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Assessing Extinction Risk for West Coast Salmon

Proceedings of the Workshop
November 13–15, 1996
Seattle, Washington

April 2003

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Preface

In 1994, after receiving several petitions to list West Coast salmonid (*Oncorhynchus* spp.) populations under the U.S. Endangered Species Act (ESA), the National Marine Fisheries Service (NMFS) undertook a series of coast-wide reviews of the status of seven anadromous species of salmonid: coho salmon (*O. kisutch*), chinook salmon (*O. tshawytscha*), pink salmon (*O. gorbuscha*), chum salmon (*O. keta*), sockeye salmon (*O. nerka*), steelhead trout (*O. mykiss*), and cutthroat trout (*O. clarki*).

This workshop was convened to provide NMFS with scientific expert opinion regarding the best methods for assessing the extinction risk of Pacific salmon population units for the ESA listing decisions and recovery planning. The agenda and list of panelists were assembled under the advice of a steering committee composed of Dan Goodman (Montana State University), John Emlen (National Biological Service), Mike Lynch (University of Oregon), Alex Wertheimer (NMFS Alaska Fisheries Science Center), Alec MacCall (NMFS Southwest Fisheries Science Center), and Tom Wainwright (NMFS Northwest Fisheries Science Center). The participants in this symposium were selected as having both informative and provocative viewpoints that could contribute to the improvement in the science and underlying application of the ESA to salmonid populations. The opinions expressed in the workshop proceedings are those of the individuals, and not necessarily those of NMFS.

Assessing the extinction risk of any group of organisms under the ESA requires answering two questions: 1) Is the entity in question a “species” as defined by the ESA? 2) If so, is the “species” threatened or endangered?

Fundamental Questions

The first question is one of taxonomy: is the entity a species, subspecies, or “distinct population segment” that would qualify as a “species” under the ESA. Answering that question requires examination of information regarding reproductive isolation and genetic legacy of the entity, by considering evidence regarding: 1) natural rates of straying and recolonization, 2) natural barriers to migration, 3) measurements of genetic differences among populations, 4) phenotypic and life-history traits, and 5) local adaptations and habitat structure. Due to the demographic complexity of salmonid populations, NMFS developed the concept of Evolutionarily Significant Units (ESUs) as the functional “species” unit for treatment under the ESA (NMFS 1991).

The second question considers the degree of risk facing a species or ESU. The ESA (section 3) defines the term “endangered species” as “any species which is in danger of extinction throughout all or a significant portion of its range.” The term “threatened species” is defined as “any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range.” NMFS considers a variety of information in evaluating the level of risk faced by an ESU. Important considerations include: 1) absolute

numbers of fish and their spatial and temporal distribution, 2) current abundance in relation to historical abundance and carrying capacity of the habitat, 3) trends in abundance, based on indices such as dam or redd counts or on estimates of spawner-recruit ratios, 4) natural and human-influenced factors that cause variability in survival and abundance, 5) possible threats to genetic integrity (e.g., selective fisheries and interactions between hatchery and natural fish), and 6) recent events (e.g., a drought or a change in management) that have predictable short-term consequences for abundance of the ESU. Additional risk factors, such as disease prevalence or changes in life-history traits, may also be considered in evaluating risk to populations.

According to the ESA, the determination of whether a species is threatened or endangered should be made on the basis of the best scientific information available regarding its current status. This workshop aimed at defining the best approaches and determining the most accurate information to use in answering the second question.

Issues Discussed

The Steering Committee identified a list of topics that would cover major issues. The workshop began with a series of presentations on these topics by members of a scientific panel. Each presentation was followed by a brief question/discussion period. Following these presentations, members of the audience participated in breakout-discussion groups to provide broader representation of issues and opinions. Following the public workshop, members of the scientific panel met to develop their recommendations regarding the best methods for assessing the extinction risk of Pacific salmon under the ESA. The panel attempted to address all issues discussed at the workshop.

Based on the issues identified by the steering committee, presentations were divided into several topical areas, as follows. Not all speakers submitted manuscripts for this proceedings volume, and one manuscript was published elsewhere before this volume was completed (Goodman 2002). The full agenda listing all presentations is given in Appendix 1.

- Background
  Two presentations provided an overview of key scientific issues in the ESA listing determinations and presented NMFS approaches to risk assessments under the ESA.

- Overview
  Two speakers presented contrasting reviews of factors contributing to salmon extinction risk. Topics discussed were:
  (1) What factors should be considered in evaluating risks to salmon populations and species under the ESA?
  (2) Are some factors more important than others?
  (3) Are different factors more important for different species or in different geographic areas?
  (4) Are there some factors (e.g., water regulations, habitat modifications) that might be positive for some species but negative for others, resulting in management tradeoffs?

- Ecological Issues
  Speakers in this session considered three ecological issues: 1) the role of environmental fluctuation and change, 2) population risk and habitat condition, and 3) risks and benefits of hatchery production.

- Diversity Issues
  Speakers considered issues of metapopulation structure, ecological diversity, and genetic diversity.

- Assessment Methods
  Two speakers addressed the use of quantitative modeling and the role of uncertainty in ESA risk assessments.

- Workshop Summary: Summary of Major Points Raised in Presentations and Discussions
  These presentations were followed by three breakout-group discussions allowing audience members to interact with panelists in discussing three areas: 1) habitat and environmental fluctuations; 2) genetic and ecological diversity, and hatchery issues; and 3) assessment methods.

Panel Recommendations

After the public sessions were completed, the scientific panel met to develop and present their advice to NMFS on the best approaches for ESA listing determinations. Panelists were asked to go as far as they could toward developing a framework for Pacific salmon extinction risk assessment and specific recommendations for listing and delisting criteria. Several general questions were presented for their consideration:

1) Can specific, quantitative criteria be established that indicate whether a population or ESU is presently in danger of extinction or likely to become so in the foreseeable future?
2) Can qualitative or quantitative measures be established that describe the overall degree of risk (or any particular aspect of this such as demographic or genetic risk) facing an ESU?
3) What are the best methods that can be applied to assessing the extinction risk, combining the effects of multiple factors with varying degrees of information?
4) Where should monitoring efforts be focused to best improve our ability to conduct risk assessments in the future?
5) What avenues of research or methods' development would be most productive in improving our abilities to assess the extinction risk of Pacific salmon?

A Summary of the Panel's Recommendations is included in Appendix 2. In all, over 200 people attended the workshop, providing a wide array of valuable insight during discussions. All three sections of this workshop (presentations, breakout discussions, and panel report) have contributed subsequent ESA listing and recovery deliberations within NMFS.

Acknowledgments

As with any scientific workshop, success depends upon a large cast. In addition to the Steering Committee identified above, we extend our thanks to the panelists (Pete Bisson, Gayle Brown, Bob Francis, Dan Goodman, Mike Lynch, Mark Mangel, Nate Mantua, Phil Mundy, Jay Nicholas, Brian Riddell, Stewart Schultz, and Tommy Williams) and to the workshop attendees who contributed many ideas for the panel's consideration. Recording and reporting was done by Suzanne Montgomery. This proceedings volume would have been impossible without the editorial and production assistance of Kathleen Jewett, Cheryl Read, and Cid Hughes, and the workshop would not have happened without the registration and logistics efforts of Kathleen Neely.

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Citations

National Marine Fisheries Service (NMFS). 1991. Policy of applying the definition of species under the Endangered Species Act to Pacific salmon. Federal Register [Docket No. 9120248-1255, November 20, 1991] 56(224):58612-58616.

Goodman, D. 2002. Uncertainty, risk, and decision: the PVA example. *In* J. M. Berkson, L. L. Kline, and D. J. Orth (eds.), Incorporating uncertainty into fisheries models. Am. Fish. Soc. Symp. 27:171-196.

Overview

A Review of Essential Factors for Assessing the Extinction Risk of West Coast Salmon Populations: Identifying and Defining Normative Conditions Relevant to Pacific Salmon Stock Assessment

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In order to conduct an analysis of the extinction risk of West Coast salmon (anadromous forms of *Oncorhynchus* spp.) populations which are being considered for listing under the U.S. Endangered Species Act (ESA, 16 U.S.C. §§ 1531 to 1544), it is desirable to have broad scientific agreement on the risk factors which are important to consider, and on how to apply those factors to the salmon risk assessment in consistent manner (U.S. Department of Commerce [USDOC] 1996). As recommended by a number of authorities (National Research Council [NRC] 1995), the selection of risk factors of interest in determining the risk of extirpation of West Coast salmon populations proceeded under an ecological approach which was fully inclusive of both biotic and physical factors. Published status reviews of anadromous salmonids and other authorities were consulted to identify risk factors (Table 1). To identify and establish the relative importance of factors, a primary screening criterion of demonstrated ability to impact the rate of change in population size was adopted. The screening criterion was employed in a manner designed to provide an inclusive menu of ecologically important factors from which the reader could draw combinations relevant to specific localities and salmon life-history types. Factors so selected are organized into two classes, endogenous and exogenous, which separate factors with regard to their mode of action on the individual member of the salmon population.

In populations, the extinction risk, or extirpation, is determined by a multiplicity of factors which are capable of producing changes in the average, and in the variance, of the time rate of change in living biomass. Under extinction by trend, when the rate of change in biomass is negative, the probability of extirpation becomes an increasing function of time until such time as the rate of change becomes non-negative. Under hypothetical equilibrium conditions, there may be no extinction risk, if the level of biomass is high enough that random fluctuations cannot extinguish the population. At equilibrium, the rate of change in biomass would alternate signs frequently, the population biomass would oscillate about some constant level, and the long-term average rate of change in biomass would be zero. On the other hand, under extinction by trend, when the biomass of a population is in a steady decline, the longer the rate of change remains negative, and the closer the biomass comes to zero, the more certain extinction becomes. When circumstances are such that the population cannot achieve positive growth rate, extinction is

Table 1. Factors identified by other authorities to be considered in assessing the extinction risk of salmon populations.

	Factors
1.	(Thompson 1991) In the review of models, the risk factors are endogenous population attributes. Exogenous risk factors are not treated explicitly as parameters to be estimated. Exogenous factors are lumped into stochastic elements, expressed as variability in population size through time.
2.	(Waples et al. 1991a) Made determination based on trend in abundance and present abundance.
3.	(Waples et al. 1991b) Risk factors cited are reduction in geographic distribution, alteration and reduction of spawning habitat, decline in abundance, low abundance, but no threshold established, potential threat to genetic integrity from straying of hatchery fish onto wild spawning areas. Introduces the six general risk factors to be considered in status reviews, pending availability of information: 1) absolute numbers and their spatial and temporal distribution, 2) current abundance in relation to historical abundance and carrying capacity of the habitat, 3) trends in abundance, based on indices or dam or redd counts or on estimates of spawner-recruit ratios, 4) natural and human-influenced factors that cause variability in survival and abundance, 5) possible threats to the genetic integrity such as selective fisheries and interactions between hatchery and wild fish, and 6) recent events that have predictable short-term consequences for abundance of the ESU such as changes in management or drought. In addition, risk factors are also disease prevalence, and changes in life history traits. Future effects of conservation measures were not considered and a steady state was assumed.
4.	(Matthews and Waples 1991) Risk factors considered were historical, current, and projected abundance, trends in abundance, and the geographic distribution and migratory timing. Trends in salmon abundance were analyzed using the Dennis model to compute the probability that the 5-year running sums of redd counts would fall below a fixed number of redds (15,474 threatened, 7,065 endangered) within a time period of 100 years.
5.	(Johnson et al. 1991) Risk factors identified are intense human perturbation of freshwater habitats, particularly spawning habitats, and commercial exploitation responsible for reducing numbers to near extinction of native runs in combination with habitat degradation. There was drastic reduction in geographic range, hatchery swamping of decimated native runs, continuing over harvest of native runs, blockage of habitat. (No ESU was discovered so there is no listing.)
6.	(Busby et al. 1993) Risk factors identified decline in apparent abundance to very low levels, and declining trends in abundance of sports catches. Efforts were refocused on finding the ESU. None was found so there was no listing.
7.	(Johnson et al. 1994) A wide variety of risk factors was considered, including alteration of temperature regimes, hatchery releases and supplementation, however the only conclusive evidence of risk was found to be time trends in abundance.

Table 1. Factors identified by other authorities to be considered in assessing the extinction risk of salmon populations. Continued.

	Factors
8.	(Busby et al. 1994) Risk factors evaluated are population trends, reductions in available habitat (dams, logging, mining), hatchery swamping or replacement. ESU was identified but no listing.
9.	(National Research Council [NRC] 1995) Sources of risk are habitat loss, effects of introduced species, and overharvesting. Low population numbers puts populations at risk. Risk factors identified are random changes in demographics (age structure, sex composition, vital statistics) and environmental fluctuations, catastrophes (natural disaster), accumulation of deleterious genetic factors on reduction of low population size, loss of adaptive variation within the population, habitat fragmentation, supplementation (by which is meant hatchery swamping, not support of natural populations by artificial means).
10.	(Waples 1995) Risk factors explicitly defined were: 1) loss of evolutionary legacy: loss of genetic variability which represent the reservoir for future evolutionary potential, 2) loss of genetic building blocks to preserve representative collection of components for future evolution, and 3) loss of ecological diversity. This also cites the risk factors in earlier status reviews (Waples et al. 1991b).
11.	(Waknitz et al. 1995) Risk factors considered were dam and redd count-based abundance and trends in abundance. Habitat alterations were part of the preliminary considerations of risk.
12.	(Weitkamp et al. 1995) Factors considered were habitat loss, adverse ocean conditions, hatchery practices, and harvest.
13.	(Hard et al. 1996) Risk factors listed by petitioners were habitat alterations in the form of water withdrawals during spawning times, habitat degradation as diking and sewage releases, timber harvest, hatchery releases of potentially predatory coho salmon, and mixed-stock harvests. Risk factors mentioned were present abundance, historical abundance and carrying capacity, trends in abundance, climate trends, and threats to genetic integrity from hatchery fish. Reliance on population trends from Nehlsen et al. (1991). Data evaluations of risk factors were current and historical abundance, trends in escapement, proportion of spawners due to hatcheries, geometric mean of the 5 most recent years for run size and escapement, estimated abundance, not indices. Average percent annual change in escapement regressed against year. Risk of artificial production was considered less a problem than habitat degradation. A major risk factor driving the conclusions was a trend in abundance of spawners.

Table 1. Factors identified by other authorities to be considered in assessing the extinction risk of salmon populations. Continued.

	Factors
14.	(Busby et al. 1996) Risk factors mentioned were present abundance, historical abundance and carrying capacity, trends in abundance, climate trends, and threats to genetic integrity from hatchery fish. Blockages to habitat by locality as risk factors were identified. In some cases, there were references to changes in temperature regimes. On the Oregon coast, risk of habitat blockages and shifts in temperature regimes were identified. Workhorse risk factors were trends in abundance, reduction in geographic range, degradation of habitat, introgression of hatchery fish, and present abundance (recent 5-year geometric mean).
15.	(Slaney et al. 1996) Risk factors identified are anthropogenetic habitat destruction, overutilization, disease, hatchery introgression, exotic-species interactions, and natural disasters.
16.	(Baker et al. 1996) Factors causing declines were: habitat degradation, overfishing, disease, hatchery introgression, and natural disasters. Loss of habitat for spawning and rearing due to development and logging are risk factors. Overfishing was also a factor in mixed-stock situations where enumeration of individual stocks is not feasible.

inevitable (NRC 1995). But biomass and its rate of change, as functions of time, are only crude indicators of population status, and they may be only two variables among the many which may be considered in assessing the extinction risk. Nonetheless, the criterion of the ability of a factor to control population size has been applied to identify factors of interest in determining the risk of extirpation for a population.

Among anadromous salmon populations (*Oncorhynchus* spp.) along the West Coast of North America, as in all animal populations, the rate of change in biomass is determined by the relation of births to deaths over some arbitrary time period. Note, that growth and reproduction are chosen as criteria to identify endogenous risk factors because they are explicitly related to survival for a great many fish species (Jensen 1996). Since any factor, which either decreases the birth rate or increases the death rate, is potentially of interest in determining the risk of extirpation for a salmon population, an examination and discussion of these factors is necessary for effective salmon stock assessment under the ESA. To remain effective in the face of changing environments, any salmon stock assessment requires knowledge of a suite of such critical factors, since it may not be feasible to measure all factors in every salmon-bearing locality, and since the length of time for which any given observation has been recorded may vary. In addition, identifying a suite of critical factors is desirable because no single factor can be expected to reliably serve stock assessment over all geographic ranges and time frames of interest.

The suite of factors which needs to be considered when assessing the extinction risk of West Coast salmon populations are those which define the terms on which the individual animal is allowed to exist. The terms of this ecological contract for survival fall into two categories: endogenous and exogenous. The endogenous ecological characteristics which determine the risk of extirpation of a West Coast salmon population are necessarily genetically based, phenotypic attributes of the animal that have been determined by the process of natural selection. The exogenous terms of the survival contract are the geophysical and biological forces with which the genome interacts to produce the endogenous characteristics, and the time series of annual population abundance is the resultant of the vectors formed by the interaction of exogenous and endogenous factors.

Exogenous Factors Defined

Exogenous factors determine the probability of loss for a salmon population through their control of the endogenous physiological functions of the individual salmon. The search for the relations between exogenous environmental factors, such as water movement, and the adaptive fish behaviors with which they interact to influence survival, is key to understanding the range of physical conditions which allows fish species to persist at any point in space and time. The suite of exogenous factors which directs the evolution of the species, and which defines the suite of adaptive traits (endogenous factors) which permit the species to cope with its environment, are called normative conditions. Within the bounds of normative conditions the species can express its full range of life-history diversity, occupying the environment to maximum advantage in sustaining the viabilities of its populations.

As watersheds are altered by impoundment and other aspects of human development, the suite of environmental conditions with which the species must cope in order to persist may change. Should the alterations move the exogenous conditions outside the normative, it is axiomatic that population viabilities decline as the extinction risk increases. Within some arbitrary time period, the number of extirpations of salmon populations should be proportional to the degree to which exogenous conditions coincide with the normative. In order to understand the role of changing environment in the viability of local populations of a species, it is essential to define the envelope of exogenous factors within which the extinction risk would be on the order of zero for an arbitrarily long period of time, all other factors being neutral.

As is the case with protection of a component of any aquatic ecosystem, any identification and assessment of the relative importance of factors bearing on the extinction risk of salmon populations needs to proceed with a conceptual foundation, which is appropriate to the community level of ecological organization (Tonn et al.1983). Resource management decisions made on the basis of measures of the population dynamics of a single life-history type of a single species are unlikely to address the principal sources of extinction risk which are habitat loss, effects of introduced species, and overharvest (NRC 1995). A survey of approaches available to the analysis of fish communities, for the purposes of identifying risk factors, reveals a large body of information which is currently not being used in Pacific salmon recovery measures. Approaches for the identification of exogenous risk factors generally link biological production or productivity, as measured by individual fish species or by groups of aquatic species, to the geophysical and geochemical processes which pertain to reproduction and survival.

Endogenous Factors Defined

The extent to which the quantitative and qualitative phenotypic characters of population are appropriate to the exogenous circumstances, within the range of the population, is a factor relevant to the extinction risk. In theory, the coevolution of a suite of adaptive characters is expressed as a distribution of phenotypes which provides the maximum average survival for some suite of endogenous characteristics (NRC 1995). The tails of the distribution of phenotypes provide the responses to shifts in exogenous factors. Presumably, the coadapted gene complexes, which produce the suite of endogenous factors, are selected for their ability to produce the distribution of phenotypic traits and behaviors which maximize survival.

The best understood endogenous factors which bear directly on reproduction and survival are size-at-age, fecundity and egg size, age composition, ontogenetic patterns in rheotropism, timing and geographic patterns of migrations, and disease resistance. The genetic basis of these adaptive endogenous factors has been confirmed for a wide variety of species and life-history types of anadromous salmon.

Interactions Between Endogenous and Exogenous Factors

The extent to which the endogenous properties of a salmon population may modify exogenous factors, which are important determinants of reproductive success and survival, forms

the basis for a control feedback process with consequences for the assessment of the extinction risk. Salmon populations are essential constituents of the biogeochemical cycle, and nutrient feedback from adults to their offspring can be an important factor in salmon population dynamics (Mathisen 1972). The chemical elements essential to terrestrial ecosystem function which are removed by erosion during runoff, and through emigration of anadromous, and to a lesser extent, catadromous species, are returned to the terrestrial ecosystems (Kline et al. 1990). Salmon populations are the transport mechanisms whereby marine carbon and nitrogen reach terrestrial ecosystems, and substantial portions of the food webs in salmon spawning areas are supported by materials from the decomposing carcasses.

Discussion of Exogenous Factors

Exogenous factors: Climate

Reproduction and death in salmon are functions of many exogenous factors which are ultimately dependent on climate, as the proximate agent of geophysical action on salmon. Adverse ocean conditions have been identified by the National Marine Fisheries Service (NMFS) as a principal threat to coastal coho salmon (USDOC 1996). Critical exogenous factors have been described in physical, chemical and biological terms. The interrelated annual-temporal patterns of temperature and runoff, to which natural selection has shaped the timing of salmon migrations (Quinn and Adams 1996) are critically important functions of climate, among other factors.

As the ultimate arbiter of the geographic extent and function of the ecosystem (Cushing 1982), climate is a factor important to assessing the extinction risk of West Coast salmon populations (Beamish and Bouillon 1993, Francis and Hare 1994, Williams et al. 1998). Climate impacts individual survival and reproduction in a salmon by its interaction with every component of the ecosystem. By determining the timing and location of nutrient transport, climate influences growth rates and survival by determining how much, and what, the salmon may find to eat. Climate also directly impacts reproductive success by controlling both the amounts, and the physical and chemical qualities, of the water over the spawning beds. Through its influence on temperature, climate determines the geographic distributions of salmon populations and all the populations of other species with which salmon interact. As the ultimate arbiter of the location and functioning of the ecosystem, climate is a factor important to assessing the extinction risk of West Coast salmon populations.

Exogenous factors: Anthropogenesis

Salmon populations have evolved in a freshwater environment of lotic waters, but today the assessment of the extinction risk of salmon populations must contend with the anthropogenic effects of impoundment (Raymond 1979). Risk assessment for salmon populations must address the extent to which water movement may be necessary for the persistence of the species. Consequently, the answer to the question of the extent to which the success of reproduction and

survival of a salmon population may be associated with water movement is fundamental to establishing its extinction risk.

Anthropogenic effects are the results of impoundment, agriculture, logging, and development, associated with human population growth such as road building. Negative effects on the ecological carrying capacity of salmonids in portions of the Columbia River Basin have been extensive (Bisson 1996). Alteration of the natural annual runoff patterns have degraded water quantity and quality with respect to salmon populations. Loss of seasonally flooded habitat has had serious consequences for production of salmonids (Bisson 1996). Input of sediment and removal of large woody debris are but two of the anthropogenic effects which have reduced salmon's ability to reproduce and to survive as juveniles.

Anthropogenic shifts in aquatic temperature regimes are factors of interest in assessing the extinction risk of salmon populations. A recent bibliography documents the extensive scientific basis of the effects of elevated temperature on growth, reproduction and survival in salmon populations (McCullough 1993). The insidious and potentially far-reaching effects of temperature on salmon are evident in research which indicates that temperature-dependent sex determination occurs in sockeye salmon, and that it could occur in all salmon species (Craig et al. 1996). Adult salmon have a limited ability to alter their migratory timings in response to environmental factors due to their semelparous nature (Mundy 1982, Quinn and Adams 1996). Therefore, unfavorable environmental alterations in the adult migratory corridor are factors to be considered in assessing the extinction risk of salmon populations. Potentially lethal temperatures are encountered by endangered chinook salmon and sockeye salmon species during spawning migrations in the Columbia and Snake Rivers. Water temperatures in the Snake River exceeded the threshold at which prolonged exposure could be lethal (20ºC) during the latter part of July, August, and early September, 1991. A hiatus was noted in the fall chinook salmon spawning migration into the Snake River. The hiatus was attributed to the high temperatures in the Snake River in 1991 (Bjornn et al. 1992). Endangered fall chinook salmon species attempting to pass the fish ways at John Day in 1995 were subjected to potentially lethal water temperatures for the majority of their migratory period (Dalen et al. 1996). Water temperatures in the fishways of three lower Columbia River dams reached or exceeded 21.1ºC (70.0ºF) at Bonneville Dam for 7 days (August 1-August 7, 1991), at The Dalles Dam for 16 days (July 27–August 11, 1991), and at the John Day Dam (July 25–September 23, 1991). High water temperatures in the fishways at these localities are known to occur in late afternoons, and at all times in the late summer (Dalen et al. 1996).

Exogenous factors: Habitat dependency measures

The degree to which the needs of the salmon population for habitat is met at any locality for any life-history stage, is a factor important to the assessment of the extinction risk. A number of quantitative and qualitative methods which link changes in attributes of habitat, which are critical to reproduction and survival of fishes (including salmon), are available for consideration in computation of the extinction risk. In general form, the habitat-dependency methods attempt to define the proportion of the population dependent upon various habitat attributes, or on indices of habitat attributes.

The scientific basis for predicting associations between habitat type and the nature of plant and animal assemblages is extensive. A very old and rich literature of the aquatic organisms of running waters describes the longitudinal succession of plant and animal species assemblages encountered in moving through a watershed from its headwaters to the estuary (Hynes 1970). Measures of the distribution of biomass among species in ecological communities and species diversity indices (Pielou 1966), have been used for some time to characterize temporal variability in response to natural seasonal changes in habitat for fish species assemblages, both marine (Dahlberg and Odum 1970) and freshwater (Harima and Mundy 1974). A measure of longitudinal succession, the variation in fish species assemblages as a function of stream size, has been used to predict changes in species in fish species composition as a function of habitat alteration (Mundy and Boschung 1981).

Individual measures of fish assemblages and indexes of habitat quality have been combined into two lines of research which attempt to match the suitability of available habitat to the optimum habitat requirements of individual species. These are the instream flow incremental methodology (IFIM), and the habitat suitability index (HSI), (Pajak and Neves 1987). It is interesting to note that recommendations on fish-production estimation methodology for a non-salmonid species from an HSI study on small streams in Virginia (Pajak and Neves 1987), are very similar in concept to methodologies recently proposed for salmon in the Columbia River Basin (Lestelle et al. 1996). The 1987 Virginia study recommended improving fish-production estimation by including in the study area stream sections (called bands in the 1996 study) throughout the home range of the species; or the inclusion of the annual habitat requirements of all life stages of the target species. This is a fundamental concept of the 1996 study. The 1996 study (Lestelle et al. 1996) is discussed later in this document.

An example of a habitat-dependency measure, which is the method of weighted usable area (WUA; Glova and Duncan 1985), defines the amount of usable habitat in a river for juvenile chinook salmon, adult chinook salmon, and other life-cycle stages of other fish species, based on measures of association between fish and average water velocities, depths, and substrate size expressed as habitat-suitability curves. Changes in the WUA as a function of water discharge (m^3s^{-1}) and the closely related variable, river channel width (m), can be used to illustrate the importance of discharge to different life-cycle stages of chinook salmon in maintaining diversity in channel form and flow. Levels of discharges which maintain the diversity in channel form and flow provided more WUA for chinook salmon and other species. At low discharge levels, an overall decrease in WUA was attributed to complete loss of the habitats associated with small channels (Glova and Duncan 1985).

The index of biotic integrity (IBI) is designed to evaluate the state of an aquatic resource based on the attributes of indigenous fish communities (Karr 1981). Three categories of fish community attributes are the species composition, trophic composition, and health and abundance of fish. The scores of these attributes reflect the condition of the fish community in relation to an ideal undisturbed situation. The IBI reflects the hypothesis that key attributes of the fish community change in proportion to degradation of habitat.

Even though the IBI was developed for low gradient, warm-water streams in agricultural areas, it has been successfully applied to small, mountain cool-water streams (Leonard and Orth

1986). In the cool-water stream application, a modified IBI, based on six fish-community attributes was consistent with independent rankings of stream degradation. The six critical exogenous attributes identified by Leonard and Orth (1986) are representative of those which may be important to the assessment of the extinction risk in salmon. These are: 1) total number of species, 2) proportion of individuals as creek chubs, 3) species richness, 4) composition of darters, 5) number of fish in sample, and 6) proportion of fish with disease or anomalies. With substitutions for the ecological equivalents of creek chubs and darters, the IBI may be applicable for assessing the extinction risk of salmon. An IBI as applied to small streams was found to vary spatially and temporally in conjunction with known water quality (Karr et al. 1987). None of the individual components of the IBI, such as the species diversity index, performed as consistently at ranking sites with respect to habitat quality as did the IBI. The IBI was found to reflect known habitat and water quality perturbations of both natural and anthropogenic origin over time and at a variety of locations (Karr et al. 1987).

Mathematical techniques which may quantify factors important to the assessment of the extinction risk have been developed by U.S. government scientists from agencies associated with salmon management and recovery. Models of habitat dependency for salmonids have been developed which describe freshwater salmon production as a function of habitat attributes (Murphy et al. 1990). Other relevant U.S. government models have been developed to help understand the risks posed to salmon production by government forest-management practices (Murphy 1995).

Another class of habitat-dependency measures currently being developed specifically for salmon in damaged habitats are the patient-template analysis (PTA) (Lichatowich et al. 1995), and the closely related ecosystem diagnosis and treatment method (EDT) (Lestelle et al. 1996). Both PTA and EDT are conceptually closely similar to HSI, WUA and IBI, in that they link attributes of the aquatic organisms of interest to the productive capacities of a series of critical habitats, called life-history trajectories (Lestelle et al. 1996). EDT is more narrowly focused on the indicator organism than is IBI, being based on the classic assumption that populations which are dependent on the stability of ecological processes over a large portion of a watershed can be used to help diagnose conditions for sustainability (Lestelle et al. 1996). PTA, like HSI and WUA, evaluates productive capacity of habitats for a life-history type of a species by comparing the habitat conditions presently available to support production to an optimum or historical set of habitat conditions.

A note of caution is in order for all indicator species habitat-dependency measures. Although PTA and EDT reduce the carrying-capacity problem to small dimensions of individual habitat bands and collections of life-cycle stages, EDT, in particular, is heavily dependent on the measures of habitat capacity of the individual habitat bands. Unless the habitat-capacity estimates explicitly incorporate understandings of how exogenous factors act on endogenous factors to affect reproduction and survival, the associated estimates of salmon performance and cumulative carrying capacity indices will be retrospective quantities, not prospective quantities.

As recognized by the authors of PTA and EDT, habitat-dependency measures need to be combined with understandings of interactions between exogenous and endogenous factors. A panel of scientists, convened to consider the issue of estimating salmon carrying capacities,

concluded that the approach of identifying factors limiting survival of salmon, in order to quantify the number of salmon which the environment can support, is an oversimplification of complex ecological processes (Neitzel and Johnson 1996). The panel of scientists went on to conclude that to pursue a single number or set of numbers that quantify how many salmon can be supported will not provide useful information, and that an understanding of the relations among factors that affect salmon performance in a serial fashion throughout the life cycle of the individual is needed. The panel recommended that the region approach the estimation of carrying capacity from a number of different scientific perspectives (Neitzel and Johnson 1996).

A specialized form of habitat-dependency measures of interest to the assessment of the extinction risk of sockeye salmon is the productive capacity of the nursery-lake rearing environment. Reductions in lake rearing capacity were directly proportional to losses of production in Columbia River sockeye salmon (Fryer 1995). Models of sockeye salmon escapements needed to maximize production, based on photosynthetic rates (euphotic volume), produced accurate production predictions and required only two years of data to make the predictions (Hume et al. 1996). This method shows promise for models which project the distribution of times to the extinction risk of sockeye salmon. Given the recent work on the trophic basis for stream production of salmonids (Bilby et al. 1996), it is reasonable to speculate that a similar approach for stream-rearing species such as coho salmon, steelhead, cutthroat, and chinook salmon might be worth trying.

Exogenous factors: Mixed stock harvest and bycatch

The extent to which all salmon life-history stages may be caught (not necessarily landed) in directed mixed-stock salmon fisheries is important in assessing the extinction risk of a salmon population. The risk posed to salmon populations by mixed-stock fisheries has long been understood. The understanding was that different management strategies, which result in similar sustained yields, could have markedly different effects on the relative abundance of the individual salmon populations which were harvested in the fishery (Paulik et al. 1967). In a mixed-stock harvest situation, the desirability of preserving enough genetic diversity to allow populations to respond to environmental change within a salmon run might be important enough as a management objective to rule out the application of those strategies which over-exploit small stocks to the level of extinction (Paulik et al. 1967).

The bycatch problem is potentially a serious factor of concern in the assessment of the extinction risk of a salmon population (Williams et al. 1998). Since bycatch is not landed to be sampled, the knowledge of stock composition in bycatch may be lacking or incomplete. The risk of bycatch to a salmon population would increase in proportion to the number and the magnitude of the catches in the intercepting fisheries.

Exogenous factors: Biogeochemical cycle

A very large body of evidence indicates that salmon populations are important constituents of the biogeochemical cycle, functioning as important conduits carrying the

chemical resources of the North Pacific Ocean to the terrestrial salmon-bearing ecosystems. The presence and duration of the organic matter contained in spawned-out salmon carcasses in the fresh and marine waters has been understood for over a quarter of a century (Brickell and Goering 1970). Studies (in Little Port Walter estuary, Alaska, and in its rapidly flushing tributary, Sashin Creek) of the chemical fate of pink salmon and chum salmon carcasses showed that decomposition had substantial effects on freshwater and marine chemistry for periods exceeding 6 weeks. Ammonium and dissolved organic nitrogen (N) were 5 to 10 times higher in the salmon-bearing portion of the stream than in the inaccessible control portion of the stream for up to 6 weeks during the spawning time. Similar temporal patterns in dissolved organic nitrogen were seen in the receiving estuary (Brickell and Goering 1970).

Subsequent studies in the same locality (Sashin Creek, Alaska), using stable isotope methods, found that marine-derived nitrogen (MDN) is the predominant source of N for food webs found in the lower 1,200 m of the stream where salmon spawn (Kline et al. 1990). Outside the zone of salmon spawning, in the lake above a barrier waterfall in the creek, respired carbon (measured as the isotope ^{13}C) is very important. The source of C in the remainder of the stream is C fixation by autochthonous producers and marine organic C within the salmon-spawning section. Resident fishes in the salmon-spawning section depend on marine-derived nitrogen and some of the C delivered by the annual run of returning salmon (Kline et al. 1990).

The feedback loop between the nutrients contained in adult carcasses and the chemical constituents of their offspring has been substantiated in enough cases to make it a strongly tenable hypothesis. Biota in Iliamna Lake, Alaska, had higher ^{15}N compared with control lakes, verifying a mixing model correlating ^{15}N with marine-derived nitrogen (Kline Jr. et al. 1993). Periphyton ^{15}N reflected localized input from salmon-spawning populations. Juvenile sockeye salmon had relative levels of MDN which corresponded to escapement size, suggesting the importance of large escapements (>10 million) for maintaining a predominantly MDN lacustrine N pool. Resident species, other than juvenile sockeye salmon, showed shifts in MDN between years of high and low escapements. Dual-isotope approach ^{15}N and ^{13}C showed that fish production is primarily dependent on the limnetic primary and secondary productivities. The coast range sculpin was shown by ^{15}N and ^{13}C levels to have a diet consisting heavily of salmon eggs and fry.

The role of marine enrichment in freshwater growth and productivity is not limited to the pink salmon and sockeye salmon. In coho salmon-bearing streams of western Washington State, aquatic invertebrates and juvenile coho salmon and riparian vegetation were substantially enriched by marine nitrogen from adult coho salmon carcasses (Bilby et al. 1996). Growth of age-0 coho salmon was doubled following spawning in late fall, but the highest level of enrichment of the stream biota, with the marine isotopes, came in the spring during carcass decomposition. Interestingly, uptake by primary producers was not an important avenue of incorporation of marine carbon and nitrogen. Therefore, the loss of marine enrichment due to declines in salmon abundance could have devastating effects on the productivities and structure of freshwater food webs. Loss of marine enrichment is likely to be an important factor in assessing risk of extirpation of salmon.

Exogenous factors: Spawning substrates

Loss of spawning substrate due to the loss of normal sediment transport and river renewal (Ward and Stanford 1995) and the effects of accelerated erosion and siltation of stream beds, is a factor to be considered in assessing the extinction risk of salmon populations. Although the relations between salmon survivals and spawning substrates depend on the velocity and on the depth of spawning, and the nature of the flow and fine sediments, it is well established that survival of salmon embryos regresses positively on mean particle diameter, fredle index (an index of gravel quality), permeability, and dissolved oxygen. The geometric structure of the redd can mitigate the effects of fine sediments on survival of developing embryos because it permits formation of a seal which blocks out fine sediment through accretion of small gravels (Chapman 1988). The formation of the silt-excluding cap depends on the Froud number which is a function of the square of water velocity, gravity and the depth of redd. Under high and turbulent flows, the silt cap has trouble forming, and siltation becomes a higher risk to embryo survival (Chapman 1988).

Exogenous factors: Connecting the patches

Fragmentation of habitat is an important factor in establishing the extinction risk of salmon populations for two reasons. First of all, local salmon populations may impact reproduction of other local salmon populations by providing spawners (Quinn 1984). The reproductive links among local salmon populations are evolutionarily important to survival of the species (Quinn 1984). The organization of salmon spawning aggregates into metapopulations means that the extinction risk of any one local population should be defined in terms of its degree of connectivity to other local populations (Mundy et al. 1995). In modeling studies conducted under assumptions realistic for salmon populations, patches of animals which were both subject to environmental degradation and complete reproductive isolation, from other patches, had a higher probability of extinction (became extinct much faster on average), than patches under the same environmental degradation which were allowed low levels of reproductive input from other patches (dispersal, or straying) (Berkson 1996). Secondly, fragmentation of habitat is an important factor in establishing the extinction risk of salmon populations. For salmon, as anadromous species, the connections between patches of spawners are themselves vitally important patches for other life-history types of the same and other salmon species (Lestelle et al. 1996, ISG 1996).

Given that the goal of metapopulation recovery for wildlife, including salmon, is to establish landscapes in which populations can survive and prosper by themselves (McCullough 1996), the probability of the extinction risk of a salmon population is a function of the degree to which the landscape is connected. Corridors suitable for salmon may also be suitable for other wildlife such as birds, making the probability of extinction, of even terrestrial species, covariates of the probability of salmon extinction. For example, buffers of vegetation, left along riparian zones after clear cutting, functioned to permit dispersal of juvenile birds (Machtans et al. 1996). As also noted in the bird study, the geographic scale of the corridors and patches is an important risk factor for salmon populations, since scale factors shift ecological balances as the landscape is fragmented into smaller patches (McCullough 1996). Additionally, patches altered by humans to

be suitable to one salmon life-cycle stage, or to one life-history type of a species, may be a disadvantage for other life-cycle stages or species which function on different-sized geographic ranges, or in patches of differing characteristics under anthropogenic control. For example, reducing the risk of the migratory corridor for yearling emigrant chinook salmon and steelhead, by regulating water flows upward, may in some circumstances increase the risk of loss at the same locality for subyearling chinook salmon, coho salmon, and steelhead, which use the margins of the corridor for rearing and feeding (Williams et al. 1998).

Discussion of Endogenous Factors

Endogenous factors: Threats to genetic integrity through loss of inherent vulnerability to disease

Genetically determined characteristics which confer adaptive advantage on the salmon population are factors to be considered in determining the extinction risk. An innate character of salmon populations, which is subject to natural selection, is disease resistance. Steelhead, chinook salmon, cutthroat, coho salmon, and other salmonid species are known to have a susceptibility to the mxyosporidean parasite, *Ceratomyxis shasta*. However, the actual vulnerability had been observed in some species to vary geographically, according to whether the parasite was endemic or not (Buchanan and Sanders 1983). The hypothesis that resistance to *C. shasta* is the result of natural selection was tested using three Oregon coho salmon populations known to have differing degrees of susceptibility. When coho salmon offspring from all possible crosses of the three stocks of varying susceptibility were exposed to *Ceratomyxishasta* in Willamette River water, susceptibility of crossbred individuals was intermediate to that of the original stocks (Hemmingsen et al. 1986). The hypothesis that resistance to *C. shasta* observed in some salmon and steelhead trout stocks has a genetic basis resulting from selective pressure, was validated.

Endogenous factors: Threats to genetic integrity through loss of inherent adaptive behavior

Behavior, and especially the serial ontogeny of adaptive behaviors, is a key factor in determining the survival of a migratory species which occupies a series of habitats during its life cycle. Inherent adaptive behaviors are genetically determined characteristics, which confer adaptive advantage on the salmon population, and, as such, they are factors to be considered in determining the extinction risk.

Juvenile coho salmon display a variety of life-history strategies over a fairly wide range of stream habitats which involve territoriality (Sandercock 1991). The territorial mechanisms were hypothesized to function as specific, local adaptations which provided for dispersal, prevention of contagion and parasitism, reduction of predation, and partitioning of food supply (Chapman 1966). Experimental evidence is consistent with the hypothesis that territorial behavior in juvenile coho salmon has a genetic basis which natural selection shapes into agonistic behavior suitable to the availability of food (Roseneau 1987).

Migratory timing is a genetically inherited, environmentally mediated, adaptive response which is key to the survival of both juvenile (Northcote 1984) and adult (Brannon 1984, Quinn and Adams 1996) salmon. A striking demonstration of the genetic basis for adaptive migratory behavior is available for early post-emergent sockeye salmon fry (Brannon 1967). In most local populations of sockeye salmon, the fry need to reach a lake to start feeding soon after emerging from the gravel. Sockeye salmon fry from populations spawning in lake outlets swam into the current, fry deposited from lake inlet spawners swam with the current, and fry crossbred from the two populations showed both kinds of rheotropism (Brannon 1967).

Endogenous factors: Threats to genetic integrity through loss of inherent adaptive morphological traits

Morphological traits such as size-at-age are genetically determined characteristics which confer adaptive advantage on the salmon population. Morphological traits are factors to be considered in determining the extinction risk. The size of the spawner is a genetically heritable trait which is adaptive for stream size in pink salmon and chum salmon (Beacham and Murray 1987, Beacham et al. 1988, Smoker et al. 1994). Given the importance of the geometry of salmon redd construction to the survival of salmon embryos (Chapman 1988), and given the tendency of spawning substrate to vary with the size of the river (Beacham et al. 1988), and given the territorial defense of spawning areas by males in some species (Burgner 1991), it is probable that selection for body size is quite heavy in some salmon populations. Depth of egg deposition is heavily dependent on body size of the female spawner. The ability to resist the mortalities associated with scouring floods of the spawning grounds is dependent on depth of egg deposition in coho salmon (Sandercock 1991).

Endogenous factors: Threats to genetic integrity through loss of inherent reproductive potential and egg size

The influence of the number of eggs per female on reproduction and population mortality schedules is profound. The number of eggs per female, and the reproductive potential (or fecundity) of a salmon population is an endogenous characteristic which adapts a salmon population to a particular life-history strategy. As a general rule, it is recognized that fecundity in salmon is a function of the length of the freshwater residency, an adaptive trait of evolutionary significance (Semko 1954a. in Burgner 1991). Ultimately, the number of eggs per female must be linked to the average total mortality that the population is adapted to withstand. Since, at theoretical equilibrium levels for population numbers (assuming a sex ratio of 1:1), each female must replace herself and her mate. For the semelparous salmon, in a theoretical population with a stable age distribution, the average total mortality needed to avoid declines in population size is a function of fecundity. Let

$2 = N(t)$ be the number needed for replacement at the end of one generation,
t be one generation unit, and
$N(0)$ be the average number of successfully deposited fertilized eggs per female, as the average over all reproductive age classes.

Then,

$$N(t)/N(0) = (-Zt) \ ,$$
$$\exp(-Z) = 2/N(0) \ \text{, and}$$
$$Z = \ln N(0) - \ln 2 \ .$$

Thus $Z[N(0)]$, the total instantaneous mortality as a function of average fecundity, is the maximum average total mortality for which the probability of extinction is nominally non-zero. For all $Z > Z[N(0)]$ the probability of extirpation is an increasing function of time. As long as $Z > Z[N(0)]$ the length of time to extirpation is a function of the magnitude Z and the initial number of spawners in the population.

The size of the egg is also a potentially important adaptive trait in at least some salmon species, which is linked to fecundity. Egg size has a bearing on how much yolk is available to the developing embryo, which is hypothesized to be of adaptive significance due to its influence on the time of emergence of fry in chum salmon (Beacham and Murray1987), although no such relation was found for pink salmon (Beacham et al.1988). Within a salmon population, the size of the egg is inversely proportional to the number of eggs per female. It has been suggested that for each combination of exogenous factors there is an optimum combination of egg size and fecundity (Rounsefell in Burgner 1991). The point of balance occurs where the survivals permitted by exogenous factors, favorable to rapid development and survival of the embryo, balance mortalities inflicted by exogenous factors, limiting survival of later life-history stages.

Endogenous factors: Threats to genetic integrity through loss of inherent life-history diversities

Life-history diversities, and genetically determined characteristics, which confer adaptive advantage on the salmon populations, are factors to be considered in determining the extinction risk. Loss of big-river habitats for spawning and rearing threatens the fall chinook salmon in the Columbia River Basin (ISG 1996). Mitigative measures, such as juvenile fish transportation and mechanical turbine-intake bypasses (submerged fixed and traveling screens) which discriminate against certain life-history types while providing benefits to other life-history types, apply selective pressure against life-history diversity. Transportation of juveniles and mechanical bypass are factors contributing to the risk of loss in fall chinook salmon and sockeye salmon in the Snake River basin (Mundy et al. 1994, ISG 1996) .

Endogenous factors: Abundance and age structured abundance

Abundance, the time series of age-structured abundance, and abundance by year of spawning, or stock and recruitment, are not, strictly speaking, endogenous factors in their own right. These measures bear discussion because they are the salmon population attributes most commonly employed in the assessment of extinction risk (NRC 1995). Unfortunately, trends in population abundance have not been consistently applied to assess the extinction risk of West Coast salmon populations by published authorities, so conflicting information on population

status exists in the literature (NRC 1995). Often, the definition of stock or population is inconsistent among authorities, making stock status and trends in abundance information difficult to interpret (Weitkamp et al. 1995). Stock and recruitment is a function of the factors which determine the extinction risk, hence, it is circular to use it as a means of assessing the extinction risk. When the suite of exogenous factors is moving sharply outside the normative, the historical time series of age-structured abundance and its variability may give no information relevant to assessing the extinction risk of salmon populations. For example, the declines in Columbia River Basin sockeye salmon from 1900 to 1990 was a series of declining step functions, which closely followed the occlusion of nursery lakes by impassable agricultural and hydroelectric dams (Fryer 1995). This example is apt for all species of anadromous Pacific salmon due to the enormous pressure exerted by anthropogenic factors on exogenous conditions essential for salmon reproduction and survival.

Conclusions

The exogenous factors are considered to be far more important than the endogenous factors (Table 2). Biological organisms are shaped by their environments. How the animal is capable of using its environment, and the degree to which it is still adapted to its environment, are critically important for understanding the future of the population. The loss of ecological integrity, as shown by breaks in the biogeochemical cycle and by loss of connectivity among salmon populations, is a serious threat to the survival of salmon populations. The influence of climate is all pervasive. Understanding the effects of trends in marine survival and changes in the trophic structure of marine and freshwater environments, as a function of climate, is essential knowledge. Anthropogenic factors are obviously serious threats to the survival of salmon populations throughout their range. Mixed-stock harvest and bycatch lend themselves to overharvest of salmon populations, and their effects are insidious due to the lack of monitoring and stock identification information at the level of the native population.

Endogenous factors are shaped by the environment. Genetically inherited adaptive traits are a key to how the population is suited to survive in any environment. Abundance and trends in abundance are least important among the factors identified, since they are poor substitutes for understanding the causes of changes in salmon population size. Trends in abundance work best for populations which are clearly on the verge of extinction, but yield poor information at higher population levels.

Lack of information should not drive how we approach factors for assessing the extinction risk of salmon populations. In identifying the knowledge we need, but do not have, we have taken a major step toward understanding the reliability of our conclusions. With uncertain critical information, we have uncertain conclusions. Only by improving the knowledge base can we become more certain about the future of West Coast salmon populations.

Table 2. Prioritized list of factors important to the assessment of risk in salmon populations.

1. Exogenous Factors

   Habitat Dependency Measures (Spawning Substrates)
   Biogeochemical Cycle
   Connecting the Patches
   Climate
   Mixed Stock Harvest and Bycatch
   Anthropogenesis

2. Endogenous Factors

   Threats to Inherent Adaptive Traits
   Abundance and Age-Structured Abundance

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Ecological Issues

Climatic Influences on Salmon Populations in the Northeast Pacific

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1. Introduction

A number of recent studies have verified the fact that many stocks of Pacific salmon are threatened with extinction. For example, the Wilderness Society (1993) estimates that naturally reproducing Pacific salmon are mostly extinct or imperiled in 56% of their historic range in the Pacific Northwest and California. This undesirable state of affairs has developed in response to both natural variability and a legacy of human activities that are related to land use, harvest and hatchery practices (National Research Council [NRC] 1996). In this document, we examine the role that climate variability plays in driving salmon population changes. Ultimately, we develop a paradigm for the role of climate variations in the concern over future salmon extinctions.

One of the most obvious and important characteristics of the climate system is its variability. At time scales ranging from seasonal to millennial, records of climate from around the globe all highlight the fact that the normal state of the physical environment is one of dynamic change. Throughout the history of their existence, Pacific salmon and the ecological communities they are a part of have demonstrated tremendous resilience by evolving upon and adapting to a naturally variable environmental template. Thus, from a long-term historical perspective it seems clear that natural climate variability, by itself, should not be a primary concern in maintaining salmon stocks.

Anthropogenic influences on the salmon's environment play a primary role in our discussion of climate influences on salmon extinctions. Human activities have degraded, and in some cases completely eliminated much of the Pacific salmon's historic stream and estuarine habitat in the past century and a half. In many ways, human actions have forced semi-permanent changes to the salmon landscape that parallel those typically associated with climate change (Karr 1994). For example, stream temperatures, flow regimes, sediment transports, and pool-to-riffle ratios are all subject to anthropogenic and climate changes. Karr (1994) points out that one major difference between perturbations due to natural climate events versus one caused by human activities is the time scale of the resulting impacts. A warm phase of the El Niño/Southern Oscillation (ENSO) generally impacts precipitation and stream flows over the

course of a single year, while the construction hydropower dam alters stream flows for decades to centuries.

In this document, we present results from two distinct types of analysis. In the first type, we adopt a Pacific Basin-scale perspective and search for linear relationships between climate and salmon-metapopulation variability along the Pacific Coast, from Alaska to California. This approach yields a robust large-scale pattern of salmon metapopulation responses to climate variability. In the second approach, we select a few case studies that illustrate complex, nonlinear relationships between climate and salmon population variability. With case studies, we examine a hierarchy of spatial scales, starting with a regional perspective of metapopulations, then step down to more local spatial scales, bringing us much closer to evolutionarily significant units (ESUs) of salmon populations. It is this latter approach that we see as most applicable to the issue of climatic influences on salmon extinctions and potential listings under the Endangered Species Act (ESA).

We will argue that the superposition of natural-climate variability upon anthropogenically stressed salmon ecosystems is an issue of grave concern for the sustainability of salmon populations. We offer some ideas about salmonid vulnerabilities to climate fluctuations, and discuss possible strategies to preserve and enhance salmon metapopulation resilience in the face of climate fluctuations.

The remainder of this document is organized as follows: In Section 2, we describe the data and methods of analysis used. In Section 3, we discuss two recurring patterns of Pacific climate variability generally believed to be important to Northeast Pacific salmon, the ENSO and the Pacific Interdecadal Oscillation (PDO). In Section 4, we discuss results of a retrospective study linking large-scale Pacific climate variability to that in Pacific salmon populations. Case studies detailing climate impacts on salmon populations over a range spatial scales are presented in Section 5. A discussion of climatic influences on salmon extinctions is presented in Section 6, and conclusions follow in Section 7.

2. Data and Methods

2.1. Climate and salmon landings data

Historical salmon-catch records and climate data were obtained from a variety of sources. In each case, we assembled annual values for each measure of interest, covered in the period of record 1925 to 1993, unless otherwise noted.

We obtained salmon-landings data from the following agencies: the Alaska Department of Fish and Game (ADFG) (1991), the Canadian Department of Fisheries and Oceans (CDFO), the Washington Department of Fisheries (WDF), the Oregon Department of Fish and Wildlife (ODFW), and the California Department of Fish and Game (CDFG). Following the various fisheries agencies listed above, we divided our salmon landings data into 10 regions: 1) western Alaska, 2) central Alaska, 3) southeast Alaska, 4) northern British Columbia, 5) the Strait of

Georgia, 6) west Vancouver Island, 7) Washington Coast, 8) Puget Sound, 9) Oregon, and 10) California (Figure 1).

Average annual catch of all salmon (in millions) and fractional composition by species for each region for the period of record 1925 to 1993 are shown in Figure 2. On average, the largest salmon catches have been recorded in Alaskan waters where sockeye salmon and pink salmon are the dominant species. In contrast, southern salmon catches (and populations) are primarily composed of coho salmon and chinook salmon, and overall numbers in the southern regions are typically an order of magnitude lower than those in the far north. In British Columbia, between the extremes in the Northeast Pacific salmon's range, annual-average salmon landings have been both relatively large and evenly distributed among each of the five commercially exploited species. The average landings data for the period of record studied here are regarded as generally reliable indicators for the variability in adult salmon populations (Beamish and Boullion 1993, Francis and Hare 1994, Hare and Francis 1995).

An alternative approach is to compare salmon survival to climate variability, but such information is available for only a few select stocks and for a relatively short period of time (Coronado-Hernandez 1995). It is our hope and expectation that by averaging over relatively broad regions, variability in the catch data that is coherent with that in the climate data will emerge if the relationships are robust. The results presented in Section 4 suggest that, indeed, a climate signal does exist in the admittedly difficult-to-interpret fishery data set.

Our analysis of climate relationships with coast-wide salmon populations utilizes three indices for naturally occurring marine climate variability in the Pacific Basin. These are: 1) the Pacific Interdecadal Oscillation (PDO) index, 2) an index of sea-surface temperature (SST) variability along the coast of British Columbia and Washington State (BCSST), and 3) an index for SST variability in the eastern equatorial Pacific, hereafter the cold-tongue (CT) index. Each index was chosen to represent the time history of recurring climate patterns thought to be important to Pacific salmon and/or climate variability in the Northeast Pacific. The source regions for each of the SST indices are shown in Figure 3, and the time series are plotted in Figure 4.

The PDO index, derived from a principal component/empirical orthogonal function (PC/EOF) analysis (Preisendorfer 1988) of North Pacific SST for the period of record from 1900 to April 1996, is the dominant pattern of SST variability in the extratropical North Pacific (Zhang et al. 1996). The PDO has clear signatures in North American winter-air temperatures, precipitation, stream flows, and select salmon populations (Mantua et al. 1997). PDO-related SST and sea-level pressure (SLP) patterns are shown in Figure 5a.

The CT index is the average SST anomaly in the region from latitude (lat.) 6ºN to 6ºS, longitude (long.) 180ºW to 90ºW. It is a commonly used ocean-based measure of the ENSO (a recurring phenomenon that has been linked to large-scale climate anomalies) that are similar, in many respects, to those associated with the PDO (Zhang et al. 1996). The ENSO is known to impact a number of fisheries in the nearshore waters of the eastern Pacific (Baker and Chavez 1983, Mysak 1986, Sharp and McClain 1993). CT-related SST and SLP patterns are shown in Figure 5b.

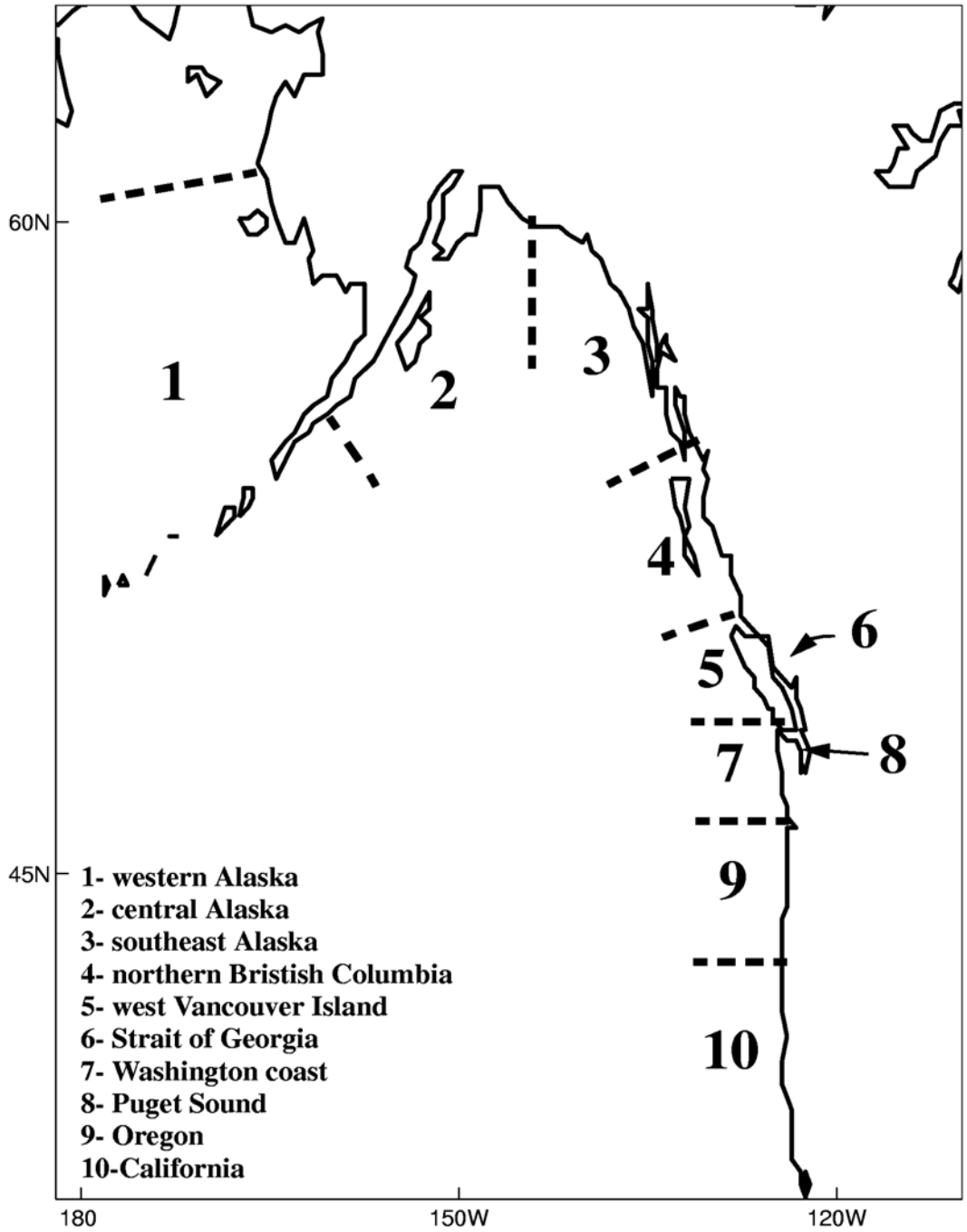

Figure 1. Salmon catch data regions.

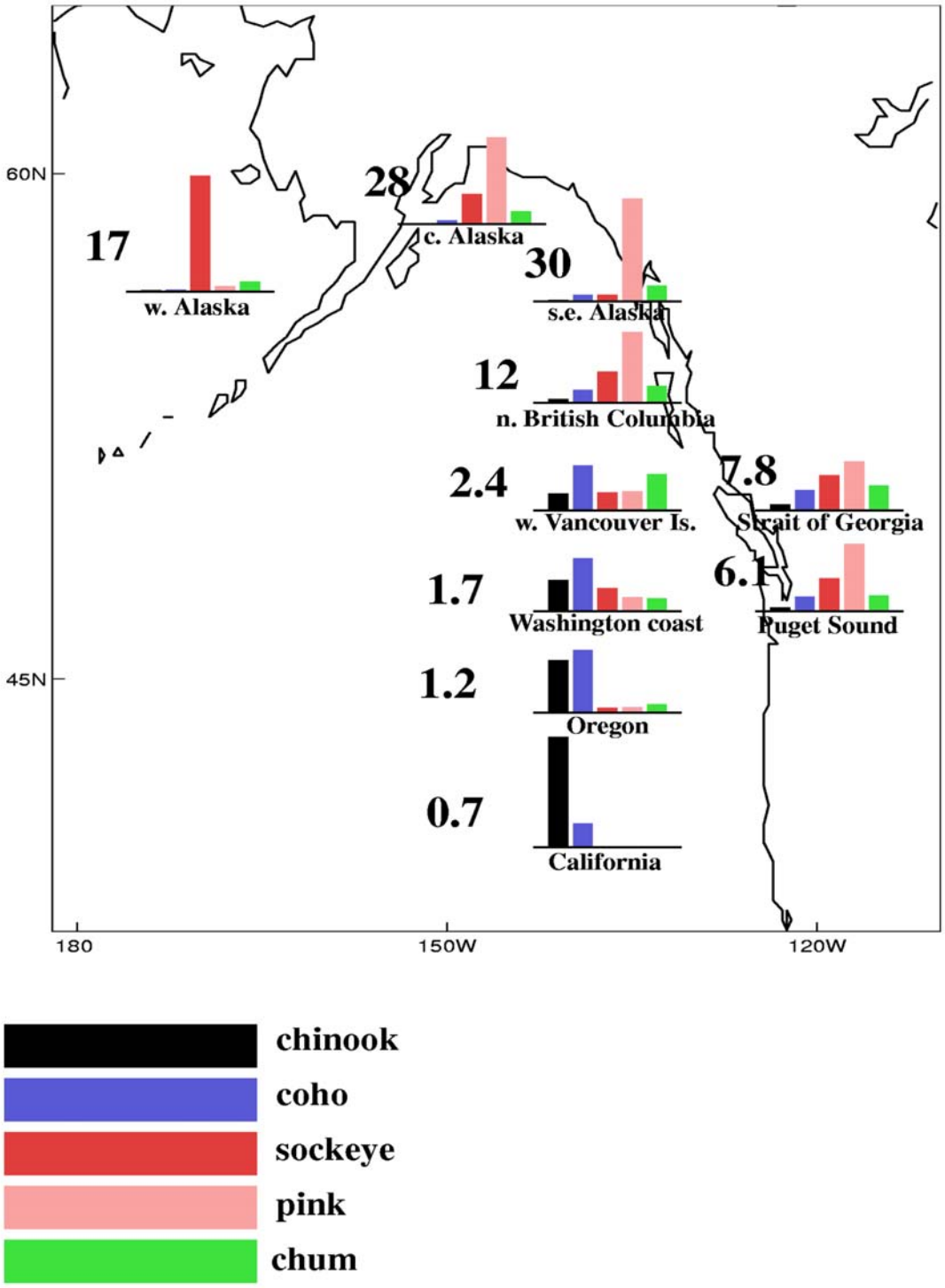

Figure 2. Annual mean total salmon catch by species for each of ten regions along the Pacific Coast of North America. Bold-faced numbers represent the annual mean catch of all salmon in millions of fish for the period of record 1925-1993. The length of each bar corresponds to the average relative contribution of each species to the catch of all salmon in the region.

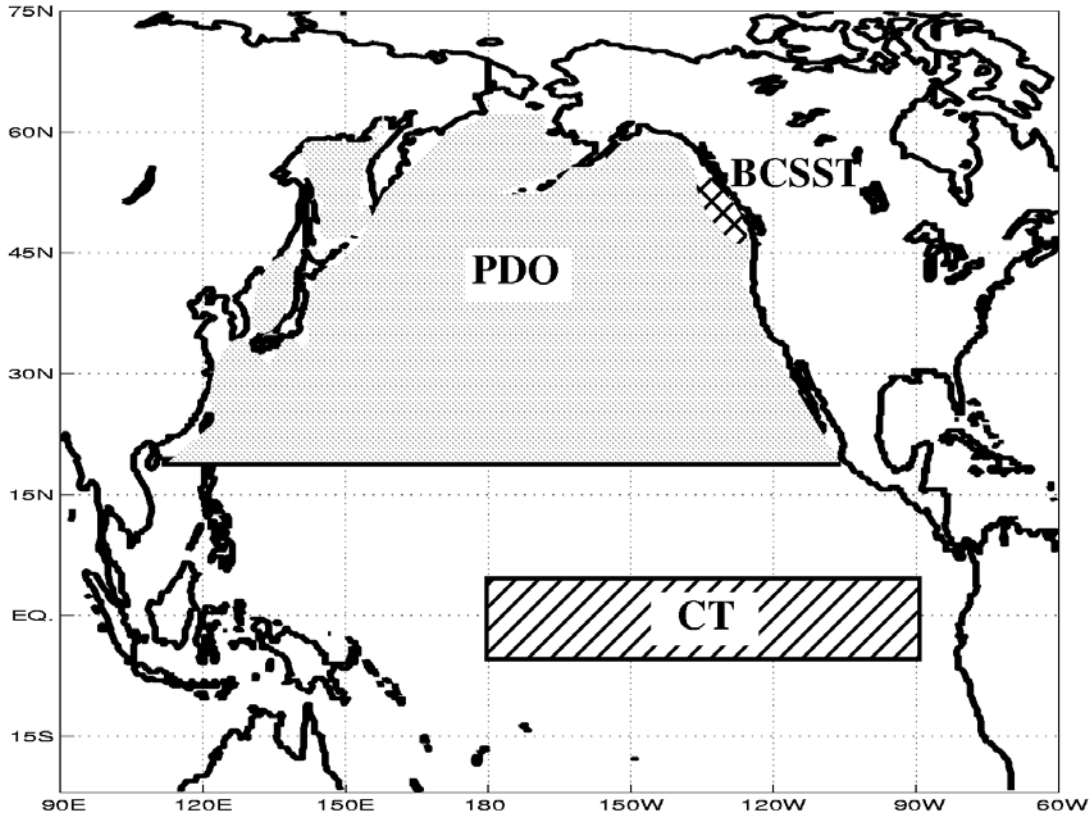

Figure 3. Source regions for the SST indices described in Section 2.1 and discussed in Section 3: Pacific Interdecadal Oscillation (PDO), coastal British Columbia SST (BCSST), and the Cold-Tongue (CT).

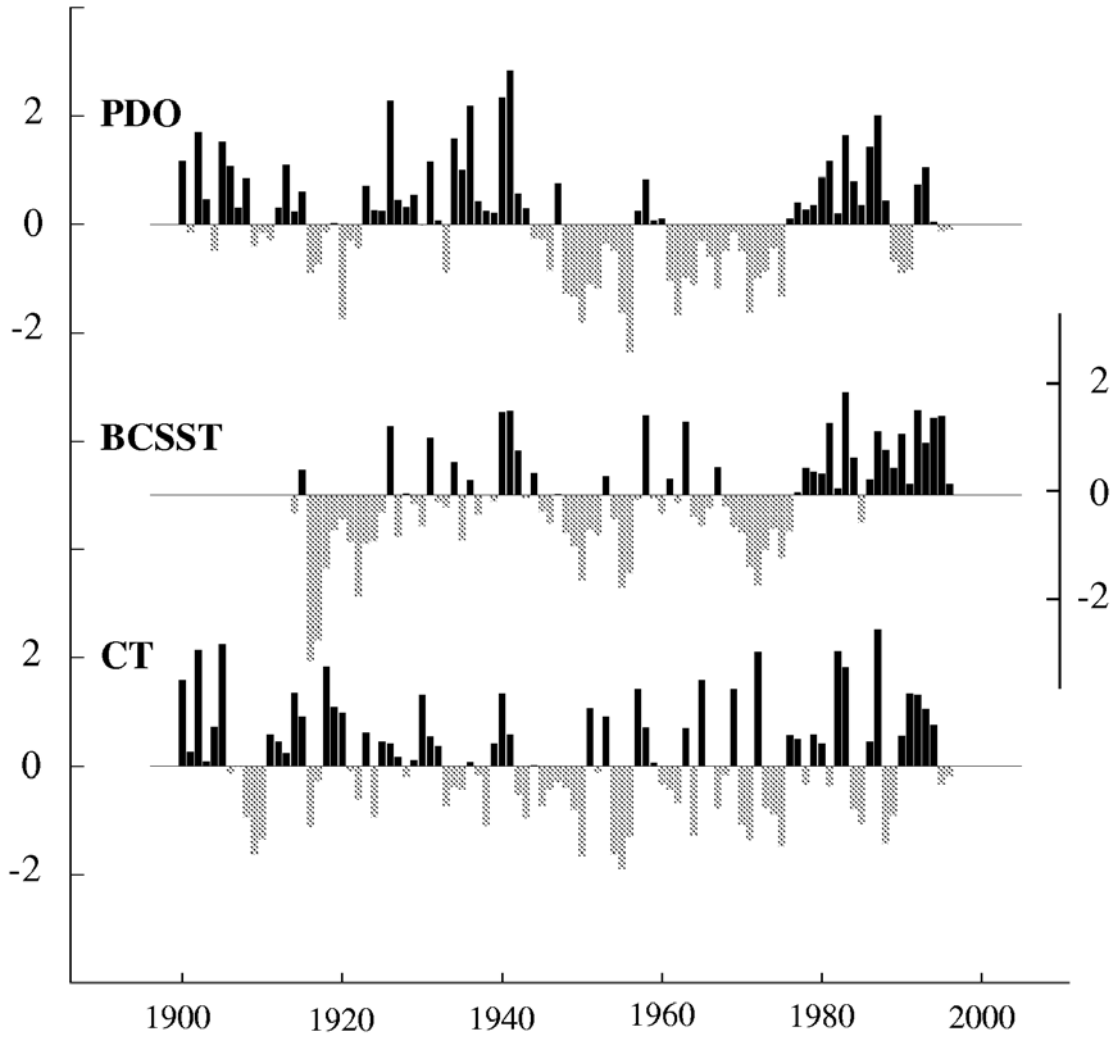

Figure 4. Annual mean normalized Pacific basin climate indices derived from SST data. Bars have been shaded such that positive values are black and negative values are grey.

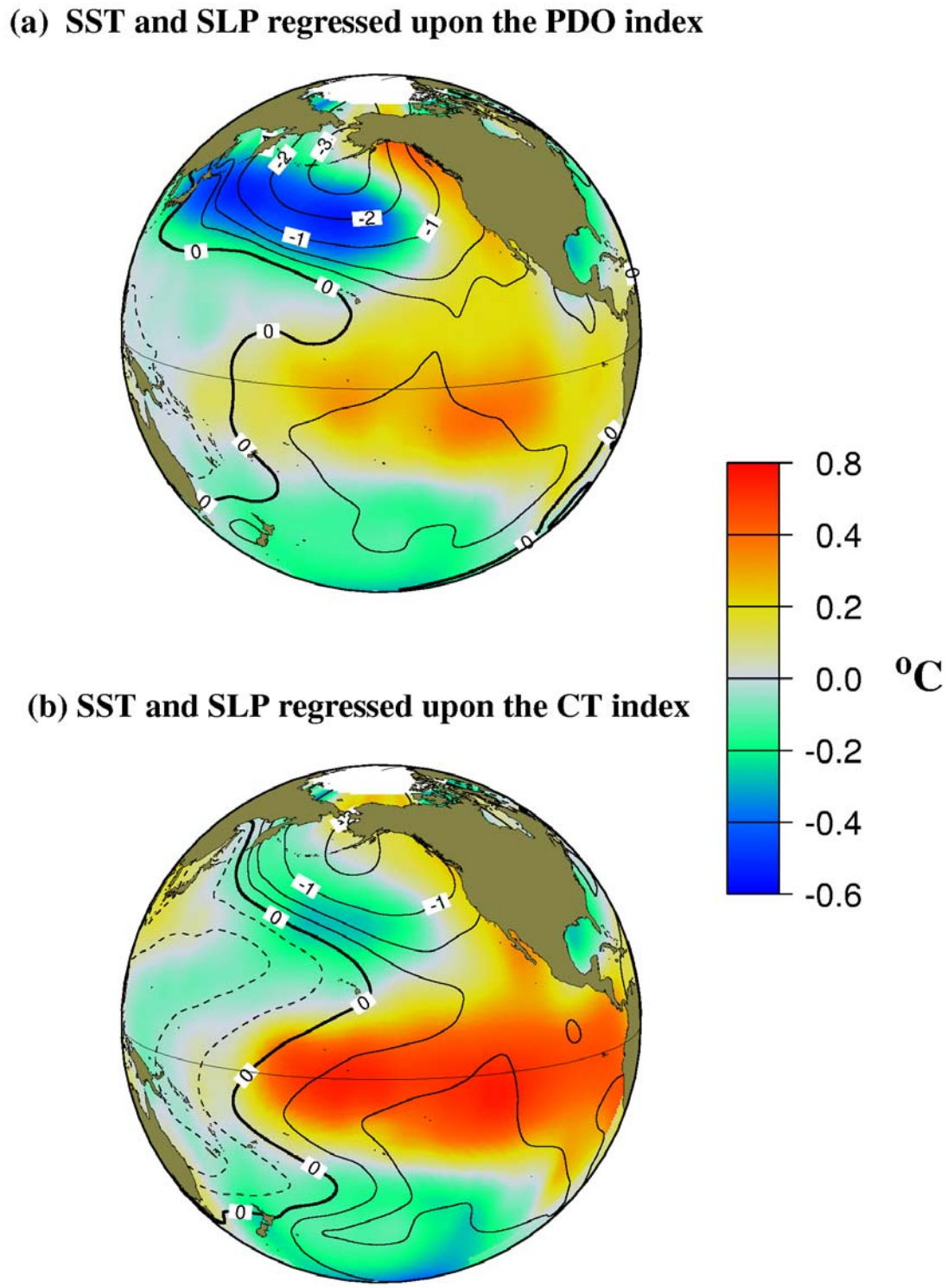

Figure 5. Winter mean (November-March) COADS SST regressed upon (a) the winter mean PDO index, and (b) the winter mean CT index for the period of record 1900-1992. Contour interval is 0.1˚C. Positive (negative) contours are solid (dashed). Reproduced from Zhang et al. (1996).

We include the BCSST index[1] (which is a regional measure of SST anomalies from shore stations between the Queen Charlotte Islands in British Columbia, Canada, and Neah Bay in Washington State) because it represents coastal marine climate variability in the center of the Northeast Pacific salmon's range. A more comprehensive discussion of the climate indices and related patterns is presented in Section 4.

A selection of regional climate data is examined in this document as well. In Figure 6, we show annual water year (October through September), streamflow indices from the Gulf of Alaska and the Pacific Northwest, wintertime surface air temperatures from the Gulf of Alaska, and coastal SST from Scripps Pier in southern California.

2.2. Analysis strategy

To objectively identify recurring patterns of climate variability in the North Pacific, a PC/EOF analysis of gridded SST data, poleward of 20ºN in the Pacific Basin, was done (compare analysis with Zhang et al. 1996). We used the covariance matrix from monthly SST anomalies provided by the Climatic Research Unit, University of East Anglica, for the period of record 1900 to April 1996 (Folland and Parker 1990, 1995). The analysis produced the PDO index shown in Figure 4.

To objectively identify linear relationships between our climate indices and salmon catch data, we follow a four-step procedure. The end products of this analysis are patterns of regional and species-specific salmon catch variability with time-varying indices. Each pattern explains relatively large fractions of the total variance in the salmon-catch data set.

First, we compute lag-correlations between each of the 47 salmon-catch records and each of the three climate indices. Before the lag-correlations are computed, each time series is prewhitened following Katz (1988).[2] This part of the analysis was done for two reasons. First, to gain insights into which part of each species' life history (e.g., early versus late in the ocean phase where the relationships with climate appear). The second reason is to provide guidance for building a data matrix to be used in the PC/EOF analysis. The time lags (number of years),

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[1] BCSST index is a composite of nine individual SST time series from coastal British Columbia, Canada, and Washington State. These stations are at: Amphitrite Point, Departure Bay, Race Rock, Langara Island, Kains Island, McInnes Island, Entrance Island, and Pine Island, in British Columbia (B.C.), Canada; Neah Bay, in the NW corner of Washington State. The time series from B.C. was obtained from the Institute of Ocean Sciences in Sidney, B.C., Canada, while that for the Neah Bay was obtained from the Scripps Institute of Oceanography in La Jolla, CA.

[2] The presence of strong autocorrelations in time series, which is a common property of environmental data sets, can introduce spurious cross-correlations at numerous time lags. Prior to computing the lag-correlations between the catch and climate time series, we removed the 1-year autocorrelation. An exception was made with the pink salmon catch records because they exhibit a clear peak in autocorrelation at 2-year lags, thus, we removed the 2-year autocorrelation from these catch records (see Hare 1996 for a more detailed discussion of problems introduced by autocorrelations in environmental data).

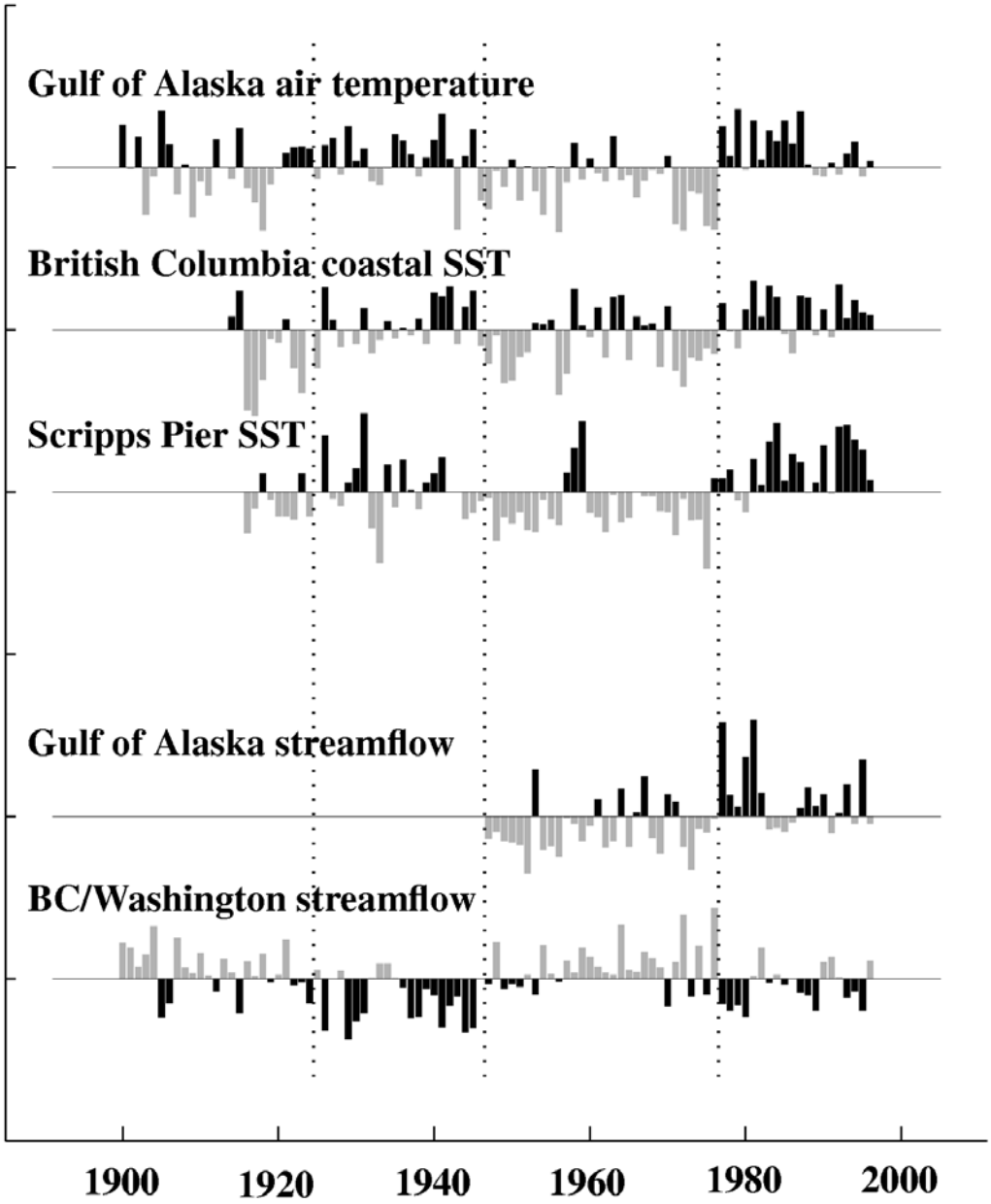

Figure 6. Selected regional climate time series with PDO signatures. Dotted-vertical lines are drawn to mark the PDO reversal times in 1925, 1947, and 1977.

for which there are statistically significant cross-correlations between the prewhitened climate and salmon time series, are recorded. From these time lags, frequency distributions for significant catch-climate lags stratified by species, are constructed (shown in Fig. 7, and discussed in Section 4.1).

In the next step, we create a data matrix composed of the 47 selectively-lagged catch records. The appropriate time lags for each species are determined by the peaks in the histograms of statistically significant lag-correlations.

In step three, we compute a population-weighted covariance matrix. The weighting amounts to a normalization of each group of catch time series, by region, such that each of the 10 fishery areas has the same total variance. Within each region, the variance for each species is weighted by its fractional contributions to the annual mean catch in that region.

In the final step, we apply a PC/EOF analysis to the population-weighted covariance matrix. The products of the PC/EOF analysis are a set of objectively derived orthogonal principal components (PCs), or expansion-coefficient time series and corresponding loading vectors. Each PC is a time series that describes the time varying amplitude of the associated loading vector. In a less formal analysis presented in Section 5, we examine three case studies, which exemplify nonlinear complex responses of salmon populations to environmental forcing, of which climate is a part.

3. A Retrospective Look at North Pacific Climate Variability

Previous work has demonstrated that climate fluctuations captured by the BCSST, CT, and PDO indices are important to marine ecosystems along the Pacific Coast of the Americas. For example, coastal SST variability represented by the BCSST index has been implicated as an important environmental forcing on nearshore marine ecosystems in the Northeast Pacific (e.g., Wooster and Fluharty 1985, Mysak 1986). Tropical SST variations marked by the CT index have been identified as a factor in pelagic fish population change in the eastern tropical Pacific (Barber and Chavez 1983, Sharp and McClain 1993). Large-scale SST fluctuations projecting onto the PDO have been linked to variability in large marine ecosystems of the Northeast Pacific and Bering Sea (Hollowed and Wooster 1992, Beamish and Boullion 1993, Francis and Hare 1994, Hare and Francis 1995, Beamish et al. al. 1995, Hare 1996, Mantua et al. 1997). In the remainder of this Section, we discuss the characteristics of the climate patterns associated with the three SST indices shown in Figure 4.

At the top of Figure 4 is the PDO index which represents the time history of the dominant pattern of North Pacific SST variability for the period of record from 1900 to April 1996. The PDO has experienced strong interdecadal fluctuations over the past century, with mostly positive values from the mid-1920s to the mid-1940s, negative values from the mid-1940s to 1976, and positive values since 1977. In this century interdecadal fluctuations in this index have closely paralleled those in the dominant pattern of North Pacific SLP (Hare 1996, Latif and Barnett 1996, Zhang 1996, Zhang et al. 1996). Thus, the PDO represents a large-scale, coherent ocean-atmosphere interaction at preferentially interdecadal time scales.

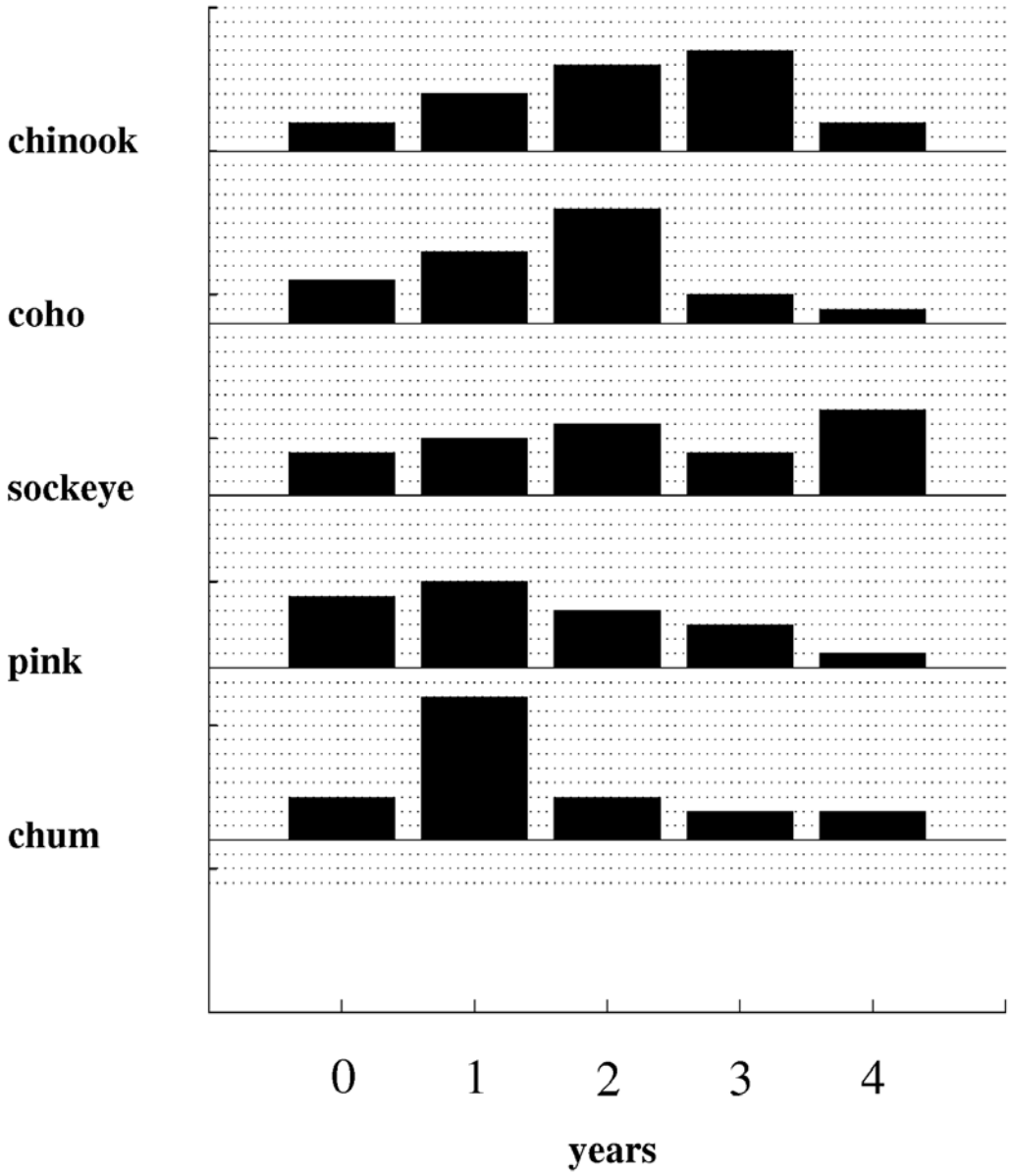

Figure 7. Histograms of statistically significant catch-climate lag-correlation, in years.

Shown at the bottom of Figure 4 is the CT index, which represents the time history of the dominant pattern of tropical Pacific SST variability. Over the past century, the CT index has varied mostly at interannual time scales and is highly correlated with an index for the leading pattern of SLP variability in the tropical Pacific. The CT index is a commonly used oceanic indicator for the well-known ENSO[3], which involves large-scale, ocean-atmosphere interactions.

Shown in the middle of Figure 4 is the BCSST index. The BCSST index has exhibited regime-like behavior that parallels behavior in the PDO for much of the common period record. Exceptions are clearly evident during the 1958 to 1962 and 1988 to 1992 periods of record when the PDO was weak or negative but BCSST was positive. Time variability in BCSST appears to contain a mix of the lower- and higher-frequency variability that is contained in the PDO and CT indices, respectively.

By regressing records of gridded wintertime SST and SLP data upon the PDO index, spatial patterns typically associated with a positive unit standard deviation of the PDO are generated (Fig. 5a). The largest PDO-related SST anomalies are found in the central North Pacific Ocean, where a broad pool of cooler-than-average surface water has been centered for much of the past 20 years. The peak amplitude of the SST regression coefficients in the cold pool are on the order of -0.5ºC. The narrow belt of warmer-than-average SST that, in the past 2 decades, has prevailed in the near shore waters along the West Coast of the Americas, is also a distinctive feature of this pattern and is consistent with the relatively strong positive correlations between the PDO and BCSST indices. The SLP anomalies (not shown) that are typical of the positive PDO are characterized by basin-scale negative anomalies between 20ºN and 60ºN. The peak amplitude of the mid-latitude wintertime SLP signature is about 4 *mb*, which represents an intensification of the climatological-mean Aleutian Low. This SLP pattern is very similar to the dominant pattern of wintertime North Pacific SLP variability (Hare and Francis 1995).

Shown in Figure 5b are the SST fields regressed upon the CT index. The map in Figure 5b shows anomalies typically associated with a unit standard deviation ENSO pattern. Comparing Figure 5a with 5b, it is evident that the tropical PDO spatial signatures are in many ways, reminiscent of canonical warm-phase ENSO SST anomalies (Rasmussen and Carpenter 1982). However, the PDO amplitudes in the tropical fields are weaker than those obtained by regressing the surface fields upon the CT index. Likewise, the PDO regression amplitudes in the Northern Hemisphere extratropics are stronger than those obtained from regressions upon the CT index (Zhang et al. 1996), both in the interior North Pacific and along the coastal strip of the Northeast Pacific.

Over the past century, the CT, BCSST, and PDO indices are positively correlated at statistically significant levels (see Table 1). With a linear multiple regression, using the CT and PDO indices as predictors, one can explain 44% of the variance in the BCSST index for the period of record between 1925 and 1993. Using the PDO index alone to model BCSST

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[3] Note that the essence of ENSO is thought to be contained within the tropical latitudes of the Pacific Basin (see Battisti and Sarachik 1995 for a comprehensive review on understanding and predicting ENSO), while that of the PDO remains an area of active research.

variability, one can predict about 40% of the variance. Using the CT index alone explains about 20% of the BCSST variance.

Table 1. Correlation coefficients between the PDO, BCSST, and CT indices.

	PDO	**BCSST**	**CT**
PDO	----	.65	.43
BCSST	----	----	.40
CT	----	----	----

There is little evidence that the BCSST region is the locus for a strong, ocean-atmosphere interaction important to larger scales of Pacific climate variability. In our view, BCSST is best understood to vary in response to the PDO, tropical ENSO, and other patterns of Pacific climate variability.

For example, the tropical ENSO is known to influence Northeast Pacific SST via two pathways. First, by so-called atmospheric teleconnections (Wallace and Gutzler 1981) and second, via coastally trapped, poleward-propagating, internal ocean waves (Gill 1982).

ENSO-related changes in tropical precipitation excite changes in the wintertime atmospheric circulation over the mid-latitude North Pacific (Bjerknes 1969, Julian and Chervin 1978, Horel and Wallace 1981, Hoskins and Karoly 1981). It is the teleconnected change in extratropical surface winds that ultimately force changes in North Pacific ocean temperatures through air-sea fluxes of heat and momentum (Namias 1969, Miller et al. 1994, Miller 1996).

ENSO-related changes in tropical winds can influence Northeast Pacific SST, via the generation of coastally trapped, upper-ocean disturbances in the equatorial Pacific (Enfield and Allen 1980, Chelton and Davis 1982). Results of empirical, theoretical, and numerical modeling studies suggest that the oceanic connections between variability in the tropical ENSO and mid-latitude coastal waters of the eastern Pacific are most robust equatorward of San Francisco. Poleward of San Francisco, coastal SST and sea-level variability are primarily driven by atmospheric forcing in the North Pacific (Chelton and Davis 1982, Parres-Sierra and O'Brien 1989, Miller et al. 1994).

Large-scale atmospheric-circulation anomalies that impact coastal SST also generate terrestrial climate variability. Typical of positive (negative) PDO and warm (cool) ENSO years are relatively warm (cool), wet (dry) winters with high (low) water-year (October-September) stream flows in the coastal regions of the Gulf of Alaska. During those same years, the Pacific Northwest tends to experience relatively warm (cool), dry (wet) winter with low (high) snowpack and low (high) stream flows (Cayan 1996, Mantua et al. 1997).

Selected climate records from western North America highlight the widespread signatures of the PDO (Fig. 6). Interdecadal fluctuations in wintertime surface-air temperature in the Gulf of Alaska, and SST near the coast from Alaska to southern California, varies in phase with the PDO. During positive PDO years the annual, water-year discharge in the Skeena, Fraser, and Columbia Rivers is on average 8%, 8%, and 14% lower, respectively, than that during negative PDO years. In contrast, positive PDO year discharge from the Kenai River in the central Gulf of Alaska region is on average about 18% higher than that during the negative-polarity PDO years (Mantua et al. 1997).

In summary, evidence suggests that it is primarily by their North Pacific atmospheric expressions that the PDO and ENSO climate phenomena influence the terrestrial and coastal oceanic environments in which Northeast Pacific salmon live. Over the past century, interdecadal variability associated with the PDO climate pattern has dominated that associated with teleconnections to the interannual ENSO (as expressed by the CT index) in the North Pacific.

4. Climate Influences on Salmon Populations

4.1. Linear Climate-Catch Data Relationships

Following the analysis outlined in Section 2.2, we generated frequency distributions for years with significant lag-correlations between the climate indices and catch records, constructed a population-weighted catch-data covariance matrix, and then applied a PC/EOF analysis to identify coherent patterns of salmon metapopulation variability along the Pacific Coast of North America.

Histograms showing the number of statistically significant, climate-catch, lag-correlations, stratified by year, lag and species, are shown in Figure 7. For this part of the analysis, we collected the significant lag-correlations from all 10 regions for each species where they exist. The histogram for chinook salmon shows statistically significant correlations at lags of 2 and 3 years, with a few significant correlations occurring at 0-, 1-, and 4-year lags as well. For coho salmon, the peak in the histogram occurs at 2 years, and there are significant lags at 0, 1, 2, and 4 years. Two- and 4-year lags emerge as the peaks in the histogram for lag-correlations between sockeye salmon catch and climate indices[4]. The histograms for pink salmon and chum salmon show that the most frequent significant correlations with the three climate indices occur at a 1-year lag.

Based on the results of the climate-catch lag-correlations, the following time lags were used to construct the catch-data matrix for the PC/EOF analysis: chinook salmon – 3 years, coho salmon – 2 years, sockeye salmon – 2 years, pink salmon – 1 year, and chum salmon – 1 year.

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[4] The 4-year lag appears to be related to year-class cycles in some sockeye salmon breeding populations (Burgner 1991). We follow Francis and Hare (1994) and Hare and Francis (1995) by focusing on the 2-year lag-correlation peak which points to an early ocean life-history connection between most Alaskan sockeye salmon stocks and climate variability.

For all but chum salmon, the years emerging as peaks in significant lag-correlations suggest that the climate patterns considered here are most often impacting salmon populations early in the ocean or late in the freshwater phases of their life histories (compare with Pearcy 1992, Francis and Hare 1994, Hare and Francis 1995, Hare 1996).

The leading pattern of salmon-catch variability, emerging from our statistical analysis of the selectively-lagged, salmon catch covariance matrix, explains 34% of the variance from the original data matrix (Figs. 8a, 8b). The leading principal component (PC1), or expansion-coefficient time series, is shown by the shaded bars in Figure 8a. The time variability in PC1 depicts an interdecadal vacillation with predominantly positive values from 1925 to 1942, negative values from the early 1940s to about 1976, and then positive values from 1977 through 1992. For the common period of record, the similarity between the PDO index (shown by the solid line with open circles in Fig. 8a) and PC1 is striking. PC1 is also positively correlated with the BCSST and CT indices, much more strongly with the former than the latter (Table 2).

Table 2. Correlation coefficients between catch data PC1 and climate indices.

	PDO	**BCSST**	**CT**
PC1:	0.55	0.46	0.17

The loading vector that corresponds with PC1 is shown in Figure 8b. Each weight is plotted as the correlation coefficient between PC1 and each individual catch record, and only those correlations which exceed a 95% confidence interval are plotted. This loading vector is interpreted as follows: temporally coherent and positively correlated with PC1 are catches of coho salmon and sockeye salmon in the three Alaska regions; pink salmon in central and southeast Alaska and Oregon; chum salmon in western and central Alaska, west Vancouver Island, and Puget Sound; chinook salmon in Puget Sound and central Alaska; coho salmon in Puget Sound; and sockeye salmon on west Vancouver Island. Temporally coherent but negatively correlated with PC1, are coho salmon landings on the Washington Coast, Oregon and California, and chinook salmon catches in west Vancouver Island, the Washington Coast and California.

To test the robustness of these results, the PC/EOF analysis was repeated with several modified versions of the catch data covariance matrix. In one case, the climate indices were added to the catch data, and a catch-climate data matrix was analyzed. The leading PC-loading vector pair that emerges is very similar to that shown in Figure 8b, and the variance explained was slightly greater at 36%. In another case, none of the catch records were lagged. The leading PC-loading vector pair from this version of the analysis again remained like that in Figure 8b, though the variance explained was slightly weaker at 33%. The PC from this analysis, like that in Figure 8a, is strongly auto-correlated with negative values from the mid-1920s through the mid-1940s, then negative values from the late 1940s to the late 1970s, and positive values thereafter.

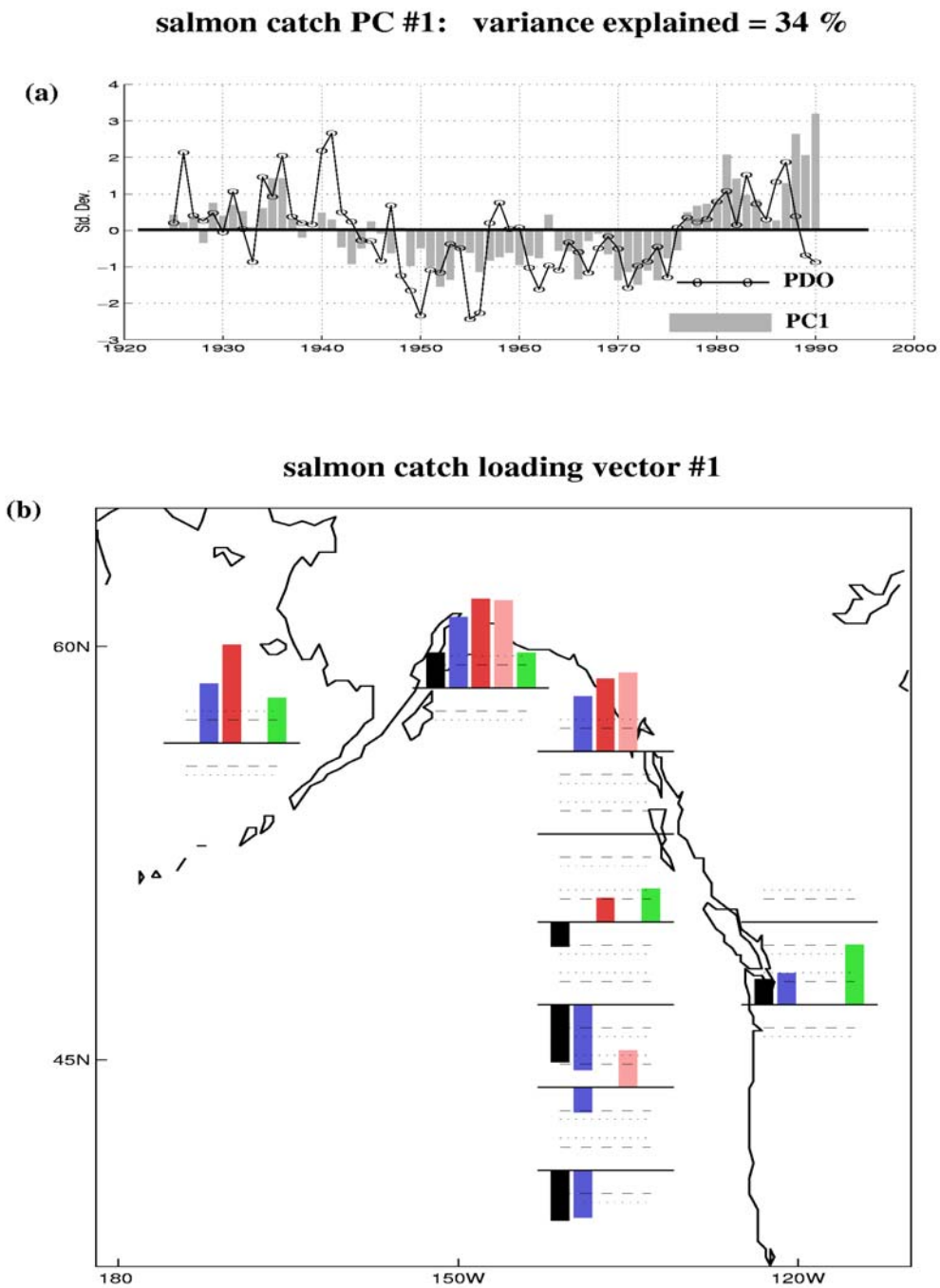

Figure 8. Results from the salmon catch PC/EOF analysis. In Panel (a) PC1 is shown with the grey shaded bars; the PDO index (from Fig. 3) is repeated with the solid line and open circles. In Panel (b) is the corresponding loading vector. Bars are plotted a correlation coefficients between PC1 and the selectivily lagged normalized time series for each catch record. The variance of the total data set explained by this PC/loading vector pair is printed in the upper right hand corner.

Based on the suite of PC/EOF analyses discussed, we are confident that the leading pattern of salmon-catch/climate variability shown in Figures 8a and 8b is robust. Clearly, the interdecadal climate variability associated with the PDO is coherent with that in many catch records, and presumably regional populations, for salmon in the Northeast Pacific.

4.2. Biophysical linkages between Pacific salmon and the PDO

Results of studies by Pearcy (1992) and Francis and Hare (1994) indicate that it is very early in the salmon's marine life history – likely just months after they enter the ocean – when many climate-related biophysical linkages to salmon populations take place. The early ocean life history also emerges as an important period in our climate versus salmon-catch lag-correlation analysis.

Recent work suggests that the marine-ecological response to the PDO-related environmental changes starts with phytoplankton and zooplankton at the base of the food chain and works its way up to top level predators like salmon (Venrick et al. 1987, Hare and Francis 1995, Roemmich and McGowan 1995, Brodeur et al. 1996, Hare 1996). This bottom-up enhancement of overall productivity appears to be closely related to upper ocean changes that are characteristic of the positive polarity of the PDO. For example, some phytoplankton-zooplankton population dynamics models are sensitive to specific upper ocean mixed-layer depths and temperatures. For the decade following the 1977 climate regime shift, such models have successfully simulated aspects of the observed increases in Gulf of Alaska productivity as a response to an observed 20% to 30% shoaling and 0.5ºC to 1ºC warming of the mixed layer (Polovina et al. 1995).

Variability in the strength of wind-driven mixing of the upper ocean is also influenced by the PDO. Wind-driven mixing replenishes vital nutrients to the light- and phytoplankton-rich, near-surface waters from below the thermocline. The strength of wind-driven mixing in the upper ocean is proportional to the cube of the SLP gradient (Garwood 1979), so that small changes in the latter field may cause relatively large changes in wind stirring. We speculate that, during positive PDO winters in the Gulf of Alaska, enhanced mixing of the upper ocean may also promote increased biological productivity.

Finally, to the extent that high- or low-stream flows favor high or low survival of juvenile salmon respectively, PDO-related stream-flow variations are likely working in concert with the changes to the marine environment in regard to impacts on salmon production. For Alaska salmon, the typical positive-PDO year brings relatively warm winter air temperatures, enhanced stream flows, and ocean mixed-layer conditions favorable to high biological productivity. Generally speaking, the converse appears to be true for Pacific Northwest salmon. In the Pacific Northwest, typical positive-PDO year stream flows are anomalously low, while nearshore upper ocean conditions appear to be unfavorable for high biological productivity.

5. Nonlinear and Complex Responses of Salmon Populations to Climate: Case Studies

In Section 4 we described a pattern of regional salmon-metapopulation variability that is related to a pattern of large-scale interdecadal climate forcing. Now, we would like to look at three cases: 1) Bristol Bay sockeye salmon, 2) Prince William Sound pink salmon, and 3) Oregon Production Index (OPI) coho salmon. For these three cases, there is more detailed information than what was presented in Section 4. These cases tend to display characteristics that are particularly important to the issues which arise around potential population extinctions. Extinctions are non-linear population events and, except on very large time and space scales (e.g., ice age/interglacial cycles), they are likely to be population responses to more than climatic forcing alone. We present the following three cases to give some perspective into complex salmon population responses to environmental forcing, of which climate is a part.

5.1. Bristol Bay Sockeye salmon

The Bristol Bay (Alaska) sockeye salmon fishery is the largest sockeye salmon fishery in the world. It appears to be extremely well-managed with the major goal of management to keep escapements to the various watersheds (Fig. 9) at optimum levels. Egegik is one watershed in Bristol Bay. From the 1950s through the 1980s, it accounted for less than one-third of the total sockeye salmon production (total run) of the region. Then in the early 1990s, production suddenly exploded to where, in 1992 and 1993, it accounted for well over 50% of the total sockeye salmon production (Fig. 10, top panel). This all occurred under relatively constant long-term escapement levels (Fig. 10, bottom panel).

This seems to us to be a classic example of a rapid and unpredictable shift in the organization of an ecosystem (Bak and Chen 1991, Waldrop 1992): in this case, the entire Bristol Bay salmon production system. It appears that it is also an example of density-dependent constraints operating from the top down (Apollonio 1994) and at the ecosystem level rather than the population level (Wilson et al. 1994). If one examines the top panel Figure 10 carefully, it appears that all systems in Bristol Bay responded to the climate-driven increase in production felt throughout Alaska starting in the late 1970s (Francis and Hare 1994). It also shows that most Bristol Bay production systems, except Egegik, declined in production in the early 1980s. During this time, Egegik became the major producer, as production once increased in the late 1980s, setting the stage for the explosion in Egegik production in the early 1990s.

What this points out to us is that in complex systems, history is important. A change in the constraint structure could have occurred in the early 1980s which set the stage for the sudden outbreak at Egegik in the early 1990s. This is the essence of self-organized criticality (Bak and Chen 1991). Hare (1996) tends to further support this, when he reports estimation failure when trying to fit the most common form of a spawner-recruit model (Ricker 1954) to Egegik data. No simple model can explain the dynamics of the stock over the past several decades – in particular, the response to the 1976/1977 climate shift, coupled with the sudden outbreak at Egegik in the early 1990s.

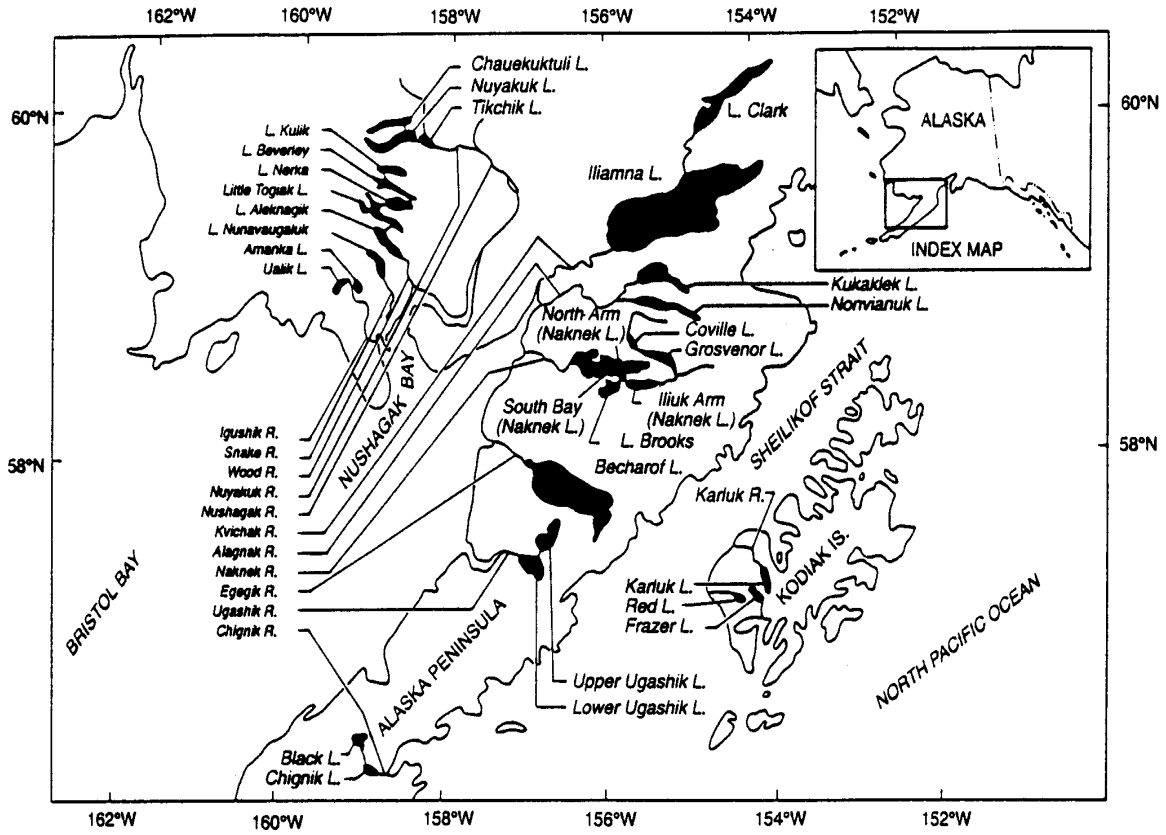

Figure 9. Sockeye salmon drainages in southwestern Alaska.

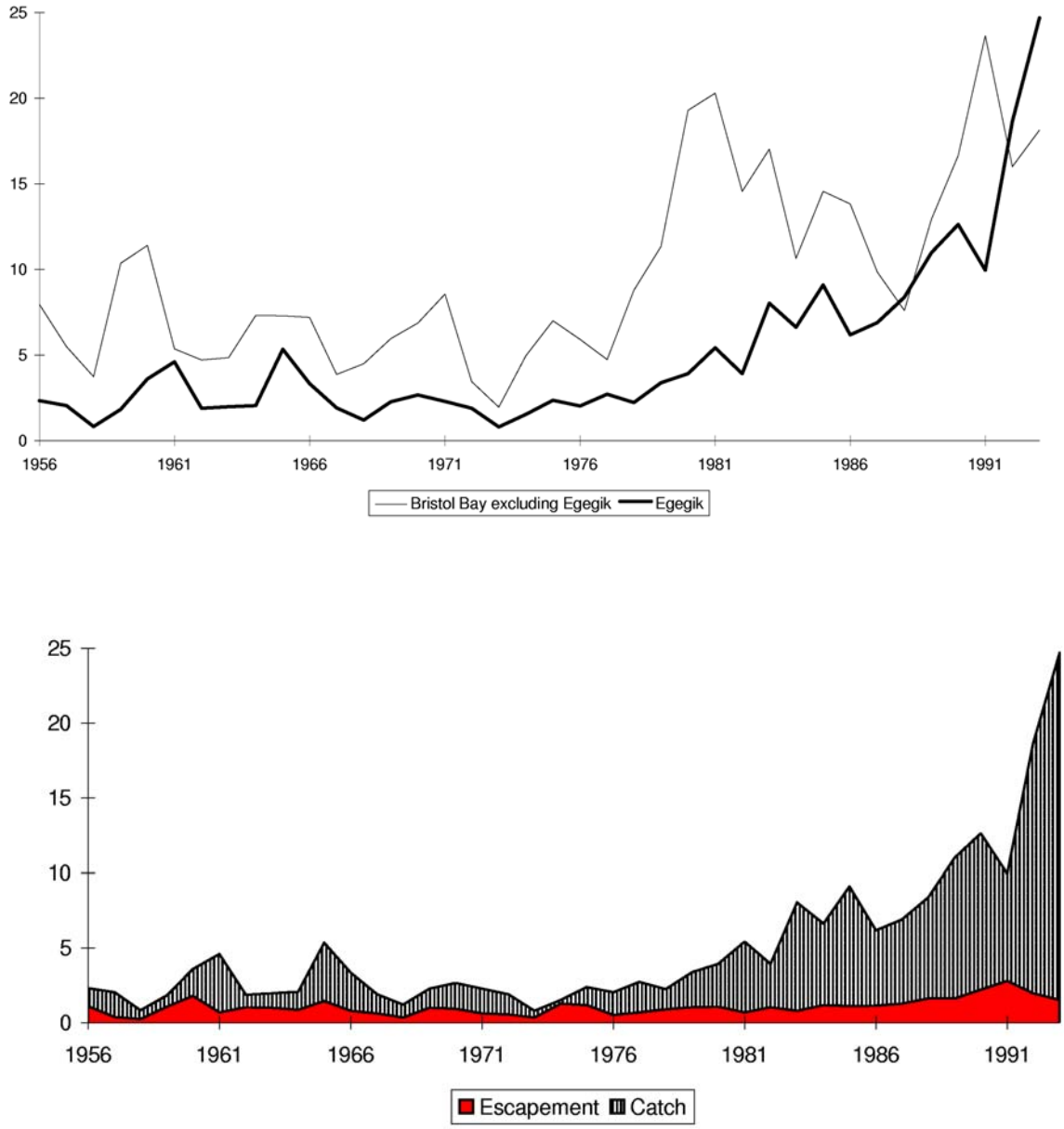

Figure 10. Top panel: Bristol Bay (excluding Egegik) and Egegik sockeye salmon total run size (millions), 1956-1993. Bottom panel: Egegik sockeye salmon escapement and catch (millions), 1956-1993.

5.2. Prince William Sound pink salmon

Our guess is that a similar thing happened in Prince William Sound (PWS), Alaska, with very different results. The top panel of Figure 11 shows the total PWS pink salmon wild and hatchery runs (catch plus escapement) from 1960 to 1994. To be brief, in the mid-1970s, when catches and runs of pink salmon in Prince William Sound (and throughout the Gulf of Alaska) had been at an all-time low for a number of years, a group of fishermen and processors formed a nonprofit hatchery corporation with the idea of enhancing depressed levels of wild production. The hope was to create runs which would provide bountiful harvests even in years when wild runs were weak. By the mid-1980s, the consortium had created the largest man-made pink salmon run in North America. In the late 1980s, however, the wild run declined significantly, while the hatchery run stayed strong. The run (mostly hatchery fish) became so large that it outgrew its market in 1990, forcing the dumping of millions of fish, which could not be sold, and then the market crashed in 1992 and 1993.

The causes of both the rapid increase in the early to mid-1980s, the decline of the wild run in the late 1980s, and the precipitous fluctuations of the total run in the early 1990s are hotly debated issues. Candidates to take credit for the increase are the new hatchery system and the marine environment. Causes for the subsequent declines and fluctuations are the 1989 *Exxon Valdez* oil spill and its effects on both freshwater and marine habitats, overfishing, over-production by the hatcheries, and changes in the marine environment.

As was mentioned earlier, it is clear that salmon production in Alaska increased significantly starting in the late 1970s due to a climatic shift in the marine environment (Fig. 12). It is clear that there was a significant increase in wild pink salmon production in the region in the late 1970s, and that it occurred long before hatchery production had become significant (Fig. 11).

The top panel of Figure 13 shows the PWS wild pink salmon run and hatchery releases the previous year. The rapid decline in wild production in the late 1980s occurred at a time when hatchery production had become significant. This decline does not appear to be related to a reduction in overall wild pink salmon escapement (Fig. 13, bottom panel), which would result from overharvest of wild populations. As a matter of fact, the exploitation rate for wild pink salmon in PWS stayed well below that for hatchery pink salmon during the late 1980s and early 1990s. The likely cause of declines in wild pink salmon production is due to competition between wild and hatchery juveniles when they first enter the marine environment (Cooney 1993). Hatchery smolts are generally released before wild smolts migrate from their natal streams into the near shore marine environment. As a result, not only do they swamp the environment due to the recent quantities of releases, but they get a competitive jump on their wild counterparts in the timing of entry. Of course, this is just speculation but it appears to be a likely scenario.

The abrupt fluctuations in both wild and hatchery production which occurred in the early 1990s could reflect a reorganization of the system in response to what happened at approximately the same time in Bristol Bay. Prince William Sound could have been in a state of severe tension, far removed from equilibrium at that time, and manifested a significant response in the early 1990s. The balance could have been tipped by an event as significant as the *Exxon Valdez*

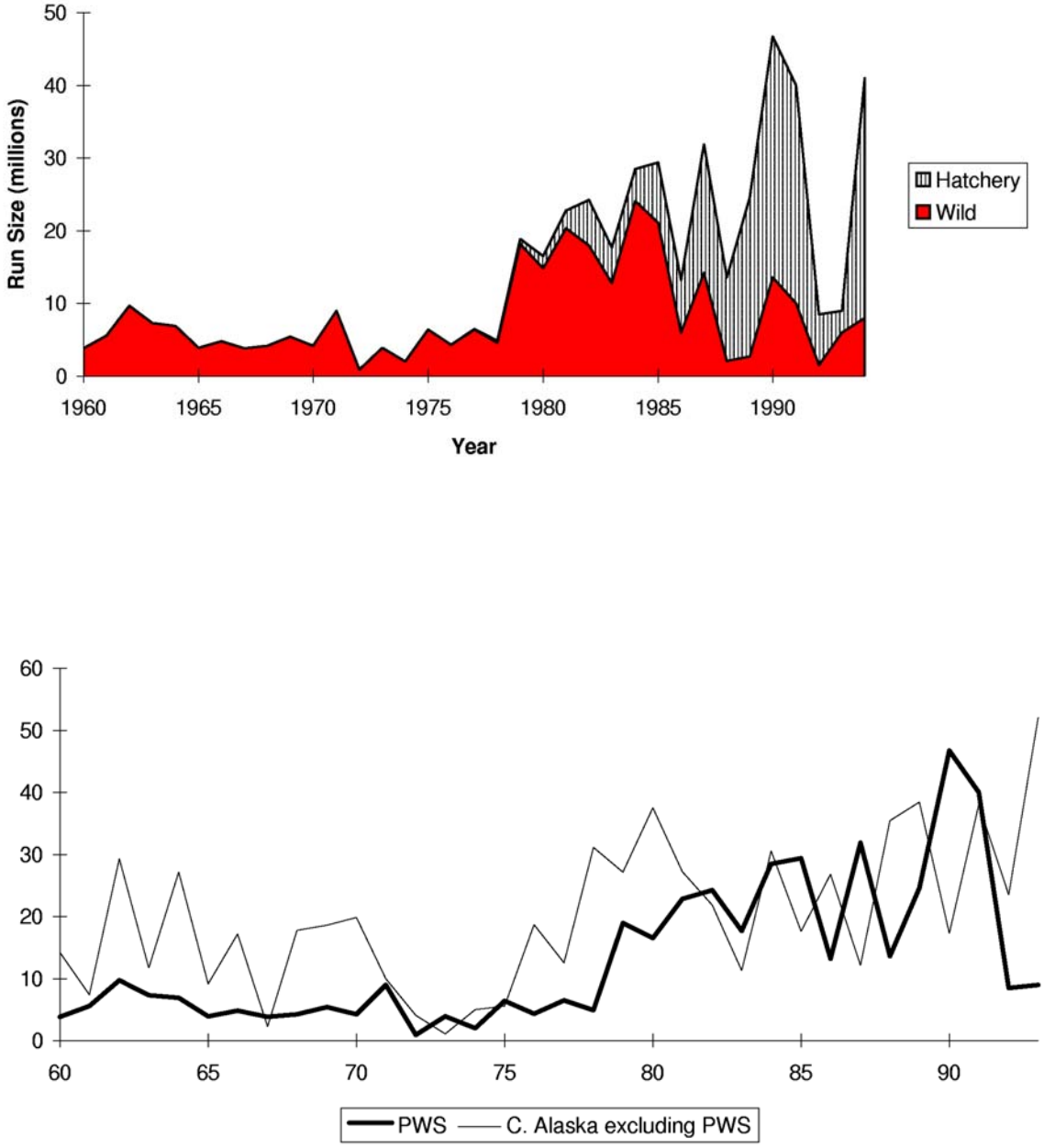

Figure 11. Top panel: Prince William Sound (PWS), Alaska, pink salmon estimated run sizes (millions), 1960-1994. Bottom panel: estimates of PWS and Central Alaska (exclusing PWS) pink salmon total run sizes (millions).

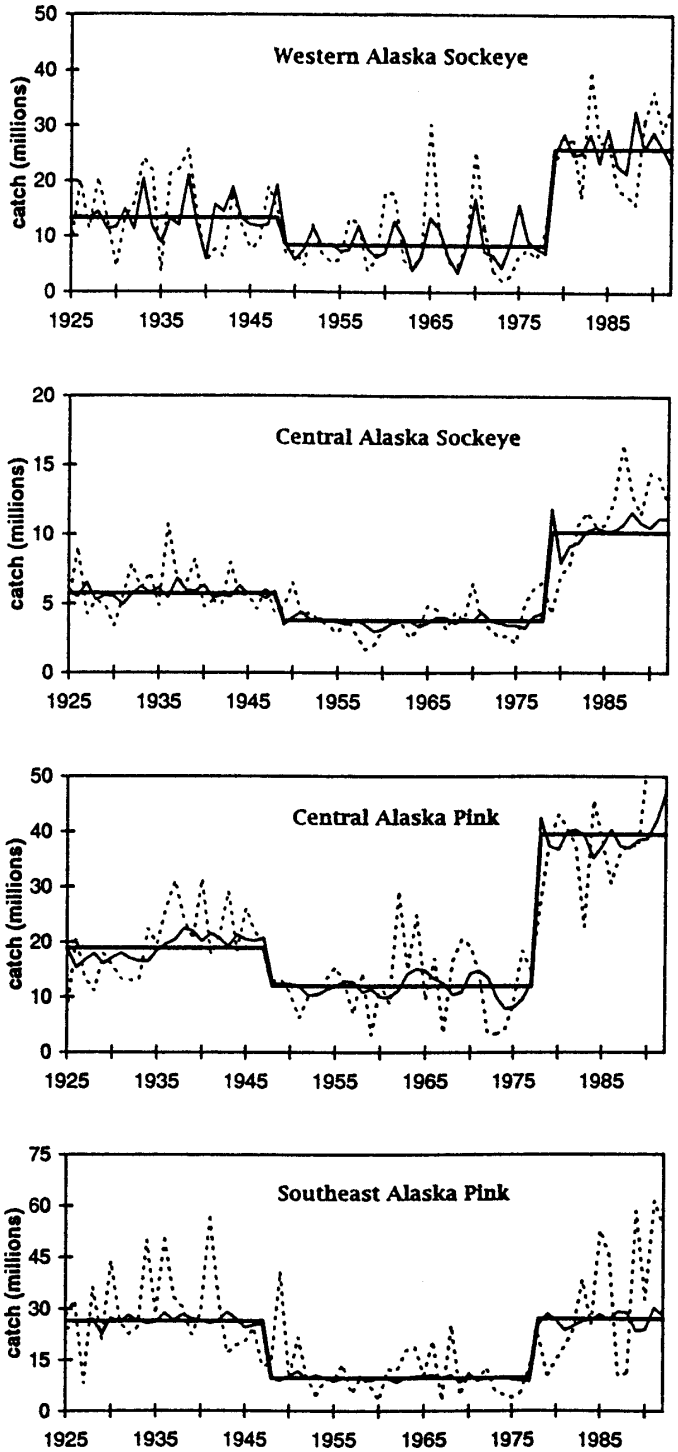

Figure 12. Time history (dashed lines), intervention model fits (thin solid lines), and estimated intervention (thick solid lines) for Alaska salmon catch time series (reproduced from Francis and Hare 1994).

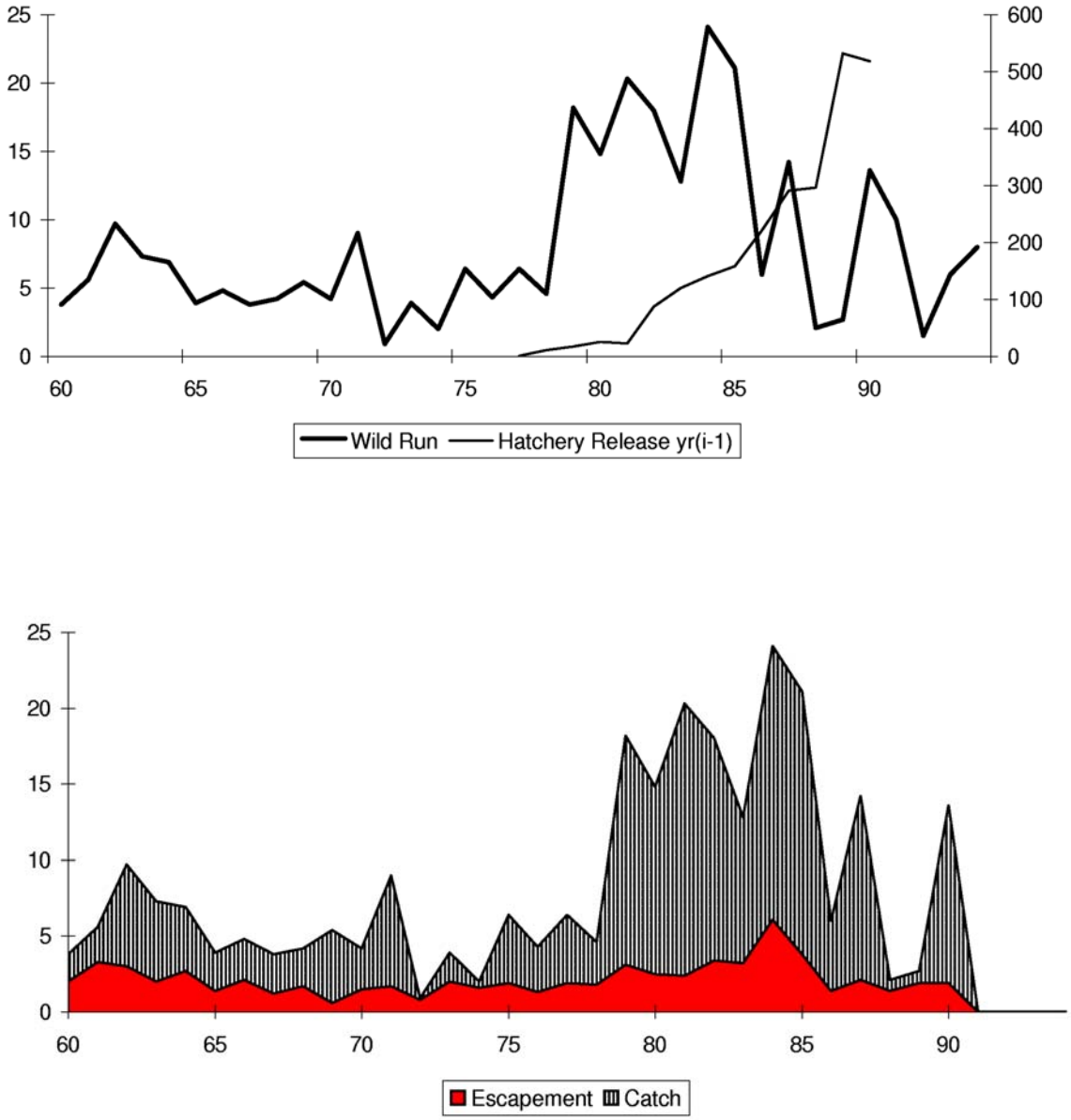

Figure 13. Top panel: Prince William Sound (PWS) wild pink salmon run in year *i* and hatchery releases in year (*i*-1) (millions), 1960-1994. Bottom panel: PWS, wild pink salmon escapement and catch (millions), 1960-1991.

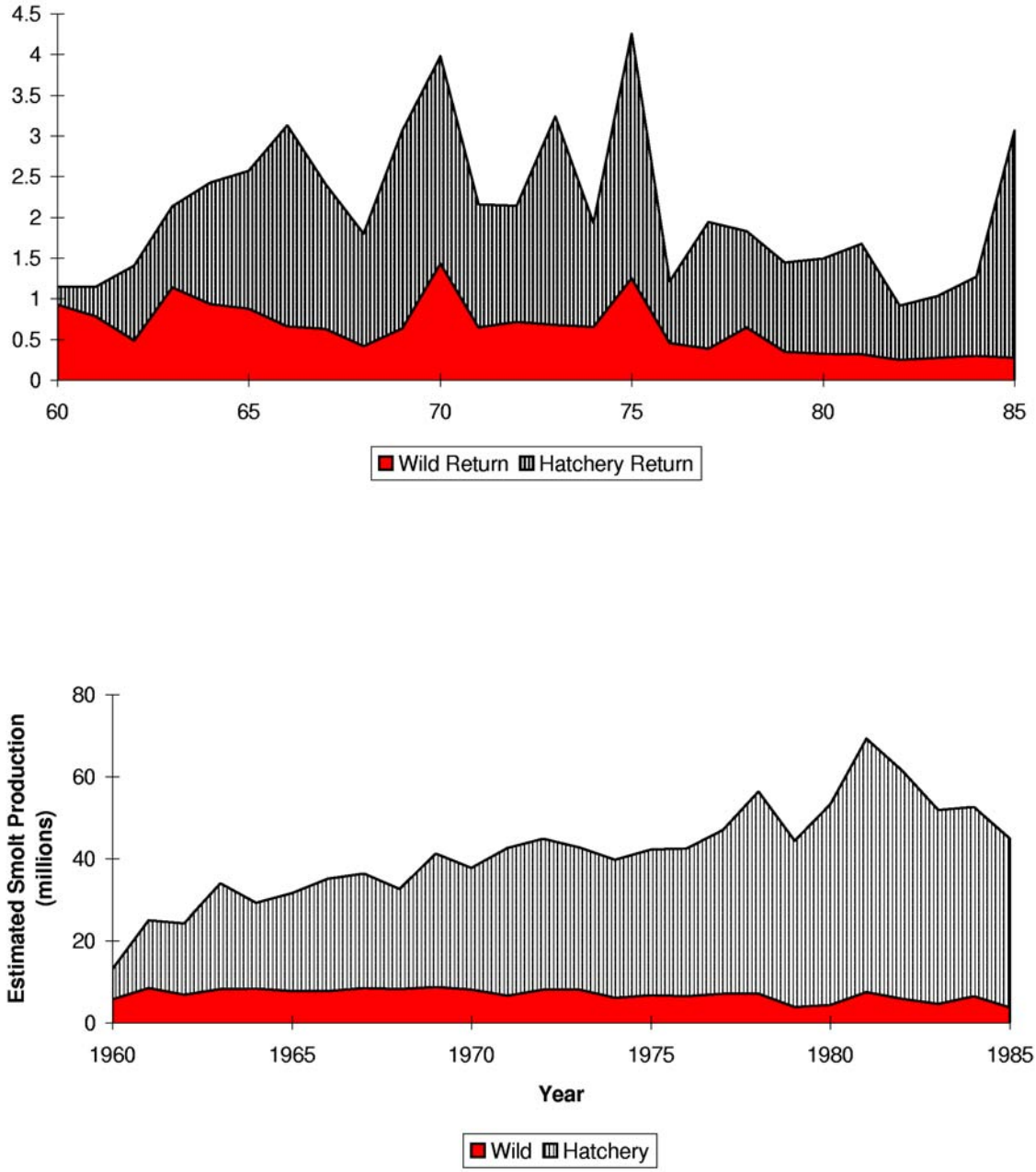

Figure 14. (Top panel) OPI coho salmon estimated run size (millions), 1960-1985. (Bottom panel) OPI coho salmon estimated total smolt production (millions), 1960-1991.

oil spill of 1989 (and its ramifications through the system), or as insignificant as a slight shift in marine climate or fishery dynamics. As Allen (1985) says, when this tension or disequilibrium reaches a certain intensity, "then many amazing and surprising things can happen."

The difference between the Prince William Sound and Bristol Bay experiences, however, comes down to one (Bristol Bay) being considered to be within the realm of normal variability around sustainable use, and the other (Prince William Sound) being considered a biological, social and economic disaster. In neither case is cause directly attributable. However, in one (Bristol Bay), human activities are clearly expected to ebb and flow with the vagaries of nature. In the other (Prince William Sound), blame is quickly passed around from one human institution to another.

5.3. Oregon production index (OPI) coho salmon

A third case involves the OPI of coho salmon. The OPI area is a portion of the Pacific coastal water bounded by Leadbetter Point, Washington, on the north and Monterey Bay, California, on the south. The top panel of Figure 14 shows coho adult salmon returns from 1960 to 1985 (Brodeur 1990, Emlen et al. 1990). The bottom panel of Figure 14 shows the corresponding increases in smolt production, all of which are due to increased hatchery output. However, it is clear that there is a point in the mid-1970s when there was an abrupt decrease in OPI coho salmon run size which persists through the end of the time series. Table 3 shows wild, hatchery and the total OPI coho salmon run size estimates (millions) for 1966 to 1975 and 1976 to 1985.

Table 3. Wild, hatchery, and total OPI coho salmon run size estimates (in millions).

	Wild	**Hatchery**	**Total**
1966–1975	0.77	2.04	2.81
1976–1985	0.36	1.23	1.59

A number of factors have been implicated in both the relatively large run sizes of the 1960s and early 1970s and the subsequent decreases in coho salmon numbers during the late 1970s and 1980s. These factors include: changes in the marine environment, compensatory and depensatory effects of increases in hatchery production, habitat loss, and overfishing. For years, the debate has been on whether the declines in both wild and total OPI coho adult salmon production are due to: 1) density-dependent factors operating early in the marine life history, which are imposed by competition between smolts (overproduction of hatchery smolts), or 2) shifts in constraints induced by the effects of large-scale climate variations in the marine environment and its productive capacity (Nickelson 1986, Emlen et al. 1990, Pearcy 1992, Francis and Brodeur 1996).

Figure 15 attempts to show how difficult it is to sort these factors out. Estimated hatchery and wild smolt-to-adult (ocean) survival rates against total smolt production by year class, are shown in the top panel of Figure 15. It is clear that as smolt production increased due to increased hatchery output, ocean survival of both wild and hatchery populations decreased. The same variables are plotted against time in the bottom panel of Figure 15. It is clear that there was a significant and abrupt decrease in ocean survival which occurred in the late 1970s and, with the exception of the 1983 year class (1985 smolt year), it has persisted to the present.

Recall that in the late 1970s, a climate-induced increase in Alaska salmon production occurred (Francis and Hare 1994). Consistent with the results of our analysis in Section 4.1 many (e.g., Francis and Sibley 1991, Hollowed and Wooster 1992) believe that climate-driven effects on biological production tend to operate in opposite directions in the California Current and Alaska Current ecosystems. As a result, corresponding to the late 1970s increase in Alaska salmon production, one would expect to see a corresponding decrease in Washington-Oregon-California salmon production (Fig. 8). The bottom line is that wild coho salmon populations in the OPI region are at very low levels, and have been petitioned to be declared endangered under the ESA (Weitkamp et al 1995).

Francis and Brodeur (1996) attempted to deal directly with this issue of compound effects on OPI coho salmon fishery production by building a simple model to explore the consequences of empirical relationships in smolt-to-adult survival:

1) between wild and hatchery fish,

2) under a range of ocean environmental (coastal upwelling) conditions believed to influence early ocean survival,

3) as a function of the total number of smolts entering the marine environment, and

4) as a function of improved freshwater spawning and rearing habitat for wild populations.

Figure 16 shows a number of the relationships that were input to the model. The top panel shows two habitat scenarios under which the model was run. Current habitat reflects the Ricker spawner-to-smolt relationship currently used by ODWF to predict wild smolt production from spawner abundance in the OPI area (P. Lawson[5]). Double Habitat reflects a modification of the Ricker relationship to reflect a doubling of the smolt production resulting from an increase of wild coho salmon spawning and rearing habitat (the Ricker b parameter was halved).

The bottom two panels of Figure 16 show the empirical smolt-to-adult survivals used in the model. These were computed as functions of total smolts entering the marine environment in a particular year, and mean coastal-upwelling volumes (March through September) partitioned

[5]P. Lawson, ODFW, Newport OR. Pers. commun. 1996.

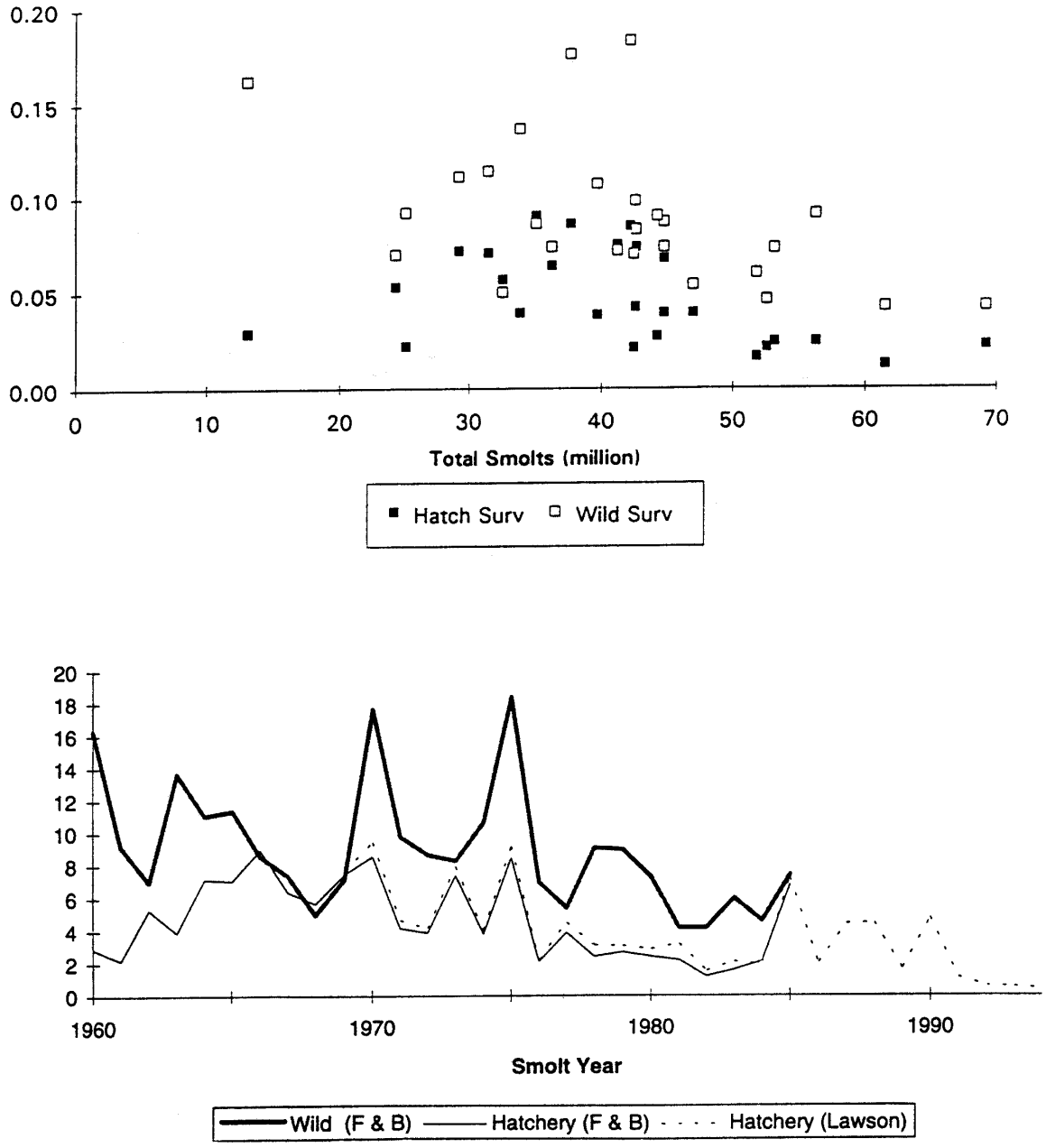

Figure 15. Top panel: OPI coho salmon wild and hatchery ocean survival versus total smolts release (millions), 1960-1985. Bottom panel: OPI coho wild and hatchery ocean survival versus year of ocean entry, 1960-1985 from Francis and Brodeur (1996, F&B). Shown with the dashed line are the official ODFW hatchery ocean survival estimates from 1970-1995 (courtesy of P. Lawson, footnote 5).

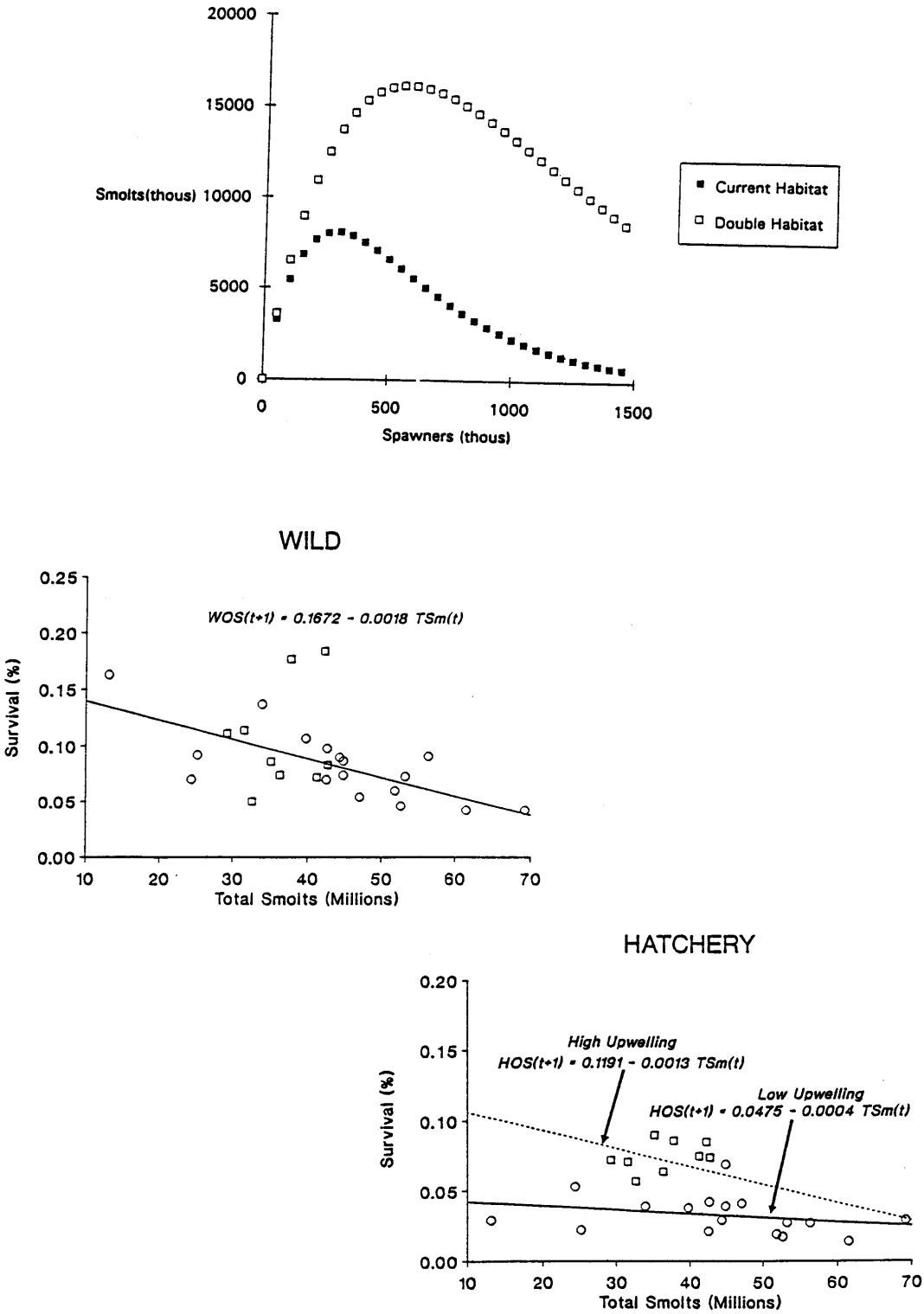

Figure 16. Top panel: OPI coho salmon spawner-to-smolt recruitment curves under current and "doubled" habitat scenarios. Middle panel: empirically derived survival of wild OPI coho salmon smolts as a function of total (wild+hatchery) smolts. Bottom panel: empirically derived survival of hatchery OPI coho salmon smolts as a function of total smolts.

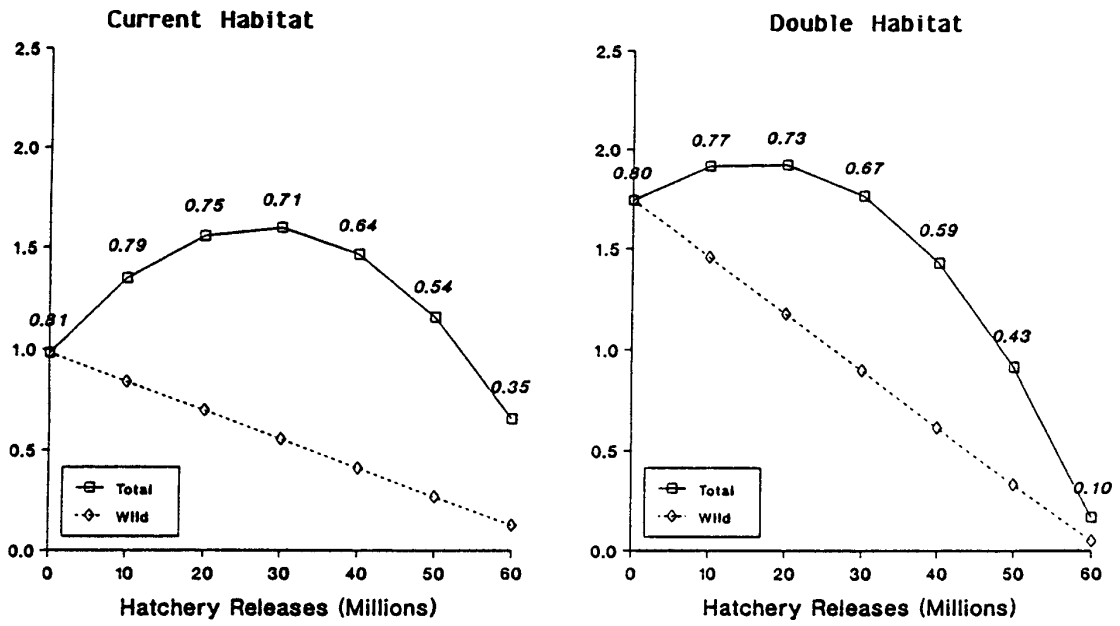

Figure 17. Model estimates for the maximum average wild and total catch (hatchery+wild) versus hatchery releases for (left panel) current habitat and (right panel) doubled habitat scenarios. Printed above each data point is the harvest rate at which those yields are obtained.

into strong and weak upwelling as defined by Nickelson (1986) for wild (middle panel) and hatchery (bottom panel) populations.

Figure 17 shows one set of model results which clearly illustrates the findings of the study. The two panels show estimates of maximum average wild catches and associated total (hatchery + wild) catches plotted against fixed levels of hatchery releases under both current and doubling of wild spawning and rearing habitat. The model was run under a time-varying pattern of ocean environmental conditions meant to reflect what was observed over the 1960 to 1981 period of record. Above each point is the harvest rate at which those yields of wild coho salmon adults are obtained. This example illustrates the apparent constraint on the production potential of wild salmon populations posed by high-levels of hatchery release, apparently similar to the Prince William Sound situation discussed previously. Two important conclusions arose from this study:

1) The levels of OPI-coho salmon hatchery releases in the late 1970s and early 1980s, which were 40-to-50 million per year, were significantly in excess of those necessary to maximize the total catch or realize increases in wild adult fishery production.

2) The more one increases wild spawning and rearing potential, the more one must reduce hatchery production in order to realize that potential in terms of wild adult salmon.

This modeling study was clearly at the metapopulation level. As Francis and Hare (1996) have pointed out, the connection between large-scale climate forcing and Pacific Northwest salmon production may relate more to interdecadal time-scale changes in the structure of the mixed-layer of the coastal ocean, than to variability in the winds that drive the coastal upwelling process. However, no matter how one represents these processes, the implications for individual breeding populations at risk seem to us to be even more acute than these model results reflect.

6. Discussion

How do the case studies relate to the issue of potential extinctions of salmonid populations? Mundy (1997) states: "What the currently prosperous salmon populations have, that the failed populations do not, is adequate habitat. In all cases where harvest of salmon apparently has been sustained indefinitely, there are two common elements; maintenance of adequate habitat, and the eventual implementation of rational limits on harvest."

One can argue that all three cases have relatively rational limits on harvest, although debate might arise in the case of OPI coho salmon. What really distinguishes the three cases is habitat. Bristol Bay is essentially pristine. Prince William Sound is relatively pristine from the physical point of view. However, the existence of massive populations of hatchery juveniles and adults likely have had a serious impact on the productive capacities of the wild pink salmon populations of the region. In this case, artificially-produced populations of pink salmon become part of the habitat for wild populations.

OPI coho salmon have experienced a quadruple whammy. First, OPI coho salmon spawning and rearing habitat is largely damaged and/or lost (Fig. 18). Second, the region has experienced a significant increase in hatchery salmon production. Third, unfavorable marine and terrestrial environmental conditions have persisted in the region for most of the past two decades. Fourth, as both the wild and hatchery populations and fisheries have declined, the fraction of the catch harvested out of the region (called interceptions) has greatly increased (Fig. 19) The end product has been disaster not only for the populations themselves but also for the fisheries which depend upon them for their sustenance.

7. Conclusions

The results of our analyses demonstrate clear linear relationships between naturally occurring and large-scale changes to the physical environment and a number of salmon populations in the Northeast Pacific. Of particular interest to the issue of climatic influences on salmon extinctions, interdecadal environmental fluctuations, associated with the Pacific Interdecadal Oscillation (PDO), appear to have significantly reduced the ecosystem(s) carrying capacity for West Coast coho salmon since the 1977 regime shift. The overall productivity of salmon in Alaska has dramatically increased during this same time period in response to PDO-related climate changes. Our results agree with those of previous studies that identify the first few months of the salmon's ocean life as the period of critical climatic influences on survival, which in turn, suggests that coastal and estuarine environments are key areas of biophysical interaction.

It seems likely that the polarity of the PDO climate pattern will continue to change at interdecadal time scales as it has over (at least) the past century. If and when that happens, West Coast coho salmon will once again experience favorable climatic conditions while Alaska salmon will be faced with poor marine and terrestrial climate conditions. However, wild West Coast coho salmon will continue to face the problems caused by the legacy of human land use, hatchery and harvest practices.

In summary, what are the lessons to be learned regarding the effects of climate on the extinction of salmon populations?

1) Climate alone is not likely to tip the balance. However, climate variability clearly has the capacity to amplify the risk and likelihood of extinction when superimposed upon salmonid ecosystems under extreme stress from humans.

2) Since climate effects on salmon seem to be much more significant at interdecadal than annual time scales, and since interdecadal time-scale climate change can only be recognized in hindsight, the effects of climate need to be hard wired into fishery management policy (e.g., different management strategies and algorithms may be required for different climatic regimes).

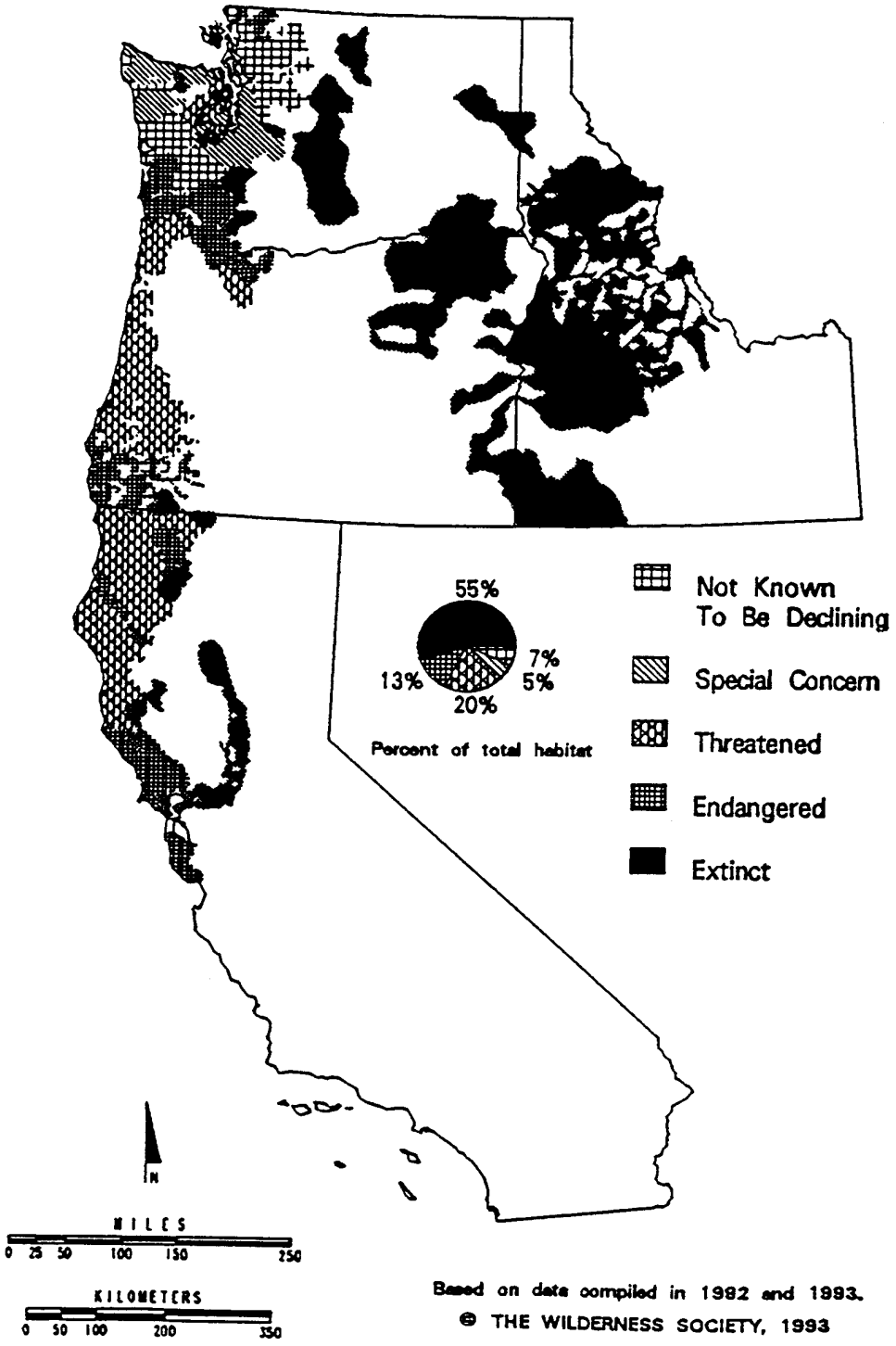

Figure 18. Status of coho salmon in the Pacific Northwest and California (reproduced from The Wilderness Society 1993).

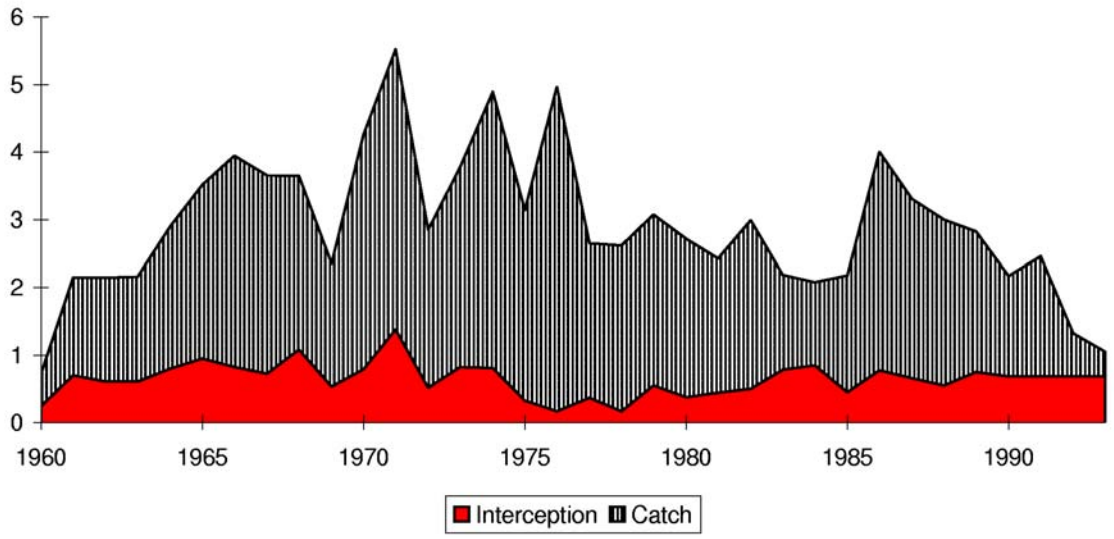

Figure 19. Washington-Oregon-California coho salmon fishery interceptions and in-area catches (million), 1960-1994.

3) Climate-related negative impacts on salmon production at the regional scale likely have much more severe implications for individual breeding populations than for metapopulations as a whole. Clearly, this has been the case for thousands of years. However, combining the effects of human activities with climate fluctuations likely amplifies a number of these negative influences.

It is also important to note that human activities have not only altered the salmon's terrestrial and estuarine environments, but they have also contributed to the envelope of climate variability by rapidly increasing the concentrations of radiatively important gases in the atmosphere. At present, our analysis of the climate record for the Pacific Basin suggests that anthropogenic climate change, if it is occurring, has been swamped by natural variability in this century. However, anthropogenic changes to the Earth's radiation budget are expected to lead to rapid changes to the climate system over the next few decades and centuries. Can Pacific salmon adapt to new climatic regimes?

It is our opinion that salmon populations in regions with healthy habitat will probably survive as long as the time scale of environmental change does not exceed their rate of adaptation. On the other hand, those populations that are presently stressed by occupying healthy, marginal or fragmented habitat, will most likely face more acute threats of extinction with the additional burden of significant anthropogenic climate changes.

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Diversity Issues

Metapopulation Ecology and the Extinction Risk of West Coast Salmonid Populations

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*(This paper was finished in fall 1996. My views on some of these subjects has changed since then, and much new work has appeared. It was not possible to revise the paper and cite this new work, but I would like to point readers towards two of my own pieces: Cooper, A. B., and M. Mangel. 1999. The dangers of ignoring metapopulation structure for the conservation of salmonids. Fish. Bull. US 97:213-226, which was motivated by a question from Andy Cooper at the workshop, and Shea, K., and M. Mangel. 2001. Detection of population trends in threatened coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 58:375-385.)*

In this paper, I address various aspects of metapopulation ecology, particularly metapopulation models, in regard to the extinction risk of West Coast salmonid (*Oncorhynchus*) populations. A metapopulation is a "population of populations" (Levins 1970) linked by immigration and dispersal. Individual locations will be characterized by extinction and colonization events, but if the collection of populations is not too closely synchronized, the metapopulation may persist for longer times than any individual population.

I briefly describe the history of metapopulation ecology, including Hanski's "practical" metapopulation model. After that, I describe characteristics of salmonids that challenge existing models. I develop models for: 1) presence/absence analysis in spatially linked stocks, and 2) metapopulation dynamics in slowly varying environments. I conclude with operational recommendations that arise from the models.

Classical Metapopulation Ecology

In the remarkable period of the late 1960s, optimal foraging theory (Emlen 1966, MacArthur and Pianka 1966), island biogeography (MacArthur and Wilson 1967) and metapopulation ecology (Levins 1969) developed. Island biogeography is concerned with the numbers of many species occupying a set of islands populated by a source of colonists, whereas metapopulation ecology deals with many populations of one species linked by dispersal. Each continues to make contributions to modern ecological science and some authors (Rosenzweig 1995) consider them to be gems of the merging of theory and experiment in biology, in terms of a strong predictive ecological theory (of which we do not have many).

The theories of optimal foraging and island biogeography developed rapidly, leading to experiments and the development of new fields, such as behavioral ecology. On the other hand, metapopulation theory languished for quite a while before a phase of development, and the subsequent development in the 1980s, was mainly theory (Hanski 1989). The rapid success of island biogeography and optimal foraging theory relative to metapopulation ecology involves two issues.

First, the developers of optimal foraging theory and island biogeography provided a prescription: 1) measure a certain set of empirically clear parameters, and 2) given these parameters, compute a quantity of interest. Levins did not do this as explicitly. Second, Levins published his seminal paper in an entomology journal and on biological control. In the heady times of the late-1960s, such "applied" biology was scorned by many colleagues.

For example, in classical rate-maximizing optimal foraging theory (Stephens and Krebs 1986), one measures handling times of, energy gain from, and encounter rates with food items, and then is able to predict the diet breadth of a foraging organism. In classical island biogeography, one measures per capita birth and death rates and carrying capacity of an island and is able to predict the mean persistence time.

On the other hand, it is not exactly clear what to measure in metapopulation theory or how to apply it. Indeed, authors still revisit the original Levins model (Hanski 1994, Loehle and Li 1996, Wahlberg et al. 1996) trying to operationalize it; see below, where Hanski's (1994) "practical" metapopulation model is described in detail. The fundamental variable in Levins's model is the fraction of occupied sites in a homogeneous habitat. The dynamics are assumed to be

$$\frac{dp}{dt} = cp\left(1-p\right) - mp, \tag{1}$$

where $cp\ (1-p)$ is the colonization rate of patches and mp is the extinction rate of patches. The parameters of c and m are rates of local immigration or extinction (Loehle and Li 1996). They determine the steady-state level of patch occupancy, which is $\left(c-m\right)/c$. Levins's description is based on assumptions of homogeneous patches, no spatial structure, no time lags, and constant probabilities of extinction and immigration (for discussion, see Gotelli 1995). The Levins model cannot be used to characterize the extinction risk of the metapopulation, except in the trivial case in which $m > c$. However, the classic notion of extinction risk in a metapopulation is one based on reliability (Martz and Waller 1982). If r_e is the probability that one of N identical patches goes extinct in a year, the probability that all of them do is $(r_e)^N$, so that the probability of persistence of at least one patch is $1 - (r_e)^N$. This function rises rapidly toward 1 as N increases, as long as the chance of local extinction is not too great (Fig. 1).

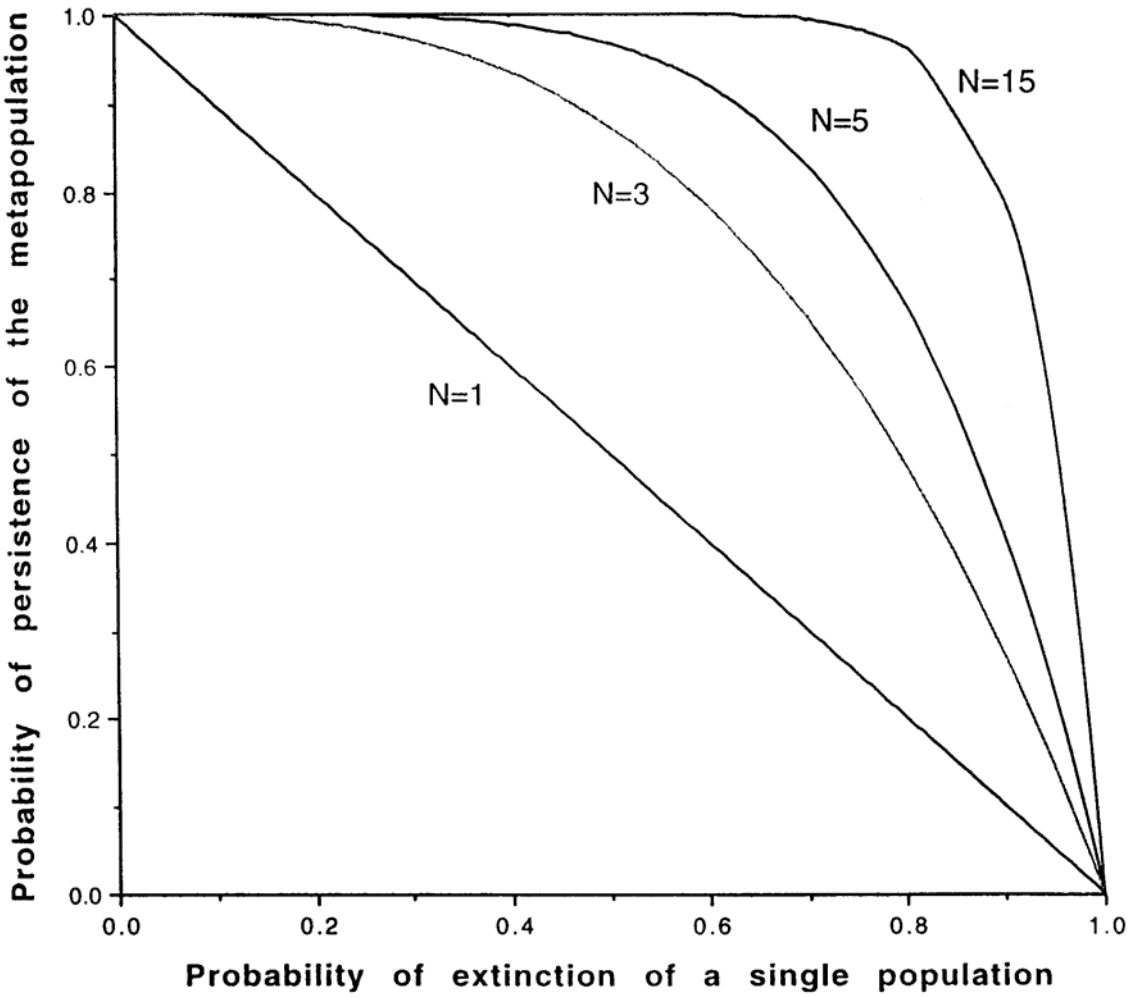


Figure 1. The reliability-theory notion of a metapopulation is that the collection of populations may persist because of redundancy.

A Practical Metapopulation Model and Evolutionarily Significant Units

Current metapopulation models (Gilpin and Hanski 1991, Gotelli and Kelley 1993, Adler and Nuernberger 1994, Hanski 1994, Berkson 1996) aim for generality and require tailoring for application. Here, I summarize Hanski's (1994) "practical model of metapopulations." Hanski et al. (1996) and Wahlberg et al. (1996) showed how it could be used effectively to understand the distribution of an endangered butterfly.

Hanski focuses on the "incidence function" J of a patch. This function is the long-term probability that the patch is occupied, assuming that its dynamics are a first-order Markov process involving colonization and extinction (see below):

$$J_i = \frac{C_i}{C_i + E_i} \tag{2}$$

Here, J_i is the incidence function for patch i, C_i is the colonization probability, and E_i is the extinction probability in patch i.

Hanski assumes that if patch i has area A_i, the extinction rate is:

$$E_i = \frac{\mu}{A_i^x} \tag{3}$$

where μ, and x are parameters.

The colonization probability is given by:

$$C_i = \frac{M_i^2}{M_i^2 + y}, \tag{4}$$

where y is a constant and the number of immigrants to patch i, M_i, is:

$$M_i = \beta \sum_{j \neq i} p_j \exp\left(-\alpha d_{ij}\right) A_j, \tag{5}$$

where α and β are constants, d_{ij} is the distance from patch i to patch j, and $p_j = 1$ if patch j is occupied and 0 otherwise, and A_j is the size of patch j. Note that colonization is independent of the number of individuals in other patches and only depends upon the area of the other patches (individuals presumed to be at constant density) and whether other patches are occupied or not.

The data requirements for this model are:

- patch areas A_i,
- pairwise distances d_{ij},

- presence or absence in a given year, and
- the parameter α that sets the strength of migration.

Given these, one estimates y, μ, β, and x based on the observed incidence. The data requirements for this analysis are stringent (see Table 1 in Hanski 1994).

Hanski et al. (1996) and Wahlberg et al. (1996) applied this model to butterfly populations with reasonable success. By simulating the metapopulation dynamics, they were also able to study the dynamics of occupancy, i.e., the fraction of patches that are occupied as a function of time. The fraction of occupied patches depends upon the level of stochasticity in the environment (see Fig. 2 of Hanski et al. 1996).

Hanski (1994) concludes that "Our main task is to make practical yet sensible assumptions about how the extinction and colonization probabilities E_i and C_i depend upon measurable environmental variables and on the life-history traits of the species."

At the present time, an Evolutionarily Significant Unit (ESU) is defined as a group of populations that: 1) are substantially reproductively isolated from other populations, and 2) contribute substantially to the ecological or genetic diversity of the biological species (Busby et al. 1996). It is not clear how metapopulations and ESUs are related, or if ESUs are defined by genetic criteria, but metapopulations are defined by dispersal criteria.

In the next sections, I describe challenges to this practical model caused by life-history traits of the salmonids. I then develop models that: 1) recognize unique aspects of salmonid life histories, 2) are operational in the sense that parameters can be measured and identified, and 3) focus on both population counts and presence-absence methods (Busby et al. 1994, Weitkamp et al. 1995).

Life-History Traits of Salmonids, Metapopulation Ecology, and Extinction Risk

For salmonids, the potential spatial structure of the potential metapopulation is clear because fish are found in drainages and not elsewhere. However, there a number of features of salmonid life history that limit the applicability of current theories (Gotelli and Kelley 1993, Hanski 1994, Halley and Dempster 1996).

Life-history variation

Most of the salmonids exhibit life-history variation in either age-at-smolting, age-at-return, or both. This is so common that salmon life histories are often summarized as *S.O.* for the number of stream years, *S*, before migration and the number of ocean years, *O*, before return for reproduction (Groot and Margolis 1991). The contribution of different life histories to reproduction varies (Tables 1 and 2). This variation has important implications for metapopulation ecology. Thus, for example, a stream that is empty in one year may have fish in

it the next year, not because of colonization from other populations but because of delayed return of adults. Salmonid populations do not follow a first-order Markov process.

Straying

Although salmonids are famous for returning to their natal streams, straying occurs. Indeed, without straying, there is no metapopulation. Straying is an explicitly spatial phenomenon. That is in general, neighboring streams are much more likely to receive strays than ones that are distant from a target stream.

Bartley et al. (1992), in a study of chinook salmon (*Oncorhynchus tshawytscha*), found that the number of migrants within five geographic groups ranged from about 4 per generation to nearly 16 per generation. Long-distance straying may occur, even in stream-dwelling fish (Fausch and Young 1995). Straying is an important way of introducing new genetic material into streams. Habitat manipulation can have positive effects beyond the site of manipulation only if other management activities assure that dispersal is effective (Gowan and Fausch 1996). If straying is mainly local, then Equation 5 simplifies it so that only adjacent streams need to be considered.

Adaptation

There is likely some level of selection for behavioral and reproductive traits in particular streams, although it is still difficult to characterize such selection and recognize it genetically. Thus, although straying provides the metapopulation structure, we should expect that strays are generally less successful in their new streams than residents. The effect of adaptation is that C_i given by Equation 4 must be modified to represent the effective number of migrants, determined by the relative performance of individuals from stream j in stream i.

Slowly varying environments

West Coast salmonids cannot escape the global consequences of the El Niño Southern Oscillation (Mangel 1994). Thus, analysis of the extinction risk of salmonid populations must explicitly take into account the environment varying on temporal and spatial scales much larger than those characterizing population dynamics (Gowan and Fausch 1996). Perforce, this means that it will be difficult to focus on steady state.

Sampling variation

To be successful over 100 million years, fish had to learn to avoid predators. One consequence of this evolution is that unless one extensively traps or electrofishes an entire stream, there is likely to be sampling variation. Most importantly, this means that "false negatives" are possible (or even highly probable). With limited sampling, we may conclude that

Table 1. Maximum percent contribution to any population of different life histories of sockeye salmon (Healey 1987).

	OCEAN YEARS				
	1	2	3	4	6
STREAM YEARS					
0	t*	0.1	t		
1	2.2	89.2	50.7	66.5	7.2
2**	1.4	58.3	64.2	8.9	
3**	1.7	15.4	4.6	t	
4**	t	0.3	t		

* t = trace (present)

** trace levels of 2.0, 3.0, and 4.0 life histories observed

Table 2. Maximum percent contribution to the Waddell Creek (California) population of different life histories of steelhead trout (based on data in Shapovalov and Taft 1954).

	OCEAN YEARS*		
	1	2	3
STREAM YEARS			
1	11.5	7.2	0.5
2	51.1	41.9	0.5
3	30.2	10.7	0.2
4	5.1	1.6	0.3

* Fish spawning for the first time. There are also second-, third-, and fourth-time spawners.

a stream does not contain fish, even though it does. Thus, we need to separate apparent and real measures of the level of incidence, based on the properties of the sampling scheme.

Characterizing Extinction Risk

Busby et al. (1996) consider a number of factors for the assessment of extinction risk: 1) absolute numbers of individuals, 2) spatial and temporal distribution of adults, 3) the relationship between current abundance and habitat capacity and the historical levels, 4) trends in abundance, and 5) threats to genetic integrity. Nehlsen et al. (1991) considered stocks to be at high extinction risk if they had declined from historic levels and were continuing to decline or if they had spawning escapements of less than 200. Stocks above 200 were considered to be at moderate extinction risk. Metapopulation models that incorporate the life-history characteristics of salmonids can contribute to the characterization of the extinction risk.

I first consider a spatial presence-absence model, in which the dynamic variables are the probabilities that a particular stream contains fish or not, with no focus on the size of the population. For simplicity, I consider only constant environments. I then develop a population-dynamics model, assuming no density dependence but a spatially and temporally varying environment. The latter models allow one to focus on questions of sampling and how sampling processes may affect perceptions about the state of the stock. Both models are first order in time, so that life-history variation in age at smolt metamorphosis and maturity is not included as this will be reported elsewhere.

A Spatial Presence-Absence Model

The model

Imagine a series of geographically contiguous streams, indexed by $i = 1$ to $i_{\max}$ that are censused on a regular basis (for definiteness assume yearly, but other time scales would work just as well). The fundamental variable is:

$$p_i(t) \equiv \text{ Probability that stream } i \text{ contains fish at the time of census in year } t. \tag{6}$$

Extinction is a property of the stream itself:

$$\mu_i \equiv \text{Probability that stream } i \text{ will not contain fish at the next census, given that it contains fish at the current census.} \tag{7}$$

Colonization is a property of the stream and its neighbors, in the sense that an empty stream is more likely to be colonized if its immediate neighbors contain fish. For simplicity, but the

results generalize, I assume that stream i is colonized by individuals from stream $i - 1$ or stream $i + 1$.

Suppose that $X_j = 1$ of a stream contains fish at the time of census, and $X_j = 0$ if there are no fish in the stream at the time of census. Colonization can then be described by

$$\lambda_i(y,z) \equiv \text{Probability that stream } i \text{ contains fish at the next census, given that it does not contain fish at the current one, and that } X_{i-1} = y, \text{ and } X_{i+1} = z. \tag{8}$$

I assume:

$$\lambda_i(y,z) = \lambda_{i0} + \varepsilon(y+z), \tag{9}$$

where λ_{i0} and ε are constants. Note, that if $\lambda_{i0} = 0$, then once a stream loses its natal fish, there is no chance of recolonization except from adjacent streams, so that ε is a measure of rescue by adjacent streams. On the other hand, if $\varepsilon = 0$, there is no linkage between different streams. In the absence of interconnection between streams ($\varepsilon = 0$), there is a steady-state level of occupancy $\overline{p}_i$ given by:

$$\overline{p}_i = \frac{\lambda_{i0}}{\lambda_{i0} + \mu_i} \tag{10}$$

Equation 7 is analogous to the "incidence" studied by Hanski (1994). It may be corrected for the "rescue effect" of simultaneous extinction and colonization:

$$\overline{p}_i = \frac{\lambda_{i0}}{\lambda_{i0} + \mu_i - \lambda_{i0}\mu_i} \tag{11}$$

When interconnection between streams occurs ($\varepsilon > 0$), the $p_i(t)$ satisfy a system of different equations,

$$\begin{aligned} p_i(t+1) = {} & p_i(t)(1-\mu_i) \\ & + (1-p_i(t))\big[\lambda_i(0,0)(1-p_{i+1}(t))(1-p_{i-1}(t)) \\ & + \lambda_i(1,0)\,p_{i-1}(t)(1-p_{i+1}(t)) \\ & + \lambda_i(0,1)(1-p_{i-1}(t))\,p_{i+1}(t) \\ & + \lambda_i(1,1)\,p_{i-1}(t)\,p_{i+1}(t)\big] \end{aligned} \tag{12}$$

The first term on the right-hand side corresponds to stream i containing fish in year t and not having an extinction between year t and $t + 1$. The next four terms correspond to the situation

in which stream i is empty in year t, which happens with probability $1 - p_i(t)$. Then stream i can be colonized in principle by its own individuals returning for spawning or those from neighboring streams and the four terms in ([⋯]) in Equation 12 capture the ways that this might happen.

Equation 12 can be solved on a desktop computer, assuming "reflection" at $i = 1$ and at $i = i_{\max}$ (so that no fish are lost through the boundaries of the metapopulation), and random initial conditions are determined according to the average occupancy probability of each stream independently (Equation 10). The results can be summarized by two measures of population performance. The first is the fraction of streams occupied at the end of a time horizon of length T:

$$\langle p \rangle = \frac{1}{i_{\max}} \sum_{i=1}^{i_{\max}} p_i(T) \tag{13}$$

and the second is the probability that all streams are simultaneously empty at T:

$$p_e = \prod_{i=1}^{i_{\max}} \left[1 - p_i(T) \right]. \tag{14}$$

Because of the assumption used in this section that the environment is constant, the dynamics in Equation 12 reach a steady state, so that unless one is concerned about transient effects, initial conditions do not matter.

A metapopulation can be considered extinct if p_e exceeds a previously agreed upon threshold (Mangel et. al. 1996). Equations 13 and 14 allow one to deal with conflicting information. For example, within a geographic region, fish may have disappeared (perhaps momentarily) from some streams but still be present in others. By using Equations 13 or 14 with pre-agreed thresholds, one avoids giving favor to one kind of information over the other and lowers the likelihood of listing species in metapopulations as threatened when they are, in fact, depressed but not in threat of extinction.

Results

For the results presented here, I used 10 streams ($i_{\max} = 10$), a time horizon of 20 years ($T = 20$), and set λ_{i0} and μ_i the same. As a check on intuition, one can consider how $\langle p \rangle$ and p_e depend upon λ_{i0} and μ_i (Figs. 2, 3). Perhaps the most interesting question, though, is how effectively can straying work as a rescue mechanism. Figure 4 is one way of answering this question, in which $\overline{p}_i$ is constant at $1/11$, but the individual values of λ_{i0} and μ_i vary. The conclusion is that the effectiveness of colonization from other streams depends strongly upon the local processes.

Operational considerations

The results suggest that before one can sensibly discuss the extinction risk of salmonid metapopulations, it will be important to gather information on the parameters λ_{i0}, μ_i, and ε. Clark and Rosenzweig (1994) and Rosenzweig and Clark (1994) describe ways for estimating λ_{i0} and μ_i

for the case when $\varepsilon = 0$. Tagging or genetic methods will allow us to estimate ε, although genetic methods might require larger sample sizes of returning fish than is practical for species considered to be at risk (Bartley et al. 1992, Brodziak et al. 1992).

Population Dynamics In Slowly Varying Environments

Oceanographic oscillations will affect the abundance of salmonids (Dunbar 1993) and it is important to understand these if we are to draw correct conclusions. An interesting historical example is provided by Dunbar and Thompson (1979) who studied the qualitative pattern of Atlantic salmon (*Salmo salar* L.) abundance in west Greenland waters:

1576–1586	Salmon probably present
1605–1625	Salmon probably abundant
18th century	Salmon scarce
1806–1812	Salmon present, perhaps abundant
1820–1850	Salmon scarce
1890–1928	Salmon scarce
1928–1931	Salmon observed in increasing numbers
1935–1958	Salmon becoming more abundant
1958–1979	Salmon very abundant

Gaps in the sequence were caused by gaps in the literature used for the reconstruction, not in the presence or absence of salmon. It is not known if this long-term variation was due to temperature fluctuations, the Great Salinity Anomaly (GSA), or other factors (Dunbar 1993).

In this section, I consider metapopulation dynamics (rather than presence-absence dynamics) in a temporally-fluctuating environment and address questions of sampling. First, I introduce the basic model, then elaborate it with temporally-fluctuating environments, and finally consider sampling.

The Basic Model

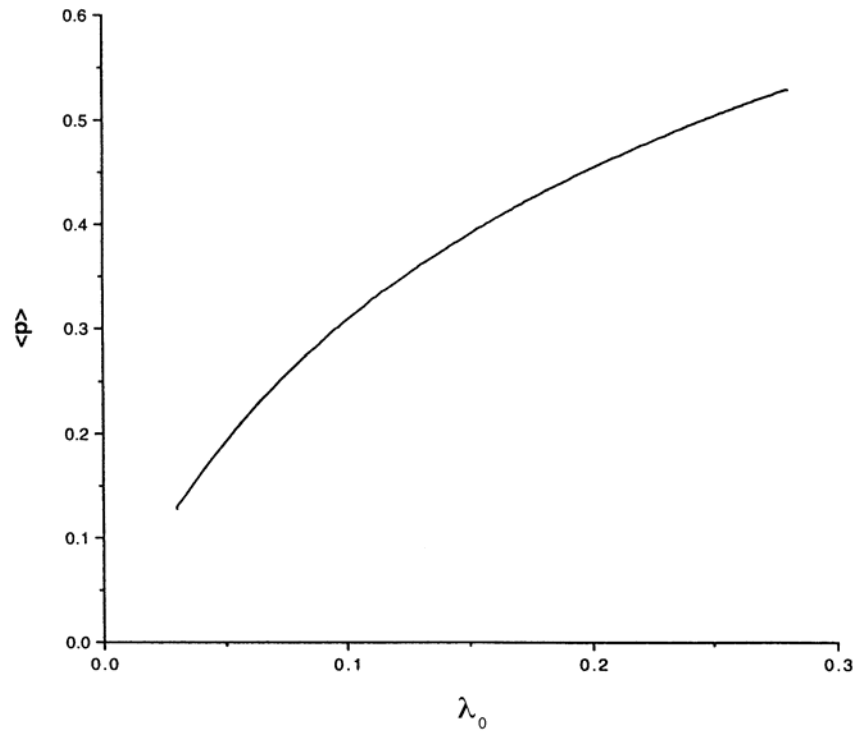
Assuming that density-dependent effects can be ignored (which, except for Allee effects, is almost certainly the case with populations potentially at risk), the fundamental variables are:

$$\begin{aligned} N_i(t) &= \text{ population size in stream } i \text{ at the time of census in year } t \\ r_i(t) &= \text{ per capita reproduction in stream } i \text{ in year } t. \end{aligned} \tag{15}$$

Assume that a fraction f of fish disperse or stray from a stream to its adjacent ones and that reproductive performance of individuals in their non-natal streams is a fraction q of that in the natal stream. With these assumptions, the population dynamics are

$$N_i(t+1) = r_i(t)\left[N_i(t)(1-f) + 0.5fq\left(N_{i+1}(t) + N_{i-1}(t)\right)\right] \tag{16}$$

a)



b)

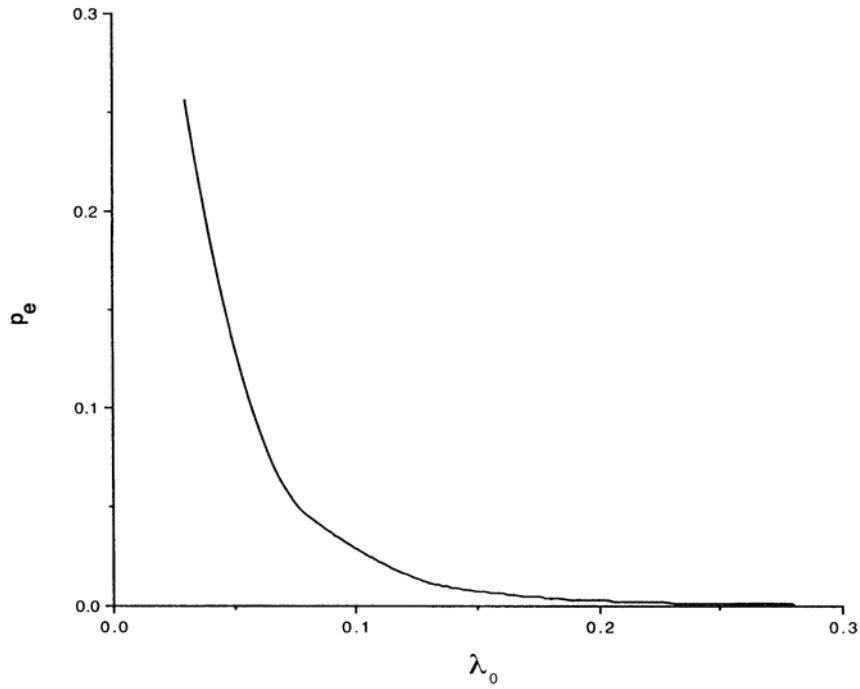
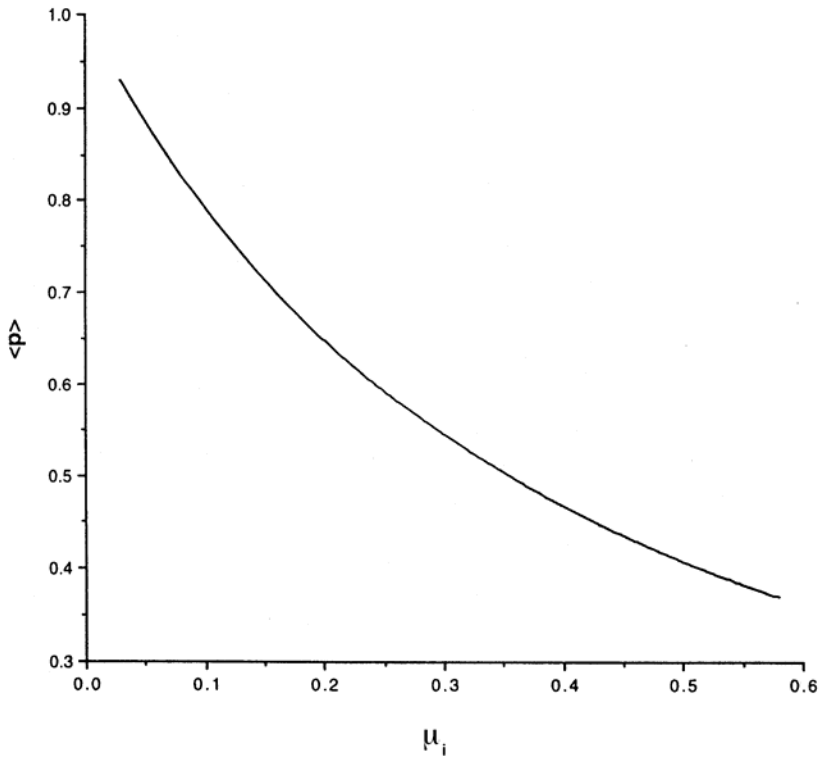


Figure 2. For the spatial birth-and-death model, $<p>$ increases as λ_{i0} increases (panel a) and p_e decreases as λ_{i0} increases (panel b). In these calculations, $\mu_i = 0.3$ and $\varepsilon = 0$.

a)



b)

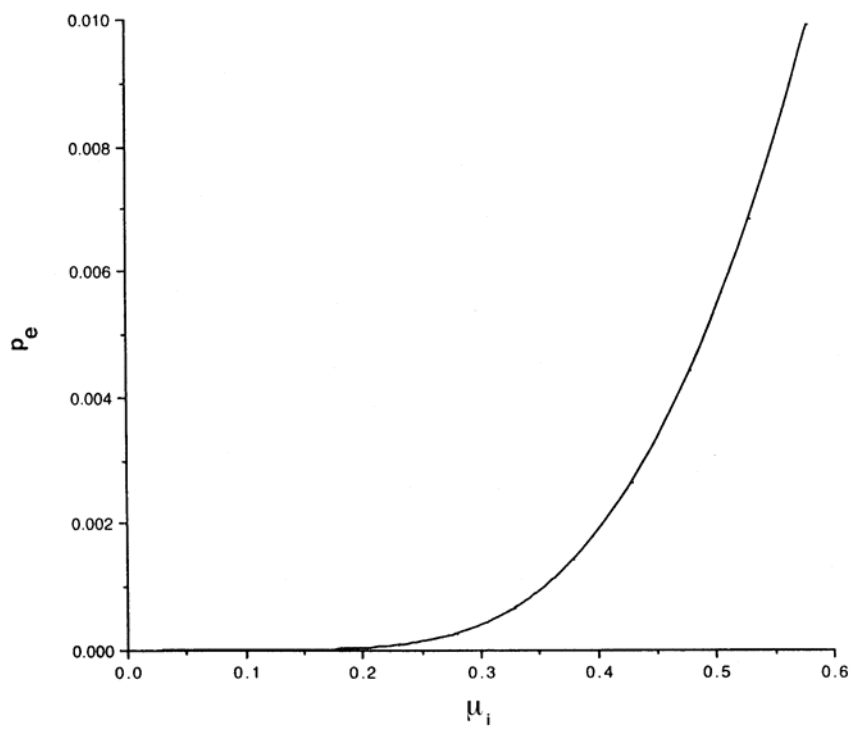
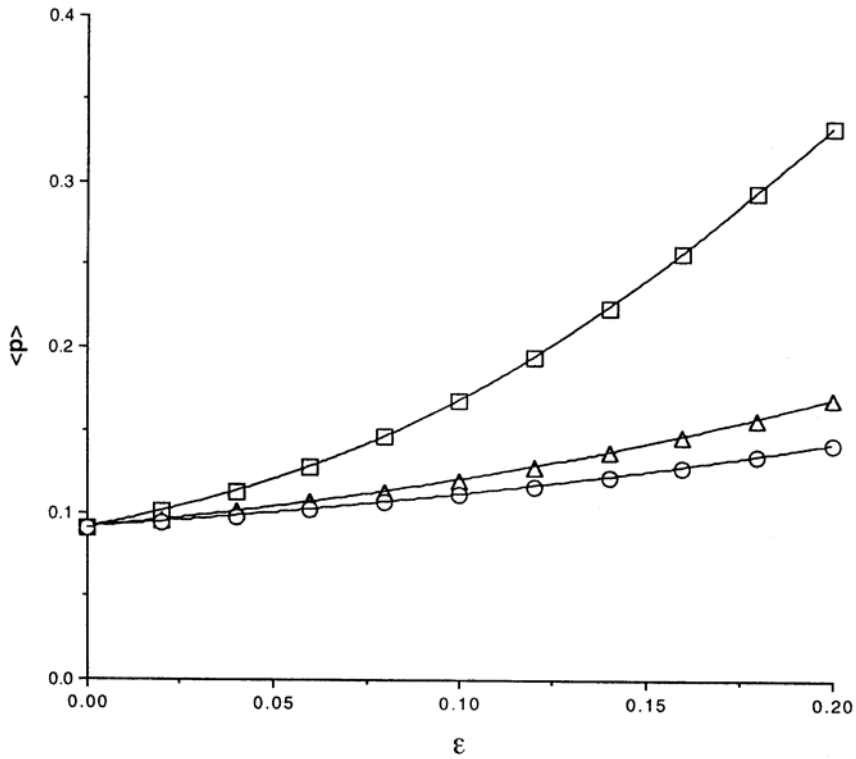


Figure 3. For the spatial birth-and-death model, $< p >$ decreases as μ_i increases (panel a) and p_e increases as μ_i increases (panel b). In these calculations, $\lambda_{i0} = 0.3$ and $\varepsilon = 0$.

a)



b)

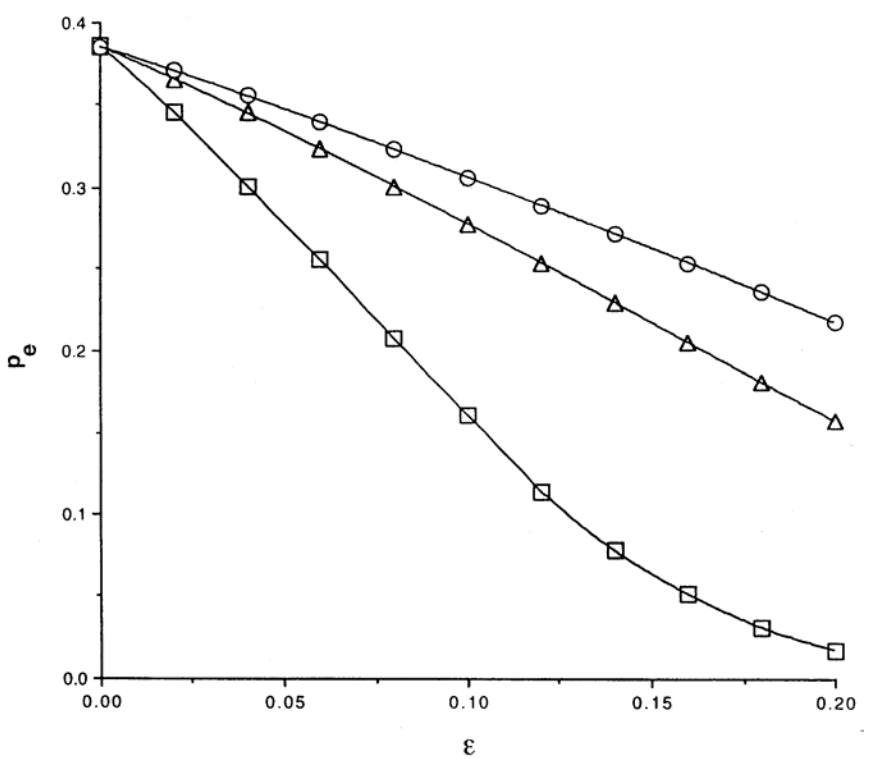


Figure 4. Although $< p >$ increases as ε increases (panel a) and p_e decreases as ε increases (panel b), the quantitative effect is strongly modulated by the values of λ_{i0} and μ_i, which are 0.03 and 0.3 (squares), 0.06 and 0.6 (triangles) or 0.08 and 0.8 (circles).

The first term on the right-hand side corresponds to reproduction by individuals who remain in the natal stream and the second two terms correspond to reproduction by individuals who stray from their natal streams (only 50% of the strays from stream $i + 1$ end up in stream i, the others go to stream $i + 2$, etc.), reducing performance. In Equation 16, I also assume a one-year cycle for reproduction. Fish that spend multiple years before either smolt metamorphosis or maturation could be included by relating $N_i(t + 1)$ to $N_i(t - 1)$, $N_i(t - 2)$ and $N_i(t - 3)$, and using the data in Tables 1 or 2 to weight the lags in reproduction. In the absence of straying ($f = 0$) and a constant environment, if $r_i(t)$ were equal to 1, then population levels would be stable.

Temporally varying environments

I assume that the per capita reproduction rate varies across both time and space and use:

$$r_i(t) = 1 + w + a \cdot \sin\left(\tfrac{2\pi}{\tau}(t + bi)\right). \tag{17}$$

In this equation, w, a, b, and t are parameters; t is the period over which the environment fluctuates, b measures the synchronicity of the environmental fluctuations across different streams, a measures the intensity of fluctuations in terms of per-capita reproduction, and w is chosen so that in the long-term, the population is stable.

Variation in the per-capita reproductive rate $r_i(t)$ could be due to variability in oceanic condition (ENSO events, as mentioned previously) or to variation in stream habitat conditions. There is evidence that West Coast oceanic conditions vary on long-term cycles (Pearcy 1992, Mullin 1993). In such a case, it is important to recognize that salmonid stocks may experience a population bottleneck but then may recover. Some of the weaker streams may be lost, but then recolonized at later points in time.

Real and apparent extinctions

We can consider a population to be functionally extinct due to Allee effects whenever its level falls below a level N_{ext}. However, due to sampling inaccuracy, we may conclude that no fish are present when fish are actually present. Even techniques such as electrofishing can underestimate population size more than 50% of the time (Riley and Fausch 1992).

I assume that sampling can be characterized by the zero-term of negative binomial distribution (Mangel and Smith 1990) with mean $N_i(t)$ and overdispersion parameter k, so that:

$$\Pr\left\{\begin{array}{l}\text{Presence-absence sample concludes that no fish are}\\ \text{present, given that the population size is } N_i(t)\end{array}\right\} = \left(\frac{k}{k + N_i(t)}\right)^k \tag{18}$$

where k is the over-dispersion parameter of the negative binomial distribution (Mangel and Clark 1988). Halley and Dempster (1996) discuss a situation in which apparent extinctions occur because the entire habitat is not sampled.

Results

I report computations for a 25-year time horizon and the following parameter values: $f = 0.1$ (so that 10% of the fish miss their natal stream on return), $q = 0.85$ (so that a fish performs at 85% of its potential when it returns to a non-natal stream), $a = 0.2$, $w = 0.205$, $b = 2$ (see Equation 12), $t = 25$ (so that the environment fluctuates on a 25-year period), and $i_{max} = 25$ (so that there are 25 streams).

Because of the spatial and temporal variation in the per capita growth rate, at any specific time, some streams will have $r_i(t) < 1$ (sink populations, Pulliam 1988) and others will have $r_i(t) > 1$ (source populations, Fig. 5) Because of the temporal variation, the relative roles of sink and source will change over time. This variation also causes oscillation in population size (Fig. 6). Similarly, the population in an individual stream will oscillate (Fig. 7). Nehlsen et al. (1991) considered populations to have a "high risk of extinction" if "fewer than 1 adult fish returns to spawn from each parent spawner." This definition makes obvious sense in relatively constant environments, but requires modification in slowly varying environments.

As shown in Figure 7, the population size in a single stream may fluctuate by a factor of about 8. In such a case, sampling considerations become important. To study sampling effects, one must specify the effective extinction level (N_{ext}) and the overdispersion parameter of the negative binomial distribution (k). One example, for $N_{ext} = 3$ and $k = 1$, is shown in Figure 8. The relationship between the real and apparent extinctions depends upon the value of N_{ext} at which the Allee effect occurs and the size of the overdispersion parameter (Table 3). When k is small, samples are highly over-dispersed (i.e., most samples will yield no fish and a few will yield many) and there is a considerable chance of obtaining a zero sample even if the mean is relatively large (Fig. 9). For example, when 100 individuals are present in the sampling region and $k = 0.25$, there is about a 20% chance that a presence-absence sample will yield no counts.

Operational considerations

The results of the population model suggest that not only should dispersal fractions and relative performance be monitored, but that one needs to have at least a rough idea of the value of the negative binomial k to determine the quality of the information provided by the presence-absence sampling. This could be determined by seeding a sampling area and then conducting presence-absence sampling when one knows the number of fish present.

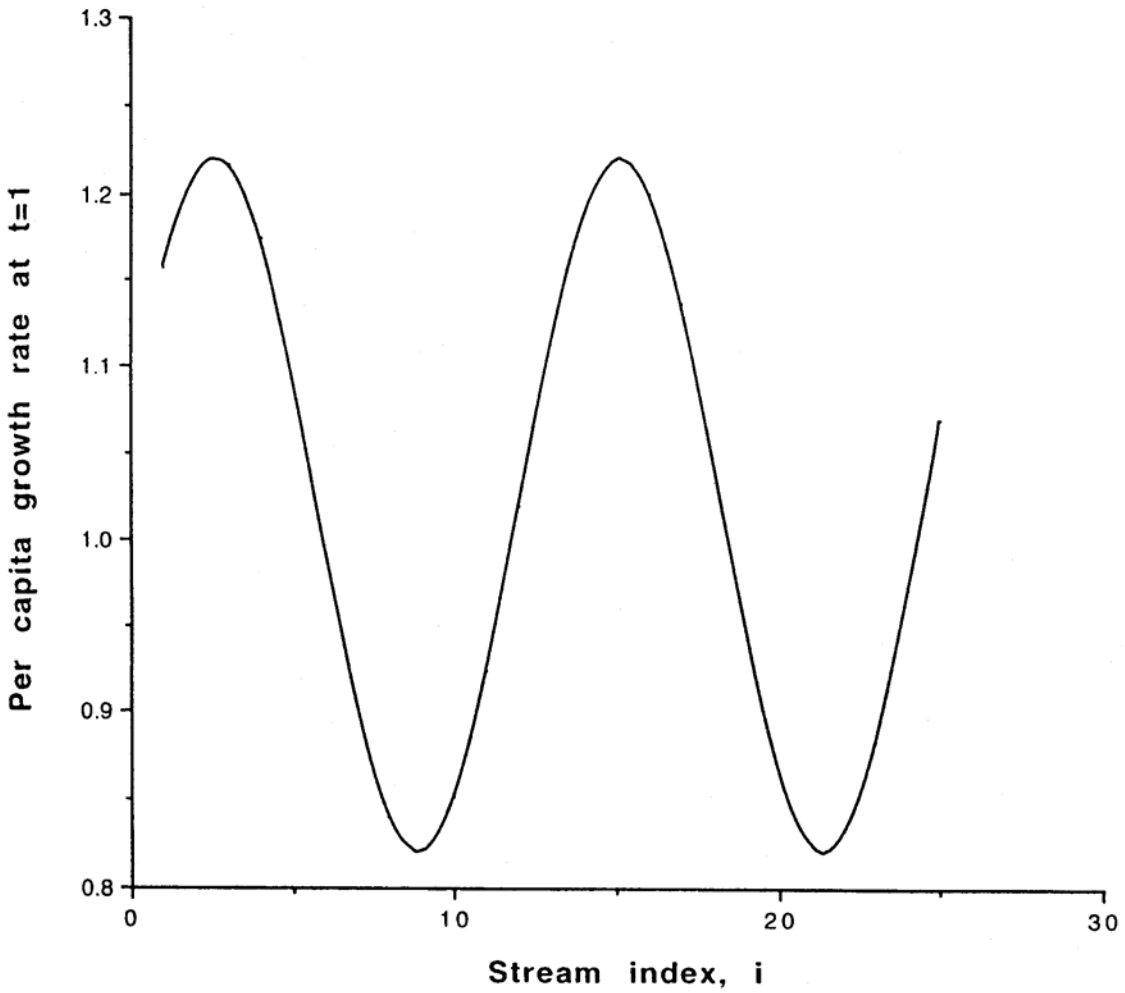


Figure 5. At a given time, some populations will have per capita growth rate less than 1 and some will have per capita growth rate in excess of 1.

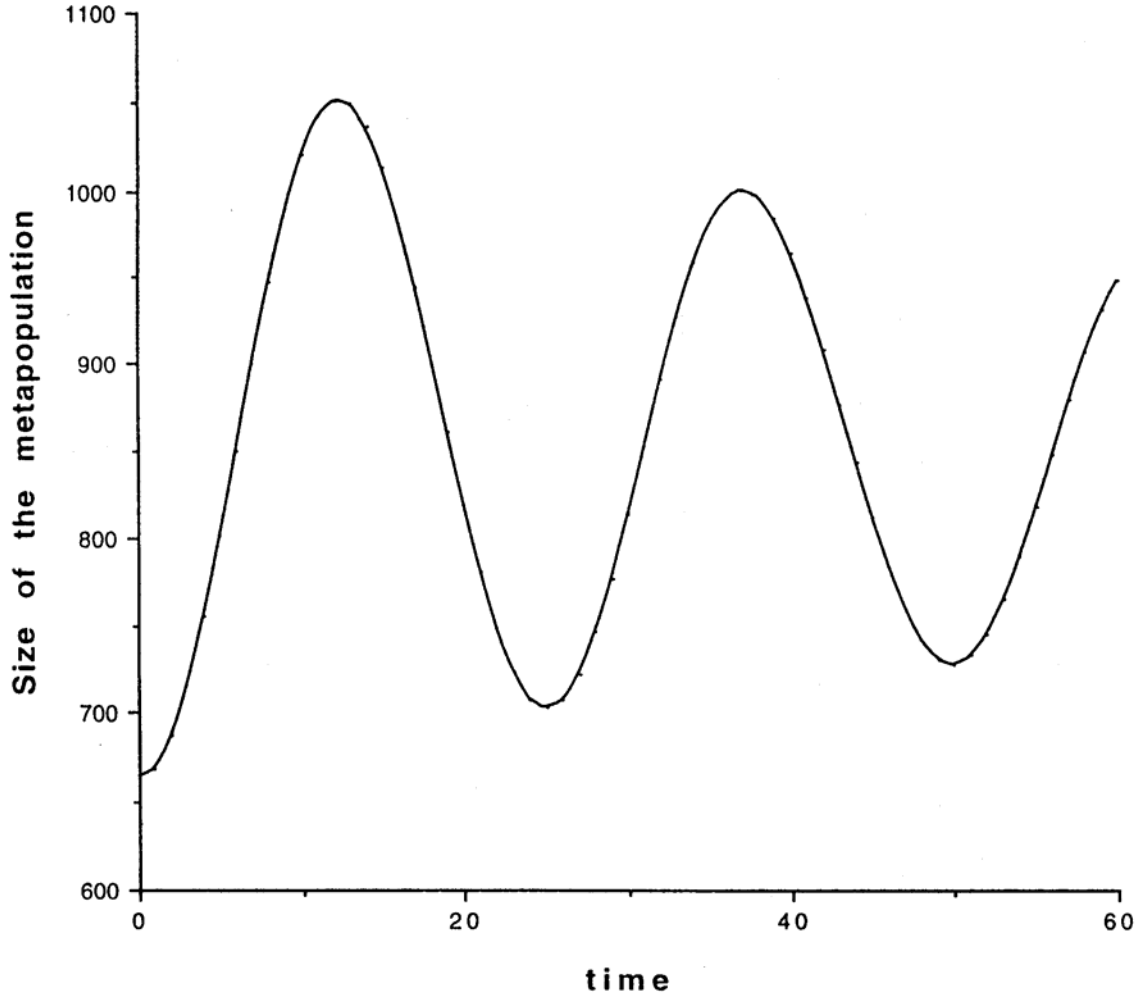


Figure 6. The total population, obtained by summing $N_i(t)$ across all streams, oscillates because of the temporal and spatial variation in the per capita growth rates.

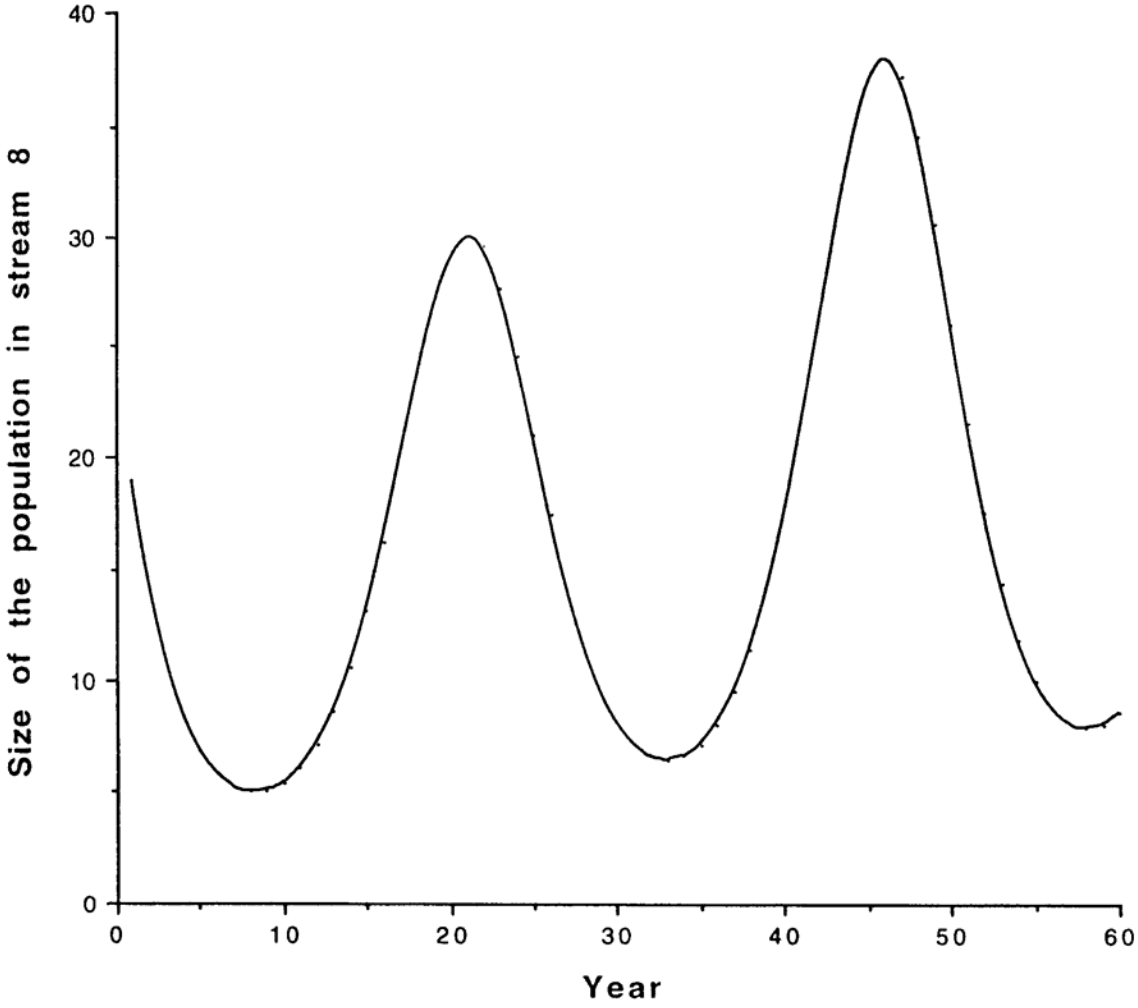


Figure 7. The population in stream 8 fluctuates over time. This is typical of other streams (although they are out of phase).

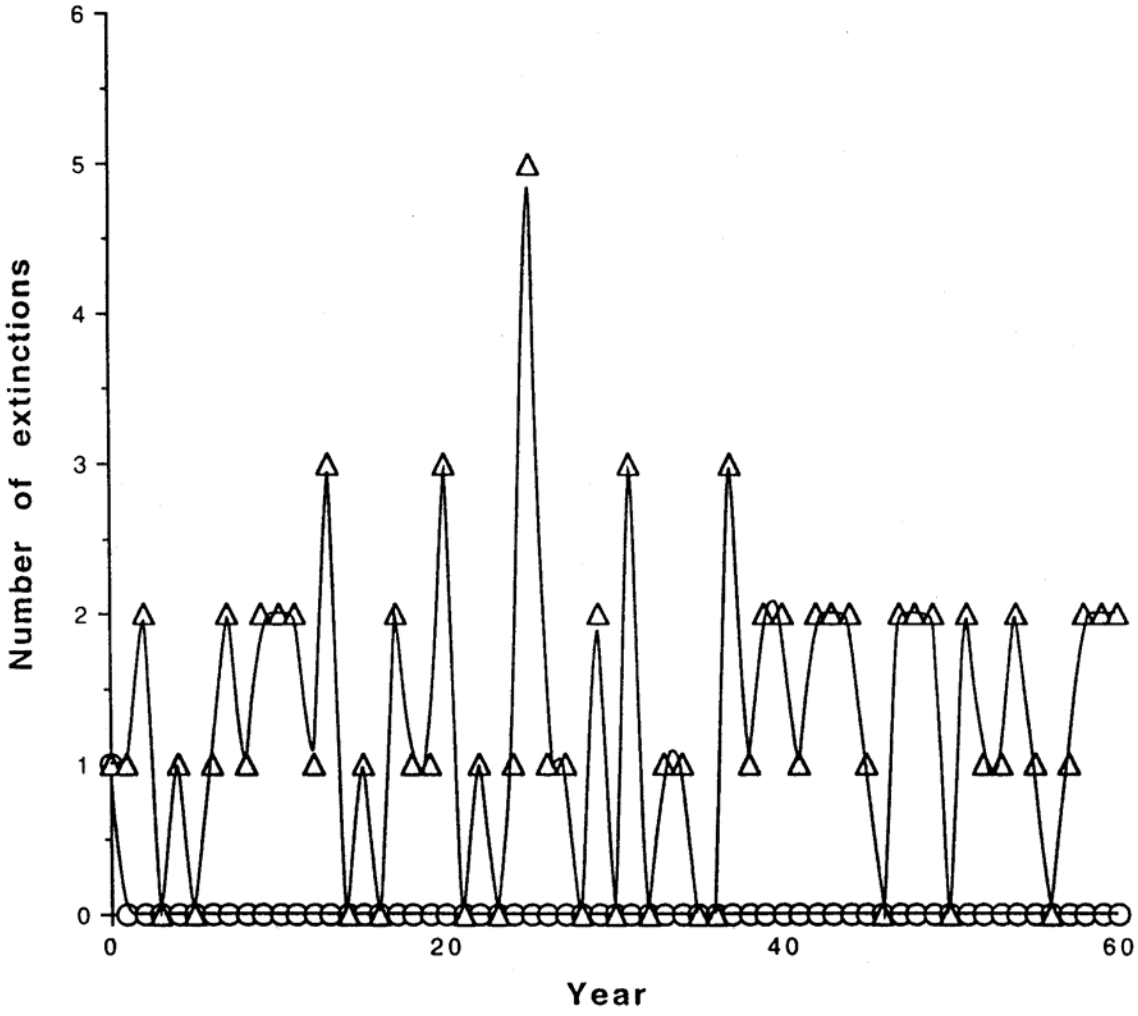


Figure 8. The average yearly number of real (circles) and apparent (triangles) extinctions over the time horizon for $N_{ext} = 3$ and $k = 1$.

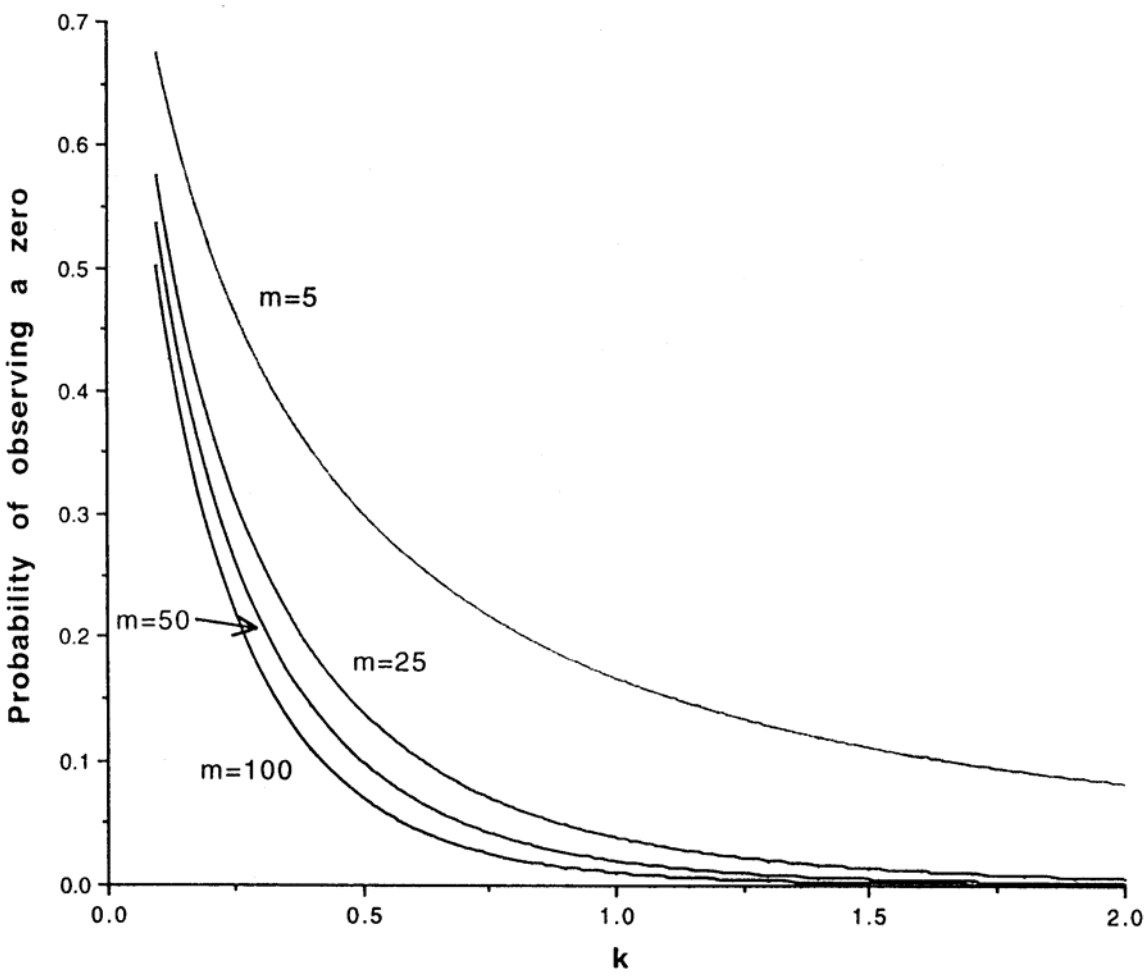


Figure 9. Presence-absence sampling for overdispersed samples can yield very high probabilities of zero-counts even when the mean (*m*) is as large as 100.

Table 3. Average number of real and apparent extinctions per year as a function of the extinction level (N_{ext}) and overdispersion parameter (k).

N_{ext}	k	Average Number of Extinctions per Year	
		Real	Apparent
1	1	0.0	1.31
1	2	0.01	0.4
1	3	0.05	0.3
1	4	0.05	0.08
1	5	0.05	0.06
2	1	0.16	1.43
2	2	0.1	0.33
2	3	0.3	0.3
2	4	0.1	0.08
2	5	0.16	0.13
3	1	0.15	1.26
3	2	0.53	0.21
3	3	0.16	0.08
3	4	0.16	0.05
3	5	0.16	0.06
4	1	0.16	1.13
4	2	0.51	0.51
4	3	0.28	0.06
4	4	0.4	0.13
4	5	0.31	0.08
5	1	1.55	1.61
5	2	0.53	0.33
5	3	0.83	0.2
5	4	1.43	0.11
5	5	1.11	0.08
6	1	0.76	0.98
6	2	1.95	0.45
6	3	1.38	0.2
6	4	2.00	0.13
6	5	1.75	0.1

Table 3. Average number of real and apparent extinctions per year as a function of the extinction level (N_{ext}) and overdispersion parameter (k). Continued.

N_{ext}	k	Average Number of Extinctions per Year	
		Real	Apparent
7	1	3.46	1.58
7	2	2.96	0.35
7	3	2.08	0.1
7	4	5.3	0.21
7	5	4.33	0.18
8	1	2.26	1.16
8	2	3.26	0.31
8	3	2.86	0.08
8	4	2.6	0.08
8	5	2.95	0.05

Conclusions

Metapopulation ecology and metapopulation models can inform the assessment of extinction risk of West Coast salmonid populations. A number of issues remain:

1) Metapopulation dynamics (either patches or actual numbers) should incorporate the life-history variation (age at smolt metamorphosis and age at maturity) found in salmonids. This will reduce generality, because various species have life-history variation patterns that differ, but increase the applicability to a particular species.

2) The practical model of Hanski and the presence-absence model developed here should be extended to the case of slowly varying environments.

3) The connection between the metapopulation (based on an ecological concept of dispersal) and the ESU (based on genetic concepts) needs to be clarified.

4) Various kinds of empirical information need to be gathered, including:

    a) What is the relationship between local extinction and stream size? Alternatively, what measure of habitat is appropriate? Although it is generally assumed that habitat is limiting for production (Gowan and Fausch 1996), the assumption that the extinction probability is inversely related to habitat needs to be verified.

    b) What is the ecological range of dispersal (versus genetic definition of an ESU)?

    c) What is the level of regional synchronicity? Long-term persistence of a metapopulation requires sufficient decoupling of the dynamics in different streams.

Finally, as good ecologists, we should expect multiplicity of causes and effects in ecological systems. For example, central California steelhead trout *(Oncorhynchus mykiss irideus*, Behnke 1992) may experience stream habitat degradation, decreased water flow, marine mammal predation, and fishing pressure. Decreasing the extinction risk is likely to require mitigating all of these factors, not just one.

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Ecosystem Diversity and the Extinction Risk of Pacific Salmon and Trout

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(The following represents our thoughts and the literature at the time of the symposium. The conservation and recovery of Pacific salmonids in the context of landscape dynamics has been fertile ground for research. In the past few years there has been much development and refinement of the underlying concepts.)

The landscape within the distributional range of Pacific salmon and trout (*Oncorhynchus* spp.) is dynamic in space and time. Geologic processes of glaciation and volcanism have shaped a large portion of the area (McPhail and Lindsey 1986). Other events such as fire and flood have shaped the landscape at smaller temporal ($10^1 - 10^2$ years) and spatial scales (watersheds and basins) (Benda 1994). These various disturbances created a shifting mosaic of abiotic and biotic conditions across the range of these fish (Reeves et al. 1995). Pacific salmon and trout are adapted to dynamic environments through life-history attributes that include straying by adults, relatively high fecundity rates, variability in age of ocean entry, variability in age structure, and mobility of juveniles (Reeves et al. 1995).

Human development of western North America has modified this mosaic of conditions and has modified the temporal and spatial distribution of the habitat conditions that Pacific salmon and trout encounter. Declines of Pacific salmon and trout populations (Nehlsen et al. 1991) and other fish species in the Pacific Northwest (Williams et al. 1989, Frissell 1993) have been observed, in part, as a result of these changes. Variability in abiotic and biotic conditions has been modified and constrained to such an extent that opportunities for Pacific salmon and trout to persist have been reduced (Reeves et al. 1995). This reduction and simplification of system diversity has occurred over various temporal and spatial scales.

Ecosystem diversity, for our purposes, represents the variability of states or conditions in the freshwater ecosystem. An ecosystem is a series of states or conditions, each with given physical and associated biological features. The particular state present at a location is primarily a function of the time since the last major disturbance and the geomorphic setting. The state or

condition of a location can be thought of as a function of the disturbance history and recovery rate, with the recovery rate highly dependent on the geomorphic setting (e.g., alluvial stream reach vs. a high-gradient stream reach). Within a basin or across a number of basins, there may be a mosaic of conditions that are dynamic in space and time.

The spatial and temporal shifting mosaic character of freshwater ecosystems is a critical component in our definition of ecological diversity. Ecosystems are a result of diverse and complex abiotic and biotic interactions occurring over several decades to centuries at the river basin scale. Understanding systems at these temporal and spatial scales is difficult because past processes and interactions are often matters of surmise. But an understanding, or recognition, of these processes is needed because it may be this diversity of conditions that provides opportunities for the development of life-history variability and for persistence of salmon and trout populations. Lack of ecosystem diversity could result in lower phenotypic diversity among individuals and a scarcity of available habitat across the landscape (den Boer 1968, Poff and Ward 1990). Appropriate scales of time and space for ecosystem conditions to move through various stages need to be considered if ecological diversity is to be protected or restored (Reeves et al. 1995). In this context, consideration of ecological diversity invites questions concerning the role of dynamic environments in shaping the structure of populations and how one might incorporate this diversity in analyses of the extinction risks of Pacific salmon and trout.

The Pacific Northwest region is a highly dynamic environment over shorter, temporal (less than 300 years) scales. Understanding the structure of local species assemblages requires a reference to regional-scale phenomena (Gaston 1996). For example, the natural disturbance regime in the central Oregon Coast Range includes infrequent stand-resetting wildfires and frequent flood events that may result in concentrated landsliding into stream channels and debris flows (Reeves et al. 1995). These naturally occurring disturbances have immediate (e.g., direct mortality, habitat loss, barriers to migration) and long-term implications (e.g., introduction of essential habitat elements – large wood and sediment, alteration of channel morphology) for Pacific salmon and trout. This episodic delivery of materials causes stream channels to alternate between aggraded and degraded sediment states, and therefore, a natural mosaic of habitat conditions (i.e., range of channel conditions) exists within and among watersheds (Reeves et al. 1995). In the central Oregon Coast Range, conditions ranged from channels aggraded with sediment and little large wood, to a variety of substrates and intermediate amounts of large wood, to bedrock and large quantities of large wood. All conditions were historically found on the landscape (Benda 1994); however, they were not necessarily in equal proportions. A given watershed potentially experienced the range of these conditions over time.

Reeves et al. (1995) found that each ecosystem condition they encountered had an associated fish assemblage. The assemblage, associated with the aggraded condition and bedrock-dominated state, contained almost exclusively coho salmon. The state with a variety of substrate and intermediate amounts of large wood had an assemblage dominated numerically by coho salmon (*O. kisutch*) (85% of the fish present). However, cutthroat trout (*O. clarki clarki*) and steelhead (*O. mykiss*) were also present in relatively large numbers (12.5% and 2.3% of the total numbers, respectively).

The persistence of a population or group of populations (e.g., metapopulation) is dependent on the presence of suitable ecosystem states and the ability of populations to track and use these patches through time. Tracking changes in ecosystem states requires a diversity of suitable connecting habitat. Variation in habitat at small spatial and temporal scales is required for a fish to complete its life cycle and to accommodate a number of life stages or species within a single habitat unit, stream segment, tributary, or watershed. The opportunity for movement across the landscape during various portions of its life cycle (e.g., spawning, over-wintering, ocean migration) is critical for the survival of a local population and opportunities for individuals to move among populations (i.e., stray) are critical for recolonization following local extinctions.

The ability to disperse depends upon distance and habitat conditions along the route of dispersal. Taylor et al. (1993) used the term landscape connectivity to express the degree to which the landscape facilitates or impedes movement among areas. Suitable ecosystem states should exist not only in areas that contain (or could contain) populations, but also across the landscape that provides opportunities for movement as well (Wiens 1997). The term mosaic management (Wiens 1997) has been used to describe efforts to manage movement patterns. This requires that a range of landscape features (i.e., ecosystem states) be considered when determining the fate of local populations in habitat patches.

Changes in type, frequency, and magnitude of natural disturbance can alter abiotic and biotic features and the resilience of an ecosystem (White and Pickett 1985, Hobbs and Huenneke 1992). Resilience of an ecosystem is the capacity of an ecosystem to return to a domain of behavior or range of conditions the system experiences following disturbance (Holling 1973). Changes in the legacy of disturbance may be important in determining the resilience of an ecosystem by altering immediate and future habitat conditions following a disturbance (Reeves et al. 1995). The legacy of a disturbance represents the conditions that exist following a disturbance, and in aquatic ecosystems these conditions are greatly affected by such things as large wood, sediment input and movement, and floodplain function. When the resilience of a system is altered, the domain of behavior may shift and a new system with new, previously unexhibited conditions or states will develop (Reeves et al. 1995, Ebersole et al. 1997). Anthropogenic disturbances, such as timber harvesting and urbanization, may result in disturbances that force systems to a different domain or set of conditions (Yount and Niemi 1990). Gurtz and Wallace (1984) hypothesized that stream biota may not have the capacity to recover from anthropogenic disturbances because they may not have evolved the appropriate breadth of habitat or reproductive requirements, and because such disturbances have no analogues in the natural disturbance regime.

Temporal synchronization of habitat conditions can also result from land-management activities. Historical habitat conditions varied across the landscape creating a shifting mosaic of conditions. Management activities over large areas have resulted in a temporal synchronization of habitat conditions that has resulted in large portions of the range of Pacific salmon and trout to be at a similar state, usually with a reduced capacity for one or more species at the same time (Fig. 1). This situation reduces the range of abiotic conditions and may limit opportunities for the development of various life-history types and for movement of individuals across the landscape. Human activities have altered and constrained the recovery potential of ecosystems,

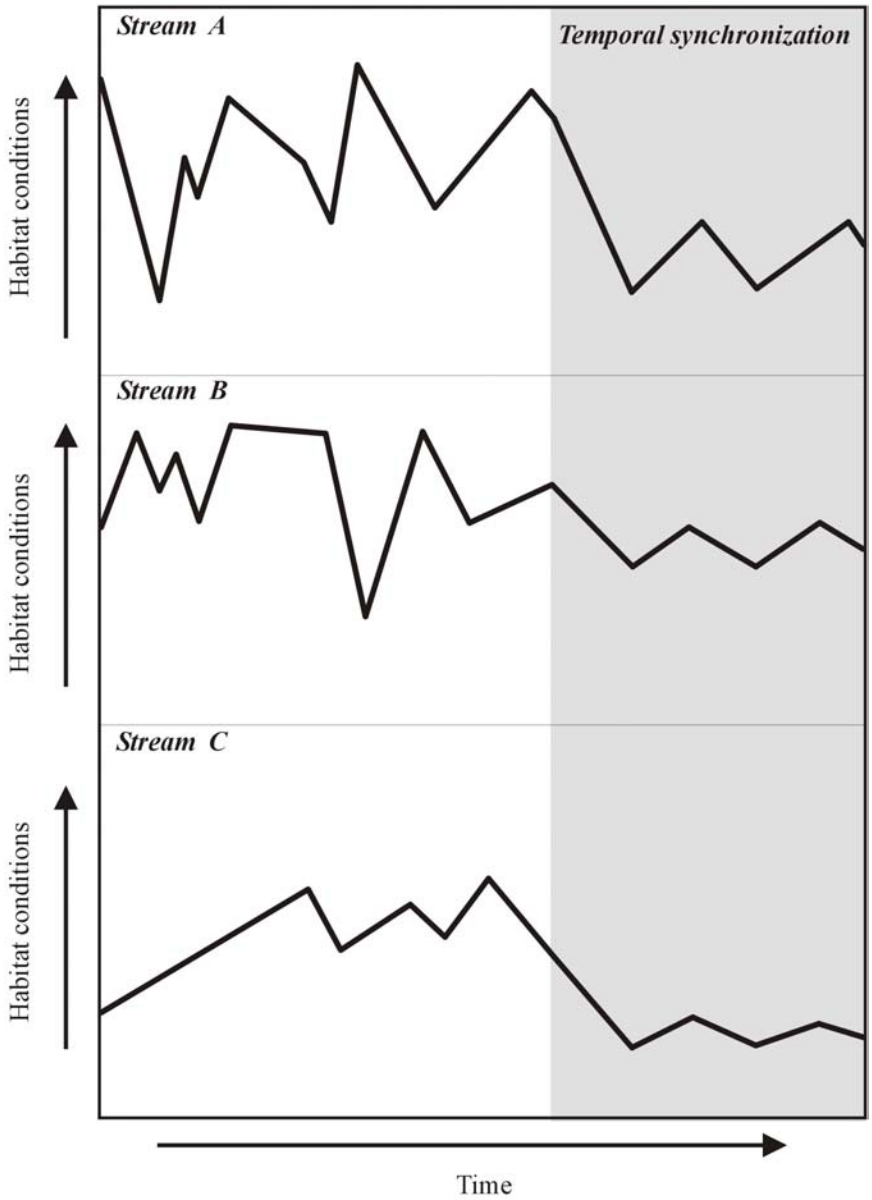

Figure 1. Hypothetical historical conditions followed by temporal synchronization of habitat conditions in three different streams within and among watersheds (Benda 1994, Reeves et al. 1995).

which may be as responsible for the decline of habitat as the direct impact of the original activity (Reeves et al. 1995, Tilman 1996, Ebersole et al. 1997).

When evaluating the extinction risk of Pacific salmon and trout, a static view of habitat conditions may lead to unrealistic expectations of persistence time. The shifting mosaic nature of habitat conditions is discounted if recovery and restoration activities rely solely on a system of reserves. For example, areas set aside for reserves will eventually shift into a less productive state. The loss of reserve habitat cannot be offset by adjacent non-reserve habitat shifting into a productive state if non-reserve habitat is not allowed to recover from human disturbance. Temporal synchronization between reserve and non-reserve areas will result in a continued loss of habitat until the ecological diversity of ecosystems across the landscape can be reestablished. Strategies used in the past for the design and management of reserves focused on species and ecosystems, often ignoring landscape scale and ecological processes relevant at longer time scales and larger spatial scales (Baker 1992). Short-term considerations should include areas with good habitat conditions and functionally intact ecosystems for those areas that remain (Reeves et al. 1995), but long-term considerations must include larger areas. A system made up of disconnected, isolated reserves that are too small to exhibit independent environmental variance (in relation to other reserve areas) increases the risk of metapopulation extinction by reducing opportunities for natural recolonization (Goodman 1987). A reserve system that includes many independent reserves (i.e., exhibit independent environmental variance) across the landscape, and allows for recolonization (i.e., adequate habitat for dispersal among areas) diversity in abiotic and biotic conditions, and adequate time for habitat recovery should provide longer persistence time. Without opportunities for dispersal and recolonization, smaller independent reserves may confer shorter persistence time than a single large reserve (Goodman 1987).

Conclusions

We have identified several critical factors that must be considered if one is to assess the extinction risk of a population or group of populations of Pacific salmon and trout. This is not to dismiss factors such as harvest, influence of hatcheries, and passage mortality. In general, the abiotic and biotic factors to consider are those that provide opportunities for life-history variation to exist, for individuals to move among populations and habitat, and for ecosystems to progress through ecological states over various spatial and temporal scales. We believe that a dynamic ecosystem context is necessary for the extended persistence of Pacific salmon and trout.

As ecological diversity is reduced or lost as a result of a reduction of the abiotic and biotic capacity of the ecological system, opportunities for the expression of phenotypic and genetic variation are reduced or lost. An inappropriate delineation of a population unit may result in an inadvertent misinterpretation of phenotypic characters unique to a particular environment as being nonadaptive, and therefore not incorporating the ecological diversity (i.e., abiotic and biotic) that has allowed that particular population or group of populations to persist. Failed attempts to establish or reestablish populations of Pacific salmon and trout, especially those with more variable life-history types (e.g., sockeye salmon, coastal cutthroat trout), suggest that the local environment is more than a stage to play out a particular phenotype. Wood (1995)

found that reproductively isolated populations of sockeye salmon were adapted to local conditions and were, in some sense, evolutionarily significant. The lack of success in efforts to establish or reestablish Pacific salmon and trout to suitable habitat seems to "fly in the face of the species' apparent phenotypic plasticity and opportunism" (Healey and Prince 1995). Despite many attempts to transplant anadromous sockeye salmon, self-perpetuating anadromous populations have rarely been established, although the establishment of nonanadromous (kokanee) populations from introduction of anadromous populations have occurred (Wood 1995). The failure of anadromous sockeye salmon transplants, despite the establishment of nonanadromous kokanee from these efforts, suggests local adaptation within the donor population for anadromous behavior of sockeye salmon (Wood 1995).

Opportunities for dispersal across the shifting mosaic landscape must be considered when evaluating the extinction risk of Pacific salmon and trout. The extent of structuring of local populations is partially related to the species' life-history patterns and its dispersal capabilities (Avise 1992). Pease et al. (1989) suggested that migration (e.g., dispersal, straying) may often be of greater importance than selection for a population in a changing environment, allowing the population to spatially track a moving environment (i.e., changing environment). Life-history patterns exhibited by a species and opportunities for dispersal are greatly influenced by habitat condition. When populations encounter constraints to tracking environmental change, the population must adapt to local environmental challenges to survive. Even with large population sizes, the extinction risk of a population can increase when opportunities for tracking environmental change (e.g., dispersal) are reduced (Pease et al. 1989). When stray rates are low (or their mortality rate is high), intra-specific variation (local adaptation) may result (Quinn 1997). As dispersal opportunities and suitable habitat are reduced or lost (i.e., greater isolation among populations) due to land use activities, an extinction rate greater than that from the simple loss of habitat area may result (Rieman and McIntyre 1995).

Although the evidence that local adaptation is pervasive and important in populations of Pacific salmon and trout is indirect and circumstantial, observations of local adaptation in other organisms show that it is the result of dynamic processes and it is these processes that must remain intact to preserve genetic diversity (Taylor 1997).

We have attempted to introduce the importance of ecosystem diversity in terms of spatial and temporal variation in abiotic and biotic conditions into the consideration of the extinction risk of Pacific salmon and trout. As Kareiva (1990) pointed out, "simply saying that the spatial environment is important is to mouth a platitude." The examples presented emphasize that variation in abiotic and biotic conditions exists within stream systems and across the landscape of Pacific salmon and trout. This variation is absolutely crucial because it provides the environmental context that these species have evolved in and the context for their recovery and persistence. It is important when assessing the extinction risk of a population of Pacific salmon and trout to recognize the ecosystem processes that generate and maintain the shifting mosaic landscape patterns (Schlosser and Angermeier 1995). Adkison (1995) considers alternatives to the concept of local adaptation. We agree with him that both basic science and conservation efforts would be improved if alternatives are considered, but with fewer and fewer functioning habitats and extent populations, the risk of not assuming local adaptation in the course of land management and conservation decisions may be irreversible.

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The Genetic Risks of Extinction for Pacific Salmonids

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A century of human activities, greatly intensified over the past fifty years, has imposed upon anadromous species of Pacific salmon a diverse array of selective challenges. These include:

- threats from overfishing,
- loss of spawning habitat due to the consequences of logging, road building and irrigation,
- blockage of access to spawning grounds resulting from the construction of dozens of hydroelectric dams,
- adverse interactions with introduced species, and
- possibly human-induced global climatic change.

There is perhaps no West Coast salmonid stock that is not confronted with at least one of these problems, and most are facing all of them. Most of these adverse factors have never been previously encountered in the entire fifty or so million years of the salmonid lineage. Due to the long time spans necessary for ecosystem recovery, most of these factors are not likely to dissipate greatly over the next several decades, even if restoration plans are swiftly implemented.

The goal of many well-intentioned environmentalists is to preserve, indefinitely, the gene pools of wild salmonid populations as they were prior to their exposure to intense human activities. This is a naive and reckless philosophy, in that lack of evolutionary change in the face of a radically changing environment can only lead to further loss of adaptation and increased risk of extinction. While evolutionary flexibility is a vital component of any species' adaptive arsenal, with the multiplicity of strong selective challenges confronting them today, such flexibility is absolutely critical to the future survival of West Coast salmonids. It is quite conceivable that populations of salmonids that do not evolve substantially over the next few decades will be doomed to extinction. Dozens to hundreds of unique stocks have already been extirpated (Nehlsen et al. 1991, Williams et al. 1992).

The genetic issues relating to the long-term viability of Pacific salmonids extend well beyond the usual considerations for other endangered species. Until recently, Oregon and Washington salmon have served as a major commercial, cultural, and recreational resource for both coastal and inland communities. The political pressures to provide conditions that restore high harvest rates are enormous. However, for the most part, the means to this end have been as short sighted as the activities that are directly responsible for species' declines. Rather than dealing directly with the ecological alterations that have led to the demise of salmonids, federal and state fishery agencies have put most of their efforts into building and maintaining dozens of hatcheries, with the primary mission to enhance the total production of fish. While occasionally

fulfilling this goal, the management policies of many hatcheries are often inconsistent with the long-term survivorship needs of native populations of fish.

This paper provides a nontechnical overview of the genetic issues that should be considered in evaluating the extinction risks of indigenous stocks of salmonids. Although studies on the evolutionary genetics of salmonids are rare (reviews appear in Allendorf and Waples 1996, and Hard and Hershberger 1995), the genetic phenomena described in the following are known to occur in a diversity of species of plants, invertebrates, and vertebrates. The principles emerging from these studies are sufficiently general to provide substantial guidance in the development of conservation genetic policies of most species, including salmonids.

I begin by providing a broad overview of the consequences of small population size for the genetic integrity of a population, with special attention being given to the approximate population size beyond which a species can be viewed as being genetically secure. Although the number of breeding adults is not the only determinant of the evolutionary potential of a population, it is the primary factor in most cases, and its relative ease of determination makes its evaluation a critical first step in any genetic risk analysis. I next consider issues involving population subdivision. Because of the extraordinary degree of homing extinct in anadromous salmonids, population substructure and local adaptation is expected to be especially pronounced, serving as an additional reservoir of evolutionary flexibility in these species. I then review how hatchery programs can greatly compromise the degree of adaptation in individual populations, as well as lead to a loss of the adaptive variation that has historically developed between populations. Finally, I consider the implications of our current state of knowledge of salmonid genetics for the application of listing criteria under the ESA.

The Genetic Effective Size of Salmonid Populations

From an exploitative or management perspective, population abundance is often taken to be a good estimate of population health, if for no other reason than the fact that such numbers are often easily acquired. However, from the standpoint of conservation genetics, the total census number of adults will almost always underestimate the genetic extinction risks, often considerably so. The relevant measure of population size from a population-genetic perspective is known as the effective population size, and is generally denoted by N_e.

The fundamental concept of effective population size can be understood by considering a randomly mating diploid population with separate sexes. For any autosomal locus, if we take a single gene from each of two random members of the population, and let P be the probability that both genes will have come from the same individual in the preceding generation, then $1/P$ is equivalent to the effective population size. In a diploid population, $1/(2\ N_e)$ is the probability that two random alleles are direct copies of the same gene in the preceding generation. In the ideal case in which there are equal numbers of males and females, completely random mating with random family sizes, discrete generations, and constant numbers of adults from generation to generation, N_e is approximately equal to the number of reproductive adults (N). However, in most natural settings, a number of factors conspire to insure that N_e will be less than N, most

notably uneven sex ratios, variance in family sizes, and temporal fluctuations in population density.

The Relevance of Effective Population Size to Risk Analysis

Even a rough estimate of the genetic-effective size of a population can be highly informative from the standpoint of risk analysis. The primary reason for this is the fact that the quantity $1/(2N_e)$ defines the magnitude of random genetic drift in a population on a per-generation basis. For genes with no selective consequences for their bearers, $1/(2N_e)$ is the expected rate of loss of heterozygosity from the population per generation. Such neutral alleles have little bearing on the extinction risk, but the effective size of a population influences the fates of a broader class of genes. The evolutionary dynamics of alleles with absolute selective effects less than $1/(4N_e)$ are almost completely determined by random genetic drift. Such alleles are said to be effectively neutral, despite the fact that they may have advantageous or deleterious effects on individual fitness. Even alleles with absolute effects as large as $1/N_e$ have fates that are somewhat influenced by chance events. These population-genetic principles have two important implications for the fitness of small populations — all alleles with beneficial effects less than approximately $1/(2N_e)$ will be subject to random loss, while mutations with deleterious effects milder than $1/(2N_e)$ will be subject to accumulation by random genetic drift. Thus, the smaller the effective size of a population, the narrower the range of beneficial alleles that can be exploited for adaptive evolutionary change, and the wider the range of deleterious alleles that can contribute to cumulative damage to the population.

Numerous attempts have been made to develop ranking schemes to identify threshold effective sizes below which the genetic integrity of a population is seriously threatened (Franklin 1980, Soulé 1980, Soulé et al. 1986, Mace and Lande 1991). All such classifications have focused on criteria such as the maintenance of 90% of the genetic variance in the ancestral (predisturbance) population for periods of 200 or so years. Goals such as these are arbitrary with respect to the magnitude of acceptable loss and time span, and the critical population size can be quite dependent on the assumptions of the genetic model. An alternative approach is to consider the critical size of a population beyond which the evolutionary dynamics are essentially the same as those of an effectively infinite population (Lande 1995, National Research Council [NRC] 1995, Lynch 1996). Recent theoretical work has led to some general qualitative conclusions about the relationship between effective population size, deleterious-mutation accumulation, and adaptive evolutionary potential, which I will now briefly review.

A universal observation from quantitative-genetic analyses is that all natural populations of diploid organisms harbor large numbers of mildly deleterious recessive alleles which, when made homozygous through inbreeding, result in substantial decreases in fitness (Lynch and Walsh 1997). The high incidence of such genes is due to the fact that the genomic deleterious-mutation rate for higher organisms is typically on the order of one per individual per generation. In large populations, where the efficiency of natural selection is high, the frequencies of most such deleterious mutations are kept low, and because low-frequency alleles exist primarily in the heterozygous state, their effects are partially masked by more dominant beneficial alleles. However, as noted above, a reduction in the effective size of a population to a small size will

release the spectrum of deleterious alleles with effects smaller than $1/(2N_e)$ from the grip of natural selection. Such alleles will drift to fixation with probabilities approximately equal to their initial frequencies.

Since the majority of deleterious alleles appear to have mild effects (on the order of 5% or less in the homozygous state), the ultimate decline in fitness that can result from the fixation of deleterious alleles in a severely bottlenecked population can be substantial. Experiments involving strong inbreeding, in normally outbreeding populations of animals, almost always result in fitness declines of at least 20% and often substantially more (Table 1). While the best estimates of the consequences of inbreeding have been derived with laboratory or domesticated species, these results are quite general (Thornhill 1993, Lynch and Walsh 1997). No quantitative estimates of inbreeding depression seem to be available for anadromous salmonids, but Kincaid (1976a, b) produced rainbow trout (a close relative of steelhead) that were up to 50% inbred. Linear extrapolation of his data suggests that intense inbreeding in these fish would eventually lead to an approximately 19% increase in the incidence of major birth defects, 62% decline in survival to 147 days, and 83% decline in weight at 1 year. Slower rates of inbreeding will have less pronounced effects due to the fact that a larger fraction of deleterious alleles will be purged by natural selection (Lynch et al. 1995a).

The fate of deleterious recessive alleles initially present in a bottlenecked population is an important consideration in any conservation management plan, and has received a substantial amount of theoretical scrutiny (Senner 1980, Lacy 1992, Halley and Manasse 1993, Hedrick 1994, Mills and Smouse 1994). However, a unitary focus on pre-bottleneck alleles can give a rather distorted view of the genetic consequences of small population size, since such alleles are only a minor component of the long-term genetic extinction risk. Recent studies on a diversity of species have demonstrated that, when a population is small enough to severely compromise the effectiveness of selection, the recurrent introduction of mildly deleterious mutations is such that mean fitness will continue to decline by up to a few per cent per generation, even after all of the pre-bottleneck deleterious mutations have been lost or fixed (Table 2). Although no data are yet available for a vertebrate, because of their larger genome sizes and longer generation times, it seems reasonable to expect that the rate of genomic deterioration of a salmonid will be at least as great as the average value in Table 2 (i.e., at least 1.5% per generation).

To gain a rough understanding of the implications of such deleterious-mutation accumulation for the long-term survival of a salmonid population, consider the fact that under optimal conditions the number of return spawners produced per spawning adult is not likely to exceed $R \simeq 5$ or so. An 80% decline in fitness in such a population would reduce R to 1. Since this is the point at which the population could just replace itself, any further decline in fitness would lead the population down a path to rapid extinction. With an expected decline in fitness of 1.5% per generation, this point would be reached in about 105 generations. For a population with $R \simeq 2$, which is common for existing salmonids, the point of genetic inviability would be reached in approximately 45 generations.

Table 1. Magnitude of inbreeding depression for a variety of fitness-related traits in flies of the genus *Drosophila*, reported as percent declines expected upon complete inbreeding. The results are averages over a large number of studies cited in Lynch and Walsh (1997).

Character	Inbreeding Depression
Competitive ability	90%
Egg-to-adult viability	44%
Female fertility	45%
Female rate of reproduction	60%
Male mating ability	73%
Male longevity	18%
Male fertility	11%

Table 2. Estimates of the rate of fitness decline (per generation) that would be expected to occur if the efficiency of selection were essentially relaxed, due for example to a very small effective population size. The decline in fitness is entirely due to the recurrent introduction of spontaneous deleterious mutations. The estimates are derived from mutation-accumulation experiments in which replicate lines are taken through bottlenecks of one or two individuals over periods of 10 to several dozens of generations. The *Drosophila* results are averaged over several studies in the literature (Lynch and Walsh 1997), while those for *C. elegans* (Vassilieva and Lynch, 1999) and *A. thaliana* (Schultz et al., 1999) are derived from recent experiments in our lab. The *Daphnia* results were extrapolated from a field population by use of the method of Deng and Lynch (1996). Here it is assumed that half of the observed mutational load is a consequence of lethals, which would not ordinarily contribute to the decline of fitness in a population.

Organism	% Fitness Loss/Generation
Drosophila melanogaster (fruit fly)	1.8%
Daphnia arenata (microcrustacean)	3.2%
Caenorhabditis elegans (nematode)	0.6%
Arabidopsis thaliana (plant)	0.5%

Whether such rates of fitness decline will occur in a population depends on the effective population size and on the average effect of new mutations. The existing studies (cited in Table 2) suggest that the average spontaneous mutation decreases fitness by approximately 1% in the homozygous state. Moreover, the distribution of mutational effects may be very L-shaped, with mutations with effects below the mean being especially common (Keightley 1994). Based on the logic outlined above, these results suggest that populations with effective sizes smaller than a few hundred individuals are highly vulnerable to the accumulation of deleterious mutations by random genetic drift. Populations for which N_e regularly exceeds several hundreds of individuals are unlikely to greatly suffer from deleterious-mutation accumulation on time scales of up to several thousands of generations (Lande 1994, Lynch et al. 1995a, b).

The empirical results cited previously clearly indicate that the vast majority of new mutations arising in a population each generation are deleterious, perhaps unconditionally so. Moreover, a comparison of standing levels of genetic variation in natural populations, with the mutational rate of input, has led to the hypothesis that most of the variance for quantitative traits may simply reflect recurrently introduced cohorts of deleterious mutations not yet eliminated by natural selection (Houle et al. 1996). If this view is even approximately correct, then conventional measures of standing genetic variance (i.e., heritabilities) may reveal little about the potential for adaptive evolution—the few polymorphisms that can actually contribute to adaptive evolutionary change will be diluted in a larger background of deleterious mutations. As pointed out in Lynch (1996), measures of molecular variation within populations will be even less informative. However, an estimate of N_e can again provide a useful indication of a population's adaptive evolutionary potential.

Since the rate of adaptive evolution in a changing environment is directly proportional to the additive genetic variance for the selected character(s), it is informative to consider the factors that influence the maintenance of adaptive genetic variance for quantitative characters. New adaptive variation is regularly created by mutation, but most forms of natural selection lead to a loss of variance, and as noted above, random genetic drift also reduces the standing pool of genetic variance by a fraction $1/(2N_e)$ each generation. Thus, for populations in drift-mutation-selection balance, the additive genetic variance for a typical quantitative trait is expected to increase with increasing N_e. However, several studies have shown that the equilibrium level of genetic variance is essentially invariant once N_e exceeds several hundred to a few thousand individuals (Keightley and Hill 1988, Bürger et al. 1989, Houle 1989, Foley 1992).

This result suggests that the adaptive potential of a population is unlikely to be greatly influenced by changes in effective population size once N_e has exceeded a thousand or so individuals. Strictly speaking, however, further increases in N_e can have some influence on the evolutionary properties of populations, since the actual amount of genetic variance in a population can drift around its expected value from generation to generation, and does so to a degree that depends on the inverse of the effective population size (Bürger and Lande 1994, Bürger and Lynch 1994). This effect can be non-negligible even in populations with effective sizes of several thousands of individuals.

To sum up the empirical and theoretical results cited above, as a first-order approximation, populations with long-term effective sizes of several hundred to a thousand individuals can be considered to be genetically secure on time scales of hundreds to several thousands of generations. Populations with long-term effective sizes on the order of 100 individuals are certainly evolutionarily compromised, and populations with N_e much less than 100 have an extremely high genetic extinction risk. Since the genetic effective size of a population is not equivalent to its actual size, it is informative to inquire what a goal of N_e = 1,000 implies in terms of total population abundance.

Effective population size and actual population size in salmonids

Since N_e is directly related to the distribution of allele copies in a progeny generation, it can be estimated directly if one has information on the pedigree structure of a population. Such detailed information is rarely available for a natural population, but approximate estimates of N_e can still be obtained if one has a good understanding of some basic demographic features of the population. The theory for the estimation of effective population size from demographic parameters is well-developed but technically complex, with recent reviews having been given by Lande and Barrowclough (1987), Crow and Denniston (1988), and Caballero (1994). However, the essential features of this theory can be summarized in a fairly simple manner.

For nonmonogamous species, such as salmon, the effective number of individuals may differ between the sexes due to differences in numbers of individuals mating and differences in mating success. The effective numbers of males and females in a particular generation are given by:

$$N_{em} \simeq \frac{2N_m}{1+C_m^2}\text{, and} \tag{1a}$$

$$N_{ef} \simeq \frac{2N_f}{1+C_f^2} \tag{1b}$$

where N_m and N_f are the actual numbers of breeding males and females, and C_m and C_f are the coefficients of variation (ratios of standard deviations to means) of progeny number for males and females. In the ideal case, in which all members of the same sex have equal fertilities, mating is completely random, and there is no selection, then family sizes follow a Poisson distribution ($C_m = C_f = 1$), and the effective numbers for each sex are the same as the observed numbers. However, as the population's reproduction becomes more dominated by a small fraction of individuals (which increases the variance of progeny number per adult), the effective size becomes smaller than the actual number of breeding adults.

Unfortunately, the information needed to estimate this degree of inflation in salmonids is lacking. Data presented in Simon et al. (1986) for coho and in Hedrick et al. (1995) for chinook suggest that C_f may be about 0.7 for hatchery-reared populations. However, with naturally spawning populations, there are numerous ecological factors that could greatly inflate the variance in female reproductive success beyond that expected on the basis of egg production. These include the ability to locate a mate, variance in mate number, and variation in spawning location and timing. Similarly, variance in male mating success is likely to be very dependent on male size and return time. A large survey of information from natural populations of plants, invertebrates, and vertebrates (Frankham 1995a) implies that coefficients of variation of reproductive success are often on the order of 2.0. The procurement of accurate estimates of these coefficients for naturally spawning salmonids will require the use of molecular markers for the ascertainment of paternity and maternity in returning cohorts.

The effective population size for any particular generation is a nonlinear function of the effective number of individuals of each sex,

$$N_e = \frac{4N_{em}\,N_{ef}}{N_{em} + N_{ef}} \quad . \tag{2}$$

When the ratio of effective numbers in each sex is even, the total effective size is simply N_{em} + N_{ef}, but as one of the sexes becomes very rare, N_e approaches 4 times the effective number of the rarer sex. As can be seen from Equations 1a and 1b, the relative values of N_{em} and N_{ef} depend on the numbers of males and females. Random fluctuations of sex ratios (N_{em} vs. N_{ef}) can become very pronounced when population sizes are small, and even fairly large populations of salmonids can regularly exhibit unequal sex ratios. For example, Oregon populations of coho routinely exhibit excess frequencies of males (K. Kostow)[1], enough so, that even with no variance in reproductive success, the total effective size would be about 10% less (on average) than the actual number of breeding adults.

Finally, when populations fluctuate in size, the long-term effective size is given by the harmonic mean of the single-generation values,

$$\tilde{N}_e = \frac{t}{(1/N_{e,1}) + (1/N_{e,2}) + \ldots + (1/N_{e,t})} \; . \tag{3}$$

The harmonic mean much more closely approximates small than large values in a series. Thus, the long-term effective size of a population is primarily determined by events that temporarily reduce population size rather than by those that increase it. For 10 Oregon coho populations for which censuses of spawning densities are available for more than 15 consecutive years, the harmonic mean is between 30% and 70% of the arithmetic mean number of spawning adults.

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[1] K. Kostow, Oregon Department of Fish and Wildlife (ODWF), 2501 SW First Ave, Portland, 97207 Portland OR. Pers. commun., 1995.

Taking the very limited demographic information cited previously into account, it is quite plausible that the long-term effective size of a typical salmonid population ($\tilde{N}_e$) is as small as 20% to 40% of the arithmetic mean annual number of spawning adults ($\bar{N}$), and it is conceivable that it is often smaller than 20% of $\bar{N}$. In a taxonomically broad survey of 56 studies in which variance in reproductive success, uneven sex ratio, and temporal change in population size were taken into account, Frankham (1995a) found that $\tilde{N}_e$ averaged only 10% of $\bar{N}$.

An alternative route to estimating N_e, that is less laborious and less assumption-laden than approaches based on direct observations of demographic parameters, is to monitor year-to-year changes in the frequencies of neutral alleles for molecular markers (Nei and Tajima 1981, Tajima and Nei 1984, and Waples 1988, 1990a, b), and to evaluate the value of N_e that is most compatible with the observed fluctuations. Still another approach, which requires data from only a single sample, is to estimate the value of N_e that is most compatible with observed levels of linkage disequilibrium for alleles at unlinked loci (Hill 1981). Waples and Teel (1990) used temporal changes in allele frequencies at allozyme loci to indirectly infer the effective sizes of hatchery populations of chinook salmon. Averaging over nine populations, results from their analyses suggest that $\tilde{N}_e$ is less than 22% of $\bar{N}$. A second study, involving six populations of naturally spawning chinook, led to an average estimate of $\tilde{N}_e / N \simeq 0.49$. Using the linkage-disequilibrium approach, Bartley et al. (1992) estimated $\tilde{N}_e / N$ to be 0.04 in a naturally spawning population of chinook.

Thus, results based on very approximate demographic arguments, as well as several molecular-marker analyses, are in qualitative agreement. Conservatively speaking, the genetic effective size of a salmonid population is on the order of 20% of the actual number of breeding adults. These results lead to the conclusion that populations of salmonids can be viewed as being evolutionarily secure when the harmonic mean number of adults ($\tilde{N}$) exceeds 5,000 or so individuals, and as having very high genetic extinction risks when $\tilde{N} < 500$. These observations imply that, from a genetic perspective, current U.S. policies for protecting species are too lax. At the time of formal listing under the ESA, the average animal species has dwindled to a total (juveniles plus adults) of 1,000 individuals (Wilcove et al. 1993). The situation, has in some cases, been more extreme for anadromous salmon. For example, Snake River sockeye salmon had long been in decline, with a total of only six adults returning in the 3 years before formal listing as an endangered species in 1991 (Waples 1995a). The average numbers of adults for the 5 years prior to formal listing are approximately 2,200 for Sacramento River winter chinook, 2,000 for Snake River spring/summer chinook, 300 for Snake River fall chinook, and 20 for sea-run cutthroat trout (J. Hard[2]).

Evidence for local adaptation

An understanding of the potential for local adaptation in semi-isolated populations is important with respect to the development of rational management strategies, recovery plans, and

[2]J. Hard, NMFS Northwest Fisheries Science Center., 2725 Montlake Blvd. E, Seattle, WA. 98112. Pers. commun., 1995.

hatchery supplementation policies for endangered species. When an entire species is essentially panmictic over its entire range, it is reasonable to treat it as a single Evolutionarily Significant Unit (ESU) in decision-making processes (Waples 1991a, 1995a), although certain segments of the population may be deemed more or less expendable from an ecological perspective. When a species has a metapopulation structure in which individual populations are locally adapted, then each population is a potentially important component of the species evolutionary legacy and evolutionary potential. To the extent that individual populations are likely to harbor unique adaptations, they may warrant consideration as independent units of protection under the ESA (NRC 1995).

Because of the substantial degree of homing fidelity in adult anadromous salmon, there is certainly the opportunity for local adaptation in these species, so the consequences of population subdivision are fundamental issues in any discussion of genetic-conservation issues involving Pacific salmonids. The degree of homing is far from perfect, so it is likely that populations from different drainage basins experience a low level of natural gene flow. A fundamental question is the degree to which local adaptations can evolve and be maintained in the face of a low degree of gene flow.

A number of large allozyme surveys have been performed on Pacific salmonids, and the general picture that emerges is one of a low-overall degree of population subdivision at the molecular level, with adjacent populations usually (but not always) being most similar, and few cases in which different populations are fixed for different alleles. The average value of G_{st} (the fraction of total gene diversity at the molecular level that is attributable to between-population differences) ranges from 0.02 to 0.013 (Table 3). While significant, this is approximately half the degree of subdivision seen in typical lake-dwelling species of fish, and about twice the degree of subdivision seen in a typical marine species (Ward et al. 1994).

If one is willing to assume that salmonid populations are in approximate equilibrium for molecular markers (such that the divergence among local populations by random genetic drift is roughly balanced by their convergence from gene flow), then using the island model of Wright (1943), one can estimate that an average of two migrants must enter each population each generation to maintain a $G_{st} = 0.11$, whereas 10 migrants per generation are required to reduce G_{st} to 0.02. Although these results assume that migration is random with respect to source and recipient populations, restriction of migration to adjacent populations would not alter the conclusion that the level of molecular divergence commonly observed for salmonid populations is consistent with only a small amount of migration.

While it is relatively easy to estimate degrees of population subdivision at the molecular level, the relevance of such data to concerns about the degree of local adaptation is by no means clear. In general, it is believed that the molecular markers upon which population-level analyses are usually performed are neutral or very nearly so. Gene frequencies associated with such loci passively diverge among populations as a consequence of random genetic drift, a slow process when effective-population sizes are large. On the other hand, when populations are exposed to different selection pressures, divergence with respect to adaptive traits can be much more rapid than that for neutral marker loci, as natural selection will promote different alleles in different

Table 3. Magnitude of population subdivision estimated in various species of anadromous Pacific salmonid from surveys of protein variation. G_{st} is an estimate of the fraction of total gene diversity (measured as heterozygosity) in a species that is distributed between populations.

Species	Geographic Range	G_{st}	Reference
Pink salmon, O. gorbuscha	AK	0.03	Gharrett et al. 1988
	WA, BC	0.02	Hard et al. 1996
Chum salmon, *O. keta*	AK, BC	0.03	Kondzela et al. 1994
	BC, WA	0.03	Phelps et al. 1994
Coho salmon, *O. kisutch*	OR, WA, BC	0.12	Milner 1993
	BC	0.09	Wehrhahn and Powell 1987
	WA	0.05	Reisenbichler and Phelps 1989
Steelhead, *O. mykiss*	Snake River	0.04	Waples et al. 1993
	WA	0.02	Reisenbichler and Phelps 1989
	OR, CA	0.02	Reisenbichler et al. 1992
Sockeye salmon, *O. nerka*	OR, WA, ID	0.03	Winans et al. 1996
	BC	0.18	Wood and Foote 1996
	AK	0.13	Guthrie et al. 1994
Chinook salmon, *O. tshawytscha*	BC, WA, OR, CA	0.12	Utter et al. 1989
	OR, CA	0.18	Bartley and Gall 1990
	AK	0.06	Gharrett et al. 1987
	Snake River	0.03	Waples et al. 1993

populations. Thus, from the standpoint of adaptive divergence, the information provided by molecular markers is asymmetric. Significant divergence at the molecular level implies that there has been ample opportunity for adaptive divergence, but lack of discernible divergence at the molecular level does not rule out the possibility of significant divergence at the phenotypic level.

Although the data needed for a direct comparison of divergence at the level of molecules and quantitative traits do not exist with salmon, results from a diversity of other plants and animals reveal a striking pattern. For phenotypic characters, such as body size, reproductive rates and so forth, an analog of G_{st} is the index Q_{st}, which provides an estimate of the fraction of the total genetic variance for a quantitative trait in a species that is attributable to between-population differences. For the few species in which both indices have been measured, there is a striking degree of correlation—species with higher G_{st} have higher Q_{st} (Fig. 1). However, the relationship between the two is far from linear—divergence at the level of quantitative traits is always equal to or greater than that for molecular markers, and the disparity increases with decreasing G_{st}, being nearly 10-fold when G_{st} is small. Since the quantitative traits involved in all of the studies in Figure 1 are fitness related, these results uphold the contention that the magnitude of molecular divergence among local populations provides a conservative (and in the case of low G_{st}, essentially uninformative) estimate of the degree of adaptive divergence. Referring to Figure 1, it is apparent that for salmonids, with G_{st} in the range of 0.02 to 0.13, at least 10 to 35% of the adaptive variation for quantitative traits is likely to be manifest in between-population differences. That adaptive divergence among partially isolated populations actually occurs is supported by direct observation.

One of the most remarkable examples of local adaptation in the absence of pronounced molecular divergence is the case of sockeye and kokanee salmon (*Oncorhynchus nerka*). Sockeye salmon are typical anadromous species, whereas kokanee spend their entire life cycle in fresh water. Molecular evidence, combined with biogeographic considerations, strongly suggests that the kokanee morph has evolved from the sockeye morph independently in many drainage basins since the last glaciation, i.e., over the past 10,000 years (Taylor et al. 1996, Wood and Foote 1996). While it is common for both species to spawn within sight of each other, there is strong assortative mating. Male kokanee occasionally fertilize female sockeye, yielding viable progeny, but gene flow between these groups has not been recorded. Remarkably, the level of molecular divergence between kokanee and sockeye salmon is no greater than that between different populations of sockeye or between different populations of kokanee. Yet, the two morphs have diverged dramatically with respect to growth rate, with adult sockeye being about 3 times the length of kokanee, despite similar ages at maturity. That such a pronounced level of physiological and morphological divergence can be maintained in the face of some gene flow suggests that the intensity of selection against hybrids must be very strong.

Such rapid and polyphyletic origin of major ecological differences among populations appears to be common in fish. For example, both Schluter and McPhail (1992), and McPhail (1993) have documented dozens of cases of incipient (and sympatric) speciation in sticklebacks, where the divergence involves feeding morphology. Similarly, molecular analyses suggest that the lake whitefish (*Coregonus clupeaformis*) has diverged into limnetic and benthic feeding morphs on many independent occasions since the last glaciation (Bernatchez et al. 1996). In this

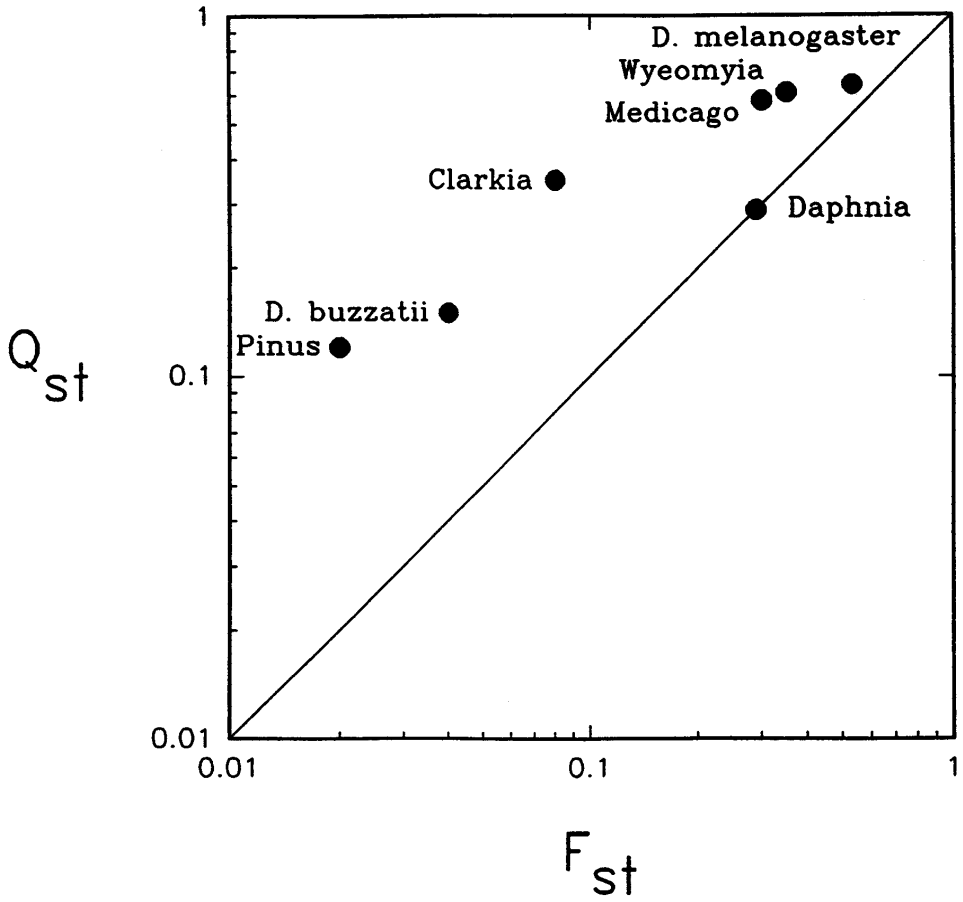

Figure 1. Estimates of genetic subdivision at the level of quantitative characters (Q_{st}) versus that at the level of isozymes (F_{st}). Most of the quantitative traits are size and reproductive characteristics. References: *Pinus contorta* (pine) – Yang et al. (1996); *Drosophila buzzatii* – Prout and Barker (1993); *Drosophila melanogaster* – Long and Singh (1995); *Clarkia dudleyana* (a flowering annual plant) – Podolsky and Holtsford (1995); *Daphnia obtusa* – Spitze (1993); *Medicago truncatula* (alfalfa) – Bonnin et al. (1996); *Wyeomyia smithii* (pitcher-plant mosquito) – P. Armbruster and J. Hard (pers. commun.)[3]. The solid line denotes the points at which $Q_{st} = F_{st}$.

[3] P. Armbruster, University of Oregon, Eugene, OR, and J. Hard, NMFS Northwest Fisheries Science Center, Seattle, WA, 98112. Person. comm., 1996.

case, the two morphs are separated by a G_{st} of only 0.01 for nuclear genes, although the degree of subdivision for the mitochondrial genome is considerably larger. Evidence for parallel ecotypic divergence also exists for smelt (Taylor and Bentzen 1993a, b), arctic char (Hindar et al. 1986), Atlantic salmon (Ståhl 1987), brown trout (Bernatchez et al. 1992), and guppies (Reznick et al. 1996). The fact that early- and late-run populations of chinook salmon within the same drainage basin are more molecularly similar than populations with the same run times from different areas has led to the suggestion that differences in run times have evolved independently many times (Utter et al. 1989), although the possibility of gene flow within drainages can not be ruled out. These types of observations are by no means limited to fish, and arguments are emerging that parallel ecotypic divergence combined with assortative mating within morphotypes may be a common initial event in the speciation process (Rice and Hostert 1993, Schluter and Nagel 1995).

While it may not be surprising that the types of life-history and morphological changes described previously can evolve on time scales of thousands of years, they may actually develop on time scales of only a few generations. In the case of salmon, for example, kokanee morphs have appeared in several lake basins (previously barren of salmon), following the human planting of sockeye (Ricker 1940, Scott 1984). Whether all sockeye stocks have the genetic resources to generate the kokanee morph is unknown. Moreover, there is no information on any system regarding the reproductive compatibility of independently evolved populations with the same morph. Answers to both of these questions are of fundamental importance from the standpoint of conservation genetics. The degree to which populations harbor the genetic variation necessary to fuel rapid adaptive divergence determines their flexibility in response to environmental change. If, however, stocks with similar phenotypes achieve their similarity via different genetic pathways, then the mixing of gene pools from different sources (e.g., via hatcheries or transplants) could result in a significant loss of fitness in a local population, an issue which will be considered in more detail shortly.

While the types of morphological change outlined previously are pronounced and obvious, more subtle physiological and developmental adaptations may be the norm in semi-isolated salmonid populations. As emphasized by Allendorf and Waples (1996), the selective challenges confronting organisms with life cycles as complex as those of anadromous salmon are enormous. The particular ecological conditions associated with different streams (e.g., the seasonality of flow regimes and temperatures, and distances to spawning sites) strongly dictate the timings of life-cycle events that are compatible with local survival and reproduction. The fact that stock transfers of Pacific salmonids to foreign drainage basins have rarely been successful (Withler 1982, Allendorf and Waples 1996) may be a simple consequence of a poor fit between local ecological demands and the adaptive features of introduced lineages.

The Genetic Consequences of Supplementation Programs

With hatcheries now playing a central role in the management programs for most Pacific salmonids, there is justifiable concern about the negative consequences of supplementation for the genetic integrity of natural populations. Although captive broodstock programs may provide a short-term mechanism for saving extremely rare stocks from extinction, as outlined in the

following, the long-term consequences of such programs can be contrary to the goal of species maintenance. Indeed, there appear to be very few, if any, positive genetic consequences of supplementation programs. Continued reliance on hatcheries for the maintenance of harvestable populations is likely to have severe negative effects on native stocks in the face of continuing degradation of viable habitat.

The ways in which a supplementation program can have negative genetic consequences for a native stock are numerous, and many of these can operate simultaneously in a synergistic fashion. Of particular significance is the fact that most of the genetic consequences of supplementation take several generations to be fully revealed. Thus, what might initially appear to be a successful management decision, leading to further supplementation, may later become a liability to the wild population. Recent reviews of the issues appear in Hindar et al. (1991), Waples and Do (1994), Hard (1995b), Waples (1991b, 1995b), Allendorf and Waples (1996), and Hard and Hershberger (1995). Here, I simply summarize the primary problems, while attempting to integrate the implications with the basic principles previously outlined. My discussion of the issues is organized into three broad categories of problems.

Outbreeding depression

While the external environment molds the evolution of local adaptations via natural selection, because of the stochastic nature of the evolutionary process, populations that are exposed to identical-selection pressures will not necessarily respond along the same genetic trajectory. The particular gene complexes that evolve in any population may largely be fortuitous, depending on the chance variants produced by mutation and/or by initial gene frequencies. Moreover, once one beneficial allele has arisen to high frequency in a population, the internal genetic environment will have been modified, thereby defining the future types of mutations that will be compatible with further adaptive evolution. By this means, local gene pools can become internally coadapted, and once this occurs, interpopulation hybridization can lead to a reduction in fitness by breaking up coadapted gene complexes (Dobzhansky 1948, Templeton 1986, Lynch 1991). It is important to realize that outbreeding depression can occur between populations that are adapted to the same extrinsic environment. Thus, when a hatchery population is started from a foreign stock, there is no guarantee that it will be genetically compatible with the local wild population, even if both populations appear to have very similar environmental settings.

It is also important to realize that the F_1 (first generation) progeny, from a hybridization event, are often uninformative with respect to the potential for outbreeding depression, and may even exhibit a transient increase in fitness, due to the masking of mildly deleterious alleles distributed in each population. Since it is not until the F_2 generation that the chromosomes from the parental lineages begin to recombine, at least two (and perhaps several more) generations of inbreeding are required for the full effects of outbreeding depression to be revealed. By the time this degree of genomic mixing has occurred, it is essentially impossible to reverse the process of introgression. In the absence of any data on the matter, it is difficult to forecast how long a period would be required for a native population to fully recover from a bout of outbreeding depression, but it is likely to be many generations.

Numerous examples exist for outbreeding depression among populations of plants and animals separated by relatively small physical distances (reviewed in Hard 1995a, Hard and Hershberger 1995, and Lynch 1996), so the possibility of coadapted gene complexes within historically fragmented lineages of salmonids must be taken seriously. However, only a single study has attempted to evaluate the genetic consequences of hybridization in salmonids. Gharrett and Smoker (1991) crossed even and odd year cohorts of Alaskan pink salmon and monitored the descendants through the F_2 generation. Since the members of this species have a perfect 2-year life cycle, there is absolute reproductive isolation among alternate-year classes inhabiting the same drainage basin. Low returns of F_2 individuals were strongly suggestive of outbreeding depression, but the sample sizes of returning fish in both F_2 hybrids and controls were small.

Displacement of locally adapted genes

Even in the absence of synergistic interactions among the gene pools of wild and hatchery-reared populations, a high degree of gene flow from hatchery to wild fish can impose a serious genetic load on a wild population as the locally adapted genes are displaced by those of the hatchery population. Because the hatchery environment is radically different from that in nature, one can expect selection to favor a different suite of genes in captivity than in nature, leading to domestication selection (Doyle 1983, Ruzzante and Doyle 1991). Moreover, the goal of all hatcheries is to provide conditions that maximize early survival, and they are usually very successful at this, with egg-to-smolt survival typically being several-fold greater than that in the wild (Waples 1991b). Thus, it is conceivable that hatcheries foster the accumulation of mildly deleterious alleles that would otherwise be eliminated by selection in the natural environment. Reisenbichler (1996) has documented dramatic reductions of the survivability of hatchery-reared fish in natural streams with increasing numbers of generations in the hatchery and other shorter-term studies have yielded similar results (Nickelson et al. 1986, Leider et al. 1990, Fleming and Gross 1992). In situations such as these, gene flow from the hatchery could only reduce the fitness of the wild population.

Given an immigration rate m to the wild population, the pool of local genes for which the selective advantage is much less than m would simply be flushed from the population. Since the selection coefficients of most alleles are unlikely to be much greater than a few percent, this implies that the rate of straying from a hatchery to a wild population need not be very great to have such a swamping effect. This is a concern because hatchery-reared fish may stray more often than naturally spawned fish. In the extreme, one can imagine a situation where relaxed selection in the hatchery environment, combined with a high degree of gene flow into the native population, leads to the erosion of fitness of the native population below the point necessary for sustainability. Such a scenario is particularly likely to develop when the hatchery population is treated as an isolated stock (i.e., when there is no gene flow from the wild to the hatchery population).

Reduction in the genetic effective population size

A high rate of migration from a hatchery population into the wild does not simply reduce the frequencies of local genes. It also dictates the genetic-effective size of the wild population, which as previously described, will have a significant influence on the evolutionary flexibility of the wild population. If the effective number of annual breeders in the hatchery is much less than that in the wild, then as the gene pool of the wild population is transformed into that of the hatchery, the wild population will also take on an effective size that is essentially the same as the hatchery. Many salmonid management programs make serious efforts to minimize gene flow between hatchery and wild populations. However, an increasingly common management strategy to boost the density of small endangered populations is the use of captive broodstock. In this case, a fraction of the wild population is brought into the hatchery each generation, and the hatchery-reared progeny are targeted toward reintegration into the wild population.

Such a procedure will have the effect of shifting the effective size of the wild population toward that determined by the annual effective number of breeders in the captive population (Ryman and Laikre 1991, Waples and Do 1994, Ryman et al. 1995). If the captive population contributes the majority of the adults in the naturally spawning population, N_e for the wild population will be very close to that for the hatchery. Thus, a long-term captive broodstock program that utilizes only a small number of adults, but successfully so, is the genetic equivalent of a population bottleneck, even if the demographic effects are an increase in the size of the wild population. In the long run, this can only increase the genetic extinction risks in the wild population, particularly if relaxed selection in the hatchery environment encourages the random accumulation of deleterious mutations for juvenile survival in the wild.

The general principles outlined argue strongly against the use of augmentation programs except as a last resort in the recovery of an endangered species. There are many serious, and potentially very long-lasting, negative genetic consequences of captive breeding and no obvious advantages. In a recent review of the evidence, Allendorf and Waples (1996) state that "We are not aware of a single empirical example in which supplementation has been successfully used as a temporary strategy to increase the long-term abundance of naturally spawning populations of Pacific salmon." Continued reliance on artificial propagation as a means for enhancing harvestable populations is highly likely to lead salmonids down an evolutionary trajectory of domestication selection and accumulation of mutations that are deleterious to juvenile survival in the wild. The longer this addiction to technological fixes proceeds, the more difficult it will be to maintain and/or re-establish naturally spawning populations.

Genetics and the Endangered Species Act

The ESA provides a legal vehicle for formally protecting any "distinct population segment" of a species. This raises special concerns for the protection of anadromous salmonids, since it is clear that such species are fragmented into semi- to completely isolated populations. Should individual populations, groups of adjacent populations, or entire species be treated as potential units for listing? Unfortunately, the ESA does not provide insight into this matter as it does not clarify how distinctiveness should be defined. To address this issue, the NRC (1995)

suggested the concept of an Evolutionary Unit (EU) be defined as "a group of organisms that represents a segment of biological diversity that shares evolutionary lineage and contains the potential for a unique evolutionary future." This concept is similar to the ESU used by the NMFS in applications of the ESA to Pacific salmonids (Waples 1991a, 1995a). An ESU is defined to be "a population (or group of populations) that: 1) is substantially reproductively isolated from other conspecific population units, and 2) represents an important component in the evolutionary legacy of the species" (Waples 1991a).

There are some important differences between the EU and ESU concepts. First, by omitting the word "significant," the EU concept makes a logical distinction between the criteria for determining whether a target for listing is distinct and the value judgments involved in evaluating whether a distinct population is also a significant one. Standard scientific procedures can be used to determine whether populations are distinct in terms of morphology, physiology, behavior, etc. (outlined in NRC 1995, and Waples 1991a, 1995a), but evaluation of significance is a personal judgment (although it can certainly be informed by scientific argument). Second, the EU concept puts less emphasis on reproductive isolation as a criterion for listing. Determining whether "substantial" reproductive isolation exists can be difficult, unless one is willing to simply take significant differences between populations as evidence of substantial isolation. Third, the EU concept places more emphasis on the evolutionary future of a species than on its evolutionary past, although in the decision-making process, NMFS clearly evaluates targets for listing in terms of their potential contribution to the evolutionary future of a species (Waples 1995a).

How does our basic understanding of the population-genetic structure of anadromous salmonids bear on the application of the EU and/or ESU concepts in evaluating targets for listing under the ESA? There are, unfortunately, no simple recipes for the decision-making process, nor are there likely to be even in the face of great enhancements of our understanding of salmonid genetics. Given the theoretical and empirical results cited above, we can be virtually certain that salmonid species have historically been separated into adaptively divergent local populations. Such specialization to local conditions, essential to long-term viability, has almost certainly been compromised (and in many cases, eliminated) by massive reductions in population size resulting from habitat destruction and overharvesting, as well as by displacement of local gene pools by those of hatchery-reared fish.

What is less clear is how different units of protection should be circumscribed in terms of geographic range. Prudence would suggest that any local population that can be shown to be genetically distinct with molecular markers should be a valid candidate for protection, as such differences are likely to be accompanied by even larger differences at the level of adaptive traits (Fig. 1). However, one must also be aware that marker differences that have arisen in recent years may simply be a consequence of random genetic drift resulting from massive reductions in population size or from gene flow from adjacent hatchery populations. Recovery could be rapid, provided local populations can be kept at moderate densities, and gene flow from hatcheries can be eliminated.

There are many additional genetic issues worthy of consideration in efforts to establish viable salmonid populations. In many cases, recovery of spawning habitat will be a very long-

term process – decades to centuries. However, even if such goals are attainable, they address only a small part of the selective pressures imposed on salmonids by human activities. An important issue that has received almost no attention from a management perspective is the effect of intensive harvesting on the evolution of salmonid life histories. Ricker (1981, 1995) and Reisenbichler (1996) have reviewed the dramatic reductions in adult sizes, age-at-maturity and changes in run times that have been recorded in most species of anadromous salmonids over the past few decades. These changes are almost certainly a consequence of the size-selectivity of commercial fishing gear and seasonal concentration of fishing activities, and in many cases, they are likely to be quite incompatible with the reproductive needs of the species. For species that breed in streams with a high degree of seasonality, inappropriate spawning times may lead to complete reproductive failure. For stocks that normally have very long migratory routes, such as those inhabiting the Snake River basin, a small body size may simply be energetically inadequate for a successful journey to the spawning grounds.

It is unrealistic to expect harvesting intensity to decline in the near future, and more likely than not, it will increase. Thus, human activity has forever transformed the evolutionary challenges faced by Pacific salmonids. Even if spawning habitat can be completely restored, it is highly likely that selective pressures imposed by commercial and sports fisheries will lead to dramatic alterations in salmonid life histories over the next several decades. To meet these challenges, salmonid populations will need all the genetic resources possible.

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Artificial Production

Potential Risks and Benefits of Hatchery Supplementation to Naturally Spawning Populations of Salmon

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Artificial propagation programs of any form (e.g., standard hatcheries, net-pen operations, or supplementation programs) pose a number of potential risks to natural-spawning populations of salmon. The risks will vary with the nature and goals of the program, however, each may impact the basic ecology and the genetic integrity of naturally spawning and rearing fish when interaction or interbreeding with artificially propagated fish occurs. Most artificial propagation programs will likely lead to multiple interacting effects upon the ecological and genetic risks to wild populations.

Ecological risks to naturally spawned fish (hereafter "wild" fish) include: 1) increased competition in rearing and spawning areas for space, food or mates, 2) increased predation by larger, hatchery-reared fish or through aggregations of other predators attracted to large numbers of hatchery-released fish, 3) increased exposure to disease, or 4) alterations in natural behavior induced in the presence of hatchery-released fish (e.g., the reported "pied-piper" effect wherein wild fish initiate premature downstream migration in the presence of migrating hatchery-released smolts). The ecological risks will depend heavily on the age at which fish are released from hatcheries, the size and concentration of the released fish relative to the wild fish, and how the released fish spatially redistribute themselves after release.

The genetic integrity (including fitness and genetic diversity) of wild populations may be affected primarily through interbreeding with genetically divergent hatchery fish. The hatchery fish may be genetically divergent because they originated from a non-local wild population or because hatchery management practices have resulted in changes in quantitative or qualitative genetic characteristics. Unintentional interbreeding (through straying of hatchery fish) or intentional interbreeding (through hatchery releases intended to produce natural spawners) have both the potential to reorganize the natural intra- and inter-populational distribution of genetic diversity and to change heritable survival-related characteristics. Interbreeding, whether desired or not, is expected to most often reduce the genetic diversity among populations currently thought to be critical for long-term persistence, and to decrease fitness for rearing in the natural environment in the short-term. Perhaps only in cases where depressed wild populations are in risk of severe effects due to inbreeding, or have already lost substantial genetic variation, may interbreeding with fish from genetically divergent populations lead to a decreased risk of further decline or extinction.

Hatchery-supplementation programs (i.e., hatchery programs producing fish for the main purpose of restoring or rebuilding wild populations) are being promoted as a conservation tool expected to have only a trivial effect on the carrying capacity or productivity of naturally spawning populations, particularly if only wild (naturally spawned) fish are used for hatchery broodstock. In other words, if hatchery fish are always only one generation removed from wild fish. This thesis is explored using existing data (Figs. 1, 2), and a simple model to evaluate cumulative effects of supplementation over several generations. This thesis is found to be false. The existing data better support the hypothesis that supplementation of naturally spawning salmon populations with hatchery fish will substantially decrease the productivity for fish spawning naturally, and will result in total production far less than anticipated if genetic changes are not considered.

Natural selection for fish that perform well in the hatchery (domestication selection) has been demonstrated for steelhead (*Oncorhynchus mykiss*), and coincides with loss in genetic fitness or survival for rearing in natural streams. This loss should reduce the carrying capacity and productivity (adult progeny per spawner) for naturally spawning steelhead populations when hatchery fish augment these populations. The magnitude of reduction, in part, depends on when the period of limiting (density-dependent) mortality occurs for naturally rearing fish (Junge 1970, Reisenbichler 1986).

The available data suggest progressively declining fitness for natural rearing with increasing generations in the hatchery—the reduction in survival from egg to adult may be about 25% after one generation in the hatchery, and 85% after many (>6) generations (Fig. 2). Such reductions for an entire population in stream systems, where the limiting period for natural production occurs at or shortly before the juvenile fish become yearlings, would reduce carrying capacity and productivity by these same amounts.

To investigate the cumulative effect of supplementation, a supplementation program is considered where all hatchery fish spawn naturally and, after one generation, all wild fish are taken into the hatchery as brood fish. The fish all mature at the same age (i.e., there is no overlap in generations), and year-to-year variation in environmental conditions is ignored. The existing data suggest that each generation of hatchery rearing moves the relative survival for a population (survival relative to that for the original wild population) 1/3 of the way to the asymptotic value (approximately 0.25 for survival to yearling or 0.2 for survival to adult). Natural selection on each generation of fish rearing in streams is assumed to likewise move relative survival 1/3 of the way to the asymptotic value for natural rearing (1.0).

This supplementation program produces a saw-toothed decline in the fitness or success for rearing in natural streams, until by the ninth generation egg-to-adult survival is reduced by 50% (Fig.3). If the naturally spawning population is limited by the amount of spawning gravel, the associated carrying capacity is reduced by 40% within four generations, and 50% after nine (Fig. 4). Application of spawner-recruit models to a reasonable set of scenarios shows that the actual production (hatchery plus natural) with supplementation can be only one-third that expected if the genetic consequences of hatchery rearing are ignored (Fig. 5). If supplementation is discontinued, the population may be in danger of extinction depending on how quickly it can regain fitness for natural rearing.

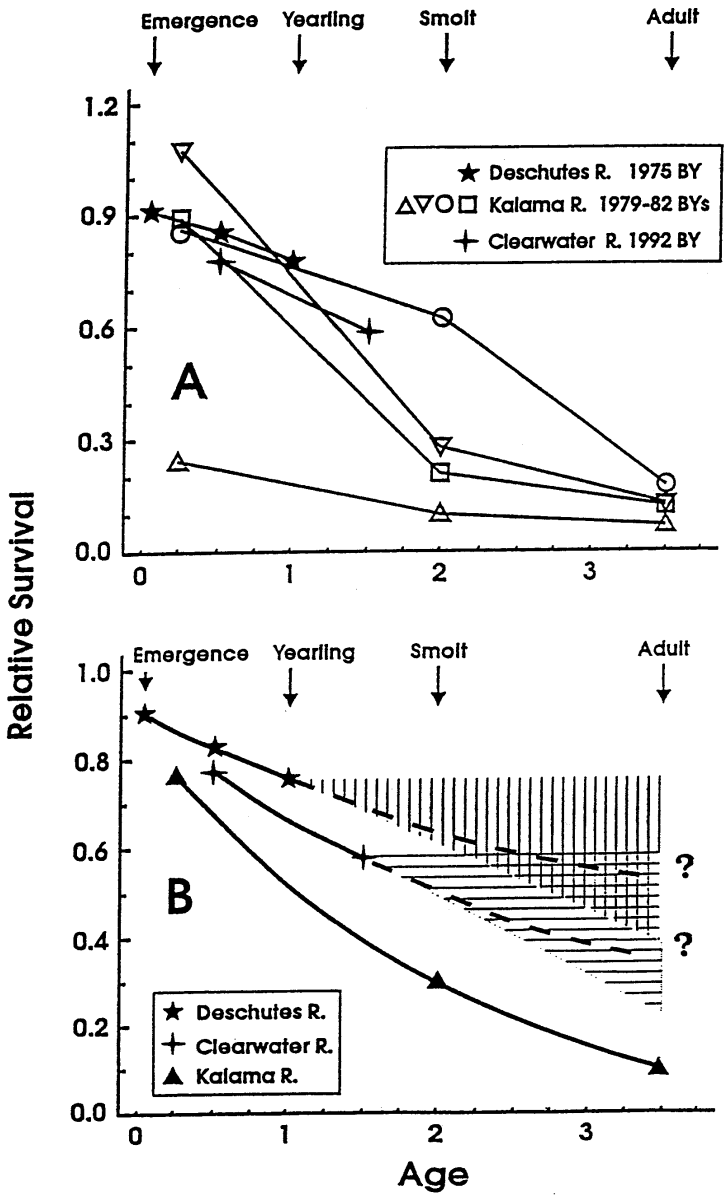

Figure 1. Survival for offspring of hatchery steelhead rearing in natural streams (or at sea) relative to that for offspring of wild steelhead at various ages or life history stages. Relative survivals were evaluated from the eyed-embryo stage at Oregon's Deschutes River (stars: Reisenbichler and McIntyre 1977), unfertilized eggs in Washington's Kalama River (open points: Leider et al. 1990), and swim-up fry in Idaho's Clearwater River (crosses; U.S. Geological Survey, unpublished data). A) Data are given for each year class separately. B) Data for the Kalama River (squares) are arithmetic means from the four year classes. Curves were fitted by eye. Dashed lines represent extrapolation of the data from the Deschutes and Clearwater rivers following a trajectory similar to that for the Kalama River. Shaded areas represent reasonable limits for these extrapolations.

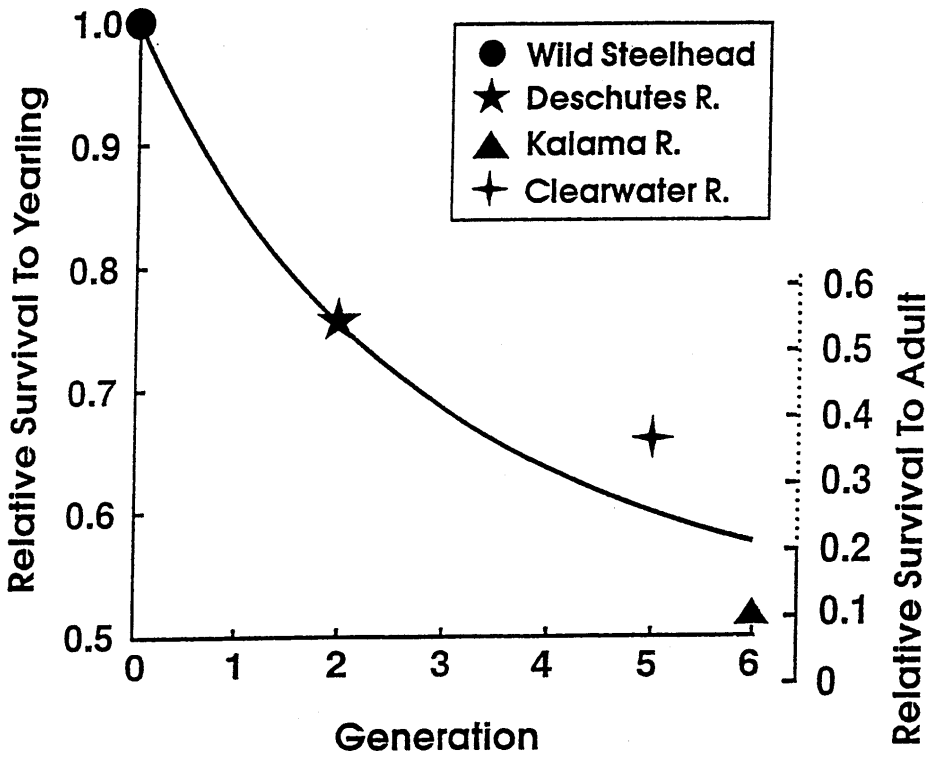

Figure 2. Survival for offspring of hatchery steelhead relative to that for offspring of wild steelhead versus number of generations the hatchery populations had been in the hatchery. Hatchery and wild fish reared together in natural streams until termination of the experiment or until migrating to sea. Survival was from the eyed-embryo or swim-up fry stage for the Deschutes River fish (stars: Reisenbichler and McIntyre 1977), the swim-up fry stage for the Clearwater River fish (crosses: U. S. Geological Survey, unpublished data), and unfertilized eggs (prior to being spawned naturally) for Kalama River fish (triangles: Leider et al.1990). The value for zero generations is one by definition.

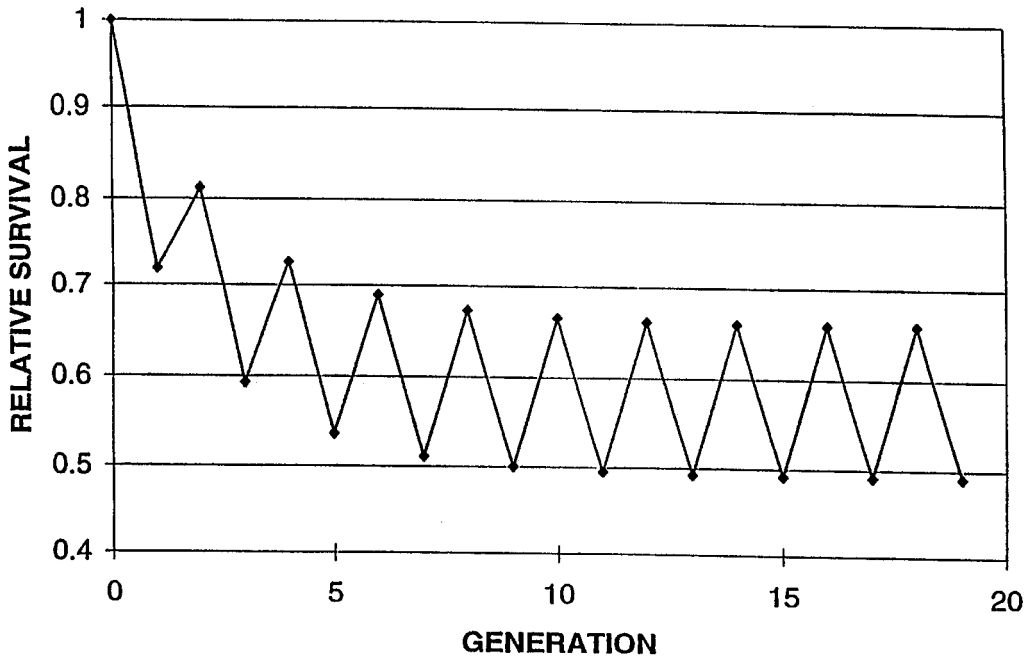

Figure 3. Predicted egg-to-adult survival under natural rearing, relative to that for the initial wild population, for a line of steelhead reared in a conventional hatchery one generation, spawning naturally and rearing in a stream the next generation, reared in the hatchery the next generation, and so on. Relative survival for natural rearing decreases with each generation in the hatchery, and increases with each generation of natural rearing.

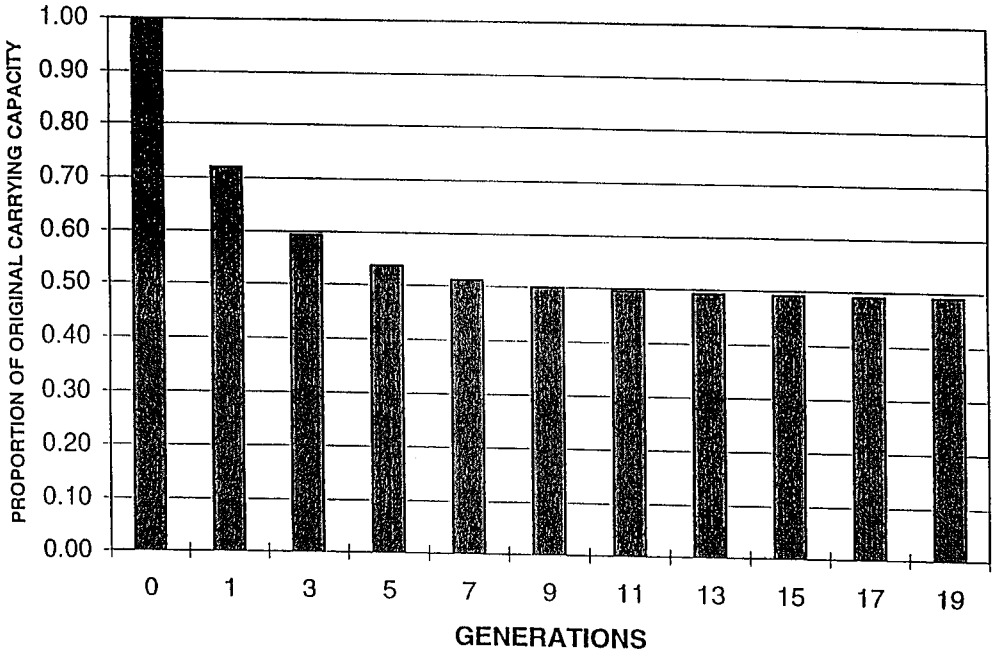

Figure 4. Decline in the carrying capacity (and productivity) for a hypothetical steelhead population after supplementation with hatchery fish. Carrying capacity is 1.0 for the original wild population before supplementation, and is reduced by 50% after nine generations of supplementation. Hatchery rearing begins in generation one, using only wild fish from the population to be supplemented. Steelhead production for this population is limited by the amount of spawning gravel.

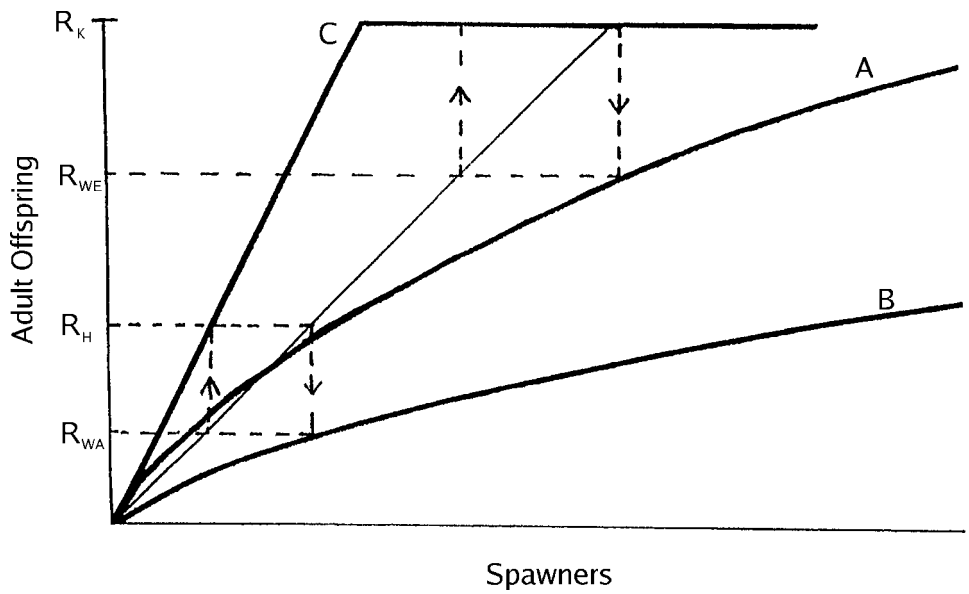

Figure 5. Hypothetical reproductive relations for a naturally-spawning population before supplementation (A) and after nine generations of supplementation (when productivity and carrying capacity are reduced by 50%) (B), and for hatchery-reared fish (C). The diagonal line simply shows where the number of progeny equals the number of spawners. Except for the first generation, all wild fish are used for hatchery brood stock and all hatchery fish are allowed to spawn naturally. R_K is the carrying capacity (measured in returning adults) for the naturally-spawning population before supplementation, and for the hatchery. Managers ignoring the genetic consequences of supplementation expect total production (natural and hatchery) to be $R_K+R_{WE}=1.7R_K$; however, realized production will be $R_H+R_{WA}=0.55R_K$, which is only one-third the expected level.

The cumulative effects of supplementation will vary with the proportion of wild fish brought into the hatchery each year, the productivities for hatchery and natural rearing, and the period of density-dependent limitation for natural rearing. Although results are presented for only one combination of these parameters, they are sufficient to show that the benefits of hatchery supplementation can be seriously overestimated if genetic consequences are ignored. They also suggest that deleterious effects to wild populations, and as a factor contributing to the extinction risk, can be seriously underestimated. Modifying hatchery (or preservation) environments to reduce domestication selection may reduce the genetic problems, but the practical level of reduction is unknown and may be slight, particularly for large-bodied, relatively long-lived fish such as the Pacific salmon species.

Additional work is needed to better describe and understand the rates of genetic change in survival or fitness (domestication and naturalization), to predict the cumulative effects of supplementation for other sets of parameter values, and to design and evaluate alternative hatchery environments for reducing domestication selection. The existing data already suggest though, that supplementation programs may not provide a general solution for depressed populations and instead, may best be considered as a “last-ditch” effort.

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Assessment Methods

Predicting Extinction in Salmon: How Far Can We Trust the Models?

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Managing salmon stocks to avoid extinction requires choosing from a complex array of options. The appropriateness of a course of action depends on several factors: its cost (both in dollars and in political currency), its probable effect on the target organisms, and its urgency. While cost is fairly easy to estimate, at least in the short term, urgency and impact can be difficult to measure, and some recalcitrant cases continue to resist our best efforts at understanding and prediction.

Urgency in the social climate has been fueled by the loss of many Pacific salmon stocks in the last 50 years, and an alarming downward trend in several populations during the last decade. Some action appears necessary. But, how necessary, and how are we to evaluate alternatives?

The rapid rise of inexpensive but powerful computers has opened up new possibilities and new hope for a method that will finally cut through the confusion and provide objective and quantitative criteria for establishing clear conservation priorities. In this paper, I introduce two general approaches to estimating extinction risk: time-series analysis and demographic modeling. I show examples of the application of these computer-intensive approaches to Oregon coho salmon-risk assessment, leading to specific predictions and evaluations of the health of populations. I conclude with predictions of my own, concerning how these techniques are likely to be used in the future for best results.

Time-Series Analysis

Salmon populations, like those of all organisms, fluctuate. In some cases, the causes of these fluctuations are known with some confidence (e.g., variations in ocean temperature, in harvest rates, and annual and seasonal changes in runoff). In other cases, fluctuations seem entirely random. For any time interval, these fluctuations in population density define the "population trajectory" during that interval.

A time series is any sequence of measurements made at regular time intervals, such as yearly harvest rate, monthly ocean temperature, monthly runoff in a particular watershed, or the population trajectory itself (e.g., the yearly density of spawning individuals in a particular reach). For the purposes of conservation, the time series of primary concern is, of course, the population trajectory. We are interested most in the future population trajectory, and specifically the

probability that population size falls to zero (or some other unacceptably low value, defined as quasiextinction) during some specified future time period.

In this context, the goal of time-series analysis is to answer that question. For example, to estimate the likelihood of extinction of a particular salmon stock in the next 50 years. Time-series analysis attempts to answer this question by searching for a set of rules that the population trajectory appears to be following, and applying those rules to extrapolate the trajectory into the future. A basic assumption is that those rules continue to apply in the future.

Two major approaches to time-series analysis have been developed: a frequency-domain (or spectral, or harmonic) approach, and a time-domain (or Box-Jenkins) approach (Box et al. 1994). Both are applicable to salmon populations.

Spectral Analysis

Spectral analysis represents a time series as a summation of pure sine waves that differ in frequency, amplitude, and phase (Hamilton 1994). Any time series can be perfectly represented by an appropriate number of appropriately shaped sine waves. This approach has been used to predict a variety of natural phenomena, such as sunspot behavior, climatic variation, and oscillating animal populations (such as the Canadian lynx). It has been used with spectacular success to generate extremely accurate predictions of ocean tides.

However, the predictive success of spectral analysis hinges on two conditions. First, the time series must be periodic. This means that, for example, the population trajectory must oscillate in a manner that is regular (although the regularity may not be visually obvious). Second, the degree of complexity of the oscillations must be commensurate with the amount of data in existence. If, for example, a time series is a summation of 10 sine waves, we need a very large number of data points in order to uncover all those sine waves accurately. If we have just 50 data points, then we might be able to uncover a few important periodicities, but our predictive power will be minimal. These criteria are fully met by oceanic tidal series, which are simple, obvious oscillations, whose underlying sine curves can be extracted easily from the available data sets, which are in many cases enormous.

Several periodicities or cycles in climate have been described in the Northeast Pacific and adjacent continent, and these undoubtedly affect salmon population trajectories to some degree. For example, a long-term cycle in ocean surface temperature has noticeable effects, with warmer years tending to reduce survivorship and population densities. Similar cycles in other climatic variables affecting both freshwater and marine habitat might also affect salmon populations. The relationship between these climatic oscillations and the population trajectory can be explored with bivariate spectral analysis. This estimates the degree of "coherence" between the two (analogous to a correlation coefficient between two variables), and the "phase difference" (analogous to the sign or direction of the correlation). Although, a full-scale spectral analysis of salmon stocks has not yet been attempted, such an analysis could prove valuable in allowing prediction of decadal oscillations in the population trajectory.

Box-Jenkins Analysis

Box-Jenkins analysis (named for the authors of a pioneering book on time-series forecasting and control, recently rewritten in Box et al. 1994) is a catch-all category that includes a great variety of techniques for analyzing time series other than spectral analysis. Box-Jenkins techniques and spectral techniques are not mutually exclusive (Box et al. 1994). Any feature of a time series that can be described by one technique can also be described by the other. The choice of technique will depend on simplicity and both may be included in a single time-series model. In general, however, the more pronounced and regular the time-series fluctuations, the more useful and simple a spectral analysis will be in comparison to techniques described in the following.

Box and Jenkins developed systematic procedures for accomplishing the three major tasks in time-series analysis (Box et al. 1994):

- identification, or the selection of a tentative model,
- estimation, or the fitting of model parameters, and
- diagnostics, or the testing of adequacy of fit (involving an analysis of residuals).

After these tasks are successfully completed, the final goal can be achieved, which is forecasting the time series. A model is simply an explicit mathematical statement of the rules believed to govern the time series, or in our case, the population trajectory. The models used in Box-Jenkins analysis fall into three major categories (Box et al. 1994):

- ARMA, or Autoregressive-Moving Average models,
- transfer function models, and
- intervention models.

Autoregressive models are those which describe a given value in the time series as a linear function of past values in the series and a random error term. Models containing a random error term are called "stochastic" models. For example, a simple random-walk model might relate the population density at time t as $N_t = N_{t-1} + \varepsilon_t$, where ε_t is a normal random error with mean zero and arbitrary standard deviation. In other words, population at time t is a random step from that at time $t - 1$. A sequence of many random steps is a random walk. If we were to make a scatter plot of population density at time t against that at $t - 1$, we would see a positive correlation, with slope 1, and intercept through the origin. Because this correlation is between a variable and itself (at a previous time) it is called an "autocorrelation ." If our random walk included a trend, an appropriate model might be $N_t = N_{t-1} + C + \varepsilon_t$, where C is a constant. If C is negative, then the population trajectory has a negative trend; the random walk tends downward from one time to the next. A scatter plot in this case would again yield a positive correlation of slope one, but the y-intercept is expected to be $C < 0$.

A more complex random walk might proceed not from the previous value of the time series, but from a weighted sum of previous values, so that $N_t = aN_{t-1} + bN_{t-2} + \cdots + \varepsilon_t$. All such (infinite) random walks can be equivalently expressed as a weighted (infinite) sum of random errors ε_t, since each value of the series can be recursively expressed in terms of previous values

and the error term for each t. Alternatively, N_t might be expressed more accurately as a weighted finite sum of previous error terms, (e.g., $N_t = a\ \varepsilon_{t-1}, + b\ \varepsilon_{t-2}$). This type of model is a "moving average" model, since a value of the series depends not on all error terms in the series, but on a finite recent sample of them, which moves with the series. In principle, the best model could turn out to be a mixture of autoregressive and moving average functions, an ARMA model.

We can identify the form of the best autoregressive function by inspecting a list of autocorrelations for the time series. We can calculate correlation coefficients for (N_t, N_{t-1}), (N_t, N_{t-2}), (N_t, N_{t-3}), and so on, and large correlations imply inclusion of these terms in the model. Similarly, we can calculate partial autocorrelations to determine the appropriateness of a moving average model.

Of course, exogenous variables might also affect the time series, making a simple ARMA model an unsatisfying fit to the data. A transfer model takes into account the effects of some external random time series (such as harvest and poaching rates, climatic variables, the rate of sedimentation, the volume of timber harvest in a watershed) on the population trajectory. This second time series is called the transfer function. In principle there is no limit to the number of transfer functions that can be incorporated into the model. We do this by including additional terms in our model, representing the values of the exogenous time series that exert an effect on the population trajectory. For example, we may set the current population density equal to $N_t = N_{t-1} + Y_{t-1} + \varepsilon_t$, where Y_{t-1} is some function of an exogenous variable, such as mean ocean surface temperature at time $t - 1$.

An intervention model takes into account the effect of presence or absence of some phenomenon or activity (called the "intervention") on the population trajectory. Examples might include a new legal penalty for poaching, a new hydroelectric dam, a new hatchery, any land use change in a watershed, change in some forest practice such as widening of the stream buffer, or the appearance of a smart sea lion at the entrance to a fish ladder.

The intervention function then is a series of ones and zeroes coded to the presence or absence of the activity. Although, we code an intervention as a binary variable, in reality its effect on population trajectory will be exerted through an effect on a continuous variable (i.e., a transfer function), most likely affecting some component of survivorship. But since we may not be able to measure this variable, focusing on the presence/absence of the intervention may be the best we can do. Even if we knew the precise manner in which an intervention affected survivorship, we still might be interested in its overall effect on the population trajectory regardless of the mechanism (e.g., to evaluate the overall effectiveness of a change in management on the population) and so we would still want to model the effect as a series of ones and zeroes.

Once we have decided on the appropriate form of the model, we must estimate its parameters. Several computational procedures are available for this purpose (Box et al., 1994). They involve using the full stochastic model to predict later elements in the population trajectory from earlier elements, as well as from elements of the transfer and intervention functions. The fit of a parameter set is calculated as the total sum of square differences between predicted and

observed values of the trajectory. Interestingly, it is a trivial mathematical truth that a large, complex model can always be constructed that fits the trajectory perfectly. This model, however, almost certainly will be useless in making forecasts. Thus, fit is not the only criterion for accuracy of the model. A criterion which is equally important is our assessment of how reasonably the model describes the mechanics of population fluctuation. Our model should be no larger than our knowledge permits, even though its fit to the population trajectory is inevitably worse than a larger, unsupported model.

Once we have an acceptable model, we are ready to use it for making forecasts. But, one may ask, how can we be sure the model, well-fitted to past observations, also applies in the future? How do we know whether any particular forecast is correct? Since a forecast is a statement of probability of a future event (in this case extinction), and the probability is never zero or one, the forecast will always allow for both the occurrence and non-occurrence of the event. So the event, or lack thereof, does little to prove the truth or falsity of the forecast. Given this, can we never have confidence in the predictions of our model? My answer is no. Our confidence is exactly as strong as our confidence in our knowledge of the population being modeled, of the reasons the numbers have fluctuated in the past, and of the reasons they will continue to fluctuate. There are only two reasons a forecast could be true: luck, or accuracy of the model. We cannot predict luck, but we can predict accuracy, as well as we understand the population in question. The model can be trusted as far as we trust our understanding.

Applications

There has been apparently no systematic analysis of salmon population trajectories in the framework of an ARMA or spectral model. However, several workers have noted trends in salmon population trajectories, and discussed the relationship between some of these trends and habitat characteristics (McGie 1981, Mysak 1986, Nickelson 1986, Holtby and Scrivener 1989, Beamish 1991, Ware and Thomson 1991, Beamish and Bouillon 1993, Lawson 1993, and Francis and Hare 1997).

Schreck et al. (1996) plotted the trajectories of several Oregon coho salmon stocks, and fitted various curves to them in an attempt to estimate extinction risk due to possible long-term trend behavior. In particular, they found an alarming downward trend in total yield (equal to the total adult population before harvest) of North Coast coho salmon during the last 15 years. This was the combined trajectory for the Nehalem, Wilson, Nestucca, Yaquina, Beaver, Alsea, and Siuslaw watersheds. The recent decline of this Northern Gene Conservation Group was attributed to a concomitant change in oceanographic conditions.

Schreck et al. (1996) fitted a linear regression to the downward trend from 1982 to 1995, which predicted extinction shortly after the turn of the century. This result led the authors to propose listing these fish as threatened if the trend continues. They then fitted the same segment of the population trajectory with an exponential function, and calculated the 95% confidence intervals around this curve. This curve was then proposed as a criterion for listing as endangered. If any future population size fell below its 95% confidence interval, Schreck et al.

(1996) proposed immediate reclassification as endangered. The authors also proposed a criterion for delisting, derived from the population trajectory. From 1950 to 1976, the population appeared to fluctuate at random around a fixed mean of roughly 80 spawners per mile.

The lowest abundance during this period was 39 spawners per mile, a density reached three times (1950, 1960, and 1969). Since 1982, the population has not exceeded this nadir. Schreck et al. (1996) proposed that these stocks should be delisted if the total population again grows above this level, and remains there for a consecutive 9 years. The authors caution, however, that their interpretation of the trend is tentative, and that any substantial change in the trajectory indicates the need for a new analysis.

The authors also plotted the trajectories for two other Gene Conservation Groups in Oregon (the Umpqua River, and the Coos/Coquille Rivers), and found considerable variation with no consistent pattern. They concluded that these populations are beyond imminent risk, but recommended continuing monitoring.

The kind of analysis performed by Schreck et al. (1996) could be expanded to include partial and full autocorrelation estimates as well as transfer and intervention functions. The recent downward trend observed in the northern populations likely follows a transfer function of an ocean variable such as mean-surface temperature. A separate model could be estimated for each Gene Conservation Group, and its fit tested with least-squares and backcasting techniques. A confidence interval around the forecasted trajectory would allow estimation of extinction risk over any time period.

For the Northern Gene Conservation Group, the lack of variation around the trend suggests that a transfer function (of ocean conditions) will be found that fits the trajectory closely, and gives a narrow 95% confidence interval. Because of this close fit, the model will very likely predict a high extinction risk over the next 10 to 20 years.

Demographic Modeling

The techniques described above allow development of an explicit mathematical model describing the fluctuations in the trajectory of a population from one year or generation to the next. These techniques make use of trigonometric functions, correlation analysis, and many statistical techniques for testing fit, estimating confidence limits, and other procedures. However, the actual ecological mechanisms that determine the demographic behavior of the population do not enter explicitly into the model-building process. Their influence is only indirect, in shaping the trajectory that is being modeled (through post-hoc spectral or autocorrelative analysis).

The purpose of demographic modeling is to approach the problem from the other direction, which is to derive a model directly from knowledge of those ecological relationships that are known or hypothesized to determine the population trajectory (Burgman et al. 1993). The fit of that model can then be tested using the same techniques (least squares, backcasting) as

in Box-Jenkins analysis, and confidence limits can also be estimated. However, there is no limit to how complex a realistic demographic model can be. Complexity, and especially non-linearity of the model, can make certain procedures (such as least-squares estimates) difficult. This is because the expected or "mean" trajectory produced by a non-linear model is not necessarily the same as that predicted by the deterministic portion of the model. Hence, one cannot simply calculate the prediction of deterministic portion, and then compare this to observations. The trajectory actually predicted by the whole model (deterministic portion plus stochastic portion) will most likely be different.

Techniques exist, however, for overcoming this problem. One is to linearize the model, using techniques that have been developed for this purpose (e.g., using a Taylor expansion and obtaining derivatives, perhaps with numerical estimates). Another is to estimate the mean prediction of the model by Monte Carlo computer simulation. Many runs of the model are made with the same observed N_t. The only difference between runs are in the error terms, which are generated randomly according to a previously chosen probability distribution. Then the grand mean N_{t+1} is calculated for each observed N_t, and this trajectory can then be compared with the true trajectory. This is done repeatedly, with different values for the parameters in the model, until the set of parameters which yields the best fit to the time series is obtained.

So, one can obtain a model for the population trajectory in two ways which are: 1) by analyzing the correlational properties of the trajectory itself, and 2) by postulating a model *a priori* from what is known about the ecological relationships of the population that produced the trajectory. Interestingly, the best fitting model generated by one technique is not likely to fit as well as the best model generated by the other, and choosing between the two may be difficult. Most likely, the best model will be a combination of both. A time-series analysis, for example, can identify long-term trends and oscillations in the population that demographic techniques ignore. Incorporating these into a demographic model will then improve its fit and forecasting accuracy.

Though I have drawn a distinction between these two general ways of building a population trajectory model, in reality they overlap considerably. For example, one might decide from demographic knowledge that the model must have a certain form, and then estimate its parameters from behavior of the population trajectory. In practice, deciding on a form is usually a matter of determining how population density affects the survivorship and reproduction of individuals. If survivorship (l) decays exponentially with density N_t, then we can write:

$$l = \exp\left(\alpha - \beta N_t\right) \tag{1}$$

where $\alpha \leq 0$ and β respectively determine the maximum survivorship at low density and the rate of decay of survivorship with increasing density. If this is the only density dependence in the population, then each survivor will contribute an average of K offspring to the next generation independently of the density of survivors, so that:

$$N_{t+1} = K\, N_t' = K\, N_t \exp\left(\alpha - \beta N_t\right), \tag{2}$$

since the number of survivors N_t' is equal to $N_t l$. The population trajectory then follows a Ricker model, which is:

$$N_{t+1} = N_t \exp\left(r - \beta N_t\right), \tag{3}$$

where $r_t = \ln\left(K\right) + \alpha$.

The previous Ricker equation gives:

$$\ln\left(R_t\right) = r - \beta N_t, \tag{4}$$

where R_t is the population growth rate from time t to $t + 1$, equal to N_{t+1}/N_t . We can add a stochastic term to this equation by allowing r to vary randomly over time, so that $r = r_0 + c_t$, where r_0 is a constant. This gives:

$$\ln\left(R_t\right) = r_0 + \varepsilon_t - \beta N_t, \tag{5}$$

Equation 5 suggests that one can estimate the parameters of the Ricker model by plotting $\ln\left(N_{t+1}/N_t\right)$ against N_t, regressing a straight line through these points, and setting r equal to the intercept and β equal to the slope. However, this procedure may give unsatisfactory results, for two reasons.

First, the stochastic term in the equation might be quite large, due to great variation in all sources of mortality throughout the life cycle. If we had a large sample of values of the population trajectory, this might not be a problem. Small sample size, however, will make our estimates of the Ricker parameters very uncertain.

Second, a plot of $\ln\left(N_{t+1}/N_t\right)$ versus N_t includes the quantity N_t in both variables. This would not be a problem if we could measure N_t and N_{t+1} with 100% accuracy. As long as Equation 5 held, the intercept and slope of the regression line would estimate r and β. However, any experimental or sampling error in our estimates of population size will introduce a negative correlation between $\ln\left(N_{t+1}/N_t\right)$ and N_t, over and above any negative correlation due to density dependence. Even if the true value of N_t were the same at every t, yet, inaccuracy in our measurements of them caused spurious year-to-year variations, a plot of $\ln\left(N_{t+1}/N_t\right)$ versus N_t would yield a negative slope. If the number of sample points were large due to many years of data, this slope could be very highly significantly less than zero. Figure 1 shows a very highly significant negative correlation in a regression of this type, even though the two variables (analogous to N_{t+1} and N_t) are two entirely independent random deviates, generated by computer from a uniform distribution between zero and 4,000. In comparison (Figs. 2, 3), Ricker plots from real data, show correlations substantially less significant. The correlations in these plots may be spurious, due to the inherent statistical dependency of the y value on the x.

How, then, should we estimate the parameters of the Ricker equation? One method is to screen off the noise caused by density-independent sources of mortality by observing directly, or designing an experiment to observe the effect of density on survivorship and reproduction of

individuals. In other words, to focus on the specific source of mortality due to density, so that other sources of mortality and its variation have no chance to interfere. In many current populations of coho salmon, the stage at which density-dependent mortality appears to operate most strongly is during the growth of hatchlings to summer parr (Nickelson and Lawson 1998). If we plotted hatchling density against proportion of hatchlings that survive to summer parr, we would find a significant negative relationship (as was found by Moring and Lantz 1975). This relationship is not lost in the noise of other sources of mortality later in life, since we are ignoring those. However, again, we have the problem of spurious correlation, because a single quantity (i.e., the number of hatchlings), is contained in both the y variable and the x variable. To ensure that the x and y are independent, we could alternatively plot the hatchling density versus the density of survivors at the beginning of summer (rather than the proportion of survivors). This would yield a curve similar to a recruitment curve, with a positive slope near the origin, and a peak or plateau at greater density. It would be harder to estimate the Ricker parameters from this scatter of points, because a straight line regression through them would be meaningless. One possible method would be to simply estimate the direct fit of various Ricker curves that differ in the magnitudes of r and β.

To do this, we first write a Ricker equation containing reasonable values of these parameters. Then, we add to the equation a random error term or terms. We then find the mean or expected prediction of this model for each of our observed hatchling densities. The fit of our model to our observations is defined by the sum of square differences between the observed and predicted number of survivors for each measured density of hatchlings. We do this repeatedly for many Ricker curves that differ in the magnitudes of r and β, until we find a curve that gives the best fit.

It is important that we test the fit of the full stochastic model, and not just the deterministic portion of the model. This is because, even though the mean of the stochastic term is zero, if it varies at all, then the deterministic portion will not give the same curve as the expected curve of the total model. Specifically, the deterministic portion of Equation 5 will underestimate the true expected value (of number of survivors for a given hatchling density), and this underestimate will increase as the variance in the error term increases.

We could of course perform this analysis on the values of the population trajectory itself. However, a plot of N_t versus N_{t+1} will almost certainly be noisier than the corresponding counts of individuals just before and after the action of density dependent factors. Moreover, the recorded population densities at any reach might never have been sufficiently large to affect survivorship and mortality, or have been sufficiently large too seldom to provide reliable information about how the population responds to high densities. This is especially likely to be true for endangered populations. Given these difficulties, probably the best procedure will be to extrapolate the Ricker parameters from a few controlled experiments to all populations of interest.

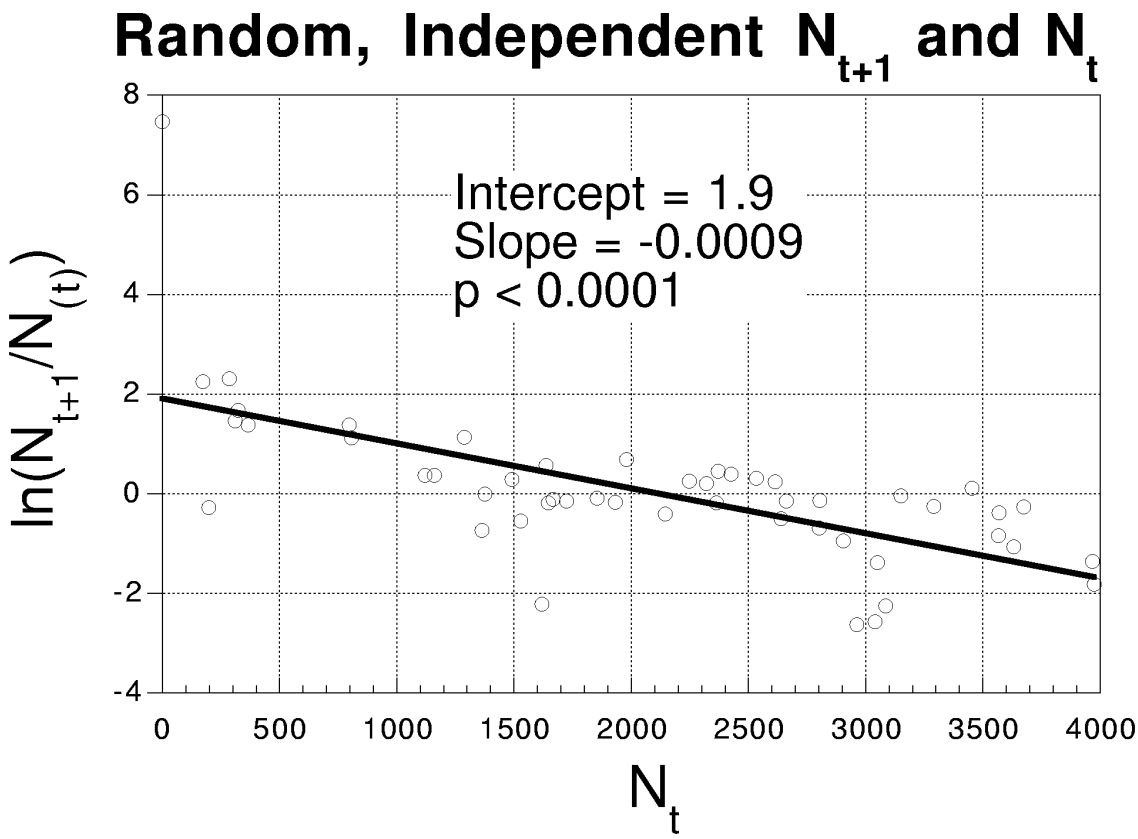

Figure 1. Plot of $\ln\left(N_{t+1}/N_t\right)$ versus N_t where N_t and N_{t+1} are two independent random deviates from a uniform distribution from zero to 4,000. A highly significant relationship is found, even though the N_t and N_{t+1} are entirely independent.

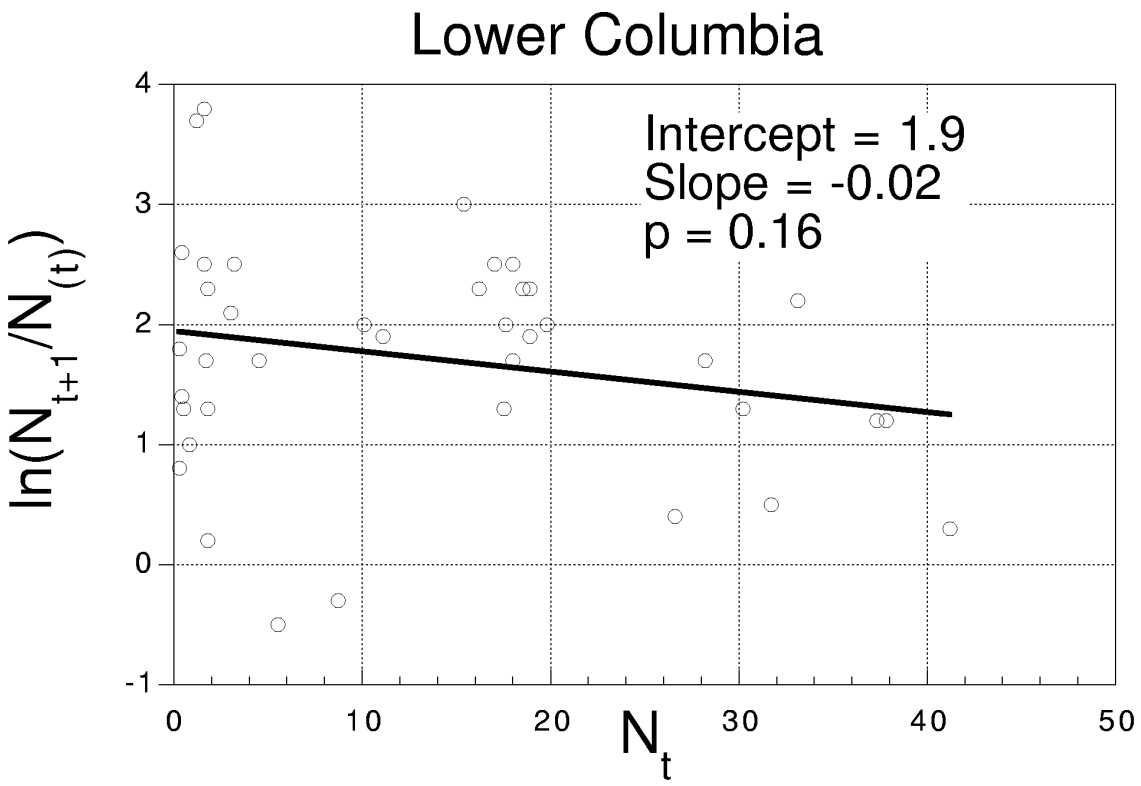

Figure 2. Plot of $\ln\left(N_{t+1}/N_t\right)$ versus N_t for the Lower Columbia River coho salmon, 1952 to 1991. Counts are per mile. N_t represents spawners, and N_{t+1} the total recruits 3 years later, including harvested fish.

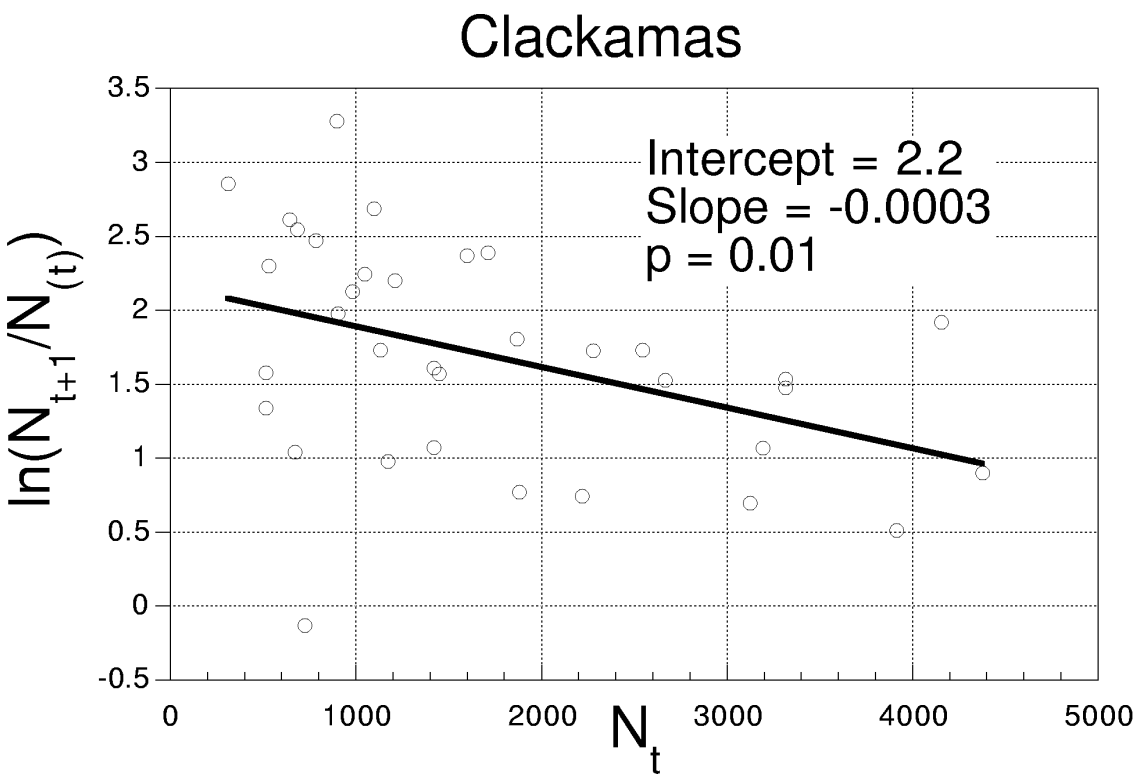

Figure 3. Plot of $\ln\left(N_{t+1}/N_t\right)$ versus N_t for Clackamas River coho salmon, 1957 to 1991. Counts at Northfork Dam. N_t represents spawners, and N_{t+1} the total recruits 3 years later, including harvested fish.

Applications

The Oregon Department of Fish and Wildlife (ODFW) has constructed several stochastic Ricker models to estimate the extinction risk in Oregon populations of coho salmon. The Coastal Salmon Restoration Initiative (CSRI) Science Team (1996) has fitted Ricker parameters from spawner/recruit ratios in 13 populations, including stochastic terms with standard deviation equal to that of the $\ln\left(N_{t+1}/N_t\right)$ versus N_t regression for each population. They performed each Ricker simulation 1,000 times for 10 generations, and recorded the proportion of simulations that ended with less than two fish per mile (or 100 fish total for the Rogue population), defined as quasiextinction. They found generally high risks of quasiextinction for several populations, particularly for ocean-survival rates less than 3-4%. If ocean survival was set to 2%, the quasiextinction probability exceeded 0.3 for the Wilson, Siletz, and Rogue populations, after just 10 generations. For a 1% ocean survival rate, this probability was close to 0.3 or higher for seven populations. In all analyses, the Wilson River population showed the highest extinction risk. The authors conclude that ocean harvest should be held sufficiently low to maintain coho salmon abundance at a minimum of one-third of full seeding in all populations.

Similar models (Nickelson and Lawson 1998) have been constructed in which the Ricker parameters were estimated not from spawner/recruit ratios, but rather from independent studies of density dependence and survivorship, and the relationship between freshwater survivorship and several attributes of freshwater habitat (including active channel width, reach type, reach gradient, density of beaver dams, and the density of pools). Ricker parameters from a large number of Oregon reaches were estimated from these relationships, and stochastic terms were added with standard deviation conforming to the data. An addition to these models was the inclusion of migration between populations. The habitat analysis suggested that freshwater habitat in Oregon coastal basins is so poor that only about 17% is of sufficient quality to allow populations to replace themselves under 3% marine survival and with no harvest. Preliminary risk-assessment results suggested (at least for marine survival rates above 1.5%) the existence of two points of equilibrium population density which are the lower unstable and the higher stable. The densities below the unstable point tend to fall rapidly to extinction, and those above tend to increase to the higher equilibrium point. The values of these equilibrium points were found to be strongly affected by marine survival. With the latter set at 2%, for example, the lower equilibrium point for the Tillamook population was roughly 100, but at 3%, the equilibrium dropped to 50.

Metapopulation Models

One goal of modeling the trajectory of a single population is an accurate estimate of the probability of extinction (or quasiextinction) of that population over some future time period. Extinction depends not only on the internal dynamics of that population, but it also depends on the rate of immigration into the population, and thus, indirectly on the dynamics of neighboring populations. Moreover, extinction can occur to any number of populations composing a species. Estimating the extinction risk of one population might not tell us much useful about the probability of extinction over the entire species. An analysis of a metapopulation (or a collection

of partially interbreeding subpopulations) attempts to incorporate the dynamics of an arbitrary number of subpopulations simultaneously. The objectives are to estimate the extinction risks of both individual subpopulations and the entire metapopulation, and include migration as an influence on the extinction risk of subpopulations (as in Nickelson and Lawson 1998).

Any given subpopulation has a chance of going extinct during some time frame, but new subpopulations are being founded at some colonization rate during the time frame. Subpopulations can be thought of as occupying a discrete habitat patch (such as a reach of a river drainage), and the patch may or may not be occupied at any given instant. One can visualize a metapopulation as blinking Christmas tree lights, with subpopulations blinking off and on as they go extinct and their patch becomes recolonized. During any instant, some fraction of the lights are on (i.e., some fraction of patches are occupied by subpopulations), but there is a finite probability that at some instant all the lights will happen to blink off (i.e., extinction of the metapopulation has occurred).

This process can be modeled qualitatively, without including the demographic details of each population if we can postulate certain relationships among probability of extinction, probability of colonization of a habitat patch, and the total density or arrangement of patches. For example, if we assume: 1) a fixed rate e of extinction of patches; and 2) the rate of colonization of vacant patches is proportional to both the density d_v of patches vacant (the more vacancies, the easier it will be for a colonist to find a patch) and the density d_v of patches occupied (the more patches occupied, the more potential colonists), then the instantaneous rate of change in the proportion of patches occupied is:

$$\frac{dp}{dt} = cd_0 d_v - ep + \varepsilon, \tag{6}$$

where c is a measure of colonist ability, and ε is a random error term.

Here we are not attempting to model individual-population trajectories, but rather the combined effects of simple assumptions about extinction and colonization on the total distribution of individuals in a metapopulation. In reality, the individual-population trajectories will determine the probability of extinction in any patch, in part through their effects on the number of emigrants from any patch (high population densities, for example, might lead to greater emigration rates).

An implication of Equation 6 is that, if the colonization component of the equation, cd_0d_v, is less than the extinction component, ep, then the proportion of patches occupied will tend to decrease. One way for this to happen is if deterioration or loss of habitat reduces the number of patches. The fewer the patches, the lower the success rate of colonists. An important and perhaps the non-intuitive point here is that, even if the eliminated patches are unoccupied, the colonization rate will decrease due to the lowered likelihood that an emigrant will find a suitable patch. Once the patch density falls below a threshold, there will be a continuing loss in proportion of patches occupied, leading to inevitable extinction of the metapopulation. In this

case, the metapopulation is said to carry an "extinction debt," which it must eventually pay, though perhaps not for many generations.

The concept of metapopulation is certainly applicable to salmonids. A given species can be thought of as a metapopulation that consists of several temporally and spatially separate breeding stocks, among which some migration occurs via straying between drainages and migration of jacks between temporally separated stocks. We can then study the balance between extinction of individual stocks and recolonization of vacant reaches of a drainage. The primary datum of such a study is the presence or absence of spawning adults at a particular reach during a particular spawning period. From this qualitative information, we can calculate the proportion of suitable reaches that are occupied, for each successive spawning period, and thereby construct a time series.

This habitat-occupancy time series for a particular drainage might remain constant at 100% over all known time periods. In this case, this simple qualitative information is of little value in assessing risk. It is more likely, however, that some suitable reaches in a drainage or group of drainages will be vacant during any particular census period. These reaches may, in future census periods, become recolonized, and other reaches vacated. The habitat-occupancy time series then fluctuates over time, just as the individual-population trajectories fluctuate. A variety of natural processes and human activities may affect both colonization and extinction rates. Chance high abundance of a stock one year might result in a higher straying rate into vacant reaches. Shifts in stream flow may alter the channel morphology and rates of erosion resulting in new regions of suitable spawning gravel. Upland erosion and sedimentation due to logging activities might eliminate spawning habitat in some reaches.

A habitat-occupancy time series can be analyzed as any other time series, with spectral or ARMA models, and the transfer or intervention functions (based perhaps on some of the previously mentioned processes) can be used to improve fit and predictive power. If we had full knowledge of all reaches occupied in some drainage for several decades, we would most likely find a long-term downward trend in habitat occupancy that correlates with spawning-habitat degradation. Although fluctuations will be superimposed on this trend (due in part to greater colonization rates during periods of abundance), Equation 6 suggests that a downward trend might continue even after habitat degradation has stopped. This would occur if density of available spawning habitat dropped to such low levels that random strays are unlikely to find newly vacant spawning habitat. Local extirpations, though uncommon, would then not be balanced by recolonizations, and the metapopulation would be facing extinction in the absence of habitat mitigation. Due to the difficulty of obtaining precise data on salmon numbers, this qualitative analysis (of a habitat-occupancy time series) may be the best we can do to assess the extinction risk of some salmon species or stocks.

Including genetics in the models

In addition to ecological and demographic factors, genetic factors also put small populations at a greater extinction risk. First, small populations have lower genetic diversity, which may make them less able to evolve in response to changes in the environment. Second,

individuals in small populations are likely to be more closely related than those in large populations. Inbreeding is more common, and inbred progeny may have a lower fitness (see Waples and Do 1994). Third, sampling error makes selection against deleterious mutations less effective in small populations. Changes in their frequency more closely approaches a true random walk, and they may become fixed in the population close to the rate at which they appear. Though each deleterious mutation may have an imperceptibly small effect, as more and more become fixed, they may greatly lower the mean fitness of the population. Eventually individuals may no longer replace themselves from one generation to the next. When this point is reached, the population will spiral rapidly to extinction.

Because the effect of deleterious mutations can be difficult or impossible to see at the population level, their effects may not appear in the population trajectory until just a few generations before extinction. This limits the utility of time-series analysis as a means of assessing the contribution of genetics to the extinction risk. Harmful mutations may be invisible because each female produces a very large surplus of progeny, of which only one female will survive on average to reproduce in a stable population. Even if all the progeny have accumulated many deleterious mutations (perhaps over tens of generations in a small population), and their fitness is quite low, nevertheless the total fecundity of a female may be so large that several progeny are nearly always guaranteed to survive the action of their mutations. Density-dependent processes will then prevent all but one of these (on average) from successfully reproducing. The population may then persist at what appears to be a normal, healthy level. But as mutations accumulate, eventually the probability of surviving will fall below the reciprocal of a female's fecundity. Then, on average, deleterious mutations will allow less than one of her offspring to survive and reproduce. When this point is reached, the population trajectory gains a permanent downward trend, and the population may survive only a few more generations as mutations continue to accumulate and reduce fitness even further.

Currently, this process of extinction due to mutation accumulation can be explored through either analytical techniques (such as diffusion theory and matrix analysis), or the use of simulation models that explicitly represent every individual in the population, the mutations contained in that individual, and the segregation of those mutations in every mating. However, genetic and demographic complexities are difficult to incorporate into an analytical treatment. Simulation models have been developed to model extinction of coho salmon due to mutation accumulation, by myself and Lynch (1997), under a contract with the ODFW.

These models build on previous work by M. Lynch and colleagues, and are based on the following assumptions:

- Occurrence of mutations follows a Poisson distribution, in which the mean and variance in the number of new mutations per zygote are equal, and is at least one.

- When homozygous, a mutation reduces the probability of survival by 5% on average.

- When heterozygous with a wild-type allele, the expression of the deleterious mutation is reduced by more than 50%; i.e., the mutation is partially recessive.

- Populations are at or near carrying capacity, and the mean effective number of offspring per mating is two.

- The effective fecundity of females is 10. This number defines the intrinsic rate of increase of the population at low density, which is not equal to the total number of eggs laid by females (roughly 2,500) because the vast majority of these will die even under the best conditions.

- The effective size of populations ranges from less than 10 to over 120 individuals. The effective size is a measure of the number of individuals in an ideal random-mating population that would have the same loss of heterozygosity as observed in the real population. If individuals vary in their mating success or the population has gone through a recent bottleneck, the effective size is expected to be substantially smaller than the actual count of spawning adults.

- The viability of a zygote depends on the total number of mutations it contains, and whether a mutation is in a homozygous or heterozygous state.

We allow mating (with separate sexes) to occur at random, and mutations to occur in each zygote at random genetic loci. We decide in advance the effective size N_e, of the population, and create zygotes at random to build a population of this size. Each zygote's viability is calculated, and we compare that viability with a uniform, random number to determine whether that zygote survives to reproduce. If a zygote carries mutations, it may not survive. In this case, the remaining fecundity of its mother is decremented by one. Deleterious mutations accumulate in the population because the population is finite, and sampling error can cause the frequency of mutations to change at random, sometimes in a positive direction. As mutations accumulate, the mean viability of the population drops. Eventually the viability drops so low that some females spend all their fecundity (i.e., produce ten zygotes) without success. Eventually, the average female produces less than two survivors, the population no longer replaces itself from generation to generation, and declines rapidly to extinction.

Some preliminary results may serve to exemplify this process. For a mean deleterious-mutation rate of one, the mean time to extinction for a population with random mating, separate sexes, ranges from 20 to over 1,000 generations, as the effective size increases from eight to 128 individuals (Fig. 4). These are the times required for mutations to accumulate until viability drops to roughly one in ten (the reciprocal of the maximum female fecundity). As effective size increases, selection is more efficient in weeding out deleterious mutations, and random drift of mutations to fixation is a much slower process.

In reality, however, the deleterious mutation rate might be greater than one. In this case, extinction occurs much more rapidly. For example, a population of effective size 64 reaches extinction at times ranging from 400 to just 50 generations as the deleterious-mutation rate increases from 2 to 10 per generation. This drop in time to extinction applies even in the presence of reasonable rates of mutation to slightly beneficial alleles, which might be expected to offset the effects of the deleterious mutations (Fig. 5).

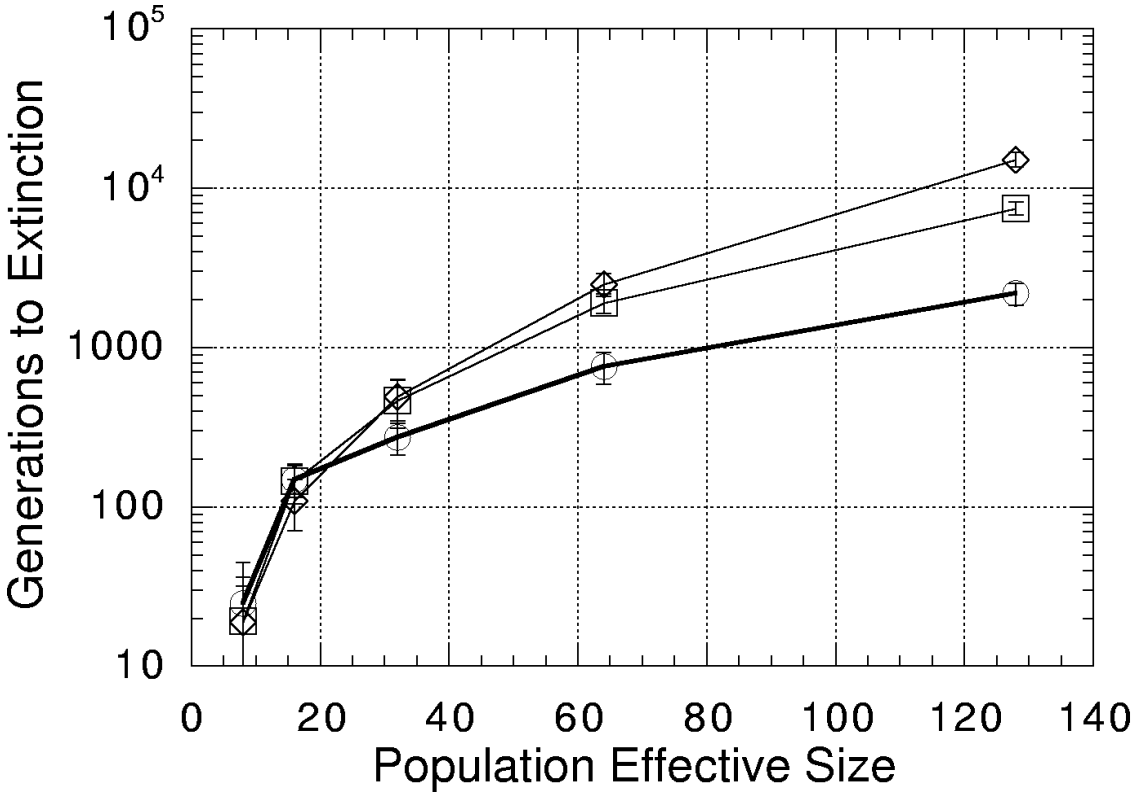

Figure 4. Generations to extinction due to accumulation of spontaneous, deleterious mutations, for populations of different effective sizes. The three curves represent different functions relating number of mutations to total fitness: circle represents multiplicative fitness, and square and diamond represent more rapid than multiplicative declines in fitness with increasing number of mutations.

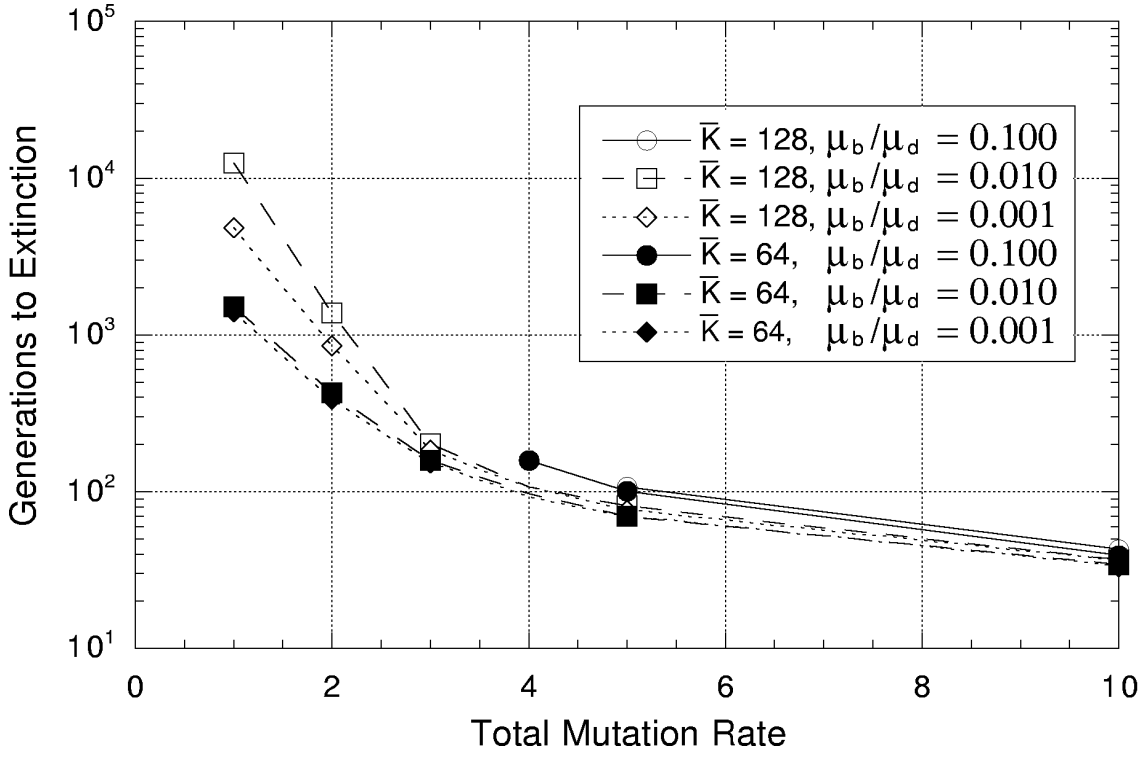

Figure 5. Generations to extinction versus total mutation rate, beneficial plus deleterious. $\bar{K}$ represents mean effective population size, and μ_b/μ_d the ratio of beneficial to deleterious mutation.

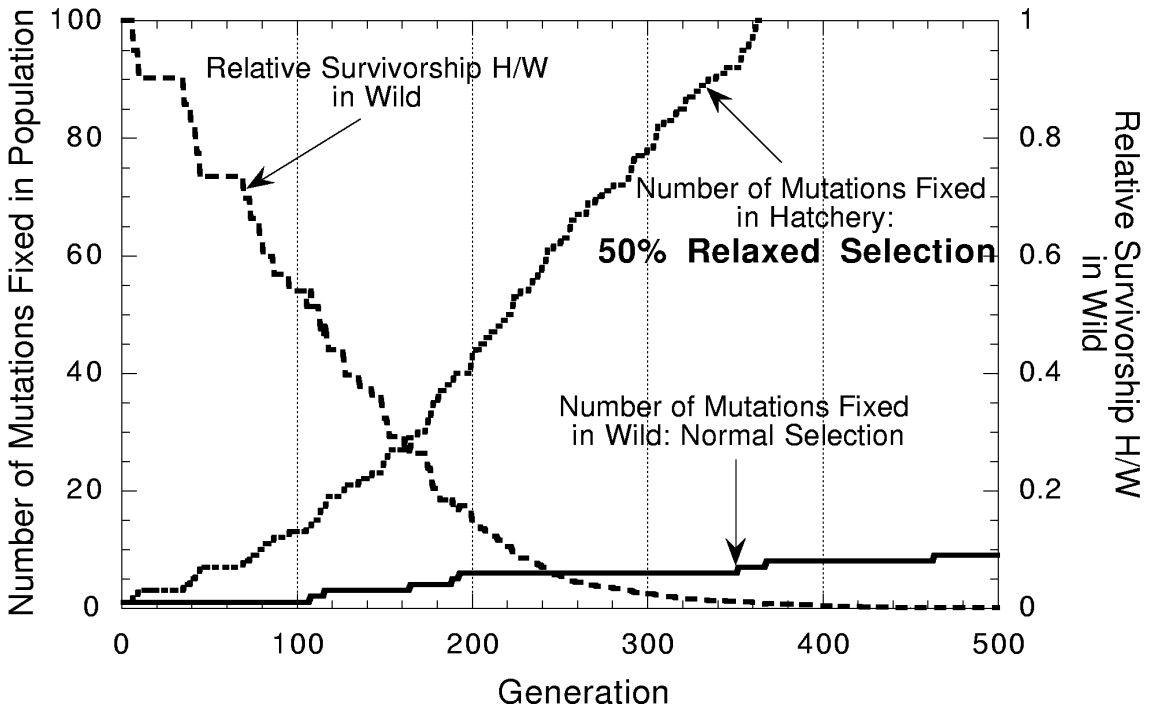

Figure 6. Accumulation of mutations and resulting loss of relative fitness in the wild for hatchery population under 50% relaxed selection and multiplicative fitness. The effective population size for both hatchery and wild is 50, and a mean of one deleterious mutation occurs each generation, with fixed effect 0.05 in the homozygous state and 0.0175 in the heterozygous state (dominance coefficient 0.35). Relaxed selection allows deleterious mutations to accumulate at roughly 10 times the rate at which they would occur in a population of the same size in the wild. As a result, fitness of hatchery fish in the wild drops to half that of the wild population in 100 generations.

Genetic effects of hatcheries on wild stocks can be explored within the framework of this model. In hatcheries, natural selection is intentionally relaxed in order to increase production beyond what would be expected in the wild. Relaxation of selection results in the survival of genotypes that would not survive the threats facing juveniles in the wild. Once adults, these fish might successfully stray into wild populations, and introduce these deleterious alleles into the wild population. This migration of deleterious alleles from hatchery to wild would have effects similar to increasing the deleterious mutation rate in the wild populations. Simulations with this model show that, under relaxed selection in hatcheries, the accumulation of deleterious mutations can occur up to 10 times as fast as in the wild, since the fitness difference necessary to weed out deleterious alleles is artificially eliminated or reduced in hatcheries (Fig. 6). As a result, fitness of hatchery fish in the wild declines exponentially, to roughly half that of the wild population in 100 generations. Thus, without regular input of wild fish in the hatchery program, the relaxed selection in hatcheries must be maintained indefinitely to avoid extinction of the hatchery population.

Conclusions

What role should models play? In a sense, the role of quantitative models in salmon risk assessment will always be central. Any risk assessment necessarily requires forecast of a population trajectory into the future. A forecast can be done only by making quantitative assumptions about the rules governing a population trajectory. These quantitative rules are by definition a model. If a forecast has any logical basis at all, that logic represents some sort of model of the population.

Nevertheless, most decisions to list a species as threatened or endangered have not been based on any explicit population model whatsoever, let alone on any quantitative estimate of extinction probability. Were these decisions erroneous, unscientific, or perhaps even irresponsible? Almost certainly the answer is no. In many cases, species have declined to such small numbers for reasons so plain that a quantitative-risk analysis would have told us only what was already obvious. The same may be true for some stocks of Oregon coho salmon.

Still, such analyses can always be performed. For example, if we believe that a population has shrunk so small that only a minor bad year is likely to cause complete mortality, we are essentially positing a random-walk model. We are asserting that, regardless of the form of the deterministic portion of the population model, the population is now so small that the stochastic portion dominates its dynamics. We can certainly express that assertion mathematically, by choosing a stochastic term with a reasonable distribution and variance. We can then use the equation to simulate the population trajectory, and perhaps find that 98% of our simulated populations go extinct after 50 years, due to one or many successive years of bad luck. Thus, our initial belief is confirmed.

To take another example, suppose we observe a long-term decline in abundance of a population. We then perform studies that conclude that a certain kind of habitat degradation is responsible for the decline. We are almost certain that continued habitat degradation is inevitable, and if it continues at the past rate, extinction will occur in 50 years. These beliefs can

be expressed in terms of a mathematical model. We are asserting a correlation between some habitat variable and the number of individuals the habitat is capable of supporting. We can express that mathematically, and include at least two stochastic terms which are: one to describe how tight the correlation is, and another to describe how almost certain we are that the degradation will continue. A simulation could again be used to conclude that the population has perhaps a 98% chance of extinction in 50 years.

One might say that in both these examples, it is no surprise that the initial assessment was validated by the model, since the model is basically a reiteration of the initial assessment. That is true and precisely the point. Any forecast can be restated using a mathematical model. In most cases, our quantitative intuition may be accurate, and the use of a model only provides confirmation of that accuracy. In cases of severe endangerment, forecasting will often be trivially easy, and no quantitative analysis will be necessary to justify a legal listing. Subsequent analysis, however, will often be useful. Models can be used to compare different recovery plans (e.g., if some of their effects are complex and stochastic in nature), and to determine when recovery has occurred.

What kind of model? Current knowledge of salmonid ecology is sufficient to allow construction of models that combine: 1) demographic mechanisms, 2) geographic variation in habitat quality, and 3) decadal cycling due to oceanographic conditions. Such models could be run on inexpensive desktop computers. More advanced computing technology will allow individual-based stochastic models that incorporate genetics and metapopulation dynamics. Several of these components have already been constructed in separate population viability analyses, with very profitable results (Emlen 1995, CSRI Science Team 1996, Nickelson and Lawson 1998, Schultz and Lynch 1997).

Quantitative or qualitative data? The full range of knowledge of a species can be incorporated into a population-trajectory model. This includes both quantitative and qualitative information. Presence or absence of an activity affecting the population can be coded as a time series of ones and zeroes. The influence of this intervention function on the population trajectory can be estimated. Presence or absence of a population at a suitable habitat patch is as much a time series as a full-population trajectory, and can be studied with the same techniques used to model the latter.

What if the model is biased? Population-trajectory models can certainly provide unbiased estimates of the extinction risk. If they represent true statements about how a population changes over time, then by definition, they must be accurate. The question is not whether unbiased models can be created but rather: How do we go about choosing the best model? The best model is our best guess how a population's numbers change over time. This guess is based on the totality of our knowledge of the population. The population model that we accept should be one that we believe represents the true mechanism of population change, or is as close to the true mechanism as our knowledge permits. If more than one alternative model appear equally accurate, or if there is controversy regarding accuracy of parameters, we can estimate the extinction risk with more than one model. In that case, we will end up with a set of equally supported (given our current knowledge) extinction risk estimates rather than one single best estimate. Of course, we should certainly use unbiased techniques to estimate the parameters of

our models. But the accuracy of these techniques does not guarantee the accuracy of the model, which is determined ultimately by the accuracy of our knowledge. The possibility of bias is a moot question until we know more. If our model is the best reflection of reality available, then its risk estimate is by definition the best estimate that our current knowledge permits.

How do we deal with a paucity of data? Our knowledge of some aspects of a population will necessarily be less complete than others. For example, we currently know little about the genetic parameters that are critical in estimating extinction due to loss of genetic diversity. We have few or no estimates of effective population size, the degree of relaxed selection in hatcheries, the rate of deleterious and beneficial mutation, and the genetic basis of traits that differ in fitness. Nevertheless, we can still model extinction due to these lesser known features of the population. We can do this by bracketing each of the poorly known parameters within a reasonable range, and generating two estimates of the extinction risk, which would be one for the most optimistic values possible, and another for the most pessimistic. In the context of extinction, the pessimistic prediction should take priority. This procedure is hardly different from that mentioned in the previous, of performing separate risk assessments with several equally supported models. We are confident that the best estimate resides within these two limits, but our knowledge is not sufficient to say precisely where. The point is that lack of information is not defeat, because we can quantify our uncertainty. If we know its limits, we can translate them directly into limits on our estimates of the extinction risk. Regardless of our incomplete biological understanding (and it will always be incomplete), we can always translate what we do know into a best estimate of the extinction risk.

Absolute, or relative risk? We can use an extinction model to predict the absolute extinction risk over an arbitrary time period. We can use it to predict whether one set of input parameters gives a greater risk than another set, regardless of the absolute risk. The latter typically would be applied to different candidate management plans. If we simply want to know whether one proposed course protects the population better, this will sometimes be a trivial question that can be answered with no simulation at all (assuming we know how each course will affect the parameters of the model).

Can our knowledge ever be so poor that we should avoid estimating an absolute extinction risk, and stick to making such easy qualitative comparisons? I would say no. First, our best estimate of absolute risk is necessary. Otherwise, we would have no reason for granting legal protection to a population, or wondering how best to protect it from extinction, in the first place. Second, making such a qualitative comparison may not at all be any simpler than performing an estimate of the absolute extinction risk. In fact, it may be essentially the same exercise. Consider the question: Are hatcheries, overall, a benefit or a detriment to total production of a drainage? This is a very complex question because hatcheries have potentially both positive and negative, deterministic and stochastic effects, and we cannot sum up those effects into a total effect on any parameter of any model. The only way this question can be answered is by running a full, complex simulation of all those effects, and observing how they interact finally to cause extinction. We would need to do this twice, in the presence and absence of hatcheries, and compare the two estimated extinction risks. In so doing we have had to calculate not one, but two, estimates of absolute extinction risk. This comparison is not easier, but twice as hard as calculating a single, absolute extinction risk. The accuracy of the relative

risk is no more accurate than either absolute risk. In fact, we might not even be able to say with confidence whether a particular hatchery has a positive or negative effect, since the uncertainties in the two absolute estimates may overlap. If they overlap, then we might know with reasonable confidence that the absolute risks fall within some range, but still could not say much about the relative risk.

Thus, predicting relative risk is not always easier or safer than predicting the absolute extinction risk. Given that we are unsure of the health of a population, there is no good reason to avoid using a model to calculate an absolute risk. The resulting estimate may have such a large uncertainty that it may be of little value, but we do not know this until we perform the exercise. The utility of the estimate will speak for itself.

Summary

Mathematical models can be used to estimate the extinction risk. The best model is that which most accurately captures the mechanics of population fluctuation. We can trust a model as far as we trust our own understanding of the population. Any forecast of a population trajectory is based, either explicitly or implicitly, on a model of the population. In extreme cases, an explicit analysis may not be necessary to justify legal listing, and will only confirm what is already obvious. Models of salmonids have been, and will continue to be, useful in monitoring the health of randomly fluctuating populations and in assessing the relative efficacy of candidate-management plans. Accurate models will be easier to develop for salmonids than for most other animals or plants, because of the wealth of information collected on this economically important group. Results of past modeling efforts suggest that some stocks of coho salmon are in danger of extinction, and should be given federal status as threatened or endangered.

Acknowledgements

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Appendix 1

Workshop Agenda

Appendix 1
Workshop Agenda

November 13, 1996

Welcome and Introductions

8:30-8:45 Alec MacCall, NMFS, Southwest Fisheries Science Center.

Background

8:45-9:00 *Key issues in ESA listing determinations for Pacific salmon:* Robin Waples, NMFS.
9:00-9:15 *NMFS' present approaches to risk assessment:* Tom Wainwright, NMFS.

Overview

Two reviews of factors contributing to salmon extinction risk:
9:15-9:45 Speaker 1: Phil Mundy, private consultant.
9:45-10:00 Questions/Discussion

10:00-10:30 Speaker 2: Jay Nicholas, Oregon Department of Fish and Wildlife.
10:30-10:45 Questions/Discussion

10:45-11:00 Break

Ecological Issues

11:00-11:30 *Climatic influences on salmon populations in the northeast Pacific:* Bob Francis and Nate Mantua, University of Washington.
11:30-11:45 Questions/Discussion

11:45-12:15 *Population risk and habitat condition:* Pete Bisson, U.S. Forest Service.
12:15-12:30 Questions/Discussion

12:30-14:00 Lunch

Diversity Issues

14:00-14:30 *Metapopulation ecology and the extinction risk of West Coast salmonid populations*: Marc Mangel, University of California.
14:30-1445 Questions/Discussion

14:45-15:15 *Ecological diversity:* Tommy Williams, Oregon State University.
15:155-15:30 Questions/Discussion

15:30-15:45 Break

15:45-16:15 *Genetic diversity:* Mike Lynch, University of Oregon.
16:15-16:30 Questions/Discussion

November 14, 1996

Artificial Production

8:30-9:00 *Risks and benefits of hatchery production:* Gayle Brown, National Biological Service.
9:00-9:15 Questions/Discussion

Assessment Methods

9:15-9:45 *Predicting extinction in salmon: How far can we trust the models?* Stewart Schultz, University of Miami.
9:45-10:00 Questions/Discussion

10:00-10:30 *Population Viability Analysis: the Risk Assessment Paradigm:* Dan Goodman, Montana State University.
10:30-10:45 Questions/Discussion

10:45-11:00 Break

11:00-12:30 Breakout groups:
Discussion groups including audience and panel members. These groups will define important issues to be considered by the panel in forming its recommendations. Each group will prepare a brief summary report to be transmitted to the panel.

Group A: *Habitat and environmental fluctuations*
Group B: *Genetic and ecological diversity and hatchery issues*
Group C: *Assessment methods*

12:30-14:00 Lunch

Summary and Concluding Remarks

14:00-15:00 Breakout group summary presentations.

15:00-15:30 *Workshop summary:* Brian Riddell, Canadian Department of Fisheries and Oceans, Nanaimo.

15:30 Adjournment

November 15, 1996

Discussions of conclusions by panelists (closed session)

Appendix 2

Panel Recommendations

Appendix 2
Panel Recommendations

Background

The panel was mandated to provide advice to NMFS regarding the best information and best techniques to use in scientific evaluations for ESA listing and delisting decisions for Pacific salmon. Prior to the workshop, the following documents were mailed to panelists to provide a common background.

- Chapter 7 "Evaluating Risk" from "Science and the Endangered Species Act" (Committee on Scientific Issues in the Endangered Species Act, National Research Council, 1995).
- "Determining minimum viable populations under the Endangered Species Act" (Thompson 1991).
- "Evolutionarily significant units and the conservation of biological diversity under the Endangered Species Act" (Waples 1995).
- NMFS status review reports for coho salmon and steelhead (Weitkamp et al. 1995; Busby et al. 1996).

Phil Mundy was elected to chair the panel working session. NMFS staff (Alec MacCall and Tom Wainwright) presented their lists of priority issues to be addressed by the panel. The panel took these as non-binding recommendations in prioritizing their work.

Alec MacCall:

1) Defining the proper management unit for assessing risks--how does it relate to ESUs, what is the scale of "local adaptation"?
2) What is a "significant portion of the range"?
3) How should genetic and demographic concerns be balanced?
4) How do we quantify habitat values?
5) How do we incorporate long-term ocean variability?

Tom Wainwright:

1) How should multiple risk factors be combined into a single risk assessment?
2) How should single population risks be translated into ESU risk?
3) How should we evaluate risks associated with hatchery production?
4) How can we deal with the uncertainty in assessing natural sustainability for mixed natural/hatchery stocks?

Panel Discussion and Recommendations

ESUs/Significant Portion of Range

The panel has concerns about the definition of ESUs and interpretation of significant portion of the range as they affect risk assessments.

The panel recommends some check of robustness of risk assessments to alternate definitions of ESUs and different interpretations of significant portion of the range, for example by doing risk assessments using different ESU boundaries to see if that affects conclusions.

NMFS should consider using the definition of Evolutionary Units (EUs) as described in the Klegg report (NRC 1995).

Abundance

Abundance should be expressed as effective breeding number (N_e) for evaluating random genetic effects – if $N_e > 1000$, random genetic effects are insignificant.

Treatment of abundance data in an empirical Bayesian format would be useful. This would involve predicting the probability distribution of future abundance (or extinction) as a function of current abundance as a comparative approach.

Measures of apparent abundance (e.g., redd counts, dam counts) are least preferred for risk assessments – measures of effective breeding number and age/sex composition would be better.

Habitat

The Nickelson type of habitat model (Nickelson 1998), utilizing multiple regression of capacity on habitat characteristics, is useful in quantifying habitat.

Such models need to be combined with life-cycle population dynamics models to assess risk. Information needs to be collected on a spatial scale that permits interspecific interactions to be evaluated.

Note/caveat: It is very time-consuming to gather data and evaluate models. Complicated habitat models may be swamped by data variability, so simple models may be as effective.

Recent Events

When evaluating the effects of recent natural events or changes in management, uncertainty in the consequences should be considered.

Balance of Genetic and Demographic Risks

This is a false dichotomy. Genetic and demographic affects interact. It is necessary to account for genetic effects on demographics (e.g., shifts in fitness affect population productivity). Non-random (directional) genetic factors (e.g., hatcheries) need to be considered.

Combining Factors into a Single Evaluation

A default quantitative model could be used for combining main effects (demographic, genetic, habitat, and hatcheries). It is feasible to develop such a model. Model development should proceed through an open cooperative process guided by a group of experts.

Ocean/Climate Variability

Incorporating ocean/climate variability into management models is problematic because there is a several-year lag before regime shifts are visible. Risk evaluation could be done in the same way as it is done for habitat, with low predictability.

Model analyses could be done with or without climate cycles, but with interannual variability superimposed. How this would change under different oceanic futures could be examined.

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Appendix 3

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Appendix 3
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