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Rapid Adaptation to a New Environment: Is it Reversible?

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Abstract

Accumulating evidence suggests rapid adaptation of fish populations when they are exposed to artificial hatchery environments. However, little is known if rapidly-adapted populations can readapt to their original, natural environment at the same rate. Here, I review recent studies on salmonid fish that address this issue. They indeed suggest rapid adaptation of hatchery populations, in which reproductive fitness under a natural environment became much lower than that in the wild population after only 1-2 generations of captive breeding. However, the reproductive fitness did not recover after one generation of natural rearing, implying that rapid adaptation to a new environment was not reversible at the same rate. I discuss potential consequences of the irreversible fitness reduction in extensively stocked fish species. Understanding the mechanism behind the irreversible rapid adaptation in fish populations will help us figure out a better, nature-friendly, and hence sustainable means of hatchery operations for human welfare.

Keywords: fish stocking, hatchery, rapid adaptation, reproductive fitness, salmonid species

Introduction

While fish has been recognized as our most important food resource long since ancient days, we keep in captivity, many fish species for personal and public viewing to ultimately enjoy their biodiversity. For example, fish catches have been around 90 million tons since 1990s, and aquaculture production has reached 60 million tons in 2011 (FAO, 2012). More than 80% of them were sold in fish markets and utilized for human consumption. While aquaculture has been developing rapidly, there is no other industry that depends so much on 'natural' resources at the moment. In addition, we have more than 400 public aquariums worldwide, and c.a. 500 thousands of people visit them each year in Japan alone. On the one hand, they make us very familiar with fish species. On the other hand, wild fish populations often became overexploited, vulnerable to environmental disturbances, and endangered worldwide. Despite the popularity of the fish species, however, our knowledge on ecology and evolution of fish in the wild is very limited. Efficient means of conservation and sustainable management of wild fish stock is yet to be established.

Salmonid species are one of such species. Although they are recognized as economically and socially important species, ecology of salmonid species in the wild is largely uncertain. In this review, I briefly summarize our knowledge on the ecology and adaptive capability of salmonid species, followed by an introduction of related information from my own research and that of my colleagues. It is hoped that this review would contribute to broad discussions on better, sustainable uses of fish for our future generations.

Ecology of salmonid species

Salmonid species are often characterized by their nature of large-scale migration and of homing behavior (Quinn, 2005). However, their life histories are very diverse among individuals, populations and species (Groot and Margolis, 1991). In brief, they are born in cold freshwater, typically in 4-10°C. After a few months from hatching, some already start their migration. Majority of Pacific salmonids, for example, have short freshwater residence as juvenile, whereas rainbow trout (*Oncorhynchus mykiss*, also a part of Pacific salmonids) and the other 'trout' species can live their whole life in freshwater. In fact, some species have multiple life history forms, typically male-biased. O. mykiss is one of them, and its sea-run form is called steelhead. Brown trout (*Salmo trutta* L.), one of the two species in Atlantic salmonids, also has a sea-run form called sea trout. Just like other salmonid species, they grow fast in the ocean and come back to their natal rivers for reproduction. The basis of their life history differentiation is still unclear, although it is most likely determined through genetic-environmental interactions.

Ocean migration takes one to a few years. Pink salmon (*O. gorbuscha*) is unique in this context because they have a strict two-year life cycle. Salmon migration range covers whole of the North Pacific for Pacific salmonid species and a northern part of the Atlantic Ocean for Atlantic salmon (*S. salar*). The time for salmon runs to the river for reproduction varies among species and among populations in the same species. If any, resident fish can spawn together with sea-run fish in the same spawning ground. Resident males often use 'sneaking' behavior for their reproductive success with sea-run females. This is part of the reasons why multiple paternity is common in salmonid species. Although majority of salmonid fish die after the first spawning, trout species and a few sea-run species can repeat the migration and reproduce multiple times in their life (e.g., Atlantic salmon).

Rapid adaptation to hatchery environments and its downside

Due to an increasing demand for salmonid species as a food resource, hatchery and domestication programs have been very popular worldwide. Hatcheries and programs were first established in the late 19th century. The rearing technique has been developed and improved for many species, most notably for Atlantic salmon. Together with developments in refrigerated cargo transportation systems, full-life cycle aquaculture enabled us to find this species in fish markets worldwide today. For majority of sea-run Pacific salmonid species however, full-life cycle aquaculture system is either not established yet or unrealistic due to economic reasons. This is why we still depend heavily on fish stocking for salmonid species, which utilizes hatcheries for juvenile development from fertilization to parr or fingerling, typically for <1 year, and releases juveniles into the wild with a hope for their successful return as adults.

One question is whether the hatchery-born fish can survive well in the wild and return to the point of release so that fisheries can gain from the hatchery fish stocking. Even more profound question is then whether adults that have returned (but not caught) can spawn naturally and reproduce successful progenies. Both questions are important but the latter one is even more critical for conservation and self-sustainable stock management. To answer this question, we used molecular genetic markers to identify individuals and the pedigree of steelhead *Oncorhynchus mykiss* in the Hood River, Oregon, USA (Araki *et al.*, 2007a, 2007b). The DNA-based parentage assignment method, together with highly polymorphic genetic markers (called 'microsatellite'), provided a powerful means of identifying parent(s)-offspring pairs in the field samples of >15,000 returning adults. We found that 'old' hatchery stock performed poor in the system, suggesting only 10-30% of successful natural reproduction compared with wild-born fish that spawned in the same river in the same year (Araki *et al.,* 2007a). The 'old' hatchery stock might have suffered, having come from a non-local origin and from multi-generation captive rearing with the surviving stock becoming forcibly adapted to the artificial rearing environment. The first generation of 'new' hatchery stock, which was designed for conservation, performed much better. Nevertheless, they still showed significantly lower reproductive success than wild fish in the wild (Araki *et al.,* 2007a). On average, the relative reproductive success of the first generation was 0.848, suggesting that they reproduced 15% less than their wild counterpart in the river. The most interesting part of the study was on the second generation of the 'new' hatchery stock – those who had a returning hatchery-born parent and they themselves were also reared in a hatchery. Their relative reproductive success to their wild counterpart was on average 0.379, which was rather close to that of the 'old' stock above (Araki *et al.*, 2007b). Together with other studies on reproductive fitness of hatchery-born salmonids, we concluded that c.a. 38% of natural reproductive fitness can be lost per captive-reared generation. This result suggests rapid adaptation of fish to the new, artificial environment coinciding with maladaptation to the original, natural environment once they are released (see also Christie *et al.*, 2012).

How general is it? Currently, there are a limited number of comparable studies, and they are all on salmonid species (Araki *et al.*, 2008). The reduced reproductive fitness of hatchery-reared fish was also suggested in Chinook salmon (*O. tshawytscha*) and coho salmon (*O. kisutch*) (Williamson *et al.*, 2010; Thériault *et al.*, 2011 but see also Hess *et al.*, 2012). In addition, there is little evidence for hatchery fish releases helping local wild stock enhancement, together with a few exceptions as a hope for better fish stock management (Araki and Schmid, 2010).

Re-adaptation to the original environment?

The next question is whether offspring of the hatchery-born yet naturally-spawned fish can reproduce well in the wild. Note that the offspring themselves are born, reared and reproduced in the wild. Therefore, if they can re-adapt to their original environment at the same rate as their adaptation rate to the captive environment, we can expect a rapid recovery of reproductive fitness. However, this was not the case for the Hood River steelhead, where we found the rapid decline of reproductive fitness of hatchery-born fish in the wild (Araki *et al.*, 2009). Among wild-born offspring of hatchery-born parent, fish from two hatchery-born parents had the lowest reproductive fitness. On average, they had 63% lower reproductive success than that of fish from two wild-born parents. Reproductive success of fish from a hatchery-born parent and a wild-born parent was intermediate (on average 13% lower), but the estimate was not significantly different from that of two wild-born parents. These results indicate that even after stopping the fish stocking, remaining wild populations can still suffer from the carry-over effect of past fish stocking (also known as "genetic pollution"). Indeed, we estimated that eight percent of the wild population might have been lost due to the carry-over effect in the case above (Araki *et al.*, 2009). This value strongly depends on the proportion of offspring from two hatchery-born parents, and hence it is most likely sensitive to the amount of fish stocking. If 50% of the mature fish were hatchery-born fish in the wild, for instance, loss of the wild population in the next generation due to the carry-over effect could be >20% in the case above.

Conclusion: For better stock management

We have seen that reproductive fitness of hatchery-born fish reduces very rapidly and that they are suffering from the reduced fitness after being stocked in the wild. And it is likely that this process is not reversible at the same rate. However, there are many questions left. Firstly, it is not entirely clear why reproductive fitness can be reduced so rapidly in captive environment but not in natural environment. The most likely reason is very strong domestication selection reducing not only the reproductive fitness but also genetic variations in the loci under selection. Once the genetic variation is lost from the population, the selection potential for re-adaptation to natural environment will also be lost. In fact, reduction of neutral genetic variation in hatchery stocks has been reported in many species, suggesting small selection potential left for these stocks (Araki and Schmid, 2010). Most importantly, however, we should identify the trait under domestication selection first because neutral genetic variation does not necessarily reflect the selection potential for re-adaptation to the original environment. This is one of the main reasons why genomic study becomes increasingly important for fishery science. Secondly, we do not know the consequences of coexistence of wild-born and hatchery-born individuals in the wild very well. Theoretical predictions suggest that stocking of hatchery fish with maladapted genetic background can have serious demographic consequences when they interbreed with their wild counterparts (Ford, 2002; Lorenzen, 2008). Using a modeling approach, Satake and Araki (2012) also suggested that intermediate levels of hatchery fish stocking can cause not only reduction in population size in the long term but also local gene pool replacement. But empirical evidence for linking hatchery fish stocking and its outcome in the status of wild stock is scarce at best. Lastly but not least importantly, social responses to the fishery activities are not well documented and predicted. We should bring and keep politicians, stakeholders and local societies in the discussions over the better stock management, so that the risk and potential advantages of fish stocking can be shared among them. It is eventually them who decide what kinds of fish and fisheries should be accepted in the societies, and we are responsible for informing them to find the best solution.

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