Spatial Organization of Pacific Salmon: What To Conserve?

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1. Introduction

The rich biological diversity in salmonids has been recognized for centuries and has been a central premise in managing salmon fisheries in this century (the "Stock Concept"). But recently, as in many other biological resources (FAO, 1981; Oldfield, 1989), increased concern has been expressed about the loss of biological diversity and the impact of harvest management on Pacific salmon. Management of Pacific salmon (*Oncorhynchus* sp.) is probably as rich in social, economic, and political issues as its resource base is biologically, and the scope of this issue continues to expand. Multiple resource management principles, such as sustainable economic development (WCED, 1987), will increase harvest and environmental issues involved in salmon management decisions. Evidence for global climate changes increases uncertainty about future salmon production. Litigation is increasingly used to protect specific interest groups. Unfortunately, in many salmon management decisions, the non-biological interests have taken precedence over the biological resource (Wright, 1981; Fraidenburg and Lincoln, 1985; Walters and Riddell, 1986). Each of these may have been a responsible decision, but in aggregate they create a serious biological problem through the gradual but steady erosion of biological diversity. An adage for similar problems in other fields of resource management is The Tyranny of Small Decisions. However, decisions favoring biological conservation are becoming more frequent, even though their effects on resource use, other resources, and communities are becoming more controversial.

In the Pacific Northwestern USA, Nehlsen et al. (1991) have identified 214 salmonid stocks of concern, 159 of which are considered to be at moderate to high risk of extinction. Since 1990, the Sacramento winter Chinook and Snake River sockeye (Redfish Lake), and spring and summer Chinook stocks have been listed as threatened or endangered under the Endangered Species Act of the United States. In Canada, a comparable inventory of Pacific salmon has not been prepared. In southwestern British Columbia, however, one-third of the spawning populations known since the early 1950s have now been lost or decreased to such low numbers that spawners are not consistently monitored (Fig. 1). This area of British Columbia has been the center of urbanization and development and is not representative of the

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Genetic Conservation of Salmonid Fishes, Edited by J.G. Cloud and G.H. Thorgaard, Plenum Press, New York, 1993

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salmon resource in the province generally, but northwestern USA is not unique in their concern for conservation of Pacific salmon populations.

In the immediate future, resource managers can anticipate being asked more frequently "what to conserve" and policy makers will have to consider "at what cost". The latter issue will be an essential one but will not be considered in this paper (see Norton, 1986). The essential biological issue is what to conserve, but there is no single answer. The answer will vary between situations depending on the species and the remaining distribution of breeding populations, population dynamics and integration of the species with its ecological system, the status of the

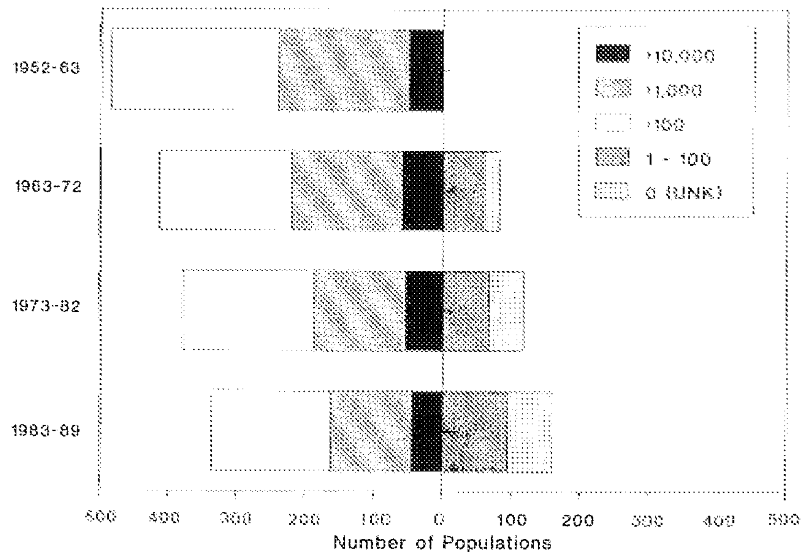

Figure 1. The number (n=495) of Pacific salmon (*Oncorhynchus nerka, O. keta, O. gorbuscha, O. kisutch, O. tshawytscha*) spawning populations by size classes (numbers of spawners by species) and time periods in southwestern British Columbia (east coast Vancouver Island and adjacent mainland areas including the lower Fraser River). The number of populations with zero spawners or unknown numbers (UNK) were combined because once a population consistently shows none or very few spawners the field staff may not monitor the stream.

resource, and the causes of the conservation problem. Each answer will be information intensive, expensive, and likely controversial. The answer to such complex situations are seldom unique or unanimously agreed upon. Further, many of the future debates will be results of past mistakes.

This paper presents a series of principles for management of Pacific salmon to conserve genetic diversity. The guidelines are admittedly pragmatic and their applicability may vary. However, they are a step towards recognizing and integrating a conservation genetic objective in Pacific salmon management while also recognizing the limitations of our knowledge in the population genetics of Pacific salmon. More scientific research is needed to improve this knowledge but the incorporation of genetic advice in fishery management decisions should not wait for the development of more rigorous quantitative guidelines.

2. Genetic Diversity in Pacific Salmon

The life history and biology of Pacific salmon have recently been reviewed in Groot and Margolis (1991). Reproduction and early juvenile rearing (of varying periods) are in

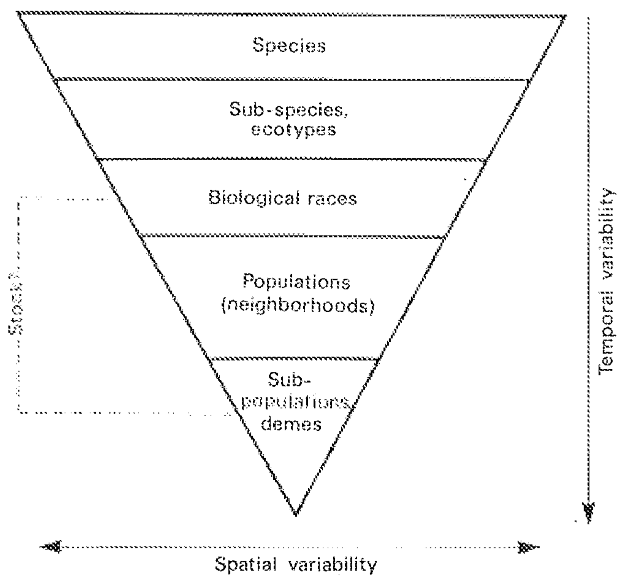

Figure 2. Schematic representation of the hierarchical organization of genetic diversity in Pacific salmon. The inverted triangle emphasizes that locally adapted, and largely reproductively isolated sub-populations or demes are the basic unit of diversity in these species. Varying definitions of "stock" would place this term in the range identified by the dashed lines.

freshwater but juveniles migrate to the sea for feeding until maturity and then return to their natal stream to spawn and die. Patterns of historical colonization following glaciation, adaptation to local spawning and rearing environments, and recent anthropogenic impacts have resulted in fragmented spatial distributions of locally adapted spawning populations (reviewed recently in Altukhov and Salmenkova, 1991; Taylor, 1991). Biological diversity within the Pacific salmon species naturally forms a hierarchical organization (Fig. 2).

Higher levels of the organization share more common life history traits, for example races of salmon defined by adult migration timing (spring and fall Chinook salmon, winter and summer steelhead trout). Lower levels within each higher division consist of more localized spawning groups adapted to finer scale environmental differences, and being largely reproductively isolated from other local groups. In population genetic theory, these isolated local groups are commonly referred to as demes (Gilmour and Gregor, 1939; Wright, 1969). The differentiation between a deme and larger population units becomes more arbitrary depending on the exchange of genes between population units. In Wright's treatise (1969), he describes several models for spatially sub-divided populations up to and including the neighborhood, defined as the population of a region in a spatial continuum. In conservation biology, the concept of the metapopulation (see Simberloff, 1988) is analogous to Wright's view of populations as being a loosely but connected group of demes.

The total genetic diversity in a species is the sum of variability between each hierarchical level and within each level, the latter including the cumulative variability from each lower level. Over time, the between population variation should increase as the species invades new territory or continues to adapt to environments within its range (temporal variability, Fig. 2). However, total diversity may not change and may even decrease over time depending on the spatial range maintained, the balance of selective versus disruptive genetic factors within the breeding populations, and the population dynamics of the species. The latter being of particular concern in Pacific salmon because of their long history of exploitation and anthropocentric impacts on freshwater habitats. At any one time though, the greatest diversity in such a hierarchically organized species exists over all hierarchical levels (populations within races, races within ecotypes, etc.) within the spatial range of the species (spatial variability, Fig. 2). Unfortunately, such a truism does not assist us in determining how much diversity is conserved over a specified area or group of populations; and the degree of differentiation between hierarchical levels differs between salmon species (Ryman, 1983; Altukhov and Salmenkova, 1991). What we can deduce from this organization is that maintaining maximum biological diversity requires maximizing the number of demes conserved over time and space.

The term "stock" has been used extensively in referring to a population of salmon, but its definition and application has been inconsistent and, at times, confusing. Consequently, stock may refer to various organizational levels in Figure 2 and may not be a useful term in conservation discussions. The word "stock" is from old English use meaning descent or lines of ancestor. Its use in fisheries literature follows from the 1938 Conference on Salmon Problems (Moulton, 1939) when stock was selected as the most desirable term to indicate that there was not necessarily a hereditary basis for differences observed between groups of salmon. No evidence was presented at this conference for hereditary factors in differences between "river stocks". Hereditary factors have, of course, now been demonstrated and, for Pacific salmon, summarized in Ricker's (1972) famous paper on hereditary and environmental factors affecting salmonid populations. Confusion in the use of stock results from its initial application in identifying intra-specific groups for fishery management, and numerous subsequent efforts to define stock in terms of population structure. A major conclusion of the 1980 Stock Concept symposium, however, was that the latter is not as important as acceptance of the stock concept to provide a genetic perspective in management decisions (MacLean and Evans, 1981). The stock concept is a conceptual summary of the genetic basis to the spatial hierarchy in Figure 2. The term "stock" though should probably not be used to describe population units in conservation since the population level it refers to is uncertain and likely varies between individuals (see Dizon et al., 1992). A common terminology to describe the spatial organization of Pacific salmon should be accepted to promote understanding of biological diversity. Terms in Figure 2 are commonly used in population genetics literature .

The term "stock" remains useful in managing fisheries and may be defined as a manageable or recognizable group of population units (Larkin, 1972). Larkin also acknowledges that "what we define as a stock is partly an arbitrary decision taken for human convenience. Any practical management definition of a stock requires some degree of treating groups collectively rather than separately." Pacific salmon demes are unlikely to be harvested discretely or to be identifiable uniquely. Consequently, managing stocks and conserving demes involves two issues: identifying the stocks in a fishery, and limiting harvest rates to maintain inter-demic diversity within stocks.

3. What Is It We Are Preserving?

Conserving biological diversity will involve trade-offs with other management objectives and will incur costs. It is appropriate then to briefly consider the values of conserving this diversity, particularly since the necessity for maintaining diversity will continue to be questioned. A notable example of this is Larkin's (1981) perspective on population genetics and fisheries management. Although Larkin had been more conservative in previous papers, in this one, he questions the emphasis on between "stock" differences and suggests that "Insofar as genetics is concerned, we should not become too hysterical about population declines to low levels. " His latter suggestion should now be rejected (see Soule, 1987), although hysterical seems to over state the point, but information on the relative fitness of different populations is still limited.

3.1. Economic Values

The most obvious values are the financial returns from fishing and tourism and the potential for future development. If the only objective in salmon management was maximizing the sustainable catch for commercial fisheries, then maintaining broad population diversity may not be necessary or consistent with this objective. Production could be sustained by the most productive natural and enhanced populations but less productive ones would be over exploited (Ricker, 1958; Kope, 1992), possibly resulting in extinction. Management objectives are not so simple, however, and over the past 15 to 20 years three major changes favouring diversity have occurred. The most significant change has likely been the development of specific catch sharing agreements (allocation) between an increasing number of user groups. These agreements have limited harvest in mixed stock and species fisheries to allow certain species and individual stocks to escape to fisheries closer to their natal streams. The obvious example of this is the sharing of Pacific salmon catches between native and non-native fishers in the United States (Clark, 1985; Blumm, 1990). The rapid expansion of recreational fishing and investment in tourism has also contributed to change. Along the west coast of Canada, recreational fishing and related tourism have been estimated to now equal the value from the Pacific salmon commercial fishery. The third change has been the substantial increase in world salmon production through mariculture, and from hatchery and wild populations. Recent high catches of salmon have reduced prices and are changing industry concerns from the supply of salmon to optimizing economic benefits from a catch limited by available markets. Distributing fishing effort and catch over time and space and stabilizing salmon production over more populations would benefit the industry and favour population diversity.

There are also indirect economic benefits. Maintaining a diverse population basis will increase habitat utilization and the stability of their natural ecosystem. Protecting and utilizing productive fish habitats may become important in negotiations with other resource developers. Efforts to preserve these habitats for salmon would be weakened if it was not utilized, particularly since natural re-colonization will be slow and salmon transfers have a very low success rate in re-establishing self-sustaining populations (Withler, 1982).

3.2. Social Values

Pacific salmon are an integral part of the social heritage of the Pacific coast of North America. The cultural significance of Pacific salmon to native peoples is without question, and salmon fishing has also been fundamental in the development of non-native communities (Lyons, 1969; Netboy, 1980; Roos, 1991). But even in the general public, Pacific salmon are an integral part of the aesthetics in this region. Large numbers of people volunteer to participate in habitat improvement and small scale salmon enhancement projects. Educational programs to foster a conservation ethic are an essential part of salmon enhancement programs. Access to salmon fishing is a valued recreational opportunity and its economic importance was noted above. It is probably not an exaggeration to suggest that a healthy Pacific salmon resource is part of the moral values in these west coast communities. Healthy salmon populations are equated to a healthy environment and good resource management practices.

Comparing these societal values with other values which can be determined quantitatively (for example, the economic value of another commodity) will be a problem, but the importance of social values in maintaining biological diversity should not be under-estimated. People live throughout most of the range of Pacific salmon and will naturally value maintaining populations in their local area. E.O. Wilson (1984) has argued that human nature has developed "in a good part because of the particular way we affiliate with other organisms." Along the Pacific coast, responsible stewardship of localized salmon populations probably has strong societal support, but it must be expressed and heard. Procedures likely need to be established to ensure that these values are considered in management decisions (Scarnecchia, 1988).

3.3. Biological Values

In a practical sense, the biological diversity presently observed is a non-renewable resource, and only an instant in the dynamic evolutionary process. The diversity has resulted from colonization events, innumerable events which changed genetic variation, and the differential fitness of individuals over past environments. Once a spawning population is lost, any unique traits it may have possessed are realistically gone forever. Consequently, the principal biological values are adaptedness in the existing populations, maintenance of population structures and the evolutionary process, and, very simply, maintaining the spatial and temporal basis for salmon production. The latter would be true even if the diversity between spawning populations did not have a genetic component since salmon accurately return to their natal habitat (summarized in Table 1 of Quinn, 1990; Gharrett and Smoker, 1993). This point was first made by W.M. Rich (1939) at the 1938 Conference on Salmon Problems. But the value of maintaining diversity for production is still frequently confused with debates about genetic variation between spawning populations and how much to conserve. The distribution of existing spawning populations and protection of the rearing habitat provides the basis for production. The existing production may not be maximal due to depressed population sizes or unutilized habitat but maximizing the number of demes maintained will likely increase juvenile production (and presumably total production unless the marine environment is limiting). Maintaining most of the demes would limit exploitation rates to those sustainable by demes with lower productivity. Spawning numbers in the demes with higher productivity would increase and juvenile production more fully utilize the habitat. Further, large spawning escapements may stimulate colonization of unused spawning and rearing environments.

Another value, but one which will probably receive little weight compared to the above, is the knowledge created by studying the present population structure and biological diversity. Our understanding of the population genetics of Pacific salmon is still very limited and concerns have been expressed about the genetic impact of harvest practices (Ricker, 1981; Healey, 1986; Riddell, 1986), and hatchery practices and production (Goodman, 1990; Hilborn, 1992). Studies of the remaining natural populations are essential to develop genetic guidelines for restoration programs and conservation of the species.

4. What Are the Major Sources of Impacts?

It is impractical in this essay to consider the variety and combinations of specific factors which have reduced diversity and population sizes. The factors involved and their relative importance will vary and will have to be identified and managed within each situation. However, to summarize sources of past impacts and concerns for the future, five categories of impacts have been identified, but their impacts are not independent. For example, the catch sustainable from a population size varies with the productivity of the population and the habitat carrying capacity. If productivity is reduced through habitat loss or environmental change then fishing pressures must be reduced to sustain that population size.

4.1. Fishing

Pacific salmon are heavily exploited species. Historically, fishing was very near or in rivers, but with the development of refrigeration in the early 1900's, fishing began to move off-shore becoming more distant from the rivers. This led to the development of ocean fisheries harvesting mixtures of many salmon populations, sequential exploitation by several fisheries on an individual population, and intense competition both internationally and domestically. The biological results were decreased spawning population sizes, changes in the biological characteristics of the spawning populations, and the creation of complex salmon management problems. The Canadian Commission on Pacific Fisheries Policy concluded that "the immediate cause of continuing declines and low levels of abundance (of salmon) is overfishing" (p.14, Pearse, 1982). Fishing has contributed to decreased diversity in Pacific salmon, but fishing is also the first impact targeted for conservation actions since fishing can be immediately controlled when necessary.

While resource managers are now acutely aware of many problems, resolving these problems and controlling fishing impacts will remain an unenviable task. Efforts to maintain a diverse resource base and increase production from depressed populations will be increasingly disruptive to fisheries, local communities, and other activities potentially affecting fish habitat. But denial and inaction will only exacerbate the eventual impact, whether it is extinction of a population or increased costs to maintain it. Frequently, the controversy about a conservation action involves denial of responsibility for the problem...some other group was the principal cause. Individual fishing groups do not believe that their impact is enough to cause the problem or lead to extinction, and they should not, therefore, be heavily impacted by the conservation plan. Management actions also seem disproportionate to the contribution of the population to a fishery. Controversy naturally arises from this situation since any one group is likely correct, but it is the aggregate impact of all groups that must be managed. Further, these debates have to be addressed even when the fishery may not be the principal cause. Future salmon production can only be developed from what is present and conserved today. Consequently, if the causes require time to correct then the population can be conserved by reducing the harvest impacts, or possibly, by more artificial actions such as gene banks (Bergan et al., 1991).

4.2. Point Source Problems

A point source problem refers to a wide variety of localized anthropocentric impacts which reduce the productive capacity of salmon habitat. The impact of 28 dams in the Columbia River hydropower system is an obvious example (Raymond, 1988). Water regulation for power, irrigation, and industry is a wide spread concern along the Pacific coast (Dorcey, 1991; Mundie, 1991) but is also only one of many habitat impacts. In a recent review of habitat impacts in the Fraser River, twelve impacts associated with human activities were identified (Table 1). Henderson (1991) associates habitat impacts (temperature, flow, etc.) with each of these activity types by habitat types (lakes, tributaries, mainstem, estuary). It is not unexpected though that a large variety of impacts were identified when 86% of the province's population lives in British Columbia's largest watershed.

Table 1. Human activities affecting Pacific salmon habitat in the Fraser River, B.C. Canada (summarized from Henderson, 1991).

Dykes and stream channelization	Argiculture and water abstraction
Municipal and industrial landfills	Logging
Port development	Silviculture
Dredging and log storage	Roads, railways, and transport of dangerous goods
Urbanization and municipal effluents	Pulp mill effluent and wood preservatives
Mining	Dams

Early development in the Fraser severely depressed salmon production following the 1913 rock slide at Hell's Gate in the Fraser canyon, and logging dams at the outlets of Quesnel and Adams lakes (Ricker, 1987; Roos, 1991). Sockeye runs to these lakes were amongst the largest sockeye runs in the Fraser. Sockeye production in the Quesnel has now recovered but returns to the Upper Adams river remain very small and the original Upper Adams sockeye are likely extinct. The logging dam on the Adams River was built in 1908 (Fig. 3) and in 1911 no sockeye were reported above the dam. Small numbers of sockeye now return to Upper Adams spawning streams but 16 transplants of non-local populations were released between 1949 and 1975 (Williams, 1987). If the original runs were not extinct following the dam, then the genetic race has likely now been lost through genetic drift and introgression. Williams reports that the Upper Adams River has 1.2 million m^2 of spawning area. Consequently, the

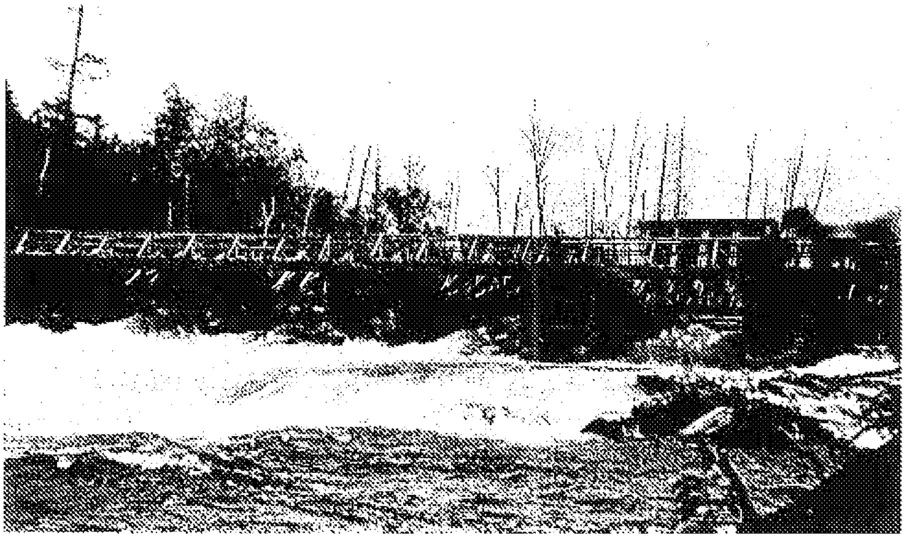

Figure 3. The Adams River logging dam 1908-1921. This dam blocked passage of summer run sockeye to the Upper Adams River, populations in this river have not recovered.

loss of this one population has cost the fishery, on average, six million sockeye per cycle year based on the productivity of other summer sockeye populations in the area (Cass, 1989).

Point source problems will have to be identified on a case-by-case basis and may not be easily addressed. Frequently, their impact on salmon production is unknown and difficult to partition from the annual environmental variation observed in salmon populations. Further, these impacts result from large industrial economic and urbanization bases. Conservation discussions will therefore contrast values associated with salmon diversity with values and ethics of other industries and interest groups (Norton, 1986; Callicott, 1991).

4.3. Urbanization and Population Growth

Population growth and urban development are obviously associated with Fishing and the Point Source Problems but are an increasingly important concern for the future. The population in British Columbia has increased by approximately 50% since the 1971 census and is expected to double by about year 2010 (Ministry of Finance and Corporate Relations, Province of BC). The direct impacts of this in salmon management are likely to be loss of small stream habitat, increased water regulation, and increased recreational fishing effort. The indirect effect may be increasingly polarized debates between conservation values and economic and health necessities of an expanding population. Resource managers would be well advised to begin planning how to meet these demands.

4.4. Biological Limitations and Climate Change

As in the Point Source Problems, numerous biological factors may influence the productivity and existence of salmon populations but each situation will likely differ. The types of biological factors involved include: intra and interspecific competition, predation, exotic introductions, and disease. Loss of biological diversity is not commonly attributed to biological interactions except for the notable exception of exotic introductions: sea lamprey (*Petromyzon marinus*) in the Great Lakes (Smith, 1968; Smith and Tibbles, 1980), the parasite *Gyrodactylus salaris* in Norway (Johnsen and Jensen, 1991), and the opossum shrimp (*Mysis relicta*) in Idaho lakes (Spencer et al., 1991). The ecological and genetic effects of fish introductions were the topic of a recent international symposium (FIN, May 17-19, 1990, Windsor, Ontario). In his synthesis paper Allendorf (1991) concludes: "Purposeful introduction rarely have achieved their objectives. Moreover, both intentional and unintentional introductions usually have been harmful to native fishes and other taxa through predation, competition, hybridization, and the introduction of disease." Several papers in that symposium showed that genetic effects of introductions constitute a threat to the long-term existence of wild populations and species.

The primary intention of identifying this type of impact was that biological factors may become more important when attempting to restore population sizes and if climate changes. If a population has been in low abundance for many years, its community may have adjusted such that the species can not expand its share of the resources or its abundance. Projections about climate change in Canada (Hengeveld, 1991; McBean et al., 1991) and the Pacific northwestern United States (Leovy and Sarachik, 1991; Neitzel et al., 1991) suggest it could have a significant effect on biological diversity in Pacific salmon, particularly in the southern portions of species' ranges. Climate change will reduce the freshwater productivity of southern salmon populations, and may threaten the survival of populations if they can not adapt. The latter will be of particular concern in small, spatially isolated demes that may not have the genetic variation remaining to adjust to a rapidly changing environment.

4.5. Hatchery Impacts

The use of hatcheries has a long history in Pacific salmon management. Hatcheries and spawning channels are used to augment catches, mitigate environmental impacts, and to supplement numbers of natural spawners. The numbers of Pacific salmon juveniles released from facilities are staggering (over 5 billion per year in the late 1980's) and McNeil (1991) has estimated that 55% of the world salmon harvest in 1990 was cultured salmon (mariculture plus ocean ranched). The economic importance of this contribution is obvious but there is clearly growing concern about the long term impact of cultured production on the genetics of natural populations (Helle, 1981; White, 1989; Goodman, 1990; Hindar et al., 1991; Nehlsen et al., 1991; Waples, 1991; Hilborn, 1992; Meffe, 1992). Waples (1991) summarizes the concerns as three issues: direct genetic effects (caused by hybridization and introgression), indirect genetic effects (due to altered selection regimes or reductions in population sizes caused by competition, predation, disease, or other factors), and genetic changes in hatchery populations which magnify consequences of hybridization with wild fish. Waples (1991) and Hindar et al. (1991) both document that hatchery production can have substantial direct and indirect genetic effects on wild fish.

Managing these concerns will again be controversial. Hatchery production is seen by user groups as a technical solution to difficult management problems or the loss of productive habitat. Basically, the controversy will contrast production objectives of users (to sustain catch) and longer term management objectives to conserve genetic diversity. However, as Waples (1991) also states, production and conservation objectives are inseparable in the stewardship of the Pacific salmon resource. The issues are how to utilize hatchery production while controlling harvest to protect wild populations, and to develop genetic guidelines for culture programs so that direct and indirect genetic effects are minimized.

5. What to Conserve?

The rhetorical response is simple: "Everything". In practice though, the response seems to have been "as much as is practical". The latter response reflects past emphasis on salmon harvest objectives and, I suggest, management confusion in applying the stock concept. In British Columbia, if a population is not large enough or identifiable in a fishery, then fishery managers refer to these populations as being passively managed. The designation resulted from practical limitations but signifies acknowledgment of a risk of population losses. Under the broader set of values discussed above, more balance between short (present harvest) and long (genetic diversity and sustained production) term objectives would be anticipated. To achieve this, managers will require clear policy statements about fishery management goals, and advice on the population dynamics, biological characteristics of the species, and how to conserve genetic diversity. The following principles are proposed for the latter, but are likely more general than a manager would desire. However, more specific advice would quickly lose its general applicability and could be applied incorrectly without a manager's appreciation. Given our limited knowledge of population genetics in Pacific salmon and their fine-scale spatial organization, it seems appropriate to advise from a conservative perspective.

These principles are listed in decreasing order of importance and assume the hierarchical model of biological diversity, and a broad spatial scale of populations impacted by harvest, habitat alterations, and the presence of hatchery populations. The priority of these principles may vary between situations in more localized areas.

(i) *In the absence of other proof, manage Pacific salmon from the premise that localized spawning populations are genetically different, and valuable to the long term production of this resource.*

To borrow from Waples (1991) and the conclusion of the FIN symposium, "First, do no harm." This is obviously an idealistic principle but aptly emphasizes the importance of maintaining genetic diversity. By managing from this premise and protecting habitat, resource managers are, first, stewards of the resource for long term production and, secondly, managers of short term utilization and impacts. Managing from the opposite premise will continue to result in lost diversity and production. **It is simply untenable to expect managers to prove value in each localized population before it will be conserved.**

(ii) *Identify higher levels of organization which are threatened.*

Genetic variation between the higher organizational units (sub-species, races, etc.) resulted from largely independent evolutionary lines. Differences observed between these units are important components of diversity but their independence also implies importance as reserves of rarer genes.

(iii) *Maintain a broad perspective of the spatial and temporal* impacts.

Too narrow a focus on production has led to conservation problems but too narrow a focus on one conservation problem may also be counterproductive. A narrow focus could mask sources of the conservation problem, generate new problems by neglecting other local populations or ecological issues, and could be detrimental to credibility in the broader resource management community.

(iv) *Maintain genetic variation within populations by maximizing the spatial and temporal distribution of demes.*

The likelihood of maintaining genetic variation, and therefore adaptability, increases as the number of salmon reproducing per deme increases and the number of demes increase. Further, maintaining demes in marginal environments is possibly more important than currently appreciated in salmon management (Scudder, 1989). Scudder suggests that conserving marginal populations and habitats is one of the "best" ways to conserve genetic diversity. By maximizing the spatial and temporal distribution of spawning populations, the numbers of spawners per deme would increase, exchange between demes would be facilitated, and new demes may develop as spawners disperse from more productive habitats

As for advice concerning a minimum spawning population size, more evaluation of this issue is required. The concept of a minimum viable population size (see Soule, 1987) for long term survival has not, to my knowledge, been applied to Pacific salmon. Further, the concept will not provide a single value to be applied to all populations (nor is this appropriate since each situation is likely unique). Rather, it considers the probability of a population surviving over a specified time, environmental variation, and the genetic effective population size (N_e, for Pacific salmon see Waples, 1990). Managers must recognize, however, that the genetic N_e can be substantially smaller than the census population observed on spawning grounds. The two values can not be confused.

(v) Maintain groupings of fragmented populations/races, and contiguous distributions between fragments to facilitate gene flow.

The loss of genetic material in small populations is dominated by random events (genetic, demographic, environmental). Consequently, the loss of genetic material in different populations should be independent. Over many such populations, a large proportion of the original genetic variation should exist.

Managers should not label these small populations as "biologically unviable" or "economically extinct" (phrases from author's experience). Their economic value is diversity and opportunities for future production, and the viability debate frequently confuses small numbers with low productivity. If viability refers to population continuance then it depends on why the population is small (habitat capacity, overfishing, etc.), productivity of the population, and stochastic variation. Small populations are at greater risk of random extinction but are not necessarily unproductive. If over-fishing is the cause, the maximum exploitation rate a population can sustain is a function of its productivity (the maximum rate of adult returns per spawner at low population size) only. For the reasons presented in principles (*iii*) and (*iv*), small populations should not be ignored and actually merit some cost to conserve them.

(vi) Identify remaining wild populations and/or areas of least disrupted habitats, and protect these over a broad spatial range.

Undisturbed habitat and populations are Nature's in situ "gene bank" and are increasingly important as biological controls and study sites. Unfortunately, over large portions of the Pacific salmons' ranges it is difficult to identify such sites. Further, for such refuges to be valuable in conserving diversity, a wide spatial distribution of them will be required and whole watersheds may be necessary to maintain ecological interactions.

(vii) Manage intensive culture programs to maintain genetic variation within the cultured populations and to minimize genetic effects on natural populations.

These topics have recently been reviewed by Allendorf and Ryman (1987) and Waples (1991). Maintaining variation in cultured populations may increase productivity and reduce concerns about direct genetic effects on natural populations. However, whether selection can be averted in intensive culture situations is uncertain. The use of non-local populations in brood stock has largely been stopped and is strongly advised against, unless in extreme situations and after thorough public review.

The development of mariculture is an additional threat of genetic effects on natural populations. The mixing of mariculture fish with wild fish will occur less frequently than from ocean ranching of hatchery fish, but the risk of genetic consequence is greater. Catastrophic mixing may occur following large scale escapes from sea pens, and the genetic composition of the mariculture population will differ from the wild because of selection and the use of non-local population in brood stocks. To protect natural diversity, the frequency of escapes must be minimized (an objective obviously shared by the industry) and guidelines developed to minimize their genetic impact.

(viii) Maintain populations with unique genetic traits or, at least, with genetic traits of important local value.

These populations are non-renewable resources and must be conserved to protect present or future opportunities. This principle seems self-evident but risks continue to be imposed on such populations. Once the gene complexes controlling these traits are altered or lost, reestablishing them is unlikely.

(ix) Maintain original source populations used in resource developments.

Maintaining large numbers of natural spawners in populations used for developments (for example, original brood sources for a hatchery or mariculture program, or a localized fishing opportunity) protects diversity and the development investment. The development of brood stocks for mariculture is an important example. If problems develop in the brood stock then the natural population provides a common source of genetic material to correct the problem. On the other hand, a large natural population may be needed to counteract potentially large numbers of escapees from the mariculture site.

(x) Maintain populations occupying atypical habitats or expressing unusual phenotypic traits.

Experience with Pacific salmon clearly indicates that phenotypic variation between populations is usually associated with some genetic variation. Further, the utilization of different habitats may have a genetic basis and these marginal environments may be important in maintaining genetic diversity (Scudder, 1989).

6. Discussion

Post-glacial re-colonization, habitat patterns, precise homing of Pacific salmon to natal streams, and evolutionary processes have resulted in a spatial hierarchy in the genetic organization of Pacific salmon. The hierarchy is based on locally adapted, largely isolated spawning groups or demes. Anthropocentric impacts during the past century have increasingly disrupted the genetic structure and habitat basis of salmon production. However, over the past 10-20 years, the focus of Pacific salmon management decisions has diversified from principally one of maximum production for commercial fisheries. Changes in resource allocation and broadening of economic benefits, coupled with rising environmentalism and expression of social values, provide increased opportunity to conserve and rehabilitate salmon populations and habitats. Genetic variation, within and between hierarchical levels, and productive habitat are the resource base of Pacific salmon, both for long-term sustainable production and continuing evolutionary processes. Opportunities to conserve this base should be vigorously pursued and tested, presumably by explicitly incorporating conservation objectives in salmon management planning and practice (for example, see Riggs, 1990; PMFC, 1992). Rehabilitation of populations (number, distribution, and size) and protection of habitat will also be essential for minimizing impacts of climate change.

The principles in this paper provide advice about how to conserve genetic diversity through Pacific salmon management. Unfortunately, a plan of how to conserve may be inadequate for successful conservation. Success will require commitment to genetic conservation in salmon management policy, processes to consider economic, social, and biological values in decision making, plus four activities also identified in Allendorf (1991): education, cooperation between management agencies, regulation, and research. Some of these will require more time to develop, particularly methods to compare different types of values and the development of decision processes, but others should proceed immediately.

An appeal for more research has almost become a cliche in scientific literature, but is appropriate in population genetics and conservation biology (including habitat requirements) of Pacific salmon. Nelson and Soule (1987) express this need very well:

> "In surveying the causes of loss of genetic diversity we are struck by how often the conspirators are not the expected Ignorance and Greed but, rather, the equally dangerous Partial Knowledge and Good Intentions."

Those authors emphasized the need for studies of population structure (determining N_e and numbers of migrants) and the effect of selective pressures generated by exploitation on life history traits. Additional requirements are for studies of genetic variation within hatchery populations (inadvertent selection, N_e, inbreeding, operational guidelines) and the genetic interaction of hatchery and wild fish. In response to concerns about climate change, genetic studies of thermal tolerance and correlated traits are advised for populations in areas expected to be affected. It is notable that increased emphasis on genetic conservation may also change public perspectives about research costs in salmon management. Under principle (i), limited knowledge should limit utilization. Investments in research may have a more tangible benefit since utilization could become less restricted as we learn what and how to conserve.

This work should proceed immediately to provide a solid information base for management but results of genetic studies will not be available for several years. In the interim, conservation interests are best addressed through evaluation of the existing resource base, and education of the public and management agencies. Evaluation includes an inventory of existing genetic and habitat resources, and assessment of present versus potential production (stock assessment, see Gulland, 1983). If spawning population sizes are less than the management goals then an immediate conservation benefit can be achieved by increasing the number of spawners and/or increasing the productivity of the population. Conservation will also be benefited by maintaining the broadest spatial and temporal distribution of demes, including the small fragmented and/or marginal demes. Education now becomes paramount. Immediate increases in the number of spawners and populations can only be achieved by reallocating catch (user groups' benefits) to breeding populations. Beneficiaries from the salmon resource are usually supportive of conservation needs but will, understandably, argue to minimize disruption of their usage.

Geneticists advising on conservation of Pacific salmon have a responsibility to user groups and the public to explain, in understandable terms, what genetic diversity is, the importance of conserving it, and the basis for recommended management principles. The essential role of education in resource management was also emphasized by the FIN symposium (Allendorf, 1991):

> "Education is a key in dealing with these issues. Many of the past and current arguments in favor of introductions have been based upon perceived societal demands for food, recreation, or economic benefits. There are two central educational issues. First, the history of introductions tells us that such introductions rarely achieve their objectives. Second, society must realize that such introductions also involve a 'cost' and we usually do not understand natural systems sufficiently to know what the cost will be."

Similar information and education problems exist for Pacific salmon. Management debates frequently involve a small but recurring set of fallacies:

a. lowering harvest rates to restore production will result in continually lower catch
b. small populations are unproductive populations
c. hatcheries are solutions to management and habitat issues (referred to as the Technological Fix Syndrome, Hilborn 1992)
d. sustaining production and conserving genetic diversity are incompatible objectives
e. only a small number of salmon are required for the preservation of populations.

These fallacies must be explained and their impacts identified before managers should expect an increased commitment to an explicit conservation objective in salmon management. Each has been addressed to some extent in this paper.

Genetic conservation in Pacific salmon is fundamentally sustainable development (WCED, 1987) providing a longer term perspective of utilization for a broader set of beneficiaries. The resource bases for sustaining production are genetic diversity (genetic variation within and between all levels of the organizational hierarchy) and the habitat utilized by all life stages of the species. Genetic diversity provides for the continuing evolutionary processes and the biological basis of future production. The first step in sustaining production is improved stewardship of existing resources, but a greater challenge for conservation may be maintaining productive habitat. Human population growth and associated economic development plus climate change can be anticipated to increasingly threaten salmon habitat. Successful conservation will also require habitat protection, educational programs, increased research, and the establishment of accountable decision processes to consider multiple resources and all types of resource values. Realistically, salmon conservation can not proceed independently of other natural resources, particularly the increasing demands for freshwater.

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