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Special Issue: Evolutionary perspectives on salmonid conservation and management

Robin Waples
NOAA, robin.waples@noaa.gov

Andrew P. Hendry
McGill University, andrew.hendry@mcgill.ca

EDITORIAL

Special Issue: Evolutionary perspectives on salmonid conservation and management

Robin S. Waples[1]* and Andrew P. Hendry[2]*

1 National Marine Fisheries Service, Northwest Fisheries Science Center, Seattle, WA, USA
2 Redpath Museum & Department of Biology, McGill University, Montreal, QC, Canada
* Guest editors

Abstract

This special issue of Evolutionary Applications comprises 15 papers that illustrate how evolutionary principles can inform the conservation and management of salmonid fishes. Several papers address the past evolutionary history of salmonids to gain insights into their likely plastic and genetic responses to future environmental change. The remaining papers consider potential evolutionary responses to climate warming, biological invasions, artificial propagation, habitat alteration, and harvesting. All of these papers consider how such influences might alter selective regimes, which should then favour plastic or genetic responses. Some of the papers then go on to document such responses, at least some of which are genetically based and adaptive. Despite the different approaches and target species, all of the papers argue for the importance of evolutionary considerations in the conservation and management of salmonids.

Introduction

Conservation and management tend to emphasize immediate demographic concerns, such as reversing population declines or maximizing productivity. These concerns have long been addressed by reference to ecological processes, but recent work has increasingly pointed to the additional importance of considering evolutionary processes. From the standpoint of conservation, adaptation might influence the collapse and recovery of populations experiencing environmental change (Bürger and Lynch 1995; Gomulkiewicz and Holt 1995; Stockwell et al. 2003; Ferrière et al. 2004; Kinnison and Hairston 2007; Carroll and Fox 2008). From the standpoint of management, evolutionary responses can influence population productivity and therefore change harvest yield (Conover and Munch 2002; Olsen et al. 2004; de Roos et al. 2006; Hutchings and Fraser 2008). In both general contexts, it is therefore important to understand how populations might evolve in response to environmental change, and how these responses might then feedback on population persistence and productivity.

What is known at present is that many species experiencing environmental change also exhibit adaptive phenotypic responses, at least some of which are genetically based (Hendry and Kinnison 1999; Reznick and Ghalambor 2001; Stockwell et al. 2003; Hairston et al. 2005). Many of these responses appear driven by direct or indirect effects that humans are having on populations or their environments. For example, adaptive phenotypic changes have often been documented in response to climate change (reviews: Bradshaw and Holzapfel 2008; Gienapp et al. 2008), exploitation (review: Hutchings and Fraser 2008), and biological invasions (reviews: Cox 2004; Carroll 2008). One taxon sensitive to all these perturbations, and many others, is salmonid fishes, which are also of considerable recreational, cultural, ecological, and commercial importance. It thus seems important to focus the light of evolution on their conservation and management.

Salmonids

Native salmonids, particularly anadromous Pacific salmon (*Oncorhynchus* spp.) and Atlantic salmon (*Salmo salar*), have been extirpated or are at risk throughout much of their native range (Nehlsen et al. 1991; Parrish et al. 1998). For example, a recent study estimated that 30% of the historic populations of Pacific salmon and steelhead in the contiguous United States have been lost, and about half of those that remain are listed under the US

Endangered Species Act (Gustafson et al. 2007). The deteriorating status of wild populations has triggered similar conservation concerns in Canada (Irvine et al. 2005), Europe (Hindar 2004), and Japan (Kaeriyama and Edpalina 2004). More generally, anadromous fishes face unusually high risks of extinction worldwide (Jonsson et al. 1999).

Extirpations and declines of salmonids are often associated with major anthropogenic influences. In particular, considerable effort has been expended in understanding effects of the 'four Hs': habitat, harvest, hatcheries, and hydropower (McClure et al. 2003). Most of this research effort has focused on how the 4 Hs influence survival, mortality, and population growth rate (e.g. Kareiva et al. 2000; McClure et al. 2003), thus casting anthropogenic influences as an ecological problem. At the same time, however, virtually every anthropogenic change that affects these key ecological and demographic parameters can also have evolutionary consequences (Stockwell et al. 2003). At present, however, the only two Hs to have received much attention from an evolutionary perspective are hatcheries (e.g. Hindar et al. 1991; Waples 1999; Ford 2002) and harvesting (e.g. Ricker 1981; Hard 2004; Fig. 1).

The other two Hs (habitat and hydropower), as well as other perturbations (e.g. climate change and biological invasions), are likely to also have evolutionary consequences. For example, Quinn and Adams (1996) showed that warming water owing to dams in the Columbia River has led to earlier migration times for sockeye salmon, although the genetic basis for this change is not known. Other work has examined phenotypic and genetic changes when salmon are introduced into, or naturally colonize, new habitats. As one example, sockeye salmon introduced into Lake Washington founded several populations that

Figure 1 Gillnet fisheries, such as this one for sockeye salmon in Bristol Bay, AK, are size-selective, which can lead to evolutionary changes in size and age at maturity. Photo by Andrew P. Hendry.

diverged in juvenile development and adult morphology (Hendry et al. 2000; Hendry 2001). As another example, chinook salmon introduced into New Zealand founded several populations that diverged in these same traits, as well as in reproductive allocation and spawning time (Kinnison et al. 2001, 2003; Quinn et al. 2001). This New Zealand work is particularly informative because it has confirmed the action of selection, the genetic basis for evolutionary divergence, and the consequences for survival and reproductive success (Kinnison et al. 2001, 2003, 2008). In short, phenotypic responses to environmental change have been found wherever one has looked for them.

This special issue

The motivation for the present special issue came from two international meetings. The first, held in December 2006 in Seattle, WA, was a symposium and workshop entitled 'Evolutionary changes and salmon: consequences of anthropogenic changes for the long-term viability of Pacific salmon and steelhead' (http://www.nwfsc.noaa.gov/events/workshops/index.cfm). This meeting brought together salmon biologists and evolutionary biologists to focus on salmon datasets amenable to evolutionary analysis. The second meeting, held February 2007 in Los Angeles, CA, was an international summit entitled 'Evolutionary change in human-altered environments' (http://www.ioe.ucla.edu/cTR/ioesymposium.html). This meeting focused on similar issues to the first, but with a broader geographic and taxonomic range. Many papers from the Los Angeles meeting have now been published (Smith and Bernatchez 2008), and these have stimulated valuable discussions about how evolution is important in conservation and management. Our hope is that the present special issue will have a similar impact with respect to salmonids. We therefore invited contributions from participants in the original Seattle meeting, as well as from other biologists working on related topics. The resulting papers cover multiple salmonid species (chum salmon, chinook salmon, sockeye salmon, brook charr, brown trout, and rainbow trout), examine multiple anthropogenic impacts (climate change, hatcheries, habitat alteration, hydropower, selective harvesting), and employ multiple analytical approaches (reviews, syntheses, mathematical models, empirical analyses). The following paragraphs provide a brief overview of these contributions.

Past evolutionary history will influence future evolutionary trajectories, an issue taken up in several papers. Carlson and Seamons (2008) review genetic variation for phenotypic traits in salmonids – because this variation will be critical to their evolutionary potential. The authors report a broad range of heritabilities and genetic

correlations, thus highlighting the need for population/trait-specific estimates. Einum et al. (2008) consider how density-dependence shapes adaptive landscapes experienced by salmonid populations. They present evidence that reduced densities owing to anthropogenic disturbances will dramatically alter the nature and intensity of selection. Waples et al. (2008) describe a complex history of environmental changes that have shaped the genetic diversity of Pacific Salmon, including chinook salmon in Puget Sound and the Columbia River. These dynamic processes have structured this species into regionally/temporally distinct lineages with particular life history characteristics. Wood et al. (2008) perform a similar analysis for sockeye salmon but find a different pattern: large differences among populations of the lake ecotype (even at small spatial scales) but small differences among populations of the sea/river ecotype (even at large spatial scales). These contrasting outcomes for chinook salmon versus sockeye salmon highlight the need for species-specific evaluations of how evolutionary history shapes conservation concerns and future evolutionary potential.

Climate warming is an emerging concern for salmon (e.g. Battin et al. 2007), just as it is for other species (Thomas et al. 2004; Malcolm et al. 2006) Crozier et al. (2008) consider potential responses to climate warming in the suite of traits that characterize some Columbia River populations. They emphasize the complicated interplay between plastic and genetic responses that play out across multiple life history stages. Williams et al. (2008) show how warmer conditions for chinook salmon juveniles associated with hydropower development in the Columbia River have caused a shift in the age at which smolts migrate. The magnitude of this shift raises the crucial question of what will happen to selection, evolution, and fitness when the dams are ultimately removed? Angilletta et al. (2008) estimate the fitness consequences of warming water in relation to the temperature sensitivity of juvenile salmonid performance. The authors argue that temperature changes associated with dams are unlikely to directly threaten most population, but that they might well exacerbate other impacts.

Habitat loss has been one of the greatest contributors to population extirpations in salmonids (Nehlsen et al. 1991; Parrish et al. 1998) and other species (Hughes et al. 1997; Brooks et al. 2002). Habitat loss will also have evolutionary consequences, as will any habitat gains through remediation or improved access. McClure et al. (2008a) consider the disappearance of formerly productive habitats owing to dams or other blockages to migration. A result is the differential elimination of certain habitat types (e.g. higher level tributaries), which reduces biocomplexity and future adaptive potential. Haugen et al. (2008) analyze the reverse situation, where a new

fish ladder eased the upstream migration of brown trout. This increased accessibility changed selection from directional (disfavouring small fish) to stabilizing (disfavouring both large and small fish), which then caused the apparent evolution of smaller and less variable body sizes.

Biological invasions are a major ecological and evolutionary concern throughout the world (Mooney et al. 2005; Sax et al. 2005). Salmon are often the culprits, having been introduced to many locations around the world where they now have strong ecological effects. Miller and Vincent (2008) describe the reverse situation – where a native salmonid has recently come under selection from an introduced organism. Over the decade since first detection of whirling disease, wild native trout have substantially improved their ability to resist the disease's effects. Another sort of biological invasion occurs at the level of genes, rather than species (Saltonstall 2002). For example, genes from hatchery stocks that invade wild populations might decrease local adaptation. Araki et al. (2008) review data on how genetic changes in hatchery fish can dramatically reduce their success in the wild – after only a few generations. They argue that the rapidity of these fitness declines points to the evolution of multiple traits throughout the life cycle. McClure et al. (2008b) further review the evolutionary impacts of hatchery propagation, and argue that its use as a conservation measure should be decided on a case-by-case basis. In general, however, they recommend that artificial propagation should only be used as a last resort – because it invariably reduces fitness in the wild.

Harvesting is a potential selective force on the life history and behaviour of many fish species (Hutchings and Fraser 2008), including salmon (Ricker 1981; Hard 2004). Fukuwaka and Morita (2008) show how size-selective gillnets in high seas fisheries for Japanese chum salmon led to the evolution of a smaller size at maturity. Cessation of this fishery then lead to the evolution of larger size at maturity, a recovery from harvesting that seems to have eluded other species (Olsen et al. 2004; de Roos et al. 2006). Hard et al. (2008) review multiple studies of harvested salmon and confirm that age and size at maturity do frequently decline. They point out, however, that few studies have been able to conclusively disentangle genetic and environmental effects, or to confirm that the change is indeed the result of harvest selection. Thériault et al. (2008) extend the consideration of harvesting effects to a new trait: the probability of migration. They show that increased fishing, in this case recreational, on the migratory portion of a population should lead to reduced migration, and that this change can negatively influence population productivity.

Conclusion

Research on salmonids has contributed heavily to the emerging perspective that human-caused environmental change leads to contemporary phenotypic changes that can be adaptive and genetically based (Hendry and Kinnison 1999; Reznick and Ghalambor 2001; Stockwell et al. 2003; Hairston et al. 2005; Hendry et al. 2008). These phenotypic changes might enhance individual fitness and perhaps also population productivity and persistence (Bürger and Lynch 1995; Gomulkiewicz and Holt 1995; Kinnison and Hairston 2007; Kinnison et al. 2008). The present volume amplifies these intuitions by showing how human influences on salmon populations and their habitats can alter selection and lead to phenotypic change. At the same time, ambiguity often remains as to the genetic versus plastic basis for observed phenotypic changes, as well as to the relationship between phenotypic traits and fitness. Many investigators realize the need to resolve this ambiguity, and so we anticipate rapid future advances in the application of evolutionary principles to salmonid conservation and management.

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