

Probabilistic maturation reaction norms of sockeye salmon spawning populations of Bristol Bay, Alaska

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Goal

To estimate probabilistic maturation reaction norms (PMRNs) for length and age at maturation of locally adapted sockeye salmon spawning populations of the Wood River system, Bristol Bay, Alaska.

Background and motivation

Humans can influence life history traits of domesticated and wild animals through selective processes. Fishing is often deliberately size-selective for economic and biological reasons (Walters and Martell 2004). Size-selective fishing mortality is often associated with directional selection and changes in life history traits such as age and size at maturity (Law and Grey 1989, Policansky 1991). Short term and sustainable fishery yields can fluctuate due to life history evolution in harvested populations. Therefore, the evolution of age and size at maturity, phenotypic traits associated with yield, are of particular interest when assessing the effects of fishery selectivity (Law 1979, 2000).

While it is undeniable that age and size at maturity are shaped by environmental factors (Bigler et al. 1996, Pyper and Peterman 1999), numerous studies on wild and experimental fish populations have demonstrated that size-selective exploitation can affect these life history traits (Ricker 1981, 1995, Conover and Munch 2002, Walsh 2003, Olsen et al. 2004, Munch et al. 2005). Still, the selective effects of fishing and phenotypic changes it can cause have not been considered a great deal in fisheries management (Hamon et al. 2000, Law 2000). Specifically, less research has been conducted on evolutionary and fishery management implications of size-selective harvest for semelparous species.

Quantitative genetics and reaction norms are used to analyze the phenotypic and genetic variation that conditions the response to selection (Stearns 1992). Norms of reaction show the ranges of potential phenotypes, such as different ages and sizes at maturity, that a given genotype could develop if an individual is exposed to different environmental conditions (Stearns and Koella 1986). The probabilistic maturation reaction norm of a genotype or population describes the phenotypic maturation schedule of individuals, stocks, or species and is defined by the probabilities of becoming mature in the next season as a function of an individual's size and age. Across populations or within populations across time, differences in age and size at maturity associated with variation in growth and mortality may represent plastic responses to the environment if they follow the same reaction norm. Variation in age and size at maturity can be interpreted as a plastic response if the variability in growth rates is mainly due to environmental determinants (Heino et al. 2002a, Heino et al. 2002b, Hutchings 2004). Selection, due to many causes, may act on age and size at maturation and cause the reaction norm of an individual or population to shift in position (Stearns and Koella 1986, Heino et al. 2002b) or change shape (Haugen 2000).

It is important to characterize the maturation reaction norms in various populations. With this information, one can better understand variability in phenotypic traits, such as age and size at maturity, between populations of a given species that exhibit life history differences. Research has shown that in some cases human-induced selection, for example due to fishing, can change the shape or position of maturation reaction norms. A study on northern cod, which were heavily harvested in the 1970s and 80s and who suffered major stock collapses in the early 1990s, is a prime example of this. As harvest mortality on female northern cod increased throughout the 1980s and early 90s, the maturation reaction norm shifted continually toward smaller sizes and younger ages (Olsen et al. 2004). Research has also shown that even with low fishing pressure on Newfoundland stocks of American plaice, their maturation reaction norms have shifted towards maturation at younger age and smaller sizes (Barot et al. 2005). In these examples, and in others, alterations of the maturation reaction norms suggest that changes in age and size at maturation resulted not only from phenotypic plasticity due to variations in growth rate but from underlying genetic, and thus evolutionary, changes. Maturation reaction norms may help to disentangle phenotypic plasticity associated with different growth and mortality conditions from genetic effects that influence maturation as a result of reaction norm evolution (Heino et al. 2002a, Heino et al. 2002b). Thus, they may reveal changes in maturation schedules associated with size-selective fishing. From a management perspective, it is important to understand if life history trait changes over time, specifically in age and size at maturity, are genetic changes or plastic phenotypic responses (Morita et al. 2005), as genetic changes may have more long-term consequences.

While PMRNs have been developed for a number of iteroparous fish species, little work has been done understanding reaction norms for semelparous species, such as Pacific salmon. Bristol Bay, Alaska has some of the most diverse and abundant sockeye salmon (*Oncorhynchus nerka*) populations in the world. The Wood River system of the Nushagak fishing district is home to dozens of genetically and ecologically distinct sockeye spawning populations. Spawning sites include streams, rivers, and beaches, and fish are locally adapted to their site. We possess a great deal of data on life history traits of individual spawning populations so can examine if these populations differ in their PMRNs. An economically important commercial gillnet fishery has exerted strong, size-selective fishing pressure on these salmon since 1884. Fishery catch and escapement data and spawning ground data on age and size at maturity have been collected yearly since 1946. Additionally, the management of the Bristol Bay sockeye salmon fishery has varied over time but has been well documented (Link et al. 2003, Hilborn 2006).

Research questions

For this proposed study, I plan to calculate PMRNs for age and size at maturation of different Wood River system sockeye salmon spawning populations from the 1960s through the present. With these PMRNs, in the future I can understand changes in life history traits over time and will evaluate if the fishery selection has the potential to cause life history evolution. I can also use the reaction norms to later create an eco-genetic model of the effects of different size-selective harvest regimes.

Methods and work plan

To calculate PMRNs, I will use data collected on the Nushagak district and Wood River spawning ground sockeye salmon populations. Daily counts of the numbers of salmon caught in the Nushagak district and escaping into the 3 main freshwater sys-

tems are available yearly since 1946. In addition, age, sex, and length measurements from samples of the catch and escapement have been taken yearly. Count, age, sex, and length data from many of the spawning populations of sockeye salmon within the Wood River system are available during many, though not all, years since the 1940s. Finally, we have a great deal of information on past fishery management practices over time (Link et al. 2003, Hilborn 2006).

To calculate PMRNs of age and size at maturation for the spawning populations within the Wood River system, I will use the methods described by Heino et al. (2002a, 2002b) and Morita et al. (2005). Approximately 10 spawning populations, from the three main habitat types (streams, rivers, and beaches), with long-term data available, and with consistently large population sizes, will be chosen for assessment. Because semelparous species spawn only once before their death, it is easy to determine first-time spawners. We also have age and size data from yearly time intervals, consistent with the methods described by Heino et al. (2002a, 2002b).

In the Wood River system, juvenile sockeye salmon from all spawning populations rear for 1-2 years in 4 main nursery lakes. Environmental conditions are similar in these lakes (Burgner et al. 1969). Little is known about growth of fish from the different spawning populations, as genetic or other markers have not been developed to identify individual fish or populations. Thus, growth and mortality conditions are assumed to be similar for fish from all populations. After completion of rearing in the nursery lakes, sockeye migrate to the ocean, where they put on 99% of their body weight. In this stage little if anything is known about different growth and mortality conditions of fish from different spawning populations, so the same growth and mortality conditions will also be assumed for all fish. After completion of their ocean growth phase, sockeye salmon home to where they were born to spawn and die. As they are migrating back into freshwater, Bristol Bay sockeye are exposed to a heavy commercial gillnet fishery, which takes up to 80% of the run. This fishery is size-selective, and imposes greater mortality on some individual fish and populations due to their size. For example, large fish spawning in rivers and beaches may be more heavily exploited during some years than are small fish who can escape through the gillnets (Kendall et al. in prep.). Therefore, adult mortality of the different sockeye spawning populations can differ at this point.

To determine PMRNs, representative samples of both maturing and immature fish are required (Heino et al. 2002b). Because we only sample mature sockeye salmon that are returning to the Wood River system to spawn, we must reconstruct unobserved size distributions of immature fish. With our present data, we can calculate length- and age-based maturity ogives for the different Wood River sockeye spawning populations. The reconstruction procedure is outlined by Heino et al. (2002b) and includes one initialization step followed by a cycle of three steps. This reconstruction method requires the assumption of a growth model for immature fish. In this study a length-linear juvenile growth model will be used.

Another way to reconstruct the fork length of immature fish is that described by Morita et al. (2005), which uses a back-calculation method based on otolith measurements using a biological intercept method (Campana 1990). Otoliths are currently being measured from two Wood River spawning populations, and hopefully more populations and those from additional years will be examined in the near future. This data will also help to corroborate the findings of the growth model used to reconstruct immature sockeye lengths at age. Morita et al. (2005) describe a similar way to that of Heino et al. (2002b) to calculate the probability of a fish maturing. They used their results to examine the rule of age and size at maturity.

Given the mature and the immature reconstructed length at age data and maturity ogives for the Wood River system, PMRNs for length and age at maturation will be calculated.

Relevance and link to EEP's research plan

This research will estimate PMRNs for locally adapted populations of a major commercial fish and thus falls under EEP's research focus on evolutionary fisheries management. My research project will also expand the scope of EEP's research to fish of the Pacific Ocean and with a semelparous life history, and set up the opportunity to create an eco-genetic model for these fish.

Expected output and publications

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

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