

SALMON RECOVERY SCIENCE REVIEW PANEL
Report for the meeting held
December , 2004
Southwest Fisheries Science Center
National Marine Fisheries Service
Santa Cruz, CA

This introductory material (pp. i-iii) is available on the RSRP web site, but as an aid to the reader we are now including it with individual reports.

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Recovery Science Review Panel

The Recovery Science Review Panel (RSRP) was convened by NOAA Fisheries to guide the scientific and technical aspects of recovery planning for listed salmon and steelhead species throughout the West Coast. The panel consists of seven highly qualified and independent scientists who perform the following functions:

1. Providing scientific support to Technical Recovery Teams, specifically:
 - a. Reviewing core principles and elements of recovery science;
 - b. Ensuring that well-accepted and consistent ecological and evolutionary principles form the basis for all recovery efforts;
 - c. Encouraging consistent application of core principles across populations, ESUs, and recovery domains;
2. Providing scientific support to scientists at the Northwest and Southwest Fisheries Science Centers who work on Pacific salmon and steelhead;
3. Providing general advice for salmon science.

The panel meets 2-3 times annually, submitting a written review of issues and documents discussed following each meeting.

Expertise of Panel Members

Panel members have all been involved in local, national, and international activities. They have served on numerous National Research Council committees and have published many papers in prestigious scientific journals.

Dr. Joseph Travis (chair), Florida State University

- *Field of expertise:* Population ecology and genetics, physiological ecology, ichthyology
- *Awards:* Fellow, American Association for the Advancement of Science; Dennis Chitty Lecturer, University of British Columbia; Distinguished Visiting Scholar, University of Zurich; Robert O. Lawton Distinguished Professorship, Florida State University
- *Scientific Leadership:* President, American Society of Naturalists; Past Chair, Science Advisory Board, National Center for Ecological Analysis and Synthesis; Past Editor, *The American Naturalist*; Member of several editorial boards; Member of scientific advisory boards on state and local conservation and management activities
- *Research:* More than 110 scientific publications

Dr. Russell Lande, University of California-San Diego

- *Field of expertise:* Evolution and population genetics, management and preservation of endangered species, conservation and theoretical ecology
- *Awards:* Sewall Wright Award from the American Society of Naturalists; Guggenheim Foundation; MacArthur Foundation; Fellow of the American Academy of Arts and Sciences
- *Scientific Leadership:* Past president of the Society for the Study of Evolution; International recognition: developed scientific criteria for classifying endangered species adopted by the International Union for Conservation of Nature and Natural Resources (IUCN)
- *Research:* More than 140 scientific publications

Dr. Marc Mangel, University of California Santa Cruz

- *Field of expertise:* Theoretical and mathematical biology
- *Awards:* Koopman Paper Prize, Operations Research Society of America; JASA-Applications Invited Paper, American Statistical Association; Fellow, John Simon Guggenheim Memorial Foundation; Fulbright Senior Fellowship, Oxford University; Distinguished Statistical Ecologist, International Association for Ecology; Fellow, California Academy of Sciences; Fellow, American Association for the Advancement of Science
- *Scientific Leadership:* Founding Director, Center for Population Biology, University of California Davis; Chair, SIAM-AMS Committee on Mathematics in the Life Sciences; Past Editor, Behavioral Ecology; Member, Committee of Scientific Advisors, US Marine Mammal Commission; Member, NMFS Ecosystem Advisory Panel; Member, Science Advisory Board, National Association for Ecological Analysis and Synthesis
- *Research:* More than 200 scientific publications

Dr. Ransom A. Myers, Dalhousie University

- *Field of expertise:* Ecology, Conservation, and Management of Marine Animals, Modeling and Statistical Ecology, Population dynamics
- *Awards:* The Great Auk Lectureship (1999), Awarded first Killam Chair in Ocean Studies, Dalhousie University (1996)
- *Scientific leadership:* Member of Science Advisory Boards for Sierra Club of Canada (2003), Oceana (2003), and Atlantic Policy Congress (2000), Member of Board of Directors: The International Oceans Institute of Canada (2000) and Natural Resource Modelling Association (1994-1999). Asked to testify at the U.S. Senate Commerce Committee Hearing on Overfishing (2003) and the House of Commons (Canada) Standing Committee on Fisheries and Oceans (2003)
- *Research:* More than 110 scientific publications.

Dr. Charles Peterson, University of North Carolina Chapel Hill

- *Field of expertise:* Marine community ecology, restoration ecology
- *Awards:* Pew Foundation Scholar in the Environment
- *Scientific Leadership:* Member of many National Research Council panels; Member of several editorial boards; Founding Chair, US GLOBEC Scientific Steering Committee; Past Chair, Scientific Advisory Board, National Center for Ecological Analysis and Synthesis
- *Research:* More than 140 scientific publications

Dr. Mary Power, University of California Berkeley

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- *Awards:* Kempe Award for Distinguished Ecologist, Umea University and Swedish Agricultural University; Jasper Loftus-Hills Prize of the American Society of Naturalists; John and Margaret Gompertz Chair in Integrative Biology, University of California, President-Elect American Society of Naturalists (2005), G. Evelyn Hutchinson Medal (American Society of Limnology and Oceanography, summer 2005)
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- *Field of expertise:* Community ecology, conservation biology, invasion biology
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- *Research:* More than 260 scientific publications

RECOVERY SCIENCE REVIEW PANEL (RSRP)
Southwest Fisheries Science Center, Santa Cruz, California

December 1-3, 2004

INTRODUCTION

Coastal rainbow trout *Oncorhynchus mykiss irideus* is considered to be a single subspecies with two forms, one, migratory/anadromous (steelhead) and the other, resident (rainbow trout) (Behnke 2002). In some geographic areas, these forms appear as separate subpopulations; in other areas, they occur as a polymorphism, with most individuals exhibiting distinct morphological, physiological and behavioral characters associated with one or other life history. The existence of two forms raises several issues for the conservation of *O. mykiss*, from determining appropriate inclusion of subpopulations into ESU's (evolutionarily significant units) (BRT 2003) to devising appropriate recovery plans. The issues are made more complicated by the potential effects of hatcheries, which can produce substantial numbers of both anadromous and resident forms (RSRP 2004).

We are concerned that planning for the recovery of *O. mykiss* include the restoration, maintenance, and protection of the full life-history diversity in this species. In particular, we are concerned that incomplete understanding of the proximate and ultimate causes of the life history diversity in *O. mykiss* may foster complacency concerning the impact of recent extirpations of the anadromous form and failure to appreciate that preserving life history diversity is vital to long-term viability of *O. mykiss* ESUs.

In this light, we devoted most of our meeting of December 1-3, 2004, in Santa Cruz, California, to this subject. In this report, we review the fundamental elements of this life-history variation and assess existing knowledge on the sources of this variation. We conclude that anadromous fish, either within a polymorphism or as a component of a larger population, represent a complex life history that cannot be easily reconstituted from a purely resident stock. In the final section, we comment upon two facets of general viability models in response to specific presentations by the TRTs (Technical Recovery Teams).

RELATIONSHIPS BETWEEN ANADROMOUS AND RESIDENT FORMS

The two forms of *O. mykiss* represent different phenomena in different locations, from a polymorphism within some populations to a secondary contact between divergent subpopulations to reproductively isolated, long-separated lineages (presentation of Carlos Garza). Steelhead population structure, as estimated from molecular genetic markers, is generally concordant with geography. For steelhead, genetic distance between populations is correlated strongly with the geographic distance between them, as measured by coastal distance plus stream distance between spawning localities. Massive outplanting and translocation, mainly into resident populations, has not greatly disrupted the natural population structure of anadromous steelhead, despite the common occurrence of one-way gene flow from land-locked resident populations to anadromous ones. In a few cases, such as the Russian and Eel Rivers, a resident population was introduced above a natural barrier where none had previously existed; these populations remain phylogenetically distinct from the anadromous population below the barrier, in spite of one-way gene flow across the barrier into the anadromous population. These observations are consistent with strong local adaptation in natural steelhead populations and low fitness of introduced fish.

The two life histories appear to be adaptations to different ecological circumstances and evidence suggests that the adaptive distinctions include substantial tradeoffs. In particular, two case studies show that the evolution of residency is associated with a decreased capacity for successful migration. The first

example is the case of a resident population in Sashin Lake, Alaska, descended from a 1926 introduction of juvenile *O. mykiss* from the outlet stream below a natural waterfall that is impassable to upstream migrants. The resident population produces some fish each generation that undergo smolting and migrate over the waterfall separating the lake from its outfall stream. These fish have lower survival to adulthood as anadromous migrants than that of the typically anadromous fish found downstream, with the major contributing factor to that reduced survival being their poor performance in the marine environment (presentation of Jeff Hard; Thrower et al. 2004a, RSRP 2003). These results are consistent with experimental studies from this resident population that indicate negative genetic correlations among traits that can constrain the response of residents to selection for anadromy (Thrower et al. 2004b). The second example comes from the fate of hybrids between residents that escape from the stream above Big Creek Falls in Scott Creek, California and anadromous fish found below the falls; genetic signals of hybridization are found in smolts but not in returning anadromous adults (presentation of Sean Hayes).

The reduced fitness of anadromous phenotypes produced by a long-term resident population is consistent with well-known genetic deterioration of unused or vestigial characters, which typically show decreased expression, diminished function, reduced correlation with related traits, and increased variability (Darwin 1859, Kurten 1953, Pannebakker et al. 2004). This is the same pattern seen through the domestication of hatchery fish in adapting to an artificial environment and losing fitness in the wild (RSRP 2004).

The tradeoff in fitness and the propensity for resident populations to lose the capacity for successful migration is consistent with historical evidence. The anadromous life history appears to be the ancestral condition in salmonids (McDowall 2002). For over a century, *O. mykiss* have been stocked around the world and resident populations have been established from resident, steelhead, and mixed stock (Behnke 1992). This history indicates that resident populations can be established easily behind migration barriers. However, the converse is not true; there is only one published report of anadromy developing from a resident population, that of Pascual et al. (2001) from the Santa Cruz River, Patagonia, Argentina. While there is no dispute that anadromy has evolved from the introduced stock, there is controversy over whether the introduced stock was composed of pure resident genotypes (Behnke 2002, Pascual et al. 2002, Rossi et al. 2004). Moreover, this same stock was used in a number of introductions around the world and anadromy has apparently emerged in only this single case. Members of the RSRP have conferred with colleagues in Eastern Canada, Scotland and Scandinavia, who report no known cases of a true rainbow population developing anadromy.

These considerations indicate that, when the alternative life histories represent distinct populations separated by longstanding natural barriers, they should not be considered part of the same ESU. This point is not in question (BRT 2003).

ANADROMY AND RESIDENCY AS A POLYMORPHISM

In many locations, particularly at intermediate latitudes within the species range (McDowall 1987), the two life histories are more closely associated. This association ranges from examples in which discrete populations of residents are isolated from populations of anadromous fish on an ecological time scale (but not an evolutionary one) to cases in which the two forms appear to represent a genuine polymorphism within a single population. The polymorphisms are longstanding and appear to be adaptive, although the selective forces maintaining them are not completely understood. Frequent formation of sand bars across estuaries blocking access to the ocean, with variable times or occurrence of breaching among years, is apparently one of the main ecological factors favoring this life history polymorphism (presentation by Churchill Grimes). However, variability in relative food availability in freshwater and the ocean (with consequent growth and survival opportunities) also appears to play an important role (Gross 1987).

The expression of alternative life histories is the result of a complex interaction between genetic variation and environmental conditions. In some polymorphic populations, each type of parent typically gives rise to both anadromous and resident phenotypes, as judged from observations on element ratios in otoliths (presentation by Chris Donohoe) and segregation in experimental genetic crosses (presentations by Richard Carmichael, Jeff Hard). Offspring from different types of crosses show different propensities for smolting and different migratory tendencies (Thrower et al. 2004b).

The situation is different in other natural populations, as inferred from field surveys using otolith microchemistry. In some locations, there appears to be a significant asymmetry in the production of one type of fish from a parent of the other type, specifically, that an anadromous parent is more likely to produce a resident offspring than vice-versa. Richard Carmichael described surveys from the Columbia River that indicated that 5-20% of hatchery steelhead do not migrate but complete their life histories in fresh water. Similar analyses implied that 17% of anadromous adults to have had resident mothers; conversely, from 54-70% of resident adults appear to have had anadromous mothers. The same asymmetry, albeit with smaller sample sizes, was demonstrated by Zimmerman and Reeves (2000) in *O. mykiss* from the Babine River in British Columbia. However, Zimmerman and Reeves (2000) also demonstrated a very different result from the Deschutes River in Oregon; in this river, there was no evidence that anadromous and resident parents produced surviving offspring of the other life-history type, indicating reproductive isolation between them.

These results are concordant with those from other studies of trout populations, revealing that whether an individual migrates is a complex function of its genetic constitution and the opportunities for growth provided by its environment (Jonsson and Jonsson 1993, Pirhonen and Forsmann 1999). This pattern is consistent with considering anadromy as an adaptive response to ecological circumstances. In this light, it is important to understand this phenomenon to preclude the temptation to expect that, because anadromy and residency can occur as a polymorphism, it would be a simple matter to reconstitute an anadromous population from a resident or mixed population.

The evolution of diadromy has been reviewed repeatedly (Gross 1987, McDowall (1987, 1988, 2002). Gross (1987) emphasized the importance of bottom-up effects, i.e. production, in determining migration. In his view, when the ocean is more productive than freshwater, anadromy develops; when freshwater is more productive than the ocean, catadromy develops. For *O. mykiss*, the frequency of the resident life history tends to increase with distance of spawning sites from the ocean (presentations by Chris Donohoe, Churchill Grimes, Pete Adams), consistent with an important role for energetic considerations. However, Dingle (1996, pg 268) noted that “If nutrition were the only factor involved in selecting between the two modes of migration, the transition in frequencies should manifest itself across the 40° productivity boundary. That it occurs instead between 20° and 40°, where freshwater habitats are only somewhat more productive, suggest that other factors could be involved as well” (Figure 1). Indeed, in the Atlantic biota, eels are catadromous in the same rivers in which salmon are anadromous, so food availability alone is unlikely to explain the pattern. Currently, other factors influencing the degree of anadromy are largely unknown, but one might surmise that habitat quality and predation on juvenile life stages (Lowe-McConnell 1975) might be important.

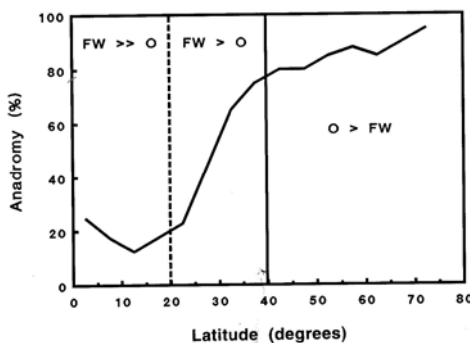


Figure 1 (Figure 10-3 of Dingle 1996):
Relative proportion of anadromy among
diadromous fishes as a function of latitude.

Migration needs to be understood in the context of maturity: migration is optional for successful reproduction but maturation is not and migration delays maturation. Policansky (1983) showed that fish will mature at the earliest opportunity provided to them. The scientific issue then becomes: what is the requisite opportunity? In addition, since the physiological machinery required for life in freshwater and the ocean is very different, smolting and residency/maturation entail developmental conflict (Thorpe 1987). To illustrate this point, Thorpe (1994) reports a study of sockeye salmon in Japan, where there are no anadromous sockeye, and only a few lake populations (hime salmon) that live in waters warmed geothermally. Thorpe (1994) cites works in which potentially maturing juvenile hime salmon were exposed to low temperature surface-water conditions in the winter prior to expected maturation, which inhibited maturation on that cycle. Instead, these fishes smolted. Fish treated this way were released to sea, and returned at maturity as sockeye. This work suggests that smolting should be considered in the context of maturation, as occurring in individuals that were unable to mature in freshwater.

Taylor and Taylor (1977) argue that migration should be understood as a response to adversity: animals move when the current location is not meeting their needs. Johnsson et al.'s (1993) "common tank" experiment using rainbow trout, steelhead trout and their hybrids illustrates this point (Figure 2).

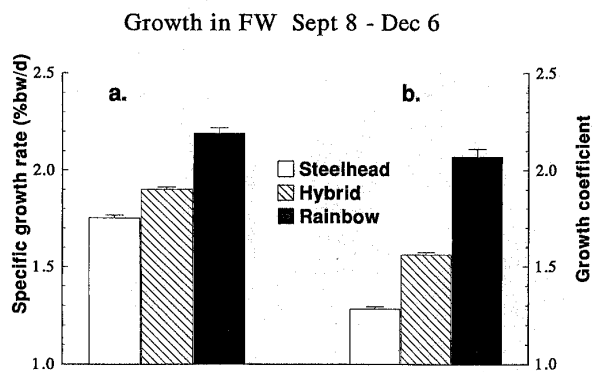


FIG. 2. (a) Mean specific growth rate and (b) coefficient of growth for pooled replicates of steelhead ($n = 353$), hybrid ($n = 353$), and domesticated rainbow trout ($n = 60$) from September 8 to December 6 in fresh water. Mean water temperature was 12.3°C. Vertical bars denote standard errors of mean growth rates.

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Figure 2. Results of the common tank experiment of Johnsson et al (1993). (Specific growth rate in the interval 0 to t is $G = \ln(W(t) / W(0)) * 100$ and coefficient of growth is $GC = \frac{W(t)^{1/3}}{W(0)^{1/3}} + \frac{Tt}{1000}$ where T is the mean temperature during the growth interval).

Note that the growth rate of steelhead offspring in fresh water is only about 60% of that of rainbow offspring and that the hybrid is intermediate. This experiment, however, only demonstrates a difference in growth-rates; it does not inform about difference in the rates of smolting among the three categories. Even with that caveat, one interpretation of Policansky (1983), Taylor and Taylor (1977) and the results of Johnsson et al. (1993) is that a juvenile *Oncorhynchus mykiss* becomes a steelhead rather than a rainbow trout because it is unable to sequester resources at a sufficiently high rate in freshwater for successful reproduction there.

Taken together, these observations lead to the conclusion that resident and anadromous (or polymorphic) populations can be considered part of the same ESU if it can be demonstrated, through careful experimentation, that (i) resident fish still have the genetic capability to develop anadromy when faced with poor growth opportunity (see Thrower et al. 2004b), (ii) anadromous offspring of resident

parents have the ability to complete seaward migration successfully and return for reproduction and (iii) that the fitness of anadromous fish derived from resident parents is sufficiently high to make a positive contribution to the overall viability of the population in a fluctuating environment, rather than acting as a demographic drain on the population.

THE VITAL IMPORTANCE OF RECOVERING AND PRESERVING THE ANADROMOUS LIFE HISTORY

We have reviewed evidence that anadromous fish represent a complex life history that cannot be easily reconstituted from a purely resident stock. Here we discuss the evidence that anadromous fish contribute substantially and irreplaceably to any measure of *O. mykiss* productivity and viability.

Studies of character distribution, mating behaviors, and reproductive success are consistent with interpreting the polymorphism as a product of adaptive evolution. Detailed study of quantitative characters in polymorphic populations often reveals continuous but bimodal distributions (presentations by Sue Sogard, Sean Hayes, Jeff Hard), suggesting that the life history polymorphism is maintained by disruptive natural selection against intermediate types, perhaps augmented by assortative mating. There are indications that anadromous females may tend to avoid spawning with resident males, which implies strong selection against resident genes in the anadromous phenotype. Disruptive selection has been implicated in maintaining life history polymorphism in other fish species, potentially involving even sympatric speciation, e.g. between resident kokanee and anadromous sockeye salmon, *O. nerka* (Wood and Foote 1994), and between benthic and limnetic sticklebacks (Bolnick 2004).

This evidence points to anadromy as an evolutionarily significant component of *O. mykiss* diversity and places this diversity firmly within a larger context of similar systems that have been studied by evolutionary biologists. Experiments on other organisms have shown that disruptive selection and reduced gene flow in a population occupying two distinct environments is often reflected in fitness tradeoffs (negative genetic correlations in fitness) among genotypes from the two environments (Via 1984a,b, Via and Lande 1985, Schlichting and Pigliucci 1998). As discussed above, there is evidence that tradeoffs exist at least between the development of residency and subsequent performance in marine environments. This evidence reinforces the notion that, in polymorphic populations, anadromy is a significant component of *O. mykiss* diversity. We suggest that observations on quantitative characters and fitness, using molecular genetic markers, could be done to measure selection on quantitative traits at Sashin Creek or Scott Creek (similar to ongoing work at Minter Creek discussed in our previous report [RSRP 2005]), which echoes a previous suggestion (RSRP 2003). Such research would help to reveal how selection is operating to maintain the life history polymorphism. Carlos Garza said that such experiments were being planned.

The anadromous component of a salmonid ESU, by maintaining the population's access to ocean habitat and food resources, can affect productivity over the short term and the probability that the ESU can persist in the long term. The spatial extent of marine habitat used by anadromous salmonids dwarfs the range used during freshwater phases, including areas used by resident members of the same ESU. Steelhead tagged on the high seas that returned to estuaries and rivers of North America have been recovered from 7,107,000 km² of the North Pacific (Figure 3). In contrast, an estimated 2200 km² of freshwater lakes and rivers large enough to accommodate fish lie within the native range of steelhead from California to Alaska (although much of this habitat is no longer accessible to fish or suitable as salmonid habitat). Taken together, these estimates suggest that eliminating the anadromous component of steelhead eliminates fish from 99.97% of their potential natural habitat.

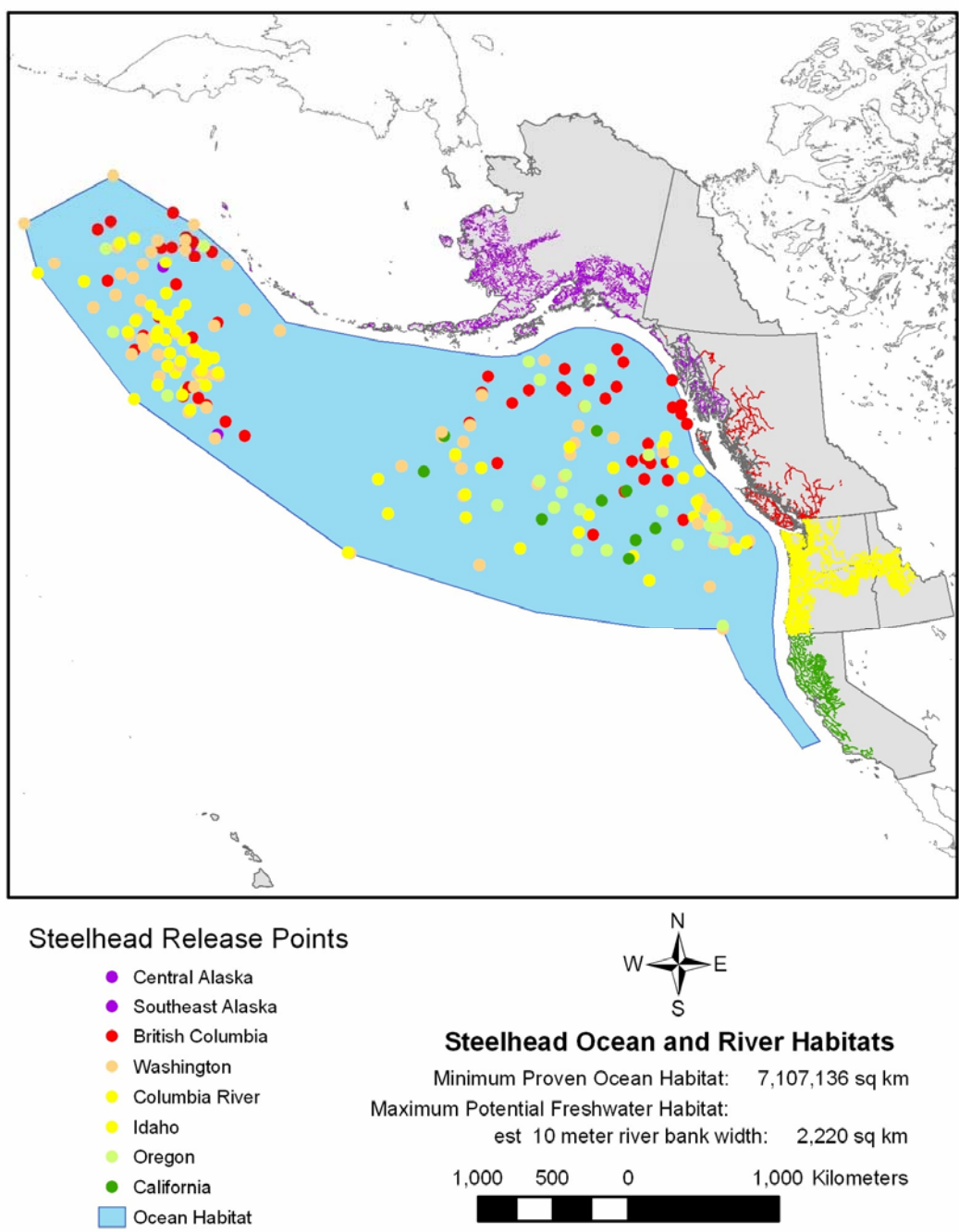


Figure 3 GIS analysis of habitat use based on recapture records of tagged steelhead using data compiled by Myers et al. 1996; dots represent ocean recaptures, coded by color to the freshwater system in which the fish were tagged. This is undoubtedly an underestimate of the actual area of ocean habitat used by North American steelhead.

The marine habitat is important for *O. mykiss* because anadromous individuals that return to breed contribute disproportionately to the population productivity of their ESU and therefore to the gene pool available for future reproduction. The number of years spent by steelhead at sea has a profound influence on their ultimate size, whereas the number of years spent in the less productive freshwater habitat has little or no effect (Sutherland 1973). Comparisons of weights of tagged steelhead smolts leaving estuaries versus adults returning to spawn suggest that these fish acquired more than 98% of their body mass at sea (unpublished data compiled by Dr. Beth Sanderson, NOAA Fisheries). Fecundity of salmonids, including steelhead, increases markedly with size; anadromous forms of the coastal rainbow trout are approximately three times more fecund than resident forms (Stolz and Schell 1991).

Preserving anadromy in *Oncorhynchus* ESUs is particularly crucial in light of changes in the freshwater ecosystems of the western US that are anticipated to continue over the next several decades. Diversions, impoundments, pollution, and ground water mining have already greatly reduced and degraded fresh water habitats of salmonids (Lichtowich 1999, Power et al. 1997, many others). Land and water use will only intensify as human population density increases. Water shortages and distribution problems will be exacerbated by global warming, which is predicted to alter spatial and temporal distribution of precipitation, raise sea level, and cause more intense storms and heat waves (Hengeveld 2000, Field et al. 1999, National Assessment Synthesis Team 2000). These changes are particularly important because much of the freshwater habitat of salmonids depends upon water from snowmelt (which at present contributes 75% of all water in western US streams: Service 2004). Total snow accumulation is declining, particularly in the Cascades of Oregon and Washington, where decreases of up to 60% since the 1950s have been observed (Mote, cited in Service 2004). Snow is also melting earlier in the spring throughout the California Sierra (Cayan, Stewart and Dettinger cited in Service 2004), so less will be stored to maintain summer stream flows. As the amount and quality of freshwater habitat declines, the fitness of the resident life history will decrease relative to the anadromous life history because anadromy allows access to an oceanic environment that promotes greater somatic growth, higher survival, and greater fecundity. In addition, because the ocean environment is much more open to migration, anadromous fish would have a greater opportunity than resident fish to seek conditions to which they are adapted. Selection in this environmental condition will favor an increase in adoption of anadromy and a diminution in frequency or complete loss of the resident life history. If, as is predicted, these environmental changes occur rapidly and become permanent, there will be a premium on the existence of anadromous or mixed populations to maximize the viability of an ESU.

This scenario offers a clear example of how life history diversity can promote the long-term viability of an ESU.

The importance of recovering and protecting anadromous life histories reaches beyond *O. mykiss*. For example, anadromy permits straying, which promotes gene flow between drainages that helps to maintain genetic variability within local populations that could otherwise be significantly reduced by finite population size in small completely isolated populations. Straying also allows fish to re-colonize a basin in which a previous salmonid population has gone extinct (Hendry et al. 2003). The arguments we outlined for the critical role of the marine phase of the life cycle in promoting population growth and ultimate resiliency can be applied to other western North American salmonids.

THE LONG-TERM VIABILITY OF *O. mykiss* ESUs

The collected evidence has important implications concerning the long-term viability of *O. mykiss* ESUs. In polymorphic populations, the occurrence of resident and anadromous life histories helps to buffer a population against fluctuating environmental conditions in fresh water and the ocean as well as variable access to the ocean from sandbars blocking estuaries. The loss of anadromous fitness in land-locked resident populations, and the unidirectional evolution from anadromous or polymorphic

populations to resident populations, clearly indicates that resident populations by themselves should not be relied upon to maintain long-term viability of an ESU. To be sure, a resident population *recently* created from an anadromous or polymorphic population will continue to produce anadromous fish that could, in principle, help to re-establish an anadromous run in the short term. However, the feasibility of re-establishing an anadromous run from a resident population is expected to diminish rapidly in evolutionary time. If it could be done at all, it would be most easily accomplished within a few or perhaps several, but not many, generations after extinction of a self-sustaining anadromous run.

In particular, in cases where an anadromous run is extinct or not self-sustaining, there is no scientific justification for the claim that the long-term viability of an ESU could be maintained by a land-locked resident population alone, or by a land-locked resident population connected by one-way gene flow into an anadromous population (see Cramer et al. 2005). In fact, the results from Sashin Lake (Thrower et al. 2004a) and Scott Creek (presentation of Sean Hayes) suggest a stronger conclusion, that there is scientific evidence **against** the feasibility of establishing a viable anadromous population from a pure resident population. The prospects for doing so are similarly poor if the life-history diversity is maintained primarily by hatchery input, where the anadromous fish spawning in the wild are not self-sustaining. This militates against a position being explored by the NMFS Policy branch, as presented to us by James Lecky, that loss of the anadromous component of an *O. mykiss* ESU does not impair its long-term viability because of the facility with which an anadromous run could be re-established from a pure resident population.

Artificial extirpation, or even substantial reduction, of either life history within a polymorphic population inevitably alters the natural evolutionary trajectory of that population. The alteration will be exacerbated if the population is being fed by gene flow from hatchery strays. Sufficient alteration of the evolutionary trajectory of a population can, in the long term, cause its phenotype to become so distinct that it should no longer be classified as part of the same ESU. A parallel process occurring at the species level in long-term evolution is called "phyletic extinction," or "pseudoextinction," in which the morphology of a species changes so much that at some point the original species is considered extinct and the same lineage is considered to have become a different species (Simpson 1953, Raup and Stanley 1978, Ridley 1996).

We believe that recovery plans for *O. mykiss* ESUs listed under the Endangered Species Act should place a high priority on the maintenance and restoration of naturally occurring life-history diversity, including the restoration of extirpated anadromous runs. We suggest that these issues should be included in the workshop revisiting ESU definitions. We recommend that the NMFS working concept of an ESU be redefined to focus on the evolutionary process rather than on current genetic taxonomy, concentrating on the evolutionary future in addition to the past evolution of an ESU, including the critical role of natural life history variation (and artificial hatchery influences) in determining the evolutionary trajectory and long-term viability of an ESU.

VIABILITY MODELS AND SUBDIVIDED POPULATIONS

The Effective Size of A Subdivided Population

A question posed by Steve Lindley during the TRT Chairs Meeting with the RSRP concerned measures of effective population size, N_e , for a geographically subdivided population, and how to assess the risk of loss of genetic variability in an ESU with a known substructure. He alluded to previous theoretical results suggesting that single populations with N_e in the range of 500 to 5,000 are thought to maintain typical levels of heritable variation in quantitative characters due to a balance between loss of variation from random genetic drift and creation of variation by spontaneous mutation (Franklin 1980, Soulé 1980, Lande 1995, Frankham and Franklin 1998, Lynch and Lande 1998). Lindley mentioned

explicit formulas for N_e of a subdivided population and discussed that of Whitlock and Barton (1997), which depends on the productivity of local populations (or subpopulations) and indirectly on dispersal rates through Wright's F statistic between pairs of populations. Lindley suggested that understanding the degree and pattern of population subdivision might be useful in determining genetic risks to the long-term viability of a subdivided population, as well as to the local populations that compose it.

Formulas for N_e by themselves typically concern only the loss of selectively neutral variation by random genetic drift, neglecting other factors such as mutation, that are necessary to maintain genetic variation in a finite population. Strobeck (1987) and Slatkin (1987) showed that, in a finite subdivided population with stable geographic structure, the expected heterozygosity maintained within each local population by neutral mutation is independent of the dispersal rates among local populations and equivalent to the expected heterozygosity that would be maintained if the subdivided population were panmictic (randomly mating), provided that all of the local populations are connected by appreciable dispersal. Thus, if there are no absolute barriers to gene flow, the degree of subdivision among local populations does not influence the amount of neutral heterozygosity within local populations. An analogous result also holds for additive genetic variance in quantitative traits (Lande 1992).

These results can be surprising at first glance. To understand them, consider first that smaller local population sizes and greater geographic isolation (lower gene flow) will decrease genetic variation within local populations. But in this case, a local population will tend to be genetically differentiated from its neighbors, and individuals from such a population that immigrate successfully to a new population are, on average, genetically more distinct and so introduce more genetic variation to the recipient population. When populations are larger and more connected, there is more local genetic variation and less genetic differentiation such that successful immigrants are not so distinct and thereby introduce less genetic variation to the recipient population. The two effects, local population size and migration rates, exactly cancel on average, so that the genetic variability maintained by mutation within local populations is independent of dispersal rates among local populations, provided that all the local populations are connected by dispersal. In contrast, the *total* genetic variability within and among localities is increased by geographic subdivision (Strobeck 1987, Slatkin 1987, Lande 1992).

The clear implication of these results is that population substructure within an ESU poses no genetic risk to the long term viability of local populations, provided that they are not completely isolated. However, total genetic variability among populations within an ESU divided by geography and/or seasonal variation in spawning times is increased by random genetic drift and local adaptation through diversifying selection toward different optimum phenotypes among localities, which amplifies the opportunity for adaptive evolution in response to environmental changes, thereby increasing long-term viability of the ESU. High rates of local extinction and colonization from a few founders can reduce the metapopulation N_e and genetic variability (Slatkin 1987, Lande 1992, Whitlock and Barton 1997, Waples 2002), but this scenario does not appear to apply to salmonids. Of course, these considerations are purely genetic and evolutionary, and do not directly address demographic and ecological risks to ESU viability (Doak and Morris 2002, Lande et al. 2003).

Population Viability Models

We heard reports on viability, including models for population viability, models for scaling up from population-level viability to stratum-level and ESU-level viability, and how to assess viability when data are scarce. Most, but not all, models were based in the framework of the VSP (Viable Salmon Population) approach. In general, the models are complicated and have great detail; their structure is at least reasonable and often incorporates information about the biology of particular species and even particular populations. The models often give quite precise results, such as probabilities of survival of a population, a stratum, or an ESU. Because they are detailed, formal models, they have the benefit of

forcing consideration of many factors that affect viability, and of being able to generate and compare various alternative scenarios for achieving viability.

This approach has a persistent shortcoming that could be addressed with extensive sensitivity analyses. The models contain assumptions that have not been empirically verified, and many (but not all) of the parameters are difficult to estimate with available information. Therefore, although they produce quantitative estimates and allow comparisons, it is disconcerting that we do not know how confident we should be in the results. The quantification could even give a false sense of accuracy. Sensitivity analyses could be used to explore how robust the results are to changes in model structure and to variation in parameter estimates. It would be particularly interesting to know if slight changes in structure, or in one or more parameters, could produce very different predictions.

A different approach might be to use more general models with fewer assumptions and parameters. Statistical theory, bolstered by simulations of specific cases (Ludwig and Walters 1985, Linhart and Zucchini 1986, Hilborn and Mangel 1997, Burnham and Anderson 1998), indicates that the best predictions of dynamic processes are achieved by simple models with a small or intermediate number of parameters, rather than by complex models with many parameters that can only be estimated with low accuracy from limited data. It is possible that more general models with fewer parameters could be developed, at least for one or a few populations, in order to compare their predictions with predictions generated from larger, more complicated models. These simpler models would not be used to generate precise quantitative predictions but to facilitate comparing, qualitatively, the probable outcomes of various management scenarios.

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