Alternative stable states and shifts in competitive dominance in size-structured fish communities

Magnus Huss (1,2), André de Roos (3), Anieke Van Leeuwen (3), Michele Casini (4) and Anna Gårdmark (1)

(1) Department of Aquatic Resources, Institute of Coastal Research, Swedish University of Agricultural Sciences, Skolgatan 6, SE-742 42 Öregrund, Sweden; (2) Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06520, USA; (3) Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O.Box 94248, 1090 GE Amsterdam, The Netherlands; (4) Department of Aquatic Resources, Institute of Marine Research, Swedish University of Agricultural Sciences, Turistgatan 5, SE-453 21 Lysekil, Sweden. Presenter contact details: magnus.huss@slu.se, Phone +1 203 215 8792

Summary

Patterns of coexistence among competing species that exhibit size- and food-dependent growth remain largely unexplored. Here we study mechanisms behind shifts in competitive dominance and mechanisms causing alternative stable states in a size-structured fish community. We use a framework of physiologically structured population models, applied to competing populations representing sprat and herring stocks in the Baltic Sea. Degree of resource overlap and size-dependent mortality were studied as functions of resource productivity. We found that the identity of the dominant species in our model system shifted between low and high productivity, but that the importance of varying productivity was dependent on mortality level. In addition, we show how population cycles driven by size-based competitive asymmetries may result in priority effects leading to alternative stable community states, including one-species states and a state where sprat and herring could coexist. To better understand how changes in major ecosystem drivers, such as resource productivity and mortality, influence community structure and dynamics in exploited marine fish communities we argue that accounting for size- and food-dependent development is necessary.

Introduction

A major factor governing population and community dynamics is size-dependent mortality, but the effects of size-dependent mortality in systems explicitly characterized by size variation among individuals in populations have rarely been focus of study. Still, competitive interactions fundamentally depend on body size, as body size scaling of foraging capacity strongly influences competitive ability (Persson *et al*. 1998). For predator–prey systems, the relative importance of competition and mortality in determining community patterns has been extensively explored (e.g. Bohannan and Lenski 2000). For pure competition systems, however, little is known about the importance of a mortality–productivity interaction for community structure. Here we aim to advance our understanding of factors governing the structure and stability of food webs with coexisting consumers exhibiting food-dependent growth by studying an example of competing zooplanktivorous fish, representing sprat and herring. We studied (1) the effects of resource overlap and the possibility of undergoing an ontogenetic diet shift on community structure as functions of resource productivity and (2) the significance of cyclic population dynamics driven by cohort interactions for different levels of size-dependent mortality as a mechanism causing alternative stable states (ASS) based on priority effects.

Materials and Methods

We used the framework of physiologically structured population models (PSPMs) (de Roos and Persson 2001), which distinguish individual (*i*), population (*p*), and environmental (*e*) states. The *i* state represents the state of the individuals in terms of a collection of physiological traits (e.g., body size), the *p* state is a frequency distribution over all the *i* states, and the *e* state describes, in our case, the current density of the different food resources. The PSPM analyzed describes the interaction between sprat and herring and their respective resources, including two zooplankton and one benthic prey. Resource densities decrease following consumption, which, in turn, decreases the amount of food available for other consumers. Consequently, we explicitly considered the feedback between individuals and their environment, leading to food-dependent individual growth as well as competition for resources. Our model represents a mixed continuous-discrete time system where growth, survival, consumption, and resource production are continuous processes but reproduction occurs as a discrete process. The model formulation consists of a mathematical description of how individual growth, survival, and reproduction depend on individual physiology and food densities. We investigated the asymptotic dynamics of the model by means of bifurcation analysis using long numerical integrations, in which we systematically varied one of the parameters of interest in small steps. To assess regions of different sprat–herring community states we identified the extinction and invasion boundaries (for details, see Huss et al. 2012).

Results and Discussion

The dynamics and growth patterns of sprat and herring were heavily dependent on the level of size-dependent mortality. Increased mortality on small individuals resulted in stabilized population dynamics. At low size-dependent mortality, both sprat and herring experienced cohort cycles in which a cohort of juvenile individuals dominates the population until they reach maturity, after which they produce the next dominant cohort.

Stable coexistence between sprat and herring could be accomplished by a compensatory balance between the smaller size at maturation of sprat and the capacity of herring to tolerate lower food levels. However, the likelihood of stable coexistence decreased as the intensity of interspecific competition increased. Whereas zooplankton productivity influenced community structure irrespective of the level of mortality, the influence of benthos productivity depended on size-dependent mortality. Herring only gained a competitive advantage by exploitation of a benthic resource when mortality and hence zooplankton density was high. Thus, one cannot by default assume that high benthos productivity favors herring over sprat.

Our results also show how endogenously driven population cycles resulting from interactions among size cohorts may lead to ASS in competition systems through priority effects. Several ASS were identified across a productivity gradient, including coexistence and one-species states. This suggests that reestablishment following extinction of one of the species could be difficult. The prerequisites for the type of ASS identified in our model were (1) populations exhibiting cohort-driven dynamics, (2) different maturation sizes for the two species (leading to variation in age at maturation and hence in cycle length), and (3) strong interspecific competition.

In light of our results, we argue that, to better be able to predict changes in community structure in exploited communities of competing fish, the roles of food-dependent growth and size-dependent interactions are crucial. Likewise, the advantages of an individual and size-based approach hold for studies of all ecological communities with species exhibiting complex life cycles.

References

Bohannan, B. J. M., and Lenski, R. E.. 2000. The relative importance of competition and predation varies with productivity in a model community. American Naturalist, 156:329–340.

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

Huss, M., Gårdmark, A., Van Leeuwen, A., and de Roos, A. M. 2012. Size and food-dependent growth drives patterns of competitive dominance along productivity gradients. Ecology, 93:847-857.

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