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Status Review of Coastal Cutthroat Trout from Washington, Oregon, and California

January 1999

U.S. DEPARTMENT OF COMMERCE
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National Marine Fisheries Service

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Status Review of Coastal Cutthroat Trout from Washington, Oregon, and California

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EXECUTIVE SUMMARY

This status review examines coastal cutthroat trout (*Oncorhynchus clarki clarki*) in California, Oregon, and Washington to determine whether they face a risk of extinction if present conditions continue. The National Marine Fisheries Service (NMFS) initiated this status review, which was also requested by a 1997 petition seeking listing of all *O. c. clarki* in those three states as threatened or endangered under the federal Endangered Species Act (ESA). The NMFS decision to conduct this status review follows the agency's announcement, in response to earlier petitions and to general concerns about the status of Pacific salmon throughout the region, to initiate ESA status reviews for all species and populations of anadromous salmonids, including coastal cutthroat trout, in Washington, Idaho, Oregon, and California.

The ESA allows listing "distinct population segments" of vertebrates and named species and subspecies. The policy of the NMFS on this issue for anadromous Pacific salmonids is that a population will be considered "distinct" for purposes of the ESA if it represents an evolutionarily significant unit (ESU) of the species as a whole. To be considered an ESU, a population or group of populations must 1) be substantially reproductively isolated from other populations, and 2) contribute substantially to the ecological or genetic diversity of the biological species. Once an ESU is identified, a variety of factors related to population abundance are considered in determining whether a listing is warranted.

A team of NMFS scientists conducted this status review, which the ESA stipulates be based on the best available scientific and commercial information. This Biological Review Team (BRT) reviewed and evaluated information from federal, state, and tribal fisheries agencies, as well as individuals.

The BRT did not as part of this review evaluate likely or possible effects of conservation measures, and therefore did not make recommendations as to whether identified ESUs should be listed as threatened or endangered. The BRT did, however, draw conclusions about the risk of extinction faced by ESUs under the assumption that present conditions will continue.

Umpqua River Coastal Cutthroat Trout

A status review of coastal cutthroat trout from the Umpqua River basin in southern Oregon was conducted by the NMFS in 1994. The BRT for that review concluded that all life-history forms in the Umpqua River were part of the same ESU but was unable to reach a conclusion on the ESU's geographic extent. The BRT also concluded that the anadromous portion of the ESU was precarious and that its loss would be an ESA concern; anadromy is based (at least in part) on genetics and contributes substantially to the ESU's ecological/genetic diversity.

In July 1996, the NMFS published a final rule listing Umpqua River cutthroat trout as an endangered species. However, in doing so, NMFS committed to reevaluate the status of the species within 2 years. This current coastwide review of coastal cutthroat trout reevaluates biological data on the status of the Umpqua River species and identifies Umpqua River coastal cutthroat trout as part of a larger Oregon Coast ESU, which is evaluated as part of this review. This review, however, does not completely resolve the Umpqua River ESU boundary question, and the possibility that smaller ESUs should be recognized has not been excluded.

Difficulties in Reviewing Coastal Cutthroat Trout Status

Reviewing the status of coastal cutthroat trout was difficult because they are one of the most biologically diverse and least-studied groups of West Coast salmonids. Two factors made ESU determination and risk assessment for this group especially challenging:

- Relevant biological information on the subspecies is meager compared to data collected for Pacific salmon because, as cutthroat trout are not a commercial species, much of the information useful for their management and conservation is obtained only incidentally during biological surveys for commercially caught Pacific salmon species.
- Coastal cutthroat trout express a wide diversity of life-history attributes. This diversity includes several migratory pathways: They may migrate to estuaries and other marine environments (a form known either as "anadromous" or "sea run"); they may remain in fresh water (freshwater forms) as river/lake migrants or in upper headwater tributaries as nonmigrants; or they may follow migratory pathways that combine these behaviors. Genetic and environmental influences on these migratory pathways and life-history attributes are poorly understood.

The BRT felt strongly that life-history forms in each ESU represent diverse genetic and phenotypic resources important to its evolutionary ecology, and the BRT unanimously concluded that each ESU include all of these life-history forms. Team members concurred that loss of any individual life-history form could increase risk to the ESU as a whole.

Another challenging problem for the BRT was to evaluate the significance of various migration barriers that separate the different life-history forms of coastal cutthroat trout in some watersheds. The BRT was divided on whether populations above long-standing barriers (i.e., those that effectively preclude migration for hundreds or even thousands of years) should be included in ESUs. The primary argument for inclusion centered on the fact that populations above barriers are often most closely related to those below them; this close relationship makes it unclear to which ESU above-barrier populations would belong if not to the ESU including below-barrier populations. The argument for exclusion focused on the complete reproductive isolation between the above- and below-barrier populations and, consequently, the different evolutionary trajectories followed by these groups of populations. Only under very special circumstances would the above-barrier populations be useful in recovery of the below-barrier populations.

This problem also involved barriers that permit some one-way migration (i.e., downstream migration of smolts but not upstream passage of adults). The majority of BRT members believed that populations above these barriers should be included in ESUs. The basis for this conclusion is two-fold: 1) populations above barriers may contribute demographically and genetically to populations below them, even if the frequency of successful one-way migrants per generation is low, and 2) populations above barriers may represent genetic resources shared by populations below them (and thus may be a significant component of diversity for an ESU).

Coastal Cutthroat Trout ESUs

The BRT considered several possible ESU configurations for this subspecies based on biogeographic, life history, and genetic information. After considerable discussion, a majority of BRT members supported a scenario involving six ESUs: Puget Sound, Olympic Peninsula, Southwestern Washington/Columbia River, upper Willamette River, Oregon Coast, and Southern Oregon/California Coasts. Alternative scenarios considered at length by the BRT were 1) a single ESU corresponding with the range of coastal cutthroat trout and 2) multiple ESUs corresponding to small geographic units, such as major river basins. However, the BRT ultimately concluded that available information best supported the scenario of six ESUs. These six ESUs show strong similarities to ESUs designated for other species, especially coho (*O. kisutch*) and chinook (*O. tshawytscha*) salmon, and steelhead (*O. mykiss*); however, there are significant dissimilarities that reflect species differences in genetic structure and life-history variation.

Figure ES-1 shows the six ESUs; descriptions follow.

1) Puget Sound ESU

This proposed ESU includes populations of coastal cutthroat trout that enter protected marine waters in northwestern Washington; its boundaries correspond roughly with the Puget Lowland ecoregion.

Life-history data indicate that coastal cutthroat trout from Puget Sound generally smolt at a smaller size and younger age than those entering coastal marine waters. Genetic data indicate that these populations are separated from those in southwestern Washington and farther south. Populations in Puget Sound and Hood Canal and on the Olympic Peninsula are highly heterogeneous genetically; nevertheless, some evidence exists for coherent genetic separation of Olympic Peninsula populations from those in the eastern Strait of Juan de Fuca, northern Puget Sound, and Hood Canal. Populations in Hood Canal and along the Strait of Juan de Fuca are distinctive but show no clear evidence of a transition zone between Puget Sound and southwestern Washington. There are genetic distinctions between populations from the upper Nisqually River (a system in southern Puget Sound with strong glacial influences) and other southern Puget Sound populations. Based primarily on these life-history and genetic patterns, the BRT concluded that this ESU includes all streams in Puget Sound and the Strait of Juan de Fuca west to, and including, the Elwha River. The northern boundary for this ESU is unclear, but

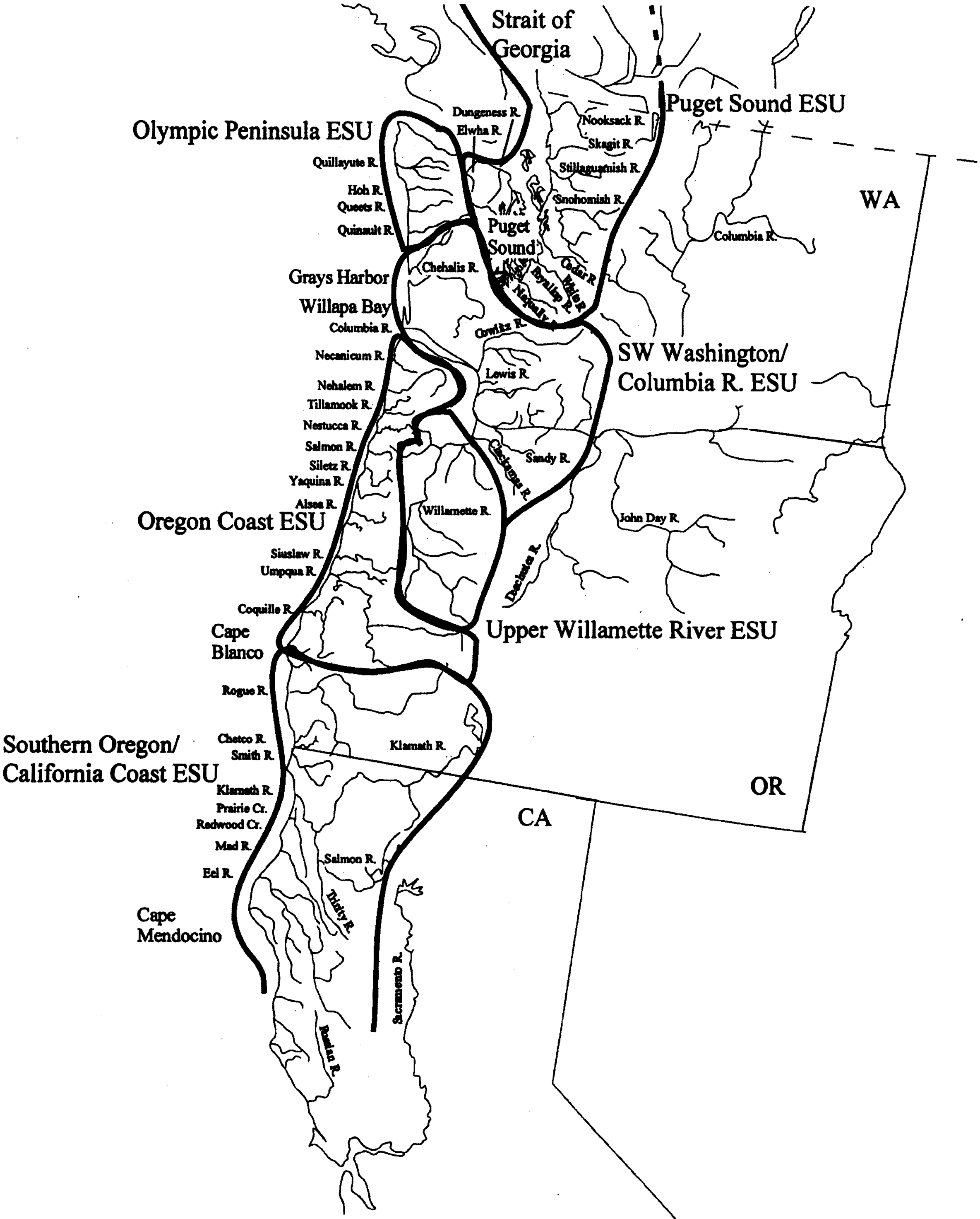

Figure ES-1. Proposed Evolutionarily Significant Unit (ESU) designations for coastal cutthroat trout.

unpublished data lend support to the hypothesis that this ESU extends into southern British Columbia, including populations along eastern Georgia Strait north of Vancouver.

In general, this ESU's boundaries reflect an ecoregion in which river drainages have relatively high flows due largely to high precipitation, snow melt, and temperatures moderated by the marine environment. The southern and western boundaries are similar to those previously identified for chinook, coho, chum (*O. keta*), and pink (*O. gorbuscha*) salmon, and steelhead. The northern boundary differs from the one for chinook and coho salmon (which does not extend into Canada) and for pink, chum, and coho salmon (which does not include eastern Vancouver Island).

2) Olympic Peninsula ESU

This proposed ESU includes coastal cutthroat trout in populations from the Strait of Juan de Fuca west of the Elwha River and coastal streams south to, but not including, streams that drain into Grays Harbor. The proposed boundaries of this ESU are similar to those for steelhead and coho salmon. Support for this ESU relies primarily on the ecological distinctiveness of this area, which is characterized by high precipitation, cool water temperatures, and relatively short high-gradient streams entering directly into the open ocean.

Coastal cutthroat trout from this area are relatively large as smolts, and a higher proportion appears to mature at first return from seawater than is the case in most Puget Sound populations. Olympic Peninsula populations are genetically distinctive, but show a greater similarity to populations in Puget Sound and Hood Canal than to those along the Strait of Juan de Fuca east of the Elwha River.

Based primarily on these genetic data, a minority of the BRT concluded that populations from the Olympic Peninsula should be considered part of a combined Puget Sound-Olympic Peninsula ESU. Other BRT members pointed out that the Olympic Peninsula ESU may represent a genetic transition zone between the Puget Sound and Southwestern Washington/Columbia River ESUs.

3) Southwestern Washington/Columbia River ESU

The proposed boundaries of this ESU are similar to the Southwestern Washington/Lower Columbia River ESU for coho salmon and extend upstream in the Columbia River to Celilo Falls. Support for this ESU designation comes primarily from ecological and genetic information. Ecological characteristics of this region include the presence of extensive intertidal mud and sandflats, similarities in freshwater and estuarine fish faunas, and substantial differences from estuaries north of Grays Harbor and south of the Columbia River. The coastal cutthroat trout samples from southwestern Washington show a relatively close genetic similarity to samples from the Columbia River.

A minority of the BRT supported a split of Columbia River from southwestern Washington coastal cutthroat trout populations. Tagging and recovery data for chinook, coho, and chum salmon indicate different marine distributions for fish from the two areas. The limited dispersal ability of anadromous cutthroat trout may restrict genetic exchange among populations in the two areas, which exhibit different physical estuarine characteristics. Also, an important salmonid parasite, *Ceratomyxa shasta*, occurs in the Columbia River but has not been observed in Willapa Bay or Grays Harbor. However, the majority of BRT members concluded that available data did not provide compelling evidence for splitting populations along the southwestern Washington coast from those in the Columbia River.

4) Upper Willamette River ESU

Cutthroat trout are one of only three species of anadromous Pacific salmonids that historically occurred above Willamette Falls. Upper Willamette River populations of the other two species (spring chinook salmon and winter steelhead) have been identified as separate ESUs in previous status reviews, based on ecological factors, substantial genetic differences from other Columbia River populations, and physical and hydrological conditions.

The upper Willamette River above the falls encompasses a large area with considerable habitat complexity that evidently supports several different populations of coastal cutthroat trout. Based on information provided by the Oregon Department of Fish and Wildlife, Willamette Falls in its present configuration is a nearly complete barrier upstream and downstream in summer and early fall to anadromous fish, including summer steelhead as well as coastal cutthroat trout. The BRT concluded that the upper Willamette River has probably never supported a substantial anadromous population of cutthroat trout, although freshwater forms are common. Upper Willamette River coastal cutthroat trout exhibit a genetic structure consistent with the hypothesis that the falls is a strong reproductive barrier between populations above and below it. *Ceratomyxa shasta* in the Willamette River below the Marys River and high temperatures in the lower Willamette River in summer and fall probably limit the survival of the very few migrants known to drop over the falls. Although the populations above the falls are highly heterogeneous genetically with several outlier populations, they form a somewhat coherent cluster of apparently isolated and semi-isolated populations.

A number of factors—physical and genetic evidence of a migration barrier, habitat and ecological differences above and below Willamette Falls, and the lack of anadromous populations and prevalence of freshwater migratory forms above the falls—led the majority of the BRT to conclude that coastal cutthroat trout above Willamette Falls should be considered a separate ESU.

5) Oregon Coast ESU

Genetic data indicate marked genetic differences between coastal cutthroat trout from coastal Oregon and those in the Columbia River and along the Washington coast. Samples of coastal cutthroat trout south of the Columbia River indicate a large heterogeneous group of populations along the Oregon coast. Furthermore, several ecological differences exist between rivers along the Oregon coast and those farther north. The Oregon coast is characterized by relatively high precipitation, moderate temperatures, and short low-gradient streams with few migration barriers. Tagging studies in Alaska and elsewhere indicate that anadromous cutthroat trout follow shorelines when in seawater; thus, the known migratory patterns of this species are consistent with the hypothesis that the Columbia River, which is several miles wide and relatively deep at its mouth, is a migratory barrier between coastal populations in Oregon and Washington.

The proposed boundaries of this ESU are similar to the ESUs identified for coho and chinook salmon and steelhead. The southern boundary of this proposed ESU is at Cape Blanco, Oregon. Genetic data provide only weak evidence for a split between populations north or south of Cape Blanco, but ecological data support it. The Cape Blanco area is a major biogeographic boundary for many marine and terrestrial species and has been identified as an ESU boundary for chinook and coho salmon and steelhead on the basis of strong genetic, life-history, ecological, and habitat differences north and south of this landmark. Also, unpublished meristic data point to a difference between coastal cutthroat trout populations north and south of Cape Blanco (Williams unpubl. data).

6) Southern Oregon/California Coasts ESU

A majority of the BRT members concluded that populations of coastal cutthroat trout from Cape Blanco south to the southern extent of the subspecies' range represent a separate ESU. Several members did not consider the genetic and ecological data strong enough to support this split. However, as described above, meristic (and, to some extent, genetic) information lends support for a separate coastal cutthroat trout ESU south of the major biogeographic boundary at Cape Blanco. In addition, the limited dispersal capability of coastal cutthroat trout and anecdotal evidence for marked differences in population dynamics for populations north and south of Cape Blanco support a split at that landmark. Finally, the majority of river systems in this ESU are relatively small with limited estuaries and heavily influenced by a maritime climate. Many of these systems are characterized by physical and thermal barriers to movement by anadromous fish; notable systems that lack such barriers are the Eel, Klamath, Rogue, and Trinity rivers.

Assessment of Extinction Risk

The ESA defines "endangered species" as "any species which is in danger of extinction throughout all or a significant portion of its range." "Threatened species" is defined as "any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range." According to the ESA, the determination of whether a species is threatened or endangered should be made on the basis of the best scientific information available regarding the species' status, after taking into consideration conservation measures proposed or in place.

One of the most challenging aspects of risk assessments for coastal cutthroat trout is the scarcity of available information. This lack of data is far more pervasive than for other species of Pacific salmonids. Current or historical abundance information, especially for adult coastal cutthroat trout, is available for only a very small proportion of the known populations within any ESU. In contrast to status reviews of the other species of Pacific salmonids, the BRT for coastal cutthroat trout had to base its risk evaluations more heavily on abundance estimates for a small number of populations spanning only a few years, on presence/absence data, and on professional judgements by biologists familiar with coastal cutthroat trout in specific geographic regions. Information on risks from hatchery-origin fish and on hybridization with steelhead and rainbow (the freshwater form of *O. mykiss*) trout also is very limited for coastal cutthroat trout.

The BRT wrestled with a fundamental dilemma stemming from the lack of data, which can result in two alternative conclusions:

- There is insufficient evidence to demonstrate that coastal cutthroat trout are at significant risk of extinction
- There is insufficient evidence to demonstrate that coastal cutthroat trout are *not* at significant risk of extinction

This dilemma existed for many of the coastal cutthroat trout ESUs. For some BRT members, uncertainty about a given ESU's status stemming from insufficient information and from a collective sense among many local biologists that coastal cutthroat trout were in decline led to a conclusion that there is a risk of extinction. For other BRT members, insufficient information led to a conclusion that there is *not* significant risk. The BRT stressed that the latter conclusion does not necessarily indicate that an ESU is healthy; rather, it may simply indicate that there is insufficient information to demonstrate that it is *not* healthy.

Summary of BRT Risk Conclusions

- A majority of BRT members concluded the Puget Sound, Olympic Peninsula, and Southern Oregon/California Coast ESUs are not presently in danger of extinction, nor are they likely to become so in the foreseeable future. For each of these three ESUs, a minority of the BRT believed there is a likelihood of endangerment in the foreseeable future.
- All BRT members agreed that the Oregon Coast ESU is not presently at risk of extinction, but the team was evenly split on whether the ESU is likely to become endangered in the foreseeable future.
- The BRT unanimously concluded that the Southwestern Washington/Columbia River ESU is likely to become endangered in the foreseeable future. The conservation status of the ESU in the upper Willamette River, a tributary of the Lower Columbia River, was not formally evaluated by the BRT because available evidence indicates that few if any anadromous coastal cutthroat trout are produced in this ESU.

A summary of the rationale for risk conclusions for each ESU follows.

Puget Sound ESU

The BRT noted with concern that there are few existing data relative to those for steelhead and Pacific salmon concerning historical and present abundance of coastal cutthroat trout in the Puget Sound ESU region. Anecdotal reports suggest relatively high abundance of coastal cutthroat trout in northern Puget Sound and low abundance in southwestern Puget Sound streams. There are some data indicating that juvenile coastal cutthroat trout are relatively well distributed in the Skagit and Stillaguamish river basins and along the Strait of Juan de Fuca. The BRT acknowledged that widespread habitat degradation and loss has occurred in the Puget Sound region. This reduction in habitat capacity constitutes an important and ongoing risk to coastal cutthroat trout that has not been well quantified.

Trend data for this ESU available to the BRT were from downstream migrant and adult counts for a few streams. Apparent declines in downstream migrants in the Skagit River basin may not accurately depict coastal cutthroat trout abundance—but may at best be rough indicators of true trends—because the trap locations and dates trapped were designed to estimate coho salmon smolt numbers. Increases in coastal cutthroat trout smolt numbers in some eastern Hood Canal streams coincided with declines in coho salmon abundance, suggesting to the BRT that interactions between these two species may be reducing the abundances of coastal cutthroat trout in some streams. Historical estimates of smolt abundance were not available, so no definitive conclusions about the risks to coastal cutthroat trout populations could be made from smolt count data.

In addition to information about population sizes and trends in abundance for coastal cutthroat trout in this ESU, the BRT considered another important risk factor—the potential loss of life-history diversity. The anadromous life-history type in particular appears to be declining in some streams. However, the BRT believed that risks to the ESU's integrity and long-term sustainability due to loss of life-history diversity were relatively low compared to those of the other five coastal cutthroat trout ESUs, which have more streams with documented declines in anadromous life-history types. The influence of hatchery coastal cutthroat trout in the Puget Sound ESU is probably low compared to the scale of hatchery propagation of other Pacific salmon.

A majority of the BRT members believed the Puget Sound ESU is not presently in danger of extinction, nor is it likely to become so in the foreseeable future. A minority believed that the ESU is likely to become endangered in the foreseeable future. The uncertainty underlying these assessments was high: most BRT members reported certainty scores of 2 or 3 for their risk evaluations. The BRT concluded that widespread, often irreversible, degradation of freshwater and estuarine habitat has occurred, due to effects of development, logging, and agriculture. Thus, extant habitat capacity is clearly lower than historical levels. A number of biologists familiar with coastal cutthroat trout believe fishing mortality on cutthroat trout is an important source of risk. The BRT expressed concern that historical and continuing reduction in habitat quality, combined with very little information with which to assess status, led to great uncertainty in evaluating risk for Puget Sound coastal cutthroat trout.

Olympic Peninsula ESU

The BRT had very little information to estimate population abundances for coastal cutthroat trout in this ESU. The general impression from state and tribal fisheries biologists is that juvenile coastal cutthroat trout are widely distributed in streams along the western Strait of Juan de Fuca and northern Washington coast, and the BRT believed there are probably some highly productive coastal cutthroat trout streams in this region. On the other hand, the BRT acknowledged that ongoing habitat destruction, primarily from logging and associated activities continue to be a source of risk to coastal cutthroat trout in many Olympic Peninsula streams.

The only quantitative data available to the BRT for this ESU were counts of downstream migrants on tributaries of the Clearwater (1978-present), Dickey (1992-1994), and Hoko (1986-1989) rivers and in Salt Creek along the Strait of Juan de Fuca (1998). The trends among Clearwater tributaries were mixed. The BRT did not weigh increasing trends from the Hoko River heavily in its risk determinations because these data are not current; the Dickey River trends were also not weighed heavily because they are based on only 3 years of trapping designed to estimate coho salmon production. It was difficult to interpret outmigrant data because of a lack of smolt-to-adult survival estimates and because production declines may have occurred before 1981, when earliest data collection began.

The BRT indicated that the risks to the Olympic Peninsula ESU from loss of life-history diversity were relatively low. This ESU received a lower risk score for this source of risk than did any other ESU. Risks associated with hatchery coastal cutthroat trout also are considered low in this ESU.

A majority of the BRT concluded that the Olympic Peninsula ESU is not presently in danger of extinction, nor is it likely to become so in the foreseeable future. One member considered the ESU likely to become endangered in the foreseeable future. These risk evaluations, however, must be considered in light of the very high uncertainty expressed by the BRT. Certainty scores for this risk assessment were the lowest of all of the cutthroat trout ESUs, with most of them 1 or 2. The BRT believed that there are indications of productive cutthroat trout habitat to support this ESU, but information was not available to confirm such a possibility. Continuing habitat degradation throughout the region was a significant source of concern to the BRT.

Southwestern Washington/Columbia River ESU

According to the Washington Department of Fish and Wildlife, the southwestern Washington-Lower Columbia River region historically supported healthy and highly productive coastal cutthroat trout populations. Coastal cutthroat trout, especially the freshwater forms, may still be widely distributed in most river basins in this region, although probably in numbers lower than historical population sizes. Severe habitat degradation throughout the Lower Columbia River area has contributed to dramatic declines in anadromous coastal cutthroat trout populations and two near extinctions of anadromous runs in the Hood and Sandy rivers. The BRT was concerned about the extremely low population sizes of anadromous cutthroat trout in Lower Columbia River streams indicated by low incidental catch in salmon and steelhead recreational fisheries and low trap counts in a number of tributaries throughout the region. In contrast, local biologists told the BRT that freshwater forms of coastal cutthroat trout are widespread in streams throughout the region.

In the southwestern Washington portion of this ESU, trends in anadromous adults and outmigrating smolts are all declining. Returns of both naturally- and hatchery-produced coastal cutthroat trout in almost all Lower Columbia River streams have been declining markedly for the last 10 to 15 years.

A significant risk factor for coastal cutthroat trout in this ESU is reduction in life-history diversity. The limited information available suggests that, in many streams, freshwater forms of coastal cutthroat trout are widely distributed and in high abundances relative to anadromous cutthroat trout in the same stream. The BRT believed that smolt production by freshwater forms does occur, but that it has not resulted in demonstrably successful reestablishment of anadromous forms. Habitat degradation in stream reaches accessible to anadromous cutthroat trout and poor ocean and estuarine conditions probably have combined to severely deplete this life-history form throughout the Lower Columbia River Basin. Without the appropriate freshwater and estuarine habitat for expression of the anadromous life history, a greater risk of extinction may occur. The significance of this reduction in life-history diversity to the integrity of the ESU and the likelihood of its long-term persistence were major sources of concern to the BRT.

Negative effects of hatchery coastal cutthroat trout may be contributing to the risks facing natural coastal cutthroat trout in this ESU. The Lower Columbia River tributaries are the only streams in Washington still receiving hatchery-origin coastal cutthroat trout, although the total numbers of released hatchery fish have been substantially curtailed recently. The BRT emphasized that the ultimate effects of hatchery fish depend on the relative sizes of hatchery and natural populations, the spatial and temporal overlap of hatchery and natural fish throughout their life cycles, and the actual extent to which hatchery fish spawn naturally and interbreed with naturally produced fish. In addition, the extent to which natural coastal cutthroat trout are incidentally harvested in fisheries targeting hatchery coastal cutthroat trout and other salmonids also affect the magnitude of the risks to coastal cutthroat trout due to hatchery fish.

The BRT was unanimous in concluding that the Southwestern Washington/Columbia River ESU was likely to become endangered in the foreseeable future. Certainty scores ranged from 2 to 4; although these scores reflect only a moderate degree of certainty regarding the risk assessment, they were on average higher than for any other ESU. The BRT was especially concerned about the widespread declines in abundance and small population sizes of anadromous cutthroat trout throughout the Lower Columbia River. The severe reductions in abundance of this life-history form could have deleterious effects on the ability of this ESU to recover from widespread declines. Reductions in the quantity and quality of nearshore ocean, estuarine, and riverine habitat have probably contributed to declines, but the relative importance of these risk factors is not well understood. The BRT was encouraged by recent steps taken by the states of

Washington and Oregon to reduce mortality in this ESU due to directed and incidental harvest of coastal cutthroat trout.

Upper Willamette River ESU

The conservation status of this ESU was not formally evaluated by the BRT. Since few anadromous cutthroat trout are produced in this ESU, the U.S. Fish and Wildlife Service has jurisdiction for these populations.

Oregon Coast ESU

Coastal cutthroat trout in the Oregon coastal region occur mostly in small populations that are relatively widely distributed. Most of the abundance information considered by the BRT for this ESU was for juveniles and smolts, with the prominent exception of adult counts at Winchester Dam on the North Umpqua River. In general, the BRT was encouraged by the numbers of juveniles in coastal streams with relatively large basins. These data are available for only the last 2 years, however, so it is not known how well these juvenile counts translate into adult abundances or longer-term population trends.

Conflicting information about the abundance and distribution of coastal cutthroat trout in the South Umpqua River basin suggested to the BRT that there is insufficient information to determine the status of coastal cutthroat trout in that drainage. The numbers of adults returning to the North Umpqua River have been critically low in recent years (5-year geometric mean = 18 fish), although the last 3 years have produced counts of 79, 81, and 135 (through November 15, 1998) at Winchester Dam on the North Umpqua River. The BRT noted that widespread habitat degradation due to logging, road construction, and development along coastal streams probably constitutes a significant reduction in habitat capacity relative to historical conditions.

Smolt production in two small drainages (Cummins and Tenmile creeks) in central Oregon has shown an increasing trend over the past 7 years. All other streams on the Oregon coast for which data were available are experiencing moderate declines in adults and juveniles. In some areas, declines may have occurred primarily in anadromous cutthroat trout populations, and the BRT was concerned about such reductions throughout this ESU. The BRT believed risks associated with possible reductions in historical connections among streams by migratory coastal cutthroat trout could be a significant threat to the ESU.

Risks due to interactions with hatchery coastal cutthroat trout are probably moderately low in this ESU. Nevertheless, widespread releases of Alsea River hatchery broodstock in Oregon coastal streams have stopped only recently. Hybrids between coastal cutthroat trout and *O. mykiss* were detected in genetic samples from the Coquille River Basin and a few other streams in this ESU. Some degree of hybridization between *O. mykiss* and coastal cutthroat trout may occur naturally without the direct influence of hatchery-origin fish. However, risks to coastal cutthroat trout populations due to hybridization may increase if either changes in habitat conditions or an increase in the abundance of hatchery-origin *O. mykiss* increase the frequency of natural hybridization or change its fitness consequences.

All BRT members agreed the Oregon Coast ESU is not presently at risk of extinction. However, the BRT was evenly split in determining whether or not the ESU is likely to become endangered in the foreseeable future. The certainty in this assessment was fairly low: the certainty scores were mostly 2 or 3. The BRT was concerned about habitat degradation that continues within this region, and the scarcity of abundance information for major drainages limited the BRT's efforts to conduct a risk evaluation. Hatchery records indicate that the Alsea River coastal cutthroat trout stock was released widely in streams throughout the Oregon coastal region. Recent reductions in releases of hatchery-origin coastal cutthroat trout and coho salmon fry, coupled with a statewide catch-and-release recreational fishery policy for "wild" coastal cutthroat trout, may have reduced risks associated with those factors. The BRT noted that reduced nearshore ocean habitat quality is probably a significant threat to coastal cutthroat trout in this region, but quantifying those effects on coastal cutthroat trout abundance is very difficult. Finally, the BRT was concerned about incidental mortality of coastal cutthroat trout in this ESU due to fishing pressure on Pacific salmon and steelhead.

Southern Oregon/California Coasts ESU

Coastal cutthroat trout in this ESU are thought to be widely distributed in many small populations. Two possible exceptions are populations in the Rogue and Smith river basins, where abundance may be comparatively large. Population sizes are thought to be relatively small in other streams throughout this region, in part because it is the southern limit of this subspecies. The BRT believes that severe habitat degradation has occurred in this region, primarily due to activities associated with agriculture, flood control, logging, road construction, and some local development that have contributed to a reduction in habitat capacity relative to historical levels. In addition, seasonal dewatering of stream mouths occurs naturally in Northern California, sporadically blocking access to the sea for anadromous fish in those streams. Also, large water withdrawals in several of the larger coastal river basins (e.g., the Rogue, Klamath/Trinity, and Eel rivers) and several of the smaller coastal rivers have reduced the quantity and quality of the remaining riverine and estuarine environments in this ESU.

Biologists familiar with this region believe, and anecdotal evidence suggests, that major declines in coastal cutthroat trout populations have occurred since historical times, but that some populations appear to have been relatively stable or increasing. The data available to the BRT indicate increasing short-term trends in smolt abundance in Mill Creek as well as increasing short-term trends in adult abundance in the lower Klamath River tributaries and its estuary and in the Smith River Basin. Exceptions include recent declines in the incidence of coastal cutthroat trout in Redwood Creek.

Reductions in the anadromous form of coastal cutthroat trout are not thought to be a significant source of risk to the overall ESU. Although declines in some anadromous runs have occurred, there was no evidence presented to the BRT that these declines have occurred throughout a significant portion of the ESU.

Risks due to interactions with hatchery coastal cutthroat trout are probably low in this ESU. Other risks the BRT noted for coastal cutthroat trout in this region were possible deleterious interactions with naturally occurring or hatchery-derived coho salmon and steelhead, and incidental catch of coastal cutthroat trout in sport fisheries targeting steelhead and coho salmon. The BRT was encouraged by recent changes in harvest regulations aimed at reducing risks to natural trout from direct and indirect harvest mortality.

A majority of the BRT believed that the Southern Oregon/California Coasts ESU is not presently in danger of extinction, nor is it likely to become so in the foreseeable future. A minority concluded that the ESU was likely to become endangered in the foreseeable future. Most BRT members indicated their risk evaluations were associated with a low level of certainty (scores ranged from 1 to 4, but most members indicated a score of 2). As in considerations of many other ESUs for coastal cutthroat trout, the BRT was hindered here by the scarcity of abundance information for this ESU. The BRT emphasized that continuing threats to the quality of freshwater and estuarine habitat for coastal cutthroat trout in this region are sources of concern.

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INTRODUCTION

The U.S. Endangered Species Act (ESA) is intended to conserve threatened and endangered species in their native habitats. The ESA allows listing of named species, subspecies, and distinct vertebrate populations segments. According to National Marine Fisheries Service (NMFS) policy, a salmonid population or group of populations is considered "distinct" and a "species" under the ESA if it represents an evolutionarily significant unit (ESU) of the biological species.

In response to earlier petitions for ESA listing of a variety of salmonid species and to more general concerns about the status of Pacific salmon throughout the Pacific coast, NMFS (1994) announced that it would initiate ESA comprehensive status reviews for all species of anadromous salmonids in the Pacific Northwest. This proactive approach was intended to facilitate more timely, consistent, and comprehensive evaluation of the ESA status of Pacific salmonids than would be possible in a series of reviews of individual populations. Since 1994, the Northwest Fisheries Science Center (NWFSC) has conducted a series of status reviews to identify ESUs in these species and evaluate their risk of extinction. These status reviews include coho salmon (*Oncorhynchus kisutch*) (Weitkamp et. al. 1995), pink salmon (*O. gorbuscha*) (Hard et al. 1996), steelhead (the sea-run form of *O. mykiss*) (Busby et al. 1996), chum salmon (*O. keta*) (Johnson et al. 1997), sockeye salmon (*O. nerka*) (Gustafson et al. 1997), and chinook salmon (*O. tshawytscha*) (Myers et al. 1998). This review of coastal cutthroat trout (*O. clarki clarki*) is the final coastwide review in this series.

This status review also addresses a petition received by NMFS on December 5, 1997, from the Oregon Natural Resources Council (ONRC) and others (listed in "Summary of Coastal Cutthroat Trout Petition," p. 5) to "list the sea-run cutthroat trout as threatened or endangered throughout its range in the states of California, Oregon, and Washington" (ONRC 1997, p. 2).[1]

A third purpose of this status review is to update information gathered for an earlier status review of Oregon's Umpqua River coastal cutthroat trout (Johnson et al. 1994), which was initiated in response to a petition to NMFS by the ONRC, the Wilderness Society, and the Umpqua Valley Audubon Society (ONRC et al. 1993) to list the North and South Umpqua River sea-run cutthroat trout as a threatened or endangered species under the ESA. NMFS accepted the petition and conducted a status review, concluding that coastal cutthroat trout in the Umpqua River basin did constitute an ESU (Johnson et al. 1994). On August 9, 1996, NMFS issued a final ruling that listed the Umpqua River coastal cutthroat trout as an endangered species under the ESA (61 Fed. Reg. 41514). However, at the time of this determination, NMFS indicated that it would reconsider this determination in 2 years or as new scientific information became available (61 Fed. Reg. 41521). Consequently, the portion of this status review that pertains to

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[1] "Sea-run cutthroat trout," one of several common names for *O. c. clarki* and the name used in the petition, refers only to one life-history form in the subspecies (fish that migrate to seawater). This report uses coastal cutthroat trout (or cutthroat trout) as the common name for this subspecies (see "Terminology," p. 6).

Umpqua River coastal cutthroat trout will focus on new information developed for this ESU since the 1994 status review.

Scope and Intent of the Present Document

This document reports results of the comprehensive ESA status review of all life-history forms (both anadromous and nonanadromous) of coastal cutthroat trout from Washington, Oregon, and California. To provide a context for evaluating U.S. populations of coastal cutthroat trout, biological and ecological information for coastal cutthroat trout in British Columbia and Alaska were also considered. Therefore this review encompasses, but is not restricted to, contiguous U.S. sea-run populations identified in petitions for coastal cutthroat trout received by NMFS in 1997.

Because the ESA stipulates that listing determinations should be made on the basis of the best available scientific and commercial information, NMFS formed a team of scientists with diverse backgrounds in salmonid biology to conduct this review. This Biological Review Team (BRT) reviewed and evaluated scientific information compiled by NMFS staff from published and unpublished literature. Information was also considered that was presented at a series of public meetings in 1997 and 1998 in Arcata, California; Gleneden Beach, Corvallis, Portland, and Roseburg, Oregon; and Seattle and Olympia, Washington. In addition, the BRT reviewed technical information submitted to the ESA administrative record.

Key Questions in ESA Evaluations

In determining whether a listing under the ESA is warranted, two key questions must be addressed:

1. Is the entity in question a "species" as defined by the ESA?
2. If so, is the species threatened or endangered?

These two questions are addressed in "Information Relating to the Species Question" (p. 21) and "Assessment of Extinction Risk" (p. 135). If it is determined that a listing(s) is warranted, then NMFS is required by law (1973 ESA Sec. 4(a)(1)) to identify one or more of the following factors responsible for the species' threatened or endangered status: 1) destruction or modification of habitat; 2) overutilization by humans; 3) disease or predation; 4) inadequacy of existing regulatory mechanisms; or 5) other natural or human factors. This status review does not formally address factors for decline, except insofar as they provide information about the degree of risk faced by the species in the future.

The "Species" Question

As amended in 1978, the ESA allows listing of "distinct population segments" of vertebrates as well as named species and subspecies. However, the ESA provides no specific guidance for determining what constitutes a distinct population, and the resulting ambiguity has led to the use of a variety of approaches for considering vertebrate populations. To clarify the issue for Pacific salmon, NMFS published a policy describing how the agency will apply the definition of "species" in the ESA to anadromous salmonid species, including coastal cutthroat trout and steelhead (NMFS 1991). A more detailed discussion of this topic appeared in the NMFS "Definition of Species" paper (Waples 1991a,b). NMFS policy stipulates that a salmon population (or group of populations) will be considered "distinct" for purposes of the ESA if it represents an ESU of the biological species. An ESU is defined as a population that 1) is substantially reproductively isolated from nonspecific populations, and 2) represents an important component of the evolutionary legacy of the species.

The term "evolutionary legacy" is used in the sense of inheritance—something received from the past and carried forward into the future. Specifically, the evolutionary legacy of a species is the genetic variability that is a product of past evolutionary events and that represents the reservoir upon which future evolutionary potential depends. Conservation of these genetic resources should help to ensure that the dynamic process of evolution will not be unduly constrained in the future.

For each of the two criteria (reproductive isolation and evolutionary legacy), NMFS policy advocates a holistic approach that considers all types of available information as well as their strengths and limitations. Important types of information to consider for reproductive isolation include natural rates of straying and recolonization, evaluations of the efficacy of natural barriers, and measurements of genetic differences between populations. Data from protein electrophoresis or DNA analyses can be particularly useful for this criterion because they reflect levels of gene flow that have occurred over evolutionary time scales. Isolation does not have to be absolute, but it must be strong enough to permit evolutionarily important differences to accrue in different population units.

The key question with respect to the evolutionary legacy criterion is this: Would extinction of the population represent a significant loss to the ecological/genetic diversity of the species? Again, a variety of types of information should be considered. Phenotypic and life-history traits such as size, fecundity, migration patterns, and age and time of spawning may reflect local adaptations of evolutionary importance, but interpretation of these traits is complicated by their sensitivity to environmental conditions. Data from protein electrophoresis or DNA analyses provide valuable insight into the process of genetic differentiation among populations but little direct information regarding the extent of adaptive genetic differences. Habitat differences suggest the possibility for local adaptations, but do not prove that such adaptations exist.

Artificial Propagation

NMFS policy (Hard et al. 1992, NMFS 1993) stipulates that in determining 1) whether a population is distinct for purposes of the ESA, and 2) whether an ESA species is threatened or endangered, attention should focus on "natural" fish, which are defined as the progeny of naturally spawning fish (Waples 1991a,b). This approach directs attention to fish that spend their entire life cycle in natural habitat and is consistent with the mandate of the ESA to conserve threatened and endangered species in their native ecosystems. Implicit in this approach is the recognition that fish hatcheries are not a substitute for natural ecosystems.

Nevertheless, artificial propagation is important to consider in ESA evaluations of anadromous Pacific salmonids for several reasons. First, although natural fish are the focus of ESU determinations, possible effects of artificial propagation on natural populations must also be evaluated. For example, transfers of fish from one area to another might change the genetic or life-history characteristics of a natural population in such a way that the population might seem either less or more distinctive than it was historically. Artificial propagation can also alter life-history characteristics such as smolt age, migration, and spawn timing. Second, artificial propagation poses risks to natural populations that may affect their risk of extinction or endangerment (see "Assessment of Extinction Risk," p. 135). In contrast to most other types of risk for salmon populations, those arising from artificial propagation are often not reflected in traditional indices of population abundance. For example, to the extent that habitat degradation, overharvest, or hydropower development have contributed to a population's decline, these factors will already, for the most part, be reflected in population abundance data and accounted for in the risk analysis. The same is not true of artificial propagation. Hatchery production may mask declines in natural populations that will be missed if only raw population abundance data are considered. Therefore, a true assessment of the viability of natural populations cannot be attained without information about the contribution of naturally spawning hatchery fish. Furthermore, even if such data are available, they will not in themselves provide direct information about possibly deleterious effects of fish culture. Such an evaluation requires consideration of the genetic and demographic risks of artificial propagation for natural populations. The sections on artificial propagation in this report are intended to address these concerns.

Finally, if any natural populations are listed under the ESA, then it will be necessary to determine the ESA status of all associated hatchery populations. This latter determination would be made following a proposed listing and is not considered further in this document.

The "Extinction Risk" Question

The ESA (Section 3) defines the term "endangered species" as "any species which is in danger of extinction throughout all or a significant portion of its range." The term "threatened species" is defined as "any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range." NMFS considered a variety of information in evaluating the level of risk faced by an ESU. Important considerations included: 1) absolute numbers of fish and their spatial and temporal distribution; 2) current abundance in relation to historical abundance and carrying capacity of the habitat; 3) trends in abundance, based on indices such as dam or redd counts or on estimates of recruit-to-spawner ratios; 4) natural and human-influenced factors that cause variability in survival and abundance; 5) possible threats to genetic integrity (e.g., selective fisheries and interactions between hatchery and natural fish); and 6) recent events (e.g., a drought or a change in management) that have predictable short-term consequences for abundance of the ESU. Additional risk factors, such as disease prevalence or changes in life-history traits, may also be considered in evaluating risk to populations.

According to the ESA, the determination of whether a species is threatened or endangered should be made on the basis of the best scientific information available regarding its current status, after taking into consideration conservation measures that are either proposed or currently in place. In this review, we do not evaluate likely or possible effects of conservation measures. Therefore, we do not make recommendations as to whether identified ESUs should be listed as threatened or endangered species because that determination requires evaluation of factors we did not consider. Rather, we have drawn scientific conclusions about the risk of extinction faced by identified ESUs under the assumption that present conditions will continue (recognizing, of course, that natural demographic and environmental variability is an inherent feature of "present conditions"). Conservation measures will be taken into account by NMFS Northwest and Southwest Regional Offices in making listing recommendations.

Summary of Coastal Cutthroat Trout Petition

On December 5, 1997, NMFS received a petition to list what petitioners called sea-run cutthroat trout *(O. c. clarki)* along the coasts of California, Oregon, and Washington under the ESA. The petitioners were the ONRC, Coast Range Association, Native Fish Society, Northwest Ecosystem Alliance, Save the West, Siskiyou Regional Education Project, Siskiyou Audubon, Trout Unlimited of California, Western Ancient Forest Campaign, Salmon Defense Association, Salmon Forever, California Sportfishing Alliance, Oregon Wildlife Federation, Clark-Skamania Fly Fishermen, and the Washington Rivers Council. A summary of their petition follows.

The biological information in the ONRC et al. (1997) petition consists of two short sections that summarize an extensive 38-page status review of *O. c. clarki* written by a private fisheries consultant, Patrick C. Trotter. From data presented in Trotter's status review, the petitioners concluded that coastal cutthroat trout abundance was reduced from historic levels across the subspecies range, especially in the Willamette River and the Lower Columbia River on both the Oregon and Washington sides. They believe that available data show that abundance of "wild" populations is "dangerously low" in these two rivers.

The petitions asserted that available data indicate natural coastal cutthroat trout populations along the California and Oregon coasts are at "seriously low levels" and "in danger of becoming threatened or endangered." Exceptions to this scenario are populations in the Smith and Winchuck rivers on the California-Oregon border, which the petitioners asserted are "more robust than any of those around them."

The petitioners also concluded that the only "healthy populations" of *O. c. clarki* along the West Coast are north of the Snohomish River in Puget Sound, Washington.

Terminology

Coastal cutthroat trout are the least studied of the seven *Oncorhynchus* species native to the Pacific Northwest. Both sport and scientific literature often do not differentiate coastal cutthroat trout from other species of salmonids (especially steelhead, the sea-run form of *O. mykiss*) and simply categorize them as "trout" or "other fish." Another difficulty is that these sources of information often refer to coastal cutthroat trout with a variety of confusing local names, including "harvest" (perhaps most common historically), "blueback," "salmon," "steelhead cutthroat," and "sea" trout (Schultz 1936, Roth 1937, Clemens and Wilby 1946). In fresh water, the subspecies has often been simply identified as "trout," but also as "native," "mountain," "speckled," or "brook" trout (Behnke 1972, 1992).

Because *O. clarki* is a polytypic species (Allendorf and Leary 1988; see also the "Life History" section, p. 38) with different life-history forms that are often difficult or impossible to distinguish, even the recent biological literature can be confusing. Several life-history forms have been identified (see Trotter 1989) (Fig. 1), with a variety of regional names. For example, coastal cutthroat trout observed in rivers have been identified as "resident," "fluvial," "adfluvial-fluvial," "river-migrating," and "potamodromous" (Trotter 1989, 1991). However, "resident" and "fluvial" have also been used to refer only to trout that inhabit upper headwater tributaries and are considered "nonmigrants." "Potamodromous" has been used to mean all freshwater forms (Northcote 1997b) or any of those migrating within river (Tomason 1978). Also, although all life-history forms of the subspecies *O. c. clarki* may possess the ability to go to sea and could be considered anadromous, "sea-run cutthroat trout" usually refers only to fish in the subspecies that regularly enter seawater. Coastal cutthroat trout also migrate from sea water to fresh water not only to spawn but also for winter refuge and perhaps to feed. For this subspecies, "amphidromous" (Stearley 1992, Williams et al. 1997a) is more scientifically correct than "anadromous." However, "anadromous" has broad general acceptance in the scientific community, and we will use it in this document to describe coastal cutthroat trout migrating between fresh water and sea water.

This document uses a simplified and consistent terminology for the subspecies and its life-history forms (Fig. 1). The entire subspecies (all life-history forms) will be referred to as coastal cutthroat trout (or simply cutthroat trout). Fish that migrate to sea water (estuary or open ocean) will be termed *sea run* or *anadromous*. Fish that do not enter sea water are *freshwater forms,* which may be *migrants* within river systems (riverine) or lake systems (lacustrine), or *nonmigrants* moving only short distances within headwater tributaries. We have avoided the

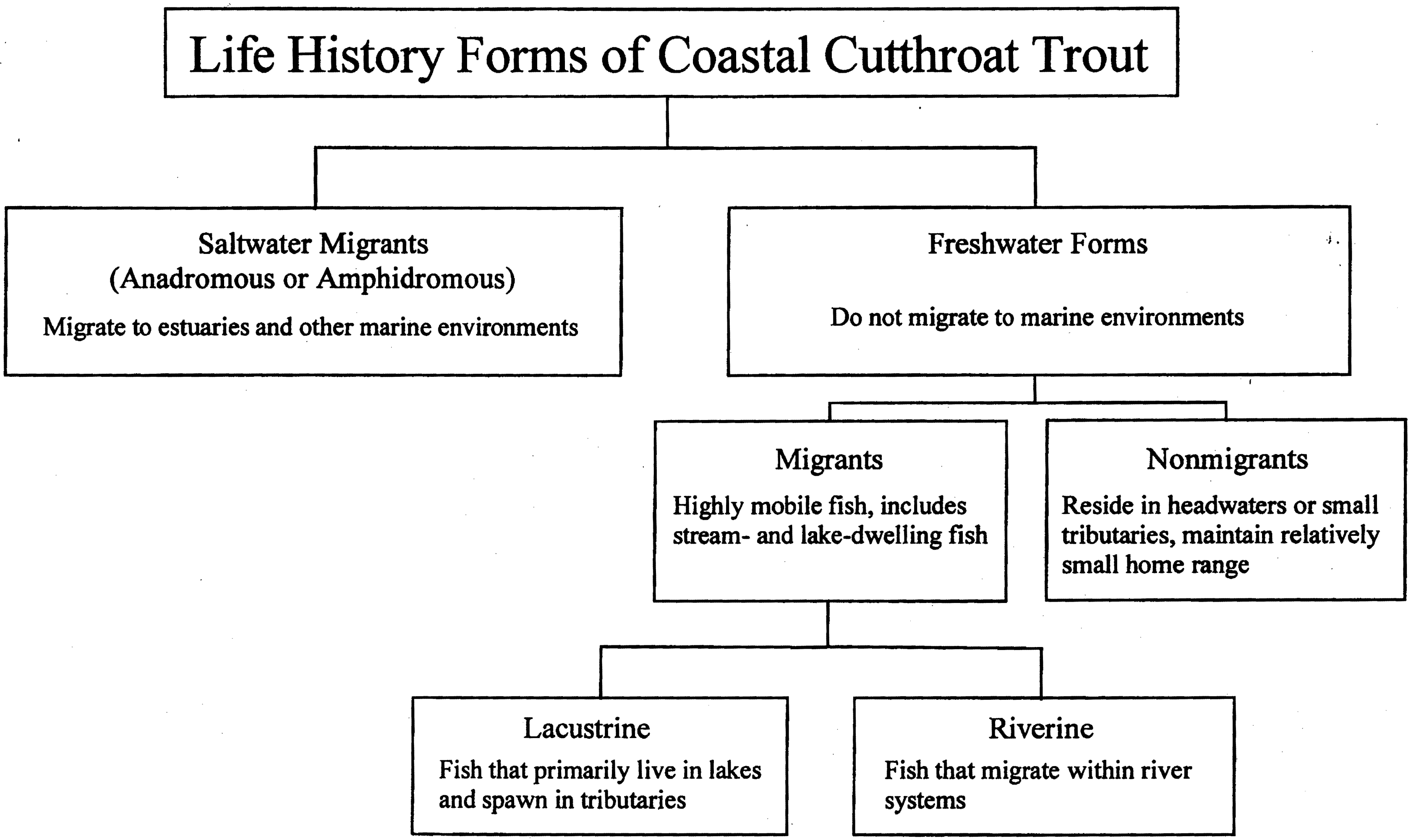

Figure 1. Terminology of coastal cutthroat trout life-history forms used in this document and a description of their general habitats and behaviors (adapted from Garrett 1998).

terms "resident," "fluvial," and "potamodromous" due to their ambiguity. Our terminology is only a general guide as fish from any life-history form may, under the right set of circumstances, become any other form. (See the "Life History " section, p. 38, for a detailed description of these life-history forms).

Another source of confusion from the literature arises from the use of the terms “wild fish” and “natural fish.” In a number of management contexts, it is useful to distinguish fish returning to a river based on their origin (e.g., offspring of parents from the local stream, from a different stream, or from a hatchery) and whether they spawn naturally in available habitat or in a hatchery. Different state and tribal entities have very different definitions for these terms (WDF et al. 1993, Kostow 1995), so, to avoid confusion, this document uses a simplified and consistent terminology for the origin and spawning location of coastal cutthroat trout. We use *natural* to describe those fish produced by parents spawning in a river or lake rather than in a controlled environment (such as a hatchery). Natural fish may include what are sometimes called *wild* fish; *wild* in that usage usually refers to fish native to a stream and naturally spawning with little or no hatchery ancestry. However, because local and regional interpretations of *wild* fish vary, we avoid using the term in this status review. (See “Assessment of Extinction Risk,” p. 135, for discussion of natural fish in the context of risk evaluations).

General Biology

Coastal cutthroat trout are found in the coastal plains of western North America from southeastern Alaska to northern California (Trotter 1989) (Fig. 2). They belong to the same genus as Pacific salmon and steelhead, but are generally smaller, rarely overwinter in the sea, and do not usually make extensive oceanic migrations. Unlike Pacific salmon, coastal cutthroat trout are iteroparous rather than semelparous, and adults have been known to spawn each year for more than 6 years (Trotter 1989).

Various phylogenies or evolutionary histories of coastal cutthroat trout have been proposed (e.g., Stearley and Smith 1993, Behnke 1992, 1997). Based upon fossil records, Stearley (1992) and Stearley and Smith (1993) suggested that trout diverged from a common salmonid ancestor somewhere in eastern Asia, probably more than 6 million years ago. Behnke (1992, 1997) suggested cutthroat and rainbow trout were native to western North America and diverged from a common "trout" ancestor somewhere in what is now the Snake/Columbia River Basin (Fig. 3) at the beginning of the Pleistocene Era, approximately 2 million years ago. Behnke (1997) argued that in the middle of the Pleistocene Era, approximately 1 million years ago, the cutthroat trout group diverged again into a coastal group (presently *O. c. clarki*) with a characteristic 68- or 70-chromosome karyotype set and an interior group (presently the westslope cutthroat trout group, *O. c. lewisi*) with a characteristic 66-chromosome set. The coastal group has essentially remained intact, colonizing coastal rivers from northern California to Prince William Sound in Alaska. The interior group evidently diverged again into a third component with a 64-chromosome set. This group contained two isolated groups: the Lahontan cutthroat

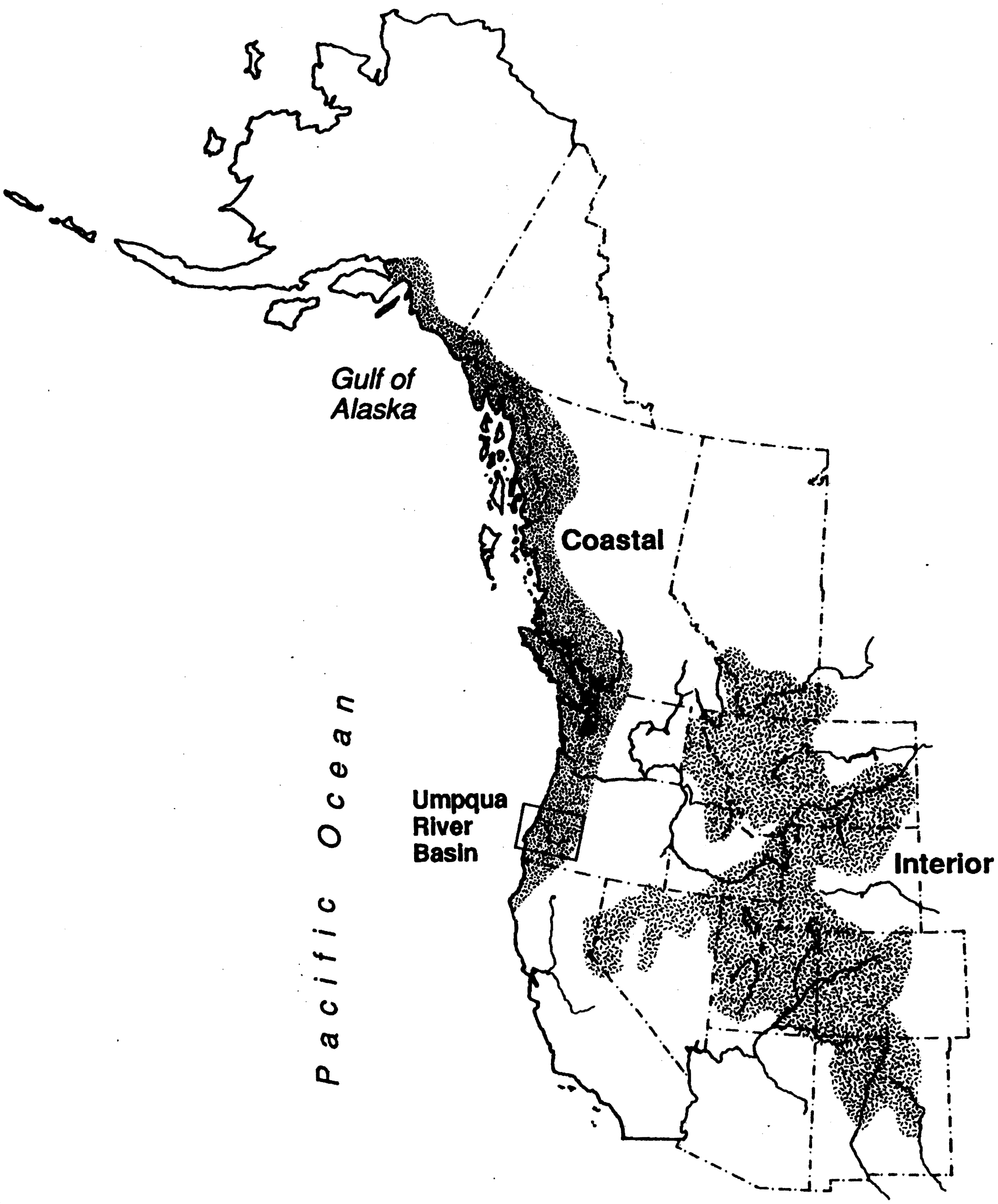

Figure 2. Range of coastal cutthroat trout (*Oncorhynchus clarki clarki*) (shading on coast) and of 13 interior subspecies (*O. c.* subspp.) (shading inland). Framed area represents Umpqua River Basin.

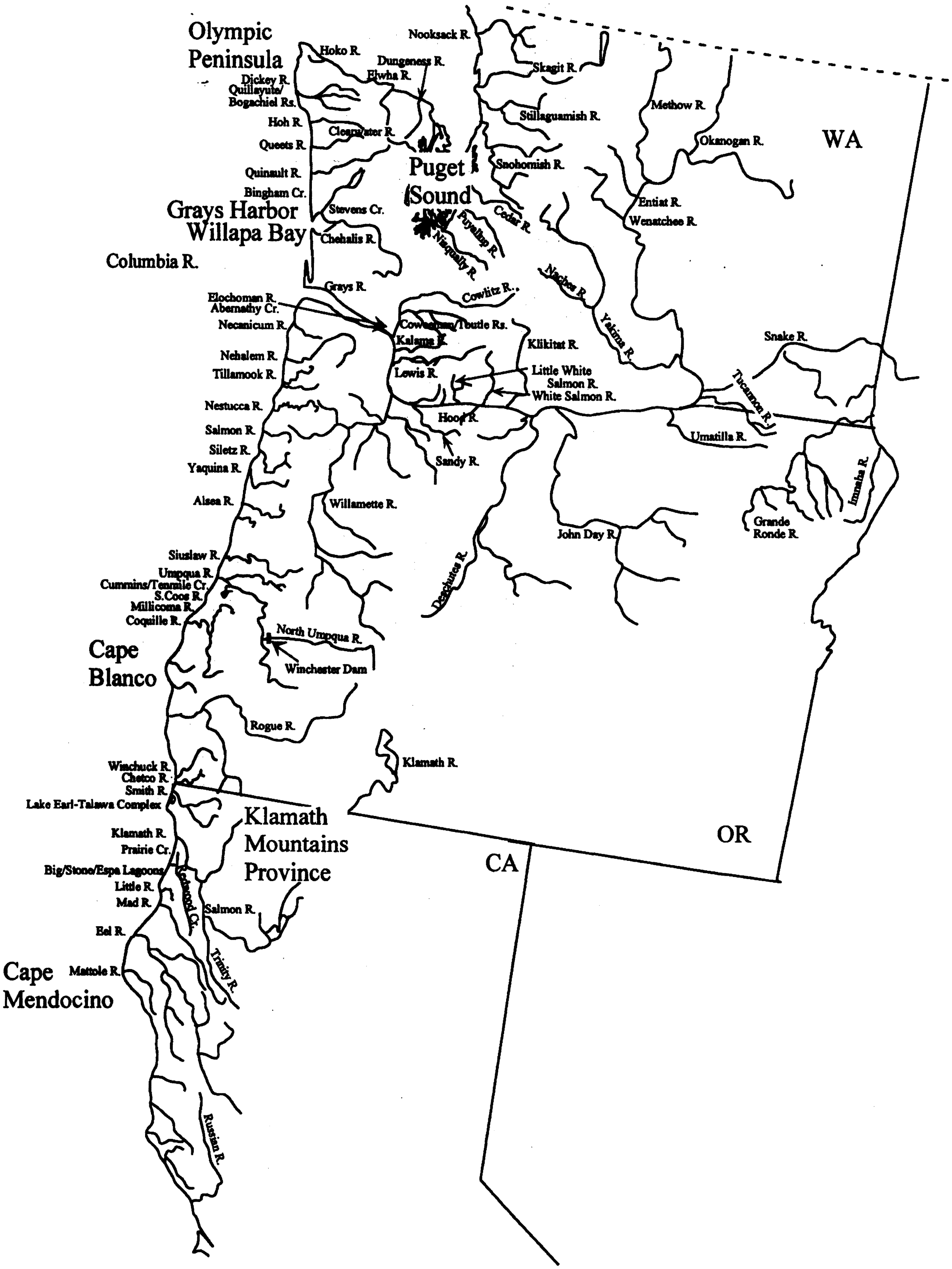

Figure 3. Map showing major rivers and other key geographic features discussed in this document.

trout in the Lahontan Basin of the western Rocky Mountain range (*O. c. henshawi*), and the Yellowstone cutthroat trout in the Snake River Basin (*O. c. bouvieri*).

Based upon this evolutionary scenario, Behnke (1992, 1997) proposed 14 extant subspecies of *O. clarki* grouped into what he describes as four "major" subspecies (coastal, westslope, Lahontan, and Yellowstone cutthroat trout). These subspecies have a genetic divergence time of more than 500,000 years, while what Behnke calls the 10 "minor" subspecies were recently derived from the Lahontan or Yellowstone ancestors (Behnke 1992, 1997). The coastal subspecies occurs in the coastal rainforests of North America and east to the Cascade crest. The interior subspecies have not successfully penetrated the coastal mountains and generally remain in the northern river basins of the western Rocky Mountains.

The coastal subspecies differs from other cutthroat trout in a variety of ways. For one, *O. c. clarki* has a karyotype (2n) of 68 (Gold et al. 1977) or 70 (Simon 1963, 1964, Simon and Dollar 1964) that is unique among cutthroat trout subspecies (Simon and Dollar 1964, Gold et al. 1977, Loudenslager and Thorgaard 1979, Thorgaard 1983, Behnke 1992), as well as several unique alleles detected by protein electrophoresis (Leary et al. 1987, Allendorf and Leary 1988). Phenotypically, coastal cutthroat trout differ from all other trout by their profusion of small- to medium-sized spots of irregular shape (Behnke 1992). In addition, they do not develop the coloration associated with interior cutthroat trout. Further, while at sea and during seaward migrations, this coloration and spotting are obscured by the silvery skin color common to anadromous salmonids. At maturity, freshwater life-history forms of coastal cutthroat trout tend to be darker, with a "coppery or brassy" sheen (Behnke 1992).

The life history of coastal cutthroat trout may be the most diverse of any Pacific salmonid (Northcote 1997a; also see "Life History" section, p. 38). Their populations show a bewildering diversity in size and age at migration, timing of migrations, age at maturity, and frequency of repeat spawning. Part of this diversity reflects the way individual fish can move between feeding, refuge, and spawning areas. Even populations where the vast majority of fish are anadromous may have members that do not migrate to sea every year. In other populations, some coastal cutthroat trout simply remain in headwater tributaries, while others may migrate within rivers or lakes and return to headwater tributaries only to spawn. Some lake forms remain in the lakes for their entire life cycle, spawning in shallow inlets or outlets (e.g., Crescent Lake, Washington) (reviewed in Trotter 1989, 1997; Behnke 1992, 1997; Northcote 1997a).

Historically, interior and coastal cutthroat trout subspecies represented one of the most broadly distributed salmonid species in western North America (Behnke 1979, 1992). Interior cutthroat trout were often the only salmonid present (sometimes the only fish) in many lakes and streams throughout the interior American west, and they were far more broadly distributed than steelhead, rainbow trout, or other salmonids (Behnke 1979, 1992). In recent years these interior subspecies have been precipitously replaced by rainbow trout or other introduced species in many parts of their range (Gresswell 1988, Young 1995). Perhaps most destructive was the widespread release of hatchery rainbow trout (*O. mykiss*) throughout the native range of interior cutthroat trout (Gresswell 1988, Young 1995). The two species readily hybridize, often to the extreme detriment of *O. clarki*, and it has been estimated that "just within the last century perhaps 99 percent of the unique cutthroat strains of interior drainages have been lost forever" (Willers 1991, p. 10). Behnke (1988, p. 1) estimated that "in less than 100 years after the first [United States] settlements in the West, the cutthroat trout vanished from most of its vast range." This hybridization with rainbow trout, habitat degradation, and other factors have caused many of these interior subspecies to decline in numbers to the extent that they are now protected by state and federal endangered species legislation (Table 1) (Johnson 1987).

Some authors have suggested that coastal cutthroat trout are the healthiest subspecies of cutthroat trout because they have experienced the least amount of habitat destruction, hybridization with introduced species, or overfishing (reviewed in Pauley et al. 1989, Trotter 1989, Trotter et al. 1993). Still, the Endangered Species Committee of the American Fisheries Society (AFS) identified all populations of anadromous coastal cutthroat trout as being at some risk of extinction and coastal cutthroat trout from all Oregon streams as being at moderate risk of extinction (Nehlsen et al. 1991[2]). NMFS has listed coastal cutthroat trout in the Umpqua River basin as an endangered species under the ESA (Johnson et al. 1994, Fed. Register Notice 50 CFR Part 222).

The incongruity of being considered the "healthiest" cutthroat trout subspecies while being identified by the AFS as having a moderate risk of extinction across its range reflects in part a lack of information on the status of the fish. There has never been a coastwide effort to collect the type of information about coastal cutthroat trout traditionally collected on commercially important species of Pacific salmon and routinely used by management agencies to manage stocks. Consequently, data on the subspecies are generally collected incidentally, during studies targeting other salmonids (e.g., smolt traps for coho salmon [Garrett 1998] or dam counts [Loomis et al. 1993]) and to provide information most pertinent to the recreational angler (e.g., creel counts, presence/absence, feeding habitats).

The lack of information about coastal cutthroat trout in the Umpqua River was noted in 1946 by the Oregon State Fish Commission (FCO and OSGC 1946, p. 25) in a comment that is still apt for much of the subspecies range:

> Very little is yet known about these fish and they have been rightly called the "problem children" of the State Game Commission . . .

Ironically, the Umpqua River Basin is one of the few areas across the range of *O. c. clarki* where long-term counts of migrating coastal cutthroat trout *have* been made. For example, Pacific salmonids have been counted since 1946 (the same year as the commission report) at Winchester Dam on the North Umpqua River near Roseburg, Oregon (Table 2, Fig. 4). These counts revealed two dramatic declines in coastal cutthroat trout passage, in the late 1950s and the late 1970s (Fig. 5). In fact, more coastal cutthroat trout were counted passing Winchester Dam in 1946 (1,138) than from 1977-93 combined (fewer than 1,049 in total) (Loomis et al. 1993).

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[2] The authors of Nehlsen et al. (1991) were members of the AFS Endangered Species Committee and the paper "states the opinions of the Committee and does not necessarily reflect AFS policy" (p. 4).

Table 1. Subspecies of cutthroat trout and their federal and state protection status (Johnson 1987, Allendorf and Leary 1988). The eight major subspecies are endemic to large geographical areas (Behnke 1979). Subspecies of Special Concern are according to The Natural Heritage Network (1998). CO = Colorado, ID = Idaho, MT = Montana, NM = New Mexico, NV = Nevada, US = United States, UT = Utah, and WY = Wyoming.

Common name	Subspecies	Legal protection	Special concern
Major subspecies			
Bonneville	*Oncorhynchus clarki utah*	UT	US, ID, NV, WY
Coastal	*O. c. clarki*	US (Umpqua R.)	OR
Colorado	*O. c. pleuriticus*	UT	US, CO, WY
Greenback	*O. c. stomias*	US, CO	
Lahontan	*O. c. henshawi*	US, OR, UT	
Rio Grande	*O. c. virginalis*	NM	CO
Westslope	*O. c. lewisi*		US, ID, MT
Yellowstone	*O. c. bouvieri*		US, ID, MT
Minor subspecies			
Alvord	*O. c. alvordensis*	extinct	
Bear Lake	*O. c. subsp.*		ID
Humboldt	*O. c. subsp.*	--	--
Mountain	*O. c. alpestris*	--	--
Paiute	*O. c. seleniris*	US	
Snake River	*O. c. subsp.*		ID
Willow/Whitehorse	*O. c. subsp.*		US
Yellowfin	*O. c. macdonaldi*	extinct	

Table 2. Numbers of returning adult coastal cutthroat trout passing Winchester Dam on the North Umpqua River, Oregon from 1946 to 1998 (a counting year at Winchester Dam begins in March) and releases of Alsea River hatchery cutthroat trout immediately below Winchester Dam from 1961 to 1976, in Smith River from 1975 to 1993, and in Scholfield Creek from 1982 to 1993 (Loomis et al. 1993, D. Loomis[3], ODFW 1998, StreamNet 1998). For locations, see Figure 4.

Year	Number of smolts released below Winchester Dam	Number of smolts released in Smith River	Number of smolts released in Scholfield Creek	Number of returning adults
1946	-	-	-	1,138
1947	-	-	-	974
1948	-	-	-	437
1949	-	-	-	439
1950	-	-	-	664
1951	-	-	-	1,508
1952	-	-	-	761
1953	-	-	-	1,838
1954	-	-	-	706
1955	-	-	-	960
1956	-	-	-	982
1957	-	-	-	87
1958	-	-	-	108
1959	-	-	-	48
1960	-	-	-	106
1961	5,000	-	-	306
1962	10,000	-	-	308
1963	10,000	-	-	142
1964	10,000	-	-	420
1965	20,000	-	-	796
1966	20,000	-	-	2,364
1967	20,000	-	-	2,200
1968	20,000	-	-	1,031
1969	20,000	-	-	942
1970	19,000	-	-	1,880
1971	20,000	-	-	289
1972	19,000	-	-	1,094
1973	20,000	-	-	1,712
1974	20,000	-	-	622
1975	17,000	9,900	-	427
1976	9,000	7,500	-	544
1977	-	10,000	-	123
1978	-	15,100	-	104
1979	-	11,100	-	25
1980	-	12,700	-	74
1981	-	20,100	-	86

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[3] D. Loomis, District Biologist, Oregon Department of Fish and Wildlife, Roseburg District Office, 4192 North Umpqua Highway, Roseburg, OR 97470. Pers. commun. to O. Johnson. April 1998.

Table 2. (Continued).

Year	Number of smolts released below Winchester Dam	Number of smolts released in Smith River	Number of smolts released in Scholfield Creek	Number of returning adults
1982	-	19,100	2,600	156
1983	-	9,100	2,700	43
1984	-	15,800	4,500	104
1985	-	15,800	4,500	88
1986	-	1,200	4,000	53
1987	-	8,100	8,000	35
1988	-	11,900	4,000	47
1989	-	12,000	4,000	38
1990	-	12,000	4,000	34
1991	-	12,000	4,000	10
1992	-	12,000	4,000	0
1993	-	12,000	4,000	29
1994	-	-	-	1
1995	-	-	-	79
1996	-	-	-	81
1997	-	-	-	91
1998	-	-	-	135 (by 11/15)

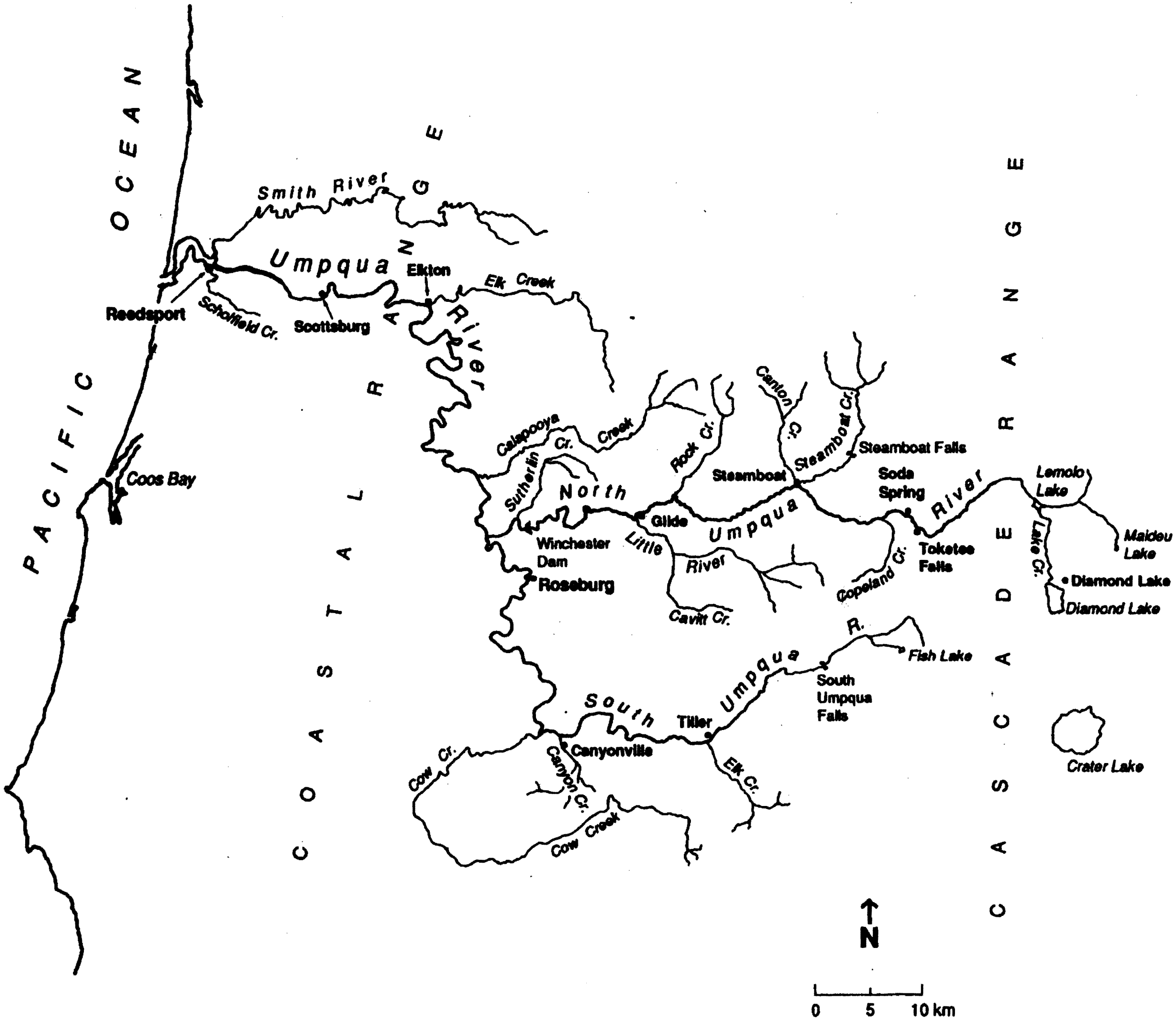

Figure 4. Map of the Umpqua River Basin on the Oregon coast (see also Figure 2).

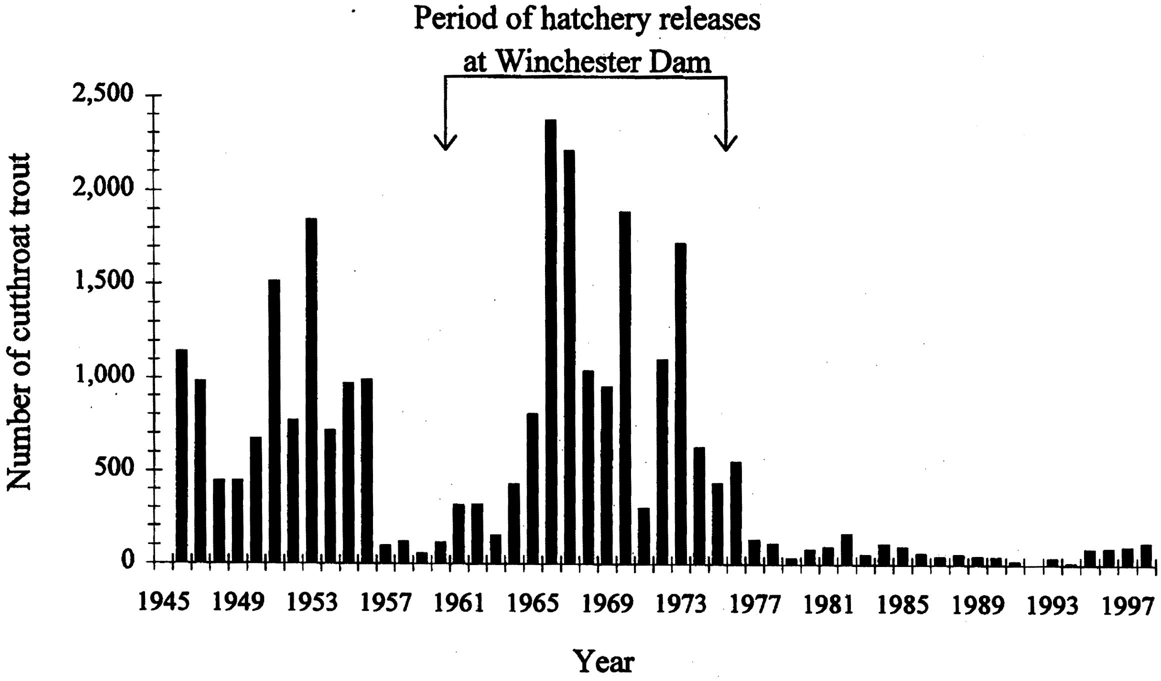

Figure 5. Yearly counts of adult coastal cutthroat trout passing Winchester Dam on the North Umpqua River, 1946-98 (ODFW 1998, StreamNet 1998). Alsea River hatchery cutthroat trout were released into the North Umpqua River Basin immediately below Winchester Dam, 1961-76.

However, it has been suggested (Cramer 1998, Loomis footnote 3) that fish in some of the earlier counts may not have been coastal cutthroat trout, but were instead misidentified hatchery rainbow trout or even coho salmon jacks (Bauer 1998). In the mid-1990s, few to no coastal cutthroat trout were counted passing Winchester Dam, but more recent data suggests a relative resurgence, with more than 80 fish per year counted in 1996 and 1997 (Loomis footnote 3). In 1998, 135 fish were counted by November 15 passing Winchester Dam for the highest count since 1982. On most days only a single coastal cutthroat trout was counted passing the dam, but 43 coastal cutthroat trout passed the dam over 2 days (30 on 28 July, 13 on 29 July). These two days also coincided with the warmest water temperatures of the year (24.5°C) up to that time.

Geographic Distribution

The distribution of coastal cutthroat trout is broader than that of any other cutthroat trout subspecies. It extends along the Pacific coast of North America from the Eel River in northern California (DeWitt 1954) to the Prince William Sound area of Alaska, extending to Gore Point on the Kenai Peninsula (Scott and Crossman 1973, Behnke 1992). The eastern range of the subspecies rarely extends farther inland than 160 km and usually is less than 100 km. The eastern range appears to be bounded by the Cascade Mountain Range in California, Oregon, and Washington, and by the Coast Range in British Columbia and southeastern Alaska (Fig. 2). This range coincides closely with the coastal temperate rain forest belt defined by Waring and Franklin (1979). The subspecies appears highly adapted to this region; even when the fish have access beyond the coastal rainforest, as in the Columbia or Stikine rivers, they penetrate only a limited distance inland (Sumner 1972; Trotter 1987, 1989).

The distribution of coastal cutthroat trout on the Pacific coast is reviewed in Hall et al. (1997) by the following authors: for California by Gerstung (1997), for Oregon by Hooton (1997), for Washington by Leider (1997), for British Columbia by Slaney et al. (1997), and for Alaska by Schmidt (1997). As reported by Gerstung (1997), California coastal cutthroat trout have been observed in 182 named streams (approximately 71% of the 252 named streams within their range in California) and an additional 45 streams (17% of the named streams) likely support populations. Reproducing populations occur throughout most of the Humboldt Bay tributaries, the Smith and Little river basins, the lower portions of Redwood Creek and the Klamath, Mad, and Eel rivers, and numerous small named and unnamed coastal tributaries (Gerstung 1997). They also occur in five coastal lagoons and ponds—Big, Stone, and Espa lagoons, and the Lake Earl-Talawa complex—with about 1875 ha of occupied habitat (Gerstung 1997). Gerstung (1997) also reported that in California almost 46% of coastal cutthroat trout occupied habitats in the Smith and Klamath river drainages. Historically, coastal cutthroat trout have been distributed farther south along the northern California coastline down through the Russian River in Sonoma County. There are still anecdotal reports of coastal cutthroat trout in several streams from the Mattole River down to the Garcia River (Gerstung 1997); however, there are currently no known self-sustaining populations south of the Mattole River or Cape Mendocino. Recently, snorkel surveys of entire stream drainages throughout the state have been initiated to provide more complete information on the subspecies distribution in California.

In Washington and Oregon, coastal cutthroat trout are widespread west of the crest of the Cascade Mountains. Historically, the range of anadromous *O. c. clarki* may have extended past the Cascade Crest into tributaries of the Columbia River, as far eastward as the Klickitat River at River Kilometer (Rkm) 290 (Bryant 1949). At present, freshwater forms (migrants and nonmigrants) of *O. c. clarki* are found at least to the Klickitat River on the Washington side of the Columbia River (WDFW 1998a), and to 15-Mile Creek on the Oregon side (K. Kostow[4]). Leider (1997) indicated that current distribution of sea-run fish appears to be confined to tributaries downstream from Bonneville Dam (Rkm 235). At present the Washington Department of Fish and Wildlife (WDFW) has identified 46 "stock complexes" in Washington (WDFW 1998a).

In Oregon, two interior subspecies of *O. clarki* are also present: the Lahontan cutthroat trout in southeastern Oregon, and the westslope cutthroat trout in the John Day River basin of northeastern Oregon (Hooton 1997). Both of these interior subspecies live east of the Cascades and neither has an anadromous component (Hooton 1997). In Washington, westslope cutthroat trout reportedly occur naturally in the Lake Chelan drainage (Behnke 1988) and perhaps throughout isolated headwater streams in the upper Columbia River basin (Behnke 1992). A variety of interior subspecies have also been planted in numerous streams and lakes throughout the Pacific Northwest.

The apparent lack of coastal cutthroat trout in Asia is puzzling. It seems unlikely that a fish that thrives in nearshore coastal waters did not successfully invade Asia when the Beringia land bridge was present during the ice ages. A potential solution to this mystery was uncovered in 1994 when several specimens of a "new" trout were caught in the Tigil River of western Kamchatka (in Eastern Russia, off the Bering Sea). These fish had the distinguishing physical characteristics that separate a cutthroat from a rainbow trout (e.g., basibranchial teeth and nine pelvic fin rays) (Savvaitova et al. 1995, Behnke 1996). However, analysis of the mitochondrial DNA in 12 of these presumptive coastal cutthroat trout from the Tigil River, using a set of markers developed at the NWFSC in Seattle, indicate that these fish are *O. mykiss,* not *O. clarki* (J. Baker[5]).

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[4] K. Kostow, ODFW, Fish Division, 2501 SW First Ave., PO Box 59, Portland, OR 97207. Pers. commun. to O. Johnson. Oct. 1998.

[5] J. Baker, University of Washington School of Fisheries, Marine Molecular Biotechnology Laboratory, 3707 Brooklyn Ave. NE, Seattle, WA 98195. Pers. commun. to O. Johnson. May 1998.

INFORMATION RELATING TO THE SPECIES QUESTION

This section summarizes environmental and biological information relevant to determining the nature and extent of coastal cutthroat trout ESUs in the Pacific Northwest. The focus of this document is on populations in the contiguous United States; however, information from Alaska and British Columbia was also considered to provide a broader context for interpreting results. Furthermore, ESU boundaries are based on biological and environmental information and do not necessarily conform to state or national boundaries.

Environmental Information

Environmental information was used to indicate possible ESU boundaries. We identified areas where the physical environment appeared to change based on environmental characteristics (i.e., river flow patterns, ocean conditions, water temperatures, climate, etc.), and on the distributions of other organisms. Areas with different habitat types may have different selective pressures that may lead to local adaptations within specific areas. The distributions of organisms sympatric with coastal cutthroat trout were considered because the distributions may reflect environmental, ecological, or historical processes that also affect these trout.

Geological and Climatic Events

The climatic events of the last 20,000 years have provided opportunities for isolation, colonization, and population interbreeding. In determining ESU boundaries, it is useful to understand the factors that may have shaped present-day coastal cutthroat trout population distributions. Much of the present distribution of aquatic and terrestrial species in western North America is a legacy of the volcanic, tectonic, and glacial forces that shaped this region. Events such as headwater transfer or stream capture altered the flow of major rivers and the aquatic species that inhabit them.

The Cordilleran ice sheet was the last major glacial event to affect the distribution of coastal cutthroat trout and other salmonids in the Pacific Northwest. At its height (10-15,000 years ago), the ice sheet covered vast areas of Alaska, British Columbia, Washington, and Idaho (McPhail and Lindsey 1970), creating a discontinuous distribution of salmonid populations. Two major ice-free refugia existed: Beringia, composed of the Bering land bridge connecting Eastern Siberia and Western Alaska, and Cascadia, composed of the lands south of the mid-Columbia River drainage (McPhail and Lindsey 1970). An additional ice-free refuge existed on the coast of the Olympic Peninsula in the area of the Chehalis River. The drop in sea level during the glacial periods may have created minor refugia along the coast of Vancouver Island or the present-day Queen Charlotte Islands. As the ice sheet receded, salmonids from the Cascadia and Beringia refugia began to colonize the newly exposed freshwater habitat (McPhail and Lindsey 1986).

Coastal cutthroat trout conduct extensive freshwater migrations, which may have allowed them to quickly colonize the headwaters of new streams emerging from retreating glaciers (c. 10,000 years ago). This colonization may have occurred in a number of ways. Coastal cutthroat trout may have entered newly opened rivers on overwintering or feeding migrations. Ice dams and land expansion after the retreat of glacial ice sheets caused rivers to alter course and change watersheds. Spawning adults may have strayed into these new habitats by chance or because their natal streams were inaccessible. As an example, during the last deglaciation, parts of the Fraser River drainage flowed into the Columbia River via the Okanogan River and Shuswap Creek (McPhail and Lindsey 1986). Further, several southeastern Alaskan and northern British Columbia rivers (e.g., the Stikine, Skeena, and Nass) that now flow westerly into the Gulf of Alaska drained, at various times, easterly into the Fraser River Basin (McPhail and Lindsey 1986). These watershed exchanges may have allowed a mixture of species among the Columbia River, Fraser River, coastal Washington and Puget Sound, and southeastern Alaskan coastal rivers.

Ecoregions

The fidelity with which anadromous salmonids, including coastal cutthroat trout, return to their natal stream implies a close association between a specific population and its freshwater environment. The selective pressures of different freshwater environments may be responsible for differences in life-history strategies among populations. As an example, Miller and Brannon (1982) hypothesized that local temperature regimes are the major factors influencing variables such as time of emergence, food availability, growth, and other life-history traits. Gresswell et al. (1994) suggested that local adaptations in interior cutthroat trout may occur at a river basin or stream tributary scale. Boundaries of distinct freshwater habitats coinciding with differences in life histories would suggest a degree of local adaptation. Therefore, identifying distinct freshwater, terrestrial, and climatic regions may help identify coastal cutthroat trout ESUs.

The ecoregions used in the document are a compilation of relevant information; ecoregions for the contiguous United States retain designations assigned by the Environmental Protection Agency (EPA) to its ecoregion system (Omernik 1987). The EPA system of ecoregion designations is based on soil content, topography, climate, potential vegetation, and land use. These ecoregions are similar to the physiographic provinces determined by the Pacific Northwest River Basins Commission (PNRBC 1969) for the Pacific Northwest. Historically, the distribution of coastal cutthroat trout in Washington, Oregon, and California included six of the present-day EPA ecoregions (Fig. 6). Hughes et al. (1987) noted a strong relationship between ecoregions and freshwater fish assemblages.

The ecoregions for the contiguous United States include physiographic information presented by PNRBC (1969), present-day water use information (USGS 1993), river flow information (Hydrosphere Products, Inc. 1993), and climate data from the U.S. Department of Commerce (1968) into the appropriate ecoregion description (Omernik and Gallant 1986,

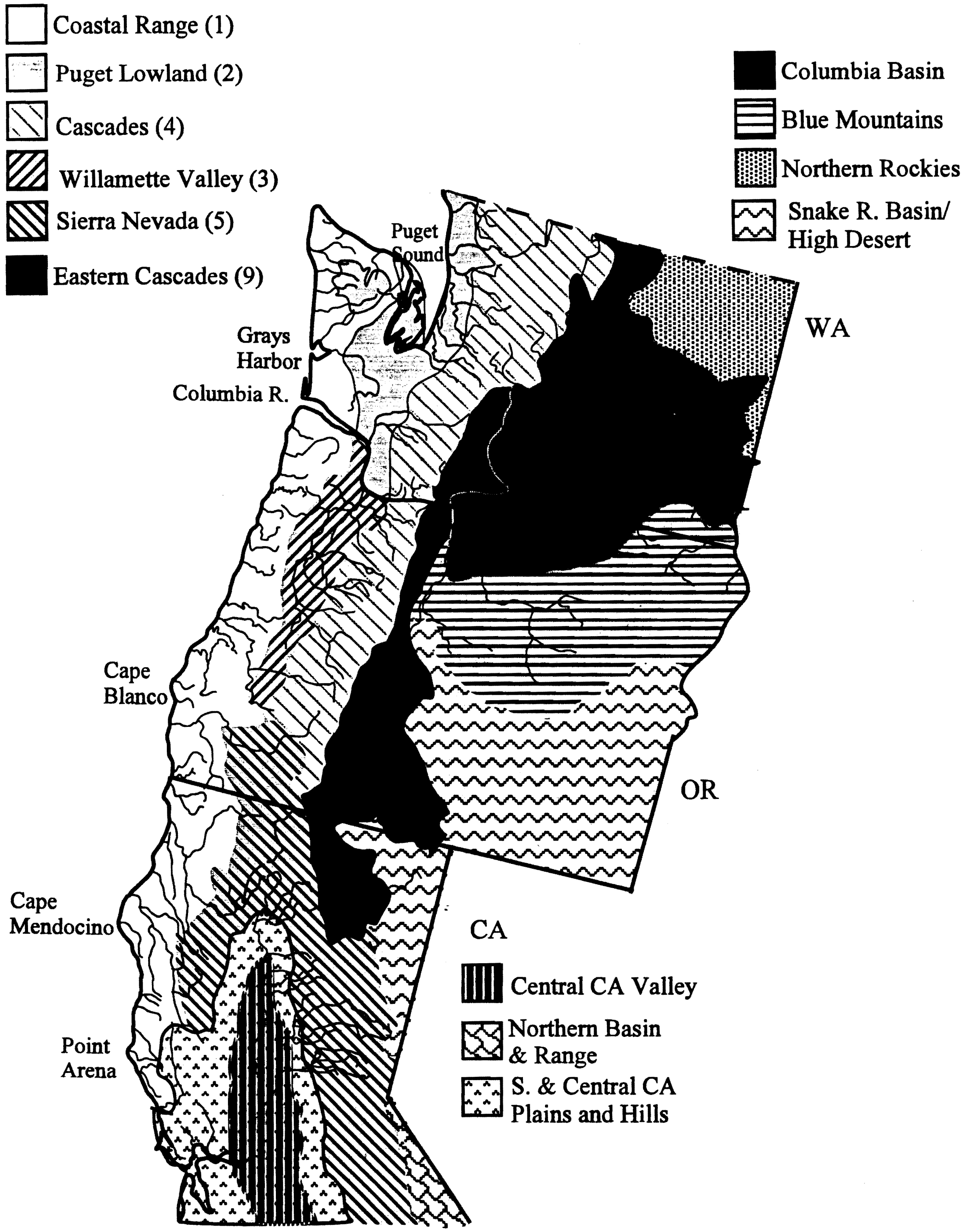

Figure 6. U.S. Environmental Protection Agency ecoregions for California, Oregon, and Washington (Omernik and Gallant 1986, Omernik 1987). Regions are based on land use, climate, topography, potential natural vegetation, and soils. Ecoregions with number designations are described in the text.

Omernik 1987). Additional information for British Columbia (Environment Canada 1977, 1991) and Alaska (ADFG 1978, Alaska Geographic Society 1978) is included for comparative purposes. The ecoregions we use are wholly or partially within the historical natural range of coastal cutthroat trout in Washington, Oregon, and California.

Ecoregion descriptions follows. As noted earlier, names and associated numbers reflect the EPA system (Omernik 1987).

Coast Range Ecoregion (#1)

Extending from the Olympic Peninsula through the Coast Range and south to the Klamath Mountains and San Francisco Bay, the Coast Range ecoregion is influenced by medium to high rainfall levels due to adiabatic cooling as marine weather systems intercept mountains of the region. Topographically, the region averages 500 m in elevation, with mountains less than 1,200 m high. These mountains are generally rugged with steep canyons. Between the ocean and mountains lies a narrow coastal plain composed of sand, silt, and gravel. Tributary streams are short and have a steep gradient; therefore, surface runoff is rapid and water storage is relatively short term during periods of no recharge. These rivers are especially prone to low flows during times of drought. Regional rainfall averages 200-240 cm per year (up to 380 cm in the Olympic Mountains) (Fig. 7), with generally lower levels along the southern Oregon coast and northern California. Average annual river flows for most rivers in this region are among the highest found on the West Coast when adjusted for watershed area (Fig. 8). River flows peak during winter rain storms common in December and January (Fig. 9). Snow melt adds to the surface runoff in the spring, providing a second peak in flows, and there are long periods when the river flows maintain at least 50% of peak flow (Fig. 10). There is usually very little precipitation in July or August, a dry period that may expand to 3 months every few years. River flows are correspondingly at their lowest (Fig. 11) and temperatures at their highest during August and September (Fig. 12).

This region is heavily forested, primarily with Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), Douglas fir (*Pseudotsuga menziesii*) and western red-cedar (*Thuja plicata*). Forest undergrowth is composed of numerous types of shrubs and herbaceous plants.

Primary land use in this region has been timber harvesting and agricultural development. Splash dams were common features on many coastal streams throughout Washington and Oregon at the turn of the century. Extensive stream cleaning and channelization occurred in many coastal rivers to facilitate log drives (Sedell and Luchessa 1982), and the legacy of these activities continues to influence conditions in many coastal streams today (Reeves et al. 1997).

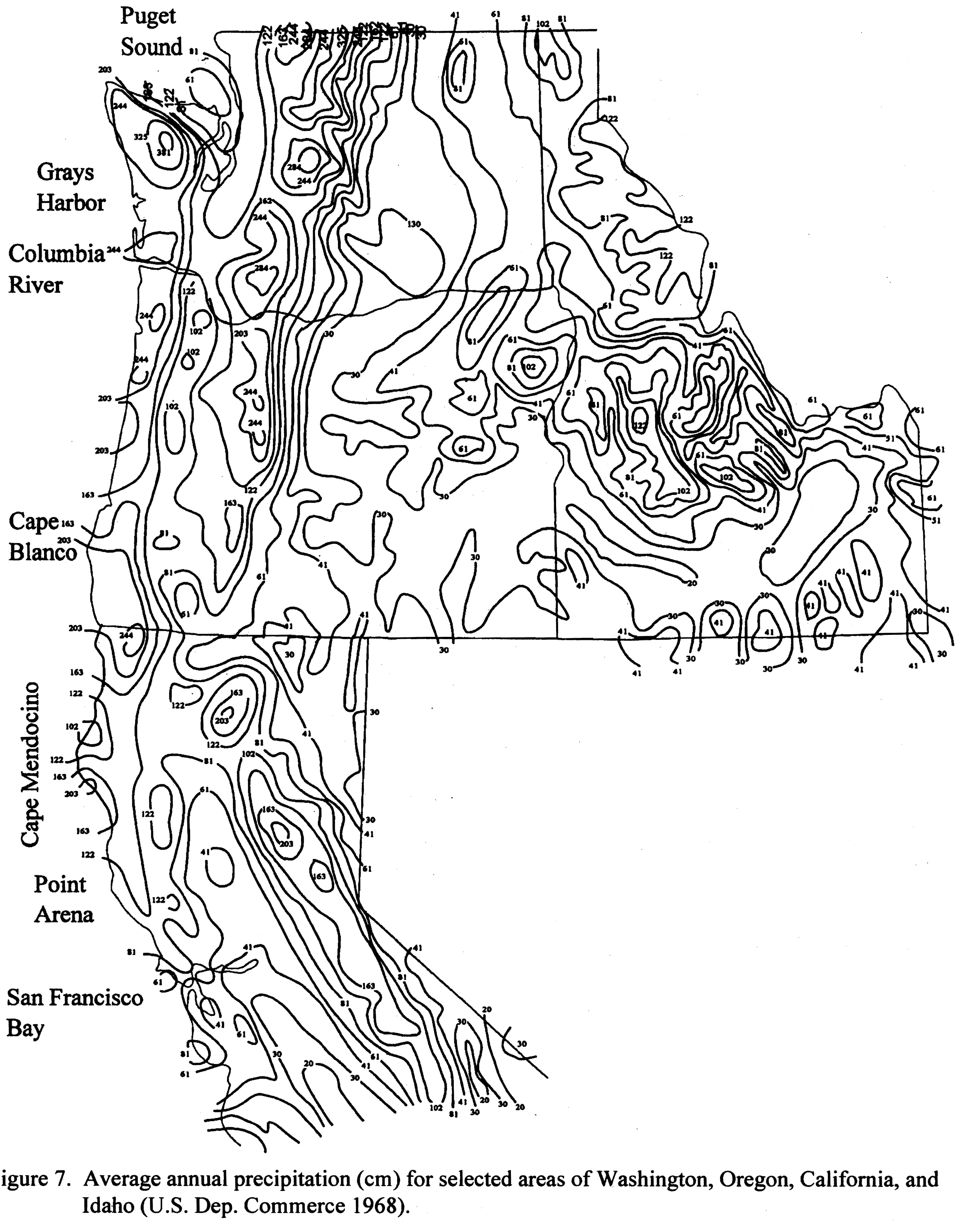

Figure 7. Average annual precipitation (cm) for selected areas of Washington, Oregon, California, and Idaho (U.S. Dep. Commerce 1968).

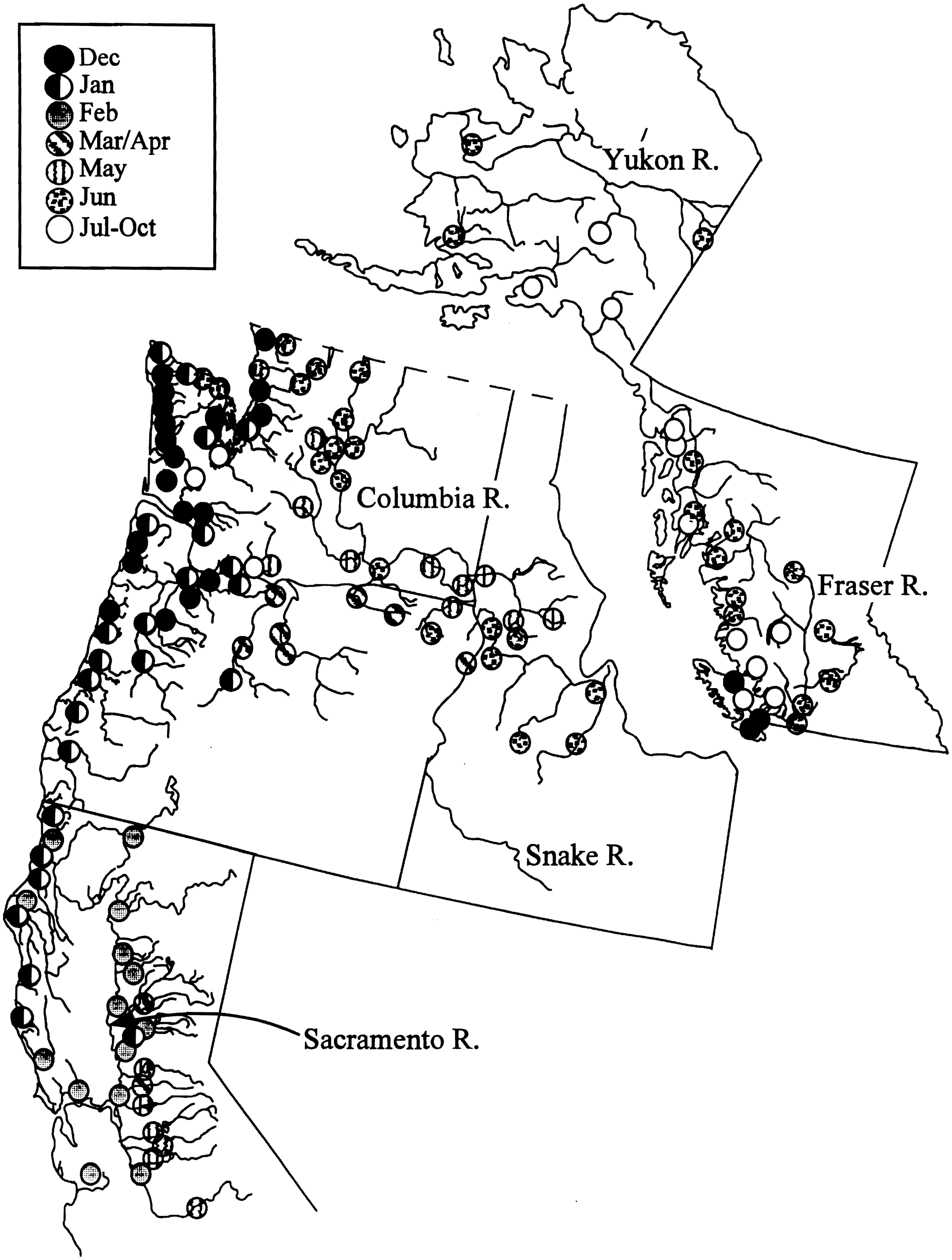

Figure 8. Timing of annual peak flow (by month) for selected river basins in Alaska, British Colombia, Washington, Oregon, California, and Idaho. If two peaks in flow occur, the higher of the two peaks is represented. Based on United States Geological Survey (USGS) streamflow data (Hydrosphere Data Products, Inc. 1993) and Inland Water Directorate streamflow data (Environment Canada 1991) (modified from Weitkamp et al. 1995).

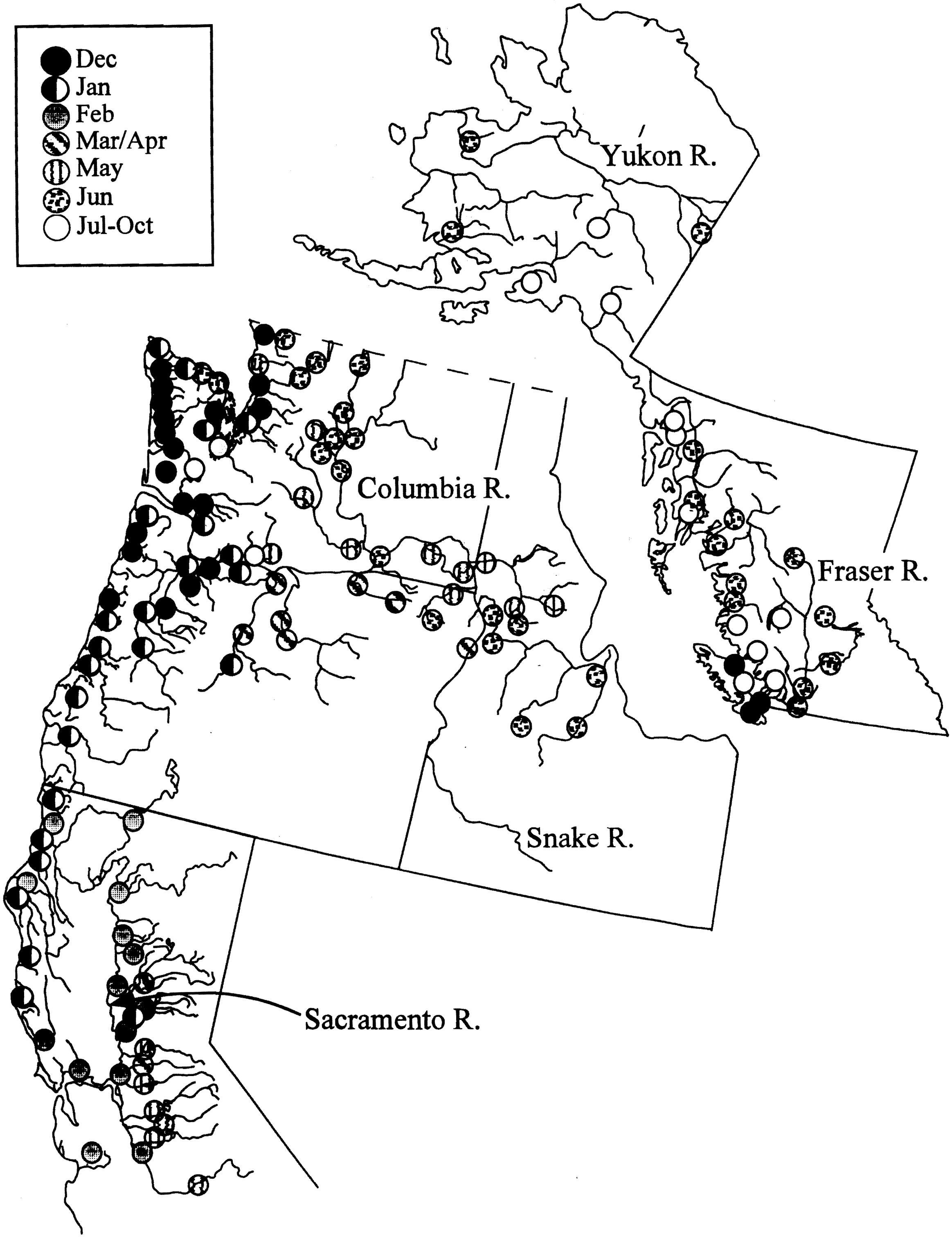

Figure 9. Timing of annual peak flow (by month) for selected river basins in Alaska, British Colombia, Washington, Oregon, California, and Idaho. If two peaks in flow occur, the higher of the two peaks is represented. Based on United States Geological Survey (USGS) streamflow data (Hydrosphere Data Products, Inc. 1993) and Inland Water Directorate streamflow data (Environment Canada 1991) (modified from Weitkamp et al. 1995).

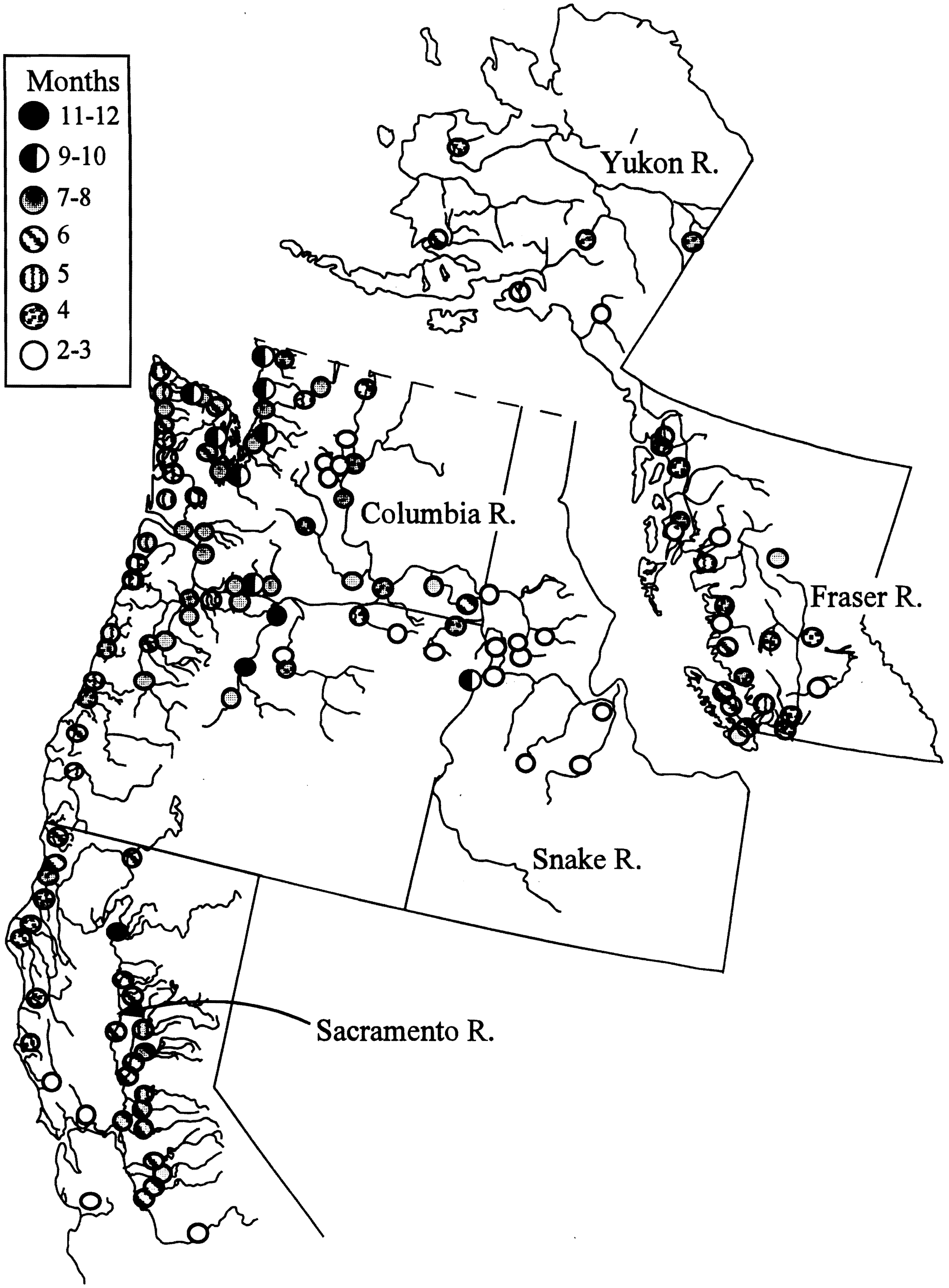

Figure 10. Duration of high flows (number of months when flow is equal to of exceeds 50% of peak monthly flow) for selected river basins in Alaska, British Columbia, Washington, Oregon, California, and Idaho. Based on United States Geological Survey (USGS) streamflow data (Hydrosphere Data Products, Inc. 1993) and Inland Water Directorate streamflow data (Environment Canada 1991) (modified from Weitkamp et al. 1995).

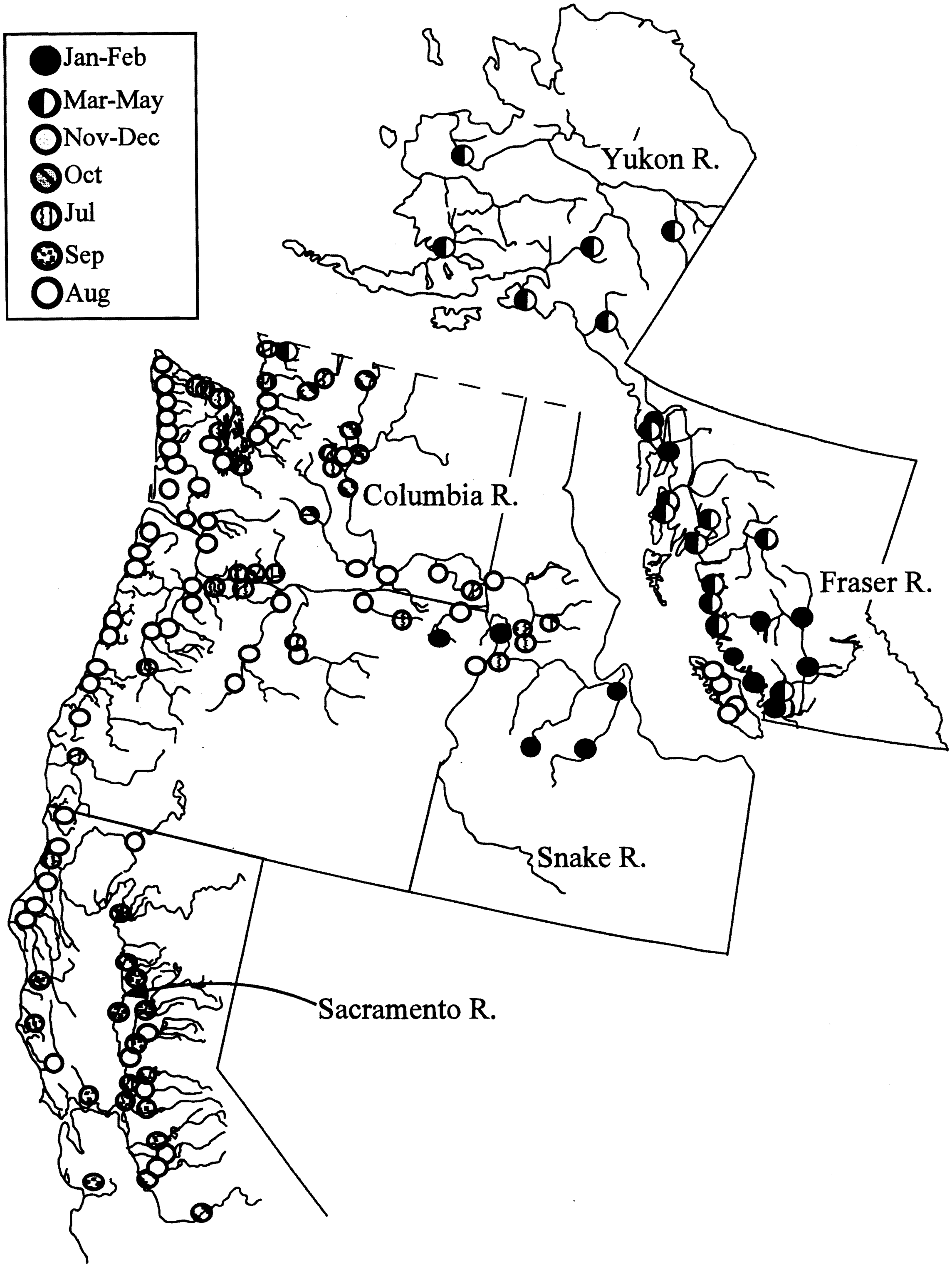

Figure 11. Timing of annual low flow (by month) for selected river basins in Alaska, British Columbia, Washington, Oregon, California, and Idaho. If two peaks in flow occur, the higher of the two peaks is represented. Based on United States Geological Survey (USGS) streamflow data (Hydrosphere Data Products, Inc. 1993) and Inland Water Directorate streamflow data (Environment Canada 1991) (modified from Weitkamp et al. 1995).

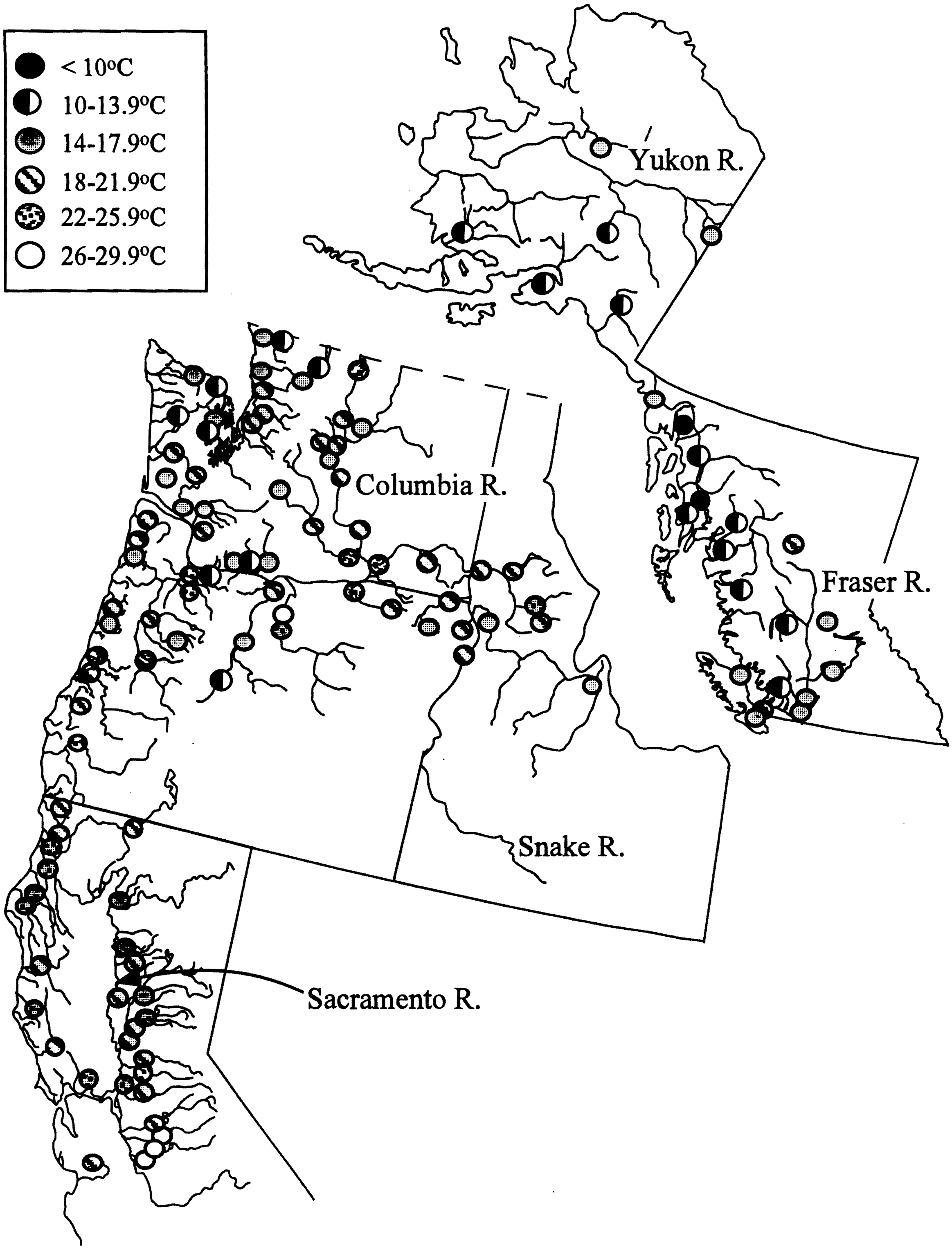

Figure 12. Annual maximum monthly stream temperatures (^{O}C) for selected rivers in Alaska, British Columbia, Washington, Oregon, California, and Idaho. Based on United States Geological Survey (USGS) streamflow data (Hydrosphere Data Products, Inc. 1993) and Inland Water Directorate streamflow data (Environment Canada 1991) (modified from Weitkamp et al. 1995).

Puget Lowland Ecoregion (#2)

Situated between the Coast Range and Cascade Range ecoregions, this region experiences reduced rainfalls (50-120 cm) from the rain-shadow effect of the Coast Mountains. The area is generally flat, with high hills (600 m) at the southern margin of the ecoregion. Soils are alluvial and lacustrine deposits. These deposits are glacial in origin north of Centralia, Washington. This area tends to have large groundwater resources, with groundwater from the bordering mountain ranges helping to sustain river flows during drought periods. Peak river flow varies from December to June, depending on the decadal climate cycle and the contribution of snowpack to surface runoff for each river system. Rivers tend to have sustained flows (5 to 8 months of flows at 50% of the peak or more), and low flows are generally 10-20% or more of the peak flows.

Douglas fir is the primary subclimax forest tree species, with other coniferous species such as lodgepole (*Pinus contorta*), western white (*P. monticola*), and ponderosa pine (*P. ponderosa*) locally abundant. Prairie, swamp, and oak, birch, and alder woodlands are also common. The land is heavily forested, and wood-cutting activities (such as building roads and splash dams) contribute to soil erosion, river siltation, and river flow and temperature alteration.

Because the Puget lowland surrounds one of North America's largest protected bays with access to marine shipping, it has been become heavily urbanized, especially along the western slopes of the Cascade Mountains and the shore of Puget Sound (major cities surrounding Puget Sound include Everett, Seattle, Tacoma, Olympia, and Bremerton). Domestic and industrial wastes, urban runoff, and sewage treatment degrade the quality of local water systems. Exceptions are river systems draining into the Hood Canal region and northern Puget Sound. However, even here, extensive diking, agricultural use, logging operations, housing developments, and other changes have altered the physical geography and flows of river systems (Brody 1991, Ashbaugh 1994). Glacial sediment also influences water quality, especially in the Skagit, North Fork Nooksack, Nisqually, and Puyallup/White river basins.

Willamette Valley Ecoregion (#3)

The Willamette Valley, which adjoins the southern border of the Puget Lowland ecoregion at the Lewis River, was not glacially influenced. A rainshadow effect, similar to the one influencing the Puget Lowland ecoregion, limits rainfall to about 120 cm per year. River flows peak in December and January and are sustained for 6-7 months of the year. Low flows occur in August and September, although the volume is generally 20% of the peak flow.

Much of the land has been converted to agricultural use, with Douglas fir and Garry oak (also known as Oregon white oak [Randall et al. 1990]) (*Quercus garryana*) stands in less-developed areas. Irrigation is common, and stream flows, especially in the southern portion of this ecoregion, can be significantly reduced as a result. Agricultural and livestock practices contribute to soil erosion and fertilizer/manure deposition into stream systems.

As in the Puget Lowland ecoregion, water quality in the Willamette Valley is degraded by agricultural, timber, and urban activities, especially near at the mouth of the Willamette River and along parts of the Lower Columbia River (e.g., Portland, Oregon, and Longview, Washington). Many water quality problems are exacerbated by low water flows and high temperatures during the summer. Pulp and paper mill discharges of dioxin into the Columbia and Willamette rivers are considered another water quality concern, although this situation has improved (USGS 1993).

Cascades Ecoregion (#4)

The Cascades ecoregion is composed of the Cascade Range in Washington and Oregon and contains the headwater tributaries of many coastal cutthroat bearing rivers, including the Skagit, Stillaguamish, Willamette, Umpqua, and Rogue. Mountain peaks above 3,000 m are distributed throughout the region. The crest of the Cascade Range (averaging 1,500 m) captures much of the ocean moisture moving eastward and poses a biological barrier to many terrestrial and aquatic animals. Precipitation can average 280 cm per year, much of it in the form of heavy snowfall. Intense rainstorms (those depositing more than 2.5 cm per hour) are rare. Rainfall is generally spread over the year, with most of it between October and March. There is little capacity for long-term groundwater storage except where porous rock substrate exists. In these porous areas, streams receive 75-95% of their average discharge as groundwater and are able to maintain flows during dry periods. Surface water flow originating in the Cascade Range influences river flows throughout this region.

The area is primarily forested with Douglas, noble (*Abies procera*), and Pacific silver fir (*A. amabilis*) (all subclimax species), whereas western hemlock and western red-cedar are common climax species. At higher elevations, these trees are replaced by Engelmann spruce (*Picea engelmannii*), whitebark pine (*P. albicaulis*), grand fir (*A. grandis*), and mountain hemlock (*Tsuga mertensiana*). Forest undergrowth tends to be dense on the western slopes of this region and sparse on the eastern slopes. A combination of heavy rainfall and wood-cutting activities has increased soil erosion.

Sierra Nevada Ecoregion (#5)

South of the Cascades Ecoregion is a similar ecoregion comprised of portions of the Klamath, Sierra, Trinity, and Siskiyou mountains. The Sierra Nevada ecoregion includes the present-day southern extent of coastal cutthroat trout (at the Eel River in California). Annual rainfall varies considerably, from 40 cm to more than 150 cm, depending on elevation and the degree of rainshadowing. Most of the rain falls in winter, with summers being hot and dry. Topographically, the region rises to over 2,000 m, with an average elevation of 1,000 m.

This ecoregion contains the headwaters for the Rogue, Klamath, and Sacramento rivers. Historically, peak flows occurred in February, with lowest flows in August, September, or October; however, water diversion and impoundment activities changed this pattern and flows are now more evenly distributed throughout the year. This change occurred primarily through irrigation/flood-mitigation-related reductions in peak flows and less so through increased spillage during the historical time of minimum flows.

Douglas fir is the predominant tree species, but mixed coniferous/oak stands are common. Soils tend to be unstable, and timber harvest or livestock grazing can result in severe erosion. Hydraulic placer mining has had a considerable impact on stream quality and hillslope stability.

Eastern Cascades Slopes and Foothills Ecoregion (#9)

Anadromous coastal cutthroat trout are believed to have historically inhabited this ecoregion at least as far east as the Klickitat River (Bryant 1949), but only freshwater forms are now believed to be present (Leider 1997). This ecoregion marks the transition between the high rainfall areas of the Cascades Ecoregion and the drier basin ecoregions to the east. The area receives 30-60 cm of rainfall per year. Streamflow is intermittent, especially during the summer dry season. Surface and groundwater contributes to flows in the Yakima, Deschutes, Klickitat, and White Salmon rivers.

Ponderosa and lodgepole pine are common throughout the region, with little forest undergrowth. Soils tend to be volcanic, young, and highly prone to erosion. Primary land uses are timber harvest and mixed grazing/timber areas. Agriculture is limited to valleys and irrigation is commonly employed.

Coastal British Columbia

The maritime climate of the Olympic Peninsula continues north along the west coast of Vancouver Island and along the British Columbia mainland north of Vancouver Island. The Fraser River, which drains into the Strait of Georgia at Vancouver, dominates about one-fourth of the province of British Columbia and is the largest single river producer of Pacific salmon in the world (Northcote and Atagi 1996).

Limited hydrographic data (Farley 1979) indicate that river flow patterns in coastal British Columbia are similar to those on the Olympic Peninsula, with relatively high flows throughout the year. There is a general decrease in summer air temperatures to the north—the Olympic Peninsula coast is generally a few degrees warmer than the southwest coast of Vancouver Island, which is a few degrees warmer than the northwest coast and the mainland north of Vancouver Island. Annual rainfall and snowfall average 111 cm and 55 cm respectively in Vancouver and 240 cm and 140 cm respectively in Prince Rupert (Environment Canada 1996).

Anadromous cutthroat trout are found in at least 756 streams throughout the region, but information was available for only 120 populations in a recent assessment of population status (Slaney et al. 1997). More than half of the 120 populations were determined to be at some level of risk, and several populations within the lower Fraser River and Georgia Strait were considered extinct. Habitat degradation attributed to urban development was reported as posing the greatest threat to coastal cutthroat trout populations (Slaney et al. 1997).

Southeastern and southcentral Alaska

A maritime climate dominates the southeastern coast of the Alaska panhandle and continues north along the coast to the southcentral region of Prince William Sound. This area marks the northern extent of the distribution of coastal cutthroat trout. Average annual rainfall and snowfall for Annette Island in southeastern Alaska are 260 cm and 130 cm, respectively, while Cordova in southcentral Alaska receives an average of 240 cm of rainfall and 300 cm of snowfall per year (CDC 1961-98).

The crest of the Coast Range in southeastern Alaska forms the Alaska-Yukon-British Columbia boundary (ADFG 1978). This coastal area is characterized by numerous islands, bays, and short steep stream channels. The southcentral region includes the drainages that enter the Gulf of Alaska and is dominated by the Copper River basin. The estuary of the Copper River, numerous islands, and hundreds of small coastal streams create thousands of miles of habitat in Prince William Sound for rearing salmonids, including coastal cutthroat trout (ADFG 1978).

Western hemlock and Sitka spruce dominate the forests, with some western red-cedar, Alaska-cedar (*Chamaecyparis nootkatensis*), and red alder (*Alnus rubra*) scattered throughout the region. Natural resources have long dominated the economy including forest products, mining, fishing, tourism and recreation (Alaska Geographic Society 1978).

Biogeography

Vegetation

Forest communities have specific requirements, which means that dominant vegetation types are a valuable indicator of relative precipitation, temperature, soil type, solar radiation, and altitude. Changes in vegetation types indicate changes in the physical environment, which may affect freshwater coastal cutthroat trout habitat. The following discussion of vegetation was compiled from Viereck and Little (1972), Franklin and Dyrness (1973), Barbour and Major (1977), Farley (1979), and Whitney (1985).

Sitka spruce zone

Coastal regions in Oregon, Washington, and British Columbia are forested with a Sitka spruce-dominated floral community, which includes western hemlock, western red-cedar, red alder, and Douglas fir as major species. This vegetation type is restricted to coastal regions and river valleys; only over coastal plains does it extend more than a few kilometers inland, even then exceeding elevations of 150 m only in areas immediately adjacent to the ocean. This vegetation type is typified by a uniformly wet and mild climate. Sitka spruce forests could be considered a variant of western hemlock forests of higher elevations and inland areas, but are distinguished by frequent summer fogs, higher moss concentrations, lichen abundance, and proximity to the ocean (Franklin and Dyrness 1973).

Along the coast, Sitka spruce forests grade into redwood forests in southern Oregon and northern California, and into western hemlock-dominated forests along the Strait of Juan de Fuca to the north. Sitka spruce forests also extend up the Columbia River to approximately the Clatskanie River (RKm 80), beyond which point the vegetation increasingly reflects the drier climate east of the Coast Range.

Redwood zone

Beginning in the Chetco River basin in southern Oregon (Fig. 3), Sitka spruce and western hemlock are replaced by redwood forests slightly inland and in river bottoms along the coast. This forest type forms the dominant coastal vegetation south to Monterey at elevations between 30 and 800 m. From the redwood zone along the coast, vegetation on the moist western slopes changes to Douglas fir/hardwood forests at lower elevations, followed by Shasta red (*A. magnifica shastensis*) and white fir (*A. concolor*), and finally mountain hemlock at higher elevations. Vegetation in the upper basins of the Rogue and northern California rivers is adapted to a more arid climate than those closer to the coast, and consequently is distinct from upper-basin vegetation types either north or south. These vegetation types include areas with Garry oak, mixed evergreen, and Klamath montane, coastal montane, and oak/pine forests and chaparral. South of the Mattole River, upper basins are not as arid and the vegetation is more like the coastal type: primarily redwoods with patches of mixed evergreens and mixed hardwoods, and coastal prairie-scrub around the San Francisco Bay area.

Western hemlock zone

Along the Washington and Oregon coasts, the western hemlock-dominated plant community replaces Sitka spruce at elevations above 150 m. In the Puget Sound/Strait of Georgia area, the western hemlock community forms the dominant vegetation from sea level to 700-1,000 m. This vegetation type includes western hemlock, Douglas fir, red alder, and western red-cedar as major species. The transition point between Sitka spruce and western hemlock along the Strait of Juan de Fuca appears to be approximately the Elwha River on the U.S. side and Sooke Inlet on the Canadian side. South of the Columbia River, the western hemlock zone extends southward along the Coast Range to the Klamath Mountains and southward along the Cascade Mountains to the Umpqua River (Fig. 3). Forests in the Puget Sound area are often considered a special type of western hemlock community: the area's lower precipitation and glacial soils make drought-stress-tolerant western white, lodgepole, and occasionally ponderosa pine major species, whereas they are considered minor species elsewhere in the western hemlock zone.

Alpine and subalpine zones

The headwaters of rivers draining higher mountains, such as the Olympic and Cascade mountains and the British Columbia and Oregon Coast ranges, begin in alpine meadows and subalpine parklands before the change to western hemlock-dominated forests below 700 to 1,000 m. The higher alpine regions are typified by a mosaic of meadows and tree patches with extensive and deep snow cover. The subalpine zone is dominated by mountain hemlock and subalpine fir, has less extensive snow cover than higher alpine areas, and is wetter and colder than areas at lower elevations.

Analyses of vegetation types

In his factor analysis of western U.S. floras based on the distribution of more than 9,000 plant species, McLaughlin (1989) defined three floristic areas within the range of coastal cutthroat trout: the Vancouverian, Sierra Nevada, and California areas. The Vancouverian area includes the Sitka spruce zone described above, the western hemlock zone (excluding the central and southern Oregon Cascade Mountains), and the redwood zone from its northern boundary to approximately Cape Mendocino. The California floristic area includes the redwood zone south of Cape Mendocino and lower elevation portions of the Sacramento/San Joaquin Valley, while the Sierra Nevada area covers the central and south Oregon Cascade Mountains, the interior Klamath Mountain Province, and the Sierra Nevada Mountains. In a similar analysis based solely on Pacific coast beach vegetation, Breckon and Barbour (1974) identified a "temperate" eco-floristic zone from lat. 54° N to lat. 36°30' N. This zone is subdivided into a northern North Coastal Zone and a southern Mediterranean Zone with the boundary at lat. 43°30' N (approximately the Coos River, about 70 km north of Cape Blanco).

Zoogeography

Like vegetation types, the distribution patterns of marine and freshwater species indicate variations in the physical environment these species share with coastal cutthroat trout. These variations in the physical environment may affect coastal cutthroat trout habitat and put different selective pressures on coastal cutthroat trout in different zoogeographical areas.

Marine fishes

There are two distinct faunal boundaries for marine fishes within the range considered in this status review: Point Conception in California (lat. 34°30' N) and the northern tip of Vancouver Island (approximately lat. 50° N) (Allen and Smith 1988). Marine fishes north of Vancouver Island are primarily coldwater subarctic species, those between lat. 50° N and lat. 34°30' N primarily temperate species, and those south of Point Conception primarily subtropical. Although not a distinct faunal boundary, Cape Mendocino represents a southern limit beyond which many northern species do not routinely occur (Horn and Allen 1978).

Marine invertebrates

The distribution of marine invertebrates shows transition points between major faunal communities similar to those for marine fishes (Hall 1964, Valentine 1966, Hayden and Dolan 1976, Brusca and Wallerstein 1979). Invertebrate faunal boundaries along the west coast of North America occur at approximately Dixon Entrance (directly west of Prince Rupert), the Strait of Juan de Fuca, and Point Conception, with a minor boundaries at Cape Mendocino and Monterey Bay (Hall 1964, Valentine 1966). The primary cause of this zonation is attributed to temperature (Hayden and Dolan 1976), but other abiotic (Valentine 1966) and biotic (Brusca and Wallerstein 1979) factors may also influence invertebrate distribution patterns.

Freshwater fishes

Freshwater fishes in southern and central British Columbia, Washington, and most of coastal Oregon are populations of Columbia River origin (McPhail and Lindsey 1986, Minckley et al. 1986). Variation in the makeup of freshwater fish communities in these areas reflects the varied dispersal patterns of fishes between river basins. The Stikine River in northern British Columbia is the point at which freshwater fishes from the north displace the Columbia River fish fauna (McPhail and Lindsay 1986). The Sixes River in southern Oregon marks the southern extent of the Columbia River freshwater fish fauna (Snyder 1907, Minckley et al. 1986). Freshwater fishes in the Klamath-Rogue Ichthyofaunal Region, which includes the Klamath and Rogue rivers, differ from the Columbia River-dominated assemblages to the north and the Sacramento/San Joaquin River-dominated faunas to the south (Snyder 1907, Moyle 1976, Minckley et al. 1986). Freshwater fishes in northern and central California between Redwood Creek and Carmel River are derived from the Sacramento-San Joaquin River system. However, many of the smaller basins have no exclusively freshwater fishes, but only species that move readily through salt water (Moyle 1976).

Estuarine fishes

Estuarine fishes also show regional differences based on presence or absence of species and can be roughly divided into five groups within Washington, Oregon, and northern and central California (Monaco et al. 1992). Two large groups with considerable overlap extend from Willapa Bay in Washington to the Eel River in California. The differences between these two groups appear related to the size of the estuaries. In Washington, two groups have been identified: one overlaps to some extent with the two large groups and encompasses Grays Harbor, Willapa Bay, and the Columbia River estuary; a second group is restricted to Puget Sound and Hood Canal. Differences between these two groups also appear to be related to the size of the estuaries. A final group extends from Tomales Bay to Morro Bay in California.

Amphibians

Many amphibian species have very restricted distributions and may serve as indicators of subtle differences in environmental conditions and historical distributions. The distributions of many amphibians appear to begin and end at several common geographical areas within the range of coastal cutthroat trout in Washington, Oregon, and California. For example, the Strait of Georgia and Vancouver Island is the northern extent of the distributions of many amphibians, including tailed (*Ascaphus truei*) and red-legged (*Rana aurora*) frogs and Pacific giant (*Dicamptodon tenebrosus*), western long-toed (*Ambystoma macrodactylum macrodactylum*), western red-backed (*Plethodon vehiculum*), Oregon (*Ensatina eschscholtzii oregonensis*), and brown (*A. gracile gracile*) salamanders (Cook 1984). The Cape Blanco area of southern Oregon is the northern extent of southern long-toed (*A. m. sigillatum*), Del Norte's (*P. elongatus*), and California slender (*Batrachoseps attenuatus*) salamanders, and the southern extent of western red-backed salamanders (Stebbins 1985, Leonard et al. 1993). Cape Mendocino is the northern extent of the southern red-legged frog (*R. a. draytonii*), red-bellied newt (*Taricha rivularis*), and arboreal salamander (*Aneides lugubris*), and the southern extent of the northern red-legged frog (*R. a. aurora*) and Del Norte's salamander (Stebbins 1985). Additionally, the Olympic torrent salamander (*Rhyacotriton olympicus*) occurs only on the Olympic Peninsula, while the Pacific giant and Dunn's (*P. dunni*) salamanders occur in most areas in western Washington and Oregon *except* the Peninsula (Leonard et al. 1993).

Life History

Several types of life-history information were considered in evaluating the diversity of coastal cutthroat trout. Life-history traits examined included smolt size and outmigration timing, age, river entry timing, size, and frequency of spawning. However, the use of such traits to help define coastal cutthroat trout ESUs is complicated by several factors.

First, long-term data sets are rare, and data collected from different locations during different years may obscure regional patterns in life-history traits. Moreover, differences in collection methods can hinder meaningful comparisons. For example, traits such as age and size at migration will likely be very different for fish caught by angling and for those caught in rotary traps or tributary weir traps. Nearly all gear types are selective for size and species (Hayes et al. 1996). For coastal cutthroat trout, tributary weir traps can be more selective than rotary traps for both size and age of captured fish (Garrett 1998).

Second, the difficulties with aging cutthroat trout by scale analysis may hinder meaningful comparisons among studies. Coastal cutthroat trout scales are notoriously difficult to read and interpretations of scale patterns often vary greatly between readers (Knudsen 1980). Cutthroat trout tend to easily lose their scales and the rate of regeneration has been shown to increase as the fish gets older. Cooper (1970) examined the proportion of regenerated scales to nonregenerated scales from cutthroat trout of several size classes. In his study, Cooper found that about 40% of the scales collected from yearling fish (40-49 mm FL) were regenerated, whereas more than 80% of the scales collected from fish larger than 140 mm showed regeneration. Furthermore, evidence suggests that large spacing between annuli is not a clear indicator that the fish has spent time in salt water. Highly productive freshwater habitats may confer scale patterns in cutthroat trout that are indistinguishable from saltwater growth (Tomasson 1978, D. Saiget[6]). In a study in Petersburg Lake, Alaska, Jones (1977) found very little difference in age and length data between freshwater and sea-run cutthroat trout. This problem was also discussed by Sumner (1962), who expected that tidewater growth should be intermediate between stream and saltwater patterns. Rather, Sumner (1962) and Giger (1972) found that tidewater growth was similar to stream growth patterns. Otolith analysis may provide a more reliable means of establishing life history patterns and ages, but the technique has not been widely applied in cutthroat research as it is costly, time consuming, and requires killing the fish.

Third, fish exhibiting different life histories are often morphologically indistinguishable, particularly as juveniles (Tomasson 1978, Fuss 1982). Direct comparisons of coastal cutthroat trout life-history traits between stocks have not been made under controlled conditions. Differentiating life-history forms is further complicated by a lack of definitive terms in the literature to distinguish between these forms (see "Terminology," p. 6).

Fourth, the sensitivity of life-history traits to environmental and genetic influences may allow their alteration by anthropogenic activities such as land-use practices (Hartman et al. 1984, Holtby 1987), harvesting (Ricker 1981), or artificial propagation (Steward and Bjornn 1990, Hard et al. 1992, Campton 1995, Flagg et al. 1995). The effects of anthropogenic activities on coastal cutthroat trout life-history traits are unclear and consequently difficult to factor out. To help limit any bias introduced by artificial propagation, life-history trait comparisons in this status review have focused on naturally spawning populations. Life-history trait information from hatchery populations was used only when information from naturally spawning populations was insufficient.

Finally, relatively less is known of the migratory pathways of coastal cutthroat trout than of pathways for the other species of Pacific salmon. Research into Pacific salmonid migrations has been dominated for decades by studies on the long-distance transoceanic aspects of the life cycle. Much of the research into long-distance migrations has focused on the migrational timing and pathways important to the commercial fishing industry. Coastal cutthroat trout do not make transoceanic migrations, nor are they a commercial species. For these reasons, minimal attention has been given to the short-distance estuarine or freshwater migrations of these fish.

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[6] D. Saiget, U.S. Dep. of Agriculture, Forest Service, Zig Zag Ranger District, 70220 E. Hwy 26, Zig Zag, OR 97049. Pers. commun. to A. Garrett, Aug. 1998.

Patterns of Life-History Variation

The life history of coastal cutthroat trout is perhaps the most complex of the Pacific salmonids (Northcote 1997a), with reproductive and migratory behaviors at least as diverse as those of steelhead and sockeye salmon and perhaps more similar to some species in the genera *Salmo* (e.g., Atlantic salmon [*S. salar*] and brown trout [*S. trutta*]), *Salvelinus* (e.g., bull trout [*S. confluentus*], Dolly Varden [*S. malma*], and Arctic char [*S. alpinus*]), and *Hucho* (Stearley and Smith 1993). Unlike many Pacific salmonids where all (e.g., chum or pink salmon) or almost all (e.g., coho and chinook salmon and steelhead) members are anadromous, coastal cutthroat trout populations may contain both migratory and nonmigratory individuals within the same population (reviewed in Hall et al. 1997). Although all coastal cutthroat trout populations with access to the sea are believed to have an anadromous component, not all members of the subspecies migrate to the sea (Giger 1972, Sumner 1972, Trotter 1989). Most cutthroat trout that do enter seawater do so as 2- or 3-year-olds, but some remain in fresh water for up to 5 years before entering the sea (Giger 1972, Sumner 1972). Other coastal cutthroat trout never outmigrate at all, but remain in small headwater tributaries. Still others migrate only into rivers or lakes (Nicholas 1978a, b; Tomasson 1978; Moring et al. 1986; Trotter 1989) even when they have seawater access (Tomasson 1978). For example, anadromous, freshwater migratory, and nonmigratory life-history forms of coastal cutthroat trout have all been reported in southern Oregon's Umpqua River Basin (Trotter 1989, Loomis and Anglin 1992, Loomis et al. 1993, Hooton 1997).

Multiple life-history forms frequently coexist within the same watershed and even the same stream (June 1981, Johnston 1982). Where multiple forms exist together, spatial and temporal differences in reproductive behaviors may be large enough to promote genetic differentiation (June 1981, Zimmerman 1995). On the other hand, similar environmental conditions (such as water temperature and velocity) may facilitate reproductive overlap of life-history forms. Allelic and meristic variation among coastal cutthroat trout populations in the Nisqually River's Muck Creek basin led Zimmerman (1995) to suggest that the expression of anadromy probably differs among populations within a basin even when no geologic barrier exists. Thus, some populations may be entirely anadromous some may be entirely freshwater forms, and some may have multiple life-history forms.

Direct comparisons of coastal cutthroat trout life-history traits among populations or individuals have not been made under controlled conditions; even so, it is unclear to what extent such comparisons would be applicable to natural populations. Information from other species suggests that anadromous forms may occasionally have nonanadromous progeny, and vice versa (Nordeng 1983, Kaeriyama et al. 1992, Burgner et al. 1992, Mullan et al. 1992). Both of these relationships may occur in coastal cutthroat trout, according to otolith microchemistry analysis of fish in Oregon's Elk River (Griswold 1996). Griswold (1996) found that some sea-run cutthroat trout had signals in the otolith primodia that indicated their maternal parent was in fresh water at the time of yolk formation and that they migrated to the marine environment. Other fish had strontium/calcium signals that indicated their maternal parent was in the marine environment at the time of yolk formation and that they also migrated to the marine environment.

Only in a few instances, however, have larger migratory (possibly sea-run) female coastal trout been observed paired with small "cryptically colored" males during spawning periods (Northcote 1997a, Saiget et al. in prep). Females observed by Saiget et al. (in prep.) ranged from 300 to 359 mm and males ranged from 100 to 180 mm. It is unclear what the observations of these five fish might imply for the reproductive behaviors of coastal cutthroat trout. Two possibilities are that some males in anadromous populations may mature at a young age and small size (precocious maturation) and perhaps never migrate to sea, or that fish of one life-history form will readily interbreed with other life-history forms. However, information about other species suggests that behavioral differences in mate selection would probably promote some degree of assortative mating between sympatrically spawning anadromous and freshwater forms (Neave 1944, Foote and Larkin 1988).

The migratory patterns of coastal cutthroat trout suggest that patterns may vary within as well as among populations. Some populations of coastal cutthroat trout are split into migratory and nonmigratory individuals, a phenomenon termed "partial migration" by Jonsson and Jonsson (1993). For example, Heggenes et al. (1991) studied local movements and spatial stability of 413 coastal cutthroat trout in the Musqueam-Cutthroat Creek system, British Columbia. A total of 587 recaptures were made of marked coastal cutthroat trout between winter and late summer. Heggenes et al. (1991) found that nearly two-thirds of the marked fish had not moved more than 10 m; only 17.9% moved more than 50 m. The authors acknowledged that within this "resident" group some proportion was likely to be anadromous, though the correlation (based on 246 observations) between distance moved and fish size was weak ($r^2 = 0.0333$, $P = 0.0039$). These authors also found that large fish were still in the stream after anadromous spawners typically would have emigrated, which led them to speculate that a substantial proportion of the mobile individuals were not anadromous (Heggenes et al. 1991). In other studies describing movements of presumably freshwater migratory coastal cutthroat trout, Waters (1993) (Table 3) and Moring et al. (1986) observed that fewer than 10% of the fish moved extensively; Moring et al. (1986) found that 93% of the recaptured coastal cutthroat trout were recovered in the same pool or riffle.

These studies illustrate that while the vast majority of fish within a population probably behave similarly, some individuals may exhibit migratory behaviors that differ from their cohorts. The notion that all fish in a population fit neatly into one category or the other may not be true (Gowan et al. 1994). In a study on brown trout, Harcup et al. (1984) found no evidence to suggest that the migratory component of the population was composed of permanently mobile individuals. Rather, they found that individual brown trout switched between migrating and not migrating, and migratory fish were no more likely to move in subsequent sampling periods than nonmigratory fish.

Environmental conditions, particularly those affecting growth rate, have been shown to markedly alter the degree of residency expressed in some salmonid species (Jonsson 1985, Hindar et al. 1991, Northcote 1992). In an intensive study on Arctic char, Nordeng (1983) reared the progeny of experimentally produced crosses of freshwater and anadromous individuals under different feeding regimes and found that increasing the amount of food significantly increased the proportion of freshwater individuals to anadromous fish. Not only could each form produce

Table 3. Mobility of radio-tagged coastal cutthroat trout from a study on the North Umpqua River, Oregon (Waters 1993).

Date of tagging	Total length (mm)	Weight (g)	Number of detections over 51 days	Number of different locations when detected	Home range (m)	Total distance moved (m)
McConnas Creek						
12/22/92	166	35	3	2	9	9
12/22/92	210	70	22	4	59	188
12/23/92	169	39	22	1	5	0
12/24/92	206	72	22	3	66	98
12/26/92	215	83	22	5	52	120
12/26/92	170	40	22	1	5	0
12/26/92	205	75	22	2	23	46
12/26/92	154	32	22	4	12	69
12/26/92	173	39	22	2	5	33
12/27/92	220	84	22	3	33	66
1/5/93	234	89	10	5	42	55
Kelly Creek						
1/18/93	164	38	2	1	5	0
1/19/93	191	53	22	2	8	8
1/26/93	194	52	5	2	68	68
1/26/93	186	46	17	5	152	181
Harrington Creek						
2/3/93	165	32	14	4	20	51
2/3/93	191	52	26	14	433	1,305
2/3/93	200	80	25	3	33	41
2/5/93	159	30	2	2	45	45
2/9/93	205	72	23	1	4	0
2/9/93	170	38	14	5	27	63
2/10/93	186	52	4	2	12	12
3/9/93	206	54	12	2	21	21
3/9/93	162	32	12	1	6	0
3/11/93	184	50	11	6	130	288

progeny of any form, but single individuals could also change forms during their lifetimes. The age at sexual maturity of the parents, however, influenced the age at sexual maturity of their offspring. Thus, the offspring of small freshwater fish produced more early maturing (nonmigratory) offspring and fewer smolts than did the offspring of anadromous parents (Nordeng 1983).

Some salmonids, as illustrated in the above example, have a behavioral flexibility that allows them to respond to environmental conditions. There is some empirical evidence to suggest that coastal cutthroat trout migratory behaviors may be flexible, but the extent to which such a strategy occurs is unknown. In an ongoing study that began in the spring of 1997, the Alaska Department of Fish and Game (ADFG) started PIT (passive integrated transponder) tagging coastal cutthroat trout as they outmigrated to sea from Auke Lake (D. Jones[7]). During the fall of 1997, an upstream migrant trap was operated and all immigrating coastal cutthroat trout were counted. Previously tagged fish were individually identified and recorded by their PIT tag number and immigration date. Again, in the spring of 1998 coastal cutthroat trout were recorded leaving the lake and all unmarked fish were tagged. During the summer of 1998, ADFG surveyed the lake for freshwater forms of coastal cutthroat trout and found three fish that had been PIT tagged on their emigration to sea in 1997, returned to the lake in the fall of 1997, and apparently opted to remain in the lake in 1998.

Other empirical evidence supports the idea that life-history patterns can vary within individual coastal cutthroat trout over time. For example, some sea-run cutthroat trout may spawn before their first saltwater migration (Giger 1972, Tomasson 1978, Fuss 1982, Jones footnote 7), and others may not return to sea after spawning but may instead remain in fresh water for a year (Tomasson 1978).

Research on other species suggest that even very small individual differences in behavior and physiology, particularly during the first few weeks of life, can affect life-history patterns (Metcalfe 1993). Thorpe (1989) proposed that there is a critical period in which some characteristic of performance, such as a threshold level of growth, will define the direction of individual development. The role that growth plays in determining life-history patterns is complex, as residualization may occur in fish that grow either too quickly or too slowly. An abundant food supply may promote residency (Northcote 1992) and may induce early or precocious maturation. Furthermore, at any point along the migratory path or even at the microhabitat level, individuals of a cohort may respond differently to environmental factors (e.g., temperature, food availability, and predation). The ability of an individual to modify its behavior in response to food abundance, threat of competition, risk of predation, and experience suggests many fish species possess some degree of adaptive flexibility (Dill 1983).

This diversity in life history may reflect an adaptive generalist strategy that allows coastal cutthroat trout to exploit habitats not fully utilized by other salmonids (Johnston 1982, Northcote 1997a). For example, their small size at maturity may give coastal cutthroat trout an adaptive

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[7] D. Jones, ADFG, Div. of Sport Fish, Douglas, AK 99824. Pers. commun. to A. Garrett. Oct. 1998.

advantage for using small streams for spawning and rearing and reduce interspecific competition with other anadromous spawning salmonids (Pearcy et al. 1990). Conversely, post-spawning coastal cutthroat trout or those on feeding migrations are larger than outmigrating juveniles of other Pacific salmon species, which allows coastal cutthroat trout to prey on these fish in a variety of freshwater and estuarine habitats (Pearcy et al. 1990, Northcote 1997a). For these reasons, Northcote (1997a) suggested that, historically, coastal cutthroat trout were probably present year round in a wider variety of climatological conditions and diversity of marine and freshwater habitats than any other salmonid in the coastal Pacific Northwest (Northcote 1997a).

Life-history forms

The diversity of migratory behaviors in coastal cutthroat trout makes identification of fish by life-history form particularly challenging. One way to separate coastal cutthroat trout into population groupings is to classify them by the physical locations where they are caught (e.g., Wyatt 1959, Tomasson 1978, June 1981, Moring et al. 1986). These classifications, however, are somewhat arbitrary as fish may move from one area to another (Northcote 1997a). Consequently, the location and timing of sampling may affect which life-history category migratory individuals are chosen to represent (Fausch and Young 1995). For instance, coastal cutthroat trout believed to be freshwater forms one year may migrate to sea another year (e.g., some fish do not make their initial migration to sea until age 6 (Sumner 1962, Giger 1972) and some sea-run cutthroat trout may not enter saltwater every year after their initial smolt migration, but may instead stay in fresh water (Tomasson 1978, Jones footnote 7). For these reasons, we define the three general life-history forms of coastal cutthroat trout as follows (see also Fig. 1).

Nonmigratory coastal cutthroat trout—This life-history form includes fish generally found in small streams and headwater tributaries near spawning and rearing areas. These fish typically undertake only small-scale migrations and maintain relatively small home territories compared to forms that make more extensive migrations. In general, nonmigratory coastal cutthroat trout appear to grow more slowly than other life-history forms of trout (Tomasson 1978, Trotter 1989), are smaller at maturity (seldom larger than 150-200 mm in length), and rarely live longer than 2 to 3 years (Wyatt 1959, Nicholas 1978a, June 1981). However, as June (1981) points out, the lack of older fish in his study may be due not only to age-dependent mortality, but also to scale-aging problems or outmigration of older larger fish from the study area.

The proportion of coastal cutthroat trout within a basin that exhibit this nonmigratory life history is often difficult to determine. As an example, in a study by Wyatt (1959) of presumably nonmigratory coastal cutthroat trout in Lookout Creek, a small tributary of Oregon's Willamette River, only 14% of 1,112 fish originally marked were recovered. Of these 155 recoveries, 150 (97%) had not moved more than 180 m from the original point of marking. No fish marked in the three upper seining stations were recovered in the lowermost stations, which led Wyatt to suggest that probably no major downstream movement occurred during the study period of June 1955 to September 1957. The distribution of the remaining marked fish was not determined.

Freshwater-migratory coastal cutthroat trout—This freshwater or potamodromous (e.g., Myers 1949, Tomasson 1978) life-history form includes fish that migrate entirely within fresh water. A variety of distinctive population migrations are frequently recognized within this general classification, including populations that migrate from large tributaries to small tributaries to spawn (fluvial-adfluvial), populations that inhabit lakes and migrate upstream to spawn in the lake inlet (lacustrine-adfluvial), and populations that live in lakes and migrate downstream to spawn in the lake outlet (allucustrine) (Varley and Gresswell 1988, Trotter 1991).

These freshwater-migratory populations are best documented in rivers and lakes with physical barriers to anadromous fish, such as above Willamette Falls in the Willamette River. Historically, these falls apparently barred access of anadromous fish to the upper river; above this barrier, schools of coastal cutthroat trout were found to migrate from natal spawning areas to mainstem feeding areas and back (Dimick and Merryfield 1945; Nicholas 1978a,b; Moring et al. 1986). River-migrating coastal cutthroat trout have also been reported as schooling in large streams above migration barriers in southwest Oregon (e.g., upper Chetco River and upper Silver Creek [Illinois Basin]) (ODFW 1993b).

Only rarely have nonanadromous river-migrating schools of coastal cutthroat trout been reported below barriers or in locations with access to anadromous fish. The Rogue and Umpqua rivers are two locations where this behavior has been documented. Tomasson (1978) was first to identify migratory coastal cutthroat trout in the Rogue River with access to seawater that did not enter the marine habitat, but moved only within the river. He was also first to identify potamodromous fish sympatric with sea-run fish, and to document that at least some sea-run fish in the Rogue River migrated only to the estuary and did not enter the open ocean. It is unclear how widely this form occurs in sympatry with anadromous cutthroat trout, partly because the two forms are indistinguishable at the juvenile stage, and differences in growth and appearance may not always be apparent in adults (Jones 1977, Tomasson 1978). In his work on the Rogue River, Tomasson differentiated between the anadromous and nonanadromous fish by chemical analysis of scale tissue.

Saltwater-migratory coastal cutthroat trout—In most areas, this is the most familiar life-history form of coastal cutthroat trout, and most of the biological information presented in "General Biology" (p. 8) and the following sections was derived from studies on saltwater migratory individuals. The juvenile fish migrate from freshwater natal areas in the late winter and spring to feed in marine environments (estuarine or nearshore) during the summer. They then enter fresh water in the winter to feed, seek refuge, or spawn, typically returning to sea water in the spring.

Trophic migratory model

The classification of coastal cutthroat trout into life-history forms may be based more on convenience than on true biological categories (e.g., Gross 1987), considering the inherent difficulty in distinguishing between forms and the wide variability in migratory patterns. One way to consider migratory movement in coastal cutthroat trout is proposed by Northcote (1997a) in terms of functional processes in a "migratory/residency spectrum" or cycle (Fig. 13). Not all

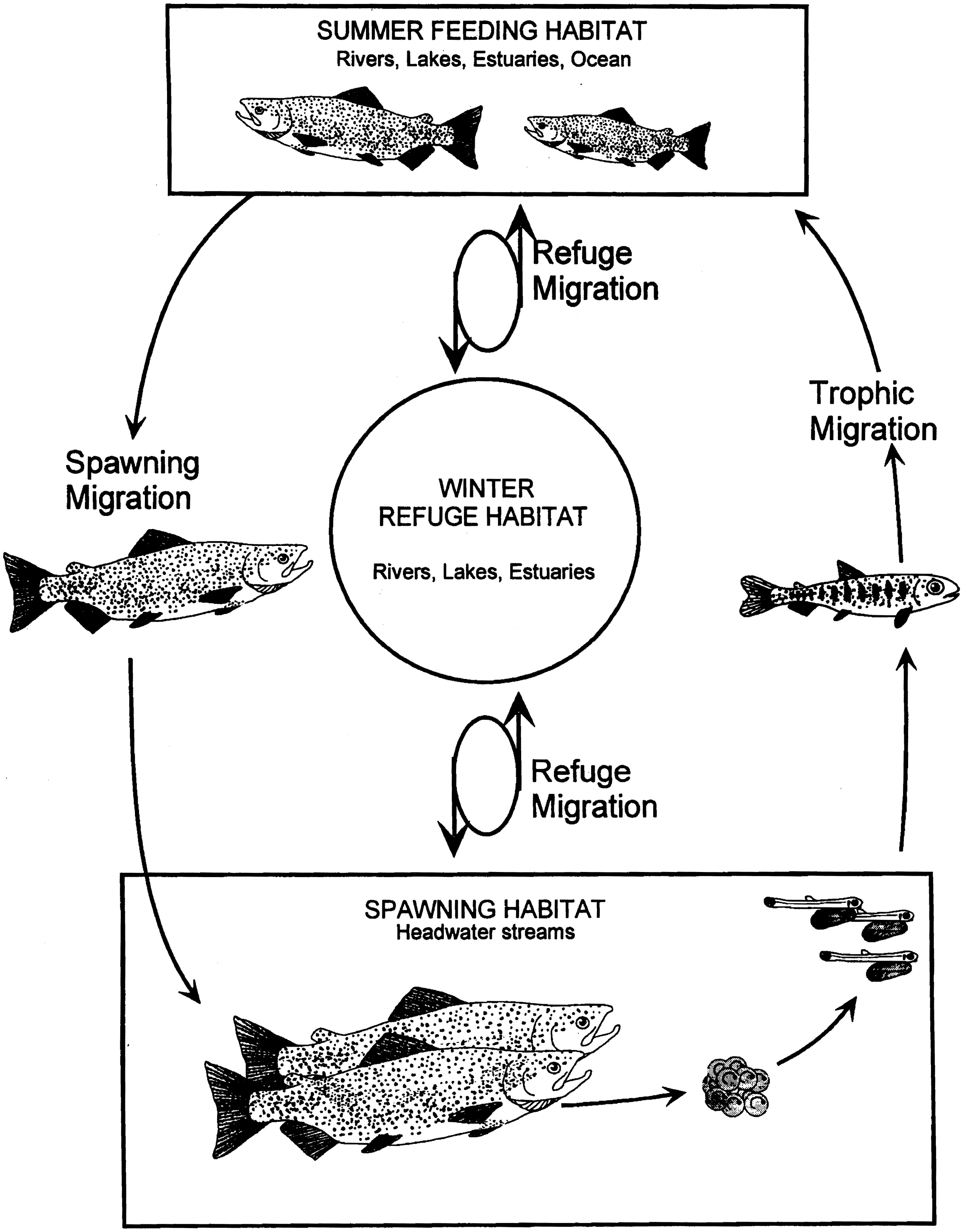

Figure 13. Life-history patterns of cutthroat trout (*Oncorhynchus clarki*). Trophic migrations can occur within rivers, lakes, estuaries, and out into the open ocean. All fish overwinter in estuaries or in freshwater refuges (adapted from Northcote 1997a).

individuals in a population may be involved in such a cycle, and in some systems two or more different migratory cycles may be present.

In Northcote's model (1997a), juveniles migrate from natal rearing areas to feeding habitats, which may be an ocean, estuary, river, or small headwater tributary. They may then migrate to a refuge area for overwintering; the migration may be from the sea to the river or from the river to the headwater tributary. In the spring, the individual may migrate back to a feeding habitat (and repeat this for several years), or may migrate to the spawning area and begin the cycle all over again. This individual behavior does not exclude the likelihood that natural selection has led to adaptations in some populations primarily for anadromous migrations or for remaining in headwater areas. The migratory cycles suggested for coastal cutthroat trout by Northcote may be considerably more complex than those proposed for anadromous Dolly Varden in Alaska by Armstrong and Morrow (1980) and Bernard et al. (1995). Armstrong and Morrow (1980) hypothesized that Dolly Varden may follow two basic migratory pathways. The first pathway applies if the fish spawn in a watershed with a lake: they simply move in the spring to the marine environment and in the fall to a lake in their natal watershed. They feed during the summer in the marine environment and overwinter (and eventually spawn) in the natal watershed. The second pathway occurs if the natal watershed lacks a lake. In this case, the fish follow the first pathway until the fall, when they must find a nonnatal watershed with a lake for overwintering. They return to the natal watershed only to spawn and must leave after spawning to return to the lake in their nonnatal watershed. Bernard et al. (1995) suggested these pathways may be oversimplified, and argued that some fish (14-58% in their study) may overwinter at sea for at least 1 year.

Mechanisms of life-history expression

For any organism, life-history diversity represents both opportunities for and constraints to adaptive evolution. An organism's life history is its repertoire of attributes affecting its fitness (Roff 1992, Stearns 1992), what Williams (1966) called its "design for survival." These attributes are those affecting development, growth, dispersal, and reproduction, including traits such as fecundity, offspring size, migratory propensity, size and age at maturity, and reproductive schedule. The high degree of genetic differentiation (at presumably neutral genes) among some coastal cutthroat trout populations demonstrates that there is also ample opportunity for local adaptations to arise. The complexity of life-history variation in coastal cutthroat trout undoubtedly reflects in part such adaptations, but major life-history trait variations also can occur due to genetic drift in isolated populations or in those founded by few individuals. Understanding the underlying basis of variation in life-history traits is necessary in order to make predictions about the responses of coastal cutthroat trout populations to changes in their environment.

Life-history traits, like most quantitative traits, are thought to reflect expression of several (perhaps very many) genes, many of which have small effects on the phenotype (Falconer 1989). The form of gene expression can be very complex; in addition, life history traits are typically sensitive to environmental as well as genetic influences (Hard 1995). The observation that heritabilities of life-history traits in fishes are generally low has been used to infer that genetic variation is lower for these traits than for other quantitative traits (Kirpichnikov 1981, Allendorf et al. 1987, Tave 1993, Hard and Hershberger 1995), possibly owing to past selection. However, because it is a relative measure, low heritability may reflect high environmental variance more than low genetic variance (Price and Schluter 1991); therefore, life-history traits may have substantial genetic variance and can still respond rapidly to selection. Consequently, life-history variability can represent a potentially enormous store of genetic resources in a population.

The range of total phenotypic variation observed in a population is due to the net effects of genotypic and environmental variation and the interaction between genotypes and their environment (Falconer 1989). Understanding the underlying causes of phenotypic variation is important for predicting individual and population-level responses to changes in the selective environment. At one extreme, phenotypic variation in a population could be due entirely to genetic variation—that is, novel phenotypes each are associated with a novel genotype. At the other extreme, phenotypic variation could be purely a reflection of variation in environmental conditions, with absolutely no genetic variation existing among individuals. In this latter scenario, a population fixed for a particular genotype could still exhibit a broad phenotypic distribution because of high levels of spatial or temporal environmental variation experienced by individuals. Phenotypic variation resulting from the range of phenotypic responses from a particular genotype under different environmental conditions is called "phenotypic plasticity" (Stearns 1989, Via 1993). The actual underlying control of the variation observed in many phenotypic traits is likely to be a combination of these two scenarios.

Regardless of the mechanisms producing phenotypic variation in a population, changes in the environment will result in a shift in the range of observed phenotypes in a population. However, the expected longer-term response of a population to environmental change will be greatly influenced by the underlying control of phenotypic variation. If the range of phenotypic variation observed in a population is due to genetic variation, changes in the environment would result in a shift in the observed phenotypic distribution because certain genotypes would be favored over others. In such a case, the range of phenotypes that could be produced in the future is reduced during every generation of selection. Alternatively, a population whose phenotypic variation is due to phenotypically plastic responses of genotypes to environmental variation can continue to produce a broad array of phenotypes generation after generation.

Phenotypic plasticity can be a less costly means of increasing a population's phenotypic repertoire without the genetic costs incurred by polymorphism and appears to be favored in environments that are highly variable, either spatially or temporally (Bradshaw 1965, Via 1987). However, the evolutionary benefit afforded by phenotypic plasticity depends in part on how reliably organisms can "anticipate" environmental change (Bradshaw 1986): if organisms cannot produce an appropriate phenotype in response to an environmental challenge, plasticity provides no advantage over genetic polymorphism as a mechanism for maintaining phenotypic variation.

Phenotypic plasticity may manifest itself as the "flexibility" in life history that an individual might express over the course of its life cycle. Such flexibility probably involves more than simple behavioral or physiological adjustment to environmental variation. This plasticity should be most pronounced when the temporal variability in the environment within generations is greater than that between generations. But the effect on the phenotypic response of individual genotypes also depends on the degree of spatial environmental heterogeneity, which tends to lead to higher specialization if the spatial component is large and the within-generation temporal component is small (Lynch and Gabriel 1987). For coastal cutthroat trout, some evidence supports the existence of "generalist" life-history phenotypes, which could arise rapidly if both spatial and temporal heterogeneity in the environment are substantial.

There is evidence that at least some individual coastal cutthroat trout adopt a complex (and perhaps plastic) migratory strategy. For example, an individual might spend several years in a nonmigratory or freshwater migratory phase before migrating to seawater for a period of up to a few months, return to fresh water to spawn or overwinter, and then repeat this cycle (or a variation of it) one or more times (see Giger 1972, Tomasson 1978, Fuss 1982). This diversity expressed by individual fish may represent several possible responses to environmental conditions, options that are rare in Pacific salmon. Why? It is possible that Pacific salmon exhibit fewer migratory behaviors because reproductive options are limited, especially after smoltification (Thorpe 1987).

There are a number of possible adaptive explanations for the observed range of phenotypic variation in life history traits in coastal cutthroat trout. Behavioral or physiological adjustment (including dispersal or migration) that allows individuals to cope with environmental variation probably occurs to some degree. The success of such adjustments is typically highest when environmental variation is relatively weak and/or the spatial scale of environmental variation is small relative to the scale over which dispersal occurs. Selection also may favor a form of "bet hedging" when individuals must spread their reproductive risk (den Boer 1968, Stearns 1976) by producing a wide array of offspring phenotypes, only a fraction of which might be able to cope with the environment they encounter (Kaplan and Cooper 1984, Bull 1987). This tactic has a high cost, however, and is expected to be favored only in highly unpredictable environments (Hard 1995). For salmonids like coastal cutthroat trout that show mixed migration strategies, Jonsson and Jonsson (1993) suggested that in a single mating parents may produce offspring with different migratory strategies, but this has not been confirmed experimentally for coastal cutthroat trout.

The observed complexity in life-history traits in coastal cutthroat trout likely reflects (at least in part) unique adaptations to local environments–attributes that are important to the diversity of an ESU. Another significance of this complexity may be to provide populations with a fundamental means of coping with environmental change. In fact, the extent of this variation in systems in which migratory fish are present may also constitute our most reliable indicator of population resilience and ESU status. For example, anecdotal evidence for several river basins points to relatively healthy nonmigratory coastal cutthroat trout populations but weak or declining anadromous populations, which strongly suggests that saltwater migratory–and even freshwater migratory–coastal cutthroat trout within the same river basin can experience selective regimes that are markedly different from their nonmigratory counterparts. However, the consequences of this disparity in population trends depend heavily on the extent to which this life-history variation is genetically controlled. Unfortunately, we are unaware of any information that bears directly on the genetic basis of life-history variation in any coastal cutthroat trout population.

Life-History Stages

Spawning

Anadromous cutthroat trout spawning typically starts in December and continues through June, with peak spawning in February (reviewed in Pauley et al. 1989, Trotter 1989). In California, spawning is reported to begin in November, with peak spawning in late December in larger river basins and late January and February in the smaller coastal rivers and streams (e.g., Howard and Albro 1995, 1997; Gale 1996, 1997; Taylor 1997). Redds are primarily built in the tails of pools in streams with low stream gradient and low flows, usually less than 0.3 m^3/s during the summer (Johnston 1982). The size of coastal cutthroat spawning streams is well summed up by R. Dimick, founder of Oregon State University's Department of Fisheries and Wildlife: "You can step across a cutthroat spawning stream, but you have to jump a steelhead stream" (C. Bond[8]).

Generally, spawning occurs upstream of coho salmon and steelhead spawning zones, although some overlap may occur (Lowry 1965, Edie 1975, Johnston 1982). It is believed that this choice by coastal cutthroat trout of spawning sites in small tributaries at the upper limit of spawning and rearing sites of coho salmon and steelhead has evolved to reduce competition for suitable spawning sites and reduce competitive interactions between young-of-the-year coastal cutthroat trout and other salmonids. Reduction of juvenile competition may be particularly important at this early life-history stage, as coastal cutthroat trout typically emerge later and at a smaller size than fry of these other species (Johnston 1982, Griffith 1988). These spatial separations may limit hybridization between coastal cutthroat trout and rainbow trout or steelhead. In many drainages where rainbow and coastal cutthroat trout coexist, a slight difference in spawn timing between the two species is believed to reduce the opportunity for hybridization (Cramer 1940, DeWitt 1954, Sumner 1972, Glova and Mason 1977, Johnston 1982). However, as discussed in "Hybridization between cutthroat trout and *O. mykiss*" (p. 76), hybridization between coastal cutthroat and rainbow trout has been documented in a variety of locations throughout Washington, Oregon, and California where spawning areas and time of spawning overlap (Campton and Utter 1985, Hawkins 1997, Taylor 1997; see also "Genetic Information," p. 70).

Cutthroat trout are iteroparous, and the incidence of repeat spawning appears to be higher than in steelhead (Sumner 1953, Giger 1972, Busby et al. 1996). Some fish have been

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[8] C. Bond, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331-3803. Pers. commun. to O. Johnson. February 1994.

documented to spawn each year for at least 5 years (Giger 1972), although some do not spawn every year (Tomasson 1978) and some do not return to seawater after spawning but instead remain in fresh water for at least a year (Giger 1972, Tomasson 1978). In general, coastal cutthroat trout exhibit considerable variation in age and size at maturity. Nonmigratory coastal cutthroat trout typically mature at an early age (2 to 3 years) whereas sea-run cutthroat rarely spawn before age 4 (Trotter 1991). Larger fish, because of their size, can obtain the best spawning sites and produce larger eggs (Trotter 1997). In two British Columbia lakes, Jonsson et al. (1984) found significant differences between sexes, with mature females significantly larger than mature males. Furthermore, the sex ratio of upstream migrant coastal cutthroat trout shows a preponderance of females in the migrants (Sumner 1953; Jones 1974, 1975; Wenburg 1998). This observation, combined with anecdotes about large "sea-run" females spawning with small "cryptically colored" males (discussed in "Patterns of Life-History Variation," p. 40), suggest that male coastal cutthroat trout may possess the alternative reproductive tactic of precocious maturation, similar to coho salmon (Gross 1984) or brown trout (Jonsson 1985). Although large males tend to be the principal spawners in most populations, small males can dart in and fertilize some of the eggs. This tactic could be particularly successful for coastal cutthroat trout because they spawn in small streams that often have numerous places for a small male to hide near a spawning pair (Jonsson et al. 1984). When large migrant males are absent, small males may become principal spawners (Jonsson 1985).

Spawners may experience high postspawning mortality due to weight loss of as much as 38% of prespawning mass (Sumner 1953) and other factors (Cramer 1940, Sumner 1953, Giger 1972, Scott and Crossman 1973). Still, in one Oregon stream, over 39% of one year's spawning population returned to spawn the next year, 17% for the third year, and 12% for the fourth year (Sumner 1953). However, in another stream with an intense sport fishery, only 14% returned to spawn in the second year (Giger 1972).

Cutthroat trout are among the salmonids most vulnerable to overharvest by angling (Gresswell and Harding 1997) (see "Assessment of Extinction Risk," p. 135), especially during postspawning outmigrations to summer feeding areas. This relatively heavy harvest mortality on repeat spawners has been a concern of biologists in the Pacific Northwest for many years (Giger 1972, Johnston 1982, Gresswell and Harding 1997), especially as first-year coastal cutthroat spawners often have fewer and poorer quality eggs than do repeat spawners (J. Hunter[9]).

Incubation and emergence

Eggs begin to hatch within 6-7 weeks of spawning, depending on temperature; alevins emerge as fry between March and June, with peak emergence in mid-April (Giger 1972, Scott and Crossman 1973). At emergence, fry quickly migrate to channel margins and backwaters, where they remain throughout the summer (Glova and Mason 1976, Moore and Gregory 1988). Coastal cutthroat trout are found in streams with channel gradients that vary from low (< 2%) to

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[9] J. Hunter, WDFW, 600 Capitol Way N., Olympia, WA 98501-1091. Pers. commun. to O. Johnson. June 1998.

moderate (2-3%) or steep (> 4%), with narrow widths (0.7-3.0 m) (Hartman and Gill 1968, Edie 1975, Glova 1978, Moore and Gregory 1988, Jones and Seifert 1997), and often in small watersheds with drainage areas under 13 km^2 (Hartman and Gill 1968).

There is some disagreement in the literature regarding the preferred habitat type of coastal cutthroat trout fry. When they are the only salmonid in the stream, age-0 coastal cutthroat trout are more abundant in pools, but use riffles and glides as well (Glova 1984). In contrast, in sympatry with coho salmon fry and sculpins, coastal cutthroat trout are fairly evenly distributed between all three habitat types (Glova 1978, 1987). The reduced use of pools while in sympatry has been interpreted as evidence that coastal cutthroat trout are relegated to riffles by socially dominant coho salmon (Glova 1978, 1984; Johnston 1982; Trotter 1997). Other authors have found that underyearling coastal cutthroat trout select the shallower and faster waters in riffles (June 1981, Bisson et al. 1982, Bisson and Sedell 1984, Mitchell 1988) but may reduce their use of this habitat type in the presence of steelhead (Bisson et al. 1982). In winter, coastal cutthroat trout move to pools near log jams or overhanging banks (Bustard and Narver 1975).

Juvenile movements

Coastal cutthroat trout parr generally remain in upper tributaries until they are 1 year of age, when they may begin moving more extensively throughout the river system. Once these movements begin, it is difficult to determine whether fish caught in upstream or downstream traps are parr making a freshwater migration, or smolts on a seawater-directed migration; many unpaired coastal cutthroat trout of similar size caught in these traps have characteristics of either life-history stage or intermediate characteristics (Tomasson 1978, Fuss 1982). In Oregon, Lowry (1965) and Giger (1972) found that downstream-directed movement by juveniles in the Alsea River system began with the first spring rains, usually in mid-April with peak movement in mid-May. Giger (1972) also reported that some juveniles entered the estuary and remained there over the summer but apparently did not smolt or migrate to the open ocean. He was unable to determine how many of these "parr" continued moving seaward and how many remained in the estuaries. Such movement further confounds the difficulty in separating nonanadromous downstream migrations from seaward migrations.

In Oregon, Washington, and British Columbia, upstream movement of juveniles with parr marks from estuaries and mainstems to tributaries began with the onset of winter freshets during November (Giger 1972, Moring and Lantz 1975, Cederholm and Scarlett 1982, Hartman and Brown 1987, Garrett 1998) and continued through the spring, frequently peaking during late winter and early spring (Cederholm and Scarlett 1982, Hartman and Brown 1987, Garrett 1998). Many of these yearling fish averaged less than 200 mm in length (Moring and Lantz 1975, Garrett 1998) and were found in streams that ran through ponds or sloughs (Hartman and Gill 1968, Garrett 1998).

Smoltification and seawater entry

Smoltification involves a number of behavioral, morphological, and physiological changes that prepare juvenile salmonids for their trophic migration to the sea (Fontaine 1975, reviewed in Clarke and Hirano 1995). Some authors consider the transformation of juvenile salmon from freshwater parr to seaward-migrating smolt as a "metamorphosis" (Wald 1958). An essential part of smoltification is an increase in euryhalinity, which allows the smolt to live in salinities varying from fresh water to full-strength seawater. For Pacific salmon and steelhead, the biochemical transformation during smoltification has been well studied (Clark and Hirano 1995), and several "smoltification indices" have been developed (e.g., Zaugg and McLain 1970, 1972; Zaugg and Wagner 1973; Folmar and Dickhoff 1980, 1981; Zaugg 1981). Visually, smoltification is characterized by morphological changes in color and body shape. The first change is most obvious: smolts lose their juvenile parr marks (oval-shaped and darkly pigmented melanin bars on the lateral surface) and take on a silvery sheen caused by the accumulation of guanine and purine in the scales and superficial dermal layers of the skin. Secondly, the weight-to-length ratio declines, resulting in a more streamlined body shape.

No studies have been conducted to develop a biochemical "smoltification index" for coastal cutthroat trout. Furthermore, some coastal cutthroat trout migrate to estuaries in the spring and, at least on the Oregon coast (Giger 1972, Sumner 1972, Tomasson 1978) and in the Cowlitz River on the Lower Columbia River (Tipping 1981), will remain in the estuary throughout the summer, returning to fresh water in the fall. In the Rogue River, Tomasson (1978) concluded from chemical analysis of scales that coastal cutthroat trout did not enter the open sea, but remained in the estuary throughout the summer. Tomasson (1978) speculated that sea-run Rogue River coastal cutthroat trout may remain in the estuary to avoid predation by steelhead called "half-pounders" that do not conduct long oceanic migrations, instead residing during the summer in the nearshore ocean where sea-run cutthroat trout usually occur. Still, all fish that enter and reside in an estuary for several months need to be able to adapt to varying concentrations of salt water, especially during summer months when freshwater flow and runoff is minimal.

Some coastal cutthroat trout do undergo complete smoltification, and these fish have been best identified from open ocean samples. Loch and Miller (1988) and Pearcy et al. (1990) both report capturing sea-run cutthroat trout as far as 66 km offshore that lacked the marking of sea-run *O. c. clarki* caught in estuaries. The fish caught in the open ocean were "very silvery, and could only reliably be distinguished from steelhead by the presence of basibranchial teeth" (Pearcy 1997).

Researchers have found that coastal cutthroat trout that enter the sea generally do so after 2-4 years in the freshwater environment (Sumner 1962, Lowry 1965, Giger 1972, Michael 1980, Fuss 1982) (Table 4, Fig. 14). (Notable exceptions to this are summarized in studies from Alaska that indicate a majority of the emigrants are between 4 and 6 years of age at initial seawater entry (Armstrong 1971, Jones 1978) (Table 4, Fig. 14). Time of initial seawater entry of smolts bound for the ocean generally occurs between March and July (Table 4, Fig. 15), varies by locality, and

Table 4. Life-history data (out-migration timing, mean length, and predominant age) for coastal cutthroat trout at initial seawater entry.

Region River System	Peak timing	Average length, mm (range)	Major age-class	Percent of major age-class represented (Total no. aged)	Citation	Notes
Southeastern Alaska						
Petersburg Cr.	June	246 (144-480)	5	52.4 (21)	Jones 1972	
	mid-June	247 (120-481)	5	34.7 (95)	Jones 1973	Majority age 3-6.
	early June	258 (131-460)	5	34.6 (75)	Jones 1974	Large cutthroat trout dominated early in the runs, average-sized fish dominated the peak of out-migration, while the latter portion of the outmigration was dominated by small cutthroat trout. Data from 1972-75.
	mid-May to mid-June	262 (110-508)	4	38.2 (55)	Jones 1975	
	May	243 (86-515)	4	35.6 (59)	Jones 1976	
			4-6	78.2 (286)	Jones 1977	Scale analysis revealed sea-runs are at least age 3 at first outmigration.
			4-6	78.2 (129)	Jones 1977	
Eva Lake	May-June	284 (125-390)	6	30.1 (196)	Armstrong 1971	Of 88 fish with a growth band considered to be from initial saltwater entrance, 80% were age-3 fish.
British Columbia						
Carnation Cr.		~145 (120-155)			Hartman and Scrivener 1990	
North Coast Washington						
Soleduck (Quillayute basin)		169	2	64 (21)	Fuss 1978	Small sample size; back-calculated age at entrance.
Dickey Cr. (Quillayute basin)		211	3	83 (12)	Fuss 1978	"
Goodman Cr.		255	3	80 (5)	Fuss 1978	"
Hoh R.		224	3	78 (18)	Fuss 1978	"
Clearwater R. (Queets basin)		220	3	63 (37)	Fuss 1978	"

Table 4. (Continued).

Region River System	Peak timing	Average length, mm (range)	Major age-class	Percent of major age-class represented (Total no. aged)	Citation	Notes
Clearwater R. (Queets basin)		215	4	59 (105)	Fuss 1982	Two fish captured intertidally did not exhibit saltwater morphology and scale patterns did not indicate saltwater growth.
Clearwater R. (Queets basin)	May	225	4		Garrett 1998	Ages inferred from length-frequency distributions of catch.
Puget Sound						
Stillaguamish R.			2	90 (88)	Johnston 1979	
Snow and Salmon Cr.	May		2	76 (35)	Michael 1989	
Washington and Oregon coasts						
Purse seine catch	July	241	2	45 (110)	Pearcy et al. 1990	More captured in July, absent in Sept.
Columbia River						
Gobar Cr.	May	161	2	68.8 (32)	Chilcote et al. 1980b	Tributary of Kalama (RKm 31.2).
Kalama R.		168	2	63.2 (38)		Columbia tributary on SW slopes of Mt. St. Helens.
Gobar Cr.		151	2	69.9 (55)	Chilcote et al. 1980a	Captured in 1979.
Kalama R.		150	2	64.3 (126)		
Oregon coast						
Sand Cr.	April-May	150(68-278)	3	46.2 (253)	Sumner 1962, 1972	These are downstream migrants under 28 cm, some may be what Sumner called non-sea-runs, however, age at entrance closely corresponds with number of stream annuli on most sea-runs (3 annuli [46.2%]).
Alsea estuary	late April-early May	146(104-177)	2.4	(155)	Giger 1972	Parr captured in the estuary, separated here according to presence of parr marks or silvery appearance, coefficient of condition, and timing of migration.
		231(170-295)	3.4	(483)	"	Smolt ages were calculated from fall sea-run catch.
Siuslaw R.			3.3	(782)	"	

Table 4. (Continued).

Region	River System	Peak timing	Average length, mm (range)	Major age-class	Percent of major age-class represented (Total no. aged)	Citation	Notes
	Rogue R.	April to May	122 (at 2nd annulus)	2	53.9-85.9 (13-205)	Tomasson 1978	Coastal, sampled in estuary, 4 years of data, 1974-77.
	Deer Cr.	April to May	125-150	2	48.3 (300)	Lowry 1965	Downstream migrants, aged by length-frequency analyses.
	Flynn Cr.	April to May	125-150	2	64.4 (365)	Lowry 1965	"
	Needle Branch Cr.	April to May		1	42.4 (144)	Lowry 1965	"
	Umpqua and Smith R.		165-254	2		OSGC 1947	Oregon State Game Commission, Lower Umpqua River Study, Annual Report.
	Umpqua and Smith R.			3		OSGC 1949	Oregon State Game Commission Annual Report - Lower Umpqua River Study.
California							
	Smith R.	late April-early May	150 (119-174) 232 (76-400)			Voight and Hayden 1997	Smolts of various ages.
	Klamath R.	April-May	192 (127-292)	2		McCain unpubl. data	
	Redwood Cr. estuary	April	225 (110-381)	3	61.3 (143)	Redwood National Park 1983, 1988-93	
	Mad R.	April				T. Wesloh[10]	

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[10] T. Wesloh, California Trout, 870 Market St. #859, San Francisco, CA 94102. Pers. commun. to G. Bryant. May 1998.

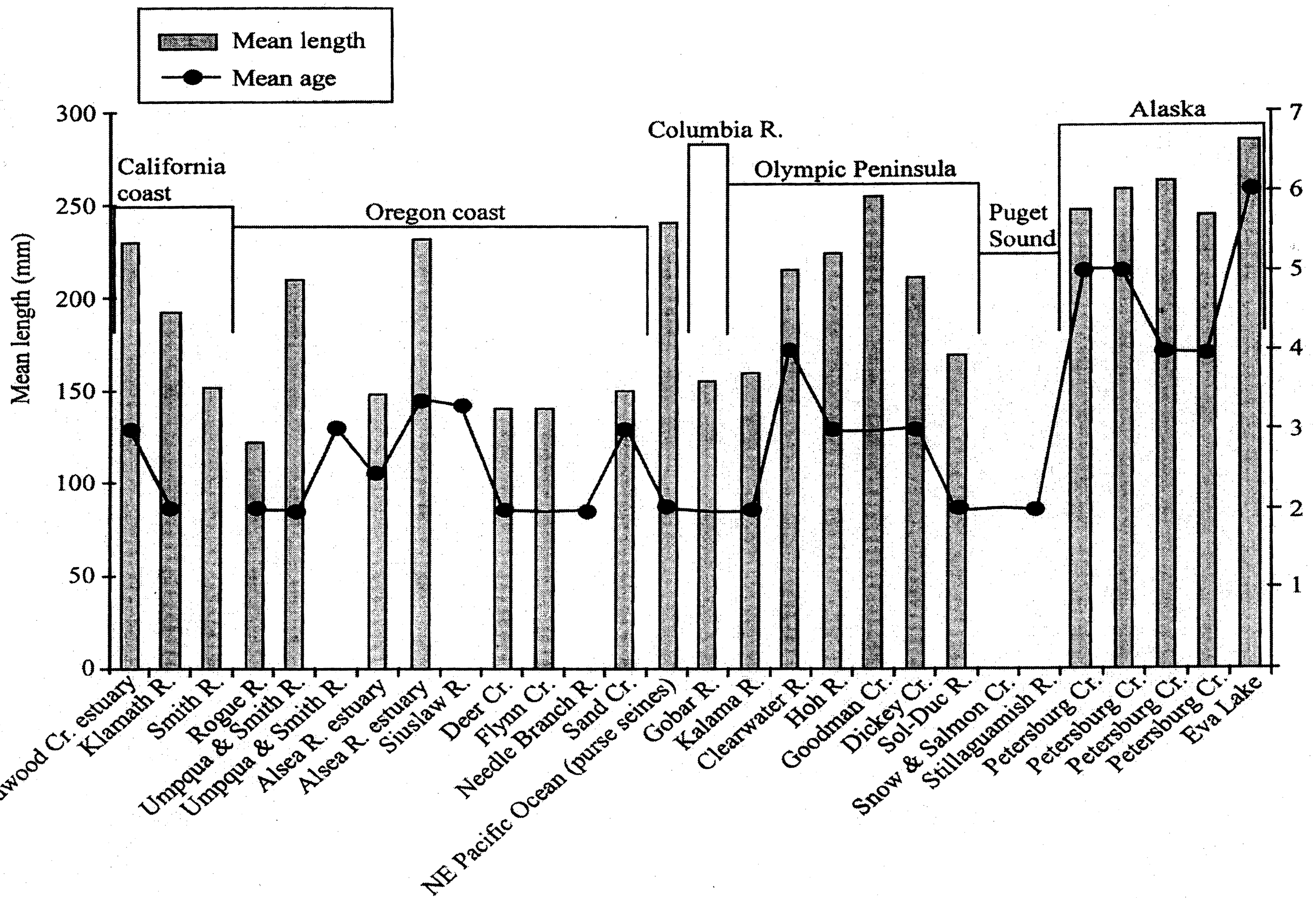

Figure 14. Mean age and length of coastal cutthroat trout at saltwater entrance. Repeated locations represent data from multiple publications. (OSGC 1947, 1949; Sumner 1962, 1972; Lowry 1965; Armstrong 1971; Giger 1972; Jones 1973, 1974, 1975, 1976; Fuss 1978, 1982; Tomasson 1978; Johnston 1979; Chilcote et al. 1980a; Redwood National Park 1983, 1988-1993; Michael 1989; Pearcy et al. 1990; Voight and Hayden 1997; McCain unpubl. data.)

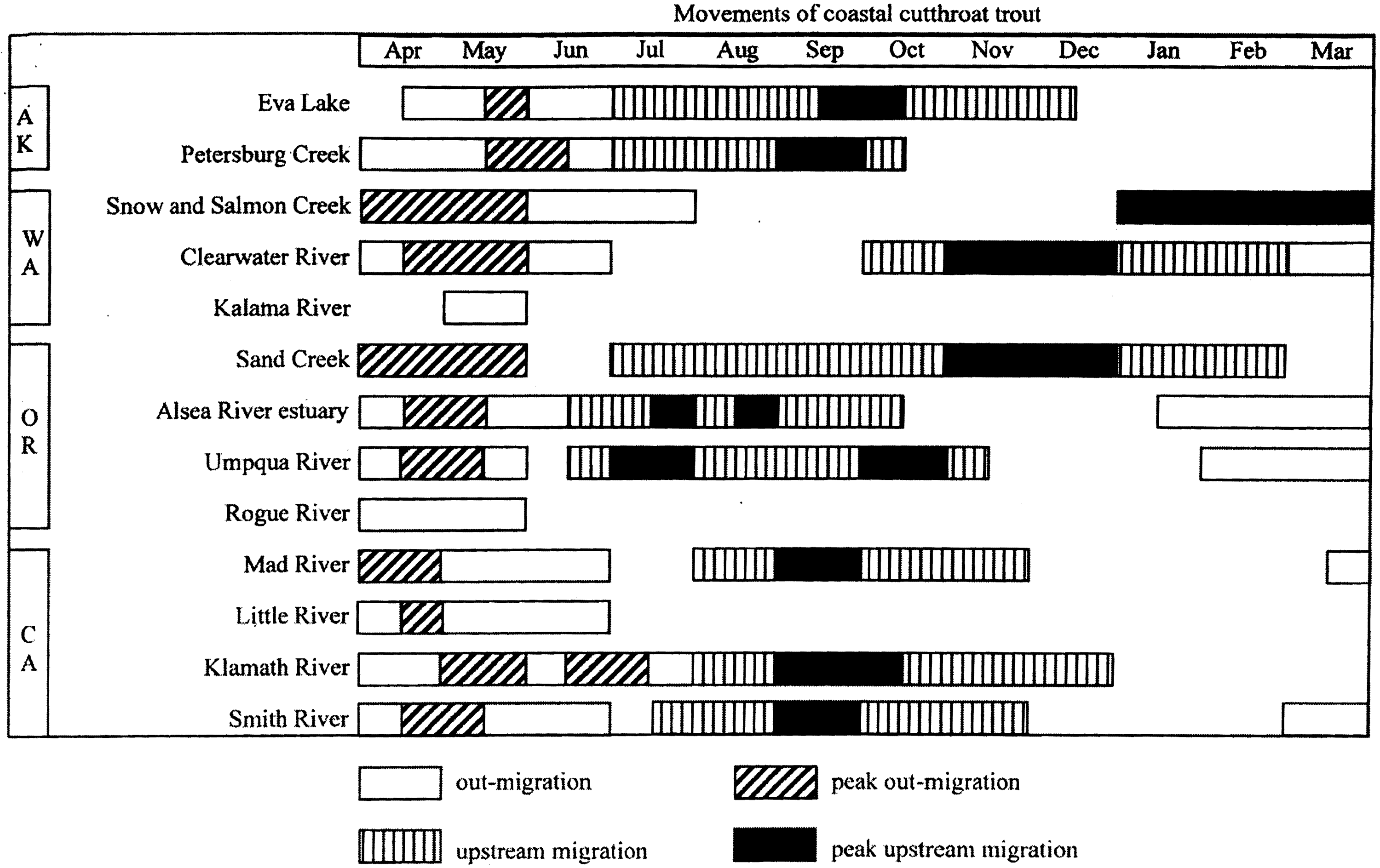

Figure 15. Migrational timing of coastal cutthroat trout from populations along the Pacific Coast. Data compiled from Sumner 1962, 1972; Armstrong 1971; Giger 1972; Jones 1978; Tomasson 1978; Chilcote 1980b; Michael 1989; Johnson et al. 1994; Howard and Albro 1997; Garrett 1998; Voight and Hayden 1998; McCain unpubl. data; and Wesloh footnote 10.

may be related to marine conditions or food sources (Sumner 1953, 1972; Lowry 1965, 1966; Giger 1972; Johnston and Mercer 1976; Trotter 1989). In California, smolt emigration typically begins in March and continues through June and July, with peak migration in April and May (Redwood National Park 1983, 1988-1993, 1997, 1998; Brown 1988; Mitchell 1988; Lintz and Noble 1990; Lintz and Kisanuki 1991; Shaw and Jackson 1994; Gale 1996, 1997; Simondet 1997; Voight and Hayden 1997). In Washington and Oregon, entry begins as early as March, peaks in mid-May, and is essentially over by mid-June (Sumner 1953, 1972; Lowry 1965; Giger 1972; Moring and Lantz 1975; Johnston 1982). In Alaska, the migration begins in April and peaks in late May or early June (Baade 1957, Armstrong 1971, Jones 1976), although two additional surges may occur in mid-June and mid-July. Jones reported that the mid-June surge was composed of outmigrating coastal cutthroat trout over 250 mm and indicated "these were not believed to be initial migrant smolts." Jones (1976) also found that the average size of outmigrants in a mid-July migration peak at Petersburg Creek in Alaska was less than 200 mm (Table 4). This run occurred at night on moderate stream flows and stopped during extreme high or low stream flows.

It has been suggested that seaward migration of smolts to more protected areas (e.g., Puget Sound or the Columbia River) occurs at an earlier age and smaller size than migration to more exposed areas (e.g., the outer Washington coast) (Johnston 1982). Johnston (1982) also reported that in Puget Sound and the Columbia River smolts make their first migration at age 2, at a mean size of about 160 mm (Table 4). On the California, Oregon, and Washington coasts, coastal cutthroat trout make their initial seawater migration between ages 2 and 3, with a few age-4 migrants of mean sizes ranging from 150 to 255 mm (Lowry 1965; Giger 1972; Sumner 1972; Fuss 1982; Redwood National Park 1983, 1988-93; USFS 1995). However, studies on age and size at initial seawater entry are rare (Table 4, Figure 14; see also Table C-2 in Appendix C for additional life-history data acquired after the final BRT meeting), and ages or lengths at initial entry are often back-calculated using scales from returning adults in creel surveys (Knudsen 1980). These back-calculations are difficult and may often be inaccurate (Knudsen 1980). While Johnston's hypothesis (1982) is plausible, more studies are needed to confirm its validity. The oldest recorded initial age of seawater entry was a 6-year-old 280-mm fish from the Alsea River in Oregon (Giger 1972).

Estuary and ocean movement/migration

Coastal cutthroat trout that enter nearshore waters reportedly move moderate distances along the shoreline but do not cross large bodies of open water (e.g., Jones and Seifert 1997, Pearcy 1997). Sumner (1953, 1972) reported that, in the Nestucca River and Sand Creek, Oregon, coastal cutthroat trout moved from stream to stream for more than 68 km. Studies by Giger (1972) in Oregon and Jones (1973, 1974, 1975) in Alaska indicated that coastal cutthroat trout, whether initial or seasoned migrants, remained at sea an average of only 91 days, with a range of 5 to 158 days. In these studies, the majority of coastal cutthroat trout seemed to migrate in similar patterns from year to year, rarely crossed bodies of water more than 8 km in width, and closely followed shorelines, sometimes for up to 71 km. Jones and Seifert (1997) radio-tagged coastal cutthroat trout in Auke Lake and Lake Eva in southeastern Alaska to monitor their movement. These fish traveled a maximum of 52 and 26 shoreline km, respectively, but did not cross extensive open-water channels.

However, these shoreline migratory patterns may not represent the behavior of all coastal cutthroat trout. For example, two fish captured and tagged offshore migrated much further distances (Pearcy et al. 1990): One fish, released near Cape Disappointment on the northern Oregon coast, was recovered in the Umpqua River, 290 km to the south; another fish released off Yaquina Head was recovered 43 days later in the Siuslaw River, 72 km to the south. Pearcy (1997) argued that these and other data (e.g., Giger 1972, Pearcy and Fisher 1988) suggest that sea-run cutthroat trout along the Oregon coast may swim and/or be transported with the prevailing currents long distances during the summer.

It is not clear how far offshore coastal cutthroat trout migrate. Most researchers have found that the subspecies remains in nearshore waters. Sumner (1953, 1972) reported that coastal cutthroat trout were routinely caught up to 6 km off the mouth of the Nestucca River. Jaenicke and Celewycz (1994) did not catch any cutthroat trout using offshore purse seines in southeastern Alaska, but these fish were captured with beach seines inshore of the same area (Pearcy 1997).

The hypothesis that coastal cutthroat trout will not cross large bodies of open water may not hold true near the Columbia River plume. In offshore sampling studies with fine-meshed purse seines, coastal cutthroat trout were captured between 10 and 46 km offshore (Dawley et al. 1978, 1979, 1980; Loch and Miller 1988; Pearcy et al. 1990). These fish may have been carried out to sea in the freshwater plume of the Columbia River, or they may have moved offshore in search of prey. As previously discussed, these fish were silvery in color, lacking the spotting of their nonmigratory or estuarine counterparts, and could only be distinguished from steelhead by the presence of basibranchial teeth (Pearcy 1997). These reports might imply that sea-run cutthroat trout are more common offshore than previously reported but are often misidentified as steelhead.

The relatively brief exposure of sea-run cutthroat trout to seawater, compared to other anadromous salmonids, should not necessarily be construed as an indication that the marine phase of the life cycle is less important for sea-run cutthroat trout. The relative importance of the marine phase may vary among populations, at least on relatively large geographic scales, depending on conditions in estuaries and nearshore habitats (Reeves et al. 1997). In some coastal cutthroat trout populations, only a small proportion of the individuals may be anadromous (DeWitt 1954, Gerstung 1997), a condition also found in *O. nerka* and *O. mykiss* but rare in other Pacific salmonid species. Thus, although the marine phase can be very important to sea-run cutthroat trout in enhancing opportunities for growth and dispersal to neighboring drainages, the freshwater phase may be relatively more important for juvenile growth and survival in sea-run cutthroat trout than for other anadromous salmonids, at least in some populations where estuaries are small or nearshore habitat is limited.

Adult freshwater migrations

Coastal cutthroat trout may return to freshwater feeding/spawning areas from late June through the following April (Table 5, Fig. 15, and Table C-2). Re-entry timing has been found to be temporally consistent from year to year within streams, but varying widely between streams (Giger 1972). As in other species of anadromous salmonids, entry to large rivers seem to occur consistently earlier than to shorter coastal rivers (Giger 1972, Johnston and Mercer 1976, Johnston 1982). In small streams, such as Carnation Creek in British Columbia, Minter Creek in Washington, and Sand Creek in Oregon, peak returns occur in December and January, and fish may continue to return through March (Sumner 1953, Anderson and Narver 1975, Johnston 1982). These streams usually have low flows (< 0.6 m^3/s). Sumner (1953) found fall-winter movements in Sand Creek, first with large adults (up to 10 years old), followed by smaller (<25 cm) mature freshwater migrants coming from the lower reaches of the estuary. In the Nestucca River, Sumner reported a late reproductive migration in early to mid-May, with large ripe females in rivers as late as June.

In large river systems within Washington and Oregon (such as the Stillaguamish, Columbia, Cowlitz, Alsea, and Umpqua rivers), coastal cutthroat trout return migrations usually begin as early as late June and continue through October, with peaks in late September and October (Lavier 1963; Bulkley 1966; Hisata 1971, 1973; Duff 1972; Giger 1972; Wright 1973; Tipping and Springer 1980; Tipping 1981, 1986; ODFW 1993a). On the Alsea River, for example, Giger (1972) reported that the earliest known entrance dates of sea-run cutthroat trout into the Alsea River between 1965 and 1970 ranged from June 23 to July 21. Giger also noted that these first fish were the "forerunners of larger runs which peaked at later dates" and that "smaller numbers of fish were known to enter as late as early October" (Giger 1972, p. 11). He also suggested that the early run of fish in the Alsea River may consist of older fish, with first-time spawners making up the later October-November run. Similarly, in the Umpqua River, Oregon Department of Fish and Wildlife (ODFW) biologists (ODFW 1993a) reported that coastal cutthroat trout at Winchester Dam historically began upstream migrations in late June and continued to return through January (Fig. 15), with bimodal peaks in late July and October.

In California rivers with year-round access to the Pacific Ocean, adult immigration typically begins in late July and continues through December, with peak migration in September and October (CDFG 1980-89; Voight and Hayden 1997; McCain unpubl. data; Gale 1996, 1997; Simondet 1997). In smaller California rivers and coastal lagoons with seasonal river sand bars that block access to the ocean, adult immigration begins with the first opening of the sand bar (usually with the first large freshet in November or December) and continues through March, with peak migration typically in January and February (Redwood National Park 1983, 1988-93; Taylor 1997).

Table 5. Life-history data (age, mean length, and sex) of coastal cutthroat trout at initial return to fresh water from the ocean.

Region River System	Entrance timing (peak mo.)	Mean age at return (% total)	Age at maturity (% mature)	Average size, mm (range)	Sex	Sample Size	Citation	Notes
Alaska								
Petersburg Cr.	Aug-Oct (Sept)	4 (47.4)		306 (140-513)		76	Jones 1972	Fifty-six percent of the immigrants were immature.
	Jul-Oct (Sept)	4 (33.7)		274 (140-460)		101	Jones 1973	Fifty-three percent of the immigrants were immature.
	Jul-Oct (Sept)	6 (27.2)		245 (135-471)		81	Jones 1974	Some immigration through weir as early as April but not considered part of the sea-run immigration; 54.1% immigrants were immature; averaged 730 eggs per female.
	April-Oct (Sept)	4 (41.2)		261 (130-444)		51	Jones 1975	Forty-eight percent of immigrants were immature; averaged 880 eggs per female.
		5 (33.3)		260 (117-432)		27	Jones 1976	Observed spawners only during hours of darkness; counts of immigrants were hampered by high flows. Thirty-nine percent (27) were immature (angler bias); 862 eggs per female.
							Jones 1978	Vol.19 summary; note normally mature when age 5 or 6, sea-run cutthroat trout typically do not live more than 9 or 10 years, whereas freshwater cutthroat trout can live to age 15. Jones suspects osmoregulation is responsible for short life span of sea-run cutthroat trout.

Table 5. (Continued).

Region River System	Entrance timing (peak mo.)	Mean age at return (% total)	Age at maturity (% mature)	Average size, mm (range)	Sex	Sample Size	Citation	Notes
Eva Lake	May-Nov (Sept - Oct)						Armstrong 1971	No indication as to spawning condition of fish. Reference noted for immigration timing.
British Columbia								
Carnation Cr.	Feb-May (Mar)						Hartman and Scrivener 1990	
Washington								
Snow and Salmon Cr.	(Jan-Apr)			303 (203-438)			Michael 1989	First return fish dominate immigration. (Some fish were immature but proportion not noted in paper).
Clearwater R.	not determined (probably Sept-Oct)		5 (84%)	292 (251-355)		25	Fuss 1982	Termed anadromous by scale analysis. Five of age-5 fish spawned again at age 6; a higher percentage of returns are mature compared with (Puget Sound) populations.
			5 (57%)	237 (216-272)		14		Freshwater forms identified by a spawning check at age 3 or older in absence of saltwater growth, and small body size at age 4 or 5.
Stillaguamish R.	not determined		(20-27%)	322 (235-420)	total	52	Johnston 1979	Creel census data. Eighty-five percent were first returns (60% of first returns would not spawn); ages of mature fish not given.
				301	males	26		
				342	females	26		

Table 5. (Continued).

Region **River System**	**Entrance timing (peak mo.)**	**Mean age at return (% total)**	**Age at maturity (% mature)**	**Average size, mm (range)**	**Sex**	**Sample Size**	**Citation**	**Notes**
Oregon								
N. Fork Willamette R.	Jan		5				Nicholas 1978a	Freshwater cutthroat blocked by dam at RKm 1.6 and impassable falls at RKm 62.
				304			OSGC 1949	Sea-run cutthroat trout p. 9; avg. length for adults captured on initial migration.
Sand Cr.	July-Feb (Nov)		5	345 (254-472)			Sumner 1962	Oldest - age 10.
Alsea estuary	June-Sept (July)						Giger 1972	
Alsea R.		3 (52.4)					Giger 1972	
Siuslaw R.		3 (60.4)					Giger 1972	
Nestucca R.		3 (37.4)					Giger 1972	
Flynn Cr.	Oct-Mar (Dec)	sea-run 4 (41.2) freshwater form 4 (43.2)					Moring and Lantz 1975	The authors distinguished between forms by scale analysis. Large spacing in scale circuli were considered indicative of ocean growth. Fish without evidence of large growth periods were deemed freshwater fish.
Deer Cr.	Oct-Mar (Dec)	sea-run 4 (47.9) freshwater form 3 (48.6)					Moring and Lantz 1975	"
Needle Branch Cr.	Nov-Jan (Dec/Jan)	freshwater form 3(55.9)					Moring and Lantz 1975	"

Table 5. (Continued).

Region River System	Entrance timing (peak mo.)	Mean age at return (% total)	Age at maturity (% mature)	Average size, mm (range)	Sex	Sample Size	Citation	Notes
Rogue R.	not determined (prob. Feb-Mar)						Tomasson 1978	Of 27 in second season in estuary, only 14 spawned previous spring.
California								
Smith R.	late July-November			(232-390)			Howard and Albro 1997	
Redwood Cr. estuary	July- Sept (Sept)						Redwood National Park 1983, 1988-93	
Mad R.	Aug-Nov (Sept)						Wesloh footnote 10	

Straying and refuge or feeding migrations versus reproductive straying

Few tagging studies of coastal cutthroat trout (e.g., Giger 1972; Jones 1975,1976; Jones and Seifert 1997) address the question of straying rates. Studies that have been conducted often use hatchery fish (Giger 1972), whose behaviors may differ from natural fish. Most studies are also confounded by the difficulty in distinguishing overwinter nonreproductive migrations from spawning migrations (Jones 1975, 1976; Jones and Seifert 1997).

In tagging studies on Petersburg Creek in southeastern Alaska, Jones (1975, 1976) reported that many tagged natural fish wandered to nearby streams during their first year's return to fresh water. As second-year migrants, a much higher proportion of tagged fish were captured in their home stream. Overall, Jones (1976) found that less than 50% of initial returning migrants were sexually mature and suggested that first-year fish found wandering to nonnatal rivers were on feeding runs.

From 1966 to 1970, Giger (1972) conducted more than 23 separate releases of marked Alsea River hatchery fish into the Nestucca, Alsea, and Siuslaw rivers in Oregon. A planned comparative study with natural fish could not be assessed because of low numbers of outmigrants tagged and tag losses at sea. Unfortunately, most of the data collection occurred in the same year or the year following the release, and it is not possible to tell whether these were true strays or juveniles on feeding or refuge migrations. However, extensive data were collected and analysis reveals a complex pattern of coastal cutthroat trout movement among these three rivers. Apparent directional straying southward along the coast was found in four of the five years studied. Giger attributed the directionality in straying to marine conditions such as ocean currents rather than to behavioral characteristics. He also suggested the straying may result from poor imprinting on rivers where the fish are released due to the speed of out-migration after release. The average percentage of fish straying varied from 0% (Siuslaw to Nestucca rivers) to 18.4% (Alsea to Siuslaw rivers). The greatest magnitude of straying for a single release (out of a total of 23 separate release groups) was for a May 1967 Alsea River release from which nearly 30% of the fall returns were taken in the Siuslaw River fishery.

Like Jones (1976), Johnston (1982) suggested that sexually immature first-year migrant coastal cutthroat trout may conduct feeding runs to nonnatal rivers. Johnston also proposed that the fish will home to natal streams the following year, when a larger proportion are sexually mature.

Interactions of Coastal Cutthroat Trout with Other Salmonids

Studies of the fossil record and natural distributions of Pacific salmon and trout suggest that coastal cutthroat trout may have been the first salmonid to colonize the western United States (Behnke 1992). Many coastal cutthroat trout populations became well established before other species of salmonids were abundant, and they remained isolated from these other species for thousands of years (Behnke 1979, 1992; Johnston 1982). As an example, the only native fish historically present with the Yellowstone cutthroat trout in Yellowstone Lake, Wyoming, was the longnose dace (*Rhinichthys cataractae*) (Gresswell and Varley 1988). In another example, only eight other fish species historically occurred in the Lahontan Basin in Nevada and California along with the Lahontan cutthroat trout (Behnke 1992).

Because of this isolation, many interior species of cutthroat trout never competed with other salmonid species, and introductions of other salmonids (primarily rainbow trout) into the American west resulted in a dramatic decline of many interior cutthroat trout populations (Greswell 1988, Behnke 1992). This decline occurred in part through habitat modification and destruction (e.g., Clancy 1988), but is primarily attributed to interspecific interactions such as introgressive hybridization (Behnke 1992; Allendorf and Leary 1988), predation (reviewed in Marnell 1988), and competition (Griffith 1988).

It is worthwhile noting that one study (Platts 1974) found that westslope cutthroat trout density peaked at a channel gradient of about 10%, a steeper gradient than is associated with peak densities of bull trout, rainbow trout, or brook trout (*Salvelinus fontinalis*). Platts suggested that the cutthroat trout in this study represented populations in gradients least preferred by other salmonids.

Coastal cutthroat trout are believed to have been less severely affected by these interspecific interactions because they evolved in close contact with other salmonids. Coastal cutthroat trout have developed a variety of habitat-partitioning techniques and life histories, all of which may reduce competition with other species and help reduce opportunities for hybridization (Johnston 1982, Campton and Utter 1987, Griffith 1988).

Cutthroat trout have been documented to change their behavior in the presence of other salmonids such as steelhead/rainbow trout (reviewed in Griffith 1988), char (Andrusk 1968, Andrusak and Northcote 1970, Northcote 1995) and coho salmon (Glova 1984, 1986). In studies where cutthroat and rainbow trout or steelhead occupied the same watersheds, cutthroat trout have been found primarily in the headwater tributaries, while steelhead and rainbow trout occupied the larger river reaches (Hartman and Gill 1968, Edie 1975, Hanson 1977, Jones 1978, Nicholas 1978a, Johnson et al. 1986). Nicholas (1978a) also found that cutthroat trout in western Oregon streams grew more slowly and matured at an earlier age than did sympatric rainbow trout. Cutthroat trout also spawned earlier in the spring and in smaller or different tributaries than did rainbow trout. Nicholas believed this resource partitioning reduced the opportunity for hybridization and helped maintain the integrity of the cutthroat trout populations.

In a study of lacustrine populations, Nilsson and Northcote (1981) found that coastal cutthroat trout showed changes in behavior, prey, and growth in the presence of rainbow trout. In laboratory studies, the rainbow trout were consistently more aggressive and quickly killed coastal cutthroat trout when paired together. However, the two species successfully coexisted in natural lake environments (Nilsson and Northcote 1981).

Dolly Varden and bull trout have also evolved sympatrically with coastal cutthroat trout in the Pacific Northwest (Brown 1992). Like coastal cutthroat trout, these char may use a variety of habitats, including lakes, marine areas, rivers, ponds, and headwater tributaries. However, these species seem to be partitioned by a temperature gradient, and char are seldom found in streams with summer temperatures exceeding 18°C (Allan 1980, Shepard et al. 1984). In northern Puget Sound tributaries, Dolly Varden apparently also spawn and rear higher in headwater tributaries than do coastal cutthroat trout. Kraemer[11] suggests this is due to an 8°C spawning threshold for Dolly Varden. In Washington, Wydoski and Whitney (1979) report Dolly Varden spawning activity was most intense at 5°C to 6°C. Studies of Dolly Varden and coastal cutthroat trout occurring together in lakes have generally concluded that, in competitive situations, the char tend to be excluded from the upper water column and feed on benthic prey while coastal cutthroat feed on surface prey (Andrusak and Northcote 1971, Schutz and Northcote 1972).

Juvenile coho salmon have also been shown to be dominant over juvenile cutthroat trout in field (Giger 1972, Glova 1984) and laboratory studies (Glova 1986, Sabo and Pauley 1997). However, in both kinds of studies, coho salmon were dominant only when they were larger than cutthroat trout (Sabo and Pauley 1997). In the absence of larger coho salmon, cutthroat trout prefer to rear in pools (Giger 1972). When coho salmon are present, they virtually always dominate cutthroat trout fry because the juvenile coho salmon emerge from redds earlier and are large (Giger 1972, Sabo and Pauley 1997). Cutthroat trout juveniles then move to less-preferred lower-gradient riffle areas, where they remain until winter flows force changes because of displacement (Glova 1984, 1987; Glova and Mason 1977).

At least one subspecies of interior cutthroat trout has evolved sympatrically with other Pacific salmonid species; westslope cutthroat trout and rainbow trout/steelhead coexist in the Snake River Basin (Hanson 1977). In a study of abundance and distribution of the two species, Hanson (1977) found that in drainages where both occurred, cutthroat trout occupied upper portions of the stream and *O. mykiss* the lower portions. Hanson also determined that age-0 steelhead were larger than age-0 cutthroat trout and displaced previously established age-0 cutthroat trout, but that the smaller cutthroat trout could not displace steelhead. Hanson suggested there is "interactive segregation" of the co-occurring species despite–or because of–their apparent coexistence for thousands of years.

The effect of these interactions is not clearly understood and may differ depending on a variety of factors. Although cutthroat trout may be competitively excluded from preferred rearing habitats by larger coho salmon (Glova 1984, 1986, 1987) and steelhead (Hartman and Gill 1968), it has been suggested that in some cases this interaction may be positively correlated to anadromous cutthroat trout abundance. In Cummins Creek, which is contained within a wilderness area on the Oregon coast, cutthroat trout seem to grow more slowly and fewer smolts outmigrate in years with poor coho salmon runs. Coho salmon may consume some age-0 cutthroat trout, but it has been suggested that this may allow the remaining cutthroat trout to

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[11] C. Kraemer, WDFW, 16018 Mill Creek Blvd., Mill Creek, WA 98012-1296. Pers. commun. to O. Johnson. July 1998.

grow faster and result in better survival of anadromous cutthroat trout populations (T. Nickelson[12]).

Temperature Tolerance in Coastal Cutthroat Trout

Coastal cutthroat trout are exposed to a wide range of water temperatures across their distribution and, relative to other salmonids, little information on their habitat requirements is available (Hunter 1973, Golden 1975, Bjornn and Reiser 1991). Still, like other salmonids, coastal cutthroat trout have evolved to take advantage of temperature regimes in their home ranges. When abrupt changes occur in water temperatures or other physical factors, the fish usually compensate by seeking refugia, but changes from the normal pattern can reduce their survival (Golden 1975, Bjornn and Reiser 1991).

In several studies (Hunter 1973, Golden 1975, Behnke and Zarn 1976, Behnke 1992), cutthroat trout, like other salmonids, were not usually found in water temperatures higher than 22°C, although they could tolerate temperatures as high as 26°C for brief periods. Typically, adult fish appeared stressed when water temperatures rose above 22°C. At 28°C to 29°C the fish lost equilibrium and died, even if temperatures were gradually increased 1-2°C per day (Behnke and Zarn 1976). Juvenile cutthroat trout preferred water temperatures around 15°C. They also lost equilibrium and died between 28°C and 30°C (Heath 1963). A literature review by Bell (1986) reported lower and upper lethal temperatures of 0.5°C and 23°C for coastal cutthroat trout. Optimum temperatures for spawning ranged from 6.1°C to 17.2°C and for egg incubation from 4.4°C to 12.7°C.

Golden (1975) conducted experiments specifically on coastal cutthroat trout to determine the effects of fluctuating temperatures on lethal tolerance limits. He found acclimation significantly affected survival in the subspecies. Fish acclimated to temperatures of 13 to 23°C had lower survival rates when exposed to high temperatures than did fish acclimated only to 23°C or to temperatures ranging from 13 to 25°C. He also found that fish acclimated to both the 23°C and 13 to 23°C temperatures could withstand exposures to large diel cycles of up to 13 to 27°C daily variation with 10% or less mortality over 7 days.

Dwyer and Kramer (1975) calculated metabolic rates and scope for activity for an interior subspecies of cutthroat trout from a hatchery in Logan, Utah. In their experimental fish, active metabolism and the scope for activity was greatest at 15°C and lowest at 5°C. There was also a metabolic decline at 24°C, which the authors concluded is near the upper lethal temperature for this subspecies of cutthroat trout.

Temperature tolerance is difficult to study. Behnke (1992) described redband trout (*O. mykiss newberrii*) in eastern Oregon that seem to have adapted over thousands of years to high water temperatures. He reported that these fish actively feed and apparently thrive in waters

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[12] T. Nickelson, ODFW, P.O. Box 59, Portland, OR 97207. Pers. commun. to O. Johnson. Nov. 1993.

of 28.3°C. Other populations do not seem to successfully adapt to high temperatures. In the Firehole River, Yellowstone National Park, introduced redband trout have lived for 60-70 years in water temperatures that may reach 29.5°C (Kaya 1977). Adaptation to this warm water might be expected, but in a series of experiments Kaya (1978) found that these redband trout survived less than 2 hours at 29.5°C and stopped feeding at 23°C to 24°C, even when water temperature was gradually increased. He suggested that the fish, rather than adapting to the hot water, were able to find refuge in cooler water and avoid the higher temperatures.

Based on the above information, the biological significance of temperature, as seen in southern Oregon and northern California (e.g., the Rogue and Umpqua rivers) and discussed in the "River Water Temperature" section in Johnson et al. (1994), remains unclear.

Genetic Information

Previous sections examined evidence for phenotypic and life-history differences between populations or groups of populations of coastal cutthroat trout that might be used to identify ESUs. The genetic basis of many phenotypic and life-history traits, however, is often weak or unknown, and consequently population differences in these traits provide little information on reproductive isolation between populations. The BRT considered molecular genetic evidence that might be used to define reproductively isolated populations or groups of populations of coastal cuttroat trout. These genetic markers are presumably unaffected by selection but may change in response to mutation, genetic flow, and genetic drift. The analysis of the geographical distributions of these markers may reveal historical dispersals, equilibrium levels of migration (gene flow), and past isolation. Most of this evidence is based on the analysis of protein variants (allozymes), microsatellite loci (variable numbers of short tandem deoxyribonucleic acid [DNA] repeats), and mitochondrial DNA (mtDNA). Genetic variability among populations of coastal cutthroat trout has been examined throughout much of the geographical range of this species with allozyme electrophoresis, and in some regions with mtDNA or microsatellite loci. Available genetic data were also used to assess the relationship between migratory and nonmigratory populations to understand the effects that nonmigratory populations might have on anadromous populations. The BRT's deliberations on defining population units also considered the effect hybridization with steelhead or rainbow trout would have on genetic population structure. Unlike other West Coast species of Pacific salmon, coastal cutthroat trout show evidence of widespread hybridization with *O. mykiss*.

Statistical Methods

Several standard statistical methods have been used to analyze molecular genetic data to detect reproductive isolation between populations. Comparisons of genotypic frequencies in a sample with frequencies expected under random mating (Hardy-Weinberg proportions) may be used to infer the breeding structure of a population or to detect population mixing (Wahlund's effect). Contingency table comparisons of allozyme or microsatellite allele frequencies among population samples with chi-square or G (log likelihood ratio) test statistics or with randomization tests have been used to detect significant differences between populations, which may be evidence of reproductive isolation.

Another way of assessing genetic isolation between populations is to analyze genetic distances based on allele-frequency estimates. Several genetic distance measures (e.g., Cavalli-Sforza and Edwards 1967; Nei 1972, 1978) have been used to study the population genetic structure of anadromous salmonids. It is unclear, however, which measure is most appropriate in a particular case or whether one measure is always most appropriate. Discussions of the features of genetic distances appear in Nei (1978), Rogers (1991), and Hillis et al. (1996). Most of this discussion has focused on the merits of the various measures for phylogenetic reconstruction among species or higher taxa. To our knowledge, no one has quantitatively evaluated the performances of these distances in assessing genetic differentiation among populations within species such as anadromous salmonids, which typically show small genetic distances between conspecific populations (populations of the same species). An attractive feature of Cavalli-Sforza and Edwards' distance (D_c) is that it satisfies the triangle inequality; that is, given three populations (A, B, C), the sum of the distances between A and B and between B and C is always greater than the distance between A and C. Neither of these genetic distance measures, however, employs a correction for sample size, so distances are biased upward, especially for small sample sizes. In contrast, Nei's (1978) unbiased genetic distance, D_n, corrects for this bias but does not always satisfy the triangle inequality.

Sample sizes and heterozygosity may also influence the power of the genetic distance approach to resolve genetic population structure. When sample sizes used to estimate allelic frequencies are 50 individuals or more, the difference between Nei's genetic distance (Nei 1972) and Nei's unbiased genetic distance (Nei 1978) is small, but might still be a substantial proportion of D if D is small. When genetic distances between populations are also small, as they often are between populations of both salmon and anadromous trout, low but significant levels of genetic differentiation may not be detected by an unbiased distance measure because sample size corrections may reduce estimates of genetic distance to zero. Another consideration is that D_n may be affected by different levels of heterozygosity between populations, whereas D_c apparently is not.

Since it is unclear which distance measure is most appropriate in any given application, we analyzed sets of data with Nei's unbiased and Cavalli-Sforza and Edwards' genetic distances to identify results that were robust to the choice of the distance measure used. D_n tends to minimize distances between genetically similar samples consisting of only a few individuals and ranges from 0.0 (no difference) to infinity. D_c, on the other hand, tends to magnify distances between closely related samples and diminish distances between distantly related samples. This measure ranges from 0.0 (identity) to 1.0 (complete dissimilarity). In most cases, the different genetic distance measures yield highly correlated results.

The degree of reproductive isolation between populations can be inferred from an analysis of the pattern of genetic distances between populations. Clustering methods, such as the unweighted-pair group method with averages (UPGMA), (Sneath and Sokal 1963) and the neighbor-joining method (Saitou and Nei 1987), find hierarchical groupings of genetically similar populations. Multivariate methods, such as multidimensional scaling (MDS) (Kruskal 1964) or principal components analysis (PCA), find groupings of genetically similar populations in several dimensions, which are depicted here in two or three dimensions. MDS analysis produces a plot of samples in which the distances between samples in the plot are linearly related to the genetic distances between them. When the geographical distribution of genetic variability is not hierarchical or disjunct, such as in a clinal or reticulate pattern of differentiation, MDS and PCA more accurately depict relationships among samples than do agglomerative methods such as the UPGMA (Lessa 1990). In a UPGMA analysis, information about the relationship between the incoming sample and the individual samples already in the cluster is lost; this algorithm compares the genetic distance of an incoming sample to the average genetic distance between samples already in a cluster. MDS, on the other hand, is a nonmetric ordination technique that attempts to find the shortest genetic distances between samples in *n*-dimensional space without averaging. A related technique, applying PCA to allelic frequencies, can also be used to examine genetic relationships among populations. In our experience, the results of a PCA are usually similar to MDS ordinations for a set of data. A minimum spanning tree between samples can be used to detect distortions in three-dimensional views of a PCA or MDS ordination. Samples that appear to be close to one another in one view of an ordination may be far apart in another view. Reproductive isolation between populations can be inferred from a visual examination of these plots to find clusters of genetically related populations that were consistent with sample geography in the clusters.

Various studies have estimated levels of genetic variability within populations because the level of within-population variability may reflect evolutionary or historical differences in population size and migration patterns between populations. Within-population gene diversity was measured by the expected proportion of heterozygous genotypes in a population of randomly mating individuals averaged over the number of loci examined (H). Estimates of H based on a small number of individuals are usually accurate, as long as enough loci (>30) are surveyed for variability (Nei 1978).

Genetic differentiation between populations at various hierarchical levels has been estimated in many studies with a gene diversity analysis (Nei 1973, Chakraborty 1980), which apportions allele frequency variability among populations into its geographical or ecological components. For example, the proportion of the total genetic variability in a set of samples that is due to differences among populations may be estimated with $G_{ST} = (H_T - H_S)/H_T$, where H_S is the average within-population heterozygosity and H_T is the total heterozygosity in the pooled samples disregarding geographical subdivision. The standardized variance of allele frequencies among populations, F_{ST}, is equivalent to G_{ST} when only two alleles occur at a locus. Most genetic variability in salmonids occurs as genotypic differences among individuals within a population (Ryman 1983). A smaller proportion of the total variability is due to hierarchical differences between regions, river systems, tributaries and streams within a river system, between years, or between run types. The range 0.05-0.15 for G_{ST} or F_{ST} indicates moderate differentiation, and the range 0.15-0.25 indicates strong genetic differentiation among populations (Wright 1978). These statistics facilitate comparisons among groups of populations that may reveal regional differences in gene flow between populations, or the effects of hatchery strays on levels of differentiation between populations.

Migratory vs. Nonmigratory Populations

One important consideration in defining population units for conservation is to understand the genetic relationships between the various life-history types of coastal cutthroat trout, which often occur in the same river drainage. Freshwater migratory and nonmigratory forms have also been observed in other salmonids, including Arctic char, brook trout, brown trout, rainbow trout, and sockeye salmon. Small (but significant) allele frequency differences have been observed between landlocked and anadromous populations of brown trout (Hindar et al. 1991, Skaala and Naevdal 1989), sockeye salmon (Foote et al. 1989), rainbow trout (Allendorf and Utter 1979, Currens et al. 1990, Northcote 1970), and Atlantic salmon (Ståhl 1987). The relationship between migratory and nonmigratory individuals, however, varies between species and between populations of the same species.

For example, Northcote's study (1969) of migratory behavior in rainbow trout populations in the Pacific Northwest found a greater tendency for downstream migration in juvenile rainbow trout from populations below waterfalls than for juveniles from populations above waterfalls. Rivers below waterfalls would be expected to be more productive than rivers above falls, due in part to nutrients contributed by returning anadromous fish. More productive rivers result in faster-growing juveniles with perhaps a greater tendency to outmigrate. A genetic tendency for nonmigratory behavior would be advantageous at localities above waterfalls and where downstream migration would lead to the loss of individuals from the upstream population (Northcote 1992). Historical biogeographic considerations imply that landlocked populations in each species have been derived from anadromous populations in the same general area, even though detectable genetic differences occur between nonmigratory brown and rainbow trout populations isolated by falls or in lakes and nearby sea-run populations of the same species.

The variability of relationships between migratory and nonmigratory individuals is illustrated by several studies of brown trout in Scandinavia. In a study of allozyme variability, Hindar et al. (1991) found that samples of sea-run and nonmigratory brown trout (identified by scale patterns) clustered by locality, rather than by life-history type. Jonsson (1982) found that juvenile brown trout captured in a lake with sea access migrated downstream more often than fish captured in a lake above an impassable waterfall migrated upstream. Nevertheless, Jonsson (1982) found that both sea-run and nonmigratory parents gave rise to progeny that could follow either life-history pattern. In another study of brown trout, Jonsson (1985) measured migration, age distribution, age at sexual maturity, growth, and fecundity in migratory and nonmigratory individuals, and concluded that different life-history types were components of the same genetic population. In a study of brown trout populations in France, Baglinière et al. (1989) found both spatial and temporal separation in spawning between migratory and nonmigratory segments of a population in the same stream.

In coastal cutthroat trout, the genetic significance of nonmigratory, freshwater migratory, or anadromous fish in populations has been difficult to assess. It is not always possible to identify individuals in a genetic sample that have migrated or may have been destined to migrate to the ocean. Scale analysis can be used to infer whether coastal cutthroat trout have migrated to sea, but analysis of scale growth patterns is not always a reliable means of establishing migratory behaviors (see "Life History," p. 38, for a brief discussion of the problems in coastal cutthroat trout scale analysis). Analysis of otolith growth patterns or microchemistry may provide more accurate results, but is costly and time consuming and has not been widely used to identify sea-run fish in genetic studies. Based on studies of other salmonids with sea-run and nonmigratory life-history patterns, nonmigratory individuals may co-occur with anadromous individuals in the same stream (e.g., Hindar et al. 1991). The extent to which sea-run and nonmigratory life-history forms of coastal cutthroat trout co-occur in a particular stream is unknown. Most assessments of the genetic relationships between migratory and nonmigratory populations of coastal cutthroat trout have been made by comparing populations above and below barrier waterfalls. Although the fish may not be able to swim upstream, downstream migration over some waterfalls may still be possible and may lead to at least one-way gene flow between migratory and nonmigratory populations.

The level of genetic divergence between migratory and nonmigratory populations of coastal cutthroat trout also appears to be variable, as are the levels of divergence between life-history types in other trouts. Some freshwater populations of coastal cutthroat trout above barrier waterfalls (possibly nonmigrants or freshwater migrants) show strong genetic differences from below-barrier populations in the same area. For example, in a study of allozyme variability in coastal cutthroat trout populations in Hood Canal and northern Puget Sound, Campton and Utter (1985) found that sea-run populations tended to be genetically more similar to one another than to an above-barrier freshwater population (Howe Creek) in the Hood Canal drainage.

A study of coastal cutthroat trout populations in a tributary of Washington's Nisqually River by Zimmerman (1995) also showed the largest genetic differences between sea-run and putative nonmigratory populations. Zimmerman (1995) surveyed allele frequency variability at 14 polymorphic allozyme-encoding loci in samples from six localities in Muck Creek and found the greatest number of significant differences in allele frequency between a sample from Chambers Lake (with sea-run individuals) and samples taken upstream (considered by their size and appearance to be from nonmigratory populations). No clear barriers to migration were present between these sea-run and apparently nonmigratory populations. The amount of divergence between these two groups, however, was small; genetic distances between the anadromous population and nonmigratory populations averaged about $D_n = 0.01$.

Other studies show variable degrees of divergence between sea-run and freshwater migratory/nonmigrant populations of coastal cutthroat trout. Griswold (1996) sampled coastal cutthroat trout above and below waterfall barriers (populations below the barrier had access to the ocean) to measure genetic divergence between putative sea-run and freshwater coastal cutthroat trout populations in the same stream. Griswold (1996) collected samples in two widely separated river drainages: Vixen Inlet in southeastern Alaska and Elk River, Oregon. Samples were examined for variability at 41 allozyme loci; 12 were polymorphic in the Elk River samples and 9 were polymorphic in the Vixen Inlet samples. One of the below-barrier Elk River samples appeared to contain genetic markers indicating a large number of *O. clarki* × *O. mykiss* hybrids and was not used to make comparisons. For the Elk River samples, the sums of chi square contingency table tests of allele frequencies between samples were significant for all pairs of samples except one above- and below-barrier comparison. However, a correction for multiple tests of the same hypothesis apparently was not made, so the significance of some of these tests may be due to Type I error. In the Vixen Inlet drainage, all chi square tests were significant except for one comparison between below- and above-barrier samples. These data together indicate that below- and above-barrier populations may or may not be genetically different from each other.

In summary, the few existing studies of cutthroat trout show that, although both allele frequencies and morphology may differ between populations above barriers and potentially sea-run populations below barriers, these life-history forms generally show close genetic relatedness in the same drainage relative to genetic population differences among drainages. These results indicate that sea-run and freshwater migratory/nonmigratory populations appear to represent a single evolutionary lineage in which the various life-history patterns have repeatedly appeared in different geographic regions. Variability in migratory behavior within populations may nonetheless have some genetic basis.

Hybridization and Introgression

Genetic divergence among subspecies of cutthroat trout

As many as 15 subspecies of cutthroat trout have been recognized, and all but one, *O. c. clarki*, are limited to inland waters. A phylogenetic analysis of seven of these subspecies and of rainbow trout indicated that Yellowstone cutthroat trout consisted of at least five closely related nominal subspecies (Yellowstone, Colorado, Snake River, greenback, and Rio Grande) that, as a group, showed substantial biochemical genetic divergence from westslope, Lahontan, and coastal cutthroat trout (Allendorf and Leary 1988). Nei's genetic distance between the Yellowstone complex of subspecies and the remaining three subspecies averaged 0.212 (Allendorf and Leary 1988), which is typical of values between related fish species. Westslope, Lahontan, and coastal cutthroat trout showed considerably greater divergence from one another than did the five subspecies of Yellowstone trout. Unexpectedly, a sample of Westslope, Lahontan, and coastal cutthroat trout were as similar to rainbow trout as they were to the subspecies in the Yellowstone complex. Coastal cutthroat trout showed nearly the same level of divergence from rainbow trout ($D_n = 0.099$) as it did from Lahontan cutthroat trout ($D_n = 0.077$). In contrast, morphological (Behnke 1992), karyotypic (Gold et al. 1977, Loudenslager and Thorgaard 1979, Thorgaard 1983), and mtDNA (Gyllensten et al. 1985, Shedlock et al. 1992) data indicate that the major subspecies of cutthroat trout are more closely related to one another than they are to rainbow trout. The reason for the close relatedness of rainbow trout to some subspecies of cutthroat trout is unclear, but may be the result of persistent hybridization in areas where the species have come into contact with one another.

Hybridization between cutthroat trout and *O. mykiss*

Several studies have reported hybridization between various subspecies of cutthroat and rainbow trout and between coastal cutthroat trout and steelhead. Although there is a substantial genetic (Loudenslager and Gall 1980, Leary et al. 1987, Allendorf and Leary 1987) and karyotypic divergence in chromosome number between westslope cutthroat ($2n = 66$) and Yellowstone cutthroat ($2n = 64$) trout (Loudenslager and Thorgaard 1979) and between these subspecies and rainbow trout ($2n = 60$, Gold 1977), westslope cutthroat trout hybridize with both taxa. Allendorf and Leary (1988) found evidence of hybridization between westslope cutthroat trout and Yellowstone or rainbow trout (or both) in 32 of 80 samples (40%) considered to be pure westslope trout. A genetic analysis of samples from the Flathead River drainage in Montana showed that only 2 of 19 headwater lakes harbored populations of pure westslope cutthroat trout and that gene flow was occurring between introgressed and downstream populations (Marnell et al. 1987). Extensive hybridization has also been documented between Yellowstone cutthroat trout and rainbow trout (Allendorf et al. 1987, Martin et al. 1985), between Paiute and coastal cutthroat trout (Busack and Gall 1981), and between coastal cutthroat trout ($2n = 68$, Gold 1977) and steelhead (Campton and Utter 1985). Although chromosome numbers may differ between these taxa, the total number of arms (104-106) is similar among taxa, and Robertsonian (chromosome arm fusion) polymorphisms are common within these trout species (e.g., Thorgaard 1983). Similarity in chromosomal arm number and substantial gene duplication in salmonids permits these taxa to hybridize without major developmental incompatibilities (Ferguson et al. 1985, 1988).

Hybridization between coastal cutthroat trout and *O. mykiss* has been detected with molecular methods in many West Coast drainages (Table 6). Neillands (1990) surveyed genetic variability in nine tributaries to Prairie Creek and in five tributaries to Redwood Creek (both in Northern California), and in a sample from the Redwood Creek embayment. The Campton and Utter (1985) hybrid index (relative probability that the multilocus genotype of a particular fish could have arisen by random mating within two species) was used to identify pure and hybrid individuals from allozyme genotypes, and gametic disequilibrium (nonrandom association of alleles between loci) was used to measure the consequences of hybridization. Four loci (*IDDH-2**, *IDHP-3,4**, *MEP-4**, and *PEP-A**) appeared to distinguish between coastal cutthroat trout and *O. mykiss*. The hybrid index indicated that 8 of the 15 samples had hybrid index values that indicated the presence of hybrid individuals. Departures from Hardy-Weinberg genotypic proportions in some samples indicated they were composed of individuals from more than one population. Estimates of gametic disequilibrium were significantly greater than zero in the coastal cutthroat trout components in four streams and for the hybrid component in one stream. None of the *O. mykiss* subsamples showed evidence of gametic disequilibrium. These results indicate that hybridization in the Redwood Creek drainage is extensive and that introgression

Table 6. Streams and broodstock reported to have putative hybrids between coastal cutthroat trout and *Oncorhynchus mykiss*. Method of detection: A = allozymes; M = microsatellites; P = PINEs (paired interspersed nucleotide elements).

Locality	Method	Reference
Washington		
Nooksack R.		
Double Ditch Cr.	A	NMFS et al. unpubl. data
	M	Wenburg et. al. 1998
Skagit R.		
Wiseman Cr.	A	NMFS et al. unpubl. data
Bulson Cr.	A	NMFS et al. unpubl. data
Stillaguamish R.		
Stream No. 172	A	NMFS et al. unpubl. data
Harvey Cr.	A	Campton and Utter 1985
	A	Hawkins 1997
Covington Cr. (Green R.)	A	NMFS et al. unpubl. data
	M	Wenburg et al. 1998
Southern Puget Sound		
Johns Cr.	A	NMFS et al. unpubl. data
Kennedy Cr.	A	NMFS et al. unpubl. data
Burley Cr.	A	NMFS et al. unpubl. data
Hood Canal		
Tarboo Cr.	M	Wenburg 1998
Big Beef Cr.	M	Wenburg 1998
Seabeck Cr.	M	Wenburg 1998
Stavis Cr.	A	NMFS et al. unpubl. data
	M	Wenburg et al. 1998, Wenburg 1998
Big Mission Cr.	A	Campton and Utter 1985
	M	Wenburg 1998
	A	Hawkins 1997
Courtney Cr.	M	Wenburg 1998
Bear Cr.	M	Wenburg 1998
Strait of Juan de Fuca		
Gierin Cr.	M	Wenburg et al. 1998
Salt Cr.	A	NMFS et al. unpubl. data
	M	Wenburg et al. 1998
Whiskey Cr.	A	NMFS et al. unpubl. data
Olympic Peninsula		
Goodman Cr.	M	Wenburg et al. 1998
Southwestern Washington		
Aberdeen Fish Hatchery	A	NMFS et al. unpubl. data

Table 6. (Continued).

Locality	Method	Reference
Columbia R.		
Beaver Cr. Fish Hatchery, WA	A	NMFS et al. unpubl. data
Multnomah Cr., OR	A	NMFS et al. unpubl. data
	P	Spruell unpubl. data
Clackamas R.		
Oak Grove Cr.	P	Spruell unpubl. data
Sandy R.	P	Spruell unpubl. data
Hood R.		
Tony/Bear Cr.	P	Spruell unpubl. data
Robin Hood Cr.	P	Spruell unpubl. data
Lower Dog R.	P	Spruell unpubl. data
Upper Dog R.	P	Spruell unpubl. data
Mill Cr.	P	Spruell unpubl. data.
Oregon		
Willamette R.		
McKenzie R.	A	NMFS et al. unpubl. data
Oregon coast Yaquina R.	A	NMFS et al. unpubl. data
Alsea R.	A	NMFS et al. unpubl. data
Elk R.	A	Griswold 1996
Umpqua R.		
Coffee Cr.	A	NMFS et al. unpubl. data
Pass Cr.	A	NMFS et al. unpubl. data
Coos R.		
Fall Cr.	A	NMFS et al. unpubl. data
Coquille R.		
E. Fork Coquille R.	A	NMFS et al. unpubl. data
Camas Cr.	A	NMFS et al. unpubl. data
Wooden Rock Cr.	A	NMFS et al. unpubl. data
Rogue R.		
Williams R.	A	NMFS et al. unpubl. data
Saunders Cr.	A	NMFS et al. unpubl. data
Southern Oregon		
Wilson Cr.	A	NMFS et al. unpubl. data
California		
Tarup Cr. (Klamath R.)	A	NMFS et al. unpubl. data
Redwood Cr.		
Tom McDonald Cr.	A	Neillands 1990
MacArthur Cr.	A	Neillands 1990
Prairie Cr.		
Larry Dam Cr.	A	Neillands 1990
May Cr.	A	Neillands 1990
Boyes Cr.	A	Neillands 1990

Table 6. (Continued).

Locality	**Method**	**Reference**
Headwaters Prairie Cr.	A	Neillands 1990
Godwood Cr.	A	Neillands 1990
Wolf Cr.	A	Neillands 1990

between coastal cutthroat trout and steelhead in some streams has been occurring over several generations, which is long enough for the decay of gametic phase disequilibrium by chromosomal recombination.

An analysis of paired interspersed nucleotide elements (PINEs) of genomic DNA was used to identify coastal cutthroat trout, *O. mykiss*, and hybrids between these taxa in 29 samples from the Clackamas, Sandy, and Hood rivers and from streams entering the Lower Columbia River (P. Spruell[13]). Seven samples contained individuals of only *O. mykiss*, while 11 samples contained only coastal cutthroat trout. Seven samples contained a substantial proportion of hybrid fish in addition to apparently pure coastal cutthroat trout and *O. mykiss*. Some streams appear to harbor hybrid swarms between the two taxa. These results showed a mosaic distribution of coastal cutthroat trout, *O. mykiss*, and hybrids among streams.

In a survey of genetic variability in coastal cutthroat trout, Campton and Utter (1985) found hybrids between cutthroat trout and *O. mykiss* in 2 of 23 streams. To estimate the extent of hybridation in these two streams and to understand the nature of hybridization, they sampled Big Mission Creek in Hood Canal at three sites, 0.8, 5.4, and 8.8 km from the mouth, and Harvey Creek, a tributary to the Stillaguamish River, at 1.9, 2.4, 2.9, and 3.2 km from the mouth. They found that the geographic pattern of the occurrence of hybrids differed between these streams. In addition to these occurrences of hybridization in natural populations, they found a large proportion of hybrids in the Beaver Creek Hatchery coastal cutthroat trout brood stock. Given the distributions of genotypes among individuals, it appeared that many of the hybrid fish represented backcrosses and matings between first-generation (F_1) hybrid individuals. However, few fish with coastal cutthroat trout × *O. mykiss* features or hybrid genotypes have been observed as adults. Although hybridization occurs extensively, as evidenced by the many underyearling (0^+) hybrids, natural selection among older fish may greatly reduce the numbers of hybrids reaching maturity.

Hawkins (1997) used allozyme and mtDNA variability to identify hybrids in samples collected in 1992-94 from Big Beef and Big Mission creeks in Hood Canal and from Harvey Creek in the Stillaguamish River. The number of steelhead and coastal cutthroat trout mtDNA haplotypes among 23 individuals identified as hybrids with allozyme markers was similar; 12 had cutthroat mtDNA haplotypes and 11 had steelhead. Nine of the 12 hybrids with cutthroat haplotypes were identified as backcrosses or introgressed individuals with allozymes. Five of the 11 hybrids with steelhead haplotypes were backcrosses or introgressed individuals.

Hawkins (1997) also studied several behavioral, morphological, and performance traits in artificially produced hybrids between hatchery strains of coastal cutthroat trout and steelhead. In one study, Hawkins measured egg size and time of emergence in pure strains of coastal cutthroat trout and steelhead from the Aberdeen (Washington) Hatchery and Eels Springs Hatchery, Shelton, Washington, and in hybrid individuals. These results indicated that decreased fertilization success or decreased embryonic viability did not appear to act as a post zygotic isolating mechanism between these coastal cutthroat trout and steelhead. Most of the differences

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[13] P. Spruell, University of Montana, Div. Biol. Sciences, Missoula, MT 59812-1002. Pers. commun. to S. Grant. Sept. 1998.

between coastal cutthroat trout and steelhead early development were correlated with larger egg size in steelhead. Hybrid individuals were intermediate between the pure strains for mortality from fertilization to hatching, time to hatching, body weight at hatching, body weight at emergence, growth 40-52 days post fertilization, and time to 50% change in yolk mass.

In a study of hybrids between hatchery strains of coastal cutthroat trout and steelhead, Hawkins and Quinn (1996) made reciprocal cutthroat-steelhead crosses and measured critical swimming speed in pure and hybrid individuals. Since migration is a pervasive and important feature of salmonid life histories, selective disadvantages in hybrid individuals may be apparent as swimming impairment. They found that hybrid fish had critical swimming speeds that were intermediate to speeds in pure hatchery strains, and that no paternal or maternal effects were apparent in hybrid performance. They also found that hybrid body shape was intermediate between coastal cutthroat trout and steelhead. These results are consistent with inherited differences in life-history patterns between coastal cutthroat trout and steelhead.

Several of these parameters may have fitness consequences in natural populations. In pure strains of coastal cutthroat trout and steelhead, the rate of development is presumably matched to larval body size and yolk size so that alevins emerge from the gravel when the stage of development is most conducive to survival. Hybrids, however, appear to develop too slowly from small eggs or too quickly from large eggs, depending on maternity, so they emerge with too little or too much yolk. The mismatch between egg characteristics and emergence time may limit the success of hybrids in natural populations and may therefore limit introgression. Swimming speed may also influence fitness. Steelhead tend to inhabit faster-moving water than do coastal cutthroat trout, and steelhead make longer marine migrations than do coastal cutthroat trout.

In summary, the results of these studies lead to these conclusions:

1. Hybridization between coastal cutthroat trout and steelhead is widespread throughout the range of coastal cutthroat populations on the West Coast.
2. Hybrid individuals have been detected most often among age 0^+ and 1^+ fish, but seldom among adults. However, the presence of introgressed individuals implies that hybrids can grow to maturity and reproduce.
3. Repeated sampling after about five generations in the same stream indicates that hybridization is ongoing in some areas (Big Mission Creek in the Hood Canal and Harvey Creek in the Stillaguamish River) and is not a sporadic event.
4. No developmental abnormalities (except for too much or too little yolk) appear to occur in hybrids. However, morphological and behavioral characteristics of hybrids may be disadvantageous in the natural environment, and may tend to limit the success of hybrids in the wild.

Studies of Regional Patterns of Genetic Variability

Only a limited number of studies of the genetic population structure of coastal cutthroat trout populations in the Pacific Northwest have been published in the last few years. Other studies are in graduate theses that have not yet been published. All but one of these studies included samples from a limited geographic range. NMFS, WDFW, and ODFW recently initiated a coastwide study of biochemical genetic variability in coastal cutthroat trout to help delineate groups of populations for management and conservation. Samples collected for this study were analyzed in the laboratory by NMFS and WDFW, and these data have been combined and summarized in this review. The NMFS/WDFW/ODFW study is discussed in "New Genetic Data" (p. 85); summaries of previous studies follow.

In the earliest genetic study of coastal cutthroat trout, Campton and Utter (1987) surveyed genetic variability with protein electrophoretic methods in populations of coastal cutthroat trout in 21 streams in Hood Canal and North Puget Sound. Analysis of allele frequencies at 31 loci in these samples revealed considerable within- and between-population genetic diversity. Twenty-one loci (68%) were polymorphic in at least one population, and sample heterozygosities (H, averaged over loci) ranged from 0.080 to 0.129 and averaged 0.097 among samples. A gene diversity analysis of allele frequencies reflected the results of the analysis of variance (ANOVA); diversities for year classes, streams, drainages, and regions were 1.17, 2.41, 1.01, and 1.24%, respectively. Seven of the 12 loci analyzed in the ANOVA were significant for stream effects, two for drainage effects, and seven for regional effects. A principal coordinate analysis (Everitt 1978) in two dimensions resolved at least two groups: 1) a north Puget Sound group including the Skagit and Stillaguamish rivers, and 2) a Hood Canal group. These results indicate that not only does significant regional differentiation between Puget Sound and Hood Canal exist on a scale of about 300 km, but also that significant small-scale differences exist between streams on a scale of a few kilometers.

On a geographic scale of about 20 km, Zimmerman (1995) measured genetic and morphological variability in six unreplicated samples of coastal cutthroat trout in Muck Creek of the lower Nisqually River, Washington. Fourteen of the 52 allozyme encoding loci examined with electrophoresis for Mendelian variability were polymorphic with a common allele frequency of $p < 0.95$. Average sample heterozygosities ranged from 0.042 to 0.057 and averaged 0.051 over samples. No geographic pattern appeared in the distribution of H among samples. Pairwise tests for allele-frequency differences and UPGMA cluster analyses of Nei's (1972) genetic distance indicated that the largest divergence was between the Chambers Lake sample and the remaining samples. These results show that significant, but weak, allele-frequency differences can arise between populations separated by only a few kilometers in the same drainage.

The analysis of microsatellite loci also indicated that allele-frequency shifts can occur over short distances. Wenburg et al. (1998) examined geographic variability at six highly polymorphic microsatellite loci in samples from 13 presumed sea-run populations of cutthroat trout in Washington State and in an outgroup sample of Yellowstone cutthroat trout. The sampled populations extended from southwestern Washington through the Strait of Juan de Fuca to Hood Canal and southern Puget Sound and were a subset of samples examined with protein electrophoresis by the WDFW (1998a). Individuals that appeared to be hybrids between coastal cutthroat trout and *O. mykiss* were identified by diagnostic alleles at two microsatellite loci and excluded from the statistical analyses. After removal of hybrid individuals, sample sizes for the microsatellite analysis averaged 38 fish each and therefore provided moderately precise estimates of allele frequencies.

High levels of microsatellite variability were detected. Mean sample heterozygosity averaged 0.67 with an average of 24 alleles per locus. Excluding the Yellowstone cutthroat trout outgroup sample, a gene diversity analysis of variance components indicated that 87.9% of the total gene diversity was due to within-sample variability, 5.4% was due to allele-frequency differences between streams within the six regions, and 6.7% was due to differences between the six regions in Washington State. Estimates of gene flow (private-allele method, Slatkin 1985) between streams within six regions averaged 1.7 fish per generation. The estimate of the number of effective migrants between all streams sampled was 3.2 fish per generation. This latter value may underestimate gene flow between neighboring streams if the pattern of exchange between streams follows the stepping-stone (rather than the island) model of migration.

In the Wenburg et al. (1998) study, Mantel's tests for association between geographic distance and pairwise F_{ST} and R_{ST} (an analogue of F_{ST} developed for microsatellite data) estimates of divergence were not significant, indicating an apparent lack of isolation by distance on the geographic scale of the study. However, geographically nearby samples tended to cluster together in a neighbor-joining tree of Cavalli-Sforza and Edwards (1967) distance; an exception was Covington Creek (southern Puget Sound), which clustered most closely with Salt Creek (Strait of Juan de Fuca). The neighbor-joining tree depicted an outer coastal group of samples and a group consisting of samples from Strait of Juan de Fuca, Hood Canal, and northern and southern Puget Sound. These results together indicate that migration between streams is sufficiently restricted on different geographic scales so that genetic differences can arise between streams as well as between regions.

On a small geographic scale, Wenburg (1998) examined variability at 10 microsatellite loci in 10 samples collected in Hood Canal, Washington that were separated by 2-100 km of shoreline distance. One sample was collected from a population located above a barrier falls. *O. mykiss* alleles appeared in seven of the 10 samples (24 of 472 fish). After removing putative hybrid individuals, he found large sample heterozygosities that ranged from 0.66 to 0.73 and averaged 0.69. Tests for genotype-frequency differences between two age-class samples collected from Stavis Creek were not significant for five of six microsatellite loci, indicating that (at least for this stream) annual variability was small compared to variability between streams.

Wenburg (1998) also estimated gene flow between streams along the eastern shore of Hood Canal in two ways. First, tag and recapture experiments provided an estimate of gene flow by recording the physical movements of fish between streams. Corrections were made for incomplete tagging, tag loss, and sampling efficiency. Expansions of direct counts of migrants between Big Beef Creek and three adjacent streams (Stavis, Little Anderson, and Seabeck creeks) ranged from 0 to 32.1 fish per generation. The physical presence of a fish in a stream is a necessary but not sufficient condition for estimating gene flow, and may substantially overestimate actual levels of gene flow. Second, indirect genetic estimates of gene flow were made by the private-allele method (Slatkin 1985) and by observed estimates of genetic differentiation between populations and the island model of migration. These indirect estimates of gene flow between Big Beef Creek and each of the three adjacent streams averaged 11.8 (range 3.8-22.1) fish per generation and were similar to direct estimates of straying from tag and recapture experiments. On a larger geographic scale, including nine streams in Hood Canal, indirect estimates of gene flow ranged from 6.0 (private alleles model) to 8.4 (F_{ST} and island model) fish per generation. These latter estimates were larger than previously estimated by Wenburg et al. (1998) between streams scattered over a similar geogaphic scale.

WDFW (1998a) presented the results of an allozyme analysis of 47 samples collected from seven broadly defined regions in Washington: 1) northern Puget Sound, 2) southern Puget Sound, 3) Hood Canal, 4) Strait of Juan de Fuca, 5) Olympic Peninsula, 6) southwestern Washington coast, and 7) Lower Columbia River. Most streams were sampled only once. A subset of samples from each of these regions was analyzed by Wenburg (1998) for microsatellite variability. After the removal of hybrids, WDFW (1998a) analyzed the samples in two ways. First, a contingency-table analysis (G-test) of allele frequencies was used to search for reproductive isolation between populations, but without Bonferroni corrections for multiple tests of the same hypothesis with different polymorphic loci. These results, therefore, probably overestimate the amount of reproductive isolation between populations and between population groups, due to Type I error (chance significance). Generally, contingency table tests of allele frequencies showed highly significant ($p < 0.001$) differences at all 33 polymorphic loci tested between samples within drainages except samples in Harvey Creek (Stillaguamish River) collected 1.2 km from each other. Highly significant differences were also found between samples from each of the seven regions, apparently indicating a high degree of reproductive isolation between regions.

The second approach used to search for distinct population groups was to construct UPGMA dendrograms from Cavalli-Sforza and Edward's (1967) genetic distances, D_C, between samples. Although dendrogram analysis is not a formal test of stock structure, such an analysis may be useful for depicting genetic relationships among stocks and for summarizing levels of genetic diversity among stocks. The dendrogram indicated the presence of two large groupings of coastal cutthroat trout populations, which was consistent with the results of Wenburg et al. (1998) for microsatellite variability. In addition to the two large groups, four samples, each from different regions, were outliers that fell outside the two major groups. One major group consisted of populations in Puget Sound, Hood Canal, and the Strait of Juan de Fuca. Within this group, the samples from northern Puget Sound formed one cluster and samples from southern Puget Sound, Hood Canal, and the Strait of Juan de Fuca formed another. Some samples from southern Puget Sound clustered most closely with samples from Hood Canal and the Strait of Juan de Fuca. A second major group consisted of populations from coastal Washington and the Lower Columbia River. In this group, samples from the Olympic Peninsula were distinct from samples from southwestern Washington and the Lower Columbia River.

Williams et al. (1997a, b) examined allele frequency variability and meristic characters in populations ranging from Northern California to Prince William Sound, Alaska. In an analysis of allelic frequencies for 43 populations, they found that coastal cutthroat trout were characterized by higher levels of genetic heterogeneity among local populations than were populations of Pacific salmon and other trout. Williams et al. (1997b) reported a G_{ST} value of 0.19 for the 43 populations surveyed and found that estimates of genetic distances (Nei 1978) between populations ranged from 0.01 to 0.063. Sample heterozygosities averaged 0.102 (range 0.071 - 0.157) (T. Williams[14]). In addition, Williams et al. (1997a, b) reported consistent genetic differences among populations in Alaska, Washington, Oregon, and California, but apparently less geographical structure within regions than has been observed among populations of other Pacific salmon and trout. A preliminary cluster analysis of Nei's (1978) genetic distances between populations in British Columbia indicated that southern mainland populations were genetically similar to coastal cutthroat populations in northern Puget Sound. Populations on Vancouver Island clustered separately from populations in Washington and mainland British Columbia (Williams footnote 14).

New Genetic Data

In our assessment of the degree of reproductive isolation between populations or groups of populations of coastal cutthroat trout, NMFS and WDFW jointly analyzed tissue samples collected from 97 localities in British Columbia (*n* = 1), Washington (*n* = 45), Oregon (*n* = 45), and California (*n* = 6) (Table 7, Fig. 16). We also included in some analyses comparable data for westslope cutthroat trout collected from hatchery broodstock (Anaconda, Montana), and steelhead trout from the Yaquina River, Oregon. A complete set of data is available for these 50 loci:

*mAAT-1** *sAAT-1** *sAAT-3** *ADA-1** *ADA-2** *ADH**
*mAH-1** *mAH-3** *sAH** *CKA-1** *CKB** *FH**
*bGLUA** *bGALA** *GDA-2** *GPIA** *GPIB-2** *G3PDH-1**
*GR** *IDDH-1** *mIDHP-1** *mIDHP-2** *sIDHP-1** *sIDHP-2**
*LDHA-1** *LDHA-2** *LDHB-1** *LDHB-2** *LDHC** *sMDHA-1**
*sMDHB-1** *sMEP-1** *sMEP-2** *mMEP-1** *MPI** *NTP**
*PEPA** *PEPB-1** *PEPD-1** *PEPLT** *PGDH** *PGK-1**
*PGK-2** *PGM-1** *PGM-2** *sSOD-1** *TPI-1** *TPI-2**
*TPI-3** *TPI-4**

Only the Alsea River (Oregon) was sampled in more than one year (1995 and 1997), but these samples were not combined for the analyses. Several factors, including the presence of hybrid individuals, uneven geographic sampling, and genetic outliers, dictated an extensive genetic

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[14] T. Williams, NMFS, SWFSC, PO Box 271, La Jolla, CA 92038. Pers. commun. to S. Grant. Oct. 1998.

Table 7. Locations, sample size (N), average heterozygosity (H), and probable migratory status (1 = above suspected barrier to sea access; 2 = below barriers, has sea access) of coastal cutthroat trout samples used in the genetic analyses conducted for this status review. Genetic outliers indicated with asterisk.

Locality	**N**	**H**	**1/2**
British Columbia			
Fraser R.			
1. Abbotsford Fish Hatchery	107	0.097	2
Washington			
Nooksack R.			
2. Double Ditch Cr.	47	0.101	2
Skagit R.			
3. Alder Cr.	57	0.079	2
4. Red Cabin Cr.	50	0.082	2
5. Walker Cr.	50	0.102	2
6. Wiseman Cr.	51	0.092	2
7. Bulson Cr.	48	0.098	2
8. Lake Cr.	50	0.093	2
9. Parker Cr.	50	0.084	2
Stillaguamish R.			
10. Stream 0172	50	0.075	2
11. Harvey Cr. 1.9 M	17	0.090	2
12. Harvey Cr. 3.2 M	58	0.091	2
13. Fish Cr.	52	0.090	2
14. Portage Cr.	52	0.093	2
15. Lime Cr.	15	0.065	2
Green R.			
16. Covington Cr.	46	0.075	2
Puyallup R.			
17. Fennel Cr.	43	0.095	2
Nisqually R.			
18. Muck Cr.	50	0.092	2
19. Twenty-five Mile Cr.	50	0.097	2
20. Big Cr.	50	0.097	1
21. Nisqually R. (rm 66)	53	0.082	1
South Puget Sound			
22. Johns Cr.	47	0.109	2
23. Burley Cr.	26	0.095	2
24. Kennedy Cr.	51	0.094	2
East Hood Canal			
25. Stavis Cr.	43	0.088	2
26. Gold Cr.	55	0.093	2
West Hood Canal			
27. Shine Cr.	58	0.099	2
28. Thorndyke Cr.	57	0.109	2
Strait of Juan de Fuca			
29. Gierin Cr.	60	0.099	2

Table 7. (Continued.)

Locality	**N**	**H**	**1/2**
30. Lees Cr.	55	0.094	2
31. Whiskey Cr.	48	0.102	2
32. Salt Cr.	39	0.100	2
33. Peabody Cr.	59	0.081	2
Sol Duc R.			
34. Cedar Cr.	32	0.084	2
35. Bear Cr.	53	0.017	2
Quillayute R.			
36. Goodman Cr.	32	0.103	2
Queets R.			
37. Snahapish R.	56	0.079	2
38. Octopus Cr.	43	0.096	2
39. Manor Cr.	32	0.080	1
Grays Harbor-Chehalis R.			
40. Wildcat Cr.	25	0.080	2
41. Lake Aberdeen Fish Hatchery	51	0.116	2
Willapa Bay			
42. Redfield Cr. (North R.)	36	0.102	2
43. Oxbow Cr. (Willapa R.)	26	0.101	2
Lower Columbia R.			
44. Beaver Fish Hatchery	99	0.084	2
45. Cowlitz Fish Hatchery	119	0.085	2
46. Summers Cr. (Kalama R.)	60	0.101	1
Oregon			
Lower Columbia R. (continued)			
47. Clatskanie R.	36	0.094	2
48. Sandy R. Still Cr.	26	0.090	2
49. Multnomah Cr. (83% hybrids)	0		1
Willamette R.			
50. Clackamas R. Cripple Cr.	30	0.053	2
51. Rickreal Cr.	27	0.058	1
52. Luckiamute R.	9	0.093	1
53. Soap Cr. (Luckiamute R.)	10	0.087	1
54. Greasy Cr. (Marys R.)	30	0.104	1
55. Pamela Lake Cr.* (N. Santiam R.)	53	0.084	1
56. Hackleman Cr.*	10	0.081	1
57. Hackleman Broodstock*	53	0.083	1
58. McKenzie R.	31	0.094	1
Tillamook R.			
59. Sand Cr.	41	0.083	2
Yaquina R.			
60. Yaquina R. (7 samples pooled)	44	0.096	2
Siletz R.			
61. Siletz R. (5 samples pooled)	32	0.089	2
Alsea R.			
62. Alsea R. 1995 (N. Fork)	25	0.088	2
63. Alsea R. 1997 (6 samples pooled)	31	0.097	2

Table 7. (Continued.)

Locality	N	H	1/2
64. Alsea Fish Hatchery	100	0.096	2
Umpqua R.			
65. Halfway Cr.* (Smith R.)	7	0.077	2
66. Coffee Cr.* (S. Fork)	31	0.053	1
67. Tuttle Cr. (N. Fork)	31	0.075	2
68. Pass Cr.* (E. Fork)	10	0.111	1
69. Rock Cr. (E. Fork)	31	0.068	2
70. Calapooya Cr. (Main river)	16	0.071	2
71. Cow Cr. (Middle Fork)	10	0.067	1
72. Middle Cr.	11	0.069	1
Coos R.			
73. Pony Cr. (Upper)	42	0.090	1
74. Pony Cr. (Lower)	111	0.087	2
75. Kentuck Cr.	59	0.064	2
76. Fall Cr.	57	0.076	2
Coquille R.			
77. Lockhart Cr. (S. Fork)	22	0.057	1
78. Lockhart Cr. (S. Fork)	14	0.064	2
79. Manganese Cr. (S. Fork)	30	0.099	2
80. Yellow Cr.* (S. Fork)	12	0.039	1
81. Camas Cr. (E. Fork)	29	0.054	1
82. Dice Cr. (Middle Fork)	30	0.089	2
83. Wooden Rock Cr. (S. Fork)	29	0.095	1
84. Coquille R. (E. Fork)	28	0.060	1
85. Deadhorse Cr. (E. Fork)	30	0.044	1
Elk R.			
86. Bear Cr.	50	0.071	2
Rogue R.			
87. Saunders Cr.	32	0.091	2
88. Williams R. (3 samples pooled)	14	0.081	2
89. Big Butte Ck. (2 samples pooled)	14	0.090	2
Chetco R.			
90. Wilson Cr.	43	0.088	2
Winchuck R.			
91. Willow Cr.	39	0.088	2
California			
Klammath R.			
92. Happaw Cr.	35	0.066	2
93. McGarvey Cr. (lower)	35	0.078	2
94. McGarvey Cr. (upper)	35	0.066	1
95. Tarup Cr.	33	0.065	2
North Coast			
96. Home Cr.	30	0.043	2
97. Tom Cr.	21	0.086	2

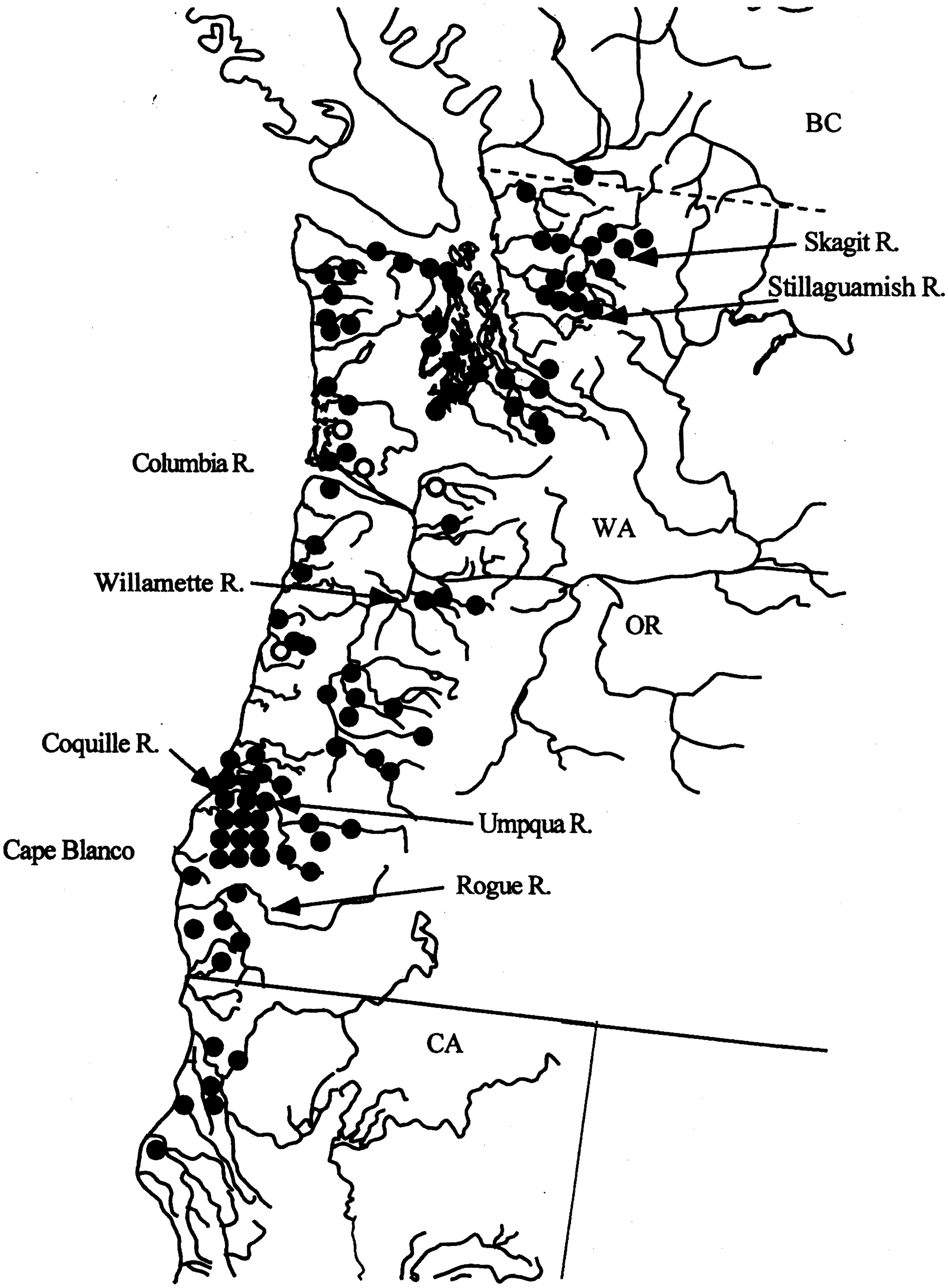

Figure 16. Localities of samples in the NMFS-ODFW-WDFW allozyme database (NMFS et al. unpubl. data). Open circles represent samples from hatcheries. List of samples in Table 7.

analysis. In our analysis, we used multidimensional scaling, in two and three dimensions, of Nei's (1978) unbiased and Cavalli-Sforza and Edward's (1967) chord genetic distances between samples to search for genetically discrete population groups.

Sampling of hybrids

Species identifications of small fish in the field were difficult because some of the characters distinguishing coastal cutthroat trout from *O. mykiss* in larger individuals are undeveloped in smaller individuals. We therefore used variability at three loci (*ADA-2**, *mAH-2**, *CKA-2*), which were fixed or nearly fixed for different alleles in coastal cutthroat trout and *O. mykiss*, to identify *O. mykiss* individuals that had been inadvertently included in the samples. These individuals were excluded from all of the remaining analyses. A three-dimensional scaling of Nei's (1978) genetic distances between samples, with *O. mykiss* individuals removed, showed that most of the samples of coastal cutthroat trout were tightly clustered together and were genetically well differentiated from westslope cutthroat trout and steelhead (Fig. 17). Nei's (1978) genetic distances between the sample of Yaquina River steelhead and coastal cutthroat trout samples ranged from 0.091 to 0.184, except for the Aberdeen Fish Hatchery ($D_n = 0.062$), Multnomah Creek (Oregon) ($D_n = 0.022$), and Pass Creek (Oregon) ($D_n = 0.056$). These latter three samples contained a high proportion of coastal cutthroat trout × *O. mykiss* hybrids that apparently produced the smaller genetic distances with the Yaquina River steelhead sample. Genetic distances between the westslope cutthroat trout sample and coastal cutthroat trout samples ranged from 0.113 to 0.200. The genetic distance between the westslope cutthroat trout sample and the steelhead sample was 0.141. These Nei's genetic distances between coastal cutthroat trout, westslope cutthroat trout, and steelhead are slightly greater than those reported by Allendorf and Leary (1988) for similar subspecies, and this difference may be due to differences in the set of loci in the two studies that were used to estimate D_n. The present results confirm previous results of allozyme studies in depicting as much genetic divergence between coastal cutthroat trout and westslope cutthroat trout as between coastal cutthroat trout and *O. mykiss*.

Comparisons of genotypes between coastal cutthroat trout and *O. mykiss* indicated that several samples collected to represent cutthroat trout populations contained hybrid individuals. Figure 18 shows an enlarged view of a two-dimensional scaling of Nei's (1978) distances between 99 samples, including westslope cutthroat and steelhead. Several samples lay outside the enlarged portion of the graph. Some regional clustering is apparent in this two-dimensional scaling: samples from Puget Sound, Hood Canal, and the Strait of Juan de Fuca tended to occupy the upper portion of the graph; samples from coastal Oregon and California occupied the lower portion of the graph; and samples from southwestern Washington and the Lower Columbia and Willamette rivers clustered between samples from Washington and those from Oregon and California.

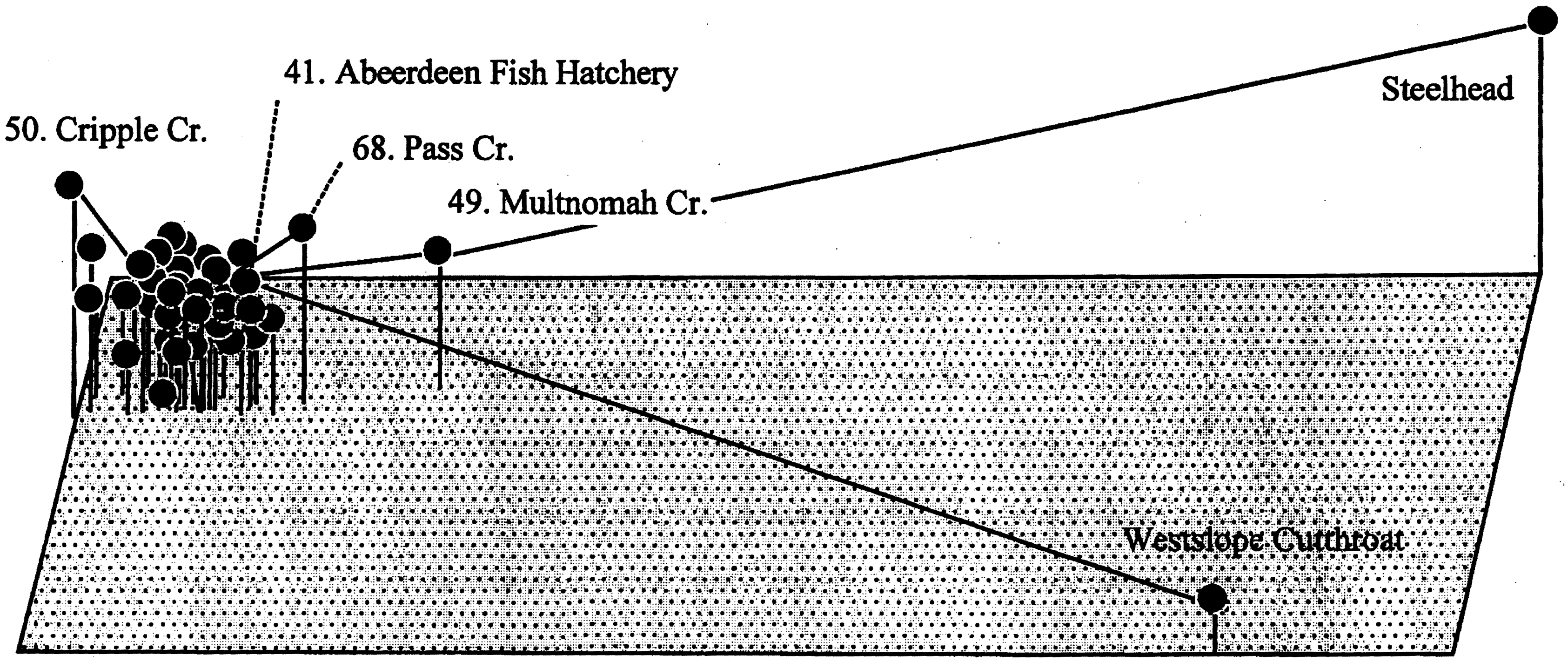

Figure 17. Three-dimensional scaling of Nei's (1978) genetic distances between samples of coastal cutthroat trout (97 samples), westslope cutthroat trout (western Montana), and steelhead (Yaquina R.). Hybrids have not been removed from putative coastal cutthroat trout samples.

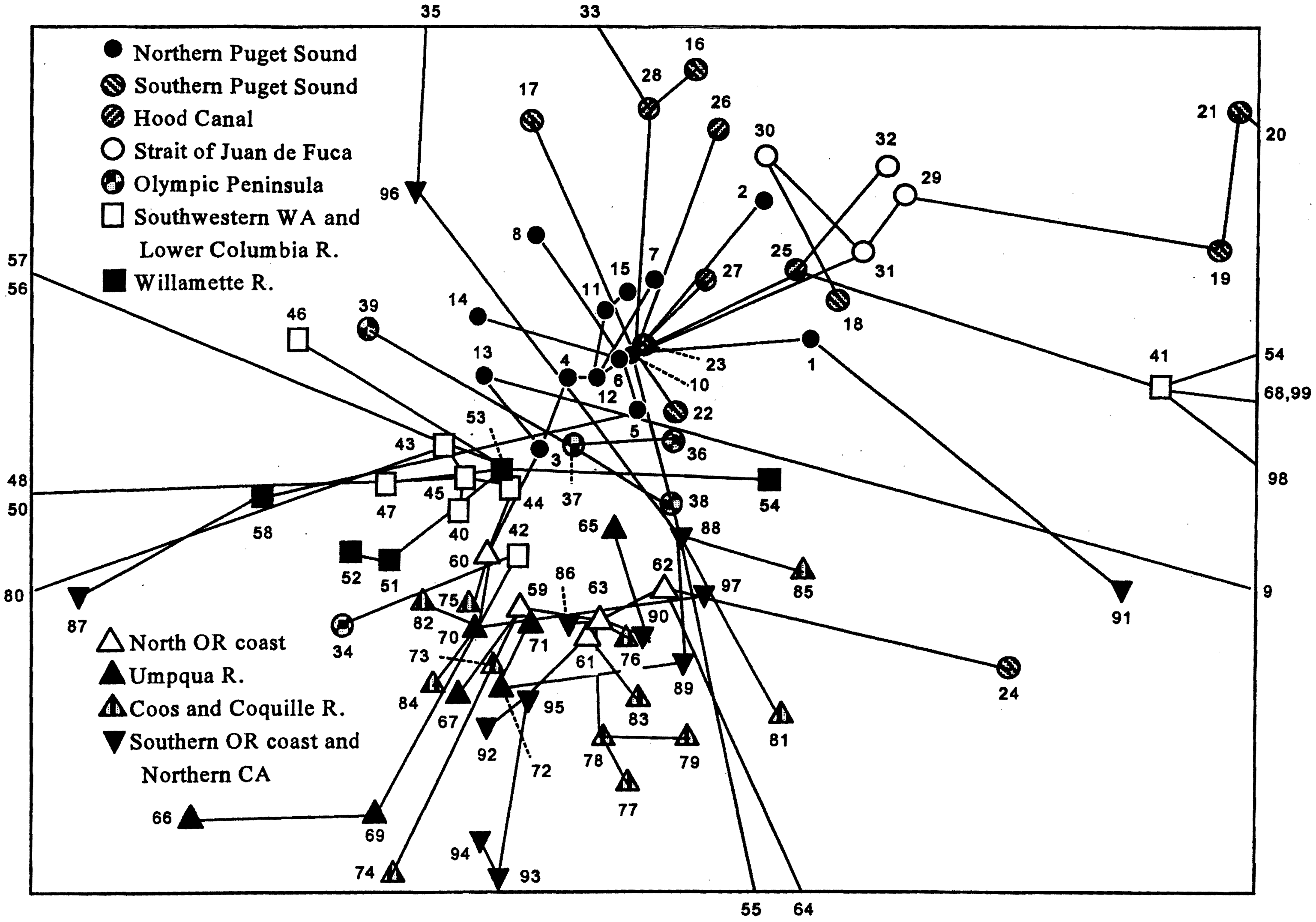

Figure 18. Enlargement of two-dimensional scaling plot of Nei's (1978) genetic distance between samples of coastal cutthroat trout (with hybrids included), westslope trout (no. 98), and steelhead (no. 99). Lines connect samples in a minimum spanning tree. Sample numbers in Table 7. (WA=Washington; OR=Oregon; CA=California.)

We attempted to remove hybrid individuals from the genetic data base because the objective of this analysis was to infer the genetic population structure of coastal cutthroat trout from allozyme data. The presence of hybrids would most likely introduce error in estimating levels of genetic divergence between coastal cutthroat trout populations. We used eight loci (*sAAT-4**, *ADA-2**, *mAH-2**, *mAH-3*, *CKA-2**, *IDDH-1**, *sIDH-2**, and *sMEP-2**) that showed strong frequency differences between coastal cutthroat trout and *O. mykiss* in an attempt to identify hybrid individuals. Some alleles might be shared between coastal cutthroat trout and *O. mykiss* because of common phylogenetic ancestry, while other alleles might be shared because of recent hybridization. Therefore, to minimize the chances of excluding individuals of coastal cutthroat trout naturally carrying *O. mykiss* alleles, we used a 50% rule in which individuals with at least one steelhead allele at four of these eight loci were considered to be hybrids. The 50% rule almost certainly allowed some introgressed individuals into the coastal cutthroat samples and alternatively excluded true coastal cutthroat trout. With this rule, 28 of 97 (29%) of our samples contained hybrids (Fig. 19). The percentage of estimated hybrid individuals in 28 samples containing hybrids ranged from about 1% to 84% (Multnomah Creek). The samples from Pass Creek (82%) and the Aberdeen Creek Hatchery (48%) also contained a high proportion of hybrids. Most of the hybrid individuals appeared to represent introgression from the second generation or later, since only a single individual was found in this study with heterozygous genotypes at all diagnostic loci. We removed hybrid individuals from the database and recalculated allelic frequencies to estimate genetic distances between samples. We also removed the sample from Multnomah Creek because it consisted chiefly of hybrid individuals and represented a population isolated above impassable falls.

These results permit two tentative conclusions. First, samples with hybrid individuals were distributed over most of the sampling area and did not appear to be associated with any particular area or kind of habitat, although no attempt was made to quantitatively assess the habitats from which samples were collected. Second, the proportions of hybrids in these samples probably represent minimal estimates of the extent of hybridization between coastal cutthroat trout and *O. mykiss*, since the samples were collected to represent coastal cutthroat trout and not to assess the extent of hybridization (i.e., sampling attempted to avoid steelhead and hybrids). Additional sampling, without regard to identifying hybrids in the field, is required to assess the full extent of hybridization between coastal cutthroat trout and *O. mykiss*.

A two-dimensional scaling of chord distances between samples of only coastal cutthroat trout with hybrids removed appears in Fig. 20. The chord distance is based on a model that assumes only random drift as the cause of population divergence and may be more appropriate than distances, such as Nei's genetic distance, which are based on models that also incorporate mutation. The same general clusters appeared as in Figure 18, but with greater separation between clusters. British Columbia, Puget Sound, Hood Canal, and Strait of Juan de Fuca samples appeared in one cluster; southwestern Washington, Lower Columbia River, and Willamette River samples appeared in another cluster; and coastal Oregon and California samples appeared in a third cluster. However, some samples were unusual. One group of these unusual samples included extreme outliers unlike the other samples and included Nos. 9, 30, 35,

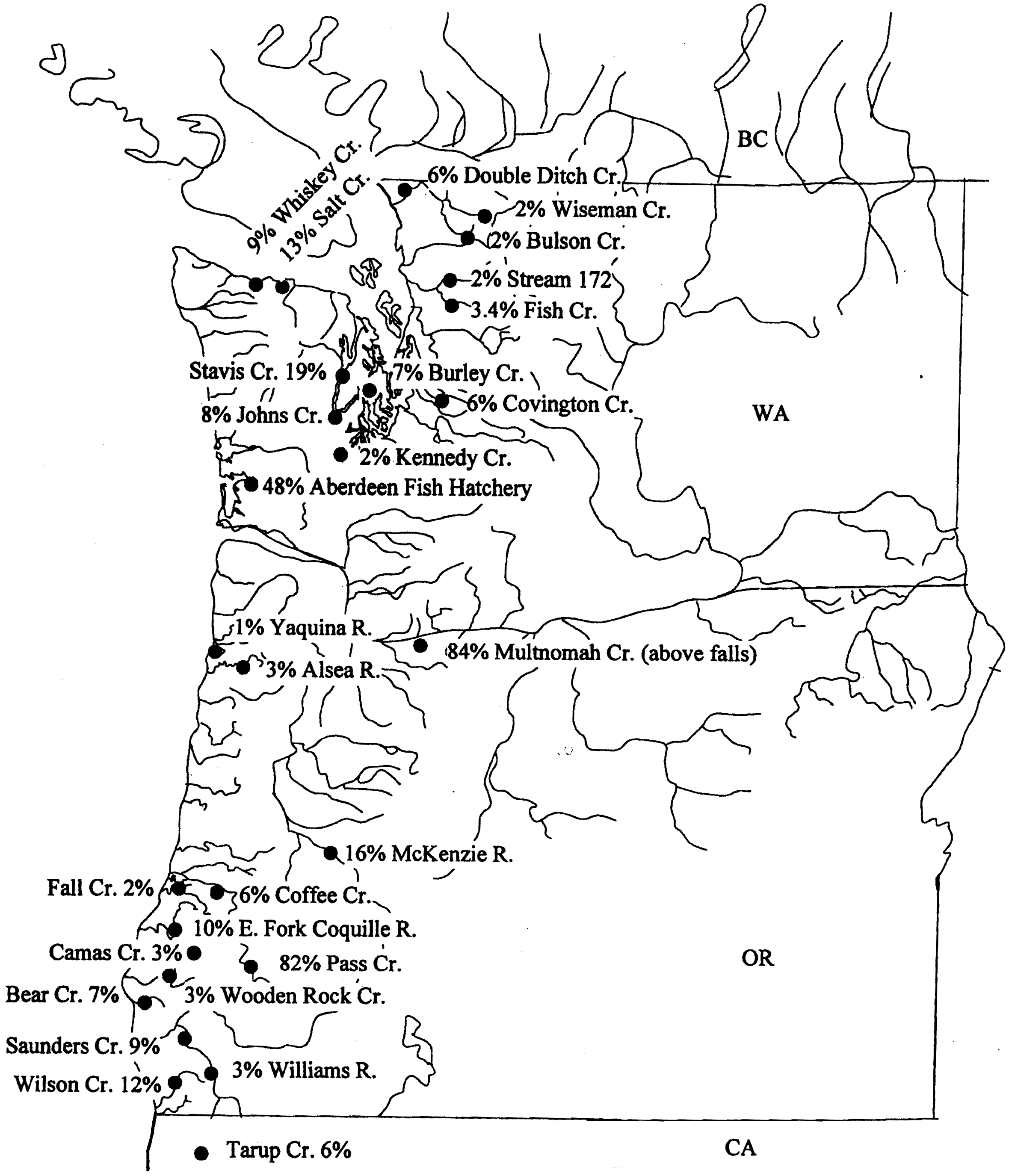

Figure 19. Percentage of hybrid fish in samples that contained hybrids (29 out of 97) of putative coastal cutthroat trout in the NMFS-ODFW-WDFW coastwide allozyme database (NMFS et al. unpubl. data). Hybrid fish were identified by the presence of steelhead alleles at eight loci showing strong allele frequency differences between coastal cutthroat trout and *Oncorhynchus mykiss*.

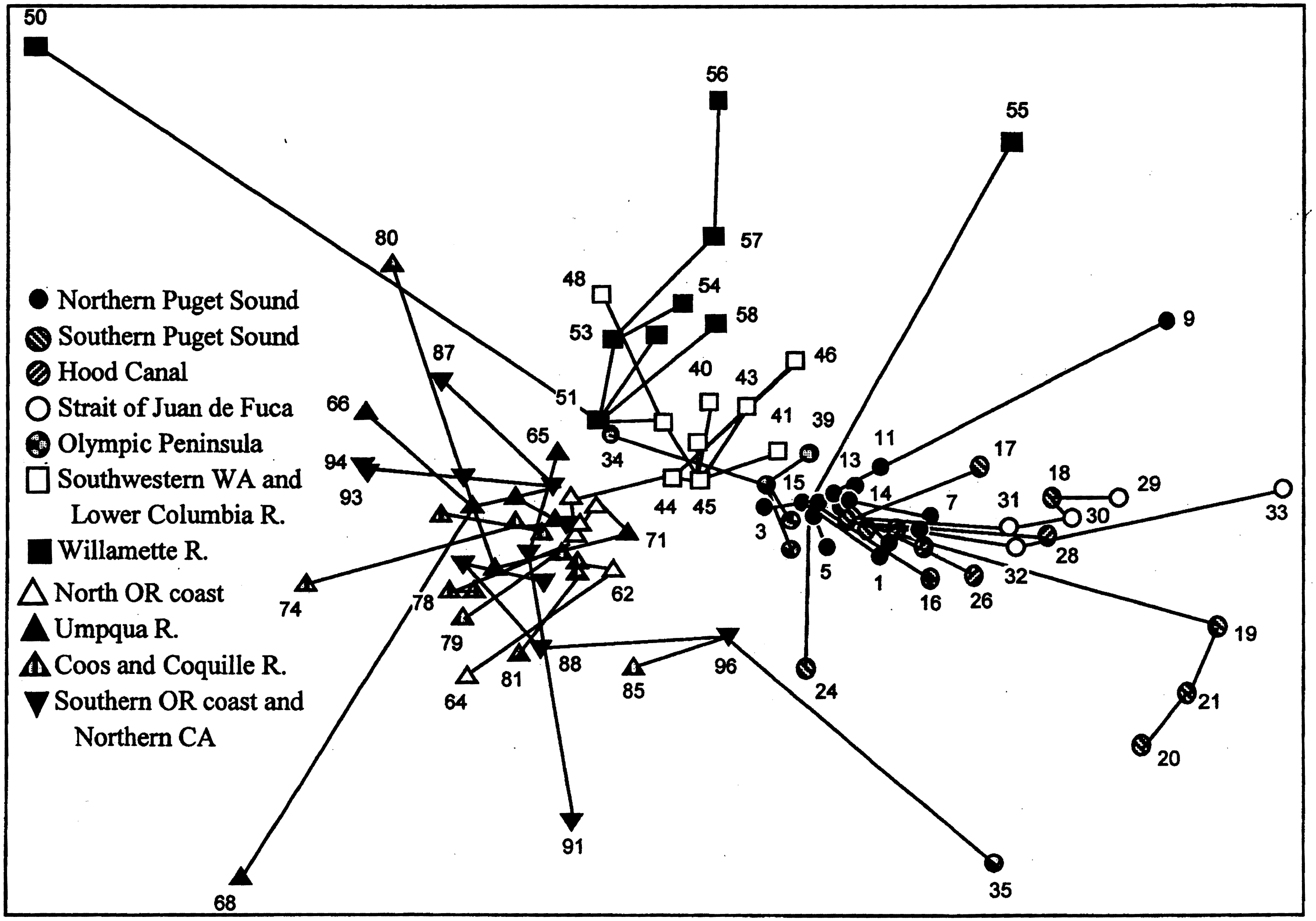

Figure 20. Two-dimensional scaling of chord distances between 96 samples of coastal cutthroat trout with hybrid individuals removed. Lines connect samples in a minimum spanning tree. Sample numbers in Table 7. (WA=Washington; OR=Oregon; CA=California.)

50, 55, 56, 68, and 91. Another group included several samples that were genetically similar to samples from other geographic areas.

Uneven geographical sampling

One caution in inferring genetic relationships among samples is that the outcome of an analysis may be influenced by uneven geographical sampling. Four river drainages were sampled much more than others in this data set. Seven samples were collected in the Skagit River, six were collected in the Stillaguamish River, eight were collected in the Umpqua River, and nine were collected in the Coquille River. An enlarged view of the two-dimensional scaling shown in Figure 20 appears in Figure 21. This enlargement shows that most of the samples from the Skagit and Stillaguamish rivers clustered more tightly than did multiple samples from other rivers. However, the overrepresentations of samples from these rivers could possibly distort the positions of the other samples from drainages with fewer samples.

Ideally, a jacknife or bootstrap analysis of multidimensional scaling results might have assessed this problem quantitatively but was not feasible within the constraints of this study. To aid in understanding the effects of uneven sampling on clustering topology, we reanalyzed two smaller sets of samples that excluded all but two samples from each of these four river drainages. Two samples with the largest sample sizes were selected from each of these four drainages for one set of samples, and two different samples from each drainage, also with large sample sizes, were selected for a second set of samples. Enlarged views of two-dimensional scalings of these two reduced data sets appear in Figures 22 and 23. Both of these analyses depicted the same three major clusters that appeared in a two-dimensional scaling of the complete set of samples. A comparison of the positions of samples common to the two-dimensional scalings shown in Figures 21, 22, and 23 indicates only slight variations in the positions of these samples relative to one another. We conclude that the uneven representation of some river drainages in the coastal cutthroat genetic data set did not obscure genetic patterns among samples in our analyses or create spurious relationships. The following analysis of genetic population structure, therefore, included all of the samples in these four drainages.

Genetic outliers

After removal of hybrid individuals, a two-dimensional scaling of chord distances between the remaining samples revealed three large clusters of samples. Fifteen samples (Nos. 9, 24, 33, 35, 48, 50, 55, 56, 57, 66, 68, 74, 80, 87, and 91) were not close to their geographically nearest neighbors (Fig. 20). Several factors may have produced these genetic outliers. First, three of these samples (Nos. 56, 68, and 80) consisted of only 10-12 individuals, and sample error may have produced larger-than-expected genetic distances between these samples and the remaining ones. These samples were still strong outliers when Nei's unbiased genetic distance was used (Fig. 18), so sample size per se may not be the reason for apparent genetic uniqueness. The remaining 12 genetic outliers, however, consisted of sample sizes ranging from 26 to 111 individuals (median = 50) and were similar in size to the remaining samples.

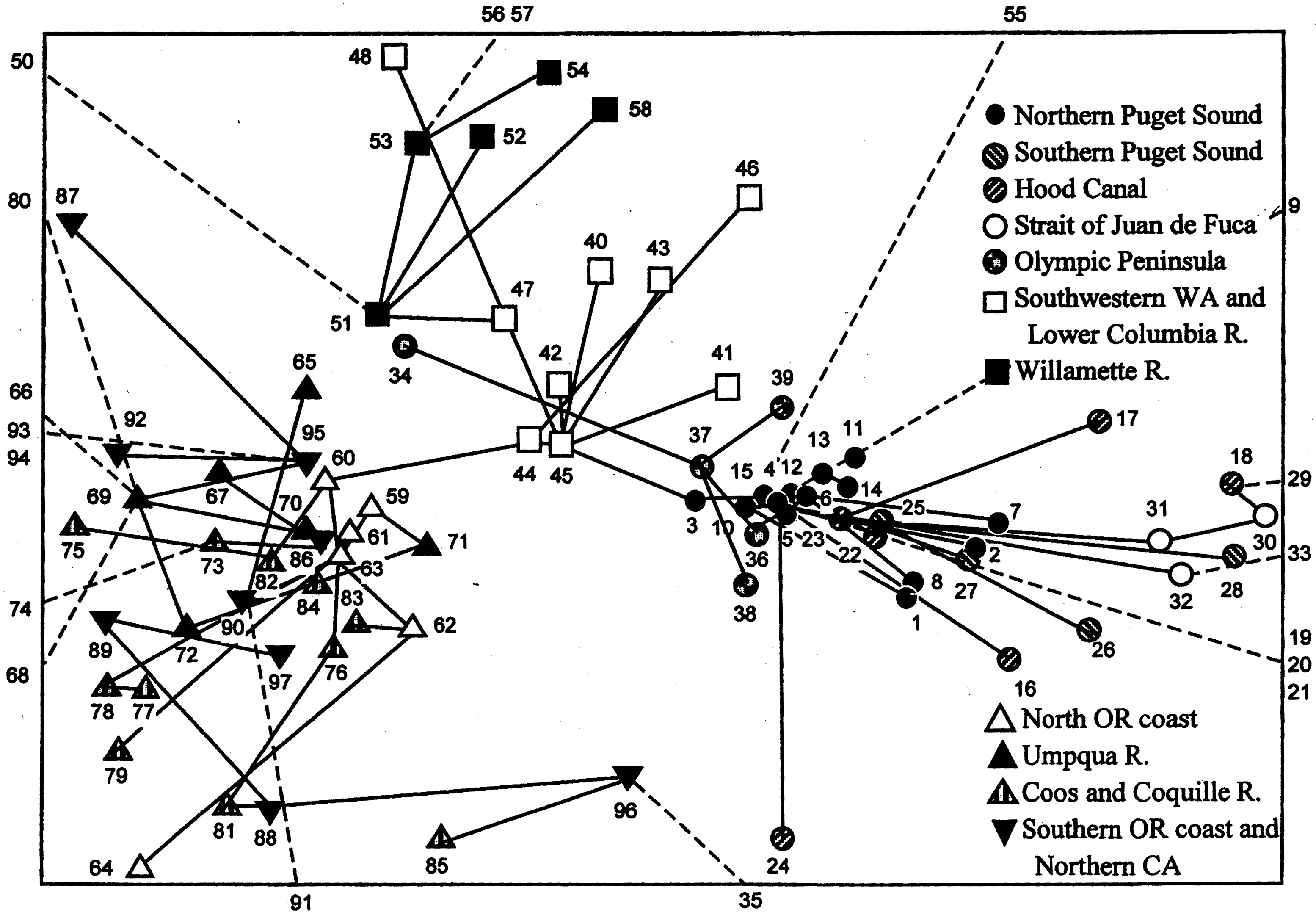

Figure 21. Enlargement of scaling of chord distances between 96 samples of coastal cutthroat trout with hybrids removed. Lines connect samples in a minimum spanning tree. Sample numbers in Table 7. (WA=Washington; OR=Oregon; CA=California.)

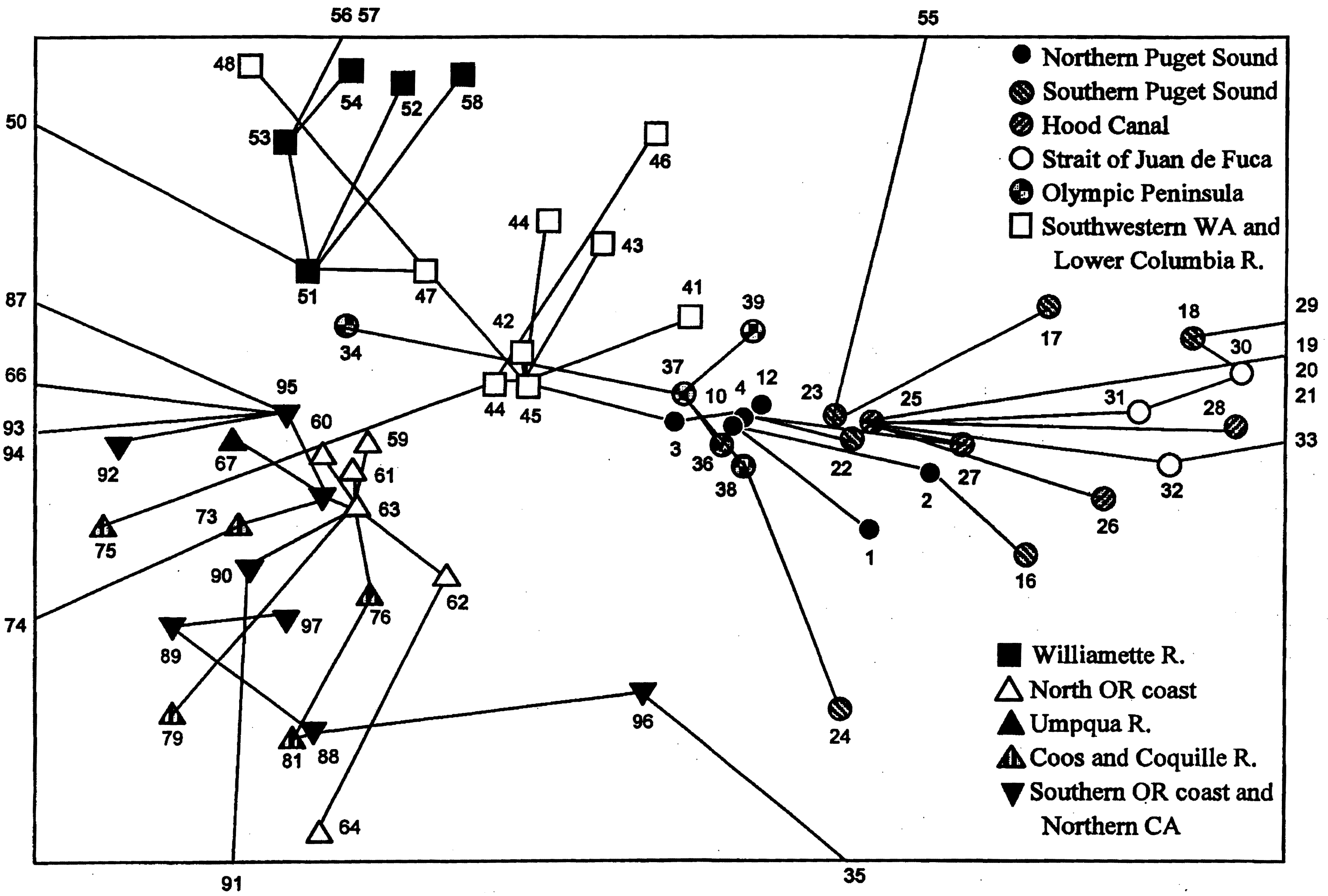

Figure 22. Enlargement of two-dimensional scaling of chord distances between 74 samples of coastal cutthroat trout with hybrids removed. Only two samples each have been included from the Skagit, Stilliguamish, Umpqua, and Coquille rivers. Lines connect samples in a minimum spanning tree. Sample numbers in Table 7. (WA=Washington; OR=Oregon; CA=California.)

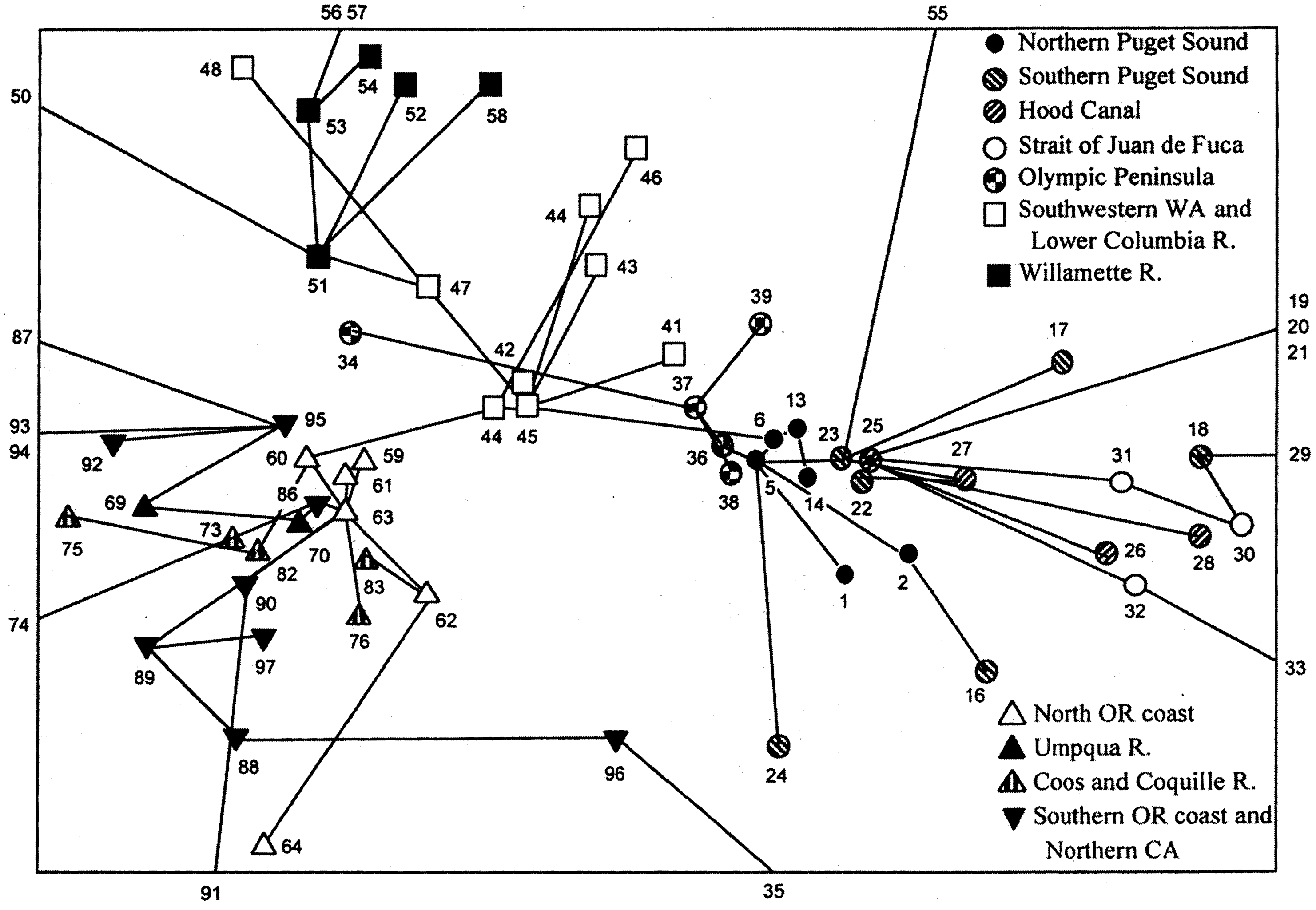

Figure 23. Enlargement of two-dimensional scaling of chord distances between 74 samples of coastal cutthroat trout with hybrids removed. Two samples from the Skagit, Stilliguamish, Umpqua, and Coquille rivers have been included. Lines connect samples in a minimum spanning tree. Sample numbers in Table 7. (WA=Washington; OR=Oregon; CA=California.)

Genetic outliers may also have arisen because the samples included the progeny of only a few individuals from a larger population. The presence of linkage disequilibrium between loci might provide evidence of offspring from the same parents in a sample, but the constraints of this study did not permit this analysis.

Random genetic drift in isolated populations and founder effects can lead to populations with unusual genetic makeups. Allele frequencies can shift substantially from those of nearby populations if some populations have been initiated with only a few founders. Large genetic divergences can also arise as a consequence of isolation by natural barriers to migration such as waterfalls and landslides, by manmade barriers such as impassable culverts and dams, or by the fragmentation or loss of sea-run migrants that would otherwise facilitate gene flow between populations. Theory indicates that average heterozygosity (H) of selectively neutral genes is lost at a rate of $1/2N_e$ each generation (Crow and Kimura 1970), where N_e is the effective population size (the size of a hypothetical population with equal sexes in which gene diversity is lost at the same rate as it is in the population in question). The loss of heterozygosity over time is greater for small populations than it is for large populations (Fig. 24). For example, an isolated population consisting of an effective population size of 40 will lose 40% of its gene diversity (H) in about 40 generations. In the coastal cutthroat trout data set, several genetic outliers had heterozygosities that were smaller than the mean heterozygosities of samples collected in the same drainage or area (Fig. 25). Reduced heterozygosity values are consistent with greater physical isolation in some populations. Heterozygosity values for sample Nos. 33 (Strait of Juan de Fuca), 35 (Olympic Peninsula), 50 (Willamette River), 66 (Umpqua River), and 80 (Coquille River) were less than the range of heterozygosities in nearby samples. These results are consistent with greater physical isolation in these samples.

Random drift also accelerates genetic divergence from neighboring or from parental populations following colonization (Fig. 26). Divergence from drift is most important in small populations. In populations with effective sizes of 80 or fewer fish, F_{ST} (a measure of genetic differentiation) increases rapidly in only a few generations. For example, F_{ST} is expected to increase to about 0.20 in 20 generations, which represents about 60 years for cutthroat trout. At smaller population sizes, divergence from neighboring populations increases even more rapidly. Divergence between coastal cutthroat populations in a river drainage averaged about 0.074 in the present study, with extreme values between genetic outliers and neighboring populations reaching 0.20 or more. These extreme levels of divergence could appear in just a few generations in completely isolated populations, with the small effective population sizes expected in coastal cutthroat trout. Strong allele-frequency shifts observed in a sample from Cripple Creek (No. 50, Clackamas River), for example, would be consistent with complete isolation for tens of generations.

Another reason for genetic outliers may be allele frequency shifts because of introgression by migrants or outplanted fish from genetically differentiated populations. One piece of evidence that outplants can genetically influence local populations is the genetic similarity between Alsea Hatchery coastal cutthroat trout and populations in streams in the

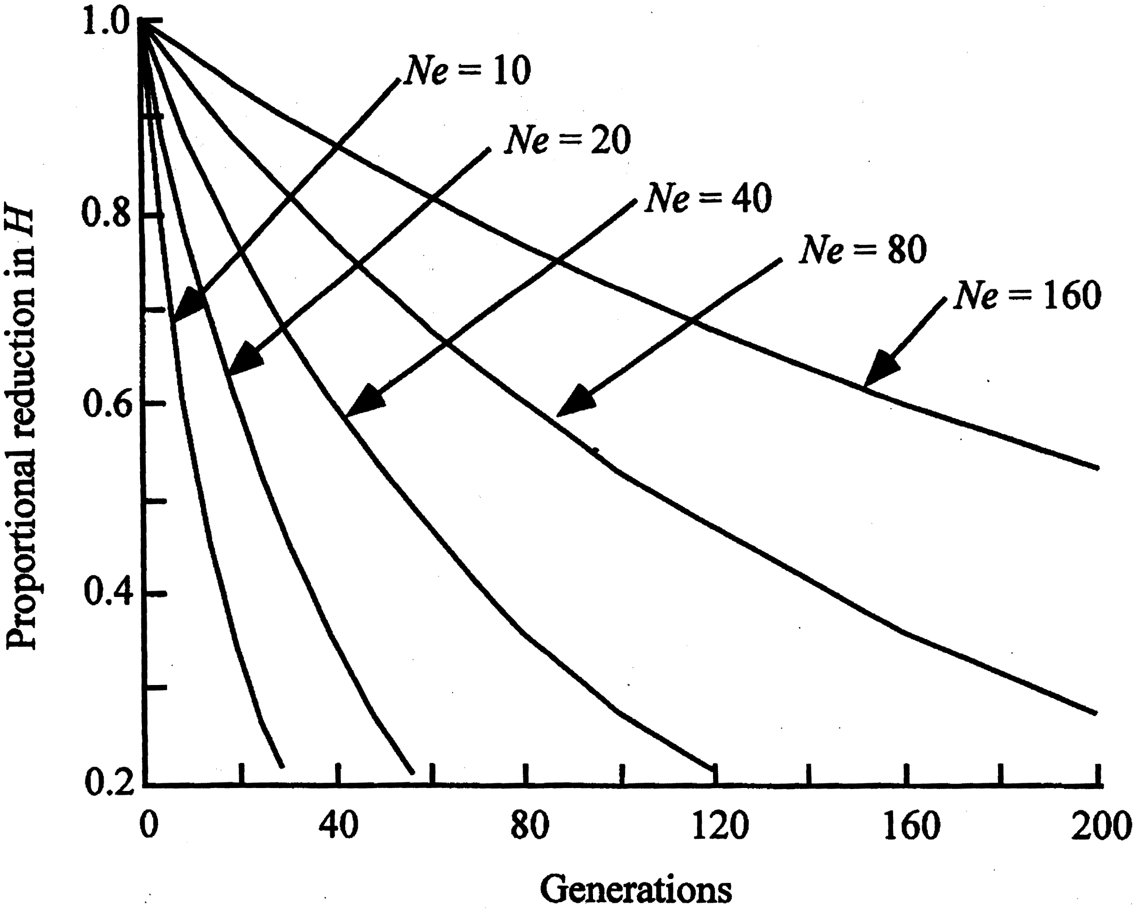

Figure 24. Proportional reduction in heterozygosity (*H*) with time and effective population size (*Ne*) in completely isolated populations.

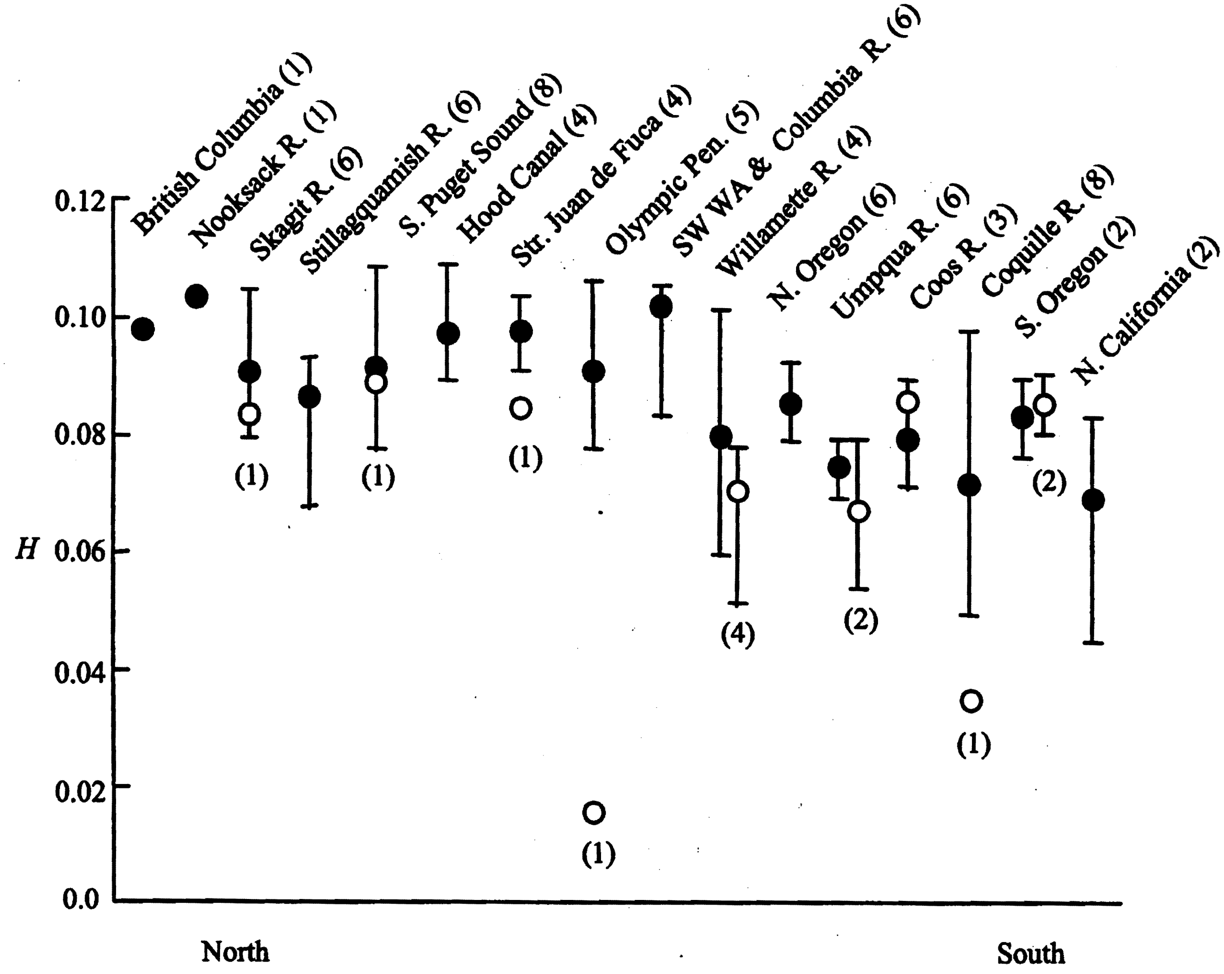

Figure 25. Mean unbiased heterozygosity (*H*) in samples of coastal cutthroat trout (closed circles). Open circles represent values or means of genetic outliers (see Table 7). Numbers in parentheses indicate the number of samples represented in the mean. Vertical bars represent the range of *H* values.

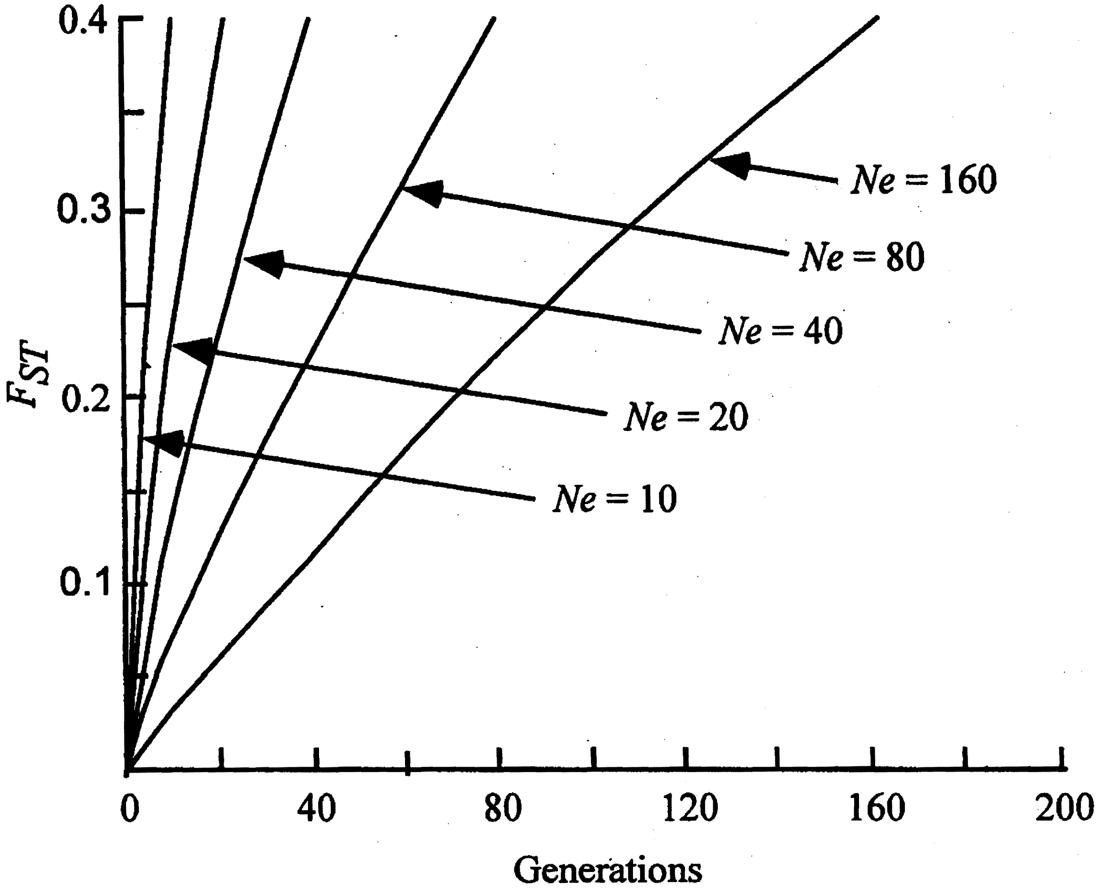

Figure 26. Increase in genetic divergence (F_{ST}) with time and effective population size (*Ne*) in completely isolated populations.

Coquille River that received Alsea Hatchery fish (P. Reimers[15]). In these cases, however, the outplantings acted like gene flow to make local populations more similar to one another and to Alsea Hatchery fish than they would otherwise be with natural levels of straying between populations. Hybridization with *O. mykiss* may also distort allelic frequencies in a sample. Even though putatively hybrid individuals were removed before allele frequencies were calculated in this analysis, *O. mykiss* alleles may still be present in these samples.

Lastly, genetic outliers may represent undersampled groups of genetically distinct populations. For example, the three samples (Nos. 19, 20, and 21) from the upper Nisqually River were very different from a sample in the lower reaches of the river (No. 18) similar to other southern Puget Sound populations. If only one sample had been collected from the upper Nisqually River, it would have been considered a genetic outlier. However, the genetic similarity between these three samples indicates that populations in the upper Nisqually River as a whole are genetically divergent from other Puget Sound populations.

Regional patterns of genetic variability

To facilitate resolving the genetic population structure, we excluded nine populations from the data set that were extreme graphical outliers (Nos. 9, 33, 35, 50, 55, 56, 57, 68, and 91 [Fig. 20]). These populations were omitted from the graphs that follow because it was not possible to enlarge the view of three-dimensional scalings of genetic distances with NTSYS-pc. Omitting these nine outlying samples from the analysis does not exclude the possibility of additional *genetic* (as opposed to graphical) outliers in the remaining sample space. A three-dimensional scaling of genetic distances might reveal genetic population structure in a third dimension.

The upper view of a three-dimensional scaling of the chord distance appears in Figure 27 and is similar to the two-dimensional scaling of populations in Figure 21, which depicted three major groups of populations. A side view of this three-dimensional scaling appears in Figure 28. A cluster in the right-hand portion of these graphs consists of samples from British Columbia, Puget Sound, Hood Canal, and the Strait of Juan de Fuca (Nos. 1-33, except genetic outliers Nos. 9, 24, and 33). The samples from drainages in southern Puget Sound (Nos. 16-24), Hood Canal (Nos. 25-28), and the Strait of Juan de Fuca (Nos. 29-33) formed a more diffuse cluster than did samples from northern Puget Sound drainages. The samples from the Strait of Juan de Fuca, however, are not close to their closest geographical neighbors in northern Puget Sound or on the Olympic Peninsula. In the third dimension, the three upper Nisqually River populations (Nos. 19, 20, and 21) were genetically more divergent from other Puget Sound populations than was apparent in the two-dimensional scaling.

Samples from the northern Washington coast on the Olympic Peninsula (Nos. 34-39) formed a widely scattered group, but were nonetheless closely connected in the minimum

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[15] P. Reimers, ODFW, 4475 Boat Basin Drive, PO Box 5430, Charleston, OR 97420. Pers. commun. to S. Grant. March 1997.

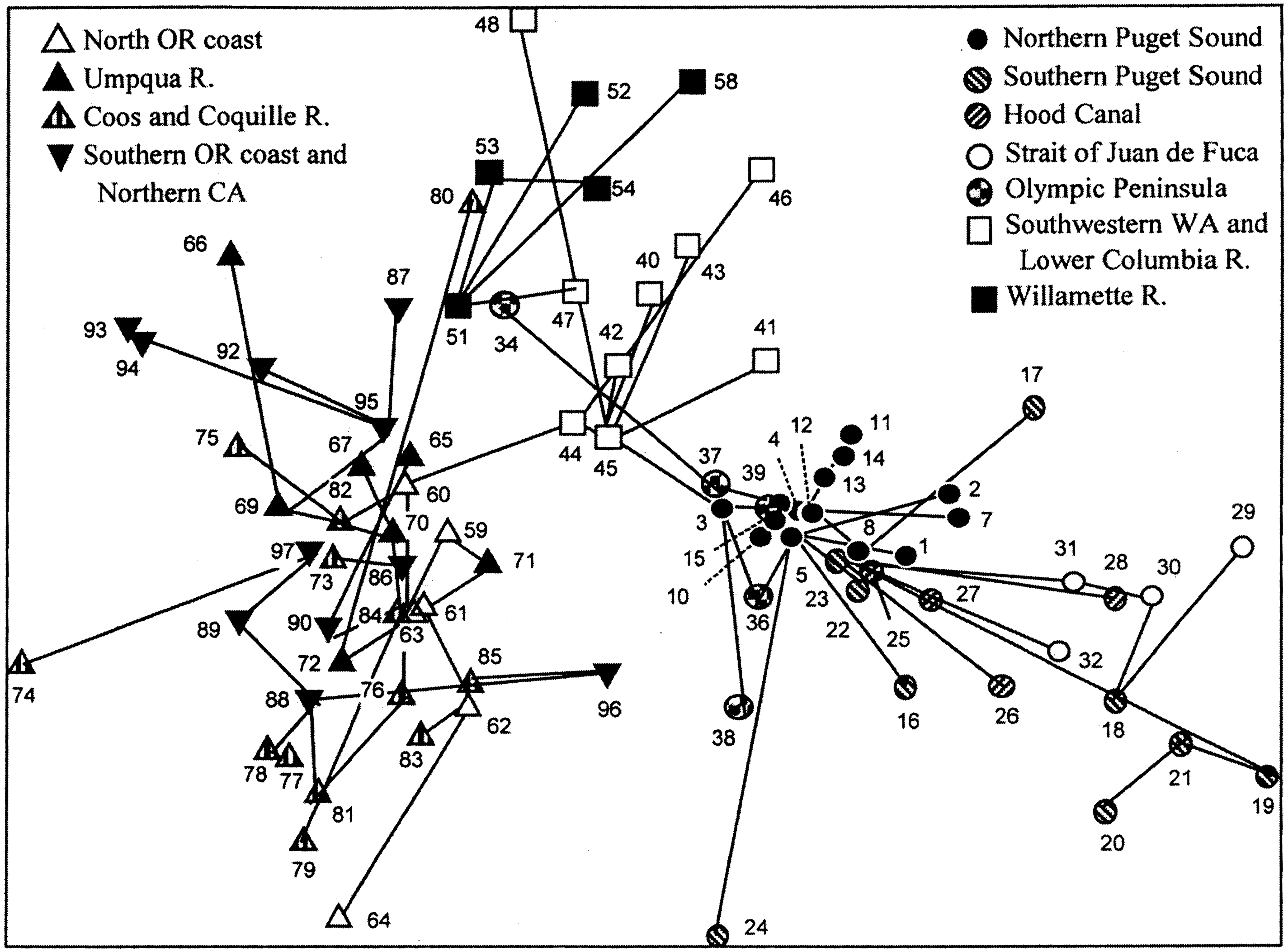


Figure 27. Top view of three-dimensional scaling of chord distances between 87 samples of coastal cutthroat trout. Graphical outliers have been excluded. Lines connect samples in a minimum spanning tree. Sample number in Table 7. (WA=Washington; OR=Oregon; CA=California.)

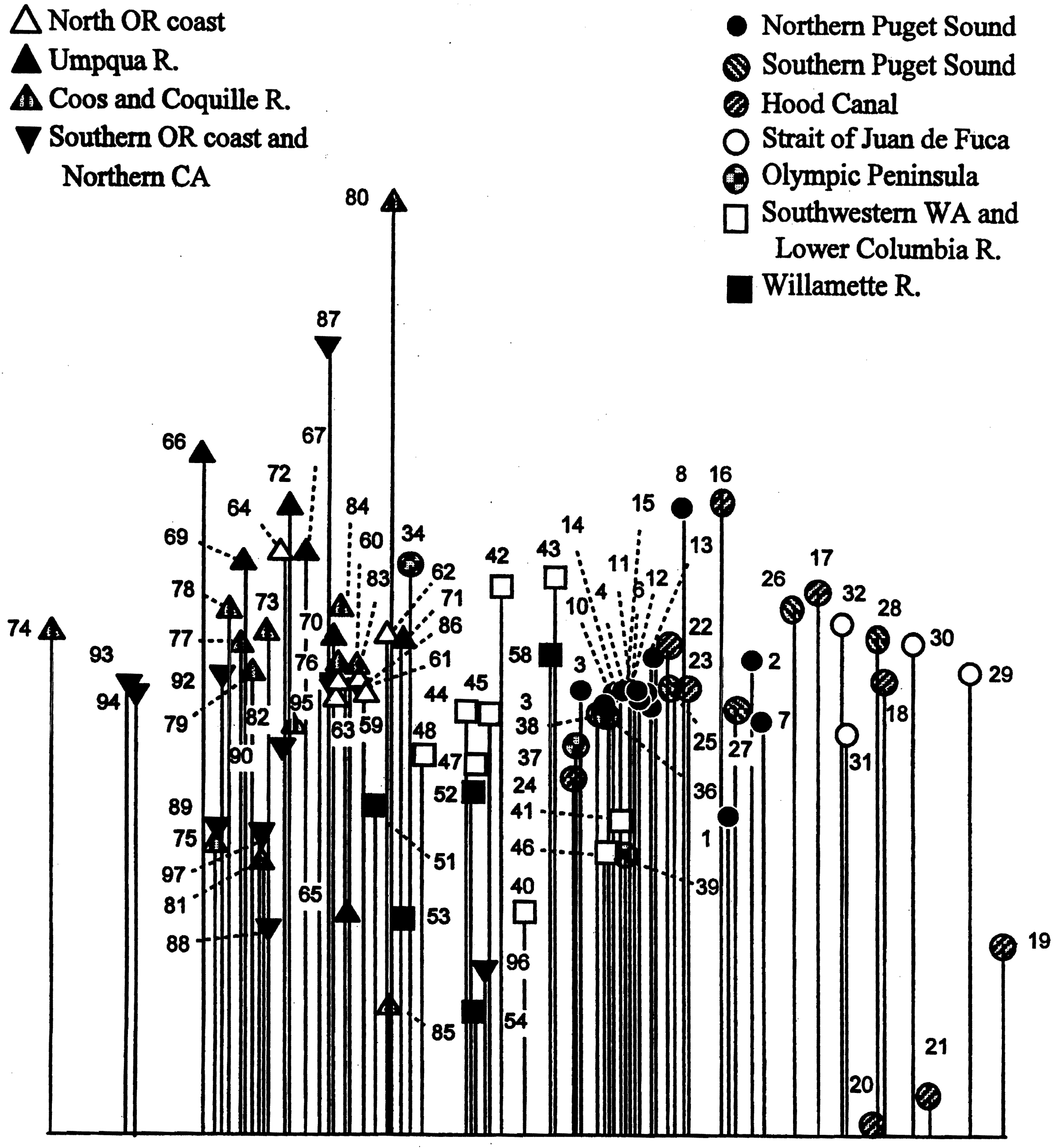


Figure 28. Side view of three-dimensional scaling of chord distances between 87 samples of coastal cutthroat trout. Graphical outliers have been excluded. Sample numbers in Table 7.

spanning network. This group was genetically intermediate between southwestern Washington samples and samples from northern Puget Sound, but was, as noted previously, distinct from the geographically neighboring Strait of Juan de Fuca samples. This geographic group contained one genetically very dissimilar sample, Bear Creek (No. 35, Sol Duc River).

A second major cluster in Figure 27 included samples from the southwestern Washington coast, the Lower Columbia River, and the Willamette River (Nos. 40-58). The minimum spanning network indicated that southwestern Washington and Lower Columbia River samples (Nos. 40-48) were more closely related to one another than to other samples. No consistent separation appeared between samples from natural populations in southwestern Washington (Nos. 40, 42, and 43) and populations in the Lower Columbia River (Nos. 46, 47, and 48). Samples from the Beaver Creek and Cowlitz River hatcheries were genetically very similar to each other, and this similarity may reflect exchanges between these hatcheries. Although the samples from the Willamette River drainage (Nos. 50-58) were related to those from southwestern Washington and the Lower Columbia River, the minimum spanning network indicated they were generally more closely related to one another than to other samples in this cluster. Even so, the samples from Cripple Creek (No. 50, Clackamas River), and from the southern portion of the Willamette River were extreme outliers (Nos. 55-57).

The third major cluster on the left side of the three-dimensional scaling depicted in Figures 27 and 28 included samples from coastal Oregon and California drainages (Nos. 59-97). Little genetic differentiation appeared between samples from different river drainages or between geographic areas. One feature of this cluster in three-dimensional scaling is that the level of genetic divergence between populations within the Umpqua, Coquille, and Klamath rivers was much greater on average than the level of genetic divergence between populations within drainages in Puget Sound. This trend holds whether or not genetic outliers are included in the analysis.

The three-dimensional scaling of Nei's (1978) genetic distances between samples confirmed these general groupings (Figs. 29 and 30). A two-dimensional view of the three-dimensional scaling showed less separation between Puget Sound-Hood Canal-Strait of Juan de Fuca samples and southwestern Washington-Lower Columbia River samples than was apparent in the three-dimensional scaling of chord distances. However, these two groups showed a greater amount of separation in the third dimension. The Strait of Juan de Fuca samples (Nos. 29-32) were also not genetically similar to their closest geographical neighbors in this three-dimensional scaling. Populations within the drainages of coastal Oregon and Northern California showed a greater amount of divergence from one another than was apparent between populations within rivers draining into Puget Sound. Although the minimum spanning tree indicated that populations within coastal Oregon and Northern California drainages were generally more closely related to one another than to populations in other drainages, no clear pattern of separation appeared between drainages.

A gene diversity analysis of allele-frequency variability (Nei 1973, Chakraborty 1980) indicated that 18% of the total variability was due to variability among populations, while 82%

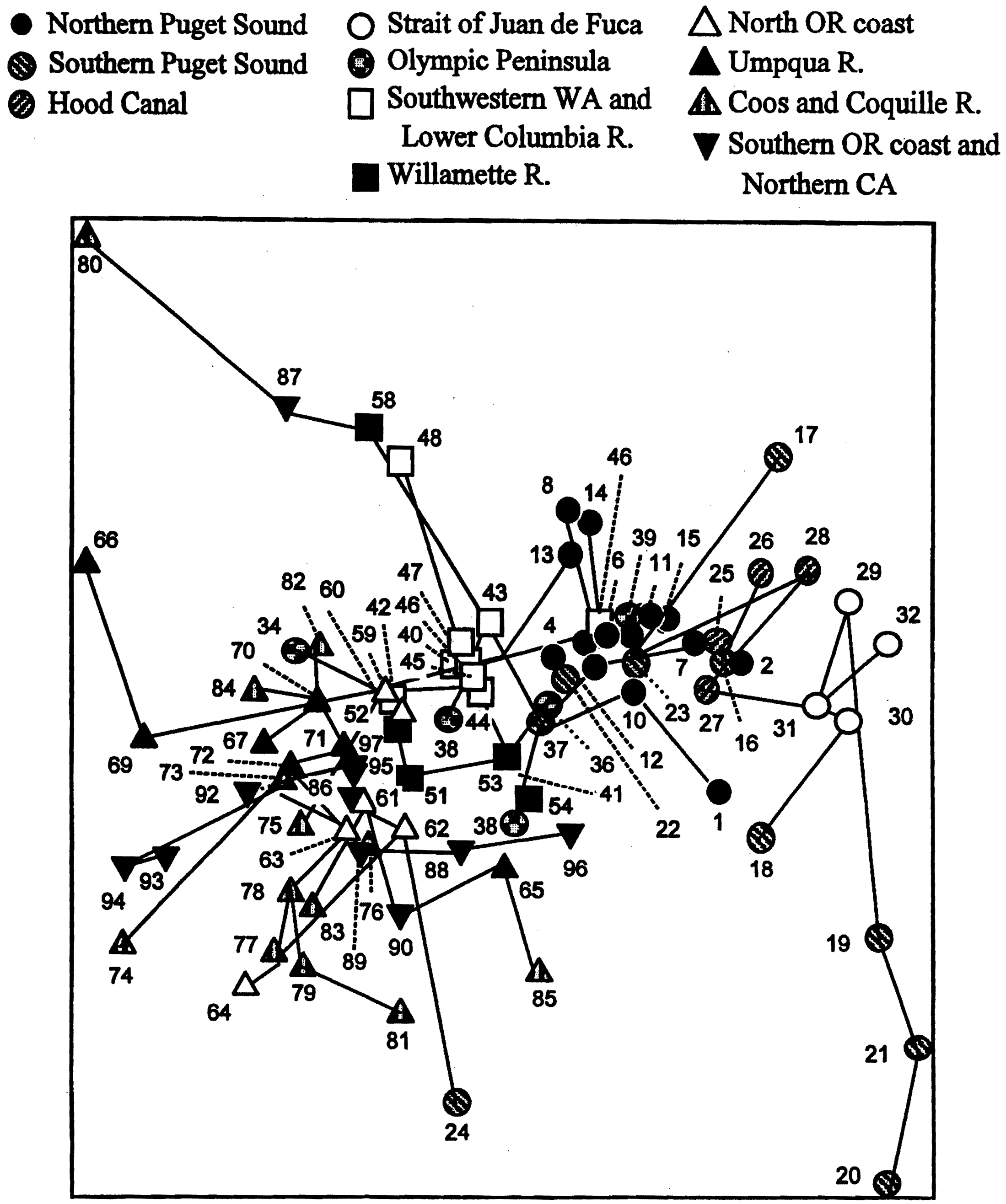


Figure 29. Top view of three-dimensional scaling of Nei's (1978) genetic distances between 87 samples of coastal cutthroat trout. Graphical outliers have been excluded. Lines connect samples in a minimum spanning tree. Sample numbers in Table 7. (WA=Washington; OR=Oregon; CA=California.)

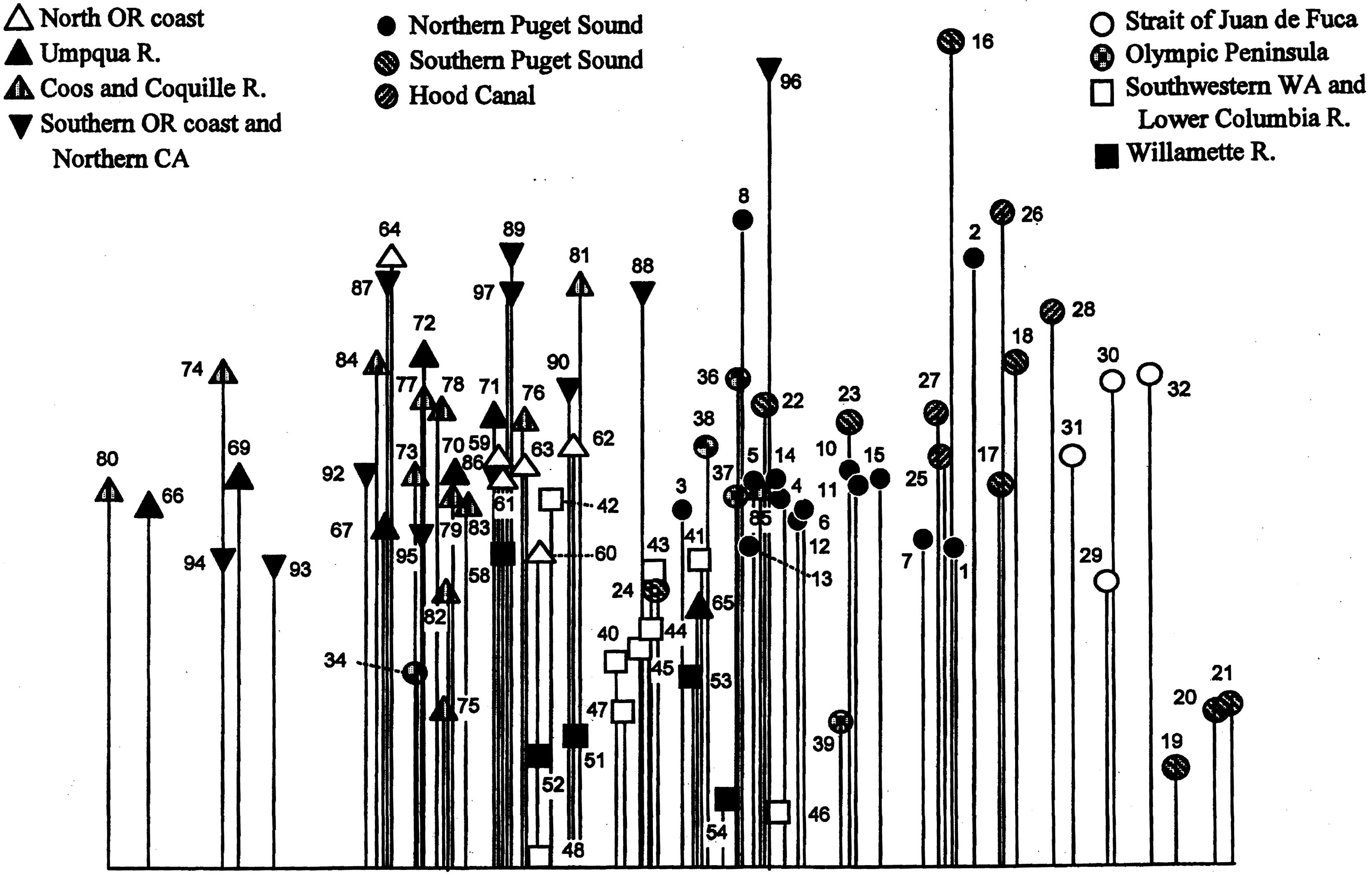


Figure 30. Side view of three-dimensional scaling of Nei's (1978) genetic distances between 87 samples of coastal cutthroat trout. Graphical outliers have been excluded. Sample numbers in Table 7.

was due to genetic differences between individuals within populations, on average. Variability between populations can be broken down further. About 5.4% was due to differences among the six major groups, 5.1% was due to differences among rivers within the six major groups, and 7.4% of the total variability was due to differences among populations within rivers, on average. Only about 0.1% of the total variability was due to differences between sea-run and non-migratory coastal cutthroat trout within streams. This estimate, however, was based on only three above- and below-waterfall comparisons and probably underestimates the average level of genetic differentiation among these life-history types. A population isolated above an impassable barrier to migration may show considerable divergence from populations below the barrier. However, this data set provided few paired comparisons for above and below barriers.

Some features of coastal cutthroat trout genetic population structure require explanations. First, a coastwide pattern of isolation by distance is apparent in the distributions of allelic frequencies. Samples from each region tended to cluster together and geographically intermediate samples from southwestern Washington and the Lower Columbia River tended to appear in an intermediate position in the cluster analysis between northern samples and southern samples. This pattern appeared in all of the results, including analyses of data sets with hybrids and with and without graphical outliers. However, a notable exception appeared within this general pattern of isolation by distance. The Strait of Juan de Fuca populations tended to be more closely related to Hood Canal and southern Puget Sound populations populations than they were to northern Puget Sound populations or to Olympic Peninsula populations. These genetic relationships may reflect recolonization patterns following the retreat of glaciers about 13,000 years ago (Thorson 1980).

Another feature of coastal cutthroat trout genetic population structure was that the amount of genetic divergence between populations differed between drainages. Samples collected within the Skagit and Stillaguamish rivers tended to be much more similar to one another than were samples collected in the Willamette, Umpqua, and Coquille rivers. One possible explanation is that, since southern drainages have long histories uninterrupted by glaciation, a greater amount of genetic divergence has accumulated between populations than has accumulated between populations in drainages that were covered with glaciers. Another possible explanation is that the sea-run life-history component of coastal cutthroat trout has been lost in southern river systems and that this loss has increased the degree of isolation, and hence genetic differentiation, among populations. Additional ecological and life-history information is needed to determine which of these nonexclusive explanations is most important.

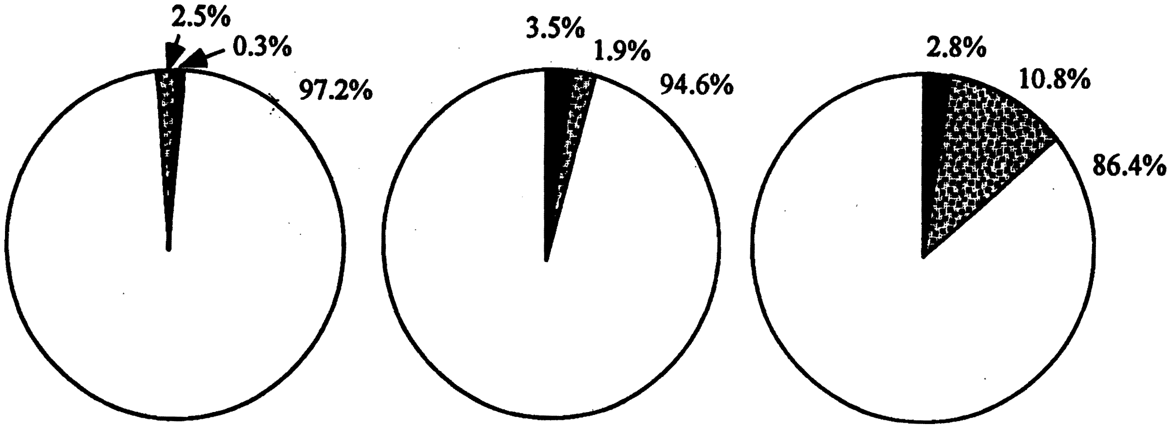
Genetic Information Summary

Coastal cutthroat trout differ from most other West Coast salmonids in that several different life-history patterns are expressed by different populations or by different individuals in the same population. Some fish remain in freshwater streams or lakes over their lifetimes, while others migrate into the lower reaches of rivers or to the ocean at various times in their life cycle. Although genetic differences that are often substantial can arise between populations consisting of different life-history types, similar life-history types did not cluster together as a groups and probably do not represent distinct taxa or distinct evolutionary lineages.

Hybridization between coastal cutthroat trout and steelhead appears widespread along the West Coast. About one-third of the samples collected by NMFS, ODFW, or WDFW in British Columbia, Washington, Oregon, and California that were thought (and intended) to be coastal cutthroat trout contained hybrid individuals. Detailed studies of hybridization show that hybrid swarms can occur in one part of a stream, while steelhead and coastal cutthroat trout coexist in other parts apparently without interbreeding. Most hybrid individuals detected with molecular genetic methods are usually 0+ and 1+ age-class fish and are seldom seen as adults. The occurrence of introgressed populations, however, implies that hybrids can mature and reproduce. Hybrid individuals tend to be intermediate between steelhead and coastal cutthroat trout in several morphological and behavioral characteristics and may have lower fitness as a result.

The NMFS et al. unpublished genetic data set consisting of 99 samples contained several apparent outliers. The origin of these outliers may be due to several factors, including 1) error in estimating allelic frequencies with small sample sizes, 2) random genetic drift in small isolated population above barriers, 3) introgression from steelhead into coastal cutthroat trout, 4) introgression from the introduction of nonnative strains of cutthroat trout, 5) and incomplete sampling of genetically divergent groups of populations. Sampling error could account for only a few of the outliers in this data set. The observation of reduced levels of gene diversity in many of the outliers (relative to neighboring populations) and genetic heterogeneity over short distances are consistent with a history of reproductive isolation for some genetically unusual populations. Allele frequency changes due to hybridization with *O. mykiss* or to introgression from nonnative cutthroat trout may also account for large genetic distances between some genetically unusual populations.

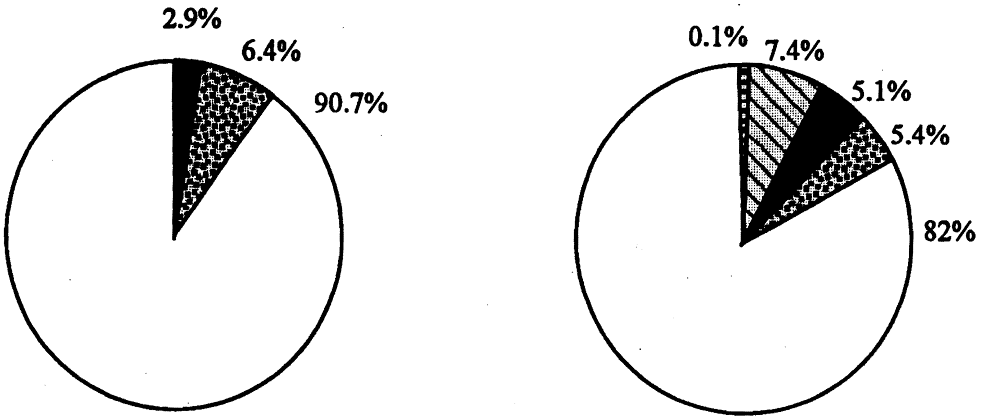
Coastal cutthroat trout differ from other anadromous Pacific salmonids in the genus *Oncorhynchus* in the distribution of genetic variation among population and life-history components (Fig. 31). For example, only a small proportion (2.5-3.5%) of the total variability among chum and coho salmon populations is due to differences, on average, between populations within major groups. A smaller proportion (0.3-1.9%) of the total diversity is due to differences between major groups. Although a similar level of diversity (2.8-2.9%) exists between populations within major groups in coastal populations of chinook salmon and steelhead, a larger proportion (10.8-6.4%) of the total diversity is due to differences among the major population groupings. Coastal cutthroat trout differ from these other salmonids in having a greater level of among-population variability (18%) over a similar geographic area. The largest proportion of this variability (7.4%) is found among streams within rivers, with smaller proportions due to differences among rivers within groups (5.1%), and among major groups (5.4%). The higher levels of genetic diversity among local populations may be due to greater amounts of reproductive isolation between populations, to genetic differences between life-history types, to higher levels of random drift in small populations, or to combinations of these factors.



Chum salmon
105 populations, 4 ESUs
British Columbia-N. Oregon
(Phelps et al. 1994)

Coho salmon
75 Populations, 6 ESUs
British Columbia-S. Oregon
(NMFS unpubl. data)

Chinook salmon
96 populations, 11 ESUs
Puget Sound-California
(NMFS and WDFW unpubl. data-a)



Coastal steelhead
137 populations, 6 ESUs
Puget Sound-California
(NMFS and WDFW, unpubl. data-b)

Coastal cutthroat trout
96 populations in Pacific Northwest (without hybrids)
6 ESUs
(NMFS et al. unpubl. data)

☐ Within populations
▨ Among ESUs
■ Among rivers within ESUs
▧ Among streams within rivers
▤ Between fish above and below barriers within streams

Figure 31. Gene diversity components of allozyme variability in selected species of salmon and sea-run trout among populations within regions. (ESU=Evolutionarily Significant Unit)

The genetic groupings of coastal cutthroat trout in our analyses of the coastwide set of allozyme frequencies is largely consistent with previous studies, which for the most part have included samples from only limited geographic areas. The three-dimensional scalings of the chord and Nei's unbiased genetic distances between samples revealed several geographic groupings of populations:

1. The northernmost group included samples from southern British Columbia, Puget Sound, Hood Canal, and the Strait of Juan de Fuca. Some geographic structure among these samples was also apparent and has been previously observed in other genetic studies (Campton and Utter 1987, Wenburg et al. 1998).
2. Another group consisted of populations on the Olympic Peninsula that did not cluster with their nearest neighbors in the Strait of Juan de Fuca. The genetic characteristics of the Olympic Peninsula populations nonetheless appeared to be transitional between populations in Puget Sound and those in southwestern Washington.
3. One group consisted of populations associated with large coastal estuaries in southwestern Washington and the Lower Columbia River.
4. Populations in the Willamette River Basin were allied with populations in southwestern Washington and the Lower Columbia River, but were distinct from them.
5. A group consisting of a large number of populations in Oregon coastal drainages extended from the mouth of the Columbia River presumably to Cape Blanco. Included in this group were populations from northern Oregon coastal streams and rivers and the Umpqua and Coquille rivers.
6. Only weak genetic support existed for a separate group consisting of populations distributed south of Cape Blanco in southern Oregon and Northern California.

Artificial Propagation

NMFS policy (Hard et al. 1992, NMFS 1993) stipulates that determination of 1) whether a population is distinct for purposes of the ESA and 2) whether an ESA species is threatened or endangered should focus on "natural" fish, which are defined as the progeny of naturally spawning fish (Waples 1991a,b). This approach directs attention to fish that spend their entire life cycle in natural habitat and is consistent with the ESA mandate to conserve threatened and endangered species in their native ecosystems. Implicit in this approach is the recognition that fish hatcheries are not a substitute for natural ecosystems.

Nevertheless, artificial propagation is important to consider in ESA evaluations of anadromous Pacific salmonids for several reasons. First, although natural fish are the focus of ESU determinations, possible effects of artificial propagation on natural populations must also be evaluated. For example, stock transfers might change the genetic or life-history characteristics of a natural population so that the population seems either less or more distinctive than it was historically. Artificial propagation can also alter life-history characteristics such as smolt age and migration and spawn timing (e.g., NRC 1996). Second, artificial propagation poses a number of risks to natural populations that may affect their risk of extinction or endangerment. (These risks are discussed in "Assessment of Extinction Risk," p. 135.) Finally, if any natural populations are listed under the ESA, it will be necessary to determine the ESA status of all associated hatchery populations. This determination would be made following a proposed listing and is not considered further in this document. The remainder of this section summarizes the nature and scope of artificial propagation activities for coastal cutthroat trout and attempts to identify influences of artificial propagation on natural populations.

Scale of Hatchery Production

West Coast hatchery production of anadromous cutthroat trout is summarized in Appendix A, which is based on a database developed under contract to NMFS (NRC 1996) and on state agency reports. Plantings of eggs or fish weighing less than 1.0 gram at release are not included in Appendix A.

Artificial propagation of coastal cutthroat trout in the Pacific Northwest has generally attempted to provide fish for recreational harvest, primarily in Puget Sound, Grays Harbor, the Lower Columbia River, and the Oregon coast (Hooton 1997, Leider 1997). In addition, starting in the mid-1970s, several programs propagated local stocks of coastal cutthroat trout (Stillaguamish River, Hood Canal tributaries, and North Fork Nehalem River, to name a few) to supplement natural spawning populations (Hooton 1997, Leider 1997, Mercer and Johnston 1979). These programs were generally considered unsuccessful and were discontinued by 1993.

The ratio of hatchery to naturally produced coastal cutthroat trout on the West Coast varies from region to region and from watershed to watershed within a particular ESU, with coastal cutthroat trout populations dominated by hatchery production in some areas and maintained by natural production in others (WDFW 1998a, Kostow 1995). Even small (but persistent) contributions from hatchery fish can affect the genetic makeup of local populations (Hard et al. 1992). In most cases, however, hatchery programs for coastal cutthroat trout have been small and of short duration compared to programs for other anadromous salmonids (Hooton 1997, Leider 1997) and have not produced substantial numbers of coastal cutthroat trout relative to natural production.

Introduction of Nonnative Coastal Cutthroat Trout into Hatcheries

In addition to the outplanting of locally derived stocks, coastal cutthroat trout have often been transferred within or between watersheds, regions, and states to either initiate or maintain existing hatchery populations. Eggs, fry, parr, and smolts from nonnative populations have also been introduced into streams to enhance recreational fishing opportunities.

It is often difficult to determine the proportion of native and nonnative hatchery fish released into a given watershed. The number and percentage of nonnative fish in a stream are often underestimated for three reasons. First, hatchery or outplanted fish designated as "origin unknown" in Appendix A (NRC 1996) were counted as native fish, even though their origin may have been unknown because they were *not* native. Second, transplanted hatchery fish routinely acquire the name of the river system into which they have been transferred. For example, coastal cutthroat trout released from the Tokul Creek Hatchery in the Snohomish River Basin in Washington are primarily descendants of stock that originated from Lake Whatcom near Bellingham, Washington (Crawford 1979), but were designated as Tokul Creek stock when released or transferred there (NRC 1996). Third, this report's release summary (Appendix A) does not include releases of coastal cutthroat trout fry smaller than 1 gram and of juveniles from egg-box programs, in part because of the presumed lower survival of smaller fish. However, unsmolted fish have been released for decades in many river basins (such as the Chehalis River Basin), sometimes in relatively large numbers, and some of these programs continue today; these fish may make some contribution to adult abundance. The validity of this premise, however, has not been evaluated.

Until recently, the transfer of hatchery stocks of coastal cutthroat trout between distant watersheds and facilities was a common management practice in Oregon and Washington watersheds (Appendix A) (Crawford 1979, WDFW 1998a, Kostow 1995). Growing concern about the genetic and ecological consequences of this practice prompted management agencies to institute policies to reduce the exchange of coastal cutthroat trout stocks among watersheds, primarily by terminating releases of fish in all but a few locations (discussed in "West Coast Artificial Propagation Activities," which follows). Coastal cutthroat trout programs in California have generally used local stocks to supplement natural populations (Gerstung 1997).

West Coast Artificial Propagation Activities

Alaska

Hatchery experimentation with coastal cutthroat trout in Alaska has been restricted to intermittent releases of smolts from Auke Creek, near Juneau, between 1983 and 1994 (Schmidt 1997). At present, no artificial propagation programs for coastal cutthroat trout are operating in Alaska.

British Columbia

Coastal cutthroat trout have been propagated in British Columbia hatcheries since 1979. Since then, about 3.1 million fish have been released, mostly into the lower Fraser River and streams entering Georgia Strait (NRC 1996). Currently, 17 hatcheries produce coastal cutthroat trout in British Columbia, using mostly local stocks to enhance recreational fisheries and supplement native spawning populations (NRC 1996).

Washington, Oregon, and California

1) Puget Sound—Before the late 1950s, hatchery production of coastal cutthroat trout in Washington consisted of nonanadromous forms. Westslope cutthroat trout, the first nonanadromous salmonid cultured in Washington state, were released into lakes and streams in eastern and western Washington as early as 1895 (Crawford 1979). The first state hatchery for coastal cutthroat trout was built in 1905 at Lake Whatcom, near Bellingham, for local distribution of fish from that lake. These fish were presumably a lacustrine form. The Lake Crescent Hatchery was built in 1913 and propagated a lacustrine strain unique to that lake until 1946 (Crawford 1979). Between 1932 and 1946, coastal cutthroat trout used to stock waters in western Washington were obtained from Cultus Lake, British Columbia, as well as from Lake Crescent, Lake Whatcom, Lake Padden (near Bellingham), and Lake Washington, in Washington State. Between 1934 and 1954, a captive broodstock of westslope cutthroat trout was reared at the Vancouver Hatchery for release in Washington waters (Crawford 1979). In the 1930s and 1940s, several hundred thousand coastal cutthroat trout eggs were taken from fish in Lake Washington tributaries and reared at the University of Washington for planting in local lakes (Lynch 1941, Donaldson 1947). Since 1949, a captive broodstock derived from fish trapped in Lake Whatcom tributaries has been held at the Tokul Creek Hatchery (Crawford 1979). Unlike several sea-run cutthroat trout stocks in Washington, this nonanadromous stock has not been mixed with other stocks at the hatchery (WDFW 1998b). In the late 1970s, this stock was augmented with wild coastal cutthroat trout eggs obtained from Lake Whatcom tributaries (Crawford 1979). These fish are used extensively for planting lowland streams, lakes, and beaver ponds in the Puget Sound region.

There may be some potential for genetic interactions between the Lake Whatcom/Tokul Creek hatchery coastal cutthroat trout stock and naturally spawning Puget Sound coastal cutthroat trout stocks. For example, it was possible to cross Lake Whatcom fish with Lake Washington fish for genetic studies at the University of Washington due to the fact that both stocks spawned at the same time (Hansler 1958). However, no studies have been conducted that demonstrate the extent of genetic exchange between coastal cutthroat trout populations in natural environments.

Releases of anadromous cutthroat trout began in the mid-1960s in Puget Sound tributaries, primarily as smolted fish. The stock source for most of these initial releases was listed in Appendix A as "unknown" because it was identified as such on the WDFW electronic database submitted to NMFS for this status review (NRC 1996). However, evidence from two reports suggests that many of these unknown releases were actually stock transfers from the Beaver Creek Hatchery in the Lower Columbia River (Johnston 1979, Hisata 1973). These early transfers did not succeed in enhancing harvest in the Stillaguamish River (Johnston 1979, Leider 1997). However, in Hood Canal streams, the short-term impact of these large-scale plants on sport harvest was apparent immediately: most fish caught in local streams were of the Beaver Creek Hatchery stock, with a substantial degree of wandering or straying from the release site (Hisata 1973). However, the overall catch rate of these Lower Columbia River fish in Hood Canal was only 0.5% (Royal 1972). Few of these fish were recaptured in seawater; most appeared to have residualized in fresh water (Hisata 1973). Royal (1972) observed that residualism of hatchery coastal cutthroat trout was far more prevalent than in steelhead, perhaps reflecting the more diverse life-history strategies exhibited by coastal cutthroat trout. Overall, the introduction of Beaver Creek sea-run cutthroat trout into Hood Canal streams appears to have had little direct effect on native populations, as few fish of spawning age were observed (Hisata 1973). Royal (1972) hypothesized that differences in rearing areas meant that hatchery-reared coastal cutthroat trout residualizing in lower river sections would not compete with most naturally produced native coastal cutthroat trout.

Anadromous cutthroat trout programs using local Puget Sound stocks were developed in the early 1970s. An early-returning (September-October) Stillaguamish River stock was reared at the Whitehorse facility on the North Fork Stillaguamish River. In addition, a late-returning Stillaguamish River stock (December-January) and a Hood Canal stock were reared in seawater net pens at the NMFS Manchester Laboratory (Crawford 1979). The Stillaguamish River broodstock was especially difficult to adapt to seawater and was phased out in 1979 (Mercer and Johnston 1979).

When it became apparent that introductions of hatchery coastal cutthroat trout had little or no effect on the abundance of coastal cutthroat trout in Puget Sound tributaries, hatchery programs were terminated. No plants of anadromous forms have been made in north Puget Sound streams since 1985, and none have been planted in south Puget Sound or Hood Canal streams since 1994 (Leider 1997, NRC 1996, WDFW 1998a).

Several hatcheries rear nonmigratory coastal cutthroat trout for planting in lowland lakes or westslope cutthroat trout for use in alpine lakes, including the Lake Whatcom, Bellingham, Arlington, Tokul Creek and Eells Springs hatcheries (Fuss and Ashbrook 1995). In 1998, coastal cutthroat trout are scheduled for releases in just a few western Washington lakes—all of which drain into Hood Canal—including Horseshoe, Tarboo, Koeneman, Wye, Benson, Cady Haven, and Trails End lakes (WDFW 1998b).

2) Olympic Peninsula—There are no hatcheries dedicated to rearing coastal cutthroat trout in this region, although occasional releases of fish reared in Lower Columbia River or Grays Harbor facilities have occurred in area streams (NRC 1996).

3) Southwestern Washington/Lower Columbia River—The principal sea-run cutthroat trout facility in Southwestern Washington is the Lake Aberdeen Hatchery, which began rearing a mixed coastal cutthroat trout captive broodstock in the early 1980s (NRC 1996, Ashbrook and Fuss 1996). This stock is a mixture of coastal cutthroat trout from tributaries of Grays Harbor and other nearby coastal streams (Ashbrook and Fuss 1996). Every few years, additional genetic material is introduced from naturally produced native adults captured in local streams.

As observed in the Puget Sound discussion about Hood Canal, releases of Beaver Creek hatchery stock resulted in extensive wandering in the North River (Hisata 1973). In total, Grays Harbor and Willapa Bay tributaries currently receive about 37,000 fish annually, primarily from the mixed stock of coastal cutthroat trout reared at the Aberdeen Hatchery (NRC 1996, Leider 1997). This accounts for about 14% of the recent hatchery effort for coastal cutthroat trout in Washington (Leider 1997).

Artificial propagation of the sea-run form of coastal cutthroat trout began in the Lower Columbia River at the Beaver Creek Hatchery in 1958, with stocks obtained from the Nemah, Green (Toutle River), and Elochoman rivers (Crawford 1979, Randolph 1986). Few returns resulted from this mixture, and the stock was not used after 1965 (Crawford 1979). Between 1963 and 1968, eggs were imported from the captive broodstock held at the ODFW Alsea Hatchery; after 1972, these fish were incorporated into the Beaver Creek Hatchery stock (Randolph 1986). In addition, cutthroat x steelhead hybrid trout were mixed into the hatchery stock in the late 1960s (Crawford 1979). However, the return rate was only 1.8%, there appeared to be a high degree of residualism, and the straying rate was high (about 30%) (Randolph 1986). To purge the hatchery stock of steelhead influence, "silvery" fish were not propagated at Beaver Creek Hatchery. Instead, only heavily spotted individuals were spawned, as these fish were thought more likely to be pure coastal cutthroat trout due to their coloration (Crawford 1979). However, this procedure may have contributed to the high rate of residualism at this hatchery, as it has been observed that anadromous cutthroat trout are silvery colored, while nonmigratory coastal cutthroat trout, which need to be cryptically colored for freshwater residence, tend to be coppery and more heavily spotted (Kostow 1995). The initial failure of the Beaver Creek Hatchery program resulted in the realization that hatchery programs for coastal cutthroat trout must be based on an appreciation of the genetic diversity of native stocks, with special considerations given to local adaptations (Behnke 1992). Returns did not improve significantly until introduction of the Cowlitz Hatchery stock in 1982, which increased returns dramatically and enabled a self-sustaining program at the Beaver Creek Hatchery.

Time of spawning of natural coastal cutthroat trout in the Elochoman River is significantly correlated with that of fish in the hatchery (Randolph 1986), which may indicate a substantial contribution of hatchery fish in the naturally spawning component. For example, between 1960 and 1965, natural and hatchery fish spawned in mid-January. After the early 1970s, natural and hatchery fish were spawning in December (Randolph 1986) due to a 3-week advancement in spawn timing that may have resulted from broodstock selection at the hatchery (Royal 1972).

The sea-run cutthroat trout program at the WDFW Cowlitz Hatchery was begun in 1968 with the Beaver Creek Hatchery stock and a few eggs from native Cowlitz River coastal cutthroat trout (Crawford 1979). This program continued until 1975 and resulted in few returns to the hatchery. After 1976, only fish returning to the Cowlitz Hatchery were spawned, resulting in an increase in returns to the fishery and to the hatchery (Tipping and Springer 1980). For example, by 1979, 60% of the Cowlitz in-river catch was hatchery fish, with a total return of 9,000 fish. Spawn timing in the hatchery stock has been advanced about 2 months earlier than in naturally produced fish since the program's start (Tipping and Springer 1980).

Currently, the largest component of hatchery efforts for coastal cutthroat trout in Washington occurs in the Lower Columbia River with about 200,000 fish released annually, mostly from the Cowlitz Hatchery (Leider 1997, NRC 1996). Approximately 75% of the total effort in Washington is dedicated to this area (Leider 1997). In 1997, coastal cutthroat trout were released into the Abernathy and Beaver creeks and the Coweeman, Cowlitz, and Lewis rivers (WDFW 1997). In addition to state hatchery programs, a cooperative project between Clark Public Utilities, Vancouver/Clark Parks and Recreation, WDFW, and Trout Unlimited is now in its fifth year of releasing fish from net pens in a pond adjacent to Salmon Creek. About 10,000 coastal cutthroat trout from the Skamania Hatchery are released from this facility each year (Shutt 1998). Leider (1997, p. 74) has suggested these hatchery releases "may also have increased the occurrence of intraspecific ecological interactions or the incidence of maladaptive gene flow from hatchery to wild sea-run cutthroat trout stocks."

The Big Creek Hatchery sea-run cutthroat trout stock, developed from the natural population in that stream, has been the primary stock used in Oregon Lower Columbia River programs (Hooton 1997, Kostow 1995); numerically, however, Alsea Hatchery stock has been used more often in the Lewis and Clark, Youngs, and Hood rivers and Gnat, Milton, and Scappoose creeks (NRC 1996). In addition, a coastal cutthroat trout stock from the North Fork Nehalem River has also been frequently introduced into Lower Columbia River streams in Oregon (NRC 1996). The effects of long-term hatchery releases of coastal cutthroat trout on natural production in Lower Columbia River tributaries in Oregon is unknown (Kostow 1995).

In Oregon, the planting of hatchery coastal cutthroat trout was discontinued in Lower Columbia River streams by 1994. Currently, only standing bodies of water such as lakes and ponds in the Lower Columbia River area are planted with hatchery fish (Hooton 1997, Kostow 1995).

4) Willamette River—Historically, tributaries of the Willamette River above Willamette Falls received hatchery coastal cutthroat trout from a variety of sources. Coast Range tributaries tended to get plants of anadromous stocks (mostly Alsea Hatchery fish), while Cascade Range tributaries tended to receive the Leeburg stock, which appears to have been derived from a local Willamette River freshwater strain native to the Long Tom River (NRC 1996). Most of the hatchery effort in Willamette River tributaries occurred in the 1950s and 1960s (NRC 1996).

Currently, the only plants of hatchery coastal cutthroat trout in the Willamette River basin are in Cascade Mountain lakes, using a native brood stock of coastal cutthroat trout known as the Hackleman stock (Hooton 1997). The effects, if any, of these introductions on naturally spawning stocks are unknown but are currently under investigation by ODFW (Kostow 1995).

5) Oregon Coast—The most notable feature of past coastal cutthroat trout hatchery programs in Oregon coastal tributaries was the decades-long reliance on the Alsea Hatchery broodstock for planting in lakes and streams over the entire Oregon coast, from Coffenbury Lake just below the mouth of the Lower Columbia River to the Chetco River near the California border (Hooton 1997, NRC 1996). Several other hatchery stocks were occasionally used, such as the North Fork

Nehalem River, Nestucca River, Roaring River, and Coquille Hatchery (derived from Alsea Hatchery) stocks (NRC 1996). The Alsea Hatchery stock has been in culture for about 40 years (Kostow 1995, Randolph 1986). The genetic consequences of these programs on the hatchery broodstocks is largely unknown (Kostow 1995).

In the last 10 years, there has been a switch from planting hatchery coastal cutthroat trout into streams to restricting plants to lakes and ponds on the Oregon coast (Kostow 1995, Hooton 1997). Planting was discontinued in south Oregon coastal streams in the 1980s, in north Oregon coastal streams in the early 1990s, the Rogue River basin in 1993, and most mid-Oregon coastal streams in 1996 (Hooton 1997). Since 1997, no hatchery coastal cutthroat trout have been planted in streams containing anadromous cutthroat trout (Hooton 1997).

6) Southern Oregon/California Coasts—Small numbers of Alsea Hatchery coastal cutthroat trout were released in South Oregon streams prior to 1985 (NRC 1996). However, few releases have occurred since then, and recent releases have been restricted to standing bodies of water.

No major programs for the enhancement or supplementation of coastal cutthroat trout stocks have taken place in Northern California, although recent interest in the species has led to the establishment of several small hatchery projects for anadromous cutthroat trout.

Coastal cutthroat trout have been reared at a hatchery facility associated with Humboldt State University since at least the early 1990s. Some of these fish have been used in a joint effort between the University, the California Department of Fish and Game (CDFG), and the City of Arcata to develop a coastal cutthroat broodstock for enhancing recreational fisheries in northern California coastal lagoons (AMWS 1998).

Between 1988 and 1992, very small releases of anadromous cutthroat trout (about 775 juveniles in total) were made from the CDFG COOP site on Prairie Creek, a tributary of Redwood Creek (CDFG 1984-97). In 1993 and 1994, eight and five adult coastal cutthroat trout, respectively, were collected at the weir on Rowdy Creek, but there is no indication that these fish were spawned (CDFG 1984-97).

Discussion of and Conclusions about ESU Determinations

As discussed below, several factors make identification of ESUs particularly challenging for coastal cutthroat trout.

Diversity of Life History

The life history of coastal cutthroat trout is perhaps the most complex of all the Pacific salmonids. Coastal cutthroat trout exhibit a diverse array of migratory behaviors and a wide range in the timing of migration and reproduction. Coastal cutthroat trout also do not necessarily die after spawning. The life-history diversity of coastal cutthroat trout poses two formidable challenges in ESU determinations: 1) understanding the factors that limit and promote this diversity within and among populations, and 2) identifying geographically based conservation units based in part on life-history variation. Unfortunately, we are not aware of direct information on the genetic basis of life-history variation in any coastal cutthroat trout population that would help address the first challenge, and the factors underlying life-history differences among populations have not been characterized well enough to help resolve the second.

For coastal cutthroat trout, it is not known to what extent behavioral or physiological adjustment, genetic polymorphism, or phenotypic plasticity contribute to life-history variation; it is also unknown whether or to what extent individual fish express different life-history strategies at different times. Possible mechanisms underlying expression of life-history variation include these: 1) the variation expressed is completely environmentally determined, 2) the variation is genetically hard wired, or 3) the variation reflects a combination of (perhaps many and small) genetic and environmental influences. In the first case, information on life-history variation would clearly be of little use in identifying meaningful ESU boundaries. At the opposite extreme, ESU determinations would be facilitated considerably by knowledge that life-history variation is genetically determined. As was discussed in "Life History" (p. 38), however, reality almost certainly lies between these extremes. The focal issue for ESU determination is the relative importance of genetic and environmental influences on life-history expression. Because data that directly address this issue are not available for coastal cutthroat trout, it is prudent to assume that both influences are important.

Consideration of life-history characteristics such as migratory behavior suggests two possible (and at least partially conflicting) implications for the evolutionary ecology of coastal cutthroat trout. On one hand, the relatively limited opportunities for marine dispersal may promote stronger reproductive isolation in coastal cutthroat trout than occurs with Pacific salmon and steelhead. Isolation of coastal cutthroat trout populations also may occur on a finer spatial scale: groups of populations from different tributaries within the same large river basin may experience reduced gene flow. All else being equal, strong reproductive isolation will promote genetic divergence more rapidly than if gene flow is more frequent. Available genetic information suggests that reproductive isolation of local populations has been a prominent feature of the evolutionary ecology of coastal cutthroat trout. Because appreciable gene flow can act to limit genetic differentiation under selection, reproductive isolation should foster more rapid development of adaptations to individual watersheds or reaches within them. The genetic evidence indicates that many of the coastal cutthroat trout populations sampled have been isolated sufficiently to permit important adaptive differences to arise (see "Genetic Information" section, p. 70).

On the other hand, although substantial reproductive isolation provides opportunities for adaptive differentiation, it may not necessarily lead to marked local adaptations in freshwater populations of coastal cutthroat trout. Marked adaptive differences among isolated freshwater populations have been difficult to detect in some salmonids that contain both migratory and nonmigratory forms. Stock transfers of kokanee (the freshwater form of *O. nerka*) and rainbow trout, for example, have been successful over broad ranges in temperate North America and on other continents, while stock transfers of anadromous sockeye salmon and steelhead within their historic range have rarely been successful (Withler 1982, Busby et al. 1996, Gustafson et al. 1997). Wood (1995) and Allendorf and Waples (1996) suggested that this result can be explained by the more complex life history of the anadromous populations. To complete its life cycle and survive to reproduce, a Pacific salmon or steelhead must perform a long series of precisely timed events, including freshwater residence, smoltification and outmigration, marine feeding and migration, and the return migration to fresh water and spawning. Disruption of a single link in this chain can substantially affect the fitness of a population. According to this argument, freshwater populations of *O. nerka* and *O. mykiss* generally have a simpler life history, with fewer conditions requiring local adaptation. On the other hand, salmonids will never be the top predator in the ocean, which is a much larger arena than a freshwater lake; the opportunity in the ocean for directed or stochastic mortality is also almost infinitely higher.

It is not clear to what extent these empirical observations for nonmigratory populations of *O. nerka* and *O. mykiss* (and inferences about the importance of local adaptations) apply to coastal cutthroat trout. Depending on the factors controlling the phenotypic expression of life history, coastal cutthroat trout may be able to respond to a wide range of conditions at several points in the life cycle. If environmental or ecological conditions are unfavorable for one phenotype, it may be possible for the population to cope with these conditions–without serious demographic or genetic consequences–through some form of life-history plasticity. This capacity to adapt to changing conditions can be found to a limited degree in some populations of *O. nerka* and *O. mykiss*, but the life-history options are generally fewer and their expression not as pervasive as in coastal cutthroat trout. One result of this life-history diversity is that coastal cutthroat trout populations may be buffered to some extent against extreme selective pressures that promote local adaptations, resulting in selection for a more generalist phenotype. Alternatively, the selection regime experienced by coastal cutthroat trout may control the degree of plasticity itself that is expressed or the range of variation in phenotypes produced by a particular mating. Available evidence is insufficient to discriminate between these alternatives, and any of them could be responsible for the observed lack of strong geographic life-history patterns for coastal cutthroat trout.

Paucity of Data

Although important data gaps have been identified in all of our coastwide status reviews of Pacific salmon and steelhead, in general these gaps apply to particular types of information and/or only to certain geographic areas. In contrast, coastal cutthroat trout are characterized by a pervasive lack of quantitative information of almost all types across the range of the subspecies. This is not to say that there is no information about coastal cutthroat trout: in fact, as discussed in the preceding sections, there is a considerable amount of information about the biology of this subspecies. However, much of this information is qualitative or descriptive, rather than quantitative. Comprehensive sets of quantitative data, such as distribution, abundance, age structure, and run timing, are largely absent for coastal cutthroat trout. The fact that coastal cutthroat trout do not constitute a commercially important species, with fewer directed recreational fisheries than for co-occurring Pacific salmon and steelhead, no doubt has much to do with the paucity of these data. Furthermore, spawning coastal cutthroat trout are more difficult to observe than spawning salmon, and there are almost no large runs that are clear targets for systematic monitoring.

In the last few years, several studies have attempted to characterize the population genetic structure of coastal cutthroat trout using allozyme and DNA markers. Although the various genetic datasets in combination are not as large as for many species of Pacific salmon, they do provide quantitative information for much of the range of the subspecies. In the other species of anadromous Pacific salmonids reviewed by NMFS under the ESA, patterns of population genetic differentiation were often substantiated by congruent patterns of life-history variation, thus providing at least two lines of evidence to support ESU determinations. For coastal cutthroat trout, this is generally not the case. A lack of life-history information, or the failure of existing life-history data to show clear geographic patterns, means that the kind of genetic, ecological, and environmental information that has proven useful for ESU determinations for Pacific salmon assumes a relatively greater importance in ESU evaluations for coastal cutthroat trout. This lack of information contributed to uncertainty in the ESU determinations, particularly for cases in which the genetic data are somewhat equivocal.

Genetic Outliers

The genetic data set for coastal cutthroat trout is distinctive in having a number of samples with allele frequencies that appear to represent extreme outliers. These outliers cover a wide geographic range, are not characterized by any particular type of collection, and are genetically distinctive, each in a unique way. It is difficult to determine how to deal with these outliers in ESU determinations without a better understanding of the reason(s) for their occurrence. Possible explanations involve four factors: sampling artifacts, founder effect/genetic drift, hybridization, and artificial propagation.

Sampling artifacts

The outlier samples could be nonrandom samples, perhaps representing progeny of just a few individuals from a larger population, or a few spawning aggregations from a larger set within a drainage. Alternatively, even random samples can seem unusual in their genetic makeup if they are based on a small number of breeding individuals.

Founder effect/genetic drift

If some populations have been recently colonized by a very few founders, allele frequencies could be shifted substantially from those of nearby populations; a similar pattern could result from substantial isolation. The outliers examined in this analysis tend to have lower-than-expected heterozygosity, suggesting that several of these populations may have experienced founder effects or appreciable genetic drift.

Hybridization

Natural hybridization with *O. mykiss* is known to complicate the genetic analysis of coastal cutthroat trout, and undetected hybridization (particularly involving backcross generations) could result in substantial allele frequency shifts from typical coastal cutthroat trout profiles. If, as hypothesized by Neillands (1990) and Hawkins (1997), hybrids tend to be selected against during the anadromous phase, hybrids would then be expected to be more prevalent in juvenile samples, such as those used in several genetic analyses of coastal cutthroat trout. If different populations of *O. mykiss* were involved to varying degrees in the various hybridization events, the genetic effects on coastal cutthroat trout populations would not necessarily be uniform and could create outliers with varying genetic signatures.

Artificial propagation

Introductions of nonnative or artificially propagated fish into a natural population may also change the genetic character of a natural population. However, the genetic influence of outplanted hatchery coastal cutthroat trout on natural populations has been largely discounted by WDFW (1998a) because hatchery fish generally have poor survival rates and are generally highly exploited by anglers. Nevertheless, genetic similarities between some populations in Oregon's Coquille River and Alsea Hatchery fish appear to be attributable to the outplanting of Alsea Hatchery fish into streams harboring these populations. These patterns could contribute to some of the genetic outliers observed in our analyses.

Collectively, these four factors do not satisfactorily explain all, or even most, of the genetic outliers. Many outliers, then, appear to reflect important aspects of the population genetic structure of coastal cutthroat trout, and probably reflect a population structure that has resulted from a wide range in the degree of reproductive isolation over small as well as large geographic distances.

In summary, the genetic and life-history characteristics of coastal cutthroat trout differ from those of other anadromous Pacific salmonids, but the implications of these differences for ESU determinations are not clear. Considering only the opportunities for strong reproductive isolation of individual populations, one might conclude that ESUs for coastal cutthroat trout would be relatively small. On the other hand, available data for life-history and other characteristics do not show strong geographic differences in traits likely to be involved in local adaptations. This lack of geographic difference among the characters may reflect common selective pressures for a generalist or highly plastic life-history strategy (in which case ESUs might be relatively large), or it may reflect an inability of available information to reveal life-history patterns that exist on small scales within a highly diverse subspecies.

There is little doubt that the distinctive life-history characteristics of coastal cutthroat trout result in interactions between the fish and their physical and biotic environments that differ from those of other anadromous Pacific salmonids. Unfortunately, this fact alone provides little information to aid ESU determinations. ESU boundaries that are congruent across several other salmon species (reflecting similar historical processes and similar responses to physical/ecological habitat factors) may not be as relevant for coastal cutthroat trout, but the existing biological data do not clearly reveal how coastal cutthroat trout ESUs should differ from those of the other species, if indeed they should differ at all.

ESU Determinations

The BRT considered several possible ESU configurations for coastal cutthroat trout. After considerable discussion, a majority of BRT members supported a scenario involving six ESUs: Puget Sound, Olympic Peninsula, Southwestern Washington/Columbia River, Upper Willamette River, Oregon Coast, and Southern Oregon/California Coasts (Fig. 32). Alternative scenarios considered at length by the BRT were 1) a single ESU corresponding with the range of coastal cutthroat trout and 2) multiple ESUs corresponding to small geographic units, such as major river basins. Although the six ESUs supported by a majority of the BRT showed strong similarities to those designated for other species (especially coho and chinook salmon and steelhead), there are a few significant differences that reflect differences in genetic structure and life-history variation.

Two general issues stimulated considerable discussion by the BRT; a summary of those issues follows.

Life-history forms

The BRT was unanimous in concluding that each ESU include all life-history forms (nonmigratory, freshwater migratory, and saltwater migratory) present. BRT members felt strongly that the diversity of life-history forms occurring in each ESU represented genetic and phenotypic resources characteristic of and important to its evolutionary ecology.

Barriers to migration

Barriers to migration separate the different life-history forms of coastal cutthroat trout in some watersheds, and evaluating the significance of these barriers proved to be a challenging problem. The BRT was divided regarding whether populations above long-standing natural barriers (i.e., those that effectively preclude all migration for hundred or thousands of years) should be included in ESUs. The primary argument for inclusion centered on the fact that populations above barriers are often most closely related to those below them; it is therefore

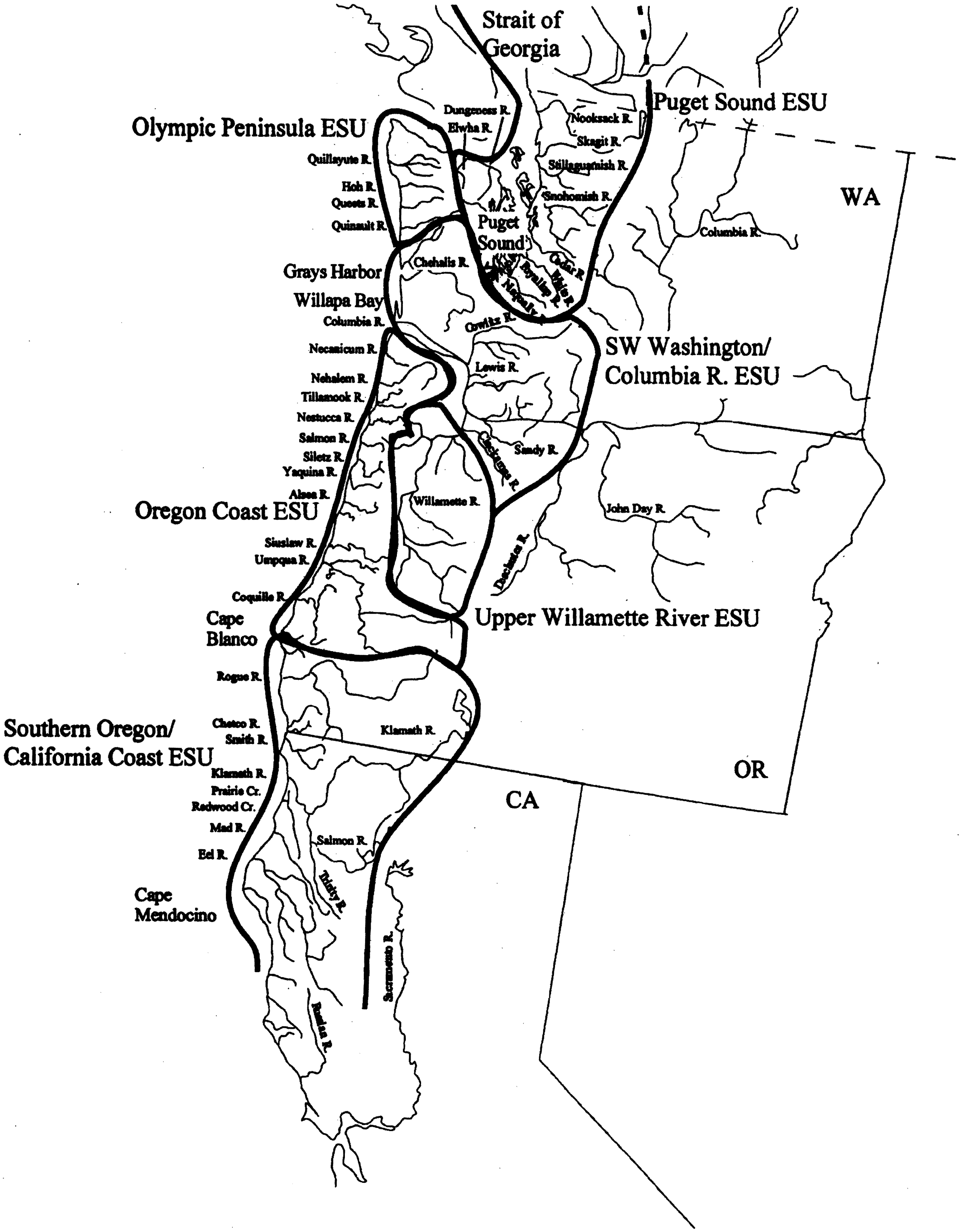


Figure 32. Proposed Evolutionarily Significant Units (ESUs) for coastal cutthroat trout.

unclear what ESU populations above barriers would belong in, if not in the ESU that includes populations below the barrier. The argument for exclusion focused on the complete reproductive isolation between populations above and below barriers and, consequently, the different evolutionary trajectories followed by these groups of populations. Therefore, only under special circumstances would the above-barrier populations be useful in recovering below-barrier ones.

With respect to barriers that permit some one-way migration (i.e., downstream migration of smolts but not upstream passage of adults), the majority of BRT members felt that populations above these barriers should be included in ESUs. The basis for this conclusion is twofold: 1) populations above barriers may contribute demographically and genetically to populations below them, even if the frequency of successful one-way migrants per generation is low, and 2) populations above barriers may represent genetic resources shared by populations below these barriers (and potentially a significant component of diversity for an ESU). In the case of the upper Willamette River, however, the BRT unanimously concluded that populations of coastal cutthroat trout above Willamette Falls are part of an ESU separate from those in the Columbia River. A primary reason for this conclusion is that the river above the falls encompasses a large area with considerable habitat complexity, and this area evidently supports several different populations of coastal cutthroat trout.

ESU Descriptions

1) Puget Sound ESU

This proposed ESU includes populations of coastal cutthroat trout that enter protected marine waters in northwestern Washington; its boundaries correspond roughly with the Puget Lowland Ecoregion. Life-history data indicate that coastal cutthroat trout from Puget Sound generally smolt at a smaller size and possibly a younger age than those entering coastal marine waters, and genetic data indicate that these populations are separated from those in southwestern Washington and farther south. Populations in Puget Sound and Hood Canal and on the Olympic Peninsula are highly heterogeneous genetically; nevertheless, some evidence exists for coherent genetic separation of populations on the Olympic Peninsula from those in the eastern Strait of Juan de Fuca, northern Puget Sound, and Hood Canal. Populations in Hood Canal and along the Strait of Juan de Fuca are distinctive but show no clear evidence of a transition zone between Puget Sound and southwestern Washington. Populations from the upper Nisqually River (a heavily glacially influenced system in southern Puget Sound) are markedly genetically distinct from their nearest geographic neighbors. The BRT was unable to ascertain the source of this distinctiveness; possibilities include strong and long-standing reproductive isolation, sharp habitat differences, or a combination of these factors.

Based primarily on somewhat distinctive life-history patterns, the BRT concluded that this ESU includes all streams in Puget Sound and the Strait of Juan de Fuca west to, and including, the Elwha River. Available genetic data are consistent with this ESU boundary. The northern boundary for this ESU is unclear, but unpublished genetic data (Williams unpubl. data) lend support to the hypothesis that this ESU extends into southern British Columbia to include populations along eastern Georgia Strait north of Vancouver. Williams' data indicate that Vancouver Island populations are genetically distinct from those on the mainland, providing evidence for reproductive isolation of these groups. In general, this ESU's boundaries reflect an ecoregion in which river drainages have relatively high flows due largely to high precipitation, snow melt, and temperatures moderated by the marine environment. The southern and western boundaries are similar to those previously identified for chinook, coho, chum, pink salmon, and steelhead; the northern boundary differs from those for chinook and coho salmon (which do not extend into Canada) and pink, chum, and coho salmon (which do not include eastern Vancouver Island).

2) Olympic Peninsula ESU

This proposed ESU includes coastal cutthroat trout in populations from the Strait of Juan de Fuca west of the Elwha River and coastal streams south to, but not including, streams that drain into Grays Harbor. The proposed boundaries of this ESU are similar to those for steelhead and coho salmon. Support for this ESU relies primarily on the ecological distinctiveness of this area, which is characterized by high precipitation, cool water temperatures, and relatively short high-gradient streams that enter directly into the open ocean. Coastal cutthroat trout from this area are relatively large as smolts, and a higher proportion appear to mature at first return from seawater than is the case in most Puget Sound populations.

Genetic data for this ESU are limited. Populations sampled from the Olympic Peninsula are genetically distinctive but show a stronger genetic affinity to neighboring populations in Puget Sound and Hood Canal than to those along the Strait of Juan de Fuca (east of the Elwha River). On the other hand, at least some of the Olympic Peninsula populations are not strongly differentiated from those in northern or southern Puget Sound, and they are well differentiated from populations to the south. Based primarily on these genetic data, a minority of the BRT concluded that populations from the Olympic Peninsula should be considered part of a combined Puget Sound-Olympic Peninsula ESU. Other BRT members pointed out that the Olympic Peninsula ESU may represent a genetic transition zone between the Puget Sound and southwestern Washington/Columbia River ESUs.

3) Southwestern Washington/Columbia River ESU

The proposed boundaries of this ESU are similar to the Southwestern Washington/Lower Columbia River ESU for coho salmon (Weitkamp et al. 1995). Support for this ESU designation comes primarily from ecological and genetic information. Ecological characteristics of this region include the presence of extensive intertidal mud and sandflats, similarities in freshwater and estuarine fish faunas, and substantial differences from estuaries north of Grays Harbor and south of the Columbia River. The coastal cutthroat trout samples from southwestern Washington show a relatively close genetic affinity to the samples from the Columbia River.

A minority of the BRT supported a split of Columbia River from southwestern Washington coastal cutthroat trout populations. Tagging and recovery data for chinook, coho, and chum salmon indicate different marine distributions for fish from the two areas. The limited dispersal ability of anadromous cutthroat trout may restrict genetic exchange among populations in the two areas, and the areas exhibit differences in their physical estuarine characteristics. An important salmonid parasite, *Ceratomyxa shasta*, occurs in the Columbia River but has not been observed in Willapa Bay or Grays Harbor. The WDFW, based on an unpublished analysis of a small number of southwestern Washington populations, observed greater genetic differentiation of populations in this ESU than was observed in the analyses described in "Regional patterns of genetic variability" (p. 104). Furthermore, WDFW argued that extensive hatchery influence in some populations may have obscured natural genetic differences between southwestern Washington and Lower Columbia River coastal cutthroat trout. However, the majority of BRT members felt that WDFW's analyses were limited and that, collectively, available data did not provide compelling evidence for a split between populations along the southwestern Washington coast and those in the Columbia River.

4) Upper Willamette River ESU

Coastal cutthroat trout is one of only three species of anadromous Pacific salmonids that historically occurred above Willamette Falls. Upper Willamette River populations of the other two species—spring chinook salmon and winter steelhead—have been identified as separate ESUs in previous status reviews, based on ecological factors, substantial genetic differences from other Columbia River populations, and physical and hydrological conditions (Busby et al. 1996, Myers et al. 1998). Based on information provided by ODFW (1998), Willamette Falls is a nearly complete barrier to anadromous fish (summer steelhead as well as coastal cutthroat trout) during summer and early fall. The BRT concluded that the upper Willamette River has probably never supported a substantial anadromous population of cutthroat trout; the primary life-history form above Willamette Falls appears to be freshwater migratory, a type that seems relatively rare below the falls.

Moreover, upper Willamette River coastal cutthroat trout exhibit a genetic structure consistent with the hypothesis that the falls is a strong barrier to reproduction between populations above and below the falls. The parasite *Ceratomyxa shasta* in the Willamette River below the Marys River and high temperatures in the lower Willamette River in summer and fall probably limit the survival of the very few migrants known to drop over the falls. Although the populations above the falls are highly heterogeneous genetically, they do form a somewhat coherent cluster of apparently isolated and semi-isolated populations.

The physical and genetic evidence of a barrier, habitat and ecological differences above and below the falls, and the lack of anadromous populations and prevalence of freshwater migratory forms above the falls led the majority of the BRT to conclude that coastal cutthroat trout above Willamette Falls should be considered a separate ESU.

5) Oregon Coast ESU

Genetic data indicate marked genetic differences between coastal cutthroat trout from coastal Oregon and those in the Columbia River and along the Washington coast. Samples of coastal cutthroat trout south of the Columbia River indicate a large heterogeneous group of populations along the Oregon coast. Furthermore, several ecological differences exist between rivers along the Oregon coast and those farther north. The Oregon coast is characterized by a strong maritime influence, including relatively high precipitation, moderate temperatures, and short low-gradient streams with few migration barriers. Tagging studies in Alaska and elsewhere indicate that anadromous cutthroat trout follow shorelines when in seawater; thus, the known migratory patterns of this species are consistent with the hypothesis that the Columbia River, which is several miles wide and relatively deep at its mouth, is a migratory barrier between coastal populations in Oregon and those in Washington. The proposed boundaries of this ESU are similar to the ESUs identified for coho and chinook salmon and steelhead.

The southern boundary of this proposed ESU is at Cape Blanco, Oregon. Although genetic data provide only weak evidence for a split between populations north or south of Cape Blanco, Oregon, ecological data do support such a split. The Cape Blanco area is a major biogeographic boundary for many marine and terrestrial species, and has been identified as an ESU boundary for chinook and coho salmon and steelhead on the basis of strong genetic, life-history, ecological, and habitat differences north and south of this landmark. Unpublished meristic data (Williams, unpubl. data) also point to a difference between coastal cutthroat trout populations north and south of Cape Blanco.

6) Southern Oregon/California Coasts ESU

A majority of the BRT concluded that populations of coastal cutthroat trout from Cape Blanco south to the southern extent of the subspecies' range represent a separate ESU. Several members felt that the genetic and ecological data were not strong enough to support this split. However, as described above, meristic (and, to some extent, genetic) information lends some support for a separate coastal cutthroat trout ESU south of the major biogeographic boundary at Cape Blanco. In addition, the limited dispersal capability of coastal cutthroat trout and anecdotal evidence for marked differences in population dynamics for populations north and south of Cape Blanco support a split at that landmark. Finally, most river systems in this ESU are relatively small with limited estuaries and heavily influenced by a maritime climate. Many of these systems are characterized by physical and thermal barriers to movement by anadromous fish; notable exceptions that lack such barriers are the Eel, Klamath, Rogue, and Trinity rivers.

Alternative ESU Scenarios

The BRT considered several alternative ESU scenarios for coastal cutthroat trout. These range from a single ESU corresponding to the entire subspecies to numerous small ESUs corresponding to individual river basins. The BRT concluded that none of these scenarios is completely satisfactory, but focused substantial discussion on two widely divergent scenarios that some members felt merited serious consideration. Although neither was favored by a majority of BRT members, the fact that both of these contrasting scenarios were taken seriously is an indication of the considerable uncertainty associated with ESU determinations for coastal cutthroat trout. These alternative ESU designations are outlined below.

Single ESU corresponding to the subspecies *O. c. clarki*

This scenario reflects one interpretation of the pattern of genetic and life-history diversity in coastal cutthroat trout. The genetic diversity of this species illustrates strong differences among populations from neighboring drainages but also substantial differences among putative populations within these drainages. Indeed, coastal cutthroat trout exhibit a substantially greater proportion of genetic variation expressed among populations than do most species of Pacific salmon (sockeye salmon is an exception). When combined with the complexity of life-history variation in coastal cutthroat trout, this pattern tends to obscure geographic patterns of differentiation.

Several lines of reasoning could support determination of a single ESU. First, it may be that, biologically, there are no conservation units of coastal cutthroat trout smaller than the subspecies that can be considered separate ESUs under guidelines in NMFS policy. Second, even if there are multiple ESUs within the subspecies, it may not be possible with current information to identify their boundaries with any certainty; in this case, treating them provisionally as a single ESU may be reasonable until better information is developed. Third, as pointed out previously, populations of coastal cutthroat trout often exhibit high degrees of genetic heterogeneity, with many genetic outliers occurring over relatively short geographic distances. These results suggest a mosaic population structure that reflects varying levels of reproductive isolation over a large range of geographic distances. This genetic heterogeneity may thus be masking, at least partially, evolutionary affinities associated with biogeographic provinces and potential adaptations within those provinces, making identification of smaller ESUs difficult to justify.

The high degree of genetic differentiation among coastal cutthroat trout populations inhabiting different river basins relative to that among ESUs (on average) could support an argument for a single heterogeneous ESU corresponding to the range of coastal cutthroat trout. However, an argument for a single coastwide ESU based on the substantial degree of genetic and life-history variation among populations (including those within basins) is problematic because available genetic evidence provides some support for a hypothesis that many populations of coastal cutthroat trout coastwide are evolving largely independently of one another. Some BRT members thought that the available data are equally consistent with a contrasting scenario involving a larger number of small ESUs. It is unclear whether additional genetic data would resolve this problem; several BRT members thought more comprehensive life-history information for coastal cutthroat trout populations probably would be helpful.

In the end, the majority of BRT members rejected this scenario in favor of one based on six smaller units because of the combination of ecological, biogeographic, and genetic evidence for finer-scale structure. Under either scenario, the BRT felt strongly that operational conservation units would likely be substantially smaller than the ESUs.

Separate ESUs in major river basins

This ESU configuration recognizes the possibility that coastal cutthroat trout in major river basins can be strongly isolated from populations in other basins and have a close affinity to local freshwater environments. Although available life-history data do not show major inter-basin differences among coastal cutthroat trout populations, environmental and ecological differences among several basins have been documented and might form the basis for adaptations of local populations. In addition, although the genetic differences observed among coastal cutthroat trout populations within an ESU tend to be greater on average than those among ESUs, substantial variation can also be detected within drainages. Thus, appreciable reproductive isolation of individual breeding populations may occur on smaller geographic scales than for other species of Pacific salmon. The genetic and life-history data are therefore not entirely consistent with ESUs based on major river basins; indeed, it is not clear what criteria would be used to identify basins that could be considered separate ESUs, or where to include populations from smaller systems not associated with major basins. However, many BRT members felt that major river basins might be useful as a template for identifying operational conservation units within larger ESUs.

Umpqua River Coastal Cutthroat Trout

In the status review of Umpqua River coastal cutthroat trout (Johnson et al. 1994), the BRT concluded that all life-history forms in the Umpqua River were part of the same ESU but was unable to reach a conclusion on the geographic extent of the ESU. This more comprehensive review has not completely resolved this question. Although Umpqua River coastal cutthroat trout are provisionally identified here as part of a larger Oregon Coast ESU, the possibility that ESUs should be recognized on a smaller scale has not been excluded.

Relationship to State Conservation Management Units

State conservation management units have not yet been completed for coastal cutthroat trout in California, Oregon, or Washington, although WDFW has proposed preliminary stock groupings as part of their draft "1998 Coastal Cutthroat Stock Inventory" (WFDW 1998a). This document follows the format of the "Salmon and Steelhead Stock Inventory" (SASSI), but its name has been changed to "Salmonid Stock Inventory" (SaSI) to reflect the inclusion of coastal cutthroat trout. The stock definition criteria used in SaSI is similar to that in SASSI, but rather than identifying "stocks," SaSI identifies groupings defined as "stock complexes." Stock complexes were developed "because of the significant uncertainties regarding the life-history, genetic, and evolutionary relationships among life-history types in local areas" for coastal cutthroat trout (WDFW 1998a, p. 31), and represented the aggregation of fish from adjacent areas with common habitat characteristics (e.g., eastern Hood Canal). The stock complexes in the SaSI draft were based on known differences in spatial or temporal distribution, "primarily in river basins in which spawning is known to occur," and "used available information on unique biological characteristics (e.g., genetic stock identification data)" (WDFW 1998a, p. 31). These stock complexes were considered preliminary, and as "additional information on genetics, life histories and ecological relations" become available, this information will be incorporated into future versions of SaSI.

Based on these criteria, SaSI (WDFW 1998a) identified 46 coastal cutthroat trout stock complexes (23 in Puget Sound and the Strait of de Fuca, 12 on the Washington Coast, and 11 in the Lower Columbia River). Stock complexes in the Puget Sound region represented 50% of the state's number, while complexes from the Washington Coast and Columbia River each contained approximately 25%.

The ESUs for coastal cutthroat trout proposed by the BRT are larger than the stock complexes proposed in SaSI (the Puget Sound ESU, for example, includes approximately 22 stock complexes). The SaSI it was concluded that "the number of individual coastal cutthroat stocks may be very large [in Washington] and that identification of stock complexes is appropriate as a first step in understanding coastal cutthroat population structure" (WDFW 1998a, p. 31-32).

In conjunction with SASSI on Pacific salmon and steelhead, WDFW identified Major Ancestral Lineages (MALs) and Genetic Diversity Units (GDUs, which represent subsets of MALs) in Washington (e.g., Busack and Shaklee 1995). According to Busack and Shaklee (1995), GDU designations were based on a combination of genetic, life-history/ecological, and physiographic/ecoregion data. The authors also said they expected that individual ESUs would often include multiple GDUs but would be unlikely to include multiple MALs. No GDUs or MALs have yet been identified by WDFW for coastal cutthroat trout.

ASSESSMENT OF EXTINCTION RISK

The ESA (Section 3) defines "endangered species" as "any species which is in danger of extinction throughout all or a significant portion of its range." "Threatened species" is defined as "any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range." NMFS considers a variety of information in evaluating the level of risk faced by an ESU. Important considerations include 1) absolute numbers of fish and their spatial and temporal distributions, 2) current abundance in relation to historical abundance and carrying capacity of the habitat, 3) trends in abundance, based on indices such as dam or redd counts or on estimates of spawner-recruit ratios, 4) natural and human-influenced factors that cause variability in survival and abundance, 5) possible threats to genetic integrity (e.g., selective fisheries and interactions between hatchery and natural fish), and 6) recent events (e.g., a drought or a change in management) that have predictable short-term consequences for abundance of the ESU. Additional risk factors, such as disease prevalence or changes in life-history traits, also may be considered in evaluating risk to populations.

According to the ESA, the determination of whether a species is threatened or endangered should be based on the best scientific information available regarding its status after taking into consideration conservation measures that are proposed or in place. The BRT did not evaluate likely or possible effects of conservation measures. Therefore, they did not make recommendations as to whether identified ESUs should be listed as threatened or endangered species because that determination requires evaluation of factors not considered by the BRT. However, the BRT did draw scientific conclusions about the risk of extinction faced by identified ESUs under the assumption that present conditions will continue (recognizing, of course, that natural demographic and environmental variability is an inherent feature of present conditions). Conservation measures will be taken into account by the NMFS Northwest and Southwest Regional Offices in making listing recommendations.

Approach

Previous Assessments

Several recent reviews have been conducted of the status of coastal cutthroat trout populations (Nehlsen et al. 1991, Chilcote et al. 1992, Nickelson et al. 1992, Kostow 1995, Gerstung 1997, Hooton 1997, WDFW 1998a). These reviews used a variety of methods and criteria for evaluating the status of coastal cutthroat trout stocks. Nehlsen et al. (1991) considered the status of populations coastwide and evaluated their risk of extinction, but reported the status only of populations they considered to be at risk of extinction, categorizing them as "possibly extinct," at "high risk of extinction," at "moderate risk of extinction," or of "special concern."

Nehlsen et al. (1991) considered populations at high risk of extinction to have likely reached the threshold for classification as endangered under the ESA. Stocks were placed in this category if they had declined from historic levels, were continuing to decline, or had spawning escapements of less than 200. Populations were classified at moderate risk of extinction if they had declined from historic levels, but presently appeared to be stable at a level of more than 200 spawners. Nehlsen et al. (1991) felt that populations in this category had reached the threshold to be considered threatened under the ESA. Populations were classified to be of special concern if a relatively minor disturbance could threaten them, insufficient data were available for them but available information suggested a decline, large releases of hatchery fish influenced them, or they possessed some unique characteristic. Nehlsen et al. (1991) also included a partial list of populations they believed to be extinct. The other reviews are limited to individual states and are thus more limited in area, but they are intended as inventories of populations and are more thorough within the areas they cover.

Washington

As noted earlier, WDFW (1998a) has extended the SASSI effort (WDF et al. 1993) to include a Salmonid Stock Inventory (SaSI) that reports on the status of char and coastal cutthroat trout in Washington State. Stock "complexes" were identified for coastal cutthroat trout because of the difficulty in identifying individual stocks. A stock complex is a "group of stocks typically located within a single watershed or other relatively limited geographic area," and includes information on genetic similarity among river systems from genetic analyses (WDFW 1998a, p. 21). The SaSI classified stock complexes by origin (native, nonnative, mixed, or unknown), production (wild, composite, or unknown), and status (healthy, depressed, critical, or unknown). Stock status was classified as healthy if recent production was consistent with current habitat conditions. The status report is complicated, however, by the WDFW (1998a) practice of combining hatchery with natural production if a hatchery was located on a stream that supported natural spawning; the status report considered only recent production status, and thus did not consider possible negative impacts of hatchery production on natural populations. WDFW (1998a) recognized 46 coastal cutthroat trout stock complexes in Washington. Of these complexes, 2 were rated healthy, 6 were depressed, none were critical, and 38 were of unknown status. The proportion of stock complexes with unknown status is much higher than for any other salmonid species inventoried in Washington (WDF et al. 1993).

Nehlsen et al. (1991) considered coastal cutthroat trout in Washington coastal and Puget Sound tributaries, as well as the Elochoman, Cowlitz, Toutle, Coweeman, Kalama, and Washougal rivers, to be of special concern. Coastal cutthroat trout populations in small tributaries on the Lower Columbia River below Bonneville Dam were considered to be at moderate risk of extinction. The stock in Rock Creek in Washington was considered to be at high risk of extinction. In contrast, WDFW (1998a) listed the status of most Puget Sound and coastal Washington coastal cutthroat trout runs as unknown. Finally, SaSI concluded that coastal cutthroat trout in the Lower Columbia River streams and smaller tributaries were depressed, which is similar to the findings of Nehlsen et al. (1991).

Oregon

Within Oregon, Nehlsen et al. (1991) considered coastal cutthroat trout in the Hood River to be at high risk of extinction. In addition, coastal cutthroat trout in Lower Columbia River streams below Bonneville Dam and in Oregon coastal streams were listed at moderate risk of extinction.

Chilcote et al. (1992) inventoried anadromous and nonanadromous coastal cutthroat trout runs in Oregon and evaluated them for gene conservation purposes under the Oregon Wild Fish Policy (Chilcote et al. 1992). This policy has two compliance criteria: a hatchery criterion that naturally spawning populations have no more than 10% strays from a genetically dissimilar hatchery stock or 50% strays from a genetically similar hatchery stock, and a numerical criterion requiring a minimum average of 300 spawners. Kostow (1995) is a revision of Chilcote et al. (1992), with newer information on stock presence or absence. Chilcote et al. (1992) considered 3 of 128 populations of sea-run cutthroat trout and 35 of 630 populations of either freshwater migratory or nonmigratory coastal cutthroat trout to be in compliance with the Wild Fish Policy criteria. For sea-run cutthroat trout populations, 6 were not in compliance due to violation of the percentages of hatchery strays and their genetic constitution, 1 population was not in compliance because its population had fewer than 300 individuals, and the remaining 118 populations were not in compliance because of lack of information. For freshwater coastal cutthroat trout populations, 595 populations were not in compliance because of insufficient information.

Nickelson et al. (1992) evaluated the status of coastal populations of coastal cutthroat trout in Oregon. They stated that most coastal populations of coastal cutthroat trout in Oregon were of unknown status due to insufficient data. They discussed anecdotal information, results from creel surveys, and fish counts at dams that all indicated that anadromous cutthroat trout populations "may be experiencing widespread decline" (p. 58).

The 1994 biennial report on wild fish status in Oregon (Kostow 1995) provided a list of all coastal cutthroat trout populations and the life-history forms of coastal cutthroat trout in each stream. The abundance of anadromous cutthroat trout in the Lower Columbia River Basin was described as having declined significantly, and populations of sea-run cutthroat trout in the Sandy and Hood rivers were described as very small to nonexistent, respectively, in 1994. The report also stated that anadromous cutthroat trout occurred only in the lower Willamette River below Willamette Falls and that occurrences in the Clackamas River were much less abundant than in the past, although freshwater forms of coastal cutthroat trout were described as "abundant and well distributed throughout headwater and lower Clackamas River tributaries" (p. 162). No abundance information was available for coastal cutthroat trout in coastal Oregon streams except for counts of fish over Winchester Dam on the North Umpqua River.

ODFW's "Status of Coastal Cutthroat Trout in Oregon" (Hooton 1997) reviewed abundance and trend information for all life-history forms of coastal cutthroat trout. Non-migratory coastal cutthroat trout were reported to be widespread and "the dominant trout in most headwater tributaries"; however, population sizes were described as likely to be lower in abundance than in the past due to habitat degradation and loss (p. 1). River- and lake-migrating forms of coastal cutthroat trout were reported to have mixed status: some populations were considered healthy, but for many, information was insufficient to determine population health. Anadromous cutthroat trout in Oregon were likely to have suffered significant declines in the past decade, according to the review. Details provided in Hooton (1997) for specific coastal cutthroat trout populations are discussed for each ESU in the "Biological Information by ESU" section (p. 158), which describes biological information used in making risk evaluations.

Umpqua River sea-run cutthroat trout status review

As discussed earlier, a status review of sea-run cutthroat trout in the North and South Umpqua rivers was conducted in 1993-94 in response to a petition NMFS received in 1993 to list those fish under the ESA (Johnson et al. 1994). The primary abundance information available for evaluating the conservation status of coastal cutthroat trout in the entire Umpqua River Basin was counts of migrating fish passing Winchester Dam on the North Umpqua River. The numbers of coastal cutthroat trout at Winchester Dam declined precipitously in the late 1950s, then increased in 1961-76, coincident with a period of releases of hatchery coastal cutthroat trout in the North Umpqua River. After hatchery releases were terminated in the mid-1970s, the numbers of coastal cutthroat trout at Winchester Dam declined rapidly. Abundances remained very low: 34, 10, and 0 coastal cutthroat trout were counted at the dam from 1991 to 1993, respectively. Angler creel censuses for 1977, 1990, and 1992 were available for freshwater forms of coastal cutthroat trout caught in the Umpqua River Basin; however, estimates of fishing effort or harvest rate were not available, so angler catch data were not expanded to estimate nonanadromous coastal cutthroat trout abundance for the basin.

In addition to declining trends in abundance, the Umpqua River coastal cutthroat trout probably also faced risks due to the effects of hatchery fish. The Umpqua River Basin has a long history of hatchery releases for a number of species, including steelhead, rainbow trout, and coastal cutthroat trout. These releases date back to the late 1880s, and their impact is unknown. Because hatchery practices were not well developed prior to the early 1950s, it is generally believed that most of these early hatchery plants had few permanent impacts on native fish populations (Johnson et al. 1994). During the period of extensive releases of Alsea River coastal cutthroat trout broodstock into the North Umpqua River (1961-73), the return timing of coastal cutthroat trout at Winchester Dam shifted to reflect the later return times characteristic of the Alsea River broodstock (Johnson et al. 1994). The shift in the run-time distribution suggested that, during the years when hatchery coastal cutthroat trout were released in the North Umpqua River, the relative abundance of native Umpqua River coastal cutthroat trout was depressed. No genetic data were available to determine whether genetic introgression between the Alsea River broodstock and coastal cutthroat trout native to the Umpqua River Basin had occurred, or whether the hatchery fish had replaced the native fish.

Scarcity of information on the status of coastal cutthroat trout in the Umpqua River Basin brought the BRT to note that a listing determination for these fish could come to one of two conclusions:

1. Since the petition was for "sea-run" coastal cutthroat trout, and nonanadromous coastal cutthroat trout were determined to be part of the Umpqua River Basin ESU, "the petition could be denied because the petitioned entities (North and South Umpqua River sea-run cutthroat trout) are not by themselves ESA 'species'" (Johnson et al. 1994, p. viii).

2. Because the anadromous portion of the ESU was suffering severe declines in abundance, the coastal cutthroat trout in the Umpqua River Basin could be considered at significant risk.

Even if it were assumed that coastal cutthroat trout in the Umpqua River constitute an ESU, the second conclusion would also involve assuming that either all life-history forms of coastal cutthroat trout in the basin were depressed, or that the anadromous portion was "a substantial and important component of the ESU and its loss would compromise the distinctness and viability of the inclusive ESU" (Johnson et al. 1994, p. ix). The BRT concluded that there was not enough information to resolve these issues with any certainty.

After considering the BRT's report, NMFS in 1994 proposed that the Umpqua River sea-run cutthroat trout be listed as endangered under the ESA. The final listing was effective in August 1996.

California

Nehlsen et al. (1991) characterized coastal cutthroat trout populations in California coastal streams as being at moderate risk of extinction.

Gerstung (1997) reviewed the status of coastal cutthroat trout in California. He concluded that most populations were depressed relative to historical abundance. Population abundance and trend data were scarce, but for those river systems with data available, trends were described as stable or increasing over the last few decades. Details provided in Gerstung (1997) for specific coastal cutthroat trout populations are discussed in this document under individual ESUs in "Biological Information by ESU" (p. 158).

Data Evaluations

Quantitative evaluations of data amassed as part of this status review included comparisons of current and historical abundance of coastal cutthroat trout and calculation of recent trends in abundance estimates. Historical abundance information for the six ESUs proposed in this report is largely anecdotal. Time-series data were available for very few populations, and the amount and quality of the data varied among ESUs. We compiled and analyzed this information to provide several summary statistics of the abundance of natural spawning populations, including (where available) recent total spawning run size and escapement, abundance indices for smolts and adults, percent annual change in abundance, and separate estimates of hatchery-derived and naturally spawning populations.

Although this evaluation used the best data available, it should be recognized that there are limitations to the few data sets that do exist and not all summary statistics were available for all populations. For example, abundance in some cases was estimated from recreational catch (which may not always have been measured accurately) or from limited survey data. In some cases, data indicating abundance of coastal cutthroat trout were incidental catch of cutthroat in traps or sport fisheries targeting other species of Pacific salmon or steelhead. In many cases, limited data also were used to separate hatchery production from natural production.

Information on stock abundance was compiled from records in a variety of state, federal, and tribal agencies. We believe this information to be largely complete with respect to long-term adult abundance records for coastal cutthroat trout in the regions included in this review. Principal data sources were fishery statistics from recreational fisheries, escapement estimates from dam and weir counts, and smolt abundance estimates from downstream migrant traps. However, although the types of data described above provide the "best" estimates of coastal cutthroat trout production for fishery comanagers, actual run size may vary from these estimates. Specific problems are discussed below for each data type.

Computed Statistics

To represent current abundance where recent data were available, we computed the geometric mean of the most recent 5 years reported (or fewer years, if the data series was for less than 5 years). Where adequate data were available, trends in abundance estimates were calculated for all data sets with more than 5 years of data, based on total escapement or an escapement index (such as fish per mile from a stream survey).

As an indication of overall trends in coastal cutthroat trout populations in individual streams, we calculated average percent annual change (over the available data series) in abundance data or indices within each river basin. Trends were calculated as the slope (a) of the regression of ln(abundance) against years corresponding to the biological model $N(t) = be^{at}$. The regressions provided direct estimates of mean instantaneous rates of population change (a). These values were subsequently converted to percent annual change, calculated as $100(e^{a-1})$. No attempt was made to account for the influence of hatchery-produced fish on these estimates. Except in cases where data were separated into hatchery and natural fish, estimated trends include any supplementation effects of hatchery fish. Trend analysis can also be influenced by climate regime shifts and other factors.

Overall Evaluation of Risk and Uncertainty

To tie the various risk considerations into an overall assessment of extinction risk for each ESU, the BRT members scored risks in a number of categories using a matrix form. The general risk categories evaluated were those outlined earlier: abundance, trends in abundance/productivity/variability, genetic integrity, and "other risks". More detailed explanation of these categories and of the nature and use of this matrix approach is provided in Appendix B.

The summary of overall risk to an ESU uses categories that correspond to ESA definitions: in danger of extinction, likely to become endangered in the foreseeable future, or neither. Note, however, that these votes on overall risk do not correspond to recommendations for a particular listing action. They are based only on the past and present biological condition of the populations and do not completely evaluate conservation measures as the ESA requires for a listing determination. The risk summary votes do not reflect a simple average of the risk factors for individual categories, but rather a judgement of overall risk based on likely interactions among risk factors and their cumulative effects. A single factor with a "high risk" score may be sufficient for an overall conclusion of "in danger of extinction," but such an overall determination could result from a combination of several factors with low or moderate risk scores.

The BRT used two methods to characterize the uncertainty underlying their risk evaluations. Because information relating to the abundance, life history, and distribution of coastal cutthroat trout is unavailable in many areas, risk evaluations were especially challenging (see "Paucity of information relating to risk," p. 195). One way the BRT captured the levels of uncertainty associated with overall risk evaluations was for each member to attach a certainty score (1=low, 5=high) to their overall risk evaluation for each ESU. For example, a BRT member who believed an ESU was very likely to become endangered in the foreseeable future (or was not currently at significant risk) would vote for that category of risk and assign a certainty score of 4 or 5; a member less certain about a given level of risk would assign a lower certainty score.

The second method for characterizing uncertainty was fashioned after an approach used by the Forest Ecosystem Management Assessment Team (FEMAT 1993). Each BRT member was given 12 total "likelihood" points to distribute in any way among the three risk categories. For example, complete confidence that an ESU should be in one risk category would be represented by most or all of the 12 points allocated to that category. Alternatively, a BRT member who was undecided about whether the ESU was likely to become endangered but who believed the ESU was at some risk could allocate the same (or nearly the same) number of points into each of the "likely to become endangered" and "not likely to become endangered" categories. This assessment process follows well-documented peer-reviewed methods for making probabilistic judgements (references in FEMAT 1993, p. iv:40-45). The BRT interpretation of these scores was similar to FEMAT's, which said the likelihoods were "not probabilities in the classical notion of frequencies. They represented degrees of belief [in risk evaluations], expressed in a probability-like scale that could be mathematically aggregated and compared across [ESUs]" (FEMAT 1993 p. iv:44).

The outcomes of the two methods for evaluating uncertainty in risk evaluations were generally consistent (see "Summary and Conclusions of Risk Assessments," p. 194). The BRT felt that clear presentation of the scientific and personal uncertainty underlying risk assessments could allow BRT members and managers to better understand the issues and make informed listing decisions.

Analysis of Biological Information

Species-wide Risk Factors Considered

Detailed information on the nature of risks in specific geographic regions is not available for a number of risk factors affecting coastal cutthroat trout. However, there is some information that provides an indication of the likely effects of these risk factors on coastal cutthroat trout or on Pacific salmonids in general. Aspects of several of these risk considerations are common to all coastal cutthroat trout ESUs. In this section, we briefly summarize information the BRT considered regarding the potential effects of each risk factor on coastal cutthroat trout. More specific discussion of factors for each of the ESUs under consideration can be found in the following sections.

Absolute numbers

The absolute number of individuals in a population is important in assessing two aspects of extinction risk. First, for small populations that are stable or increasing, population size can be an indicator of whether the population can sustain itself into the future in the face of environmental fluctuations and small-population stochasticity; this aspect is related to the concept of minimum viable populations (MVP) (see Gilpin and Soulé 1986, Thompson 1991). Second, for a declining population, present abundance is an indicator of the time expected until the population reaches critically low numbers; this aspect is related to the idea of "driven extinction" (Caughley 1994).

In addition to total numbers, the spatial and temporal distributions of adults are important in assessing risk to an ESU. Spatial distribution is important both at the scale of river basins within an ESU and at the scale of spawning areas within basins ("metapopulation" structure). Temporal distribution is important both among years, as an indicator of the relative health of different brood-year lineages, and within seasons, as an indicator of the relative abundance of different life-history types or runs.

Traditionally, assessment of salmonid populations has focused on the number of harvestable and/or reproductive adults, and these measures compose most of the data available for Pacific salmonids. In assessing the future status of a population, the number of reproductive adults is the most important measure of abundance, and we focus here on measures of the number of adults escaping to spawn in natural habitat. However, total run size (spawning escapement + harvest) is also of interest because it indicates the size of the potential spawning population if there is no harvest. Data on other life-history stages (e.g., freshwater smolt production) can be used as a supplemental indicator of abundance.

Because the ESA (and NMFS policy) mandates that we focus on viability of natural populations, in this review we attempted to distinguish natural fish from hatchery-produced fish. The offspring of all coastal cutthroat trout artificially spawned for a hatchery, restoration, or egg box program are included under the NMFS category "hatchery provided," although we recognize that different types of propagation programs will have different results. All statistics are based on data that indicate total numbers, or density, of adults that spawn in natural habitat ("naturally spawning fish"). The total of all naturally spawning fish ("total escapement") is comprised of two components (Fig. 33): "hatchery-produced fish," which are reared as eggs or juveniles in a hatchery but return as adults to spawn naturally, and "natural" fish, which are progeny of naturally spawning fish.

Life-history diversity and risk

The variety of migratory and life-history patterns observed in coastal cutthroat trout means that abundance estimates do not indicate status as clearly as they might for other species of salmonids. First, it is not a simple matter to identify a "run" of coastal cutthroat trout and count adult or juvenile individuals that contribute to that run. Because both adults and juveniles can migrate extensively within a stream or lake system throughout a year, it is difficult to determine how many downstream or upstream migrants passing a particular location should be attributed to a specific spawning population.

Second, since coastal cutthroat trout spawn multiple times, risk thresholds associated with particular levels of population size cannot be estimated in the same way as they are for Pacific salmon, which are semelparous. For example, a spawning population of salmon estimated at 100 fish per year might translate into approximately 400-500 chinook salmon per generation, accounting for multiple age classes. In contrast, 100 fish per year in a cutthroat trout population might reflect closer to 200 individuals per generation because of the relatively high frequency of repeat spawners in the population. The consequences of iteroparity exhibited by coastal cutthroat trout must be taken into consideration when evaluating estimates of population sizes.

Third, it is not clear to what extent a diversity of life-history forms within a river basin or ESU may buffer coastal cutthroat trout populations from risk. In a practical sense, this gap in our knowledge means that it also is not a simple matter to evaluate the status of coastal cutthroat trout ESUs. As discussed earlier (see "ESU Determinations," p. 125), the diversity of life-history strategies exhibited by coastal cutthroat trout may make these fish more able to adjust to changes in habitat quantity and quality. If this diversity is important, declines in one or more life-history

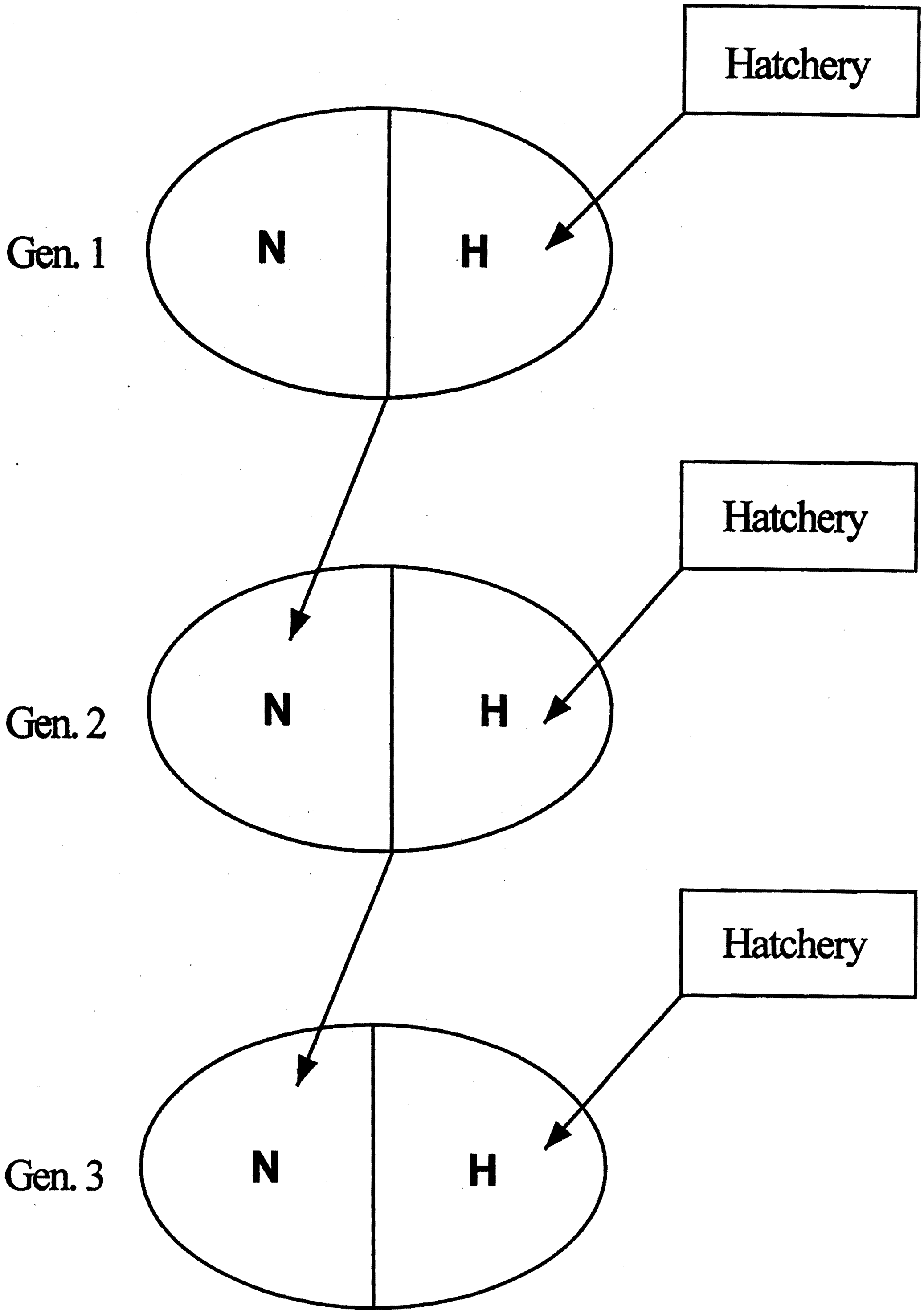


Figure 33. Schematic diagram of mixing of naturally (N) and hatchery-produced (H) fish in natural habitat. Ovals represent the total spawning in natural habitat each generation. This total is composed of naturally produced and hatchery-produced offspring of individuals in the previous generation.

forms within an ESU may represent a significant threat to the persistence of coastal cutthroat trout in that ESU. For example, loss of the anadromous form would reduce the number of larger and more fecund individuals in the population. A reduction in the number of anadromous individuals in a population would probably also have significant effects on the population age structure, spawn timing, age and size at first reproduction, degree of iteroparity, sex ratio, spatial distribution of individuals, and mate selection. In particular, migratory fish have opportunities for habitat, prey, and mate selection that may not be available to nonmigratory fish. Likewise, loss of freshwater forms would lead to a loss of potential colonists or recolonists, leading to increased genetic and demographic isolation of populations. The reduction in potential within-basin recolonists could disrupt existing metapopulation dynamics, change the spatial distribution of populations over a geographic region, and lead to a loss of unique local adaptations in nonmigratory populations. Finally, migration can provide a population with an "escape in space" (Slobodkin 1961) if rearing or spawning habitat is lost or degraded by permitting a population to persist when it otherwise might be locally extirpated (Taylor and Taylor 1977).

As an illustration of the potential consequences of reducing life-history diversity, most biologists would agree that the anadromous life-history type is crucial to the ability of coastal cutthroat trout populations to colonize new habitat (or to recolonize previously occupied habitat). Reduced opportunities for dispersal among coastal cutthroat trout populations due to reductions in the anadromous form could cause dramatic increases in local population extinctions due to the demographic and genetic effects of isolation. If too many local populations are extirpated, the metapopulation dynamics in a region may be severely disrupted, leading to the eventual extinction of an entire ESU. Unfortunately, it is not a simple matter to evaluate this possibility–abundance estimates that include a mix of life-history types may mask declines in one form that is critical to ESU persistence. In addition, even if the status of a life-history form can be determined, the risk implications of a change in relative abundance of a life-history type depend in part on the genetic control of the life history (see "Mechanisms of Life-History Expression," p. 47). In the example above, if the anadromous portion of a coastal cutthroat trout run is lost, the significance of such a loss will depend on the extent to which freshwater forms of coastal cutthroat trout in the same (or nearby) river basin can replace anadromous fish that were lost.

A related question is if the anadromous form is selected against (e.g., if an artificial barrier is imposed where there previously was none), how long will it take for the genetic variation allowing anadromy to be lost from a population? There is some indication from other species of Pacific salmon that strong selective differences on anadromous and freshwater forms can lead to rapid genetic divergence (e.g., sockeye salmon and kokanee). It also has been observed in *O. nerka* that populations above a long-standing barrier can still give rise to anadromous individuals if the conditions for migrating to sea are provided (e.g., Cultus Lake kokanee) (Foerster 1968). However, the pertinence of these case studies of other species of salmonids to coastal cutthroat trout is unknown.

Many biologists familiar with coastal cutthroat trout feel that this subspecies is well distributed in freshwater habitats throughout its range. The few data available for this status review mostly support this contention for freshwater forms of coastal cutthroat trout (see

"Biological Information by ESU," p. 158). In addition, there is some information suggesting that freshwater forms of coastal cutthroat trout in some streams can produce outmigrating juveniles that have a silvery "smolt-like" appearance (see "Patterns of Life History Variation," p. 40 and "Biological Information by ESU," p. 158). The ability of these fish to successfully migrate to salt water and return to spawn is not well quantified. In some cases, it is suspected that current habitat conditions in the lower reaches of streams or in nearshore marine environments are not of sufficient quality to allow survival of these outmigrants (e.g., in the Willamette River, ODFW 1998). In this case, freshwater life-history types would not be able to replenish anadromous forms under current habitat conditions. On the other hand, ODFW (1998) and WDFW (1998c) believe that smolts from freshwater forms of coastal cutthroat trout are contributing to adult returns in several Oregon coastal streams and in some streams in the Lower Columbia River Basin. Currently, there is not enough information to evaluate the likelihood that these alternative scenarios occur throughout the range of coastal cutthroat trout. Presumably, the ability of freshwater forms of coastal cutthroat trout to contribute to anadromous forms varies with river basin characteristics and the genetic composition of the populations within each basin.

A key question for risk evaluations of coastal cutthroat trout is whether current habitat and population characteristics (e.g., habitat quality and quantity, population sizes, age and size structure) allow for the full expression of life-history types that would be observed under pristine conditions. It is likely that human activities have altered life-history profiles of coastal cutthroat trout, but predicting the magnitude of these effects is difficult (see "Life History," p. 38). For example, impoundments in many streams throughout much of the range of coastal cutthroat trout have resulted in lower flows and higher water temperatures, conditions favorable to the parasite *Ceratomyxa shasta*. Some populations of coastal cutthroat trout in the Lower Columbia River Basin are highly susceptible to *C. shasta,* which can cause very high mortalities. It is possible that the anadromous form of coastal cutthroat trout has declined in some tributaries to the Lower Columbia River because of the effective barrier to migration posed by the presence of *C. shasta* in lower reaches of streams (ODFW 1998). Similarly, a combination of anthropogenic effects such as 1) reduced habitat quality in freshwater, estuarine and nearshore marine environments (see "Historical abundance, habitat and carrying capacity," p. 147), 2) size-selective fishing pressures from coastal cutthroat trout and salmonid fisheries, and 3) interactions between natural coastal cutthroat trout and hatchery-derived coastal cutthroat trout, steelhead, and coho salmon have probably caused a shift in the distribution of life-history forms within river basins since historical times. The incremental increase in risk due to these changes in life-history diversity is an important consideration in our conservation assessments, but it is difficult to evaluate.

In summary, as discussed earlier (see "ESU Determinations," p. 125), it is important to recognize that the observed population- or stream-level variation in life history may be due to a combination of within-individual flexibility in behavior or physiology as well as to differences among individuals in their responses to the environment. Understanding the extent of within-individual and among-individual lability in life-history expression is important for assessing responses of coastal cutthroat trout populations experiencing threats. If an ESU contains a diversity of life-history forms represented by different individuals that cannot change from one form to the other, enough individuals from each life-history form may need to be conserved to ensure persistence of the ESU. Alternatively, if an individual is flexible enough to exhibit a wide range of life histories, the numbers and types of fish needed to maintain the full expression of life-history diversity may be less, assuming habitat conditions necessary for the full expression of life-history types are achieved. Abundances needed to minimize extinction risk depend on the genetic architecture underlying these life-history traits and the ways in which the life-history diversity is maintained in populations.

Historical abundance, habitat, and carrying capacity

For coastal cutthroat trout, quantitative estimates of historical abundance generally are lacking. The relationship of present abundance to present carrying capacity is important for understanding the health of populations, but the fact that a population is near its current capacity does not in itself mean that it is healthy. The fact that a population is near capacity implies that there are limits to the effectiveness of short-term management actions in increasing its abundance. Another implication is that competition and other interactions between hatchery and natural fish may be an important consideration for increasing the abundance of naturally spawning populations because releases of hatchery fish may further increase population density in a limited habitat.

The relationship of current abundance and habitat capacity to that which existed historically is an important consideration in evaluating risk. Knowledge of historical population conditions provides a perspective of the conditions under which present populations evolved. Historical abundance also provides the basis for establishing long-term trends in populations. Comparison of present and past habitat capacity can also indicate long-term population trends and problems of population fragmentation.

Freshwater habitat conditions—Coastal cutthroat trout spend more time in the freshwater environment and make more extensive use of this habitat than do most other Pacific salmonids. The amount of time coastal cutthroat trout spend in fresh water depends on local and regional environmental conditions and on life-history strategy. Those that are anadromous typically spend 2-5 years rearing in fresh water before making their initial seaward migration. Generally, anadromous coastal cutthroat trout spend only brief periods offshore during summer months and return to estuaries and fresh water by fall or winter (Trotter 1989, Pearcy et al. 1990). Coastal cutthroat trout use a large variety of habitat types, including large and small river systems with a diversity of stream gradients, estuaries, sloughs, ponds, and lakes (see "Life-History Stages," p. 50). Because these fish make extensive use of river basins throughout all or a large portion of their life cycle, they are exposed to a variety of potentially adverse conditions associated with land-use activities.

Fisheries biologists familiar with coastal cutthroat trout believe that degradation and outright destruction of riverine and estuarine habitat for the subspecies has been widespread (Gerstung 1997, Hooton 1997, WDFW 1998a). Specific quantitative assessment of habitat degradation or attempts to evaluate the response of coastal cutthroat trout populations to specific changes in habitat are rare (Reeves et al. 1991). This lack of biological information has been attributed to two factors: 1) coastal cutthroat trout numbers are generally low relative to other salmonid species and 2) the dynamics and interrelationships between different life-history forms and their specific habitat requirements are poorly understood (Reeves et al. 1997, Williams and Nehlsen 1997).

Degraded habitat has been associated with more than 90% of documented extinctions or declines of Pacific salmon stocks (Gregory and Bisson 1997). Major land-use activities, including agriculture, forestry, urban and industrial development, road construction, and mining, have resulted in the alteration and loss of salmonid habitat and a subsequent loss in salmon production (Meehan 1991, NRCC 1996). The small streams often used by coastal cutthroat trout are particularly sensitive to changes in riparian vegetation, and they also are the ones most easily altered by human activities (Chamberlin et al. 1991). Evidence from two long-term studies, the Alsea Watershed study in Oregon and the Carnation Creek study in British Columbia, suggests that coastal cutthroat trout populations may be slow to recover from land-use activities such as timber harvest. Both of these studies have shown that coastal cutthroat trout numbers declined considerably after timber harvest and had not returned to their previous levels more than 10 years later (Moring and Lantz 1975, Hartman and Scrivener 1990, Gregory et al. in press *cited in* Reeves et al. 1997). On the other hand, coastal cutthroat trout abundance can increase following logging in shady headwater streams, presumably because of increased primary productivity under more intense sunlight (Hall et al. 1978, Murphy and Hall 1981).

The effects of urbanization also may be seen in coastal cutthroat trout population structure. Scott et al. (1986) compared two streams near Bellevue, Washington: land use in one basin was primarily urban development, while upland areas in the other basin were largely rural. The species composition of the fish community in the two drainages was not the same, and one striking difference was the predominance of early life-history stages of coastal cutthroat trout in the urbanized creek drainage. However, the difference in fish community structure was not matched by an expected increase in outmigration rates and decreased growth rates of coastal cutthroat trout in the urbanized creek relative to the control creek.

Since coho salmon and coastal cutthroat trout habitat use overlaps a great deal, effects of changes in habitat quantity and quality on coho salmon probably have had similar effects on coastal cutthroat trout production. Beechie et al. (1994) estimated that since European settlement, 24-34% of coho salmon rearing habitat has been lost in the Skagit River, Washington, with most of the habitat lost from side channels and sloughs. Three major causes of coho salmon habitat loss identified by Beechie et al. (1994) are, in decreasing order of importance, hydromodification (diking and dredging), blocking culverts, and forest practices. Similarly, McHenry (1996) estimated that since European settlement, Chimacum Creek, Washington, (northwestern Puget Sound) has lost 12%, 94% and 97% of its spawning, summer-rearing, and winter-rearing habitats for coho salmon, respectively. McHenry (1996) stated that these habitat losses were due to logging, agricultural clearing, channelization, drainage ditching, groundwater withdrawal, and lack of woody debris.

Only in the last 25-30 years has the importance of riparian vegetation to the aquatic ecosystem received much attention. Riparian vegetation provides several functions important to healthy salmonid habitat such as providing cover, maintaining stream temperatures, stabilizing streambanks and channels, maintaining undercut banks, providing an allochthonous source of energy, and contributing structural components that influence channel morphology (Murphy and Meehan 1991). In its assessment of factors leading to steelhead declines, NMFS (1996) reported that approximately 80-90% of the original riparian habitat in most western states has been eliminated. In Washington and Oregon, up to 75% and 96% of the original coastal temperate rainforest has been logged, respectively (Kellogg 1992). Only 10-17% of old-growth forests reportedly remain in the Douglas fir regions of these two states (Speis and Franklin 1988, Norse 1990). California has reportedly lost 89% of the state's riparian woodland to various land use practices (Kreissman 1991). Fisk et al. (1966) stated that over 1,600 km of streams within California had been damaged or destroyed as fish habitat by 1966.

One of the most important structural components of small streams in coastal watersheds that is contributed by riparian vegetation is large woody debris (LWD). In most river basins, the frequency and distribution of LWD has been altered through a number of human activities, many related to logging (NRCC 1996). The loss of LWD from streams results in subsequent declines in pool frequency and increases in riffle habitat (Swanson and Lienkaemper 1978, Bisson and Sedell 1984, Bisson et al. 1987, Gregory et al. 1991). FEMAT (1993) reported that there has been a 58% reduction in the number of large deep pools on national forest lands within the range of the northern spotted owl in western and eastern Washington. Similarly, there has been as much as an 80% reduction in the number of large deep pools in streams on private lands in coastal Oregon (FEMAT 1993). Overall, the frequency of large pools has decreased by almost two-thirds between the 1930s and 1992 (FEMAT 1993, Murphy 1995). Reductions in pool habitat are often related to declines in the number of age-1 and older coastal cutthroat trout (Bisson and Sedell 1984, Hartman and Scrivener 1990, Fausch and Northcote 1992, Reeves et al. 1993, Connolly 1997).

Descriptions of predevelopment conditions of rivers in Washington and Oregon that had abundant salmonid populations suggest that even big rivers had large amounts of instream LWD, which contributed significantly to trapping sediments and nutrients, impounding water, and creating many side channels and sloughs (Sedell and Luchessa 1982, Sedell and Froggatt 1984). Stream cleaning of LWD for navigation, flood control, and transport of logs occurred from the mid-1800s through the mid-1970s in many areas. In addition, past logging practices sometimes left excessive accumulations of debris in small streams that adversely affected fish production (Narver 1971, Brown 1974). Debris in streams was often viewed as something that would either impede or block fish passage and destroy channels by scour during storm-induced logjam failures. Until about 25 years ago, up to 90% of the funds for fish-habitat enhancement went for removal of wood debris in streams (Sedell and Luchessa 1982).

Beavers also had a key role in creating and maintaining many of these off-channel habitats. Beaver dams obstructed and redirected channel flows, flooded side-channels, and created large depositional areas for fine sediment storage (NRCC 1996). The use of these sloughs and other off-channel habitats by coastal cutthroat trout was probably extensive, as suggested by their present use of these freshwater habitats for overwintering and feeding (Cederholm and Scarlett 1982, Hartman and Brown 1987, Reimchen 1990, Garrett 1998).

Some of the most productive salmonid habitat has been lost by blockages to migration. The most recognized barriers to migration are dams, but many smaller barriers exist as well. Blocked or improperly maintained culverts present obstacles to coastal cutthroat trout migration and seriously reduce the amount of habitat available for spawning and rearing. In Washington, an estimated 2,400 blocked culverts have eliminated more than 3,000 miles of stream habitat (WDFW 1995). Studies by Washington Trout (unpubl. data *cited in* White 1997) suggested the problem may be underestimated and that 80% of all culverts in the Puget Sound basin may block fish passage. Furthermore, culverts designed to allow the passage of adult salmon may create water velocities that exceed the swimming ability of juveniles except during periods of low flow (NRCC 1996). The impact of migrational barriers on coastal cutthroat trout production may be particularly severe since the majority of their life cycle is spent in fresh water, and they depend upon a variety of habitats for every life-history stage. Another potential migration barrier identified by NRCC (1996) is unscreened water diversions that may entrain downstream migrants.

The declines in the number of returning Pacific salmon and the nutrients they contribute to streams also may have placed additional limitations on coastal cutthroat trout production in fresh water. Consumption of carcasses and eggs by coastal cutthroat trout may have been particularly important in nutrient-poor headwater streams (Bilby et al. 1996), where coastal cutthroat trout spawning and early rearing typically occurs. The decreased availability of this nutrient-rich food source may have contributed to a reduction in growth and overwintering survival of coastal cutthroat trout juveniles.

Conditions of freshwater habitats in which coastal cutthroat trout live today are very different from historical conditions. The 1998 "Washington State Coastal Cutthroat Stock Inventory" (WDFW 1998a) identified numerous land-use practices or habitat factors that have had a detrimental impact on coastal cutthroat trout habitat for 20 recognized coastal cutthroat trout stock complexes in Washington. Dominant land-use practices and habitat factors cited in this report include logging practices, road building, passage obstructions (e.g., dams and blocking culverts), water diversions, mining, livestock grazing, harvesting, and poaching. In Oregon, activities identified as impacting critical coastal cutthroat trout habitat are logging, grazing, road building, and land-development activities that impact water quality and flows (Kostow 1995). In most cases, separating the relative impact of one land-use activity from another is difficult since most salmon populations are subject to the cumulative effects of multiple land uses (Palmisano et al. 1993). Generally, the changes from each land use activity affect fish habitat similarly, despite differences in the activities themselves (Meehan 1991). Development and land-modification activities can act concurrently or sequentially to limit coastal cutthroat trout population size or growth during different life-history phases. In Washington, Oregon, and Northern California, the cumulative effect of these activities has led to large reductions in spawning habitat and in summer- and winter-rearing habitat for coastal cutthroat trout (Gerstung 1997, Hooton 1997, WDFW 1998a).

Estuaries—The extensive use of estuaries by coastal cutthroat trout makes them more susceptible to changes in the productivity of that environment than many other Pacific salmonid species (Giger 1972, Pearcy 1997). Although little is known about the habitat requirements or preferences of coastal cutthroat trout in estuarine habitat, estuaries are believed to provide important feeding opportunities and overwintering refuge to juveniles and adults (see "Life History," p. 38).

Estuaries historically contained large amounts of woody debris (Gonor et al. 1988). Giger (1972) suggested that temperature may be the most influential factor in determining the migration and distribution of coastal cutthroat trout in estuaries. Declines in woody debris in estuaries have likely resulted in detrimental effects on coastal cutthroat trout due to a resulting temperature increase and reduction in refuge sites. Coastal cutthroat trout are known to use such areas for protection from intense sunlight and high flows (Maser and Sedell 1994).

The loss of coastal wetlands to urban or agricultural development also would directly reduce the productivity of cutthroat populations. The primary losses in estuarine habitat are attributed to the ditching, draining, diking, and filling associated with agricultural and urban development. The degree of habitat lost in the estuarine or nearshore marine environment is difficult to quantify as there are few historical studies that include useful baseline information (Levings and Thom 1994). One of the first attempts to inventory estuarine areas in the Puget Sound region was a U.S. Department of Agriculture survey by Nesbit (1885). He surveyed 267 km^2 of tidal marshes and swamps in nine counties bordering Puget Sound, and reported approximately 320 km of dikes enclosing 4.1 km^2 of marsh. In Skagit and Stillaguamish river areas, Nesbit (1885) found that tidelands covered 520 km^2 and extended 20 km inland from the present shoreline. Nesbit found that tide marshes across the Puget Sound region in the 1880s greatly exceeded tide flats in area and that nontidal freshwater marsh area exceeded that of tide marsh by three to four times. In the 1980s, Boule et al. (1983) estimated Puget Sound had only 54.6 km^2 of intertidal marine or vegetated habitat in the entire basin and that this represented 58% of the state's total estuarine wetlands.

More recently, attempts have been made to quantify changes in estuaries within the range of coastal cutthroat trout. Bortelson et al. (1980) estimated historical changes in natural habitats in eleven major estuaries, where they found an average decrease in estimated area of subaerial wetland of 64% (SD 35%). Estimated wetland losses in the Puyallup River drainage were 100%, Duwamish River Basin losses were 99%, and Samish River Basin losses were 96%. Only in the Nooksack River drainage did wetland area increase, and that was only by 0.2%. Simenstad et al. (1982) used similar methods to calculate losses of wetland area in Grays Harbor and found a decrease of 30.3%. Hutchinson et al. (1989) estimated change in area of intertidal marshes around the Strait of Georgia and Puget Sound from the time of European settlement to the present. They found overall losses of 18% around the Strait of Georgia and 58% around Puget Sound. Dahl (1990) reported that over 33% of total (freshwater and estuarine) wetland area in Washington and Oregon has been lost and that much of the remaining wetland habitat is degraded. Levings and Thom (1994) also estimated a loss of at least 76% in marsh/riparian habitat types in eleven major deltas in Puget Sound (from 732 km^2 prior to the mid-1800s to

176.1 km^2 in the early 1990s). Dahl (1990) reported that California has lost 94% of its wetlands. Similar reductions from historical times have been reported in Washington and Oregon wetlands: 70% loss in Puget Sound, 50% in Willapa Bay, and 85% in Coos Bay (Refalt 1985).

Most reviews of estuarine modification have focused on major estuaries and at river mouths near high-intensity industrial and urban development, but this development affects only 2% of the approximately 3,620 km of Puget Sound shoreline (Canning 1997). Perhaps a better estimate of overall historical changes in intertidal and nearshore habitats are inventories of shoreline armoring (e.g., construction of rock, concrete, and timber bulkheads or retaining walls), as these habitat modifications occur primarily with residential development in relatively rural areas (Shipman 1997). Armoring has a cumulative environmental impact that eventually results in loss of riparian vegetation, burial of the upper beach areas, altered wave interaction with the shoreline, and obstruction of sediment movement (Shipman 1997). Morrison et al. (1993) found a more than 100% increase in the length of shoreline armored from 1977 to 1993 in Thurston County, Washington. Kathey (1994) inventoried armoring along Bainbridge Island in Puget Sound and found that 42-67% of the entire shoreline was armored. Estuarine habitat quality also has been negatively affected by alteration of river hydrographs due to human activities. Water withdrawals, blockages, and diversions have reduced the total amount and the timing of peaks in freshwater inflow into estuaries throughout the range of coastal cutthroat trout. These shifts in the magnitude and timing of freshwater flows have a wide range of potentially deleterious effects ranging from decreases in estuarine primary and secondary productivity, increases in the stress on salmonids waiting to migrate upriver to spawning and feeding habitat, and seasonal blockages to outmigrating salmonids during summer months with extremely low flows.

Marine habitat—Although marine migrations of coastal cutthroat trout are generally limited to nearshore habitats, these areas can be influenced by general ocean productivity. The productivity of various ocean regions has been correlated with the degree of wind-driven upwelling (Bakun 1973, 1975). Upwelling brings cold nutrient-rich waters to the surface, resulting in an increase in plankton and ultimately salmonid production (Beamish and Bouillon 1993). El Niño events suppress coastal upwelling off the Washington, Oregon, and California coasts and tend to bring warmer water and warm-water species northward (McLain 1984). The Southern Oscillation Index (an index of El Niños) reveals that these warm-water events have been occurring well above average in frequency and intensity since 1976. The Pacific Northwest Index (an index of precipitation and sea temperatures in Washington) also reveals that the period following 1976 was warm and dry compared to the cool-wet period from 1945 to 1975 (Ebbesmeyer and Strickland 1995).

These long-term climate fluctuations have resulted in periodically unfavorable ocean and nearshore conditions for salmonids in California, Oregon, and Washington. As discussed in the "Life History" section (p. 38), coastal cutthroat trout display a variety of life-history strategies that may allow them to use more productive parts of the marine/freshwater environment and avoid unfavorable ones. As the evolution of these life-history strategies has, in part, been in response to long-term geographic and seasonal differences in marine productivity and estuarine availability, these conditions may be one cause of changes in overall coastal cutthroat trout abundance or in the relative abundance of different life-history types (Pearcy 1997; W. Pearcy[16]).

Trends in abundance

Short- and long-term trends in abundance are a primary indicator of risk in salmonid populations. Trends may be calculated from a variety of quantitative data, including dam or weir counts, stream surveys, and catch data. Regular sampling has not been conducted for many coastal cutthroat trout populations, and data series are quite short for many of those populations for which sampling has been conducted. When data series are lacking, general trends may be inferred by comparing historical and recent abundance estimates, or by considering trends in habitat quantity or condition.

The role of hatcheries and other forms of artificial propagation (in the form of hatcheries) for Pacific salmonids requires careful consideration in ESA evaluations. Artificial propagation has implications for evaluating both production trends and the genetic/ecological integrity of populations. Waples (1991a,b) and Hard et al. (1992) discussed the role of artificial propagation in ESU determination, emphasizing the need to focus on natural production in the threatened or endangered status determination. Because of the ESA emphasis on ecosystem conservation, this analysis focuses on naturally reproducing fish. An important question in the threshold determination is thus: Is natural production sufficient to maintain the population without the constant infusion of artificially produced fish? A full answer to this question is difficult without extensive studies of relative production and interactions between hatchery and natural fish. When such information is lacking, the presence of hatchery fish in natural populations leads to substantial uncertainty in evaluating the status of the natural population. Hatchery production of coastal cutthroat trout in the contiguous United States has been relatively minor compared with natural production and with other species of Pacific salmonids. In most cases, therefore, there are not large numbers of naturally spawning hatchery fish to complicate the issue of sustainability of natural populations.

Factors causing variability in abundance

A variety of factors, both natural and human-induced, affect the degree of risk facing salmonid populations. Because of time lags in these effects and variability in populations, recent changes in any number of factors may affect current risk without any apparent change in available population statistics. Thus, consideration of these effects must go beyond examination of recent abundance and trends. However, forecasting future effects is rarely straightforward and usually involves qualitative evaluations based on informed professional judgement. Possible future effects of recent or proposed conservation measures have not been taken into account in this analysis, but we have considered documented changes in the natural environment. A key question regarding the role of recent events is: Given our uncertainty regarding the future, how do we evaluate the risk that a population may not persist?

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[16] W. Pearcy, Oregon State University, Corvallis, OR 97333. Pers. commun. to O. Johnson. Oct. 1998.

Variations in the freshwater and marine environments are thought to be a primary factor driving fluctuations in salmonid run-size and escapement (Pearcy 1992, Beamish and Bouillon 1993, Lawson 1993). Artificial propagation can also contribute to fluctuations in natural abundance as well as having less obvious genetic and ecological effects. These factors are assessed below and have probably made some populations less resilient to a variety of poor conditions, but these effects are not easily quantified.

Oceanic and climatic conditions are also known to have changed recently in the Pacific Northwest. Most Pacific salmonids south of British Columbia have been affected by changes in ocean production that occurred during the 1970s (Pearcy 1992, Lawson 1993). Changes in productivity in the nearshore marine environment have been implicated in declines in chinook and coho salmon abundance and productivity. Coastal cutthroat trout tend to migrate closer to shore than chinook and coho salmon, and might have been affected more significantly by changes in the nearshore environment. However, the migration patterns for coastal cutthroat trout are still poorly understood. At this time, we do not know whether these climate conditions represent a long-term shift in conditions that will continue affecting salmonids into the future, or short-term environmental fluctuations that can be expected to reverse in the near future.

Threats to genetic integrity

Artificial propagation of coastal cutthroat trout—In addition to being a factor in evaluating natural replacement rates, artificial propagation can have a substantial influence on genetic/ecological integrity of natural salmonid populations. This influence can be expressed in several ways. First, stock transfers that result in interbreeding of hatchery and natural fish can lead to loss of fitness within and loss of diversity among populations. The latter may be important in maintaining long-term viability of an ESU because genetic diversity among salmonid populations helps to buffer overall productivity against periodic or unpredictable changes in the environment (Fagen and Smoker 1989, Riggs 1990). Ricker (1972) and Taylor (1991) summarized some of the evidence for local adaptations in Pacific salmonids that may be at risk from stock transfers.

Second, because a successful salmonid hatchery dramatically changes the mortality profile of a population, some level of genetic change relative to the native, naturally produced population is inevitable even in hatcheries that use local broodstock (Waples 1991b). These changes are unlikely to be beneficial to naturally reproducing fish.

Third, even if naturally spawning hatchery fish leave few or no surviving offspring, adult spawners can still have ecological and indirect genetic effects on natural populations. On the spawning grounds, hatchery fish may interfere with natural production by competing with natural fish for territory and/or mates. If hatchery fish that are not adapted to local conditions are successful in spawning with natural fish, production may be diverted from more productive natural crosses. The presence of large numbers of hatchery juveniles or adults may also alter the selective regime faced by natural fish.

Although past hatchery practices may have substantially influenced some coastal cutthroat trout populations, the relatively small magnitude of most current hatchery programs suggests that ongoing hatchery practices are unlikely to threaten the genetic integrity of most coastal cutthroat trout populations considered in this review. Large programs have taken place in the Lower Columbia River Basin and in a few streams along the Oregon coast, and genetic concerns in these areas are proportionally greater. It is difficult to directly assess the influence that population transfers of hatchery coastal cutthroat trout have had on natural populations because, in most cases, information is lacking. However, the results from a recent genetic analysis suggest that natural and hatchery coastal cutthroat trout have been interacting in the Coquille River Basin (NMFS et al., unpubl. data). Coastal cutthroat trout in several streams in the Coquille River drainage are genetically most similar to coastal cutthroat trout in the Alsea River Hatchery broodstock. Whether this genetic similarity is due to introgression resulting from hatchery-natural matings or due to displacement of native coastal cutthroat trout by straying hatchery fish cannot be determined from the data.

For populations with low abundance (either natural or hatchery), small-population effects (inbreeding, genetic drift) also can be important concerns for genetic integrity. Inbreeding and outbreeding depression and genetic drift are well understood at the theoretical level, and researchers have found inbreeding depression in various fish species (reviewed by Allendorf and Ryman 1987, Hard and Hershberger 1995). Other studies (e.g., Simon et al. 1986, Withler 1988, Waples and Teel 1990) have shown that hatchery practices commonly used in the past with anadromous Pacific salmonids have the potential to affect genetic integrity. In addition, Allendorf and Phelps (1980) detected a significant reduction in genetic variation at isozyme loci in a hatchery stock of westslope cutthroat trout when compared to the natural population from which it was derived. The reduction in genetic variation took the form of a lower proportion of polymorphic loci, average number of alleles per locus, and in the average heterozygosity per individual. Small-population effects (such as genetic drift, mutation, and introgression) may influence coastal cutthroat trout in many of the streams throughout their range.

Hybridization between coastal cutthroat trout and *O. mykiss*—As mentioned earlier (see "Hybridization between cutthroat trout and *O. mykiss*," p. 76), coastal cutthroat trout hybridize with steelhead and rainbow trout. Risks to coastal cutthroat trout populations from hybridization with *O. mykiss* include reduction in reproductive success of coastal cutthroat trout producing hybrid offspring. Production of hybrid offspring can reduce fitness of the parental species simply by decreasing the number of parental genes passed on to the next generation; this direct loss in fitness is most rapid when hybrid offspring fitness is lower than that of pure coastal cutthroat trout offspring. Indirect fitness losses can result from hybridization if hybrid offspring are superior competitors (even if only in a particular life stage) when interacting with pure coastal cutthroat trout offspring. In addition, introgression of *O. mykiss* alleles into *O. c. clarki* genomes can contribute to risk for coastal cutthroat trout populations. The concomitant loss or alteration of "pure" coastal cutthroat trout alleles (and resulting phenotypic traits) can lead to reduced fitness if introgressed alleles alter traits contributing to local adaptation in coastal cutthroat trout. The important question to address is what the fitness consequences of hybrids are to coastal cutthroat trout in their natural environment. To date, studies on the relative selective advantages or disadvantages of coastal cutthroat trout × *O. mykiss* hybrids have been conducted only in laboratory environments. Generally, hybrids have been shown to be intermediate in performance compared to either parental species, but some hybrids exhibited early life-history traits that were expected to be selected against under natural conditions (Hawkins 1997; see also "Hybridization between cutthroat trout and *O. mykiss*," p. 76). In addition, based on allozyme samples of juvenile and adult coastal cutthroat trout, Campton and Utter (1985) and Neillands (1990) hypothesized that selection against hybrids in anadromous populations might be occurring. Furthermore, biologists familiar with coastal cutthroat trout have noted that hybrids are detected more frequently in juvenile samples than in adults, suggesting that there are negative-fitness consequences associated with coastal cutthroat trout × *O. mykiss* hybridization events. On the other hand, some hybrids detected with genetic markers appear to be offspring of backcrossed individuals, suggesting that selection against F_1 hybrids is not universally strong.

The extent of hybridization between coastal cutthroat trout and *O. mykiss* and the environmental characteristics with which it is correlated are not well understood. Identifying hybrids is not straightforward without multiple genetic markers. In addition, historical (i.e., background or "natural") levels of coastal cutthroat trout × *O. mykiss* hybridization have not been distinguished from levels of present-day hybridization. To fully address the hybridization risk, we need to know how human activities may have affected both the frequency of coastal cutthroat trout × *O. mykiss* hybridization events and the fitness consequences of such hybridizations. For example, human actions can alter the relative abundance of coastal cutthroat trout and *O. mykiss* or increase the incidence of sympatry. In addition, it is important to ask whether recent changes in physical or biotic environmental conditions have resulted in significant changes in the survival of coastal cutthroat trout × *O. mykiss* hybrid offspring. These possibilities remain important for evaluating the risks to coastal cutthroat trout from hybridization with *O. mykiss*.

Harvest

Coastal cutthroat trout are not targeted in commercial fisheries and, in many areas, the only catch of coastal cutthroat trout is incidental in recreational fisheries for other species of salmonids. Because of harvest restrictions on naturally produced coastal cutthroat trout in many areas and the lack of targeted fisheries, direct mortality due to fishing pressure is thought to be relatively low, at least in recent years (Hooton 1997, Gerstung 1998, WDFW 1998a). Nevertheless, the catch of coastal cutthroat trout in recreational fisheries targeting the species directly and in fisheries aimed at Pacific salmon was probably a significant source of mortality in the past. Cutthroat trout are especially susceptible to fishing pressure because of their high "catchability" throughout their life history (Gresswell and Harding 1997). In addition, fishing regulations establishing size and bag limits are relatively recent, and biologists familiar with coastal cutthroat trout feel that in some areas their abundance has begun to increase only recently due to imposition of these more restrictive fishing limits (WDFW 1998c, Dunham 1998). In Washington, recent fishing regulations require the release of all coastal cutthroat trout, except adipose clipped hatchery fish, in Puget Sound, Hood Canal, the mainstem of the Chehalis, Toutle, Coweeman, Cowlitz, and Grays rivers, and in several smaller streams in the Lower Columbia River Basin. Bag and size limits on recreational catch of coastal cutthroat trout are in effect in the Strait of Juan de Fuca, in coastal streams, and in all Lower Columbia River Basin streams not subject to catch and release regulations (WDFW 1998a). Hatchery coastal cutthroat trout fisheries are still fairly active in the Lower Columbia River Basin. In Oregon, catch and release regulations recently were imposed in the Rogue, Hood, and Lower Columbia rivers and in portions of the Willamette and Sandy rivers. More restrictive bag and size limits were imposed on other Oregon streams in 1995, and in 1996, harvest of coastal cutthroat trout in the Umpqua River Basin was stopped in response to the federal listing under the ESA (Hooton 1997, ODFW 1998). More restrictive bag and size limits were placed on coastal cutthroat trout in Humboldt Bay and in Stone Lagoon in California (Gerstung 1997). Active coastal cutthroat trout recreational fisheries still exist in the Smith and Little rivers and in coastal lagoons in northern California (Gerstung[17]). However, recently imposed harvest restrictions by CDFG and CFGC aimed at protecting "wild trout" in northern California should have a positive (but not yet quantified) effect on coastal cutthroat trout (Bryant 1998).

Other risk factors

Other risk factors typically considered for salmonid populations include disease prevalence, predation, and changes in life-history characteristics such as spawning age or size. With the exception of reduction in the percentage of repeat spawners in some areas and evidence for predation by marine mammals on hatchery coastal cutthroat trout in the Lower Columbia River (WDFW 1998a), there is no clear evidence for general effects of other risk factors on coastal cutthroat trout in Washington, Oregon, and California. Some of these factors may be important for individual populations or ESUs, as noted in "Discussion of and Conclusions about ESU Determinations" (p. 120).

Coastal cutthroat trout populations can also suffer as a result of ecological interactions with competitors and predators. As discussed earlier (see "Life History" section, p. 38) coastal cutthroat trout compete with other species of Pacific salmonids as juveniles for feeding and rearing sites and as adults for spawning sites (Hartman and Gill 1968, Glova and Mason 1977, Glova 1987). Both inter- and intraspecific competition can occur in freshwater habitats during early rearing, and in estuarine habitats after smoltification has occurred. Adult coastal cutthroat trout can experience inter- and intraspecific competition in nearshore marine, estuarine, and freshwater habitats. Natural levels of competition can be disrupted by changes in the relative abundance of the species with which coastal cutthroat trout interact. These changes in relative abundance can be due to natural shifts in environmental conditions or human-induced changes in interacting species. For example, estuaries may be "overgrazed" when large numbers of salmonid juveniles enter the estuary at the same time (Reimers 1973, Healey 1991). Also, coastal cutthroat trout released from hatcheries often "residualize," increasing the pressure on freshwater-habitat rearing capacity for natural coastal cutthroat trout (Royal 1972). The extent to which such residualized fish decrease abundance of natural coastal cutthroat trout has not been quantified.

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[17] E. Gerstung, CDFG, 1416-9th St., Sacramento, CA 95814. Pers. commun. to M. Ruckelshaus. Sept. 1998.

A major source of human-caused change in the relative abundance of competitors is releases of hatchery-reared salmonids into coastal cutthroat trout habitats. For example, coastal cutthroat trout have been shown to compete with coho salmon during the juvenile-rearing phase, and coho salmon hatchery fry are planted into a number of coastal cutthroat trout streams. The increased competition from hatchery coho salmon may be a prominent risk factor for juvenile coastal cutthroat trout (Tripp and McCart 1983, Peters et al. 1996a, but see Peters et al. 1996b). In support of this possibility, a majority of those streams in Washington with continuing releases of hatchery coho salmon fry after 1986 also show declining trends in coastal cutthroat trout abundance (Fig. 34). Conversely, those streams without coho fry plants had mixed trends in abundance over the same time period. We were unable to do a similar graphical analysis with Oregon streams because we did not have data on coho fry releases and coastal cutthroat trout abundance for the same streams at appropriately small geographic scales. The potential also exists for large-scale hatchery releases of fry and fingerling salmon to overwhelm the production capacity of estuaries (Lichatowich and McIntyre 1987). Finally, hatchery and natural adults with sympatric spawning distributions can compete inter- and intraspecifically for redd sites and, as habitat conditions deteriorate in a number of streams, the opportunities for increased competition at this life-history stage also may be increasing.

Predation on coastal cutthroat trout also can limit population abundances. Dramatic population increases in sea lions and harbor seals have occurred in the Columbia River, due in part to their protection under the Marine Mammal Protection Act of 1972 (WDFW 1998a). Hatchery coastal cutthroat trout returning to the Beaver Creek Hatchery in the Lower Columbia River are scored for marine mammal marks. The percentage of returning adults with scars from marine mammals has ranged from 0 to 16% (mean = 7%) since 1982 (WDFW 1998a). It is not known whether these exceed historical predation rates, but these indicators of predator-prey encounter rates suggest that in some years coastal cutthroat trout mortality due to marine mammal predation may be high.

Biological Information by ESU

Puget Sound ESU

The BRT did not receive any estimates of adult coastal cutthroat trout population sizes for streams in the Puget Sound region except for a rough estimate of 13,000 spawners returning to the Skagit River Basin in 1997 (Kraemer unpubl. data). In addition, the percentage of mature fish that are repeat spawners has declined in the Stillaguamish (from 12% in 1991 to 5.4% in 1997) and Snohomish (from 12.4% in 1996 to 8.2 % in 1997) rivers (Kraemer unpubl. data). Although these data were collected over very short time periods, the lost opportunity for multiple spawning events by older (and larger, more fecund) fish should have a negative impact on population abundance, depending on total population size.

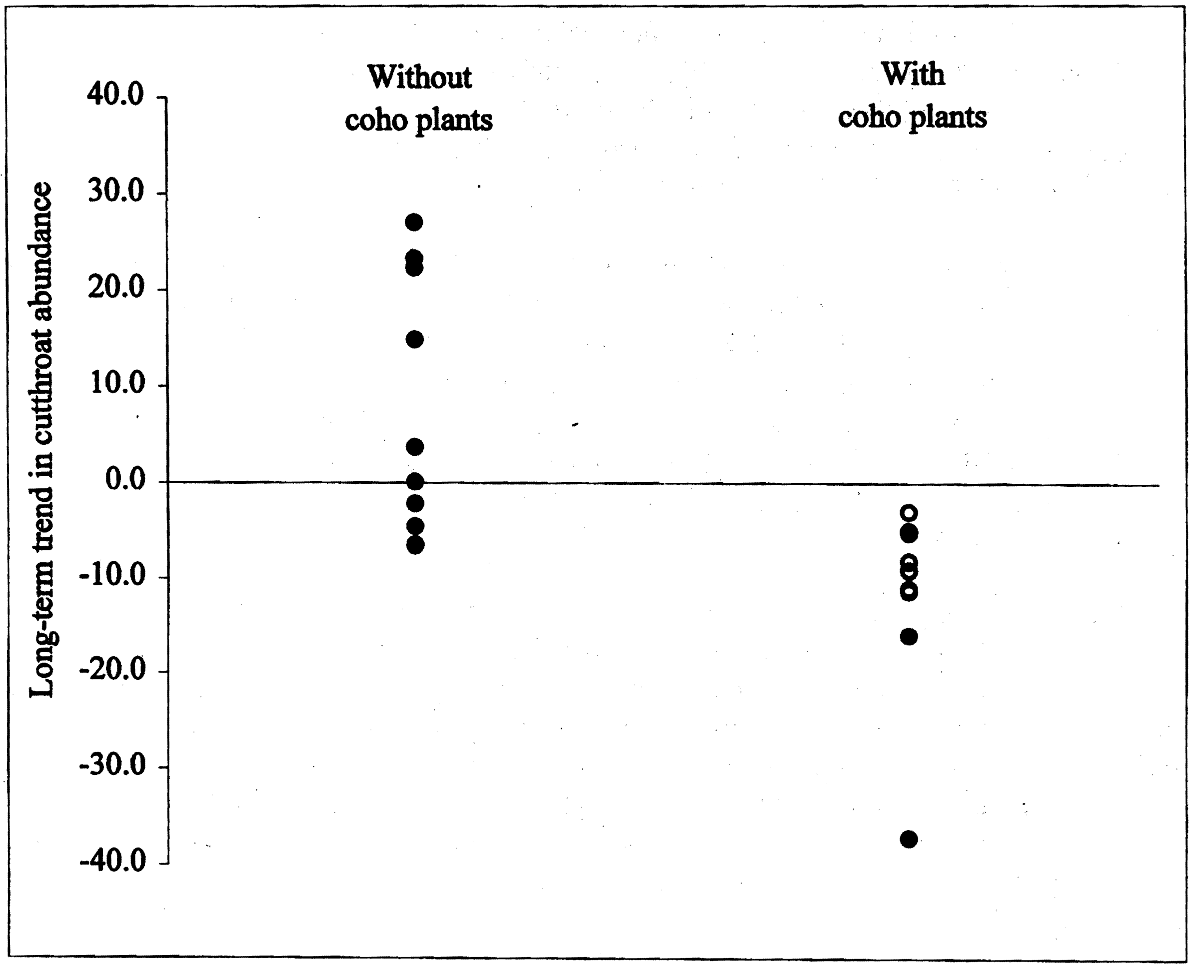

Figure 34. Long-term trend in abundance of coastal cutthroat trout in Washington streams with and without planted hatchery coho fry after 1985. Open circles indicate trends in coastal cutthroat trout adult numbers, closed circles indicate trends in coastal cutthroat trout juveniles. Trends in adults were compared to coho fry plants 4 years before.

Indices of coastal cutthroat trout abundance in a number of Lake Washington tributaries were estimated in 1996 (Ludwa et al. 1997). The numbers of coastal cutthroat trout per 50 m of stream ranged from 8 in McAleer Creek to almost 30 in Lyon Creek. Coastal cutthroat trout numbers in Kelsey Creek were 4-5 fish per 50 m of stream in 1979 (Scott et al. 1986) and increased to 23 fish/50 m in 1996 (Ludwa et al. 1997).

The only other abundance information available to the BRT for adult runs was a data set from the Oyster River in British Columbia. The Oyster River is on the eastern side of Vancouver Island, and represents one of the largest anadromous cutthroat trout runs in that area (BE and LGL 1995). Numbers of total adults (natural + hatchery) in the lower 8 km of the river ranged from 12-84 fish, of which 5-48 were estimated to be naturally produced fish (Fig. 35). Abundances in recent years have been highly variable, but the general trend has been positive since catch and release of nonhatchery coastal cutthroat trout became mandatory in British Columbia waters in 1985.

Reduction in habitat capacity for coastal cutthroat trout in the Puget Sound region has been widespread (WDFW 1998a; see also "Historical abundance, habitat, and carrying capacity" section, p. 147). In particular, numerous small streams were channelized or otherwise modified in the late 1800s and early 1900s for agricultural development. Historical records do not exist for coastal cutthroat trout in many lowland streams that were most likely very productive habitats for these fish. Estimates that 20-90% of salmonid habitat has been lost in the Puget Sound region (see "Historical abundance, habitat, and carrying capacity" section, p. 147) suggest that reduction in habitat capacity for coastal cutthroat trout is a critical, but not yet quantified, risk factor for this ESU.

All other quantitative data the BRT received for this ESU were useful only for evaluating trends in adult and smolt population sizes (Table 8, Fig. 36). Trends were mixed in the number of adults caught per hour by WDFW fisheries biologists in three northern Puget Sound rivers over the past 2-7 years (WDFW 1998a) (Fig. 37A). The Stillaguamish and Snohomish rivers showed increasing trends in catch per unit effort (CPUE), and the CPUE in the Skagit River has been declining over the past 4 years. The extremely short time periods covered by these data (especially for the Snohomish River sampling, conducted only since 1996) makes interpretation of the significance of the trends difficult. In addition, WDFW believes that much of the variation among years in adults caught was due to variable fishing conditions (WDFW 1998c).

In the Skagit River, data are available from 1990 to the present indicating the numbers of juvenile and adult coastal cutthroat trout caught in mainstem traps designed to estimate coho salmon production (Seiler et al. 1998). Both scoop and screw trap data are available for downstream migrants (1990-97 for scoop traps and 1993-97 for screw traps) (Table 8) and upstream migrants (1995-97 for scoop traps and 1996-97 for screw traps). These data are considered indices of coastal cutthroat trout abundance because trap efficiencies were estimated only for coho salmon and because the proportion of the coastal cutthroat trout population trapped is not known. Numbers of upstream and downstream migrants are likely to be underestimated because of the relatively narrow time periods during which traps were in place each year (i.e., the

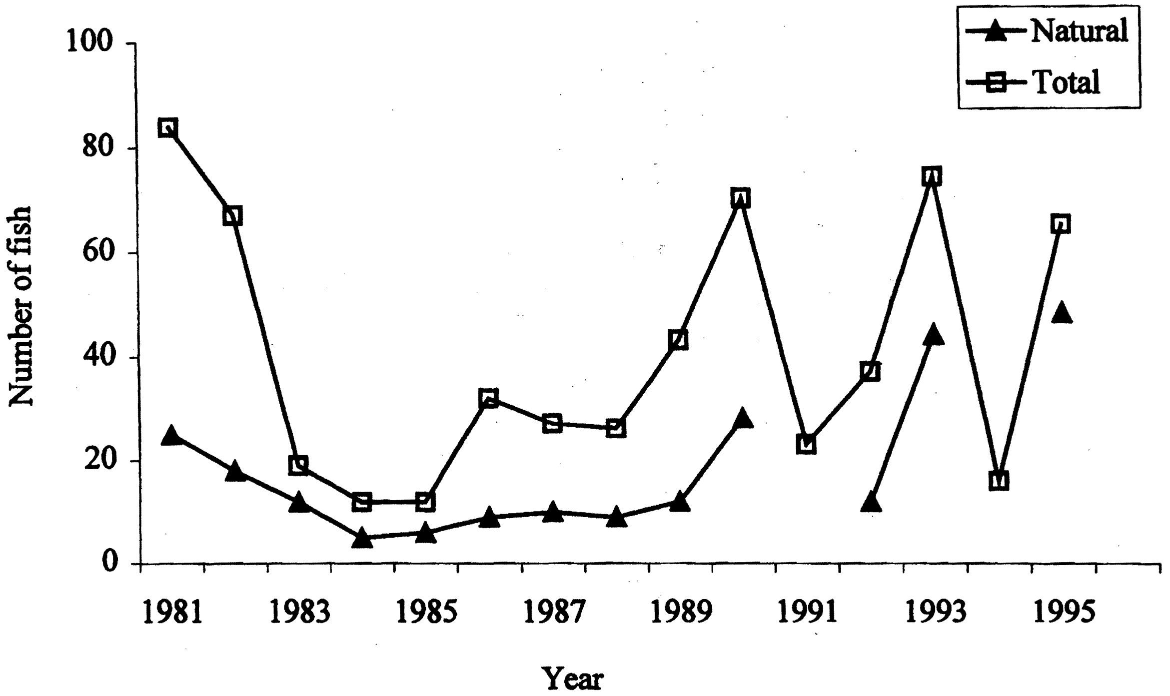

Figure 35. Abundance of natural and total (natural plus hatchery) coastal cutthroat trout greater than 28 cm long in an 8-km reach of the lower Oyster River, British Columbia (BE and LGL 1995).

Table 8. Summary of abundance information available to the Biological Review Team (BRT) for coastal cutthroat trout Evolutionarily Significant Units (ESUs) in Washington, Oregon, and California.

ESU						Recent abundance		Trends		
River Basin	Sub-basin	Production[a]	Stage	Method[b]	Data Years	Data Type[c]	5-Year Geomet. Mean[d]	Long-term[e]	Short-term[f]	Data References
1-Puget Sound										
Skagit Bay	Skagit R.	Natural	Adult & Juvenile	SC	1990-97	IN	1	-11.8	+9.5	Seiler et al. 1998
	Skagit R.	Natural	Adult & Juvenile	ST	1993-97	IN	2	-29.6		Seiler et al. 1998
	Skagit R.	Natural	Adult	HL	1994-97	CPUE		-17.3		WDFW 1998a
Puget Sound	Stillaguamish R.	Natural	Adult	HL	1991-97	CPUE		+6.7	+6.7	WDFW 1998a
South Sound	Perkins Cr.	Natural	Juvenile	TR	1981-87	OM	138	+14.9		WDFW 1998a
	Mill Cr.	Natural	Juvenile	TR	1979-87	OM	195	-5.0		WDFW 1998a
	Wildcat Cr.	Natural	Juvenile	TR	1979-87	OM	567	-2.2		WDFW 1998a
	Deschutes R.	Natural	Adult	TR	1981-97	IN	74	+10.2	+25.6	Topping unpubl. data
E. Hood Canal	Big Beef Cr.	Natural	Juvenile	TR	1978-95	OM	557	+3.7	+5.5	WDFW 1998a
	Little Tahuya Cr.	Natural	Juvenile	TR	1978-94	OM	140	+0.1		WDFW 1998a
	Big Mission Cr.	Natural	Juvenile	TR	1982-94	OM	376	-6.4		WDFW 1998a
	Courtney Cr.	Natural	Juvenile	TR	1978-94	OM	87	-6.5		WDFW 1998a
	Bear Cr.	Natural	Juvenile	TR	1978-94	OM	86	-6.6		WDFW 1998a
	Little Anderson Cr.	Natural	Juvenile	TR	1992-97	OM	547	+22.3		WDFW 1998a
	Seabeck Cr.	Natural	Juvenile	TR	1993-97	OM	334	+23.3		WDFW 1998a
	Stavis Cr.	Natural	Juvenile	TR	1993-97	OM	1,080	+27.1		WDFW 1998a
	Skokomish R.	Natural	Adult & Juvenile	TR	1986-89	OM		-68.5		PNPTC 1994

Table 8. (Continued).

ESU						Recent abundance		Trends		
River Basin	Sub-basin	Production[a]	Stage	Method[b]	Data Years	Data Type[c]	5-Year Geomet. Mean[d]	Long-term[e]	Short-term[f]	Data References
2-Olympic Peninsula										
Strait of Juan de Fuca	Hoko R.	Natural	Adult & Juvenile	TR	1986-89	OM		+31.5		PNPTC 1994
Clearwater R.	Mainstem	Natural	>70mm	SC	1981-96		35	-13.4	-1.9	Garrett 1998
	Christmas Cr.	Natural	>70mm	WC	1982-96	OMD	3	-7.3	-5.8	Garrett 1998
	Hurst Cr.	Natural	>70mm	WC	1982-96	OMD	2	-2.3	-8.6	Garrett 1998
	Miller Cr.	Natural	>70mm	WC	1982-96	OMD	3	-5.4	+2.6	Garrett 1998
	Peterson Cr.	Natural	>70mm	WC	1980-89	OM	432	-3.8		Garrett 1998
	Shale Cr.	Natural	>70mm	WC	1983-96	OMD	2	-6.6	-2.5	Garrett 1998
	Snahapish R.	Natural	>70mm	WC	1981-96	OMD	4	-4.9	+1.4	Garrett 1998
	Airport Pond	Natural	>70mm	WC	1986-96	OMD	4	+30.5	+32.2	Garrett 1998
	Coppermine Bottom Pond	Natural	>70mm	WC	1978-96	OMD		-3.9	+15.0	Garrett 1998
	Dasher's Pond	Natural	>70mm	WC	1986-96	OMD		-10.1	-8.4	Garrett 1998
	Morrison's Pond	Natural	>70mm	WC	1986-96	OMD	1	-5.7	-3.4	Garrett 1998
	Paradise Pond	Natural	>70mm	WC	1986-96	OMD		-8.5	-2.6	Garrett 1998
	Pond Two	Natural	>70mm	WC	1978-96	OMD	1	+12.2	-13.5	Garrett 1998
	Swamp Cr.	Natural	>70mm	WC	1987-94	OM	13	-29.2		Garrett 1998
	Tiemeyer's P.	Natural	>70mm	WC	1986-96	OMD	1	-7.4	-4.8	Garrett 1998
3-Southwestern Washington/Columbia River										
Chehalis R.	Hoquiam R.	Mixed?	Adult	TR	1986-95	TL	33	-5.2	-4.6	WDFW 1998a
Satsop R.	Bingham Cr.	Natural	Juvenile	TR	1982-94	OM	86	-4.6	+2.9	Big Eagle & Associates 1995
Humptulips R.	Stevens Cr.	Natural	Juvenile	TR	1982-95	OM	227	-15.4	-15.0	Seiler and Hanratty unpubl. data
Columbia R.	Abernathy Cr.	Natural	Adult	TR	1991-95	TL		-10.2		WDFW 1998a
	Abernathy Cr.	Hatchery	Adult	TR	1991-95	TL		-62.2		WDFW 1998a
	Abernathy Cr.	Mixed	Adult	TR	1972-94	SC	132	-8.1	-29.0	WDFW 1998a
	Elochoman R.	Natural	Adult	TR	1972-94	TL	5	-10.9		WDFW 1998a

Table 8. (Continued).

ESU						Recent abundance		Trends		
River Basin	Sub-basin	Production[a]	Stage	Method[b]	Data Years	Data Type[c]	5-Year Geomet. Mean[d]	Long-term[e]	Short-term[f]	Data References
3-Southwestern Washington/Columbia River										
	Elochoman R.	Hatchery	Adult	TR	1972-94	TL	287	+13.5	-21.4	WDFW 1998a
	Elochoman R.	Mixed	Adult	TR	1973-94	SC	12	-17.6	-9.0	WDFW 1998a
	Cowlitz R.	Natural	Adult	TR	1971-94	TL	1,415	-3.0	+14.2	WDFW 1998a
	Toutle R.	Natural	Adult	TR	1989-94	TE	50	+29.2		WDFW 1998a
	Toutle R.	Natural	Adult	TR	1991-95	TL		-4.8		WDFW 1998a
	Cowlitz R./ Coweeman R./ Toutle R.	Mixed	Adult	TR	1972-94	SC	162	-9.0	-28.0	WDFW 1998a
	Kalama R.	Natural	Adult	TR	1976-94	IN	4	-11.2	-8.8	WDFW 1998a
	Kalama R.	Natural	Juvenile	TR	1978-94	OM	1,410	-15.9		WDFW 1998a
	Grays R.	Mixed	Adult	TR	1972-95	SC	97	+27.6		WDFW 1998a
	Hood R.	Natural	Adult & Jacks	TR	1962-97	TL	39	-4.8		StreamNet 1998
4-Oregon Coast										
Nestucca Bay	Nestucca R.	Natural	Adult	SN	1965-95	RH	1	-1.5	-11.0	StreamNet 1998
Tillamook Bay	Trask R.	Natural	Adult & Jacks	SN	1965-95	RH	4	-2.0	+0.6	StreamNet 1998
	Wilson R.	Natural	Adult & Jacks	SN	1965-95	RH	1	-7.6	+2.1	StreamNet 1998
Coos Bay	Millicoma R.	Natural	100-200mm	SE	1978-97	CPUE	0.25	+2.4	+11.3	ODFW 1998
	Millicoma R.	Natural	>200mm	SE	1978-97	CPUE	0.12	-1.4	-9.8	ODFW 1998
	S. Coos R.	Natural	100-200mm	SE	1978-97	CPUE	0.05	+2.0	+10.6	ODFW 1998
	S. Coos R.	Natural	>200mm	SE	1978-97	CPUE	0.04	-6.8	-2.5	ODFW 1998
	Tenmile Cr.	Natural	Juvenile	WC	1992-98	OM	98	+1.2		Johnson unpubl. data
	Tenmile Cr.	Natural	Smolt	WC	1992-98	OM	331	+2.0		Johnson unpubl. data
	Cummins Cr.	Natural	Juvenile	WC	1992-98	OM	71	+30.3		Johnson unpubl. data
	Cummins Cr.	Natural	Smolt	WC	1992-98	OM	94	+30.4		Johnson unpubl. data
Umpqua R.	N Umpqua R.	Mixed	Adult	DC	1947-97	TL	18	-7.2	-6.2	StreamNet 1998

Table 8. (Continued).

ESU						Recent abundance		Trends		
River Basin	Sub-basin	Production[a]	Stage	Method[b]	Data Years	Data Type[c]	5-Year Geomet. Mean[d]	Long-term[e]	Short-term[f]	Data References
5-Southern Oregon/Northern California Coast										
Redwood Cr.		Natural	Adult	SN	1992-95	IN		-7.4		Gerstung 1998
Smith R.	Mill Cr.	Natural	Juvenile	WC	1994-97	IN		+2.9		Howard and Albro 1995, 1997
	Mill Cr.	Natural	Adult	WC	1994-97	TE		+60.0		Howard and Albro 1995, 1997
	SF Smith R.	Natural	Adult & Juveniles	SN	1991-94	TE	294	+2.1		McCain unpubl. data
	MF Smith R.	Natural	Adult & Juveniles	SN	1991-94	TE	252	+2.4		McCain unpubl. data
	NF Smith R.	Natural	Adult & Juveniles	SN	1992-94	TE		+9.4		McCain unpubl. data
Lower Klamath R.	Blue Cr.	Natural	>14"	SN	1995-97	IN		+44.9		Gale 1998
	Klamath R.	Natural	Adult	SE	1980-89	CPUE	8	+5.1		Gerstung 1998
Klamath R. Est.	Klamath R.	Natural	Adult	EF	1991-94	CPUE		+70.1		Gerstung 1998

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[a] Production: as reported by data reference.

[b] Method Codes: DC, dam count; EF, electrofishing; HL, hook/line; SC, scoop trap; SE, seine; SN, snorkel; ST, screw trap; TR, trap; WC, weir count.

[c] Data Type Codes: CPUE, catch per unit effort; FH, fish per hour; IN, index; OM, number of outmigrants; OMD, number of outmigrants per day; RH, resting hole counts; SC, sport catch; TE, total estimates; TL, total live fish count.

[d] Most recent 5 years of data used to calculate spawning escapement geometric mean.

[e] Long-term Trend: Calculated for all data collected after 1947.

[f] Short-term Trend: Calculated for most recent 7-10 years during the period 1988-1998.

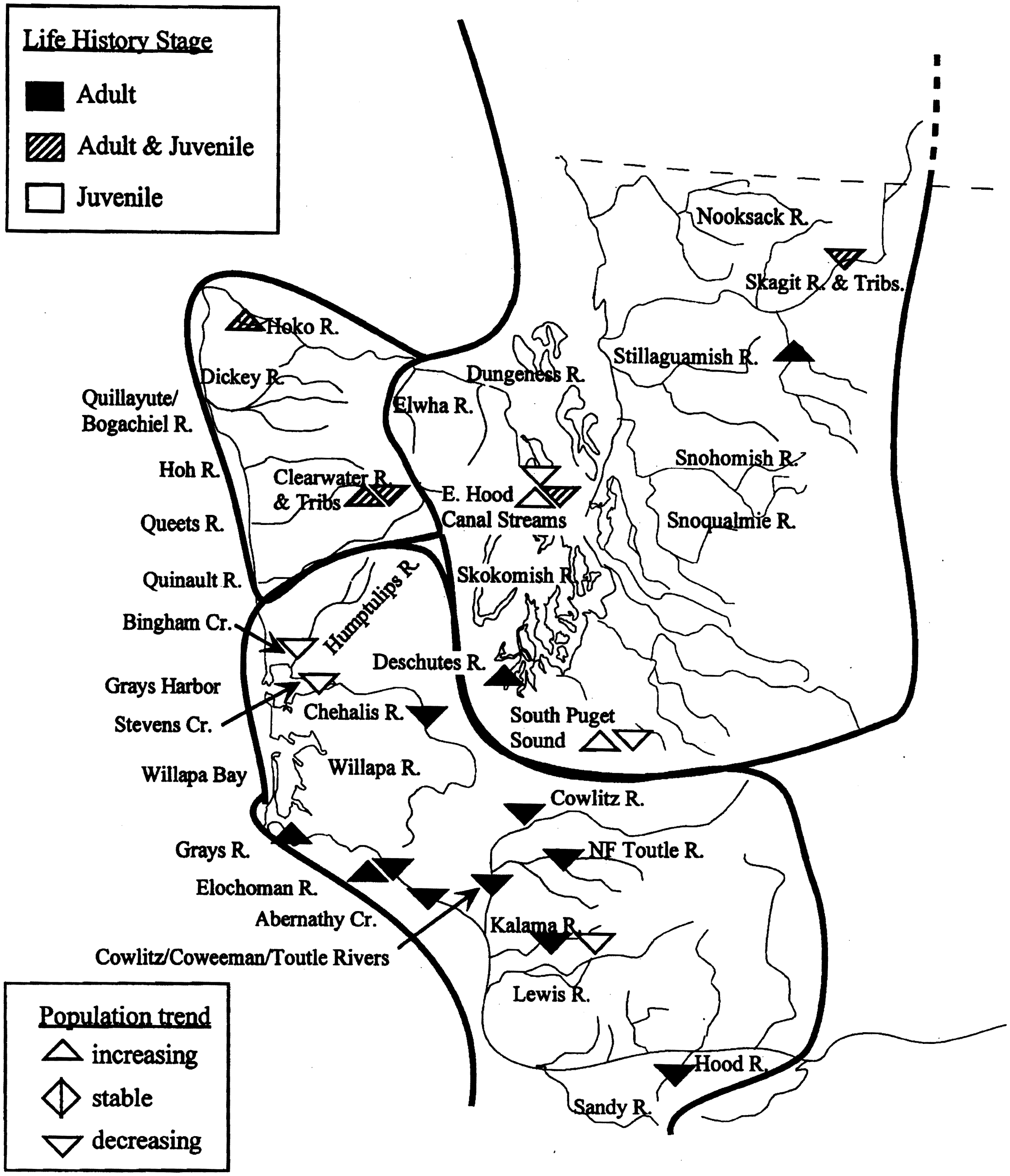

Figure 36. Trends and life-history stages for sea-run cutthroat trout in the Puget Sound, Olympic Peninsula, and the Washington portion of the Southwestern Washington/Columbia River Evolutionarily Significant Unit (ESU) (PNPTC 1994; Garrett 1998; Seiler et al. 1998; Topping unpubl. data; StreamNet 1998; WDFW 1998a).

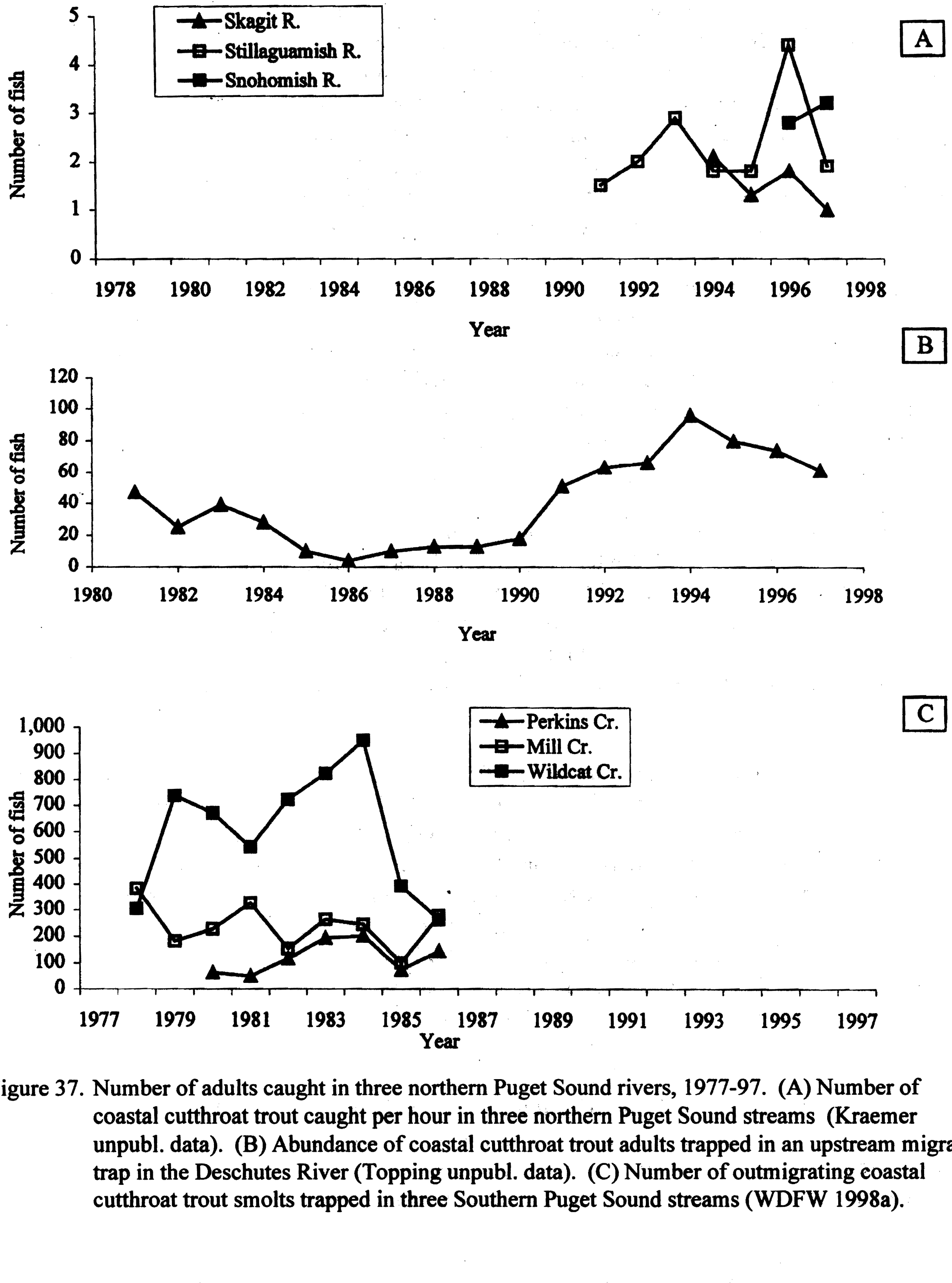

Figure 37. Number of adults caught in three northern Puget Sound rivers, 1977-97. (A) Number of coastal cutthroat trout caught per hour in three northern Puget Sound streams (Kraemer unpubl. data). (B) Abundance of coastal cutthroat trout adults trapped in an upstream migrant trap in the Deschutes River (Topping unpubl. data). (C) Number of outmigrating coastal cutthroat trout smolts trapped in three Southern Puget Sound streams (WDFW 1998a).

traps were installed during periods of known coho immigration and emigration, which occur over a more predictable and narrower window of time than do coastal cutthroat trout migration patterns) (Seiler[18]). Nevertheless, the overlap in emigration times for coho salmon and coastal cutthroat trout can be very high in some streams (Cederholm and Scarlett 1982), so underestimation for coastal cutthroat trout numbers may not be high in all instances. Trends in coastal cutthroat trout downstream migrant abundance from 1990 to present have declined by 12-30% per year; in contrast, upstream migrants increased dramatically (3-198%) over the past 3 years. It is difficult to interpret the significance of the upstream migrant data because of the high variability and short time period over which these fish have been sampled in this river basin.

Additional trend information is available for adult coastal cutthroat trout in the Deschutes River in southern Puget Sound. Immigrant coastal cutthroat trout adults trapped in a weir designed to estimate coho abundance have been counted since 1981, and their numbers have been increasing by 10% over the long term and by 26% over the most recent 5 years (Topping unpubl. data) (Table 8, Fig. 37B). Again, the absolute abundance of individuals should be considered to be an index number because the trap efficiency for coastal cutthroat trout is not known.

Data from traps for southern Puget Sound outmigrant smolts are available from the late 1970s to the late 1980s (WDFW 1998a) (Fig. 37C). Data are from Wildcat Creek (Dyes Inlet), Perkins Creek (Eld Inlet), and Mill Creek (Hammersley Inlet). Trends in smolt numbers in Wildcat and Mill creeks during this period were slightly declining (a 2-5% decrease in abundance), while Perkins Creek smolt numbers increased by 15% over roughly the same time period. No information was available to the BRT indicating the current status of coastal cutthroat trout smolts in these creeks.

Smolt abundance data from the late 1970s to the present were available from a number of streams in eastern Hood Canal (WDFW 1998a) (Fig. 38). The trends in smolt abundance were mixed, ranging from a 6.6% decline per year over 15 years to an almost 30% increase over 4 years. Smolts in the Skokomish River declined by over 68% per year from 1986-1989 (PNPTC 1994). No information about present trends in smolt abundance in the Skokomish River was available to the BRT. Upstream weir counts for one of the creeks draining into Hood Canal, Big Beef Creek, were 190 coastal cutthroat trout in 1993-94 and 86 coastal cutthroat trout in 1994-95 (Seiler et al. 1995). Additional data from Snow and Salmon Creeks in eastern Hood Canal have been submitted to NMFS but were not available for BRT deliberations (see Table C-1 in Appendix C).

No anadromous coastal cutthroat trout are presently released from hatcheries into the Puget Sound ESU. Historical information on the numbers and origin of hatchery coastal cutthroat trout released into streams in this region (see "Artificial Propagation," p. 113) provides an indication of the potential risks due to interactions with hatchery coastal cutthroat trout. For

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[18] D. Seiler, WDFW, P.O. Box 43151, Olympia, WA 98504. Pers. commun. to M. Ruckelshaus. Sept. 1998.

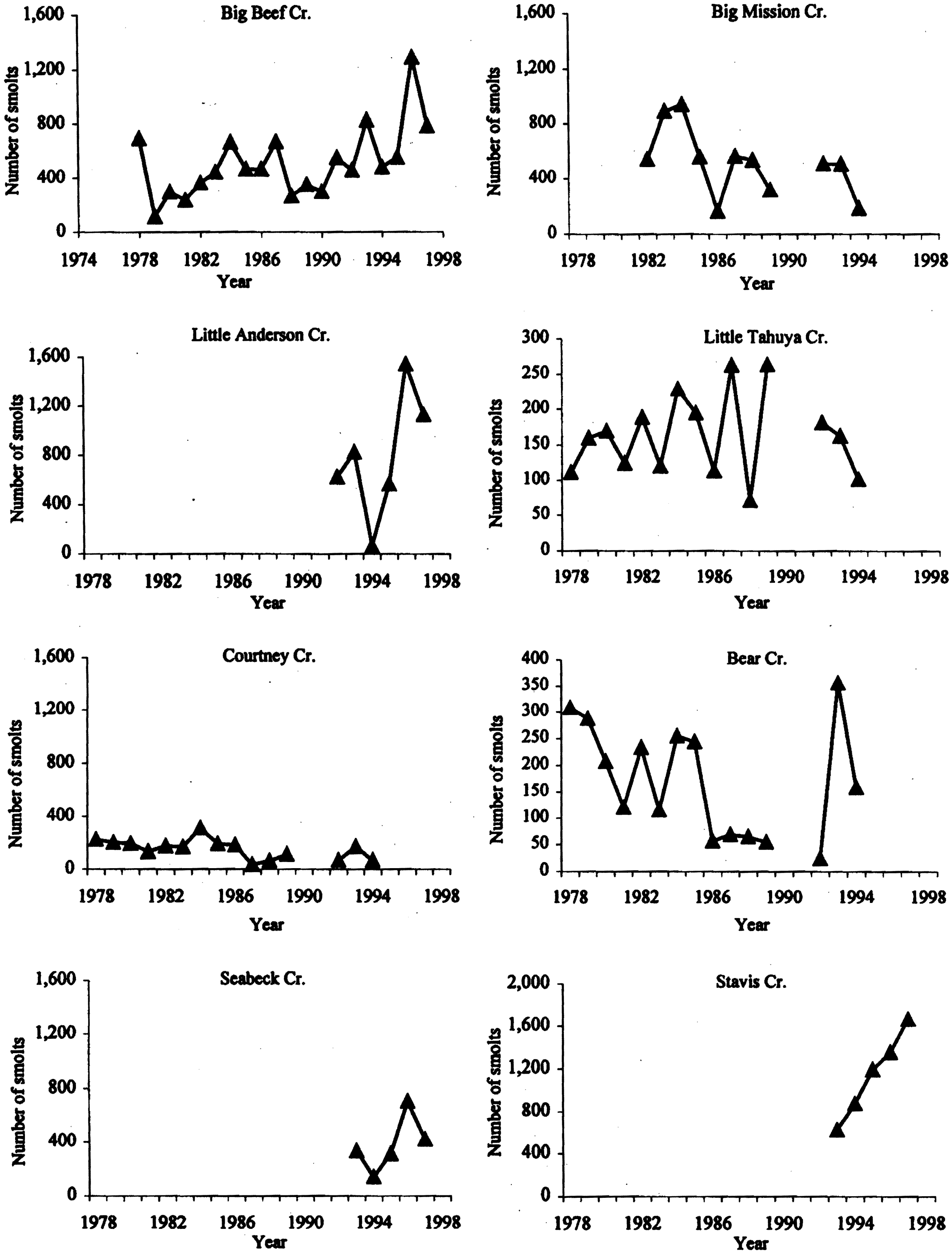

Figure 38. Numbers of outmigrating coastal cutthroat trout smolts trapped in Eastern Hood Canal streams (WDFW 1998a).

example, as discussed in the section on artificial propagation, the overlap in spawning times of the Lake Whatcom/Tokul Creek coastal cutthroat trout broodstock and native coastal cutthroat trout in Lake Washington suggest that the potential existed for interbreeding between native and hatchery fish within this ESU. In addition, WDFW considers several of the streams in northern Puget Sound to be of mixed origin (e.g., the Stillaguamish, Snohomish, and Nooksack rivers) and composite production (Nooksack River), indicating that hatchery fish of nonnative origin could potentially contribute to naturally spawning populations, depending on the release locations of hatchery coastal cutthroat trout relative to spawning grounds of native fish (WDFW 1998a, c). Hatchery coastal cutthroat trout from the Beaver Creek Hatchery in the Lower Columbia River were reported to stray when released in Hood Canal streams (Hisata 1973; see "Artificial Propagation," p. 113). On the other hand, releases of hatchery sea-run cutthroat trout were stopped in 1985 in northern Puget Sound streams, and in 1994 in southern Puget Sound and Hood Canal (WDFW 1998a). Also, some hatchery broodstocks from the Lower Columbia River released into Puget Sound did not succeed in enhancing harvest (see "Artificial Propagation," p. 113), suggesting that at least some coastal cutthroat trout of hatchery origin were not adapted to environmental conditions in Puget Sound. Finally, releases of hatchery coho salmon and steelhead continue to occur in Puget Sound and Hood Canal (WDFW 1998a).

Harvest of coastal cutthroat trout in the Puget Sound region was probably significant in the past, but most biologists familiar with salmonids in this area feel that direct and indirect fishing pressure on coastal cutthroat trout in this ESU has probably declined (WDFW 1998c). One possible exception is the continued incidental catch of coastal cutthroat trout in local gillnet fisheries targeting Pacific salmon (WDFW 1998c). Drought conditions in the mid-1980s and early 1990s also probably severely stressed coastal cutthroat trout in this region (WDFW 1998c).

Olympic Peninsula ESU

Very few quantitative data were available to the BRT for the Olympic Peninsula ESU, and the vast majority of the information came from downstream migrant traps on several tributaries to the Clearwater River, which is a tributary of the Queets River (Garrett 1998) (Table 8, Figs. 36, 39a, and 39b). Downstream migrant adult and juvenile coastal cutthroat trout have been sampled in the Clearwater River basin with a scoop trap in the mainstem and with weirs in the tributaries; trap efficiencies for coastal cutthroat trout caught in these traps are not known. The data are presented as the numbers of downstream migrants trapped per number of days the trap was operated each year. Downstream migrants in the mainstem Clearwater River have been sampled with a scoop trap since 1981, and their numbers are showing a 13% decline per year. The tributary data span 8-20 years, and they represent downstream migrant smolts and adults in streams and ponds used as feeding and overwintering habitat. The trends in abundance are mixed—some are relatively stable over the sampling period, others show declines, and coastal cutthroat trout numbers in one pond have been steadily increasing since 1988.

The other abundance data for coastal cutthroat trout in the Olympic Peninsula ESU were from the Lake Dickey screw trap, which captures downstream migrants (Seiler et al. 1997). This trap is designed to estimate coho salmon production, and the trap efficiency for coastal cutthroat

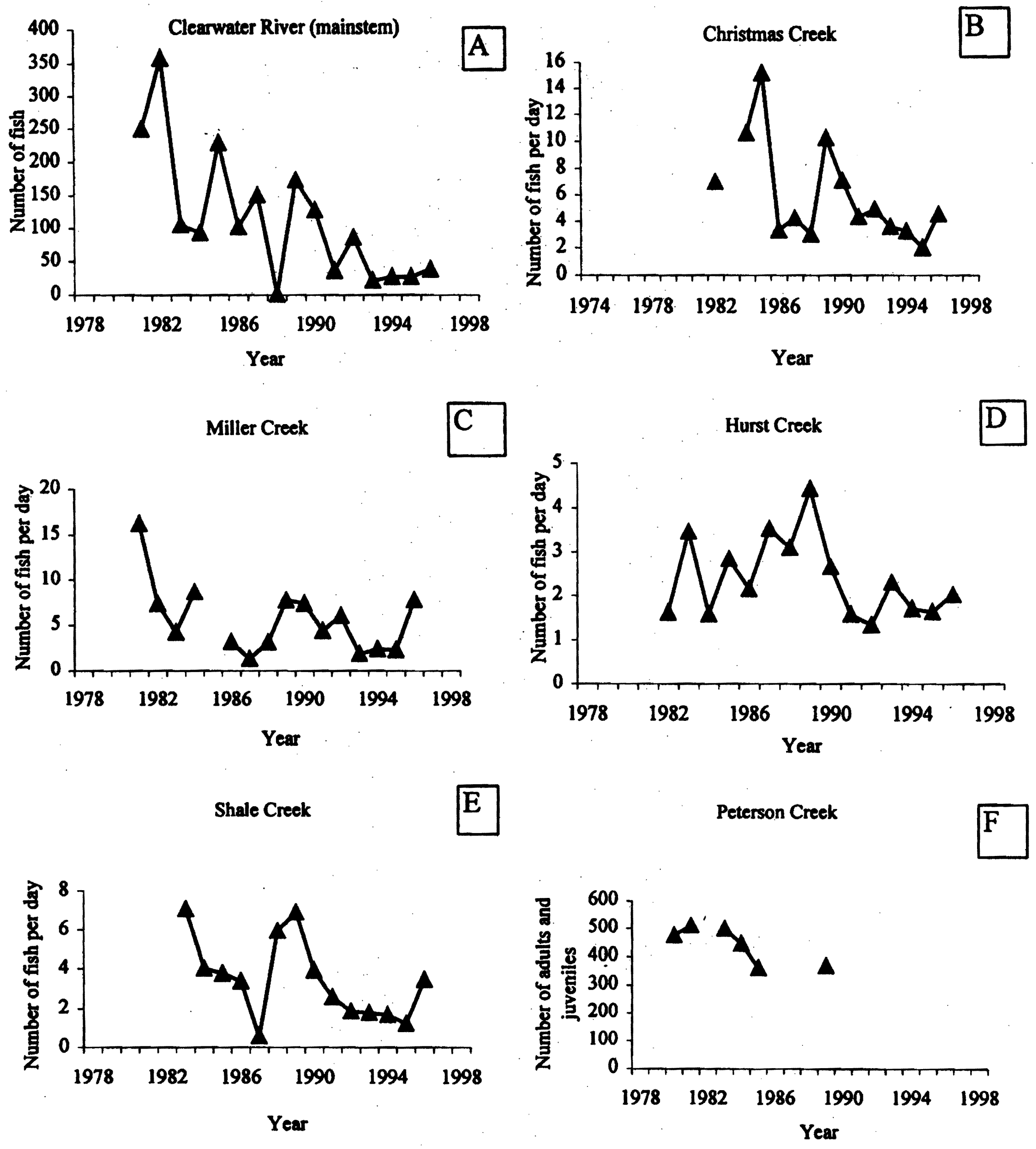

Figure 39a. Numbers of downstream migrant coastal cutthroat trout trapped in a scoop trap on the Clearwater River, a tributary to the Queets River (A). Numbers of downstream migrant coastal cutthroat trout trapped per day (B-E) and total numbers of coastal cutthroat trout trapped (F) in tributaries to the Clearwater River (Garrett 1998).

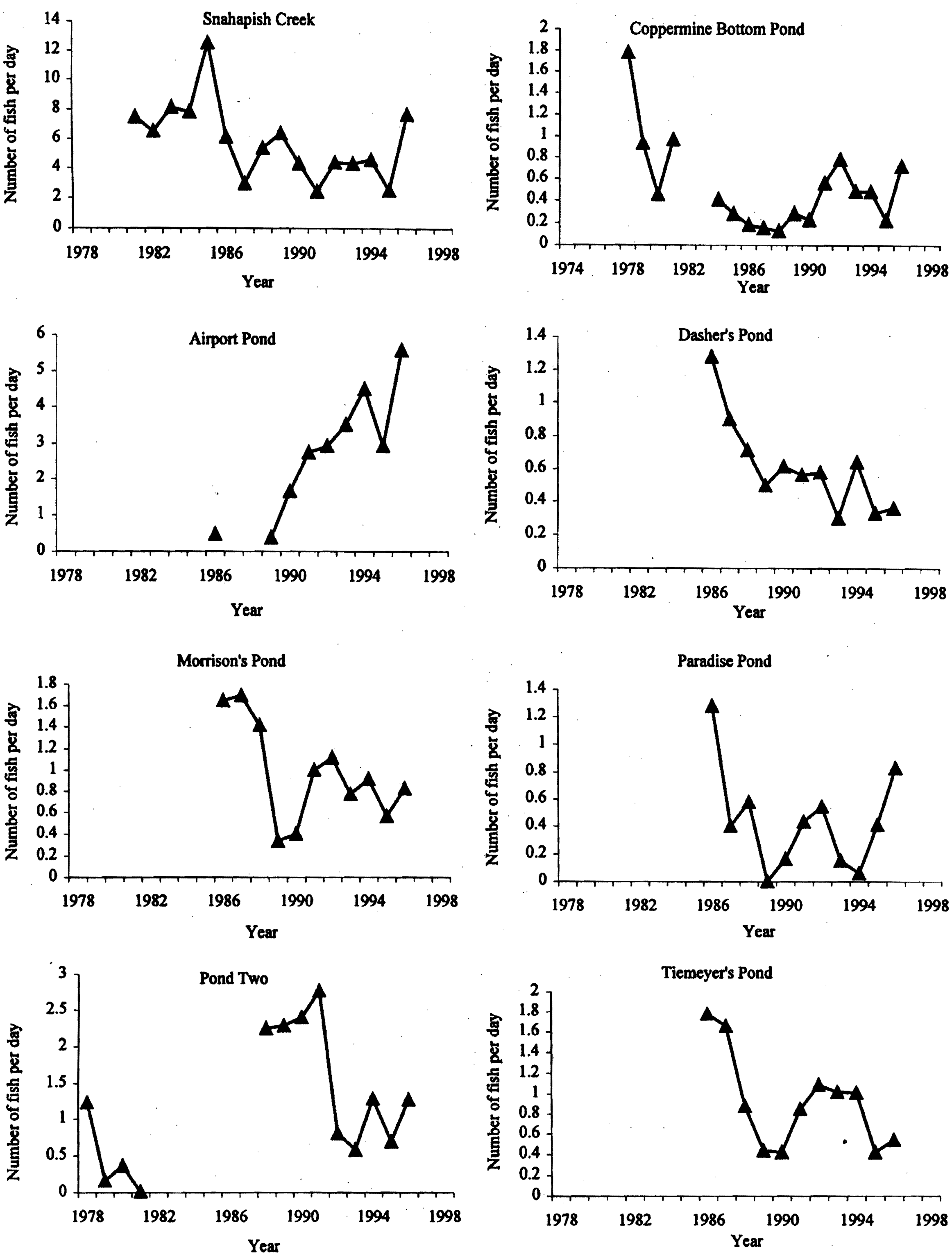

Figure 39b. Numbers of downstream migrant coastal cutthroat trout trapped per day in tributaries to the Clearwater River (Garrett 1998).

trout is not known. The numbers of coastal cutthroat trout caught in the trap from 1992-94 were 285, 138, and 269, respectively. WDFW reported high coastal cutthroat trout habitat quality in the Quinault River Basin (WDFW 1998a). In addition, the Point No Point Treaty Council coordinated sampling of downstream migrants on the Hoko River from 1986-89 (Table 8, Fig. 40) (PNPTC 1994). Weirs trapped downstream migrants at RKm 10 on the mainstem Hoko River and on the Little Hoko River at its mouth. The numbers of downstream migrants were highly variable–they increased by almost 32% per year over the time period sampled, but the high variance in the numbers of fish means this trend is not statistically significant.

Finally, WDFW has 1998 downstream migrant data for coastal cutthroat trout as a result of new sampling of coho salmon in a number of streams along the Strait of Juan de Fuca. The traps are designed to estimate coho smolt production and so were in place from April to June. Trap efficiencies for coastal cutthroat trout are not known; the proportion of the total coastal cutthroat trout population trapped in the downstream migrant traps also is not known. WDFW believes that most of the coastal cutthroat trout trapped were smolts, but a few larger fish also were caught. In 1998, the numbers of outmigrating coastal cutthroat trout in these creeks ranged from 55 in Valley Creek to 756 in Mattrotti Creek (Hanratty unpubl. data). WDFW plans to continue sampling in these streams, which should provide good indices of smolt production for coastal cutthroat trout in this area.

No information on the percentage of hatchery coastal cutthroat trout in natural spawning escapements in the Olympic Peninsula ESU was available to the BRT. There is some information on the numbers and origin of hatchery coastal cutthroat trout released into streams in this region (see "Artificial Propagation," p. 113), which provides an indication of the potential risks due to interactions with hatchery coastal cutthroat trout. In addition, releases of hatchery coho salmon and steelhead continue to occur in a few Olympic Peninsula streams.

Southwestern Washington/Columbia River ESU

Information on coastal cutthroat trout abundance was available from a few streams in the southwestern Washington portion of the geographic region encompassing this ESU (Table 8, Fig. 36). The number of adults trapped in the west branch of the Hoquiam River has ranged from 25 to 68 over the past 10 years (most recent 5-year geometric mean = 33 fish) (WDFW 1998a). Abundance in the Hoquiam River has declined by 5% per year over the past 10 years (Fig. 41A). Downstream migrants in Stevens Creek, a tributary to the Humptulips River, have been declining by 15% per year since 1982 (Table 8, Fig. 41C). The numbers of coastal cutthroat trout counted in the Stevens Creek trap should be considered an index count because the trap efficiency and the proportion of total outmigrants trapped is not known for this weir, which is designed to estimate coho salmon production. WDFW biologists who run the trap believe that most of the outmigrating coastal cutthroat trout caught in the trap were smolts, but that a few larger fish also are included in the total counts (Seiler and Hanratty unpubl. data). Smolt counts from Bingham Creek, a tributary to the Satsop River, have been variable over the past 13 years, with no clear trend in abundance (WDFW 1998a, Table 8). Over the full data set, the abundance of smolts

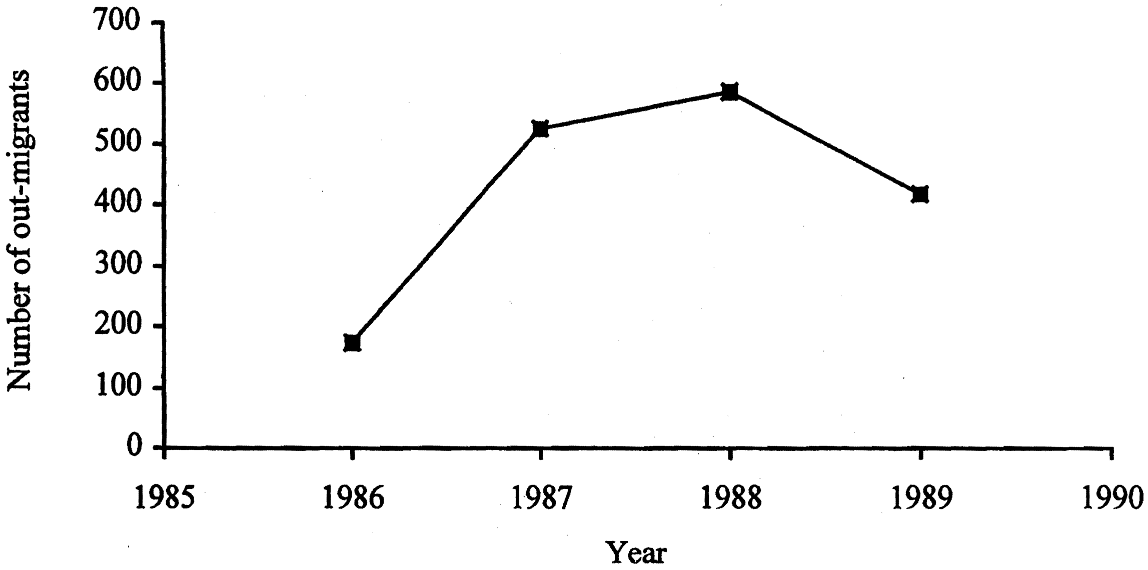

Figure 40. Numbers of coastal cutthroat trout downstream migrants trapped in the Hoko River (PNPTC 1994).

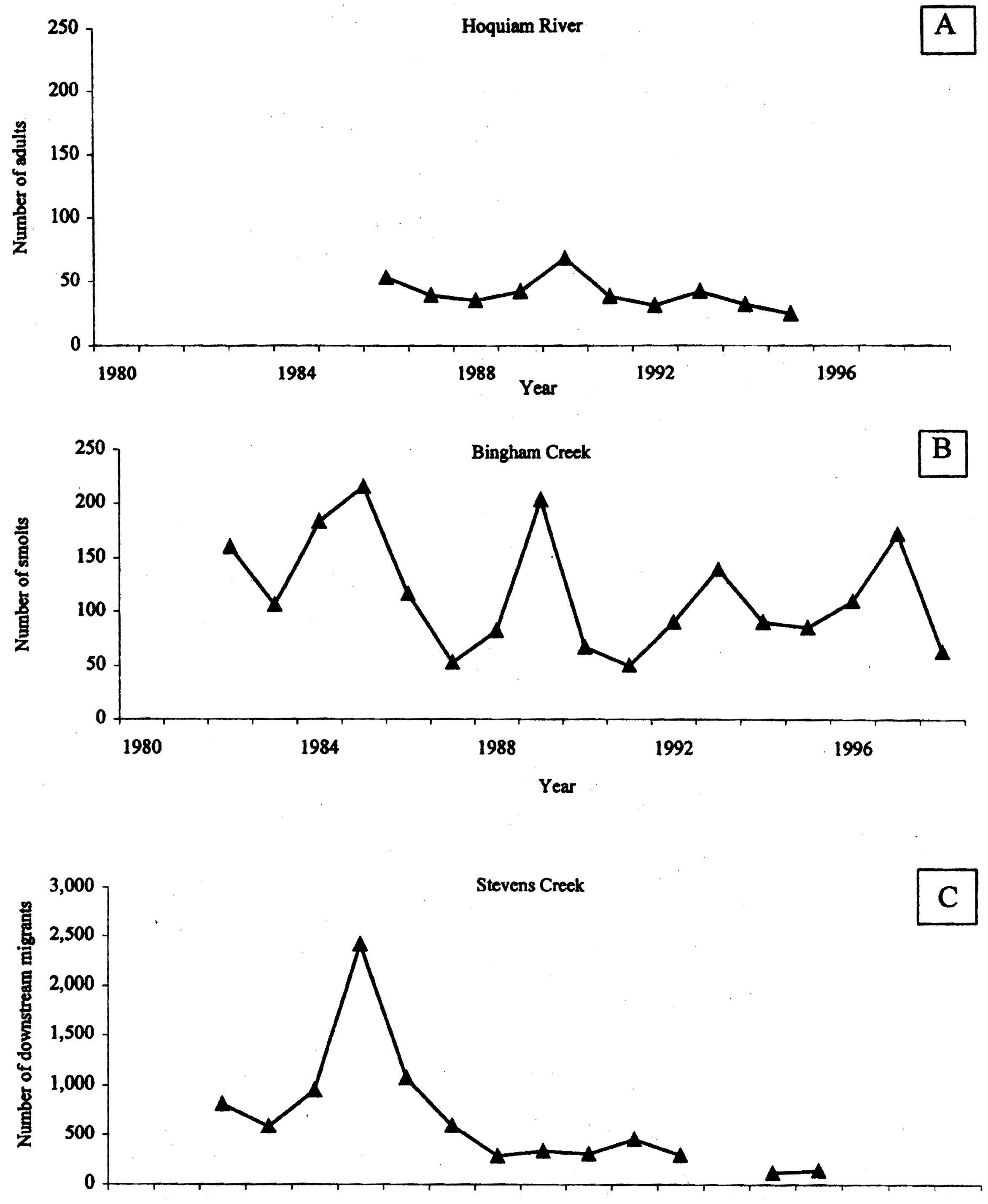

Figure 41. Numbers of coastal cutthroat trout trapped in southwestern Washington streams (WDFW 1998a). Hoquiam River adults (A) were trapped returning to the west branch of the river. Outmigrants in Bingham Creek, a tributary to the Satsop River (BE and LGL 1995) (B) and Stevens Creek (a tributary to the Humptulips River) (C) were trapped in a downstream migrant trap (Hanratty unpubl. data).

declined by 5% per year, but over the last 5 years, smolt abundance increased by 3% (Fig. 41B). WDFW (1998a) reported that the Weyerhaeuser Corporation has coastal cutthroat trout density data from more than 80 sites throughout the Chehalis River Basin, and has found that coastal cutthroat trout densities averaged 0.22-0.23 fish/m^2. These densities were higher than those found in other western Washington river drainages, such as the adjacent Willapa River Basin.

The number of anadromous adult cutthroat trout in Lower Columbia River streams is almost universally very low (Hooton 1997, WDFW 1998a) (Table 8, Fig. 42). The anadromous cutthroat trout runs in the Hood and Sandy rivers are considered to be severely depressed. Very few adults have been collected at Powerdale Dam on the Hood River—4 and 2 were collected in 1992 and 1993, respectively, and none have been collected since then except for 3 adults in 1997 (Hooton 1997, ODFW 1998). There have been no verified observations of anadromous cutthroat trout on the Sandy River in recent years (R. Hooton[19]).

The most recent 5-year geometric mean escapement of naturally produced adults in Abernathy Creek and in the Elochoman and North Fork Toutle rivers ranged from less than 1 to 5 coastal cutthroat trout (WDFW 1998a). The 5-year geometric mean abundance in the Kalama and North Fork Toutle rivers were 4 and 50 coastal cutthroat trout, respectively. The adult coastal cutthroat trout caught at the Kalama River are trapped at the falls in a trap whose spacing allows small coastal cutthroat trout to pass undetected, so the numbers are considered to be an index of abundance (WDFW 1998c). The number of coastal cutthroat trout caught at the North Fork Toutle River Fish Collection Facility is viewed as total escapement of the population following the Mt. Saint Helens eruption (WDFW 1998c). The escapement in the Cowlitz River has been higher (5-year geometric mean = 1,400 fish), but an unknown fraction of these fish are of hatchery origin. In addition, there has been a reduction in the percentage of 2-year migrants returning to the Cowlitz Hatchery from 1980-97, and the numbers of coastal cutthroat trout smolts released from the Cowlitz Hatchery have been variable but increasing over that time period (NRC 1996). Smolt-to-adult survival for Cowlitz Hatchery anadromous cutthroat trout have been 2-7% in 1991 and 1% in 1997, which are similar to estimates for wild fish: smolt-to-adult survival was 3.5% on the North Fork of the Toutle River in 1991, and it was 0.84% at Cowlitz Falls in 1997 (WDFW 1998c).

There is little information about the distribution of freshwater forms of coastal cutthroat trout in this ESU, and almost no information about relative abundances of migratory and nonmigratory freshwater forms. The WDFW (1998c) reported that observations of cutthroat trout above impassable barriers are common in a number of streams in the Lower Columbia River Basin, including the West Fork of the Elochoman River and the Cowlitz River. In their SaSI for coastal cutthroat trout, WDFW stated that there is very little information about the abundances of freshwater forms of coastal cutthroat trout in the Lower Columbia River Basin, but that their status is probably similar to that of coho salmon and winter steelhead, which are

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[19] R. Hooton, Oregon Dep. Fish. Wildl., P.O. Box 59, Portland, OR 97207. Pers. commun. to M. Ruckelshaus. Sept. 1998.

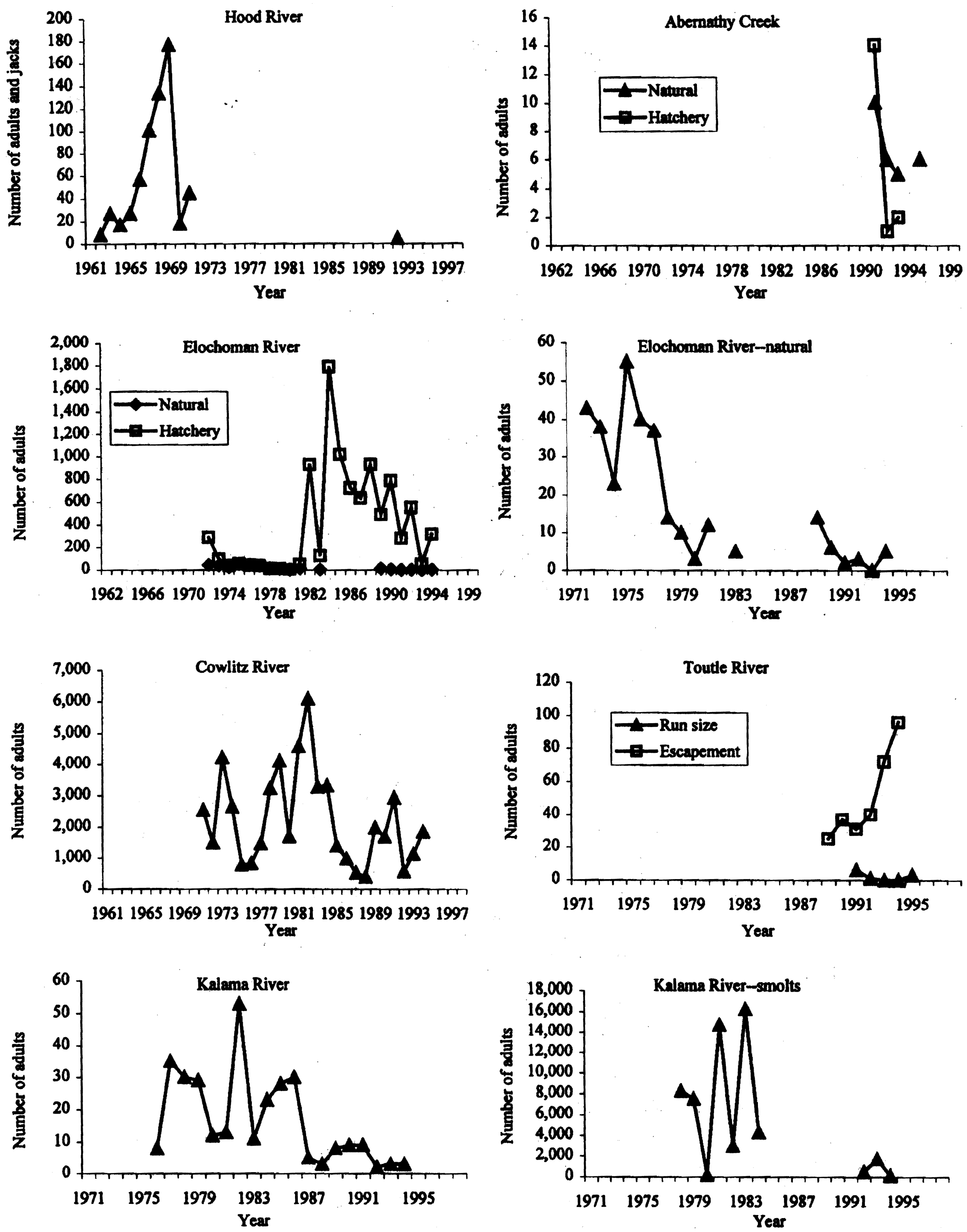


Figure 42. Number of coastal cutthroat adults and smolts in Lower Columbia River Basin streams (WDFW 1998a). Data are for escapement unless otherwise noted.

depressed (WDFW 1998a). The ODFW (1998) provided some information on the densities of coastal cutthroat trout above the anadromous zone in tributaries of the Hood River Basin. The ODFW data indicate that the freshwater form of coastal cutthroat trout does not occur in all streams sampled, but when present it can occur in fairly high densities (3-238 fish/1,000 m^2 for fish greater than 85 mm.) The BRT did not have enough information to determine how the streams sampled were chosen or how representative they were of conditions that could support local populations of coastal cutthroat trout in the Lower Columbia River Basin.

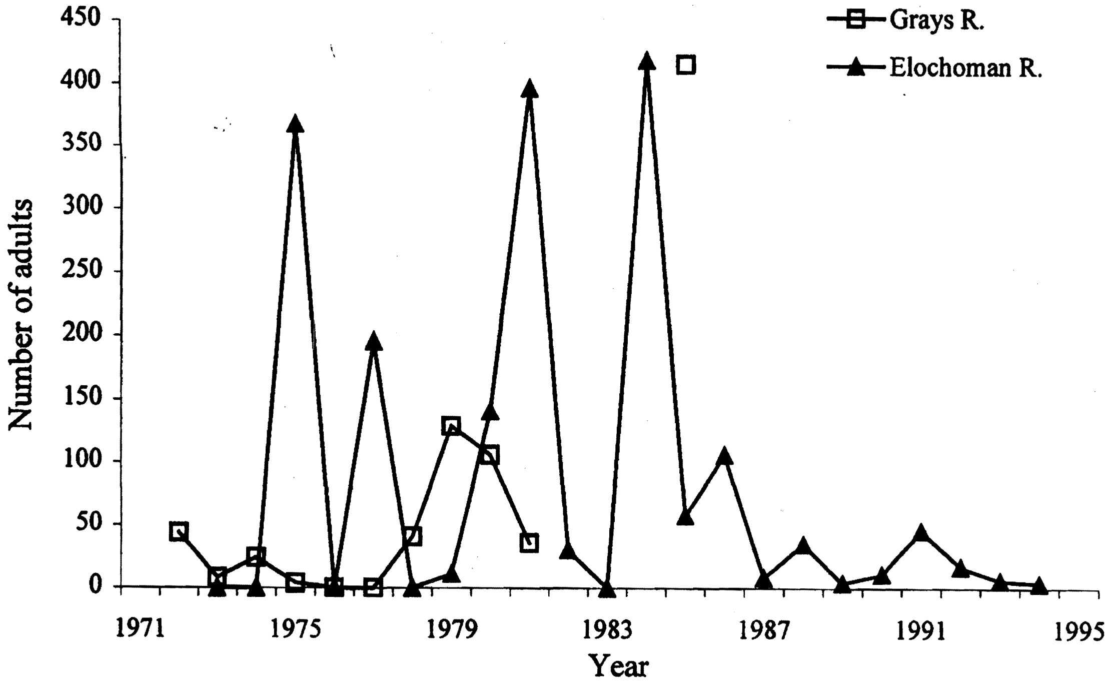
Both WDFW and ODFW provided information to the BRT indicating the possibility that freshwater forms of coastal cutthroat trout in this ESU can produce "smolts" that migrate downstream. The ODFW (1998) reported that 16-24 cutthroat trout smolts per year have been collected in a screw trap on the mainstem Hood River upstream from Powerdale Dam between 1994-98; this number can be expanded to more than 400 smolts per year after accounting for trap efficiency (ODFW 1998). The survival of these smolts after passing Powerdale Dam is not known. The WDFW (1998c) reported that a downstream migrant trap at Mayfield Dam on the Cowlitz River has captured between 60-812 smolts per year from 1978-98. There was a single release of hatchery-derived anadromous cutthroat trout above Mayfield Dam in 1981, but all cutthroat trout presently residing above the barrier are considered to be the freshwater form (WDFW 1998c). In addition, WDFW (1998c) estimated that 476-1,756 smolts were produced from the freshwater form of coastal cutthroat trout above Cowlitz Falls in 1997 and 1998. The WDFW recently has begun tagging all cutthroat trout smolts originating above Cowlitz Falls, and the otolith microchemistry was analyzed from one returning tagged fish to show that it did spend time in salt water. Additional information about the history of the population of coastal cutthroat trout above the dam was not available to the BRT. The significance of the smolt production from the freshwater form of coastal cutthroat trout depends on additional information such as how long the dam has been in place and whether there were anadromous cutthroat trout above the dam before its construction. If the freshwater form of coastal cutthroat trout above Mayfield Dam has been isolated for many generations and is still producing smolts, the potential for the freshwater form to mitigate losses in lower reaches would be greater than if the fish above the barrier have been isolated very recently. This WDFW information was received too late for discussion by the BRT, and ODFW/WDFW data lacked sufficient information for detailed BRT evaluation. Together, however, the information suggests it is possible in at least some cases for freshwater forms of coastal cutthroat trout to produce juveniles that can become anadromous, provided habitat conditions allow their survival in the lower reaches of streams and nearshore marine environments.

A number of activities have reduced habitat quantity and quality in the Lower Columbia River Basin. For example, water development projects on the Willamette and Sandy rivers and in smaller creeks in the Lower Columbia River Basin have resulted in numerous barriers that are impassable by anadromous salmonids, reducing the amount of available habitat (Kostow 1995). Dewatering below Marmot Dam on the Sandy River between 1910 and 1970 probably contributed to reduced population size of the anadromous run in that river. In addition, Kostow (1995) stated that habitat impacts due to logging activities probably have led to declines in coastal cutthroat trout population productivity in Lower Columbia River tributaries downstream of the Willamette River.

Trends in anadromous cutthroat trout abundance for Lower Columbia River streams are all negative (ranging from 5 to 11% per year declines) with the exception of fish returning to the North Fork Toutle River collection facility, which have increased by nearly 30% per year since the late 1980s decimation by the Mount Saint Helens eruption (WDFW 1998a). In addition to declines in naturally produced coastal cutthroat trout populations, hatchery populations in Abernathy Creek and the Elochoman River also have been declining precipitously over the past 6-10 years (20-60% declines). Trends in incidental catch of coastal cutthroat trout in steelhead and salmon recreational fisheries in the Lower Columbia River are similar to long-term trends estimated from escapement to streams (StreamNet 1998) (Fig. 43). The recreational catch of coastal cutthroat trout in the Lower Columbia River was approximately 5,000 fish per year in the 1970s; by the late 1980s, the catch had declined to approximately 500 per year (Kostow 1995). These catch data are not a good indication of the absolute numbers of coastal cutthroat trout since there is not good information on changes in fishing effort over the duration of the data set for this recreational fishery targeting Pacific salmon and steelhead (WDFW 1998a).

Trends in smolt abundance in the Kalama River have shown a 16% decline per year since 1978. Smolt counts in the Kalama River peaked at just over 16,000 fish in 1983 but were just over 100 in 1994. These smolt estimates are based on trapped fish in a fyke net at Kalama Falls and the trap efficiency for cutthroat was assumed to be the same as that for steelhead. Due to variation in trap efficiency, these numbers are considered to be crude estimates of total smolt production for this portion of the Kalama River (WDFW 1998c).

No information on the percentage of hatchery coastal cutthroat trout in natural spawning escapements in the Southwestern Washington/Columbia River ESU was available to the BRT. Estimates of the percentage of hatchery coastal cutthroat trout in Lower Columbia River sport catch range from 50-80% between 1979 and 1982 (WDFW 1998a). There is some information on the numbers and origin of hatchery coastal cutthroat trout released into streams in this region (see "Artificial Propagation," p. 113), that indicates potential risks due to interactions with hatchery coastal cutthroat trout. Coastal cutthroat trout released from the Beaver Creek Hatchery in the Lower Columbia River have been documented to have stray rates of up to 30% in Lower Columbia River tributaries (Hisata 1973, Randolph 1986). In addition, a shift in spawn timing of natural coastal cutthroat trout in the Elochoman River after the early 1970s reflected the spawn timing of the hatchery coastal cutthroat trout released in that river (Randolph 1986), suggesting that hatchery fish comprised a large fraction of the total run returning to the Elochoman River (see "Artificial Propagation," p. 113). Leider (1997) reported that approximately 75% of the total Washington state coastal cutthroat trout hatchery effort is concentrated in the Lower Columbia River area. Anadromous cutthroat trout hatchery releases continue in the Elochoman, Cowlitz, Washougal, and North Fork Lewis River Basins and in several creeks that drain directly into the Lower Columbia from the Washington side (WDFW 1998a). Hatchery plants of the freshwater form of coastal cutthroat trout occur in four streams above anadromous areas: Tilton River,



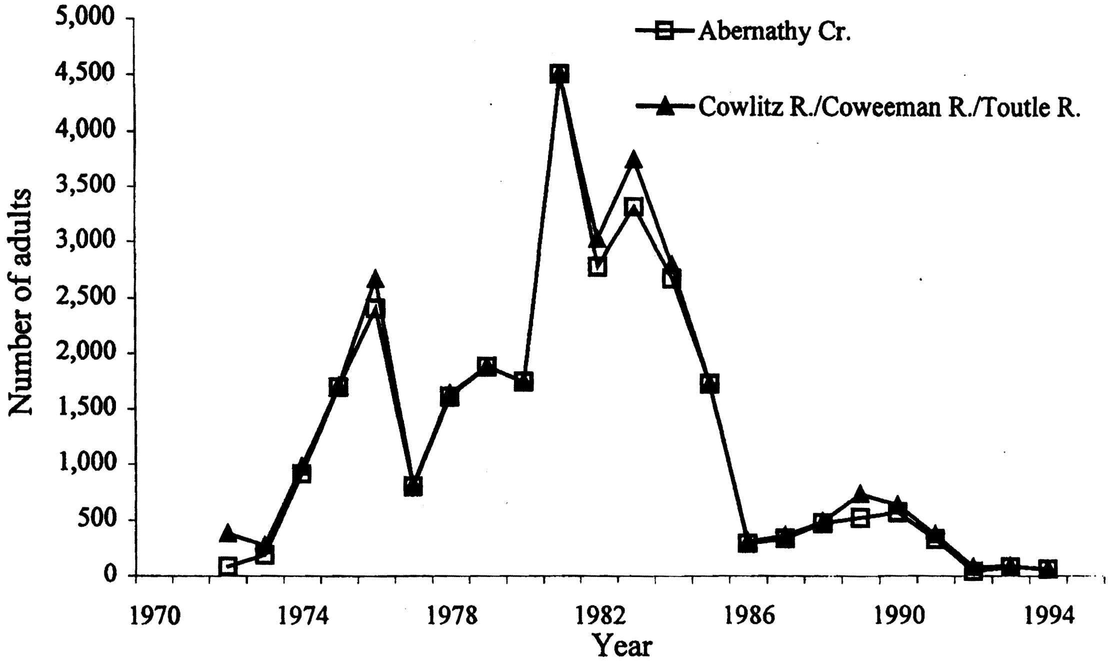


Figure 43. Catch of coastal cutthroat trout in recreational fisheries in the Lower Columbia River Basin (WDFW 1998a).

Skate, and Canyon creeks, and Little White Salmon River (WDFW 1998c). In addition, releases of hatchery coho salmon and steelhead continue to occur in a number of streams in this region.

Upper Willamette River ESU

Counts are available for the freshwater form of coastal cutthroat trout in a few tributaries in the Willamette River Basin (Hooton 1997). Biologists familiar with coastal cutthroat trout in this region have argued that streams in the Willamette River Basin support only the freshwater form of coastal cutthroat trout (both river migrating and nonmigrating) (Dimick and Merryfield 1945, Moring and Youker 1986, ODFW 1998). The ODFW (1998) has provided the BRT with several data sets supporting the idea that uniquely large populations of the river-migrating form occur in the mainstem areas of the Willamette River and its tributaries. Increasing numbers of coastal cutthroat trout have been documented by seining in three sites in the mainstem Willamette River between Corvallis and the mouth of the McKenzie River (RKm 132-175) from 1992-98. The numbers of coastal cutthroat trout longer than 60 mm caught per seine set ranged from 0.2 to 8 fish. Over the 7 years of sampling, the numbers of fish caught increased by 11% to83% per year, depending on the location (ODFW 1998). Some of this increase is due to increase in sampling efficiency (ODFW 1998). In addition, population indices for coastal cutthroat trout in the lower McKenzie River were estimated using electrofishing from1988-93 (ODFW 1998). The estimated number of river-migrating coastal cutthroat trout per mile of shoreline ranged from 113 to 333 fish per mile for fish greater than 20 cm.

Combined counts of coastal cutthroat trout and rainbow trout (15-31 cm) in index pools in the North Fork of the Middle Fork Willamette River increased between 1975 and 1991, and the counts have remained stable since then. The abundance of juvenile coastal cutthroat trout (age-1 and -2+) in an index reach of Dead Horse Canyon Creek, a tributary of the Molalla River was stable from 1981-91. Scattered sampling of the freshwater form of coastal cutthroat trout in the Santiam and McKenzie river basins in the late 1970s to early 1980s indicated that densities of all age classes combined ranged from 61 to 2,200 fish per km.

The ODFW (1998) also provided the BRT with summary information from two studies conducted in the early 1980s that estimated coastal cutthroat trout densities in streams of the Coast Range subbasin of the Willamette River. Numbers of coastal cutthroat trout ranged from 166 fish/mile in the North Yamhill River to more than 1,700 fish/mile in the Little Luckiamute River Basin.

Biologists with the ODFW (ODFW 1998) believe that the freshwater form of coastal cutthroat trout above Willamette Falls is not likely to contribute substantially to the abundance of the anadromous form in the lower Willamette River Basin. They cite two reasons for this belief: (1) very few downstream-migrating coastal cutthroat trout have been counted at the Willamette Falls bypass facility, and (2) the presence of *Ceratomyxa shasta* in the lower Willamette River below the confluence of the Marys River is thought to effectively block downstream migration of freshwater coastal cutthroat trout because of their susceptibility to this parasite (ODFW 1998).

In summary, available information indicates that this ESU produces few, if any, anadromous cutthroat trout. Information on upper Willamette River populations developed as part of this status review will be provided to USFWS, which has jurisdiction under the ESA for freshwater fish populations.

Oregon Coast ESU

Estimates of adult abundance in the Oregon Coast ESU were available for only a few streams (Table 8, Fig. 44). The most extensive data indicating abundance of adult coastal cutthroat trout in this ESU are the counts of adults at Winchester Dam on the North Umpqua River (StreamNet 1998, ODFW 1998). These data are summarized at the end of this section providing an overview of information regarding risk to the Umpqua River coastal cutthroat trout. Fisheries biologists familiar with coastal cutthroat trout in Oregon believe that coastal populations by the early 1980s had probably already suffered significant declines due to reduction in habitat quality and quantity (Kostow 1995, Hooton 1997). Habitat degradation and increases in stream temperatures have been noted in many small tributaries in the Oregon coastal region (Kostow 1995). In addition, dam counts for several Pacific salmon species on the North Umpqua River indicate consistent declines in abundance beginning in the late 1950s (StreamNet 1998).

Information on trends in coastal cutthroat trout abundance is available for a number of streams along the Oregon coast (Table 8). Catch-per-unit-effort (CPUE) data for coastal cutthroat trout > 200 mm and those between 100-200 mm in the South Coos and Millicoma rivers were variable from 1978 to the present. There is no consensus among biologists about an appropriate size cutoff for smolts and adults in coastal cutthroat trout (ODFW 1998, WDFW 1998c), and the size-stage relationship undoubtedly varies by region. The size categories reported in the South Coos and Millicoma rivers represent a mixture of life stages. The numbers of larger fish have been declining over the past 5 years in both rivers, but the trends are highly variable (StreamNet 1998) (Fig. 45).

Trends in outmigrating juvenile (> 90 mm) and smolt (> 160 mm) abundance in Tenmile and Cummins creeks have been stable or positive from 1992 to the present (Johnson unpubl. data) (Fig. 46). These numbers were corrected for efficiencies of screw traps operated on these streams. The ODFW believes the outmigrants > 160 mm are anadromous because they show definite smolting characteristics (silvering, loss of condition) and because the traps are essentially at the mouths of these small creeks that drain directly into the ocean (S. Johnson[20]). In addition to the juvenile and smolt data, ODFW also has been monitoring immigrant adults in Tenmile Creek for the last 2 years from late June through mid-September: 15 and 38 adult cutthroat returned to Tenmile Creek in 1996 and 1997 respectively (Johnson unpubl. data). Additional adult cutthroat may have returned to Tenmile in late September through November when fall freshets forced the removal of the weir (ODFW 1998). The average size of these

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[20] S. Johnson, ODFW, 2040 SE Marine Science Drive, Newport, OR 97365. Pers. commun. to M. Ruckelshaus. July 1998.

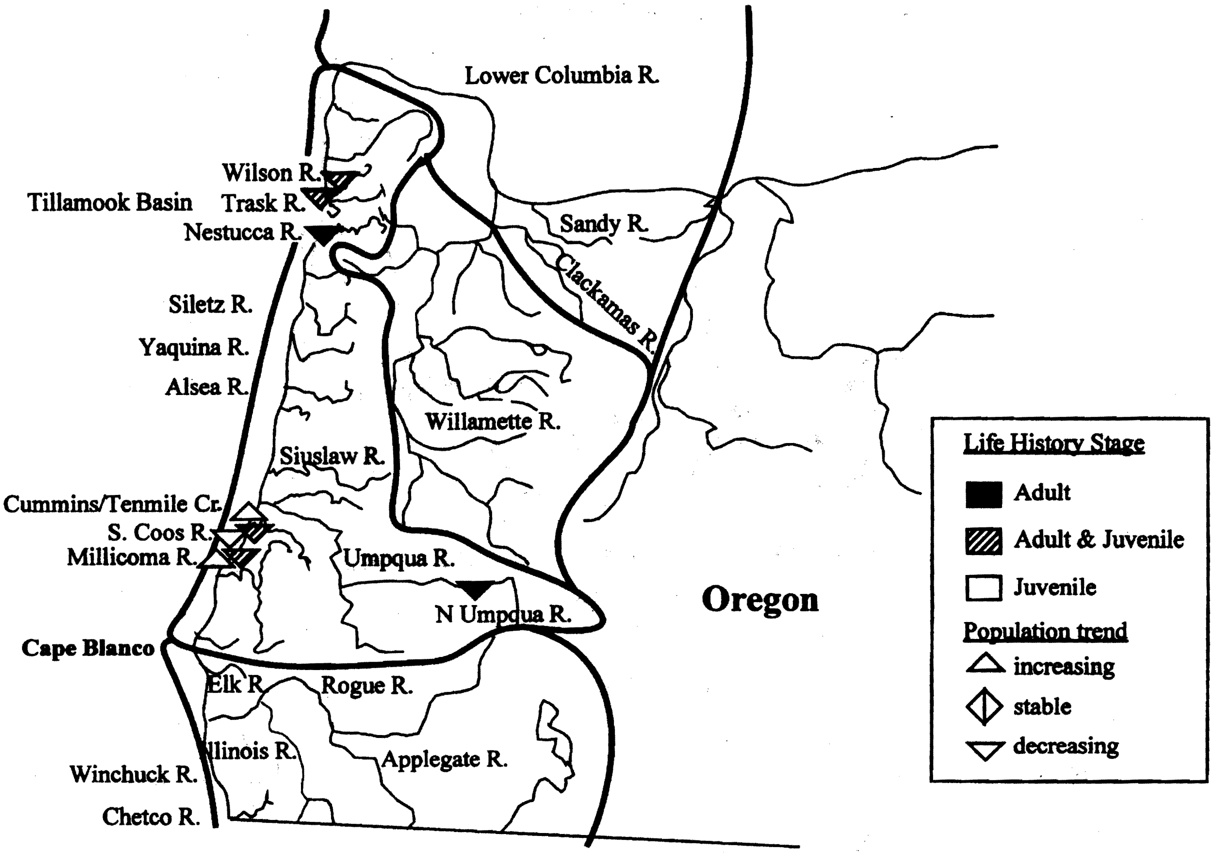

Figure 44. Trends for coastal cutthroat trout in the Oregon portion of the Southwestern Washington/Columbia River Evolutionarily Significant Unit (ESU), the Upper Willamette River, and Oregon Coast ESUs, and the Oregon portion of the Southern Oregon/California Coasts ESU (ODFW 1998, StreamNet 1998).

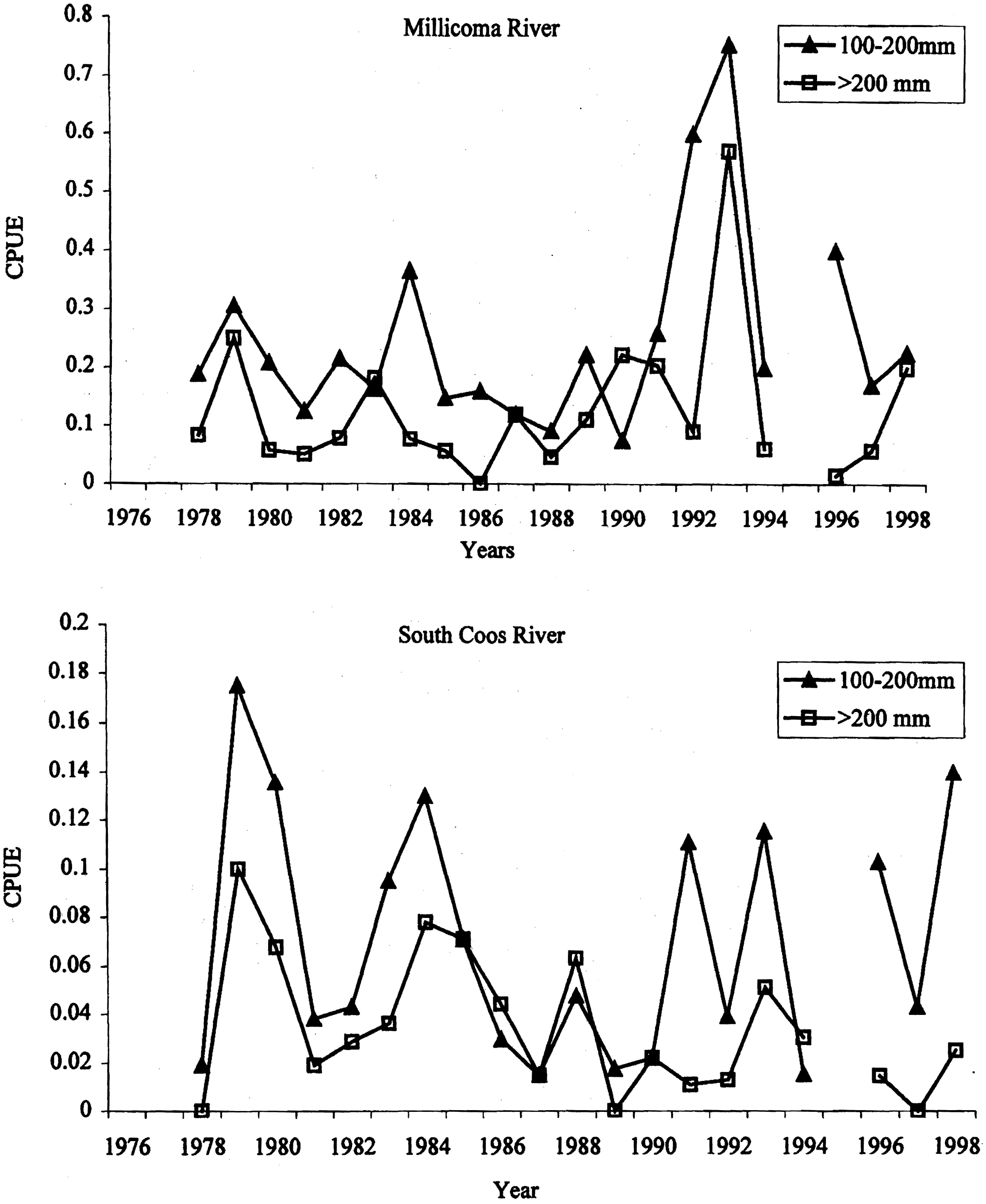

Figure 45. Catch-per-unit effort (CPUE) (number of fish-per-seine haul) of coastal cutthroat trout in the Millicoma and South Coos rivers (ODFW 1998).

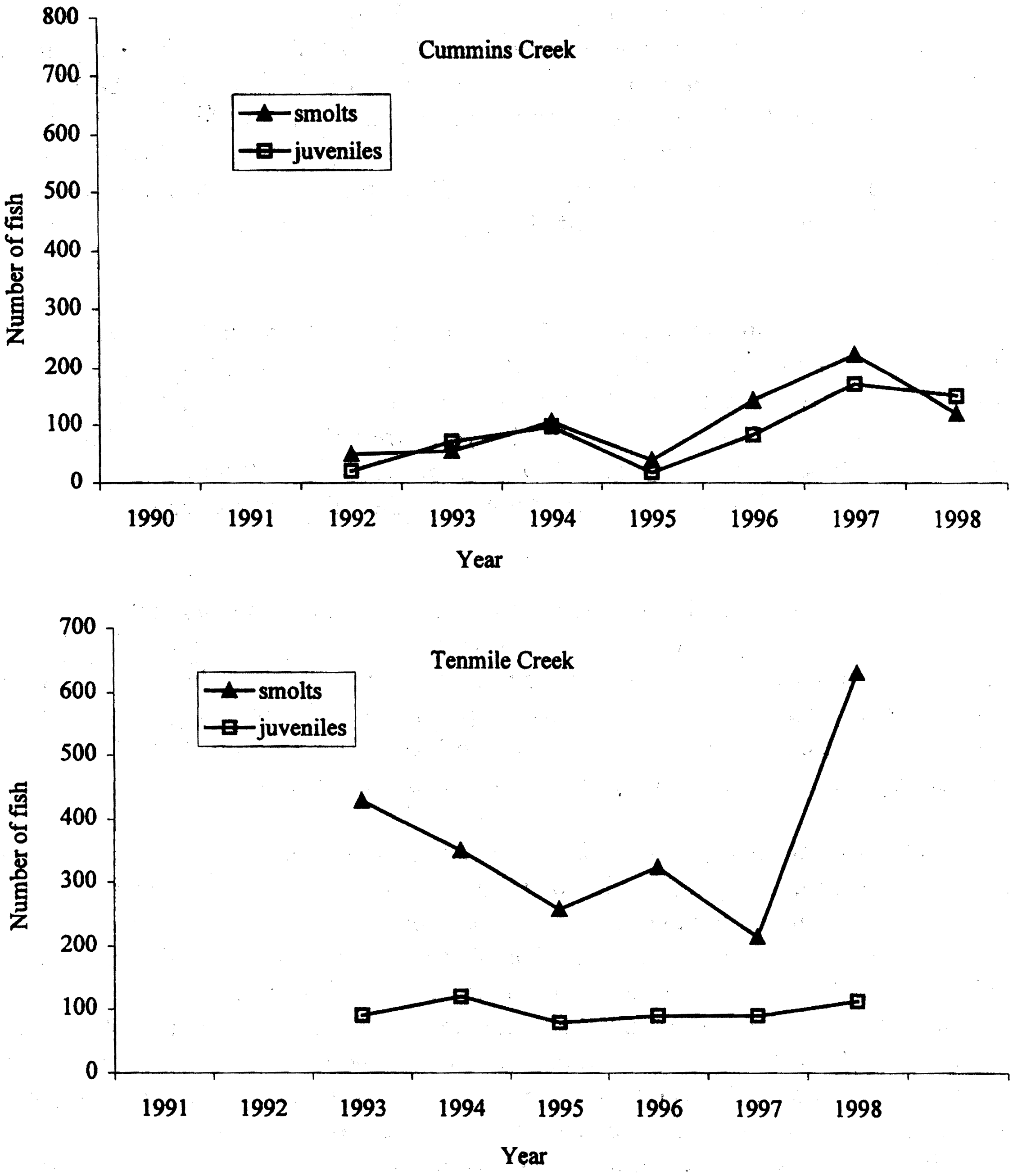

Figure 46. Numbers of smolt and juvenile coastal cutthroat trout trapped in two central Oregon coastal streams (Johnson unpubl. data).

returning adults was similar between years (325 and 332 mm in 1996 and 1997), and these lengths were similar to those reported by Giger (1972) for cutthroat returning for their initial spawning migration in several Oregon coastal rivers from 1965-70. Finally, ODFW reported that scale samples collected from the adults returning to Tenmile Creek in 1996 and 1997 indicated a survival rate of 6% for coastal cutthroat trout between their first and second years of spawning (Johnson unpublished data). In contrast, Giger (1972) estimated a 14-39% survival rate for coastal cutthroat trout during the same life-history transition in Oregon coastal streams in the 1960s and 1970s.

Resting hole count data indicating trends in adult population sizes are available for three central Oregon coast streams (Table 8). Snorkel surveys in 12 standard pools in the Nestucca, Trask, and Wilson rivers from 1965-95 indicated that the mean number of anadromous cutthroat trout per pool declined during the more than 30-year period (StreamNet 1998) (Fig. 47). Updated resting hole count data through 1998 were provided to NMFS for these three rivers. These data were received too late for consideration by the BRT, but are reported in Table C-1 (Appendix C).

The ODFW began its Life-Cycle Monitoring Project in 1998 in a number of coastal Oregon streams. Estimates of the number of downstream-migrating juvenile coastal cutthroat trout from trapping data are available for the first year of this program (Johnson unpubl. data). Numbers of fish greater than 160 mm migrating past the traps in 1998 ranged from 140-780, and the numbers of coastal cutthroat trout smaller than 160 mm ranged from 400-2,200. Numbers of outmigrating juveniles roughly corresponded with total watershed size.

Additional information on trends in adult and juvenile coastal cutthroat trout abundance is available in a report compiled by Hooton (1997). The BRT did not have the actual data for review from these studies, but the trends were considered in the BRT's deliberations on risks facing the Oregon Coast ESU, and results from these studies are summarized here. Hooton (1997) reported the number of coastal cutthroat trout per pool from several central Oregon coastal streams over a 10-year period; the trends were relatively stable from 1980-90. In addition, catch of coastal cutthroat trout in recreational fisheries was reported for the Siuslaw, Alsea, and Yaquina river basins (Hooton 1997). In some instances, changes in angler effort were known, helping to interpret data on angler catch. In other cases, no information was available on angler effort during the time period for which angler catch data were collected. Catch of anadromous cutthroat trout has declined dramatically in all river systems except the Yaquina River. In some river systems, the recreational catch data showed strong declines despite increases in hatchery coastal cutthroat trout releases. Hooton concluded "that abundance of wild coastal cutthroat trout has declined significantly and that this trend is reflected in reduced angler effort, a lower percent return of hatchery fish to angler creels, and dramatically lower catches of wild coastal cutthroat trout" (Hooton 1997, p. 11). Declining trends in anadromous cutthroat trout in recreational fisheries in the Siuslaw and Alsea river basins were not matched by declines in abundance of nonmigratory coastal cutthroat trout (Hooton 1997). Hooton (1997) cited several ongoing studies and field observations of nonmigratory coastal cutthroat trout populations, indicating that their status in these river basins is relatively stable.

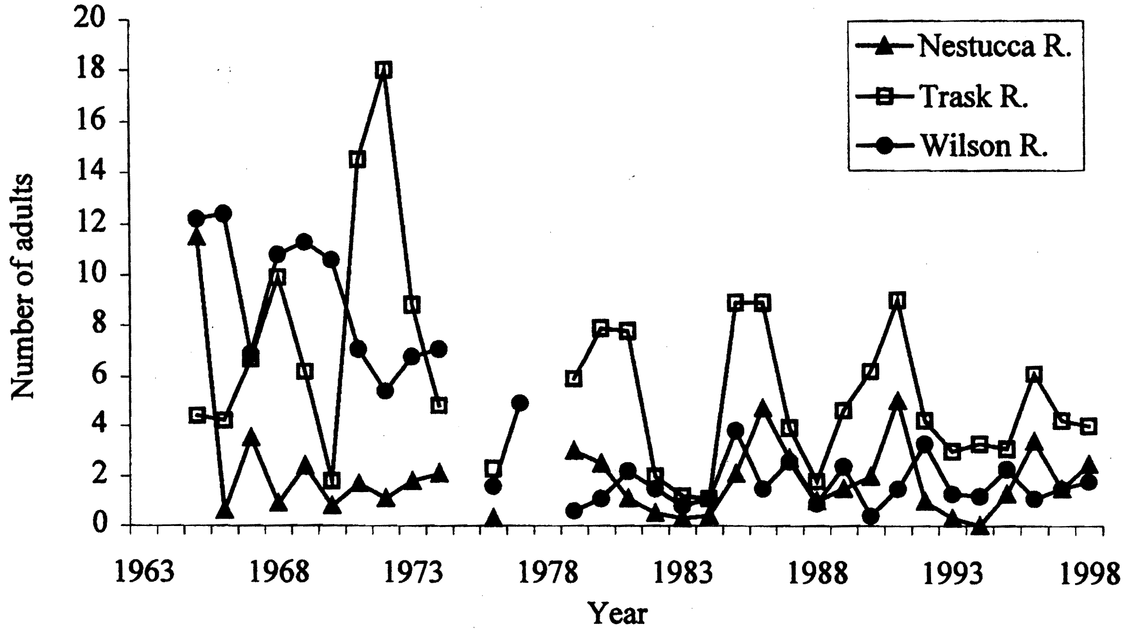

Figure 47. Resting hole counts of coastal cutthroat trout adults in the Nestucca, Trask, and Wilson rivers on the Oregon Coast. The average number of adults in resting holes in index reaches for each river are shown (ODFW 1998, StreamNet 1998).

No information on the percentage of hatchery coastal cutthroat trout in natural spawning escapements in the Oregon Coast ESU was available to the BRT. There is some information on the numbers and origin of hatchery coastal cutthroat trout released into streams in this region (see "Artificial Propagation" section, p. 113), which indicates the potential risks due to interactions with hatchery coastal cutthroat trout. Relative to other coastal cutthroat trout ESUs, the numbers of hatchery smolts released in Oregon coastal streams over the last few decades are high. A factor potentially aggravating this risk is that a single source population, the Alsea River broodstock, was the primary one used for most of the hatchery coastal cutthroat trout released in this region. Coastal cutthroat trout from several streams within the Coquille River drainage are closely genetically related to Alsea River broodstock (see "Genetic Information" section, p. 70), indicating either that introgression between hatchery and natural coastal cutthroat trout has occurred, or that hatchery coastal cutthroat trout have displaced naturally produced native coastal cutthroat trout in those streams. Releases of hatchery coastal cutthroat trout were stopped in Oregon coastal streams by 1997 and, in many streams, much earlier (see "Artificial Propagation" section, p. 113). Releases of hatchery coho salmon and steelhead continue to occur in a few Oregon coastal streams.

The Umpqua River sea-run cutthroat trout status review included a risk assessment of coastal cutthroat trout in this river drainage up through 1993 (Johnson et al. 1994). The abundance of coastal cutthroat trout at Winchester Dam was variable from 1946-74, peaking at almost 2,400 fish. After 1974, a severe decline in abundance occurred (StreamNet 1998) (Fig. 48). Abundance of coastal cutthroat trout at the dam ranged from 0-53 fish between 1986 and 1994; in 1995-98, increases occurred (79, 81, 91, and through November 15, 1998, 135—the most since 1982) (ODFW 1998; Loomis footnote 3). As noted in the original Umpqua River sea-run cutthroat trout status review, there is no way to confirm what proportion of the coastal cutthroat trout passing Winchester Dam have been or will be anadromous (Johnson et al. 1994). There has been extensive discussion about the possible causes of the dramatic fluctuations and recent declines in coastal cutthroat trout numbers in the North Umpqua River (reviewed in Johnson et al. 1994, Hooton 1997). Possible factors contributing to variation in the numbers of coastal cutthroat trout at Winchester Dam include shifts in freshwater and marine/estuarine environmental conditions, changes in counting methods at the dam, and releases of hatchery coastal cutthroat trout in the North Umpqua River. An estimate of the historical abundance of coastal cutthroat trout in the Umpqua River Basin suggested that the population size was approximately 30,000 fish before the 1970s (Lauman et al. 1972).

Snorkel surveys were conducted in 1997 in small channel streams in each of the three main drainages within the Umpqua River Basin (Cramer 1998). Numbers of cutthroat trout (> 20 cm) per unit of stream sampled (a unit = one each of a contiguous pool, riffle, and glide) were 0.059 in the North Umpqua River Basin, 0.215 in the South Umpqua River Basin, and 0.280 in the lower Umpqua. These numbers were expanded to produce total estimated abundances of 2,900 coastal cutthroat trout in the North Umpqua, 12,100 in the South Umpqua, and 17,900 in the lower Umpqua. Cramer (1998) believed these fish were not likely to be anadromous since the snorkel surveys were conducted during the summer when sea-run cutthroat typically are feeding in marine or estuarine habitats. A different picture of the status of coastal

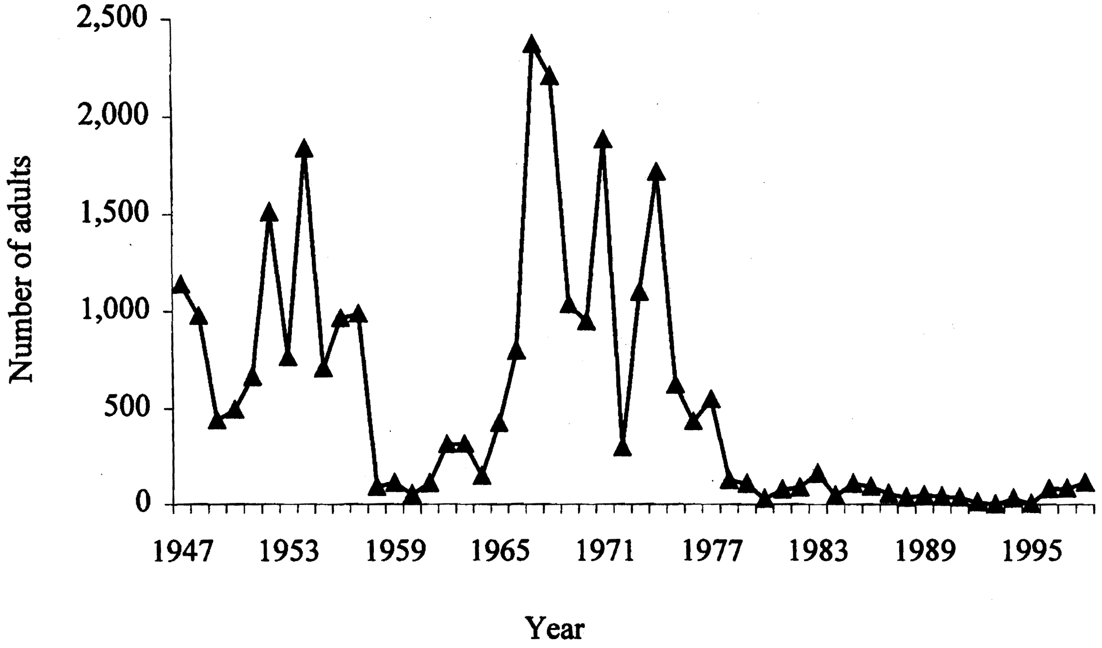

Figure 48. Numbers of adult coastal cutthroat trout counted at Winchester Dam on the North Umpqua River, Oregon (ODFW 1998, StreamNet 1998).

cutthroat trout in the South Umpqua River Basin was provided in information in Kruzic (1998a) and Roper (1995). In downstream migrant traps in the upper basin, only 14 juvenile and adult coastal cutthroat trout were trapped in total during 1991-96 (Kruzic 1998b). Trap efficiencies for coastal cutthroat trout were not calculated because of the low sample sizes, but coastal cutthroat trout that were marked indicated trap efficiencies roughly equivalent to those for coho and chinook salmon juveniles (Kruzic 1998b). In contrast to coastal cutthroat trout abundances in smolt traps, coho and chinook salmon and steelhead numbers were more than 1,000 a year from 1991 to 1996 (Kruzic 1998b). Densities of coastal cutthroat trout in the mainstem and tributaries were low or zero, which is in stark contrast to abundant cutthroat reported in Roth (1937). Kruzic (1998a) and Roper (1995) also found that the distribution of coastal cutthroat trout was not uniform in the South Umpqua River Basin—they occur primarily in headwater tributaries. Finally, Roper (1995) found that stream habitat within the South Umpqua River Basin has been degraded due to timber harvest and road construction, leading to a reduction in instream habitat complexity and a deleterious shift in stream temperature profiles.

Southern Oregon/California Coasts ESU

Information on adult coastal cutthroat trout abundance is available for only a few streams in the California portion of this ESU (Table 8, Fig. 49). Historical estimates of abundance of coastal cutthroat trout in the entire Smith River Basin were 8,500 fish (Gerstung 1998). Expansions from snorkel surveys of index reaches in the three major forks of the Smith River suggest that approximately 100-400 adult coastal cutthroat trout (> 25 cm) occurred in each of the North, Middle and South forks of the Smith River (McCain unpubl. data) (Fig. 46). The trends in abundance as indicated by these expansion estimates were positive, increasing 1-5 % annually from 1982 through 1998. Thorough surveys of coastal cutthroat trout presence/absence in a number of streams in the lower Klamath River have found coastal cutthroat trout to be widely distributed in a number of tributaries (Voight and Gale 1998, Yurok Tribal Fisheries unpubl. data). Index counts from snorkel surveys on Blue Creek, a tributary to the lower Klamath River, have found fall peak weekly counts of 10, 32, and 21 adult coastal cutthroat trout from 1995-97, respectively (Fig. 50) (Gale 1998). Fisheries biologists familiar with this area do not believe the adults in Blue Creek are spawning there, due in part to consistently negligible counts of smolts (D. Gale[21]).

Electroshocking data from a number of streams in California suggest that densities of juvenile or smolting coastal cutthroat trout (50-200 mm) are consistently between 15 and 30 fish per kilometer of stream below barriers to anadromy (Gerstung 1998). Densities of coastal cutthroat trout in the same size range above barriers were much higher, ranging from 60-400 fish per kilometer of stream. Adult densities below barriers to anadromy in the Smith River were 3-12 coastal cutthroat trout per kilometer, and 6-12 adults per kilometer were found in the Little River (Gerstung 1998). The exception to these density patterns is in Redwood Creek, where there were only 0.5 adults per kilometer of stream below barriers to anadromous fish (Fig. 50).

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[21] D. Gale, Yurok Tribal Fisheries Program, 15900 Highway 101 North, Klamath, CA 95548. Pers. commun. to M. Ruckelshaus. Nov. 1998.

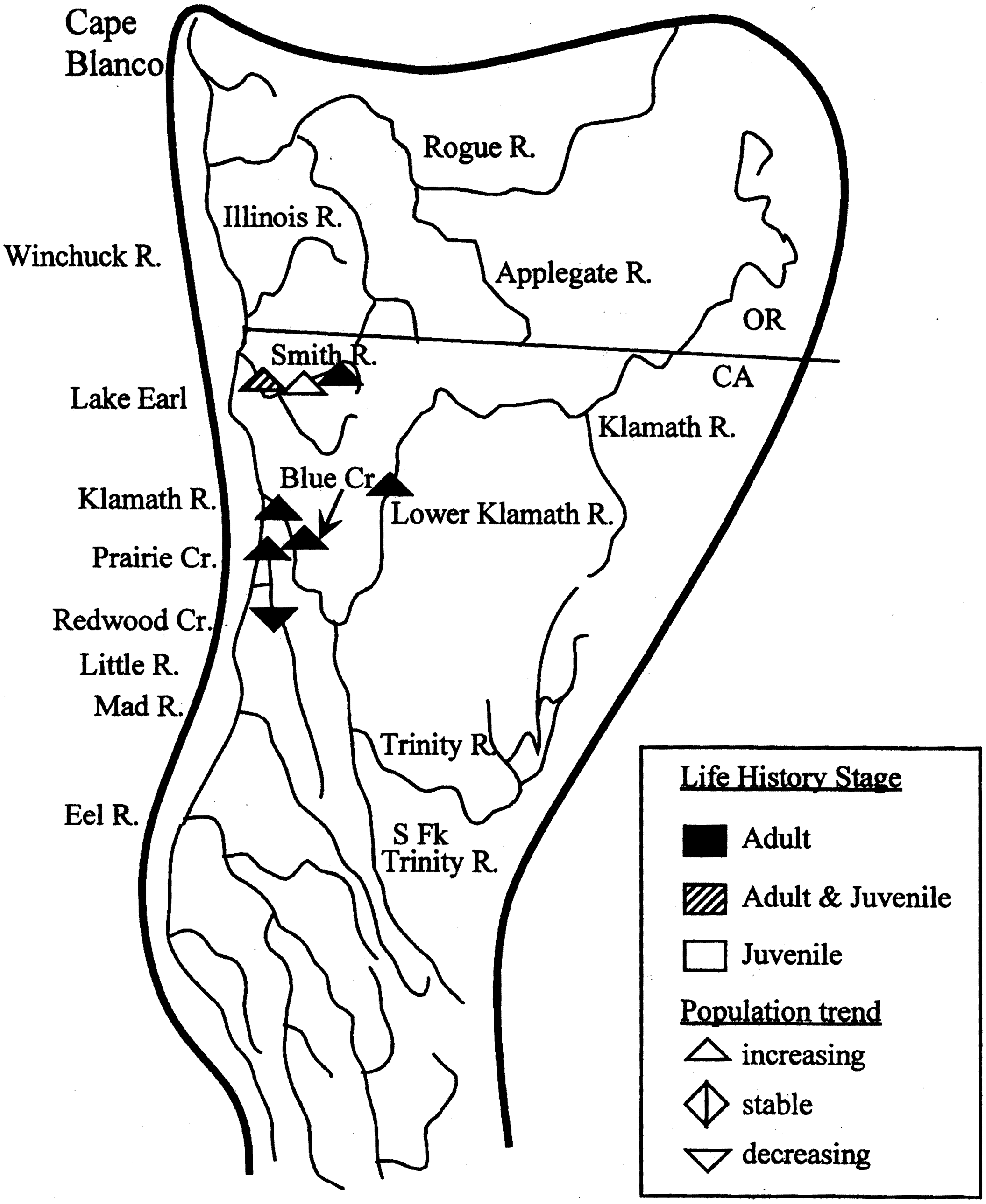

Figure 49. Trends and life-history stages for coastal cutthroat trout in the Southern Oregon/California Coasts Evolutionarily Significant Unit (ESU) (Howard and Albro 1995, 1997; Gale 1998; Gerstun 1998; McCain unpubl. data).

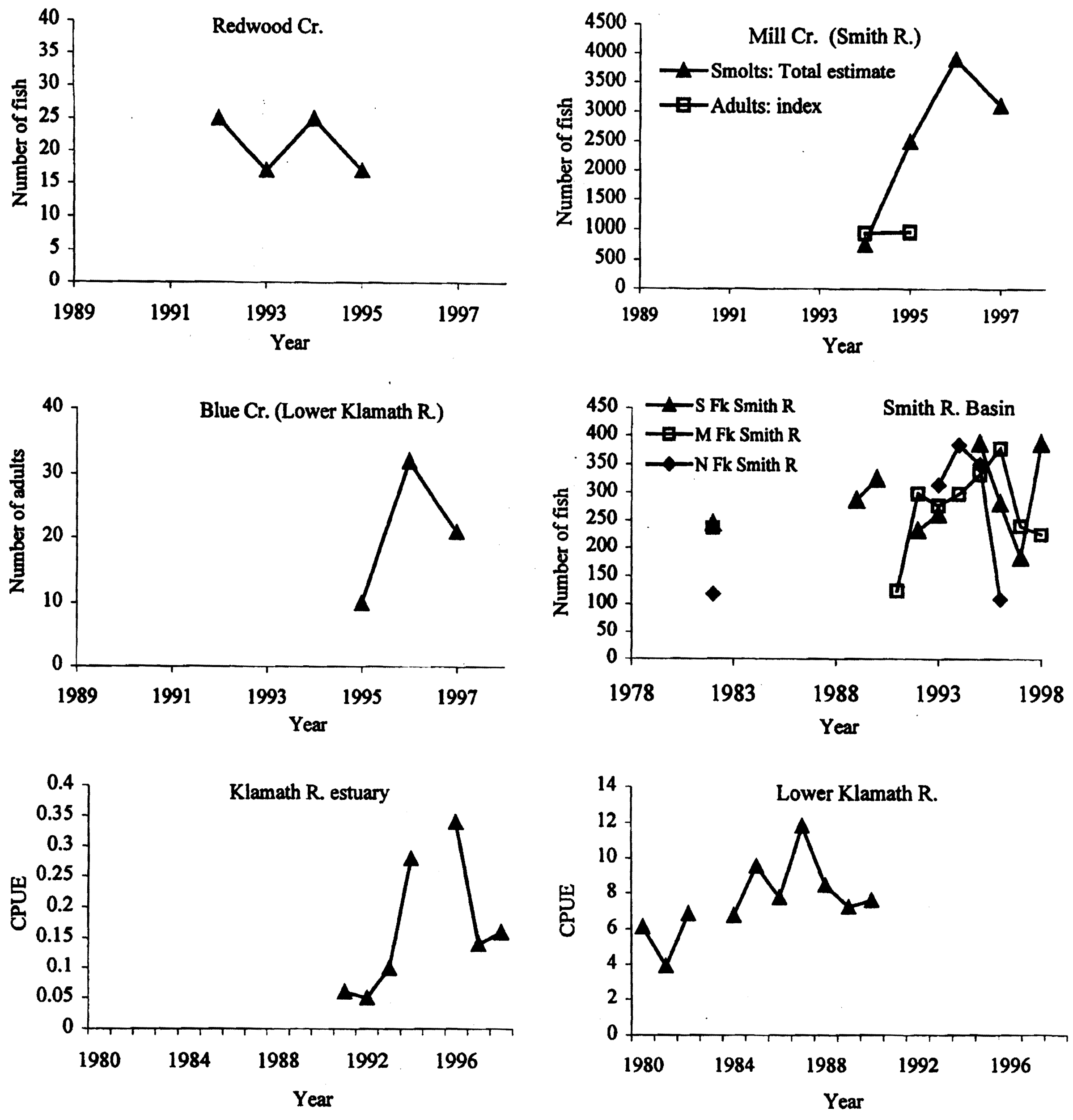

Figure 50. Number of coastal cutthroat trout adults and smolts sampled in California streams. Numbers in the Smith River Basin (McCain unpubl. data) and Redwood Creek (Gerstung 1998) are expansion estimates from snorkel surveys on index reaches. Blue Creek data are peak counts from weekly index-area snorkel censuses (Gale 1998). Catch-per-unit effort (CPUE) in the Klamath River estuary is the mean number of coastal cutthroat trout caught per minute in boat electrofishing (Gerstung 1998).

Contributing to the low densities of coastal cutthroat trout is the sharp decline in freshwater and estuarine habitat quality in Redwood Creek over the last decade (Gerstung 1998). In addition, the once-productive coastal cutthroat trout recreational fishery in the Redwood Creek drainage is no longer active (Gerstung 1998).

Smolt abundance numbers for the Winchuck River have declined over the past 3 years (2,800, 1,990, and 1,400 smolts trapped during 1996-98, respectively), but the variation in these numbers is so high that the trend is not statistically significant (Confer unpubl. data). Errors due to trap efficiencies and the very short time period over which these data have been collected make it difficult to weigh these data very heavily in risk determinations. Coastal cutthroat trout sampled in a downstream weir on Jack Creek, a tributary to the Chetco River, were stable in numbers from 1989-91, ranging from 643-667 total coastal cutthroat trout trapped (Confer unpubl. data). The BRT has only one estimate of smolt abundance in the Rogue River: from March-May 1998, a downstream migrant trap on Lobster Creek, a tributary to the lower Rogue River, caught 146 smolts, 66 juveniles and 4 adult coastal cutthroat trout (Confer unpubl. data). Correcting for trap efficiency, ODFW biologists estimated that 838 coastal cutthroat trout smolts migrated past the trap. Fisheries biologists familiar with coastal cutthroat trout in the Rogue River Basin believe that, although the mainstem is undersampled, the fish are fairly well distributed in the Rogue River. There used to be a substantial recreational coastal cutthroat trout fishery in the Rogue River, suggesting that the abundance of coastal cutthroat trout in the basin was probably fairly high (T. Confer, pers. commun.[22]).

Smolt abundance from Mill Creek, a tributary to the Smith River, has increased since 1994 (Howard and Albro 1995, 1997) (Table 8, Fig. 50). Estimated smolt numbers in this highly productive tributary ranged from 750 to nearly 4,000 fish over the 4-year sampling period. Estimates of coastal cutthroat trout smolt abundance in McGarvey (n=3,615) and Hunter (n=706) creeks in the lower Klamath River in 1997 were encouraging (Gale 1998). Catch-per-unit-effort data from the lower Klamath River between 1980 and 1991 showed a variable but relatively stable trend in the number of cutthroat caught per seine haul (Gerstung 1998) (Fig. 50). In contrast, electrofishing data from the Klamath River estuary indicated a dramatic increase in the mean number of coastal cutthroat trout caught per minute between 1991 and 1998 (Gerstung 1998) (Fig. 50).

No information on the percentage of hatchery coastal cutthroat trout in natural spawning escapements in the Southern Oregon/California Coasts ESU was available to the BRT. There is some information on the numbers and origin of hatchery coastal cutthroat trout released into streams in this region (see "Artificial Propagation," p. 113), which indicates the potential risks due to interactions with hatchery coastal cutthroat trout. Relative to other coastal cutthroat trout ESUs, the numbers of hatchery smolts released in southern Oregon and California coastal streams over the past few decades was very low. Hatchery coastal cutthroat trout releases into streams in the Oregon portion of this ESU were terminated during the mid-1980s. The Prairie Creek Hatchery, located on a tributary to Redwood Creek, stopped releases of coastal cutthroat

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[22] T. Confer, ODFW, 742 Airport Way, P.O. Box 642, Gold Beach, OR 97444. Pers. commun. to M. Ruckelshaus. July 1998.

trout in the late 1980s. Returns of coastal cutthroat trout to the hatchery were seven and eight fish in 1987 and 1988, respectively (Gerstung 1998). Hatchery coastal cutthroat trout were planted into Stone Lagoon, a coastal lagoon near Redwood Creek, as recently as 1996 (Gerstung 1998). Releases of hatchery coho salmon and steelhead continue to occur in a few southern Oregon coastal streams and in California coastal lagoons. Recent changes in angling regulations for "wild trout" in response to the proposed steelhead ESA listings in California may have a positive effect on coastal cutthroat trout (Bryant 1998).

Summary and Conclusions of Risk Assessments

Recent events considered

Recent events considered in the BRT risk evaluation include Oregon's change in angling regulations in 1995 to establish more restrictive bag and size limits on the catch of coastal cutthroat trout. Similarly, Oregon, California, and Washington have recently imposed more restrictive bag and size limits on coastal cutthroat trout in some areas. As discussed earlier, both Oregon and Washington in the early 1990s began requiring release of wild coastal cutthroat trout landed in some river drainages. In addition, the BRT's risk assessments considered potential effects of changes in hatchery management policies that have already been implemented. These changes include those affecting coastal cutthroat trout and other species of salmonids (e.g., coho salmon) that potentially interact with coastal cutthroat trout. Specific changes in harvest and hatchery practices pertinent to a particular ESU are discussed in individual ESU sections. The effects of recent (1996-97) flooding in the geographic regions included in the Oregon Coast and the Southern Oregon/California Coasts ESUs also were considered by the BRT.

General risk considerations

Habitat—As described earlier, coastal cutthroat trout tend to be found in both lower and upper reaches of streams. Coastal cutthroat trout typically utilize small tributaries of low to mid-gradients for juvenile rearing, winter refuge, and spawning habitat. In addition, juvenile and spawning adult coastal cutthroat trout are often found in small headwater streams, frequently upstream of steelhead and coho salmon spawning areas. The BRT believed that reduction in freshwater and estuarine habitat quality probably has contributed to declines in coastal cutthroat trout populations (see "Historical abundance, habitat, and carrying capacity," p. 147). Changes in nearshore habitat characteristics due to alterations in freshwater runoff, ocean circulation patterns, abundance of predator and prey species, and shifts in physical conditions could contribute to declines in coastal cutthroat trout summer growth rates or survival. The BRT noted that, coincident with continuing declines in estuarine habitat quality, coastal cutthroat trout catch in estuarine and river mouth sport fisheries has declined in a number of sites throughout the Pacific Northwest and Northern California. In addition, evidence suggests that logging practices decrease instream habitat quality due to increases in water temperature and siltation, removal of LWD that would otherwise provide important habitat structure, changes in river basin hydrology, and insertion of culverts beneath logging roads. The increased incidence of culverts in many coastal cutthroat trout streams (due to logging and nonlogging-related road construction) is a serious threat because of their effectiveness in blocking instream migration, especially for juveniles and smolts. Documented reduction in coastal cutthroat trout abundance following logging (see "Historical abundance, habitat, and carrying capacity," p. 147) was a source of concern to the BRT.

For other impacts, evidence that links a particular source of freshwater or estuarine habitat degradation to a response in coastal cutthroat trout populations is largely anecdotal. These sources include conversion of land surrounding coastal cutthroat trout streams to agricultural and commercial development, water diversions, habitat blockages, floods, changes in ocean conditions, dredging, and reduction in the presence of other salmonid carcasses for nutrient provision. Despite the lack of direct quantification of these effects on coastal cutthroat trout populations, it is clear that drastic habitat modification due to these factors has occurred in many areas. The BRT noted that most biologists familiar with coastal cutthroat trout believe that such habitat modification has led to a reduction in present habitat capacity relative to historical levels.

Hybridization—In addition to first-generation hybrids between coastal cutthroat trout and steelhead/rainbow trout, the BRT noted that coastal cutthroat trout with more fully introgressed genes have been detected in natural populations, indicating that some hybrids do survive and interbreed (back cross) with parental species. It is not clear what effect these hybridizations have on coastal cutthroat trout populations. As discussed earlier (see "Hybridization and introgression," p. 75), the extent of hybridization between coastal cutthroat trout and *O. mykiss* and the environmental characteristics with which hybridization is correlated are not well understood. In addition, the BRT discussed the importance to risk evaluations of being able to distinguish historical (i.e., background or "natural") levels of coastal cutthroat trout × *O. mykiss* hybridization from levels of present-day hybridization. Since it is not known how human activities may have affected both the frequency of coastal cutthroat trout × *O. mykiss* hybridization events and the fitness consequences of such hybridizations, evaluating the risks to native coastal cutthroat trout is difficult.

Ecological interactions—The BRT felt that the increased competition from hatchery coho salmon may be an important risk factor for juvenile coastal cutthroat trout. The BRT noted with concern that streams in Washington with continuing releases of hatchery coho salmon fry also show declining trends in coastal cutthroat trout abundance. In addition, the BRT discussed the possible effects of dramatic increases in sea lion and harbor seal populations on predation of coastal cutthroat trout, especially in the Lower Columbia River Basin. Specific information relating to risks to coastal cutthroat trout from human-induced effects on ecological interactions was not available.

Paucity of information relating to risk

The dearth of information on risks facing coastal cutthroat trout populations is more pervasive than data gaps for other species of Pacific salmonids. This situation is similar to the relative lack of data to guide decisions about ESU boundaries for coastal cutthroat trout, as discussed earlier. Current or historical abundance information, especially for adult coastal cutthroat trout, is available for only a very small proportion of the known populations within any ESU. In contrast to the situation for status reviews of the other species of Pacific salmonids, the BRT for coastal cutthroat trout has had to base its risk evaluations more heavily on abundance estimates for a small number of populations spanning only a few years, presence/absence data, and professional judgements by biologists familiar with coastal cutthroat trout in specific geographic regions. Information on risks from hatchery-origin fish and hybridization with steelhead and rainbow trout also is very limited for coastal cutthroat trout.

Biologists familiar with coastal cutthroat trout generally believe that, in some areas (e.g., Lower Columbia River Basin, Puget Sound, Northern California), anadromous cutthroat trout populations have experienced significant declines relative to historical levels of abundance (see "Biological Information by ESU," p. 158). In many cases, concrete evidence for long- or short-term declines in abundance is not available. Instead, biologists have based their opinions on such information as 1) anecdotal reports from anglers familiar with local streams, 2) success of periodic sampling of streams for coastal cutthroat trout for genetic or other life-history data, and 3) incidental observations of coastal cutthroat trout during surveys for other species of Pacific salmonids.

The scarcity of information for coastal cutthroat trout has made the risk assessments especially difficult for the BRT. The BRT wrestled with a fundamental dilemma stemming from lack of data, which is that insufficient information about key risk factors, such as abundance, can result in two alternative conclusions: 1) there is not enough evidence to demonstrate that coastal cutthroat trout are at significant risk of extinction, and 2) there is not enough evidence to demonstrate that coastal cutthroat trout are *not* at risk. This uncertainty existed for many of the coastal cutthroat trout ESUs. For some BRT members, uncertainty about status coupled with a collective sense among local biologists that coastal cutthroat trout were in decline suggested that an ESU was at risk of extinction. Finally, the paucity of information led other BRT members to conclude that one or more ESUs were not at significant risk. The BRT stressed that the latter risk conclusion does not necessarily indicate that an ESU is healthy; rather, it may simply indicate that there is insufficient information to demonstrate that it is not healthy.

The BRT continues to wrestle with how to most effectively address the inevitable uncertainty in making risk evaluations for Pacific salmonids. Developing ways of incorporating uncertainty into the BRT's risk evaluations is an evolving process. Elements of uncertainty are present in risk assessments for any species of conservation concern; the significant paucity of data for coastal cutthroat trout have made this risk evaluation especially challenging. Summaries of BRT risk votes are provided in Appendix B.

General conclusions

> If a man will begin with certainties, he shall end in doubts; but if he will
> be content to begin with doubts he shall end in certainties.
>
> Sir Francis Bacon, *The Advancement of Learning,* 1605

The two methods used by the BRT to characterize uncertainty in risk assessments generally were consistent in their outcomes (for a description of methods, see "Overall Evaluation of Risk and Uncertainty," p. 141). In the first method, each BRT member assigned a certainty score (1=low, 5=high) to the overall risk vote (in danger of extinction, not at significant risk of extinction but likely to become so in the foreseeable future, and not presently at significant risk of extinction or endangerment) for each ESU. The certainty scores for most ESUs were low (in the range of 1 to 3), reflecting considerable uncertainty regarding the conservation status of coastal cutthroat trout.

In the second method, BRT members could split their vote and allocate "likelihood points" among the three risk categories. Results from this method were generally concordant with and support information provided by the first method. That is, when the majority of BRT votes fell in a particular risk category, the majority of likelihood points also fell in the same category. For all ESUs, a small fraction of likelihood votes occurred in the "in danger of extinction" category. This result reflects the very limited information available for conducting risk evaluations for coastal cutthroat trout. Although in many cases available information did not provide conclusive evidence of high risk, it also did not clearly demonstrate that the ESUs were not at risk. As a result, at least some BRT members felt that they could not completely exclude the possibility that a particular ESU is presently in danger of extinction. However, when asked to pick only one risk category (the first method), no BRT members concluded that any ESUs are presently in danger of extinction.

Only one ESU (Southwestern Washington/Columbia River) was considered to be at significant risk by a majority of the BRT. The BRT was evenly divided as to whether another ESU (Oregon Coast) is likely to become endangered in the foreseeable future. The BRT also had some concerns about the status of coastal cutthroat trout in all of the remaining ESUs, but available information did not clearly indicate high risk in these cases. In general, although comprehensive data on the abundance of nonmigratory *O. c. clarki* are not available in most cases, qualitative observations suggest that nonmigratory forms of this subspecies are not at high risk in any ESU. Most of the concerns for the conservation status of coastal cutthroat trout focus on the depletion or loss of migratory (especially anadromous) life-history forms. Migratory forms play an important role in the evolutionary ecology of coastal cutthroat trout by forging genetic and demographic linkages among populations. Available information indicates that these life-history traits are in part genetically controlled, and their loss can have important consequences for the sustainability and future evolutionary trajectories of coastal cutthroat trout ESUs.

Summary of ESU-specific conclusions

Puget Sound ESU—Few data exist concerning historical and present abundance of coastal cutthroat trout in the Puget Sound ESU region. The BRT had almost no estimates of adult population sizes. Exceptions were a WDFW estimate of the 1997 spawning escapement in the Skagit River Basin of 13,000 fish and counts of adults at an upstream migrant trap designed for coho salmon on the Deschutes River in southern Puget Sound (5-year geometric mean = 74 coastal cutthroat trout). Anecdotal reports suggest low abundance of coastal cutthroat trout in southwestern Puget Sound streams. In general, the BRT noted with concern the lack of information regarding the distribution and abundance of coastal cutthroat trout throughout the Puget Sound region. There are some data indicating that juvenile coastal cutthroat trout are relatively well distributed in the Skagit and Stillaguamish river basins and along the Strait of Juan de Fuca. The BRT acknowledged that widespread habitat degradation and loss have occurred in the Puget Sound region. This reduction in habitat capacity constitutes an important ongoing risk to coastal cutthroat trout that has not been quantified.

Trend data from this ESU available to the BRT were downstream migrant counts from streams in eastern Hood Canal, the Skagit River basin and in southern Puget Sound (up to 1987 only), adult counts on the Deschutes River and CPUE data for adults over the past 2 to 7 years in three northern Puget Sound river basins. Trends in smolt numbers were mixed in both Hood Canal and southern Puget Sound. The BRT did not weigh the southern Puget Sound smolt trends heavily because no information on recent smolt abundance in those streams exists. In addition, the downstream migrant trends in the Skagit River basin were considered to be at best rough indicators of true trends because the trap locations and dates trapped were designed for estimates of coho salmon smolt production. The numbers of coastal cutthroat trout trapped therefore may not provide an accurate picture of abundance. Increases in coastal cutthroat trout smolt numbers in some eastern Hood Canal streams coincided with declines in coho salmon abundance. A negative correlation between abundances of coastal cutthroat trout and coho salmon suggested to the BRT that interactions between these two species may be reducing the abundance of coastal cutthroat trout in some streams. Streams with reduced coho salmon numbers may result in a relaxation of competition that allows an increase in coastal cutthroat trout abundance. Unfortunately, there is no information regarding smolt-to-adult survival in this ESU, so interpretation of the significance of smolt trends for overall risk to these populations is difficult. Furthermore, as outlined previously, the BRT discussed the possibility that smolt abundance was already depressed before these trap data were obtained. Historical estimates of smolt abundance were not available, so no definitive conclusions about the risks to coastal cutthroat trout populations could be made from the smolt count data.

The CPUE data for the Stillaguamish and Snohomish river populations showed increasing trends; the Skagit River CPUE has been declining. The BRT felt that the short time frames (2-7 years) over which these data have been collected and the possibility that significant declines in abundance occurred before data collection began reduced the usefulness of these trends in assessing population status. In addition, WDFW biologists feel that the variation in the adults caught may be due in part to annual variation in fishing conditions. Finally, there are indications that the proportion of repeat spawners in northern Puget Sound river basins has been declining. The risk posed by this decline has not been quantified and, without good estimates of the numbers of coastal cutthroat trout in spawning populations each year, the BRT concluded that the lost opportunity for larger, more fecund fish to contribute to spawning populations represents a significant threat to continued productivity.

In addition to information about population sizes and trends in abundance for coastal cutthroat trout in this ESU, the BRT considered another important risk factor—the potential loss of life-history diversity. In particular, the anadromous life-history type appears to be declining in some Puget Sound streams containing coastal cutthroat trout. However, the BRT felt that risks to the integrity and long-term sustainability of the Puget Sound ESU due to loss of life-history diversity were relatively low compared to other coastal cutthroat trout ESUs, in which there are more streams with documented declines in anadromous life-history types.

The influence of hatchery coastal cutthroat trout in the Puget Sound ESU is probably relatively low compared to the impacts of hatchery fish on the productivity of other Pacific salmon. The proportion of hatchery fish caught in the recreational fisheries for coastal cutthroat trout in Hood Canal is low. On the other hand, the BRT acknowledged that there are some hatchery-related threats to native natural coastal cutthroat trout populations in this ESU. The WDFW considers the northern Puget Sound coastal cutthroat trout populations to be of mixed origin, indicating that fish of nonnative origin may have contributed to the genetic composition of those populations (WDFW 1998a). Production in most streams within the ESU is considered "wild," indicating that hatchery fish do not contribute significantly to natural spawning escapements (WDFW 1998a). Finally, the BRT discussed the possibility that interactions between coastal cutthroat trout and naturally occurring or hatchery-released coho salmon and steelhead can negatively affect the abundance of coastal cutthroat trout in this ESU.

After considering this information, a majority of the BRT members felt that the Puget Sound ESU is not presently in danger of extinction, nor is it likely to become so in the foreseeable future. A minority felt that the ESU was likely to become endangered in the foreseeable future. The uncertainty underlying these conservation assessments was high: most BRT members reported certainty scores of 2 or 3 for their risk evaluations. The BRT felt that widespread, often irreversible, habitat degradation of freshwater and estuarine habitat has been caused by development, logging, and agriculture. Thus, extant habitat capacity is clearly lower than historical levels. Population levels and major threats appear to have been relatively constant over the past 10-15 years, although many of these populations are believed to be depressed relative to historical levels. Recent flooding events likely have contributed to declines in cutthroat trout numbers and productivity. In addition, a number of biologists familiar with coastal cutthroat trout feel that fishing mortality suffered by cutthroat trout is an important source of risk. The BRT expressed concern that historical and continuing reduction in habitat quality, combined with very little information with which to assess status, created considerable uncertainty in evaluating risk for Puget Sound coastal cutthroat trout.

Olympic Peninsula ESU—The BRT had little information with which to estimate population abundances for coastal cutthroat trout in the Olympic Peninsula ESU. The general impression from state and tribal fisheries biologists is that juvenile coastal cutthroat trout are well distributed in streams along the western Strait of Juan de Fuca and northern Washington coast, and the BRT believed there are probably some highly productive coastal cutthroat trout streams in this geographic region. For example, smolt abundances in Dickey Lake are high relative to numbers of smolts in Puget Sound and Hood Canal streams. On the other hand, the BRT acknowledged that ongoing habitat destruction, primarily due to logging and its associated activities (e.g., road building, stream blockages by culverts), continue to be a source of risk to coastal cutthroat trout in many Olympic Peninsula streams.

The only quantitative data available to the BRT for the Olympic Peninsula ESU were counts of downstream migrants on tributaries of the Clearwater (from 1981 to present), Dickey (1992-1994), and Hoko (1986-1989) rivers and in Salt Creek along the Strait of Juan de Fuca (1998). The trends among Clearwater tributaries were mixed, suggesting to the BRT that some tributary streams could be characterized as good producers and that others were declining in smolt production. The absolute numbers of outmigrants in all streams trapped was encouraging to the BRT. Nevertheless, the BRT did not weigh trends from the Hoko River heavily in its risk determinations because these data are not current; in addition, the Dickey River trends were based on only 3 years of trapping designed to estimate coho salmon production. It was difficult to interpret the outmigrant data, in part because of a lack of smolt-to-adult survival estimates and because declines in production may have occurred before 1981, when earliest data collection began. The BRT believed that continued demonstrations of consistent smolt production from outmigrant trapping could support the general sense among fisheries biologists that coastal cutthroat trout are well represented in streams throughout the Olympic Peninsula.

The BRT indicated that risks to the Olympic Peninsula ESU from loss of life-history diversity were relatively low. This ESU received a lower risk score for this source of risk than any other ESU.

Risks associated with hatchery coastal cutthroat trout are probably low in this ESU. Hatchery releases of coho salmon fry occur in some areas on the Olympic Peninsula, which may increase stress on coastal cutthroat trout due to interspecific competition levels higher than what might occur naturally.

A majority of the BRT concluded that the Olympic Peninsula ESU is not presently in danger of extinction, nor is it likely to become so in the foreseeable future. A single member felt that the ESU is likely to become endangered in the foreseeable future. However, these risk evaluations must be considered in light of the very high uncertainty expressed by the BRT. The certainty scores for the Olympic Peninsula ESU risk assessment were the lowest of all of the coastal cutthroat trout ESUs, with most scores being 1 or 2. The BRT believed there are indications that there is productive coastal cutthroat trout habitat to support this ESU, but that information was not available to confirm such a possibility. The continuing habitat degradation throughout the region was a significant source of concern to the BRT. Without data to evaluate the effects of land-use practices on coastal cutthroat trout abundance in this region, the conservation status of this ESU remains unclear.

Southwestern Washington/Columbia River ESU—According to WDFW, the southwestern Washington-Lower Columbia River region historically supported healthy and highly productive coastal cutthroat trout populations. Coastal cutthroat trout, especially the freshwater forms, may still be well distributed in most river basins in this geographic region, probably in lower numbers relative to historical population sizes. Severe habitat degradation throughout the Lower Columbia River area has contributed to dramatic declines in anadromous cutthroat trout populations and two near extinctions of anadromous runs in the Hood and Sandy rivers. The BRT was concerned about the extremely low population sizes of anadromous cutthroat trout in Lower Columbia River streams, indicated by low incidental catch of coastal cutthroat trout in salmon and steelhead recreational fisheries and low trap counts in a number of tributaries throughout the region. Although efficiencies for these traps in catching coastal cutthroat trout are not known, numbers of adults returning to traps have been consistently below 10 fish in most streams included in this region over each of the past 6 years. In contrast, the BRT believed that information on the distribution of freshwater forms of coastal cutthroat trout in this region, though mostly anecdotal, probably accurately reflected their widespread occurrence in streams throughout the region.

Trends in anadromous adults and outmigrating smolts in the southwestern Washington portion of this ESU are all declining. The BRT was aware that WDFW considers streams in this region to have relatively good coastal cutthroat trout habitat; however, data available to the BRT do not support the idea that the anadromous cutthroat trout in this area are at low risk. Returns of both naturally- and hatchery-produced anadromous cutthroat trout in almost all Lower Columbia River streams have been declining markedly over the last 10-15 years. Indeed, the only anadromous cutthroat trout population in the Lower Columbia River to show increases in abundance over the last 10 years is the North Fork Toutle River population, which is thought to be recovering from the effects of the Mt. Saint Helens eruption. In spite of its increasing trend, WDFW states that its population numbers are still critically low (approximately 100 total adults in run). The BRT also was concerned about data for hatchery-origin coastal cutthroat trout in the Lower Columbia River that indicated declines in smolt-to-adult survival since the 1980s.

A significant risk factor for coastal cutthroat trout in this ESU is reduction in life-history diversity. Serious declines in the anadromous form have occurred throughout the Lower Columbia River, and it has been nearly extirpated in at least two rivers on the Oregon side of the basin. Available information suggests that in many streams the freshwater forms of coastal cutthroat trout are well distributed and occur in relatively high abundance in comparison to anadromous forms in the same stream. The BRT discussed evidence presented from ODFW and WDFW that freshwater coastal cutthroat trout can produce smolts that migrate to saltwater. Although the BRT acknowledged that this possibility could mitigate risks to anadromous forms of coastal cutthroat trout, the observation that sea-run cutthroat trout population sizes have remained consistently low in many areas is a cause for concern. In summary, the BRT believed that, even if freshwater forms of coastal cutthroat trout have been producing occasional smolts, this production has not resulted in demonstrably successful re-establishment of anadromous forms. Habitat degradation in stream reaches accessible to anadromous cutthroat trout and poor ocean and estuarine conditions probably have combined to severely deplete this life-history form throughout the Lower Columbia River Basin. Without the appropriate freshwater and estuarine habitat for the expression of the anadromous life history, a greater risk of extinction may occur. The significance of this reduction in life-history diversity to the integrity of the ESU and the likelihood of its long-term persistence were major sources of concern to the BRT.

Negative effects of hatchery coastal cutthroat trout may be contributing to the risks facing native naturally produced coastal cutthroat trout in this ESU. The Lower Columbia River tributaries are the only streams in Washington still receiving hatchery-origin coastal cutthroat trout, although the total numbers of released hatchery fish have been substantially curtailed recently. The BRT was concerned that in the early 1980s an estimated 50-80% of the recreational catch for coastal cutthroat trout in the Lower Columbia River was composed of hatchery fish. Biologists familiar with coastal cutthroat trout believe that recreational catch data reflect true trends in coastal cutthroat trout abundance (Hooton 1997). Furthermore, the largest returns of coastal cutthroat trout in this region are to the Cowlitz River Basin, and existing information is consistent with the interpretation that a significant proportion of those fish are of hatchery origin (WDFW 1998a). The BRT emphasized that the ultimate effects of hatchery fish depend on the relative sizes of hatchery and native naturally produced populations, the spatial and temporal overlap of hatchery and native naturally produced fish throughout their life cycles, and the actual extent to which hatchery fish spawn naturally and interbreed with naturally produced fish. In addition, the extent to which natural coastal cutthroat trout are incidentally harvested in fisheries targeting hatchery coastal cutthroat trout and other salmonids also will affect the magnitude of the risks to coastal cutthroat trout due to hatchery fish.

The BRT was unanimous in concluding that the Southwestern Washington/Columbia River ESU was likely to become endangered in the foreseeable future. Certainty scores ranged from 2 to 4. Although these scores reflect only a moderate degree of certainty regarding the risk assessment, they were on average higher than for any other coastal cutthroat trout ESU. The BRT was especially concerned about the widespread declines in abundance and the small population sizes of anadromous cutthroat trout throughout the Lower Columbia River, as exemplified by near extinctions of anadromous cutthroat trout runs in the Hood and Sandy rivers. The severe reductions in abundance of this life-history form could have deleterious effects on the ability of this ESU to recover from widespread declines. Reductions in the quantity and quality of nearshore ocean, estuarine, and riverine habitat have probably contributed to declines, but the relative importance of these risk factors is not well understood. In addition, the BRT discussed the possibility that recent increases in marine mammal and bird predators may be important risk factors. The BRT was encouraged by recent steps taken by the states of Washington and Oregon to reduce mortality due to directed and incidental harvest of coastal cutthroat trout.

Upper Willamette River ESU—The conservation status of this ESU was not formally evaluated by the BRT. As stated earlier, since it is believed by ODFW that few anadromous cutthroat trout are produced in this ESU, USFWS has jurisdiction for these populations.

Oregon Coast ESU—Coastal cutthroat trout in the Oregon coastal region occur mostly in small populations that are relatively well distributed. Most of the abundance information considered by the BRT for this ESU was juvenile and smolt abundance, with the prominent exception of the adult counts at Winchester Dam on the North Umpqua River. In general, the BRT was encouraged by the numbers of juveniles in coastal streams with relatively large basins. These data are available for only the last 2 years, however, so how well these juvenile counts translate into adult abundances or longer-term population trends is not known. The estimated pre-1970s abundance of anadromous cutthroat trout in the largest river basin contained within this ESU, the Umpqua River, is 30,000 adults. A recent estimate of total run size, based on expansions of observed numbers of adults from snorkel surveys, is similar. The BRT expressed concern about assumptions underlying expansion methods to estimate anadromous run size using snorkel survey data for freshwater forms of coastal cutthroat trout in the Umpqua River basin. Conflicting information about the abundance and distribution of coastal cutthroat trout in the South Umpqua River basin suggested to the BRT that there is insufficient information to determine the status of coastal cutthroat trout in that drainage. The numbers of adults returning to the North Umpqua River have been critically low in recent years (5-year geometric mean = 18 fish), although, for the past 3 years, 79, 81, and 135 (through November 15, 1998) (Loomis footnote 3) adult coastal cutthroat trout have been counted at Winchester Dam. The BRT noted that widespread habitat degradation due to logging, road construction, and development along coastal streams probably constitute a significant reduction in habitat capacity relative to historical conditions.

Smolt production in two small drainages (Cummins and Tenmile creeks) in central Oregon has shown an increasing trend over the past 7 years. However, the percentage of repeat spawners has declined in both drainages relative to estimates in the early 1970s. All other streams on the Oregon coast for which data were available are experiencing moderate declines in adults and juveniles. In some areas, declines may have occurred primarily in anadromous cutthroat trout populations. For example, in the Alsea and Siuslaw river basins, declines in anadromous runs have occurred as indicated by recreational catch data, but ODFW believes there is no evidence for similar declines in nonmigratory coastal cutthroat trout in those same basins.

The BRT was concerned about reductions in anadromous life-history forms throughout this ESU. Information available to the BRT indicated that sea-run cutthroat trout are suffering more serious declines than are freshwater forms along Oregon coastal streams. The BRT believed that the risks associated with possible reductions in historical connections among streams by more migratory anadromous cutthroat trout could be a significant threat to the persistence of the ESU. For example, one possible interpretation of the high levels of genetic differentiation among populations in the Coquille River Basin is that populations are no longer connected by gene flow from the anadromous form. ODFW has suggested that freshwater forms of coastal cutthroat trout may be producing smolts in several coastal streams. The BRT did not have estimates of the numbers of adult anadromous trout in those streams, so it was difficult to evaluate the possibility that freshwater forms could buffer anadromous forms from declines.

Current risks due to interactions with hatchery coastal cutthroat trout are probably moderately low in this ESU. Nevertheless, the widespread releases of Alsea River hatchery broodstock in Oregon coastal streams have stopped only relatively recently. Genetic samples indicate that hatchery coastal cutthroat trout from the Alsea River broodstock have influenced the genetic composition of several coastal cutthroat trout populations in the Coquille River drainage. Hybrids between coastal cutthroat trout and steelhead/rainbow trout were detected in genetic samples from the Coquille River Basin and a few other streams in this ESU. As discussed earlier, some degree of hybridization between *O. mykiss* and coastal cutthroat trout may occur naturally without the direct influence of hatchery-origin fish. However, risks to coastal cutthroat trout populations due to hybridization may increase if either 1) changes in habitat conditions or 2) an increase in the abundance of hatchery-origin *O. mykiss* increase the frequency of natural hybridization or change its fitness consequences.

All members of the BRT agreed that the Oregon Coast ESU is not presently at risk of extinction. However, the BRT was evenly split in determining whether the ESU is likely to become endangered in the foreseeable future or not likely to become endangered. The certainty in this assessment was fairly low: the certainty scores were mostly 2 or 3. The BRT was concerned about habitat degradation that continues within this region, and the scarcity of abundance information for major drainages limited the BRT's efforts to conduct a risk evaluation. Hatchery records indicate that the Alsea River coastal cutthroat trout stock was released widely in streams throughout the Oregon coastal region. Recent reductions in releases of hatchery-origin coastal cutthroat trout and coho salmon fry, coupled with a statewide catch-and-release recreational fishery policy for naturally produced native coastal cutthroat trout, may have reduced risks associated with those factors. The BRT noted that reduced nearshore ocean habitat quality was probably a significant threat to coastal cutthroat trout in this region, but quantifying those effects on coastal cutthroat trout abundance is very difficult. Finally, the BRT was concerned about incidental mortality of coastal cutthroat trout in this ESU due to fishing pressure on Pacific salmon and steelhead.

Southern Oregon/California Coasts ESU—Coastal cutthroat trout in this ESU are thought to be widely distributed in many small populations. Two possible exceptions are populations in the Rogue and Smith river basins, where the abundance of coastal cutthroat trout may be comparatively high. Smolt abundance in Lobster Creek, a Rogue River tributary, was estimated to be over 800 fish in 1998. In addition, fisheries biologists familiar with the Rogue River Basin believe it supports many well-distributed coastal cutthroat trout populations. The estimated historical sea-run cutthroat trout population in the Smith River Basin was 8,500 fish. Expansion estimates of fish greater than 25 cm in the three major forks of the Smith River indicate that each fork supports at least 300 coastal cutthroat trout. In addition, Mill Creek, considered to be one of the most productive coastal cutthroat trout tributaries in the Smith River Basin, has had between 1,000 and 4,000 outmigrating smolts over each of the past 4 years. Again, lack of information on smolt-to-adult survival and trap efficiencies makes interpreting smolt abundance estimates in the Rogue and Smith river basins difficult. Population sizes are thought to be relatively small in other streams throughout this region, in part because it is the southern limit of this cutthroat trout subspecies. The BRT believes that severe habitat degradation has occurred in this region, primarily due to activities associated with agriculture, flood control, logging, road construction, and local development. These activities have contributed to a reduction in habitat capacity relative to historical levels. In addition, seasonal dewatering of stream mouths occurs naturally in Northern California, resulting in sporadic blockages of access to the sea for anadromous fish in some streams. Also, large water withdrawals in several larger coastal river basins (e.g., Rogue, Klamath/Trinity, and Eel rivers) and several of the smaller coastal rivers have reduced the quantity and quality of the remaining riverine and estuarine environments in the geographic region encompassing this ESU.

Biologists familiar with this region believe, and anecdotal evidence suggests, that major declines in coastal cutthroat trout populations have occurred since historical times, and that some populations appear to have been relatively stable or increasing in size since that time. The data available to the BRT indicate increasing short-term trends in smolt abundance in Mill Creek, and increasing short-term trends in adult abundance in the lower Klamath River tributaries and its estuary and in the Smith River Basin. Exceptions include recent declines in the incidence of coastal cutthroat trout in Redwood Creek.

Reductions in the anadromous form of coastal cutthroat trout are not thought to be a significant source of risk to the overall ESU. Although declines in some anadromous runs have occurred, there was no evidence presented to the BRT that these declines have occurred throughout a significant portion of the geographic area.

Risks due to interactions with hatchery coastal cutthroat trout are probably low in this ESU. Other risks the BRT noted for coastal cutthroat trout in this region were possible deleterious interactions with naturally occurring or hatchery-derived coho salmon and steelhead, and incidental catch of coastal cutthroat trout in sport fisheries targeting steelhead and coho salmon. The BRT was encouraged by recent changes in harvest regulations aimed at reducing risks to natural trout from direct and indirect harvest mortality.

A majority of the BRT believed that the Southern Oregon/California Coasts ESU was not presently in danger of extinction, nor did they believe it was likely to become so in the foreseeable future. A minority concluded that the ESU was likely to become endangered in the foreseeable future. Most BRT members indicated that their risk evaluations were associated with a low degree of certainty. Certainty scores ranged from 1 to 4, but most of the BRT members indicated a certainty level of 2. As with many other ESUs for coastal cutthroat trout, the BRT was hindered by the scarcity of abundance information for this ESU. The BRT emphasized that continuing threats to the quality of freshwater and estuarine habitat for cutthroat trout in this region are sources of concern.

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APPENDIX A: HATCHERY RELEASES

Table A-1. Hatchery releases of juvenile coastal cutthroat trout, listed by Evolutionarily Significant Unit (ESU). "Duration" indicates the time frame of releases; "years" indicates the total number of years fish were actually released within the duration. No releases of fish smaller than 1.0 g are presented. In Washington, 71% of fish released were over 10 grams in weight; in Oregon, 54% of fish released were over 10 grams. Data before 1950 are incomplete (NRC 1996). Releases in bold indicate known and possible introductions from outside the ESU. Data from Hisata (1973), Johnston (1979), Kostow (1995), NRC (1996), and WDFW (1998a).

Watershed[a]	**Duration**	**Years**	**Stock Source**[b]	**Total**
1) Puget Sound ESU				
Nooksack R.	1986	1	Hood Canal mixed H	19,776
	1968-1981	**9**	**LCR H & unk.**	**143,625**
	1984, 1985	2	NF Nooksack R.	19,877
	1983	1	Nooksack R.	1,882
	1983	1	Stillaguamish R.	3,765
Samish R.	**1966-1981**	**10**	**LCR H & unk.**	**120,430**
San Juan Is.	**1969-1981**	**11**	**LCR H & unk.**	**107,938**
Skagit R.	**1966-1981**	**13**	**LCR H & unk.**	**156,328**
North Puget Sound creeks	**1964-1981**	**12**	**LCR H & unk.**	**105,862**
Island Co.	**1964-1981**	**13**	**LCR H & unk.**	**329,648**
Stillaguamish R.	**1964-1981**	**11**	**LCR H & unk.**	**466,860**
	1982	1	Stillaguamish R.	23,360
Snohomish R.	**1967-1981**	**5**	**LCR H & unk.**	**41,243**
Lake Washington	**1987**	**1**	**mixed Coastal H**	**560**
Green R.				none
Puyallup R.	**1965-1974**	**7**	**LCR H & unk.**	**41,708**
Chambers Cr.	**1980, 1965**	**2**	**LCR H & unk.**	**6,447**
Nisqually R.	**1965-1981**	**17**	**LCR H & unk.**	**206,862**
	1988	1	Mclane Cr.	2,200
	1987-1994	3	mixed Coastal H	1,800
	1982, 1992	2	mixed South Puget Sound H	20,057

Table A-1. (Continued).

Watershed[a]	Duration	Years	Stock Source[b]	Total
Deschutes R.	**1966-1981**	**16**	LCR H **& unk.**	**334,314**
	1982, 1994	2	mixed South Puget Sound H	26,248
South Puget Sound creeks	1988-1994	6	Hood Canal mixed H	31,852
	1965-1981	**11**	LCR H **& unk.**	**204,416**
	1989	1	mixed Coastal H	2,400
	1982, 1992	2	mixed South Puget Sound H	13,671
North Hood Canal creeks	1982	1	Hood Canal mixed H	624
	1978	**1**	LCR H **& unk.**	**1,610**
Dewatto R.	1982-1991	6	Hood Canal mixed H	26,777
	1970-1981	**11**	LCR H **& unk.**	**83,920**
Tahuya R.	1982-1991	6	Hood Canal mixed H	29,991
	1965-1981	**11**	LCR H **& unk.**	**154,927**
Union R.	1986, 1987	2	Hood Canal mixed H	26,650
	1966-1979	**8**	LCR H **& unk.**	**120,513**
South Hood Canal creeks	1982-1994	7	Hood Canal mixed H	15,787
	1968-1981	**7**	LCR H **& unk.**	**152,750**
	1987	**1**	**mixed Coastal H**	**1,600**
Skokomish R.	1982-1994	12	Hood Canal mixed H	1,399,234
	1968-1981	**13**	LCR H **& unk.**	**1,123,096**
Hamma Hamma R.	1982-1989	5	Hood Canal mixed H	17,799
	1963-1967	**3**	LCR H **& unk.**	**9,316**
Duckabush R.	1986-1989	4	Hood Canal mixed H	22,836
Dosewallips R.	1986-1989	4	Hood Canal mixed H	22,527
Quilcene R.	1982-1987	3	Hood Canal mixed H	61,509
	1979	**1**	LCR H **& unk.**	**204**
Tarboo Cr.	1987-1994	6	Hood Canal mixed H	2,039
	1977-1979	**3**	LCR H **& unk.**	**20,526**
Thorndyke Cr.	1982, 1987	2	Hood Canal mixed H	8,390

Table A-1. (Continued).

Watershed[a]	**Duration**	**Years**	**Stock Source**[b]	**Total**
Elwah R.	1982-1991	4	Hood Canal mixed H	42,442
	1966-1981	**15**	**LCR H & unk.**	**301,208**
	1986-1990	**5**	**mixed Coastal H**	**47,110**
	1982	1	mixed South Puget Sound H	4,725
2) Olympic Peninsula ESU				
Bogachiel R.	**1987**	**1**	**mixed Coastal H**	**3,000**
Quillayute R.	**1961-1971**	**7**	**LCR H & unk.**	**150,518**
Quetts R.	**1984-1994**	**6**	**mixed Coastal H**	**12,675**
Copalis R.	**1984, 1989**	**2**	**mixed Coastal H**	**3,400**
3) Southwestern Washington/Columbia River ESU				
Humptulips R.	**1991**	**1**	**Hood Canal mixed H**	**10,460**
	1968-1981	**8**	**LCR H & unk.**	**29,905**
	1984-1994	10	mixed Coastal H	56,025
Chehalis R.				
	1987	1	Chehalis R.	1,980
	1982, 1991	**2**	**Hood Canal mixed H**	**32,460**
	1965-1981	**17**	**LCR H & unk.**	**1,131,339**
	1983-1994	12	mixed Coastal H	1,205,900
	1982	**1**	**mixed South Puget Sound H**	**42,615**
Willapa R.	1987	1	Chehalis R.	15,920
	1991	**1**	**Hood Canal mixed H**	**1,400**
	1973-1981	**4**	**LCR H & unk.**	**17,496**
	1984-1989	4	mixed Coastal H	21,800
North R.	**1966-1981**	**15**	**LCR H & unk.**	**133,955**
	1984-1993	5	mixed Coastal H	6,790
	1982	**1**	**mixed South Puget Sound H**	**3,825**
Palix R.	1987	1	Chehalis R.	7,920
	1978, 1981	**2**	**LCR H & unk.**	**2,500**
	1984, 1989	2	mixed Coastal H	6,000
Naselle R.	1987	1	Chehalis R.	1,500
	1973-1981	**3**	**LCR H & unk.**	**2,012**
	1987, 1989	2	mixed Coastal H	7,360

Table A-1. (Continued).

Watershed[a]	Duration	Years	Stock Source[b]	Total
Nemah R.	**1965-1981**	**4**	LCR H **& unk.**	**26,235**
	1985, 1986	2	mixed Coastal H	13,950
Pacific Co Beaver Ponds	**1973-1981**	**3**	LCR H **& unk.**	**19,062**
Willapa Bay creeks	**1973, 1981**	**2**	LCR H **& unk.**	**11,528**
	1989	1	mixed Coastal H	4,950
	1993	**1**	**mixed South Puget Sound H**	**137**
Abernathy Cr.	1986-1993	7	Beaver Creek H	37,260
	1965-1981	**17**	LCR H **& unk.**	**143,097**
Beaver Creek H	1982	1	Cowlitz H	58,960
	1984	**1**	**Deschutes R. (WA)**	**33,850**
	1982	12	Beaver Creek H	417,127
	1960-1981	**19**	LCR H **& unk.**	**544,185**
Germany Cr.	1984-1993	10	Beaver Creek H	74,581
	1965-1981	**17**	LCR H **& unk.**	**126,965**
Cowlitz R.	1982-1994	13	Cowlitz H	1,719,144
	1984-1993	10	Beaver Creek H	264,607
	1962-1994	**25**	**unk.**	**3,847,093**
	1992, 1993	2	WF Washougal R.	15,167
Lewis R.	1986	1	Cowlitz H	2,665
	1983-1993	7	Beaver Creek H	85,099
	1961-1981	**20**	LCR H **& unk.**	**1,135,417**
	1987	1	mixed Coastal H	3,000
	1961-1992	21	WF Washougal R.	1,512
Salmon Cr.	**1966-1981**	**7**	LCR H **& unk.**	**41,052**
Washougal R.	1983-1987	4	Cowlitz H	142,450
	1984, 1991	2	Beaver Creek H	51,903
	1972-1981	**10**	LCR H **& unk.**	**99,911**
	1990	1	mixed Coastal H	43,906
	1994	1	Skamania H	10,856
	1988-1994	5	WF Washougal R.	146,835
Hamilton Cr.	1989-1991	3	Beaver Creek H	13,360
	1966	**1**	LCR H **& unk.**	**450**
	1992, 1993	2	WF Washougal R.	9,997

Table A-1. (Continued).

Watershed[a]	Duration	Years	Stock Source[b]	Total
Lower Columbia R.	1991	1	Beaver Creek H	4,064
	1966-1981	**7**	**LCR H & unk.**	**25,241**
	1984-1989	3	mixed Coastal H	1,250
Klickitat R.	**1966**	**1**	**unk.**	**900**
Mid-Columbia R. creeks	1991	1	Hood Canal mixed H	300
	1987	1	mixed Coastal H	127,979
	1980, 1989	2	WF Washougal R.	16,382
Yakima R.	**1965**	**1**	**unk.**	**98,352**
Cullaby Lk.	**1956-1971**	**4**	**Alsea H**	**70,370**
	1994	1	Big Creek H	4,881
	1970	**1**	**Bandon H**	**105,131**
	1952-1956	**4**	**unk.**	**5,146**
Lewis & Clark R.	**1956-1982**	**20**	**Alsea H**	**72,348**
	1984-1990	7	Big Creek H	22,386
	1963	1	Columbia R.	20,351
	1979	**1**	**Bandon H**	**2,000**
	1955, 1974	**2**	**Cedar Creek H**	**5,009**
	1958	1	Roaring River H	4,996
	1949-1954	**4**	**unk.**	**8,618**
Youngs R.	**1957-1981**	**18**	**Alsea H**	**45,026**
	1979	**1**	**Bandon H**	**2,501**
	1955-1974	3	Cedar Creek H	6,456
	1958	1	Roaring River H	2,001
Klaskanine R.	1991-1993	3	Big Creek H	9,142
	1955	**1**	**Cedar Creek H**	**1,997**
	1940-1954	**3**	**unk.**	**10,103**
Big Creek H	**1956-1975**	**17**	**Alsea H**	**46,259**
	1980-1993	14	Big Creek H	67,362
	1955, 1974	**2**	**Cedar Creek H**	**3,502**
	1958	1	Roaring River H	4,136
	1949-1954	**4**	**unk.**	**9,427**
Gnat Cr.	**1971-1982**	**8**	**Alsea H**	**20,641**
	1985-1993	9	Big Creek H	18,593
	1979	**1**	**Bandon H**	**2,000**
	1974	1	Cedar Creek H	2,000

Table A-1. (Continued).

Watershed[a]	Duration	Years	Stock Source[b]	Total
Plympton Cr.	**1964**	**1**	**Alsea H**	**1,347**
	1949-1954	**4**	**unk.**	**4,320**
Clatskanie R.	**1956-1973**	**13**	**Alsea H**	**15,995**
	1955, 1974	**2**	**Cedar Creek H**	**2,997**
	1949-1957	**6**	**unk.**	**17,741**
LCR creeks	**1956-1972**	**12**	**Alsea H**	**11,993**
	1991-1994	3	Big Creek H	24,344
	1955, 1974	2	Cedar Creek H	3,202
	1958	1	Roaring River H	1,003
	1949, 1965	**2**	**unk.**	**9,031**
Milton Cr.	**1962-1964**	**3**	**Alsea H**	**10,899**
	1955	1	Cedar Creek H	499
	1949-1954	**4**	**unk.**	**2,285**
Scappoose Cr.	**1956-1964**	**7**	**Alsea H**	**17,036**
	1991-1993	3	Big Creek H	12,022
	1957	1	Hood R.	299
	1955	**1**	**Cedar Creek H**	**1,500**
	1958	1	Roaring River H	2,021
	1949-1963	**5**	**unk.**	**6,278**
Sandy R.	**1961**	**1**	**Alsea H**	**3,002**
	1966	1	Rapid R.	2,410
	1949	**1**	**unk.**	**1,074**
	1969	1	Utah	1,250
Clackamas R.	**1961**	**1**	**Alsea H**	**3,001**
	1963	**1**	**California**	**30,680**
	1962	1	Carson NFH	32,000
	1957	1	Hood R.	45,240
	1962	**1**	**Klamath H**	**76,800**
	1960-1975	10	Long Tom R. (Leaburg H)	372,652
	1966	1	Rapid R.	50,635
	1957-1959	3	Roaring River H	63,851
	1949-1959	**3**	**unk.**	**12,734**
	1969	**1**	**Utah**	**40,200**
	1967	1	Wickiup Res.	50,172
NF Clackamas R.	**1961**	**1**	**Alsea H**	**2,003**

Table A-1. (Continued).

Watershed[a]	Duration	Years	Stock Source[b]	Total
Sportsman Lk.	1970-1975	4	Long Tom R. (Leaburg H)	1,348
EF Hood R.	**1975**	**1**	**Alsea H**	**37,100**
	1974	**1**	**Cedar Creek H**	**24,003**
Hood R.	**1975, 1978**	**2**	**Alsea H**	**26,538**
Neal Cr.	**1975-1978**	**3**	**Alsea H**	**15,111**
	1974	**1**	**Cedar Creek H**	**5,007**
Deschutes R.	1959	1	Hood R.	370
	1960	1	Oak Springs H	12,000
Warm Springs R.	1979	1	Warm Springs NFH	67,500
Mountain Lks.	**1974**	**1**	**California**	**13,224**
	1967, 1969	2	Carson NFH	44,900
	1969-1975	6	Long Tom R. (Leaburg H)	44,890
	1967-1969	3	Paulina Lakes	2,398
	1960	**1**	**unk.**	**949**
	1969	**1**	**Utah**	**5,570**
Willamette River Basin				
Tualatin R.	**1956-1976**	**6**	**Alsea H**	**25,017**
	1957	1	Hood R.	575
	1966	1	Leaburg H	1,441
	1955, 1974	**2**	**Cedar Creek H**	**10,945**
	1949-1954	**4**	**unk.**	**26,415**
Dairy Cr.	**1956-1976**	**10**	**Alsea H**	**45,423**
	1965	**1**	**Bandon H**	**1,996**
	1957	1	Hood R.	275
	1955, 1974	**2**	**Cedar Creek H**	**5,018**
	1957, 1958	2	Roaring River H	2,496
	1949-1954	**4**	**unk.**	**17,775**
Pudding R.	**1955**	**1**	**Alsea H**	**2,999**
	1949-1955	**5**	**unk.**	**7,216**
Molalla R.	**1949**	**1**	**unk.**	**300**
Yamhill R.	**1956-1964**	**7**	**Alsea H**	**14,027**

Table A-1. (Continued).

Watershed[a]	Duration	Years	Stock Source[b]	Total
	1965	1	Bandon H	1,007
	1955	1	Cedar Creek H	2,000
	1958	1	Roaring River H	2,001
	1949-1954	4	unk.	26,967
Willamette R.	1949-1953	3	unk.	7,247
	1955-1980	3	Alsea H	3,561
	1949-1954	4	unk.	7,011
Luckiamute R.	1955-1967	3	Alsea H	9,669
	1949-1955	5	unk.	18,222
Santiam R.	1949	1	unk.	101,802
N Santiam R.	1973-1975	3	Leaburg H	1,156
	1949-1958	3	unk.	155,403
	1969-1975	5	unk.	1,904
	1969	1	Utah	1,200
Mary's R.	1955, 1960	2	Alsea H	2,181
	1949-1955	5	unk.	24,671
McKenzie R.	1955	1	Alsea H	14,339
	1955-1975	6	Leaburg H	269,753
	1949-1954	4	unk.	68,476
Mountain Lks.	1965-1975	9	Leaburg H	73,329
	1982	1	NF Nehalem R.	32,844
	1956	1	unk.	3,016
CF Willamette R.	1967-1973	5	Leaburg H	211,561
	1949	1	unk.	20,325
MF Willamette R.	1968-1973	3	Leaburg H	29,880
Long Tom R.	1966, 1974	23	Leaburg H	72
	1952	1	unk.	1,130
4) Oregon Coast ESU				
Necanicum R.	1956-1993	31	Alsea H	387,119
	1979	1	Bandon H	5,997
	1955, 1974	2	Cedar Creek H	8,999
	1986-1994	5	NF Nehalem R.	61,131
	1958	1	Roaring River H	10,748
	1949-1954	4	unk.	13,185

Table A-1. (Continued).

Watershed[a]	Duration	Years	Stock Source[b]	Total
NF Nehalem R.	1959-1981	17	Alsea H	64,777
	1963	1	Bandon H	927
	1955-1974	3	Cedar Creek H	8,072
	1982-1994	13	NF Nehalem R.	190,553
	1949-1954	**4**	**unk.**	**42,371**
Nehalem R.	1956-1981	20	Alsea H	225,822
	1963, 1965	2	Bandon H	5,646
	1975	**1**	**Big Creek H**	**3,002**
	1955-1974	3	Cedar Creek H	24,998
	1980-1993	14	NF Nehalem R.	189,290
	1956, 1957	**2**	**Oak Springs H**	**7,325**
	1958	**1**	**Roaring River H**	**5,008**
	1949-1973	**9**	**unk.**	**101,753**
Miami R.	1956-1981	20	Alsea H	42,769
	1979	1	Bandon H	2,508
	1955, 1974	1	Cedar Creek H	4,062
	1958	**1**	**Roaring River H**	**1,404**
	1949-1964	**6**	**unk.**	**64,694**
Kilchis R.	1956-1992	25	Alsea H	84,286
	1965, 1979	2	Bandon H	5,397
	1955, 1974	2	Cedar Creek H	7,411
	1984-1989	6	NF Nehalem R.	43,898
	1958	**1**	**Roaring River H**	**2,000**
	1949-1954	**5**	**unk.**	**70,047**
NF Wilson R.	1962-1978	9	Alsea H	9,220
	1974	1	Cedar Creek H	1,555
	1949-1954	**2**	**unk.**	**52,585**
Wilson R.	1956-1980	12	Alsea H	58,572
	1979	1	Bandon H	6,501
	1955	1	Cedar Creek H	3,090
	1987	1	NF Nehalem R.	15,396
	1957	**1**	**Oak Springs H**	**3,374**
	1949-1954	**4**	**unk.**	**192,313**
NF Trask R.	1965-1982	5	Alsea H	10,646
	1984-1988	4	NF Nehalem R.	6,013
Trask R.	1956-1994	27	Alsea H	190,719

Table A-1. (Continued).

Watershed[a]	Duration	Years	Stock Source[b]	Total
	1979	1	Bandon H	6,998
	1955, 1974	2	Cedar Creek H	19,073
	1984-1989	6	NF Nehalem R.	22,642
	1957	**1**	**Oak Springs H**	**693**
	1958	**1**	**Roaring River H**	**8,790**
	1952-1954	**3**	**unk.**	**135,482**
Tillamook R.	1956-1993	25	Alsea H	85,871
	1979	1	Bandon H	2,506
	1955, 1974	2	Cedar Creek H	3,200
	1983-1989	7	NF Nehalem R.	146,745
	1958	**1**	**Roaring River H**	**1,601**
	1949-1954	**4**	**unk.**	**217,006**
Sand Cr.	1956-1966	9	Alsea H	6,505
	1955	1	Cedar Creek H	163
	1958	**1**	**Roaring River H**	**805**
	1949, 1963	**2**	**unk.**	**1,936**
North Coast Ind Cr.	**1954**	**1**	**unk.**	**2,387**
Northern coastal lakes	1955-1994	33	Alsea H	1,030,413
	1963-1979	3	Bandon H	12,580
	1986-1994	**5**	**Big Creek H**	**55,400**
	1955, 1974	2	Cedar Creek H	14,408
	1958	**1**	**Hood R.**	**1,702**
	1980-1994	13	NF Nehalem R.	315,199
	1957	**1**	**Oak Springs H**	**2,003**
	1954, 1958	**2**	**Roaring River H**	**8,189**
	1950-1956	**5**	**unk.**	**157,610**
Nestucca R.	1955-1993	24	Alsea H	580,322
	1968, 1979	2	Bandon H	31,644
	1955, 1974	2	Cedar Creek H	21,383
	1983-1987	7	NF Nehalem R.	362,899
	1957	**1**	**Oak Springs H**	**1,200**
	1958, 1966	**2**	**Roaring River H**	**8,781**
	1949-1967	**6**	**unk.**	**504,898**
Hebo Lk.	1955-1994	27	Alsea H	133,929
	1965	1	Bandon H	2,292
	1974	1	Cedar Creek H	4,481
	1982-1994	10	NF Nehalem R.	113,849
	1950-1966	**4**	**unk.**	**26,561**

Table A-1. (Continued).

Watershed[a]	Duration	Years	Stock Source[b]	Total
Little Nestucca R.	1956-1992	24	Alsea H	77,682
	1979	1	Bandon H	3,003
	1984-1989	6	NF Nehalem R.	39,654
	1956	**1**	**Oak Springs H**	**1,777**
	1958	**1**	**Roaring River H**	**1,200**
	1949-1954	**4**	**unk.**	**3,149**
Three R.	1956-1994	24	Alsea H	61,950
	1963, 1979	2	Bandon H	2,285
	1955-1974	3	Cedar Creek H	6,504
	1984-1989	6	NF Nehalem R.	146,348
	1957	**1**	**Oak Springs H**	**502**
	1958	**1**	**Roaring River H**	**697**
	1952-1954	**3**	**unk.**	**7,413**
Neskowin Cr.	1956-1973	15	Alsea H	12,802
	1955, 1974	2	Cedar Creek H	1,200
	1957	**1**	**Oak Springs H**	**200**
	1958	**1**	**Roaring River H**	**201**
	1949-1954	**4**	**unk.**	**93,579**
Salmon R.	1956-1994	33	Alsea H	151,046
	1973, 1979	2	Bandon H	8,003
	1955, 1974	2	Cedar Creek H	6,195
	1957	**1**	**Oak Springs H**	**1,582**
	1949-1954	**4**	**unk.**	**10,194**
Devil's Lk.	1956-1984	16	Alsea H	1,438,516
	1965, 1963	2	Bandon H	32,966
	1957	**1**	**unk.**	**8,000**
Siletz R.	1955-1994	36	Alsea H	532,109
	1968-1979	4	Bandon H	66,968
	1974	1	Cedar Creek H	15,005
	1949-1954	**4**	**unk.**	**181,779**
Yaquina R.	1955-1960	6	Alsea H	17,496
	1949-1954	**4**	**unk.**	**89,809**
Alsea R.	1955-1994	39	Alsea H	1,516,377
	1971	1	Alsea H /Bandon H mix	561
	1965, 1979	2	Bandon H	17,703
	1974	1	Cedar Creek H	9,002
	1949-1967	**6**	**unk.**	**336,994**

Table A-1. (Continued).

Watershed[a]	**Duration**	**Years**	**Stock Source**[b]	**Total**
	1963	**1**	**Wickiup Res.**	**17,499**
Five Rivers	1955-1963	9	Alsea H	31,134
	1949-1958	**6**	**unk.**	**154,307**
Yachats R.	1955-1976	14	Alsea H	27,310
	1973	1	Bandon H	999
	1949-1954	**4**	**unk.**	**156,851**
Big Creek Res.	1955-1994	19	Alsea H	141,335
	1949-1954	**3**	**unk.**	**2,662**
Siuslaw R.	1955-1994	37	Alsea H	1,024,328
	1956-1979	9	Bandon H	135,706
	1949-1955	**5**	**unk.**	**39,270**
NF Siuslaw R.	1955-1993	24	Alsea H	124,029
	1974	1	Bandon H	4,000
	1952-1954	**3**	**unk.**	**4,424**
Mid Coast Ind Cr.	1957	1	Alsea H	222
	1953	**1**	**unk.**	**11,549**
Mid-coast Lks.	1955-1994	34	Alsea H	1,195,574
	1955-1972	10	Bandon H	306,137
	1974	1	Cedar Creek H	6,986
	1963, 1972	**2**	**Oak Springs H**	**1,115**
	1949-1965	**9**	**unk.**	**265,171**
Siltcoos Lk.	1955-1989	17	Alsea H	632,738
	1955-1965	8	Bandon H	222,191
	1969	1	Cedar Creek H	53,499
	1949-1954	**5**	**unk.**	**21,099**
Tahkenitch Lk.	1955-1986	12	Alsea H	394,419
	1955-1970	8	Bandon H	121,988
	1949-1958	**7**	**unk.**	**46,944**
Umpqua R.	1982-1993	11	Alsea H	91,308
	1963-1973	5	Bandon H	18,940
	1949-1950	**2**	**unk.**	**15,212**
NF Smith R.	1994	1	Alsea H	8,003
	1976	1	Bandon H	7,495

Table A-1. (Continued).

Watershed[a]	Duration	Years	Stock Source[b]	Total
Smith R.	1980-1984	14	Alsea H	184,716
	1955-1979	8	Bandon H	57,926
	1949-1954	**4**	**unk.**	**14,672**
NF Umpqua R.	1961-1979	14	Bandon H	198,981
	1967, 1969	**2**	**unk.**	**32,325**
Eel Lk.	1968-1985	7	Alsea H	179,228
	1954-1979	21	Bandon H	1,181,920
	1949-1969	**5**	**unk.**	**141,865**
North Tenmile Lk.	1974	1	Alsea H	52,000
	1957-1978	19	Bandon H	539,822
	1954	**1**	**unk.**	**420**
	1967, 1969	**2**	**unk.**	**36,513**
Tenmile Lk.	1955-1978	16	Bandon H	418,656
	1949-1954	**4**	**unk.**	**115,926**
	1967, 1969	**3**	**unk.**	**25,765**
Tenmile Cr.	1955-1961	6	Alsea H	4,994
	1949-1961	**8**	**unk.**	**8,116**
Saunders Lk.	1955-1978	20	Bandon H	308,475
	1967, 1968	**2**	**unk.**	**2,999**
Millicoma R.	1955, 1956	2	Bandon H	2,981
	1949, 1954	**2**	**unk.**	**17,964**
WF Millicoma R.	1980-1985	4	Alsea H	9,905
	1955-1979	20	Bandon H	34,869
	1956	**1**	**Roaring River H**	**1,000**
	1949, 1953	**2**	**unk.**	**14,475**
	1967, 1969	**2**	**unk.**	**2,000**
EF Millicoma R.	1957-1978	15	Bandon H	32,002
	1971	**1**	**Roaring River H**	**1,001**
	1967-1969	**2**	**unk.**	**4,000**
Coos R.	1963	1	Bandon H	1,001
	1953-1969	**3**	**unk.**	**47,600**
SF Coos R.	1980-1985	5	Alsea H	12,609
	1955-1979	20	Bandon H	48,319

Table A-1. (Continued).

Watershed[a]	Duration	Years	Stock Source[b]	Total
	1967	**1**	**unk.**	**1,998**
	1953, 1954	**2**	**unk.**	**4,181**
Empire Lk.	1980	1	Alsea H	551
	1960-1978	14	Bandon H	34,011
	1967	**1**	**unk.**	**4,166**
South Coast Ind Cr.	1981	1	Alsea H	6,032
	1957-1978	9	Bandon H	237,321
	1949	**1**	**unk.**	**165,757**
NF Coquille R.	1980-1985	5	Alsea H	14,024
	1955-1979	18	Bandon H	51,102
	1964	**1**	**Roaring River H**	**1,001**
	1967, 1969	**2**	**unk.**	**6,003**
	1949-1954	**4**	**unk.**	**81,972**
MF Coquille R.	1955-1973	11	Bandon H	22,987
	1967-1969	**2**	**unk.**	**3,502**
	1952-1954	**3**	**unk.**	**8,515**
EF Coquille R.	1980-1985	5	Alsea H	12,219
	1955-1979	19	Bandon H	44,348
	1967, 1969	**2**	**unk.**	**4,998**
	1949-1954	**4**	**unk.**	**83,373**
SF Coquille R.	1980-1985	5	Alsea H	13,727
	1955-1979	15	Bandon H	36,619
	1967	**1**	**unk.**	**3,998**
	1949-1954	**4**	**unk.**	**27,043**
Coquille R.	1959-1972	5	Bandon H	7,573
	1949, 1952	**2**	**unk.**	**244,625**
Bradley Lk.	1957-1978	17	Bandon H	427,256
	1949-1954	**4**	**unk.**	**68,818**
Floras Cr.	1955-1966	5	Bandon H	20,144
	1949-1954	**4**	**unk.**	**31,331**
Floras Lk.	1955-1976	12	Bandon H	62,959
	1949-1967	**5**	**unk.**	**32,848**
Sixes R.	1955-1956	2	Bandon H	4,502
	1949-1954	**4**	**unk.**	**18,014**

Table A-1. (Continued).

Watershed[a]	**Duration**	**Years**	**Stock Source**[b]	**Total**
5) Southern Oregon/California Coasts ESU				
Elk R.	**1955, 1956**	**2**	**Bandon H**	**3,076**
	1952-1954	**3**	**unk.**	**10,803**
Garrison Lk.	**1954-1976**	**14**	**Bandon H**	**61,746**
	1956	**1**	**Roaring River H**	**2,002**
	1949-1967	**4**	**unk.**	**26,810**
Brush Cr.	**1955-1963**	**8**	**Bandon H**	**8,672**
	1952, 1953	**2**	**unk.**	**2,057**
Big Butte Cr.	1973	1	Butte Falls H	128
Mountain Lks.	1973	1	Butte Falls H	6,103
	1967	1	Utah	50,192
Hunter Cr.	**1980-1985**	**5**	**Alsea H**	**4,277**
	1955-1979	**16**	**Bandon H**	**21,005**
	1967-1969	**2**	**unk.**	**2,995**
	1954	**1**	**unk.**	**998**
Pistol R.	**1980-1985**	**5**	**Alsea H**	**3,919**
	1955-1979	**14**	**Bandon H**	**24,712**
Chetco R.	**1980-1985**	**5**	**Alsea H**	**11,520**
	1955-1979	**18**	**Bandon H**	**78,132**
	1967, 1969	**2**	**unk.**	**8,398**
Winchuck R.	**1955-1979**	**14**	**Bandon H**	**19,850**
	1969	**1**	**unk.**	**2,001**
Marie Lk.	**1994**	**1**	**Alsea H**	**3,909**
	1955-1974	**16**	**Bandon H**	**211,349**
	1967	**1**	**unk.**	**2,002**
	1952, 1954	**2**	**unk.**	**152,800**

Table A-1. (Continued).

Abbreviations

[a]Watershed

NF - North Fork
EF - East Fork
CF - Central Fork
MF - Middle Fork
WF - West Fork
SF - South Fork

[b]Stock Source

H - hatchery
mixed - a mixture of two or more stocks from the same area
LCR - lower Columbia River
NFH - National Fish Hatchery
/ - a mixture of stocks from different areas
unk. - unknown
NF - North Fork
WF - West Fork

APPENDIX B: THE RISK MATRIX METHOD

APPENDIX B: THE RISK MATRIX METHOD

To tie the various risk considerations into an overall assessment of extinction risk for each evolutionarily significant unit (ESU), Biological Review Team (BRT) members used a matrix form (Table B-1) to score risks in a number of categories. The following method was used for scoring and reaching an overall conclusion regarding extinction risk for an ESU:

1. After reviewing previous documents and hearing presentations and discussions during the meeting, each BRT member filled in as much of the matrix as possible, scoring the various factors according to the relative degree of risk based on available information.
2. Scores from individual members were tallied on a single sheet and summarized.
3. The BRT reached an overall conclusion regarding the degree of extinction risk facing each ESU after steps 1 and 2 were completed and discussed.

The following is a list of factors considered. This is not a complete list, but covers considerations that have been important in past status reviews. Specific considerations within each area are discussed more fully in the main body of this report.

Risk Assessment Factors

Abundance

Questions regarding abundance can be put into three subcategories:

Small population risks—Is the overall ESU (or discrete populations within the ESU) at such low abundance that small-population risks (random genetic effects, Allee effects, random demographic or environmental effects) are likely to be significant?

Distribution—Do present populations adequately represent historical patterns of geographic distribution and ecological/genetic/life-history diversity? Does fragmentation of previously connected populations pose a risk? Is the ESU at risk in this subcategory in a significant portion of its range?

In the status review for coastal cutthroat trout (*Oncorhynchus clarki clarki*), BRT members explicitly considered the risk associated with reduction in life-history diversity.

Habitat capacity—Is abundance limited by current habitat capacity? If so, is current habitat capacity adequate to ensure continued population viability? (Here, only habitat capacity is

Table B-1. Example of a blank risk matrix for a single Evolutionarily Significant Unit (ESU). Each Biological Review Team member filled out scores on a separate form for each ESU.

Risk Factor	Comments	Risk
Abundance Small-Population Risks Distribution Habitat Capacity		
Trends/Productivity/Variability Population Trends Productivity Limiting Factors		
Genetic Integrity Loss of Fitness Loss of Diversity		
Other Risks		
Recent Events		
Summary: Overall Risk Level		
Concerns		

considered. Habitat quality as it affects trends or productivity is considered in the next section, "Trends, productivity, and variability.")

Trends, productivity, and variability

Again, considerations can be put into three subcategories:

Population trends—Is the overall ESU (or populations within it) declining in abundance at a rate that risks extinction in the near future? Is variation in population abundance, in combination with average abundance and trends, sufficiently high to cause risk of extinction?

Productivity—Has population productivity declined or is it declining toward the point where populations may not be sustainable? Is there evidence that natural populations are/can be self-sustaining without the infusion of hatchery-reared fish?

Limiting factors—Are there factors (such as poor freshwater or ocean habitat quality, harvest, human-induced mortality, or interactions with other species) that currently limit productivity to the point where populations may not be sustainable? Are such factors expected to continue? Are there natural or anthropogenic factors that have increased variability in reproduction or survival for populations beyond the historic range of environmental variability? Are there factors that have increased the vulnerability of populations to natural levels of environmental variability?

Genetic integrity

Genetic integrity can be affected through either random effects (included earlier under "Small-population risks") or directional effects. The major sources of directional effects of concern here are introduced genotypes, interactions with local or non-native hatchery fish, or artificial selection (e.g., through selective harvest or habitat modification). These directional effects pose two major types of risk for natural populations:

Loss of fitness—Has interbreeding or artificial selection reduced fitness of natural populations to the point that this is a significant extinction risk factor?

Loss of diversity—Has there been a substantial loss of diversity within or between populations?

For both types of risk, it may also be important to ask this question: Even if these interactions are not occurring at present, have past events substantially affected fitness and/or diversity of natural populations within the ESU to the extent that long-term population sustainability is compromised?

Other risks

Are there other factors that indicate risks to the sustainability of the ESU or component populations? These factors may include disease prevalence, predation, and changes in life-history characteristics such as spawning age or size.

Recent events

This category was included to recognize events (natural or anthropogenic) that have predictable effects on risk for the ESU but have occurred too recently to be reflected in abundance, trend, genetic, or other data considered by the BRT. Examples might include recent changes in management (such as harvest rates or hatchery practices), anthropogenic changes in the environment (habitat degradation or enhancement), or natural events (such as floods or volcanic eruptions). Recent changes in management were considered only where they were already fully or partially implemented and had reasonably predictable consequences.

Scoring Categories

Levels of risk—Individual factors

Risk from individual factors were ranked on a scale of 1 (very low risk) to 5 (high risk):

1) **Very low risk**—Unlikely that this factor contributes significantly to risk of extinction, either by itself or in combination with other factors.

2) **Low risk**—Unlikely that this factor contributes significantly to risk of extinction by itself, but some concern that it may in combination with other factors.

3) **Moderate risk**—This factor contributes significantly to long-term risk of extinction, but does not in itself constitute a danger of extinction in the near future.

4) **Increasing risk**—Present risk is low or moderate, but is likely to increase to high in the foreseeable future if present conditions continue.

5) **High risk**—This factor by itself indicates danger of extinction in the near future.

Levels of risk—Recent events

The "Recent Events" category does not represent specific risk factors, but rather factors that may alter the overall risk score for an ESU from the conclusion based on data available to date. This category was scored as follows:

++ Expect a strong improvement in status of the ESU
\+ Expect some improvement in status
0 Neutral effect on status
\- Expect some decline in status
-- Expect strong decline in status

Levels of risk—Overall summary

The summary score of overall risk uses categories that correspond to definitions in the Endangered Species Act (ESA): in danger of extinction, likely to become endangered in the foreseeable future, or neither. (Note, however, that these scores do not correspond to recommendations for a particular listing action because they are based only on past and present biological conditions of the populations and do not completely evaluate conservation measures as required under the ESA.)

This summary score is not a simple average of the risk factors for individual categories, but rather a judgment of overall risk based on likely interactions among factors. A single factor with a score of high risk may be sufficient to result in an overall score of "in danger of extinction"; this overall score, however, could also result from a combination of several factors with low or moderate risk scores.

Evaluation of Uncertainty

As discussed in the main document (see "Overall Evaluation of Risk and Uncertainty," p. 141), the BRT used two methods to characterize the uncertainty underlying their risk evaluations. The outcomes of the two methods were generally consistent. Results are described in "Summary and Conclusions of Risk Assessments," p. 194.

Results for the Coastal Cutthroat Trout Status Review

BRT scores for the three major categories of risk for each coastal cutthroat trout ESU are summarized in Table B-2. We do not summarize the "Other Risks" and "Recent Events" categories here because factors included in these categories varied among ESUs; these factors are discussed in the main body of this report. The Upper Willamette River ESU was not considered in risk evaluations because the U.S. Fish and Wildlife Service has jurisdiction over the coastal cutthroat trout in that ESU.

Table B-2. Summary of Biological Review Team (BRT) scores for main risk categories for coastal cutthroat trout Evolutionarily Significant Units (ESUs). As described in this appendix, each BRT member scored the level of risk for each factor (1=low risk, 5=high risk). Numbers in each cell are the mean score, with range of scores in parentheses.

ESU	Abundance	Trends/Productivity /Variability	Genetic Integrity
1) Puget Sound	3.1 (2-4)	2.8 (2-4)	2.2 (1-3)
2) Olympic Peninsula	2.3 (1-3)	2.7 (1-4)	1.5 (1-3)
3) Southwestern Washington/ Columbia River	3.9 (3-5)	3.8 (3-4)	3.1 (1-4)
4) Upper Willamette	Not applicable; BRT did not conduct a risk evaluation for this region		
5) Oregon Coast	3.2 (2-5)	3.6 (2-5)	2.6 (2-4)
6) Southern Oregon/ California Coasts	2.9 (2-5)	2.4 (1-4)	2.2 (1-4)

APPENDIX C: ADDITIONAL INFORMATION

Table C-1. Additional information on coastal cutthroat trout not included in Table 8 (acquired since the final Biological Review Team [BRT] meeting and therefore not considered in risk evaluations).

ESU						Recent abundance		Trends		
River Basin	Sub-basin	Production[1]	Stage	Method[2]	Data Years	Data Type[3]	5 Year Geomet. mean[4]	Long-term[5]	Short-term[6]	Data References
1-Puget Sound										
E. Hood Canal	Big Beef Cr.	Natural	Juvenile	TR	1978-97	OM	736	+5.1	+14.6	WDFW 1998c
	Snow Cr.	Natural	Juvenile	TR	1978-98	OM	20	+0.4	+23.1	WDFW 1998c
2-Olympic Peninsula										
Strait of Juan de Fuca	Barnes Cr.	Natural	Adult	SS	1989-98	RC	103	+20.0	+20.0	WDFW 1998c
	Lyre Cr.	Natural	Adult	SS	1994-98	RC	57	+0.1		WDFW 1998c
3-Southwestern Washington/Columbia River										
Chehalis R.	Hoquiam R.	Natural	Adult	HL	1986-95	CPUE	1	+7.7	+14.6	Hunter unpub. data
Satsop R.	Bingham Cr.	Natural	Juvenile	TR	1982-98	OM	98	-2.7	+0.5	WDFW 1998b
Satsop R.	Bingham Cr.	Natural	Adult	TR	1984-97	TL	7	+8.0	+22.8	Hunter unpub. data
Grays Harbor	Multiple streams	Natural	Adult	HL	1986-97	SC	169	+15.6	+16.6	Hunter unpub. data
Grays Harbor	Multiple streams	Hatchery	Adult	HL	1986-97	SC	40	-0.3	-4.8	Hunter unpub. data
Grays Harbor	Multiple streams	Total	Adult	HL	1986-97	SC	200	+9.9	+9.7	Hunter unpub. data
Grays Harbor	Newskah R.	Natural	Adult	HL	1986-95	CPUE	2	+6.3	+6.3	Hunter unpub. data
Grays Harbor	Johns R.	Natural	Adult	HL	1986-95	CPUE	1	+13.2	+16.3	Hunter unpub. data
Grays Harbor	Elk R.	Natural	Adult	HL	1986-95	CPUE	1	+11.4	+24.4	Hunter unpub. data
Grays Harbor	Chenois R.	Natural	Adult	HL	1986-95	CPUE	1	-4.3	-1.5	Hunter unpub. data
Grays Harbor	Andrews R.	Natural	Adult	HL	1986-95	CPUE	3	+6.5	+6.0	Hunter unpub. data
4-Oregon Coast										
Nestucca Bay	Nestucca R.	Natural	Adult	SN	1965-98	RH	1	-0.3	+3.7	ODFW 1998
Tillamook Bay	Trask R.	Natural	Adult & Jacks	SN	1965-98	RH	4	-1.5	+1.1	ODFW 1998
	Wilson R.	Natural	Adult & Jacks	SN	1965-98	RH	2	-6.7	+4.1	ODFW 1998
Coos Bay	Millicoma R.	Natural	100-200mm	SE	1978-98	CPUE	0.28	+3.7	+14.9	ODFW 1998
	Millicoma R.	Natural	>200mm	SE	1978-98	CPUE	0.09	-1.4	-1.8	ODFW 1998

Table C-1. (Continued).

ESU River Basin	Sub-basin	Production[1]	Stage	Method[2]	Data Years	Recent abundance		Trends		Data References
						Data Type[3]	5 Year Geomet. mean[4]	Long-term[5]	Short-term[6]	
	S. Coos R.	Natural	100-200mm	SE	1978-98	CPUE	0.06	+1.0	+13.1	ODFW 1998
	S. Coos R.	Natural	>200mm	SE	1978-98	CPUE	0.03	-4.5	-2.3	ODFW 1998
5-Southern Oregon/Northern California Coast										
	SF Smith R.	Natural	Adult & Juveniles	SN	1991-98	TE	289	+0.9	+0.2	McCain unpubl. data
	MF Smith R.	Natural	Adult & Juveniles	SN	1991-98	TE	289	+1.7	+5.0	McCain unpubl. data
	NF Smith R.	Natural	Adult & Juveniles	SN	1992-98	TE	222	+5.0		McCain unpubl. data
Klamath R. Estuary	Klamath R.	Natural	Adult	EF	1991-98	CPUE	0.2	+19.6	+19.6	Gale 1998

[1] Production: As reported by data reference.

[2] Method Codes: EF, electrofishing; HL, hook and line sampling; SE, seine; SN, snorkel; SS, spawner survey; TR, trap.

[3] Data Type Codes: CPUE, catch per unit effort; OM, number of outmigrants; RC, redd count; RH, resting hole counts; SC, sport catch; TE, total estimates; TL, total live fish count.

[4] Most recent 5 years of data used to calculate geometric mean abundance.

[5] Long-term Trend: Calculated for all data collected after 1947.

[6] Short-term Trend: Calculated for most recent 7-10 years during the period 1988-1998.

Table C-2. Additional life-history data on coastal cutthroat trout acquired after the final Biological Review Team (BRT) meeting and therefore not considered in determinations of evolutionarily significant units (ESUs) (this data not included in Tables 4 and 5).

Region	**River System**	**Average length in mm (range)**	**Predominant age at first saltwater migration**	**Citation**	**Notes**
Puget Sound					
	McLane Cr.	411 (229-572) females 336 (248-458) males	2	Peoples et al. 1987	July 1986 to June 1987. Fish captured by electrofishing tidally-influenced pools after high tide.
	Minter Cr.	394 (248-533) females 357 (267-470) males	2	"	"
Southwestern Washington/Columbia River					
	Chelatchie Cr. (Columbia R. tributary)	183 (89-423)		Pettit unpubl. data	Downstream migrant trap operated from 1985 to 1987.
Grays Harbor	WF Hoquiam R.	289 (171-402)	2	Hunter unpubl. data	Upstream migrant coastal cutthroat trout captured on West Fork of Hoquiam R., Oct.-Dec. 1994, and aged by scale analysis.
		285 (126-482)	2	Hunter unpubl. data	Upstream migrant coastal cutthroat trout captured on West Fork of Hoquiam R. by Quinault Department of Fisheries, 1985-1998 (N=525). Trap generally operated Oct. to Dec.
	Chenois Cr.	310-360		"	All cutthroat trout captured by angling by D. Dombrowski, early July through Nov. 1995-97. Fish measured to nearest inch (25.4 mm).
	Elk R.	310-360		"	"
	Johns R.	310-360		"	"
	E. Hoquiam R.	300-350		"	"
	Andrews Cr.	310-360		"	"
	Newskah Cr.	310-360		"	"

Table C-2. (Continued).

Region	Average length in mm (range)	Predominant age at first saltwater migration	Citation	Notes
River System				
Wynoochee R.	340-390		"	"
Barlow Cr.	320-370		"	"
Charlies and Wishkah R.	320-370		"	"
North Fork Toutle R.	173 (85-241)		Seiler et al. 1992	Downstream migrating cutthroat trout captured in the fish collection facility.
North Fork Toutle R.	318 females 286 males		Loch and Downing 1990	Upstream migrating cutthroat trout. Most of the 17 adults were immigrating for the first time and two were repeat spawners.

GLOSSARY

GLOSSARY

Note: **Bold-faced words** are defined elsewhere in this glossary.

abiotic
Devoid of life; *cf.* **biotic.**

ADFG
Alaska Department of Fish and Game

adfluvial
Fish that migrate between lakes and rivers or streams. These fish may also be called **lacustrine** and are sometimes further characterized as to whether they spawn in outlet tributaries **(allacustrine)** or inlet tributaries **(lacustrine-adfluvial)**.

AFS
American Fisheries Society

alevin
Life-history stage of a salmonid immediately after hatching and before the yolk-sac is absorbed. Alevins usually remain buried in the gravel in or near a series of **redds** until the yolk sac is absorbed, after which they **swim up** and enter the water column.

allele
An alternative form of a gene that can occur at the same location (**locus**) on homologous (paired) chromosomes. A population can have many alleles for a particular locus, but an individual can carry no more than two alleles at a diploid locus.

allochthonous
Materials from outside a system, such as leaves and insects that fall from terrestrial plants into a stream.

allacustrine
Fish that rear in lakes and spawn in outlet tributaries of lakes.

allozymes
Alternative forms of an enzyme that have the same function, are produced by different **alleles,** and are often detected by **protein electrophoresis**.

amphidromy (*adj.* amphidromous)
Migratory fishes whose migrations between fresh water and sea are not exclusively for breeding but occur regularly at some other stage of the life cycle.

anadromy (*adj.* anadromous)

The **life-history** pattern that features early juvenile development in fresh water, migration to seawater, and a return to freshwater for spawning. The coastal cutthroat trout (*Oncorhynchus clarki clarki*) is considered an anadromous subspecies, but not all members of the subspecies necessarily go to sea each year. Interior subspecies of *O. clarki* are considered **nonanadromous** because no members of those subspecies go to sea.

ANOVA (analysis of variance)

A statistical technique for estimating how much of the variability in a set of observations can be ascribed to different causes (i.e., partitioning of variance).

anthropogenic

Caused or produced by human action.

artificial propagation

Artificial propagation of salmon refers to the practice of manually spawning adult fish and rearing the progeny in hatcheries, egg boxes, remote site incubators, or other facilities before release into the natural environment.

assortative mating

Preference for mating between individuals with like **genotypes** or **phenotypes**.

basibranchial teeth

Teeth on the median ventral plate (base of tongue) overlying basibranchial bones between the gill arches. Basibranchial teeth are often considered a distinguishing feature of cutthroat trout and used to separate them from rainbow and redband trout or steelhead. However, not all populations/forms of cutthroat trout have these teeth, and some rainbow/redband populations do have them. Basibranchial teeth in juvenile fish of all three species may be undetectable.

Biological Review Team (BRT)

The team of scientists who evaluated a scientific information considered in the National Marine Fisheries Service status review.

biotic

Pertaining to life or living organisms; caused or produced by or comprising living organisms; *cf.* **abiotic.**

CDFG

California Department of Fish and Game

coefficient of condition *or* condition factor (K)

Numerical index representing the relationship between body weight and length of a fish. The condition factor can be represented by the equation $K = \text{weight}/(\text{length})^3$, with weight expressed in grams and length in millimeters.

co-managers

Federal, state, county, local, and tribal agencies that cooperatively manage **salmonids** in the Pacific Northwest.

continuous variation

Variations between individuals of a population in a character or trait in which the differences are slight and occur as a continuous series.

CPUE

catch-per-unit effort

dendrogram

Branching diagram, sometimes resembling a tree, that depicts similarities and differences between groups or samples. See **multidimensional scaling**.

discrete variation

Variations between individuals of a population in a character or trait in which the differences are marked and do not occur as a continuous gradient.

DNA (deoxyribonucleic acid)

DNA is a complex molecule that carries an organism's heritable information. The two types of DNA commonly used to examine genetic variation are **mitochondrial DNA (mtDNA)**, a circular molecule that is maternally inherited, and nuclear DNA, which is organized into a set of chromosomes (see also **allele** and **electrophoresis**).

egg boxes

Stream-side boxes where fertilized salmon eggs are incubated until the fry stage, when the juveniles swim out of the box and enter the stream.

electrophoresis

Electrophoresis is the movement of charged particles in an electric field. This process has been developed as an analytical tool to detect genetic variation revealed by charge differences on proteins or molecular weight in **DNA**. Data obtained by electrophoresis can provide insight into levels of genetic variability within **populations** and the extent of genetic differentiation between them.

endangered species

A **species** in danger of extinction throughout all or a significant portion of its range.

EPA

U.S. Environmental Protection Agency

ESA

U.S. Endangered Species Act

escapement

The fish in a population or run that "escape" all fisheries and return to the freshwater spawning area.

evolutionarily significant unit (ESU)

An ESU represents a distinct population segment under the Endangered Species Act that 1) is substantially reproductively isolated from nonspecific populations and 2) represents component an important component of the evolutionariy legacy of the species.

euryhaline

Organisms that tolerate a wide range of salinities.

FEMAT

Forest Ecosystem Management Assessment Team

fluvial

Pertaining to rivers and river action, this term for a **life-history form** of cutthroat trout has at least two regional connotations. The term may mean fish that are **nonanadromous** but conduct extensive feeding or spawning migrations within river systems (*cf.* **freshwater migrating, potamodromous,** or **riverine**). The term may also refer to fish that conduct only small migrations and reside primarily in headwater streams or upper tributaries (*cf.* **nonmigrant**). Because the term has multiple meanings, its use is avoided in this status review.

freshwater forms

An inclusive description of the life-history forms (freshwater migrants and nonmigrants)of cutthroat trout that occur within fresh water and do not enter seawater (*cf.* **nonanadromous**).

freshwater migrant/migratory

Cutthroat trout that migrate solely within the freshwater environment. These fish primarily reside in rivers or lakes while feeding or overwintering, but typically return to smaller tributaries or headwater streams to spawn (*cf.* **nonmigrant/migratory, potamodromous, riverine, lacustrine**).

fry

Stage in the **salmonid** life history when the juvenile has absorbed its yolk sac and leaves the gravel of the **redd** to **swim up** into the water column.

GDU

Genetic Diversity Unit, which represents subsets of Major Ancestral Lineages (MALs).

genetic distance

A quantitative measure of genetic difference between a pair of samples.

genetic drift

The occurrence of random changes in the gene frequencies of **populations**.

genome (*adj.* genomic)
The total genetic constitution of an organism.

genotype
The set of genes possessed by an individual organism.

haplotype
The collective genotype of a number of closely linked **loci**; the constellation of **alleles** present at a particular region of **genomic** or **mitochondrial DNA**.

hatchery produced
Any fish reared in a hatchery (*cf.* **natural fish, naturally spawning fish**).

hatchery stock
A **population** of fish associated with a hatchery. A hatchery stock is spawned and reared in a hatchery before release. Historically, hatchery stocks were often transferred among hatcheries, but this practice is now less common.

heterozygous
The condition of having two different **alleles** at a given **locus** of a **chromosome** pair.

heterozygosity
A measure of allelic diversity at a **locus** (or averaged over several **loci**) whereby alternate **alleles** at a locus are different.

homologous chromosome
Structurally similar chromosomes with the same sequence of genes and that pair during division of the cell nucleus.

hybridization
Reproduction between individuals of different genetic compositions, typically belonging to separate species, that results in hybrid offspring (e.g., cutthroat trout × rainbow trout).

karyotype
The chromosome complement of a cell, individual, or group.

introgression
Introduction by interbreeding or **hybridization** of genes from one population or species into another.

isozymes
One of several forms of an enzyme, produced by different non**allelic loci** in an individual organism's **genome**. Often misused to mean **allozyme**.

iteroparous

Having the ability to reproduce over more than one reproductive or spawning period. Among Pacific **salmonids** in the genus *Oncorhynchus,* Pacific trout such as *O. clarki* or *O. mykiss* are iteroparous; Pacific salmon, such as *O. kisutch* or *O. keta* are typically **semelparous** and die soon after spawning.

jacks

Usually used to refer to Pacific salmon; means male salmon that return from the ocean to spawn a year or more before full-sized adults return.

lacustrine

Having to do with a lake; often used synonymously with **adfluvial** to describe fish that spend most of their life in lakes.

life-history form

Used in this status review to describe coastal cutthroat trout based upon the primary activity or physical location of the fish when sampled (e.g., **saltwater migrant, freshwater migrant, freshwater forms,** or **nonmigrant**).

life-history stage

Used in this status review as a way to describe salmonids based upon the developmental stage of the fish (e.g., egg, **alevin, smolt**, or adult).

locus (*pl.* loci)

The site on a chromosome where a gene is found; often used more or less synonymously with gene *(cf.* **polymorphic locus, allozymes, isozymes)**.

LWD

Large woody debris, which is important to trout habitat in small streams in coastal watersheds.

MAL

Major Ancestral Lineage

meristic trait

A discretely varying and countable trait (e.g., number of fin rays or **basibranchial teeth);** *cf.* traits with **continuous variation** (e.g., weight, length) or **discrete variation** (e.g., male, female, mature, immature).

metapopulation

A group of partially isolated **populations** (or subpopulations) belonging to the same biological **species** (or subspecies) and connected by migratory pathways. These partially isolated populations or subpopulations can exchange individuals, which are potentially able to recolonize sites within the metapopulation from which the species or subspecies recently became extinct.

migrants

Cutthroat trout that move at regular intervals, usually seasonally, from natal spawning areas to feeding and refuge areas. Migratory movements may be to the ocean, an estuary, and/or within freshwater rivers and lakes.

minimum spanning tree (or network)

An undirected network in which all the samples are linked together with the smallest possible network. Included in the network are linkages between nearest neighbors. The network can be superimposed on **PCA** and **MDS** plots to detect local distortions, in which pairs of points may appear close in one dimension but far apart in another dimension.

minimum viable population

The smallest number of individuals necessary to give a population a high probability of surviving over a specified period of time.

mitochondrial DNA (mtDNA)

The DNA **genome** contained within mitochondria and encoding a small subset of mitochondrial functions; mtDNA is typically circular and 15-20 kilobases in size, containing little noncoding information between genes.

morphology (*adj.* morphological)

Description of an organism's form and structure, with special emphasis on external features.

multidimensional scaling (MDS)

An ordination technique for analyzing genetic distances between samples in multidimensional space (usually two or three dimensions for visualization). The technique is used to reduce the multidimensional space represented by allelic frequencies at several **loci** to a few dimensions without losing the complex genetic relationships among samples. **MDS** is considered superior to **principal component analysis (PCA)** for some genetic data because it does not assume linearity and hence does not potentially distort variation appearing in some population structures, such as step clines in allelic frequencies. MDS of genetic distances can detect nonhierarchical geographic structure without precluding detection of hierarchies.

MVP

minimum viable population

native fish

Fish indigenous to a particular region, place, or stream.

natural fish

Fish produced by parents spawning in a river or lake bed, as opposed to a controlled environment such as a hatchery. Natural fish may include "wild" fish; "wild " is often defined to mean fish native to a region and naturally spawning, with little if any hatchery ancestry. However, "wild" has a variety of local and regional definitions and its use is avoided in this status review.

naturally spawning fish
Fish spawning in a river or lake rather than in a controlled environment (such as a hatchery).

NMFS
National Marine Fisheries Service

nonanadromous
Describes fish that occur within fresh water and do not migrate to saltwater.

nonmigrant
Cutthroat trout that do not make extensive migrations but maintain small home ranges in upper tributaries or headwater streams. Nonmigrants are sometimes called **residents** or Cascade types, but this status review avoids these terms because they may have different regional connotations.

NWFSC
Northwest Fisheries Science Center

ODFW
Oregon Department of Fish and Wildlife

ONRC
Oregon Natural Resources Council

otolith
Crystalline calcium-carbonate structures within the inner ear of fish. These structures have distinctive shapes, sizes, and internal and surface features that can be used for age determination and species identification.

otolith primordia
The core region of the **otolith** first formed during embryonic development. Growth of the primordia region begins before hatching and chemical analysis can provide information about whether the maternal parent went to sea.

phenotype
The appearance (or other measurable characteristic) of an organism that results from interaction of the genotype and environment.

phylogeny
The evolutionary history of a group or lineage; the description and explanation of the temporal sequence of **morphological**, ecological, and biogeographical changes of a taxon.

PINEs
paired interspersed nucleotide elements

PIT tag

The PIT (passive integrated transponder) tag is an injectable, internal, radio-type tag that allows unique identification of a marked fish passing within a few inches of a monitoring site. The tag has been most effective in providing precise information on migrational timing and juvenile fish behavior when marked fish can be channeled past a monitoring site at a dam or weir (e.g., the fish bypass system at Snake River mainstem dams) or recaught above a barrier.

PNRBC

Pacific Northwest River Basins Commission

polymorphic

Having more than one form (e.g., polymorphic gene **loci** have more than one **allele**).

polymorphic locus

A **locus** characterized by more than one **allele** in a sample. If different alleles can be detected at a gene locus, the locus is considered polymorphic. If all alleles are of the same type, the locus is considered monomorphic. Many population genetic analyses are based on the frequency of different alleles at polymorphic loci.

polytypic

A taxon comprising more than two subordinate principle taxa or distinct **life-history forms**. Cutthroat trout are a polytypic species.

population

A group of individuals of a species living in a certain area that maintain some degree of reproductive isolation.

potamodromous

Description of an organism that either 1) migrates within river systems or 2) is non-anadromous, residing solely in fresh water. Because the term has two common usages, it has been avoided in this status review and replaced with **freshwater migrants** and **nonmigrants** or the inclusive term **freshwater forms** (*cf.* **riverine, lacustrine, anadromous, resident).**

principal component analysis (PCA)

An ordination technique for analyzing data from several variables, such as allelic frequencies or **morphological** data. The method finds linear trends (principal components) through the clouds of sample points in multidimensional space. These principal components account for the greatest amount of variation present in the data. The residual variance is removed from the data with the calculation of each successive principal component, (*cf.* **multidimensional scaling**).

protein electrophoresis

An analytical laboratory technique that measures differences in the amino acid composition of proteins from different individuals. Because the amino acid sequence of proteins is coded for by **DNA,** data provided by protein electrophoresis provide insight into levels of genetic variability within populations and the extent of genetic differentiation between them. See **electrophoresis.**

redd counts

Most **salmonids** deposit their eggs in a series of nests called **redds**, which are dug in the streambed or lake substrate by the female. Most Pacific salmon redds occur in predictable areas and are easily identified by an experienced observer by their shape, size, and color (lighter than surrounding areas because silt has been cleaned away). However, several factors, including small size, infrequent distribution, and apparent confusion with lamprey redds, make cutthroat trout redds difficult to detect; *cf.* **spawning surveys**.

resident

Life-history form of 1) coastal cutthroat trout that do not conduct extensive movements from natal spawning areas and tend to remain in upper tributaries and headwater streams; 2) any fish that does not migrate to seawater (**nonanadromous**). Because the term may have multiple meanings, its use is avoided in this status review.

riverine (river migrant)

A **freshwater migrating** cutthroat trout that primarily resides in rivers during feeding migrations, but may return to smaller tributaries or headwater streams to spawn or for winter refuge. Riverine fish may or may not go to estuaries or the open sea in some years.

rKm

river kilometer

RSI

remote site incubator

salmonid

Of, belonging to, or characteristic of the family *Salmonidae*, which includes the salmon, trout, char, and whitefish. Pacific salmonid is used in this status review to refer to fish native to the coast of western North America in either the genus *Salvilinus* (e.g., char, bull trout, and Dolly Varden) or *Oncorhynchus*, including five species of Pacific salmon (sockeye, pink, chum, chinook, and coho) and species of Pacific trout (e.g. cutthroat, golden, and steelhead/rainbow trout).

saltwater migrant/migratory

Cutthroat trout that migrate to salt water. Migration to the estuary or ocean environment generally occurs in the spring. These fish typically return to fresh water to overwinter in rivers or lakes, then migrate to smaller tributaries or headwater streams to spawn or return to the marine environment to feed (*cf.* **anadromy**).

SaSI

Salmonid Stock Inventory, which is a cooperative program by **WDFW** and **WWTIT** to inventory and evaluate the status of Pacific **salmonids** (salmon, trout, and char) in Washington State. This program follows the **SASSI** format. The SaSI report is referenced as "WDFW 1998a" in this status review.

SASSI

Salmon and Steelhead Stock Inventory, which is a cooperative program by **WDFW** and **WWTIT** to inventory and evaluate the status of Pacific **salmonids** in Washington State. The SASSI report is a series of publications from this program referenced as "WDF et al. 1993" in this status review.

sea run

Describes a coastal cutthroat trout that has gone to sea at least once (*cf.* **anadromy**).

semelparous

Having only one reproductive or spawning period and dies after spawning. Pacific salmon, such as *O. kisutch* or *O. keta*, are typically semelparous.

smolt

verb -The physiological process that prepares a juvenile **salmonid** to survive the transition from fresh water to salt water.

noun - A juvenile **anadromous** fish that has smolted.

spawning surveys

Counts of **redds** (and fish carcasses of Pacific salmon) to estimate spawner **escapement** and identify habitat being used by spawning fish. Annual surveys can be used to compare the relative magnitude of spawning activity between years. These surveys are rarely conducted for cutthroat trout due to the difficulty in identifying cutthroat trout **redds** and the rarity of carcasses in **iteroparous** species.

species

biological - A small group of organisms formally recognized by the scientific community as distinct from other groups.

legal - National Oceanic and Atmospheric Administration policy considers a species as defined by the ESA to include biological species, subspecies, and **ESUs**.

stochasticity

Random events or behaviors that are not deterministic.

swim up

The time in the life cycle of salmon when **alevins**, having absorbed their yolk sacs, transition into fry by swimming from the gravel of the **redd** into the water column.

sympatric

Describes **populations**, **species**, or taxa occurring together in the same geographical areas where they may occupy the same habitat (**biotic** sympatry) or different habitats (neighboring sympatry) within the same geographical area. Implies, especially when used in a genetic context, the opportunity to interbreed.

threatened species

A **species** not presently in danger of extinction but likely to become so in the foreseeable future.

total escapement

A combination of all counts and estimates of returning fish in a particular group (e.g., **species**, stock, run) for a river or management unit.

trophic

Pertaining to nutrition. A trophic migration would be a movement of fish to a feeding area.

USGS

United States Geological Survey

WDFW

Washington Department of Fish and Wildlife, which co-manages **salmonids** and salmonid fisheries in Washington State with **WWTIT** and other fisheries groups. The agency was formed in the early 1990s by combining the Washington Department of Fisheries and Washington Department of Wildlife.

wild

See **natural fish**.

WWTIT

Western Washington Treaty Indian Tribes, an organization of Native American tribes with treaty fishing rights recogized by the United States. **WWTIT** co-manages **salmonids** and salmonid fisheries in western Washinton in cooperation with **WDFW** and other fisheries groups.

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Northwest Fisheries Science Center

NOAA Tech. Memo.
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Most NOAA Technical Memorandums NMFS-NWFSC are available on-line at the Northwest Fisheries Science Center web site (http://www.nwfsc.noaa.gov).