# 2 The Needs of Salmon and Steelhead in Balancing Their Conservation and Use

*Carl V. Burger*

*Abstract.*—Over the past 100 years, Pacific salmon *Oncorhynchus* spp. and steelhead trout *0. mykiss* populations in the Pacific Northwest have experienced dramatic declines as a result of human population growth and associated development of the region's natural resources. Any strategy to reverse those declines will depend on achieving consensus among a diverse group of stakeholders willing to (1) restore damaged habitats and watersheds; (2) consider the biological needs of salmonid fishes; and (3) understand, conserve, and manage existing levels of biodiversity within an ecosystem context. The objective of this chapter is to review and summarize the needs of Pacific salmon and steelhead trout from perspectives that promote their sustainability and perpetuity, and, within that context, provide a framework for the development of a sustainable fisheries strategy. Although volumes of information are available on the life histories and habitat requirements of Pacific salmonids, new concepts have begun to address the importance of habitat complexity, genetic diversity among locally adapted populations, and the need for appropriate units of conservation. Habitat variability and complexity are the templates that produce diverse, locally adapted populations of Pacific salmon and steelhead trout. Molded by conditions in the environments they colonized, salmon and steelhead have unique adaptations that may have taken hundreds—perhaps thousands—of years to evolve. Any strategy to reverse the declines of salmon and steelhead must focus on conserving both current levels of genetic diversity as well as restoration and maintenance of habitats compatible with the specific needs of individual populations. An argument can be made that we know enough already about the needs of our salmon and steelhead to allow us to make appropriate decisions. There is a strong need to integrate what we know about local salmonid adaptations and habitat needs with conservation and management strategies that address the problems we have created. It may be possible to have healthy, sustainable salmonid populations coastwide if we do not wait too long to make up our minds.

## INTRODUCTION

Henry David Thoreau in his *A Week on the Concord and Merrimack Rivers* wrote:

> Perchance after a thousand years, if the fishes will be patient and pass their time elsewhere, meanwhile nature will have leveled the Billerica Dam and the Lowell factories, and the Concord River will run clear again, to be explored by migrating shoals.

The environmental impacts on the fish resources addressed by Thoreau in the northeastern U.S. soon worsened, and a similar dilemma began to materialize on the west coast of North America, in direct proportion to growing numbers of settlers who placed ever-increasing demands on anadromous fishes. The demise of fishery resources in the Pacific Northwest has become a biopolitical

crisis that directly confronts the region's primary economic interests: its hydropower, agriculture, forest, and commercial fishing industries (Allendorf and Waples 1996).

As we proceed to take on the enormous task of developing a strategy to reverse the declines of certain Pacific Northwest salmonids, and as we continue to build consensus and "buy-ins" among a diverse and growing group of stakeholders who share in common concerns, we must reflect on and consider the biological needs of our fish. What is it that they need for survival and self-perpetuation? What do they have to do to survive? And what is it that we humans have to avoid, in terms of environmental impacts, if we are to assure the health of our fishery resources into the future?

The objective of this chapter is to summarize the needs of Pacific salmon *Oncorhynchus* spp. and steelhead trout *O. mykiss* from perspectives that promote their sustainability and perpetuity and, within that context, provide a foundation for balancing the conservation and use of salmon and steelhead in the Pacific Northwest.

## HISTORICAL PERSPECTIVE

Pacific salmon and steelhead constitute spectacular resources that range from northern California, through British Columbia, to Alaska's Aleutian Islands and beyond. These resources sustained aboriginal peoples and were quite abundant through about the mid-1800s, providing substantial cultural, recreational, economic, and symbolic importance to the Pacific Northwest. For example, up to 16 million anadromous salmonids were thought to return to the Columbia River Basin during that pre-development time period (NPPC 1986)—an estimate that gradually dropped to about one eighth (2 to 3 million fish) by the 1990s (NPPC 1994; NRC 1996).

In the late 1800s, hatcheries began to appear in the Pacific Northwest in an attempt to compensate for overfishing and declining numbers of salmon and steelhead. At the turn of the century, hatcheries were deemed to be necessary in the Columbia River drainage to maintain salmon runs. By the 1920s various fishing restrictions (for example, a ban on fishwheels) were imposed on the Columbia River as salmon numbers continued their precipitous decline. Because as much as 80% of the contemporary Pacific Northwest production of anadromous salmon and trout is estimated to be of hatchery origin, natural production is probably less than 5% of what it was historically (up to 16 million) (Allendorf and Waples 1996).

Through the early and mid-1990s, various factors contributed to the ensuing decline of anadromous fishes in the Pacific Northwest, including human population growth and the associated development of the region's natural resources. Turn-of-the-century overfishing and subsequent irrigation and hydroelectric projects were the major impacts leading to declines in both the U.S. and Canada. Despite tremendous investments in hatcheries, runs began to disappear as habitat was developed and as fishing and other pressures were applied to the resource.

Historic fishery declines can be tied directly to impacts from expanded fishing, forestry, agriculture, hydroelectric, and industrial activities by increasing numbers of settlers in the Pacific Northwest. The explosive population growth in several northwestern U.S. states is apparent from census data reviewed by the NRC (1996): about 100,000 inhabitants were present during the mid- to late 1800s, over 1 million people by 1900, and 8.7 million by 1990 (annual growth rate, 2%). Not surprisingly, and largely associated with construction of dams that blocked fish passage, Pacific salmon disappeared from about 40% of their historic range in Washington, Oregon, California, and Idaho, and the numbers of fish in most remaining populations were substantially reduced (NRC 1996). Although major dams were not constructed on the Fraser River in British Columbia, a similar pattern of decline in salmon runs occurred through the 1970s (NRC 1996) from mining, logging, agriculture, and other forms of industrial development. Although Alaska did not escape historic declines, its generally stable or increasing trend of contemporary Pacific salmon production (Burger and Wertheimer 1995) likely results from conservative management since statehood and a comparatively small number of statewide inhabitants (about 600,000). Because of larger salmon population sizes, anadromous salmonids

in Alaska also may have a better ability to recover from both natural habitat disruptions as well as those imposed by human development, than populations subjected to decades of environmental impacts in southern portions of the range. Weakened by many years of human-induced pressures, some populations in non-Alaskan portions of the range contain low numbers of spawners that can no longer withstand severe winters, floods, and other natural events. With 214 populations at risk of extinction and more than 100 populations recently extinct in Washington, Oregon, California, and Idaho, we are truly "at the crossroads" (Nehlsen et al. 1991).

## LIFE HISTORY AND HABITAT NEEDS OF PACIFIC SALMONIDS

Since the earliest parts of this century, volumes of information have been written and published on the habitat and survival needs of Pacific Northwest salmon and steelhead trout. One only has to look at recent compendiums such as *Pacific Salmon Life Histories* (Groot and Margolis 1991) to find a wealth of data on the life histories and population dynamics of sockeye *O. nerka,* pink *O. gorbuscha,* chum *0. keta,* chinook *0. tshawytscha,* and coho *O. kisutch* salmon throughout their established ranges. *Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitats* (Meehan 1991) exemplifies a second collection of chapters and articles on how certain human influences affect salmonids, their life histories, and their diverse habitats. Also, countless journal publications and symposia over the past several decades have addressed the life histories, habitats, and needs of Pacific salmon and steelhead trout. Clearly, there is no shortage of material on these subjects that would preclude development and implementation of a sustainable fisheries strategy.

Fishery scientists have spent careers studying salmon and steelhead — they know the needs of these fishes quite well. And whether scientist, policymaker, politician, or layperson, all are familiar *to some extent* with what the various species of salmonid fishes need, in terms of habitat and life history requirements, for survival, reproduction, and perpetuation of their numbers. Nevertheless, and as the strategy for sustainability is developed, it is appropriate to compare and contrast some of the general needs of Pacific salmon and steelhead trout, with examples of some of the things that may adversely affect them. Also, I will try to integrate what we know about their life history and habitat needs with some key concepts — habitat complexity, genetic diversity, and local adaptation — that have implications for sustaining Pacific Northwest Salmonids.

### LIFE HISTORY OF PACIFIC SALMON AND STEELHEAD TROUT

Pacific salmon and steelhead trout are anadromous: they migrate to the ocean for maturation and return to freshwater to spawn. Although some investigators have suggested a marine origin for modern-day salmonid fishes, others have proposed a primitive origin entirely within freshwater, and that evolution of anadromy was in response to more abundant food resources in the marine, rather than freshwater environment (Gross 1987).

The migration of juvenile salmonids to the ocean can occur within several days of their emergence from spawning gravels (pink and chum salmon) or following one or more years in freshwater (chinook, coho, and sockeye salmon; steelhead trout). The length of time spent in freshwater as juveniles varies considerably among and within species; it is apparently regulated by both environmental and genetic factors that influence behavior as well as certain physiological changes prior to the seaward migration (Randall et al. 1987). Juvenile migration to the sea (smolt stage) frequently occurs at night during spring or early summer (Figure 2.1). Once at sea, initial movements appear to be oriented within estuaries and along coastlines, but subsequent marine movements occur throughout the North Pacific Ocean and Bering Sea, where distances traveled may be extensive (Groot and Margolis 1991). However, as described for sockeye salmon (Burgner 1991), offshore movements are complex and are affected by physical (season, temperature, and salinity) and biological factors (age, size, availability of food, and population-specific genetics).

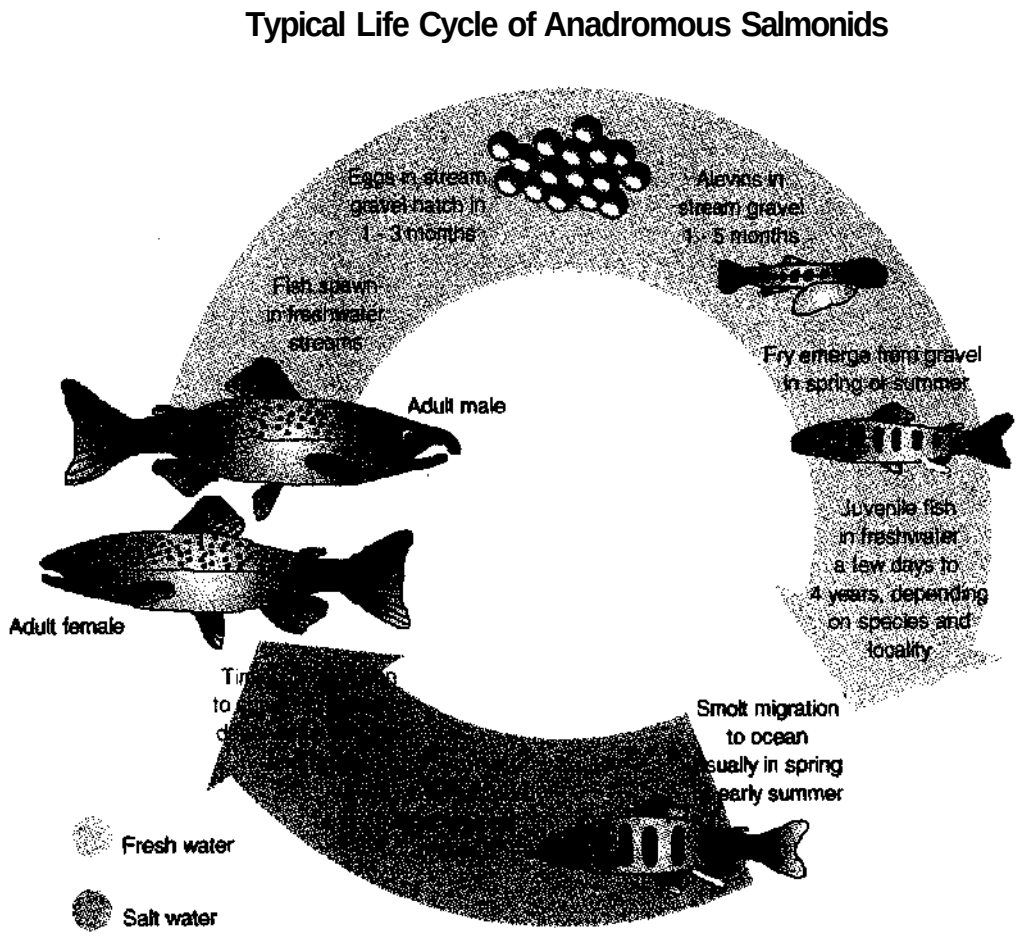


**FIGURE 2.1** Typical life cycle of anadromous salmonids (modified from Meehan and Bjornn 1991).

The length of time at sea (usually 1 to 4 years) and the age at which adult salmon and steelhead return to freshwater to spawn varies considerably among and within species (Figure 2.2).

Adult migrations to freshwater spawning areas are also variable and depend on the species, seasonal form, geographical location, and physical and biological factors. The variability in timing of return migrations to freshwater and in spawning activities encompasses virtually all seasons of the year for the five species of Pacific salmon and steelhead trout. It is beyond the scope of this chapter to provide such detail although numerous examples and summaries of species- and population-specific run and spawning times have been published (Groot and Margolis 1991; Meehan and Bjornn 1991).

Adult salmon and steelhead typically spawn during spring, summer, and fall in rivers having substrates suitable for water permeation and oxygenation of eggs that develop in the spawning nest (redd). However, there is substantial variation in the physical features (depths at which eggs are deposited, sizes of substrates used, etc.) of the spawning habitat selected (Bjornn and Reiser 1991), and in the types of environments where spawning occurs. One species (sockeye salmon) is capable of reproducing in a wide array of spawning environments including shorelines and upwelling areas entirely within lakes, lateral tributaries flowing into lakes, and outlet rivers (Burgner 1991). Adult salmon usually guard their redds against predation for one or more weeks

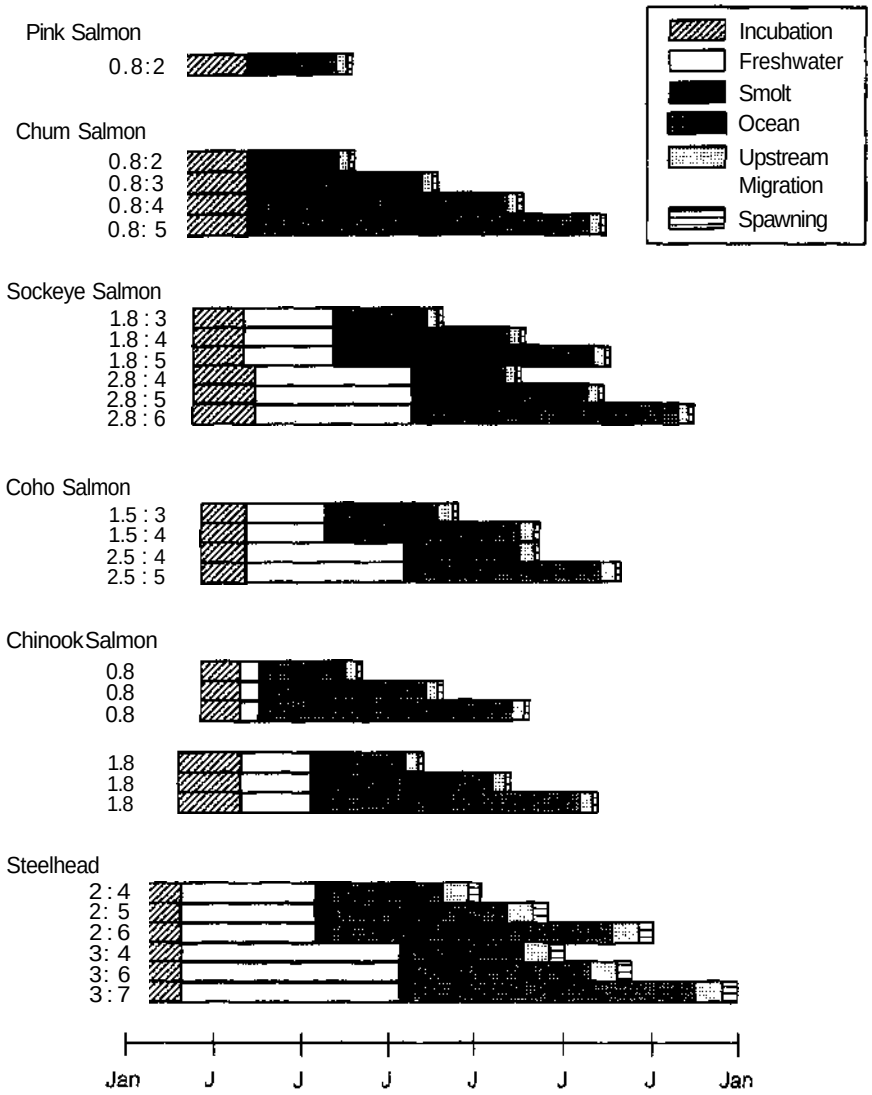


**FIGURE 2.2** Lengths of time that representative anadromous salmonids spend in various developmental stages and in fresh water or the ocean. Numbers under species names are age keys indicating the years spent rearing in fresh water from egg to smolt (first column) in relation to the total age of the fish (second column). For example, 1.5 : 3 indicates a fish in its third year of life that had spent 1.5 years incubating and rearing in fresh water before migrating to sea (modified from Meehan and Bjornn 1991).

after spawning. Whereas Pacific salmon all die following spawning-related activities, Steelhead trout are capable of surviving, and a certain percentage of Steelhead adults returns to the ocean following reproduction.

Eggs of Pacific salmon and Steelhead trout hatch within the redd from 1 to 3 months post-fertilization. The resulting alevins (yolk-sac fry) continue to reside within the protective confines of gravel substrates for 1 to 5 additional months (Figure 2.1). The juveniles typically emerge during spnng and summer to actively seek food, avoid predators, emigrate to sea (pink and chum salmon) or establish new home ranges within river drainages (chinook and coho salmon; Steelhead trout) or lakes (sockeye salmon), to commence the cycle anew.

## NEEDS OF PACIFIC SALMON AND STEELHEAD TROUT

Pacific salmon and steelhead trout have varied yet quite specific needs that must be met at different times of the life cycle. When these needs are met, distribution and abundance is maintained and production is often maximized. For example, anadromous salmonids need a sufficient volume and depth of water (at least 18 to 24 cm; Thompson 1972) with unobstructed passage, for adults to reach their spawning grounds, within the constraints of a limited amount of bodily energy. They need flow velocities that do not usually exceed about 2.1 m/s (Thompson 1972) if they are to complete their migrations. Also, they need clean, well-oxygenated, and unpolluted streams and lakes with loose, appropriately sized spawning gravel substrates (range 1.3 to 10.2 cm in diameter; Bell 1986) that are free of silt and fine sediment (Cordone and Kelley 1961). Pacific salmon and steelhead trout need cool or cold temperature regimes to optimize the success of migration, spawning, and egg incubation. Juveniles must have adequate shade and cover to escape predators and they need high aquatic productivity to ensure rapid growth to the smolt stage. A riparian interface between aquatic and terrestrial ecosystems is therefore crucial.

Bjornn and Reiser (1991) provide a very comprehensive review of the various physical and biological habitat requirements of anadromous salmonids by life history stage. There are numerous other publications on the habitat needs of salmonid fishes (for example, Marcus et al. 1990) in the available scientific literature. The point is that, within each species, the life history events and needs of both juveniles and adults are remarkably precise. The events must occur and the needs must be met within very specific windows of time for survival to be maximized.

What do Pacific salmon and steelhead trout have to do, in order to survive? Allendorf and Waples (1996) provide an excellent summary of the steps necessary for an anadromous salmonid to fulfill its life cycle. It must complete embryonic development and emerge at a time appropriate for its natal drainage; find food and avoid predators as a juvenile; locate cool water during rearing or be able to tolerate increased temperatures; undergo the physiological changes associated with the smoltification process at the most opportune time for seaward migration; enter the ocean during a window of time that promotes survival and growth as a subadult; locate food and survive at sea for one or more years; reverse the physiological process of smoltification when returning to freshwater as an adult; home to the natal spawning area and find a mate; and ensure that eggs are fertilized and deposited at an appropriate location, time, and depth. A break in any of the above processes will reduce or prevent survival in the following generation.

The various seasonal runs, races, and ecological forms within several species of Pacific salmon and steelhead trout also must escape a host of commercial, sport, and aboriginal fisheries to complete their life cycles. They need to be able to find their home streams in numbers adequate to ensure high future survival. The large numbers of adults that returned to Northwest watersheds at the turn of the century helped to confer a certain level of population resiliency toward disasters that were natural in origin. That resiliency is no longer present. Hence, salmon and steelhead resources can no longer withstand the combined effects of catastrophes (severe winters, floods, droughts, etc.), harvest rates of 60 to 70% or more in certain populations, and impacts from humans exploiting non-fish resources. Because former levels of population resiliency have been lost, modern adult escapement goals must be based on conservative standards that account for the synergistic effects of natural and human-induced activities, if perpetuation and sustainability are to be achieved.

There is another benefit from large annual escapements of Pacific salmon to home-stream spawning areas. For some time, fishery biologists have realized that the carcasses that remain after salmon spawning and death provide an important source of nutrients in otherwise nutrient-poor environments (Donaldson 1967). Although we have known that these carcasses contribute to the trophic productivity of streams, we have not always known how much. Recent research by Bilby et al. (1996) demonstrates that more than 30% of the nitrogen and carbon in the tissues

of juvenile coho salmon and steelhead trout derives from the carcasses of spawned-out salmon. Their study was conducted in tributaries to the Snoqualmie River, Washington, where they also found marine-originating N and C in invertebrate organisms and streamside vegetation, meaning that the carcasses of salmon returning from the sea are contributing to overall health of the aquatic and adjacent terrestrial ecosystems. Such results demonstrate that, as salmon escapements decline, a self-perpetuating cycle of decreasing productivity ensues, leading to fewer and fewer returning adults that can "fertilize" the home stream. An example provided by the World Fisheries Trust (1996) highlights the type of spiraling decline and the unsustainable fishery that can result from too few spawners returning to the home stream. In a population having only about 50 female salmon, perhaps 100,000 eggs will be viable. Of those, about 20,000 will hatch into fry, 1,000 will make it to the sea as smolts, 50 will survive to adulthood, and 15 salmon will escape various commercial, sport, and aboriginal fisheries to return to spawn. Thus, future generations of Pacific salmon are progressively diminished when fewer and fewer fish return to the spawning grounds. The above example underscores the necessity to consider interactions at the ecosystem level, if we want to implement conservation and management strategies that achieve the goal of fisheries sustainability.

Several additional concepts have been used to describe the biological needs and relationships among Pacific Northwest salmonids. These include habitat complexity, the concept of locally adapted populations, and the evolutionary unit concept. Along these lines, it seems appropriate to interject some results from past and present research on Alaska's wild salmonids. Because such research encompasses populations and habitats that have remained relatively pristine, results can provide new insights and implications for restoring depleted populations in more southerly portions of their range.

## HABITAT COMPLEXITY

Pacific salmon and steelhead trout need aquatic habitat with instream complexity that includes deep, unsedimented pools (Bjornn and Reiser 1991), undercut banks with overhanging vegetation (Platts 1991), and an adequate amount of natural woody debris to create resting, feeding, and overwintering areas (Everest et al. 1987). They do not benefit from overly simple, channelized streams, altered by human activities, which offer little or no complexity in which to hide, feed, and rest (Hicks et al. 1991). Nor do they need obstacles to upstream migration or streambed alterations (Atkinson et al. 1967) that can either prevent spawning or suffocate eggs deposited in once-clean gravels (Cordone and Kelley 1961). Good quality soils and forest understory along non-erosive stream banks slowly release stored water and nutrients, from riparian areas (Platts 1991). The root systems of vegetated areas also provide stream bank stability and buffer the erosive effects of water flow (Sedell and Beschta 1991). Stream banks where the forest canopy has been overcut by logging activities or overgrazed by cattle will erode when heavy rain and high flows occur, causing sedimentation of once-productive anadromous fish habitat (Chamberlin et al. 1991; Platts 1991). The result is the loss of a complex reach of stream that formerly produced high numbers of salmonid fishes.

Several studies have confirmed the benefits to juvenile salmonids from adding and simulating various types of cover that increase the complexity of streams. Juvenile salmon and steelhead abundance has been positively correlated with the addition of woody debris to increase habitat complexity in Southeast Alaska streams (Murphy et al. 1984; Heifetz et al. 1986; Johnson et al. 1986). Using unpublished data, Bjornn and Reiser (1991) showed that juvenile steelhead trout were much more abundant in channels having a combination of deep water, undercut banks, large rocks, and brush, than in pools with less cover. Combinations of cover translate into increased complexity and large numbers of fish.

## LOCAL ADAPTATION

Habitat variability and complexity are the templates (drivers) that produce diverse, locally adapted populations of Pacific salmon and steelhead trout. Because each population is adapted to its home-stream habitat, conservation and maintenance of habitat complexity promotes conservation of genetic diversity and local adaptation.

In concert with the ability to home to streams of origin after several years at sea, the variation in life history patterns that has evolved within the diverse environments used by anadromous salmonids produces many distinct local populations within a species (Altukhov and Salmenkova 1991; Utter et al. 1993). Using sockeye salmon as an example, both anadromous and non-anadromous (kokanee) forms occur throughout the range (Burgner 1991). Kokanee spend their lives exclusively in freshwater, and this form may have evolved repeatedly, in many locations, from the ocean-going variety (Foote etal. 1989). Another form (residual sockeye salmon; Burgner 1991) also matures without going to sea and is a transition between kokanee and anadromous sockeye salmon. Considerable life history diversity is apparent within the anadromous form. Although a few populations of sockeye salmon spawn in rivers having no nursery lake (Eiler et al. 1992), most anadromous populations return to drainages having lakes adjacent to the spawning grounds (Burgner 1991), where there is additional variability in choice of spawning habitat for early- and late-seasonal forms. Typical of the spawning distribution between early- and late-seasonal forms throughout Alaska, British Columbia, and Russia, early-run sockeye salmon spawn in cold, lateral tributaries of Tustumena Lake, Southcentral Alaska, whereas late-run fish spawn in considerably warmer, lake shoreline areas and in the lake's outlet (Burger et al. 1995). Despite temporal separation in spawning times between the two runs, offspring from both groups can emerge at the most favorable time for lake rearing because their life cycles are thermally adapted to, and in fine synchrony with, the temperature regimes of their specific spawning habitats (e.g., Burger et al. 1985; Brannon 1987).

Within a specific population, the timing of upstream migration and spawning is often remarkably precise from year to year and seems directly related to the temperature regime of the home stream. Spawning times among anadromous salmonids may have evolved in response to the variable temperatures of the home streams and many populations appear to have unique times and temperatures for spawning that maximize survival of fry (Bjornn and Reiser 1991). The actual temperature regime during egg incubation may be the primary evolutionary factor determining time of spawning (Brannon 1987).

A relationship between spawning time and home-stream thermal regime has been observed between the earliest (inland) and latest (coastal) runs of pink salmon in Southeast Alaska (Sheridan 1962), early and late runs of chinook salmon in Southcentral Alaska (Burger etal. 1985), and among populations of sockeye salmon spawning in the Fraser River drainage, British Columbia (Brannon 1987) and Kenai Peninsula, Alaska (Burger et al. 1995). The relationship between time of spawning and temperature promotes synchronous emergence among offspring of early and late forms during favorable periods of aquatic productivity which, in turn, promotes high survival and continued genetic selection for specific run and spawning times. Instances have been noted where life history patterns (migration timing) have changed because of environmental alterations (Atkinson et al. 1967). To the extent that Pacific salmon and steelhead trout are locally adapted to specific home-stream thermal conditions, there are implications for any human-related activities that alter temperature regimes in streams where life history events depend on a predictable annual thermal cycle (Burger et al. 1985).

The migrational behavior of sockeye salmon fry provides additional evidence for local adaptation (Taylor 1991). Fry from riverine spawning areas in lake outlets migrate upstream into the nursery lake after emergence, whereas fry emerging from spawning areas in lateral lake tributaries migrate downstream (Brannon 1972), behavior that promotes favorable feeding, growth, and survival. Similarly, laboratory studies have shown that the compass orientation of other populations of sockeye salmon fry correspond to a direction that would lead them to forage areas (Quinn 1985).

In these cases involving highly variable habitats (templates), genetic selection likely favors those behavioral adaptations that promote high juvenile survival.

Recent studies on Alaskan sockeye salmon (Tustumena Lake) suggest that the ecological differences between early- and late-seasonal forms have a genetic basis. Early-run sockeye salmon spawn in inlet tributaries to Tustumena Lake during early August, whereas late-run fish spawn from mid- to late September in the lake's outlet river. Despite temporal and spatial closeness in reproduction between the two Tustumena runs (spawning times differ by only 4 to 6 weeks; spawning areas by 20 to 30 km or less), 36% of late-run salmon had a mitochondrial DNA haplotype not observed in over 450 samples from early-run tributary spawners (Burger et al. 1997). A similar phenomenon (the most common haplotype in late-run salmon was rare or absent in respective early-run fish) was recently observed across two additional species' lines: chinook salmon from the Kasilof River, Alaska (Adams etal. 1994) and coho salmon that spawn within the Kenai River (C. Burger, unpublished data). These results suggest a high degree of local adaptation between various early- and late-seasonal forms of Pacific salmon in Alaska. The template for selection may have been the different spawning habitats used by the seasonal forms of salmon. In all three cases, late-run fish spawn in rivers downstream of (and warmed by) large lakes whereas early-run salmon spawn in comparatively cooler lake or river tributaries—environments where temperatures are substantially different. In non-Alaskan parts of the Northwest, populations of chinook salmon with different run timing from the same stream are more similar genetically than populations having similar run timing from different areas (Utter et al. 1989). Thus, greater levels of genetic diversity appear to be present among Alaskan populations of Pacific salmon than among those in some southern portions of the range. However, there also appears to be greater variability in within-drainage (home-stream) temperature regimes experienced by early- and late-seasonal forms in Alaska than occurs among seasonal forms that spawn within drainages in more southerly latitudes. Genetically diverse Alaskan populations may have resulted from low numbers of colonizers (genetic "bottlenecks") that evolved under harsh climatic conditions in variable environments.

Clearly, research on Alaska's wild populations confirms that the various seasonal runs of Pacific salmon, adapted for spawning in specific areas, have very specific ecological requirements. Because each stream or river has its own set of complex variables, the salmon inhabiting them are adapted in an equally complex way (Thompson 1965). We may never know the historic richness of the salmon and steelhead resources of the West Coast, because many populations were lost prior to our knowledge of stock structure (Nehlsen etal. 1991). However, a key point can be made: the ecological traits and adaptations (phenotypes) of surviving populations must be considered as we develop strategies to recover and restore depleted populations.

A recently completed genetic evaluation of Frazer Lake (Alaska) sockeye salmon highlights the exacting ecological needs of this species when transplanted to a new environment. Anadromous fish had not colonized Frazer Lake (impassable waterfall) prior to an introduction of sockeye salmon in the 1950s (Blackett 1979). The introduction program used three donor populations from different geographical areas. The donors also represented different ecological forms (early-run lake tributary spawners, late-run lake shoreline spawners, and fish that had reproduced in a lake's outlet river). Other introductions using the anadromous form of *O. nerka* had been largely unsuccessful (Wood 1995). However, contemporary production at Frazer Lake grew to nearly 1 million adults in some years (C. Swanton, Alaska Department of Fish and Game, personal communication). Microsatellite allele frequencies were obtained from tissue samples from the three donor populations and from seven subpopulations presently spawning in Frazer Lake or its tributaries. Genetic analysis showed that the lake outlet donor stock did not contribute to colonization of Frazer Lake—no outlet spawners were observed during spawning ground surveys at Frazer Lake (1995). However, additional genetic results (C. Burger, unpublished data) suggest an affinity between the reproductive adaptations of the donors and habitat they colonized in Frazer Lake: allele frequencies of the lake shoreline donor were most similar to two subpopulations of sockeye salmon that spawn along the lake's shoreline;

the lake tributary donor was most genetically similar to four subpopulations spawning in Frazer Lake tributaries. Apparently, the reproductive adaptations of the donors were maintained in the "new" environment.

Results of the Frazer Lake genetic analyses strongly suggest that populations ***and habitats*** need to be protected if we are to conserve salmonid genetic diversity and locally adapted populations. Localized populations need protection because they are uniquely adapted to the streams and lakes they inhabit and, consequently, are best able to survive there. Genetic differences among individuals in a local population are the basis for natural selection and adaptive evolution, whereas differences between populations reflect local adaptation to past environmental conditions: the latter represents a pool of genetic variation that is the most valuable component of genetic diversity.

Frazer Lake results may help to explain why some of the historic salmon introduction and restoration efforts have failed. Introduction programs must ensure that donor populations are adapted to the types of conditions to be encountered in the area of release. The only surprise is that we have known this for over a hundred years! Hume (1893; cited by the NRC 1996) stated:

> I firmly believe that like conditions must be had...to bring about like results, and that to transplant salmon successfully they must be placed in rivers where the natural conditions are similar to that from which they have been taken.

The main point is that the parts are not interchangeable. The examples above tell us that populations of anadromous fish are locally adapted to precise environmental conditions. Whenever we lose a specific population or habitat, we often lose a very unique life history pattern and a certain level of ecological and genetic diversity that may be slow to arise again.

Diverse life history strategies are important for population stability and persistence in salmonids (Rieman and Mclntyre 1993). Diversity may serve to stabilize populations that inhabit variable environments, and it may help to refound population segments within a species (Mullan et al. 1992; Titus and Mosegaard 1992). The adaptations to localized environments increase the overall diversity of the much larger metapopulation (Hanski and Gilpin 1991; Rieman and Mclntyre 1993). An array of small, locally adapted populations (metapopulation) within a species means that these smaller units might not respond to changing environmental conditions as a synchronous group but rather the risk of extinction is spread because the loss of all populations at any one time is lowered (Rieman and Mclntyre 1993). These authors state that, in addition, the surviving populations may be able to refound, via straying, weaker subpopulations that decline or become extinct, but that such recolonization depends on a host of factors including suitability of habitat, and it may take considerable time. However, some genetically or ecologically unusual populations may be difficult to replace in human time frames (Allendorf and Waples 1996). Salmonid adaptations have likely taken hundreds if not thousands of years, yet many of the recent human-induced changes and depletions in watersheds have occurred over decades. Despite some apparent evolutionary plasticity among anadromous salmonids, there may be insufficient time for evolutionary compensation, especially when portions of the metapopulation are now missing (NRC 1996).

## EVOLUTIONARY UNITS

A publication of the proceedings of an American Fisheries Society symposium held in Monterey, California (Nielsen 1995), presents a wealth of new information about defining evolutionary units of conservation, a subject that cannot be ignored in any discussion of the needs of salmonid fishes.

Although the Evolutionarily Significant Unit concept (Waples 1991) was introduced to describe distinct population segments in a framework for interpreting the meaning of distinct populations under the Endangered Species Act, much controversy remains over how units of conservation are defined. The Monterey Symposium provides a context for examining both the biological species concept (which defines species as being reproductively isolated) and the evolutionary species

concept that replaces reproductive isolation with spatial or temporal isolation. Evolutionary units refer to populations that maintain their identity at temporal and spatial scales, in a unique evolutionary lineage.

Defining populations of Pacific salmon and steelhead trout from a unit concept, be it based on genetic parameters or ecological considerations and requirements, is not easy. Just as one set of characteristics does not define the needs of salmonids, one size of unit will not fit all (Behnke 1995). Ecological diversity is the template for biodiversity, and temporal and spatial variability must be considered at scales that range from small sections of streams to entire watersheds (Nielsen 1995). Studies referred to previously provide good examples: even though an early and late run of salmon may spawn within 20 to 30 km of one another in a single drainage, their very different genetic structure and their concordant ecological differences suggest that the individual runs are distinct units. Such a result indicates highly restrictive gene flow between populations that spawn in closely adjacent habitat (Burger et al. 1997); this concept was validated in separate drainages used by three species of salmon. Such findings would not support any definition of a unique unit that was based on overly broad geographic boundaries. Rather, the results suggest that the individual spawning area (tributary, lake shoreline, lake outlet, etc.) may indeed be the appropriate unit of conservation and management for Pacific salmonids (Varnavskaya et al. 1994; Burger et al. 1997).

## HABITAT AND POPULATION RESTORATION

Insofar as ecological diversity is the template for biodiversity among Pacific salmon and steelhead trout, the key to sustaining and restoring populations depends on our ability to conserve and provide suitable habitat complementary to life history variation. The distinct genetic and ecological differences among salmonid populations are, after all, a consequence of the unique local environments they inhabit (Gharrett and Smoker 1993). Therefore, the key to sustaining populations of Pacific salmon and steelhead trout is to sustain their habitat using an ecosystem approach that allows for a full expression of biodiversity.

I firmly believe that a watershed approach is necessary to restore the health of the drainages used by Pacific salmonids, and that success will be possible if we focus our energies and activities at this level. We must eliminate activities that degrade habitat at their upland sources, such as erosion from clearcut areas in headwater drainage areas, that sediment downstream spawning areas. Some of the roads used to access timber harvest areas need to be removed or stabilized (storm-proofed) for the very same reason. Once the major sources of pollutants and erosion in a watershed are eliminated or stabilized, and when barriers to migration are removed, deep pools and instream complexity can be restored in downstream areas along with stream bank stability. Reeves et al. (1991) provide a wealth of information on techniques to restore and stabilize watersheds and streams. Already practiced or underway with community involvement in both the U.S. and Canada, habitat restoration activities involving broadly based societal decisions are key to any strategy to sustain Pacific salmon and steelhead trout.

What is the role of fish hatcheries in efforts to restore anadromous fish populations? Although much has been published on certain adverse effects of selection and genetic change from artificial propagation (see, for example, Allendorf and Waples 1996), re-designs and newly focused efforts may provide opportunities to reduce the risks of outbreeding depression, domestication selection, and loss of genetic variation between and within populations (Campton 1995). Hatcheries have recently begun to refocus their activities toward conservation and restoration priorities. Hatchery facilities conceptually possess the ability to conserve and maintain specific genetic resources, to assist with wild fish recovery, and to conduct research under controlled conditions to improve our understanding of life history and physiological processes. Fish culture programs and facilities are not only necessary to assist in efforts to achieve a sustainable fisheries strategy, but they may also be necessary to recover and restore depleted populations, particularly in areas impacted by habitat modifications.

Although it is beyond the scope of this chapter to discuss management techniques and options to increase escapements of salmonids to spawning grounds, it should be clear from the material presented that increased escapements are prerequisite to development of a sustainable fisheries strategy (see, for example, Knudsen 2000).

## LOSS OF FISH AND HABITATS: ARE THEY REALLY BIOLOGICAL PROBLEMS?

I hope I have accomplished my goal to provide the message that the database on the biological needs of Pacific salmon and steelhead trout is very extensive. Concurrently, I have attempted to demonstrate, using numerous examples, the extreme importance of conserving and restoring salmonid habitat complexity and the importance of variation and diversity within locally adapted populations. The Sustainable Fisheries Conference demonstrated that the declines of our Pacific salmon and steelhead are not really resource problems, but people problems, emanating from growing human needs and demands for natural resources. It was also suggested that we know enough, and that we do not really need more studies to confirm what we already know. From a perspective based on the needs of fish, I echo those sentiments.

We already know enough about the needs of our salmon and steelhead to allow us to make appropriate decisions. We can successfully raise salmonids in hatchery facilities; we can accurately predict how they will respond when we alter their habitats; we know that some of the strongest, healthiest populations exist only in pristine areas; we know their ecosystem functions and interactions; and so on. If we know all of these things, one could surmise that our problems may not relate to biology at all. Our salmonid populations could be declining primarily because we have not fully embraced a willingness to restore and maintain suitable conditions for them.

In this light there are additional needs for Pacific salmon and steelhead trout. We need to learn how to integrate what we know about the local adaptations of salmon and steelhead with management strategies that address the problems we humans have created. To protect and assure the perpetuation of salmonid resources, as well as healthy economies of those who depend on them, we need coordinated action on many fronts. I believe this can be accomplished if society is willing to

- change institutional structures for managing salmon and their habitats;
- refocus the salmon management process toward a community-based, watershed-oriented approach;
- implement true salmon ecosystem management; and
- adequately enforce existing laws and programs.

In summary, we need to act, initiate recovery, protect what we have, and restore what has been damaged. If the public and its elected and appointed decision-makers want healthy, sustainable salmonid populations coast-wide, they can have those resources—if they do not wait too long to make up their, minds.

One is reminded of the parable of the wise man approached by a trickster who, motioning to his tightly clasped hands said, "Sir, I hold in my hands a bird. Is it alive or dead?" If the wise man said the bird was dead, the trickster would open his hands to let the bird fly away. If he said it was alive, the trickster would crush the bird and kill it. But the wise man would not thus be fooled. He said to the trickster, "The life of the bird is in your hands."

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