Report of the Symposium/Workshop:

Evolutionary Changes and Salmon: Consequences of anthropogenic changes for the long-term viability of Pacific salmon and steelhead

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Meeting Summary

The public Symposium, attended by over 200 participants, provided a general introduction to this large and complex issue and helped to educate salmon biologists about evolutionary concepts, as well as evolutionary biologists about salmon biology. In the Workshop, separate workgroups focused in more detail on seven specific issues related to evolutionary changes and salmon. Key points that emerged from these sessions include:

Selective harvest.—The evolutionary consequences of selective harvest have recently been evaluated for some fish species, but no comprehensive treatment of the topic exists for salmon. Fisheries can be selective for behaviors as well as size and age. Genetic effects of fishing must be evaluated in both the short term and the long term. A key question to address will be, To what degree is genetic risk of fishing adequately dealt with by risk-averse fishery management—e.g., simply through reduction of fishing mortality? The workgroup has already drafted a paper outlining the major issues considered.

Disease.—Disease is an important factor in all ecosystems and an important agent of evolutionary change. Changing environmental conditions often trigger disease outbreaks, particularly for cold-blooded species such as salmon. Of the anthropogenic factors that could modulate the host-pathogen relationship (or host resistance for non-infectious diseases), the workgroup identified two of particular concern: isolated populations that have experienced a bottleneck of reduced population size, and introduction of novel pathogens. Both factors could substantially change selection pressure on salmon populations and hence cause an evolutionary response.

Selective loss of habitat.—Habitat loss for salmon across the Pacific Northwest has not been random; rather, it has been concentrated in two types of areas: upstream areas that are above barriers to migration, and lower river and estuary areas that have been strongly affected by urbanization and associated effects on habitat quality. These selective losses have three potentially important evolutionary consequences for salmon. First, numerical reductions in population size can erode evolutionary potential and disrupt metapopulation processes necessary for long-term viability. Second, selective loss of particular habitat types creates selective pressures against the life history traits that have evolved to take advantage of those habitats, resulting in substantial evolutionary change within the population. Third, the remnant population might be forced to utilize sub-optimal habitats, at a cost to overall population fitness.

Water temperature and flow.—This group focused primarily on the effects of water temperatures that are altered by operation of dams. Two hypotheses were developed: 1) increased variance in thermal regimes would lead to increased variance in spawn timing, migration timing, and egg development rates, and reduced variability in the environment might lead to a reduction in variance of life-history parameters such as spawn-timing or growth rate. 2) Large dams that release unseasonably warm water in the fall will increase development rates, causing fish to emerge earlier at a time that might be maladaptive. The group outlined research that could be conducted to determine whether Chinook salmon have evolved changes in spawn timing or development rate to compensate for altered thermal regimes associated with dams.

Habitat fragmentation and population structure.—This group considered the general questions, What is the relationship between salmon population structure and population fitness? and, Does loss of population structure *per se* lead to measurable reductions in population performance? The workgroup identified four steps to help improve our understanding of these relationships: 1) Make better use of recently developed population genetic models to obtain more accurate estimates of gene flow rates among populations. 2) Develop focused research projects to gain a better understanding of spatial/temporal variation in selection gradients on salmon populations. 3) Conduct analyses to determine the scale of gene flow relative to the scale of spatial heterogeneity in the environment. 4) Analyze how rates of gene flow will change with human actions.

Snake River fall Chinook salmon.—This population has experienced a wide range of anthropogenic influences that could elicit evolutionary changes. The workgroup focused on empirical data showing that the size of juveniles in June has declined substantially from the 1950s to the present. In addition, whereas virtually all juveniles historically migrated to sea as subyearling smolts, some now overwinter in the reservoirs and migrate to sea as yearlings. Evidence suggests current conditions selectively favor survival of yearling smolts, which could drive evolution of a novel life history strategy for this population. An evolutionary model indicates that the observed rate of change in juvenile size cannot be explained by random processes, but it is consistent with evolutionary rates measured in other natural populations. A strictly phenotypic response to altered environmental conditions could also explain the observed changes, and research was identified that could distinguish between the latter two hypotheses.

Climate change.—Climate change will interact with and modulate evolutionary responses to all of the anthropogenic changes discussed above. In the near future, climate change is not likely to cause local environmental changes that fall outside the range of conditions experienced by Pacific salmon. However, local populations will be challenged to rapidly adapt, move, or go extinct. Useful insights can be gained by reviewing the capacity of Pacific salmon for adaptive change and phenotypic plasticity, in the context of the magnitude of environmental changes expected to occur as a result of climate change. Some key life history traits such as spawn timing are capable of rapid response to selection and thus by themselves might not preclude adaptations to climate change. However, population fitness depends on the timing and execution of many key life history events, and changes in one trait (e.g., spawn timing) can affect timing of other traits (e.g., emergence timing and timing of smolt migration) in maladaptive ways.

Each of the workgroups identified key topics for research that could help elucidate the nature and importance of evolutionary responses by salmon to anthropogenic changes. A number of manuscripts arising from the meeting will be submitted for publication in a special issue of the new journal *Evolutionary Applications* that will be devoted to salmon evolution.

An issue that is likely to become important in future evaluations is the concept of a Darwinian debt—an evolutionary change associated with human-altered environments that must be repaid before the population can re-adapt to more natural conditions, if the human changes to the ecosystem are ever reversed. This concept is already familiar to those who have evaluated the evolutionary consequences of size-selective harvests. If harvests come preferentially from fish that are larger, the population will evolve toward a slower growth rate and earlier age at maturity, to maximize reproduction before the age at which exposure to the fishery is high. This evolution can affect not only productivity but also long-term viability (e.g., in many fishes there is a positive relationship between size and gamete quality). If size-selective harvest is terminated, it might take a long time for the population to re-evolve something approximating its historical age/growth-rate relationships, and during this period (while it repays the Darwinian debt) the population could experience reduced productivity and viability. This basic principle could apply to many anthropogenic changes associated with Pacific salmon, including hatcheries, harvest, hydropower operations, and other types of habitat modification.

Background

During the 1990s, approximately half of the existing populations of Pacific salmon and steelhead in the contiguous U.S. were listed as threatened or endangered under the federal Endangered Species Act. Anthropogenic change is believed to be at least partially responsible for many of these listings. Subsequently, considerable effort has been expended trying to quantify effects of what in the Pacific Northwest are commonly referred to as the “four Hs” (habitat, harvest, hatcheries, hydropower development) on survival, mortality, and population growth rate of listed salmon and steelhead. The implicit and widespread view is that anthropogenic change is primarily an ecological problem. However, virtually every anthropogenic change that affects these key ecological and demographic parameters will also have profound evolutionary consequences. Evolutionary responses to altered environments affect fitness and resilience, with attendant affects on long-term viability of populations. To date only the evolutionary consequences of artificial propagation, and recently those of size-selective harvest, have received much attention. This issue, however, is much more pervasive and is relevant to all anthropogenic activities. For example, consider the selective impact of the Columbia River hydropower development: selection for migration timing that maximizes survival through the current hydropower system rather than through a pristine river; selection on physiology and morphology for ability to migrate (as both juveniles and adults) through large reservoirs; selection for ability to find juvenile bypass openings or adult fish ladders; selection for the physiological capacity to survive in dramatically changed environments (temperature, flow regime, structural habitat) in the lower river and estuary; selection from invasive species (predators, competitors, disease vectors) in reservoirs; selection imposed by genetic and ecological interactions with large numbers of hatchery-propagated salmon and harvest regimes targeting these fish; etc.

More broadly, any anthropogenic activity that affects salmon and steelhead directly—or that affects their environments—has the potential to change selective regimes. Recent studies demonstrate remarkably fast responses of fish to novel selection patterns, so the concerns raised are not merely academic. We therefore expect that a broad array of anthropogenic factors will have already had – and will continue to have -- evolutionary impacts on salmon and steelhead populations. It is much less clear, however, what these changes mean for the long-term viability of natural populations in human-altered environments. Will they ameliorate the impacts of anthropogenic change, or will they potentially exacerbate them?

This is a large, complex topic that should ideally form the basis of an extended research program in the future. As an initial effort, we convened a 3-day Symposium/Workshop in December 2006 in Seattle that brought together a) top evolutionary biologists with expertise in evaluating responses of natural populations to altered selective regimes; and b) top regional scientists with detailed knowledge of salmon and the nature of anthropogenic changes to their environments. The overall goal was to explore the nature and scale of this broad issue, to identify factors that can be particularly important as agents of evolutionary change, and to help define the types of analyses, monitoring, and research that will be most productive to conduct in the future.

The Symposium (December 7) was open to the public and had two major objectives: a) to provide a public forum for discussing these important issues and raising awareness of their importance for salmon conservation; and b) to provide necessary information on salmon biology to evolutionary biologists and information on evolutionary biology to salmon biologists, in the hope of establishing substantive collaborations and exchanges. With just over 200 registered attendees, the symposium provided a lively forum for initiating discussions. The day was capped with a hosted social and poster session, with 40 posters on topics related to evolution and salmon. Abstracts for the posters and Symposium speakers are in the following sections.

The Workshop (December 8-9) included about 55 invited participants, organized into seven groups that considered evolutionary responses to specific kinds of anthropogenic change faced by Pacific salmon. To the extent possible, these workgroups focused on empirical datasets for salmon. Each workgroup included a mix of regional scientists familiar with specific datasets and evolutionary biologists who have experience in interpreting such data in an evolutionary context. Workshop topics included the following:

Evolutionary consequences of size-selective harvest
Anthropogenic influences on salmon disease prevalence and resistance
Evolutionary responses of Pacific Northwest salmon to global climate change
Selective loss of habitat types and effects on life history diversity within and among populations
Evolutionary response to changes in water flow regimes and temperature patterns caused by hydropower operation
Habitat fragmentation and population structure
Snake River fall Chinook salmon: a case study in evolutionary responses to multiple anthropogenic changes

Reports of each workgroup appear at the end of this report.

Agenda: Evolutionary Changes and Salmon Symposium
December 7, 2006 Seattle

0830 **Welcome**
0840 *Introduction/background* (Robin Waples, Northwest Fisheries Science Center)
0900 *Overview of evolutionary considerations* **(**Ruth Shaw, University of Minnesota)

Salmon Primer

0930 *The life history of salmonid fishes: nature, nurture, and the hand of man* (Tom Quinn, University of Washington)
1000 *Changes to salmon habitats, environments, and ecosystems: Pulses, presses, and spatial extent* (Mary Power et al., University of California Berkeley)

1030 Break

1050 *Harvest & hatchery impacts on salmon* (Ray Hilborn, University of Washington)

Evolution Primer

1120 *Selection* (Stevan Arnold, Oregon State University)
1150 *Evolutionary rates in natural populations of salmon and other vertebrates* (Andrew Hendry, McGill University)

1220 Lunch (provided on site)

1320 *Phenotypic plasticity: what is it and why is it important?* (Sonia Sultan, Wesleyan University)
1340 *Phenotypic plasticity: what does it mean for salmon?* (Jeff Hutchings, Dalhousie University)
1400 *Variation, selection and evolution of function-valued traits* (Joel Kingsolver, University of North Carolina)
1430 *Habitat fragmentation and population structure* (Michael Whitlock, University of British Columbia)

1500 Break

1520 *Evolution under size-selective harvesting* (Richard Law, University of York)

Case studies

1550 *Evolution of disease resistance in transplanted Chinook salmon* (Maureen Purcell, US Geological Survey, Seattle)
1610 *Response to global warming: A perspective based on Atlantic salmon* (Bill Bradshaw, University of Oregon)
1630 **Poster session** (until 1830)

Speaker Abstracts

Introduction to the symposium

Robin Waples, Northwest Fisheries Science Center, Seattle

In recent decades U.S. and Canadian populations of Pacific salmon and steelhead have experienced widespread declines, and considerable effort has been expended trying to quantify effects of the "four Hs" (habitat, harvest, hatcheries, hydropower development) on survival and population growth rate. However, virtually every anthropogenic change that affects these key demographic parameters also can have profound evolutionary consequences. These latter effects, which have received much less attention, are the focus of this Symposium. The Symposium will bring together top regional scientists with detailed knowledge of salmon and the nature of anthropogenic changes to their environment, and top evolutionary biologists with expertise in evaluating responses of natural populations to altered selective regimes. The Symposium and subsequent Workshop has two major objectives: 1) to provide a public forum for discussing these issues and raising awareness of their importance for salmon conservation; and 2) to provide necessary information on salmon biology to evolutionary biologists and information on evolutionary biology to salmon biologists, in the hope of establishing substantive collaborations and exchanges. By the end of the meeting, we hope to have a better sense of the relative importance of different anthropogenic agents in eliciting evolutionary changes in salmon, and some ideas for promising lines of future research to attack this large and complex topic.

Overview of evolutionary considerations

Ruth Shaw, Department of Ecology, Evolution, and Behavior, University of Minnesota

In considering evolutionary responses to rapid anthropogenic change, it is reasonable to expect that all of the primary processes of evolution will play important roles. I will focus on ones that seem of particular interest in relation to current concerns about salmon and emphasize the interplay between genetic and demographic consequences of evolutionary change. A potent evolutionary phenomenon is subdivision of populations, whether chronic or due to recent fragmentation, which promotes genetic divergence among demes and may enhance genetic drift. Beyond this, radical alteration of environment may impose novel selection and has, in well-documented cases, resulted in rapid adaptation to new conditions. Prediction of when to expect adaptation to keep pace with environmental change requires quantifying the components of selection response: the strength of selection, the genetic variability of traits subject to selection, and the dependence of both on environmental context. To illustrate ways these processes can be studied, with potential application to salmon, I will draw examples from research I have conducted with collaborators in populations of wild and model plants.

The life history of salmonid fishes: nature, nurture, and the hand of man

Thomas P. Quinn, School of Aquatic and Fisheries Sciences, University of Washington

The primary purpose of this presentation is to provide an introduction to the general life history patterns of Pacific salmon, emphasizing key themes that are common among species, and also the fundamental differences between species that depend on streams only for spawning and incubation of embryos (pink, chum and sockeye salmon) and those that also rely on streams for rearing by juveniles (coho and Chinook salmon, and the Pacific trout species). The secondary purpose is to follow the generalized life history of Pacific salmon, illustrating the ways in which patterns reflect genetic and environmental influences, and opportunities for direct and indirect selection from human activities. Examples include reproduction, survival of embryos, residence in streams, seaward migration (including the option not to migrate at all), ocean migration patterns, age and size at maturity, and return migration to spawn.

Changes to salmon habitats, environments, and ecosystems: Pulses, presses, and spatial extent

Mary Power[1], Beth Sanderson[2], George Pess[2], Tim Beechie[2], Michelle McClure[2],
Wendy Palen[1], and Mike Limm[1]; [1]U.C. Berkeley and [2]Northwest Fisheries Science Center

Drawing on reconstructions and ongoing research by a geomorphologists, paleontologists, and ecologists, we will contrast ancient and contemporary environments of Pacific salmon. During their early evolution, Pacific salmon confronted tectonically active coastal environments that were periodically disturbed vulcanism, earthquakes, huge landslides, and glaciation. Some of these catastrophes obliterated huge areas of salmon habitat, but river drainages that were catastrophically destroyed were probably re-habitable after years or decades. These large extent but short duration (pulse) disturbances, given vast remaining habitat and ocean life cycles that allowed straying as well as recolonization, did not threaten persistence of these fish. Their long life spans, life history variation, high fecundity, and remarkable long distance migratory capacity allowed individuals to quest far and wide for good habitat, if it existed somewhere and could be reached by swimming.

Post-European human alteration of coastal watersheds have imposed long-lasting (press) threats to salmon persistence: habitat simplification, fragmentation, and pollution; introductions of exotic biota including predators and pathogens; locally and regionally altered thermal and hydrologic regimes. These changes are also vast in spatial extent—little unaltered salmon habitat remains. Despite the large research effort directed at understanding contemporary factors limiting salmon populations, we have much to learn about the current temporal and spatial bottlenecks in salmon life histories and in their watershed and ocean environments, where restoration efforts and management could be most efficiently targeted. We also have much to learn about the extent to which variation and plasticity will support salmonid resilience through a future of accelerating environmental change. Focusing on terrestrial watershed habitats, we will briefly discuss research targeted at the environmental knowledge gaps, ranging from small scale studies of habitat effects on growth, behavior, and survival of juvenile salmonids and the food webs that support them, through attempts to parameterize effects of habitat on life stage specific stock recruitment relationships, to the remaining challenge of upscaling to link basin-specific performances of individuals to population dynamics.

Harvest and hatchery impacts on salmon

Ray Hilborn, School of Aquatic and Fisheries Sciences, University of Washington

In this talk I will review the range of impacts that harvest and hatchery practice have had on both the population dynamics, but also the potential for evolutionary impacts on salmon. Harvest impacts have been shown in numerous fisheries to be size selective, usually selecting against larger fish. Harvest may also be very selective for run timing, and age at return. Any fisheries on immature fish in the ocean will provide selection for shorter ocean life and earlier age at return. While little documentation exists some harvests may select for migration paths and areas of ocean migration. Hatcheries have been identified as providing population level impacts on wild fish through competition, disease, and genetic introgression of domestication. Each of these impacts has potential evolution impacts.

Selection

Stevan J. Arnold, Department of Zoology, Oregon State University

The aim of this talk is to review aspects of phenotypic selection that may prove useful to students of salmonid biology. I will focus on four main ideas. (1) Selection on phenotypic traits changes their statistical distributions (means, variances, covariances). (2) The mode and intensity of selection can be assessed by measuring those changes in means, variances and covariance. (3) Such measures of selection can be related to characteristics of an adaptive landscape for phenotypic traits. (4) That landscape can in turn be used to model short term as well as long term evolution. Each of these ideas will be illustrated with examples from the empirical literature.

Evolutionary rates in natural populations of salmon and other vertebrates

Andrew Hendry, McGill University

The ability of natural populations to respond adaptively to environmental change or other stressors will depend on their rate of phenotypic change. I will review rates of phenotypic change in natural populations of vertebrates to address questions about typical rates of phenotypic change and how these rates are influenced by human activities. In salmon, rates of phenotypic change are typically estimated for introduced populations or for those experiencing harvest. I will compare rates of change estimated for salmon to those observed in other vertebrates. Finally, I will speculate on the likelihood that phenotypic change in salmon can keep pace with environmental change, and the constraints on this ability. I will also discuss the likely contributions of genetic change and phenotypic plasticity to phenotypic changes in natural populations of salmon.

Phenotypic plasticity: what is it and why is it important?

Sonia Sultan, Department of Biology, Wesleyan University

Phenotypic plasticity is the ability of a genetic individual to express different phenotypes in different environmental conditions. An individual's plasticity pattern or "norm of reaction" for a developmental, behavioral, or life-history trait of interest is determined by raising genotypic or family replicates in a range of ecologically relevant potential environments. These expression patterns are trait- and environment-specific, and may vary at the genotype, population, and species levels. Accordingly, plasticity patterns can be understood as evolving traits.

Under certain conditions, adaptive plasticity can buffer populations from selective change in an unfavorable and/or novel environment. The evolutionary impact of phenotypic plasticity in a given system will depend on a number of factors, including patterns of genetic variation for plasticity, the distribution of alternative environments, and whether the expressed plasticity is adaptive or maladaptive. When environments are changed (for instance by human activities), all three of these parameters can be affected. In addition, such changes can disrupt adaptive plasticity by decoupling the environmental cues that induce plasticity from the selective conditions in which plasticity is expressed. This is particularly likely in the case of cross-generational plasticity, in which a parent's environment induces adjustments to offspring phenotype in traits such as size or developmental timing.

Phenotypic plasticity: what does it mean for salmon?

Jeffrey Hutchings, Department of Biology, Dalhousie University, Halifax, NS

The persistence of a species depends on the resistance and resilience of its populations to anthropogenic and natural environmental perturbation. Correspondingly, risk of extinction is a function of the breadth of population responses to environmental change. At the individual level, these responses are ultimately reflected by genotypic differences in phenotypic plasticity, responses that can be represented heuristically and graphically by norms of reaction. Although empirical data on fishes are comparatively few, studies on salmonids to date (including chum salmon, Atlantic salmon, brook trout, grayling) suggest that there can be considerable variability in plasticity within and among populations, notably in early-developmental characteristics and life-history traits. Regarding spatial scales of adaptation, a broadcast-spawning marine fish (Atlantic cod) with apparently high dispersal capabilities can be comprised of populations that differ genetically in their reaction norms at spatial scales undetected by microsatellite DNA. Data on brook trout and grayling further suggest how evolutionary changes to reaction norms can be affected by fishing. Key questions concerning species persistence pertain to level of genetic variability in reaction norms within and among populations, the developmental stage(s) at which reaction-norm variation is greatest, and the links that exist between plasticity, individual fitness, and rate of population growth.

Variation, selection and evolution of function-valued traits

Joel Kingsolver, Department of Biology, University of North Carolina

Many important phenotypic traits of organisms are curves or functions: body size or survival rate as a function of age; growth rate as a function of temperature or food level; 2-D or 3-D body shape. There is a useful theoretical framework for analyzing phenotypic and genetic variation, selection and evolution of such 'function-valued' traits. I will illustrate this approach with several examples from our work with insects (and maybe bacteriophage): individual and population variation in developmental trajectories (size and life stage as a function of age); quantifying variation and evolution of thermal reaction norms (growth rate as a function of temperature); and predicting how environmental (climate) variation affects selection on continuous reaction norms. I'll describe some of the benefits and limitations of a function-valued approach for different biological questions and types of data.

Habitat fragmentation and population structure

Michael Whitlock, Department of Zoology, University of British Columbia

Spatial subdivision of a species can affect its evolution in a number of important ways. The effects of space on evolution are mediated through various forms of local similarity: individuals in the same local population are more likely to experience similar selection pressures, similar habitats, and similar catastrophes. If migration is limited between local areas, then individuals chosen from the same local population will be genetically similar as well.

Evolutionary theory has many predictions about the effects of spatial population structure on evolutionary processes. Spatial structure affects a long list of important evolutionary processes and patterns, including:

- response to selection,
- local adaptation,
- mutation load (the reduction in fitness caused by recurrent deleterious mutations),
- probability of fixation of new mutations,
- heterosis and/or hybrid breakdown (the increases and decreases in fitness associated with mating among populations),
- maintenance of total genetic variance,
- partitioning of genetic variance,
- frequency dependent selection,
- the effective population size.

The effects of population structure on evolution depend on demographic features that are in principle measurable in real populations, including F_{ST} (a standardized measure of genetic differentiation among populations), migration rates, local population sizes, and the pattern of variation among populations in reproductive success.

I will discuss some of these effects of population structure. Moreover, I will emphasize when deviations from the simplest theory matter. Real populations, in particular salmon populations, do not follow the assumptions of population genetics' toy representation of space, the island model. I'll explore how isolation by distance, local catastrophe, and variation in reproductive success affect the predictions of the models.

Evolution under size-selective harvesting

Richard Law, Department of Biology, University of York

Fisheries around the world appear to be a theatre in which large scale selection experiments are being played out. The actors are first the fishery managers who set patterns of selection through regulations such as net mesh size and catch quotas, second the fishers who apply the selective mortality, and third the fish stocks that may undergo genetic change due to selection caused by fishing. This paper considers the kinds of selection on life histories that fishing can generate, and whether the conditions needed for a genetic response to such selection are likely to be met on timescales that matter in fisheries management. The evidence for genetic change in exploited fish stocks, and the implications of such evolution for management of such stocks, are also discussed.

Evolution of disease resistance in transplanted Chinook salmon

Maureen Purcell, USGS, Western Fisheries Research Center, Seattle

In the late 1960s, Chinook salmon (*Oncorhynchus tshawytscha*) from the Green River in Washington State were successfully introduced into Lake Michigan. The stock of Chinook salmon increased dramatically and contributed to a popular fishery. Beginning in 1988, large disease outbreaks associated with significant adult mortality occurred among Chinook salmon in the lake. The only pathogen consistently found was *Renibacterium salmoninarum*, the causative agent of bacterial kidney disease (BKD). *R. salmoninarum* has been endemic in the Lake Michigan stock since that time. We compared the relative BKD susceptibility in a contemporary Lake Michigan stock from Wisconsin to the progenitor stock from the Green River in Washington. The Lake Michigan groups injected with the ATCC type strain 33209 had significantly greater survival (80%) relative to the Green River group (30%) in the challenge ($p < 0.0001$). The genetic relationship between these contemporary stocks was confirmed by analyzing thirteen microsatellite loci. The data suggest that a phenotypic change in BKD resistance occurred in the Wisconsin Chinook salmon over approximately eight generations since introduction in response to intense disease selection. Recent estimates of the heritability for BKD resistance (Hard et al.) support this hypothesis.

Response to global warming: A perspective based on Atlantic salmon

Bill Bradshaw and Chris Holzapfel, Center For Ecology and Evolutionary Biology, University of Oregon

Recent rapid climate change has been attributed in large part to anthropogenic emission of greenhouse gases. In response to climate change, many species have expanded their ranges northwards or altered the timing of their seasonal activities. In fact, rapid climate change is now driving evolution (genetic change) in animal populations as diverse as insects, birds, and mammals. In each case, the genetic changes observed in animal populations relate to seasonal adaptation; to our knowledge, there are no documented examples of thermal adaptation. We use Atlantic salmon (*Salmo salar*) as a case study to predict how salmon populations are likely to evolve in response to continued global warming.

Atlantic salmon range around the perimeter of the north Atlantic basin, breed in fresh water streams and rivers and, for the most part, mature in a marine environment before returning to their natal stream to spawn. Atlantic salmon use the length of day or photoperiod in conjunction with an endogenous circannual rhythm to time smoltification, migration, and sexual maturation. Evolved differences in the timing of salmon migration and spawning are highly subject to local conditions and, as those conditions change, so also should the timing of migration and spawning. Photoperiodic responses tend to have high heritabilities and have already been shown to change in parallel with recent rapid climate change. The principal adaptation of salmon to global warming is therefore likely to be in the photoperiodic response used to time the seasonal events in their life histories, rather than in an increase in thermal tolerance or altered thermal optima.

Poster Abstracts

Note: each workgroup also presented a poster on December 7. See the workgroup reports in the next section for more details about individual workgroups.

Reproductive success and effective population size of steelhead: a case study on artificially supplemented populations in the Hood River

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While evolutionary consequences of hatchery supplementations have been evaluated theoretically, there is little empirical evidence for such hatchery effects. Here we investigate reproductive success and effective population size (N_e) of anadromous steelhead (*Oncorhynchus mykiss*), addressing 1) direct impacts of different hatchery programs on natural populations, 2) the primary factor that restricts N_e, and 3) influences of hatchery programs on the primary factor. We genetically analyzed parentage of steelhead in the Hood River, Oregon, from which an almost complete sample is available for up-migrating anadromous adults over 15 years. We found that fish from traditional hatchery programs (nonlocal, multiple generations in a hatchery) had negative impacts, not only by reducing mean reproductive success but also by increasing variance in reproductive success among breeding parents, which is the primary factor that restricts N_e. No sign of such effects was found in fish from supplementation hatchery programs (local, single generation in a hatchery). Furthermore, we found an inferred, yet significant contribution of nonanadromous parents to anadromous offspring especially when anadromous run is weak, suggesting that the nonanadromous population serves as a buffer when anadromous population size fluctuates. Thus, any anthropogenic changes that reduce the nonanadromous population size would negatively affect the anadromous populations.

Pedigrees in captive broodstock populations provide insight into reproductive success and evolutionary processes in ESA-listed Chinook salmon populations

Melissa Baird[1], Ewann A. Berntson[1], Tim Hoffnagle[2], Richard W. Carmichael[2], Paul Moran[1]
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Despite extensive artificial propagation, Snake River spring Chinook salmon (*Onchorynchus tshawytscha*) in northeast Oregon have experienced severe population decreases and potential bottlenecks in naturally spawning populations. These declines have stimulated recovery efforts, which include captive broodstock programs that raise wild-caught juveniles to adulthood, spawn them, and release their offspring. In this study we used microsatellite variation to conduct parentage analysis and quantify relative reproductive success. Preliminary analyses of 5 years of spawning data show substantial variability in relative fitness among sites, years, and mating classes, especially in early maturing jacks. In stark contrast to results from similar studies in steelhead, artificially propagated Chinook salmon show no clear pattern of diminished fitness relative to their wild counterparts. It is still unclear whether this difference is related to propagation method (conservation steelhead hatchery versus captive broodstock production) or intrinsic differences between species. We seek to put these results in a context that will provide specific guidance to managers on issues such as appropriate proportions of jacks to allow in natural spawning populations. In addition to applied information for monitoring effectiveness of artificial propagation, these pedigree studies allow detailed evaluation of selective pressures and specific factors that drive differences in reproductive success.

Consequences of gillnet-induced delayed mortality in sockeye salmon

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Sockeye salmon (*Oncorhynchus nerka*) in many commercial fisheries are caught in gillnets. While most are harvested by the fishery, many escape from nets and continue their migration to spawning areas, despite sustaining injuries. Although damaged fish are counted as part of the aggregate escapement, many seriously injured fish fail to contribute to the reproductive capacity of the escaped stocks. The effects of this unaccounted mortality may have important implications for the estimation of spawner-recruit relationships and the designation of escapement targets, especially if the incidence of injury varies year to year. Since gillnets are size selective, the effects of gillnet scarring on escaped populations of sockeye may also exert important evolutionary pressures related to morphology and life history. To explore these questions, we estimated the incidence and severity of injury in escaped fish and determined its effect on pre-spawning mortality and spawning success through field experiments in the Wood River system, Bristol Bay, Alaska (2005-2006). Specifically, we sought to: (1) estimate the incidence of scarred fish among spawning adults at natal streams; (2) determine whether scarring has a size or sex-selective bias and varies inter-annually as a function of fishing intensity; and (3) determine the severity of scarring and its relative effect on spawning success. The findings suggest that such injuries are common, inhibit spawning and may exert long-term evolutionary pressures related to the life history and morphology of exploited populations.

Life history plasticity in Sacramento River winter-run Chinook salmon: interactions among photoperiod at emergence and growth modulate smolting and early male maturation.

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Chinook salmon posess a great deal of plasticity with regard to juvenile life history traits including smolting. Smolting is a physiological process that both allows and stimulates juvenile salmonids to undertake the initial freshwater to seawater migration. The age, season, and size at which smolting occurs varies both within and among populations. Juvenile life history of Sacramento River winter-run Chinook salmon (ESA listed) is currently poorly described. We examined the relative effects of photoperiod at emergence and growth rate on smolting pattern and early male maturation rate in these fish. Pooled fry from 4 male by female crosses were ponded on the same day but under three different photoperiods, mimicking the natural range of emergence timing in this population. Physiological changes indicative of smolting were found during March and April in all treatments, similar to yearling smolting patterns found in many salmonids. Fish that emerged early and grew at a relatively high rate also demonstrated signs of smolting in autumn. Early male maturation (age 1) was dependent on growth and photoperiod at emergence. The differentiation among life history traits between Sacramento River winter-run and better described Columbia River spring-run Chinook salmon demonstrate the evolutionary potential for variation of Chinook salmon life history.

Hydrologic regime and the conservation of salmon life history diversity

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Life history diversity of imperiled Pacific salmon *Oncorhynchus* spp. substantially contributes to their persistence, and conservation of their diversity is a critical element of recovery efforts. Preserving and restoring diversity of life history traits depends in part on environmental factors affecting their expression. We analyzed relationships between annual hydrograph patterns and life history traits (spawn timing, age at spawning, age at outmigration, and body size) of Puget Sound Chinook salmon (*Oncorhynchus tshawytscha*) to identify environmental indicators of current and historic diversity. Based on mean monthly flow patterns, we identified three hydrologic regimes: snowmelt-dominated, rainfall-dominated, and transitional. Chinook populations in snowmelt-dominated areas contained higher proportions of the stream-type life history (juvenile residence >1 year in freshwater), had older spawners, and tended to spawn earlier in the year than populations in rainfall-dominated areas. There are few extant Puget Sound populations dominated by the stream-type life history, as several populations with high proportions of stream-type fish have been extirpated by construction of dams that prevent migration into snowmelt-dominated reaches. The few extant populations are thus a high priority for conservation. The low level of genetic distinction between stream-type and ocean-type (juvenile residence <1 year in freshwater) life histories suggests that allowing some portion of extant populations to recolonize habitats above dams might allow re-expression of suppressed life history characteristics, creating a broader spatial distribution of the stream-type life history. Climate change ultimately may limit the effectiveness of some conservation efforts, as stream-type Chinook may be dependent on a diminishing snowmelt-dominated habitat.

Holocene landscape evolution and potential influences on salmon life histories

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The quantity, quality, and distribution of salmonid habitats in the Skagit and Stillaguamish River basins have changed dramatically in response to post-glacial landscape evolution and volcanism over the last 14,000 yrs, and the more recent (~150 yr) history of land use. Within the first few thousand years after retreat of the Cordilleran ice sheet, streams incised more than 100 meters into valley-filling glacial sediments, sea level rose 90 m, and Puget Sound land masses rose 200 m as the continental crust rebounded from ice sheet depression. Volcanic mud flows from Glacier Peak ~12,000 ybp and ~5,500 ybp rerouted the Sauk River drainage from the Stillaguamish basin to the Skagit basin, and created an extensive low-gradient delta on the Skagit River. The interaction of these changes lengthened rivers, narrowed valley floors, and steepened tributaries. Main stems and floodplain sloughs on valley floors provided the majority of habitat, but moderate-gradient tributaries (<0.04) on terraces provided additional habitat for some salmonids. Channels in steep, bedrock terrain were too steep to support anadromous salmonids, and remain so today. Since non-native American settlers arrived in the mid-1800s, removal of beaver ponds, diking, ditching, and dredging of streams on the floodplains and deltas has isolated or obliterated approximately 50% of the coho salmon winter rearing habitat in both basins. These losses are associated mainly with agricultural practices, which occupy the same landforms as the majority of historical coho salmon habitat. Forestry activities are concentrated on the steeper slopes of the glacial sediments and bedrock terrain, and contribute to habitat losses by increasing sediment supplies and reducing wood recruitment. Understanding the interplay of Holocene landscape evolution, geomorphic processes, land use, and salmonid habitat provides a context for developing reasonable predictions for restored habitat conditions, and for understanding habitat dynamics that influence evolution of salmon life histories. Likely influences on life history evolution include reduced gene flow between the Stillaguamish and Sauk River populations while gene flow increased between Skagit and Sauk River populations, and reduction in spatial extent of cold water habitats that support the stream type life history in Chinook salmon. Recent land-uses have dramatically reduced availability of slow water habitats that provide winter refugia for stream type life histories in several salmon species.

Reproductive success of steelhead (*Oncorhynchus mykiss*) from a supplementation hatchery compared to their natural counterparts in Little Sheep Creek, Snake River basin

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Hatchery supplementation programs are designed to boost natural production; however, it can be difficult to evaluate these programs. This study investigated population genetic structure and created pedigrees for hatchery-reared and natural steelhead. We genotyped adult steelhead returning to the weir on Little Sheep Creek, as well as adult rainbow trout from upstream of the weir, and determined the parentage of sampled progeny at various life history stages. This presentation includes the initial 5 years of data for a 10-year study. Initial results suggest the relative reproductive success of hatchery fish was significantly less than that of their natural counterparts in 4 of the 5 years (30-60%). In the 5th year, a single very successful hatchery male resulted in a similar average success between hatchery and wild fish in that year. This result underscores the observation of high variance in reproductive success, especially in hatchery males. Although these supplementation hatchery fish spend just a single year of their lives in the hatchery, that year may be sufficient to cause a measurable decrease in fitness. Although the evolutionary implications are unclear, our study shows substantial impacts of hatchery fish, some of which are counter to the goals of the program.

Ten years of varying lake level and selection on size-at-maturity in sockeye salmon (*Oncorhynchus nerka*).

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Despite the many documented consequences of climate change on aquatic ecosystems, the consequences of fluctuating lake levels on organisms have received little attention. We report a case where lake level is a selective factor acting on sockeye salmon length-at-maturity because low lake levels cause large salmon to strand and die rather than reach the breeding grounds. We combined information on the level of Lake Aleknagik (southwestern Alaska) from 1952–2005 with a detailed comparison of the length of salmon that died at the mouth of Hansen Creek versus individuals that ascended to the spawning grounds over nine breeding seasons (1997–2005). The proportion of salmon stranding at the mouth varied among years from 2 to 45% in males and <1% to 19% in females. Formal selection analyses indicated that the largest individuals were most susceptible to stranding mortality, especially in years when many salmon stranded, and these were years with low lake levels. These results suggest that lake level was a strong and consistent selective force acting on this salmon population. Hansen Creek has a shallower creek mouth than most of the nearby creeks and the breeding salmon there tend to be smaller, younger, and more fusiform than conspecifics from neighboring populations.

Four decades of opposing natural and human-induced selection acting on Windermere pike (*Esox lucius*)

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The ability of natural selection to drive local adaptation has been appreciated ever since Darwin. Whether human impacts can impede the adaptive process has received less attention. Here we quantify natural selection and human induced harvest-selection acting on a freshwater fish (pike, *Esox lucius*) over four decades to test whether these selective forces typically act in concert or in opposition. Both natural selection and harvest selection were found to be remarkably consistent in direction setting up the possibility that they often act either in concert or in opposition. Specifically, directional natural selection tended to favor large individuals whereas the fishery targeted large individuals (i.e., favored small individuals). Moreover, non-linear natural selection tended to favor intermediate sized fish whereas the fishery targeted intermediate sized fish because the smallest and largest individuals were often not captured. Thus, our results unequivocally demonstrate that natural selection and fishery-induced, artificial selection acted in opposition within this natural system. Moreover, natural and artificial selection combined to produce reduced fitness overall and stronger stabilizing selection relative to natural selection acting alone. The long-term ramifications of such human-induced modifications to fitness landscapes are currently unknown and certainly warrant further investigation.

Predicting differential population responses to climate change

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Climate change is a major threat to many species. Salmon physiology and behavior are finely tuned to temperature and streamflow regimes in natal streams. How will changes in these environmental factors affect population viability? Using 12 yrs of mark-release-recapture data from the Salmon River Basin, Idaho, we detected different patterns in annual survival among populations. Summer temperature predicted annual survival in 6 of 16 populations, and fall flow predicted survival in 10 populations. We used these relationships to predict how environmental change would affect population growth using a density-dependent, stochastic life-cycle model. We input general circulation model (GCM)-predicted changes in air temperature and precipitation into a hydrological model to simulate stream flow under 2 climate change scenarios: 1) a composite of 4 GCMs and 2) the Max-Planck Institute GCM. All metrics of population viability declined under both scenarios. Temperature-sensitive populations did worse under the more moderate scenario than the flow-sensitive populations, but all populations did badly under the drier MPI scenario. A sensitivity analysis showed that the freshwater survival parameters were relatively more important under climate change. We propose a way to quantify how relative costs and benefits of occupying different habitats over the life cycle (i.e., fitness) may change, such that evolution might lessen extinction risks.

Evaluation of segregation in a steelhead (*Oncorhynchus mykiss*) hatchery system using scale pattern analysis

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Steelhead (*Oncorhynchus mykiss*) hatcheries provide a logical platform to study the effectiveness of the 'Segregated Hatchery Model' (Mobrand et al. 2005) because hatchery populations have historically been managed to return earlier than wild populations. In order to avoid risks of introgression with wild fish, it is has been recommended that the proportion of hatchery fish spawning in the wild be minimized. To demonstrate whether there is the potential for interaction *in situ*, we examined an out-of-basin steelhead fishery-enhancement hatchery at Forks Creek, WA from its inception in 1994 through 2003. Because hatchery fish were sacrificed once they return to the hatchery as adults, and hatchery fish are numerically abundant to wild fish, any evidence of spawn checks in hatchery-origin individuals indicates out-of-hatchery spawning behavior and increased risk for genetic hybridization with wild stocks. Scales were collected from both hatchery and wild adults returning to Forks Creek and analyzed to determine variation in life histories. We then estimated the proportion of hatchery fish on the spawning grounds using modeled iteroparity rates that took into account sampling error. An average of 4.6% of hatchery returning adults had spawned in the wild in previous years (range: 3.8%-10.8%). Over all parameter estimates, this system appears to exceed the recommended ratio of hatchery to wild adults on wild spawning grounds. Future work will include surveying the mating success to determine if iteroparous individuals of hatchery origin have attained reproductive success outside the hatchery. Additionally, we wish to determine whether hatchery and wild adults overlap temporally on the Forks Creek spawning grounds. These findings will aid in determining actions needed to maintain segregated hatcheries, and quantify the ecological risk these hatcheries present to wild populations.

Anthropogenic impacts on the spatial distribution of salmon populations: Patterns of philopatry and dispersal in supplemented and wild Yakima River Spring Chinook salmon.

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Philopatry in salmon is fundamental to their unique biology and management. Homing to the natal site to spawn results in genetic isolation of populations uniquely adapted for conditions in their natal streams. Homing is governed by the olfactory discrimination of home-stream water and exposure to home stream odors during appropriate juvenile stages is critical for olfactory learning (imprinting) and successful completion of the adult homing migration. While low levels of straying (dispersal) from the natal site are normal in the wild, inappropriate hatchery rearing conditions and juvenile release procedures may dramatically increase the level of straying by adult. Increased straying may have dramatic consequences on wild populations through interbreeding and direct competition. A number of conservation and supplementation hatchery programs utilize satellite acclimation facilities to seed or repopulate underutilized rivers or streams. These programs seek to exploit the tendency of salmon to imprint and return as adults to the site(s) from which they are released as outmigrating smolts. The final choice of spawning location within a watershed, however, involves complex tradeoffs between homing to the natal site, spawning habitat selection, and mate choice. The effectiveness of satellite facilities for ensuring successful imprinting, homing, and re-establishment of successful spawning in underutilized habitat while minimizing impacts on wild fish have not been demonstrated. The goal of this project was to describe the spatial and temporal patterns of homing and spawning by wild salmon and hatchery-reared salmon released from acclimation facilities in the upper Yakima River (Washington) and, to assess the efficacy of supplementation and acclimation sites in salmon recovery.

Fishing out evolution? The effects of temporally-biased fishing on migration patterns

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Migration has evolved in diverse animal taxa to optimize environmental conditions for different life stages. Migratory routes and timing are shaped by natural selection and adjusted by proximate environmental conditions. However, fisheries are a new form of selection, adding significant mortality in many cases. Exploitation by humans has well-studied selective effects on the age structure and body size in fish, and long term exposure to fishery selection pressures can cause evolutionary effects on such traits if they are under genetic control. The selective effects of fishing on the timing of migration or breeding, however, have received much less scrutiny, yet many fisheries are directly regulated by timing or are selective for the timing of migration or breeding.

This study attempts to elucidate the effect of temporally-biased fishery selection on migration timing of Pacific salmon populations. Through this research, we are attempting to show:

1) Fishing is not random and fishing pressure is temporally-biased;
2) Migratory patterns of the population have temporal structure;
3) Evolutionary consequences of temporally-biased fishing pressure on migration patterns.

Population viability of Chinook salmon following harvest selection

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There are several empirical examples of the role of harvest in causing evolution of fish populations. Few methods, however, have explicitly used quantitative genetic approaches to understand the relationships between life history variation, harvest strategies and fishery-induced evolution. We developed a genetic-based model of a Chinook salmon fishery, parameterized from empirical data and incorporating heritability values for length at age, to assess a range of harvest regimes on long-term abundance. Lengths at age for each age group were treated as different, but correlated, traits. The model showed that a constant exploitation rate above a minimum size will reduce abundance below levels predicted by a model that does not consider genetic diversity. All age groups, including those not under selection, respond to selection by becoming smaller and less fecund. When harvest occurs between a minimum and maximum size limit only, the population will evolve rapid growth to avoid the fishery, and the population may have higher abundance after 100 years than would be predicted by a non-genetic model. Under both selection regimes a faster growing population could sustain higher harvest rates and therefore had greater responses to selection.

Genetic effects of ELISA-based segregation for control of bacterial kidney disease in Chinook salmon (*Oncorhynchus tshawytscha*)

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We evaluated genetic variation in ability of Chinook salmon to resist two bacterial pathogens: *Renibacterium salmoninarum,* the agent of bacterial kidney disease (BKD), and *Listonella anguillarum*, an agent of vibriosis. After measuring *R. salmoninarum* antigen in 499 adults by enzyme-linked immunosorbent assay (ELISA), we mated each of 12 males with high or low antigen levels to two females with low to moderate levels and exposed subsets of their progeny to each pathogen separately. We found no correlation between *R. salmoninarum* antigen level in parents and survival of their progeny following pathogen exposure. We estimated a high heritability for resistance to *R. salmoninarum* (survival $h^2 = 0.890 \pm 0.256$) independent of parental antigen level, but a low heritability for resistance to *L. anguillarum* ($h^2 = 0.128 \pm 0.078$). The genetic correlation between these survivals ($r_A = -0.204 \pm 0.309$) was near zero. The genetic and phenotypic correlations between survival and antigen levels among surviving progeny exposed to *R. salmoninarum* were both negative ($r_A = -0.716 \pm 0.140$; $r_P = -0.378 \pm 0.041$), indicating that variation in antigen level is linked to survival. These results suggest that selective culling of female broodstock with high antigen titers, which is effective in controlling BKD in salmon hatcheries, may increase disease resistance of their progeny.

Long term fishery selection on length and age at maturity of sockeye salmon in Bristol Bay, Alaska

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Life history traits of wild animals can be strongly influenced by anthropogenic activities. Fishing gear, specifically gillnets, selectively remove certain individuals within fish populations and so can affect life history traits such as size and age at maturity. An increasing body of literature has warned of negative evolutionary changes resulting from fishery exploitation on wild populations. A sockeye salmon (*Oncorhynchus nerka*) gillnet fishery has been located at the Wood River system of Bristol Bay, Alaska, for over 100 years. Past research suggests that this fishery can be selective on size and age based on mesh size and fishery timing. However, fishing pressure and fishery management have varied greatly among years, and long term selection has not been examined. We are investigating the magnitude and nature of gear selectivity by this fishery on length and age at maturity of the sockeye salmon across six decades (1946-2006) to quantify underlying fishery selection. A historical reconstruction of the fishery shows large variation in vulnerability to the fishery based on fish length. Vulnerability patterns do not follow bell-shaped curves often used to characterize gillnet selectivity. Our analyses revealed variation in length vulnerability patterns between years, for a given sex, and between sexes within a year. Selection differentials reveal that the fishery has been more selective on females than on males over time, though it has become less size-selective on both males and females in recent years. This may be due to the high exploitation rate of the fishery in more recent years and changing gillnet mesh size regulations.

History of sockeye spawning channels on the Fraser River: models of domesticating selection?

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Important components of the recent evolutionary history of sockeye salmon in the Fraser River include fishing and other activities that make successful migration to the spawning grounds more difficult. For some populations, logging and road building have greatly reduced the efficacy of spawning after arrival. Spawning and incubation channels were built in the 1960s and 1970s for mitigation purposes. These channels are considered superior to typical artificial propagation in hatcheries with respect to domesticating selection: the adult salmon choose mates and dig nests (whereas gametes are manually mixed in hatcheries), and their offspring incubate, emerge, and migrate to lakes to feed similar to wild fish. There are, of course, differences between these channels and wild streams. Water flows, gravel sizes, and aquatic communities in general are likely to be more uniform in spawning and incubation channels than in wild streams. I describe spawning and incubation channels built to enhance sockeye on the Fraser River. I also present some historical data suggesting that spawning channels can reduce both size and variance in size of females in the populations that use them. Given the relationship between size and fecundity, selection on size in spawning channels could have considerable consequences for fitness and warrants further study.

Does hatchery rearing select for bold rockfish?

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Stock enhancement can potentially bolster depleted populations, but can introduce new problems if hatchery and wild fish differ behaviorally. Behavioral syndromes are one mechanism through which behavioral differences can arise. Behavioral syndromes occur when behavioral tendencies correlate with one another (e.g. a fish that feeds at high rates in the absence of a predator may also take more risks when a predator is present—a “bold” behavioral syndrome). Through such a correlation, unintentional hatchery selection for high feeding rates can change antipredator behavior and any other behavior correlated with feeding rate. We characterized behavioral variation in brown rockfish (*Sebastes auriculatus*), and tested whether hatchery rearing causes differential survival among behavioral variants. Over ten days, behavioral syndromes were stable (behavioral correlations existed on both Days 1 and 10), but individual behavioral variation was unstable (e.g. predator inspection behavior on Day 1 did not predict inspection behavior on Day 10). After 16 weeks of hatchery rearing, we detected no differential survival among behavioral variants, suggesting that there was no strong selection on the quantified behaviors. We consider a possible connection between behavioral stability/instability and selection on behavioral variants, and discuss how studying behavioral variation can inform stock enhancement programs.

The need for a common process-based view for habitat and fisheries management in restoration of endangered salmon and their ecosystems

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A new paradigm for the management of aquatic and riparian ecosystems emerged during the latter part of the 20th century. Rather than aiming to restore particular habitats, current habitat management approaches recognize the need to protect and restore the fundamental processes that shape and form habitats and biological complexes. This change resulted from the view that ecological processes operate over a spatial and temporal continuum that establishes specific ecosystem structures (habitats and biological communities) and functions that are important to the fitness and local adaptation of species and populations within specific watersheds. Furthermore, this approach admits to the variability in process, structure and function that is consistent with the evolutionary experience of aquatic organisms, such as Pacific salmon (*Oncorhynchus spp.*). In contrast, advances in fisheries management have not kept pace with this emerging view of ecosystem and population dynamics; the fishery management paradigm of selecting for the highest and most efficient rates of production, e.g., maximum sustained yield, remains dominant. This approach is inconsistent with the view of populations operating within the context of the ecosystem processes that sustain habitats and allow for a species to fully express phenotypic variation and evolutionary potential. Having two such distinctly different views of salmon management and restoration creates uncertainties and unnecessary conflicts in efforts to recover salmon populations. We suggest that a natural selection-based salmon management paradigm would help ensure that there is a common language and a basis for common ecological goals among hatchery, harvest, and habitat managers working toward protection and recovery of salmon in the Pacific Northwest.

Impacts of stormwater runoff on coho salmon in restored urban streams

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Beginning in the late 1990s, agencies in the greater Seattle area began conducting fall surveys for spawning salmon to evaluate the effectiveness of local stream restoration efforts. These surveys detected a surprisingly high rate of mortality among migratory coho females that were in good physical condition, but had not yet spawned. In addition, adult coho from several different streams showed a similar progression of symptoms (disorientation, lethargy, loss of equilibrium, gaping, fin splaying) that rapidly led to death. In recent years, pre-spawn mortality (PSM) has been observed in many lowland urban streams, with overall rates ranging from ~25% to 90% of the fall runs. Continuous daily surveys of wild coho spawners in a forested reference stream revealed <1% PSM. Although the precise cause of PSM in urban streams is not yet known, conventional water quality parameters and disease do not appear to be causal. Rather, the weight of evidence suggests that adult coho, which enter small urban streams following fall storm events, are acutely sensitive to non-point-source stormwater runoff containing pollutants that originate from highly developed landscapes. These findings have important evolutionary implications for salmonid restoration and conservation efforts in urban and urbanizing watersheds.

Comparisons of F_{ST} and Q_{ST} in populations of coho salmon

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Neutral genetic variation is commonly used to determine population structure in populations of conservation interest. However, increasing emphasis is placed on understanding the role and significance of adaptive genetic variation in determining such structure. The correlation between diversity at neutral markers and traits under selection is, in many cases, not high, and thus measures of divergence such as F_{ST} may fail to reflect population differentiation in adaptive traits. Q_{ST}, an F_{ST} analog calculated at quantitative traits, can be used to describe population divergence at traits which may be under selection or adaptive. Here we present a comparison of population differentiation between two coho populations from separate Evolutionarily Significant Units, using both F_{ST} and Q_{ST}. This comparison permits an analysis of those traits that have likely responded to selection since divergence. Q_{ST} for juvenile growth traits (length and combined growth traits) was significantly greater than F_{ST}, while for all other traits measured (alevin egg and embryo weights, juvenile weight and juvenile condition factor) there was no significant difference between F_{ST} and Q_{ST}. These results further suggest that the two populations are undergoing divergent selection for length but other traits may be under stabilizing selection.

Consequences of phenotype modification due to persistent selection for rapid growth and larger body size: A comparison of a domesticated stock of coho salmon (*Oncorhynchus kisutch*) to its parent stock.

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Animals have been selectively bred for preferred phenotypes such as faster growth, larger body size, and certain behaviors for centuries. The introduction of domesticated (and sometimes exotic) animals often proves detrimental to wild animals they come into contact with. Often their behavior can prove to be devastating to wild species. Other problems include interbreeding with wild populations that have evolved with their environment. The potential for deleterious interactions between wild and domesticated fish has been brought to the forefront of science and its interface with policy and management with the widespread expansion of salmon aquaculture.

Wild salmon are known to be highly adapted to particular river systems and the introduction of farmed fish may erode these adaptations, especially if farmed and wild fish interbreed. This study compared feed intake, growth, and nutrient and energy utilization of Dømsea coho salmon (*Oncorhynchus kisutch*), with 12+ generations of selection for rapid growth with larger body size, to its parent stock of Skykomish River coho salmon in a common culture environment. This study shows conclusively that domestication has metabolically modified the Dømsea strain, and the strain would probably be maladapted to the wild due to the tendency to utilize fat for energy instead of storing fat during winter and times of low growth opportunity.

The Oregon Hatchery Research Center: searching for answers

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The Oregon Hatchery Research Center is designed to study the mechanisms that may create differences between hatchery and wild salmon and steelhead, to develop approaches to best manage those differences to meet fishery and conservation objectives, and to help understand the role and performance of hatcheries in responsibly managing and protecting Oregon's native fishes. We already have results from studies of early development and behavior, stable isotopic analysis of diets, and feeding behavior of juvenile steelhead, *Oncorhynchus mykiss*, taking advantage of the specialized research facilities and capabilities of the OHRC, which combine experimental flexibility with capacity beyond that normally found in research facilities. Results from stable isotope studies will be used to resolve questions about the mechanisms of nutrient enhancement through salmon carcass distribution in coastal watersheds. Results from studies of early development and behavior will be applied to questions of hatchery production techniques, and the suitability of hatchery produced fish for restoration or enhancement programs. Analysis of stable isotopes links both these areas of studies, and is a powerful analytical tool for linking controlled experimental studies to large scale, long term environmental studies of salmon populations.

Health effects and potential evolutionary consequences of chemical contaminant exposure in salmonids from Pacific Northwest rivers and estuaries.

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The Ecotoxicology group at the NWFSC has monitored a number of sites throughout the Pacific Northwest in recent years for the presence of chemical contaminants and their potential health effects on juvenile salmonids. These sites include restoration sites in Commencement Bay, WA, various sites in Puget Sound, the Columbia River and it's estuary, and sites in river and estuary systems in Oregon. This poster compares some of the results of these studies and potential health effects due to chemical contaminant exposure at an early life stage. Our results suggest that the likelihood of contaminant exposure varies with species and stock. Generally, we have found that contaminant concentrations are highest in species with an extended estuarine residence time, such as chum and fall Chinook salmon. Contaminant body burdens are typically lower in species and stocks with a stream-type life history, such as coho salmon. We have also observed differences in contaminant body burdens in various stocks in the Pacific Northwest. For example, Willamette River Chinook generally have high body burden of PCBs, DDTs, and PBDEs, while Upper Columbia River fall Chinook do not. The persistent presence of chemical contaminants at Pacific Northwest sites may pose a threat to the survival of affected stocks. Concentrations of PACs, PCBs, and DDTs in sediment, prey, and fish at some sites are above concentrations associated increased risk of immunosuppression, impaired thyroid function, reduced growth, reproductive impairment, DNA damage, and delayed mortality in outmigrant juveniles. For returning adults, exposure to contaminants in stormwater may be associated with pre-spawn mortality in coho salmon, but not other stocks. Our understanding of the evolutionary implications of contaminant exposure in salmonid stocks is very limited, but exposure to contaminants might also exert evolutionary pressure on affected stocks in several ways. For example, adverse health effects due to continued contaminant exposure at these sites may over time select for fish that are more resistant to these contaminants. These selective processes may or may not be advantageous for the long-term survival of affected stocks. Evolutionary forces may also select for juvenile Chinook that spend less time in the estuary to avoid contaminant exposure, contributing to reductions in the life history diversity of salmon stocks.

Candidate loci for run timing reveal genetic differentiation among Chinook salmon (*Oncorhynchus tshawytscha*) in the Feather River, California

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Understanding the genetic basis of local adaptation is a primary interest of evolutionary and conservation biologists as it involves the role of natural selection in producing evolutionary change in response to environmental variation. Salmonid fishes are excellent subjects for the study of local adaptation because of their tendency to form reproductively isolated populations, both spatially and temporally, across diverse environments. One important temporal adaptation of anadromous salmon is the timing of migration and breeding within a reproductive season. Among Pacific salmon species, Chinook (*O. tshawytscha)* demonstrate the most intra-annual variability in migration timing with individuals belonging to one of four seasonal runs. In most river systems, neutral genetic markers are routinely employed to discriminate among these migratory runs. In California's Feather River, however, we found no evidence for genetic differentiation between the federally-listed threatened spring run and more abundant fall run at nine microsatellite loci (F_{st}=-0.0002). These data indicate that there is considerable gene flow between migratory populations. In contrast, fall and spring runs are genetically differentiated at two candidate loci for run timing, *Clock* (F_{st}=0.042), an essential gene of the endogenous circadian clock and *Ots515NWFSC* (F_{st}=0.058), a microsatellite locus homologous to two salmonid genes central to the development and maintenance of reproductive function. Evidence presented here suggests that polymorphisms in *Clock* and *Ots515NWFSC* likely play a role in mediating migration and spawning time of Feather River Chinook. Despite the extensive introgression of the fall run gene pool into that of the spring run, these genetic data combined with the existence of springtime freshwater entry, indicate that rescue of the threatened spring run is possible if separate spawning habitats can be made available in the Feather River.

Abundance, length, stock origin, and pathogen infection in marked and unmarked juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in the nearshore surface waters of Puget Sound

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To better understand major anthropogenic influences on wild Puget Sound Chinook salmon (*Oncorhynchus tshawytscha*), we studied seasonal and geographic patterns in the abundance, size, stock origin, and pathogen infection prevalence in marked (known hatchery) and unmarked (majority natural origin) juvenile Chinook. Monthly surface trawl sampling was conducted from April to October in 2003 at 52 sites in Eastern Puget Sound ranging from Bellingham Bay to the Nisqually Reach. Unmarked Chinook in the northern regions of the study area showed broader seasonal distributions of abundance and length than both marked Chinook from all areas and unmarked Chinook in central and southern Puget Sound. Unmarked fish tended to be smaller than marked fish. For genetic analysis, data from 13 standardized microsatellite DNA loci surveyed in over 60 spawning populations in Washington and British Columbia were used as a baseline to estimate the stock composition of a subset of 424 unmarked individuals. The genetic results, combined with coded wire tag (CWT) data from 283 fish, showed that juveniles in all sampling areas included individuals from a wide range of populations, and that fish from different source populations vary in terms of movement patterns and apparent residence time. Prevalence of infection by *Renibacterium salmoninarum* was related to capture location rather than stock origin. These results demonstrate that juvenile Chinook use neritic waters in Puget Sound during much of the year, but suggest more extensive use of estuarine environments by wild than hatchery Chinook, and differential use of various geographic regions of greater Puget Sound by all Chinook. In addition, length differences and infection associations have implications for interactions between hatchery and wild Chinook throughout Puget Sound.

Non-indigenous species of the Pacific Northwest: an overlooked risk?

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Non-indigenous species are recognized as one of the major threats to global diversity and have been cited as a cause of decline in 42% of species listed under the US Endangered Species Act. The Pacific Northwest is home to more than a thousand aquatic and terrestrial non-indigenous species, yet the effects of most of these species on native populations, communities and ecosystems remain unknown. During their life cycle, salmonids traverse large geographic areas spanning freshwater, estuary and ocean habitats where they encounter numerous non-native species. To date, the cumulative impact of non-indigenous species on salmonids has not been described or quantified. We examine the extent to which introduced species are a potentially important risk to threatened and endangered salmon, ultimately by contributing to higher levels of life-cycle mortality. We identify and categorize all documented introduced species in the Pacific Northwest, including fish, invertebrates, birds, plants, amphibians and others. Where data exist, we quantify the impact of non-indigenous and range-expansion species on populations of threatened and endangered salmonids. For example, birds and fish predators are reported to consume 0-40% of juvenile salmon in some habitats. These data indicate that the impact of non-indigenous species on salmon is equal to or greater than commonly addressed impacts (habitat, harvest, hatcheries and hydro-system) and suggest that managing non-indigenous species impacts may be imperative for the recovery of these fish.

Nest site selection and spawning by captive bred Atlantic salmon, *Salmo salar*, in a natural stream

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We examined the physical habitat of nest sites chosen by hatchery Atlantic salmon, *Salmo salar*, in a recovery program for this extirpated species in Lake Ontario, Canada. We compared the sites used by these captive bred fish to a set of random locations in a wide range of available habitats in a stream formerly occupied by this species. Compared to random locations in the stream, the nest sites used by the salmon were lower in the relative abundance of sediment size classes that are detrimental to embryo and juvenile survival. In addition, the process of nest construction by these captive bred fish further reduced the proportions of these detrimental sediments. Although captive breeding may have changed some aspects of the nest site selection and construction behavior, it has not caused a complete loss or major alteration of the trait and thus does not preclude hatchery fish from restoration or reintroduction programs.

Evolutionary change in human-altered environments: An international summit to translate science into policy

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Human activities are affecting the evolutionary processes that generate and maintain biodiversity. Climate change and deforestation are facilitating the evolutionary jump of animal diseases to humans. Fish farming has resulted in the spread of poorly adaptive genes to the wild. Introductions of exotic species are impacting native species and limiting their ability to adapt. In response to this developing crisis, we are convening an international summit of evolutionary biologists, conservation practitioners, and policy makers to synthesize current knowledge and to begin to develop plans to mitigate the effects. The summit will feature talks from more that 40 top evolutionary biologists, poster presentations, and working groups. A central goal of the summit is to bring the discussion beyond academic boundaries to frame real-world solutions to these problems.

Thursday, February 8 - Saturday, February 10, 2007
University of California, Los Angeles
Sponsored by the Institute of the Environment

Population-scale response of sockeye salmon (*Oncorhynchus nerka*) to un-impinging a reach of the Cedar River

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The anthropogenic customs of flow regulation and bank hardening have synergistically reduced the potential for channel/floodplain interactions by smoothing natural hydrographs and damping sediment and wood dynamics. We analyzed nearly 50 years of sockeye salmon spawning distributions in the Cedar River, Washington before and after a major channel-changing landslide event in a lower reach of the river. Historically, spawning fish more intensively utilized the upper-most reach early in the run and the lower-most reach late in the run with temporal overlap in the middle reaches. Prior to the landslide, the spatial patterns of spawning distributions indicative of the relatively fixed habitat template in this hydrologically altered river. In response to the landslide event, the spatio-temporal distribution of spawning sockeye changed throughout the river particularly in the downstream-most reach. The magnitude of this disturbance event restored enough habitat function to the affected reach that phenotypic controls on spawning sockeye distributions were overridden at a population scale by inherent mechanisms that facilitated exploitation of the newly disturbed resource. This feedback provides insight into the scale of lotic processes required to elicit an evolutionarily significant response capable of counteracting the anthropogenic disturbances that affect rivers.

Modeling the migratory behavior of juvenile salmonids (*Oncorhynchus sp.)* in the Columbia River estuary: integrating biotelemetry with environmental observation and forecast systems.

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We examined the influence of flow velocity and direction of water movement on juvenile steelhead (*Oncorhynchus mykiss*) and spring/summer and fall Chinook (*O. tschawytscha*) migration patterns within the Columbia River Estuary by integrating biotelemetry and environmental observation and forecasting systems (EOFS). The underlying methodology included analysis of the spatial and temporal movements of juvenile out-migrant salmonids with hydrological data from the (Columbia River Estuary) CORIE modeling system (http://www.ccalmr.ogi.edu/CORIE). The CORIE modeling system, an EOFS for the Columbia River and nearshore environment, integrates a real-time sensor network, data management system and advanced 3-dimensional numerical models. Numerical simulations of key physical variables (i.e., water level, velocity, and direction of flow) were generated for the precise time and location that individual juvenile salmonids implanted with radio transmitters were present in the Columbia River Estuary. Five general behavioral trends were evident from these simulations; 1) passive movement (drifting) during ebb tides, 2) active swimming with the current during ebb tides, 3) active swimming against the current during flood tides, 4) active swimming cross current during flood tides, and 5) passive drifting during the flood tide. Direction of water flow affected fish velocity. Spring/summer and fall Chinook and steelhead transported from the Snake River system in barges or those that migrated in-river past Bonneville Dam showed a positive relationship between fish velocity and simulated drifter velocity with outgoing water flow. During low water velocity (< 0.25 m/s), this relationship was only observed in barged fall Chinook. With incoming water flow, this relationship was also found with steelhead, but not found with spring/summer and fall Chinook. Analysis over a 3-year period suggested that data from the CORIE modeling system corresponded well with juvenile salmonid migratory behavior and that this methodology may be a useful tool for evaluating the impact of different hydrological conditions on fish movement.

Anthropogenic impacts in an urbanized watershed: Genetic interactions in the colonization (*re-colonization*?) of the west-side tributaries in the Willamette River basin of Northwest Oregon

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Consideration of genetic diversity and structure is essential for effective conservation and management of native steelhead (*Oncorhynchus mykiss*) populations. We genotyped 712 individuals at 15 microsatellite loci to characterize genetic structure and patterns of gene flow that likely influence evolutionary processes shaping steelhead populations in the Willamette River basin. In addition to genetically characterizing steelhead, we sought to investigate the origin of potentially recently founded populations. Steelhead are currently distributed in both east- and west-side tributaries of the Willamette River, however it is unclear whether steelhead existed historically in the west-side tributaries. We detected significant genetic structure among populations ($F_{ST} = 0.056$; $P < 0.001$), and found that most interpopulation variation can be explained by a separation between east-side and west-side tributaries. The results indicate that the genetic integrity of native east-side tributary populations appears largely unaffected by introduced hatchery stocks; whereas steelhead in the west-side tributaries appear to be of mixed hatchery and wild ancestry. Understanding the genetic structure of steelhead populations will provide necessary information for directing fishery management decisions, evaluating risk, and prioritizing recovery goals. Our study shows a mixed result with respect to anthropogenic impacts on natural genetic variation. The challenge now is to characterize the ecological correlates that drive these different results.

Influence of supportive breeding on genetic diversity of hatchery and natural Wenatchee River spring Chinook salmon

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Genetic monitoring of weak and endangered natural fish populations supplemented by hatchery fish is necessary to predict loss of genetic diversity among local, natural populations as well as the influence of genetic drift and inbreeding on the evolutionary dynamics of supplemented populations. We examined the effects of a modern salmon supplementation program on the effective population size (N_e) and genetic diversity of a natural population of Wenatchee River spring-run Chinook salmon. Demographic and genetic estimates were used to estimate N_e. Genetic estimates of N_e were obtained by linkage disequilibrium and temporal methods using data from 11 microsatellites. Despite over a decade of supportive breeding and several years of very low returns, some genetic substructure exists among natural spring-run Chinook populations within the Wenatchee watershed. Demographic estimates of N_e indicated that fluctuating population size had the most substantial impact on reducing N_e in both the hatchery and wild population, followed by variation in reproductive success. Combining information from the demographic and genetic methods of estimating N_e indicates that small brood stock sizes and episodic disproportional contributions to future generations by relatively few brood stock may have decreased N_e of the entire population below a level that would have been attained if supplementation had not been initiated.

Recolonization of *O. mykiss* above Dams: data for the Green River

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An increasing number of dams built in the early- to mid-1900's are being considered for removal or modification that will permit salmon recolonization into upper watershed habitat. The presence of resident rainbow trout *Onchorynchus mykiss* above these dams potentially complicates the reintroduction of steelhead *O. mykiss*. To what extend will the two gene pools interact and will rainbow trout contribute to recolonization of steelhead? We are using genetic and phenetic data to monitor recolonization at five dam sites in the Pacific Northwest. In 2008, steelhead will be passed over the Howard Hanson Dam, Green River, WA, in an attempt to restore anadromous fish above the dam for the first time in 80+ years. We compared resident rainbow trout above the dam with wild and hatchery steelhead below the dam at 14 mSAT loci to estimate reproductive isolation and/or gene pool mixing, at 2 MHC loci that are presumably under natural selection for disease related characteristics, and at phenotypic characters (parr markings, fin size/shape, and body shape) that may be more closely associated with natural selection in separate habitats. Genetic differences were detected for the mSAT loci and one MHC locus between hatchery steelhead and four collections of resident trout. Resident rainbow trout also differ from downstream *O. mykiss* in the shape of the caudal peduncle and the number of parr marks. We discuss similar research in the Elwha and Lewis Rivers. Results of multiple restoration studies will provide NMFS with predictive tools for stock selection and monitoring of recolonization events and help in our understanding of character evolution and adaptation in isolated populations.

Evolutionary Changes and Salmon Workshop Reports
December 8&9, 2006

I. Evolutionary consequences of size-selective harvest

Participants

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Background

The workgroup discussed and attempted to evaluate what is known, and not known, about evolutionary effects on salmon through fishing. Anadromous salmon populations—as part of their complex life history, much like aquatic insects or amphibians—must contend with environmental challenges in two distinct habitats. Many salmon populations face threats to their viability even when conditions are favorable for survival and growth. The plasticity of their life histories, the remarkable precision of their often-extensive migrations between feeding and breeding grounds, and the unusual degree of female investment in their offspring may not always be enough to cope with fluctuations in the freshwater and marine habitats that they straddle. This problem is compounded if these fish must also respond to fishing pressure, abundant hatchery fish, or climate change. Although threats to salmon viability are often well documented, what remains poorly understood is the relative importance of distinct anthropogenic factors in threatening salmon viability. Factors such as fishing may be altering salmon life histories in ways that will reduce their ability to cope with future change, but it has not yet been possible to discriminate between these effects in a way that can inform future management. Although several recent studies are attempting to attribute life history changes in some species, such as Arctic cod and large marine pelagic fishes (e.g., swordfishes), to genetic effects of fishing, the arguments are still largely circumstantial.

Key Questions

To focus their efforts, the workgroup initially identified three guiding questions:

- Can we detect genetic effects of fishing?
- Can we quantify the selection and its response (and genetic variance)?
- How important is fishing as an evolutionary factor—for future evolution, for management and conservation, and relative to other sources of anthropogenic effect?

Methods

The group members evaluated the state of knowledge for genetic impacts of salmon fishing, after considering key features of salmon biology. For salmon populations, the genetic effects of any of these human factors on viability, including those of fishing, have not yet been ascertained. Studies of effects of fishing for salmon have a long history, but these studies generally fall into one of two categories: correlative studies that aim to discriminate fishery effects from other ecological factors, or simple models that assume the effects of these other factors are negligible. In any case, fishery managers do not yet take into account the effects of fishing in formulating management plans, beyond their immediate consequences for abundance. Since Ricker's (1981, 1995) seminal work on Pacific salmon in Canada, such studies of salmon have been surprisingly rare, in large part because discriminating effects of selective fishing from changes in density-dependent growth that reflect variable patterns of environmental change or production of hatchery fish is exceedingly difficult. As a result, despite a few recent studies that have attempted to determine whether fishing selection can alter life history evolution, the jury is still out as to whether salmon life history for any particular population responds genetically to fishing. The workgroup therefore decided to proceed by addressing three central questions:

- What are the likely evolutionary consequences for salmon exposed to fishing?
- Do these consequences matter, especially when considered with other factors influencing viability?
- What are the lessons for fishery managers—how prudent is it to continue to ignore this issue in management?

For salmon, the key traits that can be direct or indirect "targets" of selection include the following:

- Size (i.e., length, weight, girth)
- Age (scales with size)
- Fecundity (scales with size)
- Egg size (scales with size)
- Growth rate
- Run/spawn timing
- Sexually selected traits (e.g., hump size, kype morphology)

The selective impacts of fishing can encompass effects on genetic and phenotypic diversity, decline in genetic quality, and directional change in life history phenotypes. For salmon exposed to fishing, the direct targets of selection typically include body size or conformation, or run timing or migratory behavior. In addition to these factors, however, fishing may also have indirect effects on several important aspects of salmon biology that can affect fitness. For example, these traits include—through density dependent selection—survival, mating and reproductive success, and genetic quality. Unfortunately, discriminating possible confounding factors that also affect these traits is exceedingly difficult (and nearly impossible from the available information).

The workgroup members felt strongly that it was important to take stock of the "knowns" and "unknowns." What data are available? What data are needed? The data that are needed for a comprehensive analysis of genetic effects of fishing include the following:

- Trends in size (at age)
- Annual survival rates
- Growth rates
- Ages at maturation

In considering these data, the workgroup felt it was important to know "What data can we work with?" and "From the available data, can we come up with reasonable estimates of heritability, selection differential, and response to selection?" In addition, workgroup members felt it was important to survey the literature to glean evolutionary lessons from exploitation of other animals, including hunted mammals and birds, as well as other fishes.

Results and Conclusions

The workgroup concluded that the problem of genetic effects of fishing must be addressed in both the short term and the long term. Harvest managers focus on the short term, so it is imperative to try to identify genetic effects that can impact short-term fishery yields. One question to answer, if possible, is “To what degree is genetic risk of fishing adequately dealt with by risk-averse fishery management—e.g., simply through reduction of fishing mortality?” However, workgroup members also felt it imperative to identify any potential long-term impacts, including those that affect viability and extinction risk through changes in demographic and life history characteristics.

Ultimately, research into the ecological and economic consequences of evolutionary change brought about by fishing, especially as they affect ecosystem structure and the fishing industry, will be important to pursue. Workgroup members spent considerable time discussing the relative importance of fishing when considered against other anthropogenic influences, such as habitat degradation and large-scale environmental trends, including climate change. Each member wondered how the knowledge of these effects has matched up, or not, with the resources have been invested into each question.

Next Steps

The harvest workgroup decided as a first step to draft a paper highlighting the importance of considering evolutionary issues in managing and conserving harvest on anadromous salmon populations. To the workgroup members’ knowledge, there is no recent summary of these issues in the published literature. After considerable discussion, workgroup members decided that the focus of the paper should be on evaluating the evidence for these evolutionary effects and their implications for salmon viability, and the members concluded that the target reader should be the salmon harvest manager. The draft paper is planned for *Fisheries* (published by the American Fisheries Society), or a similar publication outlet, because of its wide readership among salmon managers and researchers. The following is a preliminary outline of this planned paper:

Evolutionary consequences of fishing: implications for salmon

1. Introduction
2. Evolutionary consequences of fishing have received comparatively little attention
3. Question: Does fishing have evolutionary consequences for the fish being caught?
    i. Does this matter?
4. Organisms are products of evolution
5. Adaptations: Life history, behavior, morphology
    i. Evolution by natural selection
    ii. Salmon: anadromy, homing fidelity, semelparity/iteroparity with age structure, large eggs, female parental care, occur over large environmental gradients, fishing on mixed stocks, high levels of artificial propagation
6. Theory of selection and its response
7. Our understanding of the “design” process
8. Fishing as selection
9. Types of fisheries

    i. e.g. terminal vs ocean
    ii. gear types
    iii. Selection targets: esp. size and run timing
10. Genetics and adaptation
11. Evidence for genetic variability in traits affecting fitness
    i. Size, growth, age at maturity, run/spawn timing
12. Response to selection
    i. Evidence for S and h2 indicate potential for response, but…
    ii. What is the evidence for evolutionary response to fishing in salmonids?
13. Why it matters
    i. Fishing-mediated evolutionary changes likely to have effects on productivity
    ii. Not clear how important these changes are relative to other anthropogenic influences
14. Conclusion

Some workgroup members were interested in exploring further research on the topic of evolutionary effects of fishing, perhaps through NESCENT or a similar funding program. Details of this possible research remain to be worked out.

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II. Anthropogenic influences on salmon disease prevalence and resistance

Participants

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Background

Infectious disease is an important component of all functioning ecosystems, and, along with a variety of ecological (e.g. predation) and anthropogenic (e.g. harvest) factors, helps to determine population structure and abundance. However, while endemic pathogens and their natural hosts are normally in a state of relative equilibrium, outbreaks of infectious disease may result when conditions change. This is particularly true for poikilotherms, where environmental conditions (e.g. temperature) have a substantial ability to alter the disease process or to serve as stressors that reduce the innate resistance of the host. Among the environmental factors affecting the host-pathogen relationship, alterations resulting from the activities of man have been of most concern; however, the long-term, evolutionary consequences of anthropogenic changes in the ecology of salmonid diseases are not understood. In this session, we reviewed factors that affect the abundance or pathogenesis of infectious agents and the mechanisms salmonids use to resist disease. Then, we discussed how anthropogenic influences could modify the type or level of selection imposed by infectious disease and the long-term genetic consequences to natural populations of salmonids. Factors covered included: hatchery practices, changes in water quality, habitat alterations and introduction of exotic pathogens or non-native species.

Key Questions

We addressed the extent to which human activities affect the prevalence of salmonid pathogens and the ability of salmonids to resist infection or disease. Key questions included:

1) What anthropogenic factors influence pathogen abundance and virulence?
2) What anthropogenic factors affect the innate and adaptive immune systems of salmonids?
3) What types of selection results from altered host-pathogen relationships?
4) What are the resulting evolutionary consequences of changes in disease selection?

Methods

We began by creating a table (Table 1) that listed potential factors that could affect the host-pathogen relationship and scored their importance as high (H), moderate (M), low (L) or unable to determine (?) for infectious diseases and the factors affecting the pathogen, host or alternate host. We did the same for non-infectious diseases. Where possible, we also coded these factors as having some experimental support (E) or speculative (S) and needing further research. We then set those factors in bold that appeared to have the greatest potential for affecting the selection pressure imposed by disease and discussed these further. Finally, we created a list of research priorities for this topic (see below).

Table 1. Anthropogenic factors affecting the disease process for infectious and non-infectious diseases of salmonids.

	Infectious diseases			**Non-infectious diseases**
	Pathogen	Host	IE	
1. Habitat				
a. **Freshwater temp**	H/E	H/E	H/S	H/E
b. **Contaminants**	M/?	H/E	H/S	H/E
c. Sedimentation	?	M/E	H/E	L
d. Loss (change density)	M/S	H/S	?	H?/S
e. Fragmentation	M/E	M/S	?	H?/S
f. Insolation/loss of riparian cover	L	L	L	M/S
g. Human recreation/noise	L	M/S	?	L/?
h. **Hydrograph**	H/E	H/E	H/E	M
i. Hypoxia	L	H/E	M/S	M/E
j. Obstructions (stress)	L	M/S	L	na
k. Nutrient/organic changes	M/E	L	M/S	M/E
2. Fisheries Management				
a. Conservation hatcheries				
i. Amplification	M/E	M/S	L	na
ii. **Hatchery fish released**	H/S	H/S	na	H/E
iii. Broodstock selection	H/S	H/S	?	H/S
iv. Broodstock collection	L/S	M/S	?	L
v. **Vaccination**	H/S	M/S	na	na
vi. **Antibiotics**	H/E	M/S	na	na
b. **Wild transport**	H/S	H/E	H/S	M/S
c. Harvest/Lowering density	H/S	M/S	M/S	M/S
i. Food web changes	M/S	M/S	?	M/E?
ii. Selection (size/age)	H/E	M/S	?	H/E
3. Aquaculture (commercial and public)				
a. **Escapees and releases**	M	H/E	?	M/S?
b. **Amplification (cultured to wild)**	H/E	H/S	H/S	na
c. **Introduction of exotic pathogens**	H/E	H/E	H/E	na
4. Hydropower Physical injury	L/S	H/E	na	L/S
a. **Crowding**	H/S	H/S	H/E	L
b. Transport	H/S	M/S	na	L
c. Reservoir temperature	M/S	H/E	M/E	na
5. Predators	M/S	H/E	M/S	na
6. **Alien species**	H/S	H/S	M/S	H/S

Potential factors scored as high (H), moderate (M), low (L), or unable to determine (?) and having some level of experimental support (E) or speculative (S). Bolded topics were judged to be of particular concern and were discussed further in the workshop.

Results and Conclusions

Workgroup 2 was pleased with the progress made in listing, distilling and discussing the anthropogenic factors that could modulate the host-pathogen relationship (or host resistance for non-infectious diseases) and thus result in potential selection pressure on salmon populations. Overall, the group concluded that, for the most part, these factors would not result in changes in levels of selection pressure by fish diseases that were beyond the normal adaptive capabilities of natural populations of Pacific salmon. There were, however, two areas that the group agreed might represent exceptions to the general ability of salmon populations to respond to changes in selection pressures provided by disease. The first would be for stocks that are relatively reproductively isolated and, for whatever anthropogenic reasons (e.g. harvest or habitat destruction), have a sustained small effective population size. The second case would be for the introduction of exotic pathogens or new strains of endemic pathogens by human activities (e.g. transportation of fish) that resulted in subsequent exposure of essentially naive fish to pathogens for which the natural population had no historical experience. Workgroup 2 believes that these two cases represent important examples by which anthropogenic effects could result in changes whereby disease could exert sufficient selection pressure to produce a significant evolutionary response in populations of Pacific salmon.

Next Steps

Additional research/analyses that could help increase our understanding or help resolve key uncertainties include:

1. Determine the reaction norms for pathogen susceptibility linked to historical, contemporary and predicted Ne as a function of:
    - Temperature
    - Contaminants
    - Flow/velocity
    - Density
2. Understand pathogen evolution in cultured populations
    - Evolution of endemics
    - Introduction of exotics
3. Determine transmission dynamics and life cycle of hosts
    - Age prevalence curves can model transmission rates and susceptible life hx stages
4. Investigate additive verses compensatory mortality and population consequences
5. Examine allostatic overload type II and diseases susceptibility
    - Interactions of endocrine and immune system
6. Understand factors that tilt host-pathogen balance towards the pathogen by disarming the host at small effective population sizes?

III. Evolutionary responses of Pacific Northwest salmon to global climate change

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Background

Climate can be considered as the force that structures the adaptive environment of salmonids. Hence it is important to consider the role of climate when investigating current and possible future evolutionary changes in salmon. The various life histories of salmon have long been recognized as adaptive responses to an environment that is highly variable within a range of values. The historical distributions of the different salmon species and the life history variants within species may, to a large extent, reflect the limits of their capacities to adapt to a range of environmental conditions. The kinds of changes we expect to accompany global climate change will profoundly affect the adaptive landscape of salmon through interactions between the expected long-term rising trend in temperatures and changes in streamflow (*e.g.* timing shifts in snowmelt systems, warmer water temperatures year-round, longer ice-free seasons, increased frequencies of extremely high and low flows). In addition to these changes in freshwater systems we can expect complex changes in physical ocean conditions and marine food webs.

The Climate Impacts Group (CIG) at the University of Washington has taken coarse-resolution gridded outputs from global climate models and applied them to the question of likely impacts on aquatic ecosystems in the Pacific Northwest in the 21st century. For a summary see: http://www.cses.washington.edu/cig/pnwc/cc.shtml. Observations show direct effects of a changing climate on salmon habitat in the PNW region that include:

- Regional air and water temperatures have risen in the PNW since 1950.
- The timing of snow-melt and peak snow-melt runoff has advanced by several days since 1950.
- Near-shore ocean temperatures and sea surface temperatures in Puget Sound have risen since 1950.

Based on global climate model simulations organized under the work of the IPCC, these trends are expected to continue into the future.

O'Neal (2002) modeled temperature as a factor limiting the range of cold water fishes in the United States and projected the shrinkage in these ranges under different global warming scenarios. He projected that the range of habitat available to Pacific salmonids will contract in the 21st century as a result of rising temperatures. Because his analysis was restricted to the continental United States he did not consider possible expansion in the northern part of the range. Ocean conditions will likely also change as a result of global warming. These changes, according to a pair of climate model simulations, may include a shift in the pattern of upwelling to become more intense and steadier off of the Oregon coast, and to a later onset of the spring and fall transitions. Rising upper ocean temperatures will result in a shift in the distributions of many marine species including prey and predators of importance to salmonids. Patterns in the longer-term cycles, including El Niño and La Niña, and perhaps the Pacific Decadal Oscillation, may also change from the historical as the atmosphere and oceans warm, but at this time climate models provide no clear indications that the behavior of these modes of ocean-atmosphere climate variations will change.

Key Questions

In considering how salmon evolution might proceed under climate change, the workgroup quickly came to several conclusions:

- Salmon populations currently exist under a vast range of different environmental conditions (e.g., from California to Alaska: Groot and Margolis 1991; Quinn 2005). It is therefore unlikely that an incremental change in climate would ultimately preclude salmon populations from occupying particular locations except under extreme conditions, such as the southern edge of the range or areas where temperature is already a limiting factor.
- Salmon populations in different environments show dramatic adaptation in a large range of traits (Ricker 1972; Taylor 1991; Quinn 2005). With the above observation, this realization highlights the point that salmon are capable of adapting to a great diversity of climate conditions. Indeed, this diversity of natural environments greatly exceeds the changes likely wrought by climate change in the "average" location. This means that the evolutionary endpoint can most likely be reached by salmon *if the conditions are right for rapid adaptive change*.
- Precise predictions about how a given climate change would influence a specific evolutionary change would be case specific. If we are to draw general conclusions, we therefore need to avoid specific predictions about specific adaptive changes under specific climate change scenarios.

All of these observations led us to the conclusion that:

> *The critical parameters informing evolutionary responses to climate change reflect the ability of traits to respond adaptively to environmental change.*

Investigations

Adaptive potential

To assess the ability of salmon, in a general sense, to respond to environmental change, we decided that it would be profitable to first list a series of traits that might show adaptation to different environments. The potential for these traits to change adaptively would then be assessed by examining the literature for evidence of their degree of plasticity, their genetic variance, and the rate at which they have been shown to change in the past.

Table 1. Prototype table comparing heritability (H^2), plasticity, additive genetic variability and time scale for adaptive evolution for a variety of life-cycle and physiological characters. “<” or “>” under Genetic vs. plastic indicates direction and strength of difference.

Trait	H^2	Plasticity	Genetic vs. Plastic	Additive genetic variability	Time scale for adaptive evolution
Return to freshwater:					
Time	High	Moderate	>		10 gen
Size					
Age					
Spawning:					
Time	Very high	Very low	<<<		10 gen
Size					
Age					
Growth rate	Moderate	Very high	<		30 gen
Stray rate	????	Very high	<		30 gen
Egg:					
Size	low	high	<<		Post-glacial
Number	high	medium	>		30 gen
Thermal preference curves	?????	moderate	=?		20 gen
Embryo development rates		moderate			20 gen
Ocean distribution					
Ocean migration path					
Freshwater Habitat:					
Spawning					
Rearing					
Ocean entry:					
Time					
Size					
Age					

We tested this idea by defining a list of traits that are subject to natural selection. For a few of these traits we provided qualitative assessments of heritability, plasticity, additive genetic variance, and the shortest time scale of observed evolutionary change for a range of traits (Table 1). From Table 1 we can generate some crude insights. For example, egg size shows strong, seemingly adaptive, plastic responses to growth rate (Jonsson et al. 1996; Morita et al. 1999; Quinn et al. 2004). If warming conditions increased growth rate, therefore, they might be matched by appropriate changes in egg size. Spawning time, on the other hand, is not very plastic but is highly heritable within populations (Smoker et al. 1998; Quinn et al. 2000; Sato et al. 2000). Selection on spawning time leads to quite dramatic genetic responses (Flagg et al. 1995; Quinn et al. 2002). Thus, these two traits might not limit population persistence in response to climate change or some other stressor – all else being equal.

Opportunity for empirical tests

It would be desirable to understand more quantitatively how particular traits might be able to respond to climate change. This could be done by examining existing variability over, for example, clinal gradients. Latitudinal/elevational range over space might approximate the effects of an expected increase in local temperature over time in which a temperature change is manifest. We might then ask how each of the phenotypic traits varies across this latitudinal/elevational range. This would give a prediction for how much the optimal phenotypic trait value might change locally (on average) with a particular amount of warming. From the literature we could estimate whether that amount of temperature change would lead to the equivalent amount of plastic change in the correct direction. This would indicate whether the plastic responses could immediately compensate for the environmental disturbance. Simple quantitative genetic models, with estimates of heritability, could be used to predict how quickly the predicted shift in optimal trait value could be bridged by genetic adaptation.

Complex interactions

The adaptive properties of individual traits are necessary to know in order to predict an organism's response to selection. However, throughout an animal's life cycle, processes are linked in time and have undergone selection to synchronize life history events with environmental events (e.g., entry of juvenile salmon into marine habitats and the abundance of food there; Cooney et al. 2001). To understand how complex interactions among selective forces and traits, particularly in relation to the linkage between the timing of life history events and climate change, we developed a conceptual model of the freshwater residence period.

It has long been recognized that many physiological processes in salmon are mediated by temperature. These include, in freshwater, embryo development rate and fry emergence timing (Beacham and Murray 1990), and metabolic rates of juveniles with implications for rates of feeding and growth (Brett 1983; Brett et al. 1982). Growth rates and size influence competitive interactions (e.g., Abbott et al. 1995) and habitat use (Nielsen 1992). Age of smolting in some species is related to size, and the timing of the smolt migration is affected by temperature as well as photoperiod (Quinn 2005). Life-cycle timing in individual populations has evolved in response to local conditions; thus similar growth rates produce different patterns of smolt transformation and maturation in different populations. The implication is that, with warming, this adaptive life-cycle timing could be disrupted, causing a reduced fitness, but also that different populations may respond in different ways both in terms of life history and abundance (Hilborn et al. 2003).

We illustrated the nature of this problem by positing a set of scenarios relating the timing of spawning, emergence, smolting, and ocean entry, to an adaptive optimum. We then mapped hypothesized shifts in timing in response to warming and speculated about the relationship of this changed timing to the adaptive optimum (Figure 1).

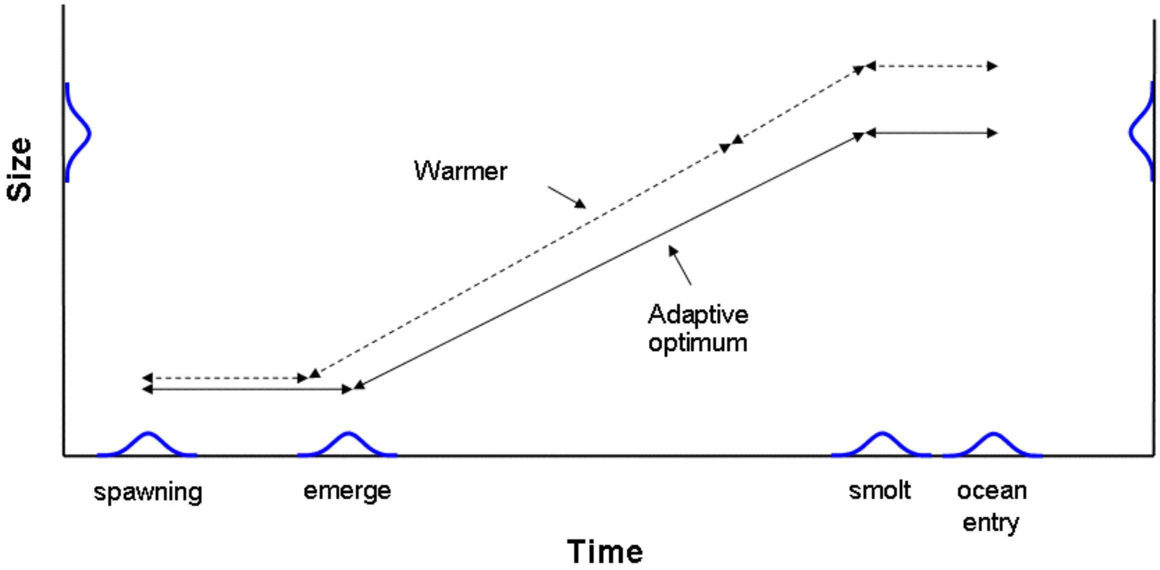

Figure 1. Possible effect of increased temperature on life-cycle parameters of a generalized salmon. The x-axis represents time from spawning through ocean entry. The blue bell-curves on the x-axis represent the distributions of optimal spawning, emergence, smolting and ocean entry times. The y-axis represents size, with the bell curve representing optimal size at smolting and ocean entry. The solid line shows an adaptive response to the optimal conditions. The dotted line shows the possible effect of increased temperature with consequent acceleration of egg development and earlier emergence, faster growth, and larger size at age.

In this scenario warmer temperatures lead to earlier fry emergence and a longer growing period with larger size at age. As a result, they may migrate to the ocean earlier in the season, at a younger age or at a larger size for their age, depending on the range of life history options open to the species (Holtby and Scrivener 1989).

We then considered a hypothetical climate change scenario to examine how the physiological changes in life history timing might relate to environmental shifts. In Figure 2 the top panel illustrates a life history adapted to environmental conditions. The middle panel illustrates how environmental events may shift; a later optimal spawn timing, earlier optimal emergence period, earlier onset of smoltification, and more variable ocean entry time with a weaker optimum. The bottom panel relates the physiological responses from Figure 1 to these changed environmental optima. The fish respond to a later optimal spawning period, and faster egg development leads to earlier emergence tracking the shifted emergence optimum. Even though the climate shift for optimal smolt timing is in the same direction as physiological smolting the accelerated rearing process slightly leads the climate shift. The more variable and weaker ocean entry timing optimum provides reduced strength of directional selection, so the ocean entry timing of the fish fails to adjust to the earlier smolt timing and ocean entry tends to be too early, disrupting this critical life history event.

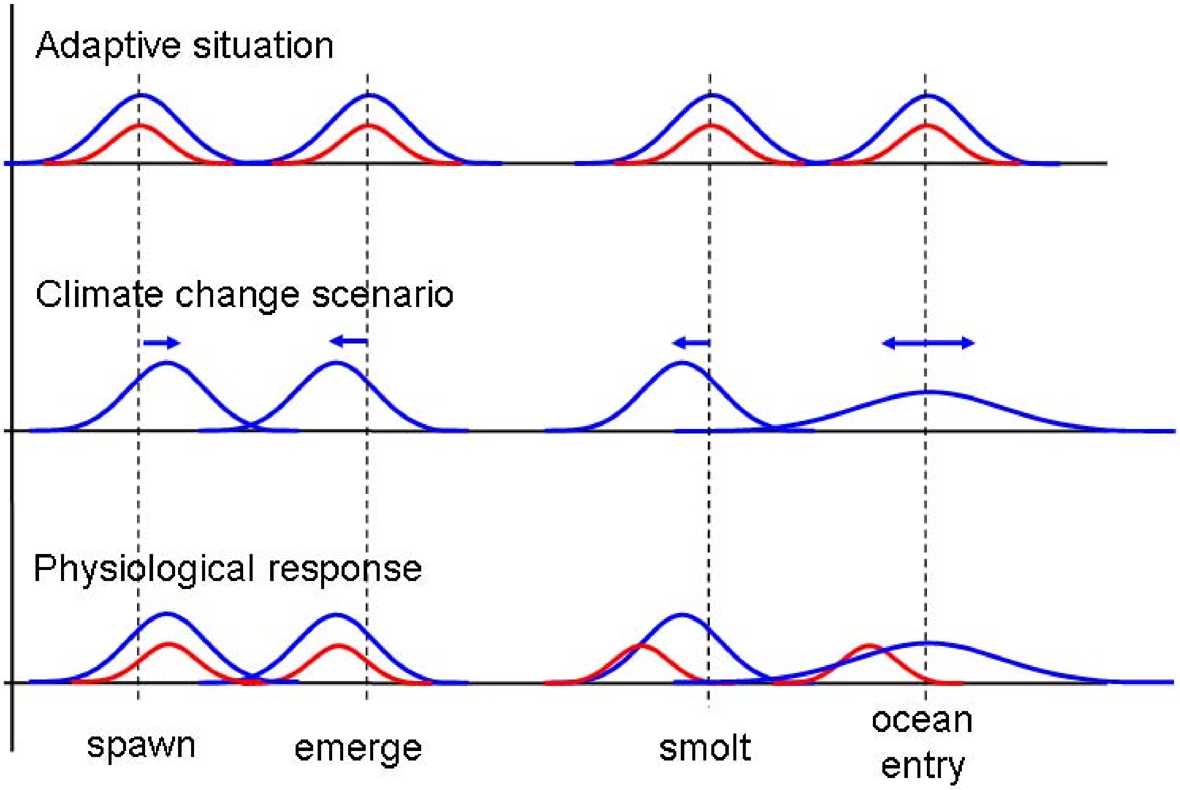

Figure 2. Hypothetical interaction between shifts in life-cycle timing and shifts in environmental optima. The X-axis represents time from spawning through ocean entry. The Y-axis represents the component of fitness dependent on timing, and the dashed vertical lines show the current optima. The higher (blue) bell curves show optimal response to the environmental conditions and the lower (red) curves show the actual biological response. The upper graph represents the situation where the response of the fish is adapted to current environmental conditions. The middle graph show a hypothetical scenario where optimal spawn timing shifts later, emergence timing shifts earlier, smolt timing shifts earlier, and ocean entry timing broadens in distribution. The bottom graph shows the likely physiological response to warmer temperatures in relation to the climate shifts.

Conclusions

We examined in a general, hypothetical way, some of the impacts climate change might have on a well-adapted salmonid population, and considered the adaptive potential of some important life history traits. Our illustrations here are intended as sketches, or prototype examples of two kinds of analysis that would improve our ability to evaluate and predict salmonid responses to climate change: (1) an analysis of the plasticity and evolutionary potential of life history traits, and (2) an analysis of potential shifts in environmental optima relative to life cycle timing, and the ability of the fish to adapt to these shifts.

We have not considered any specific cases, or even any particular salmon species. The potential influence of climate change on all salmonids is so pervasive and diverse that each specific case needs to be considered individually. Many aspects of salmonid biology not considered here may also be affected.

Our principal conclusions are that:

- There is apt to be enough variability extant in salmon populations so that climate changes of the magnitude projected for the next century are not likely to move environmental conditions out of the range suitable for salmon in the Pacific Northwest. Range changes, especially at the margins, are likely.
- There may be important disruptions to locally adapted populations as rising temperatures change finely tuned physiological rates of development and growth and as changing climate affects timing of environmental events and selection on day lengths used to time smoltification and migration.

Although our general feeling was that most salmon populations should be able to adapt to the challenges of climate change our view may be overly simplistic. For example, genetic correlations among traits under selection can profoundly affect rates of response, potentially slowing the rates of adaptation that we estimate. Another aspect we did not consider is the interaction between human societies and climate change. The lower mainland of British Columbia and eastern Vancouver Island are experiencing rapid development, as is the Puget Sound region. Human demands for water, flood control, power generation, forest resources and housing will all strongly interact with climate processes, accelerating rates of change and putting additional pressures on salmonids to adapt.

The current state of our knowledge about the nature and pace of climate change and the kinds of evolutionary pressures this will put on salmon is rudimentary. The examples in this workshop report are examples only; largely “data-free” and based on the knowledge and intuition of the workshop participants. We hope we have identified two approaches that can be applied to provide insights into the evolutionary implications of climate change to salmonids. Efforts to define and summarize the adaptive potential of salmon will be useful in a wide variety of evolutionary investigations. Case studies to elucidate the particular nature of life history adaptation and disruption will help provide understanding of the risks to salmon and their potential to meet the challenge of a rapidly changing climate.

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IV. Evolutionary consequences of habitat loss for Pacific anadromous salmonids

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Workgroup Summary

Anadromous salmonids have been blocked from large portions of historically accessible habitats in the western United States, either by passage barriers or by large-scale changes in habitat quality. The result of lost and altered habitats has been fundamental changes to environmental conditions associated with stream temperature and hydrology. Importantly, neither the loss of habitats nor the change in habitats has been uniformly distributed across habitat types. Rather, the upper reaches of rivers have tended to be blocked, often resulting in loss of access to particular kinds of habitat. For example, access to all of the high, arid reaches of the Upper Snake River – nearly 50% of the habitat previously occupied by Chinook and steelhead in the Snake drainage – is now inaccessible. Inaccessible regions in the Puget Sound, in the Willamette Valley, and in other locations throughout Oregon, Washington, California and Idaho also have unique habitats. Similarly, alterations in habitats that are at least relatively accessible may have similar effects. In the Puget Sound region, for instance, most of the Chinook populations occupying low-lying areas have been extirpated due to habitat changes. The decline of habitat quality in these regions precludes the expression of the late-run life history type unique to those regions. More minor changes, such as alterations to stream temperature or hydrograph due to irrigation practices may alter selective pressures, favoring earlier or later spawning, for instance, that would be present under normative conditions.

This loss of habitat can affect the evolutionary trajectory and long-term persistence or viability of salmonids in several ways. We identified two broad classes of effects: a) numeric effects that are a result of a smaller population size; and b) phenotypic effects that are a result of altered selective regimes. Numerical effects of habitat blockages include all the demographic effects associated with reduced population size. However, there are also evolutionary effects that can result from such a reduction. For instance, the reduction of capacity results in a lower effective population size. This, in turn, reduces the "reservoir" of variation available within the population. Similarly, extinctions (of populations or larger units) caused by blockages obviously results in the permanent loss of any traits unique to that population, but can also alter patterns of gene flow (and thus variation) among the remaining populations. Phenotypic effects are at least as great. First, because a number of anadromous salmonid life history traits, including spawn timing, run timing, and time of emergence vary with environmental parameters such as elevation, temperature and hydrology, the loss of use in these varying habitats may substantially alter the selective regime an Evolutionarily Significant Unit (ESU) or population experiences, leading to phenotypic and/or genetic changes within the group. Second, the loss of habitat may lead a salmonid population or ESU to use previously less-utilized habitats, and adapt to those novel environments. The reduction in capacity can also intensify selective pressures in the existing areas. The ultimate magnitude of effect from both these classes of impacts will be determined by the balance between changes in gene flow and changes in selective environment.

The overall impact of these habitat reductions at the species-level is probably substantial. The consequences of blocking habitat begin immediately, as capacity and population sizes are permanently reduced. In the longer term, the available genetic (and phenotypic) diversity available for the species to respond to novel or changing environments can be substantively reduced, as the loss of habitats narrows the range of habitats that are available in space and time. More dramatically, extinctions of populations and ESUs can eliminate some of that variation altogether. This combination of demographic and phenotypic effects has the potential to significantly reduce population and ESU-level viability in the long-term.

Key areas of future research include evaluating the consequences of habitat loss at various scales. This includes:

- comparative work, examining the relative life history diversity and nearly neutral genetic diversity in areas of differential habitat loss;
- characterization of phenotypic traits, examining the patterns of genetic covariance between traits involved in life history transitions and the range of tolerance to different habitat conditions;
- investigations of population and meta-population consequences of blockages, including changes in gene flow, and the rate and magnitude of fitness changes as a function of changes in habitat use.

V. Evolutionary response to changes in water flow regimes and temperature patterns

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Background

Habitat conditions such as water temperature and flow exhibit large amounts of temporal variation. Seasonal and daily variations are relatively well understood. There are clear seasonal patterns to the hydrograph that can be explained by predictable phenomena such as rainy seasons and snowmelt. Water temperature is understood to vary each day with changes in solar radiation, particularly in small streams. Water flow and temperature patterns may also exhibit variability at intermediate scales that are poorly understood but that can be quantified using wavelet analysis. Anthropogenic impacts such as dams and landscape transformation likely impact these variability patterns at daily, intermediate, and seasonal scales. There may be evolutionary consequences to changes in pattern at each of these scales. Therefore, these anthropogenic impacts may be having unknown evolutionary consequences. Salmonids are clearly adapted to natural seasonal patterns in flow as evidenced by run-timing strategies that allow passage over natural waterfalls. In addition, juvenile salmonids are adapted to daily and seasonal fluctuations in flow and temperature as can be seen in foraging timing, small-scale movement patterns and out-migration patterns. We expect that changes in water temperature regimes at multiple scales might impact spawn timing, egg size, or development rate, as well as growth rate and smolt timing.

Key Questions

- What are the potential physiological responses to changes in water temperature and flow patterns and how might those impact population-scale parameters (run timing, average morphology, life history transitions)?
- Can we relate changes in water temperature regimes to changes in growth rate or smolt timing?
- Can we relate past salmonid population performance to variability in water and flow patterns at particular scales?
- Can we detect changes in the variability of these patterns as a result of anthropogenic impacts?
- What are the evolutionary consequences of these complex patterns in habitat quality?
- Can we forecast how future changes might impact salmonid populations?

Methods

Before the workshop, we initiated an extensive literature review on two subjects. First we identified a set of key papers on impacts of land-use on flow and temperature regimes. Second, we searched for papers describing the impacts of changes in flow and temperature regimes on spawn timing in salmon. We chose this facet of salmon life history because it seemed that it might exhibit a particularly strong response to changes from natural regimes. We also identified a large set of flow and temperature data for gages in the Puget Sound area. We created a compact disk for each group member with the papers identified during the literature review and with the datasets.

Our first task in the workgroup was for each member to create a slide on a large sheet of white paper, outlining his or her ideas. The ideas presented are described in detail in the results section. This was a successful method for gaining active participation of all group members. However, it took a great deal of time. It did uncover significant confusion about salmon life history trajectories. We drew figures comparing habitat occupied and life-stage of salmonids to begin to organize and compare information on fish response and information on environmental attributes. We also spent a good deal of time defining basic terms in evolutionary ecology such as tolerance curves and plasticity. In general, the time necessary for aligning our ideas and developing a common language was much longer than most participants seemed to expect. This may have been a function of group size or it may have been an unavoidable consequence of mixing researchers with very different areas of expertise.

Once all the ideas were on the table, we began to brainstorm methods for linking the ideas into a cohesive project proposal or conclusion. Several ideas were tossed around but the group was focused on identifying and testing a hypothesis. Eventually, we settled on the idea of testing for an evolutionary response to change in thermal regimes below dams by comparing spawn timing and egg development rate between populations impacted versus not impacted by altered thermal regimes. We broke into three groups. One group worked on a conceptual model of how reaction norms might evolve and of how this might impact large-scale population dynamics. The second group aimed to identify environmental data on flow or temperature and on salmon populations. It was not possible to identify and clean the environmental data with only a few hours of time. Because we could not analyze any data, the statistical expertise within our group was also not utilized. The third group worked on how to incorporate potential evolutionary response to flow. We had a harder time making progress on flow than on temperature because of a mismatch in scales. Flow will impact salmonids at a very small scale, the speed of the water beside the fish; however, all available empirical data on flow is at a river reach scale. We generally have a daily, hourly, or maximum flow (cfs) for a particular river reach but we don’t have access to models that can then predict the water speed at the precise location of the fish. It was difficult to utilize the expertise of group members who work on flow.

By the morning of the second day, the group was very focused on designing and presenting the proposal comparing salmon populations experiencing altered versus unaltered thermal regimes. This proposal is described in the results section. In our final presentation, we outlined a plan for using existing empirical data to explore hypotheses about the potential evolutionary impact of altered thermal regimes. We also sketched out an idea for an experiment to test these hypotheses more formally.

Results

General ideas from the first day of the workgroup

Many factors influence thermal regimes including climate change, anthropogenic disturbance such as forestry and agriculture, and hydropower. These alterations can be acute or chronic. Chronic changes are the most likely to elicit an evolutionary response.

Salmon can respond to thermal change on ecological time scales as a function of their capacity for developmental or reversible acclimation. Growth rate will be one of the first things impacted by altered thermal regimes. The time scale of the thermal stress relative to the time scale required for acclimation will impact the success of any evolutionary strategy (Gabriel 1999). The predictability of the thermal stress and our ability to quantify it accurately will also be important for estimating population response (Gabriel 2005). Because salmon are tetraploids, they may be able to acclimate more readily than diploid fishes. On evolutionary time-scales, optimal phenotypes can be predicted from existing optimality models. The actual rate of evolution along the adaptive landscape will depend on the genetic structure of the populations. Relevant parameters could be estimated empirically or through model simulations.

Evolutionary change as a function of altered flow regimes depends on both discharge and channel form. Together these factors influence mean flow, variation in flow over space and time and the structure of flow over space and time. The impact of flow will depend on life history stage and fish size. The types of flow structures that are of significance include eddies and waves at all depths. These structures will vary across the width of the stream as well. Flow can be an abiotic depressor of fitness. We need to move away from only looking at mean flow data. There is a lack of flow data at the scale at which fish are experiencing flow.

Changes in the variance of flow and temperature will be important predictors of fish response. For example, studies on caterpillars demonstrated that domestication led to a loss of genetic plasticity. Have simplification of flow and thermal regimes led to a change in the plasticity of salmonids? Does increased environmental variation (scour, floods, droughts) lead to an increase in selection pressure? Is there a mechanism for maximal fitness under natural thermal and flow regimes?

What are our choices for empirical data? We could look for data on populations before and after flow or thermal change. We could use a space for time substitution. We could try to identify a selection differential, comparing those that survive with those that don't. This might be a possibility on the upper Columbia River or Snake Rivers where we monitor large numbers of fish at dams. Could otoliths be used to retrospectively assess thermal regimes?

Testable hypothesis on impacts of water temperature

Our major accomplishment was the creation of two hypotheses about how alteration of water temperature patterns is likely to generate or to have generated an evolutionary response in salmon populations. First, we hypothesized that increased variance in thermal regimes would lead to increased variance in spawn timing, migration timing, and egg development rates. And, therefore, that reduced variability in the environment might lead to a reduction in variance of life-history parameters such as spawn-timing or growth rate. Second, we considered large dams that release unseasonably warm water in the fall. This warm water increased development rates, fish emerge too early and die before they can successfully migrate to the sea. We hypothesized that the evolutionary response to altered thermal regimes such as those of the large dams on the Willamette River might include either slower egg development rates or later spawn timing so that fry would emerge later in the fall, as they would have under unaltered thermal regimes.

After the workshop, we wrote a proposal to examine whether dams are changing the evolutionary path of Chinook salmon by exerting selective pressure via altered water temperature regimes. If not, we would expect that spawn timing would be similar at dammed and undammed control sites, while egg emergence timing would be earlier at dammed sites due to faster development at higher temperatures (Fig 1A). If so, we would expect that spawn timing would be later at dammed sites so as to shift egg emergence timing back towards the optimal window for fry survival (Fig 1B). To test this hypothesis, we proposed to utilize existing water temperature and spawning survey datasets from dammed and undammed rivers in Washington, Oregon, and Idaho. Based on these datasets and both novel and conventional statistical techniques (e.g., wavelet and regression analyses), our three specific research questions were as follows:

1. Do temperatures differ during spawning and incubation at dammed and undammed sites?
2. Does predicted emergence timing differ at dammed and undammed sites?
3. Does spawn timing differ at dammed and undammed sites?

These questions are important because their answers will have major implications for scientists and managers alike. Exploration of the evolutionary consequences of human alterations to salmon habitats allows a new vision of salmon and habitat management. Given the prevalence of dams throughout the Pacific Northwest, the listing of Chinook salmon under the U.S. Endangered Species Act, and the impending effects of climate change on water temperatures worldwide, a clearer understanding of the full range of population impacts of altered thermal regimes will be required to best manage these species and their habitats.

Our research plan contained 6 major steps:

1. Select sites of two types (dammed and undammed);
2. Compile water temperature data and compute metrics;
3. Compare water temperature metrics between dammed and undammed sites;
4. Estimate and compare emergence timing at dammed and undammed sites;
5. Compile spawn timing data and compute metrics;
6. Quantify differences in spawn timing metrics over time at dammed versus undammed sites.

We also designed an experiment in which we removed eggs from populations spawning in undammed versus dammed river reaches and compared development rates in the laboratory between these two types of populations. This experiment was too costly for the grant program in which we were applying but the ideas remain interesting and can perhaps be incorporated in a larger future proposal.

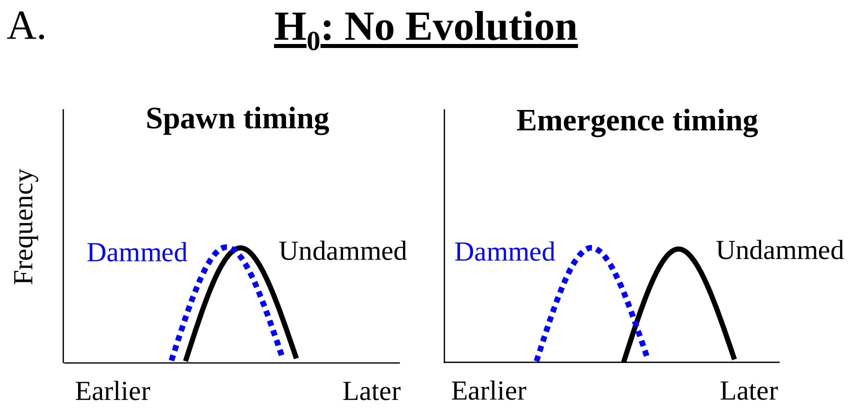
Conclusions and Next Steps

Overall our workgroup was a success. We exchanged a great deal of information and our discussions led to an innovative grant proposal and will lead to a collaborative manuscript describing our ideas. We plan to propose a manuscript for the special issue to be generated by this workshop. The manuscript will focus on the evolutionary consequences of altered thermal regimes. I expect that our group will continue to collaborate through the drafting of the manuscript and, perhaps, a second meeting or the funding of our internal grant proposal.

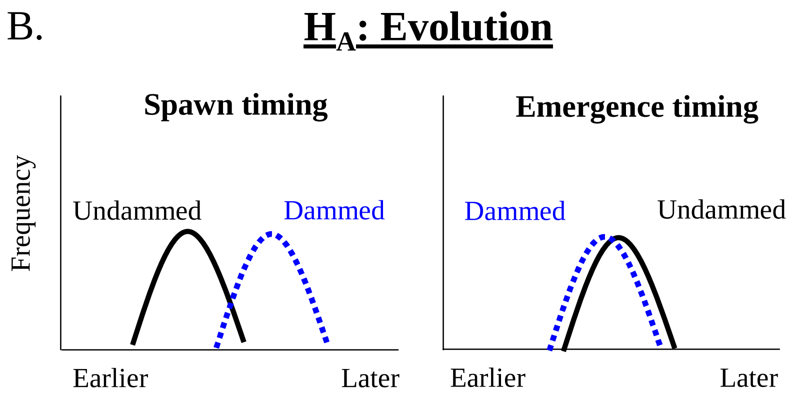
There are a few things that could have been improved. First, a group of 10 people was too large. With only 2 days, it was difficult for all ideas to be put on the table let alone to encourage discussions that included everyone. I would suggest a group of no more than 5 or 6 people for future meetings. Second, two days was too short of a time period given the large task.

It seemed that we were just warming to the subject and ideas were beginning to take shape when it was time to stop and focus on the final presentation. Thirdly, mixing two topics, e.g., flow and temperature, had serious limitations as some expertise went unused. For future groups, a more restricted topic area might help define groups in which all members could contribute evenly.

Figure 1. Conceptual diagrams depicting our proposed null (A) and alternative (B) hypotheses.



Dams increase temperatures in fall and winter but spawn timing does not evolve in response.



Selection for optimal emergence timing results in evolution of spawn timing.

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VI. Habitat fragmentation and population structure

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Background

One of the notable characteristics of salmon is that they return with varying but often high fidelity to their natal streams to spawn. The homing tendency is not absolute – a fraction of the adult fish ‘stray’ and return to breed in steams other than their natal stream. The net balance between homing and straying contributes to observed patterns of genetic variation among populations. Patterns of molecular genetic variation in salmon tend to be geographically structured, reflecting the homing tendencies of the species. Patterns of adaptive genetic variation among populations are much less studied, but available data generally suggest that salmon populations are adapted to local conditions. Changes in rates of gene flow are expected to influence salmon evolution altering patterns of local adaptation and perhaps by altering how the larger species adaptations as a meta-population.

Habitat fragmentation could affect salmon population structure in several ways. For example, fragmentation could lead to multiple smaller populations that spawn in discrete patches in place of what historically may have been a larger interbreeding population. Loss of intermediary populations might also result in a net reduction in gene flow among geographically distant populations. To the degree that habitat loss and fragmentation leads to greater geographic variance in population size, this will also influence the balance of immigration and emigration in populations. Population size is likely to influence straying in ways that are hard to predict. For example, large populations might be expected to produce more strays than small populations, but at the same time large aggregation of salmon may have a tendency to entrain fish from smaller populations, potentially leading to increased immigration into large populations. Habitat loss may also lead directly to higher rates of straying due to plastic behavior of the fish. For example, adult migrants may avoid natal areas that with high water temperatures and stray to higher quality areas.

Question of interest

What is the relationship between salmon population structure and population fitness? Does loss of population structure *per se* lead to measurable reductions in population performance?

How to answer the question

The workgroup recognized that there are both ecological/demographic and evolutionary/genetic components to these questions. There is an extensive theoretical literature on the properties of sub-structured populations (Charlesworth et al. 2003) and meta-populations (Hanski 1999). Using this background as a guide, the group developed a list of the information that would be needed to develop a practical model that could be applied quantitatively to specific salmon ESUs. This list includes:

- Number of populations
- Size of each population
- migration matrix among populations
- differences of selection functions among populations
- genetic basis for phenotypic variation that is under selection
- extinction risk of each local population
- intrinsic rates of growth for each population
- density dependence
- deleterious mutation rate

The workgroup concluded that although some information is known about each of these factors, in practice we are unlikely to obtain sufficient information to fully parameterize a "complete" meta-population evolutionary model for salmon. We therefore took a step back and asked ourselves what do we know qualitatively about the evolutionary characteristics of salmon ESUs. In general, salmon species (and ESUs) can be characterized as follows:

- Pristine salmon habitat is highly variable but highly productive. Local catastrophes (landslides, volcanoes, fires) are common, but of limited duration.
- Gene flow probably was (and now is) relatively high (2-10% immigrants per population)
- Local adaptation appears to be prevalent but is probably transitory on an evolutionary timescale (local population evolve over a period of decades or centuries to changing local conditions).

NMFS currently uses a similar characterization of salmon ESUs as the basis of its approach to developing biologically based recovery criteria (McElhany et al. 2000). In particular, after considering a similar list of factors, NMFS has generally recommended 1) conserving multiple populations spread across diverse habitats, and 2) preserve natural patterns of connectivity among them. The problem with these recommendations is that they do not allow recovery planners to compare multiple alternatives that arguably meet the recommendations.

How to improve our understanding of the relationship between salmon population structure and viability

1) Make better use of recently developed population genetic models to obtain more accurate estimates of gene flow rates among populations. Examples include using models such as the IM model (Hey and Nielsen 2004) to estimate migration parameters from genetic data, and making great use of isolation by distance (IBD) analyses to infer patterns of gene flow. As an example of the latter, the workgroup conducted a preliminary IBD analyses using microsatellite data from several populations of Snake River Chinook salmon Figure 1.

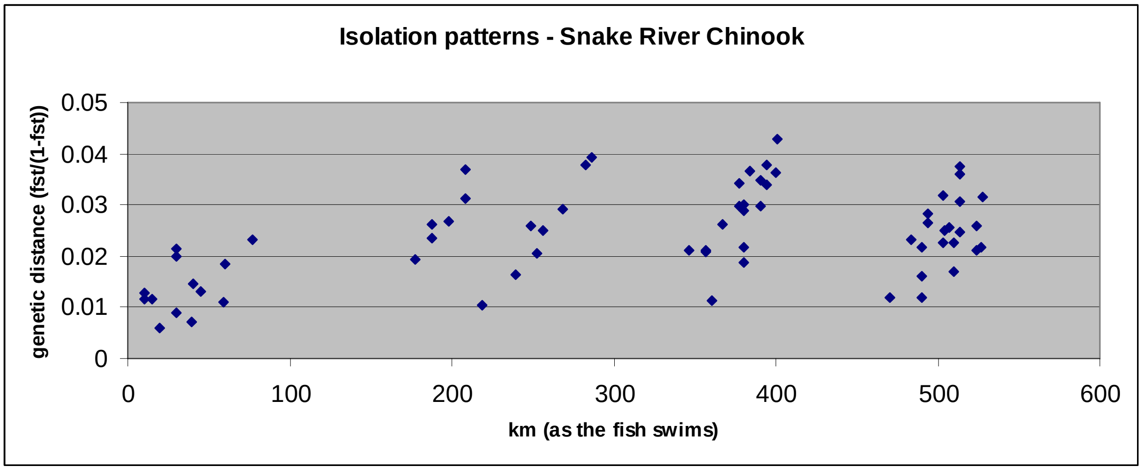

Figure 1 -- Relationship between genetic and geographic distance for Snake River spring Chinook salmon populations

2) Develop focused research projects to develop a better understanding of spatial/temporal variation in selection gradients on salmon populations. These might involve use of common garden or transplantation experiments, use of population genomic methods to identify genes involved in local adaptation, or greater use of PIT tag data to study relationships between fish phenotype and survival rates.

3) Conduct analyses to determine the scale of gene flow relative to the scale of the spatial heterogeneity of the environment. For example, although much of the discussion at the workshop was about population structure within ESUs, it is possible that gene flow among ESUs is of greater significance to population viability on evolutionary time scales than gene flow within ESUs.

4) Analyze how rates of gene flow will change with human actions. For example, small, more isolated population may be more susceptible to genetic deterioration and mutation load. Large, isolated population could become temporarily more productive due to lower migration load, but leave an ESU more prone to natural and man-made catastrophes. Artificially increased gene flow (e.g., due to hatcheries or poor habitat) may lead to lower fitness through increased migration load.

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VII. Snake River fall Chinook salmon: a case study in evolutionary responses to multiple anthropogenic changes

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Rich Zabel (NWFSC)

Background

Our workgroup was tasked with reviewing the evidence about what changes have occurred to Snake River fall Chinook salmon that might have resulted from anthropogenic actions, and whether these changes have led to possible evolutionary changes in fall Chinook salmon. We looked at a broad range of data, as follows:

1) Historical timing and size of Snake River Chinook salmon compared to the present run timing and size of juveniles. The data indicate that historically few juveniles were in the river after mid- to late June. Compared to the 1950s and 1960s, the present timing of smolts has shifted to a later distribution. ‘Actively’ migrating fall Chinook salmon from the Snake River presently spend 45-60 days migrating to/rearing in the Lower Granite Dam reservoir prior to arriving at the dam. Fish from the Clearwater River grow more slowly and take longer to migrate to Lower Granite Dam. Nearly all fish grow considerably prior to arriving at Lower Granite Dam. Additionally, in recent years (early 1990s to mid-1990s when stocks above Lower Granite Dam consisted of primarily wild fish), the wild smolts were much larger on arrival at Lower Granite Dam than were wild smolts that migrated in the 1950s and 1960s.

2) Releases of large numbers of subyearling hatchery fall Chinook salmon began in the late-1990s above Lower Granite Dam and increased from less than 250K fish in 1997 to nearly 2.45M fish in 2005. With the increased releases in hatchery fish, the size of wild fish arriving at Lower Granite has steadily decreased. The size now approximately sizes observed in the 1950s and 1960s.

3) As first identified by Billy Connor (although one might argue this type of life history characteristic was originally identified in Brownlee Reservoir in the early 1960s), not all fish migrate from the Snake River as subyearlings. A small percentage now migrates as yearlings. More importantly, however, based on scale samples of returning adults, in recent years, greater than 50% of the entire adult return passing lower Granite Dam came from fish with a yearling migration as a juvenile.

Key Questions

1) Does the change in size and timing of present day Snake River fall Chinook salmon migrants compared to historical conditions comport with the possibility of evolutionary change?

2) Will life-cycle analyses of Snake River fall Chinook salmon indicate that future populations will have life stages with different characteristics than presently exist, would viability change, and would analyses suggest that evolutionary change has occurred?

Methods

We spent most of our time discussing data and how it might inform us about potential evolutionary change. Steve Arnold had his model with him, but we didn't have the data on recent size and time. Billy Connor said he had data back at his office on the time of size of present day migrants and would get that to Arnold. Arnold's model will provide output that would indicate if changes in size and timing of SR fall Chinook salmon smolts comports with rates of evolutionary change. We also discussed the use of life-cycle models to see if changes in life-history characteristics would predict changes in future stock structure (or viability) that might vary considerable from what we see today. Rich Zabel is presently working on a life-cycle model as part of COMPASS efforts (a ne model under development for the new BiOp on hydropower operations) for Snake River fall Chinook salmon and when completed it should provide the ability to run these analyses. Billy Connor will work with Zabel to provide needed data. Jeff Hutchings said he could review Zabel's model and provide inputs/suggestions. .

Results and Conclusions

We decided that the data we discussed certainly suggested that evolutionary change may have occurred in Snake River fall Chinook salmon. We concluded that it was worthwhile to do more formal analyses to determine if we could detect some changes that might suggest that evolutionary change had occurred.

Next Steps

Our group expects to conduct some additional analyses to see if we can find evidence for evolutionary change. We have not set a time line, nor begun any work. Billy Connor will get together data for Steve Arnold's model, and Rich Zabel (and a host of others) are working on the COMPASS model. It should have the life-cycle component for Snake River fall Chinook salmon completed soon.