Speaking for the
Salmon

Continuing Studies in Science at Simon Fraser University | June 2002

Hatcheries *and the* Protection of Wild Salmon

Simon Fraser University
Burnaby, BC

edited by
Craig Orr, Centre for Coastal Studies,
Simon Fraser University
Patricia Gallaugher, Continuing Studies in Science,
Simon Fraser University
and
Jennifer Penikett, Centre for Coastal Studies,
Simon Fraser University

Hatcheries and the Protection of Wild Salmon

Acknowledgements
Continuing Studies in Science would like to thank the program sponsors for their generous support in making the briefing book, workshop, thank tank, and this publication possible. They are:

SIMON FRASER UNIVERSITY
Faculty of Science

BC Aboriginal
Fisheries Commission

Canada
Fisheries and Oceans Canada

Watershed Watch
SALMON SOCIETY

Pacific Fisheries Resource
Conservation Council

The David and Lucile Packard Foundation

Additional funding for publication of workshop proceedings was provided by:

TROUT UNLIMITED

VANCOUVER FOUNDATION
A PERPETUAL LEGACY FOR THE PEOPLE OF BRITISH COLUMBIA
ENDURING

We would also like to thank:

Workshop Moderators: Dr. Craig Orr, Centre for Coastal Studies, Simon Fraser University and
Dr. Richard Routledge, Statistics and Actuarial Sciences, Simon Fraser University

Special thanks to: Kirsten Doucette for her work transcribing the sessions and
Barb Lange for her formatting efforts.

ISBN 0-86491-230-7

Contents

CONVENERS' REPORT

Richard Routledge, Steering Committee, Statistics and Actuarial Sciences, Simon Fraser University

The conveners heartily thank all participants for the spirit of cooperation that pervaded the meeting. Discussion focused on the commonality of purpose in fostering abundant salmon populations, with as much quality habitat and genetic fitness and diversity left in place as possible to help them face an uncertain future. General agreement on this and other important fundamental principles emerged. Vigorous debates on difficult strategic issues also highlighted important information gaps. The meeting closed with a plan to create a working committee to press forward in building a consensus-based hatchery reform programme.

Commonality of Purpose
Underlying all the discussion was a sense of apprehension over the uncertain future for wild salmon populations, and a recognition that societal values and expectations have shifted in the closing years of the last century. Optimistic predictions of major increases in salmon "production" have been replaced by anxiety over possible extinctions of naturally spawning salmon in large geographic areas. Hatcheries that were built to provide enhanced fishing opportunities are now being called upon to save important salmon populations from extinction. There was general agreement that hatchery reform was needed in light of these changing expectations and needs.

In addition, a consensus emerged:

- That hatcheries and other forms of artificial enhancement cannot readily replace damaged or lost freshwater habitat;
- That we humans can never fully understand enough of the complexities of natural ecological and genetic systems to be able to maintain them artificially;
- That there can be no substitute for diligent maintenance of
  - high-quality natural habitat,
  - healthy freshwater and marine ecosystems, and
  - abundant, naturally reproducing salmon populations with their genetic fitness and diversity intact.

Several participants also stressed that restoration of damaged habitat, though valuable if properly done, was also far more expensive and less reliable than avoidance of the damage.

Shared Concerns
There was also general agreement that (i) hatcheries need to be viewed as components of complex ecological and genetic systems, (ii) hatchery evaluations need to focus on impacts on these systems. To this end, the more traditional estimates of juvenile and adult production and survival rates need to be augmented. Enhanced returns of hatchery fish might, e.g., come at a cost of reduced returns of other populations or reduced genetic fitness or diversity in wild fish populations.

Carrying capacity was also a recurring theme. There was general recognition that to overload a small stream with coho fry from a hatchery may do more harm than good. Participants also raised concerns of similar problems in overloading marine habitat with hatchery output. In addition, several participants stressed the extreme variability and uncertainty surrounding carrying capacity and associated survival rates, and emphasized that this uncertainty must be fully accounted for in hatchery reforms.

Strategic Intervention
This was the subject of lively debate. In the discussion, "strategic intervention" was interpreted as a limited use of artificial enhancement, typically including some sort of intervention in the reproductive cycle, to attempt to preserve a fish population from extinction. As currently envisaged by management agencies represented at the workshop, strategic intervention would take place when important populations were identified as facing a serious risk of extirpation. This intervention would be part of a recovery plan. This plan would delineate both an ongoing assessment strategy and specific rules for termination. Specifically, the effects would be carefully monitored with mandatory re-evaluations of the programme after each salmon life cycle, and the intervention would cease as soon as rebuilding targets were reached. Removals from the natural population would be aimed at minimizing the risk losing important genetic information in that population, and young salmon would be returned to the wild as soon as feasible.

All participants recognized the lack of clear theoretical guidance and policy for when to intervene. In the conveners' opinion, there are enough uncertainties surrounding the effectiveness of intervention strategies to question their value as conservation tools. Research on the ultimate value of such efforts is urgently needed in light of escalating numbers of declarations of threatened or endangered salmon populations. Those who supported strategic intervention listed the following as important criteria for deciding when to intervene: absolute population size, geographic extent of the population(s) at risk, rate and amount of the decline, and genetic structure and uniqueness. They also stressed that it was important not to wait until genetic losses had occurred. Participants also stated that special social and cultural values associated with individual populations might trigger earlier intervention.

Others cited evidence of potential harm from well-intended "strategic" interventions, and argued against their deployment. Some also pointed to the potential value of other, potentially less invasive conservation tools such as cryopreservation. The disagreement over strategic intervention highlighted key information gaps as outlined below.

Information Gaps

Major information gaps came to light repeatedly throughout the meeting. The following were identified as critical for making more informed decisions in hatchery reform.

- Goals: There is an overriding need for a comprehensive reassessment of the role of hatcheries in fish management. This would ideally lead to a hatcheries component in an overarching management framework. The comprehensive reassessment should eventually lead to a careful re-examination of the role of individual hatcheries, the setting of measurable goals for each hatchery, and the creation of a monitoring and evaluation scheme for assessing success in achieving these goals.

- Strategic Intervention: We need to reduce the uncertainty over whether a proposed intervention will do more good than harm. To this end, we need both

  (i) a thorough review of successes and failures of hatcheries and other interventions in conservation efforts (keeping in mind that the use of hatcheries for strategic intervention is a recent phenomenon and that there may be little to review),

  and (ii) a programme of designed experiments to develop more definitive evidence on the value of strategic interventions.

- Ecological Impacts: Ecological interactions in general were identified as high-priority items for further study. Of these, the following were highlighted:
  - Mixed-stock fishery impacts.
  - Carrying-capacity limits. Two key aspects were identified.

- The value of a better understanding of the causes of recent, large fluctuations in marine survival.

- The potential value of experimental manipulations in hatchery output to probe their ecosystem impacts. In this regard, participants noted the need for a thorough review of existing evidence, the need for an advance assessment of feasibility, including the probability of detecting a substantial carrying-capacity effect if one were present (i.e. an evaluation of statistical power), and a pilot study, possibly in a freshwater environment. Participants stressed the need for broad consensus and cooperation in an experiment that involved the manipulation of hatchery output across a broad geographic scale. For example, any experiment designed to probe hatchery impacts on the Strait of Georgia would require cooperation amongst all agencies involved in managing fisheries and hatcheries in the combined Strait of Georgia and Puget Sound regions. Furthermore, such an experiment would impact aboriginal, commercial and recreational fishing interests, hatchery workers, and others. It would require a major effort in public relations to bring these groups onside.

- Genetic Impacts: Of the many unanswered questions, the following emerged as the most important.
  - What is the comparative, lifetime success of hatchery vs. wild fish in lifetime reproductive success? Some experiments are being initiated by the U. S. National Marine Fisheries Service, but more are needed in a variety of geographic regions and on different species.
  - How soon do important genetic differences appear between hatchery and wild fish?
  - If these genetic differences infiltrate the wild gene pool, how long do they persist after a hatchery operation has been terminated?

- Zonation Issues: A map of enhancement-free salmon populations would help to assess present status. In addition, the issue was raised of creating special zones within which no salmon culture would be undertaken. The map would be a useful tool in helping to identify candidate areas for such a designation.

Implementation Issues

The group recognized the special difficulties in implementing hatchery reforms—even beyond those associated with other aspects of fish management. Both the Puget Sound and Coastal Washington Hatchery Reform initiative in Washington State and the Selective Fishing Strategy in British Columbia were praised as models to emulate. Key features that were highlighted were:

- Active participation at all stages of development and implementation from
- government agencies,
- hatchery operators,
- First Nations,
- local communities,
- commercial and recreational fishing interests,
- nongovernmental conservation organizations,
- independent scientists, and
- facilitators and communicators.

It is critical to bring all interested parties into the process to avoid alienation and polarization. In addition, the role of independent scientists in providing complementary expertise and perspective was stressed, as was the importance of involving people with the ability to facilitate consensus building and to communicate to the public the sometimes subtle, complex problems that need to be addressed. It is also important to recognize that both the hatchery reform initiative in Washington State and the Selective Fishing Strategy in British Columbia required a major commitment of resources. A similar process for hatchery reform in British Columbia would cover a much larger geographic area than the one in Washington State, and would involve more interest groups than the Selective Fishing Strategy. It would require even more resources. Participants stressed repeatedly the value, not only of creating a structure that could foster such a cooperative effort, but also of creating a network for continuing the discussions begun at this workshop. In particular, British Columbia participants stressed the value of learning from the experience in Washington State. The Think Tank session ended with a commitment to create a small working committee to pursue this vitally important objective.

INTRODUCTION AND OPENING REMARKS

Patricia Gallaugher, Director, Continuing Studies in Science and Interim Director, Centre for Coastal Studies, Simon Fraser University

I am welcoming you today on behalf of the Dean of Arts and the Dean of Science. It is good to see so many familiar faces, and we are looking forward to learning a lot, and some good discussions over the next two days, about hatcheries and wild salmon.

I would like to introduce you to Craig Orr. Craig Orr is well known for his work on fish conservation and the protection of wild salmon. He is the Associate Director of our new Centre for Coastal Studies, and he will be moderating the sessions today and sharing the moderating duties tomorrow with Rick Routledge, a professor in the Department of Statistics and Actuarial Sciences.

Craig Orr, Associate Director, Centre for Coastal Studies, Simon Fraser University, and Executive Director, Watershed Watch Salmon Society

I would like to welcome this excellent audience. I would especially like to welcome the speakers. They have come from all over North America. In fact, Ian Fleming flew in from Italy so he could be here. We are thankful for the high quality of speakers, and I hope everyone is as excited as I am to hear what they have to say on this important subject.

I would also like to thank the sponsors of this workshop, the first official workshop of the Centre for Coastal Studies, supported by Continuing Studies in Science. Our sponsors include Fisheries and Oceans Canada, and the Pacific Fisheries Resource Conservation Council; we have several members of the Council here today. Unfortunately, there is a concurrent Oceans workshop, so the Honourable John Fraser, Chair of the Fraser Basin Council, could not be here today. Other sponsors include Watershed Watch Salmon Society, the BC Aboriginal Fisheries Commission, Trout Unlimited, Long Live the Kings, and our main sponsor, the David and Lucile Packard Foundation, out of California.

The status and protection of wild salmon has been a major theme of a number of workshops at Simon Fraser University over the past few years as part of our Speaking for the Salmon series on the overall theme of wild salmon. Proceedings from those are available at http://www.sfu.ca/cstudies/science.

Why are we discussing hatcheries, and why now, especially since hatcheries have been around for more than 125 years? And are we just talking about hatcheries, or enhancement in general? Those are fair questions that several people have raised prior to this meeting. I think it is fair to say that enhancement is on the table for discussion. When you want to get somebody's attention, you use words that grab him or her, and then get them interested in the subject; that is why we mentioned hatcheries and wild salmon. However, it has been the large-scale production facilities that have garnered the most attention; attention that has focussed on numerous ecological, genetic, social and economic issues. These are the topics that we will be addressing over the next two days.

This dialogue is especially timely because as you may know, Canada is charting the future for its Salmon Enhancement Program, and attempting to finalize what many conservationists consider to be a very seminal document, the Wild Salmon Policy. At the same time, there are four separate panels in the US examining the issue of hatchery reform. We are extremely fortunate to have some of those learned reformers here today from both south and north of us. Maybe we can learn some lessons that will allow us here in Canada, and the Pacific Northwest, to provide better care for wild salmon.

Robin Waples has advised

> *"To the extent that we can depersonalize the debate about hatcheries and redirect energy to solving problems rather than trying to assess blame, the resource as a whole will benefit."*

This is a good overarching theme for dialogue over these next few days.

THE SETTING: WHY HATCHERIES?

Moderator, Craig Orr, Centre for Coastal Studies, Simon Fraser University

An Overview of Washington Hatcheries

Lee Blankenship, Hatchery Review Group, Washington Department of Fish and Wildlife

Washington State is noted for its hatchery system. Our first hatchery, the Kalama Hatchery on the Columbia River, was started in the 1890s. Since that time we have developed a full-fledged, large hatchery system. Today we have, including all government, tribal and state hatcheries, 140 hatcheries in the State of Washington. Washington releases about 180 million smolts per year and six to seven million steelhead. The adjacent state of Oregon puts out another 60 million hatchery smolts per year. It is a large system, and obviously a large part of the fisheries as well.

As we all know, hatcheries were originally designed to contribute to the fisheries. We had this fantasy of just putting fish out and there would be no end to the catch. We could just go and put more out of the hatcheries. That attitude has started to change over the years and is now coming into question. But nonetheless, even in Washington, 75% of our catch of chinook and coho still are of hatchery origin. Loss of habitat is obviously part of the reason for the hatcheries. In the Columbia River, with all the dams, about 90% of the catch is hatchery fish.

There are very few wild stocks, and of the ones we have left, several are listed under the Endangered Species Act (ESA). Even so, this last spring, for instance, we had a spring chinook fishery. The last time that I fished that personally as a recreationalist was in 1976, and I thought I would never see that fishery again in my lifetime because the stocks were going down. But thanks to good ocean conditions it has turned around. We were able to establish a fishery even though it was a mixed stock that had endangered listed salmon stocks. We had a fishery that lasted the longest since 1977 and it was based on hatchery fish. We had 75,000 angler trips in six weeks and just on the recreational side alone over $15 million was spent. There is some value there, especially where the habitat is gone. Until you can reconstruct the habitat, hatcheries do have a role to play.

Although traditionally we have always looked at them as putting fish into the catch, we have started to use hatcheries as a conservation tool. For example, we have a run of spring chinook in south Puget Sound, the only spring chinook stock in Puget Sound, and it enters the White River, which is dammed. The stock was going into a precipitous decline and in the late 1970s we were down to a dozen fish returning, and eventually down to zero adults of natural origin. Starting in 1977 we intervened with a captive brood program. This last year we had 800 adults return (all started in the hatchery, and some were returned to the river) which was more than we have had in the last 25 years. Thus, there is a new role for hatcheries as a conservation tool to bring stocks back. Obviously, without hatchery intervention, we would have lost that genetic resource, the only spring chinook of southern Puget Sound.

Another example, although it did not occur in Washington, is the Red Fish Lake sockeye. In 1990, three wild males and one female returned. From that, with a captive brood program, we have reconstructed a run. This last year there were 257 returning adults. That genetic resource would have been totally lost if we had not intervened. Granted, we did not step in until what I consider to be too late. We were down to only one female in the Red Fish Lake case. We are beginning to learn that hatcheries can be used as a tool, and we can step in before genetic resources become so limited.

These two initial programs showed us that we can use hatcheries for conservation purposes, as well as the traditional role of providing fisheries, which, is a very valued role because it gives us a clientele. In Washington, Oregon and British Columbia, catching fish is very much part of our culture, whether it is First Nations or the European transplant. If we did not have that we would not have the lobbying efforts for the habitat, or for sustaining wild fish.

The History, Goals and Direction of the Salmonid Enhancement Program (SEP) in British Columbia

Al Wood, Allen Wood Consulting

My topic is "Why hatcheries?" but it should be "Why enhancement?" as well. There are many things that take place in enhancement that raise the same concerns as with hatcheries. It is easy to think now about how anyone could have been so naïve as to build hatcheries that domesticate fish. What could they have been thinking about? In fact, your perception changes, your knowledge changes, and through time memory changes, and fades.

History of Hatcheries in BC

To understand the current setting for hatcheries, whether here or in the US, you have to go back to where we started from, where we hoped to go, and examine what we know now that we did not know then or that we did not pay enough attention to. Also, you have to address the question about where we would be if we had not enhanced.

In BC we also had hatcheries back in the 1890s. They ran for a number of years and focused mainly on sockeye. They were shut down primarily because no one could demonstrate that they were actually making a contribution to overall production. Then in the 1960s we started into a new round of enhancement. This was an unorganized program, partly stimulated by the federal Minister of Fisheries at the time, as well as by a number of different developments. It is worth taking a look at the factors that stimulated this.

First, there was a lot of success early on in the US hatcheries. There were large increases in US hatchery production of chinook and coho and were a lot of US hatchery fish being caught in BC fisheries. Second, there were early indications of success in the pre-Salmon Enhancement Program (SEP) hatcheries, spawning channels and fishways. There was also a lot of optimism about new enhancement technology such as lake and stream enrichment, Japanese-style hatcheries, and incubation boxes. Another factor was that there were really difficult ecosystem management problems and competition for habitat. For example, at that time we were dealing with a proposal for a dam on the Fraser River and proposals for a number of other hydro developments in the province. There were also increasing demands for water, industry, and agricultural and urban use. On land, transportation systems were spreading rapidly, as were logging, urban and industrial development. Most of this development was occurring down in the bottoms of valleys where it impacted salmon and rivers. Therefore, there were a lot of pressures.

At the same time, we were tied up in major salmon allocation conflicts. One was the US – Canada fish war from 1957 – 1992. Official Canadian government policy was to fish chinook and coho stocks hard to force the US into a more equitable Pacific Salmon Agreement. The focus for the fisheries was on US hatchery fish. Another allocation conflict that was growing rapidly at the time was between the commercial sectors.

Another factor in this pre-period was a general pressure for more fish. One of the reasons behind this was that the catching power of the commercial fleet was increasing rapidly and the competition between the geartypes was escalating. There was a strong salmon market and prices were high, and people were making a lot of money. There were also important calls for the rebuilding of depressed stocks on the Fraser and some other key areas. Again there was a push for more fish. I mentioned that we had a strong Minister of Fisheries, Jack Davis, at the time; as well we had an assistant deputy minister who had a strong enhancement background. Both were pro-enhancement.

The situation with the resource was quite different from what it is now. There were a lot of wild stocks around; no one was concerned about losing them like we are now. There was also a lot of diversity. You might think that we did not know a lot back then, but we were aware of most of the current problems. If you look at Peter Larkin's *Play it Again Sam*, an essay on Pacific salmon, he outlined just about all of the concerns of today. The only difference might be the emphasis; that is, a greater emphasis today on knowledge.

The Beginnings of the Salmon Enhancement Program

Before the Salmonid Enhancement Program there was a two-year well-funded planning time. It allowed us to develop a plan and test a number of strategies. One of the things that became obvious was that there was a problem of biological uncertainty with fisheries management, fisheries habitat needs, effectiveness of habitat restoration, and anything semi-natural or even quasi-natural. It was just very difficult to measure these kinds of things, especially in a very short time period.

At that time, fisheries management was still fixated on achieving Maximum Sustained Yield and there was common property management, but it was constrained somewhat by limited entry licences. It was still a long way from having controlled effort at safe levels, and it was a risk area. Habitat management was strictly a catch-up game dealing primarily with immediate impacts; most of the studies on the long-term impacts and ecosystem dynamics had not been done at that time.

Program Modeling and Analysis

By today's standards of assessment, what was done at that time was largely qualitative, just because of the difference of handling data before computer modeling was developed. Another important factor, at that time, was the confidence about enhancement. It was influenced by the capability of demonstrating an increased survival in the enhanced life stages and control of natural mortality factors. For example, in nature, the incubation *mortality* is about 90%, but once you plug the eggs into a tray, instead there is 90% *survival*. This is a number that impressed people.

Genetic Knowledge

A lot was known about genetics at the time, but it was mostly about fruit flies and plants. Nobody knew much about fish genetics, and this did not seem to be a problem.

Goals of the Salmon Enhancement Program

The first phase of the enhancement program was approved in 1977 for five years at a cost of $150 million; that is, $150 million in 1977 dollars. The program was later extended to seven years, but with no change in funding. The goals were, first, to increase production toward historic levels. The science of the day said that production was at least half the capacity that it had been historically. I quote from the cabinet document: "Salmon stocks on Canada's Pacific coast were once capable of producing catches of 300 to 360 millions pounds per year." The cabinet document also projected that without enhancement the current salmon production of 145 million pounds annually would decline a further 20 to 30% by the year 2007.

The SEP long-term goal was to increase production up to 190 million pounds per year. The phase 1 goal was to increase production by 50 million pounds per year, through the use of natural or semi-natural methods and short-term enhancement to rebuild populations. SEP was to use "a judicious mix of low, intermediate and high technology."

Another goal was to make it a profitable program. It had to be a better than a 1:1 benefit to cost ratio. This was an important factor in determining the direction of the program. It had to produce a diverse mix of benefits to be measured in five accounts: national income or economic accounts; the employment account; the regional development account; the Native people account; and, the resource and environmental account. The program also had to stake a claim on watersheds, for fish.

It was deemed important to demonstrate the value and importance of habitat and fish by investing in them. Again, from the Cabinet document: "The need for an immediate start on enhancement stems primarily from the fact that British Columbia's streams cannot continue to be protected for the production of salmonids on the argument of the potential value of production, if government is not willing to make a commitment to actually develop a productive potential." That was the BC government position then and that thinking still exists today.

Another important goal was to change public attitudes, awareness and knowledge about salmon and their needs, and to encourage public involvement in husbandry, and fish and habitat protection. There were also clear policies and directions on an array of issues. There were management considerations: to maintain the present species distribution; to extend the fishing season; to disperse the fisheries to equitably distribute the catch; to improve management capability; and, to maintain and rehabilitate small streams. There were also clearly defined enhancement technical selection criteria that dealt with manageability, enhanceability and desirability.

Another important goal was to use a "learn by doing" approach. The enhancement program was geared to respond to learning and to change the future design of operational practice. A lot was, and still is, being learned from those projects. Consequently, the program has mutated considerably to respond to learning. However, there is a lag between theory and practice. The goals, standards, and criteria that guide SEP have evolved, and those that guide non-SEP activities have evolved a little bit slower. After phase 1, SEP funding was renewed and extended, and has continued on an operational level ever since.

What We Know and
What We Did Not Pay Enough Attention To
First, I think we underestimated the importance of ecosystem and species balance and interactions. Maintaining a natural balance of production between species is very important. Looking back on the program we probably favoured chinook and coho enhancement over pink and chum salmon. We also underestimated the importance of carcasses nutrifying the watersheds and the numbers of spawners on cleaning spawning gravel.

Further, we did not pay enough attention to the importance of natural selection in maintaining the quality of a population. The genetic practices for hatcheries have evolved significantly over the past 25 years, from general, to much more specific. Many of the issues have been recognized and are considered in current guidelines. As we learn more, the guidelines are being updated. But there is a question: When fisheries on a hatchery stock are highly selective, where does the responsibility lie for fixing the situation? Should the hatchery genetic guidelines require compensation for this unnatural selection? Or is it someone else's problem?

Another sort of issue we that we underestimated, was that we had large budgets, and these types of budgets are difficult to spend meaningfully in a short time period; they tend to favour capital-intensive, "high-tech" projects. Also, economic targets limited the spending on non-production activities, such as evaluation of impacts on wild stocks, and things like that.

The other area we underestimated was variation in ocean survival. We were not as aware of the cycles in productivity as we are now. In hindsight, when you look back at that period, we were right near the peak in chinook and coho catch and production. It is probably one of the reasons that there was a lot of optimism around chinook and coho hatcheries.

Another thing that was in the background was that there was a false hope that enhancement could compress fish production into less real estate and less water and that it could be used to produce the same number of fish as natural production. This would allow for both increasing the levels of fish production and development elsewhere in the watershed. Since then it has become obvious that watersheds have a limited capacity for salmon production and development. There is a trade-off either between those uses or the amount of money it costs to maintain them. We also underestimated the time it would take to meet the agreed commitments and evaluation criteria for enhancement, particularly in relation to fisheries management. It took a long time to get to where we had originally planned. In BC we now have selective fishing so at least it is getting there.

Where Would We Be if We Had Not Enhanced?
This is an important question to ask when you are doing an evaluation. Fisheries would have been even lower on the pecking order, probably at the bottom of the list of resources. With no significant enhancement projects, other uses of water and watersheds would have had much higher priority than fish. With few public involvement projects there would have been low public awareness of the habitat needs of salmon. The public would have been more resistant to restricting development to protect fish. There would have been a greater acceptance of "writing off" of stocks. Without enhancement investment, development would have rolled all over the watersheds in the urban and developed areas. This means that there would be fewer, if any, viable salmon populations in the Georgia Basin area and much of the Fraser River.

Without a reasonable level of production, there is the question of how we would have been able to justify the cost of the environmental protection required to sustain wild stocks. With no enhancement projects we probably would have had a more natural mix of species in undeveloped areas. That may be an asset, but I am not sure. The knowledge that we acquired in preparing for, and as a result of, enhancement, would not have been available. That would include a lot of stock specific, coded-wire tagging, genetic, fish health, and other information. A case in point would be the recent stock specific protection of endangered coho stocks. It would not have been possible without the coded-wire tagging information that came primarily from SEP projects and enhancement budgets.

Because of the difficulty of measuring adult returns, too much evaluation has relied on using juveniles released, instead of adults returning. Also, hatchery evaluation is often limited to just the hatchery instead of the broader ecosystem and human impacts. The bigger picture information is costly but necessary in order to do proper assessment. The cost and difficulty of adequately monitoring the impacts on wild stocks is a significant limitation to assessing enhancement performance.

Assessment of projects that supplement natural production has been spotty. The 1994 study by Winton and Hilborn looked at four enhancement projects in BC, and concluded that they could not assess them for lack of information on wild populations. Even now, the best that can be done with current information is to compare the production in supplemented rivers with unsupplemented rivers in the same area. There is a clear picture that in many unsupplemented rivers the populations are lower than in the supplemented ones. However, there is nothing conclusive.

Effects of Selection

Some people talk about enhancement as if high survival is inherently bad. It does involve reduced selection but at the same time most enhancement methods are patterned after what we find in nature. For example, there are natural spawning areas that are more productive than spawning channels, and natural rearing areas that are more productive than artificial rearing facilities. Also, there are natural lakes that are more productive than enhanced lakes. One thing that some enhancements have is a human selection process for broodstock, matings, feedings, disease control and other factors. People are justifiably concerned about such selection.

We should also be concerned about the selective pressures of fisheries, habitat development and broader ecosystem impacts. A few years ago, Bill Ricker demonstrated a decrease in the average size of catch since the 1930s in chinook, and a bit more recently in other species. He made the case for size selective fisheries being a possible cause for this decline. A reduction in competition for spawning sites could also be a contributing factor that allows even the smallest fish to use good spawning areas and survive well. Whatever the selective pressures, the average size of fish has declined in some populations of all salmon species. These declines have been going on longer than enhancement and longer than the recent cycles of production.

The decrease in size affects more than just the size of the fish the fishery catches. It also affects the productivity in a number of ways. First, it decreases the fecundity and eggs deposited. The smaller fish cannot plant their eggs as deep as large fish, so they are more susceptible to flooding, predators, and other disturbances. Smaller salmon also produce smaller eggs that in turn develop into smaller fry. Smaller fry are more susceptible to predation and to predation for a longer time. In short, progeny from smaller spawners are expected to have a lower survival than those from larger parents. Also, unless the number of spawners is increased to compensate for this, the overall production inputs have decreased. In BC I know that they have not compensated for the decrease in size, so the number of eggs going into the gravel has gone down.

This may be outside of enhancement, but enhancement may have played a part in causing this. However, the question is: Is there an enhancement role in compensating for this kind of problem? I question geneticists' low numbers of spawners for a stock to be at risk. If that small a set of genes is enough to cope with the climate change and environmental stress that we have going on right now, I think fish already would have adapted to these changes. It will require something closer to one in a million genes or maybe one in ten million genes to cope with the kind of stressors that the fish are faced with today.

Are the few genetic markers that are currently used to identify stocks enough to capture any differences between populations? Is our science so good that we can say with confidence that the many populations now classified as a single stock are definitely a single stock? Do we pool populations into convenient stock groups so we can ignore individual populations? Is our science so good that we can be confident that lost populations can be rebuilt? The success at rebuilding populations has not been very easy, cheap or successful so far.

What Lies in The Future?

There are a couple of realities to think about when planning the future. It is very important to be realistic about what is going to happen, or what is possible in the future. For example, for salmon habitat, clearly not all will be retained; some will be traded off for the benefits of other resource development.

Climate change will aggravate current habitat problems and without intervention more salmon populations will be at risk. To compensate for these losses and to sustain overall habitat capacity and salmon production, habitat restoration and stock enhancement will be necessary in developed areas.

In fisheries management, each stock and population will not be harvested independently at appropriate rates. Mixed stocks and sequential fisheries will result in continued overharvest of weak stocks. Many fisheries will not be managed to compensate for habitat impacts on stocks. Fisheries impacts will continue to run down stock production and genetic diversity. To compensate for these impacts and sustain overall production, habitat restoration and stock enhancement will be necessary for weak stocks that the fisheries are not specifically managed for.

Such enhancements by themselves will probably have very poor economy. In enhancement, genetic changes from culturing can be reduced but will probably not be eliminated. More will be learned about how to improve the quality and enhance production. Progress will be reviewed and practices adjusted, at regular intervals. The questions will change but it will take time and resources to find the answers.

Summary

Looking back, the mistakes may be clear, but that is in 20/20 hindsight of 25 or more years of experience. One of the biggest mistakes was underestimating the complexities of salmon ecosystems, and failing to address problems of habitat protection, stock specific fisheries management and size selective fisheries. In enhancement the "learn by doing" approach and continued review processes have helped to update our understanding of many key issues. As a result of enhancement we have learned an incredible amount about salmon biology, migration behaviour, natural requirements, and genetics.

Instead of hiding from the problems we must try to solve them. Habitat restoration and enhancement should be important for effective habitat and fisheries management now and in the future. Is there anything we do that cannot be improved?

A Brief History of Fish Culture in BC and the Current Status of the Current Provincial Hatchery Program

Donald G. Peterson, BC Fisheries

I will address the history of fish culture in BC and focus first on early salmon hatcheries, and then early trout hatcheries. Then I will address current program goals and directions, including objectives and policies, and the role that the provincial hatcheries play in supporting recreational fisheries, and in small lakes as well, because I believe some of the things that are done in the non-anadromous side apply to the anadromous side, as well as our steelhead program. I will then wrap up with some of our experiences in using hatcheries to support stock restoration.

Why Hatcheries?

Here is a quote from an early paper, circa 1900 describing the circumstances leading to a need for hatcheries: "... surging economic growth, reduced stocks and political pressure from canneries." Sockeye canneries on the coast of North America were big business around 1900 and it was felt that as the huge fisheries developed to support those canneries, hatcheries could in fact make up for, or enhance, the numbers of sockeye available.

The first sockeye hatchery in BC was built on the Fraser River at BonAccord and a number of other major hatcheries were built in the ensuing years. These were not small facilities. Many of them had production objectives in the tens of millions per year and the total output of facilities in 1910 was about 500 million fish. If you look at the current production of the Canadian SEP program today, all hatcheries, spawning channels, and other operations combined, the production is around 500 million fish. Therefore, the enhancement programs of 100 years ago were very large indeed. Some of these hatcheries were on the Skeena, Central Coast, Rivers Inlet, Vancouver Island, and certainly on the Fraser River.

Concerns About Hatcheries

However, there were concerns about hatcheries even then. There was a federal commission in the early 1920s that reviewed the sockeye hatchery program, and recommended that scientific studies be conducted and operations stalled until the studies were finished. However, there was a major expansion three years later so that by 1935 there were another 10 major facilities operating. At least one major scientific study was launched at Cultus Lake, where they focused on looking at the efficiency of stocking hatchery sockeye fry against eyed-egg plants and naturally-produced fry. It concluded that the sockeye hatchery program was not making the grade at all and in fact, it was not providing much in the way of significant benefits. One scientist from the Pacific Biological Station commented that if the canneries would simply reduce their pack by about 20% they could more than make up for any of the hatchery production that was taking place.

Of course, this report came out at a very hard time for the western economy and the Privy Council in Ottawa made the decision to close all sockeye hatcheries in 1936. At that time, the federal government also transferred responsibility for sports fisheries to the Province. There were a number of sport fish hatcheries operating and in fact that was the beginning of the Provincial Fish Culture organization.

Freshwater Fish
The Province is responsible for freshwater fish. The first trout hatchery was located on Cowichan Lake, on Vancouver Island and there were facilities built in the Kootenays for the large Kootenay rainbow trout, in the Kamloops area to support the stocking of small lakes, and in the Okanagan at Summerland.

Early trout stocking programs in the province were extremely successful. The province has a dry interior plateau area with many lakes that do not have spawning areas for trout. They were fishless, yet highly productive waters, which presented ideal trout growing conditions. It was generally thought that by stocking native rainbow trout in these lakes, they could create excellent, world-class fisheries. People were coming from all over the world to fish lakes like Paul and Pinnaten, and still do so today.

Figure 1 describes the history of lakes and streams stocked in the province between 1896 and 2000. In the early years it appears that there were very few lakes and streams stocked but this is a bit misleading because many of the fish culture facilities at that time were run by fish and game clubs and there were no records kept. Certainly, the numbers in the period from 1900 to 1930 would be much higher if all the stockings had been recorded. In the period from 1975 to 1990 there was quite a large growth in the number of lakes and streams stocked and then in the last ten years or so a levelling off.

Also of historical interest is the number of trout, char and kokanee stocked (Figure 2). The numbers of systems stocked early in the century, at least the recorded ones, were small. The numbers of recorded fish stocked were equivalent or higher than what we are stocking today.

Provincial Responsibilities for Fisheries Management
Moving onto our current program goals and direction, I will describe the division of responsibilities within the Province for fisheries management, and how we manage our stocking programs, objectives and policies, as well as our role in recreational fisheries and conservation.

In BC, the Province manages freshwater fisheries and habitat and up until yesterday this was done by two organizations, the Ministry of Fisheries and the Ministry of Environment, Lands and Parks. This has changed with a new government, so the names do not apply today (today the agencies are: The Ministry of Agriculture Fish and Food and the Ministry of Water, Land and Air Protection). The federal government, through the Department of Fisheries and Oceans, manages anadromous salmon, salmon habitat and the marine fisheries. BC Fisheries, the headquarters organization of provincial fisheries, sets stocking policies, and all policies for fisheries management in freshwater for the Province.

Thus, we have an organization that is responsible for managing fisheries at a regional level. When it comes to hatchery programs, they determine which lakes will be stocked, which species, strain, number, size and whether the fish are reproductive or not. The section that I work for ensures that there is policy compliance by the regions when they select stocking programs. We go out and rear the fish, stock

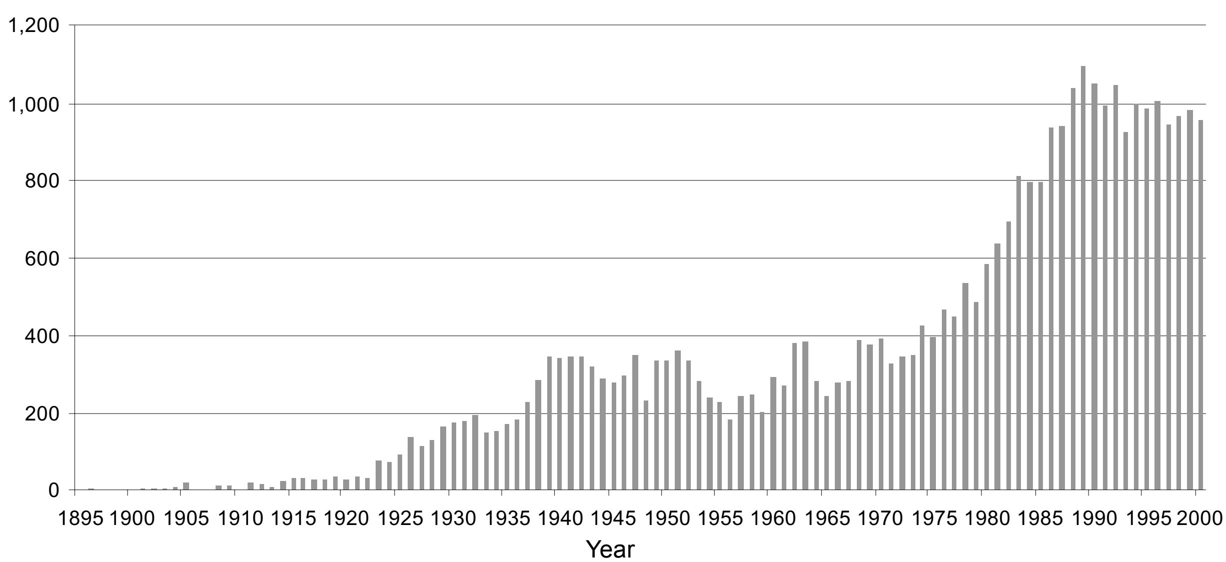


Figure 1. Lakes (and streams) stocked in B.C. 1896–2000.

the lakes and rivers and direct provincial culture carried out by others such as DFO. DFO raises steelhead on our behalf, at a number of facilities.

Provincial Government Fishery Policies

Our overall provincial stocking program objective is to deliver stocking programs that enhance angling opportunity and are consistent with wild fish conservation objectives. The provincial fishery policy has a conservation priority. We developed a new strategic plan about 15 years ago that embraced conservation of wild stocks and all our activities are supposed to be guided by putting wild stock interests first. Currently we have five major facilities; we also raise steelhead at twelve federal hatcheries and two provincial hatcheries as well as at five community and BC Corrections facilities (Table 1).

We have quite a list of policies that govern the stocking program. As mentioned, the overarching policy is for conservation. We are not supposed to conduct any stocking programs that are going to impact wild fish stocks. Our priority is to use wild, native, indigenous stocks to support hatchery production. All fish stocking and transplants are guided by a federal and provincial committee that does risk assessments on proposed stocking programs by looking at genetic, ecological and fish health factors.

We currently have a brook trout stocking policy. Brook trout are exotic to the province. However, they have been part of the stocking program since the early 1900s and there is a lot of support among the stakeholder groups to continue the stocking program. About five years ago we developed a policy to deal with the ecological risk of having this particular fish in the province. This policy includes things that direct the hatchery program to shift to stocking only non-reproductive fish and only stocking totally landlocked lakes.

We are currently developing more policies. After all we are government. Although I am making light of it, it is required. A number of policies are dated and they should be collated into an updated and more overarching approach with respect to how we are managing the stocking program.

As far as benefits go, as I mentioned, the provincial stocking program is primarily about supporting recreational fisheries. We stock about 950 small lakes each year, with about 10 million trout, char and kokanee. We raise seven species of salmonids and about 75 different stocks and strains. Again (Figures 1 and 2), over the past 10–15 years, we have been in a stable or slightly declining program. This is not because of lack of resources, but rather because of our greater attention to protecting wild stocks, refining our evaluation, and even taking lakes off the stocking list because of lack of angling interest.

I mentioned in the policy section that we want to focus on using wild stock in our hatchery production. In fact, about 80% of our production within hatcheries is coming from wild stocks. Also, about 80% of the waters we stock are small lakes, and the majority of those are considered hatchery systems, as there are no wild stocks. So it makes life much simpler than in a number of the anadromous programs and some of our programs where wild stocks are present (Table 2).

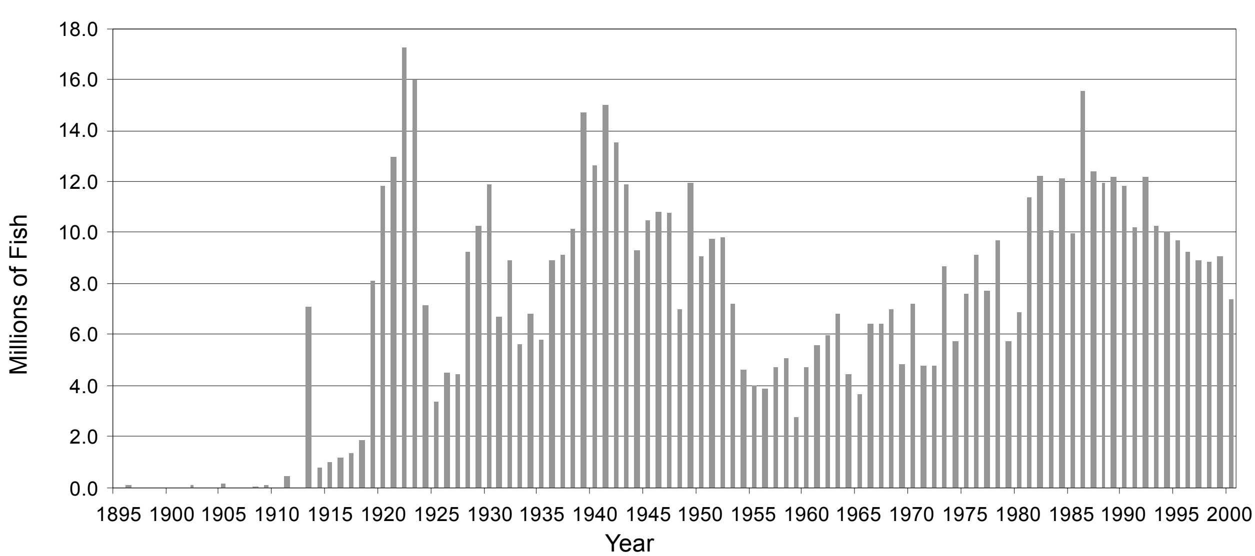


Figure 2. Number of Trout, Char and Kokanee stocked in B.C. 1896–2000.

We have a native rainbow trout focus, and a number of special rainbow trout stocks. These are wild stocks and our research group has determined specific characteristics which we are using in the hatchery program, to try to match habitat with stock type.

In terms of benefits, there are 400,000 licensed anglers in the province and the 1995 National Survey of Recreational Fishing included some questions that allowed us to determine how much effort was being conducted on hatchery lakes or stocked lakes compared with wild lakes. To our surprise, about 50% of all angling effort is on stocked lakes. This is quite interesting considering that there are 23,000 lakes in the province in total. However, not all of the lakes that are stocked are able to support a significant portion of the recreational fishery that goes on. In economic terms, there is about $400 million in angling expenditures each year, and a $250 million contribution to the provincial Gross Domestic Product.

Development of Non-reproductive Fish

We do have wild stock issues in our stocking program, and one of the ways we are trying to address these issues is through the development of non-reproductive fish. For example, we have stocked all female triploid Pennask rainbow trout in Island Lake, in the Kamloops area. Non-reproductive stock provides wild stock protection by minimizing the risk of hybridization. We have some lakes where we are stocking hatchery fish "over" a wild population. We also have lakes that have outlets where the regional biologists want to stock the lake to maintain a recreational fishery, but if the fish move out of the system they could impact wild stocks downstream. By stocking non-reproductive fish we can minimize the risk of hybridization between hatchery and wild animals. But as it turns out, by far the greatest benefit the non-reproductive program has brought is what one could call *product quality*. This is because many of the highly productive small lakes, particularly in the interior of the province, grow fish very quickly. We get early maturation in a number of our stocks, and there is also no spawning habitat, so anglers can experience catching "egg-bound" fish, fish that have not been able to release their eggs, or maturing males. We also experience a lot of male mortality after first maturation, so by stocking non-reproductive fish, we can provide anglers with silver-bright fish year round.

Figure 3 describes the growth of the non-reproductive program over the past ten years. We expect that over the next five years, where we are currently producing 1.5 million non-reproductive fish, that will probably move to represent 50 percent of our rainbow trout production.

I mentioned the brook trout stocking program and the move toward non-reproductive animals. This initiative was particularly challenging because nobody else in the world was doing this. There was some information on producing triploids, but no one had successfully produced an all-female line. Over the past five years our staff has been able to do that, and for the past three years we have been producing 100% sterile brook trout (Figure 4).

Evaluating the Program

One of the great failures of our stocking program (and of a lot of hatchery programs) is the lack of ongoing evaluation. We have gone through periods in our program in the last ten to fifteen years, up until 2000, where we were spending virtually

Table 1. Provincial Stocking Policies

Conservation • To conserve and protect all indigenous species in BC
Sources of Eggs for Fish Culture • Priority to use wild stocks for hatchery production
Fish and Invertebrate Transplant and Introduction • Fed/Prov. committee must approve any transfer/stocking • genetics, ecology, disease
Wild Indigenous Fish • management priority
Fish Stocking • priorities for stocking
Stocking New Lakes • procedures to guide selection of new lakes
Brook Trout Stocking Policy (draft) • priority to shift to sterile fish
Under development • Small Lakes Stocking "biodiversity"(2002) • Steelhead Stocking (2002)

Table 2. Wild and Other Special Brood Stocks

80% of production from "wild" brood stocks
80% of waters stocked are small lakes (generally, no wild stock issues "hatchery systems")
Native Rainbow Trout main species. • Pennask Lake rainbow • Blackwater River rainbow — Piscivorous, shoal feeder • Tzenziacut Lake rainbow — Piscivorous, pelagic

nothing on evaluating either the success or the impacts of stocking programs. Also, almost nothing is being done with regard to monitoring the health and distribution of our wild stocks.

In 2000, we were able to convince the Treasury Board to provide some funds to rectify the situation and we now have something called the Inland Sports Fish Development Initiative that has allowed us to start to enhance our monitoring program. We are looking at a number of issues (Table 3). Many of us believe that it is only through monitoring and evaluation of our enhancement programs, on an annual basis, not just once every ten years, that we can hope to move forward with an adaptive management approach.

Stocking Programs for Steelhead

The province is responsible for steelhead management. We work closely with the federal Department of Fisheries and Oceans on steelhead enhancement. The DFO provides steelhead culture at twelve facilities and we culture steelhead at two facilities. Those two facilities supply nine different systems.

The steelhead stocking program is guided by a steelhead stream classification system, which really has three categories: augmented, hatchery and wild. I have added a fourth catergory that is driven by our experimental living gene bank (Table 4). Of the roughly 890 steelhead systems in the province, the hatchery program is relatively small. There are approximately 20 augmented systems; augmented is where there is stocking in the presence of a wild population in order to produce a harvestable product. Hatchery systems are those where there are no wild stocks present, so there is no wild stock issue. The hatchery program can be mostly managed independent of wild stock concerns. In the wild classified systems, there are no hatchery enhancements permitted (Table 4).

Augementation Program Risks

I am sure that as we make our way through this workshop, we are going to be talking a lot about augmentation program risks. The risks include: domestication; hybridization; potential mixing of wild stocks through brood capture; competition and displacement risks, both in juvenile stages and in adults; and the issue of increased angling pressure on wild fish. We are certainly beginning to think that the effects of the steelhead recreational fishery on hatchery fish may be a larger issue that we first thought. There is also the issue of the hatchery programs and the fact that once they are in place and at a certain level, it becomes very difficult for governments to change them. This is difficult, even in the face of good science, because the public pressure just will not allow you to do so.

We have taken several steps to address the risk issue within the steelhead program (Table 5). We only use wild adults for brood. All hatchery smolts and fry are marked so we can differentiate them on return. We have a general stocking target of no more than one hatchery return to one wild return. Whenever possible, we release our smolts in the lower section of the rivers because experience has taught us that in most systems, smolts released into the lower section of the rivers will tend to return and the adults will

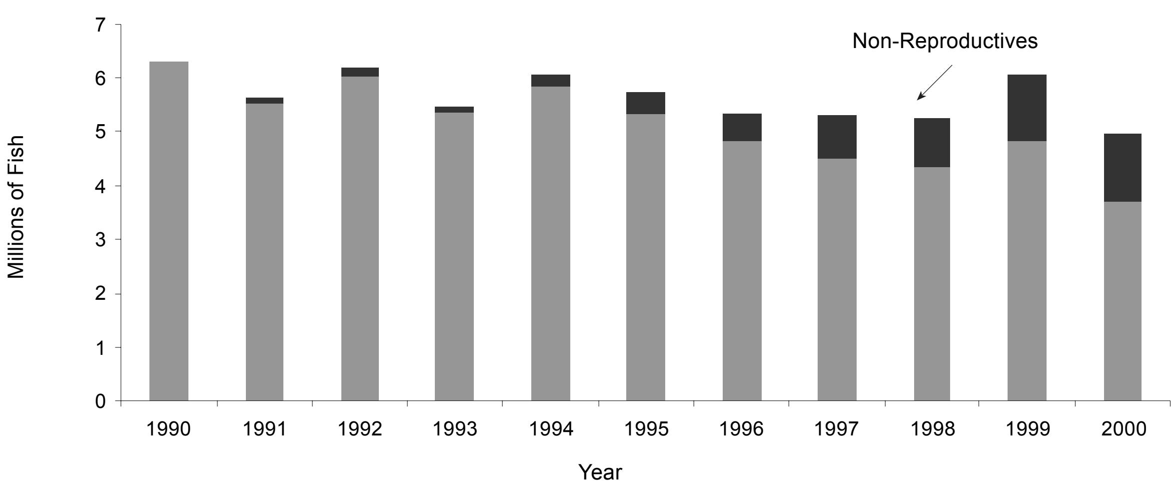


Figure 3. Rainbow Trout stocked in B.C

hang out in that area. It is not 100 % by any means, but the majority of the returns will stay in that area and the fishery can be directed on those fish, and allow at least a portion of the wild fish a refuge in the upper sections of the river. We also have the stream classification system. The majority of the province is designated as wild. Finally, there is the fish transplant committee that I mentioned.

Conservation Fish Culture

Fish culture programs present a changing role for fish culture organizations. To the south of us, our friends in the US have had some of these programs going for quite a while (20 – 25 years), but they are certainly new for us.

Within Canada and BC, recovery planning is going to be a driving force for fish and wildlife agencies. I think the Americans in the room can attest to that. The Federal Species at Risk Act (SARA) is going to be proclaimed soon. This is going to bring new urgency to both government and industry to get on with recovery of threatened and endangered populations, and fish culture does have a role there. In all cases the success of using fish culture as a recovery tool is uncertain, but in many cases it is the only alternative. Lee Blankenship mentioned the White River chinook and the Red Fish Lake sockeye. When you get wild populations dropping down to a few dozen or just a few fish you are pretty much stuck with fish culture to try to get out of that hole.

Currently, we have three conservation fish culture projects in the province, two for white sturgeon, one on the Kootenay River, in the southeast corner of the province, and one on the upper Columbia, also in the southeast corner of the province. We also have an experimental living gene bank for steelhead on Vancouver Island. We expect to have a fourth operation in the next few years for sturgeon in the central part of the province on the Nechako River.

Table 3. Inland sport fish development initiative

- Monitoring health/distribution of wild stocks/ fisheries
- Relative growth and survival of various hatchery stocks
- Cost effectiveness of stocking programs
- Biodiversity sensitive stocking policy
- Impact of various regulatory regimes (catch and release, etc.) on wild fish stocks

Table 4. Steelhead stream classification

Catergory	Number of Systems
Augmented – stocking in presence of wild population	20
Hatchery – no wild stock issue	5
Supplemented (experimental living gene bank)	3
Wild – no stocking programs	867

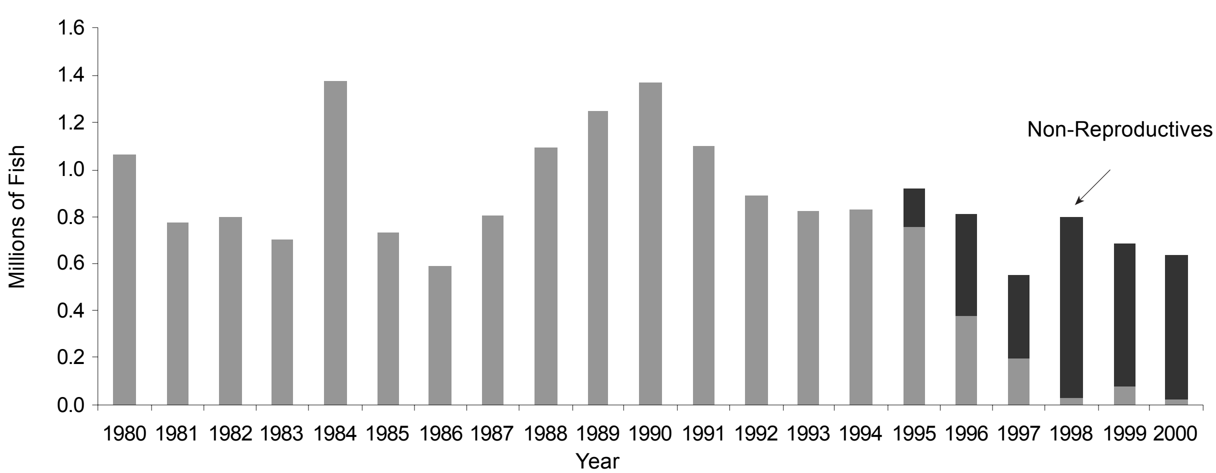


Figure 4. Brook trout stocked in B.C.

Table 5. Steelhead stocking program safeguards

- Wild adults for brood
- All hatchery smolts marked
- Stocking program target (no more than) 1:1 H/W
- Smolts released to the lower river (wild refuge)
- Stream classification system (wild, augmented, hatchery)
- Fish Transplant Committee – genetics, ecology, disease

As a fish culture organization, we find these programs to be very challenging technically. The focus has of course changed from mass production to maintaining genetic integrity of the target population. The Kootenay white sturgeon program is driven by an international recovery team led by the US Fish and Wildlife Service. The conservation hatchery program is led by the Kootenay tribe of Idaho, and they have invited us to be partners. We have built a small facility with funding from the Bonneville Power Administration and we are producing five families of 1,000 fish per year, and have completed two releases.

Living Gene Bank Project

The other example is the experimental living gene bank project on Vancouver Island. We have had a significant drop in adult returns for a number of East coast Vancouver Island stocks. Several of these stocks were in collapse, down to a few dozen fish. In 1998 we made the decision to start an experiment to determine whether a conservation hatchery approach could in fact assist with wild stock recovery. The Experimental Living Gene Bank (LGB) helps to maintain genetic variability and it works to avoid the ocean bottleneck. The LGB stocks large numbers of smolts, and allows returns to spawn naturally. In terms of mating, the LGB aims to use all available fish, randomizes female and male selection, avoids full sib pairings (where pedigrees are known), 1:1 or matrix pairings, and equalizes family contributions.

Looking down the pipe into the future with, for example, global warming trends, we thought it was quite possible that we may have many more of these situations. Are we going to go through cycles of low ocean productivity and then recover, and can hatcheries in fact help some of these stocks through these low productivity periods, and help them get back on a natural footing? We wanted to run an experiment, to see if, in fact, this was possible. We drew heavily on our American colleagues at Red Fish Lake and the Washington Department of Fisheries Dungeness chinook project. Actually we have had good success in the hatchery to date.

The program operates on collecting 100 wild smolts from three different systems, the Keogh, Quinsam and Little Qualicum Rivers. Wild smolts are brought into the facility and changed from natural diets to artificial diets, reared to maturity, and the progeny are marked and then released back into their home systems. We are going to do this for one generation only, so for five years we are going to stock these systems. All fish will be marked and we are going to run an evaluation program that will last 10 or 11 years. We will assess the returns from the program, if any, and monitor what happens on three control systems in which we are not stocking fish.

In conclusion, why do we have hatcheries in BC? We feel that when they are carefully managed and integrated within a conservation fisheries management program, hatcheries can provide significant economic and biological benefits.

Discussion

A participant asked Lee Blankenship: In 1976, when the catch was high for spring chinook, what was the percentage of hatchery relative to wild fish?

Lee Blankenship responded that he did not have those figures, but it was higher. In the catch of 1997, which are the only figures he does have, the catch was probably high in hatchery fish. It was not nearly as high as it is now. He does know that the catch this last year was 100% hatchery fish. It was the largest catch since 1973, and it was composed entirely of hatchery fish.

A participant asked: What are you expecting for the next few years of returns? Are you considering this a new trend, or is this just a one-time event?

Dr. Blankenship replied that the number of jacks that they saw this year were not as high as last year. Last year was an all time record return, the highest return that they have ever monitored on the Columbia River since they began monitoring in 1935, and again it was mostly hatchery fish. But even before there were hatcheries, or modern day hatcheries, there were abundant stocks in the 1940s of wild fish, mainly from the Snake River drainage. This return was higher than the return which was monitored this year. It is likely due to a change in ocean conditions. This year’s jack return suggests that we will have another good return next year, not as high as this last year, which was beyond everyone’s expectations, but still very high.

A question was posed to Al Wood: You talked about the use of hatcheries as a tool, actually to maintain or enhance, genetic biodiversity in areas where genetic erosion is suspected. To what degree do you have a genetic baseline for wild species, and to what degree do you monitor introgression between hatchery stocks and wild species?

Al Wood responded that this is a difficult question to answer since he has been out of the business for four years. The genetic monitoring program in BC is behind what is taking place in the US, but it is moving in across the province. Brian Pearce, Fisheries and Oceans, noted there has been some monitoring in BC, at the Pacific Biological Station.

Another question was directed towards Al Wood: Do you not think that hatcheries in BC have been put in a very bad light, because going back in history, they have been put on top of wild stocks? If they had been put in isolated areas perhaps we would now be looking at hatcheries in a different light.

Al Wood responded that if you look at the 'micro', just the hatchery and the river, that is probably true. But unfortunately, particularly for chinook and coho, their habitat is coastal. They are fished on for much of their life along the coast and it is highly mixed. When you look at most fisheries for chinook and coho you are not fishing a single stock; instead, you are probably fishing hundreds of stocks. In the 1970s they counted more than several hundred different marks from different origins, with a lot from the US, in the same central coast fishery. The only place you might be able to maintain a stock specific harvest is with river fishing but it will not solve the problem. For other species, pink and chum perhaps, this would be true. There are some areas where you have almost a pure fishery, but a lot of them are not, and it is not possible to achieve this under current fisheries management. However, with the current move toward selective harvesting it may become a lot more practical. The fishery is moving to be more selective, first species selective, and then, stock selective. That might help to address the problem.

A participant commented that Don Peterson had said that hatcheries provide significant economic benefits. Lee Blankenship mentioned something like a $15 million fishery, and Al Wood referred to this as well. Have any of the agencies actually done a cost/benefit analysis, in economic terms, not just of the revenue generated, but also the revenue expended and alternative opportunities for generating economic activity from those dollars? The participant has been searching for a full cost-benefit assessment and has not been able to find one, and wondered if there are some internal documents that might be available.

Al Wood addressed the issue from the federal government perspective noting that there are internal and external documents on the value of the federal enhancement program, and they are on the DFO website. Many of them are in public libraries as well. Probably the one to look for is the one authored by Peter Pearse in 1994.

Don Peterson noted that there has not been an all-inclusive benefit-cost analysis as was described for the provincial system. Some components of the system have been looked at in association with them going forward to build a new facility; for example, when they have had to make the economic argument for that facility. There has been some gross analysis done, based on angler use on stocked lakes and angler expenditures versus the cost of the program, but not an inclusive study.

Lee Blankenship addressed this issue by saying that he believed that the economics is important because it has always been the shortfall for all the natural resource agencies. The only information that they have, south of the border, is that the US government puts out the value of the fishery. But that really does not get to what the cost is. The closest thing for the state of Washington, was about six to seven years ago, when Natural Resource Consultants put out a document on coho salmon, describing what it cost, not just to produce, but also to manage so the production costs, as well as management costs, were in there. As he recalled, for Washington coho, it was $90 to put a fish in catch. This is the best document that he has seen on the subject. What they did was to take the value of a commercially caught fish, and the value of a recreational caught fish, and plug those figures into a benefit-cost evaluation.

Al Wood added that there is another relevant point; one of the things that is important is that a lot of the value of salmon and salmon fishing cannot be measured in dollars. A lot of the reason they are so important to the public is because of the non-dollar value and if you are going to look at evaluation, you must be sure to look at the other accounts. In SEP there was not only the economic account but also employment, renewal benefits, Native benefits, and resource and environmental benefits accounts. Therefore, you should be sure to include the whole works when you are doing your cost benefit evaluation.

A participant directed a question to Al Wood: In 1997 there was an assessment in BC and the Yukon on our wild stocks, and since then we have done nothing. When do you think we are going to get to an assessment of all the wild stocks on the coast of BC and in the Yukon?

Al Wood responded by saying that unfortunately he is not responsible for this. He noted that he does not know how you can manage something if you do not know what is out there and how much there is of it. The other thing, and that is unfortunate, is that to do this assessment is very costly.

EVALUATING SOME STATED BENEFITS OF HATCHERIES

Moderator, Craig Orr, Centre for Coastal Studies, Simon Fraser University

In this second section of this workshop Mike Berry and Bob Anstead will talk about the hatchery programs that they have been instrumental in setting up. There are a lot of hatchery managers here, so after the presentations we hope that they will also contribute what they have learned.

A Brief History of Nimpkish (Gwa'ni) Hatchery

*Mike Berry, *presenter, Inner Coast Natural Resource Centre*
Brian Wadhams, Councillor, 'Namgis First Nation

The Nimpkish Enhancement Program is the hatchery program that I am most familiar with, having worked in three hatcheries on the Nimpkish, and in various habitat restoration activities in that watershed and some others on Northern Vancouver Island. Unfortunately, at the last minute, the Nimpkish hatchery manager and field supervisor had other things to do and were not able to join us. Councillor Brian Wadhams is in the audience and can comment on resource ownership and any of the other social and economic issues.

I am mainly going to look at the history of what has happened on the Nimpkish since 1978, and the reasons we got involved in hatcheries and enhancement activities. I will look at some of the things other production facilities are doing and some of the limitations that production facilities may be facing in achieving the goals that were originally set out. The following brief history of Nimpkish River hatchery activities is not intended to be "a case history of claimed success." Rather, it is intended to stimulate discussion on the need for assessment of hatchery benefits and hazards, and to open up the discussion of factors influencing stock rebuilding that may be out of our control, or ability to measure.

The whole Nimpkish enhancement and restoration program began in the early days of SEP. We were involved in the original planning, in 1977 to 1978. It is one of the early 'kids on the block', which maybe makes it a good example for this presentation in that it has a long history.

Why did we get involved with enhancement at all, and why did we choose to go to a production hatchery? In the beginning it was not a production hatchery, it was small plywood boxes at the mouth of the Nimpkish River. Many of the early community

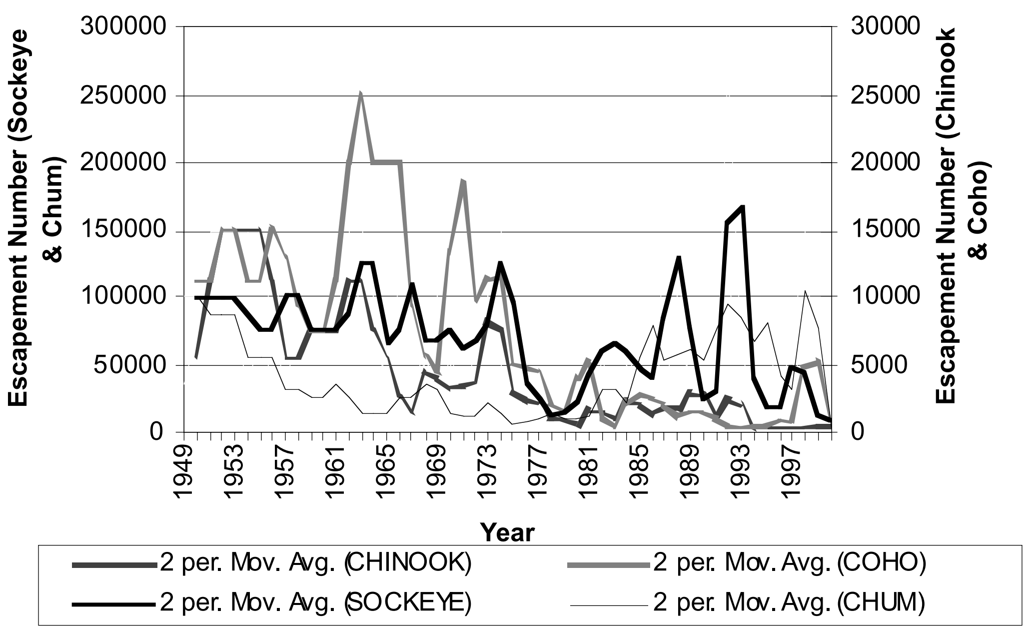


Figure 1. Nimpkish River (Gwa'ni) Escapement History

economic development hatcheries were similar small-scale operations. The question "Why Hatcheries?" has been presented. When the 'Namgis First Nation first became involved with SEP in 1978 it was in response to the drastic declines in abundance of all salmon species shown in Figure 1. The Nimpkish had, historically, been a major sockeye producer, but by 1978, returns were as low as 8,500 adults. Other species had demonstrated similar declines since the late 1950s. A combination of fishery management strategies (e.g., Area 27 closure) and enhancement appeared to be having an impact on rebuilding stocks (1988 to mid-1990s). However, we are again experiencing dramatic declines in spite of rebuilding efforts.

These are pretty broad trend lines based on escapement estimates. In the early 1970s declines were observed in all stocks. I do not think this was just a function of increased observation because we happened to have more crews on the ground. The declines of all stocks started to terrify the 'Namgis First Nation especially, who are heavily reliant for food, cultural and ceremonial purposes on sockeye and chum salmon. The numbers of sockeye in 1979, for example, were down to as low as 8,500 in a system that formerly, we think, had an abundance in the order of a 250,000 to 300,000 annual escapement, with a fairly consistent fishery on it. It was certainly a large food fishery, and perhaps in the top four on the coast. It is always a good argument with the Oweekeno Rivers Inlet people to decide whether the Nimpkish and Rivers Inlet stocks were of similar abundance, but certainly, the Nimpkish was in the third or fourth position in British Columbia as a sockeye producing system.

Hatchery activity in the Nimpkish began somewhere in the 1919 to 1920 period, with a hatchery we later discovered was in the exact location we chose to build our second hatchery operation, at the head of Nimpkish Lake. About 1.5 to 2.2 million sockeye fry were released annually at the upper end of Nimpkish Lake from 1919 to 1930. The hatchery was basically run by a number of Chinese railway workers who, once the railroad was finished, were displaced into a hatchery setting at the top end of Nimpkish Lake, in the middle of nowhere. It was kind of interesting to find old tarred incubation trays, cutlery, and all kinds of stuff buried in the bush.

Table 1 describes the history of the Nimpkish hatchery. In 1978, in the beginning part of SEP, it was strictly a couple of plywood up-welling incubation boxes running out of a couple of garden hoses at the mouth of the Nimpkish River. The water source was a beaver pond of dubious quality, and this was mostly a training exercise. We actually had started it as an aquaculture training program from 1976 to 1977, with Bill Pennell and Dan Gillis trying to set up a coho farming operation with the 'Namgis First Nation.

We had plywood incubation boxes with 60,000 – 70,000 chum in each, some fry output, zero assessment activity, followed later by a major, mostly sockeye, facility built at the head of Nimpkish Lake, at the site of the previous hatchery.

Table 1. Nimpkish (Gwa'ni) hatchery history.

1978	Plywood Incubation Boxes for Chum at Mouth of Nimpkish River
1979–1988	Sockeye, Chum, and Coho Hatchery Operated at Willow Creek (Upper Nimpkish Lake)
1984–1990	Chum, Chinook, and Coho Hatchery at Cheslakee (lower Nimpkish River)
1990–2001	Chum, Chinook, and Coho – New Major Hatchery (15M) at Cheslakee (lower Nimpkish River)

The Willow Creek hatchery turned out anywhere from 1.0-3.5 million fry annually, mainly sockeye. Later we got into coho and chinook enhancement and, illogically, we were incubating chum up there, in the totally wrong part of the watershed and wrong water temperatures. We had little knowledge of wild stock timing; as I said, I am not going to talk about all the stated benefits of the facilities we have operated over the years, nor or am I going to condemn any of them.

From 1984 to 1990, basically because of the chum question and the timing of chum releases, we ran a pilot hatchery program down at Cheslakee, which is right at the mouth of the Nimpkish River. The Nimpkish River is a huge watershed, the biggest on Vancouver Island, with an area of over 2000 km^2 and five major sockeye rearing lakes. We moved the chum facility down into some ex-school board library trailers and that was followed, in 1990, by the construction of a fairly major facility. SEP facility engineers were involved in the design and that probably defines the structure and what the hatchery looks like today. It has a potential capacity of around 15 million fish output, predominantly chum, although we are producing coho and chinook at that hatchery as well.

Sockeye incubation stopped in 1988 and the 'Namgis First Nation is extremely interested in re-establishing some level of sockeye production given that in spite

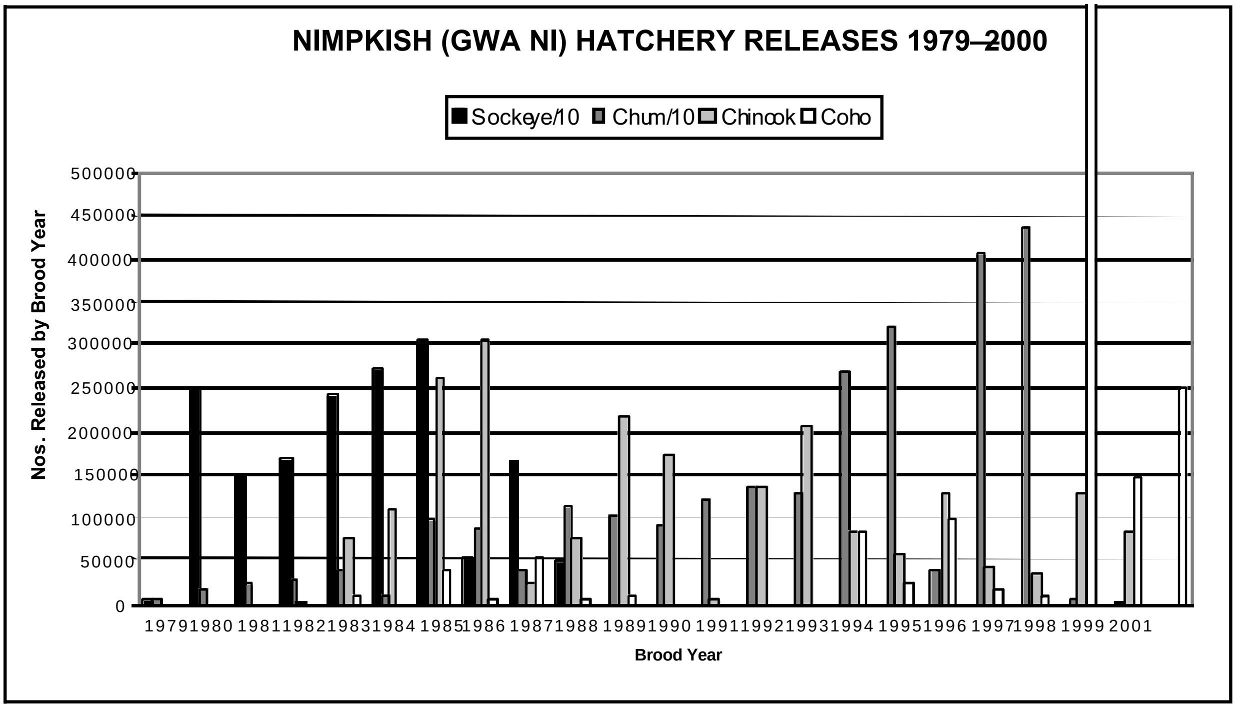


Figure 2. Nimpkish (Gwa'ni) Hatchery release history (1979–2000)

of all kinds of management effort (the Area 27 West Coast Vancouver Island fishery closure, and voluntary curbing of the First Nation food fishery since about 1978; there has not been a food fishery to speak of other than the ceremonial fishery every spring which accounts for only a few hundred fish), the sockeye have continued to decline. In spite of apparent increases in sockeye escapement in the mid-1980s to the early 1990s, when sockeye appeared to be rebounding at a fairly significant rate (to the extent of a peak year (1992) when we had 175,000 escapement into the system), last year (2000), being a low cycle year, we anticipated 38,000 sockeye returning to the Nimpkish, but in fact had only about 5,000 (Figure 1).

Once again, we heard the alarm bells that sounded in the late 1970s (8,500 fish into the system). Now that we have only 5,000 fish returning, we need to do something about it; possibly with a small incubation facility, coupled with lake fertilization that is occurring in Woss Lake.

Figure 2 provides a review of Nimpkish hatchery releases and Table 2 describes total production from the Willow Creek and Cheslakee hatcheries. In 1979 to 1988 at the Willow Creek hatchery we were involved in sockeye, basically because of its importance. Sockeye production was, on average, 1.8 million fry a year, ranging from 1.25 million to 3.5 million. What is interesting, and I will refer to it again later, is the major increase in chum production that we have been involved in since moving to the new facility. We can put 10 million chum eggs into the new facility quite easily. It has a 12,000 gallons per minute water supply, half of that being well water, and half river water.

Table 2. Total production to date from the various hatcheries (Willow Creek and Cheslakee)

Sockeye (1979–88)	16.50M
Chum	25.25M
Chinook	2.20M
Coho	1.60M
Total (all species)	**45.50M**

Sockeye

I have put together some charts overlaid on the same figure, showing the brood year releases by species, and the cycle escapement. I want to make sure that everybody understands that I am not naïve enough to make any kind of direct correlation or association between the two bars you are looking at (Figures 3 to 6). The grey bars are sockeye releases divided by 10, for the sake of scale; the black bars are cycle year escapements — brood year plus four. This is oversimplified, as there is a three-year-old component to the return, and there is no attempt

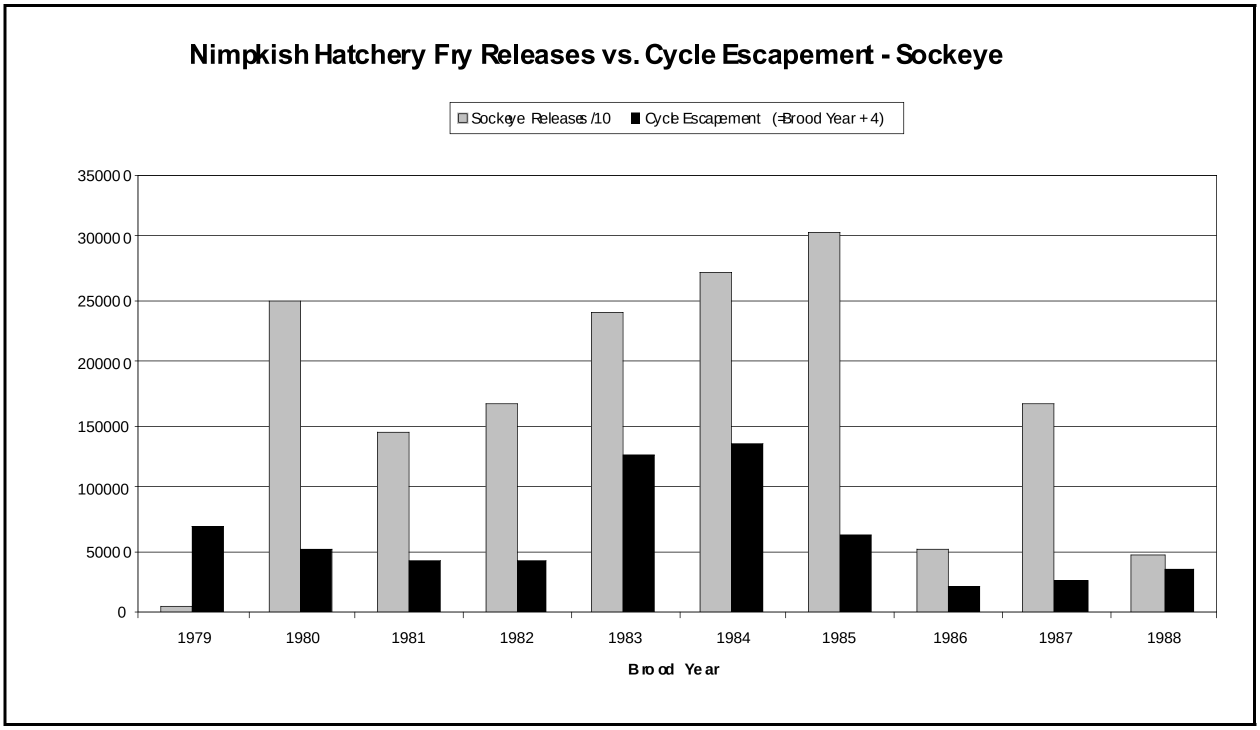


Figure 3. Nimpkish Hatchery Sockeye Releases and Cycle (Brood Year +4) Escapement

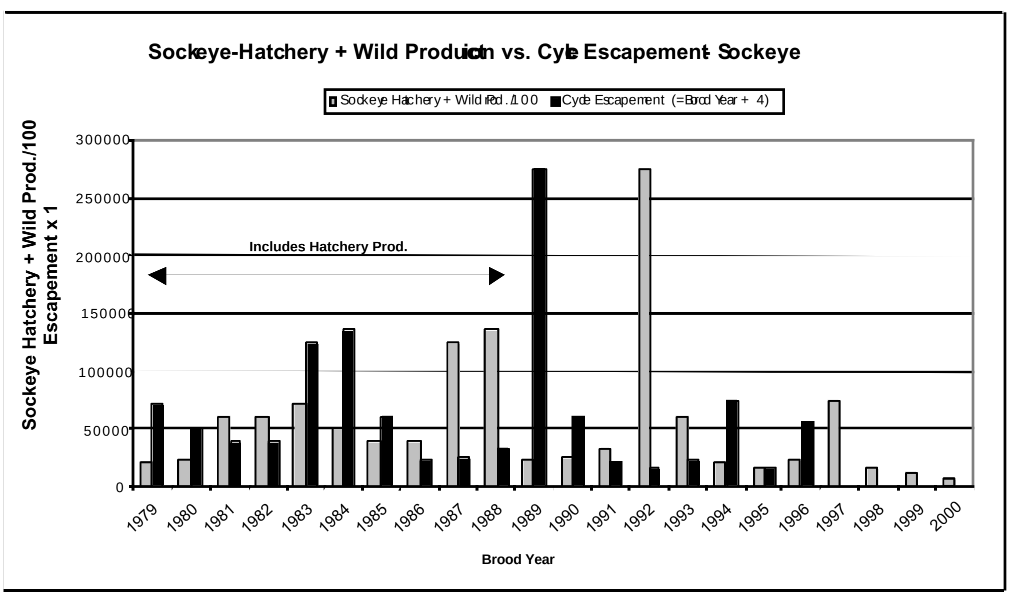


Figure 4. Nimpkish Hatchery plus Wild Production of Sockeye and Cycle (Brood Year +4) Escapement

whatsoever to look at fishing pressure exploitation rate or anything else. Please do not look at them as any attempt to provide you with a suggestion of valid correlations. Rather, these figures are presented simply to illustrate that in some cases, for example with chum salmon, there appears to be a possible connection between hatchery efforts and stock rebuilding (Figure 5).

By 1988, we pretty well tapered right out of sockeye production at Willow Creek (Figure 3). There does not appear to be a strong correlation between hatchery sockeye production and cycle escapement, with hatchery (1979–1988) or without hatchery (1989–2000) (Figure 4). Of interest, however, is the significant decline in escapement in the past six to eight years since hatchery production of sockeye has stopped. We have moved the chinook, coho and chum down to the mouth of the river. During the same time period, there was fertilization of Nimpkish Lake, the biggest nursery lake in the system. There were weekly bomber flights going out and dumping various mixtures of nitrogen and phosphorous into the lake in an attempt to increase food production. The lake fertilization program stopped about the same time as hatchery production ceased.

The release numbers are the fry production corrected to what the bio-standard of the day indicates was the fry-to-smolt survival. We know how reliable bio-standards are, if we are going to try to use the same coast-wide bio-standard for fry to smolt survival for all Nimpkish sockeye. For example, we should not dare use the same survival rates for Woss Lake, Nimpkish Lake, and Vernon Lake, because we know there is totally different fry-to-smolt survival in those three cases.

Chum

There appears to be more direct correlation between hatchery production of chum and increasing adult escapement between 1979 and 1992 (Figure 5). However, in spite of increased hatchery production, the escapement levels have dropped dramatically from 1995 to 2000. The total escapement for year 2000 was about 1,000 adults! The chum only spawn in the lower part of the river between Nimpkish Lake and the mouth of the river. This is quite a short distance, and not an easily accessible part of the river; there is no road, and it is very difficult to swim, and quite rapid in places. But it is not a bad river to assess from heli-counts. I think, since the late 1970s and early 1980s, we have done a reasonable job of estimating the escapement of chum, and I have more confidence in the numbers than I do with sockeye. I have not presented you with a coho graph because I have absolutely no faith in our assessment abilities, or our escapement counting abilities, for this species.

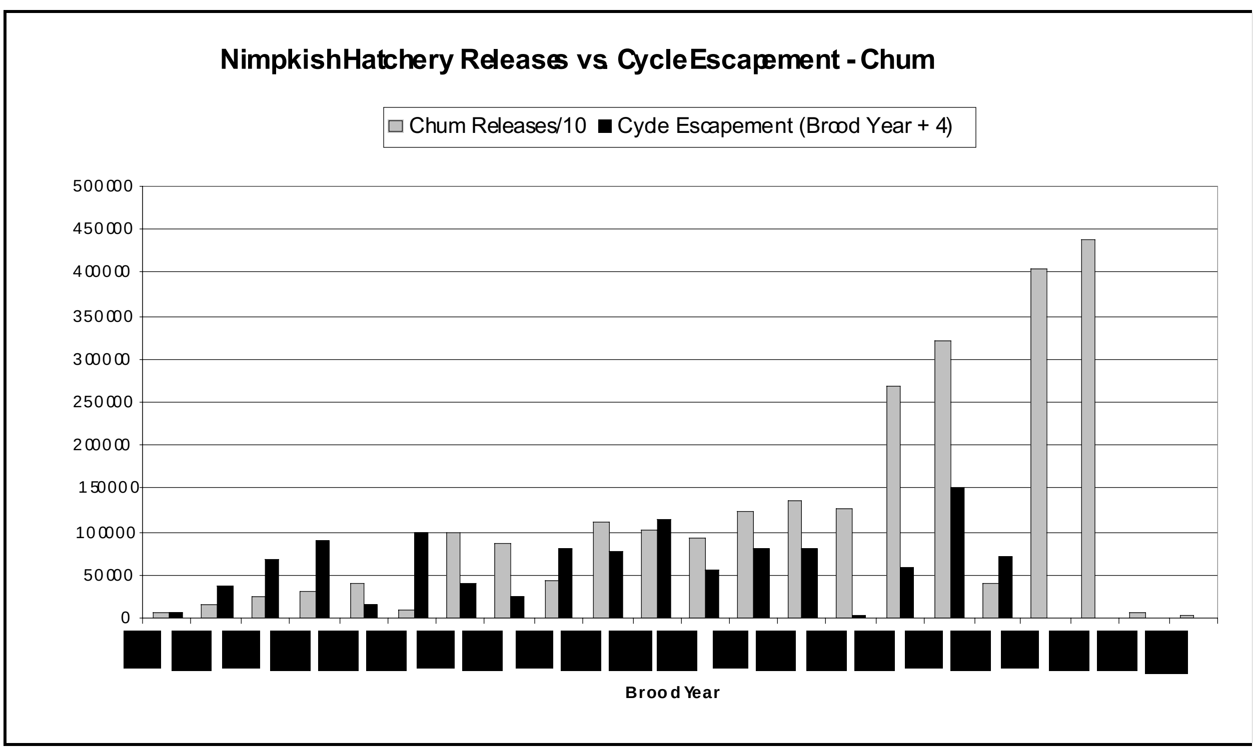


Figure 5. Nimpkish Hatchery Chum Releases and Cycle (Brood Year +4) Escapement

The four-year old chum make up about 85% of the returning population. The reason for graphing hatchery production and cycle escapement together is to determine if, in fact, there is a correlation between hatchery production and brood escapement (Figure 5). The correlation seems to be there, especially after we moved hatchery operations down to the lower river, which is more temperature controlled, with a little more attention paid to timing of release, and thus more parallel with the wild stock. There has been a large increase in hatchery production since 1994 (1.9M fry in 1998), but in 2000, somewhat less than a total of 1,000 adult chum returned to the system. It will be very interesting to see what the year 2002 returns are like given the large hatchery production of 1998.

Figure 6 shows wild production chum juveniles and cycle (brood year + 4) escapement. If there are more juvenile fish then you should have a greater escapement in the return year, with or without hatchery influences. Good examples are the 1995 and 1998 returns where both the brood years and resultant return years were fairly strong. In contrast, the extremely low return in 1999 (2,500 fish) came from a brood year of 80,000. This stock is in crisis.

The ‘Na̲mgis First Nation has targeted on chum enhancement and tried to increase the production, in the hope that at some point, with the funding limitation we all face when we are trying to run any kind of enhancement or restoration project, there would be some opportunity for self-funding through “ocean ranching,” and surplus to escapement harvest. Ocean ranching is not a very popular word in Canada, so we are trying to figure out a euphemism for it. But of interest, in spite of some apparent correlation between both hatchery and wild production and returning adults up to 1995 (whether or not the production had anything to do with it) is the fact is that the stock has again crashed (Figure 6).

In 1998 and1999 the ‘Na̲mgis First Nation again submitted a proposal, which we originally submitted in 1994, to model what it would look like if we had target escapements of 110,000 into the river and used a portion of the surplus harvested for enhancement and restoration funding activity. We never got anywhere with that proposal until 1998 when Mr. Anderson (Minister of Fisheries and Oceans) did, in fact, write a letter saying he would support such an effort on a pilot scale. He agreed that we could increase our egg take up toward the 10 million production level, rather than the 2 to 3 million we had been working on. However, the letter came in around the period of low returns, where we had only 2,500 (1999) and 1,000 (2000) returning adults. If you have to chase them all over Broughton Strait

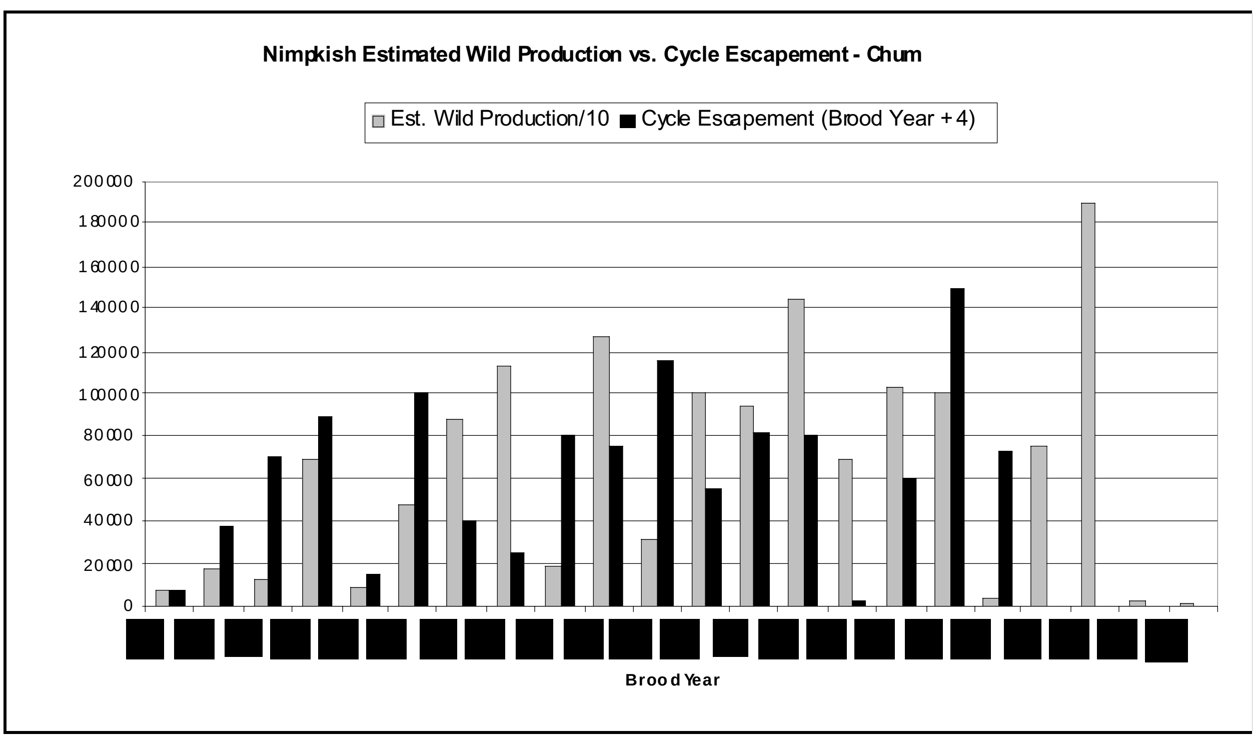


Figure 6. Nimpkish Wild Chum Production and Cycle (Brrod Year +4) Escapement

with a seine boat, trying to catch broodstock because you cannot catch broodstock in-river, all of a sudden your production levels go down. Year 2000 "eggs in the basket" were only about 32,000, because of the very low returns.

Part of what I am getting at is obvious; in spite of the chum enhancement efforts we have made over the last 20 or more years, it has been apparently all for naught. I think there are only two conclusions that we can draw from the chum production figures; that is, that enhancement has entirely annihilated the Nimpkish chum stock (although I am not going to ascribe to that one very quickly), or, that there are factors that are outside of our control and or knowledge, and knowledge is probably the most important part of that. We do not know where, or if, the Nimpkish chum are being intercepted. We have not discarded the things we couldn't possibly find out yet. Again, we need more assessment and evaluation. Is there an impact on Nimpkish fall chum in the Central Coast (Area 8) fishery or the terminal fishery at Bella Bella or are the recent low returns a result of unknown ocean survival factors? We just do not know, because we have not been able, mostly due to lack of funding or the wherewithal, to find those things out.

Chinook

In 1979, back in the beginning, we were looking at returns of 1,500 chinook. Prior to that in 1976 and 1977, DFO records indicate that the chinook run was somewhere in the order of 150 to 200, building up to the 3,000 to 5,000 range in the 1983–1992 time period (Figure 1), and then crashing again since 1993. This was in spite of hatchery production and again I cannot tell you what the impact of hatchery production is because we only had tags on them for a few years during this time period, and we have not had tags on since. So we do not know what the contribution of the hatchery is to the total escapement, and we do not know what the hatchery production is compared to the whole catch. I think that if there is anything that I am going to repeat throughout this presentation, it is that there are doubtless things that are not right with the strategies that are being used in this and other hatcheries. What those are is impossible to measure if we are not doing the appropriate assessment and evaluation of those strategies. It is absolutely critical if we are going to continue to produce chinook fry and/or smolts, that we have marks on all those animals in order to come up with some kind of evaluation technique, before we can state benefits and or hazards of the production methodologies being used.

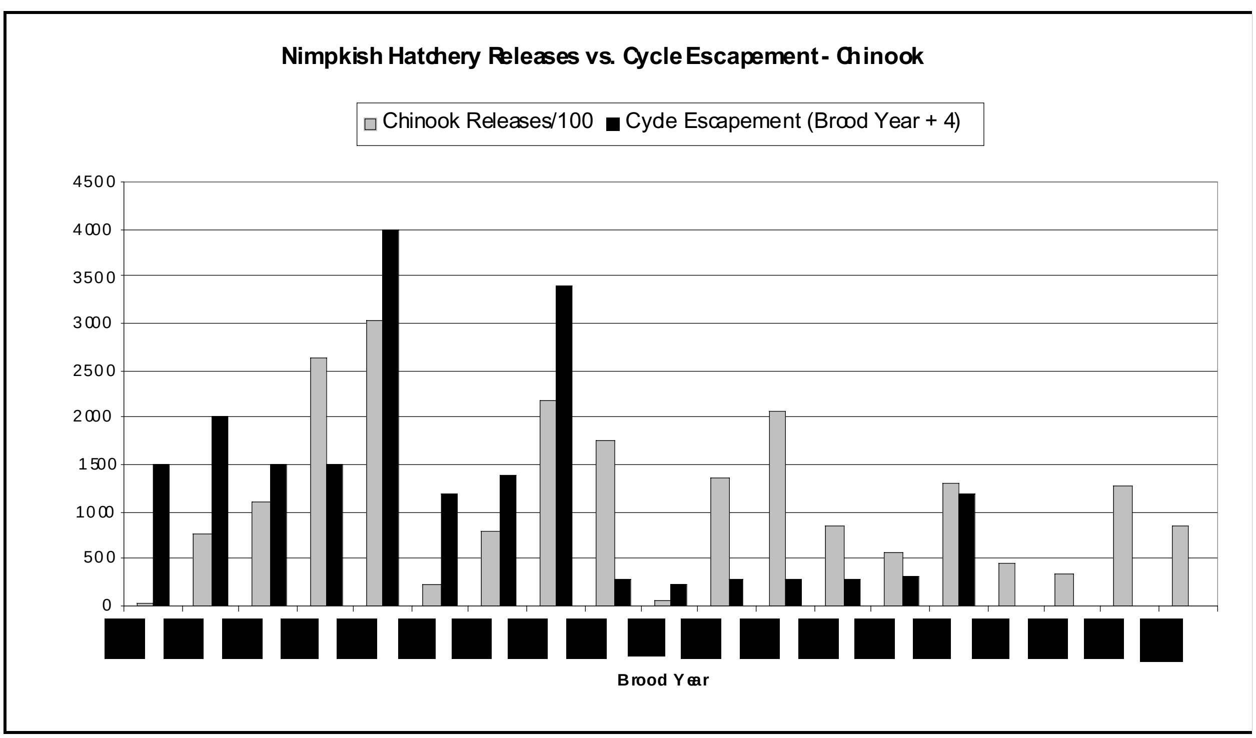


Figure 7. Nimpkish Hatchery Chinook Releases and Cycle (Brood Year +4) Escapement

In spite of some very large releases (300,000 chinook fry released in 1986), we are not really seeing a consistent correlation between hatchery production and corresponding returns in all years. For example, large releases in 1986 did appear to correspond to high returns, however, large releases in 1990 did not appear to yield the same high return rate. There is nothing that suggests that we can talk about cause and effect and benefit. There was some rebuilding of chinook escapement to the Nimpkish through the 1980s but the role that hatchery production played in this is certainly open for discussion. Again of note is the significant decline in chinook since 1990 with the average escapement from 1990-2000 being about 350 chinook/year.

Coming back to sockeye, I should have mentioned earlier that the Nimpkish is unique in that the early run sockeye, which as far as we know are extinct, came into the system as early as May and would spawn in late August and early September. The major run of sockeye, the late fall spawners, would enter the system in June and would spawn in late October and early November; it is pretty well all in by the first week of July. In the case of chum, it is probably one of the latest runs on the BC coast; they enter the estuary area, the sanctuary area adjacent to the river, in mid-October. They move upriver in November, and continue spawning right into the second week of January. It is a very distinct and late run.

Assessment

I want to talk a little bit more about assessment, and the reasons many hatcheries aren't able to do much evaluation of hatchery impacts on subsequent returns. The Nimpkish sockeye all went out unmarked; in terms of all our production, among all species, very little marking has occurred. We have three or four years of chinook coded wire tagging data that gives us some information of where they migrate through their lifecycle, and where the heaviest exploitation might take place. But we really do not have enough data to look at what percentage of the returning stock is, in fact, hatchery production, or what percentage of the exploitation is on hatchery fish. That is a critically important point.

What is your anticipated release date, what is the best time to have your releases planned for, and what temperature should you be targeting for the given species you are trying to incubate? There has been a huge amount of year-to-year variation in release strategies depending on the advisor of the day, myself included, over the 20 years. I think we have had at least a dozen biological advisors, each of whom had the best intentions and gave us great assistance throughout the project, and each of whom also had different theories on the best release and timing strategies, and best release location.

Other Benefits of Hatcheries

There are socio-economic benefits to hatcheries, including benefits of training, pride of resource stewardship, and actual income benefits. Because it is such a huge system, we wander all over "hell's half acre" looking for broodstock and doing fry releases. At this point we are operating two lake outlet fences for sockeye smolt output counts, together with Don McQueen. There are a lot of other activities other than watching water go around in the hatchery and feeding fish. There is an overall enhancement strategy and it employs a lot of people. Some of the socio-economic benefits cannot be overstressed. The pride of stewardship, the actual training, and the community status benefits for people working on the project are infectious and they run throughout the community. There are impacts on children in the public, native bands, and schools that visit the hatchery on a regular basis and follow the process. Grade five and six kids want to know what is happening. They ask, "Last year we got food fish, and this year we did not, what is going on?" Therefore there is a huge educational component associated with the project.

Table 3. Nimpkish (Gwa'ni) Hatchery
Socio-economic benefits

- EMPLOYMENT (1979–2001) — Approximately 150 person years of full time employment (and training). Approximately 84 person years of part time employment (and training).
- STEWARDSHIP — Employees, trainees, Band Council, and community members have taken a serious interest and active role in the rebuilding and management of Nimpskish River stocks.

There have been 150 full time person years of employment and about 84 part time person years (since 1979) because you have to hire six to seven extra people during broodstock collection time (Table 3).

I had hoped to have Henry Nelson (manager) and Bert Svanvik (field supervisor) here to discuss some of the "other" (non-fish) impacts of the Gwa'ni Hatchery. The 'Na̲mgis First Nation has, through its long history with the Nimpkish watershed and rebuilding of stocks, been instrumental in establishing the Nimpkish Resource Management Board – a partnership of Band, tenure holders, DFO, MOELP, and community.

Measuring benefits

You cannot measure benefits and you cannot measure impact unless you are doing the appropriate monitoring of hatchery output, whether through mass marking or individual clipping, whether it be genetic markers, or whatever. Therefore we cannot measure benefit, and I cannot really stand here and state the benefits or hazards of this particular project without the benefit of proper assessment tools (Table 4).

Table 4. How to measure benefits?

ASSESSMENT

- Need to have positive marking on all hatchery production (very few year's information to date).
- Need increased downstream assessment of marked hatchery smolt output numbers and condition (especially coho and chinook).
- Require more information on interception of both hatchery and wild stocks (all stocks and fisheries).
- Need to expand genetic "fingerprinting" program to assist in determining interception locations/levels.
- Once these are in place we can "narrow the field" for examining other impacts on returns.

You cannot do proper planning if you do not know the success and failures of your previous incubation or release strategies. You cannot do proper planning unless you have the benefit of knowing where the fish went, where they were caught, or whether they went anywhere at all. Perhaps they hit the estuary three weeks too early; for example, in the case of chum, if they are there earlier than when the copepods choose to leap off the bottom of the flats, then they are out of luck. If that is the case we need to know that. So a huge amount of assessment and work has to go into developing coherent planning. We need increased downstream assessment of marked hatchery smolts and also wild stock. We need to look at their condition and we need to look at a few other things, including the carrying capacity of stream environments that we release the fish into. We cannot just be going, driving a tank truck, and releasing 35,000 smolts. We need to do some post-watershed-restoration assessment of rearing capacity of some of the streams we are putting fish into.

We also need information on interception of wild and hatchery stocks, all stocks and fisheries. Certainly there are some exploitation rates and numbers that fisheries managers use to look at for impacts on Nimpkish fish. But we do not really know in the case of the late fall chum if we have used low numbers; for example, if there really is only a 15% potential exploitation rate, we do not know that for certain. That is a number that has been grabbed out of the air, saying yes they are late, they have probably avoided the gauntlet of the fishery, so we will stick 15% in there without any actual tagging or information.

The genetic fingerprinting program for sockeye is in place, and for now we are collecting smolt output samples. Ideally, if we had a good number of sockeye in the system we would be collecting the smolt output from at least three of the nursery lakes. One of the nursery lakes had zero smolt output as near as we can tell. Woss Lake had the largest number because that is the lake spawning population. We are just trapping, getting the results back from the lower Nimpkish trapping program. Somebody asked earlier how far are we along in BC in terms of our "library" of genetic fingerprints of stocks and races of fish on the coast. Certainly in the Nimpkish we are at the beginning of that process. Hopefully, in the future that can be used both for total escapement assessment or escapement estimates, and also to look at some of the interception issues.

Planning Needs

Over the course of our discussions, I am hoping that we can identify a number of the things that we can do something about and/or measure, and things we need to know before we can carry on hatchery programs responsibly. If, in fact, as the decision was made in the 1930s, sockeye hatchery enhancement is of zero benefit, then we ought not be wasting money doing it. However, we cannot make any of those decisions or change planning or strategies until we have got appropriate assessment tools in place. So in terms of planning we need to refine certain of our operational techniques within this particular watershed. Broodstock collection for chum, for example, is a peculiar process. We capture our chum in salt water and put them in a net pen to rest for a few days, and then we take them 40 or 50 at a time in a helicopter monsoon bucket, fly them up into Nimpkish Lake, pull the pin and drop them into a net pen in the lake. Surprisingly, the chum broodstock mortality is very low, less than one percent, even given the rather rude osmotic shock and helicopter experience. Clearly there is some refining that needs to be done. We also need to refine our release strategies, especially with respect to chum and coho. There is not much point in having warm well water, and cranking your fish out a month earlier than the wild stock, if the estuary is not tuned for that timing of release (Table 5).

Table 5. Planning needs for the Nimpkish Hatchery

- Need to refine broodstock collection and rearing strategies.
- Need to refine release strategies with respect to brood source, stock separation, timing, and release sites within the Nimpkish watershed.
- Nimpkish may become a "Pilot Planning Watershed"—may assist in refining overall enhancement and restoration plans.

One of the positive things that is happening within the Nimpkish is that it may, under the inter-government agency agreement between DFO and the Provincial Ministry, become a pilot-planning watershed so that perhaps one of these assessment and evaluation processes will in fact take place. Then we can get on with the job of stock enhancement.

The Nimpkish hatchery project has had many different people as "advisors". There has been a lack of consistency of advice regarding genetically and behaviourally sound hatchery practices. One "advisor" suggests that all chinook, for example, be released into the lower Nimpkish River. The next might advise they be released at Woss, the brood source site. Another might suggest rearing coho over winter; the next might promote early spring release with minimal rearing. Hopefully, the "best practices" advice will prevail in the future through the development of a long-term coherent plan.

Other Enhancement Activities
There is some enhancement activity in the Nimpkish other than just a monolithic facility down at the bottom end of the river. There are other things going on that create training and employment, and there are also the beginnings of some very good assessment information (Table 6).

The Woss Lake fertilization program, which was started in the mid 1980s, and which was halted for a number of reasons, was restarted in 2000. It continues this year with downstream smolt assessment or pre-smolt assessment. The genetic sampling program is being conducted in conjunction with Don McQueen, adjunct professor at SFU, with funding by NSERC and also Fisheries Renewal. A small amount of funding ($30,000) has also been approved to put a very small trailer incubation facility on Woss Lake, to see if we can step up the sockeye fry production. Also, it seems valuable to carry on with the fertilization and look at lake production from the plankton food-web point of view. It has been questioned why we are fertilizing a lake when we have 1,000 total adults in the system, 85% of which are in Woss and the progeny of which are certainly not going to be "dietarily" challenged because its an awful lot of lake and awful lot of food for that few fish.

Table 6. Other Enhancement Activities

- Woss Lake Fertilization Program restarted in 2000, continuing in 2001.
- Sockeye incubation facility to be constraucted at Woss Lake in 2001
- Sockeye genetics program started in spring 2001 (for sub-stock identification?).
- Major restoration works (especially coho habitat) through FRBC/WRP ($2.7M 1996–2001) (CANFOR/'Namgis First Nation.

The genetics program has started, along with major restoration work. It is a huge watershed and we have spent $2.7 million in the last four years on habitat restoration work on the Nimpkish. We could probably spend that much a year for the next 20 years and still barely scratch the surface of some of the things that need to be done. However, there is a fairly significant FRBC watershed restoration program going on between Canfor and the 'Namgis First Nation. They have a very strong and somewhat unique partnership in a body called the Nimpkish Resource Management Board, which involves tenure holders, and the First Nations that are associated with the area. It includes all those streams within the provincial Nimpkish Watershed Area. The 'Namgis First Nation is extremely active and proactive in the planning process. They are very concerned about the situation that is occurring with the two most precious ceremonial and food source species, sockeye and chum.

The 'Namgis First Nation and the hatchery crew appreciate that hatchery production is a "stop gap" measure that must be accompanied by a sound watershed restoration plan and, hopefully, sound stock management that will assist in the rebuilding of this once highly productive watershed. It has been demonstrated in the few years that hatchery chinook have been marked, that there is a high encounter rate in the mainland inlet sport fishery. Common sense dictates that areas of known interception should be closed until stocks are again healthy enough to support some exploitation level.

Discussion

The question was asked: How are the escapements estimated in the figure?

Michael Berry responded that "estimated" is probably even a gracious word. Sockeye are really difficult. They have tried tagging at the mouth and doing tag recovery upstream. Brian Wadhams, who is here, was involved in all kinds of tromping around, and all sorts of dead pitches. The estimates are based on some river swimming, some dead pitches, and monitoring and refining the escapement estimate based on some countable systems. The Woss River is probably an example of that. 'Estimates' is a generous term. They have a large component of about 35% of Nimpkish sockeye spawning in Woss Lake, and some possibly in Nimpkish Lake. They do not even know that total. At this point, with the reduced level of the run, of about 5,000 fish, they are looking at probably 85% of total escapement into the system in 2000 spawning in Woss Lake.

A participant asked: Is there no correlation between releases and estimated escapement?

Michael Berry replied there was nothing he would hang his hat on. He has not taken the time and energy to look at what the exploitation rates were, for example. To do that properly he would have to look at a number of factors. With chums especially there seems to be some parallels in the bars of the figure, more so than in chinook and coho.

The question was asked: Is the chum Summer and Fall combined, or is this Fall only?

Michael replied that it was Fall only, that there is no Summer run on the Nimpkish.

The question was asked: Is the fertilization just one more example of artificial human selection going on? The participant continued: In fact, you are selecting fish that respond to the addition of fertilizers. And as you commented, these are hatchery fish that should not be dietarily challenged, given the small number of fish and a big watershed. It struck me that this is another example of where artificial selection is being introduced to the system where in fact you do not know what you are selecting for.

Michael Berry responded that the genetic fingerprint between the substocks was in the Nimpkish, those being basically Vernon and Woss and main stem. Even if it was just divided into three, with Woss Lake fertilization, but no fertilization on Vernon Lake, there is a control. The control can look at differences in smolt output quality, for example, and numbers and productivity and hopefully the fingerprinting may be such that they can discern between the substocks, although the jury is out on that until they can get data back. If through micro-satellite variation they can look at those kinds of genetic differences then they will be able to assess whether it is a good thing to be doing.

A participant enquired: Given some of the concerns about the late run Fraser sockeye timing, have you noticed any changes in the timing of the Nimpkish runs?

Michael Berry responded by saying if anything, the timing is slightly later, although he would be hard pressed to prove that statistically.

A partcipant commented: My question has to do with the crash of chum. Did you look at the presence of mackerel in the area at the same time?

Michael Berry replied that there was very little mackerel. On occasion they have had small schools of mackerel observed in the estuary area but they certainly do not have the same kind of mackerel population as there has been on the West Coast of Vancouver Island.

A Brief History of Chapman Creek Hatchery

Bob Anstead, Chapman Creek Hatchery, Sunshine Coast Salmonid Enhancement Society

The Chapman Creek hatchery has been around since 1984. It was set up as an aquaculture facility raising smolts for the net pen operations, and eventually it went bankrupt. The Sunshine Coast Salmon Enhancement Society (SCSES) put together a program and raised money to purchase the facility through private sources on the Sunshine Coast and in the Lower Mainland.

Currently (and in the past), we raise chinook, coho, steelhead, sea-run cutthroat, chum, pink and rainbow trout. We are raising these fish for nine different streams and lakes on the Sunshine Coast. It is a very aggressive program for a bunch of volunteers. There is some information (handouts) available on the releases over the past seven years as well as brochures on the hatchery.

In our coho program, we raise fish for four terminal fisheries on the Sunshine Coast. We raise 50,000 for Chapman Creek and Davis Bay. We have a partnership with the Sechelt Indian Band, and we raise about 80,000 coho a year for Porpoise Bay, and about 20,000 for Halfmoon Bay terminal coho fisheries. These are all hatchery marked fish and they are raised for recreational purposes.

In addition to the Halfmoon Bay and Chapman Creek programs, we raise 150,000 chinook through another partnership with Lang Creek Hatchery in Powell River. Lang Creek provides us with 150,000 chinook eggs. Howe Sound Pulp and Paper Mill in Gibsons provides us with a building and heated wastewater, where we can incubate the eggs at 10 ºC through the winter. We can put a seven gram smolt in, in May. These fish provide recreational fishing in Davis Bay, plus wherever else they may be caught in BC. We get roughly 300 to 600 chinook back into Chapman Creek, providing another recreational fishery.

Our chum and pink program varies from year to year. We are limited to what broodstock we can get coming into Chapman Creek. The returns have not been good in the last few years, so we have not been doing much with releases. We are hoping to get roughly 200,000 to 350,000 pink salmon eggs this year, to supplement our totals.

The cutthroat program is working out well and we are getting some good returns. The 2-year smolt releases for cutthroat are all marked fish. Our steelhead program goes up and down. For the last few years we have not got enough broodstock back to put out any smolts in substantial numbers. This year we ended up with seven steelhead brought in by anglers for broodstock but seals and otters hit six out of the seven that came in. So there is a predation factor that should be looked into a little more. This gave us some indication of what is happening to our steelhead.

We provide one full time job—myself, managing the hatchery—and we have a three-day-a-week part-time person, who covers my days off. We also have a contract for the education program at Chapman Creek which is coordinated by Diane Sanford. We have a fully equipped classroom and the curriculum was developed onsite. It covers kindergarten to grade seven. The high-school classes have Streamkeeper and Stream Stewardship programs. Those are provided by Diane Sanford and one of her helpers. All the schools on the Sunshine Coast sanction the programs and last year over 2,000 students for the two-hour classroom program came to the hatchery.

The success of the hatchery depends on how you define "success". Chapman Creek, before enhancement, had a historic record of 40 to 80 coho returning. Now we have between 1,500 to 2,000 coho returning into Chapman Creek. This provides a tremendous recreational fishery and an economic benefit to the Sunshine Coast. Our fishery starts in the Davis Bay area about July and runs through to September and October in the ocean and then into Chapman Creek in November. So we have a 6-month opportunity for recreational fisheries with a two marked coho limit per day.

We literally get hundreds of people on these fisheries, and as time goes on we are getting more people scheduling vacations around the fishery. We just started promoting the Halfmoon Bay fishery last year. We did not get a lot of participation but log records from individual guides clocked as many as 60 coho per boat for the two to three month period they were fishing that area.

The Porpoise Bay partnership with the Sechelt Band has historical fisheries participating on that run. This year we expect somewhere between 4,000 and 5,000 coho back. Fish start to show up there now (June), and it will be a good five-month recreational fishery opportunity. These all have spin-offs as far as economic benefits. For example, there are at least five new independent guides that have opened up businesses on these different runs and there are people that specialize in fly-fishing only.

The Sechelt Indian Band has a historic fishery in Davis Bay for sockeye. The chinook and coho returns now supplement that fishery. For spin-off jobs, aside from the guides, there is also a creel census which we initiated. DFO funded it and we have collected some good data. We have the same person doing it this year and with funding from Fisheries Renewal BC, we will be looking at who is using the fish, and how many fish are caught, on a daily basis. We are trying to nail down just what kind of benefits these activities do provide to the Sunshine Coast. Besides the fishing there is tourism and education.

Last year the hatchery was able to donate 400 coho to the food bank in Sechelt and Gibsons. Also, through an “escapement surplus to spawning” (ESSR) licence we are able to raise a little money by selling 300 coho, which we put back into the hatchery program.

We raise roughly 400,000 to 500,000 salmonids per year. Our budget is about $120,000 per year. The DFO gives us $13,000 and we are able to raise about $65,000 to $85,000 through various fundraisers. We have a dinner and auction, a membership program, grants and donations; FRBC monies provide quite a few of the grants. We also have an aquaculture licence and we raise rainbow trout for sale. We sell roughly $600 of trout per year.

We feel we are making a big contribution to the Sunshine Coast. The amount of money that was generated by the coast to keep us going over the last eight years shows that they are happy to have us there. I am sure that there are other community-operated facilities throughout BC that are every bit as important to the communities they are in.

Discussion

The question was posed: It does not seem like the survival rate that you are getting on these fish is much higher than some of the wild coho in Georgia Strait. Do you have any idea what the survival is?

Bob Anstead said that it appears that their coho are running around three or four percent survival, but they do not have a counting fence. Their trap is set off the main stem of Chapman Creek and into the outflow water from the hatchery. He said that last year he physically had his hands on over 800 coho that came up the hatchery effluent and according to different fishermen up and down the creek, there were at least 1,000 more coho in the creek. That is the only way they can establish their numbers for fish coming back, other than their DFO Community Advisor, Grant McBain, who does a swim with some of his crew.

A participant stated that this is about 100 percent better than what they are seeing.

Bob Anstead said that they pay a lot of attention to the quality of the smolt that goes out. They raise their fish in low densities. Whether that has anything to do with it or not, he does not know. But in his experience, the bigger the smolt they can put out, the healthier the smolt, and the higher the returns.

The question was raised regarding Bob Anstead’s comment that six of the seven steelhead were attacked by predators. Figuring there are about 60,000 seals in the Strait of Georgia and fourteen days per year that they are feeding solely on salmonids, that represents a lot of fish.

Bob Anstead replied that is right. Without getting into that problem, when they first started out, before they started enhancing the coho heavily in that stream, they only had a few fish coming back, spread over several months (40 to 80 coho per year). Most of those coho were hit by otters or seals. By increasing the numbers he is sure as many fish are getting taken, but there is more than enough to support the run and the predators.

You are avoiding the so called “predator pit”?

Yes, by producing more fish.

Craig Orr asked if there are any other hatchery managers in the audience that have any indications of high survival as well?

An audience member commented that most scientific studies have indicated that marine survival for wild, compared to hatchery, coho is higher in the marine environment.

Bob Anstead replied that this is from the literature. When you evaluate the returns and the percentages of returns, there is a lot more that goes into that than just the number of fish that were released. For instance, on the Puntledge system, there would be high numbers of released fish, but there were a lot of predators taking them before they went out. All systems have their own unique problems, it can be predators, and overfishing, whether it is nets or recreational, and in certain areas it can be a lot of different problems that contribute to low releases. Rather than look at the numbers of fish that are released, you have to look at the quality of what is going out from the hatcheries. He has heard that in some cases, for example, he remembers times in Oregon and has heard rumours of it here, that if fish start showing signs of illness they may get released early in order to keep the numbers up for releases. You have to base your success on what is actually coming back.

A participant enquired: Do you keep fish health records for these fish before they go out?

No.

If you are talking about high quality, then I am assuming you have some criteria, some assessment you do?

Bob Anstead replied that uniform size, low mortalities, and vigour, are the criteria they use. Also they walk the creeks the morning after the release. He does not release fish until he can see at least 80 percent of them are full smolted and ready to go downstream. Hatchery managers have noticed that when the fish are ready to go to sea they start swimming with the current in the tanks, and that is the window of opportunity when they want to go out and let them go. But as far as condition factor goes he does not keep records of that.

A participant asked the question: Can you give us an idea of what the natural habitat on Chapman Creek is and was there a decision to enhance the natural habitat on the creek for the wild fish? Has the whole creek been impacted? Is there no habitat left and is that why you went to a hatchery? Why are you using Chapman Creek?

Bob Anstead replied that they are using Chapman Creek because it is one of the only streams on the Sunshine Coast that has enough yardage. There is about a three mile section of stream where there is no housing and no development and that allows full access for the recreational fishery. The aquaculture facility that was there was a broodstock evaluation program for the aquaculture industry. So there were coho salmon from almost every major river in BC brought to the facility to evaluate their success rates for aquaculture. Most of these escaped into the creek so there was really no genetic strain that would be disturbed by using the creek for a put and take recreational coho fishery. As far as the existing habitat that there is now, he deferred to Grant McBain, of DFO, who has done most of the work in Chapman Creek.

Grant McBain commented that based on a number of surveys, there is only room for about 5,000 to 8,000 wild smolts per year. But that has been augmented over the last three years with WRP off-channel ponds. He would not think that production would be much more than 12,000 smolts.

ECOLOGICAL ISSUES

Moderator, Craig Orr, Centre for Coastal Studies, Simon Fraser University

Can Hatchery Salmonids Contribute to the Natural Productivity of Wild Populations?

Ian Fleming, Department of Fisheries and Wildlife, Oregon State University

Ian Fleming's presentation was based on the following two papers:

Implications of Stocking: Ecological Interactions Between Wild and Released Salmonids

Sigurd Einum, Norwegian Institute for Nature Research, Tungasletta, and Ian A. Fleming, Norwegian Journal of Freshwater Research (2001) 75: 56–70

Abstract

The common management practice of introducing artificially produced fish into wild populations has raised concerns among fishery biologists. In part, these concerns arise from the observation that hatchery-produced fish commonly differ from wild fish in ways that may influence ecological interactions between them. In this review, we use a meta-analytical approach to provide quantitative tests for such differences and show that the hatchery rearing of salmonids results in increased pre-adult aggression, decreased response to predators, and decreased survival. Changes in growth rates are common, but less consistent. Changes in other fitness-related traits such as migration, feeding, habitat use and morphology also occur. Based on the presented evidence we conclude that differences between hatchery-reared and wild fish may have negative implications for the success of stocking programs. A number of studies reporting population responses to stocking support this, suggesting that the performance of hatchery fish and their interactions with wild fish is of such a character that many of the current stocking practices may be detrimental to the recipient population.

Introduction

Deliberate releases of artificially produced fish into wild populations have recently caused concern among fishery biologists (e.g. Hindar et al. 1991, Saunders 1991, Waples 1991, Thomas and Mathisen 1993, Ryman et al. 1995, Youngson and Verspoor 1998). Although such releases are often implemented to compensate for reduced production caused by human induced habitat degradation, a range of potential ecological problems may be associated with this practice. First, stocking of large numbers of fish into a limited habitat will inevitably affect population density, at least initially. Thus, any density-dependent characteristics of the environment or of the fish itself are potentially affected (cf. Elliott 1989, 1990). This numerical effect of stocking could, for example, include changes in the frequency of competitive interactions, levels of food availability, or a functional response of predators, and hence influence growth and survival of the wild fish. Theoretical considerations suggest that this may cause hatchery releases to increase temporal variability of population strength (Fagen and Smoker 1989). Second, hatchery fish may differ genetically and/or phenotypically from wild fish. Such differences may affect how stocked and wild fish interact, and thus cause effects of stocking beyond those due to pure density-dependence.

Here we review the literature dealing with such effects in salmonids, summarizing what is known about differences between hatchery- and wild-reared fish, and the implications these differences have for ecological interactions between the two types of fish. Literature data are used to examine whether the predicted effects of differences between the two types of fish have been observed in the wild. We also identify areas where research is needed to increase our knowledge about ecological interactions between hatchery and wild fish, and to establish better management practices.

Why do Hatchery and Wild Fish Differ?

Fish reared in hatchery facilities may differ from their wild conspecifics for three reasons. First, fish are highly phenotypically plastic and therefore their phenotypes may be shaped considerably by the rearing environment (e.g. Wootton 1994, Pakkasmaa 2000). The traditional way of rearing fish in hatcheries (i.e. high densities in flow-through tanks) shows little or no resemblance to natural rearing. In fact, most environmental characteristics that may influence fish development differ. This includes feeding regimes, density, substrate, exposure to predators, and interactions with conspecifics. It is not surprising that such differences can have substantial impacts on the resulting fish phenotype.

The second reason why hatchery fish may differ from wild fish is that the intensity and direction of selection differs between the two environments. Perhaps most importantly, survival during egg and juvenile stages is substantially higher in the hatchery environment than in the wild (reviewed by Jonsson and Fleming 1993). This means that genotypes that potentially are eradicated in the wild, by predation or starvation, are artificially brought through the vulnerable period of selection during early juvenile stages (Elliott 1989, Einum and Fleming 2000a, b). In theory, hatchery fish could also experience altered selection pressures. For example, the high juvenile density and abundance of food may select for behavioural and physiological traits that are disadvantageous in nature. The importance of such altered selection is unknown, but the intensity of selection may be limited due to the low levels of mortality. However, this may not necessarily be so, if traits such as body size attained in the hatchery are tightly linked to survival after release, a period of intense mortality among hatchery fish. Such genetic changes due to relaxed and/or altered selection are likely to accumulate in stocks being cultured over multiple generations (e.g., when brood stock is consistently chosen from adults originating from hatchery produced smolts). Multi-generation hatchery stocks are thus likely to differ more from wild fish than first generation stocks where most of the changes are likely to be of environmental origin.

The third reason why hatchery fish may differ from wild fish is the use of non-native fish for stocking. Such procedures may introduce novel, genetically based characters into the wild population and break up co-adapted gene complexes that may lead to outbreeding depression (e.g. Gharrett and Smoker 1991). Fortunately, the potential importance of local adaptations is being increasingly acknowledged (reviewed by Ricker 1972, Taylor 1991), and the practice of releasing non-native fish has therefore decreased in frequency.

Intentional artificial selection may also generate genetic change in hatchery populations, as has occurred with commercially farmed fish (Einum and Fleming 1997, Fleming and Einum 1997). However, such selection is rarely performed in any systematic way in non-commercial hatcheries. Thus, studies reporting differences caused by such selection have been omitted in this review.

Studies of differences between hatchery and wild fish take three forms. (1) The most common form simply documents the existence of differences and speculates about their origins. More detailed studies attempt to identify (2) the environmental and/or (3) genetic origins of the differences. The first form of study usually compares fish hatched and reared in the hatchery with fish from the wild, and while the differences observed likely have an environmental component, additional effects due to genetic differences may exist. Tests for environmental effects compare fish, of a common origin, reared in a hatchery with those reared in the wild. By contrast, tests for genetic effects compare hatchery and wild fish reared from eggs in a common environment.

Because tests of differences are usually conducted under artificial hatchery conditions, their value for predicting effects of interactions in the wild may be somewhat limited. This may be particularly problematic if genotype/phenotype by environment interactions exist, whereby the relative expression of traits between the two types of fish differs among environments. Some studies try to control for such interactions by conducting tests under differing environments (e.g., hatchery and wild), yet most studies do not. Any lack of correspondence between hatchery tests and data from the wild, therefore, may be partly attributable to this problem.

Which Characters Differ?

Ecological interactions among fish are an outcome of their behavioural traits. Thus, knowledge about behavioural differences between hatchery and wild populations is vital to understanding the potential impact from released fish. A substantial body of data that tests for such differences exists. These studies suggest that hatchery fish differ from wild fish in levels of aggression and predator avoidance behaviour (Table 1). In most studies, the effect of artificial rearing appears to result in an increase in levels of aggression (5 out of 9 studies). If we combine the probability values from the separate significance tests of the independent data sets (a meta-analytical approach described in Sokal and Rohlf (1981), p. 779; data handling described in foot-notes to Table 1) these support the hypothesis that hatchery fish exhibit increased levels of aggression relative to wild fish $\chi^2 = 85.75$, df = 30, $P < 0.001$).

Only in one study were the offspring from the wild population more aggressive than those from the hatchery population, and in this case, the hatchery population was of non-native origin (Norman 1987). Thus, population-specific levels of aggression rather than effects of hatchery rearing may be responsible for the result (e.g. Taylor 1988, Swain and Holtby 1989, Einum and Fleming 1997). Finally, in one study the direction of the difference depended on the age of the fish, with wild fish being more aggressive at emergence, and hatchery fish being more aggressive after 105 days of rearing (Berejikian et al.

1996). In the three studies where the origin of the difference was predominantly environmental, hatchery fish were consistently more aggressive than wild fish. The less consistent results appear in those studies where the difference was genetic. There has been some debate as to whether artificial selection in fish causes an increase or a decrease in levels of aggression. Both theoretical and empirical studies suggest that the direction of se-lection during artificial rearing may depend on the environment (Doyle and Talbot 1986, Ruzzante and Doyle 1991). Although these studies have focused on situations where there is intentional selection for rapid juvenile growth, and thus may not be directly applicable to most hatcheries producing fish for stocking of wild populations, they suggest that a correlated in-crease in aggression only will result if food is limited. Thus, if the environment to which fish are exposed differs among hatchery stocks this may influence the direction of evolutionary divergence of social behaviour away from that of wild fish. Nevertheless, increased aggression may evolve as a correlated response to selection for rapid growth, if such selection occurs (cf. Johnsson et al. 1996). Furthermore, evidence from guppies suggests that levels of aggression may be negatively correlated with predation rates (Endler 1995). Thus, if hatchery populations are less exposed to predators, pheno-typic or genetic correlations may cause increased aggression as well. Tightly controlled experiments are needed to further elucidate the causal relations between feeding, growth, body size, aggression and dominance under various selective regimes.

Hatchery populations do differ from wild fish in levels of anti-predator behaviour (combined probabilities $\chi^2 = 37.63$, df = 10, $P < 0.001$). The lack of exposure to predators in hatchery populations appears to result in a reduced response to predation risk, both as an environmental effect and as a response to relaxed selection in hatchery populations (Table 1).

One intriguing feature of anadromous salmonids is their long distance migrations to feeding and

Table 1. Differences in pre-adult aggression and response to predators between wild and hatchery populations of salmonids. Pos = hatchery population more aggressive, Neg = hatchery population less aggressive/lower response to predators, 0 = no significant difference, E = predominantly environmental, G = predominantly genetic, E > G = likely predominantly environmental.

	Origin			Form	
Trait	of effect	of effect	Fish	Species	Reference
Aggression	E	Pos	Native	Coho salmon	Rhodes and Quinn 1998
	E > G	Pos	Non-native	Atlantic salmon	Fenderson et al. 1968[1]
	E > G	Pos	Non-native	Cutthroat trout	Mesa 1991
	G	Neg	Non-native	Atlantic salmon	Norman 1987
	G	Pos	Non-native	Brook trout	Moyle 1969[2]
	G	0	Native	Brown trout	Johnsson et al. 1996[3]
	G	Pos	Non-native	Coho salmon	Swain and Riddell 1990[4]
	G	Pos/Neg*	Native	Rainbow trout	Berejikian et al. 1996[5]
	G	0	Non-native	Masu salmon	Reinhardt in press[6]
Predation	E	Neg	Native	Brown trout	Dellefors and Johnsson 1995[6]
	G	Neg	Native	Brown trout	Johnsson et al. 1996[2]
	G	Neg	Non-native	Rainbow trout	Johnsson and Abrahams 1991[2]
	G	Neg	Native	Rainbow trout	Berejikian 1995[7]
	G	Neg	Native	Brown trout	Fernö and Järvi 1998[2,8]

*Direction depended on age.

Comments regarding usage of data in meta-analysis:

[1] *P*-value was calculated from data.

[2] *P*-value, given as < 0.05 or just "statistically significant", was set to 0.05.

[3] *P*-value, given as > 0.6, was set to 0.61.

[4] Separate statistics were given for each of seven days of observations. Each of the *P*-values (range 0.9 – 0.001) was treated as independent.

[5] Separate statistics were given for each of three juvenile ages. These *P*-values were treated as independent.

[6] No statistics or raw data were available for inclusion of study.

[7] Separate statistics were given for two different test-environments. The two *P*-values were treated as independent.

[8] *P*-value for difference in "fleeing" was used.

breeding areas. As well as being energetically costly, such migrations potentially increase predation risk. Selection is therefore expected to mould patterns of movement to optimize fitness. It is therefore worrying that migration patterns of hatchery-reared fish often differ from those of wild fish (Table 2). For example, hatchery fish are observed to differ from wild fish in their timing of migration, which may influence both their susceptibility to predation and their energetic costs (i.e. due to different temperature and flow regimes). If this effect on timing of migration also influences breeding time, offspring survival may be compromised due to inappropriate emergence timing from nests (Einum and Fleming 2000b).

Hatchery populations may also differ from wild populations in feeding behaviour and habitat use (Table 3). However, results regarding such effects are more equivocal, potentially reflecting a time lag in adjustment to feeding on natural prey. Re-leased fish may initially behave inappropriately after being introduced into a novel environment, but with time may acclimate to the local environment. For example, L'Abée-Lund and Langeland (1995) found that the diet of released brown trout initially differed from that of wild trout, but within the first summer the released fish adopted a similar diet (see also Johnsen and Ugedal 1986, 1989, 1990).

Hatchery populations may also differ morphologically from wild fish (Table 3). Salmonid populations exhibit differences in morphological traits, and these differences have been suggested to result from local adaptations to environmental conditions (e.g. Riddell and Leggett 1981, Riddell et al. 1981). Furthermore, morphological traits are important determinants of breeding success (Fleming and Petersson 2001). Thus, any deviation in morphology from the local population may be expected to result in decreased fitness.

How Successful are Hatchery Fish in the Wild?
If hatchery fish differ from wild fish in so many respects, how successful are the released fish likely to be in the wild? Assuming that the wild populations have undergone natural selection for ten thousand years (since end of the last ice age) to

Table 2. Movement patterns of pre-adults from hatchery populations of salmonids. E = predominantly environmental, G = predominantly genetic, E + G = both environmental and genetic effects potentially important, E > G = likely predominantly environmental, G > E = likely predominantly genetic.

Origin of effect	Observations	Fish Origin	Fish Species	Fish Reference
E	Stay longer in sea.	Native	Arctic char	Finstad and Heggberger 1993
E	Stay longer in sea.	Native	Arctic char	Finstad and Heggberget 1993
E	Extended period of smolting.	Native	Atlantic salmon	Hansen 1987
E	Differences in timing of recapture of hatchery and wild fish in coastal net fishery.	Native	Atlantic salmon	Potter and Russell 1994
E	Use same oceanic areas as wild fish.	Native	Atlantic salmon	Hansen and Jonsson 1991, Hansen 1988
E	Similar oceanic migration patterns.	Native	Atlantic salmon	Jonsson et al. 1990
E	Wild fry resided in estuary longer than hatchery fish.	Native	Chinook salmon	Levings et al. 1986
E + G	Juveniles enter estuary earlier than natural produced fry. Long-term change in mean date of entry of adult fish after hatchery program initiated.	Native	Chum salmon	Lannan 1980
E + G	Earlier returns of adult fish to rivers in stocked streams.	Non-native	Coho salmon	Nickelson et al. 1986
E > G	Move more within stream.	Non-native	Brown trout	Bachman 1984
G	Low stamina during swim trials.	Non-native	Brook trout	Green 1964
G	Juveniles stay higher in water column.	Non-native	Brook trout	Moyle 1969
G	Juveniles tamer, surface oriented and lower stamina during swim tests.	Non-native	Brook trout	Vincent 1960
G	Juveniles stay higher in water column.	Non-native	Masu salmon	Reinhardt in press
G > E	Distance transferred from natal stream negatively related to recovery rate for hatchery reared fish.	Non-native	Coho salmon	Reisenbichler 1988

become adapted to the local environment (Ricker 1972, Taylor 1991), one would predict that these changes in fitness-related traits are a potential problem for released fish, and may influence their ability to survive and reproduce (see also Fleming and Petersson 2001). Their performance in the wild should therefore be expected to be inferior to that of wild fish, a pattern that is commonly observed (Table 4). In four of eight studies wild fish outgrew released hatchery fish, whereas the opposite was observed in two studies. Thus, although growth rates usually differ among hatchery and wild fish, the direction of this difference is not consistent (combined probabilities $\chi^2 = 4.07$, df = 12, $P > 0.99$). In contrast, hatchery fish consistently experienced reduced survival compared to wild fish (15 of 16 studies, combined probabilities $\chi^2 = 109.15$, df = 18, $P < 0.001$). Thus, the success of hatchery-produced fish after release appears to be con-strained by phenotypic divergence from their wild conspecifics. This is not surprising given the potential importance of local differences among wild salmonid populations in fitness-related traits and the evidence we have presented concerning the effects of hatchery environments on development and selection.

How do Naturally Produced Fish Respond to Released Fish?

Given our knowledge about the performance of hatchery-reared fish in the wild, can we predict how stocking may influence the natural productivity of salmonid populations? How will ecological interactions with hatchery fish impact wild fish? For instance, if the fish we release into a river are more aggressive than the native fish, chances are that naturally produced fish are displaced from their territories during competitive interactions (Table 5). Such effects may be modified due to competitive asymmetries caused by prior

Table 3. Pre-adult feeding, habitat use and morphology of hatcher populations compared to wild fish. E = predominantly environmental, G = predominantly genetic, E + G = both environmental and genetic effects potentially important, E > G = likely predominantly environmental, G > E = likely predominantly genetic.

Trait	Origin of effect	Observations	Fish Origin	Fish Species	Fish Reference
Feeding	E	Different diet.	Native	Atlantic salmon	Reiriz et al. 1998
	E	Lower total consumption and feeding efficiency of live prey.	Native	Brown trout	Sundström and Johnsson in press
	E > G	Reduced feeding and diet width.	Native and non-native	Atlantic salmon	Sosiak et al. 1979
	E > G	Low feeding rate.	Non-native	Atlantic salmon	Fenderson et al. 1968
	E > G	Different diet initially, similar later.	Native and non-native	Brown trout	L'Abée-Lund and Langeland 1995
	E > G	Reduced feeding.	Non-native	Brown trout	Bachman 1984
	E > G	Different diet initially, similar later.	Non-native	Brown trout	Johnsen and Ugedal 1986, 1989, 1990
	G	Similar diet.	Non-native	Brook trout	Lachance and Magnan 1990a
Habitat use	E > G	No difference in habitat.	Non-native	Brown trout	Greenberg 1992
	E > G	Different habitat.	Non-native	Cutthroat trout	Mesa 1991
	G	Similar habitat.	Non-native	Brook trout	Lachance and Magnan 1990a
	G > E	Non-native use different habitat in lake.	Native and non-native	Brown trout	Hesthagen et al. 1995
Morphology	E	Different from wild.	Native	Atlantic salmon	Fleming et al. 1994
	E + G	Increased smolt and adult body size.	Native	Brown trout and Atlantic salmon	Petersson et al. 1996
	E + G	Hatchery populations more similar to each other than to wild populations.	Native and Non-native	Coho salmon	Hjort and Schreck 1982
	E > G	Different from wild.	Non-native	Coho salmon	Taylor 1986
	G	Different from wild.	Native	Brown trout	Petersson and Järvi 1995
	G, E + G	Hatchery reared wild and hatchery population differed least. These differed substantially from wild reared wild population.	Non-native	Coho salmon	Swain et al. 1991

residency or differences in body size (cf. Johnsson et al. 1999, Cutts et al. 1999).

One intriguing question arises from the observation that even though hatchery-reared fish appear to be more aggressive than wild fish, and thus should be able to displace them in territorial contests, they suffer higher mortality in the wild. Obviously, social hierarchies are not the only determinants of mortality rates in salmonids. Other factors such as response to predators and metabolic rate relative to food availability (i.e. vulnerability to starvation) may contribute substantially to mortality rates. One might speculate that hatchery fish are to some degree able to displace naturally produced fish, but that they are unable to cope with the high cost associated with this behaviour in terms of risk of starvation or predation. If so, net fish production may actually decrease as a result of stocking (cf. Fleming et al. 2000).

An additional number of potential effects can cause releases to have detrimental effects on wild fish. For example, released fish may influence the timing of migration of wild fish. Hansen and Jonsson (1985) suggested that wild smolts were attracted to shoals of released smolts and join them when migrating downstream. Furthermore, releasing fish may influence interspecific hybridization rates. Jansson and Öst (1997) suggested that this was the reason for the high levels of hybridization between Atlantic salmon and brown trout observed in the River Dalälven, Sweden (41.5% hybrid parr). This may be

Table 4. Pre-adult growth and survival of hatchery populations in the wild. E = predominantly environmental, G = predominantly genetic, E > G = likely predominantly environmental, Neg = hatchery fish inferior performanace, Pos = hatchery fish superior performance, 0 = no observable difference.

Trait	Origin of effect	Form of effect	Fish origin	Species	Reference
Growth	E	Neg	Native	Arctic char	Finstad and Heggberget 1993
	E	0	Native	Atlantic salmon	Jonsson et al. 1991[1]
	E	Pos	Native	Coho salmon	Irvine and Bailey 1992[2]
	E > G	Neg	Non-native	Brown trout	Hesthagen et al. 1999
	E > G	Neg	Non-native	Cutthroat trout	Miller 1952[3]
	E > G	Neg	Non-native	Cutthroat trout	Miller 1953[3]
	G	Pos	Native	Atlantic salmon	Kallio-Nyberg and Koljonen 1997
	G	*	Native	Rainbow trout	Reisenbichler and McIntyre 1977[4]
Survival	E	Neg	Native	Arctic char	Finstad and Heggberget 1993
	E	Neg	Native	Atlantic salmon	Hansen 1987[5]
	E	Neg	Native	Atlantic salmon	Jonsson et al. 1991
	E	Neg	Native	Chinook salmon	Unwin 1997[3]
	E	Neg	Native	Rainbow trout	Reisenbichler and McIntyre 1977[4]
	E > G	Neg	Non-native	Brown & Rainbow trout	Weiss and Schmutz 1999[3]
	E > G	Neg	Non-native	Brown trout	Kelly-Quinn and Bracken 1989[3]
	E > G	Neg	Non-native	Brown trout	Skaala et al. 1996[3]
	E > G	Neg	Non-native	Cutthroat trout	Miller 1953[3]
	E > G	Neg	Non-native	Cutthroat trout	Miller 1952[3]
	G	Neg	Non-native	Atlantic salmon	De Leaniz et al. 1989
	G	Neg	Non native	Brook trout	Flick and Webster 1964[6]
	G	Neg	Non-native	Brook trout	Lachance and Magnan 1990b[1]
	G	Neg	Non-native	Brook trout	Vincent 1960
	G	Neg	Non-native	Brook trout	Fraser 1981[7]
	G	**	Native and non-native	Brown trout	L'Abée-Lund and Langeland 1995[3]

*Hatchery/wild hybrids outgrew pure populations.
**Wild population intermediate survival of two hatchery populations.

Comments regarding usage of data in meta-analysis:
[1]*P*-value was calculated from Table 3.
[2]*P*-value was calculated from length data in Table 3.
[3]No statistics or raw data were available for inclusion of study.
[4]*P*-value was calculated from Table 4, comparing pure hatchery strain with pure wild strain.
[5]*P*-value was calculated from data.
[6]*P*-value was calculated from Table 2.
[7]*P*-value was calculated from Table 4.

of particular concern when species are extended beyond their natural range, where prezygotic isolation mechanisms against hybridization with indigenous species may be absent (Leary et al. 1995). Releases of hatchery fish can also attract predators (including humans), and thus may cause the intensity of predation on naturally produced fish to increase (Beamish et al. 1992, Collis et al. 1995).

While little is known about the level of early maturation as parr among hatchery-reared fish, it is likely that the high growth rates that they experienced in the hatchery will increase the potential for early maturation following release. If so, this will alter patterns of sexual selection in wild populations and may ultimately affect the adaptive landscape, leading to evolutionary responses in the recipient population (reviewed in Fleming 1998).

The effects that released hatchery fish can impose on naturally produced fish should make us cautious toward implementing stocking programs to compensate for habitat degradation and to increase fisheries. Indeed, under certain scenarios, theoretical models suggest that long-term stocking may lead to extinction of the native population (Evans and Willox 1991, Byrne et al. 1992). Existing empirical studies clearly show that fish density in stocked streams may not show the desired positive response to releases (Table 5). In fact, in some cases a negative trend in population density has been associated with releases. Perhaps the best evidence for such an effect comes from a controlled study where populations of coho salmon were monitored for five years in 15 stocked and 15 unstocked streams (Nickelson et al. 1986). Stocked streams had higher densities of juveniles after stocking, but the number of adults returning to the two types of streams did not differ. Furthermore, spawning success of released fish was reduced, causing a lower density of juveniles in the stocked streams than in the unstocked ones one generation later.

Conclusions

The performance of hatchery fish and their interactions with wild fish appear to be of such a character as to suggest that many of the current stocking practices may be detrimental to the recipient populations. The present synthesis should in-cite caution in our attempts to mitigate negative effects of habitat degradation by releasing hatchery-produced fish. Although the reports published, and thus referred to here, may be biased towards negative effects of stocking, the potential for negative effects must nevertheless be acknowledged and dealt with.

A critical question we might ask ourselves is whether something can be done to avoid negative ecological effects of stocking? The answer to this question is yes and no. Better broodstock collection and mating protocols, more-natural rearing conditions, wild-fish-friendly release strategies and more focus on local broodstocks can improve the quality of hatchery fish released and reduce their impacts on wild fish. Behavioural deficits arise due to phenotypic responses to the radically unnatural abiotic and biotic environment of hatcheries, and will initially be environmental in origin but over generations of rearing will also involve genetic responses. Generally, hatcheries are psychosensory-deprived environments for fish (Olla et al. 1998). Adding complexity and enriching the environment is a common method for improving the well being of captive animals (e.g., mammals, reptiles and birds) and may have application to hatchery populations of salmonids. Such an approach could reduce environmentally induced differences between cultured and wild fish, and increase post-release survival by decreasing stress, reducing domestication and acclimating fish more appropriately for their future environments (Berejikian et al. 2000). This could be done by adding habitat complexity, altering water-flow velocities, supplementing diets with natural live foods and reducing rearing densities to produce fish more wild-like in appearance and with natural behaviours and survival (Flagg and Nash 1999). For example, increasing habitat complexity has been shown to aid in the development of appropriate body camouflage colouration and increase behavioural fitness (Maynard et al. 1995). Similarly, anti-predator conditioning can improve post-release survival, as predator recognition and avoidance behaviour in juvenile salmonids improves in fish exposed to predators (Potter 1977, Olla and Davis 1989, Berejikian 1995) or odours from injured conspecifics (Brown and Smith 1998, Berejikian et al. 1999).

The development of release strategies that minimize negative ecological effects of hatchery fish on wild fish could also be a significant improvement. Released juveniles should be within the size range of wild juveniles, if not of a similar size distribution. The greatest risk of releasing large hatchery fish is that they may out-compete wild fish, endangering the natural production of the population. Releases of hatchery fish should also complement the natural spatial and temporal patterns of abundance of wild fish in the population. That is, the number of fish released should not exceed the carrying capacity of the environment, which varies spatially within the river and through time.

Table 5. Effects of stocking on wild populations.

Performance	Observations	Fish Origin	Fish Species	Reference
Productivity	Densities similar in stocked and unstocked sections of stream.	Non-native	Brown trout	Kelly-Quinn and Bracken 1989
	Spawning among hatchery reared and hybridisation with native population demonstrated. Survival rates of 0+ three times higher in native than in hybrids.	Non-native	Brown trout	Skaala et al. 1996
	Movement of resident trout higher out of stocked sections. Total population size unaffected by stocking.	Non-native	Brown and Rainbow trout	Weiss and Schmutz 1999
	No increase in total population size. Reduced natural production.	Native	Chinook salmon	Unwin and Glova 1997
	10-fold reduction in wild spawner densities, suggested to be result of hatchery selection for early spawning and displacement of wild fish.	Native & non-native	Coho salmon	Flagg et al. 1995
	Total number of juveniles higher in stocked streams than unstocked one summer after stocking. Wild juveniles less abundant in stocked than unstocked areas. Similar numbers returned to spawn in stocked and unstocked, but lower density of resulting juveniles in stocked streams.	Non-native	Coho salmon	Nickelson et al. 1986
	After stop of stocking, large increases in natural production of rainbow and brown trout. Stocking in previously unstocked stream caused reduced production of wild brown trout.	Native*	Rainbow & Brown trout	Vincent 1987
	Stocking of high rates of rainbow (8–10 times wild density), but not lower rates, caused reduced survival of wild rainbow and cutthroat trout.	Non-native	Rainbow & Cutthroat trout	Petrosky and Bjornn 1988
Growth	Residence time and growth in estuary unaffected by presence of hatchery fish.	Native	Chinook salmon	Levings et al. 1986
	Growth of resident brown trout unaffected. Resident rainbow reduced growth in stocked sections.	Non-native	Brown & Rainbow trout	Weiss and Schmutz 1999
Hybridisation	Massive stocking of hatchery reared fish force salmon and trout to common spawning grounds, causing hybridization. 41.5 % hybrid parr in restored river section.	Native & non-native	Brown trout & Atlantic salmon	Jansson and Öst 1997
Migration	Wild smolt attracted to shoals of released smolt and join them when migrating downstream.	Native	Atlantic salmon	Hansen and Jonsson 1985
	Long-term change in mean date of entry of adult fish after hatchery program initiated.	Native	Chum salmon	Lannan 1980
Predation	Numerical response of spiny dogfish to stream mouth at time of hatchery release of smolt.	Native	Coho & Chinook salmon	Beamish et al. 1992
	Squawfish aggregate to feed on hatchery-released juvenile salmonids.	Native	Pacific salmon	Collis et al. 1995

* Both brown and rainbow trout were historically non-native species in this system, but have now established self sustaining populations.

Thus improvement in the way hatchery fish are reared and released can lead to significant strides towards reducing their negative ecological impacts on wild fish. However, as Waples (1999) points out, it is a myth to believe that these changes will make the problems disappear altogether. This is because (1) environmental and genetic changes to fish in hatcheries cannot be avoided entirely; and (2) many of the risks are negatively correlated, so efforts to reduce one risk simultaneously increases another. Clearly we need to, first and foremost, be cautious in our use of hatcheries, particularly when releases are to be used in supplementing wild populations. We need to better understand how to culture fish for release (i.e. phenotypic responses to culture and effects of domestication, and how to minimize them) and how to release these fish to minimize/eliminate potentially detrimental impacts on wild populations while contributing to an overall increase in productivity.

Acknowledgements
We thank J. I. Johnsson and E. Petersson for critically commenting on this review. Financial support was provided by the Norwegian Directorate for Nature Management, the Norwegian Research Council, and the Norwegian Electricity Association (EnFo).

References
See Appendix 1

The Ability of Released, Hatchery Salmonids to Breed and Contribute to the Natural Productivity of Wild Populations

Ian A. Fleming and Erik Petersson, Department of Animal Ecology, Evolutionary Biology Centre, Uppsala University

Nordic Journal of Freshwater Research (2001) 75:71–98

Abstract
The success and implications of hatchery release programmes are intimately tied to the reproductive capabilities of the hatchery fish in the wild. Moreover, reproductive interactions are important in understanding the ecological and genetic threats that hatchery fish may pose to wild populations. Reproductive success is a key to self-sustainability, shaping natural and sexual selection, and influencing the genetic diversity of populations. In this paper, we review the determinants of breeding success in natural populations and the implications of parental traits and decisions for offspring survival and success. We then address how rearing and release programmes affect the reproductive traits and performance of fish. A review of such programmes reveals that in the few cases where adequate assessments have been made released fish frequently fail to attain self-sustainability and/or contribute significantly to populations. Clearly, new approaches based on sound scientific research are needed and these need to be tailored specifically to the management objectives.

Introduction
Deliberate releases of salmonid fishes appear to take two main forms: (1) *fisheries releases* to increase population size for fisheries; and (2) *conservation releases* to save populations at risk of extinction or re-establish native populations that have been eradicated. Fisheries releases are the most common and in Norway, are most often undertaken for mitigation purposes, i.e. to compensate for the impacts of habitat alteration/degradation such as hydropower regulation (Finstad and Jonsson 2001, Fjellheim and Johnsen 2001, Vøllestad and Hesthagen 2001). An unfortunate consequence of this approach is that it can become acceptable to sacrifice the productivity of natural populations as long as the hatchery releases compensate for the loss to the fisheries. Little consideration is given to habitat or other improvements. This approach is also problematic because hatchery fish are often stocked on top of the natural production, which has become constrained by habitat loss (i.e. reduced natural carrying capacity), thus inducing potentially deleterious competition between the wild and released fish (reviewed in Einum and Fleming 2001, Sægrov et al. 2001). Only recently have we begun to fully appreciate that the long-term sustainability of salmonids requires conservation of natural populations and their habitats. Conservation releases are often undertaken to save populations that are likely to perish due to demographic factors (e.g., small population size). Such releases aim to use native fish as broodstock to give the population a boost (supportive breeding) and in theory, are to be considered a temporary solution until the factors responsible for the population decline are identified and alleviated.

Conservation releases may also be undertaken to reintroduce/re-establish populations that have been eradicated (e.g., because of acid rain or the parasite *Gyrodactulus salaris*). Once the cause of the extinction has been rectified, fish are reintroduced either from the population’s gene bank or from neighbouring populations inhabiting similar environmental conditions, i.e. having adaptations likely to aid in establishment.

One of the main premises/goals upon which many of the above concepts of fish releases are built upon is that they can provide a positive long-term benefit to natural populations. Yet, there appears to have been little or no attempt to find out whether this goal is achieved, and this is not a problem restricted to Norway, but a universal problem (cf. Waples et al. in press). Thus, the role of fish releases in the conservation of wild salmon populations is intimately linked to understanding the dynamics of breeding and ultimately, reproductive success between wild and hatchery released salmon. The aim of the paper is to review the determinates of breeding success and its close link with offspring success (reproductive success) in salmonid fishes, particularly Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*). Then we examine the close relation between reproductive success and the desired goals of release programs, and how they may affect the reproductive traits and performance of fish. Finally, we provide an analysis of release programs where direct and indirect information about the reproductive success of released salmonids and their potential effect on natural productivity exist.

Demographic and Genetic Consequences of Breeding Success

Breeding success is the outcome of competition among individuals to maximize the number of embryos surviving until independence (i.e. yolk absorption in salmonids) within the constraints imposed by the opposite sex (e.g., number of mates, mate choice) and the environment. Because of its link via offspring survival to individual reproductive success (a measure of fitness), it plays an important role in shaping the demographic and genetic structures of populations (cf. Vehrencamp and Bradbury 1984).

From the population perspective, the most obvious implication of variation in breeding success is its effects on annual recruitment and thus natural production. However, natural breeding also generates intense selection upon both male and female salmon that shapes life history strategies and thus the demographic structure of populations. Evidence from a series of semi-natural breeding experiments with Atlantic salmon (Fleming et al. 1996, 1997) indicate that breeding alone can generate a coefficient of variation in female success of 102% (range 71–131%) and in male success of 151% (range 60–268%). Thus, the variance in breeding success is often considerably larger than the mean success, with some individuals being highly successful while others are unsuccessful (range in female success: 0–4,644; male success: 0–11,188 embryos parented). This generates intense natural and sexual selection on male and female salmonids targeting traits such as body, hooked snout, kype, dorsal hump, caudal peduncle, and adipose fin size (van den Berghe and Gross 1989, Järvi 1990, Fleming and Gross 1994, Quinn and Foote 1994, Petersson et al. 1999). It also affects life history traits, including survival, egg production, age at maturity and the evolution of alternative reproductive tactics (e.g., sneaking versus fighting), and subsequently the demographic features of the population such as sex ratio and age structure (reviewed in Fleming 1998). Any program to conserve salmonid populations, therefore, must take account of the variation in breeding success, particularly when hatchery release programmes are being considered.

Variability in breeding success of individuals also affects the genetic structure of populations in subsequent generations, both directly through selection as described above and indirectly through its affects on a population's effective size. The effective size of a population ($N e$) is an important parameter determining the amount of genetic variability that can be maintained, particularly when the population is small (e.g., Martinez et al. 2000). It is defined as the size of an ideal population that would lose genetic variation at the same rate as a given real population (Lande and Barrowclough 1987). The loss of genetic variability influences the population's probability of long-term survival because genetic variation is requisite for evolutionary adaptation in changing environments. Things that affect $N e$ include variability in population size through time, skewed sex ratios and variability among individuals in breeding success (Lande and Barrowclough 1987, Nunney 1991). Variability in breeding success in salmonids can reduce the breeding effective size to 48–76% of the number of adults on the spawning grounds (Fleming 1994, cf. Nunney and Elam 1994).

Populations will often go extinct due to demographic problems (stochastic and/or deterministic) before loss of genetic variability can become a problem (Lande 1988). Thus demography will often be a more pressing conservation problem than genetics, though genetic diversity will remain important in maintaining the potential for adaptive evolution. Two forms of variability will affect the demography of populations at small sizes, demographic (e.g., sex ratio, age-structure) and environmental (e.g., weather, food supply, competitors, parasites). They are generally overlapping categories to describe different forms of variation that influence the demography (i.e. survival and reproduction) of a population. Environmental variability is considered to pose a greater threat to population survival (Lande 1988, 1993, Caughley 1994). Analyses by Leigh (1981) and Goodman (1987) suggest that environmental variability will usually dominate other forms of variability in populations larger than 20–100 individuals. In most real situations we are likely to have environmental variability first driving populations to low levels and demographic and genetic variability then putting on the finishing touches. The central message is that risk of extinction increases with decreasing population size and will be affected by variation in breeding success.

A final aspect where breeding success plays a critical role is in understanding the potential for gene flow. In the present context, such gene flow will frequently be one-way from cultured to native fish, though some supplementation programs will obtain a fraction of their broodstock from the wild each generation. If interbreeding is successful, the resultant gene flow may lead to the loss of genetic variability among populations, an important component of genetic variation in salmonid species and their evolutionary potential (e.g., Ståhl 1987, Allendorf and Leary 1988, Waples 1991, Hansen and Loeschcke 1994). At the within-population level, however, the effects may be negative or positive. Interbreeding may disrupt local adaptations and break up co-adapted gene complexes (i.e. combinations of genetic traits that have evolved over a long period to work complementarily) resulting in a reduction in fitness known as outbreeding depression (Templeton 1986). By contrast, it may simultaneously increase genetic variability, thereby reducing the accumulation of recessive deleterious mutations in populations suffering from inbreeding depression, and increasing within-population evolutionary potential. Despite such potential positive effects, Hindar et al. (1991) in a review of intentional (e.g., transplants) and unintentional introductions of salmon (e.g., salmon farm escapes, straying of hatchery releases) found that the effects were frequently negative (see also Gharrett and Smoker 1991).

What Determines Breeding Success?

Mating success is one of the most important factors determining breeding success. If an individual were not able to achieve matings, its reproductive output would be zero, whatever qualities the individual has in other respects. But, an ability to achieve matings does not necessarily trans-late into breeding success (e.g., due to low gamete viability or poor embryo survival). Breeding success in salmonid fishes will be determined by a variety of factors, such as body size, timing, egg production, competitive ability, attractiveness, and embryo viability. The theoretical underpinnings to understanding investments in these various traits assume that different life history components are causally related and increases in allocation to one component, for example reproduction, will be at the expense of allocation to other components, such as growth and survivorship (Williams 1966, Gadgil and Bossert 1970). However, such trade-offs may be masked in the wild because of individual variation in the ability to acquire resources, with individuals having better acquisition abilities being able to devote more energy into a wide array of traits (Reznick et al. 2000). In this section we aim to review some important elements of breeding success and how they are interrelated.

Age and Size at Maturity

Age and size are coupled in most fish species, with older individuals being generally larger than younger ones. In organisms having indeterminate growth, such as fish, the relation between growth and reproduction is potentially very important because size and fecundity are often positively related. In terms of lifetime reproductive potential, early-breeding individuals may maintain a higher cumulative reproductive output until a certain age; after which late-breeding individuals may have a higher cumulative potential (cf. Ford and Seigel 1994). This reflects the decreased growth often associated with increased reproductive investment that reduces future fecundity (cf. Williams 1966). Also, maturing at young age provides a demographic benefit in terms of decreasing generation times in expanding populations, while delaying breeding incurs an accumulated risk of dying (e.g., due to diseases, parasites, predators or senescence) (Bell 1980). Thus, the optimal size-to-age at maturity depends on growth and mortality rates, which vary with environment (Charlesworth 1980). Therefore, organisms in spatially or temporally changing environments frequently show adaptive phenotypic plasticity for this trait (Schlichting and Pigliucci 1998).

Early experimental work by Alm (1959) showed that a dome-shaped norm of reaction for size-to-age at maturity is common in fishes, with size at maturity being smaller for both fast- and slow-growing individuals than for more intermediate-growing fish. Using computer simulations, Perrin and Rubin (1990) showed that such a dome-shaped norm of reaction is optimal when assuming a finite life span and a negative relationship between production and survival rates. This latter assumption is supported by empirical data (e.g. Beverton and Holt 1959, Jensen 1985), as well as by physiological and demographic arguments (e.g. Sibly and Calow 1986). Age and size at which to mature are then among the principal components of the reproductive strategy (i.e. a genetically based life history or behaviour programme affecting an organism's allocation to reproductive effort among alternative phenotypes or tactics; Gross 1984, 1996) of a salmonid species.

Considerable variability in these traits exists among and within species, and also among and within populations of a species, including salmonid fishes (e.g., Alm 1959, Jonsson 1985, Groot and Margolis 1991, Hutchings and Jones 1998). In addition to the effects of abiotic conditions, this variability in salmonid fishes is influenced strongly by reproductive success as affected by the breeding environment (reviewed in Fleming 1998), and by the costs of reproduction (e.g., survival; Hutchings 1994). One of the most striking examples of this occurs within Atlantic salmon and brown trout, where some males mature during their freshwater stage as parr while others mature after an oceanic migration. The mature male parr may be less than a hundredth the weight, and about a third the age of ocean-migratory (anadromous) males (Fleming 1998). These two male phenotypes appear to coexist as a result of the combined effects of frequency-and status-dependent selection during breeding (Gross 1984, 1996, Bohlin et al. 1986, 1990, Hutchings and Myers 1994), where the relative success gained from using a particular tactic (anadromy versus parr maturity) will be influenced by an individual's competitive ability ("state") and the tactic used by others in the population.

Intrasexual Competition

In most salmonid species, competition among individuals of the same sex for breeding resources is intense. Moreover, because males and females fight over different resources, access to females and spawning sites respectively, the intensity of intrasexual competition differs between the sexes. The operational sex ratio (OSR, i.e. the number of sexually active males to that of sexually active females on the spawning ground) is a good predictor of contest competition for mates and to some extent mate choice. However, it will not necessarily be a good predictor of the prevalence or intensity of other mechanisms of sexual selection, such as sperm competition, infanticide or coercion (see Kvarnemo and Ahnesjö 1996). In salmonids, the OSR is highly male biased in most cases (e.g., Quinn et al. 1996). Even though the sex ratio of returning adults in some cases may be female biased (Fleming 1998), the OSR (i.e. the sex ratio on the spawning grounds) is likely to be male biased. This is a consequence of (1) asynchronous spawning by females and the male ability to spawn rapid and repeatedly; for example, female Atlantic salmon may be active on the spawning ground for 7–10 days, while males may remain so for about a month (Webb and Hawkins 1989, Fleming et al. 1996, 1997; see also Blanchfield and Ridgway 1997), and (2) the presence of early maturing male parr. It is not uncommon in salmonids to observe ten or more males, including mature parr, competing for access to a single female (Keenleyside and Dupuis 1988, Evans 1994; personal observations of wild Atlantic salmon).

Evidence from coho salmon (*Oncorhynchus kisutch*) suggests that male breeding competition can generate a 52-fold increase in the opportunity for selection (Fleming and Gross 1994). Such intense selection has likely been responsible for the evolution of elaborate secondary sexual characteristics (i.e. developed for accessing breeding resources, including mates and spawning sites), such as elongated jaws and canine-like breeding teeth, dorsal humps, bright breeding colouration and skin thickening (Schroder 1982, Järvi 1990, Fleming and Gross 1994, Quinn and Foote 1994, Petersson et al. 1999). Moreover, the studies above indicate that males are more intensively selected than females. For example, Fleming and Gross (1994) found the intensity of selection due to breeding competition to be nine times greater in male than female coho, suggesting that this was responsible for the sexual dimorphism in the expression of secondary sexual characters. Such sexual dimorphism is common in salmonid fishes.

This is not to suggest that breeding competition among females is weak, but rather less intense than that among males. While breeding sites in many rivers may appear non-limiting, females do show strong preferences for particular sites, often clumping nests in such areas (Heggberget et al. 1988, Blanchfield and Ridgway 1997, Essington et al. 1998). Competition over breeding sites can result in delays in breeding, female displacement and nest destruction by superimposition (e.g., Schroder 1981, van den Berghe and Gross 1989, Fleming 1996, Petersson and Järvi 1997, McPhee and Quinn 1998, Essington et al. 2000). Fleming and Gross (1994) found that female breeding competition generated a 6-fold increase in the opportunity for selection among female coho salmon (see also van den Berghe and Gross 1989). Thus intrasexual competition in both sexes will be important in determining breeding success, and ultimately the demographic and genetic structure of salmonid populations.

Mate Choice

Empirical and theoretical data pinpoint what most biologists intuitively know, that female mate choice is much more common than male mate choice (reviewed in Andersson 1994). In salmonid fishes, females appear to express mate choice through delays in breeding (Schroder 1981, Foote and Larkin 1988, Foote 1989, de Gaudemar et al. 2000) and aggression, sometimes directing a large proportion of their aggressive activity towards males (e.g., Keenleyside and Dupuis 1988, Fleming et al. 1997, Petersson and Järvi 1997). The choice criteria of female salmonids are still relatively unstudied, with the exception of experiments by Petersson et al. (1999) and de Gaudemar et al. (2000) showing female choice of males with relatively large adipose fins in brown trout and large body size in Atlantic salmon, respectively. It is unlikely that female salmonids gain direct, material benefits from such mate choice (e.g., territories, food, parental care), although they may gain genetic benefits for their offspring (e.g. 'good genes' or 'runaway' coevolution; see Andersson 1994), safety from disruption and injury during spawning, reduced risk of infection and assurance of fertilization (see Reynolds and Gross 1990). Recent evidence suggests males may also affect egg swelling immediately following fertilization, which may be a special case of 'male contribution' (Pakkasmaa 2000, cf. Seppä 1999), though its significance remains unclear and unstudied. The extent of female choice in salmonids, however, appears to be constrained or circumvented by male-male competition, because dominant males can monopolize access to females (Jones 1959, Järvi 1990, Fleming et al. 1996, 1997, Petersson et al. 1999). Female incitation of male-male competition, however, may be viewed as a means of 'passive' choice (cf. Cox and Leboeuf 1977), though its role in salmonid fishes is unstudied. The costs of the female choice in terms of energy, predation risk and aggression from males may often outweigh its benefits for salmonid fishes and as a result it is unlikely to play a dominant role in the mating system.

Mate choice by male salmonids is probably even less well studied than that of females. Males may show choice either for absolute female size because of its direct relation with female quality (e.g., fecundity, egg size and parental care ability; Sargent et al. 1986) or for similar-sized females because of the male's ability to obtain and control mates (Foote 1988). It is common for the number of males associated with a spawning female to increase with her size (Hanson and Smith 1967, Campbell 1977, Jonsson and Hindar 1982, Sargent et al. 1986). Asynchronous spawning by females in some circumstances, however, may constrain male mating options.

One possible outcome of the combination of mate choice and intrasexual competition is assortative mating, where males and females in a population mate more frequently with a phenotype (in a broad sense) similar to their own than expected from random. Assortative mating may arise when individuals of both sexes actively choose a mate of a similar phenotype (Burley 1983). The rapid phenotypic and genetic divergence of Icelandic Arctic char may be an example of this (cf. Gíslason et al. 1999). Alternatively, assortative mating may arise when all individuals of one sex have the same preference, but only some of them are able to achieve it (Burley 1983). For example, if all females prefer large males and all males prefer larger, more fecund females, then only the larger males are able to gain access to the preferred females. The smaller males and females, as a result, will be forced to mate with each other (cf. Petersson 1990). This pattern is most likely operating in Dolly Varden (Maekawa et al. 1993) and Japanese charr (Maekawa et al. 1994). Several other studies also report positive size-assortative mating in salmonids (Hanson and Smith 1967, Schroder 1981, Jonssson and Hindar 1982, Foote 1988). It has also been suggested that negative assortative mating based on major histocompatability complex (MHC) genes may be important in salmonids, though this remains untested (Grahn et al. 1998). Assortative mating is likely to be a common pattern in salmonid fishes.

The Link Between Adult Reproductive Traits and Offspring Success

Most of the factors contributing to embryo survival and early juvenile survival are linked to the female, as she chooses the spawning time and site, constructs the redd and deposits the nutrient-rich eggs. In Atlantic salmon, the survival of eggs in the nests not destroyed during incubation (e.g., by scouring and nest superimposition, see below) may be as high as 74–91% until hatching (Shearer 1961, MacKenzie and Moring 1988). When the eggs hatch, the small juveniles still have a considerable amount of nutrients and energy stored in the yolk-sac as a result of maternal provisioning (Einum and Fleming 1999, Berg et al. in press). Once the yolk sac is absorbed, the juveniles emerge from the gravel into the open water. Loss rates during the first weeks thereafter are very high, with 68-88% mortality during the first 17-28 days (Einum and Fleming 2000a,b). Similar patterns have been observed in brown trout, where about 80% of fry rarely feed after emergence, quickly lose weight and drift down-stream during night and die (Elliott 1986;

see also Héland 1980a, b). Incubation and early juvenile life are thus periods of intense selection (Elliott 1994, Einum and Fleming 2000a, b).

Spawning Time—A female's spawning time will dictate the thermal regime her embryos experience during development and to a large extent, their hatching and emergence time from the gravel as fry (e.g., Crisp 1981, Jensen et al. 1991). Peak spawning times between the earliest and latest breeding populations of a salmonid species may range by several months (Groot and Margolis 1991, Fleming 1996). The timing among populations correlates with water temperature during incubation (Heggberget 1988), likely to ensure optimal timing of hatching and initial feeding for the offspring (Brannon 1987, Heggberget 1988, Quinn et al. 2000). Other factors such as water-flow regime during egg incubation or limited access to the breeding grounds due to river freeze-up might also be important (Fleming 1996). Within populations, spawning may extend over many weeks (e.g., Fleming and Gross 1989, Tallman and Healey 1994, Fleming 1996, Blanchfield and Ridgway 1997), and may be temporally segregated between upper and lower reaches of the river, particularly in large systems where environmental conditions differ (Burger et al. 1985, Webb and McLay 1996). In addition to within-river variability in environmental conditions, intraspecific breeding competition may be an important factor affecting spawning times (Schroder 1981, Fleming and Gross 1993, Elliott 1994, Petersson and Järvi 1997). For the offspring, spawning time will affect emergence time, with early emerging fry having an advantage in establishing territories, and beginning to feed and grow before late emergers (Fausch and White 1986, Chandler and Bjornn 1988, Brännäs 1995). Metcalfe and Thorpe (1992) showed that Atlantic salmon emerging first were dominant, grew faster and smolted a year earlier than later emerging conspecifics. Moreover, Einum and Fleming (2000a) identified directional selection for early emergence in Atlantic salmon due to differential survival and influences on body size. The advantages of early offspring emergence and ready access to highest-quality nest sites, however, must be traded off against susceptibility to nest destruction by digging activity of later-breeding females and probability of unfavorable environmental conditions early in the spring during emergence. These trade-offs may generate adaptive variation in spawning time within populations and result in the evolution of adaptive temporal variation in life history traits ("adaptation-by-time," Hendry et al. 1999).

Spawning Site—Female choice of spawning site will dictate the environment her embryos and subsequently, her emerging offspring will experience as fry. Poor quality nests, having high concentrations of fine sediment/sand and thus poor permeabilities and low intragravel dissolved oxygen will severely reduce embryo survival (reviewed in Chapman 1988). Location will also be critical to the emerging fry, which initially remain in the nest's vicinity due to their poor swimming ability and negative buoyancy. Thus, females unable to choose and/or fight for a good site will expose her offspring to potentially harsh environmental conditions and thus high mortality immediately after emergence. For example, proximity of the spawning site to suitable nursery habitat, particularly downstream (Elson 1962, Gibson 1993), may be important as fry slowly disperse. Egg burial depth will be important in de-creasing the probability of egg destruction by scour during spates and by nest superimposition by later spawning females (e.g., Crisp 1989, van den Berghe and Gross 1989, Steen and Quinn 1999). While deeply buried embryos could suffer from inadequate water flow, evidence from chum salmon (*O. keta*) suggests this is not necessarily the case possibly because larger females, which dig deeper nests, do so in faster water than small females (Peterson and Quinn 1996). In general, egg burial depth increases with female size (reviewed in DeVries 1997), suggesting that it is selectively advantageous.

Egg Size—How a female partitions her resources available for egg production has important fitness consequences affecting the number of surviving offspring she can expect. Large eggs give rise to larger juveniles than smaller ones (e.g., Fowler 1972, Gall 1974, Pitman 1979, Thorpe et al. 1984), which in turn may afford faster juvenile growth (Bagenal 1969), higher status (Wankowski and Thorpe 1979), reduced susceptibility to starvation (Hutchings 1991), predation (Parker 1971) and parasites (Boyce 1974), or in other words, better offspring survival. However, large egg size appears to be at the cost of reduced egg number (fecundity)(Svärdson 1949, Fleming and Gross 1990, Quinn and Bloomberg 1992, Jonsson et al. 1996). Theory suggests that natural selection should maximize a female's fitness returns per unit of resource invested in egg production. This will be accomplished by dividing that investment into eggs of optimal size (Smith and Fretwell 1974, Parker and Begon 1986, Roff 1992). Thus, for a given amount of resources for egg production, egg number should vary in response to selection upon egg size. Einum and Fleming (2000b) tested this by manipulating egg size in Atlantic salmon and showed that the joint effect of egg size on egg number and offspring survival resulted in stabilizing phenotypic selection for an optimal size. A size that closely matched the mean egg size in the population, but was below that that maximized offspring survival. The results indicated that egg size had evolved largely in response to selection on maternal rather than offspring fitness.

In another study, Einum and Fleming (1999) found distinct reaction norms in the performance of juvenile brown trout from small and large eggs, with growth and survival being similar in high quality environments but becoming increasingly divergent in poorer environments. The existence of such reaction norms indicates that the optimal egg size varies across gradients of environmental quality, and this has likely shaped the evolution of egg size. This may help explain why the eggs of individual females are fairly uniformed in salmonid fishes (Fleming and Ng 1987, Fleming et al. 1996), while among females and across population eggs may differ more than twofold in weight (Beacham and Murray 1993, Fleming 1998). Like fecundity, egg size typically increases with female size, such that larger females forgo more eggs to have larger eggs for their body size than do small females. This suggests that the optimal egg size likely varies in relation to abiotic and biotic factors as affected by female size. For example, because larger females deposit more eggs on average in their nests than smaller females (Fleming 1996), sibling competition at emergence is likely to be more intense and hence select for a larger optimal egg size (cf. Parker and Begon 1986). Alternatively, female size may influence the quality of incubation habitat her eggs experience (van den Berghe and Gross 1989; modeled by Hendry et al. in press). Small females, which are often less competitive than larger females, may be forced to use sub-optimal substrate, having high proportions of fine sediment, limited intra-gravel water movement and low levels of dissolved oxygen. Such sub-optimal incubation substrate may select against large eggs, because of their higher metabolic demands and less efficient surface-to-volume ratio for acquiring oxygen (van den Berghe and Gross 1989). Quinn et al. (1995) found a positive association between egg size and substrate size in sockeye salmon (*Oncorhynchus nerka*), suggesting adaptation in response to spawning site quality. Furthermore, under conditions of intense nest competition, some large females may also be displaced into poor nesting environments and thus incur lower success than smaller females (Holtby and Healey 1986), which over time should select for a smaller average egg size within the population.

What is Known About the Reproductive Patterns of Released Fish?

As evident from the previous discussion, the evolution and dynamics of the breeding system of salmonid fishes is complex, having important consequences for the demographic and genetic structure of populations. The release of hatchery fish will almost certainly affect this structure and understanding the reproductive patterns of the released fish will be important in predicting their effect on the population's natural productivity.

The reproductive traits of released fish will reflect the stock's genetic origin, rearing history (domestication effects) and form of rearing (environmental effects). The term 'domestication' has been applied differently, though all agree that it involves animals being 'farmed by' man in a human-imposed environment. This process inevitably results in evolutionary changes due to intentional and unintentional artificial selection by humans and random genetic effects (e.g., bottlenecks, founder effects). A conservative view-point holds that domestication should be defined as involving certain irreversible changes of the animal exposed to the new environment as a result of an active selection procedure by man (cf. Hemmer 1990). From this point of view, there are very few 'true' domestic fishes in the world, though the carp (*Cyprinus carpio*), which has been intentionally selected for over 2000 years (Ling 1977), would likely qualify. A more liberal viewpoint holds that domestication involves all forms of evolutionary change due to artificial rearing, not just those due to intentional selection. The use of the term 'domesticated' for hatchery-reared fish has a long history, and was, for example, used in the 1950s (see e.g., Wood et al. 1957). For practical reasons we concur with this traditional use of the term.

Most studies examining the reproductive traits of released fish have thus far been laboratory studies, in a broad sense; i.e. comparisons of the behaviour of wild and domesticated fish in controlled environments such as aquaria, stream channels or small enclosed areas of rivers. In addition, most studies have compared wild and multi-generation hatchery fish, often of differing genetic origins, thus making it difficult to separate genetic from environmental effects. This, however, is not surprising given the scale at which these experiments must be conducted, and the fact that for most hatchery stocks their founding wild population has been altered by large-scale introgression from hatchery fish. Nevertheless, in this section we will attempt to address the environmental and genetic (domestication and non-native origin) effects of hatchery rearing on the reproductive traits of released fish.

Age and Size at Maturity

Typically, hatchery-rearing leads to rapid growth of fish due to *ad libitum* food availability, which can affect the age and size at maturity. Early (i.e. precocial) maturity among male salmonids is well known to be positively related to growth (e.g., Alm 1959, Saunders et al. 1982, Gross 1996). Thus, releases of parr that have experienced rapid growth in hatcheries may affect mating dynamics in wild populations by dramatically increasing the number of mature male parr. Rapid juvenile growth can also result in low age-at-smolting (e.g., Metcalfe et al. 1989, Økland et al. 1993) and subsequently, age-at-maturity. Moreover, the proportion of fish returning as grilse (one-sea-winter) is positively correlated with the size of smolts released (Chadwick 1988, Chadwick and Clayton 1990, Crozier and Kennedy 1993). A decrease in the age- and thus, size-at-maturity is a pattern observed in hatchery-supplemented populations of Atlantic salmon (e.g., Christensen and Larsson 1979, Sharov and Zubchencko 1993). In addition to environmental effects due to growth rate, there are indications that such responses may also reflect domestication selection in hatchery populations (Kallio-Nyberg and Koljonen 1997, also Fleming and Gross 1989). The effects of domestication on size-at-maturity, however, may not be straight forward as evidenced by the apparent lack of effect on Atlantic salmon and positive effect on brown trout of the Älvkarleby hatchery, Sweden (Petersson et al. 1996).

Homing

Generally, the homing precision of returning hatchery adults released as freshwater juveniles or as smolts in rivers is much higher than that for fish escaping or being released at marine sites, without any connection with a river (Hansen and Jonsson 1994, Hansen and Quinn 1998). Smolts and post-smolts escaping or released from a marine site return to the area in the sea from which they escaped/were released, but because of a lack of home-river imprinting, the sexually mature fish will enter several rivers in that area to spawn late in the season (Sutterlin et al. 1982, Gunnerød et. al.1988, Hansen et al. 1989). For example, experiments in the Baltic in the early 1980s demonstrated that transporting smolts to sea pens and delaying their release a few months dramatically improved survival, however, it also significantly increased their rate of straying (Anon. 1997). Similarly, hatchery Atlantic salmon released as smolts at a river mouth return there as adults at a similar time as wild fish, but ascend the river later apparently due to a lack of juvenile experience with the river (Jonsson et al. 1990, 1991; cf. McKinnell et al. 1994, Petersson and Järvi 1993). Also, the timing of release of smolts and post-smolts can affect straying, with those released during winter straying more and farther away than fish released during the rest of the year (Hansen and Jonsson 1991). As a rule of thumb, fish released at the wrong time and at the wrong site stray more, i.e. have worse homing behaviour, than those released at more appropriate (natural) times and sites (reviewed by Quinn 1993).

Spawning Time and Location

If hatchery fish differ from wild fish in location or timing of spawning the implications for offspring survival can be critical (see above). In a study of coho salmon (*O. kisutch*) in Oregon, Nickelson et al. (1986) found that hatchery fish returned and spawned earlier than the native wild fish, and concluded that this was largely responsible for the failure to rebuild populations in streams stocked with presmolt hatchery fish. Spawning time has a high heritability in salmonid fishes (Siitonen and Gall 1989, Silverstein 1993, Gharrett and Smoker 1993, Quinn et al. 2000) and evidence suggests that unintentional hatchery selection for early spawners can alter it (Ayerst 1977, Leider et al. 1984, Flagg et al. 1995, Petersson and Järvi 1993). There are also indications that hatchery rearing can affect the choice of spawning location. Not only do fish having experienced only the lower reaches of the river (as normally is the case for released hatchery-reared fish) hesitate to ascend to the upper parts where the spawning grounds lie, they also wander more within the river than wild fish (Jonsson et al. 1990, 1994). An interesting potential outcome of altered choice of spawning time and location is increased interspecific hybridization due to a break down of spatial and/or temporal isolation between species (Leary et al. 1995, Jansson and Öst 1997).

Fecundity and Egg Size

The relaxation (or perhaps even removal) of sexual and natural selection, and the artificial nature of the hatchery breeding process will likely favor those individuals that allocate their available resources to gonads instead of elaborate secondary characteristics or energy-demanding spawning activities (Fleming and Gross 1989). However, the few studies that have tested this hypothesis have been indirect (i.e. comparative or time series analyses; Table 1). To examine whether a general pattern exists among these studies we used a meta-analytical approach. Such an analysis combines the separate significance tests from the different data sets that test the same scientific (but not statistical) hypothesis. Each independent test reports a probability value for the particular outcome, assuming the null hypothesis to be correct. From the studies listed in the Table 1, we extracted probability values relevant for the trait concerned (i.e. total egg biomass). These probability values were combined according to Sokal and Rohlf (1995) to create an overall test of significance. The meta-analysis identified weak support, at best, for increased gonad allocation with hatchery rearing

χ^2 = 20.81, df = 12, P = 0.054). Such effects may be small and masked by other tradeoffs and factors, such as body condition, and thus carefully designed investigations may be needed to reveal differences.

There are indications that hatchery-rearing may affect female allocation (size-adjusted) to egg size (6 of 8 studies, Table 1), however, the pattern appears inconsistent (meta-analysis: χ^2= 13.78, df = 16, P = 0.62). Fleming and Gross (1990) hypothesized that the elimination of the constraint of gravel quality that eggs experience in nature (van den Berghe and Gross 1989, Quinn et al. 1995) will favor larger eggs in hatcheries because of survival and growth advantages. In addition, if incubation temperatures in hatcheries are higher than in nature this may also select for larger eggs because of reduced efficiency of conversion of yolk to body tissue (Heming 1982) and increased maintenance costs associated with increased water temperature (Hamor and Garside 1977). Thus, hatchery populations exposed to selection over generations may be expected to show increased egg sizes. Support for this, however, has been inconclusive and based on comparative and time-series analyses that do not fully control for other potential factors (e.g., gene flow, environment, phylogeny; Fleming and Gross 1990, Petersson et al. 1996; Beacham and Murray 1993, Petersson and Järvi 1993). By contrast, more controlled studies examining single generation (environmental) effects of hatchery rearing indicate a decrease in egg size (Jonsson et al. 1996, Fleming et al. 1997). It has been proposed on theoretical grounds that egg size should be sensitive to juvenile growth and survival (Sibly and Calow 1986, Winemiller and Rose 1993), and its expression phenotypically plastic in spatially and temporally varying environments (Perrin 1988). This appears to be the case among at least some salmonids, where egg size is negatively associated with early maternal growth (Thorpe et al. 1984, Jonsson et al. 1996, Morita et al. 1999, Tamate and Maekawa 2000). Such a phenotypically plastic response may also over time select for reduced egg size, if competition among newly emerged fry is reduced relative to that experienced in nature. While there are clear indications that hatchery rearing affects egg size, the direction of response, particularly the long-term evolutionary response remains less clear. The important point here, however, is that any alteration in egg size is likely to have important implications for the success of hatchery releases (cf. Einum and Fleming 2000b).

Breeding Morphology

Morphology affects an individual's performance, and thereby its fitness (Arnold 1983). Fish morphology is under conflicting selection pressures (e.g. Riddell and Leggett 1981, Fleming and Gross 1989, Swain and Holtby 1989), and there are clear relationships between form and function (Robinson and Wilson 1996), so that body shape affects swimming performance (e.g., Skúlason et al. 1989). The hatchery

Table 1. Differences in egg production traits between wild and hatchery populations of salmonids. Effect: whether the trait expression in the hatchery fish differs from that in wild fish and in what direction. Origin of Effect: G + E = genetic and environmental, E = predominantly environmental, G = predominantly genetic, G > E = genetic effects suspected to be greater, E > G = environmental effects suspected to be greater.

Trait	Effect	Origin of effect	Origin of Hatchery Fish	Length of Propagation	Species	Reference
Total Egg Biomass	Increase*	G + E	Native	4–83 years	Coho salmon	Fleming and Gross 1989
	Increase	G + E	Non-native	15 years	Coho salmon	Fleming and Gross 1992
	Not different	G + E	Native	25+ years	Brown trout	Petersson and Järvi 1993
	Not different	G > E	Native	25 years	Atlantic salmon	Petersson et al. 1996
	Not different	G > E	Native	25 years	Brown trout	Petersson et al. 1996
	Not different	E	Native	First generation	Atlantic salmon	Jonsson et al. 1996
Egg Size	Increase	G + E	Native	4–83 years	Coho salmon	Fleming and Gross 1990
	Increase	G + E	Non-native	15 years	Coho salmon	Fleming and Gross 1992
	Not different	G + E	Native	4–83 years	Coho salmon	Beacham and Murray 1993
	Not different	G + E	Native	25+ years	Brown trout	Petersson and Järvi 1993
	Increase	G > E	Native	25 years	Brown trout	Petersson et al. 1996
	Increase	G > E	Native	25 years	Atlantic salmon	Petersson et al. 1996
	Decrease	E	Native	First generation	Atlantic salmon	Jonsson et al. 1996
	Decrease	E	Native	First generation	Atlantic salmon	Fleming et al. 1997

* Not significant at P = 0.082

environment exposes the fish to new developmental and evolutionary forces that may not only effect juvenile (reviewed in Einum and Fleming 2001), but also adult phenotypes. Hatchery adults appear to show reduced expressions of morphological characters important during breeding, such as secondary sexual characters (Fleming and Gross 1989, 1994, Petersson and Järvi 1993, Hard et al. 2000). Both environmental and genetic (domestication) factors appear responsible for these changes (Fleming et al. 1994). Such reduced expressions of secondary sexual characters can have negative con-sequences for natural breeding success (see below).

Breeding Behaviour

Like morphology, the breeding behaviour of hatchery fish is predicted to be influenced by environmental effects and the relaxation, removal and/or alteration of natural and sexual selection. Experimental studies under semi-natural conditions indicate that these effects become evident primarily when hatchery fish breed sympatrically with, and face competition from wild fish (Fleming and Gross 1992, 1993, Fleming et al. 1996, 1997, Berejikian et al. 1997, Petersson and Järvi 1997). For hatchery females in competition with wild females, indicators of inferior competitive ability include delays in the onset of breeding (Fleming and Gross 1993), fewer nests (meta-analysis: $\chi^2 = 24.66$, df = 10, $P = 0.006$, Table 2) and greater retention of unspawned eggs (Fleming and Gross 1993, Fleming et al. 1996). This often occurs despite similar levels of overt aggression by hatchery and wild females ($\chi^2 = 5.64$, df = 12, $P = 0.93$, Table 2; but see Petersson and Järvi 1997). Hatchery females also appear more likely to have their eggs fertilized by several secondary males (most likely parr) than wild females, suggesting either poorer defense against, and/or a greater willingness to have secondary males present (Thompson et al. 1999). Ultimately, the breeding success of hatchery fish is frequently inferior to that of wild females ($\chi^2 = 19.97$, df = 6, $P = 0.003$, Table 2).

The breeding behaviour of males appears more strongly affected by hatchery rearing than that of females, reflecting the greater intensity of selection on male competitive ability during this period. Hatchery males tend to be less aggressive (meta-analysis: $\chi^2 = 24.54$, df = 12, $P = 0.017$) and less active courting females (meta-analysis: $\chi^2 = 60.38$, df = 12, $P < 0.001$), and ultimately achieve fewer spawnings than wild males (meta-analysis: $\chi^2 = 48.59$, df = 10, $P < 0.001$; Table 1). Across the studies reported in Tables 2 and 3, hatchery males suffer more from inferior breeding performance than hatchery females. This pattern also appears to carry over into the wild, where gene flow between cultured and wild salmonids is sex biased, principally involving wild males mating with cultured females (Fleming et al. 2000). The presence of male parr of cultured origin, however, could change this substantially (Fleming, unpublished data).

In most studies, environmental and genetic factors affecting the breeding behaviour of hatchery fish cannot be definitively separated. Fleming et al. (1997) in a study controlling for the genetic background of the fish, however, revealed that the environmental effects of hatchery-rearing up to smolting could be significant. They found differences in the breeding performance of hatchery and wild male, but not female Atlantic salmon. While having similar levels of aggression, hatchery males were involved in more prolonged aggressive encounters and incurred greater wounding and mortality than wild males. Furthermore, hatchery males were less able to monopolize spawnings and obtained an estimated 51% the breeding success of wild males. In another study, Fleming and Gross (1994) were able to experimentally quantify the intensity of natural and sexual selection on different male and female morphological traits, as well as behavioural differences between multi-generation hatchery and wild coho salmon. They revealed direct (i.e. independent) selection on body size, the secondary sexual trait hooked snout (significantly larger in wild than hatchery males), and hatchery-wild behavioural differences associated with breeding success. Such information provides a basis for predictions about effects of relaxed or altered selective pressures in hatcheries.

Breeding Success and the Contribution to Natural Productivity

Clearly, an array of changes in behavioural, life history and morphological traits associated with reproduction occur in culture environments and these may have important implications for the ability of released fish to contribute to natural productivity. The success of release programs must lie in their ability to allow fish to bypass the high mortality of early life in the wild (see above) and then to survive, breed and produce offspring that contribute to natural production in the wild (Waples et al. in press). The word "contribute" is important here, for it means that the released fish should not take away from the production of the wild population, if it still exists. Our aim in this section thus is to review the literature for evidence regarding the contribution of released salmonids to natural productivity.

The best examples of successful contribution come from the release of salmonids to re-establish

Table 2. Female reproductive behaviour of hatchery relative to wild salmonids. Effect: whether the trait expression in the hatchery fish differs from that in wild fish and in what direction. Origin of Effect: G + E = genetic and environmental, E = predominantly environmental, G = predominantly genetic, G > E = genetic effects suspected to be greater, E > G = environmental effects suspected to be greater.

Trait	Effect	Origin of effect	Origin of Hatchery Fish	Length of Propagation	Species	Reference
Overt	Not different	G + E	Non-Native	15 years	Coho salmon	Fleming and Gross 1992
Aggression	Not different	G + E	Non-Native	15–16 years	Coho salmon	Fleming and Gross 1993
	Not different	G + E	Non-Native*	20 years	Atlantic salmon	Fleming et al. 1996
	Not different	E > G	Non-Native*	First generation	Coho salmon	Berejikian et al. 1997
	Not different	E	Native	First generation	Atlantic salmon	Fleming et al. 1997
	Less	G + E	Native	26–27 years	Brown Trout	Petersson and Järvi 1997
Number	Not different	G + E	Non-native	15 years	Coho salmon	Fleming and Gross 1992
of Nests	Not different	G + E	Non-native	15–16 years	Coho salmon	Fleming and Gross 1993
	Fewer	G + E	Non-native*	20 years	Atlantic salmon	Fleming et al. 1996
	Fewer	E > G	Non-Native*	First generation	Coho salmon	Berejikian et al. 1997
	Not different	E	Native	First generation	Atlantic salmon	Fleming et al. 1997
Breeding	Lower	G + E	Non-native	15–16 years	Coho salmon	Fleming and Gross 1993
Success	Lower	G + E	Non-native*	20 years	Atlantic salmon	Fleming et al. 1996
	Not different	E	Native	First generation	Atlantic salmon	Fleming et al. 1997
	Lower	G + E	Non-native*	23 years	Atlantic salmon	Fleming et al. 2000

* Fish were captively reared to maturity

Table 3. Male reproductive behaviour of hatchery relative to wild salmonids. Effect: whether the trait expression in the hatchery fish differs from that in wild fish and in what direction. Origin of Effect: G + E = genetic and environmental, E = predominantly environmental, G = predominantly genetic, G > E = genetic effects suspected to be greater, E > G = environmental effects suspected to be greater.

Trait	Effect	Origin of effect	Origin of Hatchery Fish	Length of Propagation	Species	Reference
Overt	Less	G + E	Non-native	15 years	Coho salmon	Fleming and Gross 1992
Aggression	Less	G + E	Non-native	15–16 years	Coho salmon	Fleming and Gross 1993
	Less	G + E	Non-native*	20 years	Atlantic salmon	Fleming et al. 1996
	Not different	E > G	Non-native*	First generation	Coho salmon	Berejikian et al. 1997
	Not different	E	Native	First generation	Atlantic salmon	Fleming et al. 1997
	Not different	G + E	Native	26–27 years	Brown trout	Petersson and Järvi 1997
Courting	Less	G + E	Non-native	15 years	Coho salmon	Fleming and Gross 1992
	Less	G + E	Non-native	15–16 years	Coho salmon	Fleming and Gross 1993
	Less	G + E	Non-native*	0 years	Atlantic salmon	Fleming et al. 1996
	Less	E > G	Non-native*	First generation	Coho salmon	Berejikian et al. 1997
	Not different	E	Native	First generation	Atlantic salmon	Fleming et al. 1997
	Less	G + E	Native	26–27 years	Brown Trout	Petersson and Järvi 1997
Number of Spawnings	Fewer	G + E	Non-native	15–16 years	Coho salmon	Fleming and Gross 1993
	Fewer	G + E	Non-native*	20 years	Atlantic salmon	Fleming et al. 1996
	Fewer	E > G	Non-native*	First generation	Coho salmon	Berejikian et al. 1997
	Not different	E	Native	First generation	Atlantic salmon	Fleming et al. 1997
	Fewer	G + E	Native	26–27 years	Brown Trout	Petersson and Järvi 1997

* Fish were captively reared to maturity

extirpated populations (i.e. driven to extinction) once the cause(s) of extinction have been remedied or to introduce fish into areas formerly inaccessible to natural colonization due to an obvious physical barrier (Ricker 1972, Withler 1982). Success appears to reflect the presence of an open or unsaturated niche, i.e. the absence of competition from local con- and/or heterospecifics. Such programs should be short term, aiming to establish populations rapidly and then once founded, allow natural selection to shape the population to its local environment. Continued releases are only likely to hindered proper establishment, i.e. adaptation to local conditions. This may be particularly problematic if the habitat has been altered in ways that require the fish to re-adapt (e.g., following hydropower development). What is unclear about such re-leases is whether they are any better in the long term than natural colonization through straying from nearby populations, if the possibility exists. This, however, has never been addressed and unfortunately in our current environment, may be nearly impossible to examine because the vast majority of strays are domesticated fish (farm escapees and hatchery strays).

Other examples of successful contributions from released salmonids are rare, if not non-existent. The most common form of release program is aimed at the supplementation of wild populations, i.e. the intentional integration of hatchery and natural production, with the goal of improving the status of an existing natural population (Finstad et al. 2000, Fjellheim and Johnsen 2001, Vøllestad and Hesthagen 2001, Waples et al. in press). Such integration, however, entails significant ecological and genetic risks to the wild population (e.g., Hindar et al. 1991, Waples 1991, Youngson and Verspoor 1998, Einum and Fleming 2001), as well as potential benefits. Yet, despite the vast majority of release programs involving supplementation and its importance as a management strategy, astonishingly little has been done in Norway and other countries to evaluate its effectiveness to meet its principal objective/goal.

The evidence that does exist is generally qualitative and indirect, based on genetic studies of introgression and ecological studies of correlates of breeding success or semi-natural experiments (Table 4). While genetic studies often provide quantitative estimates of introgression, they provide little information regarding the actual relative contribution of the released to wild fish to the natural production. For example, frequently the levels of introgression observed are the result of large-scale releases over many years. By this process, introgression must almost be inevitable. However, what is striking from our some-what limited review of the literature is that 45% (14 of 31) of the investigations reported little or no evidence of introgression (Table 4). Thus, despite large-scale releases in many of these cases, the supplementation programs must be deemed failures. In ***none*** of the studies reporting significant introgression, is there information on whether the release program resulted in improved natural production of the population. Moreover, these genetic studies provide little clue as to the underlying determinants of introgression (e.g., relative lifetime reproductive success) or lack there of. At a broad scale, however, Utter (2000) noted a pattern of greater resistance to introgression among anadromous than among comparable freshwater populations, suggesting that more complex adaptations associated with an anadromous life history may be responsible (cf. Hansen et al. 2000).

All the ecological evidence points to diminished lifetime reproductive success and abilities of hatchery-released salmonids to contribute to natural productivity (Table 4). These studies identify critical life history episodes, particularly breeding, juvenile emergence and first year life, as key determinants of introgression (see also McGinnity et al. 1997, Fleming et al. 2000, review by Einum and Fleming, 2001). They also identify not only the directions of gene flow, but more importantly the causes for sex biases and general predictive models as to when and how such biases arise. Quantitative experimental evidence indicates that among anadromous adults, gene flow into wild populations occurs mainly via hatchery females because of the intense competition that hatchery males face from wild males (Fleming and Gross 1993, Fleming et al. 1996, 1997, 2000). However, where males have the opportunity to mature early as parr or as resident fish, such males may make significant genetic contributions to the population (Hansen et al. 2000). This likely results from their large size at release which can influence both the propensity to mature early (e.g., Alm 1959, Thorpe 1986) and competitive ability (Jones 1959, Thomaz et al. 1997) relative to that of wild fish. The most complete evidence on relative lifetime reproductive performance of hatchery fish comes from two natural experiments that suggest that released fish have approximately a tenth the ability of wild fish to contribute to natural productivity (Table 4; see also Fleming et al. 2000). Neither study, however, examined whether the contribution of the released fish actually added to, or simply replaced the natural productivity of the wild fish. Addressing this latter issue is extremely important, but difficult, requiring an experimental design that incorporates manipulations (i.e. adding hatchery fish) and controls (i.e. excluding hatchery fish) on both spatial and temporal scales. Such experiments are expensive, long term and require management vision to address this vitally important question on the contribution of released fish to natural productivity.

In probably the most thorough attempt to date to examine the ability of supplementation programs to contribute to natural productivity, Waples et al. (in press) reviewed 19 such programs developed for Pacific salmon. Of those, nine populations showed

Table 4. Evidence of the ability of salmonid supplementation programs to contribute to the natural productivity of populations.

Type of Evidence	Frequency of release	Origin of Hatchery fish	Life stage at release	Species
Significant Interbreeding/Contribution to Natural Productivity				
Genetic	Repeated	Non-local	—	Brown trout
	Repeated (1968–83)	Non-local	Eyed eggs, 0+ fry, 1+ parr	Brown trout
	Repeated	Non-local	—	Brown trout
	Repeated (6–20 years)	Non-local	0+ fry, adults	Brown trout
	Repeated	Non-local	—	Brown trout
	Repeated (20+ years)	Non-local	0+ fry	Brown trout
	Repeated	Non-local	—	Brown trout
	Repeated	Non-local	—	Brown trout
	Repeated (1944–74)	Non-local	—	Brown trout
	Repeated (1970–92)	Non-local	Eggs, fry	Brown trout
	Repeated (test over 2 years)	Non-local	—	Brown trout
	Repeated	Non-local	—	Brown trout
	Repeated (1980–1992)	Non-local	0–2+, smolts	Brown trout
	Repeated	Non-local	Primarily smolts	Chinook salmon
	Repeated	Non-local	—	Cutthroat trout
	Repeated	Non-local	—	Rainbow trout
	Repeated (1938–95)	Non-local	Fingerlings, yearlings	Rainbow trout
Strongly Diminished or No Interbreeding/Contribution to Nautral Productivity				
Experimental	Single (1989)	Non-local	Adults	Brown trout
	Repeated (1976–79)	Non-local, but same drainage	Smolts	Steelhead trout
Genetic	Repeated (1950–76)	Non-local	Fry	Atlantic salmon
	Single (1990)	Non-local	0+ parr	Atlantic salmon
	Repeated (6–20 years)	Non-local	0+ fry, adults	Brown trout
	Repeated (20 years)	Non-local	0+	Brown trout
	Repeated	Non-local	0-2+	Brown trout
	Repeated (20+ years)	Non-local	0+ fry	Brown trout
	Repeated (1980–1992)	Non-local	0–2+, smolts	Brown trout
	Repeated	Non-local	—	Brown trout
	Repeated (1966–89)	Non-local	Eyed eggs, 0+, adults	Brown trout
	Repeated	Non-local	—	Brown trout
	Repeated (1980–90's)	Non-local	0–2+, smolts	Brown trout
	Repeated	Non-local	—	Chinook salmon
	Repeated (1, 2, 4 years)	Non-local	Eyed eggs	Chum salmon

continued

Table 4. *continued*

Observation	Reference
Strongly Interbreeding/Contribution to Nautral Productivity	
Genetic admixture of native and hatchery fish (Sweden)	Ryman 1981
Natural-spawning hatchery fish 42% genetic contribution to 0+ juveniles; excessive heterozygosity (N. Ireland)	Taggart and Ferguson 1986
Introgression common (France)	Barbat-Leterrier et al. 1989
Introgression rates up to 80% in some areas (France)	Guyomard 1989
Replacement of 2 natural river populations and near elimination of another (Spain)	Garcia-Marin et al.1991
Strong introgression in 2 lake populations (Spain)	Martínez et al. 1993
Introgression rates of ca. 75% (Greece)	Apostolidis et al. 1996, 1997
Introgression rates of 30–70% at 4 of 6 stocked localities (Italy)	Giuffra et al. 1996
Natural breeding and some introgression, but positive assortative mating common (Switzerland)	Largiadèr and Scholl 1996
2–55% introgression (Spain)	Cagigas et al. 1999
10% introgression within 2 years (Spain)	Garcia-Marin et al. 1999
Introgression as high as 77% (France)	Berrebi et al. 2000
Up to 46% introgression with resident fish (Denmark)	Hansen et al. 2000
Genetic homogenisation in areas of intense hatchery culture (USA Pacific Northwest)	Utter et al. 1989
Extensive introgression between subspecies in the (USA Pacific Northwest)	Gyllensten et al. 1985
5 of 8 populations are interior-coastal hybrid swarms (Western USA)	Williams et al. 1996
Lower river pure, upper river a hybrid swarm (Oregon, USA)	Williams et al. 1997
Despite more hatchery than wild spawners, only 16-19% genetic contribution to 0+ juveniles; survival 3 times lower for hatchery-wild hybrids than wild fish to age 2+ (Norway)	Skaala et al. 1996
Success from breeding to 0+ juveniles 75–79% that of wild fish; lifetime reproductive success 11–13% that of wild fish (WA, USA)	Chilcote et al.1986, Leider et al. 1990, Campton et al. 1991
Significant Interbreeding/Contribution to Natural Productivity	
Despite large releases of anadromous fish, landlocked salmon not detectably altered (Norway)	Vuorinen and Berg 1989
No indication of genetic contribution among adult fish (Spain)	Moran et al. 1994
Introgression rates as low as 0% in some areas (France)	Guyomard 1989
No evident genetic contribution (Spain)	Moran et al. 1991
Intensive stocking with little or no evidence of genetic contribution (Denmark)	Hansen et al.1993, Hansen and Loeschcke 1994
No detectable genetic influence in several rivers (Spain)	Martínez et al. 1993
Introgression low among anadromous fish (Denmark)	Hansen et al. 1995, 2000
Introgression rates of < 10% in 2 of 6 stocked localiteis (Italy)	Giuffra et al. 1996
Reproduced and interbred, but contribution diminished over time (France)	Poteaux et al. 1998
Extensive stocking had limited genetic impact (Spain)	Garcia-Marin et al. 1999
Little or no introgression (Denmark)	Hansen et al., in press
No evidence that strays had homogenised genetic characteristics of wild population (Snake R., USA)	Marshall et al. 2000
Despite millions of released fish, genetic contribution small and disappearing (Russia)	Altukhov and Salmenkhova 1987, 1990

Table 4. *continued*

Type of Evidence	Frequency of release	Origin of Hatchery fish	Life stage at release	Species
Strongly Diminished or No Interbreeding/Contribution to Nautral Productivity				
Genetic	Repeated	Non-local	—	Rainbow trout
Ecological	Repeated (1982–88)	Local Smolts	Atlantic salmon	
(Indirect)	Single	Local	Smolts	Atlantic salmon
	Repeated (1991–93)	Local	Smolts	Brown trout
	Repeated (1980–82)	Non-local	Pre-smolts	Coho salmon
	Repeated (1988–89)	Non-local	Smolts	Coho salmon
	Repeated (decades)	Non-local	Smolts	Steelhead trout

Strongly Diminished or No Interbreeding/Contribution to Nautral Productivity	
No detectable introgression (ID, USA)	Wishard et al. 1984
14% of females and 37% of males appeared not to have spawned (Norway)	Jonsson et al. 1990
Females similar, and males 51% the breeding success of wild fish (Norway)	Fleming et al. 1997
Males lower mating success (Sweden)	Petersson and Järvi 1999
Densities of juvenile offspring lower in stocked than unstocked streams (OR, USA)	Nickelson et al. 1986
Males 62% and females 82% the breeding success of wild fish (BC, Canada)	Fleming and Gross 1993
Population productivity and proportion of hatchery fish among natural spawners negatively related (OR, USA)	Chilcote 1997 cited in Waples 1999

an increase or had remained stable in size since the start of supplementation, while the remainder (10) had declined. They also found that supplemented and unsupplemented (control) populations showed similar trends in four of the six possible comparisons, while the supplemented population outperformed the control in one case and the reverse occurred in the other. Moreover, for two programs it was possible to compare the populations' status before and after supplementation had ended, and both remained "at risk." It thus seems clear that the supplementation of depressed natural populations using hatchery fish seldom achieves the objective of increased natural production (cf. Steward and Bjorn 1990). Predicting the outcome of a release must be considered a highly complex, and as yet unresolved problem, involving ecological and genetic factors.

Conclusions

The current review indicates that understanding breeding dynamics and reproductive success are critical to predicting effects of various conservation and supplementation programs, through their effects on the demographically and genetically effective population size, and gene flow. The value of reproductive performance in hatchery fish depends on the management goal. If the goal is to re-establish or rebuild wild populations for conservation purposes (i.e. conservation releases), current hatchery practices appear to result in competitively and reproductively inferior fish that limit their effectiveness. Long-term application of such releases will moreover inhibit local adaptation and thus natural productivity. On the other hand, if the goal is to supplement wild populations to increase fisheries (i.e. fisheries releases) while reducing impacts on the wild populations, such reproductive inferiority could be advantageous, limiting the negative effects of introgression. However, the threats of ecological interference and altered selection regimes associated with the introduction of hatchery fish remain. Moreover, reproductive isolation is likely to remain incomplete and even limited introgressive hybridization may pose a concern, particularly when the scale of hatchery introductions is significantly greater than that of natural production. Clearly, the appropriate and effective use of hatcheries will be a balancing act.

Poorly managed hatchery programs can alter or even destroy biological diversity of species/ populations. This does not mean, however, that we should give up on the hatchery concept as a management tool, particularly for populations facing high short-term risk of extinction. Rather, hatcheries need to be modified to minimize the detrimental effects of hatchery rearing on fish phenotypes and genotypes, including morphological and behavioral traits, and thus increase the potential for successful enhancement. We must also recognize an inherent conflict that exists in the way hatcheries currently function, to both conserve threatened wild populations and to enhance fisheries (cf. Fleming 1994). The use of hatcheries for the enhancement of fisheries will often directly threaten the existence of wild populations, particularly those in need of conservation, through direct and indirect genetic effects (reviewed by Hindar et al. 1991, Waples 1991). Finally, we must recognize that release programs are not a solution to conservation problems, but rather should be thought of as a short-term aid for wild populations at risk. Conservation will only be successful if causes of decline in wild populations are remedied.

The biggest gap in our knowledge is understanding the performance of hatchery-produced fish and their progeny in the natural environment. Can release programs, particularly those designed for conservation, provide a net long-term benefit to natural populations? Moreover, when do we implement such programs, and then how do we best manage them to achieve this? Ideally, evaluations of supplementation programs should be conducted over a number of generations to permit distinguishing ecological and genetic effects of fish culture, and to evaluate the effectiveness of natural selection to restore fitness in natural populations of mixed hatchery-wild ancestry (cf. Waples et al. in press). Releases of hatchery fish can be a valuable management tool in our attempts to conserve wild salmon populations, yet considerable risks exist.

Acknowledgements
We would like to thank S. Einum, A. Hendry and T. Järvi for helpful comments on the manuscript and the participants of the workshop for their discussions.

References
See Appendix 1

Discussion

An audience member commented: It appears that in one example there was only one generation in the hatchery. Perhaps in some of the other ones it might be in there for many generations. Can you clarify about how long it takes to diverge and do you have a lot of different factors to look at as well?

Ian Fleming said that this was correct. In the older studies, typically you cannot actually separate environmental from genetic factors. They do not know whether these are short-term effects or long-term genetic changes. More recently, having recognized that hatcheries do cause changes to the fish, they have actually begun to quantify to what extent environmental effects and genetic effects are contributing. For instance, for breeding performance, they do not really know, because that is an extremely difficult thing to assess. But with offspring behaviour and offspring performance, there are a number of studies that show that there is both a genetic and an environmental component. For instance, response to predators has a very strong genetic component, and there is actually direct selection over time for reduced response to predators. The meta-analysis did not try to separate that; they just tried to look at characteristics. There were enough studies, seven or eight, that have looked at changes in aggression. When it comes to breeding performance, there are very few studies to reference (including three studies he himself has done). There are studies that NMFS has done, and studies in Sweden, and often those studies have combined both environmental and genetic components. In terms of breeding performance, there is a very strong environmental component.

Lee Blankenship pointed out that on the other side of the coin there is not much information that helps with how long it takes for divergence to occur. He asked if there are any studies that show how long it takes to go the other way? If we are going to keep using supplementation, we are going to need to know that answer. You are looking at mostly F1s. What about F2 and F3s?

Ian responded that there is a great scarcity of information about what is going on. You could ask yourself how many supplementation programs have gone on and suddenly we have stopped them. How quickly does the population return, in terms of characteristics, to what it looked like before? What is important and very interesting, both from a practical point of view and also a theoretical point of view, is to ask how quickly can these fish readapt.

Fred Whoriskey asked if the populations that went into fishless lakes originated from the hatcheries, and if anyone has looked at what the characteristics have become in those fish, and whether they have converged back on that wild type?

Ian Fleming responded that he did not know of any studies of this sort. For instance, in New Zealand, they are not fishless, but have introduced fish in them. They actually show quite rapid adaptation to those environments and the fish appear to have evolved to local conditions in each of these different rivers. Those differences are genetic. If you introduced just any fish into a lake and then looked at how quickly it adapted, or whether it would ever come back to the original population, then that is a completely different question.

Trevor Goff posed a question related to the Norwegian study: What was the source of the hatchery fish? Were they F1s or F2s?

Ian Fleming replied that they were F1s. The research river is the River Enza, and it has had a hatchery for about fifteen years. But each generation is created from fish captured in the wild, so they do not reuse the hatchery fish. The hatchery fish go into the wild, and so there is a complete mixing with every generation. What is wild is 'sort of' wild. You have taken hatchery and wild fish into the hatchery for broodstock from the same stock and then the eggs in both hatchery and wild fish are selected, about a week before spawning. There are substantial environmental impacts of holding fish in captivity. Both the hatchery and wild fish in captivity have eggs that are only, in volume, two thirds of the size of both the hatchery and wild eggs that have been in the natural environment all summer.

Changes in the Dynamics of Coho in the Strait of Georgia in the Last Decade

Richard Beamish, Pacific Biological Station, Fisheries and Oceans Canada

Presentation based on the following:

Changes in Coho Marine Survival in the Strait of Georgia in the Last Decade

Richard. J. Beamish, C.M. Neville, R.M. Sweeting, K.L. Poier, and G.A. McFarlane, Department of Fisheries and Oceans, Pacific Biological Station

Coho marine survival in the Strait of Georgia declined to low levels during the 1990s. In addition, in 1991 and from 1995 to 2000, virtually all coho left the Strait and did not return during the normal fishing season. In 2000, there was an abrupt increase in productivity in the Strait of Georgia that was associated with increased early marine survival and increased individual size of coho. Increased early marine survival and growth were also observed for other species of juvenile Pacific salmon. In 2001, ocean age 1 coho returned to the Strait of Georgia, but their abundance remains to be determined. During the 1990s the percentage of hatchery fish in the Strait of Georgia increased and from 1998 to 2000 the average was approximately 72%. In 2000, there was a small decline in the percentage of hatchery coho that may indicate that there was an increase in the number of wild coho that entered the Strait.

We propose that large scale climate changes in 1989 and 1998 were the factors that altered the dynamics of coho during their marine phase. The linkage between climate and survival appears to be related to the rate of growth during the first marine summer. The mechanism that alters the migratory behaviour is still unclear. The increasing percentage of hatchery-reared coho may, in a general way, reflect the percentages that enter the Strait of Georgia. There is no doubt that the dynamics of coho in the ocean in the last decade were different than previously reported. It is probable that the changes in climate expected from increasing greenhouse gas emissions will continue to alter the dynamics of coho in the ocean.

The coho catch in the Strait of Georgia is a measure of abundance because the estimated exploitation rate changed very little from 1977 to 1994, ranging from approximately 70% to 80% (Simpson et al. 2001). The total catch of coho (Figure 1B) represents the sport and commercial catch within the Strait of Georgia. From 1970 to 1979 sport catches in Juan de Fuca Strait are included. The low catches in 1991, 1994, 1995, 1996 and 1997 result from the movement of virtually all coho out of the Strait of Georgia at ocean age 0 and a failure to return during the normal fishing periods in the summer. The near 0 catches in 1998, 1999, and 2000 result from the continued absence in the Strait of Georgia and fishery closures that virtually eliminated fishing.

The proportion of Strait of Georgia coho raised in hatcheries that were caught inside and outside of the Strait of Georgia is a measure of the movement of coho out of the Strait of Georgia (Figure 1A). The catches and the recaptures of coded wire tagged coho were obtained from the MRP database (Kuhn et al. 1988). The percentage is the total catch of Strait of Georgia hatchery fish outside of the Strait/total catch of Strait of Georgia coho in all areas × 100. The percentage of coho that were available to fisheries inside the Strait of Georgia fluctuated during the

1970s and 1980s, averaging about 43%. In the 1990s, there was a dramatic change in behaviour that was unprecedented in any catch record and in the memory of biologists and fishermen. In 1991, and from 1995 to 2000, virtually all coho left the Strait of Georgia in the fall of their first marine year and did not return during the normal fishing season. In 2001, it appears that ocean age 1 coho are back in the Strait of Georgia, although the abundance remains to be determined.

The decline in abundance in the 1990s is a result of large decreases in marine survival that were synchronous throughout the southern distribution of coho (Beamish et al. 1999). In the Strait of Georgia, Puget Sound and off Washington and Oregon, the trend to declining marine survivals changed after 1989 and remained at these low levels through to 1999. In the Strait of Georgia, the average marine survival was as high as 21.8% in 1975 (year-to-sea) and as low as 1.2% in 1995 (year-to-sea) (Beamish et al. 1999).

As marine survivals declined in the 1990s, the percentage of hatchery fish in the population increased. Beginning in 1975, the percentage of hatchery coho in the catch was determined from the number of coded wire tagged coho caught in the commercial and recreational fisheries. With the virtual elimination of fishing from 1998 to 2000, hatchery and wild percentages were determined from catches of ocean age 0 in research cruises.

Reliable estimates were possible because large numbers of hatchery-reared coho received a tag or had a fin removed. The percentage of hatchery fish increased at a rate of about 2.4% a year, and from 1998 to 2000 hatchery coho averaged about 72% of the population. It is expected that the percentage of ocean age 1 coho in the Strait of Georgia in 2001 will be 69%. The percentage increased from about 47% in the 1989 catch year to 71.9% in 1998, 79.3% in 1999, and 69.3% in 2000 ocean entry years. There was a very small increase in the numbers of coho released from hatcheries during the 1990s. If only smolt releases are considered (and fry releases omitted), the production of coho from hatcheries was virtually constant. The decline in the percentage in 2000 may indicate that a greater number of wild coho smolts entered the Strait of Georgia in 2000.

Results of Recent Research

We determined the relative abundance of ocean age 0 coho in the Strait of Georgia in July and September, from 1997 to 2000 (Beamish et al. 2000) using a large rope trawl fished in the surface waters at a speed of 5 knots. We followed a fixed survey design (Figure 2) and completed between 68 and 128 tows per cruise. Abundance estimates were made using a swept volume method (Beamish et al. 2000) and catches were standardized to one hour (CPUE, Table 1).

The abundance estimates are considered to be lower estimates of the true abundance because the net was

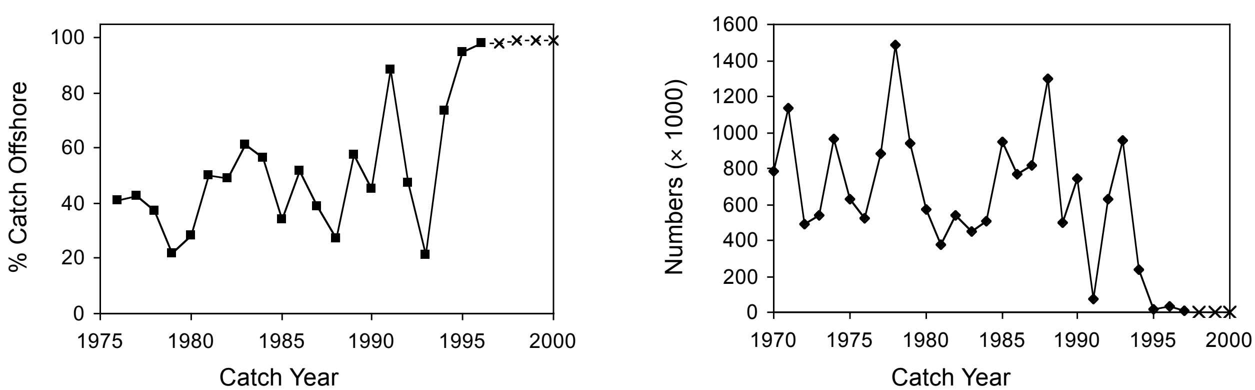


Figure 1. (A) The percentage of hatchery coho released into the Strait of Georgia that were caught outside the Strait of Georgia from 1976–1996. In 1997–2000, the percentages of Strait of Georgia coho that were outside the Strait of Georgia, were estimated from research surveys due to the closure of coho fisheries. (B) Sport and commercial catch of coho salmon in the Strait of Georgia in 1970–2000. Commerical catch includes Fraser River net fisheries. Sport catch includes Juan de Fuca sport catch for 1970–1979, 1998–2000 data are preliminary.

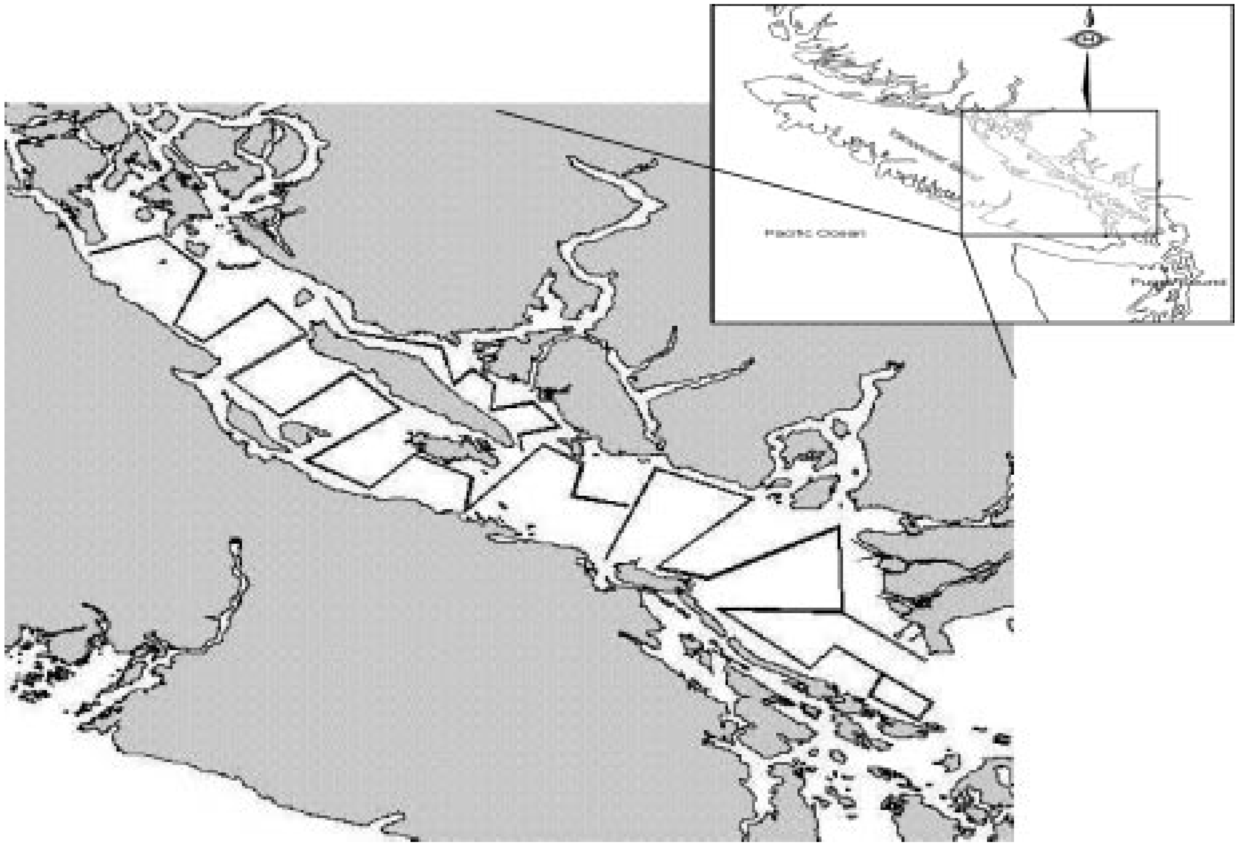


Figure 2. Fixed survey design for tow cruises in the Strait of Georgia

Table 1. Abundance estimates of age 0 coho salmon in the Strait of Georgia

Year	Date	CPUE	Total Catch	Abundance	Lower Interval	Upper Interval
1997	June 17–July 8	19	524	1,657,000	345,009	2,969,095
	Sept. 8–27	40	2380	2,994,000	1,680,377	4,307,541
1998	June 22–July 15	35	981	2,427,000	1,505,000	3,349,000
	Sept. 8–26	59	1518	3,048,000	1,566,000	4,530,000
1999	June 30–July 16	42	1649	3,397,000	2,221,000	4,574,000
	Aug. 31–Sept. 19	51	2021	4,642,000	2,293,000	6,991,000
2000	June 27–July 24	126	4628	11,220,000	6,599,000	15,842,000
	Sept 9–Oct. 1	32	1321	2,567,000	1,075,000	4,059,000

assumed to catch all juvenile coho in front of the opening. However, the abundance estimates, as well as the CPUE estimates, provide an index of relative abundances. In the June-July survey in 2000, the abundance estimate of 11.22 million ocean age 0 coho was more than 3 times larger than the previous year and larger than the three previous years combined. The September 2000 estimate of 2.567 million was the lowest of all of the September estimates. In 2000, we caught 3546 coho outside of the Strait of Georgia, 24 that had coded wire tags from Strait of Georgia hatcheries. In the four previous September cruises, 2,672 coho were caught outside of the Strait of Georgia and 8 had coded wire tags from Strait of Georgia hatcheries. This is a preliminary indication that the low abundance of coho in September 2000, relative to June-July 2000 and the previous September abundance estimates, resulted from an early movement of juveniles out of the Strait of Georgia. However, a detailed assessment of the tagging percentages must be completed to confirm that migration out of the Strait of Georgia was earlier in 2000.

There also were changes in the size of coho in the ocean among the years studied. The comparison among years are influenced by sampling dates as well as feeding conditions, so a comparison of size can be influenced by the date of sampling. However, despite some differences in the date and duration of the sampling period, the mean lengths in the July samples of 172mm, 177mm, and 172mm in 1997, 1998, and 1999 respectively (standard deviation of 23, 23, and 20 respectively), were similar (Figure 3). The mean length of 200mm (SD 24) in 2000 represented a large and significant increase in individual average length. In September, the average length of 250mm (SD 23) was the largest of the 4 samples, but it was only marginally larger than the average size of 246mm (SD 21) in 1997. In 2000, there was a doubling of the euphausiid biomass and the individual size of euphausiids also increased. These changes indicate that the productivity of the Strait of Georgia changed in 2000.

Conclusion 1

Beginning in the 1990s there were dramatic changes in the population dynamics and behaviour of coho during the marine phase of their life history. The synchrony in the decline in marine survival over the entire southern distribution of coho, and the movement of virtually all coho out of the Strait in 1991 and from 1995 to 1999 indicated that the factor causing the change probably was related to climate. The abrupt increase in abundance and average size in 2000 and other changes in the Strait of Georgia ecosystem also indicated that climate affected the dynamics of the Strait of Georgia ecosystem.

The Atmosphere Forcing Index (AFI) (McFarlane et al. 2000) is a composite of the Aleutian Low Pressure Index (Beamish et al. 1997), the Pacific Circulation Index (Beamish et al. 2000b), and the Pacific Decadal Oscillation (Mantua et al. 1997). The AFI shows distinct shifts in 1925, 1947, 1976 and 1988 (Figure 4). A change in 1999 may also be evident. The changes in the temperature in the Strait of Georgia follow trends similar to the regimes and regime shifts seen in the AFI (Figure 5). Off the West Coast of Canada, there is evidence that an index of upwelling (http://www.pfeg.noaa.gov) changed abruptly in 1998. The trend in total flows from the Fraser River is also an index of climate trends (Moore and McKendry 1996). The annual flow changed in 1977 and again in the late 1990s (Figure 6). There was not an obvious change in flow around 1989, however, there was a change in the timing of the beginning of the spring freshet. The April flows in the 1990s were the highest in the time series.

Conclusion 2

The changes in the population dynamics of coho in the ocean, and the changes in growth were closely associated with patterns of climate. The climate and ocean cycles changed quickly about 1989 and 1998. A change occurred in 1977, but it is difficult to study the impact on coho, as the relevant data are sparse prior to 1977.

How Changes in Ocean and Climate Cycles Affect Coho Populations

Climate is now generally accepted as having a major influence on the processes within the ocean that affect the survival and ultimately the carrying capacity of Pacific salmon in the ocean. It is becoming clear that changes in the environment not only change the food supply for salmon, but also that these changes occur over large areas and occur quickly. The climate impact occurs through the direction and intensity of winds that affect the amount of nutrients upwelled to the surface and thus the productivity of fishes in the surface layers (Gargett 1977). Once it is accepted that conditions in the ocean related to climate affect the productivity of salmon, we can no longer assume that the "bottleneck" to salmon production is the number of juveniles entering the ocean. The view that there was a maximum production that could be more or less sustained through management, now gives way to a view that abundance fluctuations occur as trends and

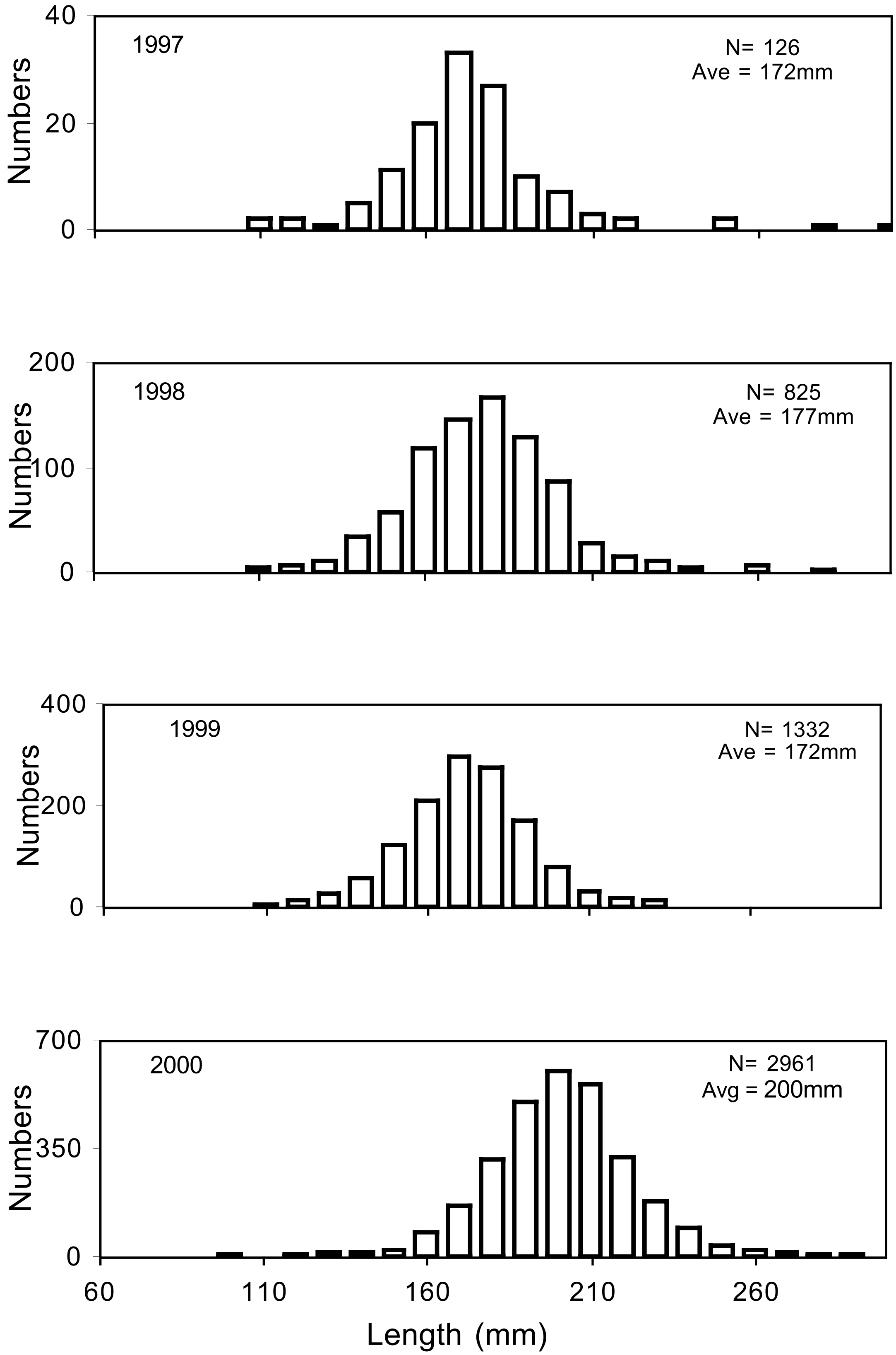


Figure 3. Length frequency of ocean age 0 coho calmon caught in the Strait of Georgia in June/July 1997 to 2000. The increase in average size in 2000 is significant ($p < 0.001$).

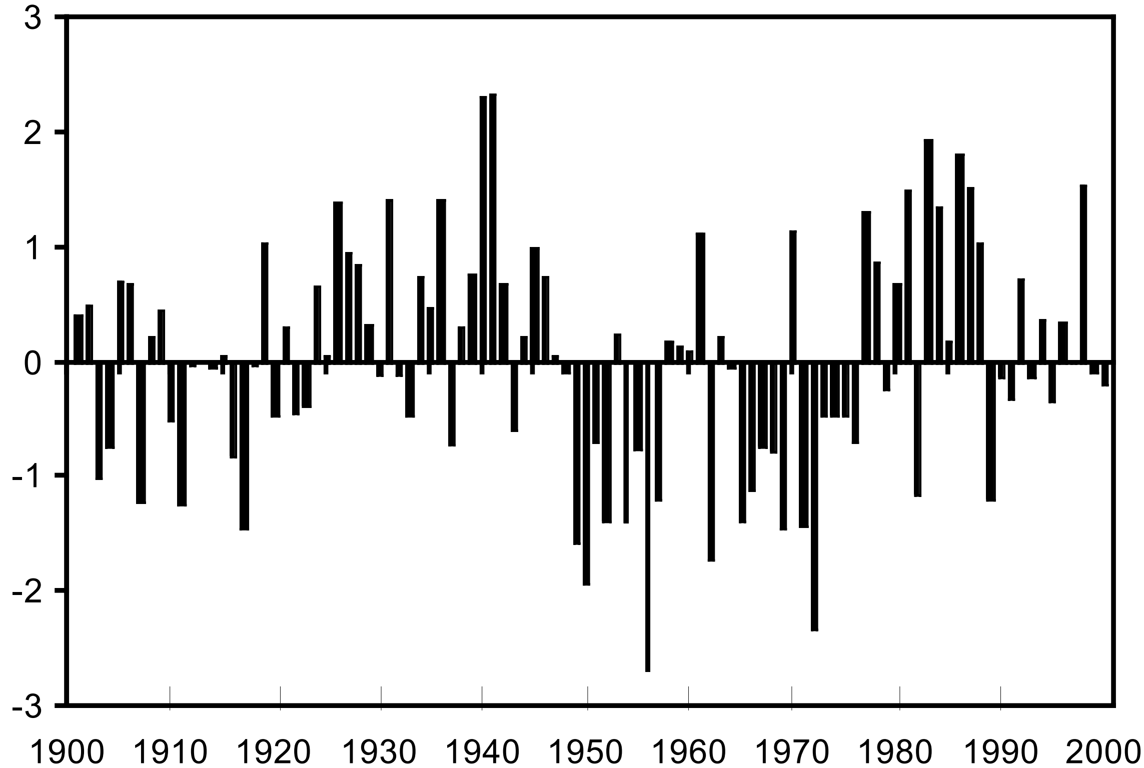


Figure 4. The atmospheric forcing index (AFI) for 1902–2000 showing distinct shifts in 1925, 1947, 1976 and 1988. Positive values correspond to intense Aleutian lows, above average frequency of westerly and southwesterly winds, cooling of the sea surface temperature in the central North Pacific and warming in North American coastal waters.

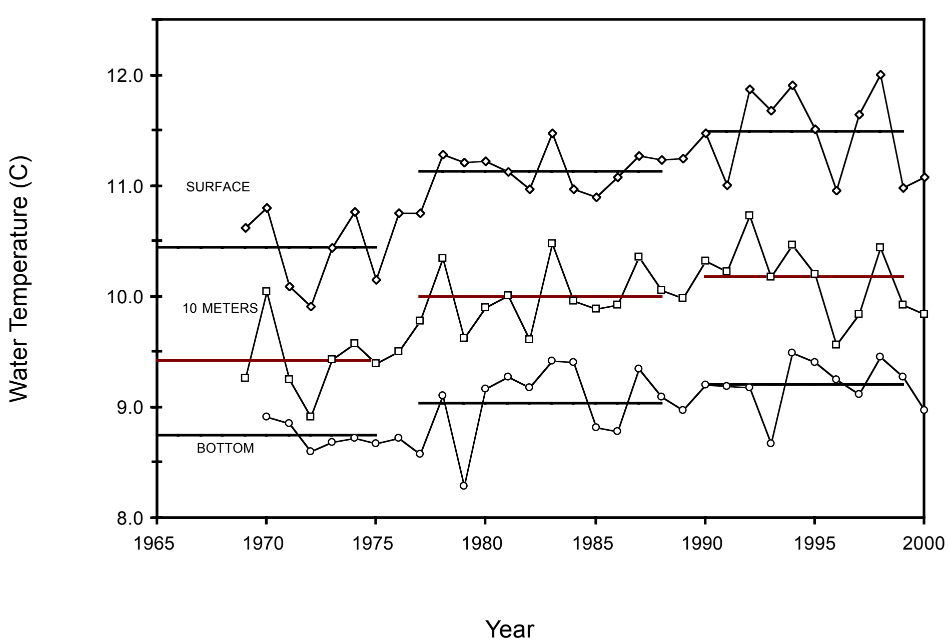


Figure 5. Average annual surface, 10m and bottom water temperatures in the Strait of Georgia from 1969–2000 sampled at the Nanoose site. Horizontal lines indicate average temperatures during 3 different regimes.

that fishing should remove a percentage of the annual abundance. Management needs to determine a safe percentage that ensures that the remaining population is able to replenish itself up to the level of the marine carrying capacity. Total abundance has been a major factor in management, but once climate and climate change become important, the diversity and resiliency of a population also become important.

Coho in the Strait of Georgia, and throughout their entire North American southern distribution, behaved unexpectedly in the 1990s. The atmospheric circulation pattern in the mid-latitude North Pacific resulted in warmer coastal surface waters that were more stratified and probably less nutrient-rich. Similar changes probably occurred within the Strait of Georgia. It is not known how the productivity of the Strait of Georgia changed in the 1990s, as this study did not begin until 1996-1997. We do know, however, that productivity increased in 2000 in association with a new climate regime in the Pacific that probably started in mid-1998.

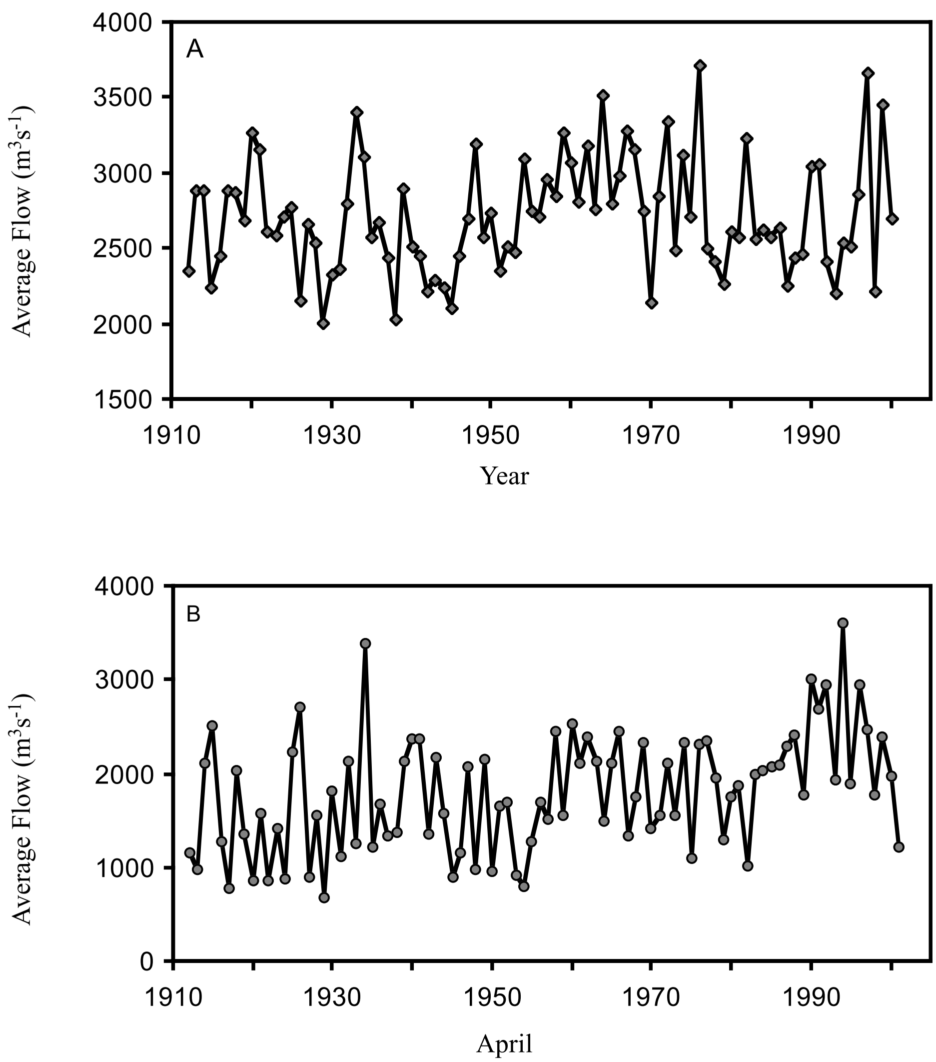


Figure 6. (A) Average annual flow (April to March) of the Fraser River from 1912–2000. The extreme variation in flow from 1996–2000 is unique to the time series. (B) Average daily flow of the Fraser River in April from 1912–2001. Increased average April flows in the 1990s indicate an earlier spring freshet. April flows decreased in 2001.

We propose that the changes in the ocean habitat of Strait of Georgia coho also influenced the number of wild coho that returned to spawn. We know that during the 1990s, the maximum total return of coho was less than in the 1960s to 1980s. Once enhancement started in the 1970s, the percentage of wild coho in this maximum return would be approximately equal to the percentage that entered the ocean. Fishing appears to have reduced the number of wild coho produced in the early 1990s and thus, even though the releases from hatcheries were almost constant, the percentage of wild coho would decline. The cessation of fishing from 1998 to 2000 would improve wild escapements and produce more wild smolts, which may explain the small decline in the percentage of hatchery coho in 2000.

We hypothesize that the linkage between the climate and ocean cycles and the population dynamics and behaviour of coho is through predation and growth-based mortality. The hypothesis is that marine survival is regulated in two stages (Beamish and Mahnken 2001). The first stage is primarily predation mortality (Pearcy 1992). The second mortality is associated with the growth the first marine summer that is needed to ensure that juveniles can survive the fall and winter conditions in the ocean. When the capacity to produce coho in the ocean is reduced, adding more hatchery-reared juveniles may add competition for food that will reduce growth and increase the growth-related mortality. This critical-size, critical-period hypothesis remains to be tested, but growth related mortality in the juvenile stage of larval fishes and other animals is an accepted concept (Cowan et al. 2000).

A final concern is global warming. It may not be a coincidence that the unexpected behaviour of coho in the 1990s was associated with unprecedented warming of the planet. The source of this warming is less important than the need to recognize that it occurred. The projections for climate change over the next few decades identify average scenarios that are several times more extreme than the past few decades. A lesson from the past might be that we need to be careful about manipulating one part of the life history of coho. A lesson for the future might be that we need dynamic management policies for wild coho, enhanced coho, and their freshwater and marine ecosystems.

References

See Appendix 2

Discussion

Lee Blankenship asked: Do you think we can get to the point with indices that will allow us to regulate on a yearly basis for hatchery fish released? He commented: We would have a fixed ecosystem that can only handle so many fish. Obviously what we want to do is reduce the number of hatchery fish to optimize wild fish production. Can we get to the point where we can regulate, or have a guess by the time we need to release hatchery fish, about how many to release?

Dick Beamish responded that the first step is that they will find a way of predicting what it is that causes regime shifts. It will probably not be anything that biologists find. There is some physicist or someone else out there that will one day say, “Hey, I know that, why did you not tell me that?” They will identify something, it might be solar, and it is going to explain an awful lot of things about cycles (it is probably in the Mayan prophecies right now) that will tell us when regimes will shift. The next stage is the answer to your question.

A participant asked: Did you say that you figured there were more wild coho entering the Strait in the last couple of years?

Dick responded that it was just last year.

The participant commented: You do not think that is a function of more hatchery fish being removed as a result of fisheries management (thinking in terms of his small part in the Interior of BC where he comes from and the spawners)?

Dick Beamish responded that it could be both, because measuring the number of hatchery fish that enter the Strait has to include the US fish. The US reduced their releases, but they think the US contributions are 11%. He would argue that there were probably more wild coho entering in 2000 than in 1999 and something happened to the hatchery percentage.

Bob Anstead commented that he thinks there has been a reduction in the opportunity for commercial impacts on chinook salmon for the last few years in BC. How much would that increase the Columbia River run?

Dick Beamish, clarifying that Bob was asking him if this is a Canadian/US Salmon Treaty issue, replied that they attribute the whole increase in the Columbia River to be based on ocean survival rates.

A participant enquired: Concerning the comment that the regime of the 1990s is now shifted into a new regime, I wonder if it is a bit early to say this? Might it not simply be a blip.

Dick Beamish replied: There is a lot of evidence that large changes are everywhere. He thinks many people now believe in this. The climate change people are buying into this and PICES is addressing this as part of their annual meeting this year in Victoria. There is a session on the so-called 1998 regime changes. There are a lot of changes; for example, the atmospheric circulation patterns, precipitation patterns, and sea ice have changed.

A participant asked: What is the relationship between survival of hatchery and wild fish? Is information available about the ratio for the survival of hatchery and wild coho in this period?

Dick Beamish replied that they always have trouble with hatchery and wild survival because when you go back in time there is some convincing evidence that wild survival was higher. But that was another regime. Wild salmon people want it to be higher, and there is some evidence that supports that. But it is really hard for him to see anything that would allow him to say one thing or another, definitively, for the 1990s.

The question was posed: What about the paper by Clara Bell with data from thirty years of coded wire tagging data, that shows hatchery and wild fluctuate by the same percentage in mortality over time? I think that makes a good comparison, and shows that hatchery and wild salmon have fluctuated at the same rate.

Dick Beamish responded that we all agree that the trends are about the same but that there seems to be some evidence that hatchery fish are just a little bit less in terms of marine survival.

An audience member disagreed with that statement.

Dick Beamish responded that in the 1990s, when the ocean conditions changed, it is hard to decide on the basis of your favourite stock; for example, when you say one thing, someone else pulls their stock out and says mine did not do that.

Effects of Hatchery Releases and Environmental Variations on Wild-stock Productivity: Consequences for Hatchery Enhancement of Pink Salmon in Prince William Sound, Alaska

Alex C. Wertheimer and William R. Heard, National Marine Fisheries Service, Auke Bay Laboratory, and William W. Smoker, University of Fairbanks Juneau Center Fisheries and Ocean Sciences

Ian Fleming described supplemental hatcheries designed to contribute to natural populations. I am going to describe the Alaskan hatchery system. The Alaskan hatchery program is also based around a supplemental hatchery concept, not to supplement natural populations, but to supplement the fisheries that are dependent on wild stocks.

How Alaska Came to Have Hatcheries

If we look at the long timeline of commercial salmon catches in Alaska we see that in the 1960s and 1970s we got down really low, and because of what was happening in Washington and BC, and certainly what was going on in Japan at the time, the Alaska Legislature, in their wisdom, said that we needed to have hatcheries. There was also a major regime shift (similar to what Dick Beamish described) that occurred right about the time that the Alaska hatchery system got started. That was coincidental of course but after that regime shift, wild stocks began rebuilding very rapidly and the hatchery program began in full bloom. Suddenly there are all-time record harvests of salmon in Alaska.

The hatchery program is based on private, non-profit, public hatcheries, most of which are now operated by regional associations. In total there are about 33 hatcheries. Unlike a lot of other areas, there are 14 hatcheries in Alaska that have been started up and then closed. Alaska is not afraid to close hatcheries if they do not work.

Siting of Hatcheries

In the siting of hatcheries, Alaska looked at what had been done elsewhere and tried to avoid some of the mistakes. For example, with exceptions, most of the hatcheries in Alaska are on water sources that do not have wild populations of salmon. Most are at, or near, tidewater, thus eliminating most of the freshwater in-stream problems. Alaska is somewhat unique in there are coexisting abundant wild stocks and a carefully structured hatchery program.

The highest priority in Alaska salmon management is to protect and maintain wild stocks. Alaska has escapement-based management where there are no fishing targets, there is vigorous habitat protection, and mixed stock fisheries are avoided, where possible. Hatcheries supplement, not replace, wild stocks, and they supplement the fisheries (e.g., see Figure 1). Importantly hatchery stakeholders pay the cost.

Figure 2 describes the contribution of wild and hatchery contributions over time and the proportion of hatchery and wild over time. The hatchery component is very high in Prince William Sound. This is primarily pink salmon that I am discussing. There are regions in the state, Western Alaska and Bristol Bay, where there are no hatcheries. If we look at the commercial harvest by species, we see that statewide, pink salmon make up a significant portion, as well as coho.

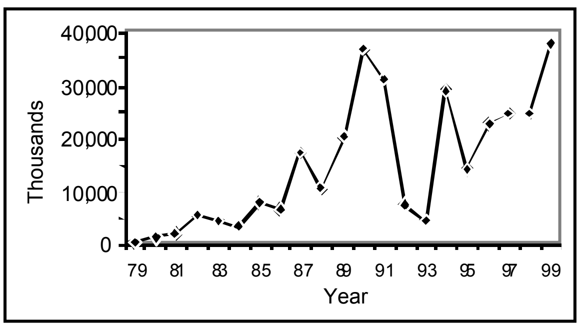


Figure 1. Catches of hatchery pink salmon in Prince William Sound

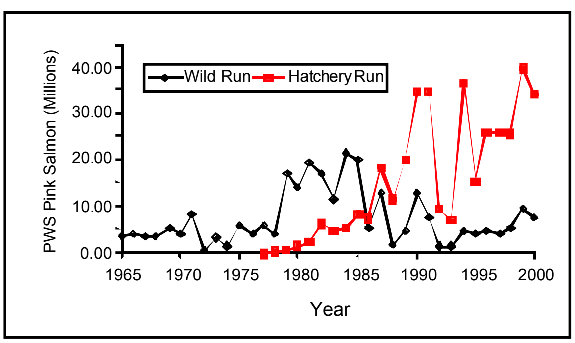


Figure 2. Hatchery vs. wild production: Cause and effect?

Prince William Sound (PWS), has a very high proportion of hatchery salmon; 70 to 80 % of the pink salmon in PWS are hatchery produced. In the Sound, there are four major salmon hatcheries, including the Armin Koernig hatchery in the Southwest corner, Main Bay, primarily a sockeye hatchery, Wally Noerenberg, Cannery Creek and the Solomon Gulch hatchery, run by the Valdez Fishery Development Association (Figure 3).

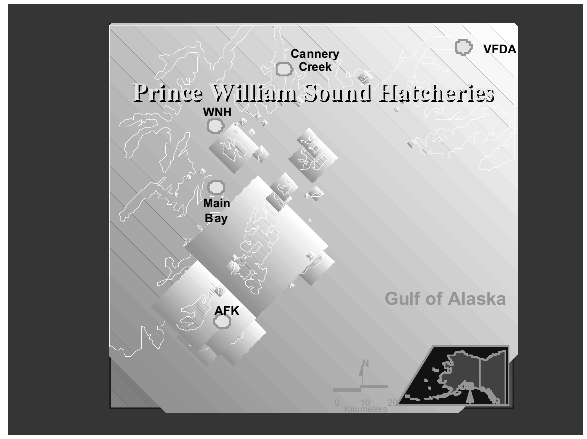


Figure 3. Prince William Sound hatcheries

Something in the order of 500-700 million pink salmon fry are released from those hatcheries. The catch in the Sound has averaged about 27 million fish over the last ten years (Figure 1). If we look at the hatchery to wild production ratio, we see that the wild run, going back to the 1960s, peaked right after the 1976 regime shift (Figure 2). Wild stocks were very high around the time the hatchery program was beginning to build. The wild run has declined and the hatchery run has increased and that has raised some questions. Some people had noted this difference and wondered if this decline in the wild run was because of the high hatchery production. I emphasize again the ten-year period (1976-1985) of high wild production (Figure 2). Was that an anomaly or could we expect that to continue in the future? A recent article published by Ray Hilborn and Doug Eggers suggests that there is little increase, if any, in total abundance due to hatchery production in PWS. They estimate about two million fish per year. A rebuttal commentary on that paper, which will be published this month (see Appendix 3), estimates the net annual gain to be in the order of 17.5 to 23 million fish from the hatchery program (Figure 4).

What I am going to discuss now is some additional analysis of that comparison. Let us look at the annual wild yield loss and the net hatchery gain. We see here the Hilborn-Eggers model, and their analysis indicates that there is basically a loss of wild production and very little net gain (Figure 4).

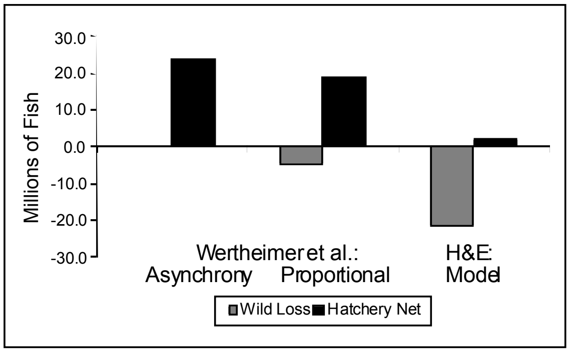


Figure 4. Estimates of annual wild yield loss and net hatchery gain

Region	"First" Regime Maximum	Inter-regime Minimum	Current Regime Maximum
PWS	1938–1947 (7.9)	1951–1960 (1.8)	1990–1999 (27.4)
KOD	1934–1943 (9.7)	1950–1959 (5.0)	1990–1999 (15.9)
SAP	1934–1943 (6.8)	1966–1975 (0.6)	1990–1999 (7.9)
SEAK	1933–1942 (36.9)	1967–1976 (8.6)	1990–1999 (50.5)

Figure 6. Timing of maximum and minimum 10-yr average catches by region

Wertheimer et al. look at two areas and note the concept of asynchrony of PWS production versus other regions in the state, and whether or not PWS and the other regions are proportional more or less across the board. We looked at a standardized ten-year running average catch of pink salmon in four regions; these are the same regions that Hilborn-Eggers examined (Southeast Alaska, Kodiak, South Alaska peninsula, and PWS) and they go back to about 1930 (Figure 5).

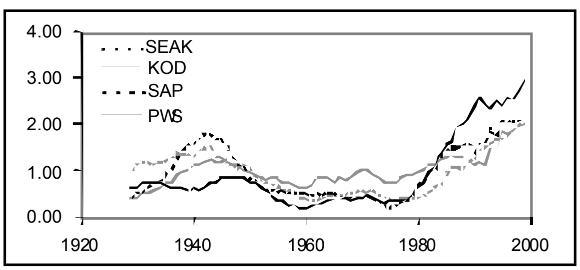


Figure 5. Standarized 10-yr running average catch of pink salmon for four regions in Alaska

These standardized averages, ten-year catches, are running averages divided by the entire time series, so that the scale is the same for all of the regions. The running averages are plotted at the end of each ten-year period; for example, 2000 represents the average 1991 to 2000 production. This shows a high production period in the 1930s and 1940s. These peaks and valleys do not actually coincide with each region in the state. If we look at the timing of the maximum and the minimum of the 10-year averages, by region (Figure 6), we note that there is a certain asynchrony in the maximum and minimum of PWS and other regions.

This first regime maximum period in PWS is offset somewhat from other regions, and so too is the degree of decline. This inter-regime minimum also is highly variable; Kodiak is declining by about 50%, South Alaska Peninsula by about 90%, and PWS 75%. The minimums in PWS and Kodiak occurred in the 1950s and the minimum in the South AK peninsula and Southeast Alaska were in the 1960s and 1970s. All regions are now at current regime maximums.

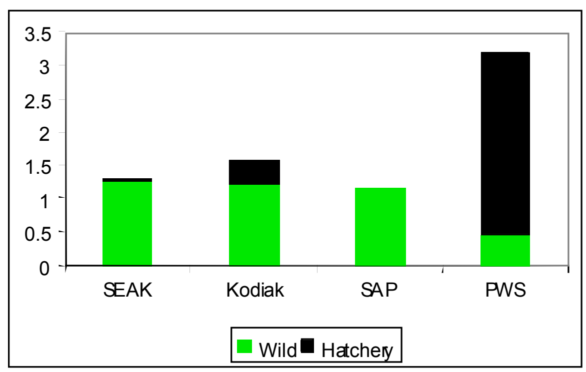


Figure 7. Relative change in 10-yr average catch: Early regime maximum to 1990s

When we compare the maximum production regime in PWS we see it has increased three-fold over the other regions. However, if we consider only wild stocks we see that PWS is actually reduced in wild stock production (Figure 7). If we expect that production between regions is proportionate across the board then we can draw a line across here and the proportion right here shows a net loss of wild production due to hatchery production, and then above the line would be a net gain due to hatchery production. If we look a little more closely though, if we re-examine that large bubble I mentioned earlier, that is in the time period 1976 to 1985 in PWS, we see that the increase here is disproportionate to other regions (Figure 8).

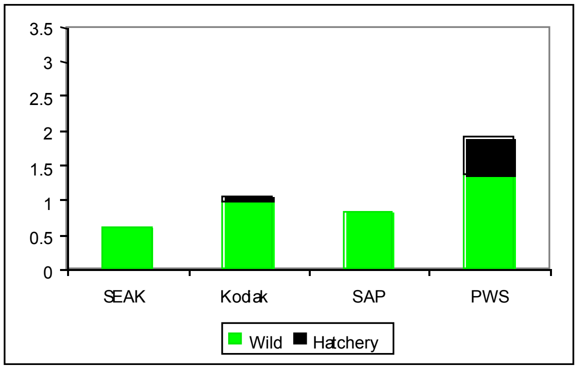


Figure 8. Relative change in 10-yr average catch: Early regime maximum to 1976–1985

It suggests that PWS production may be asynchronous with other regions and the decline in wild stock production may be due to natural cycles rather than due to hatchery influence. If we look at regional comparisons of the average return per spawner (a measure of wild stock productivity and this is to put that high bubble in production in PWS in the period 1976 to 1985 in perspective), we see it had extremely high returns for spawner average (Figure 9).

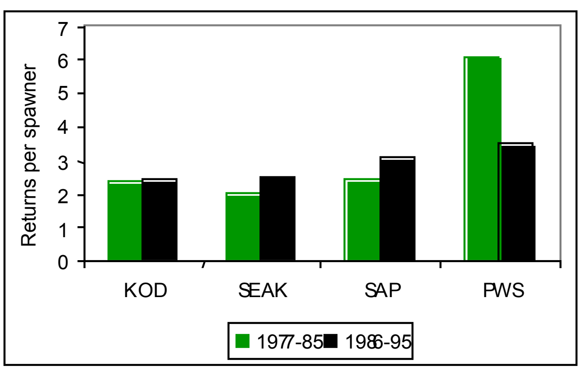


Figure 9. Regional comparisons of average return per spawner (R/S)

The current decline in wild production is the difference here, and for PWS, even with this decline, the production level of wild salmon is still the highest in the state (Figure 10). So if asynchrony occurs in PWS and other regions, then we can draw the line across here.

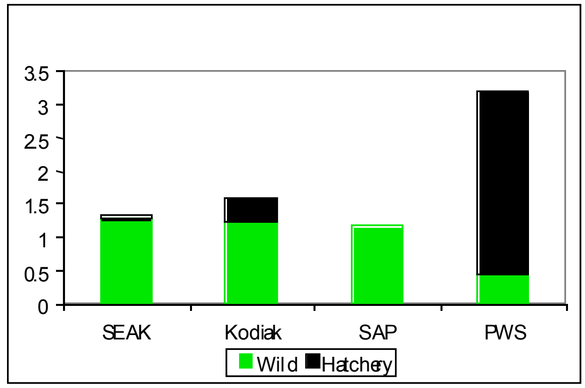


Figure 10. Relative change in 10-yr average catch: Early regime maximum to 1990s

There is something else going on there as well. This entire production from the hatcheries is a net gain. This is essentially a 23 million gain from the hatchery production in PWS. The Hilborn-Eggers model demonstrates a statistical relationship between wild stock spawner/recruit data and magnitude of hatchery releases (e.g., Figure 11). They use it to simulate wild-stock production in the absence of hatchery releases.

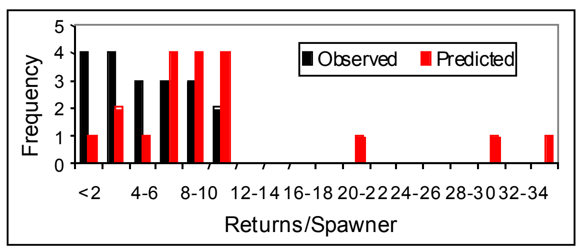


Figure 11. Frequency of observed vs. H&E predicted returns/spawner 1977–1995 BY

This is a Ricker model with an ancillary variable for hatchery releases. They simulate it by taking out hatchery releases and the output is unrealistic with returns per spawner far outside historical observation, even including those “bubble” years that had very high production. On returns per spawner, these are outliers that have never been observed under natural conditions. If we look at a regional comparison (we are going to return back to emphasize how far out those outliers are), for this “high bubble” period averaging about 6 returns per spawner, then it dropped down to the current level of about 3.5 or 4.0, which is still high (Figure 12). Those outliers are outliers not only for PWS, but also for the rest of the state.

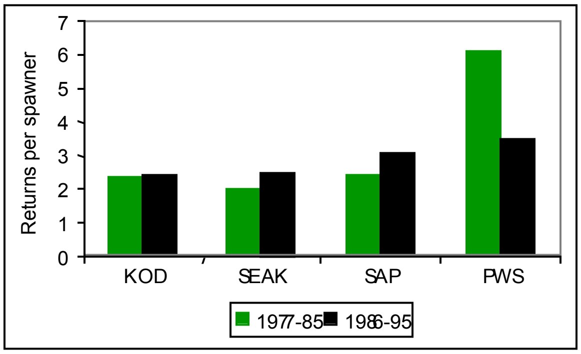


Figure 12. Regional comparisons of average R/S

The new analysis is looking at concurrent biophysical changes in the PWS system, increased hatchery releases, in the 1989 regime shift, and other regime shifts, discussed earlier by others at this conference. Biophysical variables include increased biomass of pollock; rapid increase and then collapse of herring biomass; decreased zooplankton production; decreased winter temperatures and in 1989 was also the Exxon Valdez oil spill in the Sound (Figure 13).

- Increased hatchery releases
- 1989 Regime Shift (Hare and Mantua 2000)
- *Exxon Valdez* Oil Spill
- Increased pollock biomass
- Rapid increase, then collapse of herring biomass
- Decreased zooplankton production
- Decreased winter air temperatures

Figure 13. Concurrent biophysical changes in PWS ecosystem

Now we are going to consider, using a generalized Ricker model, a broader array of environmental variables, including hatchery releases. This model is built with a forward-backward stepwise regression, where we have a less than 0.1 probability. There is a decision criterion for the regression coefficient and it is not equal to zero. Because it is a spawner recruit model we force spawners to stay in even though they do not contribute (Figure 14).

Here are the variables we consider (Figure 15). For PWS we look at winter air temperature (an indication of freshwater incubation time), spring air temperature, early marine zooplankton, and at one of the hatcheries, early marine herring biomass (potential competitors or predators). In the Gulf there is PDO that affects juveniles; we add one year to that, and we think about pink salmon biomass in the whole Gulf. There is a density-related issue. We integrate the PWS hatchery releases throughout the entire life history. And there is the real clincher that really opened our eyes when we projected PWS hatchery marine survival using this as an integration of ocean condition of all the environment variables; when we run these correlations, we are looking at these variables and we have these parameters that define what we can accept.

$$\mathrm{Ln}(R/S)=\mathrm{Ln}(\alpha)+\beta*\mathrm{Spawners}+b_1x_1+\ldots+b_nx_n$$

- Consider a broader array of environmental variables, including hatchery releases
- Model built with forward-backward stepwise regression, with $P < .1$ decision criteria for regression coefficient not equal to zero
- Spawners in model regardless of P- value for β

Figure 14. Generalized Ricker Model

• Prince William Sound	
Winter air temperature	(FW incubation)
Spring air temperature	(Early marine)
Spring AFK zooplankton	(Early marine)
Herring biomass	(Early marine)
• Gulf of Alaska	
PDO	(GOA juvenile)
PDO lagged 1 year	(GOA adult)
Pink salmon biomass	(GOA density)
• Integrated	
PWS hatchery releases	(Entire life history)
PWS hatchery marine survival	(Marine conditions)

Figure 15. Variables considered for 1980–1998 broods

First of all, for the hatchery fry it is negative, but it is not close to being significant (Figure 16). This is our significant level right here (dotted line). If we look at the hatchery survival, we get a very high degree of significance and a very high correlation. We also see that spring air temperature and zooplankton is right at the level of significance, with a positive correlation.

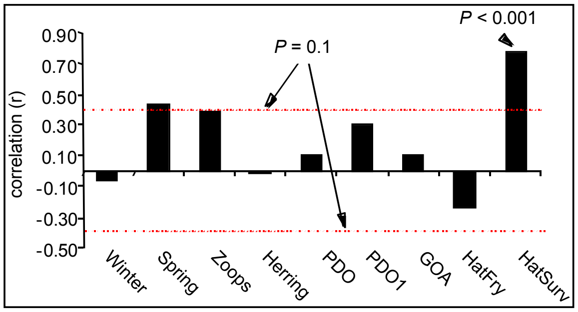


Figure 16. Correlation of environmental indexes with Ln (R/S)

Then there is the stepwise regression (Figure 17). The model includes hatchery survival, zooplankton, spring air temperature, and all are highly significant (unadjusted R-value is over 80%). Hatchery fry releases never enter the model because they are not significant.

STEP	1	2	3	4
Spawners	P = 0.367	P = 0.181	P = 0.030	P = 0.629
HatSurv		P < 0.001	P < 0.001	P < 0.001
Zoops			P = 0.048	P = 0.008
SpringTemp				P = 0.013
R_2	4.8%	65.2%	73.4%	83.2%
Adjusted R_2	0.0%	60.8%	68.1%	78.4%
C_P	53.3	12.0	8.1	3.0

Figure 17. Stepwise regression

But now there is another factor that we have to consider; the survival of hatchery pink salmon in the Sound. There are periods of higher and lower survivals of hatchery fry (Figure 18). Is this because of a density dependent effect of larger releases of fry in the latter period? The hatchery survivals decline by about the same proportion as the wild returns per spawner have declined. Are these declines due to the increased hatchery releases, or density dependence, or are they tracking some other environmental condition affecting marine survival?

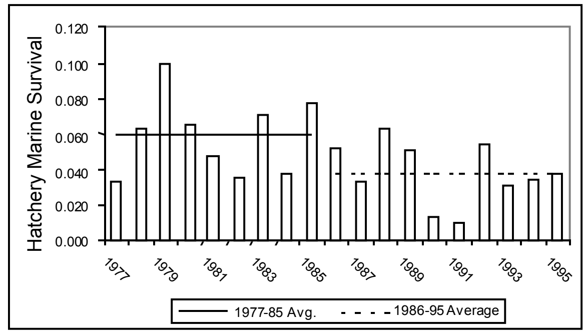


Figure 18. Marine survival of hatchery pink salmon in PWS: Density dependent

If we plot the fry releases and hatchery survival (Figure 19), we do not get much of a correlation; it is about 50/50 and we even get a negative R-value here. Probably these high early survivals with low hatchery releases represents an outlier (10% hatchery survival). There is no evidence from this of any density dependence due to fry releases.

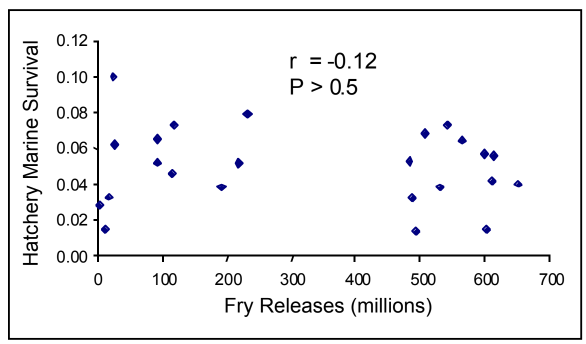


Figure 19. Correlation of hatchery marine survival to hatchery releases 1975–1998

If we run a correlation of wild returns per spawner and hatchery returns per spawner, we see two pictures (Figure 20). First of all we see a strong positive correlation and then beginning in 1984 and up to the present, when the hatchery runs are greater than half of the total pink run in PWS, R-values are highly significant. In 1979 to 1983 when the hatcheries were just getting started, the releases were small enough that apparently they did not have any effect.

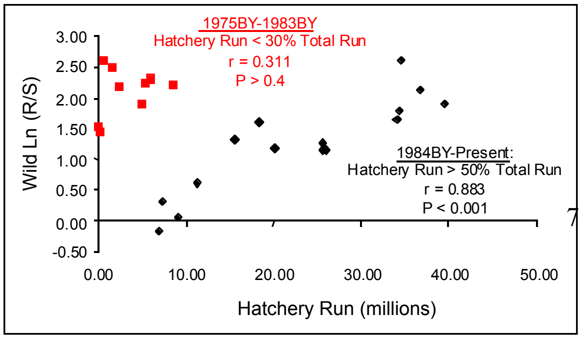


Figure 20. Correlation of wild Ln(R/S) to hatchery returns

This is not what you would expect if large hatchery production was depressing wild production. If we now simulate the hatchery impact in this new model (we are going to force hatchery releases into the model even though we know it has a negative effect), but earlier we showed this is not a significant relationship. If we force it into our stepwise model, and we use the Hilborn-Eggers approach to simulate the wild run in the absence of hatcheries, we have a high level of significance with these key biophysical variables, and of course we have to leave the spawners in the model because it is a spawner recruit model (Figure 21).

Predictor	Coefficient	SE	*P*-value
Constant (Ln(α))	1.728	0.289	<0.001
Spawners	$-1.7e_7$	$1.7e_7$	0.332
HatSurvival	22.48	5.122	0.001
Zooplankton	0.21	0.067	0.009
Sprint Temps	0.19	0.065	0.011
Hatchery Releases	$-6.6e_{10}$	$5.5e_{10}$	0.216

Figure 21. Simulate hatchery impact: Hatchery releases added to model

We can see the frequency of observed to predicted returns per spawner with this simulation (Figure 22); predicted returns per spawner are much more realistic. There is a shift to the right, indicating more wild production, and there is only one outlier which happens to be the 1988 brood. They were juveniles in 1989, which was when the Valdez oil spill occurred. We think that they may be indicative of an oil effect on marine survival but we do not have a way to get information on that now.

We can now compare the estimates of the new model, those of Wertheimer et al., and the regional asynchrony that adds about 23 million fish to the fishery (Figure 23). The region proportionately adds about 17 million. The Hilborn-Eggers model only adds 2 to 3 million, and there is a big net loss in wild production. The new hatchery survival model additions are intermediate, but it is certainly different than the Hilborn-Eggers model.

What can we conclude from this? Conditions in the marine environment explain most of the changes in wild stock production in PWS as measured by the strong positive and high correlation of hatchery marine survival and returns per spawner of wild stock. As the hatchery fish do well in the ocean, so do the wild fish. Increased hatchery production of pink salmon has caused little if any reduction in yield from wild spawners, and the contributions from hatchery pink salmon in PWS has been largely a direct enhancement for the fisheries in that region.

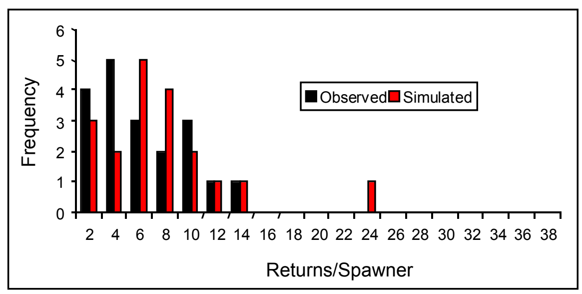


Figure 22. Frequence observed to predicted returns/ spawner fry model

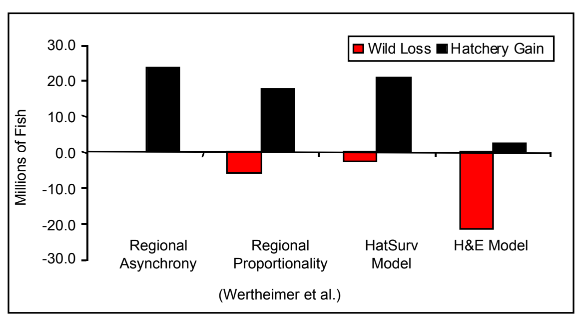


Figure 23. Estimates of annual wild yield loss and net hatchery gain

The following papers have been added to Appendix 3 to expand on Dr. Heard's presentation:

Wertheimer, A.C. et al. 2001. Comment: A Review of the Hatchery Programs for Pink Salmon in Prince William Sound and Kodiak Island, Alaska. Transactions of the American Fisheries Society 130: 712–720

Hilborn, R. and D. Eggers 2001. A Review of the Hatchery Programs for Pink Salmon in Prince William Sound and Kodiak Island, Alaska: Response to Comment. Transactions of the American Fisheries Society 130: 720–724

Discussion

Jeff Hard asked if there is any indication that in years where hatchery production increased in numbers, there is a corresponding increase in size of pink salmon in the Sound.

Bill Heard replied that there has been a general indication of a decrease over time in size in pink salmon, along with a lot of other salmon, until very recently. Things during the last two or three years may have turned around. Even with fairly high numbers, body size has begun to increase. That also applies to chum in some areas of Alaska.

Going back to the 1970s and a period of low production across the board, and why the hatchery program started in Alaska: The concept was to develop a system that would level out some of the dips in production by producing hatchery fish to support the fishery. As was pointed out, there was a regime shift in the late 1970s and everything started to look rosy, so we actually have not had a real severe down turning in ocean production. This may be based on what Dick Beamish showed. One figure which I showed, and which is not updated, shows that from 1996 to 1998, it looked like it was a sharp downward trend in Alaska. Commercial catches in 1999 and 2000 were down somewhat. It is variable, but a lot of people believe that we may be entering a time when productivity in Alaska is being considerably reduced.

Energy Inputs and Greenhouse Gas Emissions Associated with the Production of Salmon Smolts from Hatcheries in British Columbia

Peter Tyedmers, Fisheries Centre, University of British Columbia

This first part goes without saying. Hatcheries are obviously a popular fisheries management tool, or else, we would not be here. The issue I am going to address here today is the substitution of hatchery production for wild production, and the fact that that comes at a biophysical cost. When I thought about it in the last fifteen minutes I realized that may be overstating the point. Hatchery production, regardless of whether it is supplementing wild reproduction or creating a whole new fishery, comes at a real biophysical cost. The biophysical cost that I am most interested in is the energy inputs and outputs, and greenhouse gas. I thank Dick Beamish and others for at least raising the spectre of global climate change. This is the opposite side of the equation. If we are worried about what happens to salmon in the future, at the same time we should be paying a little bit of attention to what we are doing with salmon that may contribute to the problem.

Very briefly, the data I will be showing you today are the result of a larger analysis that looked at commercial salmon farming and wild salmon in BC. I will be focussing mostly on inputs and emissions on some enhancement facilities and will be contrasting some of my results with emissions and outputs associated with some private hatcheries. I will also be placing the results in the broader context of what the energy inputs to the commercial salmon fishery are as a whole. The analysis was based on data that was collected from two SEP facilities, Tenderfoot Creek hatchery and Robertson Creek hatchery. The combined data represent approximately 55 tonnes of chinook smolt production. The coho production from these two facilities is 15 tonnes, which is equivalent to about 6% of SEP production.

Peter Tyedmer’s presentation was not audio recorded properly and the rest of the session was lost.

See Appendix 4 for PowerPoint slides presented by Peter Tyedmers.

SUMMARY OF ISSUES FROM DAY 1

Craig Orr, Centre for Coastal Studies,
Simon Fraser University

As I mulled over all the information we heard yesterday, I was reminded of a recent meeting of the Pacific Salmon Endowment Fund (PSEF). The PSEF technical committee has recently completed a draft recovery plan for the Englishman River on Vancouver Island.

Since 1953, there has been an average return of 960 coho per year to the Englishman River. Wild coho were augmented for six years, between 1987 and 1993. Last year, 5,200 coho returned, the highest return ever recorded for this river. Despite this record return, and despite the fact that no augmentation has occurred for seven years, fisheries technicians collected 70 coho for brood stock from the Englishman in 2000.

When the PSEF technical committee asked those technicians why they opted to resume the augmentation—despite the record return—they were told: "Because there were lots, and it was something to do."

Clearly, there is a lack of an overall enhancement strategy in BC. Many people here may also wonder why, given this good return, this river is being recovered. The fact is, no one believes that one good return is an indication of recovery. This river still faces many threats—to its water, riparian integrity, and to other stocks.

This story also points out two other data gaps with regard to enhancement, quite apart from those addressed in our discussions on large hatcheries. First, neither the PSEF technical committee, nor the folks who enhanced the best-ever return of coho, knew enough about what was happening in the Strait, and with regime shifts. Second, the PSEF has chosen to operate according to the six draft principles of the Wild Salmon Policy.

Principle Five of that policy states that "Salmon cultivation techniques may be used for *strategic* intervention to preserve populations at greatest risk of intervention." It is safe to say that the word strategic is open to considerable discussion and interpretation—whether we are talking within the PSEF technical committee, DFO's wild salmon policy, or this room.

Many other technical committees and boards including Fisheries Renewal, BC Hydro's Bridge Coastal Restoration Program, and local enhancement groups—struggle with this word.

If, by the end of day, we could even get a little further down the road to some overarching and coordinated enhancement strategy, we will have accomplished an enormous amount. Before we get there, though, let us engage in some dialogue on some of the genetic issues.

GENETIC ISSUES

Moderator, Richard Routledge, Statistics and Actuarial Science, Simon Fraser University

GENETIC RISKS OF HATCHERY SALMON PRODUCTION TO WILD SALMON

Jeffrey J. Hard, National Marine and Fisheries Services, Northwest Fisheries Science Centre, Conservation Biology Division

Introduction

If the problems that caused the wild populations to decline (Figure 1) in the first place have not been resolved, and the hatchery supplementation program is ceased and the population then crashes back down to its original level, then the wild population is actually worse off than it was before. It now has a lower genetic variability due to the fact that more of its genes are those from the small component first brought into the hatchery. It is less of a problem, if, after the hatchery program is stopped, the population does expand, but it is still a concern. So, representative collection of broodstock is a very important component of maintaining genetic diversity in a hatchery population (Figure 2).

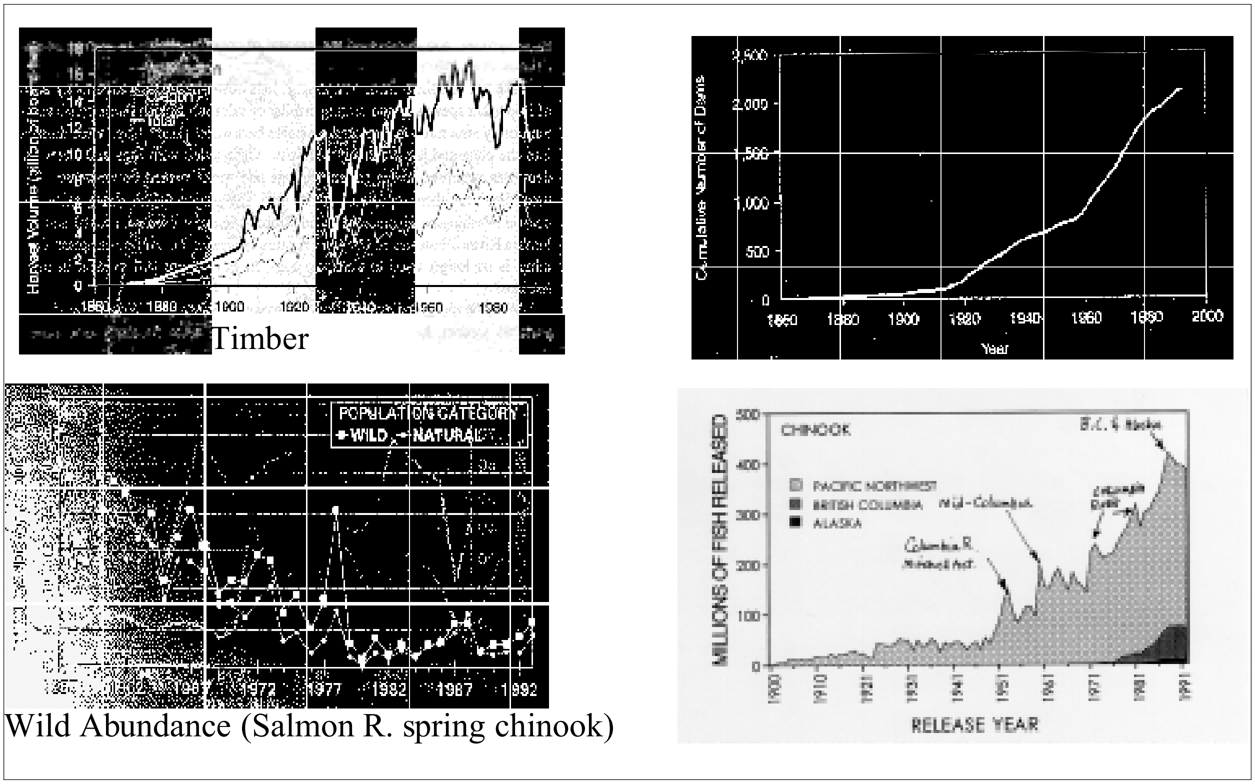


Figure 1. Hatchery use in the last century

Effects of hatchery fish

Direct biological effects

- Genetic
  - Loss of diversity within populations
    - ▲ Accumulation of deleterious alleles (small pop. size)
  - Loss of diversity among populations
  - Outbreeding depression and loss of local adaptation
  - Domestication

- Ecological
  - Competition
  - Predation
  - Disease
  - Displacement

Indirect management effects

- Overharvest of wild fish
- Masking of wild fish status
- History of optimistic prediction

Figure 2. Effects of hatchery fish

Potential genetic risks of hatchery salmon production to wild fish

Types of Effects: Genetic

Geneticists measure this diversity by what is called effective population size. The effective population size is the size that the population really is, in an evolutionary sense. If the population had equal sex ratios, random mating plus undistributed family sizes and all those things, then the population would be size X which is often much smaller than its census size. We can measure that using genetic techniques.

Loss of Diversity

This is a survey of studies, some of them unpublished or in the grey literature, using genetic methods to estimate the effective number of breeders in a given year (N_b), relative to the census number of breeders (N) (Figure 3).

You can see that they vary from about 10% to up to over 200%. Interestingly, some of the hatchery populations have very high ratios, meaning that they probably have very good mating protocols in the hatchery. Some of them have very low ratios; the overall average is around 0.2 to 0.3. In one study that is unpublished, I estimated that the effective number of breeders relative to a census number in a hatchery wild-mixture on Hood Canal for coho was about 35%. So in an evolutionary sense the population was acting, even though these fish were allowed to mate opportunistically in a wild stream setting, at low density, as if they were at 35% of the size in terms of adults.

Loss of Diversity Within Populations

Another loss of diversity we should be concerned about is phenotypic variability, particularly if that phenotype variation has a genetic component. On the lower Columbia River, coho salmon run timing has been getting earlier and there has been compression in the variation of run timing of the coho over a 15-year period (Figure 4).

N_b/N ratios

Population	N_b/N	Reference
Shasta H. (CA) rainbow trout	0.90	Bartley et al. (1992)
Secesh R. (ID) spring/summer chinook salmon	0.24	Waples et al. (1993)
Johnson Cr. (ID) spring/summer chinook salmon	0.50	Waples et al. (1993)
Marsh Cr. (ID) spring/summer chinook salmon	0.23	Waples et al. (1993)
Valley Cr. (ID) spring/summer chinook salmon	0.69	Waples et al. (1993)
Imnaha R. (OR) spring/summer chinook salmon	0.71	Waples et al. (1993)
Lostine R. (OR) spring/summer chinook salmon	0.54	Waples et al. (1993)
McCall H. (ID) spring/summer chinook salmon	2.23	Waples et al. (1993)
Sawtooth H. (ID) spring/summer chinook salmon	0.21	Waples et al. (1993)
Imnaha H. (OR) spring/summer chinook salmon	0.51	Waples et al. (1993)
Lookingglass H. (OR) spring/summer chinook salmon	0.39	Waples et al. (1993)
Sacramento R. (CA) winter chinook salmon	0.013–0.043	Bartley et al. (1992)
Sacramento R. (CA) winter chinook salmon	0.111–0.367	Hedrick et al. (1995)
Big Creek H. (OR) coho salmon	0.24	Simon et al. (1986)
Chiwawa R. (WA) spring chinook salmon	0.12	Ford et al. (unpubl. data)
Twisp R. (WA) spring chinook salmon	0.15	Ford et al. (unpubl. data)
Chewuch R. (WA) spring chinook salmon	0.18	Ford et al. (unpubl. data)
Methow R. (WA) spring chinook salmon	0.25	Ford et al. (unpubl. data)
White R. (WA) spring chinook salmon	0.84	Ford et al. (unpubl. data)
Lilliwaup Cr. (WA) coho salmon (H-wild mixture)	0.34	Hard et al. (unpubl. data)

Figure 3. N_b/N ratios for a given year

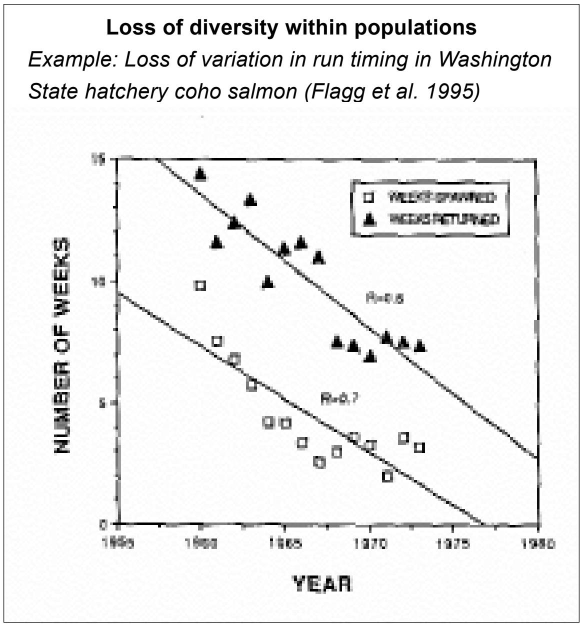


Figure 4. Loss of diversity within populations

We have seen something similar for Fall Creek Hatchery coho on the Oregon coast, where run timing has become earlier in the last 30 years, primarily due to broodstock collection practices (Figure 5).

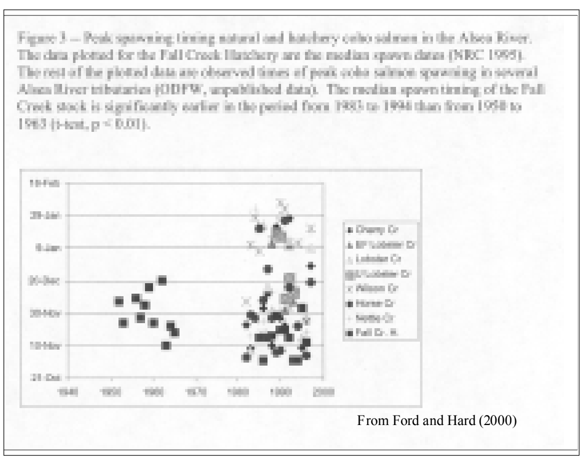


Figure 5. Peak spawning time for natural and hatchery coho salmon in the Alsea River

There are consequences from the loss of diversity; this is some unpublished data on chinook salmon combined with some published data on rainbow trout, the rainbow trout data being the circles, and the chinook salmon data being the triangles (Figure 6).

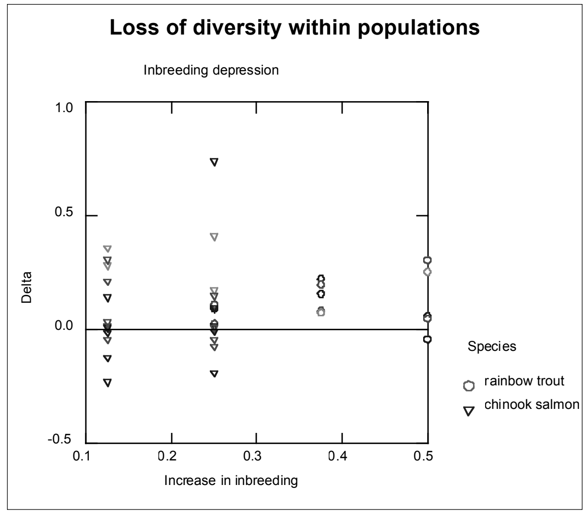


Figure 6. Inbreeding depression and increase in inbreeding for rainbow trout and chinook salmon

Each circle or triangle represents a different trait, some stage specific growth or survival characteristic. Delta is a measure of the amount of inbreeding depression, measured in terms of phenotypic standard deviations. The higher the delta the higher the inbreeding depression, or the lower the fitness. There is quite a bit of variation here. The rainbow trout, which have higher inbreeding coefficients, show inbreeding levels in the order of 0.2 to 0.3 standard deviations, at these fairly high levels of inbreeding. This is a non-anadromous fish. For chinook salmon, which have not been inbred as much, in some cases the levels of inbreeding depression for some of these characteristics are as high as we have for the rainbow trout. And for some traits, we are actually seeing heterostasis, or an increase in fitness under inbreeding, which is a curious result.

To summarize the loss of diversity within populations, the theory is well developed; it has been around for at least 60 years. There is a lot of empirical evidence for it, in many organisms. Unfortunately, there is not very much data for anadromous salmon, so more work has to be done there. The methods that we might use to reduce this sort of risk are to select as large a representative of broodstock as possible, use mating protocols that reduce the variance among prospective parents, and limit the natural spawning of hatchery fish. The major scientific uncertainties, or analytical problems associated with this issue, are meta-population structure and its effect on population structure diversity in Pacific salmon. In a biological sense, there is a moderate level of adaptive management potential to address this issue, if it was detected (Figure 7).

Loss of Diversity Among Populations

Among populations, the potential consequences of loss of diversity include loss of local adaptations, lower natural productivity, and, in the longer-term, loss of evolutionary potential, which leads to lower resilience and sustainability. This could arise through several mechanisms (Figure 8).

One is transfer of stocks between drainages, followed by genetic introgression, leading to greater homogeneity between these populations. Others include increased stray rate of hatchery fish because of inefficient ways of collecting broodstock or retaining hatchery fish once they return, or poor imprinting of hatchery fish. Broodstock collection low in a watershed could also lead to reduced diversity among populations, by mixing these fish. That has been the case, apparently, in some circumstances, as in the Grand Coulee fish maintenance project of the late 1930s, where fish were captured in the Columbia River and many of the hatchery programs that sprang up were derived from a mixture of fish from various populations in the Upper Columbia (Figure 9).

Loss of diversity within populations

Level of scientific understanding:

- Theory:
  - Well-developed theoretical foundation
- Empirical evidence that hazard exists:
  - Considerable evidence
- Methods of risk reduction:
  - Large, representative broodstocks
  - Low variance mating protocols
  - Limit natural spawning of hatchery fish
- Major scientific uncertainties or analytical problems
  - Meta-population structure and its effects on within population diversity
- Adaptive management potential:
  - Moderate (biologically)

Figure 7. Loss of diversity within populations

Loss of diversity among populations

Mechanisms:

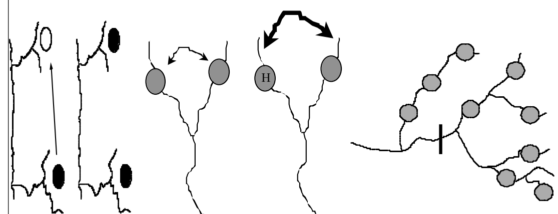
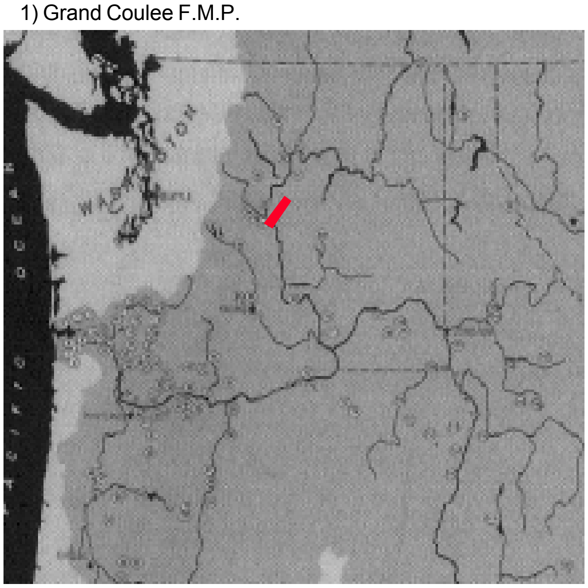


Figure 8. Loss of diversity among populations

Loss of diversity among populations

Examples:

1) Grand Coulee F.M.P.



2) Straying of Columbia R. fall chinook into Snake R.

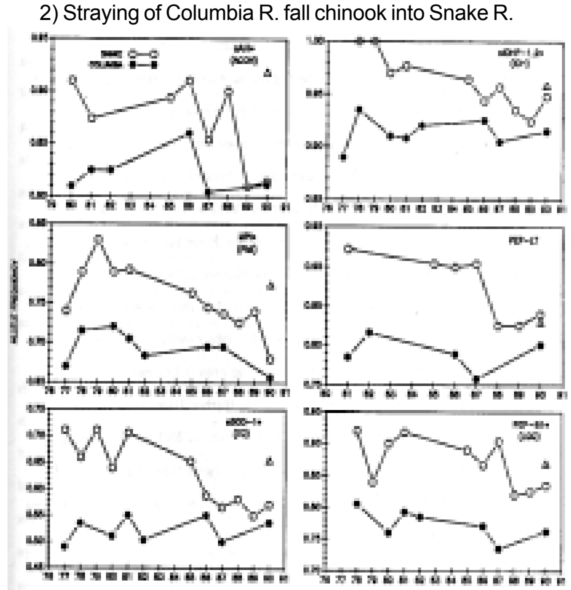


Figure 9. Straying of fish

About 10 years ago Robin Waples looked at genetic signals to see how differentiated some of these populations were. In particular he was comparing the Upper Columbia to the Snake River, in terms of allele frequency, and showed that, over time, in terms of allozymes, many of these populations became more similar, suggesting that we were losing some of the stock structure, in that area for spring chinook salmon.

This loss of diversity among populations also has a well-developed foundation and there is considerable evidence that this risk exists. The methods for reducing this risk are similar to those for avoiding loss of diversity within populations; use local broodstock, limit natural spawning of hatchery fish, and avoid this sort of straying issue. The major scientific uncertainties or analytical problems include estimating the natural levels of gene flow for populations that are connected by moderate levels of migration, which is generally true for Pacific salmon. We think that, biologically, this has a high adaptive management potential. In other words, in many cases, the problem could be corrected fairly easily, once detected (Figure 10).

Loss of diversity within populations

Level of scientific understanding:

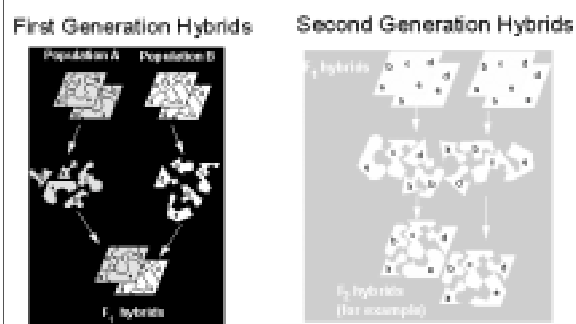
- Theory:
  - Well-developed theoretical foundation
- Empirical evidence that hazard exists:
  - Considerable evidence
- Methods of risk reduction:
  - Large, representative broodstocks
  - Low variance mating protocols
  - Limit natural spawning of hatchery fish
- Major scientific uncertainties or analytical problems:
  - Meta-population structure and its effects on within population diversity
- Adaptive management potential:
  - Moderate (biologically)

Figure 10. Levels of scientific understanding for loss of diversity among populations

Outbreeding Depression

Related to this loss of diversity among populations are the fitness consequences (i.e. outbreeding depression). There are two mechanisms for outbreeding depression. One is the loss of local adaptation, which can occur, regardless of the genetic mechanism for differentiation among populations. All that is required is that the fitness by which outbreeding depression is measured has a heritable component. Another mechanism, perhaps the more serious, is this mixing of incompatible genomes. If populations are locally adapted, and these adaptations have been forged through natural selection, over hundreds or thousands of generations, there may be interactions among loci, among genes that synergistically increase fitness, that increase local adaptation. By mixing genomes that have different solutions to different problems we can actually break apart those synergies and dramatically reduce fitness. There is a well-developed theory behind this. It has been shown empirically in many organisms now, although not in salmon, definitively (Figure 11).

Outbreeding depression



From Gharrett and Smoker (1991, 1999)

Figure 11. Outbreeding depression, F1 and F2 hybrids

This figure simply shows how outbreeding depression through this loss of co-adaptive genetic complexes might occur, and it has to do with the fact that, in many cases, you may not see a depression of fitness in the first generation, when two genetically divergent populations interact, because F1 hybrids have an intact genomic complement from each of their parents. However, in second and subsequent generations, recombination occurs, and independent assortment, and these genes become reshuffled in the F2s, and to the extent that these genes are acting synergistically to increase features in the F1, those are lost in the F2 and F3, potentially at least, and outbreeding depression can occur.

What is the Evidence for this in Salmon?

Unfortunately, there are really only a couple of published studies which provide evidence for this, both on pink salmon. The results are consistent with outbreeding depression, although they do not confirm it (Figure 12).

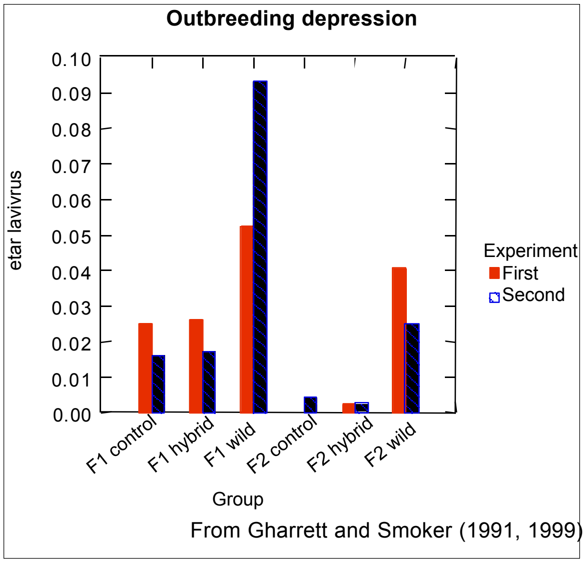


Figure 12. Outbreeding depression in pink salmon

They show a clear loss, reduced survival in the F2 hybrids between even and odd year pink salmon, relative to their F2 controls and F2 wild comparisons. The F2 controls also were quite low, the F2 controls being cryopreserved sperm from one population, the even or the odd, and then mated to females of the corresponding similar brood line whereas the F2 hybrids would be cryopreserved sperm, say, from even cross 2 females from the odd line. The reason why this may not be all that relevant to management issues for Pacific salmon is that even and odd year pink salmon are highly genetically divergent, and in fact, for all intents and purposes, they can be considered different biological species. They have been isolated for a very long time. What we do not know is if this same sort of pattern would occur in populations that are more recently derived from one another (stronger genetic relationships) (Figure 13).

The methods of reducing the risk for outbreeding depression would include using local broodstock and limiting the natural spawning of hatchery fish. The major scientific uncertainties, and there are several here for outbreeding depression, include estimating natural levels of gene flow among Pacific Salmon populations and determining levels and patterns of local adaptations. Empirically measuring outbreeding depression for various geographic or genetic distances is also a major scientific uncertainty. How divergent do populations need to be genetically before we start to see this problem? We know it happens at the inter-species level, but we do not know how distantly related conspecifics must be to produce outbreeding depression. Unfortunately, this is a problem that may be difficult to resolve, once it has happened. In other words, as the damage may have already been done, it is something we should be very concerned about.

Outbreeding depression

Level of scientific understanding:

- Theory:
  - Recently developed theory
- Empirical evidence that hazard exists:
  - Little direct evidence in salmon; considerable indirect evidence
- Methods of risk reduction:
  - Use local broodstock
  - Limit natural spawning of hatchery fish
- Major scientific uncertainties or analytical problems:
  - Estimating natural levels of gene flow
  - Determining levels and patterns of local adaptation
  - Empirically measuring outbreeding depression for various geographic or genetic distances
- Adaptive management potential:
  - Low (biologically)

Figure 13. Level of scientific understanding of outbreeding depression

Domestication

We heard something about domestication yesterday. I will define domestication as the loss of fitness in wild fish due to domesticated hatchery fish spawning in the wild. Mechanisms are thought to include selection for genotypes favored in the hatchery environment, due to either intentional artificial selection in some cases, but probably more important, the inadvertent natural selection that occurs due to adaptation to the hatchery environment (Figure 14).

Domestication

Potential consequence: Loss of fitness in wild

Mechanisms: Selection for genotypes favored in hatchery environment

- Intentional artificial selection
- Inadvertent selection
- Relaxation of selective constraints

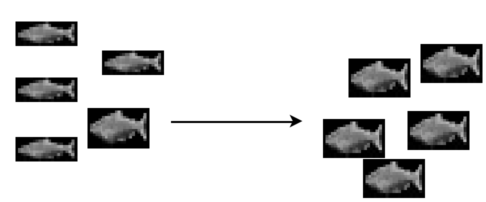


Figure 14. Consequences and mechanisms of domestication

Hatcheries are very different from wild systems and it is difficult to believe that there is no genetic response of these fish to a hatchery environment. To the extent that the genetic response occurs, it may be at the expense of adaptations to the wild, of course in the hatcheries, because we are allowing many more fish to survive than in nature. Many people believe we are actually relaxing selective constraints, at least in the hatchery. The problem is that there may be a tradeoff once those are released to the wild. We have already heard a little bit of evidence suggesting that hatchery fish have lower survival rates in the wild, and this could be a consequence of improved survival to the smolt-release stage.

What is the evidence that domestication is a problem? There is a well-developed theory from population and qualitative genetics which allows you to predict, given certain assumptions, how domestication will occur, and in which traits it would be most expressed. Low survival and mating success, compared to wild fish in the studies that are available, has been observed, and there are fairly important differences in morphology, behavior and life history of hatchery and wild fish which may be important in the domestication process, thereby reducing success of hatchery fish in nature and corresponding wild fish as well. The uncertainties and caveats associated with this domestication-poor wild fitness problem include the fact that we do not know if the domestication process is reversible or not. Presumably it is, but if so, how long would it take? In other words, if we had highly domesticated hatchery fish with a fitness level in the wild, X, we do not know whether that level of fitness is recovered over an ecological meaningful time frame, due to re-adaptation to the wild. That is an important question, if, in fact, hatchery fish fitness is depressing wild fish fitness in the wild.

There have been few specific case studies to test this issue. Some of the data you saw yesterday from Ian Fleming (see pp 29-53) showed some of the morphological differences between hatchery and wild fish, coho in particular. These morphological characteristics, particularly the secondary sexual characteristics, may be very important because of the mating structure of salmon in the wild. By bringing fish into the hatchery, we essentially remove the sexual selection process. The variance in reproductive success of fish in the hatchery is primarily determined by differences in fertility of males and fecundity of females. But in the wild, it is determined by many other factors; mate selection, fighting ability among males, and so on.

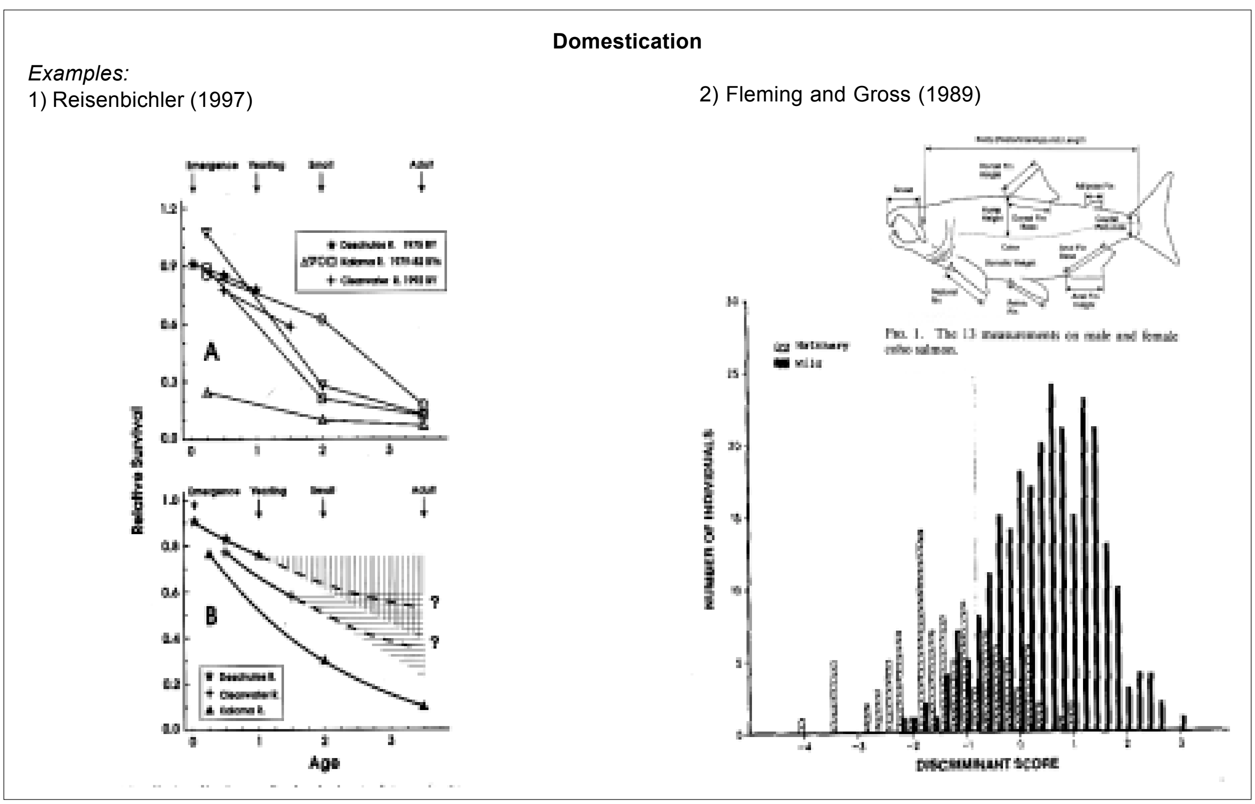


Figure 15. Relative survival for hatchery and wild fish

Figure 15 presents some of the data from one of Reg Reisenbichler's papers for steelhead on the Columbia and the Snake rivers and their tributaries, and shows the relative survival of hatchery and wild fish for several different studies, as we march through the life cycle. The relative survival of these hatchery to wild fish is quite low by the time we get to the adult stage for these steelhead. Figure 16 shows a more recent version of that graph from the 1999 Reisenbichler and Rubin review.

Wild fitness of hatchery fish

Example: Relative survival of H and W steelhead (Reisenbichler and Rubin 1999)

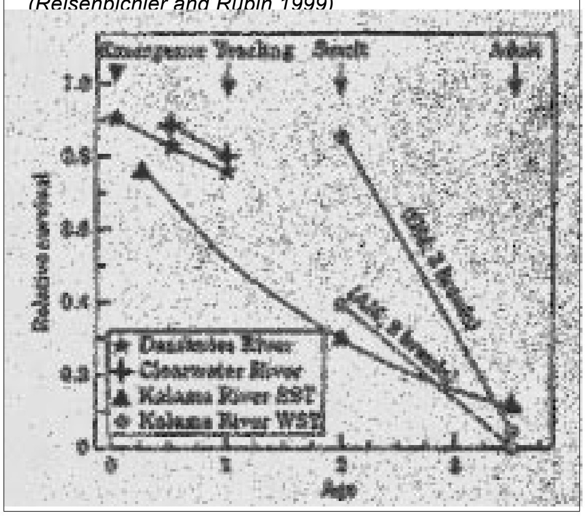


Figure 16. Relative survival of hatchery and wild steelhead

Again, it shows the relative survival of hatchery and wild steelhead for these different studies. All have limitations, but taken collectively, they suggest that the hatchery fish tend to survive at a much lower rate than the wild fish to the adult stage. These Kalama River studies are different methods of looking at two or three different broods, through arithmetic means and geometric means.

The fish in Figure 17 are not hatchery fish, they are captive reared fish. The figure on the right shows some of the shape changes that can occur in captive versus wild females and captive versus wild males. When subjected to a multivariate canonical discriminant analysis you can unambiguously assign these fish to different groups, based on these characteristics. What we found was that the reproductive success of these fish was strongly correlated with morphological and behavioural characteristics that differed between captive and the natural fish. These are clearly some components of the fitness that we are talking about.

One of the differences between the captive-wild comparison and the hatchery-wild comparison is that presumably in the captive-wild comparison, these differences are almost entirely environmentally induced, whereas in the hatchery-wild comparisons, presumably there is some genetic component to the differentiation between these hatchery and wild fish, and even though the differences are subtler they may actually be more important.

Morphological domestication

Example: Changes in adult coho body shape (Hard et al. 2000)

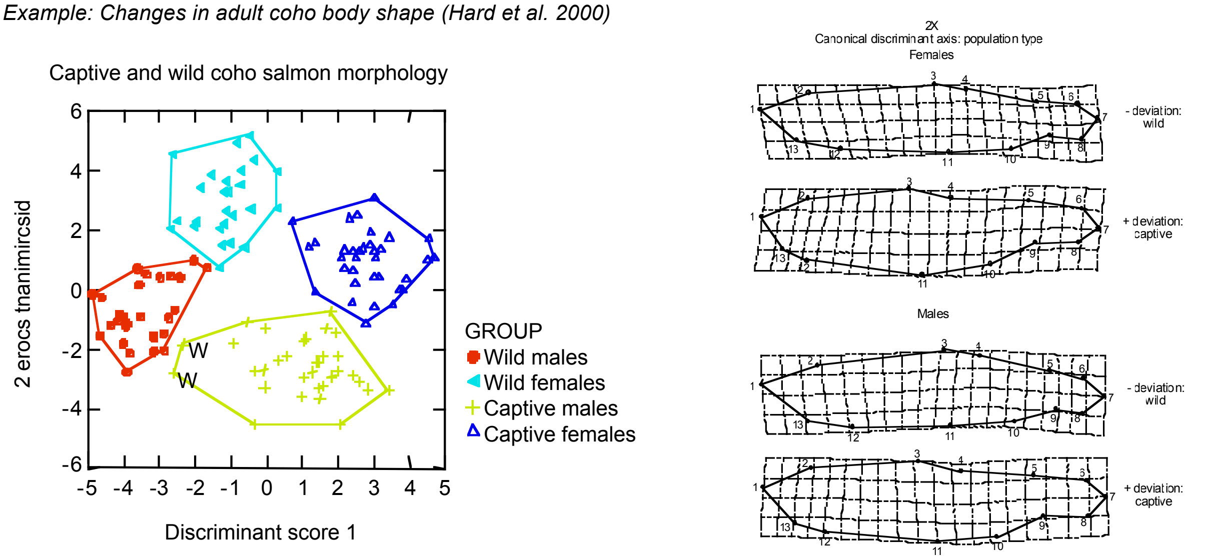


Figure 17. Changes in adult coho body shape

Behavioural Domestication
The data in Figure 18 shows greater frequencies of courting behaviors and breeding success for wild coho relative to hatchery coho.

The figure on the right [bottom] is from some of our work showing greater frequencies of different types of mating behaviours in the male wild coho relative to captive wild coho. While it is important to know that the captive fish and the hatchery fish are not doing as well as the wild fish, it is also important to note that they are expressing the same behaviours; they are just not doing it as well. There is the potential to improve hatchery practices and culture practices to possibly alleviate some of these problems; perhaps not to remove them entirely, but to alleviate them.

Behavioral domestication

Example: Changes in adult coho behavior (Fleming and Gross 1993; Berejikian et al. 1997)

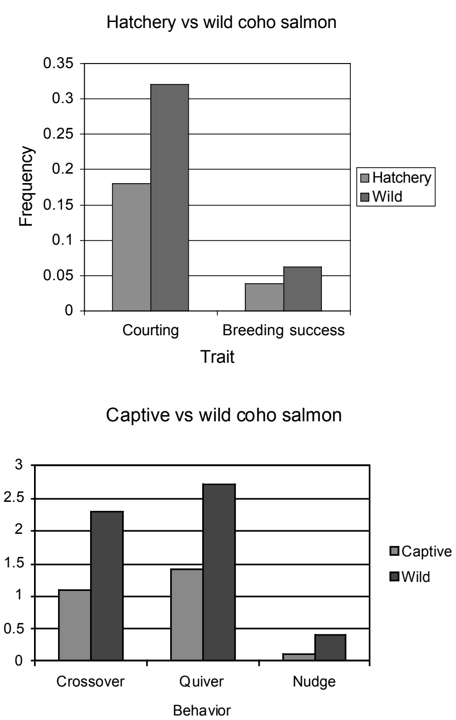


Figure 18. Changes in adult coho behaviour

The theory behind domestication is a well-developed theory (Figure 19). However, in general, it is poorly developed for specific applications involving salmon. The empirical evidence that this risk exists is fairly substantial for domestication in general, but limited evidence exists for its negative consequences for natural populations. Thus, more studies are needed to specifically look at this sort of question.

The methods of risk reduction include limiting natural spawning of hatchery fish and then thinking about adopting rearing and mating methods in the hatchery that better mimic what goes on in the wild.

Major scientific uncertainties or analytical problems include a need for better models of salmon domestication, and more empirical data on the domestication process; what traits, specifically, are most important in terms of domestication, and which ones can we reverse more easily. Unfortunately, the adaptive management potential for domestication is low, at least in the short term.

Domestication

Level of scientific understanding:

- Theory:
  - Well-developed general theory; poorly developed for specific application
- Empirical evidence that risk exists:
  - Substantial evidence for domestication; limited evidence for negative consequences to natural populations
- Methods of risk reduction:
  - Limit natural spawning of hatchery fish
  - Natural rearing and mating methods
- Major scientific uncertainties or analytical problems:
  - Need for better models
  - Need for more empirical data on domestication process
- Adaptive management potential:
  - Low (biologically)

Figure 19. Level of scientific understanding of domestication

Applying the Precautionary Principle
When applying the precautionary approach to risks from hatchery production, there are four components. One is that we need to identify and assess the risks, and weigh those against the benefits of the hatchery. There clearly are potential benefits to using hatcheries, but these need to be weighed against some of those risks I have talked of, in addition to ecological risks that I have not discussed. We need to manage for genetic diversity and integrity and not wait for the consequences if either is lost. We need to take a more proactive approach. We need to use culture and management methods that reduce the risks, and we know what some of these are. However, we do not know what all of them are. Finally, we need to develop and maintain natural reserve areas to limit potential losses, and along with that, a strong monitoring and evaluation component to any hatchery program involved in natural stock

supplementation. There is more scientific certainty about the risks to diversity and the consequences of its loss; Craig Busack and Ken Currens pointed this out in their risk paper back in 1995. I think that there is more potential for adaptive management here.

Culture and Management Guidelines that Reduce Risks

In terms of culture and management guidelines that reduce risks, the guidelines for preserving diversity within populations and, to some extent, between populations, are well understood. The guidelines for preventing domestication and outbreeding depression are not as well understood. More research would be welcome in that area.

Developing and maintaining natural reserve areas, where it should be hands-off in terms of hatcheries, is worth considering. There may be some populations that we identify that we think are critical to the evolutionary legacy of the species as a whole, and that we should probably just leave alone; leave alone, not only in terms of hatcheries, but also in terms of habitat. This serves at least a couple of purposes. It helps to protect from loss in case risk-reduction methods fail, and it provides a natural reference population for populations for adaptive management. One area where this was thought about was in one version of the draft final Snake River recovery plan for chinook salmon, where drainages were identified for different purposes (Figure 20).

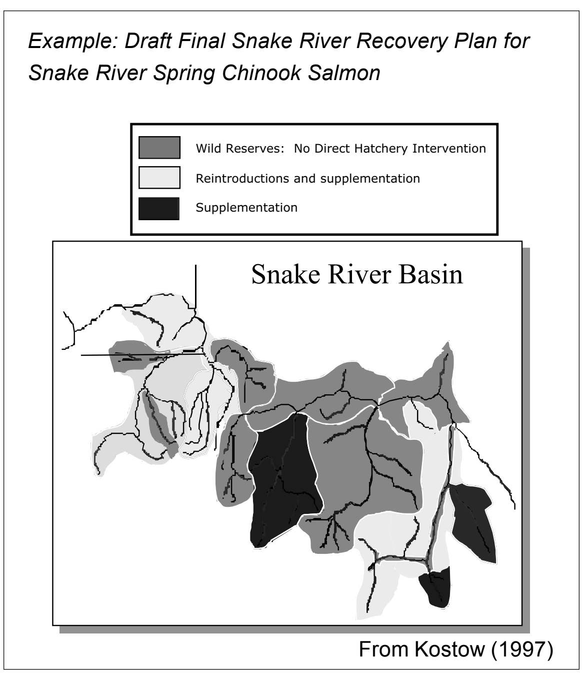


Figure 20. Draft final Snake River recovery plan for Snake River spring chinook salmon

A mixture of approaches was recommended. The Middle Fork of the Salmon and parts of the Salmon River, were recommended for wild reserves with no direct hatchery intervention. The South Fork of the Salmon is a place where supplementation was considered. Lemhi River, and the Grand Run River in northeast Oregon, other areas where some supplementation was recommended, given the appropriate stock, and where reintroduction could occur, where individual stocks had been extirpated, or nearly so.

Ian Fleming discussed the study by Robin Waples and Mike Ford on salmon supplementation. It is worth going through this once again quickly to address what we do know about the success of supplementation (Figure 21).

Salmon supplementation survey

Objective	Was it met? Y	N	?
Broodstock collection			
Age	10	2	7
Run timing	8	2	9
Integrity	14	5	–
Hatchery survival			
Prespawning (90%)	13	4	2
Egg-smolt (70%)	16	2	1
Adult-adult (2 ×)	9	3	7
Population increase	6	12	1
Natural spawning	1	2	16
Sustainable	–	–	19

Figure 21. Results from salmon supplementation survey

If we are recommending this technique to recover natural populations, what is the track record? In nineteen studies looked at, and this did not include the Englishman River population that Craig mentioned this morning, none met the criterion for sustainability. In other words, in all or most cases, none had “turned off” the hatchery, or had applied some other methods, so that you could estimate whether the supplementation had actually boosted the natural production. In only one case was natural spawning apparently successful. In most of the others it was either unknown or it had been shown not to be successful. In only six of those nineteen was population increase observed. Therefore, it is worth being very cautious about this approach because it does not have an overwhelming track record. The conclusions, in general, were that the production goals were often met. We know that these hatcheries can produce fish back to the hatchery.

Unfortunately, most programs are not rigorously evaluated for effects on natural populations, and the long-term benefits remain to be demonstrated.

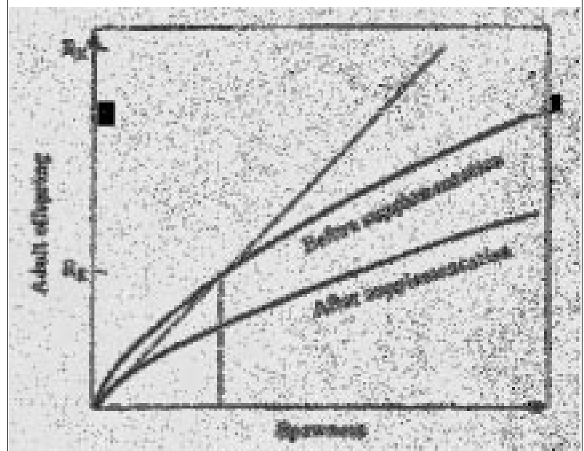
Loss of Local Adaptation

What do we know about local adaptation in salmon? We know that to some degree there is genetic isolation among these populations, there is a spatial and varying environment, these habitats differ, and there is genetic variability. There is a standing stock of genetic variability present, so evolution can occur. In other words, in experiments where genetically differentiated populations were brought into a common environment and differences were evaluated, there is a heritable basis for those differences. The vast majority of attempted translocations of anadromous salmon, at least within their natural range, have failed. That is something we ought to always think about when we are thinking about bringing one stock into another area.

Uncertainties and caveats surround this issue. There are very few case studies, so in any specific instance, it is difficult to predict what will happen. The rate of adaptation is something we have no idea of how quickly it operates, and we have no idea how many generations it takes for a population to adapt to a system. Spatial scale is another unknown. We do not know how widely we can draw fish away from a home stream without running into problems, and without reducing local adaptations. The direct effects on the receiving population are very difficult to quantify.

Figure 22 is from a recent review and I think it is an instructive thought experiment. This spawner-recruit curve, just a hypothetical one, might be a population where we are considering hatchery supplementation, which shows the value for productivity, and an equilibrium value of recruits per spawner. If what I have said is true, bringing hatchery fish in, maybe even derived from this population, even though they have become genetically diverse through domestication or some other means to the point where depression of fitness of these fish is possible, may cause the curve to drop down and these fish will no longer be able to replace themselves. That is one possibility. In fact, what may happen is this population will then become dependant on the hatchery population, or the supplementation program, to maintain itself. This is a situation that we all agree we want to avoid.

A supplementation dilemma



From Reisenbichler and Rubin (1999)

Figure 22. Spawner-recruit curve

Conclusion

In the spirit of data gaps, I will close with a question: What sort of research do we need? I think we need an estimation of lifetime reproductive success, adult to adult, over the whole lifecycle. This is our best measure of fitness. We need it to access multiple generations in natural habitats, comparing fish from a common ancestry. We need to identify the major components of fitness; in other words, which are the behavioural, morphological, physiological aspects of these fish that are most important in determining their fitness in the wild? We need to comprehensively evaluate the risks and benefits of hatchery supplementation, ideally, before we start these programs. In many cases that will not be a possibility, but it certainly will be possible for those we have not started yet. We need to characterize how fish adapt to the wild and to the hatchery. Are they fundamentally different, or are they just variations on a theme? We need to determine whether domestication is reversible and if so, what sort of time frame are we talking about? Finally, we need some rigorous evaluation of the effectiveness of supplementation.

Discussion

A participant took issue with leaving open the question of "Can domestication be reversed?" The issue was raised that, assuming we have a wild situation which shows a great spectrum of genetic diversity, and assuming that domestication is, in fact, selecting among that spectrum, we are choosing a small slice, choosing that slice as we domesticate, and selectively representing that slice to a much higher extent in following generations. How can we possibly reverse that process? We have, in fact, lost a tremendous amount of genetic information in the process of domestication, so how can we leave open the question, is this reversible?

Jeff Hard answered that he should not use the word reversible, in terms of loss of fitness. What he meant was that we may not get back to the point from which we started, but certainly he does not think that it is unreasonable to expect that we could actually get an improvement in fitness of those fish as long as they readapt to the wild. It may be along a different trajectory than they took to get to the domestication process. He is not arguing that they go back up the same way. They would take a different route to get there, perhaps, because genetic characteristics, by definition, are different.

The question was raised: What happens when a population is going through a natural abundance decline? We are thinking very seriously of using strategic enhancement to help us conserve stocks. We have populations under 1,000, then 100, then 50, then 20, and at some point, you reach a balance where what is happening in the natural spawning population is worse than what might occur as a result of intervention, with a hatchery. To put another spin on the question, we do have catastrophic natural events; for example 1-in-50 year floods during incubation should have a massive selective effect on natural spawning populations. Drought for several years in a row has the opposite effect. Is there any information that describes the impacts of these kinds of events on natural spawning populations and their recovery? Having a balance in terms of understanding these kind of impacts, relative to the fish culture potential impacts, would help give us a better sense of where to use things like strategic enhancement.

Jeff Hard noted that this is an important point. There are risks for doing nothing, and not implementing a hatchery program also has risks and that has to be weighed into the equation. Sure, we can lose individual populations through floods and that kind of thing. We can also lose them through pump failures in a hatchery. There is protective culture in the hatcheries, but, it is not without risk as well, but the point is taken.

Al Wood noted that hatchery production triggers a fisheries response. Fisheries tend to react to the increased abundance and those kind of responses can do a lot of things that Jeff described, for example, the change in stock timing. Quite often it is the early part of the run where you get the lowest harvest rate and the fishery reacts more later on. Also, it can cause the same kinds of decreases in wild stock abundance, just from mixed-stock fishing on a hatchery stock. Similarly, with a low wild escapement you will get the same kind of reduction in natural selection for area and for mates. And there is a tendency right now to not fill the spawning grounds, to over-harvest wild stocks. Is there any work you are aware of for separating out those kind of selective impacts of hatcheries from fishing?

Jeff replied that there is no empirical work. They are working on applying genetic data to some models to get at selective effects of fisheries, independent of the hatchery process.

A participant commented on a point that Jeff Hard had made about identifying the major components of fitness. It is a rather large thing to try and do, especially given some of the things Dick Beamish pointed out, in terms of the changes that we seem to be going through with regimes and global climate. It makes us reflect on this idea of reserve areas. It is a very interesting idea and especially in terms of plant genetic conservation, or, as they refer to it "*in situ*" genetic conservation. How are we going to know what kinds of things the genome is going to need to adapt? Do we really know what to expect? You also talked about the Snake River Plan, but when I think about the entire coast, the entire range of salmon on the Pacific Coast, what a population might need in one region compared with another creates a lot of uncertainty.

Jeff Hard noted that there is no shortage of studies required, and one study is not going to answer this question. We all know the idiosyncrasies of the different populations adapting to difficult circumstances, but getting at determining lifetime reproductive success of hatchery and wild fish, in particular systems, and how that is constructed from the behaviour, morphology and physiology, would get us a long way there.

Bill Heard asked if Jeff would reflect on the comments made yesterday by Lee Blankenship, on the greatest return of spring chinook on record, mostly from hatcheries into the Columbia River, and Dick Beamish's comments about regime shifts. As a geneticist and theorist, tell us, with the base assumption that there is enough water in the Columbia that the fish have a chance, what should be done with all of those fish, the spring chinook, in the Columbia River, this year, from a genetics point?

Jeff Hard responded that it is good news for all, but, that you should not get too optimistic. This return and perhaps next year's return, and last year's jack return may just be a blip on the radar screen. They certainly reflect one or two strong cohorts moving through. It is a little early to tell what is going to happen in the longer term; unfortunately, it is a bad water year.

Stock Status of Wild Atlantic Salmon Populations: A Brief Overview

Fred Whoriskey, Research and Environment, Atlantic Salmon Federation

I do not know how familiar you are with the Atlantic salmon and the Atlantic salmon's lifecycle and distribution, so I would like to give you a quick overview of what we are dealing with. Basically, it is a species that spans the area form North America to Europe. Populations used to go as far south as Portugal. They also came over as far east as the Komi Republic in Russia. In North America, they used to come down at least as far as the Connecticut River. They make their way up at least as far as the Ungava Bay. There is one relic population, and there may have been sea-run populations over in the Hudson Bay area, but the Hudson Strait in the spring time has an average temperature of about -1.73ºC. At the time the salmon have to be migrating back to the rivers in the Bay of Fundy zone their blood would freeze at -0.83 ºC. We have probably lost those, and all that remains in the Hudson Bay region is one relic estuarine population that behaves like a sea trout population. It comes out of the river system into the estuary for three months a year and then works its way back upstream.

Ocean Migration of Atlantic Salmon
The oceanic migration of the Atlantic salmon is actually quite varied. One is off the Faeroe Islands and the second is off west Greenland. These are freezing zones for Atlantic salmon. What happens is there is a tendency for the fish, the two sea winter fish, the large females, the egg supply for which we are managing, that come out of the southern European complex, to drift up. Some of them come up into that Faeroe Islands area, but some of them actually get across the prevailing currents and end up off west Greenland where they mix with the two sea winter fish that are coming out of the North American populations. Some of our fish from North America, on an erratic basis, do tend to crop up in those feeding grounds off the Faeroe Islands, but it is a fairly rare event. There are only three records of fish off the Faeroes finding their way back into North American rivers in the last four to five years. And the Northern European complex, which is from the Fendo-Scandinavian and the Russian zone primarily, congregate off the Faeroe Islands. These are the two sea winter fish. Your one sea winter fish, which you would call jacks in your Pacific salmon (we call them grilse) are off fairly locally, and come back after one winter. We do not believe that they find their way up into those particular zones.

The reason I am going into such detail over this is in terms of management, and in terms of determining the abundance, the International Council for the Exploration of the Seas (ICES) is fixated on developing something called the pre-fishery abundance estimate. How many fish are out there off the Faeroe Islands or off west Greenland just before the first mixed-population fisheries occur in these zones. That is the first point where these Atlantic salmon are going to enter into some form of fishery, and that is information that I would like to present to you as well. One final point here is that, in Greenland, there is only one anadromous Atlantic salmon population. In other words, the feeding area does not actually support any wild populations of Atlantic salmon in its rivers. The Faeroe Islands has none. The Faeroe Islands do, however, have a 400,000 metric ton a year aquaculture industry.

Trends in Abundancy of European Atlantic Salmon
Since 1971, the earliest year for which we have numbers, there has been an overall declining trend in the North East Atlantic Commission area of the North Atlantic Salmon Conservation Organization, basically, Europe. The two and one sea winter fish are coming down. We have no evidence for a shift upwards in a regime that would be generating larger abundances of salmon over the next thirty years. However, you can further break this down into a southern group of salmon that will tend to migrate both to the Faeroes and over to West Greenland, versus a northern group that tend to congregate in the Faeroes. We can also look at the Southern European complex, with the

more abundant side being always the one sea winter fish. What you see is that it is the southern populations that is driving this downward decline. They are in trouble. However, while there is a long-term trend downwards, we still have millions of fish coming back into the European rivers. By contrast, the northern populations are fluctuating a little but they have stayed relatively stable.

North American Trends in Abundance

Coming back to the North American situation, again what we see is a long-term decline. We have had some fluctuations, and some big ones. We cannot explain the reasons why the recruitment would go up and down like that. Over a thirty year period, what we are looking at is a long, steady decline down to the point that we are well below the conservation limits that we think meet the minimum spawning escapement levels in the North American river systems. We are in trouble, and that trouble is evenly distributed. As we look at the map of the salmon rivers (next page), if you were to draw a line, anything above the Northern side is in relatively good shape. We are about at the levels of spawning conservation targets; some rivers are exceeding them and supporting relatively healthy fisheries. Everything below this is in a desperate status and it gets especially interesting when you deal with little zones like where the headwaters of the rivers that go this way mix with the headwaters of rivers that going down that way. Those are well above their conservation targets; down here we are in desperate trouble. They are sharing the same geographic areas, but showing very different population problems.

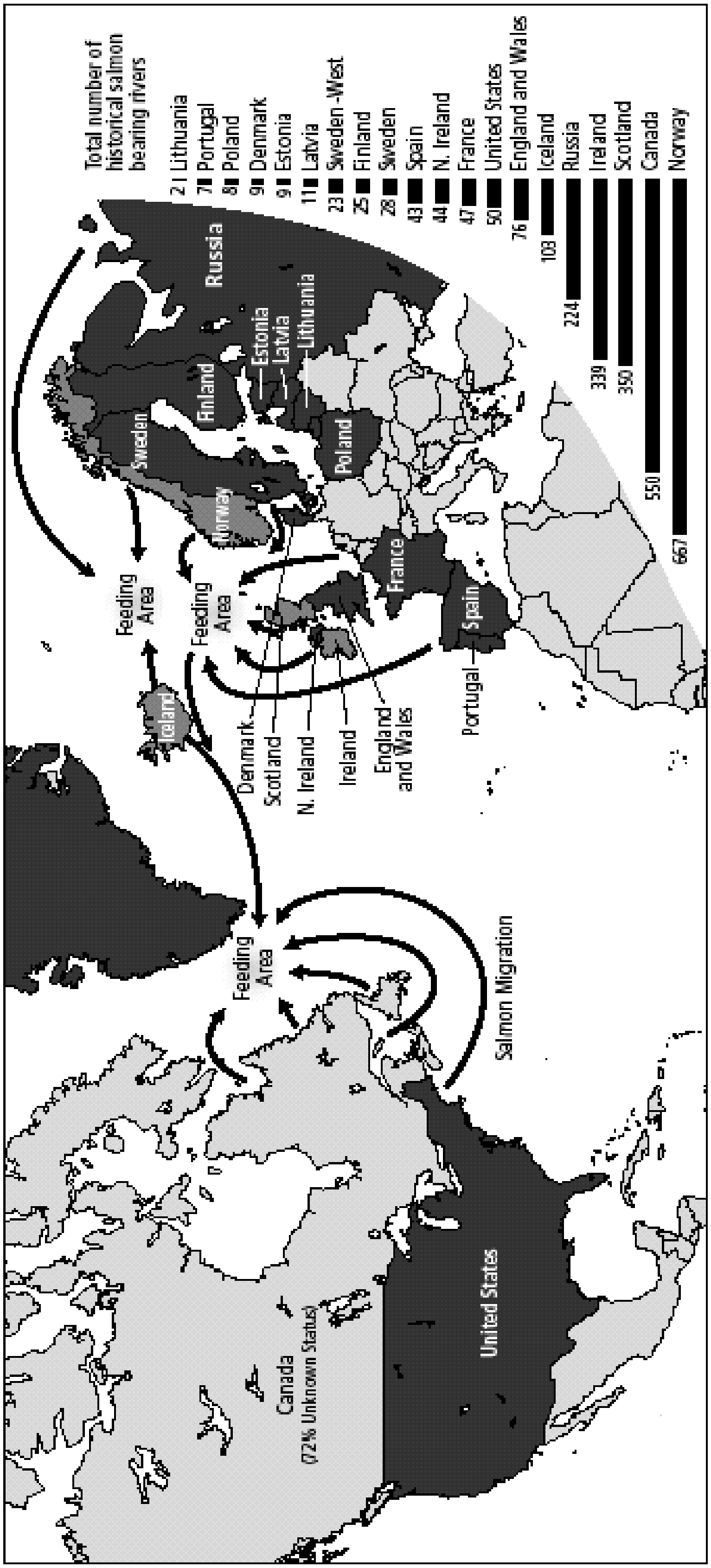
In terms of the threats, we have identified some fairly well. Looking along the coast of Nova Scotia we have a major acidity problem. Acid rain never really went away, it was just replaced by global warming, ozone and other environmental crises. We are now in the position where fish in a large numbers of these rivers are extinct, or broken into populations that, each spring during the snow melt period, are still getting pulses of acid coming into the salmon redds that are in the order of pH 3.5. We are talking about a major acid slug and until such time that the acid rain problem is taken care of, it is not going to get better.

Coming south of the border, into Maine, the US federal government in November of last year listed eight populations of Atlantic salmon as endangered under the ESA. These are believed to be the last remnants of the original wild stocks of Atlantic salmon. What we are looking at here are watersheds that have these endangered populations, most of them up to the north. There is another one, the Sheepscott, a small one called the Duck Trap, and a tributary of the Penobscott system; these populations are all down. We do not know what caused all the declines but they are the focus of a major recovery effort on the part of the United States government.

Bay of Fundy Stocks

The Bay of Fundy basically has two groups of salmon. If you were to draw a line across the Bay, the upper zone contains the Inner Bay of Fundy salmon populations. The two groups are different genetically and in terms of their life history characteristics and their migratory patterns. We basically believe that the fish, primarily one sea winter stock when it returns, does not really migrate very far from the Bay of Fundy. They come out of their rivers, stay in the Bay of Fundy, or may only go slightly offshore, and we have actually had some of them going south. We have had tag recaptures from places like Swampscott, Massachusetts, showing the fish moving south as opposed to heading north towards the normal feeding grounds. Those populations are in desperate trouble. The Committee On the Status of Endangered Wildlife In Canada (COSEWIC) last month listed those 33 Inner Bay of Fundy populations as endangered. Trevor Goff and Patrick O’Reilly will be dealing with this in more detail (see p. 88). Meanwhile, there is this complex of rivers, the Western Fundy Rivers, and they are in similar desperate shape, they had a two-sea winter component. The only one we have a complete count for is the Magaguadavic River. Our counts there go back to the early 1980s, at which point we were dealing with about 900 to 1,000 fish per year. What we see is a decline to the point that in 2000 we were down to a grand total of 14 fish, of which only one was a female.

I am embarrassed to stand here in front of you and talk about effective population size. In terms of where we stand with Atlantic salmon right now, we know we are coping with a number of problems. We have acid rain, but we have on top of that things like poor marine survival. Our return rates, in the six rivers for which we have time series showing the number of smolts out and the rate at which the smolts come back, are almost an order of magnitude below what we see anywhere else or see in historic time periods for those rivers. In the rivers like the Magaguadavic, down in that danger zone, the return rate for smolts was 0.1%. With those kinds of rates we are not going to be bringing populations back in any sort of quick way.



Map showing the wild Atlantic salmon's range in 2000 and its known migration routes. Aggregated categorization data on a country-by-country basis as reported in this study is also shown.

Causes of Decline
We have 63 officially sanctioned DFO hypotheses as to what is causing the decline of Atlantic salmon, and we do not have enough information to dismiss any one of those. In the meantime, our immediate future is all about live gene banks. However, our reality is that, as we moved into this conservation crisis in this zone, the response of the DFO was to close eight of its federal hatcheries in the region. The rationale behind it was that there was no conservation reason to keep these hatcheries open. It went something like this:

> *"You look at the Nova Scotia coast; we have an acid rain problem. If we put fish back into those rivers, there is no chance that they are going to survive and really the only reason we are doing that is to prop up the sport fishery,* ergo, *this is not really about conservation, because we have no chance of ever establishing a sustainable population. It is really about maintaining the sports fishery. Really the users should be paying for and running those hatcheries, so we are going to get out of the hatchery program, and we will close them all down."*

Actually, the ninth hatchery that still existed there was put in as a mitigation measure for a large hydroelectric dam on the Saint John River system, and they wanted to close that one, too. It was only under threat of a lawsuit that that one remains in operation. In the meantime, down in Maine, where the Endangered Species process is underway, there are hatchery support programs that have been *developed* in order to prop up those rivers. However, the Maine State government is vehemently opposed to the listing of Atlantic salmon in Maine as an 'endangered' species, to the point that they are actually bringing forth a court challenge. This is the first time an endangered species listing has ever been attacked in the courts, with an attempt to overturn it.

Review of Hatcheries in Maine
As that is happening, two other things have come along, including a $500,000 allocation to the National Sciences Foundation to conduct a review of the status listing of the salmon in Maine, especially the impacts of the hatchery program upon the fish that are in the river. There have been accusations that the hatchery program has been poorly managed, and has created a "mongrel" fish that really represents nothing about the wild salmon that used to exist in those areas. The hope is that the National Sciences Foundation review will somehow sort that one out. In case it does not, the governor of Maine is trying to get another review done by another institution. So there will be two separate reviews of the hatchery systems proceeding at the same time with no coordination, all in order to come up with an answer as to what the hatcheries are doing. In the meantime, we are praying for an upturn; we are looking for an ocean regime shift. The Magaguadavic estimate for wild smolts this year may be in the order of 200, even with a 10–15% return rate. We are not talking about something that is going to rapidly rebuild these populations.

Discussion

A participant commented: You mentioned that government wanted to have users pay for those facilities. Did they do so? And where they did, were they unsuccessful, and is that why they are closed?

Fred Whoriskey responded that the hatcheries had been privatized and two of them went bankrupt, and have since been reabsorbed by the DFO. One of them is now primarily cultivating sturgeon, and one is the property of the University of PEI, which is using it for research purposes and not for things like live gene bank programs.

Genetic Analyses of Broodstock, and the Development of a Mating Plan to Minimize Inbreeding and Loss of Genetic Variation in Inner Bay of Fundy Atlantic Salmon

Patrick O'Reilly, Fisheries and Oceans Canada, Atlantic Region

What I hope to get out of this presentation is feedback from you, what we are doing right, what we are doing wrong. Some of the participants in our program are involved in three different technical groups: the hatchery, genetics, and monitoring groups. Many of these people are providing their time free of charge. Peter Amiro from DFO is in charge of the monitoring group. Shane O'Neil and Trevor Goff are chairs of the hatcheries group, Ellen Kenchington from DFO chairs the genetics technical group, and Roger Doyle was responsible for coming up with the mating plan that I will be describing.

The Inner Bay of Fundy is between Nova Scotia, Maine and New Brunswick. It is comprised of approximately 30 to 35 rivers, depending on who you are talking to (Figure 1). The rivers shown in solid lines still have salmon. The rivers in hatched lines are now devoid of salmon. Fred Whoriskey mentioned some of the things that make the Inner Bay of Fundy salmon unique. They have different migratory patterns. Instead of moving off to Greenland, they hang around the Inner Bay. In addition, the Inner Bay has some of the highest tides of anywhere in the world and so there are extremely strong currents, and all sorts of possibilities for there being unique adaptations in salmon from this region. There have also been several studies on the genetics of salmon in this region, including by Eric Verspoor. Verspoor has looked at the mitochondrial DNA of fish from the Inner Bay of Fundy, fish from other areas of New Brunswick, Nova Scotia and Newfoundland, and he has found one mitochondrial clade that is very common in Inner Bay of Fundy fish, and very rare outside the Inner Bay of Fundy.

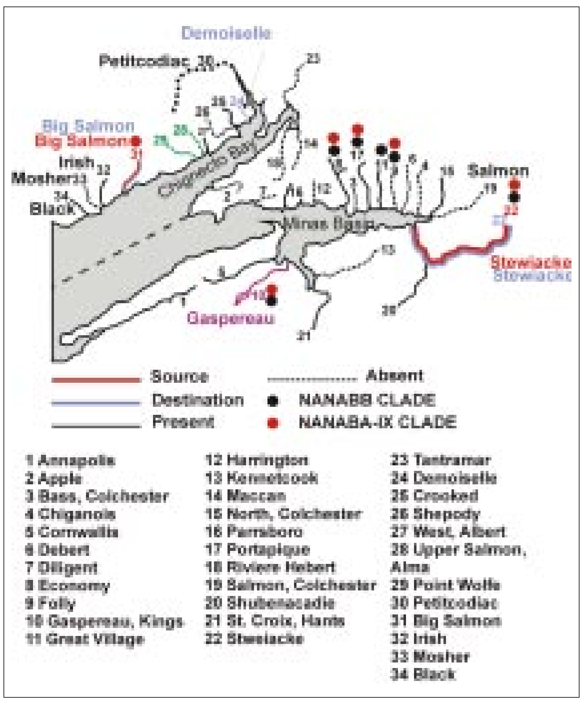


Figure 1. Inner Bay of Fundy

Tim King has also recently published a paper based on twelve microsatellite loci, showing the Inner Bay of Fundy salmon to be genetically distinct as well. There are several reasons for this group of 30 or so rivers to be fairly distinct. Again, salmon in half of the rivers are extinct. Of the remaining rivers, there are very few adults returning, and we think that next year, or the year after, we might not be able to find any parr in those rivers. We think that not too long ago there were 40,000 adult salmon returning to the Inner Bay. Last year we maybe had 200 adult salmon. The last information that I want to mention is that the return rate of smolts is approximately 1 in 1,000, so basically, that means that salmon that leave these rivers are not making it back.

The Inner Bay of Fundy Gene Banking Program

The overall goals of the Inner Bay of Fundy program are, simply, recovery and restoration, and then we plan on getting out of the picture. The specific objectives of the Inner Bay of Fundy gene-banking initiative are to minimize inbreeding, accidental loss of variation, and domestication selection, and to facilitate ongoing kinship and inbreeding analyses, and research into some of the more likely causes of decline in the Inner Bay of Fundy.

I am going to describe some of the details of the Inner Bay of Fundy gene-banking program. Again, our idea is to get feedback from you as to what you think of our overall design. First, there is an ongoing search for and collection of wild parr. We then transport the parr to the hatchery and rearing facilities, and conduct ongoing rearing of previous parr and repeat spawning adults, tissue sampling of new parr, laboratory analyses, DNA extraction of PCr and allele scoring, etc. Then we undertake a rigorous analysis of genetic information. We incorporate multiple redundant samples into our genetic analyses, to check accuracy. We then conduct a maximum likelihood mark chain method devised by Herbringer and Smith, which is being published in *Genetics* this year.

We use molecular genetic information for reconstructing family groups, full-siblings, half-siblings and cousins, primarily for implementing the gene-banking program, but also for estimating relatedness using Ritland's MME estimators of pairwise relatedness and allele sharing methods. We use the information from different analyses to check the accuracy of allele scoring methods. If we find errors we loop back to an earlier step, and if we do not, we continue on. We also compare and contrast the different methods and if they are in concurrence, we proceed. If not, we loop to the previous step or further to where analysis began. We then devise a mating strategy based on mean kin-ness, gender, spawning state and so on, making allowances for possible poor survival of certain crosses, so we will keep a couple of individuals from both the family lineages and cross those. Again, we try to avoid crosses between individuals with high and low mean kin-ness values, and I will confirm that the strategy makes sense. All the analyses I have mentioned take a great deal of time and three or four different people working on them. We do that and then consider the possibility of getting additional information and then we reconduct all of the analyses. The reason why we do this is because we want to have a backup mating plan. We will try to devise a mating program based on the latest available information, the last spawners to come in, information on mortality, spawning status, and so on.

Then we return a subset of each of the families (50-100), enough to account for mortality and sex bias, as next generation broodstock. We also keep individuals in the river as brood stock. We retain the offspring from the matings in the hatchery as briefly as possible, and then we return them to the wild as eggs and unfed fry as part of the initial restoration efforts and the live in-river gene-banking component. We retain some of the first time spawners for one more round of mating, and retain the repeat spawning salmon until the following fall. Just before spawning season we release them and hope that they will go up the river, as opposed to straying. We then monitor the program to gauge success. We look at in-river survival of offspring of the hatchery crossed salmon, based on the location of release and captures and genetics. The possibilities are that we could be looking at salmon from our hatchery crosses, salmon from third matings that are mating in the wild, progeny of any possible wild remaining adult of non-native farmed salmon and non-native wild salmon. We are gauging, again, the success of the program, so we want to identify that we are looking at progeny from our hatchery cross versus something else. We also monitor for genetic variation, look for changes in individual and population inbreeding coefficients, check for domestication selection, look at quantitative traits over time, and monitor adult return and test the origin of parr. We want to find out whether the adults that are returning are from the wild or wild crosses or from our hatchery crosses.

Research in the Gene Banking Program

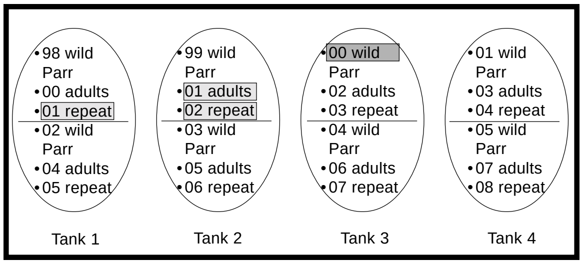
Some of the research we are conducting through the program is to assess the numbers or density hypothesis. Some people believe we need a certain number of salmon out there, possibly to form schools or overwhelm predators, or provide salmon for something. There is an ongoing project called the Salar Marine Acoustic Program (MAP) project which is being conducted right now to identify the time and location of at-sea mortality, and to provide numbers for the at-sea Inner Bay of Fundy capture studies where they are seining areas of the Inner Bay of Fundy and trying to recover smolts and assess condition and so on, and then assessment for between-family differences in fresh water survival. And then we again assess survival of non-native gene-bank salmon from different source locations and in various Inner Bay of Fundy Rivers currently unoccupied.

Gene Bank Operations and Strategy

Figure 2 shows a schematic of the mating strategy. We like to think of it as two different gene banks, a hatchery gene bank and an in-river gene bank. Basically, what we do is to capture fish from the river, and then put them into a hatchery. We have 1998 wild parr in tank 1, 1999 wild parr in tank 2, parr we have captured in the year 2000 in tank 3, and so on. These individuals were spawned in the year 2000; the 1998 wild parr and offspring were placed into the river as six-week old fry, fall fingerlings and smolts. In the future we are planning on placing only unfed fry back into the river. The 1999 wild parr will be spawned this year, 2001, then offspring will be placed into the river, and so on. By the year 2002, all 1998 wild parr, the adults, and repeat spawners, will be gone. Then we will be replacing those with parr collected from the wild in 2002. And then this cycle will repeat itself, so we should be able to maintain the gene bank with just these four tanks (Figure 2).

What could happen if, for example, we bring disease into the hatchery, inadvertently, in the year 2000? The hatchery is a closed system, and if we do find disease in wild parr and bring it in and see traces of that disease somewhere in the year 2000 and 2001, we still have repeat spawners from 1998 and adults and repeat spawners from 1999 to recover the population. Similarly, if something catastrophic happens in the hatchery we still have the in-river live gene bank. So we are trying to put our eggs into two baskets so to speak.

The other thing I wanted to mention is that in the year 2002 we will be collecting wild parr from the river and these are probably descendants from our earlier hatchery efforts. We will also have the 50-100 individuals that we have returned from each of the family crosses. Whenever possible we will be taking wild parr from those families and we will be using genetic information to do this, from specific families. If, however, we do not find any of those families present in the wild parr we bring in, we will resort to the hatchery parr that we have retained from each of these families. So, we are going to opt first of all for those fish that are kept in the in-river live gene bank. But, if we do not find those, then we will resort to the hatchery families.



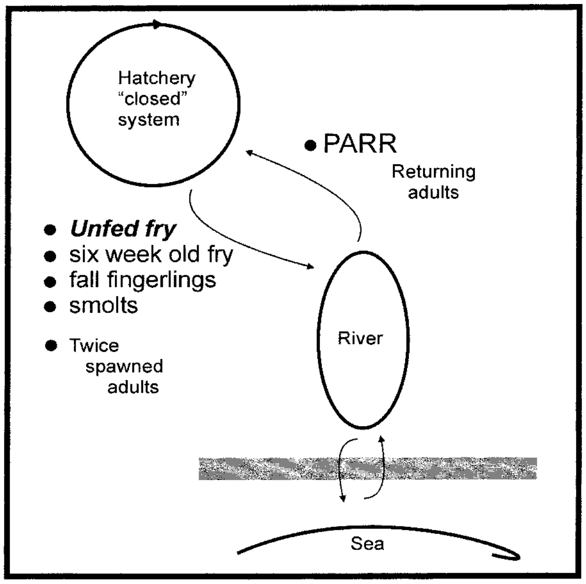


Figure 2. Schematic of Mating Strategy

Mean Kinship MK

$$MKi = \frac{\sum_{j=1}^{N} fij}{N}$$

where...

N = number of living animals in the population

fij = kinship coefficient, or the probability that alleles drawn at random from each of two individuals (i and j) are identical by descent (Falconer, 1981)

The mean kinship of individual i (MKi) is defined as the average of the kinship coefficients between that individual and all living individuals including itself.

Figure 3. Mean Kinship Formula

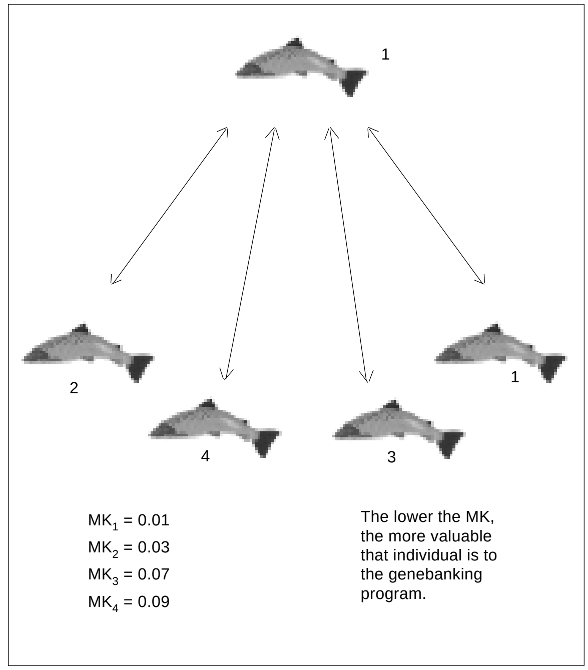
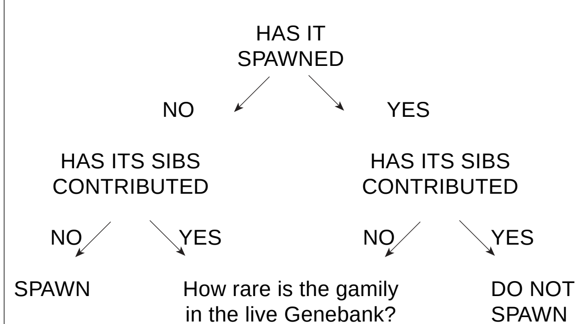


Figure 4. Mean kinship

Inner Bay of Fundy Mating Strategy



If rare ... SPAWN

If common ... DO NOT SPAWN

Rarity is based on Mean Kinship ascertained by (1) kinship analyses according to Smith and Herbinger (Genertics, in press) and Ritland's MME estimator of relatedness

FISH ID.	MEAN KINSHIP
1	0.01
2	0.01
3	0.02
4	0.02
5	0.04
→ :	:
386	0.18

FISH ID™	GREEN LIST ¢	YELLOW LIST ¢	ORANGE LIST ¢	RED LIST ¢
12	7,22,89	63,66	119,198	201
26	3,42,53	75,79	122,188	201
28	17,51,99	93,166	95,155	201
34	53,93,101	64	188	201
76	33,72,88	18,122		201
:				
359				

Figure 5. Inner Bay of Fundy mating strategy

We originally wanted to base the mating scheme or strategy on mean kin-ness, which is being done with most species, if you take a look at the literature (Figure 3). This strategy is designed to minimize the loss of genetic variation and avoid inbreeding. However, when you take a look at what is going on in a hatchery, we found that basing a system completely on this was unreasonable. With Tamarinds or Tigers, they give an individual population a mean kinship value based on pedigree information, and then they rank them all 1, 2, whatever, and then they try to cross individuals based on that mean value, shying away from crossing individuals with very high and very low mean kin-ness values, but generally avoiding individuals with high mean kinships values (Figure 4). After they take two individuals, they recalculate the mean kinship and then choose two more individuals, recalculate kinship for all the individuals they have not chosen, and then select two more. We found this was not feasible in a hatchery. You have hundreds of individuals, all with specific tags. Imagine yourself in a situation where you grab one fish, and then look at a list that tells you that individual would have to be mated with female number 432. You could possibly find that fish, but it may take you a half an hour to an hour. Then you have to do that again with another hundred crosses. Instead, we developed the following strategy.

The mating strategy is basically as follows. First we take a fish, and check if it has spawned (Figure 5). If it has not, we look at a chart and determine if its siblings have contributed. If none have, we spawn that fish. If the siblings have contributed we then look at how rare that family is in the live gene bank. If it is rare the fish is spawned, and if common, we do not spawn. We determine if it is rare or not based on mean kinship values. We then have a fish in hand, a female for example, and we refer to the mean kinship list, and look at the value. Is it high or is it low? We have another list, the green, yellow, red and orange list. What you do is look at the next male you grab, determine whether its mean kinship was high or low, and whether it was a green list individual, meaning it was unrelated, yellow list individual meaning it was related but more distantly, then orange, then red, with red referring to something that was not a native individual. We are also screening individuals for non-native status, and for farm fish as well. So depending on the green, yellow, orange or red list status, we decide whether or not to cross that individual male with the female we picked up first of all. But, just to continue through the flow chart, if the individual has spawned, you ask if its siblings have contributed. If no, again you assess how rare the family is in the gene bank and then continue on. If its siblings have contributed, then we do not spawn that individual. The plan must be continuously updated based on the availability of genotypes and returning adults from the wild, spawning condition, and so on, so we have very little time between when all these calculations are made, and when the spawning starts. The gender of salmon is not known until late summer, early fall.

Addressing Concerns About the Gene-Banking Program

There are some concerns that have been expressed about the program. One is that we are interfering with the salmon and they are better off on their own. I do not believe this to be the case. Based on the numbers, Atlantic salmon in the Inner Bay of Fundy will be gone without some intervention. The program is not natural. The stated goal is to equalize family representation, and that does not go on in nature. Some lineages are rare, some are common in the wild. We are bringing all the rare ones up in frequency so that we can avoid them due to small sample size and random effects. The idea is that we want to maintain these families and release them into the wild again. At least there is original genetic variation upon which selection can act. If we take the alternative strategy and do what some people want us to do, which is to maintain these lineages more or less in the proportions they occur in the wild, we run a greater risk of losing those rare lineages.

Some people are saying that of course there may be two alternating strategies within the Bay of Fundy; that is, some fish actually do go to Greenland and some fish do not, and by instituting a gene-banking program, we may be interfering with that pattern. Disease in the hatchery could also wipe out the remaining salmon. We are trying to mitigate that by having an in-river and an in-hatchery program. For domestication selection, what we are trying to do is to get these fish out as soon as possible as unfed fry into the river system so that they will experience the least domestication selection. We are also going to try to avoid any acceleration type programs, trying to extend, if possible, the generation time.

Ignoring possible local adaptations in the river is one other concern. There could be differences between drainages and we are bringing them all into one gene bank. Again, I do not see how we could get around that. I guess the only possible solution is to try to encompass as much as possible of the original family lineage as is present in the population, put them back in the wild when conditions in the ocean recover, and hopefully let nature sort it out.

Research Opportunities
I just want to say something about the possible research opportunities in the Inner Bay of Fundy associated with the implementation of the live gene bank program. First, we have the opportunity to compare the survival of the fall of year one to the fall of year two salmon put out as eyed eggs, unfed fry, six-week fry, and parr. This gets at the idea of consequences of domestication, both environmental and genetic, and compares survival in the wild of the offspring of full sibling crosses, half sibling crosses, crosses of unrelated individuals, F1 of farmed fish, F4 of farmed fish, F4 wild farm and F1 hatchery fish. We are in a unique position in that we have representatives from all these groups from the same river so we can conduct the experiments within a source population. In addition, we can do studies on freshwater survival on salmon from neighbouring source versus salmon from geographically distant rivers still within the Inner Bay, with similar habitat indices and destination rivers. We can get at several issues including possibly out-breeding depression, and ultimately, if marine survival improves, investigating fitness of different phenotypes, and life history strategies.

These are some of the unique characteristics of the Inner Bay of Fundy relevant to conducting research. We have the availability of efficient genotyping methods based on tetranucleotide microsatellites developed by Eric Verspoor and others. We have the ability to use hatchery resources as a part of the live gene-banking program. Because of the high at-sea mortality, and the availability of vacant freshwater habitats that are suitable for salmon research, we have a need for information on which stocks might be suitable for which rivers. We have low at-sea survival, further decreasing the risk of non-native salmon straying into adjoining rivers still supporting remnant salmon populations. We have the availability of farmed native hatchery salmon from the same river and a growing genetic database of Inner Bay of Fundy offspring or their parents on which to conduct all sorts of studies down the road.

Trevor Goff, Mactaquac Biodiversity, Fisheries and Oceans Canada

An Overview of Salmon Hatcheries in New Brunswick
This is a brief overview of hatchery facilities in which we are doing the live gene bank program that Patrick just described to you for the Inner Bay of Fundy stocks. There are two rivers being live gene banked. The two major rivers of the 32 to 33 rivers in the Inner Bay are the Big Salmon River in New Brunswick and the Stewiacke River in Nova Scotia (see Figure 1, p. 89). Those were historically the two most productive rivers in the region, if you do not include the biggest one, which is the Petitcodiac, which has been destroyed for many years because of a causeway built at the mouth of the river. Some people are now trying to have the causeway removed and replaced by a bridge to restore the river to its original condition. Historically, the Petitcodiac was the largest salmon-producing river in the Inner Bay of Fundy, and in the late 1800s and early 1900s it used to contribute as much salmon as the Restigouche River. The Restigouche is one of the largest rivers in New Brunswick. The two rivers, the Stewiacke and the Big River, up until the mid-1980s, had anywhere from to 2,000 to 4,000 adult salmon returning. They were meeting their spawning escapement targets, and the collapse happened very rapidly from the late 1980s through the 1990s. These rivers have completely collapsed now with maybe 200 adults left.

Last year, in 30 rivers there were insufficient adult fish coming back to even consider collecting wild brood stock; at the adult stage, you would have too few parents to really do an effective program. So we went into the rivers and collected juveniles before the last of the juveniles disappeared. Basically what is happening is that the smolts go out, and one in 1,000 come back. Last year in the Stewiacke, a major producing river, all 37 electro-fishing sites, which always produced normal densities of juveniles, were vacant of fry. No young of the year were seen; no zero plus parr were seen in more than 30 sites. There are still a few 1 and 2+ parr left in that river. The Big Salmon River is in the same situation, so in 1998, 1999, 2000 we collected wild parr and we have about 900 fish in total in the living gene bank in New Brunswick.

We have the same number for the Stewiacke River in Nova Scotia at a DFO hatchery. The private sector operator could not afford to keep this hatchery running, because all fisheries were closed and no one was willing to put money into running a facility if there was no opportunity to fish. DFO recovered two of these facilities for live gene banking for biodiversity. One of them is currently, for research reasons, rearing the Atlantic whitefish, which is another fish listed under the COSEWIC endangered status. The Mactaquac Hydro Electric dam was built in 1968, and the hatchery, at which we are doing the live gene banking, was built to compensate for the dam.

The St. John River is one of the largest in Canada. It drains Quebec and Maine. The head pond behind the dam inundated 100 kilometers of salmon habitat. When DFO permitted New Brunswick Power to go ahead with that development they forced them to pay the capital construction of the hatchery as compensation. The hatchery was designed to rear smolts downstream, in compensation for the loss of the smolts from the lost river habitat, and also for the approximately 50% turbine mortality that occurs for wild smolts migrating through. There are actually three dams in the system, but this is by far the largest one. We use the waste heat from the dam in an accelerated rearing facility. The water is pumped up to a filter building and it flows by gravity to an early rearing facility to maximize fish husbandry quality for juveniles. This enables us to produce a one-year smolt which significantly reduces operating costs.

There is a blind fishway on the dam and it is about 90 to 95% effective for upstream fish passage. The adults come in live, and are transported two kilometers downriver into the sorting building. Every fish that goes upriver is sorted, and we do an assessment on the run for our assessment biologists. One of every five fish is scale sampled, and biological data is collected on every fish, whether it is hatchery or wild. The run right now is typically 3,000 to 5,000, which is severely depressed. In 1980 there were 27,000 fish. The greatest concern is the wild component of the run. Most of the wild fish originate three dams up, and are subject to 50% cumulative smolt mortality through three power facilities. The production out of this facility is about 300,000 one-year smolts a year and about an equivalent number of fall parr, which are released in the headwater habitat.

Operations at the Mactaquac Gene Bank Facility

The first parr and smolts arrived at Mactaquac in 1998. They were held at the St. John hatchery over winter. At that point we had to decide where we were going to rear them. A decision was made to bring them to our facility. The facility that they were in had a problem and it was not suitable for long-term rearing. It was on a town water supply but frequently there was leakage of chlorine from an aging pipeline and there was a risk that the entire group of parr could be wiped out by a chlorine spill. The fish were transported to Mactaquac where we are rearing them on groundwater. We have five very large wells and are sitting on an aquifer, as we are basically on the floodplain. We have 4,000 gallons per minute of groundwater pumped by 100 to 200 horsepower pumps. Unfortunately our power bill is $100,000 per year. When they negotiated for the dam, DFO did not ask for free power. They would have been given it, but in 1968 power was so cheap (the oil embargo did not happen until 1973) and no one ever considered that power would be a problem.

As said, the parr were collected in 1998 but transported to Mactaquac in the spring of 1999. Most of them were at the smolt stage, though some were not large enough to be smolts, about 30 grams. The temperature of the water in the winter ranges from 6-9^{o}C , and in the summer ranges from 9-14^{o}C. The overall range for rearing these fish is about 6-14^{o}C. They grow very rapidly. In July of 2000, these fish would have spawned. The average size of the fish at spawn is about 56 cm, which is quite typical for a one-sea winter grilse. We managed to get these fish reared completely in fresh water to a size similar to what a wild and sea winter fish would be. Tissue samples were taken, put in 95% ethanol and DNA analysis was performed. The technique that Eric Verspoor uses has been transferred to the Dalhousie University gene probe lab. These fish have to be tagged after a DNA sample has been taken. We have an external tag and we also inject a PIT tag, so that every fish has two tags in case it loses one. Otherwise when it comes to spawn we would not know which fish was which.

The 1998 and 1999 wild parr were in a pond. The 1998 wild parr, smolts in 1999, were spawned in the year 2000. Some 1998 wild parr will be spawned for the second time in the year 2001. Not all the fish mature the first year. Inner Bay stocks tend to be one-sea winter spawners, but there is a small component of two sea-winter fish, possibly a survival mechanism. If there is one of the marine regime shifts, maybe it favours long distance migration because something has gone seriously wrong at the Bay. Maybe that favours those fish that leave the Bay in terms of their survival. It is probably important to protect both, and not change the selection for either all one-sea winter spawners or all two-sea winter spawners. That mix is probably important to the ecology, the migration and the long-term survival of the fish.

When we spawned these fish the first time, not all spawned successfully in the year 2000. The fish that did spawn will be spawned the second time in 2001. The fish that did not will be spawned for the first time in the year 2001 and then those fish will be spawned the second time in 2002. Our objective is to spawn each fish twice in the gene bank. At that point these fish will be released to spawn in the wild. We are selecting the mates by DNA analysis. We are not mating brothers and sisters and we are avoiding mating siblings. Last year we mated no siblings and no cousins. All the matings were good matings based upon the DNA analysis, so this year we will have the second year class of parr. They were smolts in 2000, which means the first spawners will be in 2001. Those fish will be spawned the second time in 2002, some for the first time, and then the second sea winter fish will be spawned the second time in 2003. The one-sea winter fish will have been spawned twice and they would be released at this point. Only the two-sea winter fish (two years in fresh water) would be released after the second spawning. We estimate that we will have about 2.5 million eggs per year through this process, which we estimate will yield about 1.8 million fry. We are stocking most of the progeny of the live gene bank as unfed fry to avoid problems of domestication selection in the hatchery. But with the marine survival right now, all we expect to get out of the 2.5 million eggs is maybe 18 to 36 returning adults. This is not a recovery. Until there is a marine shift, or something changes in the marine environment, or we identify a man-caused problem, or a combination of both, all we can do is keep this stock alive. We cannot realistically do anything about the recovery until there is a change in the marine survival.

The parr come in initially into tanks and spend one year there, and then they are transferred. This fall we will be bringing in the 2001 parr. Their ultimate destination is one of the ponds, but they will initially come into the tanks first, and then a year later will go into a large pond. Eventually the process repeats. Fish go here in 2003. This pond will become available for the 2002 parr. Remember that the 2002 parr will first go into the tanks and spend a year there, so the 2002 parr won't actually go into the pond until 2003, the fall of 2003, and then this pond will be available.

By preference we are stocking unfed fry so that we bring family groups back into the hatchery. We would prefer to get those from the river in the fall so they would be coming from the live gene bank in the river and also any wild fish, if we can get any. And the DNA typing will tell us if we have a new family or new material. By taking the farm fish from the river we are hoping to minimize domestication selection. If they are not available from the river then the in-house gene bank is the backup.

Discussion

A participant asked: Is there an acid rain problem in the rivers?

Trevor Goff responded that this problem is in the Southern Uplands, not in the Inner Bay of Fundy.

Another question was posed: Why are you using fry, rather than holding to smolts, given the seriousness of the problem of abundance? It seems to me that you will get a quicker response from smolts.

Trevor Goff replied that the long-term plan is to go to fry when they have a large number of fry. Then they could literally saturate the habitat with what would be normal escapement numbers of eggs. They would then be putting the juveniles in early, but at a density that would be normal if the right number of wild adults had spawned. In the short-term, there have been very small numbers of fish. He explained how they put the first fry out this spring, about 200,000, and are retagging some of those fish to go out as six-week fry. Some are going out as fall parr, at 12 centimeters, and some are being kept for smolts.

Patrick O'Reilly mentioned the Salar MAP program. The Atlantic Salmon Federation has been the driving force behind this program. They are putting pinger tags inside the smolts and tracking their migration through the Bay of Fundy. The batteries will last four to eight months. They put these pinger tags on four different stocks this year in the Bay and they also have one DFO Coast Guard ship, a 150 ft. vessel, that has a Norwegian trawl that is catching live smolts at sea, to look for sea lice and disease problems. There is a lot of research in this Salar MAP program trying to find out what is happening to these fish in the ocean.

It is not enough to just keep some alive in the river. They want to address the research issues and try to find out what is happening to fish in the marine environment. There is room for smolts in the program too. They need fish for research. This year, Dr. Gilles Lacroix, who is conducting the Salar MAP study out of St. Andrews, is probably catching the last wild smolts to leave the Big Salmon River. This is the last year he can put these tags on wild fish, and that is important because, as has been pointed out, wild fish behave differently from hatchery fish. Even with hatchery fish that have been reared under the most hatchery-reformed environment, there will still be morphological and behavioural differences.

It was important to try to get some of the tags on hatchery fish and that was done last spring. In the future, research is likely going to depend on either smolts that are reared in hatcheries, or the progeny that are released in the river. Maybe they can be captured at the smolt stage. There are a lot of smolt wheels in New Brunswick these days catching wild smolts for assessment purposes.

The question was asked: Is there enough primary production in the rivers to support increased production of the fry when they are put into the rivers?

Trevor Goff responded that they are not going to look for increased production of fry; there are no wild fry left in these rivers, they are absent in most of them. What they try to do is to put the fry back in these rivers that had electro-fish sites on them because there is historical assessment data on these rivers. They know what the normal fry levels were, and are not trying to go beyond that, but are trying to put the fish back.

The participant added: Has primary productivity been affected because of the non-return of adults that would decrease the primary productivity?

Trevor Goff responded that Atlantic salmon multiple spawn and do not necessarily die after spawning, so there is no nutrient transfer from the ocean to fresh water.

The dialogue continued:

Is that still not a problem?

We never had that nutrient transfer.

Would it be a problem though?

The rivers, where the collapses have occurred, have had no change in freshwater habitat that can be identified. So some people have said, "How do you know it is a marine problem, maybe it is a freshwater problem?" There was an instance a few years ago where smolts came from Big Salmon River wild stock. They were cage-reared in a cooperative project with an aquaculture company and then these cage-reared fish were released as adults to spawn in the Big Salmon River. There were pulses of fry and parr. This demonstrated that the habitat was fully productive. If you put eggs in there, in this case it was done through adults, you would get juveniles in the subsequent year classes. Again, these went to sea and nothing came back.

The question was asked: You are raising fish, but what are you feeding them?

Trevor Goff replied that they are captured as wild parr. Initially they are fed on a mixture of dry food and freeze-dried krill. There are two species of different sizes so there is size variation for the different-sized parr. These parr have never seen a krill before but they look like insects and they are orange and they go for them. The krill are freeze-dried and can be stored at room temperature, but they are certainly not nutritional. They do not want to keep them on krill at $169 per kg, so instead they are fed a mixture of krill and dried food, where they gradually reduce the proportion of krill. There has been a 74% survival to the eyed stage, which is better than some of the wild one-sea winter fish. He noted that they do not think there is a nutritional problem.

The point the participant was wanting to make is that there is a potential conduit for increasing contaminants in the fish as you are rearing them as a consequence of using that kind of feed.

Trevor Goff replied that his understanding is that the feed they are using is not high in contaminants.

The dialogue continued:

Have they been tested?

The manufacturer has said they do not have those levels. He understood that in the Suzuki study on contaminants in fish feed most of the diets they looked at were European ones.

The participant stated that the diets that were studied were locally produced in British Columbia.

Trevor Goff stated that their manufacturer uses local maritime herring.

It was suggested that Trevor Goff should test the food.

Mr. Goff responded by saying that it is a good point. They certainly do not want to be adding contaminants, when they already have a mortality problem.

The participant noted that the potential exists for increasing the contaminant loads in these fish. If this occurs it will be passed on to the fry through the egg.

A participant inquired: Why is the turbine problem not being addressed while you are spending all this money on the hatchery program?

Trevor Goff replied that the St. John River is a different issue. They have about 4,000 to 5,000 coming back. Historically, the majority of these would have been wild fish. The hatchery component was typically only 25 to 30% of the run. The scary thing that has happened in recent years is that they have had an increasing proportion of hatchery fish in the run and a decreasing proportion of wild fish. The wild fish have the most difficult situation because the principal spawning habitat of the St. John River is the Tobique River; it is about a six-hour drive from the dam to the headwaters of the Tobique River. That is about 60% of the spawning-nursery habitat for salmon. Unfortunately, there are three dams downstream of the Tobique. The mortality at the Tobique Narrows dam is about 19%, at the Beechwood dam about 15%, and at the Mactaquac it is around 15%. If you add those up for Tobique-origin fish, you get a cumulative mortality of about 50%. That is direct mortality from the turbines; there is also indirect mortality. Many of these fish spend two to three weeks trying to find their way around the dam, and eventually go through the turbine. They end up at Mactaquac, and are referred to as "slinks," as they have no body fat left. They are emaciated, are all fins, and their bodies are pathetically thin. Even if these fish get into the seawater, they have no body reserves left. If marine environment conditions are unfavourable, then these poor fish have two or three strikes against them, even before they get to the estuary.

Even in the best upstream facilities, 85 to 90% passage is all you are going to get. Downstream is hit or miss. Sometimes it works fairly well, sometimes it does not work at all. What works in one system sometimes does not work in another, even when similar. But it is certainly a developing area of technology and things are evolving. Engineers and biologists are working on the problem. There is a committee being struck for the St. John River which would like to invite an expert from the west coast on downstream fish passage, and also one from the east coast. They hope that the committee will make a recommendation for a downstream fish passage facility. The power company has indicated an interest in participating. There is hope in the next few years that they will have some form of downstream fish passage at the most important dam for the wild fish, Tobique Narrows, and then build on that. They would eventually like to have downstream fish passage facilities at all three dams.

A participant commented that three sources of fish were mentioned in the living gene bank program, wild, hatchery and farmed fish, and asked: How is that going to be used?

Patrick O'Reilly replied that one of the potential threats to Inner Bay of Fundy salmon, especially as populations decline, is genetic introgression and ecological interactions with farmed fish. There are many fish farms in the Inner Bay of Fundy and some of these farm fish are making it into the rivers and potentially spawning. An idea would be to set up crosses between wild fish and farm fish, and farm fish and farm fish. Not all farm fish or hatchery fish are alike. One way you can distinguish them is the number of generations. It would be interesting to cross F1 farm fish, farm fish that have been in captivity one generation, and then farm fish in captivity for more generations, set up crosses between them and wild fish, and then look at the difference in survival and growth of offspring.

Trevor Goff added that what Patrick was proposing was a possible research experiment for a river that is completely devoid of fish, which would answer some of the questions about whether there is a reversal of domestication. It was a proposal for a research project; they are certainly not using farmed fish in their gene bank. In fact, the farm fish are being screened out; they are red-listed fish. Out of the 280-odd fish that were genetically screened last year, five of them were potentially of farm origin. It is done by an assignment list; St. John River stock is what is used in the aquaculture industry.

The question was asked: How do you deal with the equalization problem, particularly when you release them at different stages—fry, parr, and smolts? There are equalization issues all the way along. What was done with the surplus that did not match the equalization numbers?

Patrick O'Reilly replied that right now the program is really in its infancy. Equalization will come into play down the road. What is being done in captive rearing programs is for individuals with very low family representation or mean kinship values so that their family is relatively rare in the wild. They could be mated multiple times so that is the first thing you can do to bring up those lineages in the hatchery program. Then they would be released as unfed fry in the future, like the remaining family lineages. In a sense then after you release them there would be equal footing, but you will increase their contribution by increasing the number of crosses, either by increasing the number of crosses between individuals within these rare families, or by mating those individuals two or three times.

Rick Routledge expressed concern about the issue that Ted Perry raised earlier about using hatcheries to supplement a population that is dying out rather quickly, like the example from the East Coast. Some people feel, with some evidence, that they may be doing more harm than good by introducing hatcheries into these situations

A participant was concerned about the implications of the depression of the genetic pool, and the domestication of hatchery stocks. If the same level of concern exists in other enhancement opportunities such as sockeye or chum spawning channels, what are the issues related to channels and the genetic implications to channel production and enhancement, as well as the interactions of wild stocks and channel stocks?

Ian Fleming responded to Rick Routledge's question about when you begin using hatcheries in these populations that are declining. He noted that the question is really, when do we make that decision? He suggested that that is what we do not know, what we do not have enough information about. If you come in too early there may be detrimental effects on the population. If you come in too late, you may have missed the opportunity. So the real question is when do you make that decision? There is not very much research out there to actually address that. That should be one of the priority areas in terms of the use or application of conservation hatcheries.

Rick Routledge asked what kind of information is needed so that you can make those kind of decisions with more certainty?

Patrick O'Reilly replied that he thought a good place to start is to find out what the effective population size is, for the remaining population. Obviously if you have 12 individuals left and 8 are females, 4 are males, then you are starting a program with a very poor genetic base. There is a lower limit where it may be too late. Much below 25 or 30 individuals is maybe a little too late.

A participant commented: If you look back through the last 100 years, the gene pools have been pillaged, and the runs have been reduced. There has got to be a way that you can go back. The Alaskans have shown they are production-oriented. A case can be made for the coastal inlets, various places on the coast where that type of hatchery facility can be used. There is a place for aquaculture, salmon ranching, salmon farms, but there has to be a vision to realize what the potential is on this coast. You can talk about all the genetics, but not until you get a vision and create an action plan on how to achieve this within the next 10 or 15 years. DFO has abandoned the west coast in terms of the salmon fishery, and it is up to the coastal people to take things into their own hands and try to get that support back, to get support from Ottawa and get funding to restore the fishery. It is time to say that hatcheries have got a place for salmon ranching, or they have got a place for community development.

Ben Greene of Trout Unlimited stated that he is from Anchorage, and is speaking as an Alaskan who is not at all happy with what Alaskans are doing. There are two overlapping situations that have been talked about. There are situations in watersheds that have been either extirpated or are on their way to be extirpated. You are desperately trying to hold on, trying to do something to re-establish or hold on to anadromous salmon runs. Then you have the situation like Alaska where you have salmon runs which are still for the most part robust, healthy, high census numbers and yet you have data coming from several different fields suggesting there are risks, serious risks, involved with artificial propagation, culturing, sea ranching, of salmonids.

He noted that Jeff Hard's talk summarized a lot of data regarding the genetic risks of artificial propagation. There are theoretical studies and theoretical indicators, but there is very little empirical data. There is very compelling data suggesting a high likelihood that many human activities, including ocean ranching, potentially threaten wild salmon populations. And it is the wild gene pool that is the basis for everything.

There are two overlapping scenarios. If you have watersheds that have been depleted completely or nearly depleted, what do you do then? There are situations like Alaska, where it really is not broken, and his suggestion is do not fix it if it is not broken. You need to lay way off of the ocean ranching bandwagon before you ruin a situation that is still hanging on. If Dick Beamish's projections are right, what is good in British Columbia, may not be good in Alaska. If you are entering a new ocean regime in BC, then Alaska may have just entered what will be a 10, 15, or 20 year low productivity regime in the Northern Pacific, and massive large-scale ocean ranching is going to bring up a whole lot of issues, including ocean carrying capacity, and density dependent competition. You need to be careful.

A participant commented that they were not a fan of hatcheries and they would love to see it go back to the situation where we are dealing with strictly wild stock, but that is not going to happen. This is recognized in many of the south coast areas of the province. If you want to have stable numbers of fish and all the related social and economic benefits, then hatcheries are perhaps a necessary evil. In far too many areas the freshwater and estuary habitat has been degraded to the point where, despite all the restoration efforts, you are not going to get it back.

One example is the Thompson River. Over the past several years the exploitation rates on these stocks have declined dramatically. It is now down to 2 or 3% on those stocks of fish. They should have seen a response proportionate to the response from the West Coast Vancouver Island coho, but this has not happened. There is considerable scientific opinion that some of these stocks are endangered or at risk, even with no fishing at all. The option may be to risk some genetic manipulation of the gene pool or have no gene pool at all. Rather than debate whether hatcheries should exist or not, it should be determined how to make them more productive, cost effective, and less impacting on wild stocks. An example is the chinook hatchery at Robertson Creek that is pumping out millions of fry, and the cut-off at which no fishing is allowed is higher than the returns to that native system before the hatchery was built. There is a bottleneck there somewhere, probably in the estuary. We should be looking at things like marine net pen rearing so as to eliminate the competition in these bottleneck areas with the wild stocks and to rear the hatchery stocks to the optimum size for release into the marine environment. There are a lot of things that can be done to improve the situation in hatcheries; to suggest that we should just shut them down and let the wild stocks do their thing, is just not an option anymore.

Lee Blankenship responded to the comments of the last two speakers. Things are broken in a lot of cases, and are not going to come back. You have to utilize hatcheries and you have to utilize them in a better way. There has been a lot of focus on the risk, but we also have to focus on all the benefits. Genetic material, even to those who are scientists, is a very real benefit that can be gained from some of these intervention programs, as well as the social and economic benefits that scientists have a tough time recognizing. As scientists, you have to come up with some prescriptions for policy makers with respect to when to step in with these programs. There are intervention programs that have less impact, less risk, compared with gene banking. What is needed is to come together and identify those levels, when you get down to those levels, and when you should bring in supplementation. Gene banking is the last place you want to go, but you have to identify that too. You really need to focus on some prescriptions that can be used for policy makers, instead of scientists debating when to step in. They can use those prescriptions and come in at a more appropriate time.

A participant stated that humans have come to accept technology to such an extent that perhaps they are less concerned than they should be about wild salmon. Just as the technology might affect the fish themselves, it affects humans. Population growth, technology and consumerism are the three biggest enemies to face. And as long as they go unchecked, the salmon's chances are very, very slight. The precautionary principle urges us to protect what is before going anywhere else. You have got to separate the business of saving salmon from harvesting them, and you have to swallow a lot of individual goals so that the fish themselves have a chance. Full-cost accounting should include what is left for the future. There are both direct and indirect ways of getting there. The participant thought that so far the focus has been on direct ways, the science, but you also have to look at the indirect ways. Indirectly, the public's concern, the public's interest at large, and the future, should be an enormous part to factor into the things that we try to accomplish.

Ian Fleming noted that what is being discussed is where we cannot have hatcheries, the good, the bad, and the ugly. He thought that you could consider having places where you have production hatcheries, places that are not going to be able to maintain a wild stock where populations have been decimated for whatever reason, or the habitat will not be recovered. You can have a hatchery with a production goal at the same time, as Jeff Hard so nicely brought out earlier, as conserving some of that integrity of the natural populations, by identifying those populations that are worth particular protection. You could create parks, call them reserves, for wild populations, the strong, important populations. Ian suggested that there needs to be a plan to identify what is important and what is not. He noted that it is not so much unimportant as it is in a state where you cannot recover what was originally there. These may be areas where you can have production for creating the fishery, for maintaining those social values we would like to see, in terms of catching fish, both commercially and sportfishing. There may also be other places where we actually conserve that original resource for the future and just for our social benefits. It is possible to think of a general plan for BC where you actually identify these areas of particular importance, or basically create a series of marine parks for salmon.

A participant noted that on the Central Coast, from Toba Inlet right up to Prince Rupert, the salmon stocks there are down to all time lows. He stated that DFO might show that they have got 5,000 on the river, but then you go and check and there are maybe 100. He felt that the coastal communities, what few there are left, wanted to get involved in hatchery production, get involved with aquaculture, salmon farming. The participant believes that what is holding the coastal people back are elements of the federal government who have their own ideas as to what they want to see happen on the west coast.

Rick Routledge asked the participant to elaborate a little bit on what their vision is for the Central Coast.

The participant thought that there is a place for salmon farming, and that there should be designated areas for salmon farming. You could develop a transportation system, and have processing facilities. You could be looking at it from an approach similar to what Norway did with salmon farming. They devised a system of transportation, electrical, processing, marketing, a business plan, and they did very well. When they came over here and saw the tremendous opportunity, they rushed in.

A participant stated that they thought British Columbia was still in a very fortunate position in that there is a lot of potential and there are healthy wild populations. By maintaining that diversity, the future is going to be extremely bright but it looks like this is being viewed as some sort of decrease in opportunity. She thought that ultimately it will result in greater opportunities, in every respect, with fisheries and everything else. You have to look at this in terms of the opportunity and potential of maintaining the wild salmon diversity.

Ted Perry from DFO wanted to note that a number of good points have been raised. There are ideas that suggest that really what is needed is to have a better strategic plan on how to manage the salmon resources and other resources in the region. He pointed out a number of recent initiatives. One is Watershed Fish Sustainability Planning, which is an approach to managing fish within a region and within particular watersheds. He pointed out that this initiative had recently been released and some pilot projects were being set up. The concept is: this is a region, maybe the Fraser River or the Interior Fraser; these are the resources; these are the pressures that are being faced; these are the kinds of things we need to sustain those for the future, as well as coming to a consensus with all the interested parties on what to do with these resources. On the one hand, one extreme would be to maintain every unique genetic characteristic of all the salmon resources as well as having zero risk of extinction, which is, of course, impossible. Another view may be that you back off of that a little bit, because all the fish in these 20 streams have some genetic similarity, and you can live with 5 or 20% risk that you lose one of these sub-populations. The kind of thinking that goes beyond the biological scientific framework actually becomes a socio-political kind of decision-making process. One other initiative is the draft Wild Salmon Policy for the Pacific Region, which has some of the same concepts. The other initiative is the Oceans Act which was passed several years ago. It calls for integrative management planning in the marine areas, which gets at the issue of integrating natural resource plans with industry, transport, salmon farming, and other uses of the natural resources, including the water, the land and so on.

The participant also wanted to address the issue of polarity. There are people who are champions of hatcheries. They think what they are doing is good if they happen to be a hatchery employee or public volunteer. There is the other extreme where there are people saying you are going to cause genetic damage. It does not matter how things are done, it really is polarized. But there is a chance to bring the sides closer together. He stated that the people who are out there trying to rebuild stocks using technology have every good intention. They do not want to cause damage. What they need is advice, the kind of advice that this workshop has given in terms of mate selection, rearing practices, and so on. But he thought it could go a lot further, and the scientists could be much more helpful. The scientists could increase the understanding where these different levels of intervention, that Lee Blankenship referred to, might or should kick in. As the risks are going up, there should be a higher level. What are those levels where you need to start thinking about new ways of handling the resource management problems? If scientists could start thinking in that direction it would help bring the sides closer together, for the people who are actually out there getting their hands smelly and wet, and secondly it would legitimize the things that they are doing.

A participant suggested that the phrase “champions of hatcheries” comes back to the theme: What are the hatcheries for? The participant noted that they had worked in a hatchery, and there are different ways of rearing salmon; for example, you keep them there longer, and then they get used to no predation. A domesticated strain of fish that has been cultured for 20 or more generations is completely different than if you take some broodstock that just came back this season, do your stuff and let them go next year. What is needed is to map out what is a hatchery fish, and what are the purposes of hatcheries. There is a need to distinguish between salmon aquaculture in cages, or if it is moved on to land, that is a whole other debate. The participant spoke of a study that he had heard about where they were actually training fish by placing objects that looked like herons or other predators overhead. So there are possibilities that are not black and white; for example, is ocean ranching bad or good, and what does it do to the genetics of the stock. The participant wanted to hear a little more creative dialogue mapping some of these kinds of things.

Summary of Discussion, Rick Routledge, Moderator
Rick Routledge summarized what he thought were the key points from this discussion. The first point that is pretty clear to everybody is that a vision is needed. What kind of vision could be debated, but they clearly need a vision, and in that vision there is a role for hatcheries, at least from what had been expressed. Also, hatcheries are going to be here to stay, one way or the other.

Another point is that there is a need to reorganize the way hatcheries operate. There needs to be a lot of changes. In particular, along with the hatcheries, they need to consider this notion of reserves, reserves that would be free of hatchery or any cultural intervention. There is also the concern that has been raised twice very effectively and appropriately about the Central Coast, and the lack of involvement of coastal communities. Ted Perry picked up on that point in a slightly different way and raised this terribly trouble-some issue of the polarity between people who are really trying to work towards the same goals. Perhaps if we, who happen to be scientists, can get involved some way, maybe we can do these sorts of things that Lee and others were talking about. And that is the sense I am taking away from this discussion today.

HATCHERY REFORM: GOALS, DATA GAPS, MEASURES OF SUCCESS

Moderator, Richard Routledge, Statistics and Actuarial Sciences, Simon Fraser University

Hatchery Reform in Puget Sound and Coastal Washington

Lee Blankenship, Hatchery Review Group, Washington Department of Fish and Wildlife

I represent the Hatchery Reform group of scientists and a facilitation team, and I am here as a speaker for that group. What I would like to do is describe the process we started about a year and a half ago, that we call hatchery reform, and incorporate a lot of what we have talked about here. We are going to split this talk into two parts. Kathy Hopper with the facilitation team Long Live The Kings (LLTK) will get into the 'nitty gritty' of how we are doing the hatchery-by-hatchery, region-by-region reviews. I will give you the history and structure, and describe how we operate and the tools we developed. Kathy will give you a little more detail on these tools and describe the actual hatchery reviews that we have just started.

The process of hatchery reform started in late 1988 when a science advisory team was put together by Congress. We had just had some listings come forth under the ESA for Puget Sound. The listing of fall chinook in Puget Sound was the first time a species had been listed under the Endangered Species Act in a highly urbanized area. So it was a big deal and everybody was concerned. We heard, "What is this going to mean? Is it just going to stop everything? Where are we going with this?"

Congress was starting to pour money into habitat, so the science advisory team was asked to come together and look at what role hatcheries might play, if any, in the recovery of these endangered wild stocks. That advisory team put together a paper that in essence said, yes, the potential exists for hatcheries to have a major impact or positive effect on recovery of these listed wild stocks. They said that to do it could have an impact in a few years at a relatively small cost compared to the money it is going to cost to fix the habitat. They also said this is not to minimize that effort. We have to go forth with that process of at least not losing more habitat and recover where we can. We realize we cannot recover habitat in downtown Seattle, but we should maintain what habitat we can. There was a bipartisan acceptance of these recommendations that the committee put forth. Both sides in the House, as well as the Governor of the State, endorsed it. And then Congress passed funding appropriations.

The hatchery reform process that was launched (Figure 1) was meant to be a systematic process that was science driven, and it was to be a redesign of how hatcheries were to be utilized. It described two new purposes: to help recover and conserve naturally spawning populations, as well as the traditional role of supplementing sustainable fisheries. The appropriation language provided for the establishment of an independent science team to serve as a foundation for the reform. It also provided for a competitive grant process that would address some of the issues that the science team thought were the issues that were unknown, such as those that Jeff Hard mentioned this morning, the ecological and genetic issues.

Puget Sound and Coastal Washington Hatchery Reform Project launched by Congress in FY 2000

"The potential exists for hatcheries to have a major, positive impact on the recovery of wild salmon, in just a few years and at relatively small costs."

— Congressional Hatchery Science Advisory Team

Figure 1. Hatchery reform project launched in 2000

It provided $700,000 per year to start addressing those issues. The money was given to the State and the tribes to develop a science team within the agencies and to start the monitoring and work of the science team. It also provided for a facilitation team, an independent third party, to facilitate the process and to help ensure implementation of the reform. When this legislation came out, the co-managers of the State, tribes, and both the federal agencies, the US Fish and Wildlife Service and the National Marine Fisheries Service (NMFS), embraced the idea. Originally it was targeted at working on this ESA problem in Puget Sound. The co-managers embraced this idea, but they wanted to go beyond just mitigating the negative aspects of hatcheries on chinook in Puget Sound. They also wanted to address all the species in Puget Sound, and coastwide, and look at the bigger picture. They met with the facilitation team and the science team and both groups endorsed this, so a coordinating team was developed with the leadership of those agencies. The director of my agency sits on this coordinating committee, as well as the lead policy director of NMFS. The tribes, US Fish and Wildlife Service, the facilitation team, and Long Live The Kings also sit on that coordinating group. The original members of the Congressional science advisory team, those who were not part of the science team, also participated.

This ended up giving us a three-legged stool. Congress had specified that we have the hatchery scientific group and the facilitation team. Now we have added a hatchery reform coordinating committee, so that we have a policy, science and facilitation and communications team. This is really the basis of the structure, a three-legged stool, and all three legs are really important. I have been involved with a few other processes like this and have seen others where you just had an independent science team or maybe a policy team, and some of those processes end up on the shelf or dying.

The purpose of the coordinating committee is to ensure a successful working relationship between the individual science panel and the staff within the agencies, and their responsible implementation. That is the first leg of the stool. The facilitation and communication team was specified by Congress to be Long Live The Kings and they brought in another group, Gordon, Thomas, Honeywell, Jim Waldo. Those from South of the border may recognize that name. That group is known for its role in many natural resource issues in the Northwest. We have got a very strong facilitation team and they facilitate both the Hatchery Scientific Review Group (HSRG) (Figure 2) and the coordinating committee, and play that intervention role between these two, as well as provide staff support and communications. The Congressional language stated that the third independent group would report to Congress on the progress that the group is making. That is going to be important for continued funding. The first year we were funded for $3.6 million, and in the second year, they managed to put us in at $5 million. We have just started our second year, and we just got word today that we are in the budget for the year 2002, so it is going well. I see this group as being the key, even though they are a non-governmental organization. Before this process, they were a non-profit group that looked at rebuilding chinook salmon in the Puget Sound area. They have been a player, but now they are a key player in this process.

The HSRG, or the independent scientists, was established by Congress to ensure that this process has a scientific foundation. The objective of this group is to assemble and organize, and to guide the policy makers in implementing hatchery reform. They have no authority and it is really up to the managers to do it, but the same group also reports to Congress. If it is status quo and agencies are just using this money to pump out fish and not really do hatchery reform, that money is going to dry up. So with these three players, it is a check and balance system.

Hatchery Scientific Review Group

John Barr (Vice Chair) NWIFC	**Lars Mobrand, PhD (Chair)** Mobrand Biometrics
Lee Blankenship (Vice Chair) WDFW	**Robert Piper** USFWS (retired)
Donald Campton, PhD USFWS	**Lisa Seeb, PhD** Alaska Dept. of Fish & Game
Trevor Evelyn, PhD Fisheries & Oceans Canada (retired)	**William Smoker, PhD** University of Alaska
Conrad Mahnken, PhD NMFS	

Figure 2. Hatchery Scientific Review Group

The HSRG is composed of nine scientists; five are totally independent of the agencies. The past-president council of the American Fisheries Society (AFS) nominated them from a pool of candidates, and then the science advisory committee picked these five people. With the nine scientists we have a large variety of expertise within the group. Trevor Evelyn is noted worldwide, and has a reputation for being a very good pathologist and microbiologist, and he adds a lot to our group; he is the only Canadian on the review group. John Barr represents the Northwest Indian Commission, and he has been a long-time hatchery manager. I represent the Washington Department of Fish and Wildlife, and Don Campton is a geneticist with US Fish and Wildlife. Conrad Mahnken is an ecologist with NMFS and Lars Mobrand, an independent biometrician, chairs the group. Bob Piper also sits on the group. Any of you who work in hatcheries or culture fish probably know the name. For a long time he was editor of the AFS fish culture magazine and has written the "bible" of fish culture, used by almost every person who has worked in fish culture. Lisa Seeb, from Alaska Department of Fish and Wildlife, an ecologist, is also in the group.

We started in March of 2000. During our first year of operation, we spent the first couple of months soliciting for grants and putting those grants out. After those first two months we then thought about a scientific framework on which to base our work, and that took about six months, and by the end of 2000, we did our second series of grants. Our first set of 12 grants totaled about $600,000. We just issued another 15 grants for $700,000. We also issued a progress report to Congress, the first summary after we organized.

I will briefly describe that Scientific Framework. It is the basis of a lot of our work, and it took us six months of hard work to devise. We met three days every month, in person, and we did a lot of work in between. It has got to the point where a lot of us are joking about our day jobs, because this is taking a lot of time. Between being Type A personalities, and a very driven and aggressive schedule by the facilitation team, we do accomplish a lot in a short time. The purpose of our Scientific Framework (Figure 3) is to recover and conserve natural populations and/or to provide for sustainable fisheries. We asked: What are the conditions for success? What are the things that will lead to success? We identified that we need healthy, viable hatchery populations, that hatcheries either need to contribute to conservation and/or harvest, that they need to be accountable for their performance, and that there had to be goals that could be measured. We wanted to benefit, or do no harm to, the native wild populations and the environment. Obviously we cannot do zero-harm, but the idea was that we lay out the benefits and we lay out the risks and the known things from science that show us what risks we are taking.

The result was a document called the Scientific Framework for the Artificial Production of Salmon and Steelhead. We use it to develop other tools, for operational guidelines, benefit-risk tools, and monitoring and evaluation. It is really the basis, our foundation, when we go to the policy makers and say why we are recommending this suite of things. It also creates a repository of knowledge from which we can talk with other scientists and to the public (Figure 4). It took us six months to develop. We put it out for review to about 15 other scientists and, after that formal review, we put it out for informal review to another 200 scientists, stakeholders and the public. We revised the document according to the input we received. We still consider it a living document, and we continually update it.

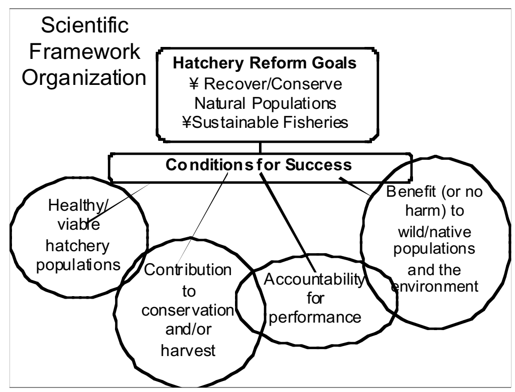


Figure 3. Scientific framework organization

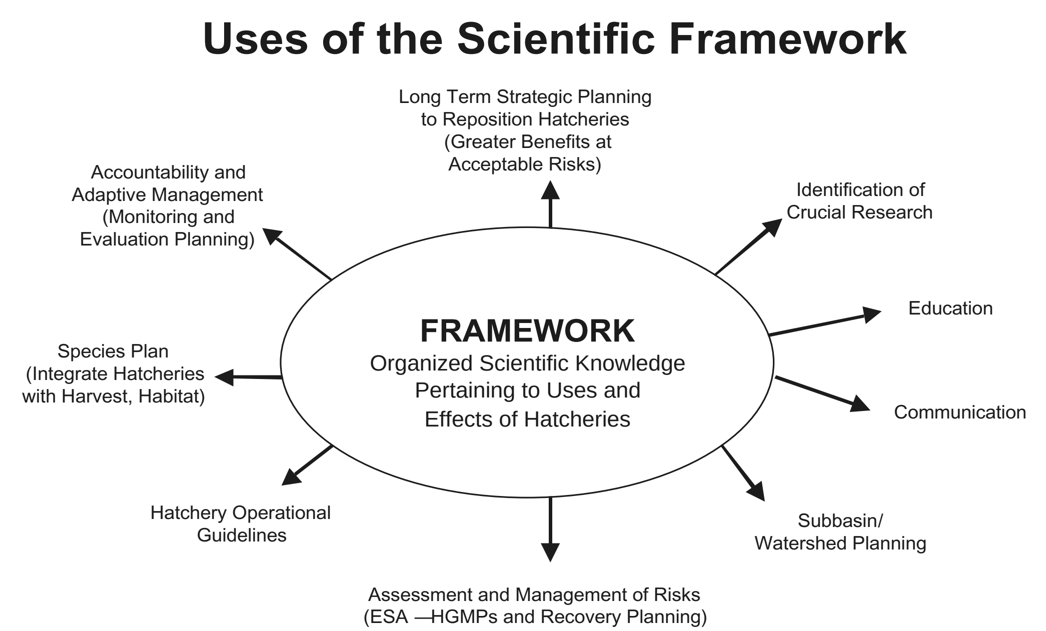


Figure 4. Uses of the scientific framework

That took about the first nine months of our existence. Then we laid out a work plan for the next year, starting in January (Table 1). The first couple of months we needed to go back, do our research grants, which we have done, and finally, by May, we can get to the meat of things: a hatchery-by-hatchery, region-by-region review of hatcheries. But first we had to develop more tools. One was a benefit-risk tool, which we developed with the co-managers who laid out the benefits provided by hatcheries, whether for conservation, or for fisheries harvest, as well as the risks. This benefit-risk tool has to do with the viability of the genetic resource in an area. For example, if there was only one stock of spring chinook in Puget Sound, it was obviously very important to protect it, as opposed to the ten fall chinook stocks. Where there is poor habitat, such as in an urban area like Seattle, we would be more willing to take risks, compared to an area that still had good habitat, or the possibility of rehabilitation. That is how our benefit-risk tool was laid out.

Table 1. Work plan for 2001

2001 Work Plan			
Task	*Jan–Apr 2001*	*May–Oct 2001*	*Nov–Dec 2001*
HSRG research	——►	——►	——►
Regional reviews		Initial regional reviews	Remaining regions
Benefit/ risk tool	Develop simplified	Field test in initial regions	Revise if needed
Operational guidelines	Develop draft hatchery operational guidelines	Field test in initial regions	Revise if needed
Monitoring & evaluation	Develop draft M&E matrix	Field test in initial regions	Revise if needed
Outreach & communi-cations	Meetings w/ decision makers	Report to Congress	
Agency science teams	Integrate activ-ities, program & facility improvements	Conduct scientific studies, improve HGMPs & HatPro	Add M&E, work w/ NMFS on BiOps

We also recently finished an operations guideline that the scientific framework laid out. These are the operations for success, but it was not prescriptive. We needed more detail and prescription of details of how you would do things in a hatchery, getting down to mating protocol, disease protocols, and that whole suite of things. We also needed to have a monitoring and evaluation component and we are currently working on this item. We will take all these tools and then use them when we do our regional evaluation. Kathy Hopper will describe these tools in more detail.

Part of the work of the facilitation team was to work with Congress to ensure continued funding. It is not just Congress; we consider the money from Congress as seed money. My institution went through and looked at hatchery structures. While today we have looked at ecological and genetic risk, an area that is often overlooked and, in my opinion, is towards the top of the list as far as risk to the fish themselves, are the structures themselves, whether it is water quality coming out of the hatcheries, or blockage to upstream or downstream migration of wild individuals. In my agency we have a lot of hatcheries and we looked at how we have to modify those structures. I know of a hatchery that was pulling in through an unscreened intake from a river that had listed fish. These are the types of things that the tools will address.

This is a $150,000 project (one hatchery), so $5 million from government to do this is only a start. It is going to be a big picture item, but at least we are identifying those things and prioritizing them, and getting a start. As I said, this last year funding jumped from $3.6 million to $5 million, so we can at least pick off the top of the priority list

The agency teams are also working with the HSRG. As they get input, they are implementing some things, and trying to meet the monitoring and data needs that the HSRG has.

I will briefly describe where we are going with the regional reviews. After a year and three months we are getting our feet and hands wet as we tour these facilities. We have divided Puget Sound and the coast into ten regions (Figure 5). We will review a region two months at a time. We will spend two to four days of meetings at each region before moving on to the next. The first one we picked is the Eastern Strait, across from Victoria. We have had our first meeting and next week we will have the second half of the two-month meeting. We have only two hatcheries there, so it is a nice one to get started with. Most of what these hatcheries are doing is restoration projects, so we have not got into a lot of harvest conflict yet.

Once we do three of these regional reviews, we are going to stop, take a break, analyze the process we have been using and get feedback from the managers on how this is working out, address how we think it is working out, and then modify the process, and dive back into the final seven regions.

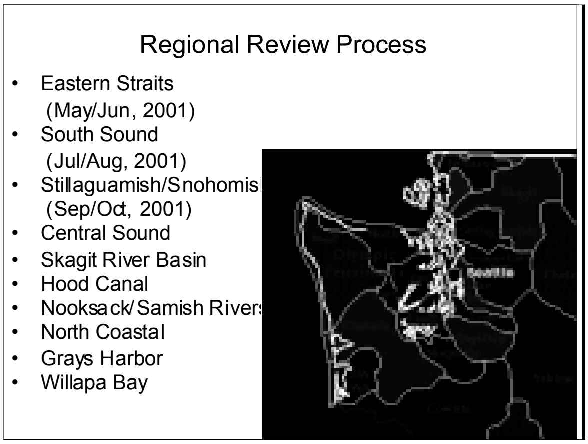


Figure 5. Regional review process

We request a lot of information before we even go into the region. The first thing we ask is: What are your regional goals for conservation, harvest and other purposes? What is the purpose and goal of your hatchery? We ask that of the hatchery managers, the harvest managers and the habitat people. While this may sound trivial, it is a big deal. For the first time we will have goals established for this area. Even though the agencies talk about reforming hatcheries and changing the way they do business, we still have hatcheries that are just plugging out fish because that is what they have always done. Identifying these goals is very important because it also gives us a way to evaluate what they are doing.

For example, let us look at stock status. Stock status to us is the biological significance and the population viability. These are really genetic issues. What is a population size and how important are those genetics in the river? We look at the habitat, and we ask for a 10-year and a 50-year projection of where we think we will be in terms of habitat. For example, downtown Seattle which has a river running through it called the Green River, which also has a hatchery on it. We know we are not going to change that watershed. However in the Eastern Straits we have two main drainages there is the Elwah and a dam that is coming out in 2004, and there is pristine habitat above that because it is in a park. We also have the Dungeness River, which the tribes and the State have poured a lot of money into, reshaping, buying up the easement, and rebuilding the river. We know that in that system we will be a lot better off in the future. Then we go in and ask the hatchery programs for detailed explanations: how are they doing business, what are their mating protocols, how do they treat diseases, what are their pond loading densities, etc.?

In conclusion, I am extremely confident and pleased with the progress that we have made in the 15 months since we first met. Most important, the co-managers have embraced this, and they have joined us in working towards this redesign of hatcheries, to provide benefits both for sustainable fisheries and for conservation of threatened stocks. I am also excited about the three-legged structure, because my agency has been talking about change, and we have been doing piecemeal efforts such as on the Dungeness. We have breeding protocols and captive broodstock, similar to what we heard this morning. We have got a wild salmonid policy that is embraced in some places but not all, and we have a disease policy. We are thinking about change, but moving slowly. This structure I really believe is going to manage change. That is where we are headed and I am confident we can make a significant difference in decreasing the risks of hatcheries and increasing the benefits (Figure 6).

"We are confident that by working together... we can achieve our goal of returning wild salmon stocks to abundance. Reforming hatchery practices is another step on the road to wild salmon recovery."

Billy Frank, Jr.,
Chairman, Northwest Indian Fisheries Commission

Figure 6. Endorsement of review process

Discussion

The question was asked: Is this hatchery-reform project integrated with the watershed analyses and other initiatives going on in Washington State, in the general framework of adaptive management?

Lee Blankenship replied that they are brought in and they provide input when they go into a region-by-region review. Their input comes mostly in the way they are structured and the habitat section of things. It is not just the agencies that are providing information, it is also any interested group.

The question was asked: From your knowledge of BC, is there any reason why this structure would not work here?

Lee Blankenship replied that he may be a bit biased, but he thinks that it is a really great structure. It is not just an independent science panel coming in and saying what should be done; it has agency input in that independent science review and it has a facilitation team that is really important. It is a third independent party and it is a nexus between policy and science. It is the first time he has seen this type of structure and that is why he is excited about the potential success they may have. The group is new, and has only been in existence for 15 months and they are doing their first review. Lee Blankenship suggested looking at it again in three months, after they have done their first review.

A participant asked: Are the hatcheries that are being reviewed all state-run hatcheries? Are the community hatcheries involved as well?

Lee Blankenship responded that there are state, tribal, federal and private NGO-type hatcheries. The first region to undergo review only has one state and another hatchery. But there will be different types of hatcheries in other areas.

The question was posed: Is the service that you provide available to all the hatcheries?

Lee Blankenship replied that, yes, when he says systematic, it is meant to be encompassing.

The Puget Sound and Coastal Washington Hatchery Reform Project. Hatchery Reform: Goals, Data

Kathy Hopper, Long Live the Kings

I would like to answer some of those questions a bit more. I have worked with hatcheries for my entire professional career. I think the question about watershed analysis is a great one. We are taking great care not to duplicate other processes and our Executive Director sits on the steering committee for the Shared Strategy for Salmon Recovery in Puget Sound, and in other such processes. We are trying not to do something someone else is already working on, and we are taking in available information as we can. That is another one of our roles. Regarding the question about community-based hatcheries, we are very aware that they are an important part of the process. The area we are in right now has just a very few community hatcheries and they are mostly educational. But they are included in the scientific consideration and we fully anticipate getting into some thorny discussion areas. However, we wanted to do a relatively simple area first so that we could test the process and the tools.

I am also going briefly describe what Long Live the Kings (LLTK) does. If you work for government, or are not really familiar with NGOs, it is just a little different spin on the world. We are able to do things that maybe government cannot, because of regulations. Many of the photos I am going to show you today are from our facility. We operate three facilities and have been doing so for all of our organization's history over the last fifteen years. If you would like to learn more we have a wonderful website: www.lltk.org.

We are a non-profit organization; we are not a political advocacy group. Our mission is to restore wild salmon to the waters of the Pacific Northwest. A very experienced, talented and interested Board of Directors guides us (Table 1). For those of you who may not be familiar with some of these names, William Ruckelshaus was the US envoy to the US-Canada salmon negotiations; David Troutt and Larry Wasserman are experienced leaders in our tribal community; Bill Nordstrom and some of the others are civic leaders in the greater Seattle area. These are people who are not just names on the Board. They work very closely with us, they have power and influence, and they love ssalmon. That is their niche and they have decided to devote time, and work very closely with our Executive Director, Barbara Cairns. She takes their input and considers it and listens and translates that to the rest of us.

Table 1. Board of Directors

James W. Youngren
Chairman

Douglas P. Beighle The Boeing Company	Jay D. Hair, Ph.D. Natl. Wildlife Federation	Douglas S. Little Perkins Coie	Gary T. Smith The Gallatin Group
Douglas T. Boyden Wm. M. Mercer, Inc.	Douglas F. Henderson Western States Petrol.	Denny Miller Denny Miller Assoc.	David A. Troutt Nisqually Tribe
Diane Ellison Ellison Timber & Props.	Patricia Herbold Attorney/Volunteer	William E. Nordstrom Nordstrom	Larry Wasserman Skagit Systems Cooperative
Diana Gale Seattle Public Utilities	Gerald D. Hermanson Hermanson Corporation	Tom Ohaus Angling Unlimited, Inc.	Sally Yozell Battelle Memorial Institute
Peter D. Grimm, D.O. Seattle Prostate Institute	Robert J. Jirsa Plum Creek Timber	Gary Reed Simpson Investment Co.	
Gerald Grinstein Delta Airlines, Inc.	John S. Larsen Weyerhaeuser Company	William D. Ruckelshaus Madrona Investment	

Barbara J. Cairns
Executive Director

BOARD OF DIRECTORS

We form creative partnerships with the private sector and with government. An example of this is on the Hamma River, which is on the Hood Canal. Access to this river is through private property, and we would not be able to be there without these very willing landowners, who want to see the fish back on the anadromous part of their river. Here we have state and federal employees, local and community volunteers, and LLTK staff, which gives us an idea of how we are able to bring together the various expertise and local knowledge, and the private property people. These particular property owners are fairly leery of government and we have to be sensitive and recognize their unique role.

We have been getting our boots wet with a variety of fish enhancement and restoration projects for the last 15 years. We have a facility on Orcas Island in the San Juans Islands where we have created a terminal fishery for chinook. We use it as an opportunity to bring in urban people and leaders and show them these magnificent animals. Even though it is a hatchery, it still reminds them to give us money or pay more attention to the endangered species listings or those sorts of things.

As Lee Blankenship mentioned, the hatchery reform effort has two goals: helping to recover and conserve naturally spawning populations, and supporting sustainable fisheries. These are the goals of the LLTK as well. It is for this reason that LLTK was specified by US Congress as a third-party facilitator for this hatchery-reform effort. The HSRG and the coordinating committee, includes LLTK and our subcontractor Gordon, Thomas, Honeywell. The US Fish and Wildlife Service is a federal agency in the Department of the Interior. They are responsible for inland fish and wildlife, such as bull trout. The NMFS is in the Department of Commerce and they are responsible for marine species and anadromous species such as salmon and steelhead. The Northwest Indian Commission is a support organization for the tribes in western Washington. They provide things like genetics and fish pathology help and leadership for the tribes. The Congressional hatchery science team is the remaining group of scientists who are not part of the HSRG. They are still in the loop because they were instrumental in getting the initial funding.

Figure 1 shows all the hatchery locations in the State of Washington. The area we are talking about is western Washington, cut off at the Columbia. We are working right now in the Eastern Straits. There are three state, and one tribal, hatcheries in that area.

As Lee Blankenship described, we are taking a regional approach. We have scheduled the first three pilot areas and we will be moving into the next seven areas.

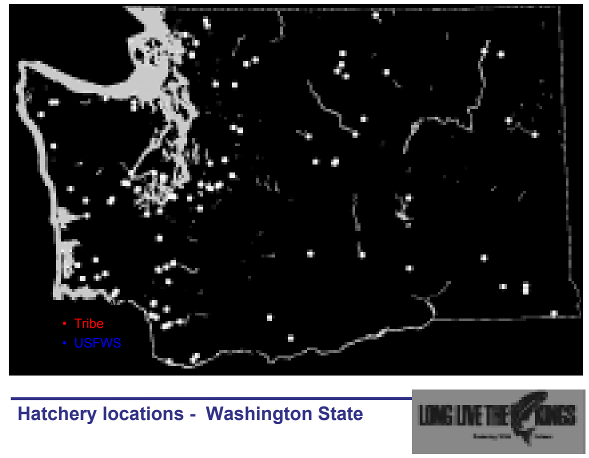


Figure 1. Hatchery locations in Washington state

For example, Grays Harbor was a major sport and commercial fishing area and it is now coming back as a sport fishery, as is Willapa Bay. The regional review schedule is described in Table 2. The first day we do regional field tours, and then we have a briefing with the co-managers about the management goals and stock status. The third day we get back together. I am telling you how it was planned; we actually did it for the first three days and we got back together with the scientists on the third day and discussed what information we did not have. They had asked specific information questions but the answers do not always come back in the form you expect. We then made assignments, which we have been working on ever since. We will see how much they get done by next week and then the following week we will begin the second half of the regional review. We will get together with just the scientists for the first two days to go over the tools and actually get down and do the analyses of benefits and risks of the hatchery operations and try to put some context into what they have been doing. On the sixth day, there will be an informal review with the co-managers. In other words, with the hatchery managers, the harvest managers and the tribal people, we will address what they think they are doing right and wrong. This won't be written down, so it is a little less scary for the managers who are concerned about their programs and what might be their downfall. If it is something simple that they could correct, it is a lot easier to have that face-to-face connection, prior to the written report, which will be done at the end of the pilot session. Again, for the three regional pilot reviews, we are in the Straits now, and then we will go to South Puget Sound and Snohomish and Stillaguamish. Each of those areas are quite different.

Table 2. Regional Review Schedule

- ➢Day One—Regional field tours
- ➢Day Two—Briefings on regional management goals, stock status, habitat, hatchery programs
- ➢Day Three—Identify information gaps, other essential information, assignments for next meeting
- ➢Day Four—Review additional regional information, discussions on actions needed in region
- ➢Day Five—Complete decision-making for region
- ➢Day Six—Informal review of region, prepare for next region

Regional Review Schedule

When we go to the Eastern Straits, we will ask: What are the regional management goals for conservation and harvest and other purposes? What is the status of the salmonid stocks in that region? What is the current and future habitat? Do the current hatchery programs fit with the goals, the stock status and the status of the habitat?

These photographs describe our first trip (not shown here). We started on our first regional review and the scientists are heading out into the region. The Dungeness River is a short river; it heads from the Olympic Mountains north to the Strait of Juan de Fuca. It was settled by Europeans and logged in the late 1800s, and dyked and used for farming. So it has had a long history of river misuse. There was once an active shellfish business in Dungeness Bay but they have not been able to harvest shellfish there recently because of contamination by fecal coliform. This is a photo of a Jamestown S'Klallum Nation biologist showing us a map with the dykes they want to take out. They are actively working at restoring the floodplain. The community is embracing it, largely because these are the people whose land is supposedly protected by the dyke. They are looking at all of the positive aspects of opening up the floodplain.

This gives you an idea of the unique circumstances the review is considering. You have to have the whole picture in order to make decisions about hatcheries.

There is an irrigation withdrawal canal situated about river mile eleven, just before the river starts to go up into the higher reaches. It is very close to the Dungeness hatchery. The Dungeness hatchery and its satellite, Hurd Creek, have been very instrumental in the restoration of chinook salmon. Dungeness River chinook salmon have been in a captive broodstock for six generations and they are looking at phasing it out. That is one of the unique questions that the co-managers brought to the scientists: What do we do next? Recognizing that this has been a very successful captive brood program, they have fry that are planted in the upper reaches of the river. The technology works, but they want to know what to do next? The Hurd Creek hatchery was built specifically for this recovery plan; there were individual family tanks and they would identify the fish. A lot of people have done a lot of work with these fish. It was helpful to be on-site with the hatchery people and talk to them.

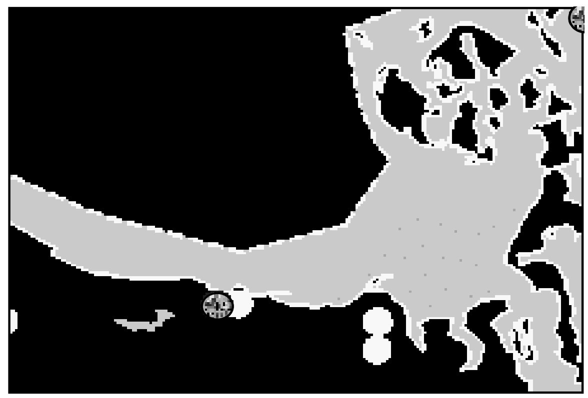


Figure 2. Eastern Straits of Juan de Fuca. Grey dots represent tribal hatcheries, and the black dots represent state hatcheries

Then we went over to the Elwah River. The Elwah is another short river that comes out of the mountains and goes down to the Strait of Juan de Fuca. It was dammed early in the 1900s by two large dams. The first one is at about river mile four; the other one is actually located in the State Park about another 20 miles upstream. The important thing is that they are both scheduled to be removed. The chinook salmon on the Elwah River have been reared in hatchery production basically to keep them going. It has been difficult because the water fed to the river comes from the top of the reservoir, and it is very warm. That poses a unique problem. These fish still know they want to go upstream; they butt their noses at the base of the dam. They are magnificent fish, not as big as they used to be, but large fish. The second dam is 200 feet high. The dams will start to be removed in 2004.

The fishery managers are keenly interested in what the scientists have to say about their hatchery programs. The habitat above the second dam, in the park, is pristine. We went to the Lower Elwah tribal staff and were briefed on their particular issues. They operate a hatchery very close to the estuary, and have a unique viewpoint. You hear different things when you sit down with these different people. The scientists spent a long day doing so, and they got a lot of good information. The Lower Elwah hatchery is used primarily for steelhead, coho and chum production. The photo was taken from a large dyke. They have managed the area between the dyke and the river for floodplain. There is a rearing channel operated by the Department of Fish and Wildlife, as mitigation for those dams. It was built as a spawning channel, but never used as such. It was always used for rearing.

As I said, the Lower Elwah River, where the Fall chinook return to spawn, gets really warm in the Fall. They have a tremendous problem with *Dermacystidium*, a parasite that kills the wild fish. They were able to develop a well on this property and they go out into the river and take chinook salmon and bring them into the facility and keep them alive and take the eggs. It is of significance that this run is listed as part of the Puget Sound Evolutionarily Significant Unit (ESU). Many of the hatchery stocks are not listed in that ESU, and so it further raises the importance and the seriousness of what they do here.

We went back to the meeting and discussed and clarified the issues. The regional people asked for very specific advice such as an evaluation of the Elwah fish restoration plan, and how they could keep the fish alive while releasing the sediments from the dams. These are big questions, and I think the scientists will offer some advice. I wanted to show again the slide of the scientists that I am privileged to work with. They have been a wonderful group. They do have other jobs for the most part, and some are retired like Trevor, and they work dually hard between gardening and things like that. They have several deliverables that are very important and these deliverables are going to be used by the co-managers and other people such as yourselves.

I would like to go into the details of the deliverables with you. The first one is the Scientific Framework for Artificial Propagation. It is available on our website, as are the meeting materials, submissions, and any applicable information about the Hatchery Reform project. The Scientific Framework was very well received; the only major criticism was that it was not prescriptive enough. That is why we have moved in with the tools. The simplified benefit-risk assessment procedures is in draft form, and is not yet available on the website. There was also a document called BRAP, Benefit Risk Analysis Procedure, that the NMFS, tribal and state geneticists worked on that was incorporated into this. Again, we are not trying to duplicate other work. The HSRG wanted to go beyond that. To read from the introductory paragraph of the BRAP: “The purpose of this simplified benefit-risk assessment is to analyze the current hatchery program relative to short- and long-term goals for conservation, harvest and other specific needs, and to identify opportunities for improvement.” Benefit and risk refer to the likelihood and extent to which these goals are, or are not, met. The assessment involves six steps. We have done the first three; classify all the stocks in the region in terms of habitat condition and stock status; identify short- and long-term goals for natural population components in terms of conservation, harvest and other benefits; and, given the goals for natural production, identify the short- and long-term goals for hatchery production.

Next week, the scientists will be moving forward in applying this benefit-risk tool. They will be prioritizing the conditions for hatchery success using the framework, and comparing the current hatchery operations and practices with the operation guidelines they have developed, and the monitoring criteria, to see which high priority conditions are met, and which are not. Then they are going to summarize the conclusions and recommendations in a kind of report card. When we put together briefing book material for the Eastern Straits it was derived from how the questions were answered. One of the things that happened on our last day of our meeting last month was that we realized it did not read cohesively, so we are writing it in an outline format that is more understandable. Then the evaluations and the recommendations will go at the bottom of that, so that anyone will be able to understand how the recommendations were derived.

The hatchery operation guidelines is also in draft form. Here is how the scientists put it in words:

> *“These guidelines are intended to describe operation practices that are most likely to meet conditions for success at hatcheries, as defined in the HSRG Scientific Framework. They were developed primarily for use by the scientific group in its regional review of the hatchery system in Puget Sound and Coastal Washington. Since goals as well as habitat and stock status*

vary among its programs, conditions for success may also vary among programs. No program is expected to meet all guidelines discussed in this document. Hatcheries are by their very nature a compromise, where risks must be balanced against benefits. For example, to meet survival goals, some genetic or ecological risk may be acceptable. The purpose of these guidelines is to ensure that potential risks and benefits are clearly identified and managed."

So this is a set of guidelines that go back to the Framework. For instance, the biological condition of fish health goes through a checklist of operational procedures that should be in place in order to produce healthy populations, reduce costs of correcting disease problems, reduce the need for using anti-microbial compounds, and reduce the effects of disease transfer. Those are the words out of the Framework. They just took that and made a checklist.

One of the interesting things that the scientists grappled with was how to get that information from hatchery managers and operators. I am quite sensitive to the fact that hatchery people, since I used to be one, have a lot of work to do. They raise fish and they also get a lot of requests for information. Another questionnaire coming in the mail, particularly with this list of all these things they are supposed to be doing - how would that be received by the hatchery managers? We decided that what we needed was a subgroup to go around and talk to these people. Again, we did not have very much time between meetings, but I went out with an employee of Lee Blankenship's to the hatchery people, with the operation guidelines, and went through them one by one. For instance, where it says mate one to one as a goal, they may have answered "No" because what they actually do, in almost every case, is to take all the females and mix the eggs and then allot them into individual buckets and put one male's milt in each bucket. There was no category in this questionnaire for that. We found out about how they deal with their carcasses, and all kinds of anecdotal information that is there if you sit and talk with them. Most of these people love their river, they know the fish, and you just have to get the information from them. I am a little leery of some of the surveys that get translated into literature, because you lose that flavor.

When I was showing you the map of western Washington with all those hatcheries, the reason why our hatchery reform method is a little bit different is that when you look at all those numbers they had kind of a scattershot approach to reform. Either there was a stock in peril, or a legal requirement. That is where the money and effort went. In some cases there were some broad-based dicta like: "Stop all net-pen rearing." They tried to apply that to big geographic areas and sometimes in response, legitimately, to things like endangered species listings. But you really need to go into this regional approach to understand what the regional issues are. That is why I spent so much time describing that first area.

Discussion

The question was asked: How did this package come together and go forward to Congress? Was there a specific impetus to get it started?

Kathy Hopper responded that there were a couple of impetuses. First of all the Board of Directors was interested in applying some of the experience they had in trying to make hatcheries a part of the recovery process. Also, there was on the ground experience, which they wanted to apply in order to help the co-managers be successful. Similarly, the Endangered Species listings in Puget Sound were imminent, and the congressional leaders from the State of Washington were saying, "Where is the best place to put money?" The former US Senator, Slade Gordon, asked some of his contacts in the state to put together a team. They sat down and wrote a report recommending hatchery reform as a package that should be funded by Congress in the short term. They pointed out that habitat is being dealt with through a lot of other venues, but there were those hatcheries operating, that have funding, and are not going away, so let us get some concerted effort in. Everybody saw this as a positive effort, so Senator Gordon, a conservative Republican, and our Democratic governor and the Democratic leaders from our House of Representatives, all said that this is a great project.

Hatchery Reform: What Should We Do With Hatcheries?

Mart Gross, Department of Zoology, University of Toronto

Introduction

Salmon, among the most biologically complex and commercially valuable fish in North America, exemplify both the potentials and the pitfalls of hatchery production. Salmon are bred and cultivated in hatcheries for three separate and largely irreconcilable goals: fishery augmentation and introduction (where hatchery-bred individuals are released into the wild in large numbers for harvest); livestock production (where individuals are selected, bred and raised for many generations in farms, and kept for all or part of their lives before going to market); and conservation (where captive individuals form so-called 'living gene banks' and are either re-introduced or their offspring are introduced as biodiversity-restoration measures). Of these three goals, only the first two (fisheries and livestock) fall under the auspices of commercial propagation. The third goal (conservation), while in some ways suggested and assisted by advances in commercial production, is largely non-commercial in purpose and methodology. Commercial salmon aquaculture has demonstrated explosive economic growth and a potential to supply demands for salmon that exceed wild production capacity. But it has also raised a suite of concerns for wild salmon populations, including genetic, ecological and disease-related issues. It is important to realize that the three interests (wild fish, capture fisheries and fish farming) are all competing over the same salmon ecosystem. It may therefore be necessary to reduce conflict by allocating the salmon ecosystem, possibly through zonation of marine environments similar to the zonation of terrestrial environments. Allocation decisions will require a comprehensive risk assessment to quantify the genetic, ecological, and pathological interactions between salmon produced through the two forms of commercial captive breeding and their wild counterparts.

Fishery Aquaculture and Wild Salmon

There is an ever-increasing dependence on artificial hatchery rearing to rehabilitate dwindling fishery stocks worldwide (e.g., Lichatowich 1999). Salmon abundance has declined to historic lows throughout the world, and numerous stocks are either extinct or threatened with extinction (e.g., Slaney et al. 1996). Augmentation of wild populations with large numbers of hatchery-bred individuals is one of the most common practices used to mitigate this decline and to maintain harvest. Hatchery propagation involves collecting spawning wild salmon, physically removing eggs and milt, artificially fertilizing eggs, rearing fry and parr in captivity, and releasing parr or smolts into the wild. While hatcheries greatly improve egg and juvenile survival, recent concerns regarding this practice include the potential for negative impacts on wild fish.

One source of impact is the 'mixed-stock' fishery, where harvest of wild stocks is over-inflated due to the presence of hatchery stocks (NRC 1996). Other significant concerns include the behavioral, morphological and genetic changes in hatchery fish that result from captive breeding. For example, when reared in hatcheries, individuals lack information about predators, food sources and habitat structure, have altered morphologies, and undergo genetic changes associated with sampling and selection in the hatchery environment. All of these changes reduce the performance of hatchery-bred salmon in the wild. Hatchery salmon, particularly males, are competitively inferior to wild males. Behavioral and DNA-fingerprinting studies show that they are denied access to ovipositing females, partake in fewer spawnings, hold more distal positions in spawning hierarchies, and may attain only 46% of the breeding success of wild males (Fleming and Gross 1993, Gross et al. unpublished data). Hatchery females suffer greater delays in the onset of breeding, fail to spawn as many eggs, lose more eggs to nest destruction by other females, and may attain only 82% of the breeding success of wild females (Fleming and Gross 1993). However, even with reduced reproductive success, the large numbers of released hatchery individuals relative to their wild counterparts can alter the gene frequencies of a population, replacing wild adaptations with domestic adaptations to the hatchery (NRC 1996). In addition, there are now indications that, in mixed populations, hatchery fish decrease effective population size (N_e), an important measure of individual genetic contribution, relative to pure and wild hatchery populations (Gross et al. unpublished data). Thus, supplementation of wild populations with captive-bred hatchery fish may be a larger conservation concern than is generally realized.

In recent years, the growing awareness of impacts resulting from production hatcheries has prompted proposals for 'dual-role' conservation hatcheries that would serve for both fishery augmentation and biodiversity preservation (e.g., 'living gene banks'). Unfortunately, the protocols for conservation hatcheries that might prevent loss of genetic quality and divergence of hatchery fish from wild fish are yet to be fully developed or tested. On-going experiments in the Gross laboratory suggest that female mate choice may be important in maintaining genetic quality of offspring through female choice for males with 'good genes' or 'complementary genes'. Current genetic protocols in hatcheries do not incorporate such female mate choice. This suggests that conservation hatcheries are only experiments in progress and not yet fully functioning tools for biodiversity protection.

'Livestock' Aquaculture and Wild Salmon
The principal 'livestock' salmonid cultivated in fish farms is Atlantic salmon (*Salmo salar*). Historically, the native range of Atlantic salmon held roughly 20 million wild adults. Today, due to over-fishing, habitat destruction and environmental change, as well as aquaculture, that number has dropped to well under 0.5 million. By contrast, in the early 1970s salmon aquaculture began to develop as a commercial enterprise, and its success is evidenced by the industry's growth to support some 160 million adult Atlantic salmon in fish farms around the world. Thus, today over 99% of Atlantic salmon live in farms and less than 1% are in the wild.

To successfully farm Atlantic salmon, breeders have used selection to alter their genetics in an effort to delay age of maturity, increase growth rates and food conversion efficiency, and improve disease resistance. In addition to genetic changes, the farmed fish are developmentally altered as a consequence of captive rearing conditions. They are heavier in weight, have rounded dorsal and caudal fins, smaller hearts, and misshapen adult mandibles. Concurrently, traits for fitness in the wild have been altered, especially those related to adult breeding and early juvenile survivorship. This massive alteration of both phenotype and genotype, while adapting the fish to the aquaculture niche, has also maladapted them to the wild niche. Recent studies have shown that farmed fish have altered mating behaviors, differ in levels of aggression, and have only 16% the lifetime reproductive success of wild native Atlantic salmon (Fleming et al. 1995,1996, 2000). Gross (1998) proposed to recognize this extensive change in the biology of Atlantic salmon by 'naming' those in aquaculture *S. domesticus* and retaining *S. salar* as the name for those in the wild.

S. domesticus escape from the net pens in which they are raised. With a loss rate of roughly 2–5% per year and 160 million individuals in farms, there are 3–8 million *S. domesticus* entering the wild each year. About 75% of this escapement is back into the native Atlantic Ocean range, and thus some 3.8 million farmed fish re-enter the waters now occupied by less than 0.5 million wild *S. salar*. The remaining 25% of escapement is into non-native ranges, including the Pacific Ocean. *S. domesticus* have been observed in non-native ranges including British Columbia (Canada) and Chile, which are significant producers of farmed Atlantic salmon.

The entry of *S. domesticus* into the Atlantic Ocean results in a collision of biologies with *S. salar*. Impacts can be categorized as genetic, ecological, and disease/parasite-related. Genetic concerns are largely due to interbreeding and the production of hybrids which may 'genetically pollute' the remaining *S. salar* populations by reducing their fitness (e.g., potentially to a mere 16% of previous levels [Fleming et al. 2000]). Ecological concerns include competition for adult nesting sites (since *S. domesticus* typically breeds later and thus can dig up *S. salar* nests) and competition for food among juveniles (since *S. domesticus* juveniles are more aggressive than *S. salar*). Production of Atlantic salmon in a native stream was shown to decrease to 70% of its potential when *S. domesticus* are present (Fleming et al. 2000). Finally, diseases and parasites are transferred from *S. domesticus* to *S. salar*. Sea lice from salmon farms have been known to decimate *S. salar* populations, and recently infectious salmon anemia, or ISA, has swept through *S. domesticus* populations and may now be affecting *S. salar* (Whoriskey 2000).

In addition to their impact on *S. salar*, escaping *S. domesticus* have been found in the Pacific Ocean (e.g., Gross 2000, Volpe et al. 2000). Three rivers in British Columbia have been found to contain *S. domesticus* juveniles, and free-swimming adults are found in the Pacific Ocean from Washington State through Alaska (Gross 2002). This raises additional biodiversity concerns, since native Pacific salmon species are already endangered (NRC 1996). The introduction of exotics is generally regarded as the third largest concern for biodiversity after habitat change and exploitation (World Conservation Union [IUCN] 2000 Red List). Thus, invasion of the Pacific by *S. domesticus* is an important issue to consider.

Another important issue is that native Pacific salmon (*Oncorhynchus*) are also being used in Pacific Ocean salmon farms, and since domestication of these species only reduces but need not prevent interbreeding, the genetic impacts of these native farmed salmon may greatly exceed those of exotic farmed Atlantic salmon (Gross 2002). The Gross laboratory is therefore working with ecological, genetic and pathology research specialists in Canada and the US to investigate the relative risk of *Salmo* (exotic) and *Oncorhynchus* (native) farm fish losses in BC. Both the Provincial and Federal governments support the development of this new research program.

Facilitating Coexistence Between Commercial Captive Breeding and Wild Salmon
The aquatic ecosystem available to salmon is limited. The Pacific Ocean currently receives 5–6 billion hatchery smolts, 1 billion livestock smolts, and 20 billion wild smolts per year, all of which must compete

for food, space, and waste-absorption (e.g., Levin et al. 2001). The future of salmon will therefore depend upon reducing conflict between these three interests (and others). An integrated and comprehensive salmon management plan is necessary to recognize the legitimate interests of wild fish, capture fisheries and fish farming. Such a plan must adopt an ecosystem approach and recognize that each interest affects the others, since all draw on the production capacity of a single ecosystem. The allocation of resources may require marine zonation similar to that found on land, including such regions as wild salmon sanctuaries, industrial zones for capture fisheries and fish farming, and 'public abuse' zones. The plan should also recognize the metapopulation structuring of salmonid populations, where quasi-extinction is a natural process, and allow for potential recolonization of 'empty' habitats.

To achieve comprehensive management of the interest groups, it will be necessary to acquire detailed data. For salmonids, research has progressed beyond the anecdotal to the empirical. What we still lack in our decision-making, however, is a predictive capacity to address the outcomes of genetic, ecological and pathological interactions at different levels of hatchery release and farm escapement. What we now need is a holistic risk assessment supported by coordinated empirical studies to synthesize and structure information and enumerate the direct environmental costs and benefits of commercial captive breeding in the salmon industry.

Summary

Hatchery reform requires clearly identifying what hatcheries are for (goals), determining if these goals are defensible (cost:benefit analysis), conducting empirical research to fill the holes in the cost:benefit analysis, explicitly dealing with uncertainty (risk analysis), and creating an integrated management plan (other stakeholder goals). An integrated and comprehensive, coast-wide and interior, fisheries management plan is necessary for reducing conflict among stakeholders. The plan must recognize the legitimacy of multiple users: wild fish (wilderness/nature), fisheries aquaculture (ranching industry), livestock aquaculture (fish farming industry), and sport and other cultural fisheries (recreational industry, spiritual industry, First Nation's interests). It must have an ecosystem approach, explicitly recognizing that each 'user' impacts the other since all draw on the capacity of a single ecosystem. Finally, it may need to consider 'zonation', a policy that is widely applied to terrestrial habitats (e.g., urban zones, industrial zones, parks, sanctuaries). Throughout this exercise we must remember that we are not reforming hatcheries (tools), but their application to better meet the needs of society.

References

Please see Appendix 5.

* This presentation was turned into text by Cory Robertson, and on behalf of the Wild Salmon Center (Portland, Oregon) and the IUCN Salmonid Working Group, presented as a contribution by M. Gross and C. Robertson at the Commerical Captive Propogation Workshop held in Florida on 7–9 December 2001. I thank Cory for his efforts.

Discussion

A participant thought that Mart Gross should distinguish between ocean ranching, the form carried out by Alaska, and the form carried out by DFO. They commented that the aspect of ocean ranching which is probably most appropriate for discussion is the fact that the fish are out there and in contact with wild fish. In the case of net cage culture, if we can help it, the fish are not in contact with the wild fish. We want to keep them and sell them; that is the point of the exercise. There is an entirely different exposure ratio and it is an extremely different situation. In BC, the salmon farming industry is not ocean ranching.

Mart Gross responded that he would like to clear that up. You want to recognize that ocean ranching, which Mart Gross believes he heard the participant say, and he is in agreement, is largely the hatchery practice in BC. They are just not recognized as a privatized form of it, but it is essentially a public produced industry, which is ocean ranching. Over here is your fish farming, that is a distinct industry, raising fish in net-pens. So by and large there is less contact with the wild fishes, but there is also more domestication and more divergence. Mart Gross proposed that rather than think of them as a diverged life form, you need to think of them as a new species. Through time they are a new species, just like cows and pigs and sheep are. They are *domesticus*. That is what an ideal goal of fish farming should be because then you have got a really well-developed organism. It is the escapement issues with the environmental protection of the wild fishes type that people are worried about when you have extremely diverged different species. But you are right; we have to keep them apart.

A participant commented: Of course there is a benefit of a mate choice in terms of increased survival, but when you have a very small effective population size there is going to be a cost to the strategy. You are suggesting that there will be an increase in the loss of family lineages. The question is: Have you done any studies to demonstrate that the benefits you are suggesting will more than offset the increased cost of the loss of family lineages?

Mart Gross responded that he had not. The issue is when population sizes become very small in mate choice, because we have a preference for certain individuals, means other individuals will not be able to breed. Generally, most of the females will be able to breed, but some of the males will be excluded. This could reduce the effective population size. This is an interesting balance issue. The tradeoff is loss of genetic diversity with the loss of good gene effects on genetic quality; genetic diversity is for future evolution, genetic quality is for adaptation in the present, which gives populations their population size and resilience. There is a tradeoff, of course. He has initiated an experiment in his laboratory that has been running for about a year and Ian Fleming is running a similar kind of experiment in his research facility. They are working with the stock population and have divided it into three lines. One line of guppies is running in the minimized kinship regime, which is the maximized genetic diversity. One is the mate choice lineage, and one is a random lineage. The experiment will run for several generations. They will look at performance, disease resistance, growth rates, fecundities and perhaps eventually they can look at their evolutionary capacity by changing their environment and seeing which population responds first.

Fred Whoriskey commented that he is looking at cost-benefit analyses using dollars as a common currency. Fred Whoriskey asked the question: Wearing your COSEWIC hat, what is the baseline value for the extinction of a species?

Mart Gross responded that what Fred would like to put a value on, an intrinsic value, is kind of like the Mona Lisa, and what would you give me for the Mona Lisa?

Fred Whoriskey commented that he can see how you would spin upwards from salmon from a baseline value. You have got a lot of dollar values you cannot assign to things, the employment opportunities and everything else. But when push comes to shove, a process has been established, the COSEWIC process, whether it is a butterfly, a snake, or a salmon. You are sitting down there and evaluating that. There must be an inherent value to this, and he would be curious to know what it is.

Mart Gross responded that it becomes very complicated. There will have to be forms of utility evaluation of nature developed, because society is by and large a decision maker on the dollar. Even the federal minister is going to be challenged with making calculations of these values. The very simplistic way we could generate a dollar figure is by looking at what does the COSEWIC Secretariat cost us. That is an indication of how society values endangered species. Of course this is still a trivial cost relatively speaking.

A participant commented that Mart has raised the idea of spatial planning, and she wanted to contrast that to the way that we traditionally manage fisheries. What you are getting at really starts to get into coastal zone management because you are only talking about salmon here, but lots of activities are also occurring in the coastal zone. She has worked for Fisheries and Oceans on the Central Coast Land and Resource Planning process, which is one of the first processes on the west coast that was looking at doing that on a large scale. That is exactly where she goes when she hears what you are saying. Once you start a process like that it might as well consider the whole picture. I would actually zoom out and if you are going to give talks in other places it might be worth while mentioning this.

Mart Gross restated the point made: If we are going to do zonation policy development as part of this global fisheries management plan, we certainly have to integrate it with other uses of coastal zones and indeed even interior zones.

A participant commented that they wanted to come back to the debate and discussion of how things get valued. What has to happen is you have to bring the interests together. That is happening in these processes in BC. The different interests come together and eventually you have to make social and ethical decisions. You can put the dollar values on certain things, but there are other accounts that were raised yesterday. There are things called multiple accounts where you cannot always put dollar values. There are First Nations, which have special cultural considerations. What is the value of a Pacific salmon to a recreational fisherman and to a First Nations person? You are not going to get the same number. It is always going to come back to political and social decisions.

Mart Gross responded that those political and social decisions will have to be guided by some framework and ultimately that will be a financial accounting; that is what all of our society has ended up gravitating towards. People die everyday in Canada because we have made a decision of how much money we will put into investing to save them. These are very hard decisions to make, but we have to do it, it is our only currency of decision-making in the end. They are difficult decisions and we should not trivialize them, and we should not conceal this and pretend that is not the way it works in the end.

A participant commented that they thought that zonation is a very useful concept in the terrestrial ecosystem, but they are not convinced that it is doable in the aquatic or marine environment. The concept of developing these zones, where you may have a hatchery production zone which would be integrated into other aspects of coastal resource management, is really an interesting concept.

Peter Broomhall, Watershed Watch Salmon Society, commented that they are hearing about some very ancient problems, the kind of confusion between the physical and the metaphysical worlds. Sometimes we know the cost of one thing and the value of another, but he is enlightened here too because of the move towards full cost accounting in the public good, and recognizing that eco-economics is going to have to wrestle with things that have not been wrestled with reflectively before. It does not mean there are easy answers. It will mean that it is kind of a dynamic rod. You will have to learn to think in new ways. You will have to think that there is a value to joy, the smiles on people's faces, to laughter. For example, some of you know that studies show that the average adult laughs 14 times per day. The average child laughs 400 times per day. When you value things like health, whether this is now or for the future, you will have to think of the health that is derived from walking streams, from perhaps even days lost from not walking streams, and hospitalization, depression. Some of these things will be easy to factor in, others won't. How will we factor in the stimulation to science, to art, to literature, to thought? Much of it will depend on where you live, whether it is above or below the neck, whether you think a lot or whether you feel a lot, whether you grasp a lot or grasp little. One question that can be answered is: Does this interbreeding cause a specific kind of problem, can it modify migratory effectiveness?

Mart Gross thought Ian Fleming would be able to comment on the migration work with his colleague from ENSA.

Ian Fleming replied that a lot of migration work suggests that if the releases are done appropriately it does not affect it. That is assuming that migration is strictly based on an environment. There are populations, near Harrison Lake, that, when they emerge, have a genetic program in terms of what direction to migrate.

The participant responded that there are only two ways; it is either born in or it is beat in. It seems until we know a little bit more about the migratory behaviour, we are playing Russian roulette with Mother Nature.

Trevor Goff added that there is some evidence for outbreeding depression to be disastrous if migration patterns are coded for. They have never had any success on the East coast when they have tried long distance transplantation. They would get survival, get lots of tags back, lots of ocean survival, but no success to river. When they switched the river of origin they had more success. The reason the transplants were not a success was that it interfered with their natural migrations; sometimes you have a North facing river, sometimes a South facing river, so the fish do not know which way to turn to go to Greenland if they are switched.

A participant commented that he thought the idea of this zonation is going to come down in the future. The description of benefit-cost analysis, and the fact that the Minister, and other decision-makers bring things down to money, and our society as a whole brings things down to dollars, is pretty bleak. Some of the values just cannot be quantified in terms of dollars. You did say that they are going to need a framework under which to make those decisions. Well the framework already exists and it is called the Canadian Constitution. There are a couple of people sitting in this room that have a Constitutional right to the resource, and the rest do not. It is that that is going to provide the framework to make the decisions, and to make sure that wild salmon and their habitats exist in the future.

Mart Gross thanked the participant for those comments. He commented that he was not so sure you cannot quantify all the joys and laughter. People go to amusement parks and they tell you how much they are willing to pay to laugh. And if they laugh more, how much more are they willing to pay? There are actually ways to at least start addressing these issues. In terms of the First Nations communities, they themselves, because of the large holdings, might want to consider these ideas within even their areas, like zonation and what to do with industrialized ocean ranching versus fish farms versus wild fish protection. He commented that he was pleased to have a dialogue on these things.

A participant commented that as an economist, not a fisheries economist, he would like to make a comment that relates to a point that was just made. All the technocratically beautiful comprehensive management plans are not going to work, certainly not on this coast and he doubted on the east coast, until the issue of property rights is resolved. Property rights are now in a state of flux. He was not suggesting that we have to necessarily privatize the fisheries, or we have to go to individual transferable quotas and so on. But the issue of property rights needs to be clarified and as long as there is some kind of doubt on that, you can have all the theoretically, most beautifully comprehensive management plans you could possibly dream up and it's not going to work. Based on the observation that virtually every reasonably accessible open access fishery in recent history, that has been managed by fisheries biologists and fisheries ecologists (who have been a strong source of scientific and technocratic support for what he would call a low wage economy vision for the coastal area management of natural resource extraction) has at one time or another gone into crisis. Are your colleagues aware of this, and is that attitude ever going to change in the future? Do your colleagues really care?

Mart Gross replied that he is not a fisheries ecologist, so he does not have any of those kinds of colleagues per se. He is a conservation biologist, and did not come out of the fisheries profession. People who call themselves fisheries scientists are well aware of those figures and are very concerned by it and are attempting to understand why that should be. Fisheries scientists are very rarely in the position to make policy decisions, which lead to these collapses. They are simply people providing information, and they themselves are very rarely the decision-makers on quotas, allocations or anything like that. You might want to direct some of those concerns to the people who are responsible for making the eventual decisions. From the cod fishery, it is a wonderful example of how politics can subvert science and DFO fisheries scientists were unable to even speak to the press or the public about what their concerns were as the numbers were going down and as quotas remained high. There, the decisions were out of the scientists' hands.

APPENDIX 1 – IAN FLEMING'S REFERENCES

Implications of Stocking: Ecological Interactions Between Wild and Released Salmonids

Sigurd Einum 1,2, and Ian A. Fleming 1,3*

1 Norwegian Institute for Nature Research, Tungasletta
2 N-7485 Trondheim, Norway 2 Department of Zoology, Norwegian University of Science and Technology, N-7034 Trondheim, Norway
3 Coastal Oregon Marine Experiment Station and Department of Fisheries and Wildlife, Oregon State University, Hatfield Marine Science Center, Newport, OR 97365, USA
* Author for correspondence

References

Bachman, R.A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. – Trans.Am. Fish. Soc. 113: 1-32.

Beamish, R.J., B.L. Thomson and G.A. McFarlane. 1992. Spiny dogfish predation on chinook and coho salmon and the potential effects on hatchery-produced salmon. – Trans. Am. Fish. Soc. 121: 444-455.

Berejikian, B.A. 1995. The effects of hatchery and wild ancestry and experience on the relative ability of steelhead trout fry (*Oncorhynchus mykis*s) to avoid a benthic predator. – Can. J. Fish. Aquat. Sci. 52: 2476-2482.

Berejikian, B.A., S.B. Mathews and T.P. Quinn. 1996. Effects of hatchery and wild ancestry and rearing environments on the development of agonistic behavior in steelhead trout (*Oncorhynchus mykis*s) fry. – Can. J. Fish. Aquat. Sci. 53: 2004-2014.

Berejikian, B.A., R.J.F. Smith, E.P. Tezak, S.L. Schroder and C.M. Knudsen. 1999. Chemical alarm signals and complex hatchery rearing habitats affect anti-predator behavior and survival of chinook salmon (*Oncorhynchus tshawytsch*a) juveniles. – Can. J. Fish. Aquat. Sci. 56: 830-838.

Berejikian, B.A., E.P. Tezak, T.A. Flagg, A.L. LaRae, E. Kummerow and C.V.W. Mahnken. 2000. Social dominance, growth, and habitat use of age-0 steel-head (*Oncorhynchus mykis*s) grown in enriched and conventional hatchery rearing environments. – Can. J. Fish. Aquat. Sci. 57: 628-636.

Brown, G.E. and R.J.F. Smith. 1998. Acquired predator recognition in juvenile rainbow trout (*Oncorhynchus mykis*s): conditioning hatchery reared fish to recognize chemical cues of a predator. – Can. J. Fish. Aquat. Sci. 55: 611-617.

Byrne, A., T.C. Bjornn and J.D. McIntyre. 1992. Modelling the response of native steelhead to hatchery supplementation programs in an Idaho river. N. Am. J. Fish. Manage. 12: 62-78.

Collis, K., R.E. Beaty and B.R. Crain. 1995. Changes in catch rate and diet of northern squawfish associated with the release of hatchery-reared juvenile salmonids in a Columbia river reservoir. – N. Am. J. Fish. Manage. 15: 346-357.

Cutts, C.J., N.B. Metcalfe and A.C. Taylor. 1999. Competitive asymmetries in territorial juvenile Atlantic salmon, *Salmo salar.* – Oikos 86: 479-486.

De Leaniz, C.G., E. Verspoor and A.D. Hawkins. 1989. Genetic determination of the contribution of stocked and wild Atlantic salmon, *Salmo salar* L., to the angling fisheries in 2 Spanish rivers. – J. Fish. Biol. 35: 261-270.

Dellefors, C. and J.I. Johnsson. 1995. Foraging under risk of predation in wild and hatchery-reared juvenile sea trout (*Salmo trutta* L.). Nord. J. Fresh. Res. 70:31-37.

Doyle, R.W. and A.J. Talbot. 1986. Artificial selection for growth and correlated selection on competitive behavior in fish. – Can. J. Fish. Aquat. Sci. 43: 1043-1064.

Einum, S. and I.A. Fleming. 1997. Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. – J. Fish Biol. 50: 634-651.

Einum, S. and I.A. Fleming. 2000a. Highly fecund mothers sacrifice offspring survival to maximize fitness. – Nature 405: 565-567.

Einum, S. and I.A. Fleming. 2000b. Selection against late emergence and small offspring in Atlantic salmon (*Salmo sala*r). Evolution 54: 628-639.

Elliott, J.M. 1989 Mechanisms responsible for population regulation in young migratory trout, *Salmo trutt*a. I. The critical time for survival. – J. Anim. Ecol. 58:987-1002

Elliott, J.M. 1990. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta.* II. Fish growth and size variation. – J. Anim. Ecol. 59: 171-185.

Endler, J.A. 1995. Multiple-trait coevolution and environmental gradients in guppies. – Trends Ecol. Evol. 10: 22-29.

Evans, D.O. and C.C. Willox. 1991. Loss of exploited, indigenous populations of lake trout, *Salvelinus namaycus*h, by stocking of non-native stocks. – Can. J.Fish. Aquat. Sci. 48 (Suppl.1): 134-147. Fagen, R. and W.W. Smoker. 1989. How large-capacity hatcheries can alter interannual variability of salmon production. – Fish. Res. 8: 1-11.

Fenderson, O.C., W.H. Everhart and K.M. Muth. 1968. Comparative agonistic and feeding behavior of hatchery-reared and wild salmon in aquaria. – J. Fish. Res. Board Can. 25: 1-14.

Fernö, A. and T. Järvi. 1998. Domestication genetically alters the anti-predator behaviour of anadromous brown trout (*Salmo trutta*) – a dummy predator experiment. – Nordic J. Freshw. Res. 74: 95-100.

Finstad, B. and T.G. Heggberget. 1993. Migration, growth and survival of wild and hatchery-reared anadromous Arctic char (*Salvelinus alpinus*) in Finnmark, northern Norway. – J. Fish Biol. 43: 303-312.

Flagg, T.A. and C.F. Nash (eds.) 1999. A conceptual framework for conservation hatchery strategies for Pacific salmonids. – U.S. Dept. Commer. NOAA Tech. Memo. NMFS-NWFSC-38, 54 p.

Flagg, T.A., F.W. Waknitz, D.J. Maynard, G.B. Milner and C.V.W. Mahnken. 1995. The effect of hatcheries on native coho salmon populations in the lower Columbia River. – Am. Fish. Soc. Symp. 15: 366-375.

Fleming, I.A. 1998. Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. – Can. J. Fish. Aquat. Sci. 55 (Suppl. 1): 59-76.

Fleming, I.A. and S. Einum. 1997. Experimental test of genetic divergence of farmed from wild Atlantic salmon due to domestication. – ICES J. Mar. Sci. 54: 1051-1063.

Fleming, I.A. and E. Petersson. 2001. The ability of hatchery-reared salmonids to breed and contribute to the natural productivity of wild populations. Nordic J. Freshw. Res. 75: 71-98.

Fleming, I.A., B. Jonsson and M.R. Gross. 1994. Phenotypic divergence of sea-ranched, farmed, and wild salmon. – Can. J. Fish. Aquat. Sci. 51: 2808-2824.

Fleming, I.A., K. Hindar, I.B. Mjølnerød, B. Jonsson, T. Balstad and A. Lamberg. 2000. Lifetime success and interactions of farm salmon invading a native population. – Proc. R. Soc. Lond. B 267: 1517-1524.

Flick, W.A. and D.A. Webster. 1964. Comparative first year survival and production in wild and domestic strains of brook trout, *Salvelinus fontinalis.* – Trans. Am. Fish. Soc. 93: 58-69.

Fraser, J.M. 1981. Comparative survival and growth of planted wild, hybrid, and domestic strains of brook trout (*Salvelinus fontinalis*) in Ontario lakes. – Can. J. Fish. Aquat. Sci. 38: 1672-1684.

Gharrett, A.J. and W.W. Smoker. 1991. Two generations of hybrids between even-and odd-year pink salmon (*Oncorhynchus gorbuscha*): a test for outbreeding depression? – Can. J. Fish. Aquat. Sci. 48: 1744-1749.

Green, D.M. 1964. A comparison of stamina of brook trout from wild and domestic parents. – Trans. Am. Fish. Soc. 93: 96-100.

Greenberg, L.A. 1992. The effect of discharge and predation on habitat use by wild and hatchery brown trout (*Salmo trutta*). – Regul. River 7: 205-212.

Hansen, L.P. 1987. Growth, migration and survival of lake reared juvenile anadromous Atlantic salmon *Salmo salar* L. – Fauna Norveg. A 8: 29-34.

Hansen, L.P. 1988. Status of exploitation of Atlantic salmon in Norway. p. 143-161. – In: Mills, D.H. and D.J. Piggins (eds.) Atlantic salmon: planning for the future. Croom Helm, London.

Hansen, L.P. and B. Jonsson. 1985. Downstream migration of hatchery-reared smolts of Atlantic salmon (*Salmo salar* L.) in the river Imsa, Norway. – Aquaculture 45: 237-248.

Hansen, L.P. and B. Jonsson. 1991. Ranching of Atlantic salmon in the River Imsa, Norway. – Int. Counc. Explor. Sea CM 1991/M:35.

Hesthagen, T., O. Hegge, J. Skurdal and B.K. Dervo. 1995. Differences in habitat utilization among native, native stocked, and non-native stocked brown trout (*Salmo trutta*) in a hydroelectric reservoir. – Can. J. Fish. Aquat. Sci. 52: 2159-2167.

Hesthagen, T., L. Fløystad, O. Hegge, M. Staurnes and J.Skurdal. 1999. Comparative life-history characteristics of native and hatchery-reared brown trout, *Salmo trutta* L., in a sub-Alpine reservoir. – Fish. Manag. Ecol. 6: 47-61.

Hindar, K., N. Ryman and F. Utter. 1991. Genetic effects of cultured fish on natural populations. – Can. J. Fish.Aquat. Sci. 48: 945-957.

Hjort, R.C. and C.B. Schreck. 1982. Phenotypic differences among stocks of hatchery and wild coho salmon, *Oncorhynchus kisutch,* in Oregon, Washington, and California. – Fish. Bull. 80: 105-119.

Irvine, J.R. and R.E. Bailey. 1992. Some effects of stocking coho salmon fry and supplemental instream feeding on wild and hatchery-origin salmon. N.Am. J. Fish. Manag. 12: 125-130.

Jansson, H. and T. Öst. 1997. Hybridization between Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in a restored section of the River Dalälven, Sweden. – Can. J. Fish. Aquat. Sci. 54: 2033-2039.

Johnsen, B.O. and O. Ugedal. 1986. Feeding by hatchery-reared and wild brown trout, *Salmo trutta* L., in a Norwegian stream. – Aqua. Fish. Manage. 17: 281-287.

Johnsen, B.O. and O. Ugedal. 1989. Feeding by hatchery-reared brown trout, *Salmo trutta* L. released in lakes. – Aqua. Fish. Manage. 20: 97-104.

Johnsen, B.O. and O. Ugedal. 1990. Feeding by hatchery-and pond-reared brown trout, *Salmo trutta* L., fingerlings released in a lake and in a small stream. – Aqua. Fish. Manage. 21: 253-258.

Johnsson, J.I. and M.V. Abrahams. 1991. Interbreeding with domestic strain increases foraging under threat of predation in juvenile steelhead trout

(*Oncorhynchus mykiss*): an experimental study. – Can. J. Fish. Aquat. Sci. 48: 243-247.

Johnsson, J.I., E. Petersson, E. Jönsson, B.T. Björnsson and T. Järvi. 1996. Domestication and growth hormone alter anti-predator behavior and growth patterns in juvenile brown trout, *Salmo trutta.* – Can. J. Fish. Aquat. Sci. 53: 1546-1554.

Johnsson, J.I., F. Nöbbelin and T. Bohlin. 1999. Territorial competition among wild brown trout fry: effects of ownership and body size. – J. Fish Biol. 54: 469-472.

Jonsson, B. and I.A. Fleming. 1993. Enhancement of wild salmon populations. p. 209-238. – In: G. Sundnes (ed.) Human impact on self-recruiting populations. Tapir Press, Trondheim.

Jonsson, B., N. Jonsson and L.P. Hansen. 1990. Does juvenile experience affect migration and spawning of adult Atlantic salmon? – Behav. Ecol. Sociobiol. 26: 225-230.

Jonsson, B., N. Jonsson and L.P. Hansen. 1991. Differences in life history and migratory behaviour between wild and hatchery-reared Atlantic salmon in nature. Aquaculture 98: 69-78.

Kallio-Nyberg, I. and M.-L. Koljonen. 1997. The genetic consequence of hatchery-rearing on life-history traits of the Atlantic salmon (*Salmo salar* L.): a comparative analysis of sea-ranched salmon with wild and reared parents. – Aquaculture 153: 207-224.

Kelly-Quinn, M. and J.J. Bracken. 1989. Survival of stocked hatchery-reared brown trout, *Salmo trutta* L., fry in relation to the carrying capacity of a trout nursery stream. – Aqua. Fish. Manage. 20: 211-226.

L'Abée-Lund, J.H. and A. Langeland. 1995. Recaptures and resource use of native and non-native brown trout, *Salmo trutta* L., released in a Norwegian lake. – Fish. Manage. Ecol. 2: 135-145.

Lachance, S. and P. Magnan. 1990a. Comparative ecology and behavior of domestic, hybrid, and wild strains of brook trout, *Salvelinus fontinalis,* after stocking. – Can. J. Fish. Aquat. Sci. 47: 2285-2292.

Lachance, S. and P. Magnan. 1990b. Performance of domestic, hybrid, and wild strains of brook trout, *Salvelinus fontinalis,* after stocking: the impact of intra- and interspecific competition. – Can. J. Fish. Aquat. Sci. 47: 2278-2284.

Lannan, J.E. 1980. Adaptive and behavioral responses to artificial propagation in a stock of chum salmon, *Oncorhynchus keta.* p. 309-312. – In: McNeil, W.J. and D.C. Himsworth (eds.) Salmonid Ecosystems of the North Pacific. Oregon State University Press, Corvalis.

Leary, R.F., F.W. Allendorf and G.K. Sage. 1995. Hybridization and introgression between introduced and native fish. – Am. Fish. Soc. Symp. 15: 91-101.

Levings, C.D., C.D. McAllister and B.D. Chang. 1986. Differential use of the Campbell River estuary, British Columbia, by wild and hatchery-reared juvenile chinook salmon (*Oncorhynchus tshawytscha*). – Can. J. Fish. Aquat. Sci. 43: 1386-1397.

Maynard, D.J., T.A. Flagg and C.V.W. Mahnken. 1995. A review of innovative culture strategies for enhancing the post-release survival of anadromous salmonids. – Am. Fish. Soc. Symp. 15: 307-314.

Mesa, M.G. 1991. Variation in feeding, aggression, and position choice between hatchery and wild cutthroat trout in an artificial stream. – Trans. Am. Fish. Soc. 120: 723-727.

Miller, R.B. 1952. Survival of hatchery-reared cutthroat trout in an Alberta stream. – Trans. Am. Fish. Soc. 81: 35-42.

Miller, R.B. 1953. Comparative survival of wild and hatchery-reared cutthroat trout in a stream. – Trans. Am. Fish. Soc. 83: 120-130.

Moyle, P.B. 1969. Comparative behavior of young brook trout of domestic and wild origin. – Prog. Fish-Cult. 31: 51-56.

Nickelson, T.E., M.F. Solazzi and S.L. Johnson. 1986. Use of hatchery coho salmon (*Oncorhynchus kisutch*) presmolts to rebuild wild populations in Oregon coastal streams. – Can. J. Fish. Aquat. Sci. 43: 2443-2449.

Norman, L. 1987. Stream aquarium observations of territorial behaviour in young salmon (*Salmo salar* L.) of wild and hatchery origin. – Salmon Research Institute Report, Sweden 1987: 2, 7 p. (In Swedish with English abstract.)

Olla, B.L. and M.W. Davis. 1989. The role of learning and stress in predator avoidance of hatchery-reared coho salmon (*Oncorhynchus kisutch*) juveniles. – Aquaculture 76: 209-214.

Olla, B.L., M.W. Davis and C.H. Ryer. 1998. Understanding how the hatchery environment represses or promotes the development of behavioural survival skills. – Bull. Mar. Sci. 62: 531-550.

Pakkasmaa, S. 2000. Morphological and early life history variation in salmonid fishes. – Ph.D. Dissertation, Department of Ecology and Systematics, University of Helsinki, Finland.

Petersson, E. and T. Järvi. 1995. Evolution of morphological traits in sea trout (*Salmo trutta*) parr (0+) through sea-ranching. – Nord. J. Freshw. Res. 70: 62-67.

Petersson, E., T. Järvi, N.G. Steffner and B. Ragnarsson.1996. The effect of domestication on some life history traits of sea trout and Atlantic salmon. – J. Fish Biol. 48: 776-791.

Petrosky, C.E. and T.C. Bjornn. 1988. Response of wild rainbow (*Salmo gairdneri*) and cutthroat trout (*S. clarki*) to stocked rainbow trout in fertile and infertile streams. – Can. J. Fish. Aquat. Sci. 45: 2087-2105.

Potter, B.G. 1977. Body size and learned avoidance as factors affecting predation on coho salmon, *Oncorhynchus kisutch,* fry by torrent sculpin, *Cottus rhothaus.* Fish. Bull. 75: 457-459.

Potter, E.C.E. and I.C. Russel. 1994. Comparison of the distribution and homing of hatchery-reared and wild Atlantic salmon, *Salmo salar* L., from north-east England. – Aqua. Fish. Manage. 25 (Suppl. 2): 31-44.

Reinhardt, U.G. Selection for surface feeding in farmed and sea-ranched salmon juveniles. – Trans. Am. Fish. Soc. (In press.)

Reiriz, L., A.G. Nicieza and F. Braña. 1998. Prey selection by experienced and naive juvenile Atlantic salmon. – J. Fish Biol. 53: 100-114.

Reisenbichler, R.R. and J.D. McIntyre. 1977. Genetic difference in growth and survival of juvenile hatchery and wild steelhead trout, *Salmo gairdneri.* – J. Fish. Res. Board Can. 34: 123-128.

Reisenbichler, R.R. 1988. Relation between distance transferred from natal stream and recovery rate for hatchery coho salmon. – N. Am. J. Fish. Manage. 8: 172-174.

Ricker, W.E. 1972. Hereditary and environmental factors affecting certain salmonid populations. p. 19-160. – In: Simon, R.C. and P. A. Larkin (eds.) The Stock Concept in Pacific Salmon. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver.

Rhodes, J.S. and T.P. Quinn. 1998. Factors affecting the outcome of territorial contests between hatchery and naturally reared coho salmon parr in the laboratory. – J. Fish Biol. 53: 1220-1230.

Riddell, B.E. and W.C. Leggett. 1981. Evidence for an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile Atlantic salmon *Salmo salar.* – Can. J. Fish. Aquat. Sci. 38: 308-320.

Riddell, B.E., W.C. Leggett and R.L. Saunders. 1981. Evidence of adaptive polygenic variation between two populations of Atlantic salmon *Salmo salar* native to tributaries of the S. W. Miramichi River, N. B. – Can. J. Fish. Aquat. Sci. 38: 321-333.

Ruzzante, D.E. and R.W. Doyle. 1991. Rapid behavioral changes in medaka (*Oryzias latipes*) caused by selection for competitive and noncompetitive growth. – Evolution 45: 1936-1946.

Ryman, N., F. Utter and K. Hindar. 1995. Intro-gression, supportive breeding, and genetic conservation. p. 341-365. – In: J. D. Ballou, M. Gilpin and T. J. Foose (eds.) Population management for survival and recovery. Analytical methods and strategies in small population con-servation. Columbia University Press, New York.

Saunders, R.L. 1991. Potential interaction between cultured and wild Atlantic salmon. – Aquaculture 98: 51-60.

Skaala, O., K.E. Jorstad and R. Borgstrøm. 1996. Genetic impact on two wild brown trout (*Salmo trutta*) populations after release of non-indigenous hatchery spawners. – Can. J. Fish. Aquat. Sci. 53: 2027-2035.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. – W. H. Freeman and Company, San Francisco.

Sosiak, A.J., R.G. Randall and J.A. McKenzie. 1979. Feeding by hatchery-reared and wild Atlantic salmon (*Salmo salar*) parr in streams. – J. Fish. Res. Board Can. 36: 1408-1412.

Sundström, L.F. and J.I. Johnsson. Experience and social environment influence the ability of young brown trout to forage on live novel prey. – Anim. Behav. (In press.)

Swain, D.P. and L.B. Holtby. 1989. Differences in morphology and behavior between juvenile coho salmon (*Oncorhynchus kisutch*) rearing in a lake and in its tributary stream. – Can. J. Fish. Aquat. Sci. 46: 1406-1414.

Swain, D.P. and B.E. Riddell. 1990. Variation in agonistic behavior between newly emerged juveniles from hatchery and wild populations of coho salmon, *Oncorhynchus kisutch.* – Can. J. Fish. Aquat. Sci. 47: 566-571.

Swain, D.P., B.E. Riddell and C.B. Murray. 1991. Morphological differences between hatchery and wild populations of coho salmon (*Oncorhynchus kisutch*): environmental versus genetic origin. – Can. J. Fish. Aquat. Sci. 48: 1783-1791.

Taylor, E.B. 1986. Differences in morphology between wild and hatchery populations of juvenile coho salmon. – Prog. Fish-Cult. 48: 171-176.

Taylor, E.B. 1988. Adaptive variation in rheotactic and agonistic behavior in newly emerged fry of chinook salmon, *Oncorhynchus tshawytscha,* from ocean- and stream-type populations. – Can. J. Fish. Aquat. Sci. 45: 237-243.

Taylor, E.B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. – Aquaculture 98:185-207.

Thomas, G.L. and O.A. Mathisen. 1993. Biological inter-actions of natural and enhanced stocks of salmon in Alaska. – Fish. Res. 18: 1-17.

Unwin, M.J. 1997. Fry-to-adult survival of natural and hatchery-produced chinook salmon (*Oncorhynchus tshawytsch*a) from a common origin. – Can. J. Fish. Aquat. Sci. 54: 1246-1254.

Unwin, M.J. and G.J. Glova. 1997. Changes in life history parameters in a naturally spawning popula-tion of chinook salmon (*Oncorhynchus tshawytscha*) associated with releases of hatchery-reared fish. – Can. J. Fish. Aquat. Sci. 54: 1235-1245.

Vincent, R.E. 1960. Some influences of domestication upon three stocks of brook trout (*Salvelinus fontinalis* Mitchill). – Trans. Am. Fish. Soc. 89: 35-52.
Vincent, E.R. 1987. Effects of stocking catchable-size hatchery rainbow trout on two wild trout species in the Madison River and O'Dell Creek, Montana. N.Am. J.Fish. Manage. 7: 91-105.
Waples, R.S. 1991. Genetic interactions between hatchery and wild salmonids: lessons from the Pacific Northwest. – Can. J. Fish. Aquat. Sci. 48 (Suppl. 1): 124-133.
Waples, R.S. 1999. Dispelling some myths about hatcheries. – Fisheries 24: 12-21.
Weiss, S. and S. Schmutz. 1999. Response of resident brown trout, *Salmo trutta* L., and rainbow trout, *Oncorhynchus mykiss* (Walbaum), to the stocking of hatchery-reared brown trout. – Fish. Manage. Ecol. 6: 365-375.
Wootton, R.J. 1994. Ecology of teleost fishes. – Chapman & Hall, London.
Youngson, A.F. and E. Verspoor. 1998. Interactions between wild and introduced Atlantic salmon (*Salmo salar*). – Can. J. Fish. Aquat. Sci. 55 (Suppl. 1): 153-160.

The Ability of Released, Hatchery Salmonids to Breed and Contribute to the Natural Productivity of Wild Populations

Ian A. Fleming, 1 and Erik Petersson†*

* Norwegian Institute for Nature Research, Tungasletta 2, N-7485 Trondheim, Norway.

† Department of Animal Ecology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18 D, SE-752 36 Uppsala, Sweden and National Board of Fisheries, Laboratory of Stream Water Ecology, Brobacken, SE-814 94 Älvkarleby, Sweden.

1 Current address: Coastal Oregon Marine Experiment Station and Department of Fisheries and Wildlife, Oregon State University, Hatfield Marine Science Center, Newport, OR 97365-5296, USA.

References

Allendorf, F.W. and R.F. Leary. 1988. Conservation and distribution of genetic variation in a polytypic species, the cutthroat trout. – Cons. Biol. 2: 170-184.
Alm, G. 1959. Connection between maturity, size and age in fishes. – Rep. Inst. Freshw. Res., Drottningholm, 40:1-145.
Altukhov, Yu.P. and E.A. Salmenkhova. 1987. Stock transfer relative to natural organization, management, and conservation of fish populations, p. 333-343. – In: Ryman, N. and F.M. Utter (eds.) Population genetics and fishery management. University of Washington Press, Seattle.
Altukhov, Yu. P. and E.A. Salmenkhova. 1990. Introductions of distinct stocks of chum salmon, *Oncorhynchus keta* (Walbaum) into natural populations of the species. – J. Fish Biol. 37 (Suppl. A): 25-33.
Andersson, M. 1994. Sexual selection. – Princeton University Press, Princeton.
Anon. 1997. Report of the Baltic salmon and trout assessment working group, Charlottenlund, Denmark, 7-16 April 1997. ICES CM 1997/Assess: 11.
Apostolidis, A.P., Y. Karakousis and C. Triantaphyllidis. 1996. Genetic differentiation and phylogenetic relationships among Greek *Salmo trutta* L. (brown trout) populations as revealed by RFLP analysis of PCR amplified mitochondrial DNA segments. – Heredity 77: 608-618.
Apostolidis, A.P., C. Triantaphyllidis, A. Kouvatsi and P.S. Economidis. 1997. Mitochondrial DNA sequence variation and phylogeography among *Salmo trutta* L. (Greek brown trout) populations. – Mol. Ecol. 6: 531-542.
Ayerst, J.D. 1977. The role of hatcheries in rebuilding steelhead runs of the Columbia River system. – Am. Fish. Soc. Spec. Publ. 10: 84-88.
Arnold, S. J. 1983. Morphology, performance and fitness. – Am. Zool. 23: 347-361.
Bagenal, T.B. 1969. Relationship between egg size and fry survival in brown trout, *Salmo trutta* L. – J. Fish Biol. 1: 349-353.
Barbat-Leterrier, A., R. Guyomard and F. Krieg. 1989. Introgression between introduced domesticated strains and Mediterranean native populations of brown trout (*Salmo trutta* L.). – Aquat. Liv. Res. 2: 215-223. 91
The Ability of Hatchery Salmonids to Breed
Beacham T. D. and C.B. Murray. 1993. Fecundity and egg size variation in North American Pacific salmon (*Oncorhynchus*). – J. Fish Biol. 42: 485-508.
Bell, G. 1980. The cost of reproduction and their consequences. – Am. Nat. 116: 45-76.
Berejikian, B.A., E.P. Tezak, S.L. Schroder, C.M. Knudsen and J.J. Hard. 1997. Reproductive behavioral interactions between wild and captively reared coho salmon (*Oncorhynchus kisutch*). – ICES J. Mar. Sci. 54: 1040-1050.
Berg, O.K., A.P. Hendry, B. Henrikson, C. Bech, J.V. Arnekleiv and A. Lohrmann. 2000. Maternal provisioning of offspring and the use of those resources during ontogeny: variation within and between Atlantic salmon families. – Funct. Ecol. (In press.)
Berrebi, P., C. Poteaux, M. Fissier and G. Cattaneo-Berrebi. 2000. Stocking impact and allozyme diversity in brown trout from Mediterranean southern France. J. Fish Biol. 56: 949-960.
Beverton, R. J. H. and S.T. Holt. 1959. A review of lifespans and mortality rates of fish in nature, and their relation to growth and other physiological

characteristics, p. 142-180. – In: Wolstenholme, G.E.W. and M. O'Connor (eds.) Ciba Foundation Colloquia on Ageing, Volume 5.Churchill, London.

Blanchfield, P.J. and M.S. Ridgway. 1997. Reproductive timing and use of redd sites by lake-spawning brook trout (*Salvelinus fontinalis*). – Can. J. Fish. Aquat. Sci. 54: 747-756.

Bohlin, T., C. Dellefors and U. Faremo. 1986. Early sexual maturation of male sea trout and salmon – an evolutionary model and some practical implications. – Rep.Inst. Freshw. Res., Drottningholm 63: 17-25.

Bohlin, T., C. Dellefors and U. Faremo. 1990. Large or small at maturity – theories on the choice of alternative male strategies in anadromous salmonids. Ann.Zool. Fennici 27: 139-147.

Boyce, N.P.J. 1974. Biology of *Eubothrium salvelini* (Cestoda: Pseudophyllidea), a parasite of juvenile sockeye salmon (*Oncorhynchus nerka*) of Babine Lake, British Columbia. – J. Fish. Res. Board Can. 31: 1735-1742.

Brännäs, E. 1995. First access to territorial space and exposure to strong predation pressure: a conflict in early emerging Atlantic salmon (*Salmo salar* L.). – Evol. Ecol. 9: 411-420.

Brannon, E. L. 1987. Mechanisms stabilizing salmonid fry emergence timing. – Can. Spec. Publ. Fish. Aquat. Sci. 96: 120-124.

Burger, C.V., R.L. Wilmot and D.B. Wangaard. 1985. Comparison of spawning areas and times for two runs of chinook salmon (*Oncorhynchus tshawytscha*) in the Kenai River, Alaska. – Can. J. Fish. Aquat. Sci. 42: 693-700.

Burley, N. 1983. The meaning of assortative mating. – Ethol. Sociobiol. 4: 191-203.

Cagigas, M.E., E. Vázquez, G. Blanco and J.A. Sánchez. 1999. Genetic effects of introduced hatchery stocks on indigenous brown trout (*Salmo trutta* L.) populations in Spain. – Ecol. Freshw. Fish 8: 141-150.

Campbell, J. S. 1977. Spawning characteristics of brown trout and sea trout, *Salmo trutta* L. in Kirk Burn, River Tweed, Scotland.-J. Fish Biol. 11: 217-229.

Campton, D.E., F.W. Allendorf, R.J. Behnke and F.M. Utter; Chilcote, M.W., S.A. Leider and J.J. Loch. 1991. Reproductive success of hatchery and wild steelhead. – Trans. Am. Fish. Soc. 120: 816-827.

Caughley, G. 1994. Directions in conservation biology. – J. Anim. Ecol. 63: 215-244.

Chadwick, E.M.P. 1988. Relationship between Atlantic salmon smolts and adults in Canadian Rivers, p. 301-324. – In: Mills, D. and D. Piggins (eds.) Atlantic salmon: Planning for the future. Croom Helm, London.

Chadwick, E.M.P. and R.R. Clayton. 1990. Predict-ability in a small commercial Atlantic salmon fishery in western Newfoundland.-Fish. Res. 10: 15-27.

Chandler, G.L. and T.C. Bjornn. 1988. Abundance, growth, and interactions of juvenile steelhead relative to time of emergence. – Trans. Am. Fish. Soc. 117: 432-443.

Chapman , D.W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. – Trans. Am. Fish. Soc. 117: 1-21.

Charlesworth, B. 1980. Evolution in age-structured populations. – Cambridge University Press, Cambridge. 300 p.

Chilcote, M. 1997. Conservation status of steelhead in Oregon. – Oregon Department of Fish and Wildlife, Portland, OR.

Chilcote, M.W., S.A. Leider and J.J. Loch. 1986. Differential reproductive success of hatchery and wild summer-run steelhead under natural conditions. – Trans. Am. Fish. Soc. 115: 726-735.

Christensen, O. and P.-O. Larsson, P.-O. (eds.). 1979. Review of Baltic Salmon Research. – Int. Counc. Explor. Sea, Coop. Res. Rep. No. 89.

Cox, C. and B.J. LeBeouf. 1977. Female incitation of male competition: a mechanism in sexual selection. – Am. Nat. 111: 317-335.

Crisp, D.T. 1981. A desk study of the relationship between temperature and hatching time for the eggs of five species of salmonid fishes. – Freshw. Biol. 11: 361-368.

Crisp, D.T. 1989. Some impacts of human activities on trout, *Salmo trutta,* populations. – Freshw. Biol. 21:21-33.

Crozier, W.W. and G.J.A. Kennedy. 1993. Marine survival of wild and hatchery-reared Atlantic salmon (*Salmo salar* L.) from the River Bush, Northern Ireland, p.139-162. – In: Mills, D. (ed.) Salmon in the sea and new enhancement strategies. Fishing News Books, London.

de Gaudemar, B., J.M. Bonzom and E. Beall. 2000. Effects of courtship and relative mate size on sexual motivation in Atlantic salmon. – J. Fish Biol. 57: 502-515.

DeVries, P. 1997. Riverine salmonid egg burial depths: review of published data and implications for scour studies. – Can. J. Fish. Aquat. Sci. 54: 1685-1698.

Einum, S. and I.A. Fleming. 1999. Maternal effects of egg size in brown trout (*Salmo trutta*): norms of reaction to environmental quality. – Proc. R. Soc. Lond. B 266: 2095-2100.

Einum, S. and I.A. Fleming. 2000a. Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). – Evolution 54: 628-639.

Einum, S. and I.A. Fleming. 2000b. Highly fecund mothers sacrifice offspring survival to maximize fitness. – Nature 405: 565-567.

Einum, S. and I.A. Fleming. 2001. Implications of stocking: ecological interactions between wild and

released salmonids. – Nordic J. Freshw. Res. 75: 56-70.
Elliott, J. M. 1986. Spatial distribution and behavioral movements of migratory trout (*Salmo trutta*) in lake District stream. – J. Anim. Ecol. 55: 907-922,.
Elliott , J. M. 1994. Quantitative ecology and the brown trout. – Oxford University Press.
Elson, P. F. 1962. Predator-prey relationships between fish-eating birds and Atlantic salmon, *Salmo salar.* – Freshw.Biol. 25: 61-70.
Essington, T.E., P.W. Sorensen and D.G. Paron. 1998. High rate of redd superimposition by brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in a Minnesota stream cannot be explained by habitat availability alone. – Can. J. Fish. Aquat. Sci. 55: 2310-2316.
Essington, T.E., T.P. Quinn and V.E. Ewert. 2000. Intra-and inter-specific competition and the reproductive success of sympatric Pacific salmon. – Can. J. Fish. Aquat. Sci. 57: 205-213.
Evans, D.M. 1994. Observations on the spawning behavior of male and female adult sea trout, *Salmo trutta* L., using radio-telemetry. – Fish. Manag. Ecol. 1: 91-105.
Fausch, K. D. and R.J. White. 1986. Competition among juveniles of coho salmon, brook trout, and brown trout in a laboratory stream and implications for Great lakes tributaries. – Trans. Am. Fish. Soc. 115: 363-381.
Finstad, B. and N. Jonsson. 2001. Factors affecting the yield of smolt releases in Norway. – Nordic J. Freshw. Res. 75: 37-55.
Fjellheim, A. and B.O. Johnsen. 2001. Stocking of salmonid fry and fingerlings in Norway: status and future management. – Nordic J. Freshw. Res. 75: 20-36.
Flagg, T.A., F.W. Waknitz, D.J. Maynard, G.B. Milner and V.W. Mahken. 1995. The effect of hatcheries on native coho salmon populations in the Lower Columbia River. – Am. Fish. Soc. Symp. 15: 366-375.
Fleming, I.A. 1994. Captive breeding and the conservation of wild salmon populations. – Conserv. Biol. 8: 886-888.
Fleming, I.A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. – Rev. Fish Biol. Fish. 6: 379-416.
Fleming, I.A. 1998. Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. – Can. J. Fish. Aquat. Sci. 55(Suppl. 1): 59-76.
Fleming, I.A. and M.R. Gross. 1989. Evolution of adult female life history and morphology in a pacific salmon (coho: *Oncorhynchus kisutch*). – Evolution 43: 141-157
Fleming, I.A. and M.R. Gross. 1990. Latitudinal clines: a trade-off between egg number and size in Pacific salmon. – Ecology 71: 1-11.
Fleming, I.A. and M.R. Gross. 1992. Reproductive behavior of hatchery and wild coho salmon (*Oncorhynchus kisutch*): does it differ? – Aquaculture 103: 101-121.
Fleming, I.A. and M.R. Gross. 1993. Breeding success of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in competition. – Ecol. Appl. 3: 230-245.
Fleming, I.A. and M.R. Gross. 1994. Breeding competition in a pacific salmon (coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. – Evolution 48: 637-657.
Fleming, I.A. and S. Ng. 1987. Evaluation of techniques for fixing, preserving and measuring salmon eggs. – Can. J. Fish. Aquat. Sci. 44: 1957-1962.
Fleming, I.A., B. Jonsson and M.R. Gross. 1994. Phenotypic divergence of sea-ranched, farmed, and wild salmon. – Can. J. Fish. Aquat. Sci. 51: 2808-2824.
Fleming , I.A., B. Jonsson, M.R. Gross and A. Lamberg. 1996. An experimental study of reproductive behavior and success of farmed and wild Atlantic salmon (*Salmo salar*). – J. Appl. Ecol. 33: 893-905.
Fleming, I.A., A. Lamberg and B. Jonsson. 1997. Effects of early experience on the reproductive performance of Atlantic salmon. – Behav. Ecol. 8: 470-480.
Fleming, I.A., K. Hindar, I.B. Mjølnerød, B. Jonsson, T. Balstad and A. Lamberg. 2000. Lifetime success and interactions of farm salmon invading a native population. – Proc. Roy. Soc., Lond. B 267: 1517-1524.
Foote, C. J. 1988. Male mate choice dependent of male size in salmon. – Behaviour 106: 63-80.
Foote, C. J. 1989. Female mate preferences in Pacific salmon. – Anim. Behav. 38: 721-723.
Foote, C. J. and P.A. Larkin. 1988. The role of male choice in the assortative mating of anadromous and non-anadromous sockeye salmon (*Oncorhynchus nerka*). – Behavior 106: 43-62.
Ford, N. B. and R.A. Seigel. 1994. An experimental study of the trade-offs between age and size at maturity: effects of energy availability. – Func. Ecol. 8: 91-96.
Fowler, L. G. 1972. Growth and mortality of fingerling chinook salmon as affected by egg size. – Prog. Fish. Cult. 34: 66-69.
Gadgil, M and W. Bossert. 1970. Life historical consequences of natural selection. – Am. Nat. 104: 1-24.
Gall, G.A.E. 1974. Influence of size of eggs and age of females on hatchability and growth in rainbow trout. – Cal.Fish. Game 60: 16-35.

Garcia-Marin, J.L., P.E. Jorde, N. Ryman, F.M. Utter and C. Pla. 1991. Management implications of genetic differentiation between native and hatchery populations of brown trout (*Salmo trutta*) in Spain. – Aquaculture 95: 235-249.

Garcia-Marin, J.L., N. Sanz and C. Pla. 1999. Erosion of the native genetic resources of brown trout in Spain. – Ecol. Freshw. Fish 8: 151-158.

Gharrett, A.J. and W.W. Smoker. 1991. Two generation of hybrids between even- and odd-year pink salmon (*Oncorhynchus gorbuscha*): a test for outbreeding depression? – Can. J. Fish. Aquat. Sci. 48: 1744-1749.

Gharrett, A.J. and W.W. Smoker. 1993. Genetic components in life history traits contribute to population structure, p. 197-202. – In: Cloud, J.G. and G.H. Thorgaard (eds.) Genetic conservation of salmonid fishes. Plenum Press, New York.

Gibson, R.J. 1993. The Atlantic salmon in fresh water: spawning, rearing and production. – Rev. Fish Biol. Fish.3: 39-73.

Gíslason, D., M.M. Ferguson, S. Skúlason and S.S. Snorrason. 1999. Rapid and coupled phenotypic and genetic divergence in Icelandic Arctic char (*Salvelinus alpinus*). – Can. J. Fish. Aquat. Sci. 56: 2229-2234.

Giuffra, E., R. Guyomard and G. Forneris. 1996. Phylogenetic relationships and introgression patterns between incipient parapatric species of Italian brown trout (*Salmo trutta* L. complex). – Mol. Ecol. 5: 207-220.

Goodman, D. 1987. The demography of chance extinction, p. 11-34. – In: Soulé, M.E. (ed.) Viable populations for conservation. Cambridge University Press, Cambridge.

Grahn, M., Å. Langefors and T. von Schantz. 1998. The importance of mate choice in improving viability in captive populations. p. 341-363. – In: Caro, T. (ed.) Behavioral ecology and conservation biology. Oxford University Press, Oxford.

Groot, C. and L. Margolis (eds.). Pacific salmon life histories. – University of British Columbia Press, Vancouver. 564 p.

Gross, M.R. 1984. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes, p. 55-75. – In: Potts, G. and R.J. Wootton (eds.) Fish Reproduction: Strategies and Tactics. Academic Press, London.

Gross, M.R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. – Trends Ecol. Evol. 11: 92-98.

Gunnerød, T.B. , N.A. Hvidsten. and T.G. Heggberget. 1988.Open sea releases of Atlantic salmon smolts *Salmo salar,* in central Norway, 1973-83. – Can. J. Fish. Aquat. Sci. 45: 1340-1345.

Guyomard, R. 1989. Diversité génétique de la truite com-mune. – Bull. Fr. Pêche Piscic. 314: 118-135. (In French).

Gyllensten, U., R.F. Leary, F.W. Allendorf and A.C. Wilson. 1985. Introgression between two cutthroat trout sub-species with substantial karyotypic, nuclear and mitochondrial genomic divergence. – Genetics 111: 905-915.

Hamor, T. and E.T. Garside. 1977. Size relations and yolk utilization in embryonated ova and alevins of Atlantic salmon, *Salmo salar* L. in various combinations of temperature and dissolved oxygen. – Can. J. Zool. 55: 1892-1898.

Hansen, L.P. and B. Jonsson. 1991. The effect of timing of Atlantic salmon smolt and post-smolt release on the distribution of adult return. – Aquaculture 98: 61-71.

Hansen, L.P. and B. Jonsson. 1994. Development of sea ranching of Atlantic salmon, *Salmo salar* L., towards a sustainable aquaculture strategy. – Aquacult. Fish. Manag. 25(Suppl. 1): 199-214.

Hansen, L.P. and T.P. Quinn. 1998. The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. Can. J. Fish. Aquat. Sci. 55(Suppl. 1): 104-118.

Hansen, L. P., B. Jonsson and R. Andersen. 1989. Salmon ranching experiments in the River Imsa: is homing dependent on sequential imprinting of the smolts? p. 19-29. – In: Brannon, E. and B. Jonsson (eds.) Proceedings of the salmonid migration and distribution symposium. School of Fisheries, University of Washington, Seattle.

Hansen, M.M. and V. Loeschecke. 1994. Effects of releasing hatchery-reared brown trout to wild trout populations. p. 273-289. – In: Loeschecke, V. and S.K. Jain (eds.) Conservation Genetics. Birkhäuser Verlag, Basel.

Hansen, M.M., V. Loeschecke, G. Rasumussen and V. Simonsen. 1993. Genetic differentiation among Danish Brown trout (*Salmo trutta*) populations. – Hereditas 118: 177-185.

Hansen, M.M., R.A. Hynes, V. Loeschcke and G. Rasmussen. 1995. Assessment of the stocked or wild origin of anadromous brown trout (*Salmon trutta* L.) in a Danish river system, using mito-chondrial DNA RFLP analysis. – Mol. Ecol. 4: 189-198.

Hansen, M.M., D.E. Ruzzante, E.E. Nielsen and K.-L.D. Mensberg. 2000. Microsatellite and mito-chondrial DNA polymorphism reveals life-history dependent inter-breeding between hatchery trout and wild brown trout (*Salmo trutta* L.). – Mol. Ecol. 9: 583-594.

Hansen, M.M., D.E. Ruzzante, E.E. Nielsen and K.-L.D. Mensberg. Brown trout (*Salmo trutta*) stocking impact assessment using microsatellite DNA markers. – Ecol. Appl. (In press.)

Hanson, A. J. and H.D. Smith. 1967. Mate selection in a population of sockeye salmon (*Oncorhynchus nerka*) of mixed age groups. – J. Fish. Res. Board Can. 24: 1955-1977.

Hard, J.J., B.A. Berejikian, E.P. Tezak, S.L. Schroder, C.M. Knudsen and L.T. Parker. 2000. Evidence for morphometric differentiation of wild and captively reared adult coho salmon: a geometric analysis. – Environ. Biol. Fish. 58: 61-73.

Heggberget, T.G., T. Hauke, J. Mork, and G. Ståhl 1988. Temporal and spatial segregation of spawning in sympatric populations of Atlantic salmon, *Salmo salar* L. and brown trout, *Salmo trutta* L. – J. Fish. Biol. 33: 347-356.

Heggberget, T.G. 1988. Timing of spawning in Norwegian Atlantic salmon (*Salmo salar*). – Can. J. Fish Aquat. Sci. 10: 1681-1698.

Héland, M. 1980a. The downstream migration of brown trou*t, Salmo trutta,* fry. I Characteristics in an artificial environment. – Annales de Limnologie 16: 233-245.

Héland, M. 1980b. The downstream migration of brown trout, *Salmo trutta,* fry. II Activity of downstream migrants compared with that of non-migrants. – Annales de Limnologie 16: 247-254.

Heming, T.A. 1982. Effects of temperature on utilization of yolk by chinook salmon (*Oncorhynchus tshawytscha*) eggs and alevins. – Can. J. Fish. Aquat. Sci. 39: 184-190.

Hemmer, H. 1990. Domestication: the decline of environmental appreciation. – Cambridge University Press, Cambridge.

Hendry, A.P., O.K. Berg and T.P. Quinn. 1999. Condition dependence and adaptation-by-time: breeding date, life history, and energy allocation within a population of salmon. – Oikos 85: 499-514.

Hendry, A.P., T. Day and A.B. Cooper. Optimal propagule size and number: allowance for discrete stages, and effects of maternal size on total reproductive output and offspring fitness. – Am. Nat. (In press.)

Hindar, K., N. Ryman and F. Utter. 1991. Genetic effects of cultured fish on natural fish populations. – Can. J. Fish. Aquat. Sci. 48: 945-947.

Holtby, L.B. and M.C. Healey. 1986. Selection for adult size in female coho salmon (*Oncorhynchus kisutch*). – Can. J. Fish. Aquat. Sci. 43: 1946-1959.

Hutchings, J. A. 1991. Fitness consequences of variation in egg size and food abundance in brook trout *Salvelinus fontinalis.* – Evolution 45: 1162-1168.

Hutchings, J. A. 1994. Age- and size-specific costs of re-production within populations of brook trout, *Salvelinus fontinalis.* – Oikos 70: 12-20.

Hutchings, J. A. and R.A. Myers. 1994. The evolution of alternative mating strategies in variable environments. – Evol. Ecol. 8: 256-268.

Hutchings, J.A. and M.E.B. Jones. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar.* – Can. J. Fish. Aquat. Sci. 55(Suppl. 1): 22-47.

Jansson, H. and T. Öst. 1997. Hybridization between Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in a restored section of the River Dalälven, Sweden. – Can. J. Fish. Aquat. Sci. 54: 2033-2039.

Järvi, T. 1990. The effects of male dominance, secondary sexual characteristics and female mate choice of the mating success of male Atlantic salmon *Salmo salar.* – Ethology 84: 123-132.

Jensen, A.J., B.O. Johnsen and L. Saksgård. 1991 Temperature requirements in Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), and Arctic char (*Salvelinus alpinus*) from hatching to initial feeding compared with geographic distribution. – Can. J. Fish. Aquat. Sci. 46: 786-789.

Jensen, A.L. 1985. Relations among net reproductive rate and life history parameters for lake white fish (*Coregonus clupeaformis*). – Can. J. Fish. Aquat. Sci. 40: 1395-1404.

Jones, J. W. 1959. The salmon. – Collins, London.

Jonsson, B. 1985. Life history patterns of freshwater resident and sea-run migration brown trout in Norway. – Trans. Am. Fish. Soc. 114: 182-194.

Jonsson, B. and K. Hindar. 1982. Reproductive strategy of dwarf and normal Arctic char (*Salvelinus alpinus*) from Vangsvatnet Lake, western Norway. – Can. J. Fish. Aquat. Sci. 39: 1404-1413.

Jonsson, B., N. Jonsson and L.P. Hansen. 1990. Does juvenile experience affect migration and spawning of adult Atlantic salmon? – Behav. Ecol. Sociobiol. 26: 225-230.

Jonsson, B., N. Jonsson and L.P. Hansen. 1991. Differences in life history and migration behaviour between wild and hatchery-reared Atlantic salmon in nature. – Aquaculture 98: 69:78.

Jonsson, N., L.P. Hansen and B. Jonsson. 1994 Juvenile experience influences timing of adult river ascent in Atlantic salmon.-Anim. Behav 48: 740-742.

Jonsson, N., B. Jonsson and I.A. Fleming. 1996. Does early growth cause a phenotypic plastic response in egg production of Atlantic salmon? – Func. Ecol. 10: 89-96.

Kallio-Nyberg, I. and M.-L. Koljonen. 1997. The genetic consequences of hatchery-rearing on life-history traits of the Atlantic salmon (*Salmo salar* L.): a comparative analysis of sea-ranched salmon with wild and reared parents. – Aquaculture 153: 207-224.

Keenleyside, M.H.A. and H.M.C. Dupuis. 1988. Courtship and spawning competition in pink salmon (*Oncorhynchus gorbuscha*). – Can. J. Zool. 66: 262-265.

Kvarnemo, C. and I. Ahnesjö. 1996. The dynamics of operational sex ratios and competitions for mates. – Trends Ecol. Evol. 11: 404-408.

Lande, R. 1988. Genetics and demography in biological conservation. – Science 241:1455-1460.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. – Am. Nat. 142: 911-927.

Lande, R. and G.F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management, p. 87-123. – In: M. Soulé (ed.) Viable populations for conservation. Cambridge University Press, Cambridge.

Largiadèr, C.R. and A. Scholl. 1996. Genetic introgression between native and introduced brown trout (*Salmo trutta* L.) populations in The Rhône River Basin. – Mol. Ecol. 5: 417-426.

Leary, R.F., F.W. Allendorf and G.K. Sage. 1995. Hybridization and introgression between introduced and native fish. Am. Fish. Soc. Symp.15: 91-101.

Leider, S.A., M.W. Chilcote and J.J. Loch. 1984. Spawning characteristics of sympatric populations of steelhead trout (*Salmo gairdneri*) of summer and winter races in the Kalama River, Washington. – Can. J. Fish. Aquat. Sci. 43: 1398-1409.

Leider, S.A., P.L. Hulett, J.J. Loch and M.W. Chilcote. 1990. Electrophoretic comparison of the reproductive success of naturally spawning transplanted and wild steelhead trout through the returning adult stage. – Aquaculture 88: 239-252.

Leigh, E.G. 1981. The average lifetime of a population in a varying environment. – J. Theor. Biol. 90: 213-239.

Ling, S.W. 1977. Aquaculture in southeast Asia – a historic review. – University of Washington Press, Seattle.

MacKenzie, C. and J.R. Monring. 1988. Estimating survival of Atlantic salmon during the intragravel period. – N. Am. J. Fish. Manage. 8: 45-49.

Maekawa, K., T. Hino, S. Nakano and W.W. Smoker. 1993. Mate preference in anadromous and landlocked Dolly varden (*Salvelinus malma*) females in two Alaskan streams. – Can. J. Fish. Aquat. Sci. 50: 2375-2379.

Maekawa, K., S. Nakano and S. Yamamoto. 1994. Spawning behavior and size-assortative mating of Japanese char in an artificial lake-inlet stream system. – Env. Biol. Fish. 39: 109-117.

Marshal, A.R., H.L. Blankenship and W.P. Connor. 2000. Genetic characterization of naturally spawned Snake River fall-run chinook salmon. – Trans. Am. Fish. Soc. 129: 680-698.

Martinez, J.L., P. Moran, J. Perez, B. DeGaudemar, E. Beall and E. Garcia-Vazquez. 2000. Multiple paternity increases effective size of southern Atlantic salmon populations. – Mol. Ecol. 9: 293-298.

Martínez, P., J. Arias, J. Castro and L. Sanchez. 1993. Differential stocking incidence in brown trout (*Salmo trutta*) populations from Northwestern Spain. –Aquaculture 114: 203-216..

McPhee, M.V. and T.P. Quinn 1998. Factors affecting the duration of nest defense and reproductive lifespan of female sockeye salmon, *Oncorhynchus nerka.* – Env. Biol. Fish. 51: 369-375.

McKinnell, S., H. Lundqvist and H. Johansson. 1994. Biological characteristics of the upstream migration of naturally and hatchery-reared Baltic salmon, *Salmo salar* L. – Aquacult. Fish. Manag. 25(Suppl. 2): 45-63.

Metcalfe, N.B. and J.E. Thorpe. 1992. Early predictors of life-history events: the link between first feeding date, dominance and seaward migration in Atlantic salmo*n, Salmo salar* L. – J. Fish. Biol. 41(Suppl. B): 93-99.

Metcalfe, N.B., F.A. Huntingford, W.D. Graham and J.E. Thorpe. 1989. Early social status and the development of life-history strategies in Atlantic salmon. – Proc. R. Soc. Lond. B 236: 7-19.

Moran, P., A.M. Pendas, E. Garcia-Vazquez and J. Izguierdo. 1991. Failure of stocking policy of hatchery reared brown trout (*Salmo trutta*) in Asturias, Spain, detected using *LDH-5** as a genetic marker. – J. Fish Biol. 39(Suppl. A): 117-122.

Moran, P., A.M. Pendas, E. Garcia-Vazquez, J.T. Izquierdo and D.T. Rutherford. 1994. Electro-phoretic assessment of the contribution of trans-planted Scottish Atlantic salmon (*Salmo salar*) to the Esva river (northern Spain). – Can. J. Fish. Aquat. Sci. 51: 248-252.

Morita, K., S. Yamamoto, Y. Takashima, T. Matsuishi, Y. Kanno and K. Nishimura. 1999. Effect of maternal growth history on egg number and size in wild white-spotted char (*Salvelinus leucomaenis*). – Can. J. Fish. Aquat. Sci. 56: 1585-1589.

Nickleson, T.E., M.F. Solazzi and S.L. Johnson. 1986. Use of hatchery coho salmon (*Oncorhynchus kisutch*) presmolts to rebuild wild populations in Oregon coastal streams. – Can. J. Fish. Aquat. Sci. 43: 2443-2449.

Nunney, L. 1991. The influence of age structure and fecundity on effective populations size. – Proc. R. Soc. Lond. B 246: 71-76.

Nunney, L. and D.R. Elam. 1994. Estimating the effective population size of conserved populations. – Conserv. Biol. 8: 175-184.

Økland, F., B. Jonsson, A.J. Jensen and L.P. Hansen. 1993. Is there a threshold size regulating seaward migration of brown trout and Atlantic salmon? – J. Fish Biol. 42: 541-550.

Pakkasmaa, S. 2000. Morphological and early life history variation in salmonid fishes. – Academic dissertation, Helsinki University, Faculty of Science, Edita Oy, Helsinki.

Parker, G.A. and M. Begon. 1986. Optimal egg size and clutch size: effects of environment and maternal phenotype. – Am. Nat. 128: 573-592.

Parker, R.R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. – J. Fish. Res. Board Can. 28: 1503-1510.

Perrin, N. 1988. Why are offspring born larger when it is colder? Phenotypic plasticity for offspring size in the cladoceran *Simocephalus vetulus* (Müller). – Func. Ecol. 2: 283-288.

Perrin, N. and J.F. Rubin. 1990. On dome-shaped norms of reaction for size-to-age at maturity in fishes. – Func. Ecol. 4: 53-57.

Peterson, N.P. and T.P. Quinn. 1996. Spatial and temporal variability in dissolved oxygen in natural egg pockets of chum salmon, in Kennedy Creek, Washington. – J. Fish Biol. 48: 131-143.

Petersson, E. 1990. Age-assortative mating patterns in two swarming caddisfly species (Trichoptera: Leptocerida). – J. Insect Beh. 3: 797-803.

Petersson, E. and T. Järvi. 1993. Differences in reproductive traits between sea-ranched and wild sea-trout (*Salmo trutta*) originating from a common stock. – Nordic J.Freshw. Res. 68: 91-97.

Petersson, E. and T. Järvi. 1997. Reproductive behavior of sea trout (*Salmo trutta*) – consequences of sea-ranching. – Behavior 134: 1-22.

Petersson, E., T. Järvi, N.G. Steffner and B. Ragnarsson. 1996. The effect of domestication on some life history traits of sea trout and Atlantic salmon. – J. Fish Biol. 48: 776-791.

Petersson, E., T. Järvi, H. Olsén, I. Mayer and M. Hedenskog. 1999. Male-male competition and female choice in brown trout. – Anim. Behav. 57: 777-783.

Pitman, R. W. 1979. Effects of female age and egg size on growth and mortality in rainbow trout. – Prog. Fish Cult. 41: 202-204.

Poteaux, C., D. Beaudou and P. Berrebi. 1998. Temporal variations of genetic introgression in stocked brown trout populations. J. Fish. Biol. 53: 701-713.

Quinn., T.P. 1993. A review of homing and straying of wild and hatchery-produced salmon. – Fish. Res. 18(1-2): 29-44

Quinn, T.P. and S. Bloomberg. 1992. Fecundity of chinook salmon (*Oncorhynchus tshawytscha*) from the Waitiki and Rakaia Rivers, New Zealand. – N.Z. J. Mar. Freshw. Res. 26: 429-434.

Quinn, T.P. and C.J. Foote. 1994. The effects of body size and sexual dimorphism on the reproductive behavior of sockeye salmon, *Oncorhynchus nerka.* – Anim. Behav. 48: 751-761.

Quinn, T. P., A.P. Hendry and L.A. Wetzel. 1995. The influence of life history trade-offs and the size of incubation gravels on egg size variation in sockeye salmon (*Oncorhynchus nerka*). – Oikos 74: 425-438.

Quinn, T.P., M.D. Adkison and M.B. Ward. 1996. Behavioral tactics of male sockeye salmon (*Oncorhynchus nerka*) under varying operational sex ratio. – Ethology 102: 304-322..

Quinn, T.P., M.J. Unwin, and M.T. Kinnison. 2000. Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding by introduced chinook salmon populations. – Evolution 54: 1372-1385.

Reznick, D., L. Nunney and A. Tessier. 2000. Big houses, big cars, superfleas and the costs of reproduction. – Trends Ecol. Evol. 15: 421-425.

Reynolds, J.D. and M.R. Gross. 1990. Coasts and benefits of female mate choice: is there a lek paradox? – Am. Nat. 136: 230-243.

Ricker, W.E. 1972. Hereditary and environmental factors affecting certain salmon populations, p. 19-160. – In: Simon, R.C. and P.A. Larkin (eds.) The stock concept in Pacific salmon. H.R. MacMillan Lectures, University of British Columbia, Vancouver.

Riddell, B.E. and W.C. Leggett. 1981. Evidence of an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile Atlantic salmon (*Salmo salar*). – Can. J. Fish. Aquat. Sci. 38: 321-333.

Robinson, B.W. and D.S. Wilson. 1996. Genetic variation and phenotypic plasticity in a trophically polymorphic population of pumpkinseed sunfish (*Lepomis gibbosus*). – Evol. Ecol. 10: 631-652.

Roff, D. A. 1992. The evolution of life histories. – Chapman Hall, New York. 535 p.

Ryman, N. 1981. Conservation of genetic resources: experiences from the brown trout (*Salmo trutta*), p. 61-74. – In: Ryman, N. (ed.) Fish gene pools. Ecol. Bull. (Stockholm) 34: 111 p.

Sægrov, H, Urdal, K., Hellen, B.A., Kålås, S. and Saltveit, S.J. 2001. Estimating carrying capacity and presmolt production of Atlantic Salmon (*Salmo salar*) and anadromous brown trout (*Salmo trutta*) in west Norwegian rivers. – Nordic J. Freshw. Res. 75: 99-108.

Sargent, R.C., M.R. Gross and E.P. van den Berghe. 1986. Male mate choice in fishes. – Anim. Behav. 34: 545-550.

Saunders, R.L., E.B. Henderson and B.D. Glebe. 1982. Precocious sexual maturation and smoltification in male Atlantic salmon (*Salmo salar*). – Aquaculture 28: 211-229.

Schlichting, C.D. and M. Pigliucci. 1998. Phenotypic evolution: a reaction norm perspective. – Sinauer, Sunderland. 387 p.
Schroder, S.L. 1981. The role of sexual selection in deter-mining overall mating patterns and mate choice in chum salmon. – Ph.D. thesis, University of Washington. 274 p.
Schroder, S.L. 1982. The influence of intrasexual competition the distribution of chum salmon in a experimental stream, p. 275-285. – In: Brannon, E. L. and Salo, E. O. (eds.) Salmon and trout migratory behaviour symposium. School of Fisheries, Univ. Washington, Seattle.
Seppä, T. 1999. Growth and size variation in Saimaa Arc-tic char (*Salvelinus alpinus*). – Academic dissertation, Helsinki University, Faculty of Science, Edita Oy, Hel-sinki.
Sharov, A.F. and A.V. Zubchenko. 1993. Influence of human activity on properties of Atlantic salmon populations, p. 62-69. – In: Stokes, T.K., J.M. McGlade and R. Law (eds.) The exploitation of evolving re-sources. Springer-Verlag, Berlin. 264 p.
Shearer, W.M. 1961. Survival rate of young salmonids in streams stocked with green ova. – ICES CM 1961 (98).
Sibly, R.M. and Calow, P. 1986. Physiological Ecology of Animals. – Blackwell Scientific Publications, Oxford. 179 p.
Siitonen, L. and G.A.E. Gall. 1989. Response to selection for early spawn date in rainbow trout, *Salmo gairdneri.* – Aquaculture 78: 153-161.
Silverstein, J.T. 1993. A quantitative genetic study of size, growth rate and timing of sexual maturation in coho salmon (*Oncorhynchus kisutch*). – Ph.D. thesis, University of Washington, Seattle.
Skaala, Ø, K.E. Jørstad and R. Borgstrøm. 1996. Genetic impact on two wild brown trout (*Salmo trutta*) populations after release of non-indigenous hatchery spawners. – Can. J. Fish. Aquat. Sci. 53: 2027-2035.
Skúlason, S., D.L.G. Noakes and S.S. Snorrason. 1989. Ontogeny of trophic morphology in four sympatric morphs of Arctic char *Salvelinus alpinus* in Thing-vallavatn, Iceland. – Biol. J. Linn. Soc. 38: 281-301.
Smith, C.C. and S.D. Fretwell. 1974. The optimal balance between size and number of offspring. – Am. Nat. 108: 499-506.
Sokal, R.R. and F.J. Rohlf. 1995. Biometry. 3 rd edition. – W.H. Freeman and Company, New York.
Ståhl, G. 1987. Genetic population structure of Atlantic salmon, p. 121-140. – In: Ryman, N. and F. Utter (eds.) Population genetics and fishery management. University of Washington Press, Seattle.
Steen, R.P. and T.P. Quinn. 1999. Egg burial depth by sockeye salmon (*Oncorhynchus nerka*): implications for survival of embryos and natural selection on female body size. – Can. J. Zool. 77: 836-841.
Steward, C.R. and T.C. Bjornn. 1990. Supplementation of salmon and steelhead stocks with hatchery fish: a synthesis of published literature. – Technical Report 90-1, Bonneville Power Administration, Portland, Oregon.
Sutterlin, A.M., R.L. Saunders, E.B. Henderson and P.R. Harmon. 1982. The homing of Atlantic salmon (*Salmo salar*) to a marine site. – Can. Tech. Rep. Fish. Sci. 1058: 1-6.
Svärdson, G. 1949. Natural selection and egg number in fish. – Rep. Inst. Freshw. Res., Drottningholm 26: 1139-1149
Swain, D.P. and L.B. Holtby. 1989. Differences in morphology and behavior between juvenile coho salmon (*Oncorhynchus kisutch)* rearing in a lake or in its tributary stream. – Can. J. Fish. Aquat. Sci. 46: 1406-1414.
Taggart, J.B. and A. Ferguson. 1986. Electrophoretic evaluation of a supplemental stocking programme for brown trout (*Salmo trutta* L.). – Aquacult. Fish. Manag. 17: 155-162.
Tallman, R.F. and M.C. Healey. 1994. Homing, straying, and gene flow among seasonally separated populations of chum salmon (*Oncorhynchus keta*). – Can. J. Fish. Aquat. Sci. 51: 577-588.
Tamate, T. and K. Maekawa. 2000. Interpopulation variation in reproductive traits of female masu salmon, *Oncorhynchus masou.* – Oikos 90: 209-218.
Thomaz, D., E. Beall and T. Burke. 1997. Alternative reproductive tactics in Atlantic salmon: factors affecting mature parr success. – Proc. R. Soc. Lond. B 264:219-226.
Thompson, C.E., W.R. Poole, M.A. Matthews and A. Ferguson. 1999. Comparison, using minisatellite DNA profiling, of secondary male contribution in the fertilisation of wild and ranched Atlantic salmon (*Salmo salar*) ova. – Can. J. Fish. Aquat. Sci. 55: 2011-2018.
Thorpe, J.E. 1986. Age at first maturity in Atlantic salmon, *Salmo salar*: freshwater period influences and conflicts with smolting. – Can. Spec. Pub. Fish. Aquat. Sci. 89: 7-14.
Thorpe, J.E., M.S. Miles and D.S. Keay. 1984. Develop-mental rate, fecundity and egg size in Atlantic salmon, *Salmo salar* L. – Aquaculture 43: 289-305.
Utter, F. 2000. Patterns of sub-specific anthro-pogenic introgression in two salmonid genera. – Rev. Fish Biol. Fish. (In press.)
Utter, F.M., G. Milner, G. Ståhl and D. Teel. 1989. Genetic population structure of chinook salmon in the Pacific Northwest. – Fish Bull. U.S. 87: 239-264.
van den Berghe, E.P. and M.R. Gross. 1989. Natural selection resulting from female breeding competition

in a pacific salmon (coho: *Oncorhynchus kisutch*). – Evolution 43: 125-140.
Vehrencamp, S. L. And J. W. Bradbury 1984. Mating systems and ecology, p. 251-278. – In: Krebs, J.R. and N.B. Davis (eds.) Behavioural ecology, an evolutionary approach, 2 nd edition. Blackwell Scientific Publications, Oxford.
Vøllestad, L.A. and T. Hesthagen. 2001. Stocking of fresh-water fish in Norway: management goals and effects. – Nordic J. Freshw. Res. 75: 143-152.
Vuorinen, J. and O.K. Berg. 1989. Genetic divergence of anadromous and nonadromous Atlantic salmon (*Salmo salar*) in the River Namsen, Norway. – Can. J. Fish Aquat. Sci. 46: 406-409.
Wankowski, J.W.J., and J.E. Thorpe. 1979. Spatial distribution and feeding in Atlantic salmon, *Salmo salar* L. juveniles. – J. Fish Biol. 14: 239-247.
Waples, R.S. 1991. Genetic interactions between hatchery and wild salmonids: lessons from the Pacific Northwest. – Can. J. Fish. Aquat. Sci. 48(Suppl. 1): 124-133.
Waples, R.S. 1999. Dispelling some myths about hatcheries. – Fisheries 24(2): 12-21.
Waples, R.S., M.J. Ford and D. Schmitt. Empirical results of salmon supplementation: a preliminary assessment. – In: Bert, T.M. and J.L. Nielsen (eds.) Ecological and genetic implications of aquaculture activities. Kluwer Academic, New York. (In press.)
Webb, J.H. and A.D. Hawkins. 1989. The movements and spawning behavior of adult salmon in the Girnock Burn, a tributary of the Aberdeenshire Dee, 1986. – Scott. Fish. Res. Rep. No. 40.
Webb, J.H. and H.A. McLay. 1996. Variation in the time of spawning of Atlantic salmon (*Salmo salar*) and its relationship to temperature in the Aberdeenshire Dee, Scotland. – Can. J. Fish. Aquat. Sci. 53: 2739-2744.
Williams, G. C. 1966. Adaptation and natural selection. – Princeton University Press, Princeton.
Williams, R.N., D.K. Shiozawa, J.E. Carter and R.F. Leary. 1996. Genetic detection of putative hybridization between native and introduced rainbow trout populations of the Upper Snake River. – Trans. Am. Fish Soc. 125: 387-401.
Williams, R.N., R.F. Leary and K.P. Currens. 1997. Localized genetic effects of a long-term hatchery stocking program on resident rainbow trout in the Metolius River, Oregon. – NA J. Fish Manag. 17: 1079-1093.
Winemiller, K.O. and K.A. Rose. 1993. Why do most fish produce so many tiny offspring. – Am. Nat. 142: 585-603.
Wishard, L.N., J.E. Seeb, F.M. Utter and D. Stefan. 1984. A genetic investigation of suspected redband trout populations. – Copeia 1984: 120-132.
Withler, F.C. 1982. Transplanting Pacific salmon. – Can. Tech. Rep. Fish. Aquat. Sci. No. 1079. p. 27.
Wood, E.M., W.T. Yasutake, A.N. Woodall and J.E. Halver. 1957. The nutrition of salmonid fishes I. Chemical and histological studies of wild and domesticated fish. – J. Nutr. 61: 465-478.
Youngson, A.F. and E. Verspoor. 1998. Interactions between wild and introduced Atlantic salmon (*Salmo salar*). – Can. J. Fish. Aquat. Sci. 55(Suppl. 1): 153-160.

APPENDIX 2 – RICHARD. J. BEAMISH'S REFERENCES

Changes in the dynamics of coho in the Strait of Georgia in the last decade

Richard. J. Beamish, C.M. Neville, R.M. Sweeting, K.L. Poier, and G.A. McFarlane
Department of Fisheries and Oceans, Pacific Biological Station

References

Beamish, R.J., C. Neville and A.J. Cass. 1997. Production of Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to decadal-scale changes in the climate and the ocean. Can. J. Fish. Aquat. Sci. 54: 543-554.

Beamish, R.J, G.A. McFarlane and J.R.King. 2000. Fisheries Climatology: Understanding the decadal scale processes that naturally regulate British Columbia fish populations. pp 94-145. *In* P.J. Harrison and T.R. Parsons, Fisheries oceanography: An integrative approach to fisheries ecology and management. Blackwell Science Ltd., Osney, Mead, Oxford: 347 pp.

Beamish, R.J., D.J. Noakes, G.A. McFarlane, W. Pinnix, R. Sweeting and J. King. 2000. Trends in coho marine survival in relation to the regime concept. Fish. Oceanogr. 9: 114-119.

Beamish, R.J., K.L. Poier, R.M. Sweeting and C.M. Neville. 2000. An abrupt increase in the abundance of juvenile salmon in the Strait of Georgia. (NPAFC Doc. 473) Pacific Biological Station, Nanaimo, B.C.

Beamish, R.J. and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog. Oceanogr. (*in press*).

Cowan, J.H. Jr., K.A. Rose and D.R. DeVries. 2000. Is density-dependent growth in young-of-the-year fishes a question of critical weight? Reviews in Fish Biology and Fisheries 10: 61-89.

Gargett, A.E. 1997. The optimal stability "window": a mechanism underlying decadal fluctuations in North Pacific salmon stocks. Fish. Oceanogr. 6: 1-9.

Kuhn, B.R., Lapi, L. and Hamer, J.M. 1988. An introduction to the Canadian database on marked Pacific salmonids. Can. Tech. Rep. Fish. Aquat. Sci. 1649, 56p.

McFarlane, G.A., J.R. King and R.J. Beamish. 2000. Have there been recent changes in climate? Ask the fish. Prog. Oceanogr. 47: 147-169.

Mantua, N.J., S.R. Hare, Y. Zhang, J.M. Wallace and R.C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. J. American Meteorolog. Soc. 78 (6): 1069-1079.

Moore, R.D. and I.G. McKendry. 1996. Spring snowpack anomaly patterns and winter climatic variability, British Columbia, Canada. Water Resour. Res. 32: 623-632.

Pearcy, W.G. 1992. Ocean ecology of North Pacific salmonids. Seattle, WA: Univ. Washington Press, 179 pp.

Simpson, K, D. Dobson, R. Semple, S. Lehmann, S. Baillie, and I. Matthews. 2001. Status in 2000 of coho stocks adjacent to the Strait of Georgia. PSARC Working Paper S2001-11.

APPENDIX 3 – COMMENTS

APPENDIX 4 – PETER TYEDMERS' SLIDES

ENERGY INPUTS AND GREENHOUSE GAS EMISSIONS ASSOCIATED WITH THE PRODUCTION OF SALMON SMOLTS FROM HATCHERIES IN BRITISH COLUMBIA

Peter Tyedmers, Fisheries Centre, University of British Columbia

Rationale/Background

- Hatcheries are popular fisheries management tools
- The substitution of hatchery production for wild reproduction comes at a biophysical price

Methods

- For each species, inputs quantified included:
  - electricity use,
  - fossil fuel consumption by type, and
  - feed consumption.

Methods

- Part of a larger analysis of commercial salmon fishing and salmon farming in BC
- Focus on inputs and emissions from Salmon Enhancement Program (SEP) facilities
  - contrast results with private hatcheries, and
  - place the results in the broader context of the commercial fishery

Methods

- In both public and private hatcheries, feeds are a major input
- Production of composite feeds is highly industrialized

⇨ consequently, conducted a detailed analysis of the energy inputs to a typical dry salmon feed

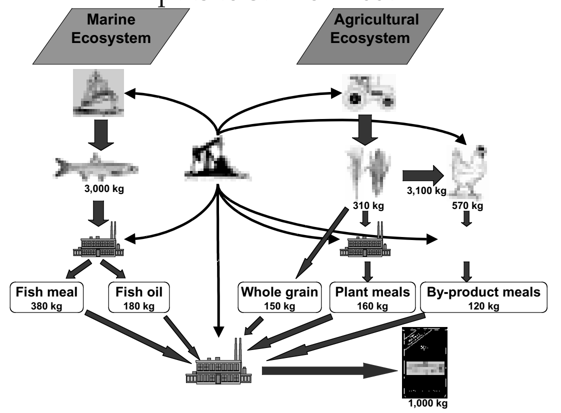
Methods

- Solicited production and operational input data from two SEP hatcheries
- Combined data represents:
  - 55 tonnes of chinook smolt production (~18% of annual SEP production)
  - 15 tonnes of coho smolt production (~6% of annual SEP production)

Methods

- For comparison, inputs to five private hatcheries also analyzed
  - together produced almost 330 tonnes of smolts
  - primarily Atlantic and chinook salmon for farms

Inputs to Salmon Feed



Methods

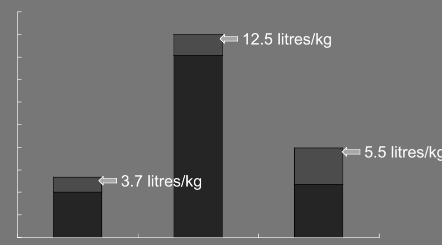
- To address energy quality problem electricity inputs re-expressed as fossil fuel equivalents
- Resulting greenhouse gas releases based on energy form specific emissions

Results - Major Inputs

- Mean unadjusted inputs per kilogram smolts produced

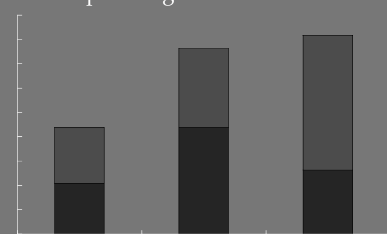
Results - Comparative Energy Inputs

Energy Inputs per kilogram Smolts Produced



Results - Comparative GHG Emissions

Emissions per kilogram of Smolts Produced

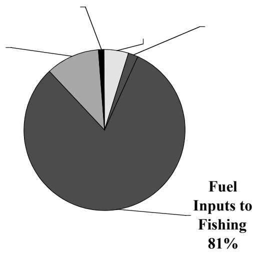


Results

- How do these results translate into adult salmon production?

Results - Inputs in Context

- Energy inputs to commercially caught chinook

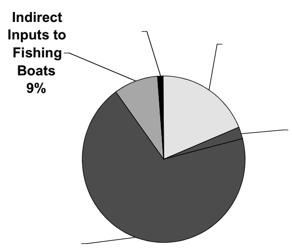


Conclusions

- Substitution of hatcheries for wild reproduction has a substantial biophysical "cost"
  - largely unaccounted for
  - contributes to climate change that in turn impacts salmon
- These costs vary between species being cultured
- Generally correlate with time spent in culture

Results - Inputs in Context

- Energy inputs to commercially caught coho



Acknowledgements

- Glen Rasmussen, Robertson Creek hatchery
- David Celli, Tenderfoot Creek hatchery
- Greg Steer & Diane Plotnikoff, SEP
- Numerous salmon farmers

APPENDIX 5 – MART GROSS' REFERENCES

Hatchery Reform: What Should We Do With Hatcheries?

Mart R. Gross, Department of Zoology, University of Toronto

References

Fleming, I.A. and M.R. Gross. 1993. Breeding success of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in competition. Ecological Applications 3(2): 230-245.

Fleming, I.A., B. Jonsson and M.R. Gross. 1995. Phenotypic divergence of sea-ranched, farmed and wild salmon. Canadian Journal of Fisheries and Aquatic Sciences 51: 2808-2824.

Fleming, I.A., B. Jonsson, M.R. Gross and A. Lamberg. 1996. An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*). Journal of Applied Ecology 33: 893-903.

Fleming, I.A., K. Hindar, I. Mjolnerod, B. Jonsson, T. Balstad and A. Lamberg. 2000. Lifetime success and interactions of farm salmon invading a native population. Proceedings of the Royal Society of London B 267:1517-1523.

Gross, M.R. 1998. One species with two biologies: Atlantic salmon (*Salmo salar*) in the wild and in aquaculture. Canadian Journal of Fisheries and Aquatic Sciences 55 (Suppl. 1): 131-144.

Gross, M.R. 2000. Will farmed Atlantic salmon invade the ecological niches of wild Pacific salmon? In, Aquaculture and the Protection of Wild Salmon (P. Gallaugher and C. Orr, eds). Continuing Studies in Science, Workshop Proceedings, Simon Fraser University, British Columbia, July 2000.

Gross, M.R. 2002. Potential impacts of fish farming on wild salmon stocks in British Columbia. Raincoast Conservation Society Wild Salmon Project: 18 pages, in press.

Levin, P.S., R.W. Zabel and J.G. Williams. 2001. The road to extinction is paved with good intentions: negative association of fish hatcheries with threatened salmon. Proceedings of the Royal Society of London, Series B 268: 1153-1158.

Lichatowich, J. 1999. Salmon without rivers: a history of the Pacific salmon crisis. Island Press, Washington, D.C.

National Research Council. 1996. Upstream: Salmon and Society in the Pacific Northwest. National Academy Press, Washington, D.C., USA.

Slaney, T.L., K.D. Hyatt and T.G. Northcote. 1996. Status of anadromous salmon and trout in British Columbia and Yukon. Fisheries 21: 20-35.

Volpe, J.P., E.B. Taylor, D.W. Rimmer and B.W. Glickman. 2000. Evidence of natural reproduction of aquaculture escaped Atlantic salmon (*Salmo salar*) in a coastal British Columbia river. Conservation Biology 14: 899-903.

Whoriskey, F. 2000. Infectious salmon anemia: a review and the lessons learned for wild salmon on Canada's east coast. In, Aquaculture and the Protection of Wild Salmon (P. Gallaugher and C. Orr, eds). Continuing Studies in Science, Workshop Proceedings, Simon Fraser University, British Columbia, July 2000.