Maturation Reaction Norm Evolution in Smallmouth Bass Populations

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Goal

To model and understand the evolution of maturation reaction norms in two recently diverged populations of smallmouth bass.

Background and motivation

Patterns of divergence in introduced populations derived from a common source can provide valuable insights into the processes that create life history variation and that drove the formation of new species. In general, rapid divergence of life history traits can occur in populations that are spatially segregated and evolve differentially in response to selective forces in the new environment. In particular, such divergence can occur when fish populations are introduced into novel environments. Such introductions are common, often mediated or caused by humans (Pimentel et al. 2000). Recent studies have observed life history evolution in grayling (*Thymallus thymallus*) populations separated for less than a century (Haugen 2000, Haugen and Vollestad 2000, Haugen and Vollestad 2001, Koskinen et al. 2002). Other studies have shown adaptive divergence of life history traits within at most 30 generations in newly colonized chinook salmon (*Oncorhynchus tshawytscha*) populations (Quinn et al. 2001) and within 30-60 generations in translocated guppy (*Poecilia reticulata*) populations (Reznick et al. 1990). These types of studies provide a rare and important glimpse at the processes creating widespread life history variation across populations and the natural evolution of new populations.

For the proposed project, the divergence of two smallmouth bass (*Micropterus dolomieu*) populations will be modeled. The two populations were introduced in the early 1900's, from the same source population (Orendorff 1983). Smallmouth bass are littoral predators that inhabit freshwater lakes throughout North America and elsewhere throughout the world. They are ecologically important predators that often shape littoral fish communities (Jackson 2002) and are an economically important sport fish. Our two study populations are from Provoking Lake and Opeongo Lake, located in Algonquin Provincial Park, Canada. Studies completed in the 1980's (Orendorff 1983) and more recently, revealed that the Provoking population had a high population density and extremely slow-growing adults, whereas the Opeongo population had a lower population density and faster-growing adults. The sizes and ages at maturation also differ between the populations. Therefore, although the populations had the same source, at the present time their growth and maturation differ substantially. Preliminary research suggests that low availability of large-sized prey has contributed to the slow growth rates of the Provoking Lake population. Research also suggests that the Provoking Lake population has higher adult mortality (possibly due to low food availability) and lower predation on young-of-the year (YOY) smallmouth bass (due to a lack of predatory species in the lake community) than the Opeongo Lake population. In the proposed study, a modeling approach will be used to determine if differences in YOY predation and adult mortality could have contributed to an evolutionary divergence between these populations.

Mortality has been shown to influence growth and maturation in several fish populations. In the experiments of Reznick and colleagues (i.e. Reznick et al. 1990) on guppies (*P. reticulata*), high ratios of adult to juvenile predation selected for younger ages and smaller sizes at maturation while high ratios of juvenile to adult predation selected for older ages and larger sizes at maturation. Thus, it is possible that differential mortality at particular life stages (i.e. YOY and adult stages) in the Provoking and Opeongo smallmouth bass populations has contributed to the divergence in growth and maturation.

One method of characterizing the growth and maturation of a population is through its maturation reaction norm. Growth rates can vary plastically in response to environmental conditions. The sizes and ages at maturation are not independent of each other and are bound to vary with growth rates in a plastic way. This range of growth rates and the subsequent range in size and age at maturation within a population determine its observable maturation reaction norm (Stearns and Koella 1986). In general, a reaction norm characterizes the phenotypes that a particular genotype expresses across a range of environmental conditions (Stearns and Koella 1986). The maturation reaction norm of a genotype or population is defined by the probabilities of becoming mature in the next season as a function of an individual's age and size. Across populations, or within populations through time, differences in the sizes and ages at maturation that are associated with differences in growth, may represent plastic responses to the environment because they follow the same reaction norm (Stearns and Koella 1986). Interpreting variation in age and size at maturity as a plastic response is justified if the underlying variation in growth rates is mainly environmentally determined (Heino et al. 2002). In addition, selection may act on the ages and sizes at maturation and cause the reaction norm of a population to shift away from its original position (Heino et al. 2002, Stearns and Koella 1986) or to change its shape (Haugen 2000).

There are a few interesting examples of how selection can influence the shape or position of maturation reaction norms. In a study on arctic grayling (*T. thymallus*) populations, as harvest mortality on adults increased, age at maturation became less plastic and the maturation reaction norm became more vertical (Haugen 2000). In a different study on North Sea plaice (*Pleuronectes platessa*), the maturation reaction norm shifted to smaller sizes at maturation in response to selective harvest (Grift et al. 2003). In both cases, changes in the position and shape of the maturation reaction norm suggested that changes in age and size at maturation were genetically determined, and not merely plastic responses to variations in growth rates. Estimating maturation reaction norms can therefore help disentangle the plastic effects of growth on the age and size at maturation from any genetic changes that may occur in the age and size at maturation as a result of reaction norm evolution (Heino et al. 2002). From a management perspective, it is important to determine if changes over time in a population are genetic adaptations or plastically based, as genetic changes are more difficult to reverse. Modeling maturation reaction norm dynamics in the Provoking and Opeongo smallmouth bass populations should provide insight into the relative contribution of phenotypic plasticity and genetic adaptation to the observed divergence of life history traits.

Previous models of maturation reaction norm evolution have employed deterministic continuum dynamics at the population level (e.g. Ernande et al. 2004). This was justified because population abundances of the species modeled were large. Population abundances of smallmouth bass populations are considerably smaller than those of the commercial marine species modeled previously, motivating the use of individual-based models for this study system. Individual-based models are being used more frequently as they allow an intuitive approach for merging genetics and demography (i.e. Chambers 1993, Jager 2001). Using an individual-based model in this study will provide a powerful approach to modeling maturation reaction norm dynamics in the Provoking and Opeongo smallmouth bass populations.

Research questions

For the proposed study, I plan on constructing a model to predict how variations in YOY and adult mortality between populations are expected to influence their maturation reaction norms. For this purpose, I will be modeling maturation reaction norm evolution under different levels (i.e. low, moderate, and high levels) of mortality on either YOY or adult smallmouth bass. This work will provide clues as to, (1) the possible cause of life history divergence between smallmouth bass populations, (2) how fish community composition influences introduction/invasion dynamics of populations, and (3) the speed at which evolution occurs in freshwater sport fish populations.

Methods and work plan

I will construct an individual-based simulation model to predict maturation reaction norm evolution in response to selective forces in the environment of newly introduced populations. I will be using data collected on the Provoking and Opeongo Lake smallmouth bass populations to parameterize the model. Such data will come from an annual angler survey that has been conducted on Opeongo Lake since the 1930's (Shuter et al. 1987) and from detailed studies of growth and maturation conducted recently on both populations.

The model will incorporate the following components. The bi-phasic somatic growth model proposed by Lester et al. (2004) will be used to simulate growth. Growth will be linear before maturation and follow the Von Bertalanffy growth model after maturation. The reduction of adult growth rates relative to juvenile growth rates will represent reproductive investment (following an approach similar to that of Roff 1983). A density-dependent growth function will be used to define the empirical function between growth and population abundance (based on empirical data). Growth will be limited for adults in the Provoking population to mimic the absence of large-sized prey in the diet. Density-dependent natural mortality will also be incorporated into the model. Maturation reaction norms will be linear with a constant envelope and modeled with an evolving intercept and slope. To simulate introduction, individuals in the founding population will be yearlings with a pre-determined body size (based on the empirical body size distribution of yearlings). Simulations will run on a discrete, one-year time step for approximately 100 years with maturation, reproduction, growth, and death occurring annually. Predation on YOY bass and adult mortality will be manipulated to determine their influence on maturation reaction norm dynamics. Different scenarios (i.e. low, medium, and high level of YOY/adult mortality) will be simulated to mimic introduction into Provoking and Opeongo Lakes. Increased complexity (i.e. dynamic maturation envelope, non-linear maturation reaction norm, dynamic growth reduction after maturation) will be added to the model as time permits.

Relevance and link to ADN's research plan

This project models dynamics of maturation reaction norms in populations of a freshwater sport fish and is thus directly linked to ADN's research focus on Fisheries-Induced Adaptive Change.

Expected output and publications

This work will be included in my PhD thesis and is intended for publication as a co-authored research article.

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