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NOAA Technical Memorandum NMFS-NWFSC-30



Genetic Effects of Straying of Non-Native Hatchery Fish into Natural Populations

Proceedings of the Workshop
June 1-2, 1995
Seattle, Washington

May 1997

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

NOAA Technical Memorandum NMFS

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Genetic Effects of Straying of Non-Native Hatchery Fish into Natural Populations

Proceedings of the Workshop
June 1-2, 1995
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Edited by
W. Stewart Grant

National Marine Fisheries Service
Northwest Fisheries Science Center
Coastal Zone and Estuarine Studies Division
Conservation Biology Program
2725 Montlake Blvd. E., Seattle, WA 98112-2097

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INTRODUCTION

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The last decade has seen an increasing awareness of the importance of considering genetic issues in the management of Pacific salmon (*Oncorhynchus* spp.) (Simon et al. 1986, Allendorf and Ryman 1987, Withler 1988, Waples et al. 1990, Riddell 1993, Park et al. 1994, Currens and Busack 1995, NRC 1996). At the same time, it has become clear that available scientific information is often insufficient to allow reliable predictions of the genetic consequences of different management actions, particularly those involving artificial propagation. One issue with both scientific and management implications is straying. Straying among, as well as homing to, natal populations is part of the evolutionary ecology of Pacific salmon. However, human manipulation of salmon and their ecosystems can also affect the nature and magnitude of straying. In particular, artificial propagation can result in higher rates of straying than would occur naturally and may also cause salmon to stray into areas that they would not normally reach.

Both scientific and management issues related to straying have been discussed for some time. Recently, this issue has been brought to a head as a result of two related developments in the Pacific Northwest. First, since 1990, several "distinct population segments" of salmon have been listed as threatened or endangered "species" under the federal Endangered Species Act (ESA) (see Waples 1995 for discussion). Under the ESA, the National Marine Fisheries Service (NMFS) has jurisdiction over marine and anadromous species, including Pacific salmon, steelhead (*O. mykiss*), and anadromous cutthroat trout (*O. clarki*). Guided by the ESA's emphasis on conserving species in their native ecosystems, NMFS has developed a policy on the use of artificial propagation in conservation and recovery and to limit the potential of hatchery fish to adversely affect listed natural populations (Hard et al. 1992). Although many of these effects have been known for some time, existing regulatory mechanisms have often failed to adequately protect natural populations. The ESA provides a much more powerful legal framework for conservation.

The second development is that empirical data have shown that non-native[1] hatchery fish are straying in significant numbers into natural spawning areas for two ESA-listed species: Snake River fall-run chinook salmon (*O. tshawytscha*) and Snake River spring/summer-run chinook salmon. The articles in this volume by Crateau and Carmichael provide background and details for the hatchery programs and natural populations involved. For example, stray hatchery fish of non-native origin

[1]In general, a non-native stock consists of fish that are not from the local area, but come from at least one river away or from another river basin. The term was not defined more explicitly because we wanted the panel to consider a wide range of scenarios.

have made up the majority of natural spawners in many streams in the Grande Ronde Basin in recent years.

Straying from these hatchery programs has presented a major challenge to fishery managers. On the one hand, Sewall Wright showed long ago (Wright 1931) that only a few migrants per generation will prevent substantial divergence among populations due to genetic drift. Low levels of gene flow can also rapidly break down existing population genetic structure. Furthermore, even a small percentage of strays from a productive hatchery population can represent a substantial fraction of a depressed natural population. On the other hand, the hatchery programs involved (Columbia River fall chinook salmon released into the Umatilla River and Rapid River stock spring chinook salmon released from Lookingglass Hatchery in the Grande Ronde Basin) were both initiated to satisfy tribal treaty obligations and to mitigate reductions in natural production caused by hydropower development on the Columbia and Snake Rivers. Stringent controls to limit straying could make it impossible to meet these legal obligations under current conditions.

In 1994, following ESA Section 7 consultations about the effects of straying by non-native hatchery fish from these two programs, NMFS established an interim standard to limit the proportion of stray, non-native hatchery fish to no more than 5% of any natural spawning population. This value was chosen in part arbitrarily, and in part as a compromise between several factors. There was a scientific basis for imposing some upper limit for straying, but exactly what that limit should be and how it should be applied was not clear. Some researchers thought that straying at a level of 5% per year was too high and would eventually erode the fitness of natural populations and alter their population genetic structure. Others thought that the level was too low and that it would seriously limit hatchery programs designed to meet other goals. Some believed that straying might be beneficial to depressed natural populations by increasing abundance and genetic diversity.

Because of the considerable interest surrounding this issue, NMFS proposed that a workshop be held to address the scientific evidence for the effects of straying by non-native hatchery fish. This workshop, which featured a panel of 12 experts in evolutionary biology and salmon biology, was held in Seattle, Washington on June 1-2, 1995. Panelists included Dr. Craig Busack, Washington Department of Fish and Wildlife; Mr. Richard Carmichael, Oregon Department of Fish and Wildlife; Mr. Kenneth Currens, Oregon State University; Dr. Joseph Felsenstein, University of Washington; Dr. Tony Gharrett, University of Alaska, Fairbanks; Dr. Michael Gilpin, University of California, San Diego; Dr. Michael Lynch, University of Oregon; Dr. Thomas Quinn, University of Washington; Dr. Nils Ryman, Stockholm University; Dr. Dolph Schluter, University of British Columbia; Dr. Eric B. Taylor, University of British Columbia; and Dr. Ruth Withler (Chairman), Department of Fisheries and Oceans, Canada. Dr. Stewart Grant, National Marine Fisheries Service, served as rapporteur. This volume is the proceedings of that workshop.

The panel was asked to consider a general scenario involving one-way straying of non-native hatchery fish into natural spawning areas at levels higher than would occur naturally. Increased levels of straying might occur if non-native stocks are imported and released near natural spawning areas, or if artificial propagation elsewhere leads to long-distance straying. Although the impetus for the workshop was concern for the listed Snake River populations of chinook salmon, the straying

issue is more generally applicable to a wide range of hatchery programs for all species of anadromous Pacific salmonids throughout the region. Therefore, the panel was asked not to limit their evaluations to any species or geographic region.

The panel was also not expected to make management decisions or to formulate policy for NMFS or anyone else. Rather, the panelists were asked to consider the following fundamental question: What are the genetic consequences for natural populations of straying by non-native hatchery fish? The panelists were asked to consider both short- and long-term effects, and to consider these effects as they relate to population structure and diversity as well as to the fitness of natural populations. In evaluating this basic issue, the panelists were also asked to consider a variety of related questions. Some examples follow.

- Can effects of hatchery straying be predicted with any certainty? If so, how? If not, what are the ramifications of the lack of certainty?

- Can hatchery straying be beneficial for natural populations? If so, how and under what circumstances?

- Is any non-zero level of hatchery straying consistent with conservation of natural populations? If not, why not? If so, what level is acceptable?

- Do short-term and long-term effects of straying differ? If so, how and why?

- How do effects of straying depend on the following factors?
  - Magnitude of straying
  - Duration of straying
  - Genetic differences between hatchery and natural populations (and how the differences are measured)
  - Number of natural populations affected

- Are the effects of hatchery straying likely to be permanent? If not, over what time frame would initial conditions be restored?

- What are appropriate units to consider in evaluating straying: the absolute number of stray fish, or the proportion of the population they represent?

- What research should be undertaken to help resolve uncertainties surrounding this issue?

The workshop did not attempt to address several related issues. For example, the panel was not asked to answer the question, Do hatchery fish stray? Empirical evidence makes it clear that some hatchery fish stray, and others do not. Rather, the panelists focused on evaluating the consequences of straying in those cases in which it does occur. Similarly, the workshop did not focus on the effects of fish culture per se; rather, the focus was on the effects of non-native fish that reach natural spawning areas because of artificial propagation. Finally, the panel did not attempt to

evaluate the effects of supplementation programs that use local broodstock. These and other hatchery issues are important but were judged to be too complex to be dealt with in a single workshop.

This volume follows the organizational structure of the workshop, which attempted to balance two goals: encouraging interactions by having an open session to take advantage of the expertise of the approximately 140 fishery biologists in the audience, and allowing the panel time for intensive discussion on the various difficult issues they were asked to address. In the introductory session, representatives of various state, tribal, and conservation groups from the region were asked to provide background information, offer comments on scientific or management issues, and pose additional questions for the panel to consider. The rest of the first day was taken up with a series of six presentations by panel members on key issues in evolutionary biology and salmon biology. These presentations were intended to provide a common framework for addressing the key issues. Audience questions and discussion that followed these presentations are included in these proceedings.

On the second day, the panel met in closed session to discuss theoretical and empirical information relevant to the key questions. At the end of the day, the panel chairman, Dr. Ruth Withler, summarized the panel's conclusions to the audience, who had spent the second day discussing various strategies for dealing with the listing of hatchery fish under the ESA. A written summary of the panel's conclusions follows the proceedings.

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Definition of the Problem:
Straying from Hatchery Populations

STRAYING OF HATCHERY ORIGIN SPRING/SUMMER-RUN CHINOOK SALMON IN THE GRANDE RONDE BASIN

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The Lower Snake River Compensation Program is a hatchery program consisting of 23 fish-rearing facilities and satellite stations designed to mitigate for the loss of salmon (*Oncorhynchus* spp.), steelhead, and rainbow trout (*O. mykiss*) caused by the construction of four dams on the lower 250 km of the Snake River. The U.S. Fish and Wildlife Service (USFWS) administers and funds the program, and state and tribal agencies operate the hatcheries and conduct hatchery evaluations. The first facility, the McCall Hatchery in Idaho, began operating in 1980, and the Lookingglass Hatchery in Oregon (Fig. 1) began in 1982, so in terms of salmon generation times (about 4-5 years for chinook salmon), the program has been in operation a short time. I would like to focus on the Lookingglass Fish Hatchery Spring Chinook Salmon Mitigation Program, and Richard Carmichael will talk about the Lyons Ferry Fall Chinook Salmon Mitigation Program. The activities of these programs led, in part, to this workshop on the effects of straying.

The Lookingglass Fish Hatchery Program was designed to produce about 1.4 million spring-run chinook salmon smolts to return about 9,070 spring-run chinook salmon adults to the Grande Ronde and the Imnaha Rivers. The hatchery is operated by the Oregon Department of Fish and Wildlife and uses two stocks of fish: a non-native Rapid River stock, and a native stock from the Imnaha River. Fish from the Rapid River stock are currently released from the hatchery into Lookingglass Creek in the Grande Ronde Basin, whereas the Imnaha stock is released into the Imnaha River after acclimation at the facility on the Imnaha River. In previous years, portions of the Rapid River stock and Carson River stock maintained in the Lookingglass Hatchery were released into the Upper Grande Ronde River, Wallowa River, Catherine River, and into Lookingglass Creek itself.

The release of Rapid River stock as well as Carson River stock has resulted in an extremely high incidence of straying in the Grande Ronde Basin. In some years and at some localities, stray hatchery fish represented 35-100% of the fish found in a particular area. Most recent spawning-ground surveys revealed a considerable amount of straying, as summarized for 1990-93 in Table 1. Estimates of escapement are also shown. For example, in 1990, stray hatchery fish constituted an estimated 46.2% of the spawners in the Minam River, 77.8% in the Wenaha River, 40% in the Lostine River, 100% in Catherine Creek, and 50% in the Grande Ronde River. In 1992, the amount of straying was particularly high, probably because of low water levels that may have prevented

access to some spawning areas. In 1993, straying was somewhat lower, but still over 45% in all populations.

Because of the concern over these high rates of straying into local natural populations, we plan to end the use of the Rapid River and Lookingglass Creek hatchery strains when local endemic stocks become available through a captive broodstock program. Such a reduction, however, seriously affects our responsibilities to tribal and governmental recovery programs for the Grande Ronde Basin. We are caught between two judicial directives: the Lower Snake River Compensation Plan and the Endangered Species Act, on the one hand, which call for fish production to mitigate losses caused by hydropower development, and on the other the influence of these programs on endangered populations of spring-run chinook salmon listed under the Endangered Species Act. The USFWS, as well as other agencies, recognizes the responsibility to protect wild and endemic populations of salmon. The regional office of the USFWS wrote a vision document in 1991 to assess the status of natural populations of salmon throughout the region and to improve the information base for wild salmon populations. As a result of this effort, we are assessing the effects of hatcheries and their potential effects on naturally spawning populations.

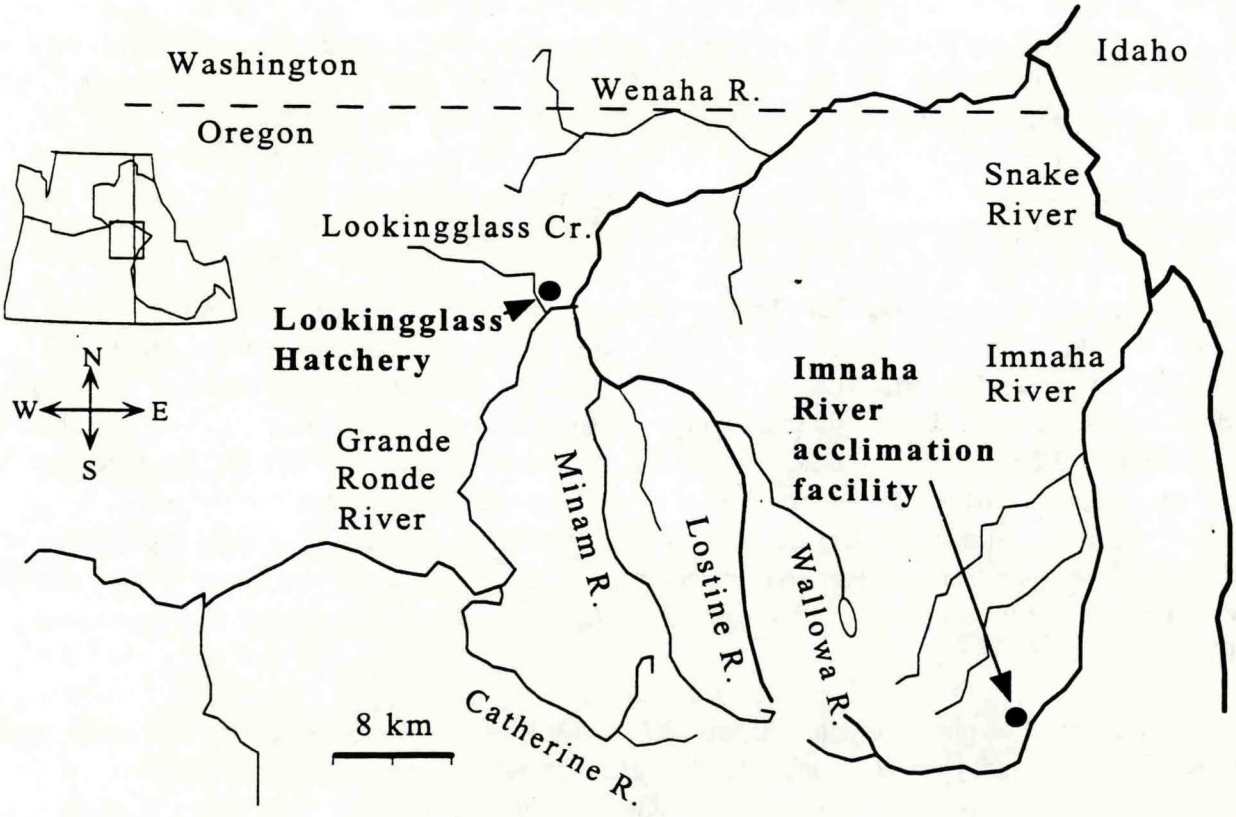


Figure 1. Locations of hatcheries on the Grande Ronde and Imnaha Rivers.

Table 1. Estimated percentage of carcasses identified as hatchery fish in the Grande Ronde River Basin, 1990-93 (based on coded wire tags, physical marks, and scales analysis).

Tributary	Year	Estimated escapement	Carcasses examined		Percentage hatchery
			Hatchery	Natural	
Minam R.	1990	161	6	7	46.2
	1991	120	5	8	38.5
	1992	266	39	3	92.9
	1993	264	17	20	45.9
Wenaha R.	1990	199	7	2	77.8
	1991	149	10	5	66.7
	1992	461	41	4	91.1
	1993	250	14	13	51.9
Lostine R.	1990	65	4	6	40.0
	1991	70	7	13	35.0
	1992	86	17	7	70.8
	1993	245	26	25	51.0
Catherine R.	1990	93	8	0	100.0
	1991	48	9	2	81.8
	1992	118	6	2	75.0
	1993	202	12	8	60.0
Grande Ronde R.	1990	76	6	6	50.0
	1991	24	0	3	0
	1992	55	55	13	80.9
	1993	247	27	8	77.1

We are now developing plans to establish captive brood stocks and captive rearing of local fish, but have several unanswered questions. What are the appropriate populations to use in a captive program? Could we use, for example, Lostine River fish, which would most likely stray into the nearby Minam and Wenaha Rivers? Is it necessary to develop several different captive broodstocks for release into specific rivers? How should broodstocks be chosen and how long should they be used? What are acceptable short- and long-term straying rates? Since straying will likely always occur, can we infuse genes from the Minam and Wenaha salmon populations into hatchery populations to insure against adverse effects of one-way gene flow? Many natural populations may be lost in the near future, and we need guidelines for our programs.

Although the problem of straying is important, the low escapement into some of these rivers is cause for more immediate concern. Many marginal populations may go to extinction in the next few years, and for many of us the problem of straying is not the highest item on a list of priorities. Over the short term, we are looking for guidelines to prevent the loss of these valuable, but imperiled, populations.

Discussion

Question: Bill Bakke (Washington Trout): You stated that you have a conflict in terms of your mitigation programs. Could you explain why you used non-native stocks in the Lower Snake River Conservation River Program, at least for the Grande Ronde?

Answer: Ed Crateau: At the time we began our program, few endemic stocks were available to us. It was an emergency, and we thought we could not get a program started with the few wild fish that remained. We wanted to jump-start the program, so we chose Rapid River fish to start the program. We now realize this may have been a mistake, but at the time our primary responsibility was for mitigation, to increase the number of returning adults. Preservation of wild populations was not a high priority at the time. We used Rapid River fish in 1980 and again in 1987. We used Carson River fish in 1982 and again in 1986, but we also tried to use adults that returned to Lookingglass Creek in years they were available. The Lookingglass stock, itself, is a mixture of local fish and returns from Rapid River releases. The Lookingglass/Carson stock is a mixture of fish from those two sources.

STRAYING OF UMATILLA RIVER HATCHERY ORIGIN FALL-RUN CHINOOK SALMON INTO THE SNAKE RIVER

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One of the issues that stimulated the development of this workshop is the straying of Umatilla River Hatchery fall-run chinook salmon into the Snake River. I thought that it would be worthwhile to provide a background on the history of the Umatilla fisheries restoration program with specific relevance to the straying issue. I believe this restoration program serves as a good example of how conflicts can arise when we pursue management activities in one subbasin that result in unexpected outcomes that conflict with achievement of objectives in other subbasins--a case in which we have conflicting cultural and societal demands.

The Umatilla River is located in the northeastern corner of the State of Oregon and enters the Columbia River at rkm 465, 58 km downstream from the confluence of the Snake and Columbia Rivers. Historically, the Umatilla Basin supported populations of summer-run steelhead, fall- and spring-run chinook salmon, coho salmon (*O. kisutsch*), and possibly chum salmon (*O. keta*). Endemic stocks of fall- and spring-run chinook and coho salmon are extinct and summer-run steelhead are depressed.

As a result of these activities, an aggressive restoration and supplementation program for fall- and spring-run chinook salmon, coho salmon, and summer-run steelhead was initiated. To guide this effort, a comprehensive plan for rehabilitation of anadromous fish in the Umatilla Basin was developed. An extensive planning and review process was completed under the Northwest Power Planning Council's Fish and Wildlife Program prior to initiation of the rehabilitation efforts. This process involved numerous agencies, tribes, and fisheries experts from the Pacific Northwest to establish management and research objectives and restoration strategies. The plan identified specific management objectives to restore the natural production of fall-run chinook salmon and to meet tribal treaty obligations. Similar objectives were established for summer-run steelhead. In both programs, efforts were made to limit the influence of hatchery stocks on resident and endemic populations. The reintroduction of anadromous salmon into the Umatilla Basin, as well as the supplementation of summer-run steelhead, was implemented only after a long, well thought-out planning process.

In addition, an array of other objectives in the areas of habitat restoration, flow enhancement, and passage improvement were developed to improve environmental conditions in the basin. Juvenile and adult passage improvements have been made at several diversion dams and ladders.

Flow enhancement projects to pump water out of the Columbia River to replace water diverted for irrigation are nearing completion, and trap and haul programs are under way to move adults and smolts up and down the river at times when river conditions are not suitable for passage.

The largest investment in the rehabilitation effort has been in the hatchery program, which is considered the cornerstone of the program. Large-scale production goals were established to meet the adult objectives that were developed in the rehabilitation plan. The Umatilla Hatchery was constructed to meet the hatchery production needs. This facility is located on the shore of the Columbia River and is supplied with well water. The plan identified the need for production and release of 7 million juvenile fall-run chinook salmon annually; however, a full program has not been achieved, and only about 3 million fall-run chinook salmon have been released annually. One surprise outcome of the fall-run chinook salmon hatchery program was the extensive degree of straying that occurred among adult fall-run chinook salmon that should have returned to the Umatilla River but returned instead to the Snake River. Table 1 shows the total escapement to Lower Granite Dam, and the composition of escapement including the number of wild fish, numbers of Lyons Ferry Hatchery[1] fish, and number of Umatilla strays. The actual number of Umatilla fall-run chinook salmon straying into the Snake River was greater than that depicted in Table 1, because a substantial number entered the Snake River but did not reach Lower Granite Dam. Several factors likely contributed to and promoted straying of Umatilla River fall-run chinook salmon. Early in the program, juveniles were released in the lower part of the river near the confluence with the Columbia River and were not acclimated prior to release. Low flows and warm water temperatures occurred in the fall at the time adults should have entered the Umatilla River and presumably discouraged adults from migrating upstream.

We have made a substantial number of improvements in an attempt to reduce the rates of straying: juveniles are released in the upper part of the river and are acclimated prior to release; all fish are marked with magnetized wire and with a unique fin clip so the fish can be trapped and removed at dams on the Snake River; and river flows have been increased in fall to provide improved water quality, greater attraction, and better migration conditions in the river. It is our belief that these changes will reduce the straying to an acceptable level. However, only future information will allow us to determine if we have reduced levels of straying to acceptable levels.

[1]This hatchery was established to propagate Snake River fall-run chinook salmon.

Table 1. Origin of fall-run chinook salmon returning to Lower Granite Dam from 1990-93. Lyons Ferry = Lyons Ferry Hatchery fish; Umatilla = hatchery fish released in the Umatilla River.

Year	Escapement to Lower Granite Dam	Number by origin			
		Natural	Lyons Ferry	Umatilla	Other
1990	575	101	308	158	8
1991	630*	318	232	76	4
1992	957	620	294	41	2
1993	1,209	777	227	195	10

*Does not include jacks.

Discussion

Question: Bob Hayman (Skagit System Cooperative): Is there a reason why you would assume that natural Umatilla chinook salmon did not also stray into the Snake River before they went extinct?

Answer: Richard Carmichael: We have not assumed anything about historical levels of straying into the Snake River from the natural populations in the Umatilla River Basin. We do know that the Snake River populations are severely depressed and that there is probably an imbalance in these numbers relative to what may have been there historically when Snake River populations were large. Historically, Snake River production probably dwarfed Umatilla River production, and straying from the Umatilla River Basin into the Snake River was not important.

REDRESS OF INDIAN TREATY FISHING RIGHTS

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By treaty, Indians were given the right to use fish resources, but the right is meaningless without the existence of the resource. The redress of Indian treaty fish rights was the impetus to reestablish salmon runs in the Umatilla River. However, since many of the salmon populations in the Umatilla River had gone extinct, there were few stocks remaining in the river that could be used to start a supplementation program that could meet the rather large objectives for artificial production. The tribes, along with the State of Oregon, developed three objectives: 1) to rehabilitate naturally spawning populations in historical spawning grounds, 2) to return fish to the basin so they could be used as a self-sustaining source of fish for artificial production, and 3) to reestablish both Indian and non-Indian fisheries.

The program has been fairly successful in meeting these objectives. The numbers of returning adults have ranged from 4,000 to 8,000 fish annually. The numbers of natural spawners have increased and several broodstocks for artificial production have been developed. Holding facilities have been developed for artificial production, and there have been both Indian and non-Indian spring-run chinook salmon fisheries in 3 of the last 6 years.

The development of hatcheries is critical to reestablishing salmon runs and increasing fish production, especially in areas such as the Grande Ronde, which lies above eight dams. In the Grande Ronde, however, hatchery facilities have not been developed nor have acclimation facilities been placed at localities that would stimulate natural spawning. The release of spring-run chinook salmon fingerlings, for example, has met with varying degrees of success, and hatchery supplementation has gained a bad reputation. One indication of the failure of this program is that the estimated return of spring-run chinook salmon into the Snake River in 1994 is an all-time low of less than 1,000 fish, of which only one third are probably wild fish. Yet, NMFS has mandated some 40 sub-population management units in the Snake River for spring-run chinook salmon. That makes an average of about 10 fish per management unit. Straying has also been an undesirable side effect of some of these efforts to supplement salmon production, and a 5% straying policy under these conditions is practically meaningless.

The right combination of hatcheries and their locations, however, has never been achieved to maximize production. Indian tribes consider hatchery supplementation an important means of achieving production goals, and to limit the use of non-native broodstock will greatly limit the ability to achieve these goals because of the lack of native fish. While the tribes do not want to continue

past mistakes, they are aware of the realities of reduced levels of fish to harvest. At what population level does the concern for inbreeding depression in a captive brood stock outweigh the concern for outbreeding depression from the straying on non-native fish from a supplementation program? The tribes would like to move ahead with some kind of non-native stock supplementation, but are not sure how to evaluate the risks involved with such a program.

STRAYING AND GENETIC DIFFERENCES BETWEEN HATCHERY AND NATURAL POPULATIONS

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I appreciate the opportunity to address this workshop. I feel the workshop is especially timely because of the recent activities by NMFS to address ESA concerns, and because it is particularly relevant to the activities of the State of Washington and the Indian tribes in their efforts to recover wild salmon stocks. For the last several years, the tribes and State have been involved in an effort referred to as the Wild Stock Restoration Initiative. One of the activities under this initiative has been the successful development of the Salmon and Steelhead Stock Inventory for the State of Washington. We are currently undertaking the development of recovery plans for all "critical" stocks identified in the inventory. We are also just beginning work on a statewide salmon habitat inventory, and for about the past year, we have been working on the development of a Wild Salmonid Policy for Washington State. The framework of this policy includes habitat restoration and conservation, harvest management, and hatchery programs, but also includes genetic conservation. One major concern within genetic conservation is the effect of straying of genetically dissimilar hatchery fish into wild populations, and how and when this straying should be limited.

I would like to focus on two questions being addressed by the workshop panel. The first is, How do the effects of straying depend on genetic differences between hatchery and natural populations, and how can these differences be measured? In developing a Wild Salmonid Policy, we have explored several alternatives to these questions in our deliberations. One is to limit the amount of straying that would be permissible based on the amount of genetic dissimilarity between the hatchery population and the natural populations receiving hatchery strays. The key problem, however, is how to measure the genetic differences between hatchery stocks and natural populations. How do we measure differences in characteristics that are important in predicting the effects that interbreeding will have on natural populations? The approach we have taken is that if hatchery and natural populations are genetically dissimilar, then the amount of allowable straying should be very small or none at all. If the hatchery and natural populations are similar, then some level of straying can be allowed. We are uncertain, however, how to predict what effects that a particular amount of straying would have and how to measure genetic differences between hatchery and natural populations. How do measurable genetic differences, allozyme frequency differences, for example, relate to fish size, fecundity, or more importantly, to productivity and survival? How do genetic interactions between non-native hatchery fish and natural spawners affect the potential for the future productivity of the resource?

The second important question is, What research should be undertaken to resolve the uncertainties of this issue? The effects of straying of non-native hatchery fish into natural populations are uncertain, and I think it is unlikely a consensus of opinion exists on the subject in the scientific community. State and tribal agencies can develop a Wild Salmonid Policy for genetic conservation that is based on population genetics theory and our best scientific opinions, but unless we have direct empirical evidence that the expected genetic consequences are actually taking place, we are not going to have much luck in getting these policies adopted. Some of the possible restrictions on levels of straying that we have considered could make major changes in how hatchery fish are produced in the State of Washington. I can envision some scenarios that would cause us to reduce radically or to alter hatchery production in Puget Sound. It will not be easy to sell a policy that might reduce hatchery production by 60-70%, unless there is good evidence to show that it is necessary to prevent the loss of future sustainable productivity. The question the State and tribal managers will ultimately be most concerned about is, How does this policy affect the ability of the fish resource to produce harvest in the future?

STRAYING AND GENE FLOW BETWEEN HATCHERY AND NATURAL POPULATIONS

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I would like to extend the discussion about straying in the context of ongoing activities between Indian tribal fishery agencies and the State. Both groups have been working on jointly developing a policy on wild salmonids that addresses straying, gene flow, and other genetic issues. The issue of salmon straying has important genetic implications for the conservation of wild stocks, harvest management, and hatchery production. Hatchery production, usually using non-local stocks, has been used to meet harvest management objectives (harvest augmentation). In contrast, the chief goal of hatchery supplementation, like that used for Snake River stocks, is to restore or increase productivity of wild stocks. Increasingly, the occurrence of declines in wild stock abundance has prompted consideration of alternative rebuilding strategies, with much focus on strategies involving supplementation. This move to emphasize natural productivity and to maintain or increase harvestable surpluses reflects a transition from the context that most fishery managers have been working within for many decades. It is important to keep in mind that salmon management, with all of its inherent complexity, is now undergoing a major transition.

The key factor when considering the genetic effects of straying is maladaptive gene flow, not just the physical presence of non-local or hatchery-origin fish in natural populations. However, direct measures of gene flow are at best difficult to obtain, and the number of strays into a spawning population may be all that we have as surrogate estimates of gene flow. Given that we need better ways of estimating the actual numbers of non-local fish spawning in the wild, we must focus on reproductive overlap between hatchery fish spawning in the wild and wild fish. Estimates of this overlap will provide one of the best surrogate measures of actual gene flow in the absence of direct measures, and thus overlap is a key part of State and tribal discussions on wild salmonids.

Several assumptions about life-history patterns and gene flow have been made during our wild-salmonid policy discussions. One is that some level of straying and gene flow occurs naturally between wild populations, but just how much and under what circumstances is uncertain. Another assumption is that human-produced elevated rates of natural straying and unintended straying from non-local hatchery sources are undesirable because of the potential loss of genetic variability within and among populations, and because outbreeding may decrease fitness and productivity. More information on the effects of outbreeding depression, as Gary Graves pointed out, is urgently needed to assist in the development of rational management policies. Another important assumption in the evolving policy is that various management strategies can be used to increase homing or to decrease

rates of straying. Several state monitoring and evaluation programs are under way to understand better the causes and effects of straying.

With respect to general guidelines in formulating Washington's wild salmon policy, the intent of the State and tribal fishery agencies is to manage gene flow to maintain genetic diversity and to conserve local adaptations, productivity, and evolutionary potential. More information is needed on the means to achieve these rather abstract goals. The underpinnings of our wild salmonid policy are clearly set out in legislation passed by the Washington State Legislature in 1993, which directs the State "to ensure that department actions and programs are consistent with the goals of rebuilding wild stock populations to levels that permit commercial and recreational fishing opportunities" (Washington State Legislature 1993, p. 73). This general directive and the Department's response to developing a wild salmonid policy under the State Environmental Policy Act (public review and comment) and in collaboration with tribal managers is intended to allow flexibility in responding to the specific requirements of different watersheds, regions, and species. A fundamental conceptual difficulty has been to decide whether a fitness-based approach or a diversity-based approach is more appropriate; to date we have leaned toward the latter. Issues related to fitness would be indirectly addressed.

In general, our diversity-based approach requires first a description of genetic diversity within and between populations of each species. Part of this need was met in the wild salmon and steelhead stock inventory (WDF 1993). In addition, we are attempting to describe the hierarchical components of genetic, life-history, and ecological diversity within each species. Our approach and methods are similar to those used by NMFS to make determinations regarding Evolutionary Significant Units (ESUs). However, as a practical, conservative approach, we will identify smaller units to manage for genetics, population status, and maintenance. Secondly, we expect to manage for specific levels of gene flow (e.g., reproductive overlap) between hierarchical population units; that is, we intend to manage unnatural gene flow between population units. This includes, for example, gene flow resulting from stock transfers and other practices, and from overlap resulting from hatchery fish that escape harvest and spawn with wild fish. Surrogate measures of gene flow will be required.

We are aware that reproductive isolation between subpopulations can occur in different ways. Some groups of fish may spawn at the same time, but in different places. Others may spawn at different times, but in the same area. Again, accommodating these subtleties of life-history patterns and migratory and spawning behavior is important. Although simply measuring the number or percentage of hatchery fish straying into a particular stream may be feasible, it will lead to imprecise estimates of gene flow. A better approach would be to estimate overlap, and to target the amount of allowable overlap between population units to be scaled to the relative genetic similarity between hatchery and wild fish in a particular watershed. We are, however, still uncertain as to what levels of gene flow or surrogate measures (e.g., overlap) should be allowed between hatchery and wild fish under various circumstances and are hoping the panel will help clarify the options and their corresponding risks. For our policy approach to be implementable and therefore successful, we need to be able to measure and to monitor suitable parameters; we are aware that various theoretical predictions are possible, but we need to have practical tools so we can monitor progress toward meeting policy objectives. Once the policy has been completed, implementation plans will consider

a broad range of strategies. Monitoring plans will include a systematic review of hatchery practices to identify and activate improvements needed to achieve compliance with wild salmonid policy goals.

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Discussion

Comment: Marta Nammack: I noticed that both Gary Graves and Steve Leider say that the burden of proof should be on the scientists to show that theoretical concepts are important. I think the burden of proof should be shifted to the proponents of hatchery programs to show that their activities do not influence wild populations.

Steve Leider: Point well taken.

STRAYING OF HATCHERY FISH AND FITNESS OF NATURAL POPULATIONS

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Pacific salmon (*Oncorhynchus* spp.) are organized into distinct populations because of homing behavior (Rich and Holmes 1939, Ricker 1972). The alternative to homing is straying, in which fish do not return to their natal streams to spawn but spawn elsewhere (Bams 1976). Even though some straying occurs among wild populations (usually less than 5%; Lindsey et al. 1959, Vernon 1957, Rich and Holmes 1928), the amount of straying between natural and hatchery stocks is of concern because it can reduce the fitness of natural populations (Fleming and Gross 1993, Meffe 1992, Leider et al. 1990, Waples 1991). Evidence shows that some transplanted stocks are less productive than locally adapted populations, and that hatchery populations are generally less productive in nature than native locally adapted populations (Leider et al. 1990, Reisenbichler 1996, Chilcote et al. 1986). Introductions of hatchery fish into a river system can also displace wild fish or reduce their abundance (Nickelson et al. 1986). The effects of hatchery fish on wild populations are well documented (see Can. J. Fish. Aquat. Sci. 1981, 38(12), Aquaculture 1991, 98(1-3)).

Much of my effort has been to get salmon management and Indian tribal agencies to pay attention to the results of these studies in their efforts to develop and manage salmonid fisheries. Given the documented effects that hatchery strays can have on wild populations, hatchery policies and funding should be subject to a scientific review process, and that is what this workshop is about. Hatcheries, however, are often treated as "sacred cows" by fishery agencies, and attempts to correct problems with straying are sometimes met with accusations of "hatchery bashing." The problem is that a formal process of hatchery evaluation is lacking in formulating budgets. For example, in fiscal 1992, the NMFS budget for its hatchery program was $13.4 million, whereas the combined funding for fishery resource management, protected species management, and habitat restoration and conservation was only $1.8 million (R. Schmitten, NMFS Headquarters, 1315 East West Highway, Silver Spring, MD 20910. Pers. commun., March 1992). The states of Oregon and Washington have similar policies for funding hatcheries, as does the U.S. Fish and Wildlife Service. Since hatchery programs constitute a large proportion of the agencies' budgets, it is reasonable for these agencies to avoid questions about hatchery programs and their influences on wild stocks.

Discussions of hatchery straying are often seen as attacks on hatchery programs, rather than as constructive criticisms intended to make things work better. Present policies inadequately regulate fish hatchery practices. Even the recent effort on the part of fish agencies to develop an integrated hatchery policy in the Columbia River Basin does not evaluate the effects of hatchery fish on the ecosystem once they are released. It deals chiefly with the coordination of protocols among hatcheries. An institutional mechanism to identify hatchery-related ecosystem problems is entirely

lacking. Consequently, even though there are ample scientific studies on the problems hatchery strays cause, an institutional means of addressing and resolving these problems is not in place because funds for a review and evaluation are not available.

Additional funds are required to acclimate juvenile hatchery fish so they imprint adequately during their down-river migration, to mark them, and to inventory spawning streams for them as adults. To reduce the rate of straying of hatchery fish, the trucking of juveniles will also have to be discontinued. Truck-transported juveniles are not imprinted well enough to find their way back up a river to their point of capture, so they tend to stray to other areas (Slatick et al. 1982) and can introduce such diseases as IHN to previously uninfected rivers. But we continue to truck juveniles because it is more economical than barging them. To deal with hatchery straying, a policy must be developed and implemented to determine if any rates of straying are acceptable, especially for small populations because they are at the greatest risk. Traps will have to be placed in streams so that marked hatchery fish can be removed.

Two primary kinds of hatchery strays include 1) hatchery fish that do not return to their release site, but stray into other streams, and 2) non-native hatchery fish used for fishery enhancement or mitigation that are transplanted from non-local populations. Both kinds of hatchery strays place native fish at risk through interbreeding and ecological interactions, and any policy on straying of non-native fish must be designed to protect the fitness and evolutionary potential of wild populations. This may mean closing a hatchery facility when it becomes too expensive or impractical to control the straying of non-native fish. Straying may also be induced when juveniles are transported for release to rivers where the hatchery fish are non-native. Examples, among many others, include the non-local release of Alsea Hatchery winter steelhead, Skamania Hatchery summer-run steelhead, Lower Columbia River hatchery coho salmon, and Rogue River chinook salmon (reared in net-pens in the Lower Columbia River). Adults returning to a release site may stray uncontrollably when they encounter unfavorable conditions. This occurred in the Umatilla River.

Converting hatcheries to raise only native brood stock may greatly reduce the effects of hatchery straying, but this hypothesis must be evaluated before it can be applied broadly to a river system. Captive brood stock may also diverge genetically from local wild stocks in traits that are important in local adaptation. Even with the use of only native brood stocks, hatchery strays may still adversely affect natural populations. Any policy on strays should also consider ecological interactions of juvenile hatchery fish with wild fish, especially in the large-scale use of non-native fish for mitigating run losses or for run enhancement.

Conserving genetic variability within and among native wild salmonid populatons is key to the success of fishery management. At this time, it is impossible to prevent selection for traits that favor survival in a hatchery environment, so hatchery fish will diverge from wild forms and become less fit for survival in nature. Thus, hatchery fish can be a form of biological pollution that must be controlled to maintain not only native salmon, but ultimately the consumptive fisheries.

I conclude with a quote by Yu. P. Altukhov and Salmenkova (1991, p. 28, 35-36): ". . . many anadromous fish are now reproduced artificially in hatcheries and reared and released into the

rivers--but the method is insufficiently effective. This is because the species' population genetic structure has not been taken into account . . . . These data testify to the negative genetic effects of existing salmonid exploitation and management practices. Artificial reproduction, commercial fisheries, and transfers result in the impairment of gene diversity in salmon populations, and so cause their biological degradation."

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Discussion

Question: Dave Johnson (Nez Pierce Tribal Fisheries): The peoples in the Pacific Northwest have eaten salmon for thousands of years, and the United States government made promises when the land was taken from Indian peoples. Among these promises was the ability to live off salmon. If, as you suggest, we manage for a particular population of salmon, we in effect lose our treaty rights and our means of subsistence is taken away. For thousands of years we have lived on salmon, and now within 100-150 years salmon have practically disappeared. We are not so concerned with the genetics of these fish, we just want the fish to eat and we support whatever hatchery programs are needed to give us those fish.

Answer: Bill Bakke: I understand your point of view, but are artificially propagated salmon as good as natural fish "from the creator" for your spiritual and cultural well-being? The Snake River has been pressed into many different uses that adversely affect salmon populations, and I hope that the tribes and others can begin to correct the problems causing the decline of salmon populations. Sustainable artificial propagation of salmon in the long term has its own problems. For example, we have a shrinking supply of eggs for the lower Snake River hatcheries and are forced to import non-native eggs. It does not appear that hatchery technology is solving the problem.

Comment: Robin Waples: I think it is good to get these ideas out, because they show the complexity of the issue and the strong feelings on all sides. The panel, however, has not been asked to deal with these social and cultural issues, but will deal only with scientific issues.

Evolutionary Biology

POPULATION DIFFERENTIATION AND EVOLUTIONARY PROCESSES

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Introduction

In the first part of this talk, I will briefly review the evolutionary forces acting upon natural populations, and in the second part, show you the results of simulations that illustrate what would happen in natural populations affected by straying from hatchery populations. The results are abstract and idealized, and the simulations have been done in nice symmetrical ways for mathematical convenience, but it is important to realize that the same principles operate in a more complicated way in real-life situations. The task is to understand what the most important principles are and how you can apply them to a real situation.

Processes Influencing Genetic Change

I will mention five basic evolutionary forces. We usually do not think of random mating as an evolutionary force, but it is. Another force is natural selection, in particular natural selection to adapt populations to local conditions. A third force that can potentially change the genetic makeup of a population is mutation. Since mutation occurs about equally everywhere, it is not in and of itself a force making populations different or more similar. Actually, mutation tends to make populations more similar to each other, but it is a minor force. Migration is another important force; for this workshop, we are concerned with hatchery straying, which is one kind of migration. Population geneticists equate migration with gene flow, the actual incorporation of migrant genes into a receiving population, and not just with the physical movement of an individual. The final mechanism that can lead to genetic changes in a population is random change from random births and deaths of individuals. This process is called random genetic drift. I will concentrate on gene flow, random genetic drift, and natural selection.

Gene flow

To illustrate the simple mathematics of gene flow between natural populations, let us imagine that we have a genetic locus (a place on a chromosome) which is variable in a set of populations. The information encoded by the locus occurs in different forms, called alleles. Each fish normally has two copies of a gene, one inherited from each parent, and the frequency of a particular allele in a natural population can be measured as the proportion of all the copies of that gene that are of one allele or another. This proportion is called a gene or allele frequency. Imagine we have a population

represented in Figure 1 as a big square, and we find--using one biochemical or molecular technique or another--two alleles, one of which is at a frequency of 0.80, or 80% of the total. In the next generation, imagine that 70% of the individuals in the population stayed in that population, but 20% came from population 2, and 10% came from population 3. In populations 2 and 3, the frequency of the same allele was 0.1 and 0.2, respectively. The allele frequency in population 1 is simply the weighted average of the frequencies in the residents and the migrants.

When the mix of individuals in population 1 begins to mate, let us assume that they mate at random, without regard to where they came from. If so, the basic units are not whole genotypes, but individual alleles that re-assort themselves each generation, and the best way to think about gene flow is to consider the flow of individual alleles rather than the flow of genotypes. Because of the peculiarities of sexual reproduction and random mating, geneticists talk about the frequencies of alleles or genes, which partially determine the frequencies of genotypes in a population. In calculating allelic frequencies in the recipient population, we have to consider migration rates. Migration rates are calculated as the fraction of new migrants in the recipient population, and population size can be important when the donating and receiving populations are very different, as is often the case for salmonid populations. For example, a migration rate of 20% in a small recipient population may represent a much smaller fraction of a large donor population. If you think about the number of individuals leaving a population, you may get the wrong impression about the effects of migration.

Random genetic drift

Suppose that we assume that natural selection is not occurring; that is, we are not favoring one allele or another and that the alleles are passively reproducing themselves at random. Following the frequencies of two alleles from one generation to the next in a population is much like tossing a coin in which each side of the coin represents an allele of the gene. If there are 100 individuals in a population, 200 copies of the gene are present--two copies for each individual. We can simulate random drift by tossing a coin 200 times to get the frequency in the next generation. But instead of having a probability of 0.5 for a particular side of the coin, the probability of getting a particular side in the toss would be the frequency of the allele in the population before reproduction, but after migration. As you know, if you toss a coin several times, you usually do not get the exact proportion that you expect. In a small number of tosses, which simulates a small population, the frequencies vary a lot from the expected. With a large number of tosses (a large population), the frequencies are closer to the expected proportion. Figure 2 illustrates the random changes in allele frequencies that might occur in a population.

In natural populations, randomness arises from three sources: randomness of deaths (some individuals may die early), randomness of births (some pairs may have a lot of offspring and others very few), and randomness of Mendelian segregation of genes during gamete formation (only one of two parental genes occurs in each gamete). These three sources of randomness lead to small changes in allele frequencies in a population from one generation to the next. An important characteristic of drift is that these small changes are cumulative; that is, the starting point for the next generation is the allele frequency of the present generation, and not the frequencies of previous generations. If

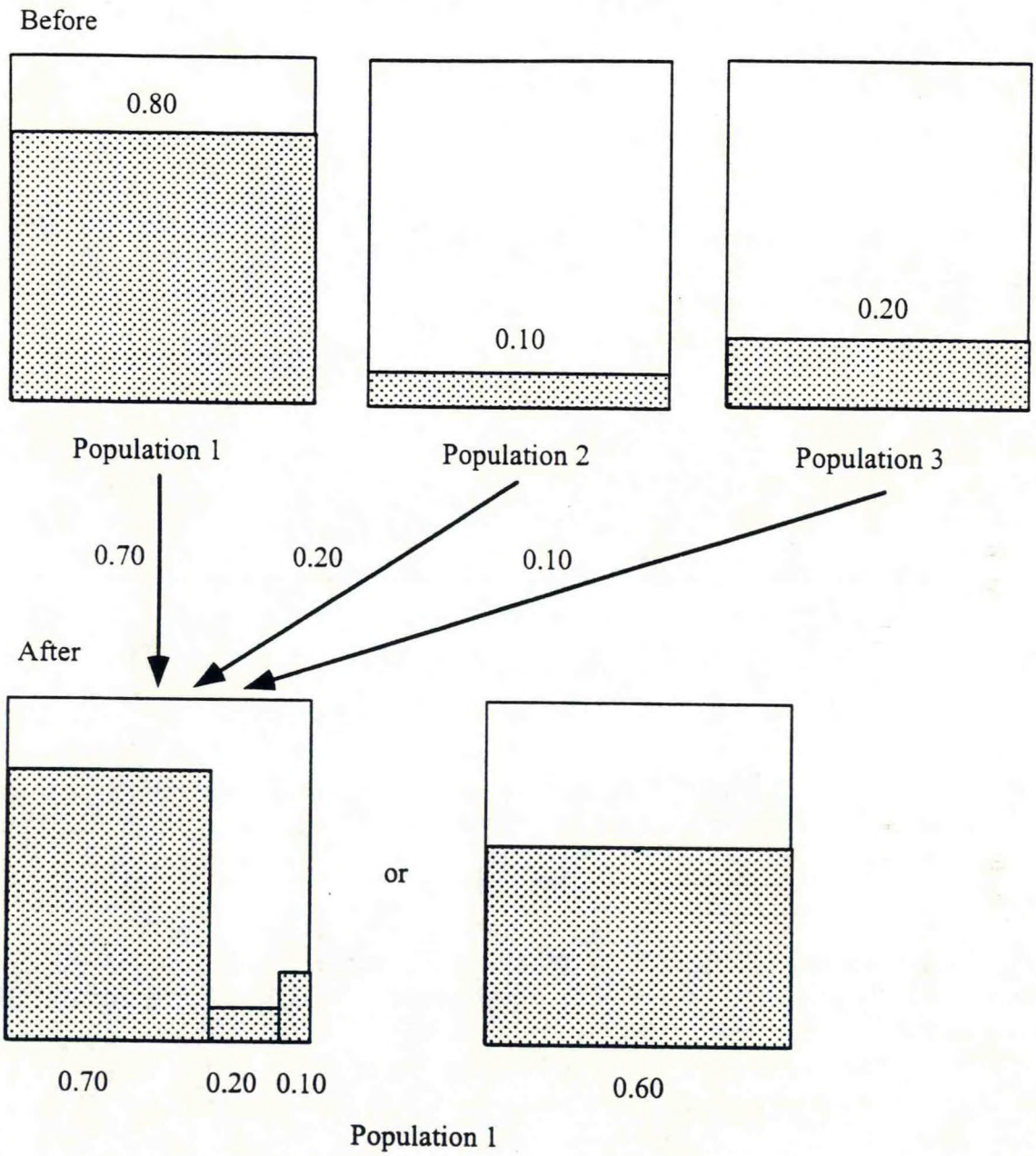


Figure 1. How gene flow affects gene frequencies in natural populations. Each rectangle is a population, and the level of shading indicates the gene frequency of an allele. One generation of gene flow is shown.

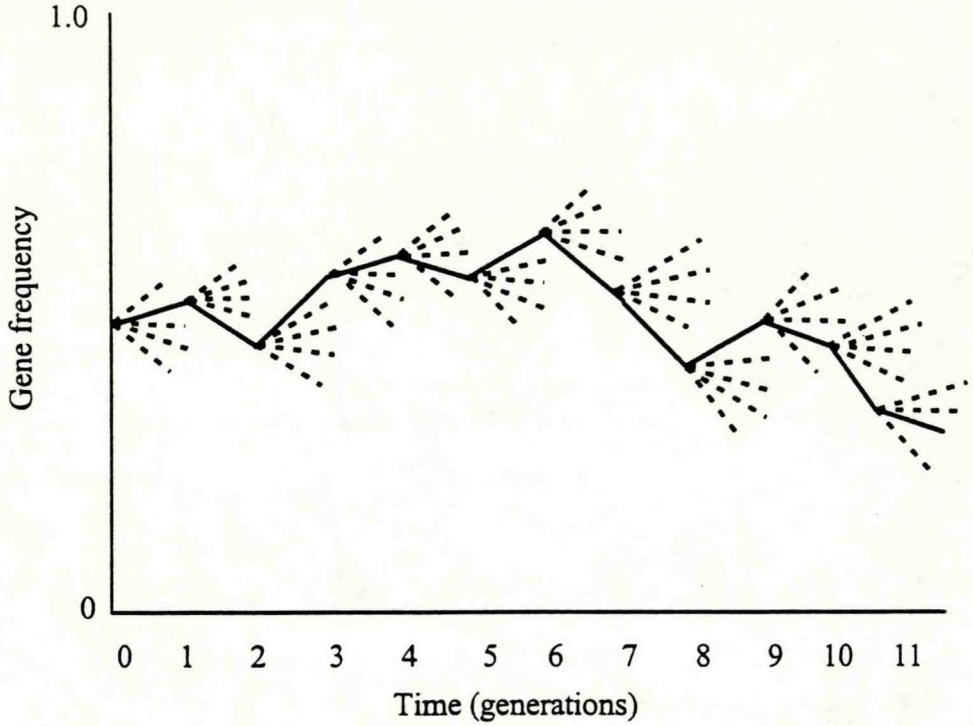


Figure 2. The process of genetic drift. In each generation, some of the possible gene frequency paths that might be taken are shown, with one of them being taken by the particular population.

frequencies change from 0.30 to 0.32 in one generation, the next generation starts from 0.32 and has no memory that the frequency was ever at 0.30. Another characteristic of random drift is that the direction of change is not predetermined. The frequency of each generation can change up or down, so the frequency can randomly "walk" away from the original frequency, then cross back over it again. If you repeat the same simulation with the same starting allele frequency, you will not get the same path each time.

Natural selection

Natural selection results in the unequal representation of different alleles in the next generation, owing to differences in survival or reproduction between different genotypes. A particular case that is of importance to this symposium is the adaptation of genotypes to the local environment. We might have an allele, *A*, that is favored in the local environment but not elsewhere. Thus genotype *AA* might have fitness 1.05, genotype *Aa* fitness 1.03, and genotype *aa* 1.00. For population genetic purposes, it does not matter what units we measure fitness in: all that matters is

the ratio of the fitnesses of different genotypes. In this case, we have arbitrarily taken genotype *aa* to have fitness 1.00. Genotype *AA* has a 5% higher fitness than *aa*, and *Aa* has a 3% higher fitness. The quantities 0.05 and 0.03 here are called selection coefficients (*s*): they give us a quick idea of how strong natural selection is.

If natural selection occurs in a randomly mating population, with no migration or genetic drift, we can easily calculate what happens to the allele frequencies. It will surprise no one that in this case, allele *A* will continue to increase in frequency until it approaches 1. The speed with which this happens is a function of the selection coefficient. If the selection coefficient is 0.01, it will take hundreds of generations for allele frequencies to change substantially. For example, with the fitnesses I just gave (1.05:1.03:1), it will take about 200 generations for the allele frequency to rise from 0.10 to 0.90. If the selection coefficient is smaller, it will take proportionally longer. For selection coefficients one-tenth as great (1.005:1.003:1), it will take about 2,000 generations instead of 200.

There are many interesting and complex results for more complex patterns of fitness (overdominance, in which the heterozygote has the highest fitness, underdominance, in which it has the lowest fitness, frequency-dependent fitnesses, temporally varying fitnesses, fitnesses dependent on multiple loci, and so on). But we will primarily deal with the simple pattern of local adaptation here.

Combining Evolutionary Forces

Migration and random genetic drift

Let us first combine the effects of migration and random drift. Migration between populations tends to average out allele frequencies so populations become more and more similar, whereas random drift tends to make populations different. Figure 3 shows three populations that are exchanging genes at a particular rate and in some kind of pattern. The allelic frequencies in each population will wander over time as they undergo genetic drift, but the amount and direction of divergence between the populations is constrained by migration between them. If one population reaches a high allele frequency, a high proportion of the migrants into the other two populations will have the high-frequency gene, and migration will tend to pull the frequencies in the other two populations in the same direction. At the same time, random drift--thermal noise like Brownian motion--will tend to pull the frequencies of the three populations apart. The result is that the whole set of populations, or the species as a whole, will change at a slower rate than individual populations.

When migration and genetic drift are operating in the absence of natural selection, the important quantity is four times the effective population size, N_e, times the migration rate m, or $4N_em$. The effective population size is the population size corrected for other factors that affect the amount of genetic drift expected in the population. These factors include unequal contributions of offspring from different individuals in the population, unequal numbers of males and females, overlapping generations, and several other factors. These factors usually reduce the effective

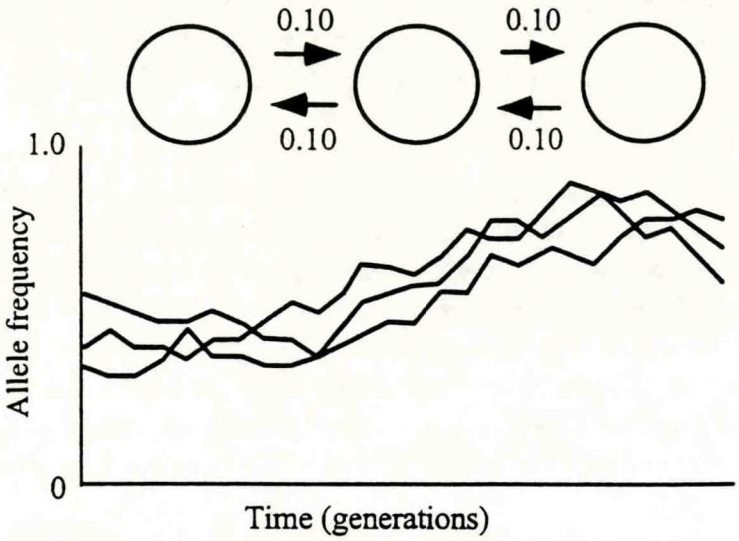


Figure 3. A diagram showing how migration and genetic drift interact. The three populations drift on the gene frequency axis, but in a correlated fashion. A model and a typical result are shown.

population size and cause more genetic drift. Population genetics theory shows that if $4N_em$ is much less than one, the populations act more or less independently of one another and allelic frequencies in a set of populations become quite dispersed. If this number is much greater than one, allele frequencies in the populations tend to be similar to one another. Note that N_em, the effective population size times the proportion of migrants coming into a population, is simply the number of migrants. If the number of migrants for a set of populations exchanging migrants is less than one per generation, the populations will tend to drift apart, and this is true whether the sizes of the populations are 100 or 1 million. The importance of genetic drift depends not on the *proportion* of migrants, but on the *number* of migrants, and the size of the population is unimportant. This is strange but true.

Population geneticists use abstract models to understand the effects of random drift and migration on sets of populations with specific geographic structures. One such model is called the *island model of migration*, in which local populations receive immigrants from a pool of migrants drawn from each population. There is really no geographic structure in the model. No two populations are closer to each other than any other two. Another abstract representation of population structure is called the *stepping stone model*, in which migration is limited to neighboring populations. Stepping stone models can be one-, two-, or even three-dimensional, depending on the biology of the species being considered. More realistic models can also be constructed in which populations can be situated anywhere with specific sizes and specific migration rates. These kinds of models, however, are complicated mathematically and are usually studied with numerical simulations.

Stepping stone migration and natural selection

Some work has been done on models similar to the one I will develop here (Haldane 1930, Hanson 1966), which I call patch swamping. Let us imagine five populations with stepping stone migration between them; that is, each population exchanges migrants only with its two neighbors at a rate $m_1/2$ so that the total fraction of immigrants is m_1 (Fig. 4). An end population receives migrants from a hatchery population, also with a migration rate of $m_1/2$. Whatever comes into the population most distant from the hatchery can get there only through the other populations by working its way down the chain of populations. Long-range straying is also possible; I am not sure what kind of gene flow is most important for salmon. In this long-range model of straying, migrants can go into any of the populations. Let us label the exchange rate between neighboring populations as m_1, and the long-distance migration rate as m_2.

First of all, let us consider an allele at a gene that has an adaptive advantage over other alleles in the local populations. In the absence of migration from the hatchery, this allele will increase in the natural populations to a frequency of 100%, except for the small effects of mutation. Next, let us add the effects of migration from a hatchery population that does not have the favored allele, so that the frequency of this allele in the hatchery is 0%. The pattern of allele frequencies among the populations depends on the relative amounts of local and long-range straying that we expect to see. The "simulations" reported here are exact calculations, by computer, of the allele frequencies that we would see in the absence of genetic drift.

In the first simulation, we set m_2 to 0.10, so that 10% of the fish in the end population are strays from the hatchery. We also set selection to 0.10, so that fish carrying the favored allele have a 10% increase in fitness for each copy of the allele they carry. If a fish is heterozygous with one non-native allele and one favored allele, it is 10% better off than a hatchery fish with two non-native

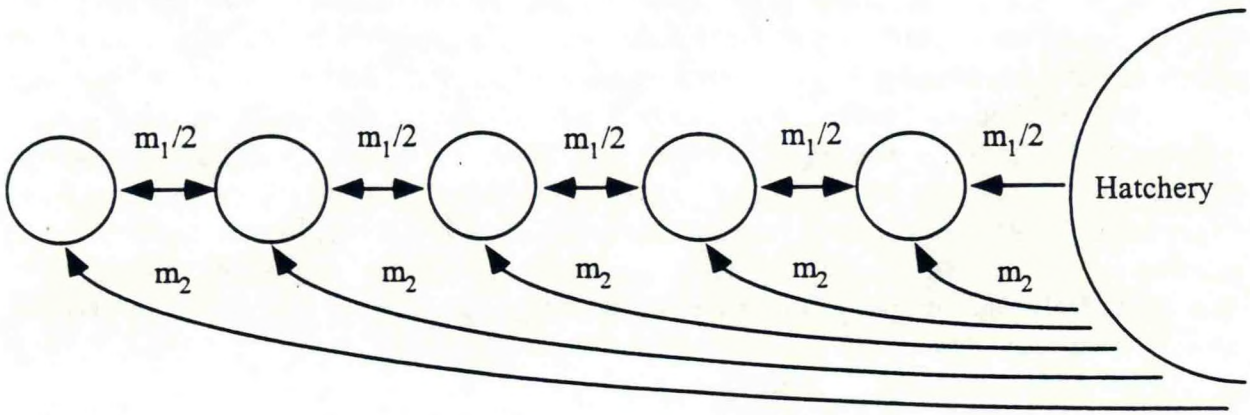


Figure 4. The model used for the computer iterations. There is both local straying and long-range straying from the hatchery.

alleles; however, if it is homozygous with two copies of the favored allele, it is 21% better off. In the first generation of the simulation, some of the non-adapted alleles from the hatchery get into the end population, so the frequency of the adapted allele is only 90% in that population (Fig. 5A; I have drawn the hatchery population twice so that its allele frequency is more visible). The frequency of the favored allele is still 100% in the remaining four populations. The simulations then continue for 5,000 generations (1, 10, and 5,000 generations are shown to give you a feel for the rate of change). As the simulation proceeds, the frequency of the non-native allele begins to increase down the chain of natural populations, but it is lower in the more distant populations. The frequency of the favored allele in the most distant population is still close to 100%, so this population is resisting the immigration of the non-adaptive allele from the hatchery. When we set the migration rate to 20%, we get a similar pattern, except that more hatchery alleles appear in the natural populations, and the frequency of the favored allele in the most distant population drops to 98%. At 50% migration, a smooth geographic pattern appears--a cline--and the frequency of the favored allele in the end population is 90% when the system stabilizes. One conclusion from these results is that for a linear string of populations with stepping stone migration, the populations have a tremendous ability to resist migration from hatcheries. But note that the selection coefficient used here was rather large.

What happens with a favored allele with only a 1% selective advantage? Such a selective value is not small in evolutionary terms, and is sufficient to make large changes in allele frequencies over long periods. In real life, however, it is difficult to measure a fitness value of only 1%, because humans can measure far fewer fish than nature can. Researchers are limited to the number of fish they can measure with the sizes of grants usually available from funding agencies, whereas nature measures millions of fish. It is also difficult to get a grant that would last 5,000 generations. We will still use 10% immigration from neighboring populations. These results show that after 5,000 generations, more of the hatchery allele is getting through to the end population, which has a frequency of the favored allele of 66% (Fig. 5B). This shows that immigration of non-adaptive alleles is more effective when selection favoring local adaptation is not strong.

If we increase the amount of migration with a 1% selection coefficient, we see the patch swamping phenomenon. At 20% migration, allele frequencies appear to form a cline after a few generations, but the cline stablizes at very low frequencies. The locally favored allele is still present, but only at a maximum of 20%, and the hatchery allele is getting through to the most distant population (Fig. 5C). At a higher migration rate of 30%, the cline collapses, and at 5,000 generations only a very small frequency of the favorable allele is present in the natural populations (Fig. 5D). The patches of local adaptation have been completely erased by migration from the hatchery into a single end population. This model does not take into consideration that the hatchery straying rate may be much higher than the natural migration rate among wild populations. It also does not account for long-distance migration beyond neighboring populations.

Long-distance migration, random drift, and natural selection

Let us now incorporate long-distance migration, by using a 1% long-range straying rate from the hatchery superimposed on a natural migration rate of 10% between the wild populations. An allele-frequency cline appears, but many more hatchery alleles move into the most distant population

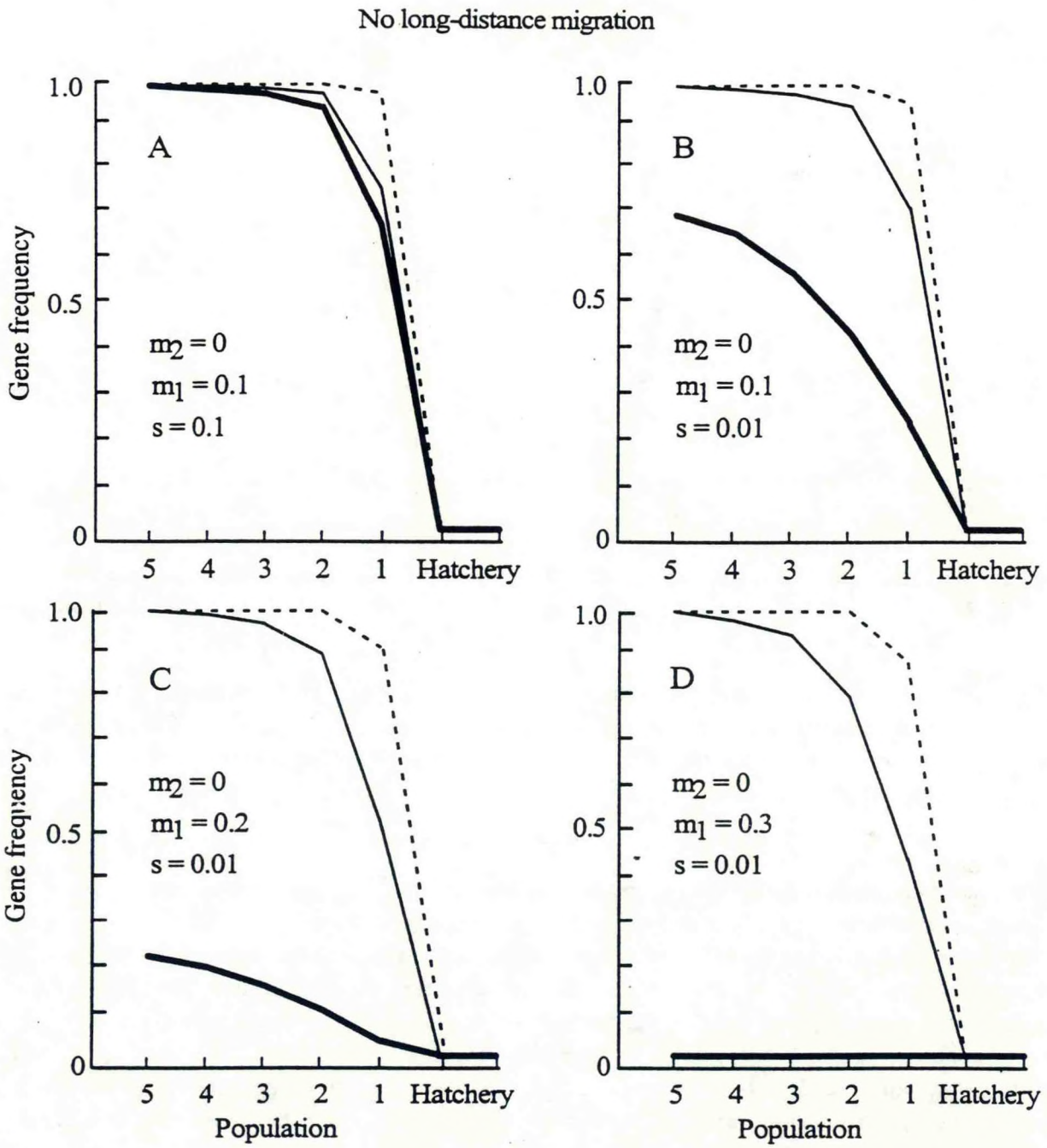


Figure 5. Allele frequency changes expected in the model of Figure 4, when there is no long-range straying. The dashed curve shows the result after one generation, the thin curve after 10, and the thick curve after 5000 generations, which is presumed to be enough to achieve equilibrium. The hatchery population is on the right, and is plotted as the rightmost two points instead of one, so that it is more visible. **A.** The results after 10 generations give a sense of the speed with which the equilibrium is approached. **B.** As less natural selection favors the locally adapted allele, hatchery alleles move farther into the chain of populations. **C.** With more local migration, the hatchery alleles penetrate farther, and the locally adapted allele is barely able to maintain itself. **D.** With even more migration, local adaptation collapses.

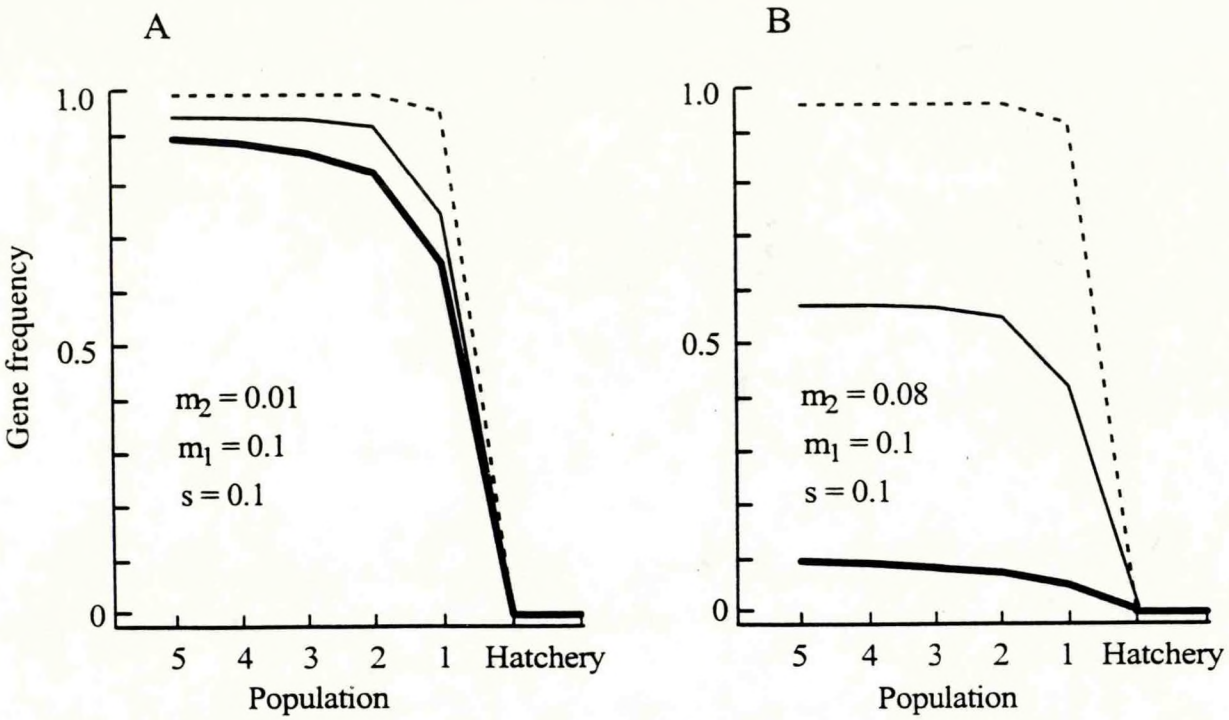


Figure 6. **A**. With some long-range migration (long-distance straying), the hatchery allele moves much farther into the chain of populations. Compare this figure with Figure 5A, which differs only in the rate of long-range migration. **B**. With a higher rate of long-range migration, the patch of local adaptation is at the point of collapsing.

than would be the case for no long-distance straying (Fig. 6A). Compare this with the same values for selection and natural migration, but without long-distance straying (Fig. 5A). Long-distance straying dramatically increases the migration of hatchery alleles. An increase in long-distance hatchery straying of 2%, 5%, and 8% progressively depresses the allele-frequency cline among the natural populations, so that the cline has virtually collapsed at 8% long-distance straying, and only a very few adaptive alleles are present in the natural populations (Fig. 6B). The point is that long-distance straying greatly erodes the populations' ability to resist the immigration of non-adaptive alleles, because the non-adaptive alleles can get to the end of chain of populations in one jump without having to travel through the string of populations.

All of these results show that the collapse of the patch of adaptation occurs at a critical ratio of the strength of selection to the migration rate, and depends on which model is used. If the rates of immigration are larger than the difference in the fitness of the adaptive and non-adaptive hatchery gene ($m > s$), locally adaptive alleles will predictably be swamped by hatchery alleles. Since this occurs locus by locus, allele by allele, a situation could arise in which a local population has several locally adaptive alleles, some strongly favored and others only weakly favored, in the face of some mix of local and long-distance migration. Weakly favored alleles may be replaced by hatchery alleles, but strongly favored alleles may persist in a clinal pattern. Because of this locus-by-locus

complexity, fish in the populations along the cline will be made up of a mix of adapted and non-adapted genotypes to varying degrees. If the alleles in the natural populations are neutral to selection and have differentiated among populations because of random drift, then hatchery alleles will push out local alleles and homogenize the frequencies of alleles among the natural populations. So, fortuitous adaptations due to genetic drift will not resist invasion from hatchery alleles. On the other hand, adaptations due to natural selection will resist the invasion of hatchery alleles to the extent that the strength of natural selection is greater than the amount of gene flow.

Linkage

In the simulations presented here, we have assumed that the effects for one locus are independent of those for other loci. This is not quite true, because loci are often physically linked together on the same chromosome. Slatkin (1975) showed that if two genes are close to each other on a chromosome, and there is little recombination between them, alleles at the two loci will tend to be associated with one another in geographically structured populations. For example, suppose we have two populations: population 1 has all capital *A* alleles at locus **A** and capital *B* alleles at locus **B**, and population 2 has all *a* and *b* alleles at the two corresponding loci. If individuals from the two populations are mixed, you would find only *A-B* and *a-b* chromosomes. After random mating, but with very low rates of recombination because of linkage, you will find not only *A-B* and *a-b* chromosomes, but also double heterozygotes with the genotype *A-B/a-b* and very few recombinant chromosomes, *A-b*, *a-B*, which also produce double heterozygotes, *A-b/a-B*, but with different states of linkage.

Let us assume that the *a-b* chromosome is from hatchery fish and the *A-B* chromosome is from adapted wild fish. A correlation appears in the population in which the adapted alleles at one locus are associated with the adapted alleles at the other locus. This association has the effect of helping favored alleles resist migration from non-favored hatchery alleles, because they travel together and natural selection favors chromosomes with both adapted alleles over those with just one adapted allele. Because they are physically linked, selection for one allele is also selection for the other. The strength of selection is as though the two individual selection coefficients are added together. For a chromosome with two linked loci each with alleles having a selection coefficient of 10%, the total strength of selection for that chromosome is 20%. Selection for linked loci provides more resistance to invasion by hatchery alleles than does selection on two similar, but unlinked loci. So to be able to predict the effects of hatchery straying in real life, we would have to know how many genes confer local adaptations, the kind of natural selection favoring them, and the strength of the linkage on the chromosome. In addition, we would have to know how much local and how much long-distance migration is occurring.

Conclusions

The genetic makeup of natural populations is potentially influenced by an interacting mix of evolutionary forces. In the absence of natural selection, the quantity $4N_em$, four times the number of

migrants, is an important quantity. If $N_e m$ is greater than one, then differentiation among natural populations from random genetic drift is unimportant. When natural selection is overlaid on migration and genetic drift, patch swamping will occur when immigration from hatcheries is greater than the strength of locally adapted selection. Patch swamping also occurs more quickly with long-distance hatchery migration than with migration into a single natural population. Linkage between loci with adapted alleles, however, increases a wild population's ability to resist the invasions of non-adapted alleles.

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Discussion

Question: Mike Lynch: If we know a specific straying rate, what you showed was the greater the strength of adaptive selection, the lower the equilibrium frequency of deleterious alleles. So from a fishery point of view, the question might be that, given a particular amount of migration and a particular strength of selection, how does a natural population "feel"? Is this analogous to mutational load where the load on the population does not depend on selection, only on mutation?

Answer: Joe Felsenstein: Yes, the analogy with mutational load is correct. The fitness of a wild population will be controlled in much the same way that the fitness of a population receiving deleterious mutations is reduced. This is the concept of mutational load. The effects of hatchery straying would be called migrational load, and you can use the principle that deleterious alleles will sooner or later be selected out. When deleterious alleles are selected out, you have one reproductive failure (death) for each copy of the deleterious allele that comes into the population. On the other hand, if the individuals being eliminated through selection carry multiple hatchery alleles, then there will be less than one death per allele, because each death eliminates more than one deleterious allele.

If migration is 10% in a set of populations that have formed a cline because the hatchery alleles are being resisted, the fitness of a population is reduced by 10%, and you do not need to know what the actual selection coefficient of the allele is. It is the migration rate that is most important in reducing fitness. However, if the adapted patches are swamped by hatchery alleles, you can "calculate" the effects by saying that the natural populations used to have an adaptive allele, but do not have it any more. In this case, the reduction in fitness depends on the selection coefficient.

Question: Gary James: You have assumed that hatchery alleles are not favorable in natural habitats, but what if the hatchery alleles do show favorable traits for local adaptation?

Answer: Joe Felsenstein: If that is the case, then only genetic drift is important. With more than 1/4 of a migrant per generation, the natural populations will all have similar allelic frequencies. If not, they will genetically diverge by genetic drift. Allele-frequency clines would not appear, patch swamping would be unimportant, and fitness in the wild populations would not change.

Question: Audience: It seems from what salmon biologists know about hatchery straying that the value of $N_e m$ is probably larger than one, so how do we use these principles?

Answer: Joe Felsenstein: If this value is greater than one, the frequencies of selectively neutral genes in the natural populations will be pushed toward the frequencies of these genes in the hatchery population. If wild alleles have higher fitness than hatchery alleles, the effects depend on the balance between the migration rate and the selection coefficient.

Question: Audience: Why did you use 5,000 generations in these simulations? Most salmon populations we work with have not been in the rivers for that long because of events in the Late Pleistocene, and selection has changed over that time and will continue to change in the future.

Answer: Joe Felsenstein: I thought 5,000 generations would be enough to show whatever might happen, but most of the changes took place in tens of generations. In most of these simulations, equilibrium conditions arrived in a short while; I continued the simulations just to make sure. I hope you do not come away with the impression that these are only very long-term problems.

Comment: Robin Waples: One of the limitations of theoretical population genetics is that it is difficult to make the transition from dealing with frequencies of alleles at a single locus to what happens in organisms as a whole, which have thousands of gene loci affecting fitness.

SELECTION AND VARIABILITY IN NATURAL POPULATIONS

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Introduction

Wild populations can potentially be affected by one-way straying of non-native hatchery fish in three ways. The first is the spread of deleterious alleles into a wild population, and as noted in the previous talk, the ability of non-native alleles to invade a wild population depends critically on selection intensities. The second potential effect of hatchery straying, also previously mentioned, is the eradication of genetic differences between hatchery and wild populations. I do not necessarily mean that some genes have no consequences for fitness, but that the different genes in hatchery and wild fish may represent equally good combinations. If, however, wild populations possess unique attributes, such as unique colors, sizes, or shapes, which do not greatly influence fecundity or other aspects of fitness, but which have some conservation value, these attributes may be eradicated by gene flow from hatcheries. This question has less to do with population fitness than with genic diversity. The third concern is with the demographic effects hatchery strays have on wild populations. Genetics and demography interact to influence wild populations in ways other than the effects brought about by gene flow. If we want to understand the effects of the immigration from hatchery populations, we also have to understand what the fates of wild populations would be in the absence of gene flow from hatcheries. Even in the absence of hatchery gene flow, wild populations may not do well, because of ecological or other non-gene flow effects from the presence of hatchery stocks in the same river. For example, a wild stock may be reduced by shared predation during harvest on both hatchery and wild stocks.

In this talk, I will address only the first issue of what selection intensities are in natural populations and will present information on what selection intensities have been measured in nature for various organisms. Unfortunately, selection has not been measured in natural populations of salmon, so we have to make educated guesses by looking at what has been measured in other organisms, some of which are fishes such as guppies and sticklebacks. I would like briefly to present the results of a survey of the literature on natural selection by Endler (1986). I will then present some caveats in drawing conclusions from these studies, to argue that we may not be able to take these estimates of selection and use them in the equations presented in Joe Felsenstein's talk. Lastly, I would like to talk about the kinds of variability in natural populations and how this variability influences population responses to selection.

Kinds of Selection

By natural selection, we mean the differential survival or reproductive success of various phenotypes. Some individuals succeed and others fail to contribute offspring to the next generation for one reason or another. This should be distinguished from evolution, which is genetic change not only by natural selection, but also by other forces such as genetic drift and migration. Sexual selection is a subset of natural selection and is brought about by differential mating success caused by differences in the phenotypes of the individuals. For example, elk males with large horns may mate with a greater number of females even though the size of the horns may not enhance the fitness of these males in other ways.

Endler (1986) grouped traits under selection into 1) morphological, 2) physiological, and 3) biochemical traits. Morphological traits include such things as external body dimensions, color variation in snails and butterflies, beak size in birds, and so on. Physiological traits include life-history traits such as fecundity, resistance to herbicides or antibiotics, tolerance to heavy metals, and so on. Biochemical traits include allozymes encoded by genetic loci which appear to be affected by selection. Allozymes are alternative states of enzymatic proteins that are encoded by the same locus on a chromosome. Just how allozymes influence an individual's appearance, size, or color is not always understood.

Criteria for Demonstrating Natural Selection

The first criterion that Endler used to include examples of selection in his survey was that the traits were heritable, or were thought to be heritable; that is, the traits had a genetic basis, at least in part. This excluded several cases in the literature that showed that selection was associated with some trait, large body size for example, but that the trait was not heritable. A *direct* demonstration of selection is made by marking a sample of individuals and measuring them for a trait before and after selection, or by repeatedly measuring a trait in an unmarked cohort of individuals in a single age class.

Using these criteria, Endler estimated that by 1986 natural selection had been directly demonstrated for 314 traits in 141 species (Table 1). Most of these examples were for morphological traits, but some were for physiological traits, especially those involving tolerance or resistance to a stress, and a few were biochemical traits. The immediate importance of these numbers is to show that natural selection is not a rare event in nature. However, it is not correct to say that natural selection occurs on morphological or physiological traits more than on biochemical traits, because at smaller scales of physical organization, it becomes progressively more difficult to measure selection. For example, it is easy to measure the size of a bird's beak, but much more difficult to characterize a bird's physiology or biochemistry, before and after selection.

Table 1. Numbers of species and traits for which natural selection has been directly demonstrated. Endler (1986, p. 156).

Kind of traits	No. of species	No. of traits
Morphological (external dimensions)	85	199
Physiological (resistance, life history, tolerance)	27	56
Biochemical (allozymes)	12	59
Two or more kinds	17	
Total	**141**	**314**

Selection Intensities in Nature

Estimates of the strength of selection in nature are crucial for using models of gene flow and selection. Let us first look at polymorphic traits, or those traits occurring in more than one easily discernible state. These include such things as eye or hair color, or other discretely varying traits such as allozyme genotypes, which can be scored for each individual. For example, a researcher measures the survival of individuals during a drought and is able to show that survival is better in individuals with particular character states. One particular genotype might be associated with 80% survival, on average, whereas individuals with another genotype may survive only 60% of the time, on average (Fig. 1). This then is natural selection, the differential survival of different genotypes or phenotypes. The selection coefficient, s, is the difference in fitness between the genotype with the highest level of survival and the genotype of interest. The genotype with the greatest fitness (w) is generally given the value 1.0, and the fitnesses of other genotypes are measured relative to this value. The range of s is then between 0.0 and 1.0. The maximal value of s is 1.0, and such a level of selection is very strong. On the other hand, a value of 0.0 means that selection is not occurring on a particular genotype or phenotype. As noted previously, the effects of gene flow depend on the amount of gene flow and the strength of selection. If the migration rate is 50%, then a selection coefficient of 50% is needed to keep adaptive alleles in the natural populations. So just what are the levels of selection in nature?

Discrete characters

Endler classified the cases of selection into two groups, varying in the types of environments: *A*, selection in undisturbed environments, and *B*, selection in disturbed environments, including selection in environments with introduced organisms and selection in enclosures (Fig. 2A, 2B). Perhaps category *B* is most relevant to hatchery straying. Endler also classified examples into two groups according to the fitness components investigated: *C*, mortality selection, and *D*, data from

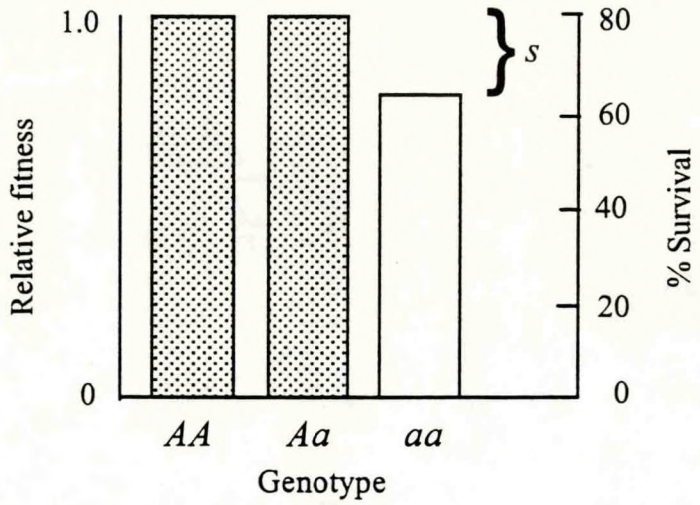


Figure 1. Hypothetical example of selection for survival. Vertical bars represent the relative fitnesses of three genotypes, *AA*, *Aa*, and *aa*.

fecundity, fertility, and sexual selection (Fig. 2C, 2D). Shaded bars represent values that are significantly different from 0.0 ($P < 0.05$). Unshaded values indicate the values were not distinguishable from chance fluctuation. The lack of significance for many of the small values may have been due to the inability of the experiment, because of small sample sizes for example, to detect small but real changes. The basic finding is that selection intensities vary considerably; some are strong, but most are weak. One problem with these distributions is that they represent a sample of values in the literature and not a random sample from nature itself. The lack of detectable selection is usually not reported, so there is a bias toward publishing large values of selection. Cases of weak, but real, selection are underestimated in the literature because the problems of measuring small intensities of selection are greater than those of measuring large selection intensities. The median of selection in undisturbed and disturbed environments is about 0.3, a high level of selection intensity.

Continuously varying characters

Next, we will look at traits, such as body mass, height, and gill raker length, that vary continuously in a population and not in discrete, countable units. Measurements of one of these traits usually show some distribution, with an average value (X) and a standard deviation (σ) as in Figure 3. The unshaded distribution represents a hypothetical population before selection, and the shaded distribution represents the same population after some kind of selection. Directional selection occurs when the mean value of the trait shifts after a period of selection. The selection illustrated in this figure is quite strong, because no one under a certain value survives. Only individuals with extremely large values survive. The standard deviation is about one-fourth of the width of the distribution and is used to scale the coefficient of directional selection. The intensity of selection (i)

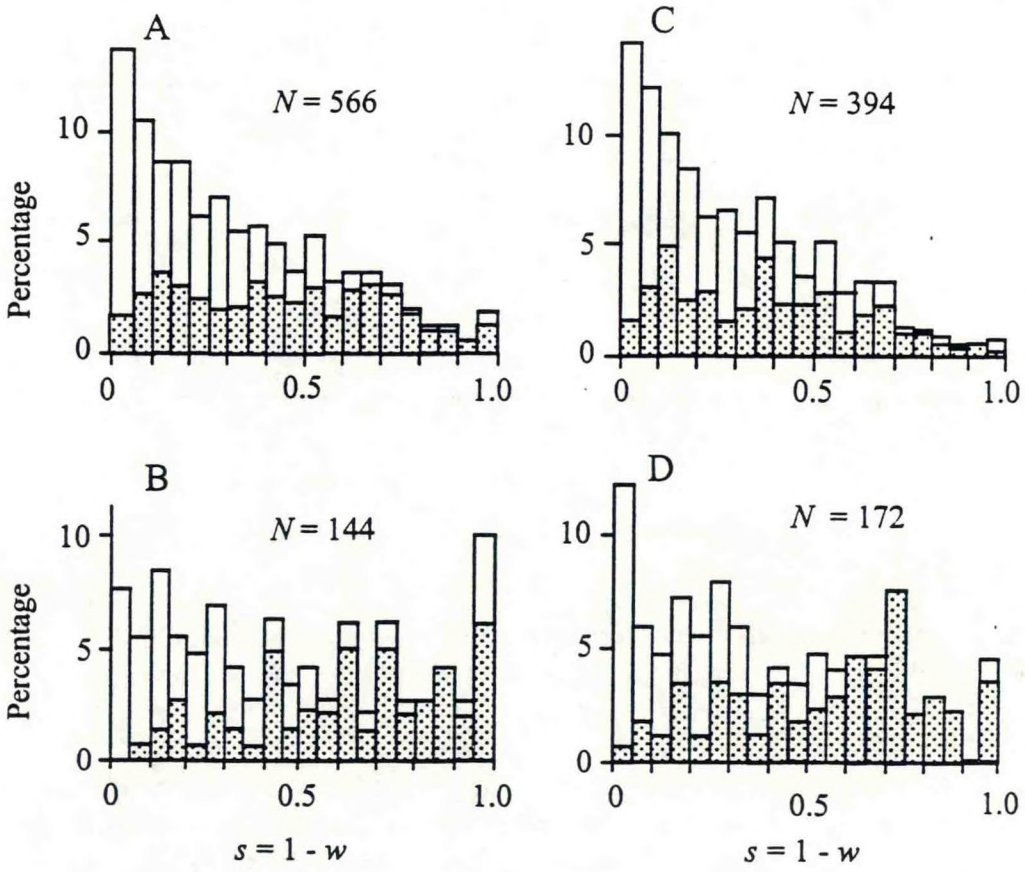


Figure 2. Distribution of selection coefficients in published studies showing selection for polymorphic traits with discrete character states. Shading indicates statistical significance, and no shading indicates measured selection values that were not statistically significant. **A**. Undisturbed populations. **B**. Disturbed populations, field cages or stressful environments. **C**. Mortality. **D**. Fecundity, fertility, and sexual selection. Endler (1986, p. 207).

is the difference between the means X_1 and X_2 divided by the standard deviation σ, and represents the amount of change in terms of standard deviation units. In this hypothetical example, the shift was about one standard deviation, which is quite large. A shift of two standard deviations is enormous. Endler used the index, i, in his survey.

The results of Endler's survey of selection, i, on continuously varying traits in natural populations appears in Figure 4. As before, shading indicates cases in which the shift was statistically significant, and did not result from chance alone. The median is about $i = 0.3$, but a few extreme values exceed 1.0. Keep in mind, however, that these are published values, and because of the tendency not to publish small values of selection, they probably under represent examples of low selection intensity.

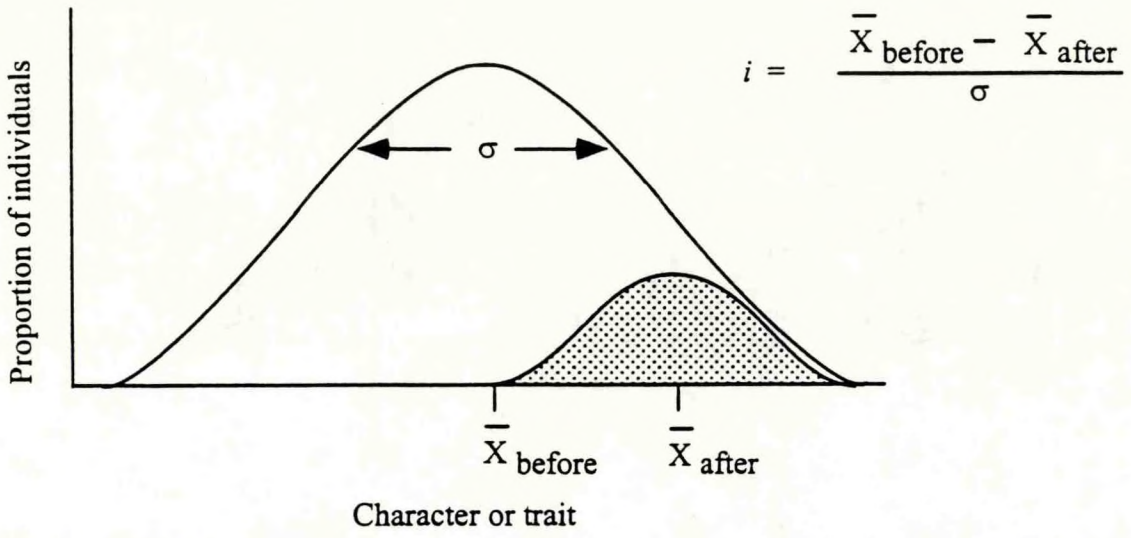


Figure 3. Graphical model of selection intensity on a continuously varying trait. The coefficient of directional selection, *i*, was used by Endler (1986) in his survey.

As a specific example, Figure 5 shows the results for a population of song sparrows on Mandarte Island in Juan de Fuca Strait, which has been studied for several years by Jamie Smith at the University of British Columbia (Schluter and Smith 1986). Tarsus (a bone in the lower part of the leg) length in millimeters is shown versus the probability of survival after the first winter of life in female birds. Symbols (+) represent individual measurements of tarsus length before winter when the birds were banded for later identification. In spring, the presence (upper row) or absence (lower row) of a bird was used as a measure of survival: if present the bird was given a value of one, if absent a value of zero. The curve, then, shows the relationship between probability of survival and variation among females in their first year of life. A difference of only 3 mm, from 18 mm to about 21 mm, produced a reduction in survival from 90% to 20-30%. This shows that large changes in the probability of survival are produced by only small changes in the length of the tarsus. Such intensities of selection are quite common and are not limited to one life-history stage. For this population, about one selection event is detectable each year for such things as juvenile and adult survival, reproductive success, and so on. This number, however, probably underestimates the number of selection events because of our limited power to detect them.

Application of these values to models

It would be tempting to use these observed values of selection in the models for migration, genetic drift, and natural selection. If we did, these large values of selection would suggest that hatchery straying will not have a large effect on the genetics of wild salmon populations. However, let me mention several caveats. The first is that in virtually all cases of selection in Endler's survey, the actual cause of selection was unknown. Although differential survival or reproductive success may be associated with a particular heritable trait, we still have no idea of the mechanism of

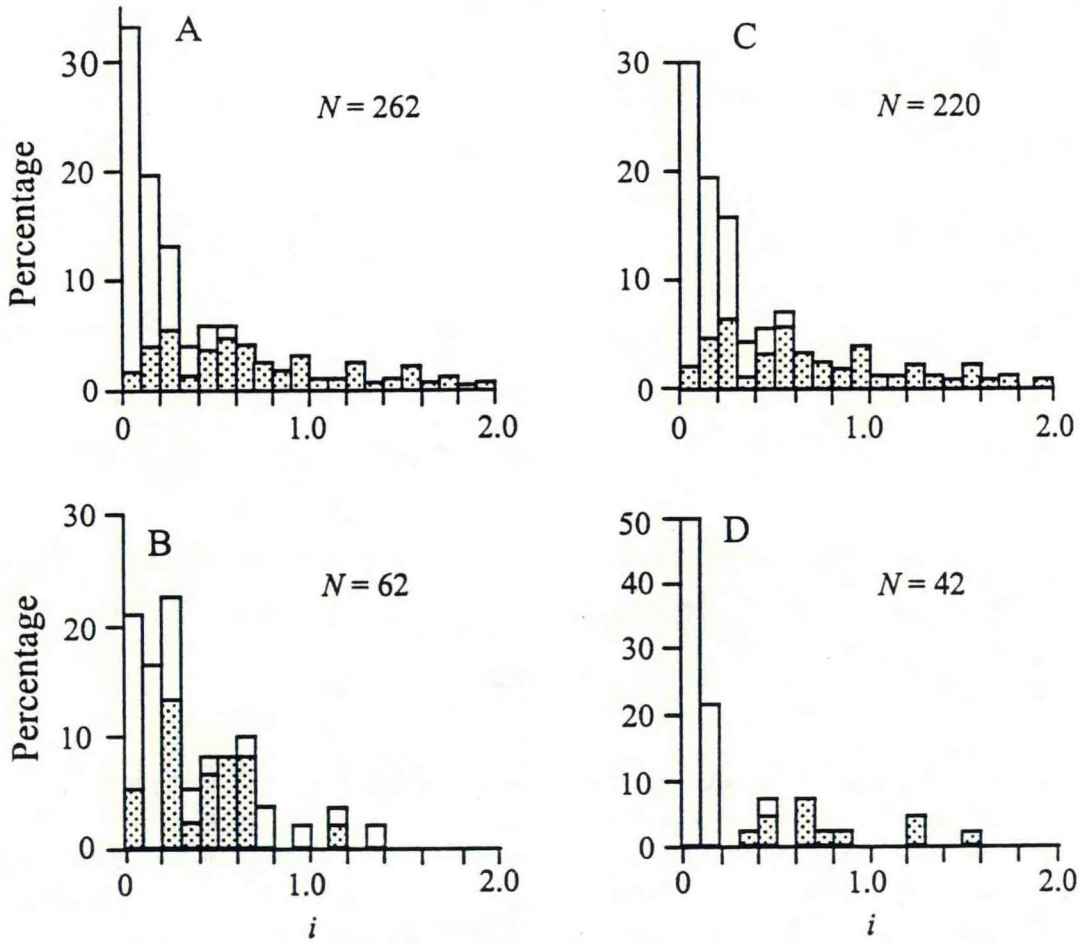


Figure 4. Distribution of selection coefficients in published studies showing selection intensities for continuously varying traits. Shading indicates statistical significance, and no shading indicates measured selection values that were not statistically significant. **A.** Undisturbed populations. **B.** Disturbed populations. **C.** Mortality. **D.** Non-mortality. Endler (1986, p. 209).

selection in most cases. Selection may actually be occurring on another unmeasured trait associated with the measured trait. Understanding the mechanism of selection is important so we can judge whether the selection is the result of factors in the local environment, or food supply, or whatever.

A second warning is that just because a trait does not show a change, it does not necessarily indicate that no selection is occurring on that trait. Strong selection may be holding the trait in place, the direction of selection may be different in the various life-history stages, or selection may be acting on another trait strongly correlated with the first in an opposing direction (Lande and Arnold 1983). A third problem is that selection may be occurring on a non-heritable trait or series of traits that are correlated with a heritable trait, so that selection is not actually acting on the heritable component of the variability. Traits that depend on the nutritional condition of an individual, such as fecundity or body size, are particularly susceptible to this kind of artifact. It is

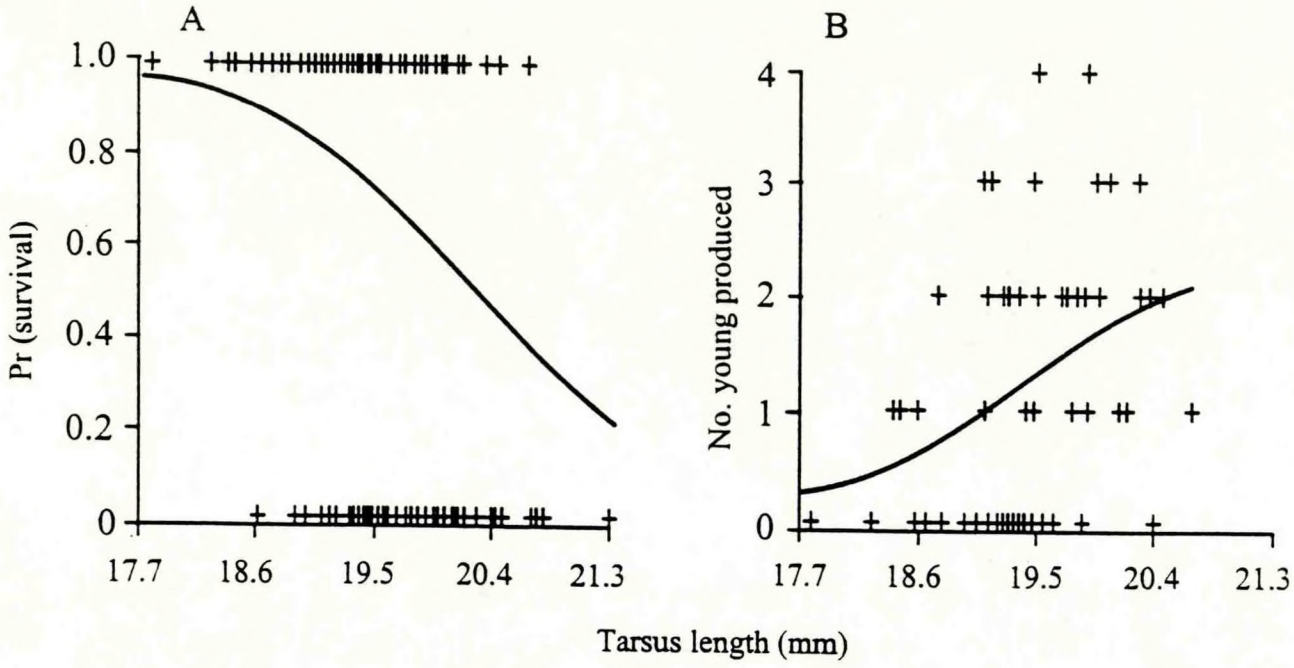


Figure 5. **A**. Survival of female song sparrows in their first year of life on Mandarte Island, British Columbia, in relation to their tarsus length. Symbols (+) indicate raw measurements for individual females from 4 years of study. Tarsus length was measured before winter. Survival was scored as 1 if females survived the winter and 0 otherwise. Nonparametric regression of probability of survival with tarsus length (Schluter 1988). From Schluter (1988) based on data in Schluter and Smith (1986). **B**. Reproductive success of adult female song sparrows on Mandarte Island. Data based on 1 year of study and are from females that survived their first winter. Nonparametric regression of mean number of fledglings and tarsus length (Schluter 1988). From Schluter (1988) based on data in Schluter and Smith (1986).

therefore difficult to extrapolate from the measurement of apparent selection to the kind of selection that may be operating.

Another problem is that only a single life-history stage was examined in most of the cases summarized by Endler. These estimates of selection, therefore, reflect only one component of fitness, and another view of selection may emerge if all life-history stages of an organism were studied. In some of the cases where selection was observed for more than one life-history stage, the directions of selection changed at the different stages (Schluter et al. 1991). For example, in the song sparrow population on Mandarte Island, selection on tarsus length operated in one direction in females in their first year, but in the opposite direction later in life (Fig. 5B). If you look over the whole life span, the two forces cancel each other out, but you would not see this if you observed only a single episode of selection.

Yet another problem is that the direction of selection may oscillate within or between generations. A well-known study of a species of Darwin's finches in the Galapagos Islands (Gibbs and Grant 1987), showed that, during a prolonged drought, 85% of the birds died, and those that survived were considerably larger for every trait (weight, wing length, beak length, etc.) measured. A subsequent, milder drought also produced changes in the same direction but on a smaller scale. When the rains associated with the El Niño returned, food abundance on the island increased and brought about selection for smaller individuals. In general, long-term studies show that the directions and intensities of selection are constantly oscillating, and the magnitudes of the selected characters tend to wobble not just within generations, but between generations. If selection is measured at only one life-history stage, it may appear that selection is powerful and operates consistently in one direction. Short-term measurements of selection tend to be large, but long-term average measurements probably tend to be smaller.

Finally, when we attempt to look at the relationship between variability for a trait and fitness, we would like to know about the intensities of selection in different populations. It is of great interest to know what kinds of selection produce differences between populations or even between hatcheries. Long-term studies of selection in a range of populations are indeed rare, but one such study does exist for the peppered moth (*Biston betularia*) in Britain. Dark pigmentation increases crypsis on tree trunks denuded of light-colored lichens by sulfur dioxide and darkened by industrial soot, and confers resistance to visual predation. The more ancestral light form was displaced by the dark form in industrial areas which produce high levels of air pollution (Kettlewell 1973). A cline developed near Liverpool, England in which most moths near the industrial area were dark and the moths farther away, 50 km or so, were more lightly pigmented. Experimental translocations of the dark and light forms allowed the researchers to measure changing natural selection pressures over the whole environmental gradient. Mortality of the light form was high near Liverpool and low farther away from Liverpool, whereas the opposite trend was seen in the dark form. Even this textbook example of selection may not be as simple as first thought; gene flow and some component of non-visual selection are necessary to explain, for example, the somewhat higher-than-expected frequency of the dark form in non-industrial areas (Brakefield 1987).

Heritability of Traits Under Selection

An important problem is to understand the extent that continuously varying traits are heritable. Many researchers assume that most of these traits are heritable, and that variation in only a few traits is caused by something other than genetic differences among individuals. Figure 6 shows the cumulative frequency distribution of heritability values in the literature for morphological traits such as beak size. This distribution suggests that the median heritability for these kinds of traits is about 40%; that is, about 40% of the variation in a trait is due to the additive effects of genes. This is quite high. Life-history traits tend to have heritabilities that are about 30%, and heritabilities for behavioral and physiological traits lie between these values.

Since life-history traits have lower heritabilities than morphological traits, you might think that the smaller the heritability, the more resistant the population is to selection; however, this is not exactly true. The unshaded curve in Figure 7 indicates the probability of survival or some other

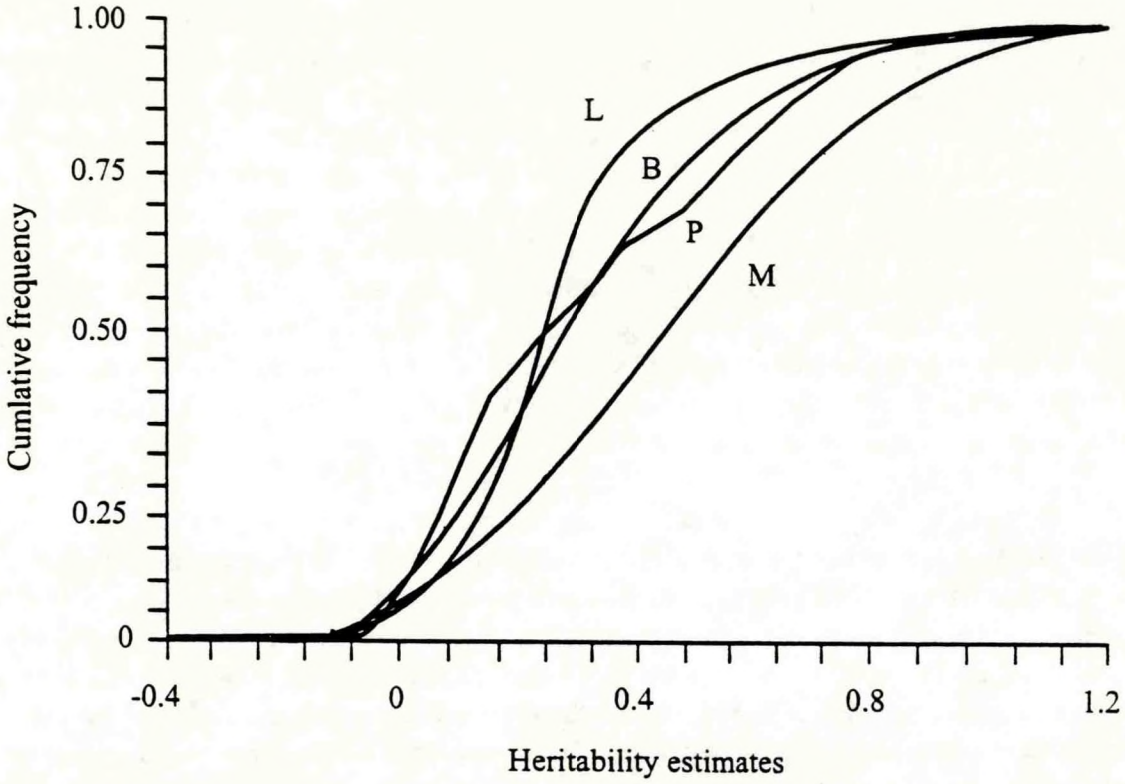


Figure 6. Cumulative frequency distributions of heritability estimates taken from the literature. Trait categories are L (life-history traits), B (behavior), P (physiology), and M (morphology). Figure from Mousseau and Roff (1987).

measure of fitness as a function of variation in that trait. The shaded curve indicates the distribution of a trait in a population experiencing selection. This relationship can be used to predict the magnitude of the response to selection in the next generation (i.e., the amount of evolution). The response is not actually determined by heritability, but by the absolute amount of additive genetic variation in the population experiencing a fitness function. The actual levels of additive genetic variation in life-history and morphological traits are about the same even though heritabilities differ (e.g., Price and Schluter 1991). Life-history traits have lower heritabilities than morphological traits because they are influenced by environmental variation to a greater degree. More environmental noise is associated with them. The message is that nearly all traits are heritable and that they do respond to natural selection.

Conclusions

My first conclusion is that natural selection is pervasive in nature, and my second is that the intensity of selection is quite strong. We have seen the patterns of selection for several kinds of single traits. However, numerous problems arise in attempting to use the estimates of selection from these limited studies, because the direction of selection may vary from one life-history stage to

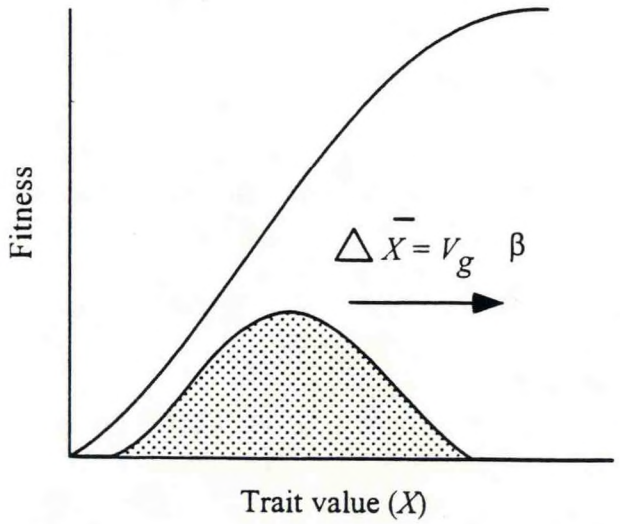


Figure 7. Graphical model of trait evolution across a single generation. Unshaded curve illustrates how relative fitness (fitness divided by the mean fitness in the population) differs among individuals for a continuous trait X. The shaded curve illustrates the distribution of the trait in a population. The change in the mean value of the trait in the next generation (X) is the product of the absolute amount of additive genetic variance in the population and the slope of the fitness function (Lande 1979).

another or because of several other factors. The third conclusion is that since most traits are heritable to some extent, local selection on life-history, morphological, physiological, and biochemical variability confers adaptation to local conditions. However, none of these conclusions implies that selection is sufficiently strong or consistent in direction to overcome the effects of migration from non-adapted genes. These conclusions also do not imply that evolution is repeatable. Just because most traits are heritable does not mean a genetically altered population can revert to its original genetic state.

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Discussion

Question: Richard Carmichael: In the distributions of selection intensities you presented for discrete and continuously varying traits, it looked as though these studies reported more statistically insignificant than significant values for selection. In calculating the average values of selection intensity, were the non-significant values treated as zero?

Answer: Dolph Schluter: The median values I reported were estimated by eye and included all the values as they were reported, significant or not. I should point out that selection has been observed in 141 species, but that several different components of selection were observed in some of the same species, so the total number of estimated selection coefficients is greater than the number of species. The problem is that some of the observations may not be independent of other observations.

Question: Nils Ryman: Do you have any idea about how strong selection must be to be observed at all?

Answer: Dolph Schluter: The most important factor in detecting selection is the interaction between the strength of selection and the sample sizes used to measure selection. Small samples sizes decrease the power of an experiment to detect small selection coefficients.

Question: Audience: You said that evolution is not necessarily repeatable, but it is striking to me how similar odd- and even-year pink salmon are to each other even though they are reproductively isolated from each other. They use the same streams in very much the same way, but in different years.

Answer: Dolph Schluter: This is an indication that similar selection pressures can produce similar phenotypes, even though biochemical data indicate odd- and even-year populations at the same locality are reproductively isolated from each other.

Question: Richard Carmichael: Do estimates of heritability suffer from the same bias that estimates of selection coefficients do, in that estimates of zero heritability tend not to be published?

Answer: Dolph Schluter: Yes, the distribution of heritability estimates also suffers from the sample size problem. Undoubtedly many researchers have dropped efforts to measure heritability when it appeared they were not going to find heritable traits.

INBREEDING DEPRESSION AND OUTBREEDING DEPRESSION

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Introduction

Fluctuations in population size and gene flow of maladaptive alleles can potentially produce inbreeding depression and outbreeding depression, both of which can reduce the fitness of a wild population.

Mechanisms Causing Genetic Deterioration

Inbreeding depression

This is the exposure of the individuals in a population to the effects of deleterious recessive genes through matings between close relatives. For a given locus, some alleles will confer more fitness on an individual than other alleles. Within the "other" class of alleles are rare deleterious recessive alleles, which when appearing as a homozygous genotype in an individual because of mating between relatives, greatly reduces the fitness of the individuals carrying them. Deleterious alleles arise constantly through mutation, so they are always present in a population at low frequencies. Suppose we have two alleles, *A* and *a*, where *A* is a normal allele and *a* is a deleterious allele. The homozygous genotype *aa* of the deleterious allele is rare in a large population, because with random mating the expected frequency of a homozygote is the square of the allelic frequency p^2, and for a low-frequency allele this is a small value. *AA* individuals are the most fit of the three possible genotypes. *Aa* individuals have the same fitness as *AA* individuals if the *A* allele is dominant over the *a* alleles, or they may have some intermediate level of fitness if the effects of the alleles are more additive. Lastly, *aa* individuals show some recessive deleterious trait that reduces their fitness.

In a large population where the *a* allele occurs at a low frequency, the *a* allele appears chiefly in the heterozygous state *Aa*, and heterozygous individuals will almost always mate with *AA* individuals. The offspring of an *AA* X *Aa* mating will be *AA* or *Aa*, and the effects of the recessive deleterious allele are masked. On the other hand, if mating occurs between relatives in which both relatives have a copy of the deleterious allele in the heterozygous state, an *Aa* X *Aa* mating, one-fourth of the offspring of the mating are expected to have the deleterious *aa* genotype. Mating

between relatives "unmasks" the effects of recessive deleterious alleles that would otherwise occur only in heterozygous individuals.

So far, we have considered only a single deleterious allele at a single locus. However, extrapolating from lower organisms and plants (Lynch et al. 1995), about 100 deleterious alleles are present in individuals of higher organisms when we look across all genetic loci (see Lynch and Gabriel 1990). The problem is therefore not trivial when all of the loci are considered. Most of these deleterious mutations produce only a small reduction in fitness of about 2%, when the alleles are made homozygous. If all of the loci in an individual are made homozygous through mating between relatives, the reduction in fitness would be on the order of 200%, enough to "kill" the individual two times over. This, essentially, is inbreeding depression.

Outbreeding enhancement

The converse of inbreeding depression is outbreeding enhancement, which is often referred to as hybrid vigor or heterosis. An example of outbreeding enhancement is the use of hybrid strains of corn, which greatly outperform inbred strains. From the standpoint of deleterious recessive genes, hybrid vigor is nothing more than the reverse of inbreeding depression; that is, it is the masking of recessive deleterious alleles by crossing individuals from different populations. Typically, different populations of the same species harbor different recessive deleterious alleles, so hybrid offspring between parents from the two populations will not be homozygous for the same deleterious alleles. The offspring are fitter than either parent because the effects of the deleterious alleles have been masked. If the hybrid offspring are allowed to mate randomly in subsequent generations, the deleterious alleles will segregate out because of the mechanics of Mendelian inheritance and produce individuals homozygous for the same deleterious allele, which will have reduced fitness. But the mean level of fitness in the population will still be higher than the level in either parental population, because the frequency of each deleterious allele has been reduced by mixing.

In summary, consider a hypothetical population in which an individual mates at random with an unrelated individual in the same population. Other individuals may mate with a sibling, a cousin, or other close relative, and as this mating between relatives continues we begin to see the effects of inbreeding depression. The more closely related two mated individuals are, the greater the depression in fitness that is expected to appear in their offspring. On the other hand, matings of unrelated individuals from genetically diverged populations of the same species may produce outbreeding enhancement, if different deleterious mutations have accumulated in the two populations.

If inbreeding depression and outbreeding enhancement were the only genetic mechanisms we had to consider and matings between individuals could be controlled, obviously the best strategy would be always to mate individuals from different populations. However, things are not so simple. So far we have considered only single-locus effects, but typically alleles at different loci interact so that complexes of genes co-evolve in a population, acting harmoniously with one another to produce a high level of fitness. Different isolated populations may evolve different complexes of genes that

interact well within a particular population, but poorly when the genes are mixed through cross-population matings. This reduction in fitness in the offspring is called outbreeding depression.

Outbreeding depression

This phenomenon can occur in two ways. One way is by the "swamping" of locally adapted genes in a wild population by straying from, for example, a hatchery population. In this case, adaptive gene complexes in wild populations are simply being displaced by the immigration of genes that are adapted to the hatchery environment or to some other locality. For example, selection in one population might produce a large body size, whereas in another population small body size might be more advantageous. Gene flow between these populations may lead to individuals with intermediate body sizes, which may not be adaptive in either population. A second way outbreeding depression can occur is by the breakdown of biochemical or physiological compatibilities between genes in the different populations. Within local, isolated populations, alleles are selected for their positive, overall effects on the local genetic background. Due to nonadditive gene action, the same genes may have rather different average effects in different genetic backgrounds--hence, the potential evolution of locally coadapted gene complexes. Offspring between parents from two different populations may have phenotypes that are not good for any environment. It is important to keep in mind that these two mechanisms of outbreeding depression can be operating at the same time. However, determining which mechanism is more important in a particular population is very difficult.

Interaction between mechanisms

Figure 1 shows the theoretical effects of outbreeding depression, relative to outbreeding enhancement and inbreeding depression. Both outbreeding depression and outbreeding enhancement may be occurring at the same time in a population receiving immigrants. As individuals in a local population mate with individuals that are genetically more and more different, outbreeding depression builds up because of the mechanisms we just mentioned. But notice that outbreeding enhancement, because of the masking of deleterious recessive alleles, may also be occurring at the same time that outbreeding depression is occurring. If you average these divergent effects, small amounts of outbreeding may lead to an increase in fitness over that in a local, randomly mating population; however, at higher levels of outbreeding, outbreeding depression may exceed the beneficial effects of outbreeding enhancement. One of the key questions is to determine at what genetic distance the detrimental effects of outbreeding depression exceed the beneficial effects of outbreeding enhancement. If populations have not diverged for a long enough time to acquire separate, co-evolved gene complexes, then it is unlikely that outbreeding depression will occur. The degree that outbreeding enhancement occurs is not predictable and must be determined experimentally.

It is also possible for a population to suffer from both outbreeding depression and inbreeding depression at the same time. Suppose we have two populations, a wild and a hatchery population, that are each fixed for two kinds of alleles for each locus because of local inbreeding (Fig. 2). The wild population has good (A) and bad (A') alleles at locus A, is fixed for a bad allele (B') at locus B,

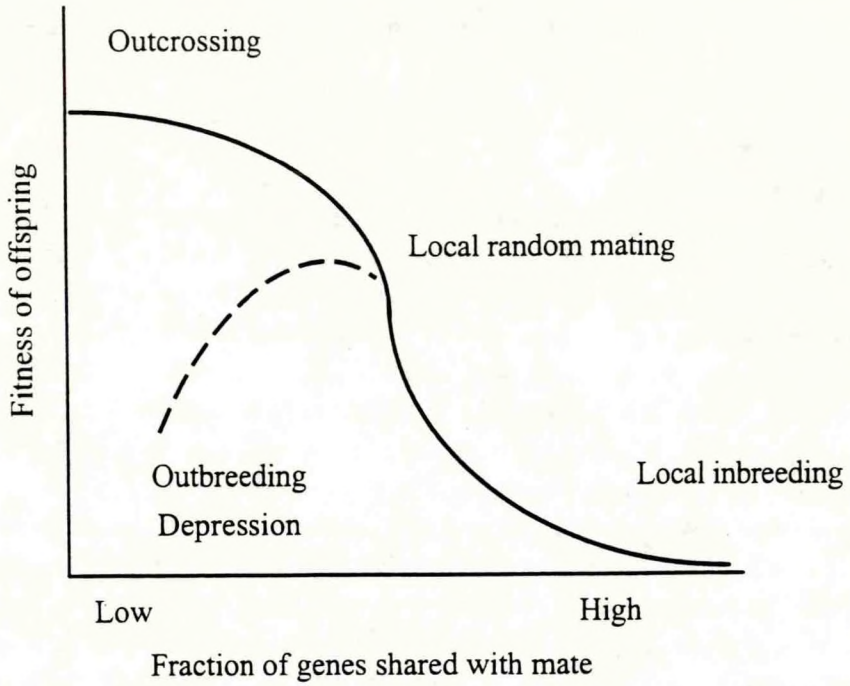


Figure 1. Relationship between fraction of genes shared by parents and the fitness of offspring.

but is fixed for a good allele (*D*) at locus D. On the other hand, a hatchery population has good (*A*) and bad (*A'*) alleles at locus A, only good alleles (*B*) at locus B, but only bad alleles (*D'*) at locus D. Suppose too that alleles *A'* and *D'* are particularly deleterious when combined in the same individual. These populations are then mixed and the hybrid population is allowed to go through several generations. Since most wild populations are small, it also undergoes inbreeding over this time. Eventually, the population may become fixed for the bad *A'* allele at locus A, for the good *B* allele at locus B, and for the bad *D'* allele at locus D. The alleles at the A and D loci therefore produce inbreeding depression. Also notice that alleles from the two different populations have become fixed in the hybrid population so that outbreeding depression has also become fixed. Two forms of genetic depression are piled on top of each other.

"Mutational meltdown"

Yet another genetic mechanism can lead to problems in wild populations, especially populations of endangered species. We have assumed that the effective sizes of populations that we have discussed are on the order of only a few individuals or a few tens of individuals at most. We know from empirical results from several organisms that deleterious mutations, mild as they may be in their individual effects, appear at a fairly high rate. About one deleterious mutation appears per individual per generation. That means that on average each fish has one deleterious mutation that was not present in either parent.

	Wild population		Hatchery population
	1 *A' B D*		1 *A B D'*
Genotype	2 *A B D*	X	2 *A' B D'*
of fish	3 *A' B D*		3 *A' B D'*
	4 *A B D*		4 *A B D'*

Hybrid population
1 *A' B D*
2 *A' B D*
3 *A' B D*
4 *A' B D*

Figure 2. Possible outcome of breeding between hatchery fish and wild fish in small populations. The prime mark (') indicates a recessive deleterious allele.

As we said, the average reduction in fitness when one of these mutations is made homozygous is only about 2%. Earlier speakers noted that the amount of random genetic drift is inversely proportional to population size, $1/2N_e$. If $1/2N_e$ is larger than the selection coefficient, the efficiency of selection against new mutations is less than the force of random drift for that population size. The result is that the "noise" of random drift will overwhelm natural selection and the new deleterious alleles will accumulate in the populations as though they were neutral alleles, even though they have deleterious effects on the individuals that carry them. Thus, if the selection coefficient is 2%, the effect will be important in populations with effective sizes of 50, or with adult census sizes of a few hundred fish. A rule of thumb is that, in small populations, new, mildly deleterious mutations will accumulate in the population at a rate that is half the mutation rate at the genomic level. Even in the absence of inbreeding depression and outbreeding depression, this accumulation of deleterious mutations will lead to a reduction in fitness of about 1% each generation. Since the effective sizes of many endangered populations of salmon are on the order of 50 or smaller, this is a major potential source of long-term genetic deterioration.

Empirical Evidence

First of all, virtually every trait that has been examined in a wide variety of species can exhibit inbreeding depression, such as by full-sib matings or by self-fertilization in the case of some plants. Some traits are more susceptible to inbreeding than others, but the fact remains that inbreeding depression occurs in all complex genetic characters. A linear decline in mean fitness with the inbreeding coefficient has been observed in a diverse array of organisms including fruit flies, flour

beetles, and many species of mammals (including humans). Because inbreeding depression is linear with the inbreeding coefficient, we can extrapolate to future generations if we know the effects of inbreeding depression in the first few generations of inbreeding.

The second point of particular importance for economically important traits in salmon is that traits most closely related to fitness are the ones that exhibit the most inbreeding depression. Again, this has been observed in numerous species, but the data for fruit flies illustrate this principle very well. Table 1 shows a summary of several studies of fruit flies. For morphological characters, the effects of inbreeding are relatively mild. The greatest changes are observed for primary fitness components, such as reproductive capacity, viability, competitive ability, and so on, and not for characters only remotely related to fitness.

The final point with respect to inbreeding depression is that all the studies presented here were done in the laboratory to ensure that observable results were acquired at the end of the experiment (reviewed in Lynch and Walsh 1997). When parallel studies were done in the laboratory and in the field under natural conditions, the effects of inbreeding were typically much greater under natural conditions. The message here is that the assertions about the negative effects of inbreeding outlined above are conservative.

Evidence for outbreeding depression is much less extensive than evidence for inbreeding depression, but outbreeding depression is nevertheless a general genetic phenomenon. One problem in studying outbreeding depression is the number of generations that may occur before outbreeding depression reveals itself. The effects of outbreeding enhancement due to the masking of deleterious alleles and outbreeding depression due to hybrid breakdown may cancel each other in the first generation after crossing individuals from two populations. So the effects of outbreeding depression may not be apparent for a few generations. A few experiments have been done in which reciprocal transplants have been made between plants separated by as little as tens or hundreds of meters. In a study of plants separated by various distances, progeny of crosses between plants separated by 10-30 meters showed greater fitness than plants separated by smaller or larger distances (Wasser and Price 1989). Many of these studies show that populations are locally adapted and that outbreeding depression occurs between genetically divergent individuals. Comparable studies in animals are rare, but it is likely that similar results occur in animals. Experiments on marine copepods in intertidal pools show that hybrid individuals between populations some tens of kilometers apart show breakdowns in salinity tolerance, prolonged development and so on (Burton 1987, 1990). In another study, clones of the microcrustacean *Daphnia* in the same lake show hybrid breakdown (Lynch and Deng 1994). The overwhelming evidence is that these genetic effects occur in every group of organisms studied, and although not much research has been done on salmon, there is no reason to believe that the genetics of salmon are any different.

Table 1. Inbreeding depression (*I.D.*) in laboratory populations of *Drosophila*. *I.D.* = 1-(z_r/z_o), where z_o and z_r are means of the random mating base, and the completely inbred population (obtained by linear extrapolation), respectively. Results marked with an asterisk were obtained from studies of only one or two chromosomes; in these cases, *I.D.* for the entire genome was extrapolated by assuming that each chromosome arm constituted 20% of the genome, and that the effects were multiplicative across chromosomes. Negative values imply an increase in character value with inbreeding.

Character	I.D. (various studies)
Competitive ability	0.84, 0.97
Egg-to-adult viability	0.57, 0,44, 0.66*, 0.48*, 0.06
Female fertility	0.81, 0.18, 0.35
Female rate of reproduction	0.81, 0.56, 0.96, 0.57
Male mating ability	0.52*, 0.92, 0.76
Male longevity	0.18*
Male fertility	0.00*, 0.22*
Male weight	0.07, 0.10
Female weight	-0.10
Abdominal bristle number	0.05, 0.06, 0.00
Sternopleural bristle number	-0.01, 0.00
Wing length	0.03, 0.01
Thorax length	0.02

Directions in Salmon Research

A question that is often raised is how to obtain information on the genetic consequences of inbreeding and outbreeding in salmon. Many managers would like to have harder evidence that these are real issues with salmonids. The only way of getting this evidence, however, is by doing experiments with salmon themselves. Demonstrating inbreeding depression is straightforward and is

done by monitoring the performance of offspring from full-sib matings, because these matings are genetically the closest possible in a sexually reproducing species. Such experiments, however, represent a substantial investment and may take a decade or so. Since the decline in fitness is approximately linear with the degree of inbreeding, useful extrapolations to small natural populations could be made from the results of these experiments.

Experiments to demonstrate outbreeding depression are also conceptually straightforward, but the work needed to complete the experiments is not trivial. To understand the effects of hatchery straying on wild populations, hatchery and wild fish would be crossed to make first generation hybrids, which would then be released for normal ocean migration. Second generation offspring would be made from returning hybrid individuals, which may represent only a small fraction of those released. The effects of outbreeding depression, however, may not be apparent in these early generations, so the crosses of further generations are required. A hybridization between odd- and even-year pink salmon made with cryopreserved sperm yielded only a small amount of evidence about outbreeding depression after several years of work (Gharrett and Smoker 1991). The bottom line is that any kind of quantitative results would take several years of hard work to generate.

Proceeding without results for salmon

Since the empirical evidence of inbreeding depression and outbreeding depression in salmonids will not be available for some time, what is the best way to proceed? The first concern for any stock, whether it is a hatchery stock or a wild stock, is with its effective population size. One way of looking at this question in an objective manner is to ask how big a population would have to be to make it behave genetically as an infinitely large population. In other words, at what point would a further increase in size fail to increase the level of genetic variability beyond that maintained in an effectively infinite population? To make a population genetically "secure" requires an effective population size of several hundred fish, or a census size of about 1,000 reproductive fish. This number is one or two orders of magnitude larger than many populations of salmon that have dwindled to only a few individuals.

The results from other species and population genetic theory can be used to make recommendations that would reduce the likelihood of outbreeding depression in salmonids. One of the most important precautions would be to minimize the degree of interbreeding between hatchery and wild stocks. The effects of outbreeding depression are not likely to appear for at least a couple of generations after outbreeding occurs. If the progeny of an out-crossed stock appear to be fine in the first few generations, this does not necessarily mean that outbreeding depression will not occur later. After genes have been mixed from two populations, it is then impossible to eradicate the potential difficulties with outbreeding depression. At that point, the only way out is to allow natural selection to sort things out, but how long this might take is unknown.

Conclusions

Relevant data for determining the potential effects of inbreeding depression and outbreeding depression in natural populations of salmonids is not yet available. However, theoretical studies and empirical results for other species show that both inbreeding depression and outbreeding depression can lead to the decline in fitness of natural populations. Both of these effects, however, may take several generations to become apparent. At this point, prevention may be better than waiting to implement corrective management policies until empirical evidence demonstrates these effects in salmon.

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Discussion

Question: Ed Crateau: In the experimental hatchery X wild salmon crosses that you mentioned to demonstrate these effects, don't you also need control experiments to show that the hatchery X wild salmon offspring are worse off in either the hatchery or natural environments? These results, however, would not show whether the problem was adaptation to another environment or outbreeding depression.

Answer: Mike Lynch: Yes. One of the big problems is to determine which mechanism is responsible for declines in fitness. To show that outbreeding depression--the breakdown of intrinsic coadaptation--was the mechanism for reduced fitness, a researcher would have to show that fitness was reduced in all environments. With the rapid habitat changes that are occurring, it is not clear which environment will be relevant several years from now. Perhaps, if fitness begins to decline in a wild population because of a breakdown in local adaptation, stopping gene flow from non-native stocks may allow the local population to recover. Such a recovery would still take several generations.

Question: Dolph Schluter: Since the experiments you described take so long, is there any way of predicting the amount of outbreeding depression that might occur in salmonids from the results of studies of other species? Is it possible to use the amount of time the stocks have been separated from each other or the genetic distance between them to make such predictions?

Answer: Mike Lynch: Few studies of outbreeding depression exist, and in these studies, the degree of outbreeding depression has not been correlated with any kind of molecular marker. So it is difficult to make statements about the time of separation or the degree of genetic differentiation in the characters affected by outbreeding from molecular markers. For the flower, *Delphinium*, outbreeding depression occurred between plants in the same field. Molecular markers could be used simply to monitor changes in genotypic frequencies in the offspring over time, to estimate mortalities in the different populations of fishes. If the different groups identified by the molecular markers show different levels of fitness, then you can be sure something is happening. If there is no differential fitness in these groups in the first few generations, however, you still cannot be sure that there is not a problem.

Question: Audience: If a hatchery stock is only one or two generations away from a local stock, does this change the likelihood of outbreeding depression in hatchery X wild crosses because of hatchery releases?

Answer: Mike Lynch: If hatchery-reared fish are only one or two generations removed from wild populations, outbreeding depression is unlikely to be a problem. If the hatchery is being used to ensure the survival of large numbers of fry, and if the brood stock is continually taken from wild populations, outbreeding depression is unlikely to occur.

Question: Richard Carmichael: I would like to clarify the kind of experiment that would be needed to show outbreeding depression. For example, someone is proposing to enhance a wild population with a non-local stock, and we want to understand if outbreeding depression might occur. We would first need to know how the hatchery stock performed in the natural environment by itself in the absence of wild salmon. Then we would need to know the productivity of the wild population apart from the hatchery stock. Finally, we need to measure the productivity of the hybrid population. Is that correct?

Answer: Mike Lynch: Yes. But in addition you should follow the hybrid population for at least two generations.

Question: Richard Carmichael: Does the size of the wild population affect the outcome? For example, would a very large population of thousands show more outbreeding depression than a small population where outcrossing may cover inbreeding through outbreeding enhancement?

Answer: Mike Lynch: Population size is important. Inbreeding is measured on a 0-1 scale, and the rate of increase in inbreeding is roughly equal to one over twice the effective population size, $1/2N_e$. If the effective size of a population is five fish, the rate of increase in inbreeding due to random mating is 1/10 or 10%. Since some of the five fish may be related, the rate of increase in inbreeding may be more. The point is that small populations become inbred very quickly.

It is really difficult to make specific predictions about outbreeding depression. The common observation from line-cross analysis in agronomy and in animal breeding is an increase in productivity traits in the first generation of a cross between two lines, followed by outbreeding depression in crosses between F_1 or later hybrids. The explanation is that hybrid vigor in the first generation results from the masking of deleterious recessive alleles in the two lines. In subsequent generations, adapted combinations of alleles break down, and this leads to outbreeding depression. The breakdown can be due to the loss of ecological adaptation or to a loss of the favorable interactions among genes. If, in fact, the migration rates are exceedingly large, on the order of 50-70% as suggested in some of the talks today, then outbreeding depression is probably not occurring. This level of flushing would simply lead to the replacement of the wild population with the hatchery populations.

Comment: Robin Waples: First, the high rates of straying of non-native fish in the Grande Ronde Basin and the Umatilla River precipitated this workshop. However, a more general issue involves a wide range of straying rates and population sizes.

Second, the theoretical treatments of migration and population size are in terms of individuals per generation, whereas fish biologists often state the number of fish returning to spawn each year. So even though 10, 20, or 50 fish may return in 1 year, a whole generation may be 4 or 5 years. The population size per generation is then the number of fish returning per year times the number of years per generation. This number is not quite so small as the returns per year mentioned earlier.

Question: Audience: How reversible is inbreeding after a population grows quickly, say from 100 to 2,000?

Answer: Mike Lynch: This point arises frequently with captive and endangered populations. Some researchers argue that inbreeding and selection could purge a population of its deleterious mutations. If the population survives, it will be better off. This strategy has been used in the captive breeding program of Spekes gazelle, which was started with four individuals. The cost of this procedure is that most lines or populations go extinct, so that in laboratory experiments with mice, for example, only about 5% of the lines survive. Replicate lines cannot usually be established for an endangered population, so that means that a population has only about a 5% chance of surviving an episode of such intense inbreeding. Also keep in mind that even if all deleterious mutations have been purged, they will eventually return to the population, because the per individual mutation rate to deleterious genes is about one per generation. If a previously inbred population grows and then experiences another reduction in population size, inbreeding depression would occur again, because of the accumulation of recessive deleterious mutations.

Question: Audience: After a population experiences inbreeding because of a strong reduction in size and grows again, you are saying that you have lost the diversity contained in the various lines of descent in the population. Is that correct?

Answer: Mike Lynch: Mutation can eventually bring new useful mutations into a population at a good rate as it grows. So if a population declines to a small size and experiences inbreeding, but its numbers recover, the population may recover genetically. This can, however, take several dozens of generations. What is critical is the transient phase when the population is small and demographic extinction is a possibility.

Question: Audience: How arbitrary is the effective population size of 1,000 individuals?

Answer: Mike Lynch: From population genetics theory, an effective population size of between 500 and 1,000 individuals is the point that, for quantitative characters (e.g., morphology), the genetic variation maintained by a balance between input by mutation and loss by genetic drift is about the same as would be expected in an effectively infinite population.

Salmon Biology

HOMING, STRAYING, AND COLONIZATION

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Introduction

The intent of this contribution is to define what is meant by homing and straying, and to describe patterns of homing and straying in salmon populations. I will explore what practices or other factors in hatcheries might encourage straying, and then outline the consequences of straying. By way of historical perspective, it was accepted by about the 1870s that most salmon homed back to their natal streams and rivers to spawn, although some biologists remained unconvinced until the 1930s. A report for the U.S. Commission of Fish and Fisheries stated that ". . . it is an established fact that adult [salmon] will always return to the place where they first made acquaintance with the water, passing directly by the mouths of streams or tributaries better adapted to their purpose, to gain their original home" (U.S. Commission of Fish and Fisheries 1874, p. lxxxii). Biologists also recognized that salmon could swim several hundreds of miles up a river to their natal areas. A later report to the Commission pointed out that a stream near Elko, Nevada "is one of the many that form the headwaters of the Columbia River, and to this point, eighteen hundred miles from its mouth, the salt-water salmon come in myriads to spawn . . ." (U.S. Commission of Fish and Fisheries 1876, p. xxviii-xxix). Milner noted "[t]he generally accepted fact in the habits of anadromous fishes that they are disposed to return to almost the exact locality where they passed their embryonic and earlier stages of growth . . . . Observations of the shad brought to the large markets shows considerable difference in the physiognomy and general contour of those from different rivers. The suggestion is natural that they are distinct and separate colonies of the same species, and thus slight characteristics are perpetuated because they breed in-and-in and do not mix with those of other rivers" (Milner 1876, p. 323).

By the 1930s, a number of biologists were aware of life-history differences among salmon populations (Moulton 1939; e.g., Clemens et al. 1939). In fact, this realization gave the first indication, before tagging studies, that salmon homed to particular localities. Salmon from various populations showed differences in morphology, body size, egg size, fin ray counts, oil content, and so on. In the 1950s to 1970s, knowledge of homing by Pacific salmon was greatly enhanced by the work of Arthur Hasler and his students (reviewed in Hasler and Scholz 1983). Their studies formed the basis for much of what we know about salmon homing. However, straying was not investigated as a behavior pattern in its own right because most salmon homed, and the focus of the research was on the sensory mechanisms of homing. Consequently, the ecological and evolutionary importance of straying from one population to another has received comparatively little attention until recently.

Today, we know that there is extensive variation among populations in many traits and that this variation often has clear adaptive value. Such local adaptations have presumably evolved because homing leads to reduced levels of gene flow between habitats, and because there is genetic control of the traits that adapt the salmon for those habitats. It has been hypothesized (Quinn 1984) that adaptations evolve most rapidly in stable habitats and that homing is likely to be positively associated with the intricacy of adaptations for freshwater habitat, and with variation in age at return. Homing and straying have adaptive value for individuals; the relative advantages may depend on environmental conditions, other life-history traits, and perhaps the relative frequencies of homing/straying (Quinn 1984, Kaitala 1990).

Homing and Straying: Definitions and Qualifications

Just what is meant by homing and straying? For a wild fish, home is the natal stream where it incubated, hatched, and emerged. Home is thus, essentially, the redd. However, when humans study salmon homing, the definition of home is influenced by how and where juvenile fish are collected and marked, and how they are recaptured as adults. These factors also influence the perception of how accurately salmon home. One might think of salmon homing through a hierarchy of spatial scales, including first a river basin, then a major tributary, a stream, and a particular point in the stream. Homing will necessarily be more accurate when measured at broader spatial scales. At the final level, the interaction between homing and spawning site selection (Blair and Quinn 1991, Hendry et al. 1995) or mate choice determines the final destination of the fish. The definitions of straying or homing, therefore, depend on the spatial scale of interest. Most research has not been sufficiently explicit in considering the spatial definition of home, and the transition between homing and spawning site selection.

For transplanted fish, the ancestral locality or the hatchery where they are reared and the locality where they were released could both be considered homes. While there is some tendency to return to the ancestral area (McIsaac and Quinn 1988, Pascual and Quinn 1994), salmon generally return to the site where they were released (Ricker 1972). For salmon released from a hatchery, the incubation, rearing, and release sites may be the same; in this case, home is the hatchery. When planted from the hatchery to a river, salmon tend to return to the point of release (e.g., Donaldson and Allen 1958, reviewed in Quinn 1993). Fish released in the lower portion of a river tend to be caught only in the lower portion of that river, and fish released in the middle or upper portion of a river tend to be caught in all parts of the river downstream from the release site (steelhead trout (*Oncorhynchus mykiss*): Wagner 1969, Cramer 1981, Slaney et al. 1993; Atlantic salmon (*Salmo salar*): Hvidsen et al. 1994, Potter and Russell 1994).

The other side of the homing "coin" is straying. Adult salmon move into non-natal streams for a variety of reasons. We know from radio-tracking data that some fish do not home directly to their natal streams, although these streams may be their final destination (e.g., Berman and Quinn 1991). Upriver migration is characterized by a certain amount of exploratory movement into non-natal streams. If a fish makes an exploratory run up a stream, is caught in a hatchery weir, and is spawned in the hatchery, this constitutes straying from a functional point of view. The fish's genes are

incorporated into the hatchery gene pool regardless of whether the fish would have left the hatchery had it been allowed to do so. Consequently, it may be difficult to accurately estimate straying frequencies using data from hatcheries. However, it is clear that some salmon spawn in rivers other than their own and so stray in the truest sense (Quinn et al. 1991).

Estimates of Straying

While many studies have provided data on the proportion of salmon that stray, almost all of these studies have been on single species, and little information exists on comparative straying rates among species. In one of the few such studies, Shapovalov and Taft (1954) reported higher levels of straying by coho salmon (*O. kisutsch*) than by steelhead into two small creeks in California. It has been speculated that pink salmon (*O. gorbuscha*) stray more than other species, but hard evidence is lacking. High levels of intraspecific variability may mask interspecific differences. The available information for coho and chinook salmon (*O. tshawytscha*), for which we have the most data, indicates large amounts of homing variability among populations, even within a small geographical area.

Another problem with the literature on homing is that wild salmon are tagged less frequently than hatchery-produced fish, and when wild salmon are tagged the data are seldom analyzed to produce estimates of straying. Consequently, little is known about straying in wild salmon populations, and most estimates of straying come from hatcheries. Hatchery-produced salmon may not stray with the same frequency as wild salmon, but so few studies have been conducted on hatchery and wild fish in the same areas that we cannot be certain (see below). Many experiments designed to estimate straying are also poorly controlled or are not replicated. In many studies, measuring variability in homing was incidental to other goals, so the data are often confounded with factors besides straying. Most studies also fail to account for straying in and out of a population; in many cases, only the dispersal of strays from the marking site is documented.

As a rough estimate, 90% +/- 10% of salmon home, and this does not include the "pathological" levels of straying that were shown earlier in the workshop for some Snake River hatcheries (Crateau, this volume) and have been documented for some hatcheries on the lower Columbia River (e.g., Grays River chinook salmon: Pascual et al. 1995). However, the overall estimate of 80-100% homing is based largely on data from hatcheries.

Straying in hatchery vs. wild populations

It is difficult to determine from the data at hand whether straying differs between hatchery and wild populations, because studies of hatchery populations greatly outnumber studies of wild populations. Comparisons between wild and hatchery-produced Pacific salmon were conducted by McIsaac (1990) and Labelle (1992). McIsaac (1990) studied fall-run chinook salmon in the Lewis River and found that wild-caught juveniles homed at a higher rate than members of the population that had been incubated and reared in the hatchery. Moreover, short-term rearing of wild fish in a

hatchery increased their rate of straying, relative to wild fish not held in the hatchery. On the other hand, Labelle's (1992) study of coho salmon on the east coast of Vancouver Island did not find a significant difference in straying rates between hatchery-produced and wild fish. Studies of Atlantic salmon also did not find differences between the straying rates of hatchery and wild fish (Jonsson et al. 1991, Potter and Russell 1994).

Regional and temporal patterns of straying

Coded wire tagging has provided a large database which can be used for homing studies (van der Haegen and Doty 1995). These data show that spatial patterns of straying vary from one river to another. The proportion of salmon that stray is not the same in all hatcheries in a region such as the lower Columbia River. In addition, the proportion of the total number of straying salmon entering a given river is not simply explained by its distance from the hatchery of origin. For example, Cowlitz River spring-run chinook salmon strayed more often to the Lewis River than to the Kalama River, even though the Kalama River is closer to the Cowlitz River than is the Lewis River (Quinn and Fresh 1984).

It appears that salmon do not stray merely because they are fatigued and cannot reach their natal spawning areas. In many cases, they stray to localities above their river of origin. The proportions of salmon straying into and out of a hatchery can vary considerably. Quinn et al. (1991) found variation from 9.9-27.5% in the proportions of fall-run chinook salmon straying from five lower Columbia River hatcheries. More dramatic, however, was the variation in attractiveness of rivers to strays. Virtually no salmon strayed into the Washougal and Abernathy Hatcheries, but about 30% of the marked salmon entering the Kalama and Lewis Rivers were strays (Quinn et al. 1991). Expanded examination by Pascual and Quinn (1994) confirmed these patterns of variation in straying and found that fish seemed more likely to enter rivers or hatcheries similar to their home than to less similar sites. For example, salmon produced in tributaries of the Columbia River seemed to stray into other tributaries rather than to hatcheries along the mainstream of the river.

In addition to differences in straying among rivers, straying can also differ from year to year. Interannual variability may be associated with catastrophic events such as the eruption of Mount St. Helens (Leider 1989). Less dramatic environmental changes such as variation in flow and temperature may also contribute to temporal variability in straying, but definitive studies do not seem to have been conducted on these subjects. There is some evidence that temporal variation in straying is associated with population size (Quinn and Fresh 1984). In years when many fish returned to the Cowlitz River hatchery, homing was better than in years when fewer fish returned. This suggests that the dynamics of small populations may be different from those of larger populations. This is an important issue and it needs to be evaluated with other data sets. There is also interannual variation in straying from a site, perhaps related to water quality, rearing conditions, or the number of returning salmon. The tendency of hatchery-produced salmon to enter their hatchery, as opposed to spawning in the river, can also vary greatly from year to year (Nicholas and Downey 1983).

Age at return also contributes to variability in straying. Older chinook salmon tend to stray more than younger fish (Quinn and Fresh 1984, Quinn et al. 1991, Unwin and Quinn 1993, Pascual et al. 1995). The difference in the rate of straying by chinook jacks and by 4- or 5-year-old fish may be an order of magnitude (Quinn and Fresh 1984). Age-specific straying rates have also been observed for coho salmon (Labelle 1992), but not for Atlantic salmon (Potter and Russell 1994). Perhaps, the longer a fish is out to sea, the more it forgets the olfactory cues it needs to return to its natal locality. The turnover of sensory epithelial cells associated with odor recognition (Nevitt et al. 1994), changes in the odors of river water, or some unknown evolutionary mechanism may be responsible for this age effect. Hatchery practices can also influence the age structure of the spawning population, which may in turn influence straying.

Straying and colonizing new areas

Little is known about the relationship between straying and the colonizing of unoccupied areas. Although most translocations of salmon have been notoriously unsuccessful, some have succeeded. For example, the inadvertent translocation of pink salmon into the Great Lakes resulted in a rapid colonization of Lake Superior and other Great Lakes (Kwain 1987). The translocation of chinook salmon to one river in New Zealand quickly led to unaided colonization of several other rivers within 15 years, but the present level of straying among rivers is not high enough to account for the widespread colonization that apparently took place after the initial introduction (Unwin and Quinn 1993, Quinn and Unwin 1993).

In addition to translocations, some natural colonization by salmon also occurs. For example, in Glacier Bay, Alaska, new habitat appears as the glacier recedes, and new habitat is colonized as it becomes suitable for spawning (Milner 1987, Milner and Bailey 1989). Straying and the ability to colonize new areas over evolutionary time is important, but little research has been done on this topic. It appears that soon after colonization, and coincident with small population sizes, straying rates may be high; however, after populations become established, only modest rates of straying occur.

Hatchery Practices and Straying

Some hatchery practices might promote straying, the most obvious being the long-standing practice of transporting individuals from one locality to another. Salmon are commonly displaced from hatcheries to "seed" nearby habitat. Most fish reared at one facility through their juvenile stages, but released at another site, return to the site of release and not to the rearing facility (e.g., Donaldson and Allen 1958, Quinn et al. 1989, reviewed by Quinn 1993). Several researchers have studied the details of the timing of imprinting and have found that fish can be imprinted not only at the smolt stage, but also to a lesser extent at earlier stages (Dittman et al. 1994, 1996). Therefore, if a rearing hatchery is in one watershed and the release site is in another watershed, fish tend to return to the release site. As the distance between the rearing facility and the release site gets closer, larger numbers of fish return to the rearing facility, especially if the facility and release site are in the same

watershed (Quinn 1993). However, the amount of "straying" from the release site is only roughly correlated with geographical distance. The release site's position within the watershed also affects homing. Johnson et al. (1990) reported that "almost all returning [coho salmon] released as yearlings at a site 23 km upstream from the rearing hatchery returned to the rearing site, whereas only 7-26% of adults originally released in a tributary 11 km downstream from the rearing hatchery returned to the rearing site" (p. 427).

In the Columbia River system, smolts are also displaced to improve their post-release survival. They may be taken from their hatchery ("point of origin" transportation) or captured during their downstream migration, trucked or barged around dams, and then released downriver. Point of origin transportation is usually accomplished by taking the fish by truck, or by truck and then by barge. Coho salmon trucked from the Little White Salmon Hatchery to Youngs Bay returned to Youngs Bay, not to the hatchery (Vreeland et al. 1975). Coho trucked 9 km downstream from Willard Hatchery and then barged to a release point below Bonneville Dam showed improved survival but impaired homing (McCabe et al. 1983). Releases in salt water also tend to increase straying. Solazzi et al. (1991) trucked coho salmon (reared at least in part at Big Creek Hatchery) to release sites below Bonneville Dam (river km 234), and Tongue Point (rkm 29). In addition, smolts were taken by boat in tanks receiving ambient water to the bar of the river (rkm 2), 19 km offshore in the river's plume, 19 km offshore outside the river's plume, and 38 km offshore in non-plume water. These six locations, progressively farther from the rearing site, produced the following proportions of salmon that returned to rivers outside the Columbia River system: <0.1%, 3.4%, 4.1%, 6.1%, 21.0%, and 37.5%. However, salmon captured as migrants and trucked long distances (e.g., from Ice Harbor Dam to Bonneville Dam) may return to the rearing site (Ebel et al. 1973, Slatick et al. 1975). Overall, the displacement studies indicate that maturing salmon tend to reverse the sequence of their outward migration as juveniles. This will lead them to the river or hatchery where they began life. Displaced salmon return first to the odors of their release site and will continue to the rearing site if its odors can be detected. If not, they seem to seek the nearest river or hatchery.

The date of release also influences homing. Fish released too early might be expected to stray more because they have not had time to imprint, or because their endocrine physiology is not synchronized with migration. Studies of Atlantic salmon (Hansen and Jonsson 1991) and of chinook salmon in the lower Columbia River (Pascual et al. 1995) and in New Zealand (Unwin and Quinn 1993) show that fish released after the smolt stage may also stray more frequently than earlier releases. It appears that exposure to site-specific water without migration is not sufficient for imprinting and will not lead to accurate homing, hence salmon held too long stray even though they were given a full opportunity to imprint (Dittman et al. 1996).

Although imprinting is a large component of homing, homing is not entirely a learned behavior. Local populations may home better than transplanted ones (pink: Bams 1976; chinook: McIsaac and Quinn 1988). Salmon may home better to their natal site than to a new site (chinook: McIsaac and Quinn 1988, Pascual and Quinn 1994; coho: Labelle 1992), and transplanted populations may show some tendency to return to their ancestral location (chinook: McIsaac and Quinn 1988, Pascual and Quinn 1994).

Interactions Between Hatchery Strays and Wild Salmon

If a hatchery produces a large number of salmon, straying by even a small percentage of them has the potential to disrupt the genetic composition of nearby wild populations. For example, the proportion of strays from an ocean-ranching facility (Oregon Aqua-Foods) was low, about 6%, but these strays accounted for about 74% of the fish in nearby Yaquina Bay tributaries (Nicholas and Van Dyke 1982). In this case, not only might there be genetic interactions, but simple stock assessment is compromised. A census of natural spawning areas would overestimate the size of wild populations, because the absolute number of strays--a small percentage of the larger hatchery population--was large relative to the local population.

While there is concern that strays from hatcheries will influence wild gene pools, wild salmon may also stray into a hatchery. Nicholas and Van Dyke (1982) estimated that 2,022 (64.7%) of the 3,124 wild coho salmon returning to the Yaquina River watershed in 1981 entered the Oregon Aqua-Foods hatchery. Such decoying of wild salmon into hatcheries both reduces the number of wild fish in the stream and contributes to genetic mixing.

Gene flow from hatchery strays may dilute beneficial genes in populations of locally adapted wild fish, or disrupt adaptive gene complexes. However, salmon mating is non-random. Factors contributing to differential reproductive success include intrasexual competition, some degree of mate choice, differences in aggressiveness between wild and hatchery fish, size effects, different return times, and so on. Differences between homing salmon and strays in distribution within a river system (e.g., Atlantic salmon: Jonsson et al. 1990) might also tend to reduce genetic interactions. Finally, since salmon can discriminate siblings from non-relatives (coho: Quinn and Busack 1985), and can distinguish fish in their own population from those of other populations (sockeye: Groot et al. 1986; coho: Quinn and Tolson 1986), the magnitude of interbreeding may not be equivalent to the proportions of wild and hatchery-produced fish. Wild fish may actively reject siblings and non-native hatchery fish as mates on natural spawning grounds.

Tallman and Healey (1994) studied small chum salmon (*Oncorhynchus keta*) populations on Vancouver Island and indicated that the level of genetic exchange between strays was lower than that inferred by the presence of strays in spawning areas. Simply counting stray hatchery fish on spawning grounds may not provide a reliable estimate of the genetic interaction between hatchery-produced and wild populations. However, genetic consequences may occur if hatchery strays spawn with locally adapted wild fish (Taylor 1991, this volume) because domestication selection and non-native stock in the hatchery might reduce the fitness of wild fish. If hatchery fish have experienced domestication selection or are a non-native stock, then they may reduce the fitness of wild fish with whom they mate (Reisenbichler and McIntyre 1977, Reisenbichler 1988, Leider et al. 1990, Hindar et al. 1991, Johnsson and Abrahams 1991).

Conclusions

Salmon as a group generally home to natal sites to spawn. Homing occurs in diverse groups of salmonids with life-history patterns differing in duration of freshwater residence, anadromy, iteroparity or semelparity, and spawning habitat. Straying between natural populations appears to be an integral part of the evolutionary biology of salmonids and may be important for colonizing new habitats or for avoiding unfavorable habitats. However, intra-specific variation ("local adaptation") presumably results from the scarcity of strays or their high mortality rate, or both, relative to locally adapted salmon. This is consistent with the generally poor survival of transplanted salmon, relative to native populations or to the population in its home environment.

It is unclear whether some species of salmon stray more than other species, but the amount of straying within a species varies considerably among populations, and older salmon tend to stray more than younger fish. It is also not clear whether hatchery-reared salmon generally stray more than wild salmon. The degree of homing in outplanted salmon often differs from that in locally-reared and released salmon, and appears to be determined by complex interactions between rearing location, release site, date, endocrine events, and migration itself. Straying fish tend to enter nearby rivers, although there are many exceptions. Homing, and therefore straying, may be influenced by such factors as water temperature, flow, presence of other salmon, habitat quality, and so on. It is not clear, however, whether fish that stray actively identify their natal breeding grounds, then migrate elsewhere, or whether strays are unable to find their natal site. The propensity to stray itself may be a genetically controlled trait, in addition to genetically based metabolic and physiological traits that make homing possible.

To the extent that there are genetic differences between hatchery and wild salmonids, straying of hatchery-produced salmon to interbreed with wild fish is cause for concern if they are less fit than wild fish. The most obvious and pressing research need is for information linking the straying of adult salmon and the exchange of genes between populations. Thus, data on the relative reproductive success of homing (locally adapted) salmon and strays, whether of wild or hatchery origin, is essential for wise management of salmon populations.

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Discussion

Question: Nils Ryman: Is it possible to select for high rates of straying? Has this been tried?

Answer: Tom Quinn: This has not been tried to my knowledge. However, a study of family-specific differences in several fitness traits such as survival, growth, age composition, fecundity, and so on, was made on Atlantic salmon in Iceland. The researchers did find family-specific differences in homing. These family differences in straying could simply reflect genetic differences among families in memory, sensory ability, swimming performance, and so on, and not differences in the direct genetic control of straying.

Question: Audience: Would it be useful to examine physiological changes in fish to estimate homing ability?

Answer: Tom Quinn: I think the patterns would be complex at best. For example, at the School of Fisheries (University of Washington), coho salmon released as zero age smolts have much lower levels of thyroid hormones than is commonly observed in other hatcheries, yet homing is very good (Dittman et al. 1994). Among adults, salmon populations return at very different states of maturity (e.g., spring- and fall-run chinook, summer- and winter-run steelhead). There seems to be no universal relationship between endocrine changes and homing. This is not to say that there is no relationship, only that it may vary considerably among populations and individuals.

Question: Richard Carmichael: Are you aware of information indicating that rates of straying among natural populations may vary between groups of salmon with different life-history patterns? For example, the Grande Ronde Basin harbors two groups of fish. Fish in one group stay their entire life in the area where they were spawned, and fish in the other group move fairly long distances into main-stem rearing areas in fall, then smolt the following year. Do these different life-history patterns produce different levels of homing?

Answer: Tom Quinn: Yes, there is evidence that stream-type and ocean-type sockeye salmon may stray more, or at least show less genetic differentiation than the conventional lake-type (Wood 1995). In the Cowlitz River Hatchery, spring chinook seemed to home more precisely than fall chinook (Quinn and Fresh 1984, Quinn et al. 1991), but the generality of this pattern among hatcheries and its application to wild populations is unclear.

Question: Mike Lynch: Are you saying that perhaps a straying rate of 2-5% might be fairly normal?

Answer: Tom Quinn: Yes. Straying rates range from almost nothing to a lot, depending on species and region. However, I must emphasize the dearth of information on wild populations.

Question: Mike Lynch: Are these estimates of straying rates compatible with those estimated from molecular data?

Answer: Tom Quinn: We seldom have estimates of straying in wild salmon populations for which we also have genetic data (but see Quinn et al. 1987 for sockeye, and Tallman and Healey 1994 for chum). There is no reason to suspect that straying rates and gene flow must be equivalent because poor survival of the progeny of strays, or non-assortative mating or some other process, may mediate the genetic interactions.

Question: Nils Ryman: Is the straying and the occurrence of jacks related? Is migratory behavior abnormal in both cases?

Answer: Tom Quinn: I am not sure I would be willing to say that jacks display abnormal behavior; they still go to sea, return to fresh water, and spawn. They may have a different marine distribution as a consequence of their younger ages, but they still migrate far enough away so they no longer have contact with their natal rivers. To the extent that there are patterns, jacks seem to stray less often than older salmon.

GENETIC POPULATION STRUCTURE

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Introduction

Most species consist of groups of individuals that are more or less isolated from one another. Isolating mechanisms may be geographical, temporal, ecological, or ethological, and the degree of isolation varies between species and their component populations. Local populations typically exhibit some degree of genetic differentiation, and the pattern of the distribution of genetic differences between populations is commonly referred to as *genetic population structure*.

Species differ both in their total amount of genetic variation and in the distribution of this variation between and within populations. In some species, such as several forest trees and marine fishes, populations show little differentiation over large geographic areas; that is, randomly selected individuals from different parts of the geographical range are genetically similar. In other species, for example many amphibians, even nearby populations may display substantial genetic divergence.

For characters that are not strongly influenced by natural selection, the extent of differentiation among subpopulations depends primarily on their size, the time since they were separated, and the degree of isolation between them. Large populations change more slowly than small ones, and even in the case of complete isolation it may take considerable periods of time before substantial genetic differences have accumulated between them. Genetically effective migration, gene flow, typically retards differentiation and prevents extensive divergence.

Implications for conservation

The strategy for conserving genetic variation within species depends on the species' genetic population structure. The extinction of a particular population may have little effect on the overall genetic resources of a species that exhibits only minor or no divergence among the constituent populations. In contrast, a corresponding extirpation in a highly differentiated species implies the loss of a significant portion of the gene pool of that species.

Depiction of genetic structure

A considerable number of studies on the genetic population structure of salmonids and other fishes have been published. The population genetic characteristics of salmonids are reasonably well known and have been discussed in several contexts. The present summary on population structure is to a large extent based on material compiled from previous publications, particularly those by Hindar et al. (1991), Utter et al. (1989), and Ryman et al. (1995a,b); the reader is referred to those original papers for a fuller discussion and for references to other articles.

Most of our current knowledge of genetic population structure has been obtained within the past two decades with biochemical genetic techniques, such as protein electrophoresis, and with the direct analysis of DNA. Genetic variation detected with these techniques is typically considered to be neutral, or nearly neutral, to natural selection. The analysis of this kind of genetic variation is generally preferred in evolutionary genetic studies, because the dynamics of selectively neutral genes is reasonably well understood theoretically, whereas variability patterns of genes affected by selection may be more difficult to interpret in an evolutionary context. Thus, selectively neutral genes may provide valuable information on evolutionary relationships among populations, their historical sizes, and the levels of gene flow between them. In contrast, such genes are typically less informative about the adaptive characteristics of a population. We would expect that loci subjected to directional selection exhibit a greater degree of genetic differentiation among populations than is observed at loci detected by various biochemical genetic techniques.

Genetic Structure of Salmonids

Biologists have long recognized intuitively that salmonid species are subdivided into more or less genetically distinct subunits. The reason for this recognition was generally based on the existence of striking ecological and morphological differences between fish of different origins. A large fraction of the variation of ecological and morphological characters is, however, caused by environmental factors. The extent that observed phenotypic differences reflected genetic divergence was difficult to determine until quite recently. Such evaluations could not be performed before techniques became available which revealed characters that were completely genetically determined and which varied independently of environmental conditions.

Salmonids are represented by both freshwater resident and anadromous species, ranging widely in the waters of the northern hemisphere. A common feature of all salmonids is the existence of genetically distinct local populations. Salmonid populations appear to maintain their genetic integrity through a remarkably accurate homing behavior.

In some species, such as brown trout (*Salmo trutta*) and cutthroat trout (*Oncorhynchus clarki*), genetically distinct populations can be found over short geographical distances. As an example from my own experience in Scandinavia, we may consider the brown trout community of Lake Bunnersjöarna in central Sweden. Lake Bunnersjöarna consists of two small basins connected by a channel that permits fish to migrate freely between the two segments of the lake. Physically, the lake

is not unusual, but we found that it harbors two genetically distinct populations of brown trout that differ at several protein coding loci, and that are markedly different in adult size. There is no apparent gene flow between the two populations, which seem to be completely reproductively isolated from each other, even though fish from both populations coexist in both lakes and can be caught in the same gill nets. Several additional, and genetically distinct, populations of brown trout occur in the same area only a few kilometers away, and finding similar levels of genetic differentiation over short geographical distances is not unusual for Scandinavia.

The genetic data that have accumulated for the salmonid species show that their population structure is more complex than was previously acknowledged. Several studies have also demonstrated that earlier concepts of genetic structure and evolutionary relationships should be modified. As exemplified in Table 1, such modifications have been justified for several species and have included populations distributed over a wide range of geographical distances. In particular, several evolutionary relationships have been revealed that were previously not recognized, and traditional classifications based on morphology or behavioral characteristics, such as time of spawning or residency vs. anadromy, have proven unreliable indicators of common ancestry.

Quantifying differentiation

A convenient method to quantify the amount of genetic differentiation within a species is the so-called gene diversity analysis. Here, the total gene diversity (H_T) estimates the total genetic variability within and among the populations sampled. H_T is the sum of the components representing the gene diversity within subpopulations (H_S), and the gene diversity due to differences among subpopulations (D_{ST}), such that $H_T = H_S + D_{ST}$. The quantities H_S and D_{ST} therefore provide a representation of the amount of differentiation among the populations sampled, and the coefficient G_{ST}, defined as

$$G_{ST} = \frac{H_T - H_S}{H_T} = \frac{D_{ST}}{H_T},$$

can be used as a measure of the proportion of the total genetic variation that is due to differences among populations. G_{ST} can take values between zero and unity, $G_{ST} = 0$, indicating that all populations have identical gene frequencies, and $G_{ST} = 1$, that the populations are as different as they can be (all variation is due to differences between populations). Of course, a fairly large number of loci is necessary to provide an accurate picture of the average variability pattern among the populations of a species. It should also be noted that G_{ST} in many cases is equivalent to the quantity F_{ST} that was originally defined by Sewall Wright for describing variation between populations at a single locus.

Table 1. Examples of biochemical genetic studies identifying new groups or modifying previous assumptions of the genetic population structure of salmonid fishes (modified and expanded from Allendorf et al. 1987, Table 1.4).

Issue	Observation	Reference
New grouping	Major genetic groups of rainbow trout (*Oncorhynchus mykiss*) correspond to geographic region (coastal-inland) rather than to drainage or life-history pattern.	Allendorf & Utter 1979
New grouping	Reproductively isolated populations of brown trout (*Salmo trutta*) coexisting in the same lake.	Ryman et al. 1979; Ferguson & Mason 1981
New grouping	Sharp genetic discontinuity in Europe of Atlantic salmon (*S. salar*) from rivers draining into the Baltic Sea and the Atlantic Ocean, respectively.	Ståhl 1987
New grouping	Genetic divergence among subspecies of cutthroat trout (*O. clarki* spp.) range from that typically observed among congeneric species to virtual genetic identity. Results suggest that the cutthroat trout taxonomy needs to be revised by recognizing westslope cutthroat trout as a distinct species.	Allendorf & Leary 1988
New grouping	Disclosure of nine major genetically defined regions of chinook salmon (*O. tshawytscha*) in the Pacific Northwest.	Utter et al. 1989
New grouping	Identification of six genetically distinct regional groups of chum salmon (*O. keta*) in southeastern Alaska and northern British Columbia.	Kondzela et al. 1994
New grouping	Recognition of three geographic clusters of genetically similar populations of odd-year pink salmon (*O. gorbuscha*) from Washington (USA) and British Columbia.	Shaklee et al. 1991
Residency vs. anadromy	Conspecificity of anadromous and landlocked forms of char (*Salvelinus alpinus*) of eastern North America.	Kornfield et al. 1981
Residency vs. anadromy	Lack of genetic divergence between anadromous and resident populations of rainbow trout, Atlantic salmon, and brown trout.	Allendorf & Utter 1979; Ryman 1983; Ståhl 1987; Hindar et al. 1991
Time of spawning	Major genetic groups of chinook salmon corresponding to geographic region rather than time of spawning.	Utter et al. 1989
Morphology	Little genetic divergence among morphologically distinct forms of cutthroat trout.	Busack and Gall 1981; Loudenslager & Kitchin 1979
Morphology	Lack of apparent genetic divergence between arid adapted (redband) and adjacent anadromous (steelhead) populations of rainbow trout.	Wishard et al. 1984

The quantity G_{ST} has been estimated from various biochemical genetic data sets for several species. For example, G_{ST} among the three races of man is about 10%; that is, about 10% of the total genetic variability is due to differences between races, and 90% of the total variability is found, on average, within each race. Caution is necessary when comparing the degree of population differentiation across species, because the various studies used different numbers of populations with various degrees of isolation and spatial separation. Similarly, sample sizes of loci and individuals

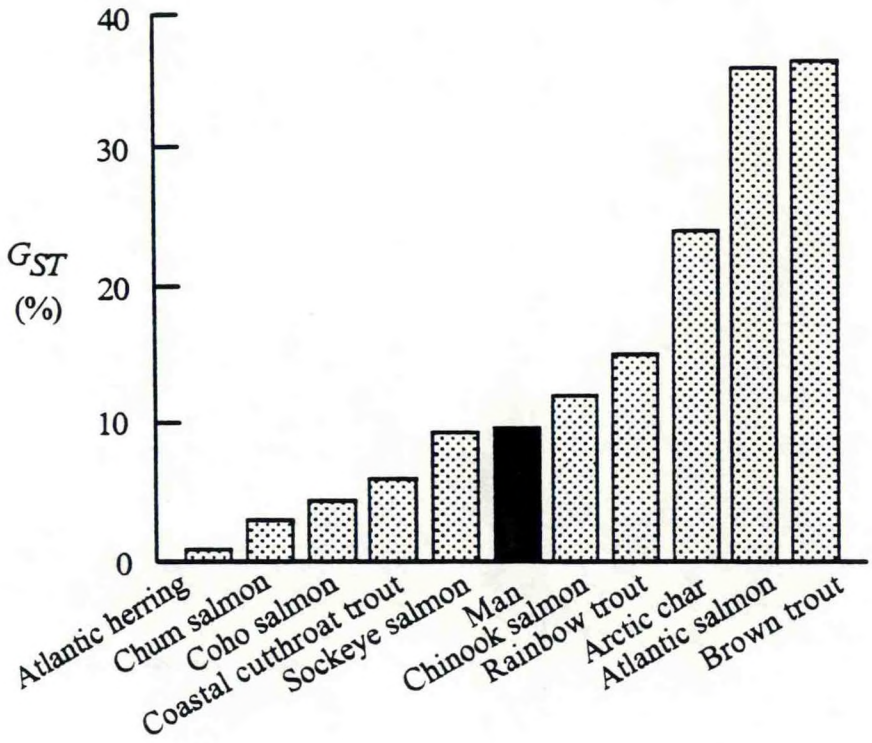


Figure 1. Percentage of the total genetic variability in various species that is due to differences between local populations (G_{ST}). Based on data from compilation of Utter et al. (1993).

examined per population sampled differed among investigations. Nevertheless, conspicuous differences appear among species in the extent of differentiation among populations.

Marine fishes, for example Atlantic herring and Atlantic cod, typically show low levels of differentiation among local populations (Fig. 1). In contrast, salmonid species are generally characterized by pronounced genetic heterogeneity between populations. In some salmonids, such as brown trout or Atlantic salmon (*S. salar*), 30% or more of the total genetic diversity may be due to differences among populations. Although most salmonids show considerable genetic differences among local populations, there are species such as chum salmon (*O. keta*) for which the differentiation appears to be less pronounced. It is not always clear why some salmonids show less differentiation among populations than others; some species may have a greater rigidity in homing behavior.

Figure 2 shows the percentage of between-population variability (G_{ST}: shaded bars) and the total variability (H_T: open bars) for several species of salmonids. The first observation is that different species have different overall levels of genetic variability (H_T), and these differences are often difficult to explain. Sometimes genetic variability is associated with the extent of a species' geographic range or with the number of populations examined. This tendency is illustrated in three studies of Atlantic salmon (Fig. 2), where H_T (as well as G_{ST}) increased as the sampling range increased from northern Sweden to northern Europe to Europe and North America. In other cases,

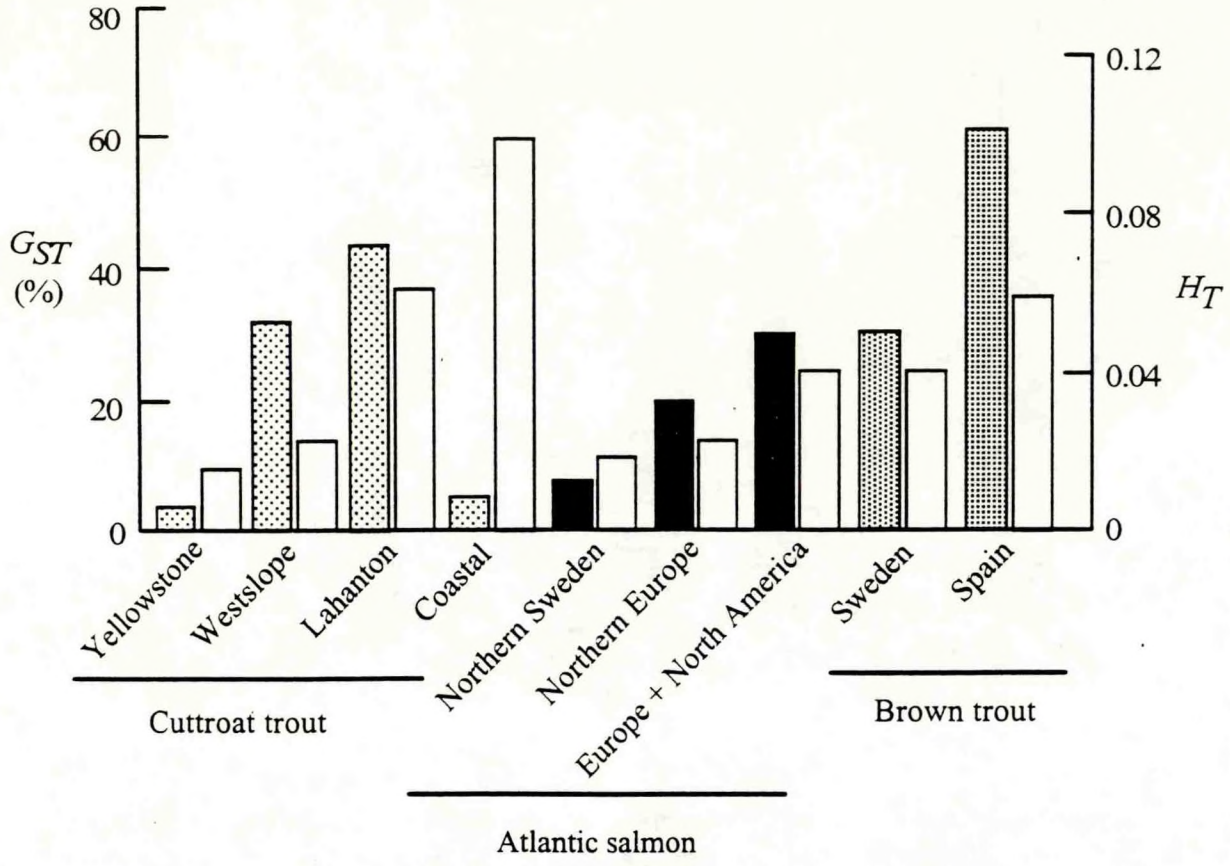


Figure 2. Total heterozygosity (H_T: open bars, right axis), and percentage of total genetic variability due to population differences (G_{ST}: solid or shaded bars, left axis) for species of salmonids. Data from Ryman (1983), Ståhl (1987), Allendorf and Leary (1988), and Garcia-Marin et al. (1991).

however, as when comparing the four subspecies of cutthroat trout (*O. clarki* spp.), no obvious relation appears between the amount of genetic variation and the geographic range covered. Second, there is no direct relationship between the amount of genetic variation (H_T) and the extent of heterogeneity among populations (G_{ST}). As for H_T, G_{ST} generally increases when more distantly located populations are included in the estimate (e.g., Atlantic salmon), except for cutthroat trout.

Species of Pacific salmon tend to be similar to other salmonids in their overall levels of genetic variability, but they tend to show less variability between populations than other salmonids. For example, chinook salmon (*O. tshawytscha*) populations of the Pacific Northwest show several population genetic groupings, even though only about 10% of the total variability is due to population differences. Utter et al. (1989) found evidence for nine genetically distinct groups of populations in chinook salmon (Fig. 3). The populations within each of these groups apparently share a common ancestral background that produces the genetic similarity between them. A closer look at the populations of chinook salmon in the south fork of the Salmon River, however, shows that populations with similar run timings (e.g., spring, summer) do not always share a common

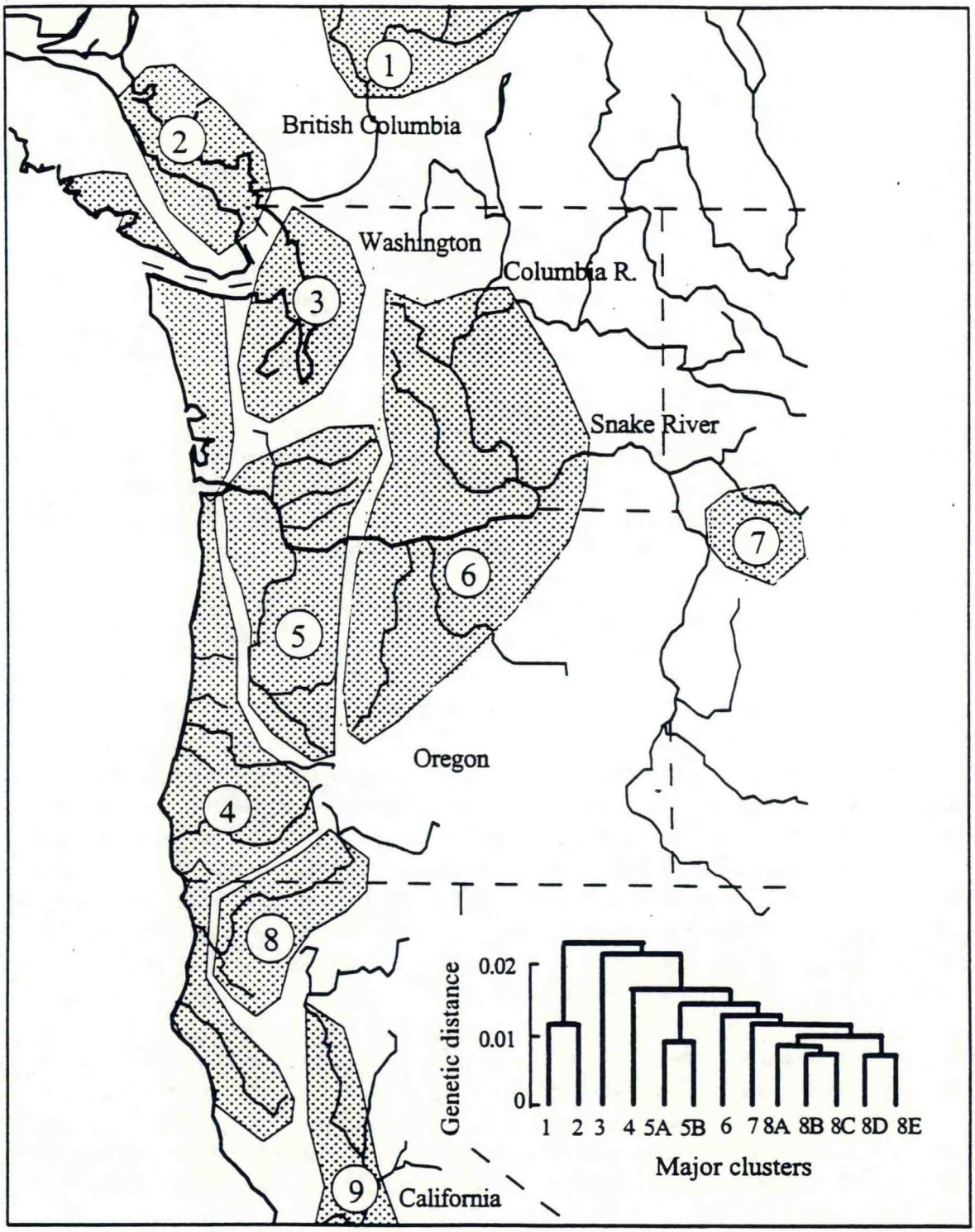


Figure 3. Dendrogram and geographic distributions of population genetic units of chinook salmon (from Utter et al. 1989).

ancestral background (Fig. 4; Waples et al. 1993). These life history characteristics have apparently arisen independently several times (Table 1).

In summary, several factors affect the amount and distribution of genetic variation among populations. In general, the larger the geographic distance between populations, the more genetic differentiation they tend to show, most likely because geographic distance enhances reproductive isolation when migration is limited. The presence of physical or geographic barriers to migration may also lead to genetic differentiation between populations because of absent or reduced levels of gene flow. Life history patterns can also influence the degree of genetic differentiation among populations. Anadromous populations of a species tend to have more genetic variation than landlocked or freshwater resident populations, but anadromous populations tend to show less genetic differentiation than do resident populations. However, even if these general tendencies exist, there are many exceptions.

These exceptions generally make it impossible to predict with reasonable precision the reproductive relationships and distribution of genetic variation among a set of salmonid populations. Therefore, direct assessment of the amount and distribution of genetic variation is necessary in any situation where information on the genetic population structure is needed for a management decision.

Temporal Variability

Allele-frequency differences that are taken to reflect population differentiation are difficult to interpret unless the variability patterns are stable over time. To date, little has been done to describe how quickly population structure can change. The data that do exist for salmonids, however, indicate that observed variability patterns are temporally stable. For example, consider the results of Waples et al. (1993) on chinook salmon from the Snake River that includes samples from 2 consecutive years (1989 and 1990) for all localities studied (Fig. 4). Clearly, samples from different years from the same locality tend to cluster together, as they should if the dendrogram depicts the relationship among samples from a set of local populations that are genetically stable over time. It should be noted, though, that the time span considered is fairly short (1 year), considerably less than a generation for chinook and other species of Pacific salmon.

The largest set of data on temporal variability in a salmonid is apparently for brown trout in central Sweden (Jorde and Ryman 1996). The populations studied were selected to represent a set of natural populations with different degrees of reproductive isolation and are as unaffected as possible by human activities (stocking, pollution, excessive harvest, and so on). Allele-frequency shifts at 14 polymorphic protein loci have been monitored for 15 years, with sample sizes of about 100 fish annually from each of four lakes (Fig. 5).

For populations in these four lakes, about 95% of the total variation was contained, on average, within lakes, and 5% was due to variation between lakes and between years (G_{ST} = 0.05; Fig. 5). These relative proportions of within and between locality variability are about the same as those frequently observed for populations of Pacific salmon, such as the Snake River chinook populations

depicted in Figure 4. The "explained" 5% component of variability among the four brown trout populations can be broken down into two sources of variation: between lakes and between years within lakes. The component corresponding to temporal variability is small and represents only about 0.5% of the total variation observed over the 15 years. This result strongly indicates that the genetic structures of the populations are quite stable over time. In turn, the biological characteristics common to salmonids in general suggest that biochemical genetic data collected at a single time for natural salmonid populations reflect geographical structures that are temporally stable.

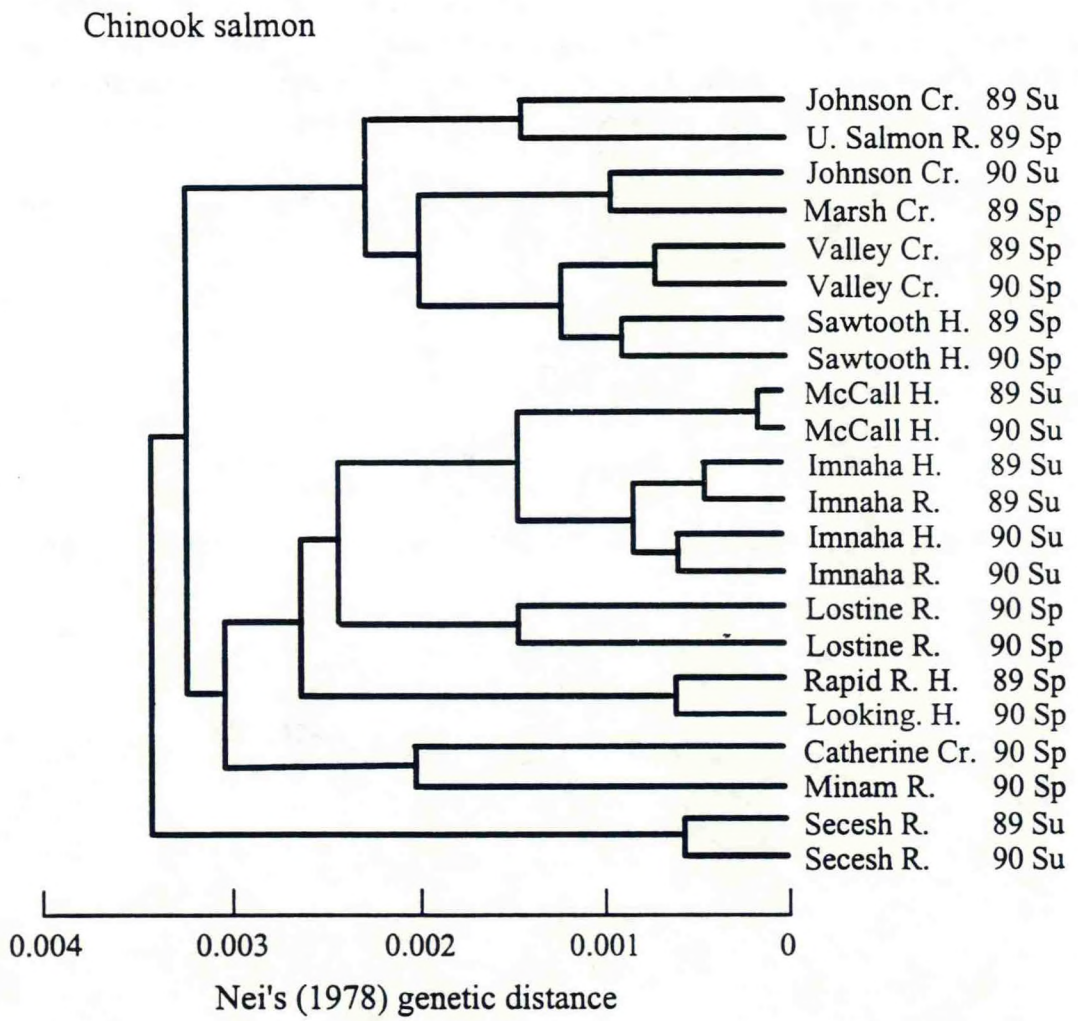


Figure 4. Dendrogram of genetic relationships among 1989 and 1990 samples of Snake River chinook salmon (from Waples et al. 1993). Sp = spring run, Su = summer run.

Migration Among Populations

The existence of genetically distinct local populations, which are typical for salmonids, indicates that the amount of genetically effective migration (gene flow) between populations is fairly restricted. In the context of straying, it is of considerable interest to have at least a rough idea of the amount of gene flow that is compatible with the level of divergence observed among local salmonid populations (see Ryman et al. 1995a).

A major difficulty in estimating natural levels of gene flow is that we are interested in genetically effective migration, which cannot be estimated by observing the movement of marked individuals. Direct observations of movement from one locality to another may lead to inaccurate estimates of gene flow, because migrants may be reproductively less successful than residents.

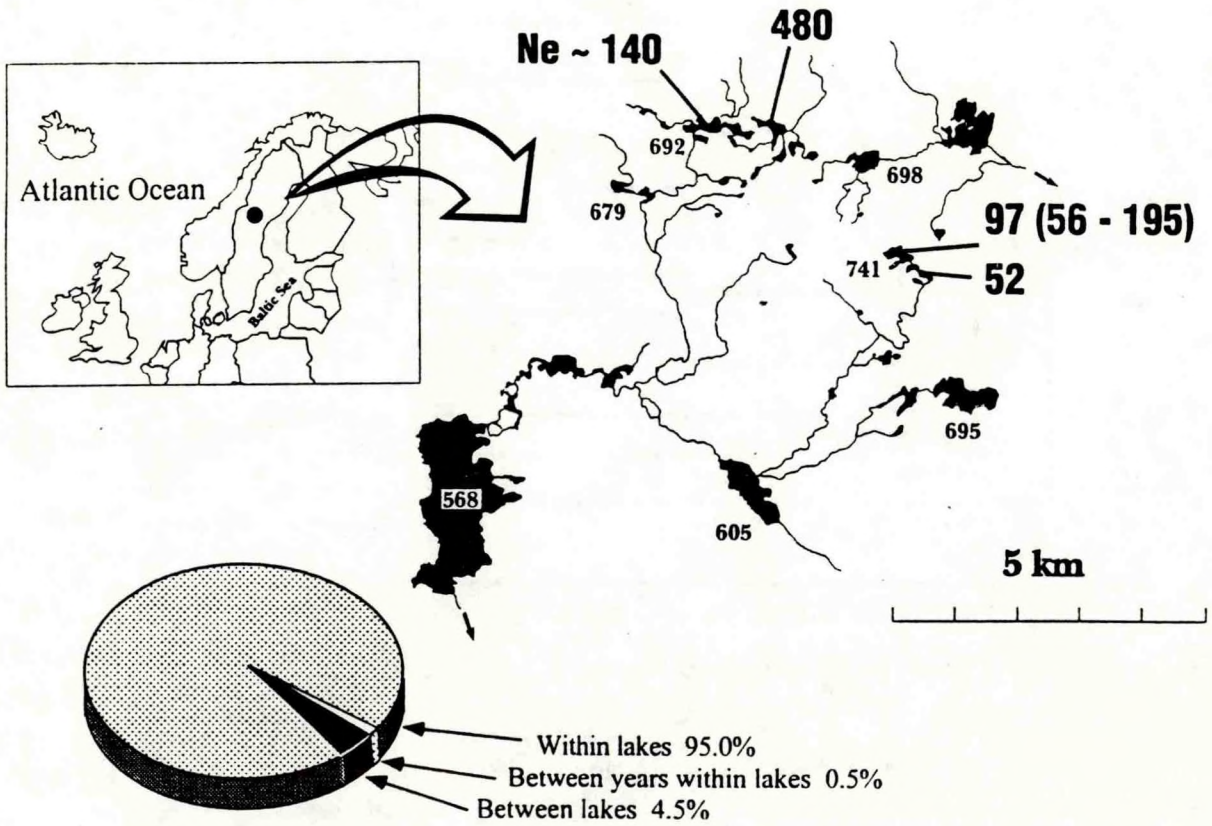


Figure 5. Temporal and spatial components of genetic diversity in four natural populations of brown trout in Sweden. Bold numbers are estimates of effective populations size (N_e), and small numbers are altitudes of the lakes in meters.

A convenient attribute of the quantity G_{ST} is that it can be related to the amount of gene flow. By assuming 1) that migration roughly follows the so-called island model of migration (see Felsenstein this report), 2) that mutation is not an important force changing allelic frequencies, and 3) that the populations are at pseudo-equilibrium relative to random drift and migration, we can estimate the number of migrants from the approximation

$$G_{ST} = 1/(4N_em + 1).$$

Here, N_e is the genetically effective population size, m the migration rate, and the product N_em is the effective number of migrants per generation. Although some care must be taken in converting G_{ST} values into estimates of migration, this approach in most cases is expected to provide a reasonably accurate estimate of gene flow, especially if a large number of protein coding loci are used and averaged (Ward et al. 1994).

The relationship between G_{ST} and the number of migrants per generation (N_em) is plotted in Figure 6. Clearly, only a few migrants are needed to prevent major differentiation among populations. For example, G_{ST} values of the order of 0.05 and 0.10, which are commonly observed among conspecific salmonid populations, correspond to an average number of migrants per generation of no more than about 5 and 2, respectively. Thus, values of G_{ST} observed for salmonids suggest that the amount of genetically effective migration or "straying" between natural populations is quite small, especially relative to the levels of straying that occur from hatchery or supplementation populations such as those of the Columbia River Basin (Waples 1991).

Results from our temporal study of brown trout populations indicate that the amount of differentiation observed may to some extent underestimate the direct or indirect gene flow among populations that are geographically distant. This impression stems from, among other things, the observation that the amount of genetic variation found within local populations is larger than would be expected from estimates of their effective sizes (N_e). This finding may be explained if larger groups of populations are connected through some gene flow that is both irregular and restricted. Such an explanation implies that low levels of gene flow between larger groups of local conspecific populations constitute part of an evolutionary strategy; gene flow between neighboring populations is small enough to permit local differentiation, but the flow within the metapopulation is large enough to maintain adequate levels of genetic variability.

The implication for management is that efforts to protect individual natural populations represent only a first necessary step in the conservation of genetic resources of salmonids. In the more ambitious program with the goal of creating opportunities for maintaining reasonable levels of genetic diversity within local populations, conservation efforts should be aimed at preserving systems of populations with the potential for a restricted gene flow between them.

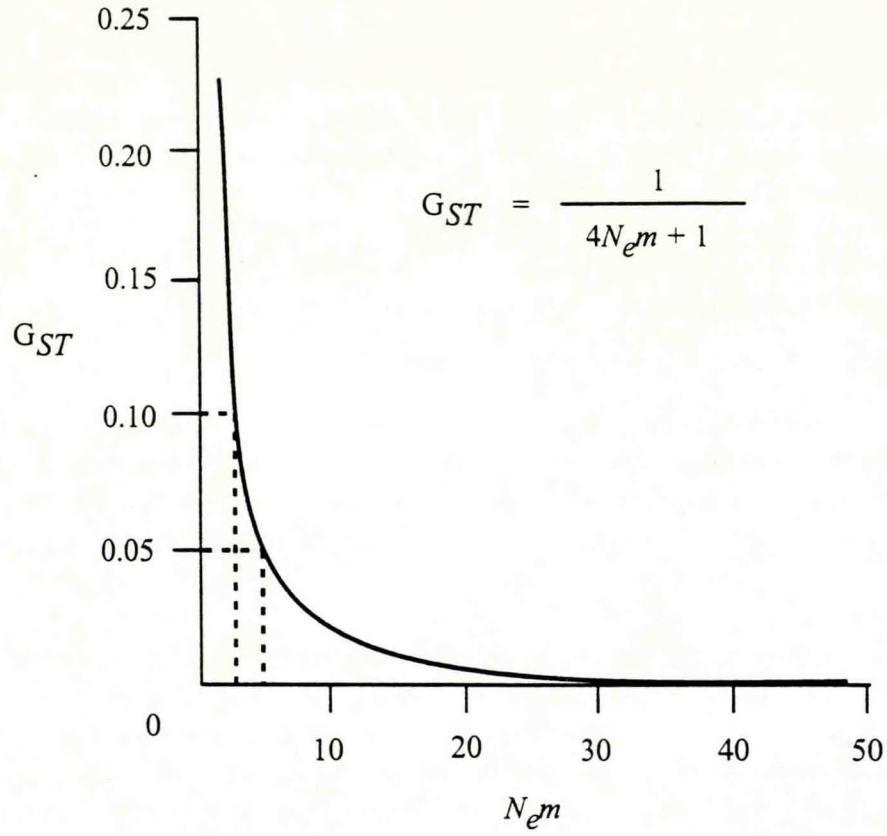


Figure 6. Approximate relationship between G_{ST} and the number of migrants, N_em, in the island model of migration.

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Discussion

Question: Robin Waples: The F_{ST} value for the Snake River chinook populations in the dendrogram of Figure 3 is about 0.035, which is fairly typical of Pacific salmon depending on species and geographic area sampled. If you sampled a larger geographic area that included divergent populations, the value of F_{ST} would be larger. The point is that, at the values of F_{ST} we find in natural populations, we are at the end of the scale in Figure 6 where a small difference in F_{ST} makes a large difference in the estimate of N_em, the number of migrants. So considering the errors associated with estimating F_{ST}, the accuracy in estimating N_em is very low. A point estimate of 10 or 20 migrants could well be 100 in nature. We generally lack the ability to draw inferences about the levels of gene flow that concern managers. Do you have any comments about this limitation on inferences from genetic data?

Answer: Nils Ryman: As you point out, we are limited in our ability to use genetic data, but this approach is the best we have for the moment.

Question: Robin Waples: Another way of expressing this concern is that if you sample a restricted geographic area, you may see fairly modest genetic differences, which are often statistically significant but which are not large. Nevertheless, when you plot that degree of differentiation against geographic distance, you see a strong correlation between genetic differences between populations and the geographic distances between them. Populations located close together tend to be more similar to one another than populations located farther apart. The result is that you have a combination of genetic differences between salmon populations that are typically not large when you compare them to a larger geographic scale.

Answer: Nils Ryman: But then we are back to the point of determining the number of populations that should be targeted for conservation in a critical geographic area. Our data indicate that gene flow occurs between natural populations, and that it is important to conserve the entire grouping rather than a particular population. In this way you escape the problem of estimating gene flow.

Comment: Joe Felsenstein: One reason you may be interested in estimating N_em that are rather large is if you were worried about fitness effects of migration on selected loci, because it may make a great deal of difference whether N_em is 40 or 80. Such values of N_em would not make much of a difference to the amount of geographic differentiation for neutral alleles, but may still be important in how much impact migration from other areas would have on local selected differentiation.

LOCAL ADAPTATION

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Introduction

One outstanding feature of salmon is how variable they are, and this variability can take many different forms within and between populations. For example, the size of adult chinook salmon (*Oncorhynchus tshawytscha*) varies greatly from medium to very large, as in some populations in British Columbia. As another example, the body shape of coho salmon (*O. kisutsch*) in British Columbia can vary greatly among populations. Variability can also be seen in coloration, behavior, and many other characteristics. A pervasive notion is that this variability is not due to environmental noise, but reflects something that is meaningful to the survival and persistence of a population in a local environment (Ricker 1972, Taylor 1991).

In this presentation, I would like to define local adaptation, outline the requirements for demonstrating adaptation in wild populations, and discuss how local adaptation is studied. I would then like to describe the extent of local adaptation in nature for a variety of traits, and illustrate the extent of temporal and spatial variability in these traits. Next, I will describe the extent of replicate adaptive evolution and discuss the relevance of hatchery straying to adaptation in wild populations. Lastly, I would like to offer several conclusions about the relevance of adaptation in wild populations and the effects of non-native hatchery straying on fitness in wild populations.

Local Adaptation Is a Dynamic Process

First of all, adaptation is a dynamic process--and I want to emphasize the word *process*--acting within populations to maintain or increase the frequency of traits that enhance the survival or reproductive success of individuals with the trait. The value of an adaptive trait to an individual is measured relative to individuals with other traits. Three criteria must be satisfied to demonstrate that a trait is adaptive:

- The trait must have an additive genetic basis.
- Variability in expression of the trait must be associated with variability in survival, reproductive success, or some other component of fitness.

- The mechanisms by which natural selection acts on the trait to increase fitness must be identified.

These are very stringent criteria. In short, to demonstrate adaptation, one must show that natural selection influences phenotypic variability and that this variability has, at least in part, a genetic basis.

Adaptation is a dynamic process, which in salmon populations has probably not reached a steady-state endpoint of optimal fitness in an environment. Adaptation is dynamic because selection varies between years, and because trade-offs in fitness at different life history stages produce a "tug of war" between various traits at different life history stages. Variability in the direction of selection was illustrated very well by the example Dolph Schluter (this volume) gave of temporal changes in body size in one of Darwin's finches on the Galapagos Islands. Years of high rainfall produced a large crop of small seeds which favored small-bodied birds with small beaks, and years of drought produced fewer, larger seeds that favored large-bodied birds with large beaks. Salmon also experience fluctuations in the directions of selection, not only between years, but between life history stages. For instance, many environmental variables thought to act as selective factors in salmon populations (e.g., water temperature, water flow, pathogens; see Taylor (1991)) fluctuate from year to year and may cause both the intensity and direction of selection to vary.

Methods of Studying Local Adaptation

One way to demonstrate adaptation is by direct experimentation in nature. This requires an estimate of the heritability of the trait or traits being studied, and a demonstration that the fitness of a phenotype is correlated with an environmental parameter. As far as I know, heritability of a trait in a natural salmon population has been measured in only a single study (Smoker et al. 1994). One way of showing the second criterion, that phenotypic variability is associated with variability in fitness, is through reciprocal transplantation experiments. However, reciprocal translocations of salmon and phenotypic correlations with environment have not been combined into single experiments to my knowledge. The result is that no one has directly demonstrated natural selection in wild populations of salmon.

Another way of demonstrating natural selection is to use indirect comparative methods, and most of the evidence for local adaptation in salmon populations comes from this kind of analysis. One approach is to search for environment-phenotype correlations among animals in contrasting environments and to use these correlations to predict how individuals might behave under experimental conditions in which performance can be tested. Another approach is to make inferences from rigorously controlled experimental manipulation.

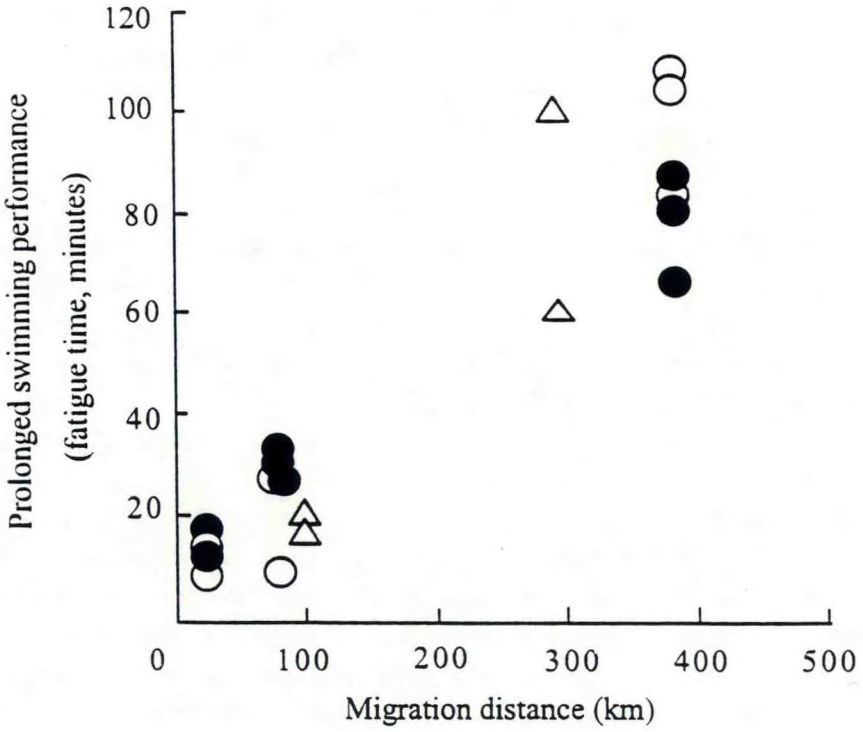


Figure 1. Prolonged swimming performance as a function of distance from natal stream to the sea for three populations of coho salmon (circles) and two populations of steelhead trout (triangles). Each point represents the mean of 10 (coho) or 30-46 (steelhead) juvenile fish. Open symbols represent laboratory (coho) or hatchery (steelhead) populations; closed symbols represent wild populations. Adapted from Taylor (1991).

Examples of Adaptation

The following are three examples of the kinds of salmon studies that have been used to demonstrate local adaptation. The first example in which the indirect comparative method was used comes from studies by Taylor and McPhail (1985) and Tsuyuki and Williscroft (1977) on fatigue time during prolonged swimming and freshwater migration distance to natal areas. Figure 1 shows the time to fatigue in coho salmon and steelhead trout for wild fish and for fish raised in "common-garden" experiments in which different populations were raised under the same conditions. Freshwater migration distances for the different populations ranged from 20-30 km to more than 400 km in the Fraser River. What we see is that fish migrating long distances have greater prolonged swimming performance (i.e., longer time to fatigue) than fish spawning at sites close to the ocean. Here the phenotype-environment interaction--a proxy for natural selection--is migration distance.

A second example comes from Atlantic salmon (*Salmo salar*) for two rivers, each with several tributaries. One river is the Dee River in Scotland, and the other is the Blackwater River in Ireland.

The frequency of the *sMEP-1*100* allele ("ME-2," malic enzyme) is positively correlated with water temperature in the two distinct watersheds (Verspoor and Jordan 1989). Although a correlation exists, no selective mechanism was suggested in the article to explain how the gene product might interact with temperature to produce the correlation. Local selection may very well be operating, but more work needs to be done on its mechanism to make this a convincing example of adaptation. This locus could also be linked to another trait that is being selected.

A third example is also a phenotype-environment correlation between the direction of migration and water flow in juvenile sockeye salmon. Some sockeye salmon, such as those in the Cedar River, Washington, spawn in the inlet stream of a lake, so that newly emerged fry must swim downstream to reach the lake where they spend their first year of life. Other sockeye salmon, such as those in the Chilco River, B.C., spawn in the outlet stream, so fry must move upstream to reach the nursery lake. Yet other fry, such as those from Weaver Creek, B.C., must first move downstream to the Harrison River, then upstream against the current into Harrison Lake. Based on the localities of spawning areas relative to the nursery lake, Quinn (1985) predicted the direction fry would orient themselves in a magnetic field after being taken from the field and raised in the laboratory. For example, Cedar River fry would be expected to orient themselves to the north so they would swim into Lake Washington. The results of these experiments followed the predictions: Cedar River fry oriented to magnetic north, on average; Chilco River fry oriented in the expected direction to magnetic south; and Weaver Creek fry oriented downstream then upstream in directions that would eventually take them into Harrison Lake.

The evidence for local adaptation in salmonids generated with indirect methods is largely circumstantial, but nevertheless compelling in that similar results appear for the same traits in several different species. For example, local adapatation has been postulated for age and size at maturity, developmental rate, temperature tolerance, disease resistance, some morphological traits, and some allozyme polymorphisms. Some of the best evidence for adaptation comes from demonstrations of increased disease resistance for salmon populations in areas of sympatry with disease pathogens.

Inferences about adaptive traits in salmon have also been made by observing the survival of hatchery fish transplanted into non-native environments. Many of these studies, however, are difficult to interpret because most of the experiments were uncontrolled and unreplicated. One of the better sets of data from this kind of experiment is on the return rate of hatchery coho salmon transplanted into non-native environments, relative to the return rate of hatchery-released fish at the hatchery (Reisenbichler 1988). The results showed a drop in the return rate as the fish were transferred farther and farther from the hatchery. Fish tranferred 700 km showed fewer returns than fish transplanted within the same watershed. The inference is that the ecological and environmental conditions become increasingly different from the hatchery at more distant localities, and fish do not have the locally adapted traits that would promote their survival in the new environments.

Geographical and Temporal Scales of Local Adaptation

The geographic extent of a local adaptation varies considerably. For example, rainbow trout fry from two tributaries of Pennask Lake, an outlet stream and an inlet stream, have different rheotactic behaviors that bring them into a common nursery lake (Kelso et al. 1981). In this case, the scale is only about 2 km. On the other hand, variability in the frequency of the *sMEP-1*100* allele among populations of Atlantic salmon across the North Atlantic demonstrates adaptation on a continental scale (Verspoor and Jordan 1989). The frequency of the 100 allele, which is associated with spawning and rearing in warm water, is low in North American populations of Atlantic salmon, which spawn in much colder waters than do European populations, which show a much higher frequency for this allele. In this case, the enzyme variant (or a selected variant at a linked locus) apparently reflects adaptation both on a small geographic scale between tributaries and on a larger scale across the Atlantic Ocean.

In considering temporal scales of adaptation, keep in mind that virtually all Pacific salmon habitats in the northern part of Washington State and in British Columbia were covered with sheets of Pleistocene ice, which started to recede about 15,000 years ago. Therefore, the considerable diversity among Pacific salmon populations in this area has, to a large extent, evolved since that time. This amount of time, therefore, might be considered the upper limit needed for salmon populations to diversify genetically and to adapt to local conditions. In reality, however, adaptations commonly arise much more quickly. For example, local differentiation has apparently developed among populations of New Zealand chinook salmon since they were introduced about 100 years ago. Experiments are now under way to determine if such differentiation reflects adaptation (T. Quinn, School of Fisheries, University of Washington, Seattle, WA 98195. Pers. commun., June 1995) and, if so, then it means that adaptive changes can occur quite rapidly. In the Pacific Northwest, hatchery populations of chum salmon (*O. keta*) can have altered developmental rates that apparently result from changes in temperature regimes in the hatchery. These genetically based changes took place in about 6 years, or about 3 generations (Lannan 1980).

I would argue that some genetic changes leading to local adaptation can occur in a single generation, not necessarily thousands of generations. Although evidence is lacking for salmon, short-term changes have been documented in other organisms. One example is the rapid change in beak size in Galapagos finches (*Geospiza* spp.), in which the driving force is the availability of differently sized seeds in different years. Another example is the rapid change in coloration in guppies that occurred in response to changes in visual predation (Endler 1986). Biochemical adaptation has been postulated for malate dehydrogenase in largemouth bass (*Micropterus salmoides*) in the central United States where water temperatures appear to favor one allele over another. The point is that although the data are lacking, many traits in salmon can most likely respond rapidly to changes in the enviroment.

Replicate Adaptive Evolution

One of the chief concerns of conservation is to perserve genetically unique population segments of a species. For many species of fish, however, adaptive traits can appear independently in several populations. One example is seasonal migration timing in adult chinook salmon. It is well known that various populations of chinook enter fresh water on their journeys to spawning grounds in spring, summer, or fall. One explanation for the diversity in migration timing might be that one-time mutations produced the different run times in an ancestral population and that the various kinds of fish colonized different areas. If this were true, we might expect all fall-run populations, for example, to be phylogenetically more closely related to one other than to populations with other migration times. When we look, however, at a phylogenetic tree depicting the genetic relationships among the populations of chinook salmon based on biochemical genetic data (Utter et al. 1989), we see that geographic proximity is a more important determinant of genetic relationships among populations than is migration timing. The populations do not cluster on the basis of run timing, but largely on the basis of geography; northern California populations cluster together, southern Oregon populations together, and so on. This clearly implies that some adaptive life history traits have evolved several times at different locations during the course of salmon evolution.

It might be argued that migration timing is not an adaptive trait--the same river can have different runs of the same species. If so, it is difficult to imagine why similar run times have evolved in so many areas independently of one another. Natural selection must be the force promoting the parallel evolution of this trait. Another useful feature of projecting quantitative traits onto phylogenies is that it focuses attention on groups of populations, and places the variability observed among populations into a more general perspective and highlights the range of habitats required to preserve the processes producing quantitative genetic diversity.

Natural Selection and Gene Flow

The most important parameter in wild populations potentially affected by the straying of non-native fish is local adaptation. The chief problem for biologists is to define the dynamic interactions between gene flow into wild populations and natural selection against "hybrid" individuals. First, selection against non-native fish and hybrids may be frequency dependent; that is, the ratio of non-native to native fish in a system may influence how well non-native fish and their genes do in natural habitats. Take for example, the very successful introduction of non-native chinook salmon into New Zealand waters. In the absence of genetic mixing, these introduced fish adapted very quickly to local habitats. Another example is the successful colonization of some Pacific salmon in the Great Lakes of North America.

Second, when genetic introgression occurs, what levels of gene flow are permissible with different kinds and intensities of natural selection? To begin to answer this question, one needs to have estimates of the strength of selection in natural habitats. Unfortunately, little data exist on the strength of selection, how often selection fluctuates, and on the kinds of selection that occur at the various life history stages. In the absence of such data, it is not possible to use population genetic

models to predict accurately what effects different levels of gene flow have on local adaptations and population fitness.

Conclusions

Although indirect and circumstantial, the evidence that local adaptation is pervasive and important in natural populations of salmon is compelling. Observations of local adaptation in several organisms have demonstrated that natural selection results from dynamic processes, and to preserve genetic diversity these processes must remain intact. Thus, research directed at measuring natural selection in wild populations is urgently needed. Although the conceptual framework for designing such experiments is straightforward, the experiments themselves require considerable effort over several generations. Without these kinds of data, however, the effect of gene flow from non-native hatchery fish on wild populations cannot be predicted with any certainty. Controlled, replicated experiments are needed to provide suitable data for understanding the effects of gene flow. Although it is difficult to say which adaptations should be studied, the migratory timing of juveniles and adults would be a good starting point.

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Discussion

Question: Audience: In one breath you talk about local adaptation and give compelling examples of why it is important, then in the next you talk about parallel evolution of life history traits. What, then, is wrong with just outplanting fish and letting natural selection sort things out?

Answer: Eric Taylor: To do that one would have to have good evidence that natural selection would in fact sort things out. The evidence from manipulative experiments suggests that perhaps this may not occur in the short term or may not occur at all. If variation is present in a population, and if the parties are willing to wait long enough--thousands of years--then natural selection would sort things out. The final product may have many of the same adaptations of existing populations, but would most likely be very different in many other traits.

Comment: Tom Quinn: Most transplanted populations do not do well. In experiments we have tried, the number of survivors has been so small that natural selection did not have a chance to sort things out.

Question: Robin Waples: We know when the last ice age ended, we know that nearly all of British Columbia was under a sheet of ice, and we know how much diversity we now have. Do we know anything about salmon populations before the last episode of glaciation or during previous glacial episodes over the last 2 million years?

Answer: Eric Taylor: Not much. About the only thing we can infer is that the various species of salmon have been around 10-50 million years. It is difficult to get information on ancestral populations, except indirectly through phylogenetic analysis of existing species with molecular methods or by the examination of fossils.

Conclusions

Panel of experts: Dr. Ruth Withler (chair), Dr. Craig Busack, Mr. Richard Carmichael, Dr. Kenneth Currens, Prof. Tony Gharrett, Prof. Michael Gilpin, Dr. Stewart Grant (rapporteur), Prof. Michael Lynch, Prof. Thomas Quinn, Prof. Nils Ryman, Prof. Dolph Schluter, Prof. Eric Taylor

CONCLUSIONS OF PANEL

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Introduction

A panel of biologists with expertise in population genetics and related fields met on the second day of the workshop to summarize the information presented by the speakers, and to evaluate, as best they could in a day, the genetic effects of the straying of hatchery fish into natural populations. Panelists agreed firstly that one-way gene flow from genetically distinct, non-native fish into a set of local populations decreases the levels of diversity among populations. Secondly, such one-way gene flow also accelerates the loss of both neutral and selectively advantageous genetic diversity within populations. The loss of diversity within populations results in the potential for decreased fitness and, hence, reduced productivity in a short time frame (50 years and less), whereas the loss of diversity among populations decreases the flexibility to adapt to changing environmental conditions and, hence, decreases productivity of local populations in a longer time frame (50+ years). It is relatively easy to identify the demographic parameters affecting genetic diversity and fitness, and to determine the general direction of impact from straying as the parameter values change (Table 1). However, it is difficult to predict the magnitude of the overall impact because of our limited ability to quantify the effects of gene flow, natural selection, and other processes on natural salmon populations.

Mechanisms of Genetic Change in Populations

Forces that bring about genetic change in populations are mutation, migration, natural selection, and random genetic drift. Most of the panel's discussion focused on the relative importance of genetic drift and natural selection on the fate of genetic variation introduced by mutation or migration under a variety of population structures. Particular consideration was given to the effects of drift and natural selection on adaptive genetic variation in small populations. Many of the assumptions made in population genetic models, such as constant population size and discrete generations, are not met in salmonid populations, and the panel attempted to outline the consequences that violation of these assumptions would have on predicting the effects of non-native straying. Before specific questions about straying are addressed, the following brief descriptions of processes bringing about genetic change and demographic factors influencing the type and extent of change in salmonid populations are outlined.

Table 1. Parameters that influence the genetic effects that straying of non-native fish has on natural populations. Values on the right generally result in larger effects on natural populations.

Parameter	Values of interest
Genetic distance between hatchery and natural populations	Small ——————> Large
Life-history traits in hatchery and natural populations	Similar——————> Dissimilar
Natural selection	Weak ——————> Strong
Magnitude of straying	Low ——————> High
Duration of straying	Short ——————> Long (1 generation) (25 generations)
Natural migration rates	High ——————> Low
Natural population size	Large——————> Small (1,000s) (10s)
Reproductive success of hatchery strays	Low ——————> High
Number of populations affected by straying	Few ——————> Many

Natural selection

The strength of natural selection for or against a trait (phenotype) is measured by the selection coefficient, s, which is the difference in fitness between the phenotype in question and an alternative form. Estimates of s for adaptive traits are between 0.0 and 0.5. However, reported values are most likely higher than the average value in nature, because the effects of small selection coefficients are difficult to detect. Moreover, for traits influenced by many genes, the quantity that affects the maintenance or loss of alleles at each locus is the strength of selection on a locus, not the strength of selection on the expressed trait.

Random genetic drift

Even in the absence of natural selection, not all spawners contribute equally to the next generation. Moreover, for any given spawner, both alleles at each locus may not be equally represented in the next generation, because of the chance segregation of alleles into gametes and because of the chance union of some gametes over others. Genetic drift is the random change in allele frequencies that occurs in finite populations due to the sampling of gametes between generations. The loss of alleles by genetic drift is unpredictable, but may be substantial in small populations, in which even beneficial alleles may be lost due to the effects of drift. A theoretical measure of the genetically effective population size is N_e, the size of a hypothetical population of equal sexes and random variation in family size that experiences the same amount of random drift as a natural population with census size N. In salmon, N_e for a population is the effective number of spawners each year times the generation length (in years).

Stray rate and gene flow

From the perspective of natural populations, the key parameter for measuring gene flow is the proportion of non-native fish actually spawning in the receiving local population(s). Only strays (immigrants) that actually reproduce in a locality result in gene flow into a local population. The observed number of strays in a local population is often used to calculate the proportion of immigrants, m, but stray fish may not reproduce, or may have reduced reproductive successes relative to local fish. Thus, m is the genetically effective rate of straying that represents actual gene flow into a population. The observed proportion of strays in a local population theoretically provides an upper limit for estimating m, assuming that strays have, at best, reproductive success equal to wild fish.

Just as the observed proportion of strays may overestimate the genetically effective proportion of strays, the census size, N, of a population typically overestimates the effective population size, N_e, that determines the genetic consequences of gene flow into a population. Studies of other organisms indicate that N_e is usually much less than N, so that N_e/N is often between 0.33 and 0.10. Since natural gene flow may increase the effective size of local populations, spawner counts alone may underestimate the effective sizes of geographically or temporally defined stocks. Such stocks

represent partially isolated local subpopulations of a much larger metapopulation, and the much larger N_e of the metapopulation determines the impact of gene flow on the total population. However, when the N_e of the immigrant population is small, gene flow can reduce the N_e of a local population.

Mutation

Mutational rates differ from one part of the genome to another, and individual mutations vary in their effect on the organism in which they occur. In large populations, natural selection will effectively limit the frequency of deleterious alleles through the elimination of individuals homozygous for them. However, the impact of individual mutations on an organism are often low, so that in small populations genetic drift may lead to an accumulation of deleterious alleles in spite of selection against them.

Heterosis or hybrid vigor

Heterosis is an increase in fitness, primarily in the first (F_1) generation after hybridization, that results after mating between individuals from genetically different populations. It can be caused by the masking of deleterious recessive genes in inbred populations, and by balancing selection (heterozygote advantage) at some loci.

Outbreeding and outbreeding depression

Outbreeding is the mating of individuals from genetically divergent populations. If the genetic differences are great enough, the result can be a reduction in fitness, termed outbreeding depression. Two types of outbreeding depression may occur.

Type 1: Reduced hybrid fitness. Mating with individuals possessing traits that are maladaptive in the local environment will result in the production of hybrid progeny with reduced fitness in that environment. This effect will occur in the first (F_1) generation after hybridization and in subsequent generations if any of the hybrid progeny survive to spawn. However, a reduction in fitness from Type 1 outbreeding depression may be masked by an increase in fitness from heterosis, particularly in the F_1 generation.

Type 2: Breakup of coadapted gene complexes. Some combinations of alleles at different loci within a population may function as a unit, or a coadapted gene complex, to confer a selective advantage upon individuals. Matings between local and non-native individuals can lead to the disruption of these gene complexes and produce a reduction in fitness. Because F_1 hybrid progeny receive one complete set of chromosomes from each parent, gene complexes generally remain intact until chromosome reassortment and recombination occurs during reproduction. Thus, Type 2 outbreeding depression will typically not be apparent until the F_2 or later generations.

Loss of Genetic Diversity Within and Among Populations

Estimates of effective population size and gene flow can be used to predict the rate of loss of neutral genetic diversity within and among populations and, to a lesser degree, the loss in fitness within populations that can result from particular levels of one-way gene flow (straying) into these populations. For populations in which the selection coefficient, s, is less than the effective stray rate, m, the time in generations for which the proportion, P, of native genes remains in a local population is

$$t_P = \ln(P)/m. \qquad (1)$$

For example, the time to a 50% loss of local, neutral genes ($P = 0.5$) is

$$t_{0.5} = 0.69/m. \qquad (2)$$

With high levels of gene flow, the loss of 50% of alleles can occur fairly rapidly:

69 generations for $m = 0.01$ (1.0% gene flow)
25 generations for $m = 0.025$ (1.5% gene flow)
12 generations for $m = 0.05$ (5.0% gene flow).

Two important consequences follow from Equation (1): First, as m increases, the fraction of alleles lost also increases, and alleles are lost more rapidly. As the fraction of locally beneficial alleles that can be maintained in the population is reduced, the frequencies of nonlocal deleterious alleles will increase. The loss of alleles of adaptive importance at high values of m leads to reduced average fitness within the local populations in the short term, if the strays have lower fitness. Second, the proportion of stray spawners in a natural population, not simply population size, determines the rate at which local alleles are replaced by hatchery alleles. However, at small effective population sizes ($N_e << 1{,}000$), the loss of adaptive genetic diversity will be greatly accelerated by genetic drift. Deleterious alleles with effects less than the reciprocal of twice the effective population size ($s < 1/2N_e$) will not be eliminated by selection, and beneficial alleles with effects less than $1/2N_e$ will be lost due to random drift.

Effects of Straying on Natural Populations

The panelists attempted to predict the magnitude of genetic effects of non-native strays on local populations that results from altering the population structure and demographic factors listed in Table 1.

Genetic distance between hatchery and natural populations

In general, measures of genetic distance among salmon populations are based on biochemical and molecular markers that are assumed to be largely neutral to selection. Thus, biochemical and molecular genetic distances may provide better estimates of the time that populations have been separated, or of the magnitude of gene flow, than the measurement of adaptive traits subject to natural selection. However, the longer two populations have been isolated from each other, the more likely it is that they have diverged genetically, even for adaptive phenotypes shared by the populations. Similar phenotypes in two reproductively isolated populations may be due to convergence in which different genotypes produce the same phenotype through different genetic mechanisms. Thus, although genetic distance based on neutral traits may not be a linear indicator of the type and extent of adaptive differences between populations, the consequences of straying on adaptive traits are likely to increase with increasing genetic distance between populations. For neutral alleles, gene flow from a hatchery population may result in the replacement of local alleles with non-native alleles regardless of the genetic distance between the populations (Equation 1). The loss of genetic diversity within a population will be modified by any population substructuring (e.g., metapopulation structure), and the loss of diversity among populations will be determined by the number of populations receiving strays from the same hatchery stock.

Life-history similarity between the non-native hatchery and local populations

As indicated above, salmon populations that appear to be phenotypically similar for adaptive traits may be genetically different. Conversely, life-history differences between populations may reflect environmental rather than genetic differentiation. Thus, the level of phenotypic similarity exhibited by hatchery and local populations is not a reliable estimator of the amount of outbreeding depression (and hence loss of productivity) that can follow hybridization. Outbreeding depression is experimentally difficult to demonstrate because hybridization and reciprocal translocation experiments over several generations are required. The type and extent of outbreeding depression in salmonids is unknown, although it probably does occur.

Magnitude of straying

Persistent one-way straying at any level will eventually lead to the loss of effectively neutral genes in a local population (Equation 1), except when selection against F_1 hybrids is absolute. Even genes under positive selection in a local population will be replaced if the proportion of effective strays, m, is greater than the coefficient of selection, s, for local advantageous alleles. Natural selection, however, is expected to maintain genes with high fitnesses in local populations in spite of immigration, except when population sizes are very small. There are few reliable estimates of selection coefficients associated with alleles producing adaptive phenotypes in salmonid populations. The number of genes influencing the variability of a morphological or life-history trait is generally unknown, so the selective value of the trait itself provides an upper limit to the selective value of any one locus influencing the trait. Traits may be selectively advantageous at one life-history stage in

one set of environmental circumstances, and selectively disadvantageous at another life-history stage or in another set of environmental circumstances. Thus, the differential in fitness between alternative phenotypes must be evaluated over the salmonid life cycle, and even then may vary over time depending on environmental conditions. It is experimentally more difficult to detect small selection coefficients than large ones, and difficult to measure the adaptive value of a trait over time. Thus, published selection coefficients are higher, on average, than values for most adaptive alleles, which likely have selection coefficients of less than 0.05 (5%). Such alleles would be lost from local populations experiencing consistent levels of gene flow of 5% and higher.

Reproductive success of hatchery strays

The reproductive success of hatchery strays is one factor that affects the magnitude of gene flow resulting from straying, as discussed above. If the reproductive successes of strays are low, the effective stray rate, m, and the rate of replacement of local genes are lower than would be estimated by simply calculating the proportion of strays in the local population. However, implications for the genetic diversity and productivity of local populations differ if selection operates on the migrants themselves rather than on their hybrid progeny. If hatchery migrants fail to compete for mates and do not otherwise disrupt normal spawning in the local population, the rate of introgression will be low, and productivity of the local population may be little affected. However, if migrants hybridize extensively with local fish but fail to produce viable progeny, much of the local, as well as the non-native, contribution to the next generation may be lost by selection against hybrid progeny. Thus, at high rates of immigration and hybridization, losses in productivity and genetic diversity in local populations may be substantial even if the reproductive success of hatchery migrants, as measured by surviving progeny, is low.

Duration of hatchery straying

The proportion of effectively neutral native alleles lost in a local population as a result of continuous one-way straying by non-native fish increases asymptotically with time (Equation 1). Long-term straying will lead to the replacement of local alleles with non-native alleles at effectively neutral loci ($s < m$). If migration from a hatchery population occurs for a short period of time (1-2 generations), or occurs only sporadically, natural selection may eliminate much of the hatchery contribution to the local population. Outbreeding depression resulting from this selection may be concentrated in the first generation after hybridization or may occur over several generations, depending on the nature of the outbreeding depression.

Local population size and structure

The proportion of migrant genes that are incorportated into the local population, not the absolute size of the local population alone, determines the effect of gene flow on the genetic composition of the local population. Populations with an N_e of 1,000 or more tend to act like

populations of infinite size, so that little genetic diversity is lost through random drift. However, even in these large populations, the replacement of local alleles with hatchery alleles will proceed through gene flow (Equation 1).

There are few estimates of effective population size, N_e, for salmon populations. Many populations are currently of such small size that if N_e were only one-third to one-tenth the number of spawners, even summing numbers of spawners over the generation time yields estimates of N_e less than 50. This indicates that as few as 1 or 2 migrants spawning in the populations each year would have a large impact within 10 generations. While many salmonid populations are at historical low levels of abundance, some species (e.g., rainbow trout, steelhead, coho salmon) appear to have persisted in small populations over time without obvious signs of inbreeding depression. Salmonids may therefore form metapopulations consisting of small, partially isolated subpopulations with some natural level of reproductively effective straying between them. Straying may not be continuous or symmetrical among subpopulations and may occur only when triggered by particular environmental or demographic conditions.

Metapopulation structure can affect the rate of introgression of hatchery alleles into local subpopulations in two ways. First, the N_e of importance in determining what proportion of the population hatchery spawners represent is the N_e of the entire metapopulation. If hatchery strays enter only one or a few local subpopulations, they constitute a much smaller proportion of the metapopulation than the local populations to which they strayed. Second, if hatchery strays spawn in only a few of the local subpopulations, hatchery alleles replace local alleles in those subpopulations at a slow rate because strays from other subpopulations replenish native genes. The flow of hatchery alleles into subpopulations not directly receiving strays would also occur, but might be greatly slowed if natural straying between the subpopulations followed a stepping-stone model of migration.

Number of populations affected

Genetic differentiation among populations can decrease, if non-native fish stray into several local populations. This is true whether the populations are isolated from one another or whether they are subunits of a larger metapopulation. When hatchery straying occurs, hatchery alleles ultimately enter all the subpopulations of a metapopulation, but the replacement of local alleles is slower in subpopulations not directly receiving hatchery migrants. Therefore, local adaptations shared among subpopulations are less likely to be lost from the metapopulation as a whole if straying occurs into only one or a few local populations.

Conclusions

Salmon have evolved so that genetic differences, both neutral and adaptive, exist between populations in the presence of natural levels of gene flow. However, we do not know which of the following is the reason that observed population structure is maintained:

- Natural levels of gene flow are very low. Low levels of gene flow may be due to strong homing behavior, or to the lack of reproductive success of stray fish in local populations, or to a combination of both factors.

- Natural gene flow occurs only sporadically and therefore has much less potential to swamp genetic diversity within or between natural populations.

- Strays tend to be exchanged among geographically nearby populations, and this stepping stone mode of gene flow to more distant populations results in a) efficient natural selection against disadvantageous genes, and b) retardation of the introgression of neutral alleles into distant populations. This latter factor leads to large-scale regional differentiation among populations, even for neutral traits such as allozymes.

Without knowing whether salmon populations, finely tuned to their environments, are structured to withstand high levels of gene flow, or whether the natural level of gene flow is low, it is difficult to predict the consequences of increased amounts of straying from genetically dissimilar populations. If the reproductive success of strays is low, the direct genetic consequences of increased straying from non-native populations may be relatively small, although indirect effects may still be important. On the other hand, natural strays may be generally reproductively successful but would not destroy population structure, either because they are from nearby genetically similar populations or because straying is sporadic. Under these circumstances, hatchery strays, which are genetically dissimilar to natural populations and which are genetically or environmentally predisposed to straying, will have a greater detrimental effect on both the diversity and the fitness of a natural population.

The expected loss of genetic diversity from gene flow is based on populations that behave as if they were infinite, with effective sizes greater than 1,000 fish. The replacement of local genes by non-native genes for neutral traits follows the predictions of Equation 1, on average, and genes with selective coefficients greater than the immigration rate will be replaced. The suggestion that large populations, because of their size, can withstand the loss of productivity from outbreeding depression is based on the assumption that local populations are currently well adapted to their environments and are currently productive enough to seed the environment to carrying capacity even with diminished fry or smolt production, or both. However, the assumptions of well-adapted populations and productivity may not be true for many populations. Human activity and natural events have changed the habitats of many salmon populations so rapidly in recent decades that populations may not be as well adapted to their environments as was historically the case. Salmon populations have already experienced a loss of productivity, because of natural selection against some genotypes that occur naturally at high frequencies in the population. Heavily exploited populations may, at least in some years, possess fewer spawners than necessary to produce optimal numbers of juvenile fish. Current populations of salmon may not be able to maintain adequate levels of fitness, because they are smaller than they were historically, and because of rapidly changing environmental conditions. Gene flow from non-native fish is an additional challenge which will affect the ability of salmon to adapt to future changes and which can greatly decrease productivity.

Replies to Questions Posed at the Workshop

What are the appropriate parameters to consider in evaluating the effects of straying?

Forces that bring about genetic change in populations are migration, mutation, natural selection, and random genetic drift. Mutation rates are typically low for most genes, and mutation was not considered in detail for the time frame of interest (< 100 years) (but see Lynch (in press) for more discussion of the role of mutation). Most of the discussion focused on the relative importance of drift migration, as well as selection under a variety of scenarios. Brief descriptions of some key terms and parameters follow.

- **Stray rate**: From the perspective of effects on natural populations, the key straying parameter is the proportion of non-native fish actually spawning in a natural population. The same number of strays can represent different rates of migration, depending on the size of the natural population. However, stray fish may not reproduce, and even if they do, they may have reduced reproductive success.

- **Gene flow**: The proportion of non-local genes that actually enter a natural population is known as gene flow and is denoted by m in the formulae presented here. Since gene flow occurs only to the extent that genes from stray fish become integrated into local natural populations, the stray rate is an approximate upper limit to the rate of gene flow.

- **Local population size**: The genetic consequences of straying depend on the effective population size (N_e) more than on census size (N). Studies of a variety of organisms indicate that the ratio N_e/N is often about 0.1 to 0.33. Since a given year-class of young return over several years for most species of salmon, the effective population size for an entire generation is the average effective size per year times the generation length (for salmon, generation length is average age at spawning).

- **Natural selection**: The strength of natural selection on a genotype or discrete trait can be measured by the selection coefficient, s, which is the reduction in fitness of a trait or genotype compared to one with optimal fitness. For traits influenced by many genes, the quantity that matters most is the strength of selection (s) per locus, not the strength of selection on the trait itself.

- **Random genetic drift**: Genetic drift is the random change in allele frequencies that occurs in all finite populations due to the sampling of gametes between generations. The effects of drift are unpredictable and can be substantial in small populations. Isolated populations with N_e of about 50 or less will lose substantial amounts of genetic variability through drift. Populations with N_e of about 1,000 or more tend to act like an infinitely large population in which drift is not important.

- **Inbreeding and inbreeding depression**: Inbreeding is the mating of related individuals. In small populations, the level of inbreeding increases, because most or all individuals are closely related. A consequence of inbreeding is an overall increase in homozygosity. Homozygosity for recessive deleterious alleles, in turn, can cause a reduction in fitness known as inbreeding depression.

- **Outbreeding and outbreeding depression**: Outbreeding is the mating of genetically divergent individuals. If the genetic differences are large enough, the result can be a reduction in fitness known as outbreeding depression. Outbreeding depression can be caused by either (or both) of two factors: 1) loss of local adaptation, and 2) breakdown of favorable combinations among gene loci. Outbreeding depression due to loss of local adaptation may occur in the first generation after hybridization, but reductions in fitness due to breakdown of gene complexes may not be apparent until the F_2 or later generations. Fitness of the local population before the hybridization event is the reference point to evaluate whether outbreeding depression has occurred.

What other parameters are important in determining the genetic effects of straying?

Several other parameters also help to determine the genetic consequences of straying (see Table 1). Some of these are described below.

- **Genetic and life-history differences between hatchery and natural populations**: In general, larger differences between natural and hatchery populations will increase the effects of straying, but the dynamics of any particular situation can be complex. If differences between natural and hatchery populations are large, substantial reductions in productivity may occur in the short term because of outbreeding depression; however, reduced survival of strays and their hybrids may help to limit the extent of introgression into the native population. More modest genetic differences may not result in such large, short-term reductions in productivity, but persistent gene flow would probably cause the replacement of local genes with non-native ones. Genetic distances derived from molecular genetic data may not reflect adaptive differences between hatchery and natural populations. Conversely, life-history differences may be due to environmental factors as well as genetic differences.

- **Magnitude of straying and strength of selection**: The effects of these two parameters must be evaluated together. Persistent one-way straying at any level will eventually lead to the loss of selectively neutral genes in a local population. The rate of swamping of genes under selection--those that form the basis of local adaptation--depends on the magnitude of straying and the strength of selection. If the migration rate (m) is larger than the selection coefficient (s), migration will swamp local adaptations, so that even low rates of migration will eventually lead to the loss of genes with small selective advantage. Natural selection, however, is expected to maintain genes with large fitness values in a local population in spite of migration (except when population size is very small, in which case the effects of drift would dominate selection). It is not clear, however, what values of s are typical for adaptive traits. Estimates

of s are biased toward large values because the use of small sample sizes in many experiments reduces the probability of detecting small but significant values.

- **Duration of straying**: The time in generations over which a particular amount of genetic diversity will be lost can be calculated. For example, the time to a 50% loss of variability for neutral and slightly adaptive genes is 69 generations for 1% gene flow, 25 generations for 2.5% gene flow, but only 12 generations for 5% gene flow. It is important to note that, as m increases, the time to a 50% loss of diversity also decreases, and the fraction of all genes subject to replacement increases.

- **Number of natural populations affected**: Greater reductions in genetic diversity among populations occur if non-native hatchery fish stray into multiple populations rather than into a single population of a metapopulation (with natural gene flow among subpopulations). Even if strays move only into a single population, they will still influence a wide range of populations, but at a much slower rate.

Do short- and long-term effects of straying differ?

Yes. A short-term infusion of non-native alleles may lead either to heterosis (increased fitness) or to outbreeding depression (decreased fitness), or both, in local populations. Although outbreeding depression and associated reduced productivity might persist in local populations for several generations after the straying occurred, selection against deleterious non-native alleles could result in the retention of primarily local genetic information. In contrast, long-term straying will eventually replace neutral genes and those with small adaptive effects ($s < m$). In small populations, the loss of genes with greater adaptive value will be accelerated by genetic drift.

Are the effects of hatchery straying likely to be permanent?

Yes. The changes in genetic structure of local populations resulting from straying are likely to be permanent. If straying stops, local populations may recover lost fitness over time through mutation, but the original genetic composition of the population will not be restored.

Can hatchery straying be beneficial for natural populations?

Theoretically, short-term straying can be beneficial under certain circumstances. The initial introduction of non-native alleles will generally increase genetic diversity in local populations. In well-adapted populations, this may cause a loss of adaptive fitness. However, in small populations experiencing inbreeding depression, the introduction of non-native alleles may mask effects of deleterious recessive genes and act to increase fitness.

Is there any safe level of hatchery straying that is consistent with the conservation of natural populations?

There are no "safe" levels of hatchery straying. Any level of long-term straying will change the structure of local populations. For neutral genes and genes with small adaptive effects, persistent straying at any level will lead to replacement of local alleles. Local alleles with adaptive values greater than migration ($s > m$) will be maintained, but selection against maladaptive non-native alleles will lead to reductions in productivity.

Can the effects of hatchery straying be predicted with any certainty?

To the extent that straying leads to one-way gene flow, initial changes in allele frequencies are predictable, as discussed above. However, the amount of gene flow resulting from a given level of straying is seldom known, and it is likely highly variable. Moreover, the fitness consequences of altered allele frequencies depend on the adaptive differences between local and non-native populations, which are seldom known. As a result, the effects of straying on average fitness in a local population, and on the long-term ability of a population to persist, are not predictable. Experimentation and long-term monitoring may be required to determine the effects of non-native gene flow into local populations. Both increased fitness from heterosis and decreased fitness from outbreeding depression may occur. Short-term monitoring of the effects of hatchery introgression may be overly optimistic because outbreeding depression may not occur until the second and succeeding generations after hybridization.

What will occur with straying at the 5% level?

As noted in the previous question, the genetic effects of straying at any given level cannot reliably be predicted, but some of the effects of gene flow are predictable. Based on estimates of gene flow from allozyme frequencies in natural populations, a value of 5% gene flow is much higher than that generally occurring between non-local salmon populations. Also based on what is known about the strength of selection in other animals, this amount of gene flow would quickly lead to the replacement not only of neutral genes, but also of locally adapted ones. Most genes in natural populations probably have selection coefficients less than 5% and would thus be subject to loss if gene flow occurred at this level. The panel found no genetic justification for allowing gene flow from non-native fish at levels as high as 5%.

What research should be undertaken to help resolve uncertainties of hatchery straying?

The following topics were identified as particularly important for research:

- The relationship between the rate of hatchery straying and the rate at which gene flow occurs.
- The nature and extent of outbreeding depression in natural salmon populations.
- Rates of straying and gene flow among natural populations.

- Selection intensities on whole traits.
- Genetic attributes of successful populations.

Citation

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