states involving catastrophic collapses. These size-structured interactions have so far been mainly demonstrated for fish and cladocerans, but do have whole lake food web ramifications.

KEY WORDS: size variation, cohort cycles, cannibalism, alternative states, intraguild predation

1. INTRODUCTION

A striking feature of natural communities is the variation in size that exists among organisms (Gaston and Lawton 1988, Werner 1988). Body size has also been a major variable to consider when unravelling the mechanisms behind the structure of ecological systems starting from Hutchinson's classical "Homage to Santa Rosalia" paper (1959). The central role of body size in ecology is not surprising given that body size is the most important variable affecting ecological performance of organisms including foraging ability, metabolism, predation risk and fecundity (Peters 1983, Calder 1984, Sebens 1987, Werner 1988, Persson and De Roos 2005). Correspondingly, body size plays a central role in a number of ecological questions like body size-abundance patterns, interaction strengths and predator-prey size ratios, body size spectra, and also forms the basis for many food web models and metabolic theory (Cohen *et al.* 1993, Williams and Martinez 2000, Kerr and Dickie 2001, Brown *et al.* 2004).

Aquatic systems are no exception to the rule that body size heavily influences ecological patterns and interactions. Typical for lake ecosystems is also that the average body mass of the individual increases dramatically from lower trophic components such as bacteria and phytoplankton to higher trophic components such as piscivorous fish (Cohen *et al.* 2003). For example, the size of the phytoplankton *Scenedesmus* amounts to 0.03 mm whereas the adult size of a top predator like pike (*Esox lucius* L.) may be as large as 1500 mm. Interestingly, we also see a major shift in the temporal and spatial scales that the organisms live on with changes in body size. The generation time of bacteria, for example, is on the time scale of minutes whereas that of piscivorous fish is on the time scale of many years (Vanni 1996). Correspondingly, the spatial scale on which small organisms live may be within a square meter, whereas that of anadromous fish may be on many square kilometres. Body size also heavily influences the ecological interactions among aquatic organisms. A well-known example is the effects of body size on the competitive ability of *Daphnia* (Gliwicz 1990). Similarly, predator-prey interactions are heavily structured by size-dependent interactions with the classical example of the effect of planktivorous fish predation on the size distribution of zooplankton (Brooks and Dodson 1965).

The studies referred to above have stressed the importance of body size for ecological patterns and interactions, but have, at the same time, restricted themselves to size variation *among* species. This contrasts to that a substantial amount of the variation in body size in ecological communities is due to variation *within* species. In particular, the fact that most organisms undergo substantial changes in size over their ontogeny is largely neglected in the above literature (Werner and Gilliam 1984, Werner 1988, Wilbur 1988, De Roos *et al.* 2003). The purpose of our paper is to give an overview of the implications of ontogenetic size variation for the dynamic of ecological communities with special reference to aquatic systems. We will consider how ontogenetic size variation will affect both the dynamics of populations (inter-cohort competition and cannibalism) as well as community structure (food chains and intraguild predation modules). Examples of dynamical consequences of within species size variation include cohort (generation) cycles and consequences for community structure include the presence of Allee effects leading to alternative states (Persson *et al.* 1998, De Roos and Persson 2002). Before considering these effects, we will first as a background give a brief overview of growth patterns in different organisms. In our treatment, we use size to refer to both length and weight considering that weight is generally a power function of length.

2. GROWTH PATTERNS IN DIFFERENT ORGANISM GROUPS

Werner (1988) showed in an overview that the majority of organisms exhibits substantial changes in size and/or morphology over their ontogeny. This pattern results partly from the dominance of organisms undergoing metamorphosis during their life cycle (85% of all taxa, 25 of 33 phyla) (Werner 1988). Even if only vertebrates are considered, individuals of 75% of all taxa still show substantial growth during most of their life, which is due to the taxonomical dominance of fish, amphibians and reptiles. Essentially, it is only among altricial birds and some mammals where the young is close to the adult body size when becoming independent of its parents (i.e. when they have to gather food themselves) (Werner 1988). It is also striking that one common trait among the two groups where the juvenile is closer to adult size when becoming independent of their parents (birds and mammals) is endothermy and a considerably higher body temperature than what is found in other groups (Case 1979, Stearns 1992). Poikilothermic organisms, which totally dominate in freshwater systems, are thus more likely to exhibit large changes in size/morphology from the moment when the individual starts to search for food independently.

The growth of organisms after that they become independent of their parents can take a number of different forms. In some organisms, such as fish, growth is relatively continuous over the whole life cycle, whereas in other groups growth occurs in discrete stages as is the case in scorpions. As already mentioned, the majority of animal species undergoes metamorphosis where growth can take place among both juveniles and adults, among juveniles only or among adults only. Restricting the focus to aquatic organisms, the degree of size variation related to ontogenetic growth correlates with both the trophic position of the organism and the temporal and spatial scales that it lives on. These relationships are essentially reflections of that the average (or rather adult) body size of a species correlates with the extent of size variation that is found over the ontogeny.

Size variation is present within populations of organisms at lower trophic positions such as bacteria, phytoplankton, heterotrophic flagellates and protozans, but intraspecific size variation is much smaller in these organisms than in organisms at higher trophic levels such as copepods, cladocerans and fish. In fish in particular, the size ratio between hatching and maturing individuals may amount to 2 orders of magnitude in length and 7 orders of magnitude in mass (Scott and Crossman 1973).

The substantial size changes that, for example, fish undergo during their life cycles impose a series of constraints on the body morphology of organisms related to both physical and biological processes (Werner 1988, Stearns 1992). For example, the Reynold numbers affecting the movement mode of the organism is vastly different between a small new-born individual and a large mature individual. For small organisms, the low Reynolds number means that they swim with friction as the propulsive mode, whereas large organisms use the inertia of the water to propel themselves (Werner 1988). Ecological constraints relate to, for example, which prey types an organism with a specific body morphology and size can efficiently utilize (Werner 1988). Size changes over the life cycle of the individual will thus affect its ecological performance as a result of both physical and biological constraints. Also the main type of interaction that an individual is engaged in will change as a result of growth (Werner and Gilliam 1984, Persson 1988, Wilbur 1988). In the following, we will consider the effects of growth for population and community dynamics starting with the most simple trophic interaction: one consumer and one resource. Although our treatment will include a substantial amount of results derived from modeling, we will not consider the modeling framework (physiologically structured population models) per se. Instead we refer the interested reader to papers by De Roos *et al.* (1990), De Roos (1997) and Persson *et al.* (1998) for an introduction to physiologically structured population models.

3. CONSUMER–RESOURCE INTERACTIONS AND ONTOGENETIC SCALING

To the ecologists in general the most well-known dynamical phenomenon resulting from consumer-resource interactions are predator-prey cycles ("paradox of enrichment cycles", "prey escape cycles") (Rozenzweig 1971, De Roos *et al.* 1990). Predator-prey cycles result from the interactions between consumer and resource and depend on two important elements of consumer and prey: a type II functional response in the consumer and logistic growth in the resource. Classical consumer-resource cycles are characterized by a time lag between the maximum number of consumers relative to the maximum number of resources equal to ¼ of the fluctuation period and also assume a stable age distribution over time. A literature review over populations where cycles were present suggests that only about 40% of the observed cycles are classical predator prey cycles, whereas the rest are cycles involving size/stage-dependent interactions (delayed feed back and single generation cycles) (Murdoch *et al.* 2002). In other words, the majority of observed cycles is not of the classical consumer-resource type, but involves size/stage dependent mechanisms.

In freshwater systems, *Daphnia* has served as a major model system to study population dynamics and cohort cycles have been found to be a dominating class of cycles in experimental studies (Murdoch and McCauley 1985, McCauley and Murdoch 1987, 1990, McCauley 1993, McCauley *et al.* 1999). Cohort cycles are characterized by 1) a lower cycle amplitude in *Daphnia* (consumer) and algae (resource) compared to predator-prey cycles, and 2) that the size (age) distribution of the consumer varies over time (Fig. 1). The latter condition results from a time lag between peaks in abun-

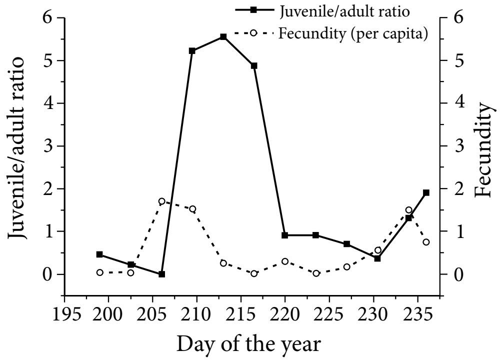

Fig. 1. Changes in juvenile/adult ratio and per capita fecundity in *Daphnia pulex* over time in a laboratory experiment (data from McCauley *et al.* 1999). Note the major change in juvenile/adult ratio over time and the suppression of fecundity by high numbers of juveniles.

dance of juveniles and adults (McCauley *et al.* 1999) (Fig. 1). In an elegant experiment, McCauley *et al.* (1999) were able to shift the dynamics from cohort cycles to predator prey cycles by exchanging produced resting eggs with juveniles suggesting that the production of resting eggs during harsh conditions is one reason for why cohort cycles dominate in *Daphnia* systems. Cohort cycles are driven by interactions between cohorts within the consumer, but although the experimental studies on *Daphnia* have clearly demonstrated the existence of cohort cycles, the mechanism(s) driving these cycles are far from understood in *Daphnia* (De Roos 1997). This concerns, for example, whether the cycles are driven by a change in adult numbers or in adult fecundity. Moreover, there exist major discrepancies between model predictions and experimental data in demographic characteristics like adult/juvenile ratios. Despite substantial efforts to unravel the reasons for the discrepancies found between experiments and modelling, the discrepancies still remain.

One reason for why it has proved to be hard to resolve the discrepancies between models and data relates to the continuous mode of reproduction in *Daphnia* making it very difficult to separate out and follow cohorts over their development. In systems where reproduction takes place as discrete events like in fish in temperate systems, there is natural separation of different cohorts. This has made it possible to rather precisely nail down the mechanisms driving the cycles in these organisms. Persson *et al.* (1998) derived a size-structured model where processes like consumption, metabolism and mortality were modelled as continuous processes whereas reproduction took place once a year at the start of the growing season resulting in a separation of cohorts born at different times. The modelling results showed that 3 main types of dynamics could evolve: cycles driven by recruiting individuals, cycles driven by larger (“resident”) juveniles and equilibrium conditions. Interestingly, it could be shown that the population dynamics observed can be understood by the individual level size scalings of 3 components: the attack rate, the handling (digestion) time and metabolism (Fig. 2 upper panels). Given the size-dependent relationships of these 3 components, the net energy surplus (intake-costs) can be calculated. Setting this energy surplus to zero, in turn, allows the calculation of the lowest resource density that an individual of a specific size needs for maintenance (the critical resource density) (Persson et al. 1998) (Fig. 2 lower panel).

In Fig. 2 is shown how the critical resource density varies with body size for 3 different size scalings of the attack rate (upper left panel) for given size scalings of metabolic rate and handling time (upper panel, 2 left panels). With a relatively shallow slope for the attack rate body size relationship ($\alpha = 0.67$), the critical resource density increases monotonically with body size leading to that smaller individuals always can tolerate lower resource levels than larger individuals. Increasing the slope of the size scaling of the attack rate (α=0.95) leads to a situation where the curve for critical resource density as a function of body size is relatively flat, i.e. differently size individuals can tolerate similarly low resource levels. Increasing the size scaling of the attack rate further ($\alpha = 1.1$) leads to a situation where the critical resource density first decreases with body size to thereafter increase for large individuals. These qualitatively different forms of the critical resource density–body size relationships translate into different population dynamics. If the critical resource density increases monotonically with body size, recruiting new-born indi-

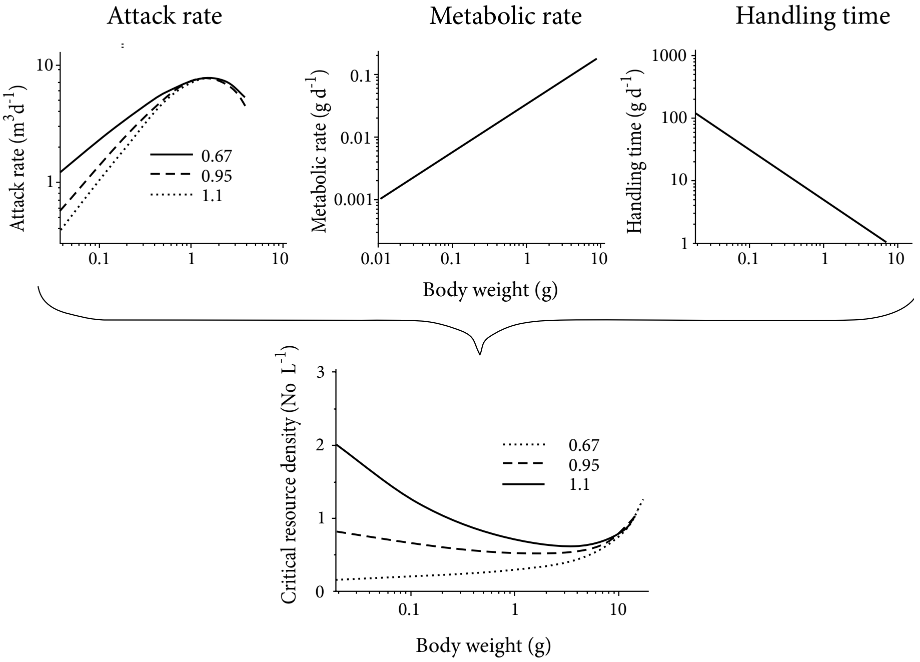

Fig. 2. Upper panels: Attack rate, metabolic rate and handling time as a function of body mass. Metabolic rate and handling time are power functions of body mass whereas the weight dependent attack rate is given by $a(w)=A(\frac{w}{w_0}\exp(1-\frac{w}{w_0}))^\alpha$ where *A* is the maximum attack rate, w_o the body size at which the maximum rate is achieved, and α a size scaling exponent. The attack rate in the upper left panel is shown for 3 different size scalings. Mechanistic reasons for functional relationships chosen are given in Persson *et al.* (1998) and Claessen *et al.* (2000). Lower panel: critical resource density as a function of body mass for the different size scalings (α) of the attack rate shown in upper left panel. See text for further explanations.

viduals will be competitively superior and their large numbers will cause a depression of the resource leading to that older mature individuals are out-competed. The dominating cohort will consequently lead to a cycle with a length determined by the time it takes for the cohort to mature (i.e. cycle length = generation time). For a relatively flat critical resource density – body size relationship, the different size cohorts are almost equal competitors leading to equilibrium conditions with coexistence of many cohorts. Finally, if the critical resource density first decreases with body size, dominating older juveniles may prevent recruitment of new cohorts by depressing the resource to a level where newborn individuals starve to death. Also this case results in cohort cycles with cycle length = generation time (Persson *et al.* 1998).

Experiments on size-dependent functional response in fish suggest that the size scalings of attack rate, handling time and metabolism are such that recruit-driven cohort cycles are expected to be rule (Persson and De Roos 2006). This expectation is supported by detailed analyses of the population cycles of different fish populations including the analysis of growth trajectories of different cohorts (De Roos and Persson 2001). The cycle length of observed cycles generally varies between 2–4 years, but also longer cycles have been observed. One example of the latter is the population dynamics of a yellow perch (*Perca flavescens* (Mitchill)) population where the cycle length amounted to 6–7 years (Sanderson *et al.* 1999, Persson *et al.* 2004a) (Fig. 3).

To conclude this section on consumer-resource dynamics, studies of cycles in *Daphnia* and fish suggest that size-dependent cohort cycles are the dominating cycles observed. For fish populations with discrete reproduction, it can actually be argued that cohort cycles should be the only cycle possible for consumer-resource interactions due to time scale differences. Finally, in the studies on fish it has also been shown that the cohort cycles induced by inter-cohort competition

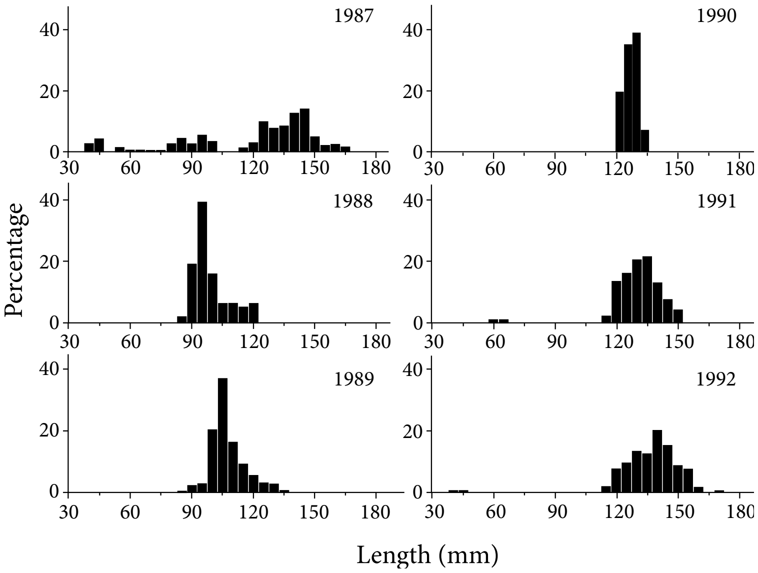

Fig. 3. Changes in size distributions of the yellow perch population in Crystal Lake during 1987–1992 (data from Sanderson *et al.* 1999). This population exhibited a 7 year cycle where the cohort born in 1985 totally dominated the yellow perch population for many years. Note the disappearance of larger size cohorts between 1987 and 1988.

feed back on lower trophic components such as zooplankton and phytoplankton (Persson and De Roos 2005).

4. CANNIBALISM AND SIZE-DEPENDENT INTERACTIONS

In the consumer-resource interactions discussed so far, we have assumed that the resource has a fixed size with no size variation. This may be a valid first approximation when studying zooplankton-phytoplankton and planktivorous fish-zooplankton interactions. In contrast, when studying the interactions among different fish species or between size classes within a species, we need to from the start consider size variation in both predator and prey. Studies of size selectivity of piscivorous fish on prey fish suggest that 2 major constraints on piscivore-prey fish interactions are present: an upper prey/predator size ratio above which prey fish escapes predation due to size-dependent escape ability or gape constraint in the predator, and a lower prey/predator size ratio below which the piscivore does not encounter the prey fish due to limitations of visual acuity (for overviews see Claessen *et al.* 2000, Juanes 2003, Juanes *et al.* 2002).

Cannibalistic interactions represent interactions that are common among aquatic organisms, and are also strongly dependent on both cannibal and victim size. Two main aspects of cannibalism have been studied in aquatic systems. First, cannibalism may serve as a "life-boat" mechanism whereby cannibalistic populations can survive periods of food shortage that would otherwise extirpate non-cannibalistic populations (Van den Bosch *et al.* 1988). The potential presence of this mechanism has been studied particularly for copepods (Van den Bosch and Santer 1993). Second, cannibalism has important population dynamical consequences (Claessen *et al.* 2000). Questions raised in relation to population dynamics include whether cannibalism may stabilize cycles induced by inter-cohort competition, and the effects of energy gain from cannibalism on population dynamics (Claessen *et al.* 2000, Persson *et al.* 2004b). The studies on population dynamics of cannibalism in aquatic systems have had their main focus on fish.

Theoretical and empirical studies on fish show that cannibalism indeed may stabelize population dynamics in otherwise widely fluctuating systems (Claessen *et al.* 2000, 2002, Persson *et al.* 2004a). The stabelizing effect of cannibalism is, however, depending on the life history characteristics of the cannibal (Claessen *et al.* 2000, 2002, Persson *et al.* 2004a). Specifically, the size range of cannibal and victim sizes that allow cannibalistic interactions to take place (the "cannibalism window") has a large influence on population dynamics (Claessen *et al.* 2002). Basically, 3 different dynamical regimes can be distinguished depending on the width of this cannibalistic window. For a small width (when cannibals cannot consume very small victims), the dynamics is characterized by *cohort competition-driven* cycles where smaller-sized, recruiting individuals out-compete older/larger individuals as outlined in the previous section before victims become large enough to be cannibalized. An example of a cannibalistic species exhibiting this dynamics is yellow perch (Fig. 3). If cannibals can consume even the smallest victims, cannibals impose a high cannibalistic mortality on victims from birth onwards, which prevents strong competition from the recruits. This *cannibal-driven* dynamics leads to equilibrium or low amplitude dynamics with coexisting cohorts (Claessen *et al.* 2002). Since most of the mortality imposed on victims takes place when they are very small cannibals gain most of their energy from the shared resource and not from cannibalism. An example of a cannibalistic species showing this dynamics is the northern pike (*Esox lucius*) (Persson *et al.* 2004a). For an intermediate cannibal efficiency, cannibals control recruiting victims through heavy cannibalism for some period, but this dynamics is intermitted by a dynamics where a strong recruiting cohort breaks through and, by depleting the shared resource, out-competes most of the cannibals. This cohort dominates the system until they mature, where after the dynamics returns to a cannibal-driven dynamics (Claessen *et al.* 2002). The few adults that survive the recruitment of the strong cohort gain a lot of energy from cannibalism and become "giants", but due to their low numbers they only impose a negligible mortality on the dominating cohort. An example of a species exhibiting this mixed type of dynamics is the Eurasian perch (*Perca fluviatilis* L.) (Persson *et al.* 2003, 2004a).

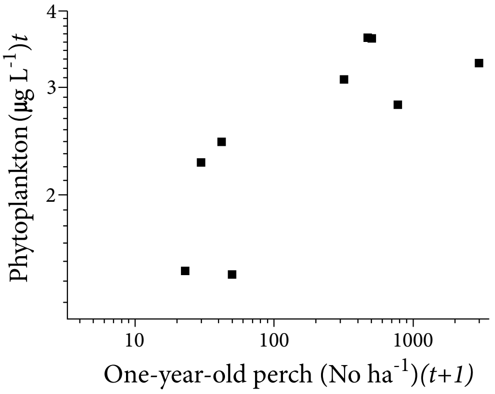

Fig. 4. The relationship between phytoplankton biomass in year *t* and one-year-old perch in year (*t+1*) in Lake Abborrtjärn 3 (data from Persson *et al.* 2003). High number of one-year-old perch in year (*t+1*) reflects high survival and hence high predation pressure on zooplankton of young-of-the-year perch in year *t*.

Both theoretical and empirical analyses show that when cannibals control their victims they extract little energy from cannibalism (see cannibal-driven dynamics above). In contrast, when cannibals do extract large amount of energy from cannibalism, they do not control victims (Claessen *et al.* 2000, Persson *et al.* 2003, 2004b). Control of victims and energy extraction from victims by cannibals thus seem to be exclusive processes that do not occur simultaneously. Finally, as for cohorts cycles cannibalistic dynamics in fish population feed back on overall lake food web dynamics showing that intraspecific interactions in fish have ramifications for overall lake ecosystem dynamics (Persson *et al.* 2003). In particular, Persson *et al.* (2003) showed that shifts in the size structure of a cannibalistic Eurasian perch population caused a 2 times variation in phytoplankton biomass (Fig. 4).

5. SIZE-STRUCTURED DYNAMICS AND COMMUNITY STRUCTURE

So far we have focused on the effects of size structure on population dynamics with examples from consumer-resource and cannibalistic systems. Studies of multitrophic systems reveal that size-dependent processes will have major effects on community structure involving alternative equilibrium states (De Roos and Persson 2002, De Roos *et al.* 2003). We will illustrate this by two examples: tritrophic food chains and intraguild predation.

5.1. Tritrophic food chains

The changes in the densities of resource, consumer and predator with productivity in unstructured tritrophic food chain models are well-known (cf. Oksanen *et al.* 1981). At low productivities, resource numbers are too low to allow the invasion of consumers, and resource numbers increase with productivity. An increase in productivity will allow the consumer to invade, and from this productivity level the consumer will gradually increase with productivity whereas resource numbers stay constant. Still higher productivities will allow the predator to invade from small numbers, where after predator and resource numbers will increase with resource productivity, while consumer numbers stay constant. New patterns emerge in such a tritrophic food chain, however, if (a) the growth rate of consumer individuals is food dependent and (b) predation by the (unstructured) predator population is size selective towards the smallest consumer individuals. As long as the predator cannot invade the system, predictions are the same as for unstructured model: the consumer increases with productivity while the resource does not. However, when the predator invades, it does not do so from small numbers but instantaneously increases to high levels (De Roos and Persson 2002). Moreover, once in the system the predator can persist down to much lower resource productivities than at which it invades. For a considerable resource productivity range, we thus have a situation with bistability (resource-consumer or resource-consumer-predator equilibrium state). The presence of this bistability also means that the system is sensitive to catastrophic collapses of the predator (De Roos and Persson 2002). This discrepancy between invasion boundary and persistence boundary reflects a depensatory growth (decreased population size leading to reduced per capita growth rate) in the predator, also termed an Allee effect. Furthermore, as this Allee effect results form pure exploitation of resources and does not involve social interactions that are often used to explain the presence of Allee effects, this Allee effect has been called an "emergent" Allee effect (De Roos and Persson 2002).

The key to understanding the appearance of the bistability lies in the food dependent growth in the consumer and size selective predation. The mechanisms can be understood by replacing the predator by a constant (i.e. non dynamic) mortality rate on small consumers. Increasing this mortality rate of small individuals relieves the competitive pressure among consumers, such that resource levels, maximum individual size and adult biomass increase, while the biomass of non-vulnerable juveniles strongly decreases. Interestingly, despite the additional mortality on small juveniles their total biomass increases significantly. The faster individual growth, which results from the higher resource levels, results in higher adult fecundity and hence in a significant increase in total population reproduction. This increased production of newborns more than compensates for the additional mortality these small individuals experience. In contrast, if a constant length-age relation is assumed and hence if higher resource levels do not increase individual growth, vulnerable juvenile and adult biomass only decrease with increasing size-selective mortality (De Roos and Persson 2002).

Size-selective predation thus leads to a positive feedback in the predator-consumer-resource system. Size-selective predators induce a shift in the size-structure of the consumers, resulting in higher biomass densities of vulnerable juveniles and adults, but lower densities of intermediately sized (Fig. 5).

The emergent Allee effect has been forwarded as a plausible explanation for the collapse and lack of recovery that has been observed in stocks of marine top predators (Carscadden *et al.* 2001, De Roos and Persson 2002). A large scale removal of a fish stock in the Norwegian Lake Takvatn provides another suggestive example of alternative states induced by the emergent Allee effect. In this case a stunted Arctic char (*Salvelinus alpinus* (L.)) population was subjected to a large scale removal where more than 70% of Arctic char were removed (Klemetsen *et al.* 2002). Not unexpectedly,

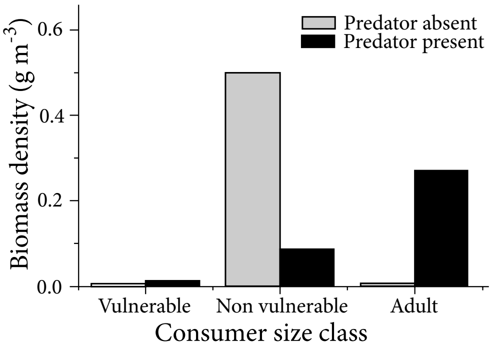

Fig. 5. Stage distributions of consumers in the absence and presence of predators with food dependent growth in consumer and size selective predation (from De Roos *et al.* 2003).

individual growth rate of Arctic char individuals drastically increased, but, more remarkably, this change in growth rate still persists after many years providing evidence for an alternative state. Evidence for that the persistent change in growth rates of Arctic char individuals can be explained by the emergent Allee effect comes from that its main predator, brown trout (*Salmo trutta* L.), that was very rare at the start of the experiment, has increased 30 times in numbers.

5.2. Intraguild predation and size-structured interactions

The fact that individuals grow will by necessity lead to that the dominating interaction they experience changes from a competitive to a predatory interaction over their life cycle (Werner and Gilliam 1984, Persson 1988, Wilbur 1988). Typically, these size-dependent shifts in interactions results in life history omnivory where the predator competes with the intermediate consumer for the shared resource when small to prey on the intermediate consumer when large (Persson 1988, Holt and Polis 1997). The dynamics of unstructured omnivorus systems with a shared resource an intermediate consumer and a predator (intraguild predation, IGP systems) have been analysed as a function of productivity in a number of papers (Holt and Polis 1997, Diehl and Feissel 2000, Mylius *et al.* 2001). The productivity-dependent community patterns differ from that of simple food chains in that the intermediate consumer will decrease with productivity once the top predator has invaded.

Furthermore, omnivory leads to the possibility for alternative states (resource-intermediate consumer-predator/ resource-predator) at intermediate productivities. Finally, at high productivities the intermediate consumer is excluded due to predation by the predator. Introducing stage structure with fixed development times has mainly quantitative effects on this pattern. If stage structure is introduced in the intermediate consumer such that large intermediate consumer individuals are not preyed upon, the relative parameter space with coexistence between predator and intermediate consumer is larger, which is mainly due to that the parameter space with bistability (either predator and resource or predator, intermediate consumer and resource) is increased (Mylius *et al.* 2001). In contrast, if stage structure is introduced in the predator such that small predators do not prey on the intermediate consumer, the relative parameter space with coexistence increases whereas that with bistability decreases. Food-dependent development in intermediate consumer and predator will qualitatively change the community patterns of IGP systems in that coexistence between intermediate consumer and predator is not possible any more (Van de Wolfschaar 2006). To test this very strong prediction of IGP models with food dependent development is an important issue for future research.

6. CONCLUSIONS

With this short overview we have given examples of how size-structured interactions may have major consequences for the dynamics of aquatic systems. The importance of size-dependent interactions increases with trophic position, but as dynamical patterns observed at higher trophic positions feed back on lower trophic components, size-dependent interactions must be considered in studies of the dynamics of aquatic systems in general. As we have shown, size variation has both dynamical and structural effects on aquatic systems. The former was exemplified with consumer-resource and cannibalistic population dynamics, and the latter with tritrophic food chain and intraguild predation modules. A key process behind many of the effects observed is food dependent development pointing to that approaches aimed at studying the dynamics of aquatic systems have to take such food dependent development into consideration.

ACKNOWLEDGEMENTS: The research based on which this paper was written has been funded by the Swedish Research Council and the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning to L. Persson and by the Netherlands Organization for Scientific Research to A.M. De Roos. We thank the organizers of the SEFS meeting in Krakow for inviting us and 3 referees for valuable comments on a previous version of this paper.

7. REFERENCES

Brooks J.L., Dodson S.I. 1965 – Predation, body size and composition of plankton – Science, 150: 28–35.

Brown J.H., Gillooly J.F., Allen A.P., Savage V.M., West G.B. 2004 – Towards a metabolic theory of growth – Ecology, 85: 1771–1789.

Calder W.A. III. 1984 – Size, function and life history – Cambridge, Harvard University Press, 431 pp.

Carscadden J.E., Frank K.T., Leggett W.C. 2001 – Ecosystem changes and the effects on capelin (*Mallotus villosus*), a major forage species – Can. J. Fish. Aquat. Sci. 58: 73–85.

Case T.J. 1979 – Optimal body size and an animal's diet – Acta Biotheor. 28: 54–69.

Claessen D., De Roos A.M., Persson L. 2000 – Dwarfs and giants – cannibalism and competition in size-structured populations – Am. Nat. 155: 219–237.

Claessen D., van Oss C., De Roos A.M., Persson L. 2002 – The impact of size-dependent predation on population dynamics and individual life history – Ecology, 83: 1660–1675.

Cohen J.E., Pimm S.L., Yodzis P., Saldana J. 1993 – Body sizes of animal predators and animal prey in food webs – J. Anim. Ecol. 62: 67–78.

Cohen J.E., Jonsson T., Carpenter S.R. 2003 – Ecological community description using the food web, species abundance, and body size – Proc. Nat. Acad. Sci. (USA), 100: 1781–1786.

De Roos A.M. 1997– A gentle introduction to physiologically structured population models (In: Structured-population models in marine, terrestrial, and freshwater systems, Eds: A. Tuljapurkar, H. Caswell) – Chapman and Hall, New York, pp. 119–204.

De Roos A.M., Metz J.A.J., Evers E., Leipoldt A. 1990 – A size dependent predator-prey interaction: who pursues whom? – J. Math. Biol. 28: 609–643.

De Roos A.M., Persson L. 2001 – Physiologically structured models – from versatile technique to ecological theory – Oikos, 94: 51–71.

De Roos A.M., Persson L. 2002 – Size-dependent life-history traits promote catastrophic collapses of top predators – Proc. Natl. Acad. Sci. (USA), 99: 12907–12912.

De Roos A.M., Persson L., McCauley E. 2003 – The influence of size-dependent life history traits on the structure and dynamics of populations and communities – Ecol. Lett. 6: 473–487.

Diehl S., Feissel M. 2000 – Effects of enrichment on three-level food chains with omnivory – Am. Nat. 155: 200–218.

Gaston K.J., Lawton J.H. 1988 – Patterns in the abundance and distribution of insect populations – Nature, 331: 709–712.

Gliwicz Z.M. 1990 – Food thresholds and body size in cladocerans – Nature, 343: 638–640.

Holt R.D., Polis G.A. 1997 – A theoretical framework for intraguild predation – Am. Nat. 149: 745–764.

Hutchinson G.E. 1959 – Homage to Santa Rosalia, or why are there so many kinds of animals? – Am. Nat. 93: 145–159.

Juanes F. 2003 – The allometry of cannibalism in piscivorous species – Can. J. Fish. Aquat. Sci. 60: 594–602.

Juanes F., Buckel J.A., Scharf F.S. 2002 – Feeding ecology of piscivorous fishes (In: Handbook of fish biology and fisheries, Vol. 1. Fish biology, Eds: P.J.B. Hart, S.D. Reynolds) – Blackwell, Oxford, pp. 267–283.

Kerr S.R., Dickie L.M. 2001 – The biomass spectrum. A Predator – Prey theory of aquatic production – Columbia University Press, New York, 320 pp.

Klemetsen A., Amundsen P.A., Grotnes P.E., Knudsen R., Kristoffersen R., Svenning M.A. 2002 – Takvatn through 20 years: Long-term effects of an experimental mass removal of Arctic charr, *Salvelinus alpinus*, from a subarctic lake – Environ. Biol. Fish. 64: 1–3.

McCauley E. 1993 – Internal versus external causes of dynamics in a freshwater plant herbivore system – Am. Nat. 141: 428–439.

McCauley E., Murdoch W.W. 1987 – Cyclic and stable populations: plankton as a paradigm – Am. Nat. 129: 97–121.

McCauley E., Murdoch W.W. 1990 – Predator-prey dynamics in environments rich and poor in nutrients – Nature, 343: 455–457.

McCauley E., Nisbet R.M., Murdoch W.W., De Roos A.M., Gurney W.S.C. 1999 – Large-amplitude cycles of *Daphnia* and its algal prey in enriched environments – Nature, 402: 653–656.

Murdoch W.W., McCauley E. 1985 – Three distinct types of dynamics behaviour shown by a single planktonic system – Nature, 316: 628–630.

Murdoch W.W., Kendall B.E., Nisbet R.M., Briggs C.J., McCauley E., Bolser R. 2002 – Single-species models for many-species food webs – Nature, 417: 541–543.

Mylius S.D., Klumpers K., De Roos A.M., Persson L. 2001 – Impact of omnivory and stage structure on food web composition along a productivity gradient – Am. Nat. 155: 200–218.

Oksanen L., Fretwell S.D., Arruda J., Niemelä P. 1981 – Exploitation ecosystems in gradients of primary productivity – Am. Nat. 118: 240–261.

Persson L. 1988 – Asymmetries in competitive and predatory interactions in fish populations (In: Size-structured populations – Ecology and evolution, Eds: B. Ebenman, L. Persson) – Springer Verlag, Berlin, pp. 203–218.

Persson L., Leonardsson K., Gyllenberg M., De Roos A.M., Christensen B. 1998 – Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model – Theor. Pop. Biol. 54: 270–293.

Persson L., De Roos A.M., Claessen D., Byström P., Lövgren J., Svanbäck R., Wahlström E., Westman E. 2003 – Gigantic cannibals driving a whole lake trophic cascade – Proc. Natl. Acad. Sci. (USA), 100: 4035–4039.

Persson L., De Roos A.M., Bertolo A. 2004a – Predicting shifts in dynamical regimes in cannibalistic field populations using individual-based models – Proc. Roy. Soc. London, 271: 2489–2493.

Persson L., Claessen D., De Roos A.M., Byström P., Sjögren S., Svanbäck R., Wahlström E., Westman E. 2004b – Cannibalism in a size-structured population – energy extraction and control – Ecol. Monogr. 74: 135–157.

Persson L., De Roos A.M. 2005 – Body size scaling and the dynamics of ecological systems (In: Food webs. Dynamic Food Webs-multispecies assemblages, ecosystem development and environmental change, Eds: P.C. de Ruiter, V. Wolters, J.C. Moore) – Academic Press, San Diego, pp.157–166.

Persson L., De Roos A.M. 2006 – Interplay between individual growth and population feed backs shapes body size distributions (In: The importance of body size in aquatic ecosystems, Eds: A. Hildrew, D. Raffaelli) – Cambridge University Press.

Peters R.H. 1983 – The ecological implications of body size – Cambridge University Press, Cambridge, 329 pp.

Rosenzweig M.L. 1971 – Paradox of enrichment: destabilization of exploitation ecosystems in ecological time – Science, 171: 385–387.

Sanderson B.L., Hrabik T.R., Magnuson J.J., Post D.M. 1999 – Cyclic dynamics of a yellow perch (*Perca flavescens*) population in an oligotrophic lake: evidence for the role of intraspecfic interactions – Can. J. Fish. Aquat. Sci. 56: 1534–1542.

Scott W.B., Crossman E.J. 1973 – Freshwater fishes of Canada. Bulletin 184 – Fisheries Research Board of Canada, Ottawa.

Sebens K.P. 1987 – The ecology of indeterminate growth in animals – Ann. Rev. Ecol. Syst. 18: 371–407.

Stearns S.C. 1992 – The evolution of life histories – Oxford University Press, Oxford, 249 pp.

Van den Bosch F., De Roos A.M., Gabriel W. 1988 – Cannibalism as a life boat mechanism – J. Math. Biol. 26: 619–633.

Van den Bosch F., Santer B. 1993 – Cannibalism in *Cyclops abyssorum* – Oikos, 67:19–28.

Van de Wolfshaar K.E. 2006 – Population persistence in the face of size-dependent predation and competition interactions – PhD thesis, University of Amsterdam.

Vanni M.J. 1996 – Nutrient transport and recycling by consumers in lake food webs: implications for algal communities (In: Food webs: intergration of patterns and dynamics, Eds: G.A. Polis, K.O. Winemiller) – Chapmann and Hall, New York, pp. 81–95.

Werner E.E. 1988 – Size, scaling and the evolution of complex life cycles (In: Size-structured populations – Ecology and evolution, Eds: B. Ebenman, L. Persson) – Springer Verlag, Berlin, pp. 60–81.

Werner E.E., Gilliam J.F. 1984 – The ontogenetic niche and species interactions in size-structured populations – Ann. Rev. Ecol. Syst. 15: 393–425.

Wilbur H.M. 1988 – Interactions between growing predators and growing prey (In: Size-structured populations – Ecology and evolution, Eds: B. Ebenman, L. Persson) – Springer Verlag, Berlin, pp. 157–172.

Williams R.J., Martinez N.D. 2000 – Simple rules yield complex food webs – Nature, 404: 180–183.

(Received after revising December 2005)