The ontogenetic niche-shift accounting for reserves and stoichiometric balances

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My current research deals with the interaction of populations with two resources. One of my main topics is how ontogenetic niche-shifts in for instance copepods affect competition with populations that do not undergo niche-shifts during their lifetime, like for instance in daphnids. Some species feed on the same set of resources throughout life, others exploit different resources during different phases of life history. A change in diet over ontogeny or ontogenetic niche-shift is widespread in nature (Werner and Gilliam 1984). Ontogenetic niche-shifts can be due to metamorphosis and migration between habitats, resulting in what is termed complex life-cycles (Loreau and Ebenhoh 1994; Schreiber and Rudolf 2008). However, niche-shifts can also result from changes in body size and accompanying changes in optimal size of resource particles that a consumer forages on without a change of habitat. Conspecific consumer individuals with different sizes or in different life-stages can thus occupy different niches and affect different resources (Werner and Gilliam 1984). I use a net-production model describing stage-structured populations in biomass (De Roos *et al.* 2008), explicitly derived from a fully size-structured population assuming food-dependent growth, maturation and reproduction (De Roos 1997; see De Roos et al. 2008, for its derivation; Metz and Diekmann 1986). Although these models are based on individual bioenergetics, they do not explicitly divide biomass into reserves and structure, and are hence simplistic in their assumptions and mathematical representation. The main advantage of these models is that qualitative effects of interactions can be easily analyzed. For instance we show using local stability and numerical bifurcation analysis that the ontogenetic niche-shift per se leads to niche partitioning; it creates a difference in competitive success where without the niche-shift it would lead to neutral coexistence. These models can be easily expanded to describe food webs. The downside of these models is that their quantitative comparison with experimental data is poor; no distinction is made between structure and reserves. Because the content of biomass is not modeled, non-equilibrium population dynamics are hard to compare to experimental data. To me, the DEB-modeling framework offers the possibility to extend my search both quantitatively and with increasing complexity concerning stoichiometric constraints on development.

My main interest in DEB is in the life-history description of ontogenetic niche-shifters, the comparison thereof with other models and the effects of this difference between model assumptions on competition.

In my previous modeling I have assumed that the ontogenetic niche-shift is caused by a change in size and accompanying change in resource preference. A change in resource use, however, can also come about because of changes in physiology. Specifically, calanoid copepods change from passively drifting to actively moving individuals over ontogeny. This change in activity is enabled by the development of rowing appendices and a sensory system at puberty. These adaptations at puberty impose different stoichiometric constraints to resources than during the juvenile or adult stage. Some species have been shown to actually shift from using protists to using algae as a food-source.

In comparison to my previous modeling, there are several relevant conceptual alterations to the assumptions and modeling given these changing stoichiometric constraints over ontogeny.

First of all, changing stoichiometric constraints over ontogeny may cause a change in food-preference (as has been assumed more phenomenologically in previous models) and it may cause a change in assimilation efficiency in one type of resource. Therewith, during physiological adaptation changes in assimilation efficiency cause a change in resource use before the individual is able to use another resource with the physical adaptations. In effect the speed of transition of use from one resource to the next is determined by the stoichiometry of the first resource. This stoichiometry of the first resource, in turn, is affected by the population dynamics of the niche-shifting population. When there are many individuals using this resource, theory predicts this resource will be depleted dependent on the stoichiometric balance between resource and individuals, making ontogeny and the transition to the next resource slower. The amount of individuals using the first resource is partly determined by life history rates controlled by the next resource (a high reproduction rate, for instance). These rates, again, are under control of the stoichiometry of the second resource. In other words stoichiometry and dynamics of both resources is intertwined with the stoichiometric constraints and population dynamics of the niche-shifters. Ontogenetic niche-shifts link the dynamics of resources through consumer life history. Changes in consumer reproduction, recruitment or maturation will hence not only affect dynamics of all resources exploited by the consumer throughout its life (Polis *et al.* 1996), but also the stoichiometric balances between resources and consumer.

Competition with a population that also feed on these resources but does not shift niche, will be affected by the variable speed of transition of use from one resource to the next in the niche-shifter. Previous modeling has shown that in case juveniles of a niche-shifter population reduce resource in excess of adults the population that does not shift niche is competitively superior, whereas when adults of a niche-shifter population reduce resource in excess of juveniles, the niche-shifter can be competitively dominant. Whether the adults or juveniles reduce resource in excess compared to the other stage depends on the resource supply. In the stoichiometric explicit case it is, however, not longer only a case of resource supply that determines these competitive outcomes. There, competitive outcome will also be affected by stoichiometric balances between resources and individuals. How these balances, and therewith resource use is affected by the presence of another population, however, is unknown up to this point in time.

To study these effects on stoichiometric balances and structured population dynamics in competition, I need a model that consistently describes all these aspects. I have to account for at least two nutrient pools, differentially divided between two basal resources and a structured population growing and reproducing food-dependently. Stoichiometric models do not consistently deal with food-dependence in growth and reproduction in structured populations. Physiologically structured population models (PSPMs) do, but most are not equipped with stoichiometric balances. The DEB-model is equipped, and applies stoichiometry to a PSPM in a consistent manner. To study equilibrium population dynamics I can translate this consistent manner to use of stoichiometry in a stage-structured biomass model.

There are several comparisons I would like to perform both between experimental data and models and between different models.

I can compare the dynamic equilibrium outcome of the DEB-model with a stoichiometrically explicit biomass model that does not account reserves. In that comparison I can assess the qualitative effect of reserves on resource use in niche-shifters. Individuals with reserves will be able to build-up the necessary building blocks to make physiological changes, while individuals without reserves will not. I expect that changes in resource supply and stoichiometry will have different reactions depending on the ability to store.

The predictions from the stoichiometric biomass model furthermore I can use to compare qualitatively with the non-stoichiometric biomass model predictions. This allows me to assess the effects of stoichiometric balances on population dynamics.

For comparison between data and models on competitive interactions, I first need to study the life-history of certain copepod species that compete for resources and shift resource-niche in different ways. Using the DEB-model as a framework, I can assess the effects of these differences on life history and obtain a mathematical description of these different life histories. The resulting life history descriptions I can then implement (in simplified form) into the different models and perform competition analyses. The outcomes of those analyses I can then compare to experimental data on competitive outcomes with the different copepod species. As stated in (Kooijman 2000), from experimental data it is hard to discriminate between the goodness of fit of net-production and assimilation models like DEB. However, that statement is based on comparison of models that describe population life-histories that do not include ontogenetic niche-shifts. When there is an ontogenetic niche-shift, the distinction between whether individuals pay maintenance from reserves or resources taken in can be made, because it influences the shift from one resource to another with changing resource supply. Furthermore, the net-production and assimilation models can be discriminated on the population dynamic level as well, through the effects of the niche-shift on competition between populations.

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