# Adaptive dynamics of size-structured populations: ontogenetic trade-offs and speciation in piscivorous fish

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The lectures and discussions at the IIASA workshop on Adaptive Speciation (December 1999) have motivated the writing of this research proposal, which has been jointly developed with Ulf Dieckmann, Project Coordinator of the IIASA Adaptive Dynamics Network, ensuring that the proposal is well integrated into ADN's research program.

## Background

There are several examples of sibling fish species that appear to have speciated by means of specialization on two different resources ('resource polymorphism'), e.g. in cichlids (Schliewen et al. 1994; D. Tautz, pers. com.), sticklebacks (Rundle et al., in press) and Arctic char (Skúlason and Smith 1995). In these cases, like in many other size-structured populations, resource use is strongly correlated to individual body size. One of the resources is a 'basic' resource that both specialists use when small, whereas the second resource is used more or less exclusively by only one specialist (the bigger one). Hence, the second 'specialist' is in fact an ontogenetic omnivore. Moreover, it is likely that their common ancestor was also capable of such ontogenetic omnivory.

### Population dynamics of piscivorous fish

In the first part of my PhD project I have studied the population dynamics of such an ontogenetic omnivore, focusing on the Eurasian perch (*Perca fluviatilis*). Small perch are mainly planktivorous but, as their size increases, they become increasingly piscivorous (Persson et al. in press). Together with André de Roos and Lennart Persson I developed a physiologically structured population model (PSPM) (Metz and Diekmann 1986, De Roos 1997) to study the impact of size-dependent competition and cannibalism on population dynamics (Claessen et al. 2000). The PSPM has been used successfully to predict population dynamics and individual development of perch. Moreover, this study offers a population dynamical (i.e. environmental, non-genetic) explanation for the occurrence of a frequently observed resource polymorphism. In populations of piscivorous fish often two distinguished life histories occur in a population: giant cannibals and planktivorous dwarfs (Smith and Skúlason 1995). Our study shows that this phenomenon emerges from size-structured population dynamics with size-dependent cannibalism and competition.

Here, I propose to extend this study by including evolution of an 'ontogenetic strategy'. Incorporation of this well-studied PSPM into the framework of adaptive dynamics will provide a sound, mechanistic platform to address questions of evolution in size-structured populations, such as the above mentioned examples.

### Ontogenetic trade-off and ontogenetic strategy

The required morphologies for efficiently capturing and processing different prey types, e.g. fish and zooplankton, differ. It is reasonable to assume that an individual cannot be maximally

adapted to feeding on both prey types simultaneously. Moreover, the ability to be piscivorous later in life imposes constraints on the efficiency of planktivory earlier in life (L. Persson, pers. comm.). In other words, there is an ontogenetic trade-off between piscivory and planktivory, that results from morphological constraints. The resource polymorphism in Arctic char illustrate that individuals may differ in their 'ontogenetic strategy'. The piscivorous morph is a worse planktivore early in life but a voracious piscivore when big, and vice versa for the planktivorous morph.

In the proposed research, an ontogenetic trade-off will be defined as a negative relation between the maximum planktivorous attack rate (at the optimal size for planktivory) and the maximum cannibalistic attack rate (at any given size). Thus two parameters in the original model will be parameterized as functions of an additional $i$-state variable, the ontogenetic strategy $z$. The value of $z \in [0, 1]$ is an index of developmental investment in morphological structure that increases the ability to capture and process fish prey. Thus $z = 0$ corresponds to the planktivorous specialist, and $z = 1$ to the piscivorous specialist. An intermediate $z$ obviously represents a generalist strategy.

## Research question and work plan

My question focuses on (1) the direction of evolution of the ontogenetic strategy, depending on the pattern of population dynamics, and (2) the role of developmental flexibility in the evolution of size-structured fish populations. Specifically, (2) addresses the question whether the possibility of a size-dimorphism given by population dynamics facilitates evolutionary branching.

($i$) The population dynamics in the possible strategy space will be explored, charting the regions with different population dynamical attractors. ($ii$) With standard methods from adaptive dynamics theory, the direction of the evolution of $z$ will be determined in these different regions in strategy space. To this end pairwise invasibility plots will be constructed. ($iii$) The potential of evolutionary branching will be investigated. In the neighborhood of evolutionary singular points I will study frequency-dependent selection on the strategy $z$, resulting from population dynamical feedbacks. ($iv$) Finally, the question will be addressed whether the size-dimorphism is a *substrate for* rather than a *result of* evolution.

During my March-May 2000 work visit with Lennart Persson, Umeå University, Sweden, I plan to make a start with the project. This will mainly concern the formulation of the ontogenetic trade-off based on empirical data and the above mentioned point ($i$).

## Relevance and link with ADN's research

In order to confront the theory of adaptive dynamics with empirical data one has to formulate testable hypotheses. A mechanistic way is to identify ecological factors that promote or inhibit evolutionary branching (Dieckmann and Doebeli 1999, and the Adaptive Dynamics workshop at IIASA). In order to do so, one has to be specific about the ecological processes in the studied system. The research proposed here is expected provide a platform for such a 'case study' to test the theory of adaptive dynamics. The PSPM for perch has been shown to correctly predict both qualitative and quantitative aspects of population dynamics of an empirical lake population (Claessen et al. 2000). Using this model, the proposed research hence potentially result in testable predictions regarding adaptive dynamics in this system.

Another interesting potential test case is provided by the suggested ongoing speciation process in Arctic char in some Icelandic lakes. The research group of Skúlason has provided evidence for a genetic basis of the resource polymorphism in certain lakes (e.g. Thingvallavatn).

Yet, on the same island there are also lakes where a size-dimorphism of piscivorous giants and planktivorous dwarfs occurs, yet without the genetic differentiation (S. Skúlason, pers. comm.). The hypothesis that the dimorphism may be induced by population dynamics is confirmed by preliminary results of the PSPM parameterized for Arctic char (Jens Andersson, unpublished results). The mechanistic approach of the proposed research may provide tools to identify the ecological factors or population dynamical patterns that promote adaptive speciation in one lake and inhibit it in another lake.

In general, an understanding of life-history adaptation in a physiologically structured population with environmental feedback extends classical life-history theory in a critical manner and is an important prerequisite for the analysis and management of many ecological systems. In this vein, the proposed research allows for applying, testing, and extending the required mathematical tools for this purpose in a well-specified ecological setting.

Finally, the research proposed here relates obviously to the research completed by last year's YSSP participant Janica Ylikarjula. Hence, this YSSP project continues and extends previous and ongoing research in the ADN project.

## Envisaged publication(s)

The proposed research is planned to result in at least one chapter in my PhD thesis. The evolution of an ontogenetic strategy in the above mentioned PSPM of perch will result in a jointly authored paper. Eventually, the case study of speciation in Arctic char, in collaboration with S. Skúlason, may lead to a second publication.

## References


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