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Independent Populations of Chinook Salmon in Puget Sound

July 2006

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Independent Populations of Chinook Salmon in Puget Sound

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Executive Summary

In developing a species recovery plan, it is important to delineate the independent populations that comprise an evolutionarily significant unit (ESU) listed under the Endangered Species Act. In 2000 the Puget Sound Technical Recovery Team (TRT) began work to identify, for recovery planning purposes, the populations that historically existed and currently remain within the geographic boundaries encompassing the Puget Sound Chinook Salmon ESU.

The TRT set forth with the goal to distinguish demographically quasi-independent groups of Chinook salmon (*Oncorhynchus tshawytscha*) within Puget Sound. To do this, the team analyzed a number of attributes indicating independence among groups of fish and examined the degree to which those attributes exhibited biologically significant differences. The TRT determined that the following 22 historical populations currently contain Chinook salmon:

1) North Fork Nooksack River
2) South Fork Nooksack River
3) Lower Skagit River
4) Upper Skagit River
5) Cascade River
6) Lower Sauk River
7) Upper Sauk River
8) Suiattle River
9) North Fork Stillaguamish River
10) South Fork Stillaguamish River
11) Skykomish River
12) Snoqualmie River
13) Sammamish River
14) Cedar River
15) Duwamish/Green River
16) White River
17) Puyallup River
18) Nisqually River
19) Skokomish River
20) Mid-Hood Canal Rivers
21) Dungeness River
22) Elwha River

Results

Based on genetic and historical evidence reported in the literature, the TRT determined that there were 16 additional spawning aggregations or populations in the Puget Sound Chinook Salmon ESU that are now putatively extinct. It was not possible in most cases to determine whether these Chinook salmon spawning groups historically represented independent populations or were distinct spawning aggregations within larger populations. Regardless of

their population status, the losses in these 16 spawning aggregations represent important losses in ESU diversity, especially among early run Chinook salmon forms.

Brief descriptions for each population are in the Conclusions section of this technical memorandum. The TRT did not assign all Chinook salmon groups spawning naturally in Puget Sound streams (WDF et al. 1993) to independent populations for two reasons:

- First, spawning adults are known to occur intermittently in certain streams—spawning in groups of tens to hundreds of fish in some years and none in others. A plausible explanation for intermittent occurrence of Chinook salmon in some streams is that those adults are part of a larger independent population that uses some spawning habitats only during years of high abundance or favorable habitat conditions. The streams that intermittently harbor spawning adults could also contain fish from more than one independent population, depending on their locations relative to the primary spawning areas of independent populations.
- Second, it is possible that some streams presently containing Chinook salmon never supported naturally spawning Chinook salmon historically. In many of these instances, the origin of the naturally spawning Chinook salmon present is most likely due to returning adults from hatchery production. As more information becomes available, it is possible that Chinook salmon in some intermittently used streams can be clearly associated with one or more populations. Their assignment will change to reflect their association with a particular population.

Methods

The TRT defined an independent population following Ricker's (1972) definition of a "stock" as "a group of fish of the same species that spawns in a particular lake or stream (or portion thereof) at a particular season and which, to a substantial degree, does not interbreed with fish from any other group spawning in a different place or in the same place at a different season." In the context of a viable salmonid population, not interbreeding to a substantial degree means that two groups are considered to be independent populations if they are isolated to such an extent that exchanges of individuals among populations do not substantially affect the population dynamics or extinction risk of the independent populations over a 100-year time frame.

The definitive information needed to identify populations is migration rates between groups and their demographic consequences. In practice, information is rarely available about salmon straying between streams and the demographic consequences of such straying. Consequently, we use different kinds of information, which are proxies for understanding the degree of reproductive isolation between Chinook salmon groups. Each type of information contributes to our understanding of population boundaries, but none alone provides us with complete confidence in our answer. The six indicators of historical population structure used, in order of the strength of inference, are:

1) geographic orientation of groups,
2) migration rates,
3) genetic attributes,

4) patterns of life history or phenotypic characteristics,
5) population dynamics, and
6) environmental/habitat characteristics.

Because populations are organized hierarchically, the basic approach to the six proxy indicators of reproductive exchange is to identify nested patterns of Chinook salmon groups that are more similar to each other than they are to other groups. The TRT distinguished biologically significant differences for each attribute among Chinook salmon groups that were judged to correspond to population-level independence. The main document describes data analyses and summary results for those indicators that were useful in population structure decisions (i.e., geography, genetics, and some life history information). The remaining indicators did not produce results that were as useful for our population structure decisions for various reasons, including irresolvable data quality problems, weak inference, and inconclusive results. The analyses for the relatively uninformative indicators are presented in Appendix A. To make final population structure decisions, the TRT (with help from others familiar with genetic data) used a population independence scoring system to delineate the degree of differences among Chinook salmon stocks. The final independence scores provided a summary of the differences among Chinook stocks among the key indicators, and thus are the basis for population delineation.

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Abbreviations and Acronyms

AIC	Akaike Information Criterion
CWT	coded-wire tag
EPA	U.S. Environmental Protection Agency
ESU	evolutionarily significant unit
GDU	genetic diversity units
GIS	geographic information system
ha	hectare
MANOVA	molecular analysis of variance
MDS	multidimensional scaling
Nb	harmonic mean of the effective number of breeders per cohort
Ne	genetic effective population
Nm	number of migrants
NMFS	National Marine Fisheries Service
NWIFC	Northwest Indian Fisheries Commission
PHYLIP	Phylogeny Inference Package
PSMFC	Pacific States Marine Fisheries Commission
SASSI	Salmon and Steelhead Stock Inventory
SPS	southern Puget Sound
TRT	Technical Recovery Team
UPGMA	unweighted pair group method using arithmetic averages
VSP	viable salmonid population
WDF	Washington Department of Fisheries
WDFW	Washington Department of Fish and Wildlife
USGS	U.S. Geological Survey

Introduction

Delineating the independent populations that comprise an evolutionarily significant unit (ESU) listed under the Endangered Species Act (ESA) is an important step in developing a recovery plan. Populations are the building blocks for recovering many salmon ESUs. Understanding the size and spatial extent of populations is critical to viability analyses, which are a necessary step in recovery planning and conservation assessments for any species. The identification of populations essentially amounts to defining the units in which most demographic feedbacks occur, which helps in the development of effective management actions designed to improve population status.

This technical memorandum identifies for recovery planning purposes the populations that historically existed within the geographic boundaries encompassing the Puget Sound Chinook Salmon ESU. As part of the recovery planning process, the seven-member Puget Sound Technical Recovery Team (TRT)[1] characterizes each population's historical and present status and identifies viability criteria. The TRT considers these populations when answering the question "What are the necessary population characteristics that will provide a high likelihood of persistence of the ESU?"

It is likely that some of the Puget Sound Chinook Salmon ESU's historical population structure was lost or substantially modified within the past 200 years due to human manipulation of watersheds and Chinook salmon (*Oncorhynchus tshawytscha*) populations. Evidence suggests that some Chinook salmon stocks in Puget Sound have gone extinct or lost major components of their life history diversity (Table 1) (Myers et al. 1998).[2] Although rigorous identification of extinct populations is not possible, the existing information is important for recovery planning and should be used to guide options for enhancing the ESU's diversity and persistence, including reestablishing populations and recovering the range of historical life history diversity.

Definition of a Population Used in this Approach

The definition of a population used in this technical memorandum is in the context of a viable salmonid population (VSP) defined by McElhany et al. (2000):

> an independent population of any Pacific salmonid (*Oncorhynchus* spp.) that has a negligible risk of extinction over a 100-year time frame due to threats

[1] The Puget Sound TRT consisted of Mary Ruckelshaus and Norma Sands, Northwest Fisheries Science Center, Kenneth Currens, Northwest Indian Fisheries Commission, William Graeber, Washington Department of Natural Resources and National Marine Fisheries Service, Robert Fuerstenberg, King County Department of Natural Resources and Parks, Kit Rawson, Tulalip Tribes, and James Scott, Washington Department of Fish and Wildlife.

[2] There likely were more historical populations than the 22 identified in this document; the TRT could not determine whether most lost aggregations were historically independent populations.

Table 1. List of putatively extinct populations or spawning aggregations of Chinook salmon in Puget Sound. Populations or spawning aggregations are included in this list if they are presumed to be extirpated or if introduced populations replaced indigenous populations (based on genetic evidence). Locations signify rivers unless otherwise noted.

Extinct spawning aggregation	**Region**	**Evidence/source**
Late-run Nooksack	Strait of Georgia	Genetic evidence/Young and Shaklee 2002
Baker	North Puget Sound	Smith and Anderson 1921
Early run Stillaguamish	North Puget Sound	Nehlsen et al. 1991, WDF et al. 1993
Early run Snohomish	North Puget Sound	Nehlsen et al. 1991, WDF et al. 1993
Late-run Sammamish	Central/south Puget Sound	Genetic evidence/Marshall et al. 1995, Marshall 1999 and 2000b
Early run Duwamish/Green	Central/south Puget Sound	Nehlsen et al. 1991, WDF et al. 1993
Late-run White	Central/south Puget Sound	Shaklee and Young 2003
Late-run Puyallup	Central/south Puget Sound	Genetic evidence/Marshall 1999 and 2000b
Early run Puyallup	Central/south Puget Sound	Nehlsen et al. 1991
Early run Nisqually	Central/south Puget Sound	Nehlsen et al. 1991
Late-run Nisqually	Central/south Puget Sound	Genetic evidence/Marshall et al.1995
Early run North Fork Skokomish	Hood Canal	Smoker 1952, Deschamps 1954, WDF 1957, Nehlsen et al. 1991, WDF et al. 1993
Early run South Fork Skokomish	Hood Canal	Smoker 1952, Deschamps 1954, WDF 1957, Nehlsen et al. 1991, WDF et al. 1993
Late-run Skokomish	Hood Canal	Genetic evidence/Marshall 1999 and 2000a
Early run mid-Hood Canal (Hamma Hamma, Duckabush, and Dosewallips)	Hood Canal	Nehlsen et al. 1991, Marshall 1999 and 2000a
Early run Elwha	Strait of Juan de Fuca	Nehlsen et al. 1991, WDF et al. 1993

from demographic variation (random or directional), local environmental variation, or threats to genetic diversity (random or directional).

The TRT defines an independent population following Ricker's (1972) definition of a stock, as "a group of fish of the same species that spawns in a particular lake or stream (or portion thereof) at a particular season and which, to a substantial degree, does not interbreed with fish from any other group spawning in a different place or in the same place at a different season." Thus in the context of a VSP, "not interbreeding to a substantial degree" means that two groups are considered to be independent populations if they are isolated to such an extent that exchanges of individuals among populations do not substantially affect the population dynamics or extinction risk of the independent populations over a 100-year time frame. The exact level of reproductive isolation that is required for a population to have substantially independent dynamics is not well understood. Theoretical work suggests that substantial independence occurs when a population's migrant proportion is less than about 10% (Hastings 1993). Thus independent populations are units for which it is biologically meaningful to examine extinction risks that derive from intrinsic factors such as demographic, genetic, or local environmental stochasticity.

Where the TRT used data from other population aggregations or reproductively based management units for analyses, the term stock is used to distinguish these groups from the populations identified. In the Salmon and Steelhead Stock Inventory (SASSI) (WDF et al. 1993), for example, Washington state and tribal comanagers also used Ricker's (1972) definition of a stock, but they did not restrict their interpretation of interbreeding to exchanges of individuals among the populations that do not substantially affect the population dynamics or extinction risk of the independent populations over a 100-year time frame as the TRT did. They delineated individual Pacific salmon (*Oncorhynchus* spp.) stocks based on geographical and temporal separation in spawning and distinct biological characteristics (e.g., population gene frequencies, return timing, fish size, age structure, etc.) and identified them by the name of the river to which they return. For some rivers they identified two different stocks that reflect differences in return or run timing, distinctions that have been used for harvest management. For example Snohomish summer Chinook salmon are the early returning stocks, whereas Snohomish fall Chinook salmon are the late-returning stocks. Although the TRT used the same indicators as SASSI and added or updated information to delineate independent populations, our results differed slightly because of different definitions. We also did not use the seasonal run timing label because of ambiguities in the definition. Where it was necessary to distinguish diversity in run timing within a river system, we describe it more generally to avoid confusion with stocks identified for different harvest management strategies.

Structure below and above Population Level

A population is a group of fish that is reproductively isolated "to a substantial degree." As a criterion for defining groups of fish, the degree of reproductive isolation is a relative measure, however, and can vary continuously from the level of pairs of fish to the degree of reproductive isolation separating species. The population-level separation defined in this document therefore may not reflect the only biologically isolated groups that can be identified. For example some Chinook salmon groups may be somewhat reproductively isolated from other groups, but not enough to be considered independent by the criteria adopted in this study. The TRT considers these groups subpopulations. The existence, distribution, and interactions of subpopulations within an independent population have important consequences for viability, because they affect population diversity and spatial structure, two of four key parameters for evaluating a population's viability.

Just as there may be substructuring within a population, there may be structure above the level of a population. This is explicitly recognized in the designation of an ESU. An ESU may contain multiple populations that are connected by some small degree of migration. Thus organisms can be grouped in a hierarchical system where we define the levels of individual, subpopulation, population, ESU, and finally species. Other hierarchical systems with more or fewer levels could be constructed. Though reproductive isolation forms a continuum, it is probably not a smooth continuum, and there exists a biological basis for designating a hierarchy of subpopulations, populations, and ESUs.

Conceptual Approach to Identifying Populations

The TRT's definition of a population implies that the populations of Chinook salmon described in this technical memorandum have been demographically independent for at least 100 years. In some cases the Chinook salmon currently within the historical geographic boundaries of these populations do not represent the genetic legacy of the fish that were present historically (e.g., if the fish are an introduced hatchery stock). The TRT's main objective is to identify geographic boundaries of historical populations of Chinook salmon as they relate to current populations. Subsequent analyses of introduced populations during the recovery planning process will determine what their role should be in recovery.

Indicators of Population Structure

The definitive information needed to identify populations is migration rates between groups and their demographic consequences. Information about salmon straying between streams, and the demographic consequences of such straying, is rarely available. Consequently we use different kinds of information that are proxies for understanding the degree of reproductive isolation between Chinook salmon groups. Each type of information contributes to our understanding of population boundaries, but none alone provides us complete confidence in our answer. In the next six subsections, the TRT discusses these information types in order of the strength of inference about population structure, everything else being equal, beginning with the most powerful. Depending on the quality and availability of the data (Data Quality subsection, page 6), however, and the genetic and demographic history of salmon in different regions, the usefulness of these indicators varies in any one area.

Geography

The geographical boundaries of a salmon population are defined in part by the spatial distribution of its spawning habitat. Physical features such as a river basin's topographical and hydrological characteristics dictate, to a large degree, where and when salmon can spawn and delimit the spatial area over which a single group of fish can be expected to interact. Geographic constraints on population boundaries (e.g., distance between streams) can provide a useful starting point from which to closely examine Chinook salmon group attributes within circumscribed geographic areas, but geographic constraints generally will not support strong inferences at finer scales (e.g., distinguishing separate populations within a small river basin). Biogeographic characteristics and historical connections between river basins on geological time scales also can be informative in defining population boundaries.

Migration Rates

The extent to which adults move between sites affects the degree of reproductive isolation and, therefore, demographic independence between sites. Straying estimates (the number or percent of fish originating from one location that are found in another) are the primary

available indicator of connectivity between spawning aggregations. Stray rates are particular to a group of fish and the season and streams in which they are estimated. Thus stray rates provide useful information about straying under those conditions. Unfortunately it is not possible to obtain estimates of the magnitude of stray rate variation over long time periods (e.g., 100 years) because the data do not exist. In contrast, compared to mark-recapture and other direct estimates of straying, indirect estimates, such as genetically based estimates of gene flow or genetic exchange, can be used to estimate exchange between Chinook salmon groups integrated over longer time periods.

Genetic Attributes

Geographical patterns in neutral genetic markers are useful in identifying salmon populations, because they indicate the extent of reproductive isolation among groups. Patterns can be difficult to interpret, because they may reflect recent introductions, effects of hatchery practices, or nonequilibrium conditions. Consequently they should be interpreted with caution. Adaptive genetic differences among Chinook salmon groups (as indicated by quantitative traits or molecular markers) are more difficult to document than discrete marker differences, but they offer good supporting evidence for distinct populations.

Patterns of Life History and Phenotypic Characteristics

Phenotypic variation can be used as a proxy for two reasons. First, many phenotypic differences are based partially on underlying genetic variation (rather than environmentally induced variation), and geographical patterns in these traits can be informative in identifying populations (defined by reproductive isolation and demographic independence). Second, phenotypic differences may indicate different selective environments experienced by salmon in different streams that could have led to adaptive differences and restricted exchange among populations.

Population Dynamics

Abundance data can be used to explore the degree to which demographic trajectories of two groups of Chinook salmon are independent of each other. All else being equal, the less correlated time series of abundance are between two Chinook salmon groups, the less likely the groups are to be part of the same population. Complicating the interpretation of correlations in abundance between Chinook salmon groups is the potentially confounding influence of correlated environmental characteristics that affect abundance. When Chinook salmon groups that are in close proximity are not correlated in abundance over time, it is likely that they are not linked demographically. The reverse is not always the case. Thus when correlations in abundance between Chinook salmon groups are detected, more work is needed to rule out confounding sources of correlation.

Environmental and Habitat Characteristics

The collective biotic and abiotic characteristics of occupied salmonid habitat can help define populations, because those ecological characteristics constitute the selective environment in which the salmon exist. Differences in these selective environments could have led to adaptive differences or restricted exchange among populations. The relative strength of

inference for these characteristics is weak, because we generally do not know which environmental variables influence fitness or whether those effects will be observed at the population level. If different salmon groups experience different selective environments and there is very little migration between those environments, we expect those groups' phenotypic characteristics to diverge.

Data Quality

An important first step in analyzing and interpreting any population structure indicator is to carefully screen the data and information for potential sources of error or bias. To minimize such error, the TRT consulted with biologists familiar with adult and juvenile sampling methods and calculations used to expand from index counts to total abundance estimates for each stream before using the data in analyses. Wherever possible (e.g., to calculate abundance trends), index counts are used in lieu of expansions in order to minimize errors or bias due to spatial variation in expansion methods (e.g., Smith and Castle 1994). Coded-wire tag (CWT) expansion methods are variable in different streams and years, for example. In cases where fish survey methods are unreliable or expansion methods are undocumented or inconsistent over time, data were not used in analyses. In many instances juvenile and adult counts include an unknown mixture of naturally produced fish and first-generation hatchery fish. Abundance measures used in these analyses refer to estimates of naturally spawning adults.

Genetic data can be rendered uninformative for population structure considerations if a stream contains nonnative, hatchery-origin fish that cannot be easily separated in a sample. Wherever possible the TRT uses the history of stock transfers and broodstock origin to determine whether a genetic sample from a stream would be indicative of the genetic makeup of native fish. Even if the existing fish in a particular stream were not native, estimates of their genetic similarity to fish in other streams can be informative in determining migration estimates if the length of time the nonnative stock has been present in the stream can be estimated.

Evaluating Similarity Between Groups

Because populations are organized hierarchically, the basic approach in using the proxy indicators of reproductive exchange is to identify nested patterns of Chinook salmon groups that are more similar to each other than they are to other groups. However this requires making difficult decisions about how similar fish must be before they are considered part of the same independent population, which is not a simple statistical exercise. For example, with advances in genetic markers, individual differences between fish can be statistically significant even though the different fish are not different populations. The TRT's goal is to distinguish biologically significant differences for each attribute among groups of Chinook salmon that the team believes would correspond to population-level independence. In general, for conservation and recovery applications, it is appropriate to assume that two Chinook salmon groups are independent unless the data indicate they should be combined into a single group. This approach errs on the side of conserving diversity that might otherwise be lost if a distinct group of fish is incorrectly lumped with a larger group.

The challenge in interpreting the results of statistical analyses is to decide how the biological differences and statistical significance can be used to inform decisions about

demographic independence. For example studies of the adaptive significance of phenotypic traits can be helpful in determining the magnitude of biological differences that might be associated with independent populations. Similarly population genetic theory can be instrumental in estimating the genetic consequences of particular migration rates and whether those rates are significant enough to indicate that they are the same population. Barring such information, however, statistical significance (or the lack of it) is informative for ruling out instances in which Chinook salmon groups should not be considered independent. If statistical power were adequate to detect differences, two Chinook salmon groups would not be considered independent populations if there were no statistically significant differences in attributes between them (unless, of course, the data were suspect—e.g., if the data were scarce or likely to be affected by the presence of nonlocal hatchery fish). The converse is not true. In some cases the TRT combined groups into a single population where there were statistically significant differences between the groups for some attributes. Such combinations occurred only when the power of the test was great enough to detect significant subpopulations within a population but the differences between group attributes were not biologically significant enough to indicate independent populations.

In a few cases reports of current Chinook salmon distribution are greater in spatial extent than estimates or reports of historical Chinook salmon distribution. In these instances the TRT assumed that the historical distribution was similar to current distribution, unless credible biological evidence to the contrary was available.

The Methods and Results section (page 8) describes data analyses the TRT conducted for indicators that were useful in population structure decisions (i.e., geography, genetics, and some life history information). At the end of the section we describe how we summarized analyses for these indicators and how we determined population structure. The remaining indicators did not produce results that were as useful for population structure decisions. Results were relatively uninformative for various reasons, including irresolvable data quality problems, weak inference, and inconclusive results. The method and results for the relatively uninformative indicators are presented in Appendix A (page 67). The TRT presents those results in Appendix A to complete the documentation of analyses and to motivate further data collection that may render such information more useful in the future.

Methods and Results

Geographic Distribution of Puget Sound Chinook Salmon

Chinook salmon in the Puget Sound ESU spawn from Dakota Creek north of the Nooksack River in the north, through south Puget Sound, into Hood Canal, and out the Strait of Juan de Fuca to the Elwha River (Figure 1). These spawning distributions are relatively well known (WDF et al. 1993) compared to information on the location of juvenile rearing areas and historical spawning distributions in most basins.

Disjunct spawning areas can suggest different populations. The TRT measured the geographic distances (km) separating spawning areas as the shortest nautical distance separating each pair of spawning sampling sites, including the river distance plus the distance between river mouths, where applicable (Table 2). Distances were measured using geographic information system (GIS) software (ERSI—Seattle, Washington) and a 1:250,000-scale map.

The theory of island biogeography (MacArthur and Wilson 1967), when applied to salmon populations, suggests that a "minimum catchment area" could exist, which defines the minimum watershed area needed to support a self-sustaining Chinook salmon population. This relationship, if known, could help identify potential historical populations, but it has yet to be defined for Chinook salmon. Catchment areas for major Puget Sound river basins vary by an order of magnitude (Figure 2). Areas range from more than 600,000 hectares (ha) in the Skagit River basin to slightly less than 20,000 ha in the Duckabush River basin. The TRT was not able to use such a minimum area criterion for analyses, because it first requires an independent assessment of populations, which the team did not have. We calculated catchment area for Puget Sound streams containing Chinook salmon using a GIS program and including the entire watershed from the river's mouth upstream to its headwaters. Exceptions are large watersheds, such as the Skagit River, which have main channel splits as well as substantial contributing tributaries. In these cases calculation of catchment area excluded portions of the watershed above major upstream confluences (e.g., the lower Skagit River includes the area from the river's mouth to its confluence with the Sauk River) (Figure 2). The smallest watershed containing what the TRT believed to be an independent population (based on multiple lines of evidence) is the South Fork Nooksack River (47,700 ha). Whether smaller watersheds can support independent populations is not possible to determine with the existing information.

Direct Observations of Migration

Some direct observations of straying among Puget Sound Chinook salmon stocks were available. Most were based on releases and subsequent recoveries of hatchery Chinook salmon marked with CWTs, available in a database maintained by the Pacific States Marine Fisheries Commission (PSMFC) (RMPC 1997). The TRT was not able to get good estimates of stray

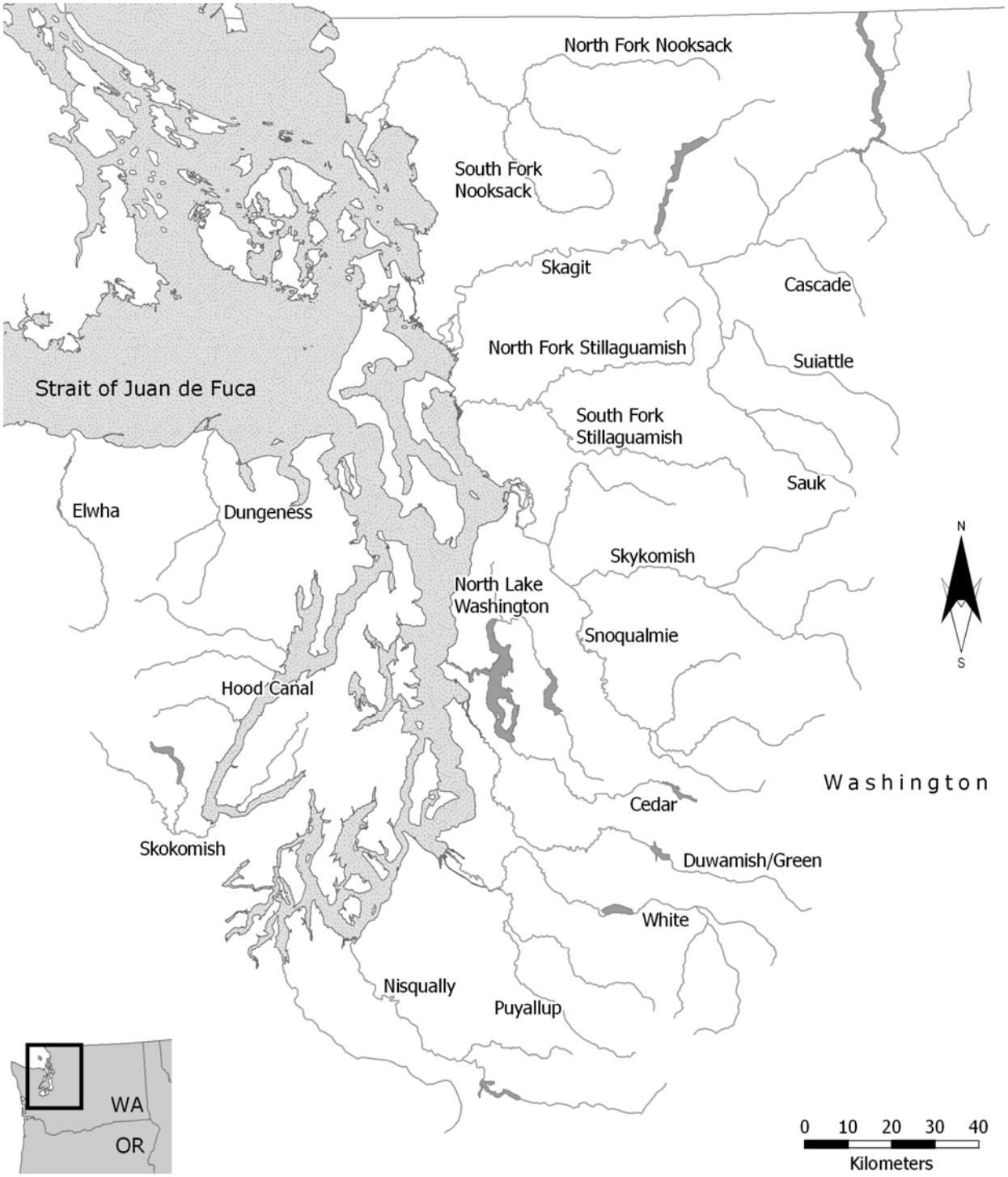

Figure 1. Major Chinook salmon spawning areas in the Puget Sound. Locations signify rivers unless otherwise noted.

Table 2. Distances (km) separating the spawning grounds of Puget Sound Chinook salmon populations.* Locations signify rivers unless otherwise noted. Source: Spawning distributions based on WDF et al. 1993.

	North Fork Nooksack	**South Fork Nooksack**	**Lower Skagit**	**Upper Skagit**	**Cascade**	**Lower Sauk**	**Upper Sauk**	**Suiattle**	**North Fork Stillaguamish**	**South Fork Stillaguamish**	**Skykomish**	**Snoqualmie**	**Sammamish**	**Cedar**	**Duwamish/ Green**	**White**	**Puyallup**	**Nisqually**	**Skokomish**	**Hamma Hamma**	**Duckabush**	**Dosewallips**	**Dungeness**	**Elwha**
North Fork Nooksack	—																							
South Fork Nooksack	5	—																						
Lower Skagit	143	138	—																					
Upper Skagit	218	213	13	—																				
Cascade	244	239	39	4	—																			
Lower Sauk	219	213	14	2	27	—																		
Upper Sauk	254	249	48	37	62	7	—																	
Suiattle	249	244	44	32	58	11	27	—																
North Fork Stillaguamish	200	195	112	187	213	188	222	218	—															
South Fork Stillaguamish	178	173	90	165	191	166	201	196	2	—														
Skykomish	251	178	188	171	196	263	206	201	67	45	—													
Snoqualmie	225	220	138	213	238	213	248	243	109	87	22	—												
Sammamish	226	221	139	213	239	214	249	244	114	92	149	127	—											
Cedar	230	225	143	218	243	218	253	248	118	96	154	131	31	—										
Duwamish/Green	215	210	128	202	228	203	238	233	103	81	137	116	41	46	—									
White	270	265	182	257	283	258	292	288	158	136	129	171	96	100	65	—								
Puyallup	268	263	181	256	281	256	291	286	156	134	190	170	95	99	64	0.1	—							
Nisqually	273	268	187	262	288	263	298	293	163	141	194	176	101	106	72	64	62	—						
Skokomish	251	246	188	263	288	263	298	293	165	143	136	178	149	154	137	191	190	194	—					
Hamma Hamma	226	221	163	238	264	239	274	269	141	119	112	154	125	129	112	167	165	170	27	—				
Duckabush	213	208	150	225	251	226	261	256	128	106	99	141	112	116	99	154	152	157	41	15	—			
Dosewallips	209	204	146	221	247	222	256	252	123	101	94	137	107	112	95	150	148	153	46	21	8	—		
Dungeness	149	109	90	165	190	165	200	195	131	109	139	144	117	122	105	160	158	163	139	115	102	98	—	
Elwha	171	166	123	198	223	198	233	228	164	142	173	177	151	155	138	193	191	196	173	148	135	131	33	—

* Distances were calculated as the shortest nautical distance separating each pair of spawning sites, including the river distance plus the distance between river mouths, where applicable. Distances were measured using GIS software and a 1:250,000-scale map.

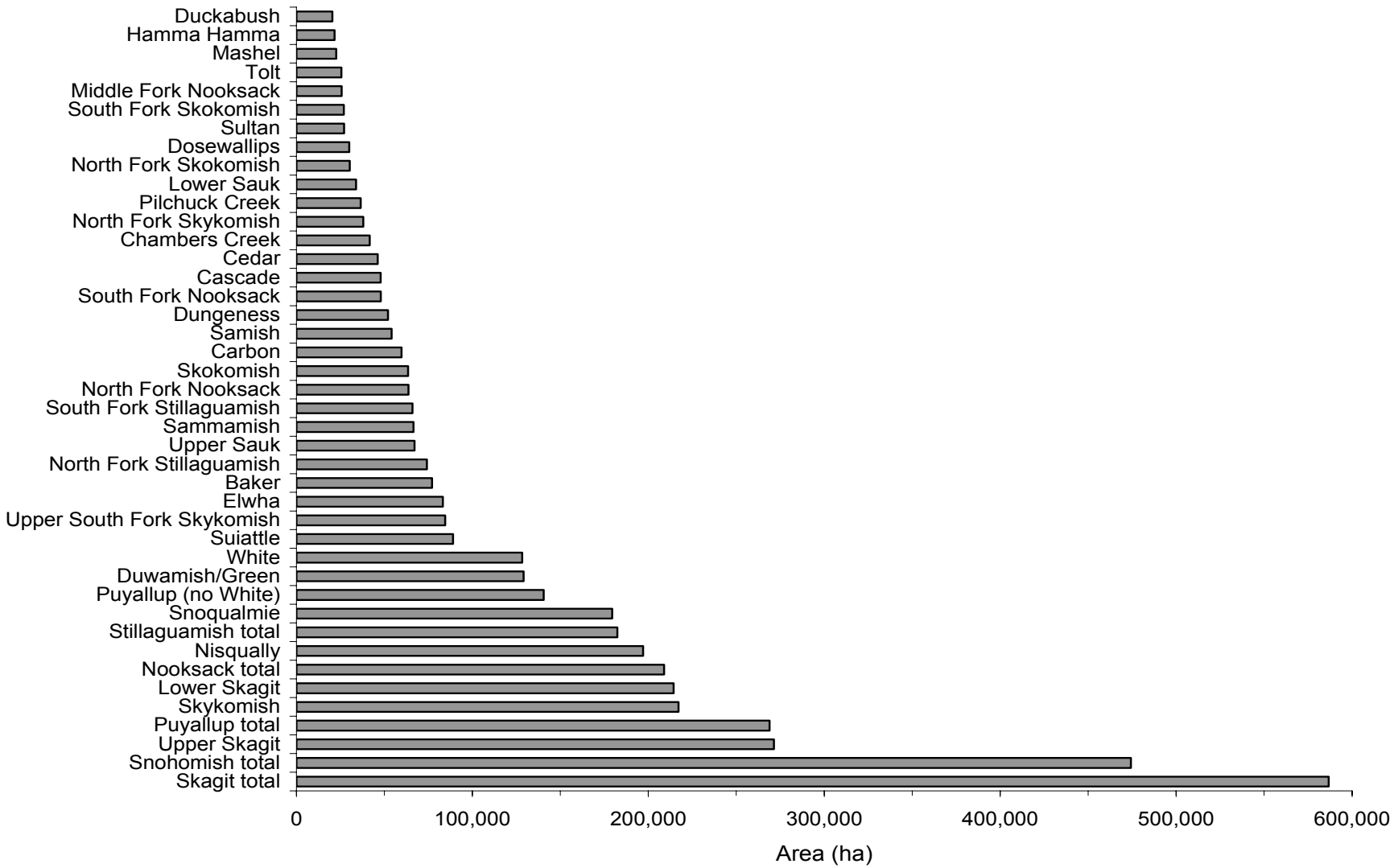

Figure 2. Basin area (ha) of rivers in the Puget Sound Chinook Salmon ESU. Total catchment area of river basins from headwaters to the mouth of the stream (or to its confluence with another large river) was calculated using GIS-based maps.

rates—the proportion of all fish in a tag group (or from a release site) that are recovered somewhere other than their tagging or release site—because methods of estimating the total number of returning tagged fish vary among recovery locations and the geographic area sampled for strays is not usually designed to estimate straying. Furthermore how well straying patterns of hatchery fish reflect those of wild Chinook salmon is not well known. Estimates of straying rates based on small-scale experimental studies were available in a few locations. More extensive estimates of stray rates of naturally produced; naturally spawning Chinook salmon are sorely needed, especially as recovery of populations proceeds. A summary of information collected and results for this indicator are reported in Appendix A (page 67).

Genetic Attributes

Methods

The Washington Department of Fish and Wildlife (WDFW) systematically samples Chinook salmon from Puget Sound streams for genetic and life history characterizations and has developed an extensive database covering multiple broodyears (1980–1996) (Table 3), which it provided for these analyses. The TRT used variation at 29 polymorphic allozyme loci to test for allele frequency differences among 35 groups of Chinook salmon sampled from Puget Sound streams to visualize patterns of genetic differences and to estimate genetic parameters of divergence and reproductive exchange. To test for differences in allele frequencies, the team used contingency table analyses of log likelihood ratio tests (G-tests) to test the null hypothesis that samples were drawn from the same population. Multiple broodyears from a site subsequently were combined, because among-site variation was greater than variation among broodyears within a site. To visualize patterns of genetic differences, the TRT used cluster analysis and multidimensional scaling. Cluster analyses of genetically similar groups of samples were based on pairwise estimates of Cavalli-Sforza and Edwards chord genetic distance (Cavalli-Sforza and Edwards 1967) and the unweighted pair-group method using arithmetic averages (UPGMA) clustering algorithm (Sneath and Sokal 1973) using the CONSENSE program in the Phylogeny Inference Package (PHYLIP) software, version 3.5c (Felenstein 1993). The team examined the robustness of the patterns by bootstrapping the allele frequencies for 1,000 iterations and constructing a consensus dendrogram using PHYLIP. The patterns of genetic differences also were visualized using multidimensional scaling (Lessa 1990) on the matrix of genetic chord distances using XLSTAT software (AddinSoft USA, New York).

To better understand the biological significance of these patterns, the TRT calculated three genetic parameters to estimate population divergence, rate of genetic exchange, and time since two groups of Chinook salmon diverged from a common population. The team estimated population differentiation, F_{ST}, using Weir and Cockerham's (1984) analog, theta (θ), which is based on using molecular analysis of variance (MANOVA) to partition the total genetic variation into components among and within groups. Theta equals zero indicates no significant differentiation; θ equals one indicates that the two groups have completely fixed genetic differences.

Table 3. Data available for analyses of population genetic structure, age at reproduction, and spawner abundance. Y = available, ND = not available. Locations signify rivers unless otherwise noted.

Name of spawning aggregation[a]	Genetics (years)	Age at reproduction	Abundance[b]
Miscellaneous streams, area 7A (North Puget Sound)		ND	Y
North Fork Nooksack spring (hatchery)	1988, 1993	Y	ND
South Fork Nooksack spring	1993–1995, 1998	Y	Y
Samish fall (North Puget Sound)	1986	Y	Y
Lower Skagit fall	1986–1988, 1998	Y	Y
Upper Skagit summer	1986, 1994–1995	Y	Y
Lower Sauk summer	1986	Y	Y
Upper Sauk spring	1986, 1994, 1998	Y	Y
Suiattle spring	1986–1990, 1998	Y	Y
Skagit spring	1990, 1993–1994, 1996	Y	
Upper Cascade spring	1993–1994	Y	ND
North Fork Stillaguamish summer	1987–1988, 1996	Y	Y
South Fork Stillaguamish fall	1992–1996	Y	Y
Snohomish (Skykomish) summer	1988–1989, 1993, 1996	Y	Y
Snohomish summer (hatchery)	1987–1988, 1996	Y	
Snohomish (Snoqualmie) fall	1988	Y	Y
Wallace (Skykomish) summer/fall	1988–1989	Y	Y
Skykomish summer (hatchery)	1987	Y	ND
Bridal Veil Creek (Skykomish) summer/fall	1987–1988	Y	ND
Sultan fall	1987–1989		
Miscellaneous streams, area 10 (South Sound)		ND	Y
Issaquah Creek fall (hatchery)	1992	Y	ND
North Lake Washington (Sammamish) summer/fall	1998	Y	Y
Cedar summer/fall	1993–1994	Y	Y
Duwamish/Green summer/fall (hatchery)	1987–1988, 1990, 1998	Y	Y
Newaukum Creek (Green) summer/fall	1992–1993	Y	ND
Puyallup summer/fall (hatchery)	1992–1993	Y	Y
Puyallup (South Prairie Creek) fall	1992–1993		
White spring	1995–1997	Y	Y
White spring (hatchery)	1991–1994		
Nisqually summer/fall	1998–1999	Y	Y
Deschutes summer/fall (hatchery)	1987	Y	Y
Miscellaneous streams, area 13 (South Sound)		ND	Y
Miscellaneous streams, area 13A (South Sound)		ND	Y
Miscellaneous streams, area 13B (South Sound)		ND	Y
Miscellaneous streams, area 10E (South Sound)		ND	Y
Skokomish summer/fall	1998	Y	Y
Hood Canal fall (Hoodsport hatchery)	1988	Y	
Hamma Hamma (Hood Canal) summer/fall	1999	Y	Y
Duckabush (Hood Canal) summer/fall		ND	Y
Dosewallips (Hood Canal) summer/fall		ND	Y
Dungeness summer/fall (hatchery)	1986	ND	Y
Elwha summer/fall (hatchery)	1988, 1991	Y	Y

[a] Miscellaneous areas and numbers correspond to the map in Figure A-5 (page 81).
[b] In some cases data were available but did not meet the TRT's sample size criteria for inclusion in analyses.

We estimated an indirect measure of gene flow following Slatkin (1985) where:

$$\theta = 1/(1 + 4Nm) \quad (1)$$

Nm is the effective number of migrants per generation. This approximation assumes an infinite island population genetic model and that the pattern of allele frequencies among populations is due to gene flow (e.g., instead of mutation, selection, or random genetic drift). Extensive simulations have shown that the approximation of gene flow using this equation is robust to violations of the simplifying assumptions (Slatkin and Barton 1989). Pairwise estimates of θ were calculated between all groups within a watershed.

In identifying populations the TRT was interested in whether divergence times between groups are greater or less than 100 years. The team estimated the time since divergence (*t*) of two groups from a common population where:

$$t/2Ne = -Ln(1 - \theta) \quad (2)$$

Ne is the genetic effective population size and *Ln* is the natural logarithm. Under this model the two groups are assumed to have diverged from a common ancestral population *t* generations ago, have had no gene flow between them since divergence, have discrete generations, mate randomly within groups, and have selectively neutral genetic variation (Weir 1996).

Although Pacific salmonids do not have discrete generations, Waples (1990) showed that this violation is not likely to greatly affect estimates of *t* over long time periods. Likewise low levels of gene flow since divergence, which may have occurred between many populations, are likely to result in underestimates of the time since divergence. The TRT estimated pairwise *Ne* between groups where:

$$Ne = gNb \quad (3)$$

g is the mean age at spawning for each group and *Nb* is the harmonic mean of the effective number of breeders per cohort. The team estimated *Nb* using census data, *N*, and an *Nb/N* ratio of 0.3, based on values from the literature for a number of salmonid species (Waples 1990, Waples et al. 1993, Ford et al. 1999).

In order to assess the spatial scale of genetic similarity, the TRT examined the association between genetic differentiation, θ, and geographic distance separating sampling sites (Figure 3). The team tested for a positive association between genetic differentiation and geographic distance using a one-tailed Mantel test with 2,000 bootstrap iterations and reduced major axis regression (Sokal and Rohlf 1981, Hellberg 1994) using Isolation by Distance (IBD) 1.4 (Bohonak 2002).

Results

Significant differences in allele frequencies among samples from different river basins and streams within basins indicated that population differentiation occurred at the geographical level of river basins or smaller. The only sample pairs that were not statistically significantly different were the Wallace River-Skykomish River, Wallace River-Bridal Veil Creek, and Bridal

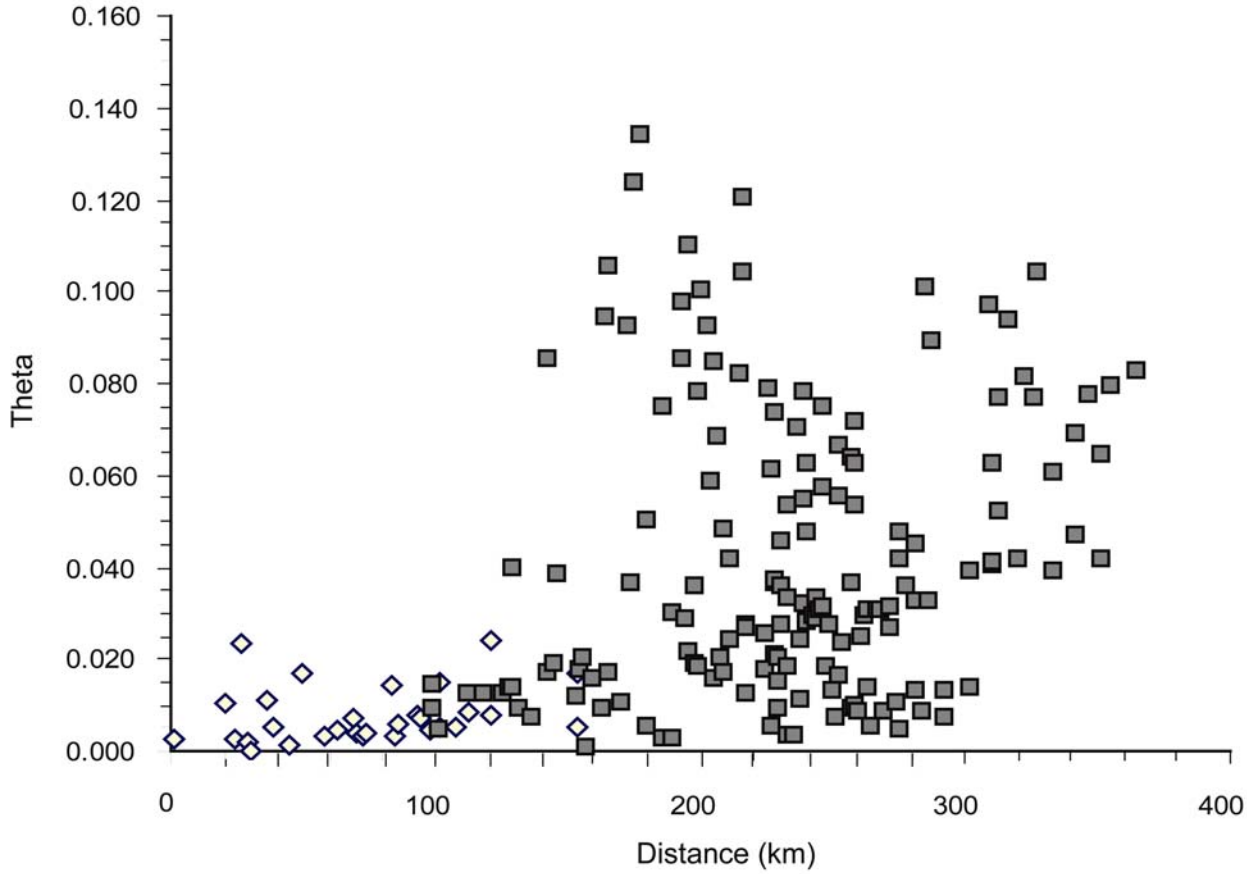

Figure 3. Relationship between genetic differentiation and geographical distance for groups of Puget Sound Chinook salmon. Open diamonds and closed squares compare samples within and between major river basins, respectively.

Veil Creek-Skykomish River in the Snohomish River basin and the Newaukum Creek-Green River comparisons. Genetic differences between aggregations generally increased with geographic distance (Mantel $Z = 1608.19$, $P < 0.001$) (Figure 3). Distances separating spawning aggregations within river basins usually occur at a scale of 120 km or less, whereas distances between river basins occur at greater than 100 km, and most river basins are separated by 160 km or more. No obvious discontinuities in the distribution of θ existed at this scale, but on average θ was 0.015, which corresponds to genetic exchange of 17 effective migrants or less per year (Table 4).

Clusters of genetically similar Chinook salmon in Puget Sound streams were consistent generally with the spatial configuration of the streams, especially in the northern Puget Sound region (Figures 4, 5, and 6). There were six major genetic clusters of Chinook salmon in Puget Sound:

1) Strait of Juan de Fuca,
2) Nooksack River early run,
3) Skagit River and North Fork Stillaguamish River,
4) Snohomish River and South Fork Stillaguamish River,

Table 4. Estimates of genetic differentiation among major geographical groups of Puget Sound Chinook salmon (θ) and genetic exchange (*Nm*) among spawning aggregations (subgroups) based on 31 allozyme loci.

Group name	Number of subgroups	θ	Lower confidence interval	Upper confidence interval	*Nm*
Puget Sound	35	0.033	0.023	0.046	7
Nooksack	2	0.017	0.004	0.036	14
Skagit	7	0.006	0.004	0.008	41
Skagit spring	4	0.004	0.003	0.006	62
Skagit summer/fall	3	0.003	0.000	0.006	83
Stillaguamish	2	0.023	0.010	0.037	11
Snohomish	7	0.005	0.003	0.009	50
Lake Washington	3	0.006	0.001	0.010	41
South Sound	6	0.013	0.006	0.024	20
Hood Canal	2	0.000	–0.003	0.004	—
Strait of Juan de Fuca	2	0.014	0.003	0.026	18

5) Central/southern Puget Sound and Hood Canal late-returning, and
6) White River early run.

The bootstrap values for the consensus tree (Figure 5) showed good statistical support for the major groups in the dendrogram. The specific relationships between individual aggregations within the major groups were less supported, especially in central and south Puget Sound and Hood Canal. Lack of definitive relationships in these regions may reflect the extensive history and continuing presence of Chinook salmon from hatchery programs. Many south Puget Sound and Hood Canal samples are very similar genetically to Chinook salmon from the Green River, which have been extensively introduced throughout those areas. Consequently patterns of genetic differentiation were not very informative for identifying historical population structure in central and south Puget Sound and Hood Canal.

Average genetic differentiation (θ) among all groups of Chinook salmon in Puget Sound was 0.033, corresponding to an estimated average gene flow between groups of seven effective migrants per generation (Table 4). Within major watersheds θ ranged from 0.000 among sites sampled in the south Puget Sound and Hood Canal to 0.023 among two stocks within the Stillaguamish River basin. In general θ values among stocks within a river basin were less than 0.02 (Figure 3).

Estimates of *Ne* for Puget Sound Chinook salmon groups varied from *Ne* = 101 for the fish in the North Fork Nooksack River to *Ne* = 7,971 for upper Skagit River fish (mean *Ne* over all groups = 1,320 fish per generation; median *Ne* = 573). Estimates of *t* between Chinook salmon groups ranged from fewer than zero generations since divergence (for Bridal Veil Creek-Skykomish River and Bridal Veil Creek-Wallace River comparisons) to 324 generations since divergence for Chinook salmon in the lower Skagit and lower Sauk rivers (Appendix B,

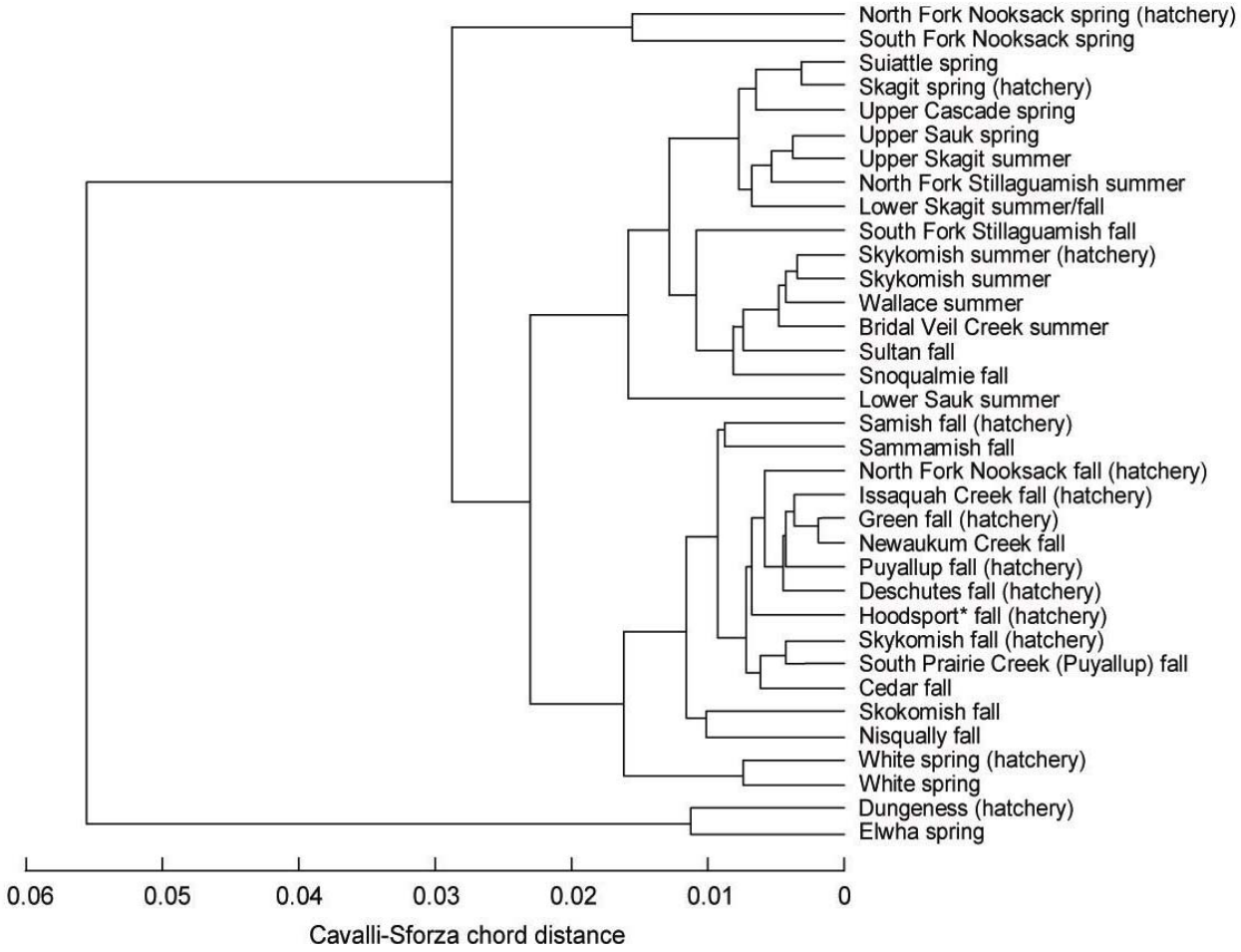

Figure 4. UPGMA dendrogram of genetic similarity of Puget Sound Chinook salmon groups. Locations signify rivers unless otherwise noted. Asterisk (*) signifies a release site.

Table B-2, pages 98–99). Mean *t* over all pairwise comparisons was 77 generations; median *t* was 25. Pairwise estimates of *t* indicate that roughly half the Chinook salmon groups (12 of 26) have been isolated for less than 100 years (assuming a 5-year generation time). As discussed in the Population Structure Decisions subsection (page 22), these low estimates of *t* need to be interpreted considering violations of assumptions in the model used to estimate *t*. For example, when low gene flow levels occur that are not demographically significant, the true time since divergence is likely to be longer than the estimated time. However high values of *t* are not likely to be misleading, so the pairwise comparisons with *t* estimates greater than 100 years are more reliable.

Patterns in Life History Characteristics

Methods

Similarities in life history or phenotypic characteristics were used as possible indicators of genetic relationships among Chinook salmon stocks. In addition examining the spatial pattern

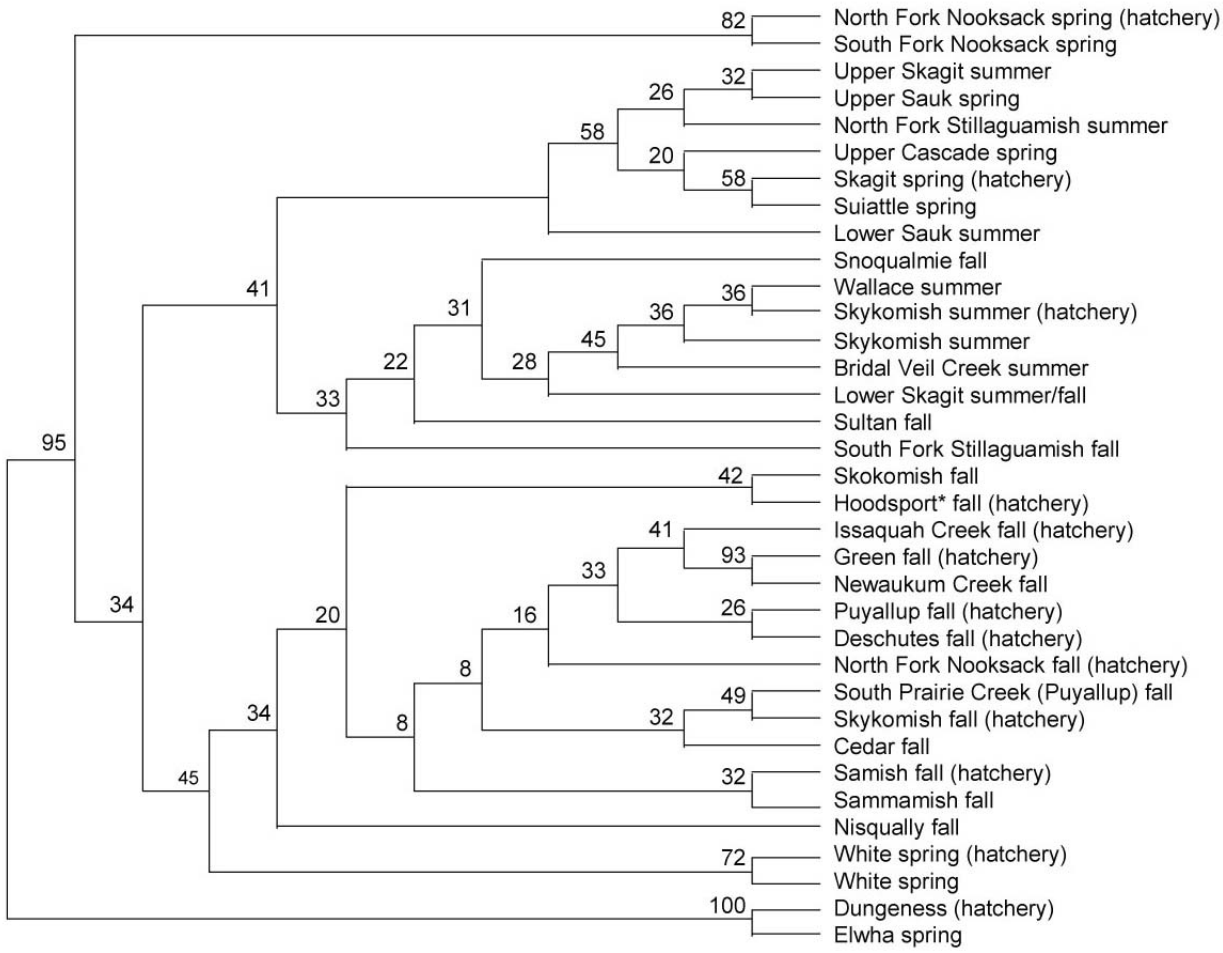

Figure 5. Consensus dendrogram of genetic similarity among Puget Sound Chinook salmon groups. Numbers at nodes indicate bootstrap support percentage. Locations signify rivers unless otherwise noted. Asterisk (*) signifies a release site.

of phenotypic variation (such as that exhibited by life history traits) can suggest differences among sites in environmental characteristics that could promote adaptive divergence of fish. More detailed analyses are needed to determine the adaptive significance of phenotypic variation, but in the context of this technical memorandum the TRT considers life history trait variation to be qualitatively informative for population identification. Four life history characteristics—age at downstream migration, age at spawning, age-specific length, and timing of spawning—were analyzed in detail. Only time of spawning was informative for our population structure decisions. Summaries of the other life history data are in Appendix A (page 67). Other life history characteristics were considered but not analyzed in detail. Ocean distribution and timing of return to the river basin of origin, in particular, have been used extensively to define and manage salmon stocks. Both of these characteristics have been well recognized as persistent attributes of Chinook salmon stocks (Williams et al. 1975, Healey 1991, Stouder et al. 1997, Meyers et al. 2003). Given other available data, and low power of these characteristics as indicators of population differences for Puget Sound Chinook salmon, the TRT did not use them. However these characteristics may be informative for further analyses of population and ESU persistence.

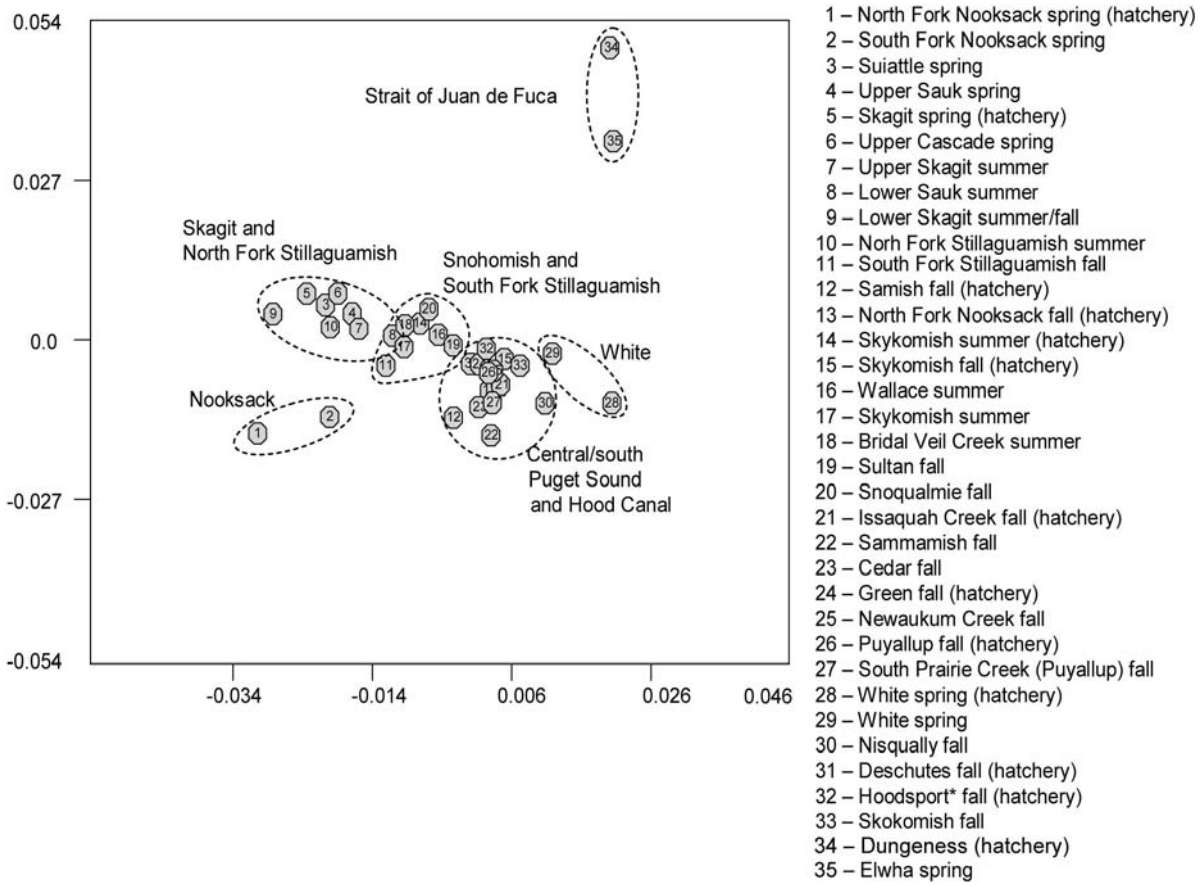

Figure 6. Multidimensional scaling of genetic similarity of Puget Sound Chinook salmon groups. Locations signify rivers unless otherwise noted. Asterisk (*) signifies a release site.

For the time of spawning analysis the TRT inferred the timing of spawning for Chinook salmon from time series of spawner densities (fish per mile) in index surveys conducted annually throughout Puget Sound. The team used only years in which at least six surveys were conducted and the densities on the first and last survey dates were at most 20% of the maximum density for the year. These criteria were intended to select annual time series that provide a reasonable estimate of the shape of the timing curve, particularly the tails. Yearly data were standardized to remove interannual variation in abundance and averaged over all years to give an average relative density curve for each index area. From each curve we calculated a weighted mean date of spawning, using the daily-average relative spawner densities as weights. The absolute value of the difference between the mean spawning dates was calculated for every pair of index areas and used as a dissimilarity matrix in a UPGMA cluster analysis.

Results

Cluster analysis based on differences in mean spawning date indicates that there are at least three fairly distinct groups, corresponding roughly to early through late August, late August through mid-September, and mid-September through late October (Figure 7). These breakpoints, however, are not obvious from inspection of the range of mean spawning dates (Figure 8), which suggests a more continuous distribution of spawn timing. At a finer level, different index areas

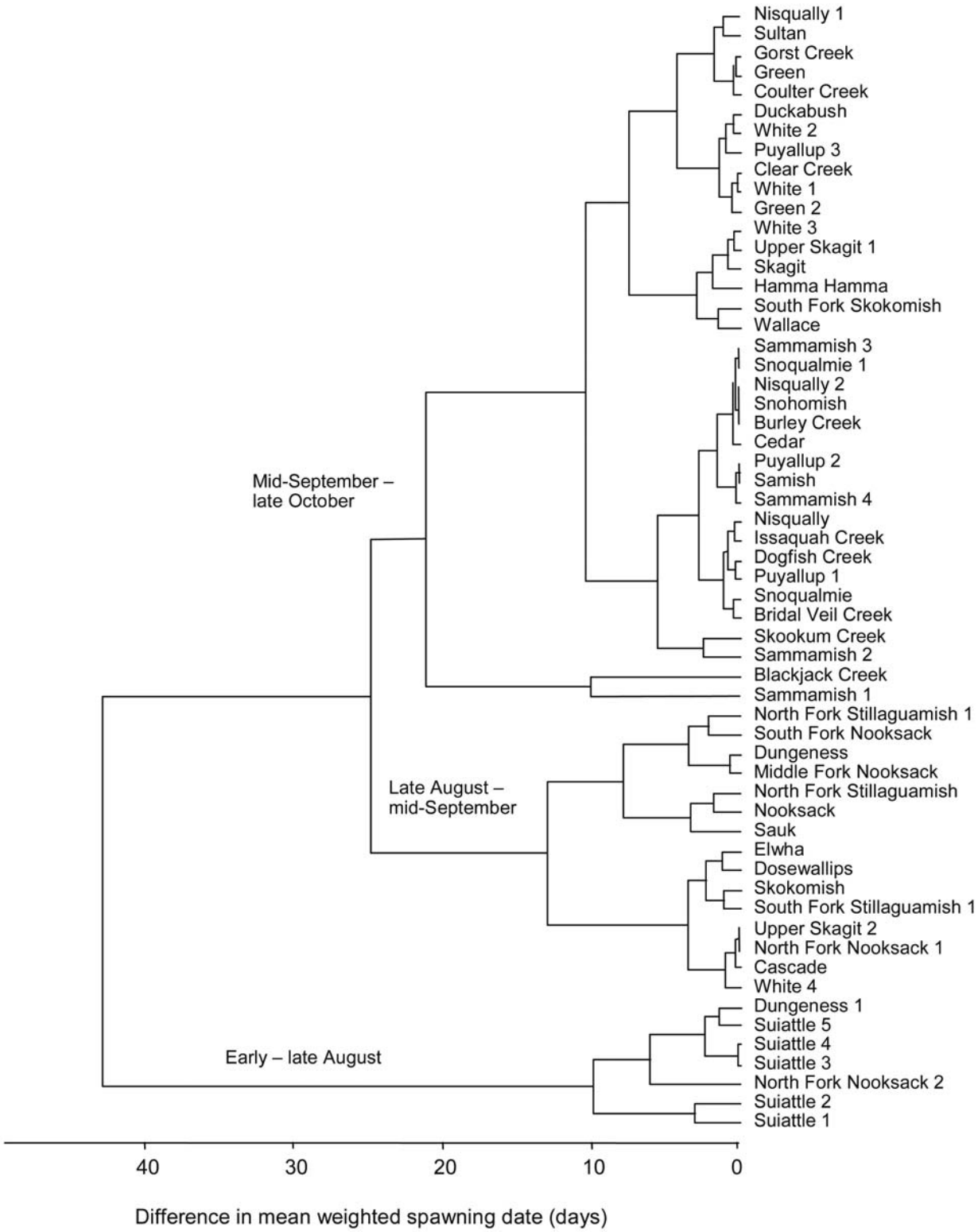

Figure 7. Similarity of Puget Sound Chinook salmon based on weighted-mean date of spawning from different index areas. Locations signify rivers unless otherwise noted.

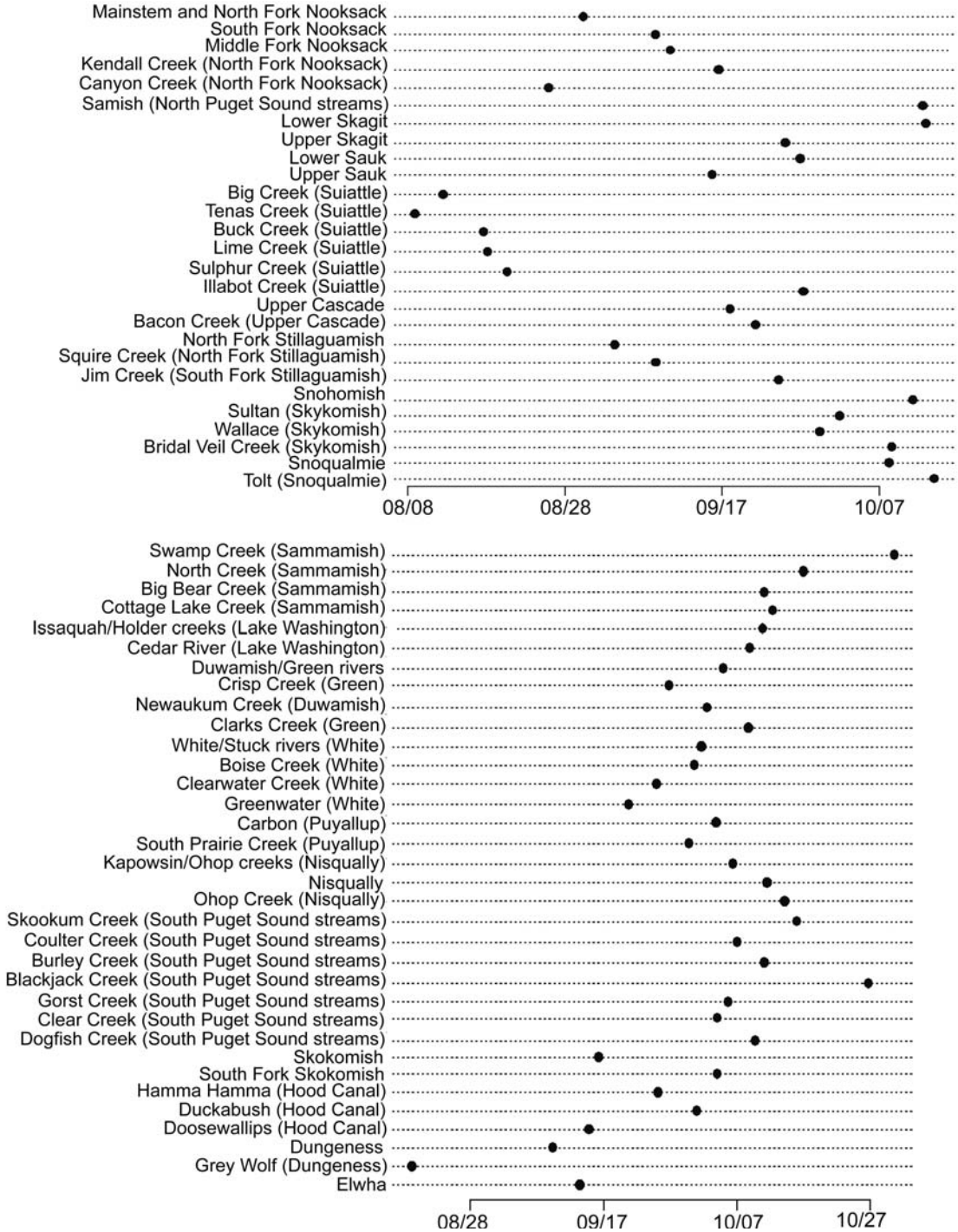

Figure 8. Weighted-mean spawning dates for Chinook salmon in Puget Sound index survey areas. The top chart is for the north Puget Sound index areas. The bottom chart is for the south Puget Sound index areas. Locations signify rivers unless otherwise noted.

within a single SASSI stock are sometimes very similar in their spawn timing (e.g., Suiattle River tributaries) but not always. In general there is a latitudinal cline in timing with earlier spawning in more northerly basins.

Spatial Synchrony in Spawner Abundance

Examining the patterns of covariation in abundance between Chinook salmon groups can, theoretically, indicate the degree to which the groups may be linked by migration. Unfortunately there is another reason why fish groups might exhibit similar population dynamics: they may experience similar environmental conditions. It is not possible to tease apart these two potentially confounding sources of covariation without experimentation. For these reasons (and the unknown proportion of hatchery fish in many groups), the results from these analyses were only partly informative for population structure decisions. On the whole the relationships among stocks suggested by correlations in abundance are not concordant with the pattern suggested by geography and genetic similarity (i.e., geographically proximate stocks do not consistently show stronger correlations in abundance than geographically distant stocks). The analytical approach to quantifying correlations and results from these analyses is reported in Appendix A (page 67).

Habitat Characteristics

Patterns of regional habitat characteristics can provide insights into the different selective environment fish experience, which may influence population structure. These analyses, which provide the weakest inference of population structure, are potentially most useful in areas where genetic, abundance, and life history data are not available. The TRT explored differences in habitat characteristics that might be correlated with different selective environments, including:

1) hydrological characteristics of rivers and streams,
2) water temperatures,
3) EPA ecoregions, which are defined by a composite of habitat features, and
4) underlying geological substrate.

Although differences in habitat characteristics among Puget Sound streams are apparent, the biological significance of those differences to Chinook salmon population structure is not known. The strength of inference from these results is relatively low, and the team did not rely on them heavily in identifying populations. The analytical approaches and results from these analyses are in the appendixes.

Population Structure Decisions

The six different indicators of population structure that the TRT used (geographical distribution, migration, genetic differences, life history differences, spatial synchrony in spawner abundance, and environmental differences) have different values for identifying independent populations. Recognizing these differences, the team examined the data hierarchically to make decisions about population structure. The members made decisions in a stepwise fashion, using geography, genetic differentiation, and differences in life history (i.e., spawn timing) as indicators of population structure. Although inferences from the other indicators (migration, spatial synchrony in spawner abundance, and environmental differences) were too weak to identify independent populations, the team used these differences as “weight of the evidence” for lending support (or increasing the certainty) to populations identified with geographic, genetic, and life history information.

The TRT first examined the geographic distribution of spawners within Puget Sound to circumscribe the watersheds considered to be the largest scale at which independent populations are likely to occur, using a list of spawning aggregations in Puget Sound derived from information in SASSI (Table 2) (WDF et al. 1993). The team began at this level because allele frequency differences among aggregations were always significant at the level of major rivers entering salt water and analysis of isolation by distance suggested minor levels of genetic exchange that were unlikely to affect persistence of independent populations. In south Puget Sound and Hood Canal, the team combined smaller watersheds draining directly to Puget Sound into a larger geographic area for consideration, usually focused around a large river system. Although the members had no formal criteria for a minimum watershed size for Chinook salmon, aggregation of these smaller watersheds reflects the general observations that many of them had little historical or anecdotal evidence of self-sustaining populations, were much smaller than the streams that have been actively managed by state and tribal fishery managers (hereafter referred to as comanagers) for natural Chinook salmon production, had lower gradients and flow, and in recent times had abundances that were largely influenced by the abundance of hatchery fish returning to nearby hatcheries.

Within each group defined by geographical separation at the largest scale, the TRT examined each possible pair of spawning groups for population independence, first using genetic data. If the genetic data did not provide strong inference for defining group identities, the team then examined life history and other indicator differences to make a decision. To standardize population data across indicators, all information for each indicator was summarized in a matrix representing the pairwise differences in the data types between all groups within a watershed (see Appendix B, pages 95–125). The TRT judged independence in two ways:

1) For genetic indicators the team relied on expert opinions of the significance of eight genetic relatedness metrics.
2) For the life history indicator the team developed a quantitatively based decision rule to decide whether a group was independent.

In each case the TRT assigned an independence score to each pair of sites within a watershed ranging from –4 (groups are part of the same population) to +4 (groups are independent populations). Scores ranging between –4 and +4 indicated the degree of difference suggested by the data and the level of confidence the scorer had in those data. For example 0 indicated that either intermediate differentiation existed between the groups or that their population structures were ambiguous from the available information. A positive score indicated that the evidence suggested that the two groups were independent populations. Scores of 3 to 4 for the genetic indicators (see the following subsection) provide strong support that the two groups were independent populations, and no further information was needed. In contrast, when independence scores for genetic indicators ranged from 1 to 2, indicating population independence but with less confidence, the TRT used life history differences to further inform its decisions. For each indicator the team summarized the independence between each pair of sites as the median independence score across scorers (with 6–10 scorers per indicator) and the distribution of independence scores among scorers (Table 5 and Appendix A, Table A-1, pages 68–69).

Table 5. Median independence scores (n = 10 scorers) based on genetic data for groups of Chinook salmon in Puget Sound watersheds.

Nooksack River basin

	South Fork Nooksack	North Fork Nooksack
South Fork Nooksack	—	
North Fork Nooksack	3	—

Skagit River basin

	Lower Skagit	Upper Skagit	Lower Sauk	Upper Sauk	Suiattle	Cascade
Lower Skagit	—					
Upper Skagit	2	—				
Lower Sauk	2	2	—			
Upper Sauk	2	2	2	—		
Suiattle	3	2	2	2	—	
Cascade	3	2	2.5	2	2	—

Stillaguamish River basin

	North Fork Stillaguamish	South Fork Stillaguamish
North Fork Stillaguamish	—	
South Fork Stillaguamish	3	—

Snohomish River basin

	Lower Snohomish	Skykomish	Sultan	Wallace	Bridal Veil Creek	Snoqualmie
Lower Snohomish	—					
Skykomish	0	—				
Sultan (Skykomish)	0	2	—			
Wallace (Skykomish)	0	–2	1	—		
Bridal Veil Creek (Skykomish)	0	–2	2	–3	—	
Snoqualmie	0	2	2	1	1	—

Lake Washington

	Cedar	North Lake Washington	Sammamish	Issaquah Creek
Cedar	—			
North Lake Washington	0	—		
Sammamish	2	0	—	
Issaquah Creek	2	0	1	—

Table 5 continued. Median independence scores (n = 10 scorers) based on genetic data for groups of Chinook salmon in Puget Sound watersheds.

South Puget Sound

	Duwamish/Green	Puyallup	White	Nisqually	Deschutes
Duwamish/Green	—				
Puyallup	1	—			
White	3	3	—		
Nisqually	1	2	3	—	
Deschutes	0	0	0	0	—

Hood Canal

	Skokomish	Hamma Hamma	Duckabush	Dosewallips
Skokomish	—			
Hamma Hamma	–1	—		
Duckabush	0	0	—	
Dosewallips	0	0	0	—

Strait of Juan de Fuca

	Dungeness	Elwha
Dungeness	—	
Elwha	3	—

Genetic Indicators

Ten geneticists from the WDFW, the Northwest Indian Fisheries Commission (NWIFC), and the National Marine Fisheries Service (NMFS) provided independence scores based on the same set of analyses (Table 5 and Appendix A, Table A-1, pages 68–69). These analyses were as follows:

- Pairwise P values from log-likelihood ratio tests (G-tests) for significant differences in allele frequencies (Appendix B, Table B-5, pages 104–105).
- Pairwise Cavalli-Sforza and Edwards genetic distances (Appendix B, Table B-3, pages 100–101).
- A dendrogram and multidimensional scaling of similarities of Puget Sound Chinook salmon based on Cavalli-Sforza and Edwards genetic distance (Figures 4, 5, and 6).
- Pairwise Nei's genetic distances (Appendix B, Table B-4, pages 102–103).
- Dendrogram (figure not shown) of similarities of Puget Sound Chinook salmon based on Nei's genetic distance (data in Appendix B, Table B-4, pages 102–103).
- Pairwise estimates of θ, a measure of genetic differentiation between groups (Appendix B, Table B-1, pages 96–97).

- Pairwise estimates of migrants per generation (*Nm*) (Appendix B, Table B-1, pages 96–97).
- Pairwise estimates of migrants per generation (*Nm*) (Appendix B, Table B-1, pages 96–97).

Analysis of the scoring indicated that *P* values from G-tests, estimates of θ, and genetic distances were most influential in assessing independence. Because of the relatively large sample sizes and statistical power of the G-tests, the group of scorers decided that if two fish groups were not statistically significantly different, they were unlikely to be in two different populations. However it is possible that a single population could contain two subpopulations that are statistically significantly different from one another in one or more genetic metrics.

The geneticists also relied on estimates of time since divergence, because any bias in the estimates would tend to underestimate the time since divergence. Most of the people scoring differences between groups indicated that they assigned scores closer to zero in cases where data were ambiguous, rather than using zero scores to indicate intermediate degrees of independence.

Life History Indicators

The TRT ranked independence using a decision rule that related the degree of potential reproductive overlap (*P*) based on spawn timing to empirical evidence of reproductive isolation among sympatric populations. The team scored groups as follows:

- Independent if *P* is less than 0.01.
- Likely to be independent if *P* is less than 0.100.
- Unsure because of insufficient information if *P* is greater than 0.100.

This approach assumes that the degree of temporal overlap between spawning groups is a good estimate of reproductive independence (i.e., spatial distances separating groups and behavioral isolating mechanisms are not included in this estimate). Values of *P* from sympatric groups of winter and summer steelhead (*Oncorhynchus mykiss*) and summer and fall chum salmon (*O. keta*) were used to set threshold values that corresponded to different levels of confidence that the populations were independent (Appendix A, Figure A-1, page 74).

Migration Indicators

Estimates of straying from CWT groups were the only direct indicators of migration available. These data were not designed to address the question of population independence. Consequently estimates were only mildly informative. Nevertheless a matrix of straying estimates and dispersal curves generated from the CWT database (Table 2 and Appendix A, Figure A-1, page 74) were helpful in identifying where straying has occurred between sites and the distances over which fish traveled to stray.

Population Dynamics Indicators

Correlations in the time series of abundance were available for some groups of Chinook salmon in Puget Sound (Appendix A, Figure A-4, page 79). Because of the potentially

confounding effects of correlated environmental conditions, these analyses were only mildly informative.

Habitat Indicators

The most informative habitat information for identifying population structure that we examined was the correlation in flow from unregulated gauges in Puget Sound rivers. Correlations in flow between those gauges in close proximity to spawning aggregations were used to score similarity in flow regime between sites (Appendix A, Figure A-8, page 87). Other habitat-related characteristics such as temperature during incubation (Appendix A, Figure A-9, page 89), EPA ecoregions (Appendix A, Figures A-10 and A-11, pages 90–91), and geological characteristics (Appendix A, Figure A-12 and Table A-3, pages 92–93), provided some corroborative information. The TRT did not use these indicators to identify independent populations, but they did offer support for (or added certainty to) conclusions based on the three primary indicators.

Conclusions

This section lists and describes the extant demographically independent populations of Chinook salmon the TRT defined for recovery planning in the Puget Sound Chinook salmon ESU (Figure 9) as follows:

1) North Fork Nooksack River
2) South Fork Nooksack River
3) Lower Skagit River
4) Upper Skagit River
5) Cascade River
6) Lower Sauk River
7) Upper Sauk River
8) Suiattle River
9) North Fork Stillaguamish River
10) South Fork Stillaguamish River
11) Skykomish River
12) Snoqualmie River
13) Sammamish River
14) Cedar River
15) Duwamish/Green River
16) White River
17) Puyallup River
18) Nisqually River
19) Skokomish River
20) Mid-Hood Canal Rivers
21) Dungeness River
22) Elwha River

In all cases the populations reflect the TRT's best estimate of the corresponding populations that spawned and reared in these streams under historical conditions and that presently contain fish. As stated earlier, in some watersheds the fish present do not represent those that were there historically. Likewise some watersheds have lost populations and major components of historical Chinook salmon diversity that have not been replaced. The potential roles of these populations in recovery will be determined in subsequent documents. Table 6 offers a more detailed summary of the within-population life history diversity types that likely occurred historically within the Puget Sound ESU. The narratives following the populations briefly summarize the data and information the TRT has assembled to date.

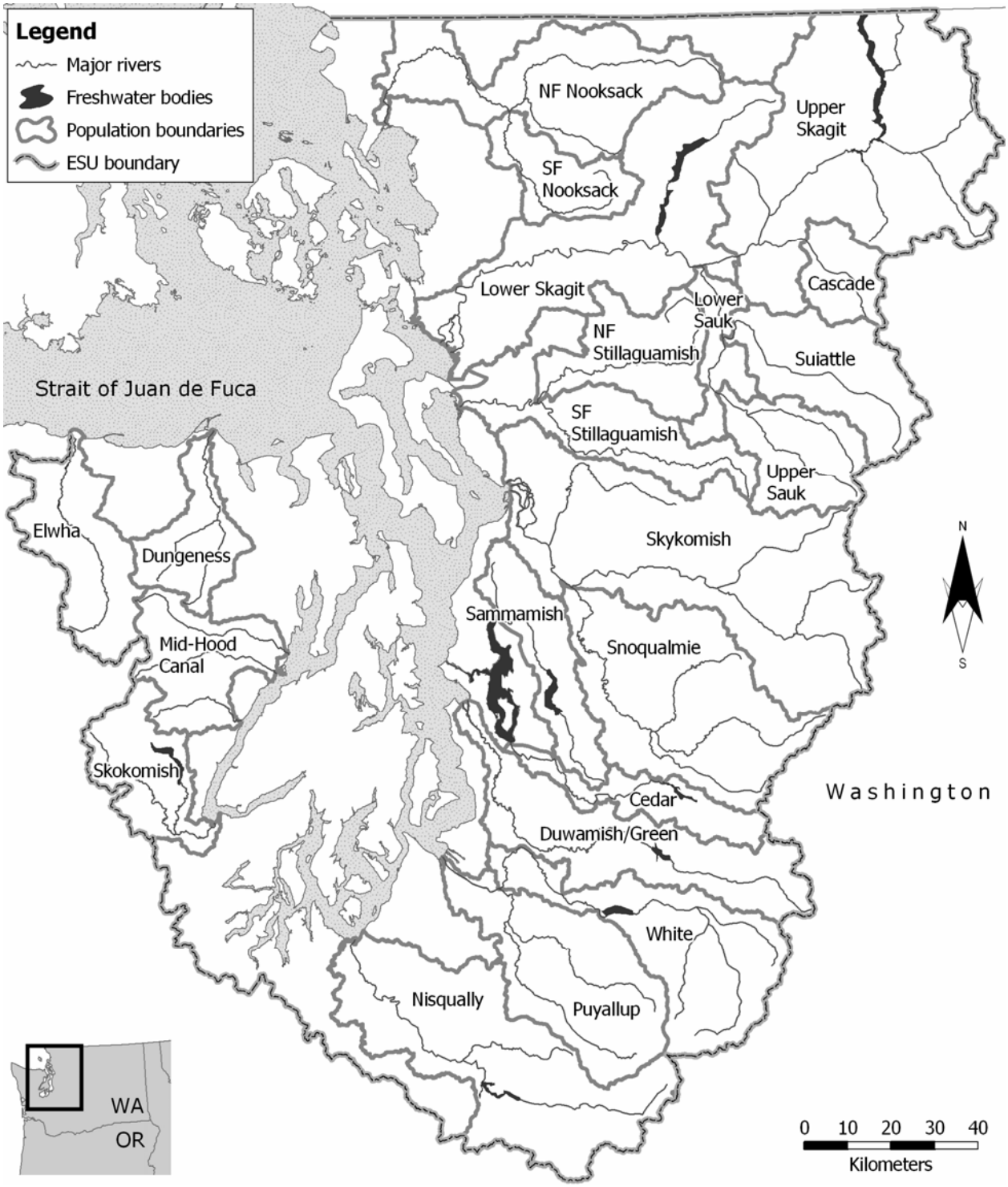

Figure 9. Proposed independent populations of Chinook salmon in the Puget Sound evolutionarily significant unit (ESU). Locations signify rivers unless otherwise noted.

Table 6. Summary of losses in Chinook salmon diversity in Puget Sound river and drainage basins.

River/ drainage basin	Diversity lost	Summary findings	Independent populations identified
Nooksack	Late run	Historical diversity in late run form is no longer extant	North Fork Nooksack South Fork Nooksack
Skagit	Baker River	Baker River diversity form is no longer extant; no evidence that this form represented an historically independent population	Lower Skagit Upper Skagit Cascade Lower Sauk Upper Sauk Suiattle
Stillaguamish	Early run	Early run diversity form is extinct; not clear whether this form represented an historically independent population	North Fork Stillaguamish South Fork Stillaguamish
	Main stem	Historical and current status are unknown; no evidence that this form represented an historically independent population	
Snohomish	Early run	Early run diversity form is extinct; not clear whether this form represented an historically independent population	Skykomish Snoqualmie
Lake Washington	Sammamish Basin	Historical diversity in Lake Sammamish form is no longer extant	Sammamish Cedar
Duwamish/Green	Early run	Early run diversity form is extinct; not clear whether this form represented an historically independent population	Duwamish/Green
Puyallup	Early run	Early run diversity form is extinct; not clear whether this form represented an historically independent population	Puyallup White
	Late-run upper Puyallup/White	Historical diversity in late run form is no longer extant	
Nisqually	Late run	Historical diversity in late run form is no longer extant	Nisqually
	Early run	Historical diversity in early run is extinct; not clear whether diversity form represented an historically independent population	

Table 6 continued. Summary of losses in Chinook salmon diversity in Puget Sound river and drainage basins.

River/ drainage basin	Diversity lost	Summary findings	Independent populations identified
Skokomish	Late run	Historical diversity in late run form is no longer extant	Skokomish
	Early run	Early run diversity form is no longer extant; not clear whether early run diversity form represented one or more historically independent populations	
Mid-Hood Canal	Late run	Historical diversity in late run form is no longer extant	Mid-Hood Canal
	Early run	Early run diversity form is extinct	
Dungeness	Late run	The late- and early run groups currently spawning in the Dungeness River are part of the historical diversity	Dungeness
Elwha	Early run	Early run diversity form is extinct; not clear whether this form represented an historically independent population	Elwha

Habitats and Fish Outside Primary Spawning Areas: Implications for Recovery Planning

Naturally Spawning Chinook Salmon not Assigned to an Independent Population

The TRT did not assign all groups of Chinook salmon spawning naturally in Puget Sound streams (WDF et al. 1993) to independent populations for two reasons:

1) Spawning adults are known to occur intermittently in certain streams—spawning in groups of tens to hundreds of fish in some years and none in others. A plausible explanation for intermittent occurrence of Chinook salmon in some streams is that those adults are part of a larger independent population that uses some spawning habitats only during years of high abundance or favorable habitat conditions. The streams that intermittently harbor spawning adults also could contain fish from more than one independent population, depending on their locations relative to the primary spawning areas of independent populations.
2) It is possible that some streams presently containing Chinook salmon never supported naturally spawning Chinook salmon historically. In many of these instances, the origin of the naturally spawning Chinook salmon present is most likely due to returning adults from hatchery production. Some streams may therefore contain Chinook salmon only because of the presence of a hatchery or releases of hatchery fish, and these streams would not have represented historical Chinook salmon spawning habitat that could sustain an independent population.

As more information becomes available, it is possible that Chinook salmon in some intermittently used streams can be clearly associated with one or more populations, and their assignment will change to reflect their association with a particular population. For the purposes of specifying viable population criteria and evaluating ESU recovery scenarios, Chinook salmon occurring in small streams that are not within the geographic boundaries of independent populations should be considered possibly to contribute to the population dynamics of independent populations in Puget Sound.

Importance of Habitats Outside Watersheds Containing Primary Spawning Areas

It is important to remember that the geographic boundaries of independent populations defined in this technical memorandum focus on spawning habitat and do not include all habitats that may be important to population viability or ESU recovery (Figure 9). Habitats used by Chinook salmon throughout the life cycle and their potential importance to recovery—including those used occasionally by spawning adults—must be identified throughout the Puget Sound

region. For example habitats used by juveniles for freshwater, estuarine, and nearshore rearing and foraging typically will not be included in the geographic boundaries of independent populations identified in this study. That does not mean that those habitats are unimportant to recovery. Many are likely to be critical to the ESU's viability, as discussed in detail in McElhany et al. (2000). The challenge for forthcoming analyses conducted by the TRT and others is to identify which habitats are the most important to protect or restore to ensure the viability of populations and the ESU. An important step in conducting these analyses is identifying which habitats fish occupy throughout their life history and the population origins of fish in particular areas.

Independent Populations in Puget Sound

Nooksack River Basin

Chinook salmon in the Nooksack River basin are distinctive from Chinook salmon in the rest of Puget Sound in their genetic attributes, life history, and habitat characteristics, indicating support for the geographical evidence of independence of these fish. Although some Chinook salmon from the Nooksack River basin may sometimes stray into other Puget Sound rivers (based on releases from Kendall Creek Hatchery), the low numbers probably have not had a significant effect on the population dynamics of other populations. The TRT identified two existing independent populations in the Nooksack River basin (The numbering sequence follows the list of populations in the Conclusions section, page 28.):

1) North Fork Nooksack River (including Middle Fork Nooksack River)
2) South Fork Nooksack River

The Nooksack River may have lost some of the Chinook salmon diversity that once occurred in the basin (Table 1). Historical evidence suggests that a later-returning life history occurred in the Nooksack River. Summer and fall Chinook salmon were reported entering the river beginning in July, with spawning occurring in mid-September and October, in contrast to the remaining populations of Chinook salmon that continue to enter the river beginning in March and spawn beginning in mid-August (Williams et al. 1975, WDF et al. 1993). A long history of introductions of late-returning fish from other basins, especially from the Green River (Myers et al. 1998), has obscured genetic evidence of historical later-returning spawning aggregations. The TRT concluded that this life history was part of the historical diversity of Chinook salmon within the basin, but the team had insufficient information to determine whether it existed as an independent population or as a part of the diversity of another population or other populations.

Summary of information used in population structure decisions

Chinook salmon historically had access to spawning areas in the north fork, middle fork, south fork, and mainstem of the Nooksack River. A diversion dam eliminated spawning in the most of the middle fork, but spawning has continued in the other areas.

Genetic data showed strong support for independence of early returning Chinook salmon from the north and south forks (independence score = 3). Allele frequencies were significantly different ($P < 0.0000$) (Appendix B, Table B-5, pages 104–105). Genetic population

differentiation ($\theta = 0.024$) was one of the largest observed between spawning aggregations within a river basin in the Puget Sound; it indicated only 2–3 genetically effective migrants exchanged between the two populations annually, which should not significantly affect either population's demographic independence. Likewise the genetic distance separating fish from the two forks is the second largest in the dendrogram for the entire Puget Sound region (Figure 4). The estimated time of divergence ($t \approx 28$ years), however, is lower than expected and suggests that this estimate may be biased downward because 1) there were low levels of gene flow, 2) t was calculated using recent low effective population sizes, or 3) the divergence is relatively recent because of large amounts of genetic drift. Previous analyses (Marshall et al. 1995) also considered the Chinook salmon in the two Nooksack River forks to be independent, designating them as separate genetic diversity units (GDUs), based on genetic differences, geographic distribution, and life history. Chinook salmon in the north and south forks are of natural origin and the limited influence of hatchery fish in spawning escapements (WDF et al. 1993, Myers et al. 1998) would not have affected the data.

Spatial isolation within the watershed and life history information support the TRT's decision on population structure. The primary spawning areas of the two groups of fish are separated by at least 10 km. Peak spawning time between fish groups from the main stem and north and south forks differs by approximately two weeks (Figure 8 and Appendix B, Table B-7, pages 110–112), with south fork Chinook salmon spawning later on average and over a longer time (Figure 8). The differences in spawn timing of Chinook salmon in the two forks may reflect a mixing of late return, nonindigenous Chinook salmon that now spawn in the south fork with the early returning south fork spawning population (see the Data needs and remaining uncertainties subsection, page 35). These nonnative, later returning Chinook salmon primarily are from the Samish Hatchery broodstock; they were released from several hatcheries within the basin. Furthermore the spawn timing information in Figure 8 for the mainstem and North Fork Nooksack River includes unknown fractions of late- and early returning fish. A third factor complicating the interpretation of the differences in spawn timing between the two forks is that survey efforts missed most of the spawning that occurs in July in the north and middle forks.[3]

The TRT had no genetic, life history, or migratory data to determine whether Chinook salmon that historically spawned in the middle fork were an independent population. If an independent population did exist, it was extirpated. Consequently the team used geography and environmental information as rationale for including the middle fork in the north fork population for recovery efforts. The middle fork joins the north fork to form a single fork of the river, whereas the south fork enters the main stem as a tributary lower in the system. The middle and north forks are influenced by glacial-origin waters and flow through steep mountainous terrain.

The TRT had no genetic, life history, or migratory data to determine whether an independent population of late-returning Chinook salmon historically existed in the Nooksack River. Evidence for an historical population includes historical catch records, which indicate that late-returning Chinook salmon existed in the Nooksack River, although these fish may have been part of populations with a broader distribution of return timing than exists now. In addition introduced late-returning fish have become established in the river, which suggests that the habitat and opportunity once existed for an historical population. The team concluded that the

[3] N. Currence, Nooksack Indian Tribe, Natural Resource Dept., Deming, WA. Pers. commun., 23 March 2001.

late-returning life history was part of the historical diversity of Chinook salmon within the basin, but could not determine whether it constituted an independent population.

Summary of additional information

Information about straying is mixed. Genetic data indicate that straying was low in the past, but may have increased in recent years. CWT data from 1973 to 1997 (RMPC 1997) indicate that some straying has occurred from the Kendall Creek Hatchery on the north fork and from the Skookum Creek Hatchery on the south fork, although the data are inadequate to quantitatively estimate stray rates. Marshall et al. (1995) concluded that straying between the two forks was very low based on mixed CWT recoveries (n = 10 fish from 1984 to 1992). Recent studies suggest much more straying occurs between the forks, although it may reflect hatchery releases of early returning north fork fish and late returning Green River fish. Hatchery strays of north fork Chinook salmon have been detected in the South Fork Nooksack River in recent years, and later returning Chinook strays have been found in north fork and south fork spawning areas.[4] Young and Shaklee (2002) noted that of the naturally produced juveniles migrating from the south fork, 9% were of south fork genetic origin, 7% were of north fork genetic origin, and 84% were late-returning fish of predominantly hatchery origin.

Additional life history information supports the TRT's decision. Age distributions of spawning fish from the two forks are very different. More Chinook salmon from the south fork tend to spawn as 5-year-olds. There are slight differences in marine and Puget Sound inland water distributions of Chinook salmon from the north and south forks, according to CWT data (Marshall et al. 1995). Marshall et al. (1995) reported a greater proportion of subyearlings from the north fork than the south fork, but more recent analyses do not support that difference (TRT no date). Length at age of maturity of fish from the two streams is not significantly different.

The north and south forks have habitat differences, but they are subtle relative to differences among basins across the Puget Sound region. The two forks occur in different hydroregions. The north fork is predominantly dominated by snowmelt, and the south fork is dominated by mixed rain and snowmelt (Appendix A, Figure A-8, page 87). Geological substrate in the north fork is distinct from that in the south fork (Appendix A, Figure A-12 and Table A-3, pages 92–93).

Data needs and remaining uncertainties

As noted in the previous subsections, a major uncertainty is whether a separate population of later-returning Chinook salmon occurred historically in the Nooksack River. Although some information exists about the historical distribution of Chinook salmon in the Nooksack River basin (Norgore and Anderson 1921, Pollock 1932, Williams et al. 1975), the return timing of adults and their spawning distributions is not well known. A long history of introductions of late-returning fish from other basins, especially from the Green River (Myers et al. 1998), has obscured genetic evidence of historical population structure in current late-spawning aggregations. Microsatellite DNA analysis of late-spawning aggregations and wild juveniles show that current spawners typically closely resemble Green River late-returning

[4] N. Currence, Nooksack Indian Tribe, Natural Resource Dept., Deming, WA. Pers. commun., 2 March 2004.

fish, and that they are reproducing successfully in the river (Young and Shaklee 2002). Therefore the TRT concluded that the historical late-returning life history is likely genetically extinct (Table 1) and that, at this time, there is insufficient information to determine whether the lost group was an independent population or diversity associated with the two remaining historical populations (Table 6).

The potential straying of nonnative, late-returning Chinook salmon and its effect on the two early returning populations is another critical uncertainty. Although recent studies indicate that late-returning fish use habitat in the north fork, south fork, and mainstem of the Nooksack River, the extent of hybridization between the late-returning fish and the early returning fish is unknown, and how this might influence the trend toward population recovery or extinction of the early returning fish is unclear. Information about the origins and geographical and temporal distribution of these groups, where they may overlap, and genetic studies of hybridization is essential to prevent the extinction of the historical populations. The distribution of juvenile rearing areas for Chinook salmon in the Nooksack River basin is poorly understood, although the Nooksack Indian Tribe and the Lummi Nation are conducting freshwater and estuarine studies that will improve the understanding.

The extent to which present patterns of genetic distinctness between fish in the north and south forks have been influenced by hatchery production is another uncertainty. Hatchery production in the south fork stopped in 1993 (Marshall et al. 1995). Likewise the origin of north fork fish is ambiguous because of extensive hatchery inputs from the north fork itself and releases of hatchery-origin fingerlings throughout the upper north fork (WDF et al. 1993, Marshall et al. 1995). In addition recent sampling of outmigrants from the Nooksack River basin indicates that naturally produced outmigrants are in very low abundance relative to hatchery-produced fish (Conrad and MacKay 2000). Because there currently are no marks on hatchery fish in the basin, further genetic testing of natural-origin outmigrants is needed to better estimate the fraction of outmigrants that are naturally produced.

Samish River

Chinook salmon may have used the Samish River historically because they do so today. The TRT has no evidence that an independent population of Chinook salmon existed in the Samish River. To evaluate ESU recovery scenarios, Chinook salmon occurring in the Samish River are considered a spawning aggregation that possibly contributes to other independent populations in north Puget Sound.

Skagit River Basin

Chinook salmon in the Skagit River basin occupy a large diverse river drainage. Spawning areas are geographically the most removed from other Puget Sound tributaries (Figure 1 and Table 2). Chinook salmon in the Skagit River basin are somewhat genetically distinct from Chinook salmon in other Puget Sound rivers (Figures 4, 5, and 6). Marshall et al. (1995) assigned all Skagit and Stillaguamish Chinook salmon stocks to the same GDU, based on life history, genetic, and habitat similarities within the Skagit River and Stillaguamish River basins (The numbering sequence follows the list of populations in the Conclusions section, page 28, and is continued from page 33.):

3) Lower Skagit River
4) Upper Skagit River
5) Upper Cascade River
6) Lower Sauk River
7) Upper Sauk River
8) Suiattle River

The Skagit River basin may have lost some of the Chinook salmon diversity that once occurred there. However the loss appears relatively less severe than it has been in other areas of the ESU. Historically Chinook salmon used the habitat in the upper Baker River (i.e., above the present dam site) but apparently not in great numbers (Smith and Anderson 1921). The TRT could find no evidence that the upper Baker River supported an independent population of Chinook salmon.

Summary of information used in population structure decisions

Geographically different tributaries of the Skagit River have disjunct Chinook salmon spawning distributions, except for the mainstem Skagit and lower Sauk rivers, where spawning areas adjoin or are in close proximity (Figure 1 and Table 2). For example the early run spawning areas currently are separated from the late-run stocks lower in their tributaries by 12–16 km of unsuitable spawning habitat (Table 2) (Marshall et al. 1995).

Genetic data showed moderately strong support for independence of the six populations (median independence = 2, Table 6). Allele frequencies were highly significantly different (P = 0.000–0.009) (Appendix B, Table B-5, pages 104–105). Genetic differentiation ranged from high between the lower Sauk River and Suiattle River and Cascade River populations (θ = 0.237–0.376) (Appendix B, Table B-1, pages 96–97) to small between the lower Sauk River, upper Sauk River, and lower Skagit River populations (θ = 0.013–0.016). This corresponded to 0.1–5 genetically effective migrants per year under the island model, which the TRT would not expect to affect the demographic independence of the populations. Likewise time since divergence ranged from 17 to 313 generations (Appendix B, Table B-2, pages 98–99). The lower estimates of time since divergence may be biased downward (Appendix B, Table B-1, pages 96–97), or they may indicate that independence has not quite lasted 100 years between the upper Sauk River and upper and lower Skagit River populations.

Summary of additional information

Quantitative estimates of migration rates were not possible and did not inform the TRT's decisions. Data indicate that fish do move among basins, but the demographic consequences are unknown. For example Chinook salmon from the North Fork Stillaguamish River were recovered in the upper and lower Skagit River (Table 3; Appendix A, Table A-2, pages 71–73). In addition out-of-system Chinook salmon collected at Baker trap in the lower Skagit River represented a large proportion of the trap returns, and they came from as far away as Vancouver

Island, British Columbia, Canada.[5] Hatchery-origin, early and late-run Chinook salmon from the Skagit River also have been recovered in the Stillaguamish River and Snohomish River basins. Likewise, within the Skagit Basin, Chinook salmon stocks reared at Marblemount Hatchery have been recovered in the mainstem Skagit River, as well as tributaries such as Illabot Creek, Jordan Creek, and the Cascade River (Appendix A, Table A-2, pages 71–73).

Life history characteristics also showed differences among some populations in the Skagit River. Upper and lower Skagit River Chinook salmon had similar lengths, whereas the three early run populations did not cluster with one another or with late-returning Skagit River populations (Appendix A, Figure A-2, pages 71–73). Age distributions of early returning Chinook salmon populations in the Skagit River basin were somewhat distinct, but the degree of differences in smolt-spawner age distributions did not depend on the stock return times (Appendix B, Table B-7, pages 110–112). The spawn timing of Suiattle Chinook salmon was distinctively earlier than that of the other two early run stocks (Figure 6). Juvenile migration patterns derived from scale data suggest that Suiattle River, Cascade River, and upper Sauk River Chinook salmon populations also had a relatively high proportion of yearling outmigrants (Marshall et al. 1995).

Spatial synchrony in spawner abundance also indicates differences among populations. Regardless of the model used to estimate correlations in abundance, the three late-run Skagit Basin stocks were always clustered together (Appendix A, Figures A-4 and A-5, pages 79 and 81). In contrast the two early run stocks for which we have data were very different in abundance over time from all other Skagit Basin stocks. In general the influence of hatchery stray Chinook salmon on the population dynamics of early run Chinook salmon in the Skagit Basin is minimal.

Differences exist in habitat among spawning aggregations. In the lower Skagit and lower Sauk rivers, Chinook salmon spawned in the low-precipitation and low-elevation hydroregion; in the upper Skagit, Chinook salmon spawned in the low-precipitation and low- and high-elevation hydroregions. All three early run streams in the Skagit Basin had snowmelt-dominated hydrographs (Appendix A, Figure A-8, page 87). The upper Cascade River was in the low-precipitation/high-elevation hydroregion, and the upper Sauk and Suiattle rivers were in the high-precipitation/high-elevation hydroregion. The geology of the three river basins was somewhat distinctive. The lower Sauk and lower Skagit rivers had similar lithology, whereas the upper Skagit River was somewhat distinctive (Appendix A, Figure A-12 and Table A-3, pages 92–93).

Remaining uncertainties and data needs

More extensive genetic sampling of stocks throughout the Skagit River basin may clarify uncertainty in population structure determinations, especially if sampling evenly spans the existing spawning areas. The contiguous spawning distribution and genetic differentiation of Chinook salmon spawning in the lower Skagit, upper Skagit, and lower Sauk rivers, for example, suggest that these groups may be linked demographically. Information about the extent of

[5] B. Hayman, Skagit River System Cooperative, La Connor, WA. Pers. commun., 6 August 2003.

straying among the three late-returning stocks within the Skagit River basin would help interpret genetic differences.

Although Chinook salmon stocks in the Skagit River basin are of native origin (WDF et al. 1993), the effects of hatchery practices on stock composition are unknown. Interpreting historical patterns of population structure from genetic data may be confounded by late-run Green River Chinook salmon at the Skagit hatchery. Likewise broodstock collections for the Skagit Hatchery early run Chinook salmon relied on timing differences to separate spring, summer, and fall Chinook salmon broodstocks. This was difficult because run-timing distributions overlapped (Marshall et al. 1995). Errors in assignment to different stocks during culture could have affected inferences of historical patterns of differentiation.

Although the TRT did not use life history information in the determinations, it provided some corroborating evidence of different populations. The genetic and length at age of maturity data for lower Sauk River fish were based on one sample year, 1986; so the extent to which these data were representative is not known.

Stillaguamish River Basin

Chinook salmon in the North and South Fork Stillaguamish River are geographically distinct from Chinook salmon in other major Puget Sound basins and from each other. The geographic distances separating Stillaguamish River Chinook salmon spawning areas from other rivers (Table 2) and their population dynamics indicate that Stillaguamish River Chinook salmon are not part of a larger population encompassing fish in other river basins. Although different Chinook salmon within a river basin generally are genetically more similar to each other than to populations in other basins, this pattern does not hold true in the Stillaguamish River. North Fork Stillaguamish River Chinook salmon were more similar to Skagit River basin fish, and the South Fork Stillaguamish River Chinook salmon were most closely allied with Snohomish River basin Chinook salmon (Figure 4 and Figure 6). This genetic diversity pattern may reflect a complex geological history. Before the Sauk River-Suiattle River headwaters were diverted to the Skagit River, they flowed into the Stillaguamish River basin (Weisberg and Riedel 1991). The TRT identified two independent populations in the Stillaguamish River (The numbering sequence follows the list of populations in the Conclusions section, page 28, and is continued from page 37.):

9) North Fork Stillaguamish River
10) South Fork Stillaguamish River

Although the North and South Fork Stillaguamish River populations remain, the Stillaguamish River may have lost some of the Chinook salmon diversity that once occurred in the basin (Table 1). Historical evidence suggests that an early returning life history occurred in the Stillaguamish River. These fish entered the river beginning in mid-April and spawned beginning in mid-August, in contrast to summer north fork and fall south fork Chinook salmon, which currently enter the river beginning in mid-June and August, respectively (Williams et al. 1975, WDF et al. 1993). Between 1966 and 1971, abundances of early returning Chinook salmon ranged from 50 to 300 (Williams et al. 1975). The TRT concluded that this life history

was part of the historical diversity of Chinook salmon within the basin, but the team could not determine whether it constituted an independent population.

Summary of information used in population structure decisions

Genetic data show strong genetic support for two independent Chinook salmon populations in the Stillaguamish River (independence score = 3; Table 6). Allele frequencies were significantly different (P = 0.000, Appendix B, Table B-5, pages 104–105). Genetic differentiation was moderate (θ = 0.51) and corresponded to exchange of approximately one genetically effective migrant per year under the island model, which the TRT concluded would not be expected to affect the demographic independence of these populations (Appendix B, Table B-1, pages 96–97). Estimated time since divergence was 26 generations (Appendix B, Table B-2, pages 98–99). Genetically North Fork Stillaguamish River Chinook salmon are more similar to Skagit River Chinook salmon than to South Fork Stillaguamish River Chinook salmon, which are more similar to Snohomish Basin Chinook salmon (Figure 4). The WDFW concluded that North Fork Stillaguamish River Chinook salmon are indigenous, but origins of the South Fork Stillaguamish River Chinook salmon were unknown (WDF et al. 1993, Marshall et al. 1995).

Summary of additional information

Quantitative estimates of migration rates were not possible and did not inform our decisions. Data indicated that fish do move among basins, but the demographic consequences are unknown. Chinook salmon from the North Fork Nooksack River (Kendall Creek Hatchery) have been recovered in the North Fork Stillaguamish River. North Fork Stillaguamish River Chinook salmon also have been reported in the upper and lower Skagit River and the Snohomish River basin (Appendix A, Table A-2, pages 71–73). Within the basin, Chinook salmon reared at the Stillaguamish Tribal Hatchery on the North Fork Stillaguamish River have been recovered at north fork tributaries such as Boulder River and Squire Creek, but no Chinook salmon from the Stillaguamish Tribal Hatchery have been recovered in the south fork.

Life history differences corroborated genetic patterns of differentiation. Age distributions and length at age of maturity of North Fork Stillaguamish River Chinook salmon also are more similar to Chinook salmon spawning in the lower portions of the Skagit River basin than they are to Chinook salmon in the South Fork Stillaguamish River. Spatial synchrony in spawner abundance in the two Stillaguamish River forks is not strongly correlated, although statistical power may have been inadequate to detect a significant relationship (Appendix B, Table B-9, pages 114–116).

The habitat characteristics experienced by Chinook salmon in the two forks of the Stillaguamish River are similar. The hydrographs are mixed for both streams: in the upper reaches of the streams, hydrographs are mixed snowmelt and rainfall, and hydrographs for lower river tributaries are rainfall dominated. Both streams are in the low-precipitation and low-elevation hydroregion, although the north fork drains more high-precipitation areas (Appendix A, Figure A-8, page 87). Mean incubation temperatures in the two streams are very similar (Appendix B, Table B-11, pages 122–125). In contrast each fork is in a different EPA ecoregion

(Appendix A, Figures A-10 and A-11, pages 90–91) and geological characteristics of the two forks are different (Appendix A, Figure A-12 and Table A-3, pages 92–93).

Remaining uncertainties and data needs

The historical and current status of two different spawning aggregations in the Stillaguamish Basin are unknown. One is the early returning Chinook salmon in the Stillaguamish River. The comanagers did not identify these fish as a distinct stock or describe their return timing as a part of the summer or fall stocks (WDF et al. 1993), which suggests that they are no longer present. Nehlsen et al. (1991) described them as extinct. The second group whose status is unknown is Chinook salmon spawning in the mainstem Stillaguamish River below the forks. The additional historical diversity in life history may have contributed to broader geographic and temporal distribution of Chinook salmon originating from this watershed, both within the watershed and in marine environments, and may have been an important part of the viability of Chinook salmon in the watershed. Further evaluation will be needed to understand the roles these spawning aggregations may have or still play in Stillaguamish River population viability.

Although the genetic and life history similarities between North Fork Stillaguamish River Chinook salmon and Skagit River late-run Chinook salmon may reflect common ancient ancestry, the genetic origins of the south fork population are less well known. Hatchery introductions may have played a role in producing the observed differences. Late-returning Green River-origin Chinook salmon have been introduced into the south fork (Marshall et al. 1995, Myers et al. 1998), and their genetic influence is unknown (WDF et al. 1993).

Snohomish River Basin

Chinook salmon in the Snohomish River basin are geographically distinct from Chinook salmon in other Puget Sound streams (Figure 1 and Table 2). Genetically the Snohomish River Chinook salmon form a group that includes the South Fork Stillaguamish (Figures 4, 5, and 6). Because of their genetic distinctness and the geographic distances separating the nearest spawning areas outside of the Snohomish River basin (Table 2), the TRT concluded it was unlikely that Chinook salmon in the Snohomish River basin were part of a larger population that included Chinook salmon from other rivers in the Puget Sound. The team identified two independent populations in the Snohomish River basin (The numbering sequence follows the list of populations in the Conclusions section, page 28, and is continued from page 39.):

11) Skykomish River
12) Snoqualmie River

Although the TRT identified at least two independent populations in the Snohomish River, an important component of the basin's diversity may have been lost (Table 1). Historical evidence suggests that an early returning life history also occurred in the Snohomish River. These fish entered the river in May through July and stayed in deep pools before spawning in mid-August and September in accessible areas of the North and South Fork Skykomish River and possibly the Snoqualmie and Tolt rivers (Williams et al. 1975). These returns occurred at different times than current returns to similar areas (WDF et al. 1993). Between 1966 and 1971,

annual abundances of early returning Chinook salmon ranged from 150 to 500 (Williams et al. 1975). The team concluded that this life history was part of the basin's historical diversity of Chinook salmon, but could not determine whether it constitutes an independent historical population.

Summary of information used in population structure decisions

Geographically disjunct spawning grounds for Chinook salmon in the Snoqualmie River and Skykomish River basins support their delineation as separate populations (Table 2). Chinook salmon spawning in the mainstem Snohomish River have continuous distributions with those in the Skykomish River, however, which suggests that Snohomish mainstem spawners belong in the Skykomish River population.

Genetic data indicate moderately strong support for considering Skykomish River Chinook salmon as a separate population from those spawning in the Snoqualmie River basin (genetic independence score = 2) (Table 6). Wallace River and Bridal Veil Creek stocks were genetically very similar to each other and to the Skykomish River stock (genetic independence < 0). Consequently these stocks were included together within the Skykomish population. Allele frequencies between Skykomish River and Snoqualmie River stocks were significantly different ($P = 0.001$). Genetic differentiation was low, however ($\theta = 0.005$–0.013), and corresponded to exchange of 5–10 genetically effective migrants per year under the island model (Appendix B, Table B-1, pages 96–97), although we concluded this would not affect the demographic independence of these populations. Time since divergence ranged from 7 to 19 generations (Appendix B, Table B-2, pages 98–99). This may reflect downward bias in the analysis (Appendix B, Table B-1, pages 96–97), or it may indicate that independence lasted not quite 100 years.

Summary of additional information

Quantitative estimates of migration rates were not possible and did not inform our decisions. Good documentation exists for straying of Chinook salmon from the Wallace River Hatchery. Studies of the distribution of hatchery fish using thermally marked otoliths suggest that many naturally spawning Chinook salmon in the Skykomish River and its tributaries originate from the Wallace River Hatchery (Rawson et al. 2001). Chinook salmon from the Tulalip Hatchery also make up a fraction of the naturally spawning Chinook salmon in the Snoqualmie River system, especially Tokul Creek. Wallace River Hatchery fish rarely are found in the Snoqualmie River system.

Life history differences support the genetic differences. Skykomish River Chinook salmon from the Wallace River had a distinct spawner-smolt age distribution from the Snoqualmie River Chinook salmon sampled from Tokul Creek (Appendix B, Table B-7, pages 110–112). The Snoqualmie River sample is based on a single year of data, so how distinct Chinook salmon are in each major Snohomish River basin tributary needs more study. Likewise, based on the available data, little overlap in spawn timing existed among Snohomish River basin stocks (Figure 8), although the true spawn timing may be later than that depicted in the database

because sampling was uneven across years and throughout the season.[6] In contrast length at age of maturity data suggest that Bridal Veil Creek and Snoqualmie River Chinook salmon were very similar (Appendix A, Figure A-2, page 75), but Wallace River, Skykomish River, and Sultan River Chinook salmon were in a separate cluster. The distinctive length at age of maturity of Bridal Veil Creek and Snoqualmie River Chinook salmon, however, may reflect the small number of years of data (2 and 1 years, respectively) included in those samples.

Differences in spawning and rearing habitat also exist within the Snohomish River basin. Chinook salmon in the Pilchuck, Sultan, Snoqualmie, and lower Skykomish rivers spawn in streams with rainfall-dominated hydrographs. In contrast Bridal Veil Creek Chinook salmon experience a mixed hydrograph that exhibits snowmelt and rainfall peak flows. As a result of hydrograph patterns Bridal Veil Creek Chinook salmon spawn in the rainfall or snowmelt-transition hydroregion, and all other Snohomish Basin Chinook salmon are in the low-precipitation or low-elevation hydroregion (Appendix A, Figure A-8, page 87). Bridal Veil Creek also occurs in a different EPA ecoregion and has a different lithology (Appendix A, Figures A-10 and A-11, pages 90–91; Figure A-12 and Table A-3, pages 92–93).

Remaining uncertainties and data needs

More information is needed about genetic and demographic relationships of several spawning aggregations in addition to the two independent populations the TRT identified. Lack of adequate genetic and migration data hampered the team's ability to identify the population structure of Chinook salmon spawning in the lower Snohomish and Pilchuck rivers. Likewise the relationship of Sultan River aggregations to other Skykomish River or Snoqualmie River stocks needs resolution. The Pilchuck River and Sultan River watersheds are smaller than the smallest watershed area with an identified independent population in the Puget Sound area, the Cedar River (Figure 2). Consequently it is difficult to tell whether the Pilchuck River and Sultan River watersheds are big enough to have supported an independent population or subpopulation. The best way to classify these fish would be to conduct genetic sampling and analysis from the Pilchuck and lower Snohomish rivers, with concurrent sampling from the Skykomish River and Snoqualmie River populations. Samples from the South Fork Stillaguamish River should be collected at the same time because of the apparent relationship between this population and Snohomish River Chinook salmon populations.

The historical and current status of early returning Chinook salmon in the Snohomish River basin also is unknown. The comanagers did not identify these as a distinct stock or describe their return timing as a part of summer or fall stocks (WDF et al. 1993), which suggests that they were no longer present during that assessment. Nehlsen et al. (1991) describe them as extinct. This life history diversity may have contributed to broader geographic and temporal distribution of Chinook salmon originating from this watershed, within the watershed and in marine environments, and it may have contributed to the viability of Chinook salmon in the watershed (Table 6).

The influence of hatchery fish on the population structure in the basin remains unclear. The Wallace River stock may have been heavily influenced by introductions, including Green

[6] C. Kraemer, Washington Dept. Fish and Wildlife, Mill Creek, WA. Pers. commun., November 2001.

River fall fish, Skykomish River summer stock, and possibly some wild stocks that strayed into the river (WDF et al. 1993). In contrast the Snohomish River and Bridal Veil Creek stocks are considered to be of native origin (WDF et al. 1993).

Central and South Puget Sound

This region includes the Lake Washington (Sammamish River and Cedar River watersheds), Duwamish/Green, Puyallup, and Nisqually basins, as well as small, independent tributaries to Puget Sound. Extensive human alterations to historical hydrologic connections that shaped metapopulation structure, dynamic geological histories, and the confounding effects of hatchery releases made population identification in this region even more challenging than in watersheds to the north. Most existing spawning aggregations are genetically similar and appear to reflect extensive influence of hatchery releases, mostly from the Green River broodstock (WDF et al. 1993, Myers et al. 1998). Life history variation also was not very informative for identifying population structure. Most Chinook salmon in this region have similar spawn timings (Figures 7 and 8; Appendix B, Table B-6, pages 106–109), and few data are available for other life history traits. Because genetic and life history data do not provide good evidence of historical population structure, to interpret the current genetic and life history patterns the TRT relied heavily on information about historical connections between the Lake Washington, Green River, Puyallup River, and White River drainages.

Chinook salmon spawning areas in central and south Puget Sound are geographically disjunct from each other and from other Puget Sound river basins (Table 2). Because of the geographic separation of the basins, the TRT considered each major basin's Chinook salmon to be distinct and independent from Chinook salmon populations in other major Puget Sound rivers (Figure 1). Although humans modified hydrological connections among streams during the past century, the geologic history of these watersheds as separate tributaries to Puget Sound suggests that Chinook salmon spawning aggregations were historically more geographically isolated from one another than they are now. After the glaciers retreated and streams were colonized by salmonids from the Columbia River (McPhail and Lindsey 1986) but before the Osceola Mudflow (4,800 years ago), Lake Washington and the Green, White, and Puyallup rivers each drained independently to an arm of Puget Sound that is now the Kent-Auburn and Puyallup valleys. Subsequent episodic volcanic events as recently as 600 years ago disrupted the post-glacial morphology of this subbasin and created the geomorphology present at the time of European settlement of these watersheds (Crandell 1963, Dragovich et al. 1994, Barnhardt et al. 1998, Scott et al. 1995).

The TRT reviewed genetic and historical evidence of independent populations or spawning aggregations in small, independent tributaries to south and central Puget Sound (Table 1). The team concluded that Chinook salmon using smaller streams in south and central Puget Sound probably did not occur there in large numbers historically and were not independent populations. Although the TRT did not establish a minimum watershed size that might indicate a self-sustaining independent population, many of these watersheds are much smaller than those we are confident have supported independent populations.

It is not obvious to what extent the spawning habitat potential of the small, independent tributaries in south and central Puget Sound may have contributed to viability of nearby

independent populations and the overall persistence of the ESU. It is possible that Chinook salmon spawning in small, independent tributaries of this region are present only because of relatively recent hatchery releases. Alternatively these smaller streams may have contained satellite populations that were never very large historically and that relied on contributions of spawning adults in significant numbers during years when self-sustaining, independent populations, such as those in the Nisqually or Puyallup rivers, had strong returns (WDF et al. 1993). It is difficult to test these possibilities with existing data. Recoveries of CWT Chinook salmon throughout southern Puget Sound suggest that hatchery Chinook salmon move readily within this region (Appendix A, Table A-2, pages 71–73), but the data are inadequate to determine how spawning in smaller, independent tributaries was related to population dynamics of larger populations. It would be useful to summarize historical records of spawning presence, timing, and abundance of Chinook salmon in other south Puget Sound streams in order to estimate their population structure. In addition the extent to which the straying behavior of hatchery Chinook salmon reflects behavior of native, naturally spawning fish under historical conditions is not known. This same discussion applies to other small, independent tributaries throughout Puget Sound.

Within this region, the TRT identified six independent populations (The numbering sequence follows the list of populations in the Conclusions section, page 28, and is continued from page 41.):

13) Sammamish River
14) Cedar River
15) Duwamish/Green River
16) White River
17) Puyallup River
18) Nisqually River

Although the TRT identified six independent populations in this region, important components of the basin's historical diversity may be lost (Table 1). These include early returning life histories that no longer are expressed and genetic diversity among late-returning populations that was lost due to extensive introductions of nonnative hatchery fish. Early returning life histories once occurred in the Green, Nisqually, and potentially the upper Puyallup rivers (Williams et al. 1975). Nehlsen et al. (1991) considered these extinct populations. The limited data available suggest that these fish returned approximately a month earlier than later-returning Chinook salmon and abundances were small. Consequently these fish also might have been early returning life histories of a larger population. The TRT concluded that these life histories were part of the historical diversity of Chinook salmon within the region, but the team could not determine whether they constituted an independent population or independent populations.

In the Puyallup and Nisqually rivers, strong genetic similarities of extant populations to Green River Chinook salmon (Figures 4, 5, and 6) suggest that the historical genetic differences between the indigenous, late-returning populations were replaced or substantially altered by Green River-origin fish, which were extensively released in the region (Myers et al. 1998).

Consequently, although the TRT identifies these watersheds as having independent populations, Chinook salmon in these rivers no longer represent historical populations. Likewise late-returning Chinook salmon in the White River, where the extant population is a genetically distinct, early returning life history, also are characteristic of Green River-origin Chinook salmon (Shaklee and Young 2003). Consequently these fish may represent:

- a life history that was a distinct historical population,
- a later-returning form that was once part of the historical White River population but was replaced by nonnative Chinook salmon,
- a part of the historical late-returning Puyallup River population that used the lower White River, or
- recent establishment of the life history in the White River from introductions of Green River-origin hatchery fish (Table 6).

Lake Washington

Summary of information used in population structure decisions

The Lake Washington watershed includes the Sammamish River and Cedar River populations. Geographically, spawning areas in the two tributaries are separated by Lake Washington and are as distant from each other as they are from the Green River (Table 2). Prior to construction of the ship canal in 1916, Lake Washington discharged through the Black River into the Duwamish River and the Cedar River was a tributary to the Black River. It is not clear whether the historical Duwamish River watershed provided more or less geographical separation among historical populations.

Genetic data provide moderately strong support for the current independence of Chinook salmon spawning in the Sammamish River basin and the Cedar River (genetic independence score = 2) (Table 6). Allele frequencies were significantly different (Appendix B, Table B-5, pages 104–105). Genetic divergence was minor ($\theta = 0.008$ to 0.012), corresponding to a genetic exchange of 5–8 migrants per year (Appendix B, Table B-1, pages 96–97). Genetic differentiation is most likely influenced by extensive use of Green River-origin Chinook salmon in the Sammamish River, which do not occur regularly in the Cedar River. Chinook salmon released from Issaquah Hatchery in the Sammamish River were Green River stock (Marshall et al. 1995), and naturally spawning Chinook salmon in tributaries to the Sammamish River were genetically similar to the hatchery stock (Marshall 2000b). The Cedar River basin has not received many hatchery introductions (WDF et al. 1993, Myers et al. 1998), but there is evidence that hatchery strays into the Cedar River have occurred in recent years.[7]

Summary of additional information

Quantitative migration rate estimates were not possible and did not inform the TRT's decisions. The available data indicate that hatchery Chinook salmon may move between the Sammamish River (Issaquah Hatchery) and Duwamish/Green River basins (Appendix A, Table

[7] H. Berge, King County Water and Land Resources, Dept. Natural Resources and Parks, Seattle, WA. Pers. commun., 15 March 2005.

A-2, pages 71–73). In addition a few Green River-origin Chinook salmon released from south Puget Sound and north Kitsap Peninsula hatcheries have been recovered in the Lake Washington drainage and Sammamish River basin.

Life history variation also was not very informative for estimating population independence. Most Chinook salmon in this region have similar spawn timings (Figures 7 and 8; Appendix B, Table B-6, pages 106–109), and few data are available for other life history traits. Likewise the population dynamics of Chinook salmon in Lake Washington (Sammamish and Cedar rivers) and the Duwamish/Green River were closely correlated (Appendix B, Table B-9, pages 114–116), but because no straying data support the correlated population dynamics within Lake Washington, the abundance correlations were not useful as independent evidence for population structure. It is likely that those correlations reflect similar patterns of hatchery releases, harvest levels, or other environmental conditions, rather than high rates of demographic exchange.

Although the current Sammamish River population is largely supported by naturally spawning hatchery fish, the basin area suggests it had the capacity to support a self-sustaining, independent population. The cumulative catchment area of tributaries draining into the Sammamish River and from Swamp, North, Bear, Little Bear, and Issaquah creeks is more than 60,000 ha, which is larger than the smallest watershed containing an independent population in the TRT's analyses (the South Fork Nooksack River, Figure 2).

Remaining uncertainties and data needs

The history of hatchery releases in the Sammamish River raises two key uncertainties. First, although the TRT identified an historical population associated with this river, the Chinook salmon that currently use the watershed likely do not represent the historical population. This population is believed to be genetically extinct because of many factors for decline, including an extensive history of introductions of Green River-origin hatchery fish (Table 1). The historical connection and currently limited gene flow between Lake Washington and the Duwamish/Green River Chinook salmon via the Black River also may have limited extensive divergence and may have influenced these populations' similarity to Green River Chinook salmon. The characteristics of this historical population are unknown, but it represents a loss of historical diversity in this region and in the Puget Sound ESU. Likewise status and potential contributions (if any) of lake-spawning Chinook salmon life histories in Lake Washington are unknown. The significance of these diversity losses to the ESU's viability is unknown.

Better information on stray rates among streams in the Lake Washington area will help interpret the genetic differences the TRT observed. In 2000 the City of Seattle, the WDFW, the U.S. Fish and Wildlife Service, and the Muckleshoot Indian Tribe began a cooperative effort to mark hatchery fish reared at the Issaquah Hatchery. Preliminary results indicate a high incidence of hatchery fish in the natural spawning areas.[8] Monitoring marked hatchery fish will help determine presence of hatchery fish in the wild.

[8] See footnote 5.

Duwamish/Green River

Summary of information used in population structure decisions

The Duwamish/Green River basin contains the Duwamish/Green River population. The TRT considers this population independent based on geographic distance from other rivers with independent populations (Table 2). Genetic data also provide some support for independence from Puyallup River and Nisqually River Chinook salmon (genetic independence score = 1, Table 6) and strongly support independence from White River Chinook salmon (genetic independence score = 3, Table 6), based on current differentiation patterns. Allele frequencies between the Duwamish/Green River and Puyallup River samples were not significantly different, but they were significantly different from the Nisqually River and White River Chinook salmon (Appendix B, Table B-5, pages 104–105). Genetic differentiation was minor ($\theta = 0.001$ to 0.026), although the differentiation between White River and Duwamish/Green River Chinook salmon was an order of magnitude greater than the others (Appendix B, Table B-1, pages 96–97). These levels of differentiation most likely reflect homogenization from extensive hatchery introductions of Green River-origin Chinook salmon in the Puyallup River and Nisqually River watersheds (Myers et al. 1998).

Summary of additional information

Quantitative estimates of migration rates were not possible and did not inform the TRT's decisions. A few fish from Grovers Creek on the north Kitsap Peninsula have been recovered in the Green River (Appendix A, Table A-2, page 71–73), but stray rates generally are unknown.

Life history variation also is not very informative. Most Chinook salmon in this region have similar spawn timings (Figures 7 and 8; Appendix B, Table B-6, pages 106–109), and few data are available for lengths of age at maturity (Appendix A, Figure A-2, page 75), smolt-spawner age distributions (Appendix B, Table B-7, pages 110–112) or other life history traits. Likewise analysis of spatial synchrony in spawner abundance is not informative, because abundance trends are confounded by different management actions. The TRT detected few correlations in spawner abundance that might indicate demographic associations between the Green River and other river systems (Appendix B, Table B-9, pages 114–116).

Remaining uncertainties and data needs

The historical characteristics of Green River Chinook salmon are unknown. Although Green River-origin Chinook salmon were used as a broodstock in the basin since hatchery production was established more than a century ago, the long period of fish culture and wide distribution of hatchery fish throughout the basin most likely resulted in significant genetic changes. The historical and current status of early returning Chinook salmon in the Green River also is unknown. The comanagers did not identify these as a distinct stock or describe their return timing as a part of the summer or fall stock (WDF et al. 1993), which suggests that they were no longer present in significant numbers during that assessment. However the additional diversity in life history may have contributed to broader geographic and temporal distribution of Chinook salmon originating from this watershed, both within the watershed and in marine

environments. This diversity may have been an important part of Chinook salmon viability in the watershed.

Puyallup River

Summary of information used in population structure decisions

The Puyallup River basin includes the Puyallup River and White River populations. The TRT used geographic and genetic information to identify these populations. Geographically, Chinook salmon spawning areas in the Puyallup River are disjunct from other Puget Sound populations. The closest river drainages containing independent populations, the Duwamish/Green River and Nisqually River, are 83 km and 60 km away, respectively (Table 2). Recent modifications to the river's physical configuration, water management, and fish passage regimes, however, disrupted access to habitat in the White River and Puyallup River basins and may have led to current patterns of habitat utilization that differ from historical distributions (WDFW et al. 1996).

Genetic data also support independence from Duwamish/Green River and Nisqually River Chinook salmon (genetic independence score = 1, Table 6) and strongly support independence between the Puyallup River and White River Chinook salmon (genetic independence score = 3, Table 6), based on current patterns of differentiation. Allele frequencies are significantly different between Puyallup River and White River Chinook salmon ($P = 0.000$, Appendix Table B-5, pages 104–105). Genetic differentiation is minor ($\theta = 0.019$), which corresponds to genetic exchange of 2–3 migrants per year (Appendix B, Table B-1, pages 96–97). These current differentiation levels most likely do not completely reflect historical patterns, however, because of extensive hatchery introductions of Green River-origin Chinook salmon in the Puyallup River watershed (Myers et al. 1998). Genetically Puyallup River Chinook salmon are very similar to Green River Chinook salmon (Figures 4, 5, and 6; Appendix B, Tables B-1, pages 96–97, and B-5, pages 104–105). The White River early run hatchery and wild genetic samples are very similar, reflecting the effects of the broodstock program that began in the 1970s (WDFW et al. 1996).

Summary of additional information

Quantitative estimates of migration rates were not possible and did not inform the TRT's decisions. CWT Chinook salmon reared at the White River Hatchery have been recovered in Puyallup River tributaries, such as Voights and South Prairie creeks. Fish movement has been recorded between the Puyallup River and Green River basins, but no movement has been reported between the Puyallup River and Nisqually River basins (Appendix A, Table A-1, page 68-69).

Life history differences support genetic and geographical evidence of different populations. White River Chinook salmon return earlier, beginning in late May, than Puyallup River Chinook salmon, which begin entering the river in late July (WDF et al. 1993). Length at age of maturity for White River Chinook salmon is different from Puyallup River Chinook salmon (Appendix A, Figure A-2, page 75; Appendix B, Table B-8, page 113). Age distributions of White River Chinook salmon (hatchery and wild) are similar to those of the

Puyallup Hatchery Chinook salmon, although Chinook salmon from South Prairie Creek in the Puyallup River are slightly different in their age distributions (TRT no date). Mean spawning dates of Puyallup River and White River Chinook salmon are similar (Figure 8).

Spawner abundances of White River and Puyallup River aggregations were not correlated with other stocks (Appendix A, Figures A-4 and A-5, pages 79 and 81; Appendix B, Table B-9, pages 114–116), but this is not necessarily strong evidence of population independence. The population dynamics of both populations were influenced by hatchery programs and environmental alterations to the rivers.

Habitat differences support genetic and geographical evidence of different populations. White River early run Chinook salmon spawn in a mixed snowmelt and rainfall-dominated river, whereas the Puyallup River is at a lower elevation and its hydrograph is mostly rainfall-dominated (Appendix A, Figure A-8, page 87). Based on their historical distribution above the Buckley trap, in the past an even greater proportion of White River Chinook salmon spawning areas would have been in the snowmelt transition hydroregion. Furthermore the dynamic and high glacial sediment load of the historical lower White and Stuck rivers (Crandell 1963, Mullineaux 1970, Salo and Jagielo 2003) probably rendered those areas inhospitable to spawning. These areas may have served to maintain separation between spawning aggregations that existed in the independent drainages prior to the Osceola Mudflow. Not surprisingly, incubation temperatures in the Puyallup River are variable but differ from temperatures in the White River (Appendix A and Table B-11, pages 122–125). The Chinook salmon spawning areas in the White and Puyallup rivers also occur in different EPA ecoregions (Appendix A, Figure A-10, page 90) and have different lithology (Appendix A, Figure A-12 and Table A-3, pages 92–93).

Remaining uncertainties and data needs

The inability to reconstruct historical patterns of genetic similarity among Chinook salmon because of extensive Green River-origin hatchery transfers is problematic. The TRT concluded that late-returning Chinook salmon in the Puyallup River were historically an independent population, although the existing population does not represent the historical one. To verify our conclusions, we need better data on straying, homing, and historical distribution of spawning or rearing Chinook salmon in smaller tributaries throughout south Puget Sound, including utilization of smaller, independent marine tributaries (e.g., Garrison and Chambers creeks). Also needed are CWT and genetic information to determine hatchery influence on the naturally spawning population (WDF et al. 1993).

The historical and current status of early returning Chinook salmon that used the upper Puyallup River (Williams et al. 1975) are unknown. Nehlsen et al. (1991) considered this population extinct. The comanagers did not identify these as a distinct stock or describe their return timing as a part of the summer or fall stock (WDF et al. 1993), which suggests that they were no longer present in significant numbers during that assessment. The TRT lacks information to determine whether these are either an independent population or part of a broader return timing of the historical population.

The origins of late-returning Chinook salmon in the White River also are uncertain. Genetic evidence indicates that the extant population is characteristic of Green River-origin Chinook salmon and genetically distinct from the early returning White River population (Shaklee and Young 2003). These fish may represent:

- a life history form that was a distinct historical population,
- a late-returning form that was once part of the historical White River population but was replaced by nonnative Chinook salmon,
- a part of the historical late-returning Puyallup population that used the lower White River, or
- recent establishment of the life history in the White River from introductions of Green River-origin hatchery fish.

The effects of disruptions to habitats and fisheries on the spatial and temporal distribution of salmon in the Puyallup Basin are unclear. Alterations in flow, temperature, fish passage, and harvest management strategies probably altered utilization relative to historical distribution patterns. This makes reconstructing historical patterns difficult. The additional life history diversity within the Puyallup River watershed may have contributed to broader geographic and temporal distribution of Chinook salmon from this watershed, both within the watershed and in marine environments, and may have been an important part of the viability of Chinook salmon in the watershed.

Nisqually River

Summary of information used in population structure decisions

The Nisqually River basin contains the Nisqually River Chinook salmon population. The geographic location of spawning grounds within the Nisqually River basin suggest that, historically, Chinook salmon in the Nisqually River may have been an independent population from the Chinook salmon spawning throughout the rest of central and south Puget Sound (Figure 1, Table 2). The closest river drainages containing independent populations, the Duwamish/Green and Puyallup rivers, are 60 km and 70 km away, respectively (Table 2).

Genetic data also provide moderate support for independence of the Nisqually River Chinook salmon from White River, Puyallup River, and Duwamish/Green River populations (median genetic independence score = 2, Table 6), based on current differentiation patterns. Allele frequencies are significantly different (P = 0.000–0.026) (Appendix A and Table B-5, pages 104–105). Genetic differentiation is minor (θ = 0.002–0.019), which corresponds to genetic exchange of 3–40 migrants per year (Appendix B, Table B-1, pages 96–97). These patterns of differentiation and exchange most likely reflect extensive hatchery introductions of Green River-origin Chinook salmon in the Nisqually River (Myers et al. 1998, WDF et al. 1993), which interbred with or replaced the historical population. Genetically Nisqually River Chinook salmon are very similar to Green River Chinook salmon (Figure 3; Appendix B, Table B-1, pages 96–97; Table B-5, pages 104–105) (Marshall 1999 and 2000b). Evidence that Nisqually River Chinook salmon evolved differently from the Puyallup River, which also has received

large introductions of Green River-origin Chinook salmon (Appendix B, Table B-1, pages 96–97) suggests that Nisqually River Chinook salmon are demographically independent.

Summary of additional information

Quantitative estimates of migration rates were not possible and did not inform the TRT's decisions. Life history data also were not informative for reconstructing historical population structure. Chinook salmon in the Nisqually River have the same general life history traits of other late-returning Chinook salmon in central and south Puget Sound. Spawner abundances of Nisqually River Chinook salmon were not correlated with other stocks (Appendix A, Figures A-4 and A-5, pages 79 and 81; Appendix B, Table B-9, pages 114–116), which might suggest natural demographic independence, but this evidence is not necessarily strong. The population dynamics of Nisqually River Chinook salmon have been influenced by hatchery programs, environmental alterations to the river, and fishery management regimes.

Three dams on the Nisqually River restrict the present distribution of Chinook salmon from their historical spawning areas and have altered flow regimes in the river. Over a large scale, however, habitat differences are similar to other central and south Puget Sound streams except the White River. Nisqually River Chinook salmon experience the same rainfall-dominated hydroregion and lithology (Appendix A, Figures A-8, page 87, and Figure A-12 and Table A-3, pages 92–93), although the Nisqually River lies in a different EPA ecoregion (Appendix A, Figure A-9, page 89).

Remaining uncertainties and data needs

The historical characteristics of Nisqually River Chinook salmon are unknown. Historical returns and distributions to the basin were affected by construction of dams, fishing, and the introduction of nonnative hatchery fish. Better data on movement of wild and hatchery Chinook salmon among streams would be useful to verify our conclusions of independence and to determine hatchery influence on this population.

The historical and current status of early returning Chinook salmon that used the Nisqually River is unknown. Smoker (1952) noted that historical peak harvest, which is usually closely correlated with entry timing, occurred more than a month earlier than current harvests on naturalized, nonnative, Green River-origin Chinook salmon, which begin entering the river in early July (Williams et al. 1975). Current entry timing also corresponds to the lowest flows in the historical hydrograph (which are now controlled by flow regulation), suggesting that historical entry timing must have been different. Nehlsen et al. (1991) considered this population extinct. The TRT lacked information to determine whether these early returning fish were a distinct independent population or part of a broader return timing of the historical population that has since been lost. Before dams limited the distribution of Chinook salmon and altered river flows, this life history diversity may have contributed to broader geographic and temporal distribution of Chinook salmon originating from this watershed, both within the watershed and in marine environments, and it may have been an important part of the viability of Chinook salmon in the watershed.

Hood Canal

Hood Canal streams are geographically isolated from other streams in the Puget Sound ESU (Figure 1). The two closest river basins to the Dosewallips River (the northernmost primary spawning aggregation identified in Hood Canal) are the Snohomish and Dungeness rivers, which are 97 km and 103 km away, respectively (Table 2). The Skokomish River is even farther from streams in other regions. Because of the geographic isolation of the Hood Canal streams, the TRT concluded that Chinook salmon spawning historically in Hood Canal streams were independent populations from other Chinook salmon spawning aggregations in Puget Sound.

Within Hood Canal, Chinook salmon spawn in the Skokomish, Hamma Hamma, Duckabush, and Dosewallips rivers, which drain the Olympic Mountains to the west and which are larger, steeper, and deeper than streams to the east. On the eastern shore, Chinook salmon use the Tahuya, Union, and Dewatto rivers in limited numbers (Williams et al. 1975, WDF et al. 1993). Identifying historical independent populations within Hood Canal from these extant spawning aggregations is problematic because of early alterations to habitat, fish passage, and fisheries; limited historical and life history data; and introductions of nonnative hatchery fish, which likely confounded genetic patterns. Genetically most of this region's present spawning aggregations are similar and appear to reflect the extensive influence of hatchery releases in the region, mostly from the Green River broodstock (Figures 4, 5, and 6) (WDF et al. 1993, Myers et al. 1998, Marshall 1999 and 2000b). Nevertheless the TRT used information on historical distributions and life histories to identify at least two independent anadromous populations. A nonanadromous extant aggregation of unknown age and origin also occurs in Lake Cushman in the Skokomish River.

The TRT identified two independent populations within this region. (The numbering sequence follows the list of populations in the Conclusions section, page 28, and is continued from page 45.):

19) Skokomish River

20) Mid-Hood Canal Rivers (Dosewallips, Duckabush, and Hamma Hamma)

Although the TRT identified two independent populations in this region, the team concluded that extensive diversity of the historical Skokomish River population or populations has been lost. These losses include early returning life histories that no longer are expressed, and genetic diversity that was lost due to extensive introductions of nonnative hatchery fish. Early reports on salmonid use of Hood Canal streams documented early returning life histories in the Skokomish, Dosewallips, Duckabush, and Hamma Hamma rivers and late-returning life histories in the Skokomish River (Royal 1932, Smoker 1952, Deschamps 1954, WDF 1957). More recently, Williams et al. (1975) noted the historical occurrence of early returning life histories and reported late-returning life histories in the Dosewallips, Duckabush, and Hamma Hamma rivers; however, whether these fish represented historical population components or introductions of nonnative hatchery fish remains unclear. Nehlsen et al. (1991) considered the early returning populations extinct, and the comanagers concluded that if these fish still existed in the Skokomish River, they were at very low abundances (WDF et al. 1993). The strong genetic similarities of extant populations to Green River Chinook salmon (Figures 4, 5, and 6)

(Marshall 1999 and 2000b) suggest that the historical genetic characteristics of the early and late-returning populations were replaced or substantially altered by Green River-origin fish, which have been released extensively in the region (Myers et al. 1998).

Summary of information used in population structure decisions

The TRT identified the Skokomish River as an independent population because of the watershed's size, available habitat, isolation from other streams, and historical information. The Skokomish River is the largest Hood Canal stream (Figure 2), and historically it produced Chinook salmon with extensive life history diversity. These characteristics indicate that it was a stable and productive watershed in the region. Historically three Chinook salmon run-timing groups were reported to have occurred in the Skokomish River (Smoker 1952). Early returning Chinook salmon (i.e., spring and summer fish) were reported to have migrated above the upper dam site on the North Fork Skokomish River (Deschamps 1954, WDF 1957). Early returning Chinook salmon also occurred in the upper South Fork Skokomish River and the lower south fork from the canyon to Vance Creek. In contrast late-returning Chinook salmon spawning was documented only in the lower north and south forks and in the main stem below their confluence (Deschamps 1954, WDF 1957). The return timing and distribution suggest there might have been two different populations, but the degree of geographical separation was equivocal. The historical geographic separation of the upper north fork spawning area from other Skokomish watershed spawning areas was approximately 21 km, which is comparable to separation between populations in other river basins. The geographic separation between the spawning habitats in the upper and lower south fork and mainstem Skokomish River is less than 3 km, however, which is at the extreme lower end of reported geographic separations of other Puget Sound Chinook salmon populations (Table 2). Although the TRT did not find a minimum watershed area that could support an independent population, the overall size of the north fork (30,000 ha) and the south fork (27,000 ha) Skokomish River watersheds are smaller than the Cedar River watershed area (46,000 ha), which is the smallest watershed for which the team confidently identified an independent population. Because the TRT could not confidently identify two historical populations in the Skokomish River, we concluded that there was at least one historical population.

Assigning the naturally spawning Chinook salmon in the Dosewallips, Duckabush, and Hamma Hamma rivers to independent populations was more difficult. The balance of information the TRT has at this time supports treating these three spawning aggregations as an additional independent population, although other categorizations are possible. The degree to which these spawning aggregations were historically demographically linked is not clear, and only further monitoring and evaluation will resolve the relationships. The similarity of the freshwater and estuarine habitats, environmental conditions, and proximity of these three mid-Hood Canal watersheds suggests that their collective area could support a single independent population. The combined overall size of the three watersheds (72,000 ha) is larger than other watersheds for which the TRT identified independent populations (Figure 2). Most Chinook salmon spawning in the mid-Hood Canal streams likely occurred in the Dosewallips River, because it is larger and has more area accessible to anadromous fish. Unpublished WDF survey records from 1932 documented a smaller-than-expected Chinook salmon run in the Dosewallips River given the size of watershed (Royal 1932). This may have led others to conclude that self-sustaining production in these streams was limited. The TRT's research

revealed, however, that at the time of the survey, in 1932, an impassable dam built many years before at river mile 3 had been destroyed and had only allowed passage for a period of several years (Royal 1932). Consequently the early reports likely did not represent the historical population, which may have already been lost. Habitat capacity analysis also supports the hypothesis that the Dosewallips River (the largest watershed) and the other two streams had sufficient spawning and rearing habitat to support an independent population. Although the three spawning areas are separated by small distances (8–21 km), juvenile Chinook salmon are thought to leave the three streams early to rear in the shallow estuarine and nearshore habitats at the mouths of the three rivers.

Summary of additional information

Genetic data were not informative in reconstructing population structure under historical conditions. Allele frequencies between Skokomish River and Hamma Hamma River Chinook salmon are not different ($P = 0.136$) and probably reflect the use of Green River-origin broodstock for hatchery programs in Hood Canal. Extant Hood Canal Chinook salmon belonged to the same genetic cluster as late-returning Chinook salmon in south Puget Sound streams, all of which have been stocked with Green River broodstock (Figures 4, 5, and 6). Genetic data available for Chinook salmon from Lake Cushman also were not informative for reconstructing historical population structure because their origin is unknown and they reflect a history of low population abundance that could have resulted in the loss of historical characteristics.

Quantitative estimates of migration rates were not possible and did not inform our decisions. However, compared to other regions, Chinook salmon spawning in Hood Canal streams do not have to travel far to move between streams (Figure 1 and Table 2). Spawning areas are mostly in the stream's lower reaches because the upper reaches extend to high-gradient regions of the eastern Olympic Range. The only straying data available were recoveries of Chinook salmon from the Skokomish River and Hoodsport Hatchery programs and from saltwater net pens (which were discontinued). The Hoodsport Hatchery has received a number of Chinook salmon from the Skokomish River, possibly because of its location near the southern end of Hood Canal. Some strays from George Adams and Hoodsport hatcheries and the hatchery net pens also have been recovered in natural spawning areas on the Skokomish, Dosewallips, Union, and Dewatto rivers.[9]

Life history information for the extant populations was not useful in discriminating different independent populations. Mean spawn timing of the extant spawning aggregations in Hood Canal rivers (ranging from mid-September to early October) was somewhat earlier than in south Puget Sound. Within Hood Canal, spawning occurred earlier in the Dosewallips and North Fork Skokomish rivers than in the Hamma Hamma, Duckabush, South Fork Skokomish, and Skokomish rivers (Figures 6 and 7; Appendix B, Table B-6, pages 106–109). Average age of spawners at Hoodsport and George Adams hatcheries was highly dissimilar. Lack of correlations in abundance of spawners suggest that the Chinook salmon in the Dosewallips, Duckabush, Hamma Hamma, and Skokomish rivers could be demographically isolated from one another (Appendix B, Table B-9, pages 114–116), but these patterns were suspect because the methods for estimating abundance in north Hood Canal streams were inconsistent over time.

[9] T. Johnson, Washington Dept. Fish and Wildlife, Montesano, WA. Pers. commun., 8 April 2002.

Habitat differences do exist within the Hood Canal basin. The biggest differences are between the streams draining the Kitsap Peninsula lowlands, where the TRT did not identify independent populations, and those draining the Olympic Mountains, which are in different ecoregions (Appendix A, Figures A-10 and A-11, pages 90–91). On the western shoreline, the Dosewallips River occurs largely in the snowmelt-transition hydroregion (Appendix A, Figure A-8, page 87), whereas the Skokomish River basin hydrograph is rainfall-dominated and it is distinguished in its lithology (Appendix A, Figure A-8, page 87; Figure A-12 and Table A-3, pages 92–93).

Remaining uncertainties and data needs

The historical characteristics of Hood Canal Chinook salmon are largely unknown. Historical returns and distributions of Chinook salmon to this region have been affected by construction of dams, habitat degradation, fisheries, and the introduction of nonnative hatchery fish. Better data on movement of wild and hatchery Chinook salmon among streams would be useful to verify the TRT's conclusions of independence and to determine hatchery influence on these populations.

The largest uncertainty is the degree to which Chinook salmon spawning aggregations are demographically linked in the Dosewallips, Hamma Hamma, and Duckabush rivers. Further evaluation is needed to resolve this issue. Several alternative scenarios also are possible:

- Chinook salmon spawning in the Hamma Hamma, Duckabush, and Dosewallips rivers were subpopulations of a single, large Hood Canal Chinook salmon population with a primary spawning aggregation in the Skokomish River. Only a few historical reports document Chinook salmon spawning in the mid-Hood Canal streams, which might suggest that they were not abundant in any one stream before hatchery supplementation began in the early 1900s. In addition the overall size of each watershed and the area accessible to anadromous fish are small relative to other independent populations.
- Chinook salmon in the Hamma Hamma, Duckabush, and Dosewallips rivers each are independent populations.
- An additional uncertainty is the degree of demographic independence among the historical Chinook salmon spawning aggregations in the upper north fork, upper south fork, and the lower reaches of the Skokomish River. Further evaluation is needed to understand their relationships. Two alternative scenarios should be considered for the Skokomish River:
    - First, early returning Chinook salmon spawning in the upper forth fork and upper south fork are a separate population from another population of Chinook salmon spawning in the lower Skokomish River.
    - Second, early returning Chinook salmon spawning in the upper north fork are a separate population from another Chinook salmon population spawning throughout the upper south fork and lower Skokomish River. The geographic separation of the upper North Fork Skokomish River from the rest of the watershed and the north fork's physically distinctive character support this scenario.

The plausibility of the above hypotheses needs to be examined using a variety of information, including demographic evidence. First, monitoring abundance of the Chinook salmon spawning aggregations in these rivers may help determine whether their dynamics are likely to be quasi-independent. Information about fish movement and straying between streams also will be useful. Finally additional documentation of Chinook salmon spawning and rearing habitat in Hood Canal streams under historical conditions, if it exists, would help in determining the likelihood of these hypotheses.

As is the case throughout Puget Sound, it is not clear to what extent Chinook salmon spawning regularly or occasionally in smaller independent tributaries may have been demographically linked to independent populations the TRT identified. Further work is needed to determine the relationship of Chinook salmon that may intermittently utilize those streams to the overall population structure at the population and ESU levels. The Northwest Fisheries Science Center (NWFSC) assessed the status of Chinook salmon populations in eastern Hood Canal streams and concluded that the Union, Tahuya, and Dewatto rivers probably did not historically support self-sustaining Chinook salmon populations and that Chinook salmon presently occurring in these streams were primarily the result of hatchery introductions or straying from hatchery releases in other Hood Canal streams (NOAA 1999). As with Chinook salmon occurring in small streams that are not within the geographic boundaries of independent populations, further work is needed to determine the relationship of Chinook salmon that may intermittently utilize those streams to the viability of independent populations and the recovery of the ESU.

Estimates of straying among Hood Canal streams by naturally spawning Chinook salmon are lacking, but hatchery adults have been recovered in natural spawning grounds. In addition the length of time certain broodstocks were introduced into the Skokomish and Hoodsport hatcheries is information that will help in interpreting any potential biological significance of differences in life history data. Finally independent and consistent sampling to estimate spawner escapements, which began in 1998, will reduce uncertainty in assessments for each of the four main western Hood Canal streams.

The origins and significance of the Chinook salmon in Lake Cushman also are unknown. Although they originated from anadromous fish, the age and source remains a mystery. Genetic analyses indicated that these fish either originated from a few founders or suffered a severe population reduction in the past (Marshall 1995). Loss of genetic variation makes it difficult to determine whether they are descended from historical Hood Canal populations or introduced hatchery fish. They are genetically different, smaller in size (and presumably less fecund) than their anadromous counterparts (Myers et al. 1998). What biological role, if any, these Chinook salmon may play in the recovery of Hood Canal Chinook salmon remains unclear. The NWFSC considers them to be part of the Puget Sound Chinook salmon ESU (Myers et al. 1998, NMFS 1999), but the TRT did not identify them as a remnant of the historical population or a viable independent population.

Strait of Juan de Fuca

This Strait of Juan de Fuca region includes the Dungeness River and Elwha River basins and adjacent independent tributaries, such as Morse Creek. The TRT identified two independent

populations in this region, based on geographical and genetic information (The numbering sequence follows the list of populations in the Conclusions section, page 28, and is continued from page 53.):

21) Dungeness River

22) Elwha River

Although the TRT identified two independent populations in this region, important components of historical diversity may have been lost (Table 1), including early and late-returning life histories that no longer are expressed and genetic diversity lost to nonnative hatchery fish introductions. Historical evidence suggests that an early returning life history occurred in the Elwha River before construction of the lower Elwha Dam eliminated access to habitat in 1914. The team concluded that the early returning life history in the Elwha River was a significant part of the historical diversity of Chinook salmon within that basin and that information was insufficient to determine whether the lost form was an independent population or within-population diversity. In contrast in the Dungeness River extensive human disruptions, including introductions of nonnative hatchery fall Chinook salmon, may have more severely impacted late-returning life histories (Williams et al. 1975, Jamestown S'Klallam Tribe 2003). Questions remain about the population structure of the Chinook salmon spawning in the basin. Nehlsen et al. (1991) identified the late-run fish as being at high risk of extinction. More recent assessments indicate that only one Chinook salmon stock with no discontinuity in spawning distribution through time or space exists in the basin (Marlowe et al. 2001). Based on available evidence, the TRT concluded that the late-returning life history in the Dungeness River was a significant part of the historical diversity of the Chinook salmon population, which remains at high risk of extinction.

Chinook salmon also spawn in Morse Creek. The TRT concluded that they were not historically independent from the Elwha River or Dungeness River populations. Current return timings suggest that these fish are more similar to Elwha River Chinook salmon than to those in the Dungeness River (WDF et al. 1993). For that reason the team assigned the Morse Creek spawning aggregation to the Elwha River population.

Summary of information used in population structure decisions

Geographically Chinook salmon spawning areas in the Dungeness and Elwha rivers are disjunct from other populations in east Puget Sound and Hood Canal. The closest independent populations to the Dungeness River in east Puget Sound and Hood Canal are in the lower Skagit River and Dosewallips River, which are 95 km and 103 km away, respectively. The Elwha River is even farther from these populations (Figure 1). In contrast spawning areas in the Dungeness and Elwha rivers are only 37 km apart (Table 2).

Genetically Chinook salmon in the Dungeness and Elwha rivers are distinctive from other Puget Sound populations and from each other (Figures 4, 5, and 6; Table 5). Because of their geographic location, Dungeness River Chinook salmon were often presumed to be genetically intermediate between Elwha River Chinook salmon and those from east Puget Sound tributaries. The TRT's analyses do not support this; the data show equal or greater divergence of Dungeness River Chinook salmon from other groups in Puget Sound (Figure 6). Because no data exist for

wild, adult Dungeness Chinook salmon, the team used data from fish taken from redds and reared in the hatchery for genetic analyses.

Summary of additional information

Quantitative estimates of migration rates were not possible and did not inform our decisions. Information about Chinook salmon straying from the Dungeness River is available as part of the Dungeness captive broodstock program,[10] which was designed to restore the population.

Life history differences support the TRT's decision, based on genetic and geographical criteria. The Elwha River and Dungeness River populations have some of the earliest spawn timings of Puget Sound Chinook salmon. Spawning in the Dungeness River, however, began earlier and was less protracted than in the Elwha River (Figure 8) (WDF et al. 1993). Spawning in the Dungeness River begins significantly earlier in the upper main stem and in the Grey Wolf River, a tributary, than in the main stem below the confluence with the Grey Wolf (Appendix B, Table B-6, pages 106–109), which is similar to spawn timing in the Nooksack River (Figures 7 and 8). Elwha River and Dungeness River Chinook salmon also have different smolt-spawner age distributions (Appendix B, Table B-7, pages 110-112).

Trends in population abundance of Chinook salmon in the Dungeness and Elwha rivers were largely uncorrelated (Appendix B, Table B-9, pages 114–116), but this probably reflects the influence of different hatchery programs in those rivers (WDF et al. 1993).

Habitat differences exist between the Dungeness and Elwha rivers and other Puget Sound streams. The Dungeness River has a fairly large spawning area accessible to Chinook salmon that reaches into the snowmelt-transition hydroregion. Historically Elwha River Chinook salmon also would have used spawning areas in the snowmelt-transition hydroregion (Appendix A, Figure A-8, page 87). The Elwha River is in a different EPA ecoregion than other Puget Sound streams, (Appendix A, Figures A-10 and A-11, pages 90–91), and it is geologically different from other nearby streams (Appendix A, Figure A-12 and Table A-3, pages 92–93).

Remaining uncertainties and data needs

The historical population structure and diversity of the Elwha River are unknown because the population's current distribution is severely constrained by the two dams. Likewise the Dungeness River population's historical and current structure and diversity are poorly understood. In both rivers, past and present habitat alterations, hatchery programs, and harvest management strategies almost certainly altered population structure relative to historical patterns.

As is the case throughout Puget Sound, it is not clear to what extent the Chinook salmon spawning (regularly or occasionally) in smaller independent tributaries may have been demographically linked to independent populations the TRT identified. Williams et al. (1975) noted that the few Chinook salmon were known to use independent tributaries in this region. In Morse Creek, current return timings suggest that these fish are associated with Chinook salmon

[10] B. Sele, Jamestown S'Klallam Tribe, Sequim, WA. Pers. commun., 14 August 2000.

from the Elwha River (WDF et al. 1993). Further information is needed about fish movements and population dynamics to determine the relationship of Chinook salmon that may intermittently utilize smaller streams along the Strait of Juan de Fuca to the overall population structure at the population and ESU levels.

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Appendix A: Methods and Results for Less Informative Population Indicators

Appendix A contains data analyses and results for population indicators that were not as influential in delineating population boundaries as those reported in the body of this technical memorandum. For each indicator the Technical Recovery Team (TRT) summarized the independence between each pair of sites as the median independence score across (with 6–10 scorers per indicator) and the distribution of independence scores among scorers (Table A-1). The relatively informative indicators are discussed in the main document. In contrast the indicators reported in Appendix A are those believed to be informative for identifying independent populations in a theoretical sense; however, because of data quality issues, confounding sources of variation, or uncertainty in interpretation of results, the TRT did not rely heavily on these results to make its determinations. The team included the analyses and results in Appendix A for completeness. Furthermore we hope to encourage further data collection, experimentation, or discussion of the natural levels of variation in these indicators and how they might suggest something about the population structure of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound.

Direct Observations of Migration

Methods

Some direct observations of straying among Puget Sound Chinook salmon stocks were available. Most of these observations are based on releases and subsequent recoveries of hatchery Chinook salmon marked with coded-wire tags (CWTs); the observations are available in a database maintained by the Pacific States Marine Fisheries Commission (RMPC 1997). The TRT searched the database for all records of tagged Chinook salmon reared in Puget Sound or Strait of Juan de Fuca watersheds and recovered at or near the probable spawning location (i.e., hatchery rack, spawning ground, carcass survey, and freshwater trap). These data allowed the team to estimate straying rates; straying is defined as recovery of a tagged fish at a location other than its rearing site. Stray rate refers to the proportion of all fish in a tag group (or from a release site) that is recovered somewhere other than their tagging or release sites. However stray-rate estimates must be viewed with caution, because methods of estimating the total number of returning tagged fish vary among recovery locations, and the geographic area sampled for strays is not comprehensive or selected based on a spatially stratified design. Estimates of straying rates based on small-scale experimental studies were available in a few locations.

The TRT graphically examined the relationship between straying rate and dispersal distance in all CWT release groups that produced at least 20 freshwater recoveries (n = 3–98 groups per release site). The team selected and summarized 16 release sites distributed throughout Puget Sound. For these sites we measured straying rates separately for each release

Table A-1. Distribution of independence scores for each pairwise comparison of streams. Each number represents a score by a different genetic scorer. Locations signify rivers unless otherwise noted.

Skagit River basin

Upper/ Lower Skagit	Lower Skagit				Upper Skagit				Lower Sauk			Upper Sauk		
	Lower Sauk	Upper Sauk	Suiattle	Cascade	Lower Sauk	Upper Sauk	Suiattle	Cascade	Upper Sauk	Suiattle	Cascade	Suiattle	Cascade	Suiattle/ Cascade
–2	2	2	3	3	1	–1	2	2	2	2	2	1	1	1
2	2	4	4	4	2	4	4	4	4	4	4	4	4	4
1	1	2	3	2	1	1	1	1	1	2	2	1	1	2
2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
2	3	3	3	3	2	2	3	1	3	3	3	3	3	3
0	1	2	2	2	0	1	2	1	1	2	2	1	1	1
3	4	2	3	3	3	4	3	3	3	4	4	3	3	2
2	2	3	2	2	2	2	2	2	2	2	2	2	2	2
1	1	2	2	3	1	2	2	2	2	2	3	2	2	2

Stillaguamish River basin	**Snohomish River basin**									
	Skykomish				Sultan			Wallace		Bridal Veil Creek/ Snohomish
North fork/ South fork	Sultan	Wallace	Bridal Veil Creek	Snohomish	Wallace	Bridal Veil Creek	Snohomish	Bridal Veil Creek	Snohomish	
4	2	–2	–2	3	–1	2	3	–1	3	3
4	2	–3	–3	3	2	2	2	–3	1	1
4	2	–3	–3	2	1	2	3	–3	2	2
3	2	–2	–2	2	1	1	2	–2	1	2
3	3	–2	–2	1	1	2	3	–3	1	2
3	2	–2	–2	1	0	1	1	–2	1	1
4	1	–3	–3	1	0	2	0	–3	0	0
3	2	–3	–3	2	2	2	2	–3	1	1
3	2	–2	–1	2	–3	1	2	–2	2	1

Table A-1 continued. Distribution of independence scores for each pairwise comparison of streams. Each number represents a score by a different genetic scorer. Locations signify rivers unless otherwise noted.

Lake Washington			**Nooksack River basin**	**Hood Canal**
Cedar		Sammamish/ Issaquah	North fork/ South fork	Skokomish/ Hamma Hamma
Sammamish	Issaquah			
	2		3	–2
–1	–1	–1	2	–2
2	2	2	3	–2
1	1	1	1	0
2	0	0	3	0
2	1	0	3	–2
2	2	1	2	0
2	2	1	3	–1
2	2	1	3	0

Central/south Puget Sound

Duwamish/Green				Puyallup			White		Nisqually/ Newaukum Creek
Puyallup	White	Nisqually	Newaukum Creek	White	Nisqually	Newaukum Creek	Nisqually	Newaukum Creek	
3	4	3	–4	3	4	3	4	3	4
3	4	1	0	4	3	0	4	0	0
1	3	1	0	3	2	0	3	0	0
1	2	2	0	2	2	0	2	0	0
–2	3	1	–4	3	2	1	3	3	–2
1	2	1	–3	2	2	0	3	3	1
1	3	1	0	3	2	0	3	0	0
1	1	2	–3	2	2	2	3	3	2
3	3	3	–4	2	3	0	3	0	0

group as the proportion of recoveries that occurred at a given nautical distance from the release location.

Results

The pattern of releases and recoveries of tagged Chinook salmon (Table A-2) suggests that migration rates between basins or major subbasins in Puget Sound are generally quite low. For most stocks more than 95% of the tag recoveries from spawners occurred within the same subbasin where the juveniles were released (but see the caveat in the Methods subsection [page 67] regarding estimates of stray rates based on these data). However some migration between major basins does occur. For example spring- and summer-run Chinook salmon released at Kendall Creek Hatchery on the North Fork Nooksack River have been recovered in the North Fork Stillaguamish River, and summer-run fish from the North Fork Stillaguamish River have returned to the Snoqualmie Basin. A small number of adults have been recovered outside of Puget Sound (e.g., spring-run Chinook salmon of Suiattle River origin released from Marblemount Hatchery have returned to the Cowlitz Hatchery on the Cowlitz River in the lower Columbia River basin).

The dispersal curve for all locations and release groups (Figure A-1) shows a strongly nonlinear decline in straying rate as a function of distance between release and recovery locations, with the steepest decline occurring between 0 and approximately 75 km. The TRT did not attempt to model this relationship statistically. The individual dispersal curves from 16 individual release sites suggest that the shapes of dispersal distributions are highly variable among streams and stocks. For example the number of fish recovered farther than 100 km from the source was very low for a number of release groups (e.g., those from Grovers, Skookum, and Garrison creeks and Wallace River). In contrast fish recoveries farther than 100 km from the source occurred from tag groups originating in the Elwha River, North Fork Stillaguamish River, Marblemount Hatchery, Skokomish River, and Kendall Creek.

Patterns in Life History Characters

Methods

Data on spawner age and age at outmigration (WDFW 1995) were gathered by reading scales collected from carcasses on the spawning grounds. Scale samples for spawner age were taken from the same wild and hatchery stocks used in the genetic analyses, and sample sizes varied among stocks ($n \geq 40$). Log-linear models were used to test for overall heterogeneity in age distributions among stocks, between sexes, and between hatchery and wild spawners; 5+ and 6+year-old age-classes were pooled for these analyses. An index of percentage overlap in age distributions (Krebs 1989) was calculated for both spawner age and spawner and outmigrant age for each pairwise combination of stocks. The resulting similarity matrix was used in a UPGMA cluster analysis, with 1 minus percent overlap as the distance measure.

Similar to the age-structure data, length (fork length or post-orbital length or both) was measured from all Chinook salmon adults collected for genetic analyses on the spawning grounds. The TRT grouped fish by age (3, 4, and 5 years old) and sex for initial length analyses. If multiple broodyears within an age and sex class existed, the team combined them to increase

Table A-2. Straying matrix for Puget Sound Chinook salmon. Except where indicated, data are based on CWT recoveries from Chinook salmon reared at hatcheries within Puget Sound.[a] Bold = recoveries within the same basin or subbasin where reared (i.e., successful homing). Italics = estimates based on otolith-marking study of Chinook salmon reared at Wallace Hatchery. Recoveries are summed over 1997 and 1998 return years. Locations signify rivers unless otherwise noted. Source: RMPC 1997.

	Stock or rearing location[b]																
	Nooksack Basin		Skagit Basin			Stillaguamish Basin	Snohomish Basin		Lake Washington Basin	Green Basin	Puyallup Basin	Nisqually Basin	South Puget Sound	Kitsap Peninsula	Skokomish Basin	Dungeness Basin	Elwha Basin
Recovery basin	Kendall spring	Skookum spring	Marblemount spring	Marblemount summer	Wild Skagit summer	North Fork Stillaguamish summer	Wallace summer	Wallace fall[c]	Issaquah fall[c]	Soos Creek fall[c]	White spring	Nisqually fall[c]	Garrison (Chambers Creek) fall[c]	Grovers Creek fall[c]	Skokomish fall[c]	Dungeness spring	Elwha fall
Nooksack	**58.00**	**6.00**								2.03							
North Fork Nooksack	**4,966.11**	10.19															
Middle Fork Nooksack	7.00																
South Fork Nooksack	6.35	**2,38.26**															
Samish	1.00						1.00			2.08							
Skagit	5.37			**20.00**	7.00	20.40											
Lower Skagit	1.00					6.00											
Upper Skagit	7.02		**1,465.70**	**1,15.03**	**3.13**	4.00		2.03						1.00			
Cascade	6.74		**77.26**														
Stillaguamish						**5.00**											
North Fork Stillaguamish	15.01		1.00			**1,050.97**											
South Fork Stillaguamish				3.00													
Snohomish							5.69	9.00						1.02			
Skykomish							*16.12/ 1,099.00*										
Wallace			2.03	1.00		10.06	***752.48/ 8,913.00***	**369.10**		3.00							
Bridal Veil Creek/ North Fork Skykomish							*636.00*										

Table A-2 continued. Straying matrix for Puget Sound Chinook salmon. Except where indicated, data are based on CWT recoveries from Chinook salmon reared at hatcheries within Puget Sound.[a] Bold = recoveries within the same basin or subbasin where reared (i.e., successful homing). Italics = estimates based on otolith-marking study of Chinook salmon reared at Wallace Hatchery. Recoveries are summed over 1997 and 1998 return years. Locations signify rivers unless otherwise noted. Source: RMPC 1997.

	Stock or rearing location[b]																
	Nooksack Basin		Skagit Basin			Stillaguamish Basin	Snohomish Basin		Lake Washington Basin	Green Basin	Puyallup Basin	Nisqually Basin	South Puget Sound	Kitsap Peninsula	Skokomish Basin	Dungeness Basin	Elwha Basin
Recovery basin	Kendall spring	Skookum spring	Marblemount spring	Marblemount summer	Wild Skagit summer	North Fork Stillaguamish summer	Wallace summer	Wallace fall	Issaquah fall[c]	Soos Creek fall[c]	White spring	Nisqually fall[c]	Garrison (Chambers Creek) fall[c]	Grovers Creek fall[c]	Skokomish fall[c]	Dungeness spring	Elwha fall
Snoqualmie						30.87	*119.00*			3.25							
Issaquah									1,094.07					3.07			
Lake Washington										1.00			1.00				
Green								9.77	5,766.90				8.90				
Puyallup									1.34	6.03							
White									1.00	3,530.89			1.00	1.03			
Garrison Hatchery	1.04								3.00	2.01			74.60	18.32			
Nisqually												1,347.30					
McAllister Hatchery												1.00	1.00	8.60			
Capitol Lake									20.10					6.44	2.24		1.00
Burley Creek														5.41			
Coulter Creek														1.00	7.74		
Minter Hatchery									1.00					11.02	1.00		
Hupp Spring Ponds														1.02	1.01		
Grovers Creek Hatchery													1.01	1,0830.37	1.00		3.02
Skokomish															1,530.36		
Hoodsport Hatchery															15.29	1.00	1.01
Dungeness																2.00	

Table A-2 continued. Straying matrix for Puget Sound Chinook salmon. Except where indicated, data are based on CWT recoveries from Chinook salmon reared at hatcheries within Puget Sound.[a] Bold = recoveries within the same basin or subbasin where reared (i.e., successful homing). Italics = estimates based on otolith-marking study of Chinook salmon reared at Wallace Hatchery. Recoveries are summed over 1997 and 1998 return years. Locations signify rivers unless otherwise noted. Source: RMPC 1997.

	Stock or rearing location[b]																
	Nooksack Basin		Skagit Basin			Stillaguamish Basin	Snohomish Basin		Lake Washington Basin	Green Basin	Puyallup Basin	Nisqually Basin	South Puget Sound	Kitsap Peninsula	Skokomish Basin	Dungeness Basin	Elwha Basin
Recovery basin	Kendall spring	Skookum spring	Marblemount spring	Marblemount summer	Wild Skagit summer	North Fork Stillaguamish summer	Wallace summer	Wallace fall[c]	Issaquah fall[c]	Soos Creek fall[c]	White spring	Nisqually fall[c]	Garrison (Chambers Creek) fall[c]	Grovers Creek fall[c]	Skokomish fall[c]	Dungeness spring	Elwha fall
Elwha							1.04										1,539.17
Outside Puget Sound				11.38		1.02								1.00	1.00		1.00
Total	5.074.64	2.54.45	1.545.99	150.41	10.13	1.128.32	7.76.33/ *1.0767.00*	380.10	1.127.94	5.782.60	3.536.92	1.348.3	77.61	1.0898.17	1.560.67	3.00	1.545.20

[a] Counts of CWT recoveries should be interpreted cautiously for the following reasons:

- Straying rates of hatchery Chinook salmon likely differ from straying rates of wild fish, particularly where the hatchery stock has been substantially influenced by out-of-basin introductions.
- Most counts shown in the table are summed over multiple tagged release groups and brood years, and the number and date of releases differ among stocks.
- Counts from different locations or years may not be directly comparable because of differences in methods used to estimate the total number of returns based on the number of tags sampled and sampling efficiency. In particular, some recoveries do not provide an estimate of sampling efficiency and simply report the number of tags observed. Thus the counts should not be directly interpreted as estimates of straying rates.

[b] In general hatchery stocks were included in the matrix only if the original broodstock was of local wild origin or if the present-day stock is genetically similar to the local wild population. Note that recoveries are grouped geographically and may include both hatchery returns and wild spawners within a given basin.

[c] Stocks with substantial out-of-basin influence are included to increase geographic coverage area.

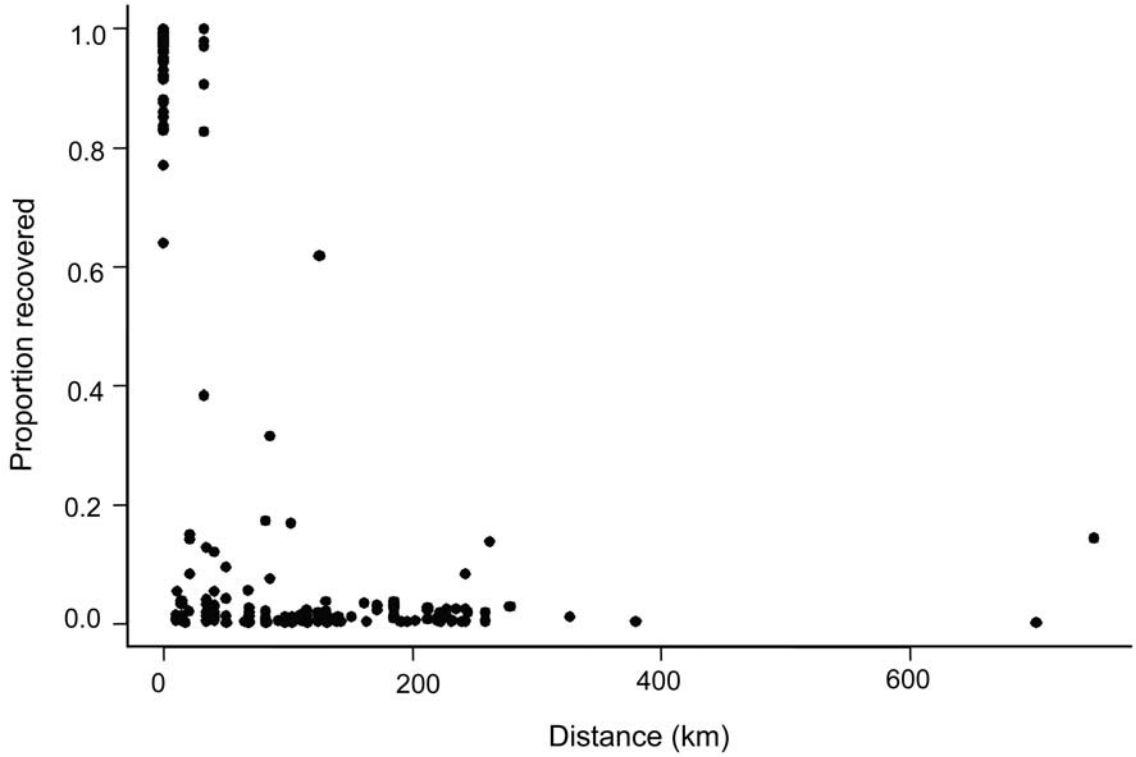

Figure A-1. Dispersal curve for Puget Sound Chinook salmon based on coded-wire tag recoveries. Data shown represent a total of 167 tagged release groups from 15 hatcheries for which at least 20 tagged spawners were recovered. Each point is the proportion of recoveries that occurred at a given distance from the release location. Proportions were calculated separately for each release group, so multiple dispersal "curves" are overlaid in the figure.

the number of stocks with adequate sample size for analyses. Only 3-year-old males and 4-year-old males and females had large enough sample sizes for length at age of maturity cluster analyses ($n \geq 40$). In most cases the TRT reported length data as either fork length or post-orbital length, so the team performed regressions within each age and sex class to standardize lengths to post-orbital length (regression [R^2] ranged from 0.80 to 0.93). Differences in length between 4-year-old males and females were not statistically significant (ANOVA $df = 1$, $P > 0.12$), so we pooled the sexes for cluster analyses of 4-year-olds. The team computed differences in the mean length at age of maturity between all sites sampled and used them to generate a difference matrix for 4-year-old males and females combined. The analysis included hatchery and wild stocks. The TRT then used the matrix in a UPGMA cluster analysis to generate a dendrogram (Figure A-2).

Results

Representative age distributions of Puget Sound Chinook salmon spawners based on carcass samples are shown in Figure A-3. A log-linear model including only naturally produced stocks detected highly significant overall heterogeneity in spawner age distributions ($G^2 = 674.83$, $df = 63$, $P < 0.0001$). In general the cluster analysis based on overlap in spawner

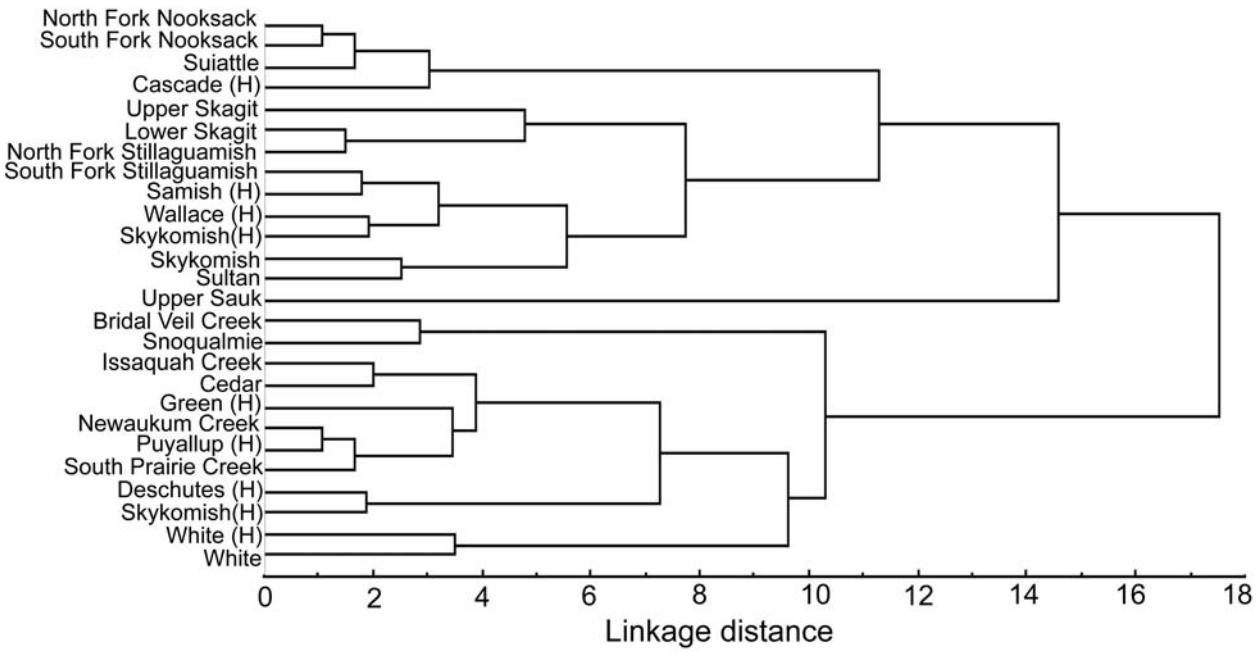

Figure A-2. Dendrogram of Puget Sound Chinook salmon stocks based on similarity in length at age of maturity (4-year-old females and males). The distance measure used in the UPGMA cluster analysis was Euclidean distance of mean length at age of maturity of 4-year-old fish. The analysis included wild and hatchery-produced stocks (stocks with an H in their name are hatchery stocks). Sample sizes and the numbers of broodyears sampled vary among stocks. Locations signify rivers unless otherwise noted.

age distributions does not indicate any strong patterns of similarity concordant with the spatial distribution of stocks, although there are some exceptions (e.g., stocks from the Cedar River and the Issaquah Hatchery cluster together, as do the upper Cascade River spring, lower Sauk River summer, and Cascade Hatchery stocks). Distributions of age at outmigration and spawning also are shown in Figure A-3. An overall test for heterogeneity was not performed on distributions of age at outmigration and spawning. The UPGMA dendrogram developed from the combined data on age at outmigration and spawning shows two main clusters, one containing all spring-run stocks and a few summer or fall stocks (i.e., Wallace, Sauk, Snoqualmie, and Elwha rivers). The other main cluster in the dendrogram is a collection of summer or fall stocks from throughout Puget Sound, with no geographic pattern to the degree of similarity in juvenile or spawner age distributions.

Age-specific length varies significantly among 26 stocks of Puget Sound Chinook salmon (ANOVA $F = 8.24$, $df = 25$, $P << 0.001$; Figure A-3). The UPGMA dendrogram indicates that, unlike the age data, patterns in length at age of maturity of Puget Sound Chinook salmon are fairly concordant with the spatial arrangement of streams. Fish in streams that are closer together have more similar length at age of maturity than fish from streams that are farther apart.

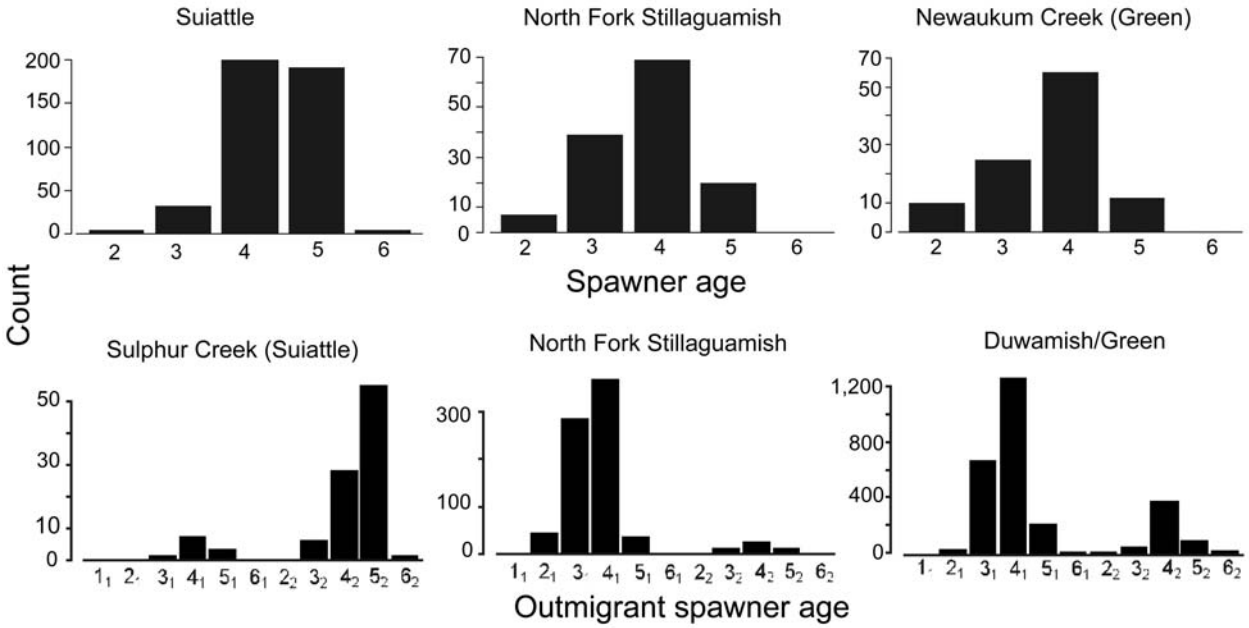

Figure A-3. Representative age distributions for Puget Sound Chinook salmon stocks, based on scale samples from carcasses on spawning grounds. The distributions of spawner age are on the top row and the distributions of age at outmigration (the subscript number) and spawning (the large number) are on the bottom row. All ages are expressed as year of life, beginning with egg deposition. Locations signify rivers unless otherwise noted.

Spatial Synchrony in Spawner Abundance

Methods

The TRT obtained time series of spawner abundance for Puget Sound Chinook salmon from StreamNet (no date). Time series with less than 10 years of data were excluded from the analysis, as were abundance data for hatchery-produced stocks, although natural spawners in some areas include a substantial proportion of first-generation hatchery strays. Using these criteria, the team selected 31 stocks (loosely defined in this study to mean any fish group for which relevant data were available) to use in the analysis. Most of these stocks correspond to SASSI stocks (WDF et al. 1993), but we also included several spawner groups in small, independent Puget Sound tributaries not described by WDF et al. (1993). The time series for each stock consists of annual total spawning escapement, as estimated from counts of live spawners, carcasses, or redds in selected index stream reaches. The series range in length from 10 to 30 years, and most include 1997 as the most recent sample year. In order to meet the requirements of statistical time-series models, the team interpolated missing observations that were not at the beginning or end of the series by averaging the abundance in the years immediately preceding and following the missing point. Only four values were interpolated, so the error introduced by this procedure was minimal.

The TRT filtered the abundance data using standard time-series methods prior to the correlation analyses. Because the goal was to examine covariation in abundance that might be due to the exchange of migrants between stocks, the team first attempted to eliminate sources of

variation within stocks that were not likely attributable to immigration or emigration (cf Hanski and Woiwod 1993, Bjørnstad et al. 1999). Statistically these sources of variation include 1) long-term temporal trends (which might be caused by changing environmental conditions due to natural or human causes), and 2) temporal autocorrelation (due to density-independent variation in cohort strength or autocorrelation in climate or other environmental variables). The team assumed that these relatively long-term patterns are driven by deterministic processes over long time scales, because migration rates in salmonid populations are more likely to vary over short time scales (see references in McElhany et al. 2000). The TRT recognizes that, after accounting for trends and autocorrelation, we cannot assume that all sources of spurious correlation in abundance time series were completely removed. Therefore inferences about possible migration rates between groups based on these abundance time series should be made with caution.

Temporal trend was estimated separately for each time series using a third-order polynomial multiplicative model (Thomas 1996):

$$N_t = N_0 \lambda_1^t \lambda_2^{t^2} \lambda_3^{t^3} e^{\varepsilon_t} \tag{4}$$

where N_t is abundance in year t, lambda$_i$ (λ_i) are the trend parameters, and epsilon$_t$ (ε_t) is a normal random variable. Equation 4 is equivalent to:

$$\log N_t = \beta_0 + \beta_1 t + \beta_2 t^2 + \beta_3 t^3 + \varepsilon_t \tag{5}$$

where beta$_0$ (β_0) = log N_0 and β_i = log λ_i for i greater than 0.

The TRT chose a third-order polynomial model because it was sufficiently complex to describe most obvious long-term patterns in the abundance data. We estimated the parameters in Equation 5 (hereafter called the trend model) by least squares, then used a stepwise procedure to find the most parsimonious model, based on Mallow's C_p-statistic (Weisberg 1985, using the S-PLUS 5 program (MathSoft 1998). Thus the final trend model for any particular stock does not necessarily include all three polynomial terms, only those that contributed to the overall explanatory power of the regression.

The TRT visually inspected residuals from each polynomial trend regression to check the assumption that ε_t are normally distributed. Residuals for many stocks showed significant temporal autocorrelation, so the team fitted a time-series model with trend and autoregressive parameters (Edwards and Coull 1987) to each abundance time series. This model (hereafter called the trend-AR) is:

$$\log N_t = \beta_0 + \beta_1 t + \beta_2 t^2 + \beta_3 t^3 + \alpha_1 \log N_{t-1} + \alpha_2 \log N_{t-2} + \cdots + \alpha_p \log N_{t-p} + \varepsilon_t \tag{6}$$

where N_{t-1} is the abundance in year $_{t-1}$ and alpha$_i$ (α_i) are autoregressive parameters.

The TRT chose the order p of the autoregression for each stock by fitting various autoregressive models (with $p \leq 8$) to the residuals from the trend model and selecting the most parsimonious model based on the Akaike Information Criterion (AIC) (Burnham and Anderson 1998). Once the team determined the autoregression order, we simultaneously estimated the parameters in the trend-AR model by least squares.

The residuals from the trend and trend-AR time-series models formed two new data sets, which served as the input for the correlation analyses. The TRT used each set of residuals to

compute a matrix of product-moment correlation coefficients between all pairs of stocks. The length of the residual time series varied among stocks, so the team computed correlations between residuals from the trend model in two ways: using pairwise deletion of missing observations (so that elements in the correlation matrix are based on differing sample sizes) and using casewise deletion (so that all correlation coefficients are based on $n = 10$ observations corresponding to years 1987–1996). The TRT could not use casewise deletion of missing observations in the correlation matrix based on trend-AR residuals because the data set had too few years with data on all stocks.

The TRT examined patterns of cross-correlation between stocks by UPGMA cluster analysis, with $1-r$ as the pairwise distance measure. The team assessed the robustness of the resulting clusters by jackknifing over years. Each of the 30 years in the escapement data set was successively deleted, and we recalculated the correlation matrix on the reduced data set. The TRT used each correlation matrix in a UPGMA cluster analysis and found a consensus tree based on the 30 dendrograms using the CONSENSE program version 3.5c (Felenstein 1993). This procedure allows an evaluation of the sensitivity of the correlation matrix to inclusion of extreme observations in particular years. The jackknifing analysis was performed only on the data set consisting of residuals from the trend-AR model.

The TRT investigated spatial autocorrelation in abundance by testing the association between pairwise correlation coefficients and pairwise geographic distances separating the spawning grounds of stocks, as described previously in this subsection. In addition the team statistically modeled the relationship between distance and correlation in abundance in order to estimate the spatial scale of demographic synchrony. We used a Gaussian model (Myers et al. 1997, Bradford 1999):

$$\rho(d) = \rho_0 \exp\left(-\frac{d^2}{2\sigma^2}\right) \tag{7}$$

in which the demographic correlation, rho (ρ) × distance (d), between two stocks declines monotonically with increasing distance, starting at an initial value of ρ_0 when $d = 0$. This model can accommodate a "threshold" at which the correlation decays most rapidly. The model was fit using nonlinear least squares. The TRT made no attempt to account for the nonindependence of elements in the correlation and distance matrices.

Results

For a majority of stocks, residuals from the trend model show significant serial autocorrelation, indicating that the trend-AR model is the more appropriate model for these stocks. Interestingly there is no general pattern of strong autocorrelation at a lag of 3–5 years, as would be expected to result from density-independent variation in cohort strength, given the predominant age at reproduction of Puget Sound Chinook salmon.

The jackknifed consensus tree for the cluster analysis, based on trend-AR residuals, indicates that low-level structure in the correlation matrix (i.e., clusters of 2–4 stocks) is generally robust to the deletion of single years from the data set. Higher-level structure, however, is much more sensitive to the inclusion or exclusion of particular years. The relationships among stocks indicated by the dendrogram (Figure A-4) are summarized

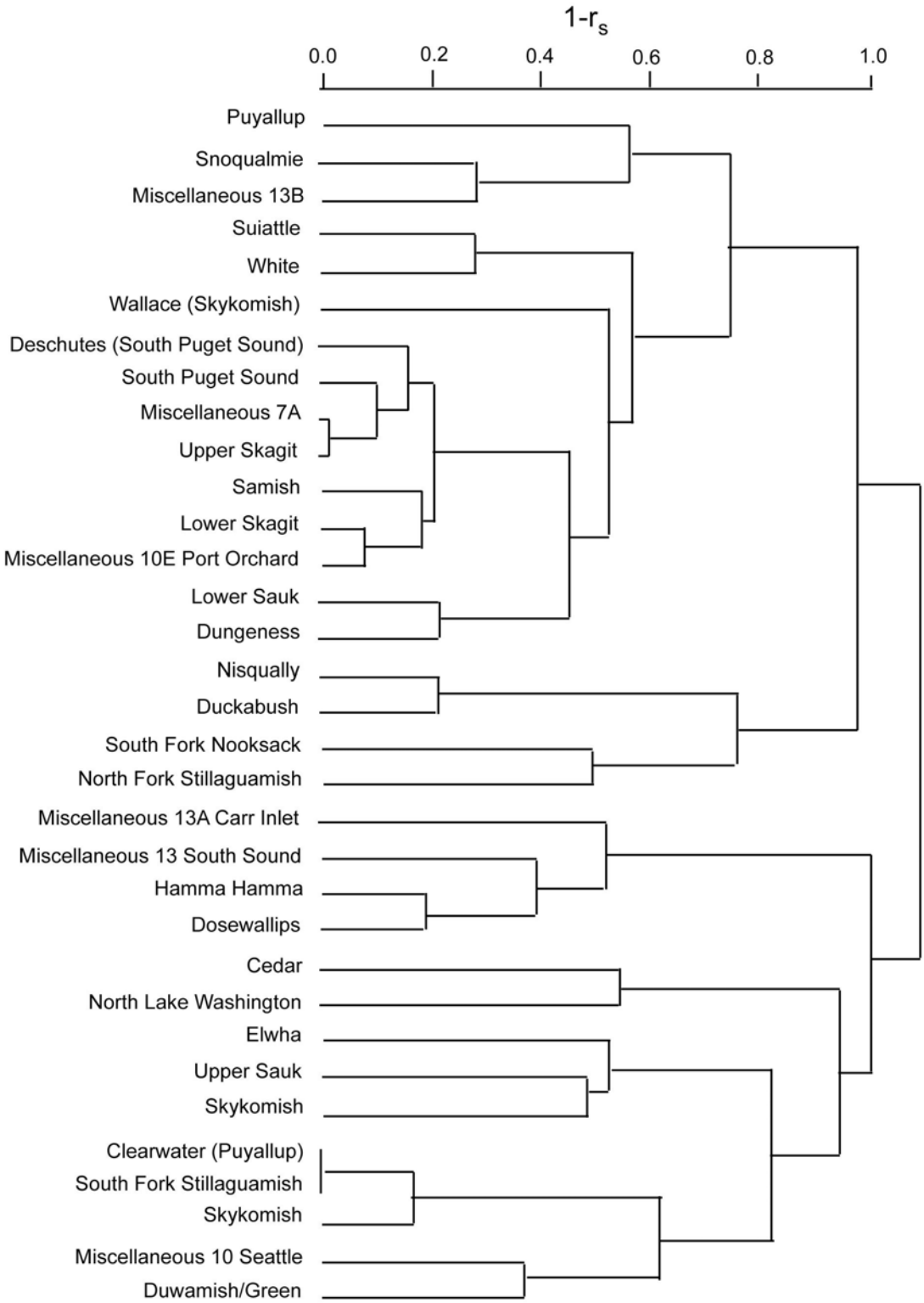

Figure A-4. Difference in the temporal correlation ($1\text{-}r_s$) in abundance time series from stocks of Puget Sound Chinook salmon. Product-moment correlation coefficients were computed between all pairs of stocks, based on residuals from time series models. Results below are from a UPGMA cluster analysis using ($1\text{-}r_s$) as the distance measure. Locations signify rivers unless otherwise noted.

graphically in Figure A-5. Stock clusters depicted in Figure A-4 are those clusters that are joined at a linkage distance less than or equal to 0.55 in the dendrogram. This linkage distance corresponds roughly to a statistically significant correlation coefficient for a sample size of $n = 9$, which is the smallest sample size used in the correlation matrix.

On the whole the relationships among stocks suggested by correlations in abundance are not concordant with the pattern suggested by geography and genetic similarity (i.e., geographically proximate stocks do not consistently show stronger correlations in abundance than geographically distant stocks). This conclusion is supported by inspection of the spatial correlogram based on trend-AR residuals (Figure A-6). Although a one-tailed Mantel test indicated a significant ($P < 0.05$) negative association between the correlation coefficient and geographic distance, the relationship is weak. Figure A-6 shows the fit of the Gaussian decay model. The estimate of the "threshold" parameter is sigma (σ) = 86.6, indicating that positive correlations tend to occur at a distance of equal to or greater than 86.6 km. This value is significantly different from zero (approximate t-test, $P < 0.001$). However the initial correlation is quite low ($\rho_0 = 0.15$), although it too is significantly different from zero ($P < 0.01$).

One of the most striking examples of a group of neighboring stocks with highly correlated dynamics is the group consisting of the lower Skagit River fall-, upper Skagit River summer-, and lower Sauk River summer-run stocks. This cluster is robust to different methods of computing the correlation matrix and filtering the abundance time series. However these Skagit Basin stocks also cluster with the geographically distant Dungeness River and area 7A stocks (Figure A-4). The upper Sauk River and Suiattle River spring-run stocks, which spawn in the upper reaches of the Skagit Basin, appear unrelated to the lower Skagit Basin stocks in all the cluster analyses. The summer- and fall-run stocks in the Stillaguamish River cluster together, but only when the correlation matrix is based on trend-AR residuals (Figure A-4). In contrast the summer-run stocks in the Stillaguamish and Snohomish rivers appear related when the correlation matrix is based on residuals from the trend model (results not shown). In the analysis based on trend-AR residuals, the Duwamish/Green River, Cedar River, and north Lake Washington stocks form a cluster, as do the Wallace River and Snohomish River summer-run stocks.

Environmental Effects on Population Synchrony

Methods

In order to investigate the possibility that the observed cross correlations in abundance were due to correlated environmental influences (i.e., the Moran effect) rather than demographic exchange (e.g., Harrison and Quinn 1989, Lande et al. 1999, Bjørnstad et al. 1999, Ripa 2000, Kendall et al. 2000), the TRT examined the relationships between annual spawner abundance and some environmental variables. The rationale for this approach was that if the environmental variables explain a significant amount of the variance in abundance, then their effects could be removed from the abundance time series and the between-stock correlations could be recalculated.

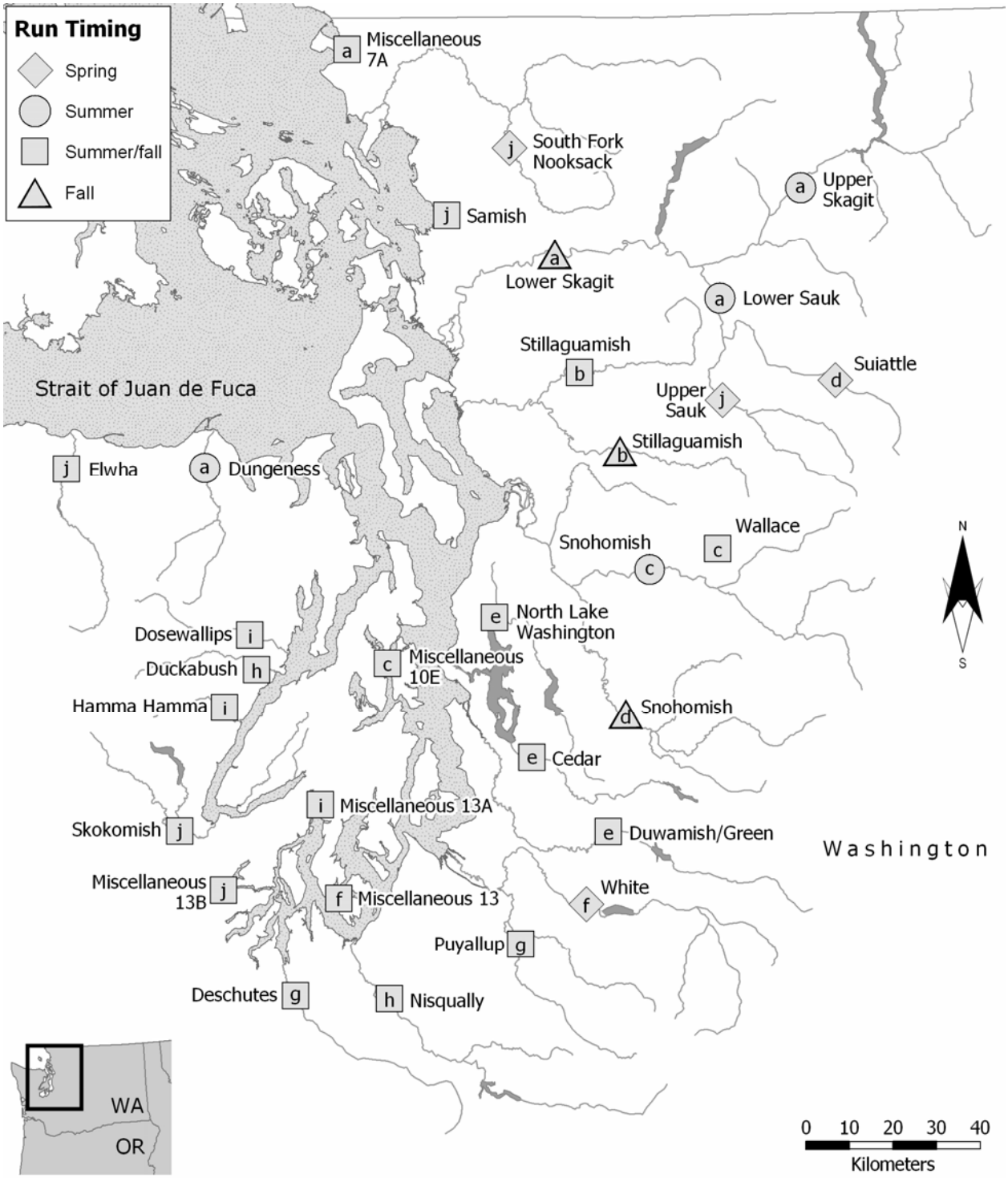

Figure A-5. Relationships among Puget Sound Chinook salmon stocks, based on UPGMA cluster analysis using temporal correlation in abundance as the similarity measure. The correlation matrix was calculated from trend-AR model residuals, using pairwise missing data deletion. Clusters were defined by taking all groups in the dendrogram that were joined at linkage distance greater than or equal to 0.55. Streams within a cluster are represented by the same letter.

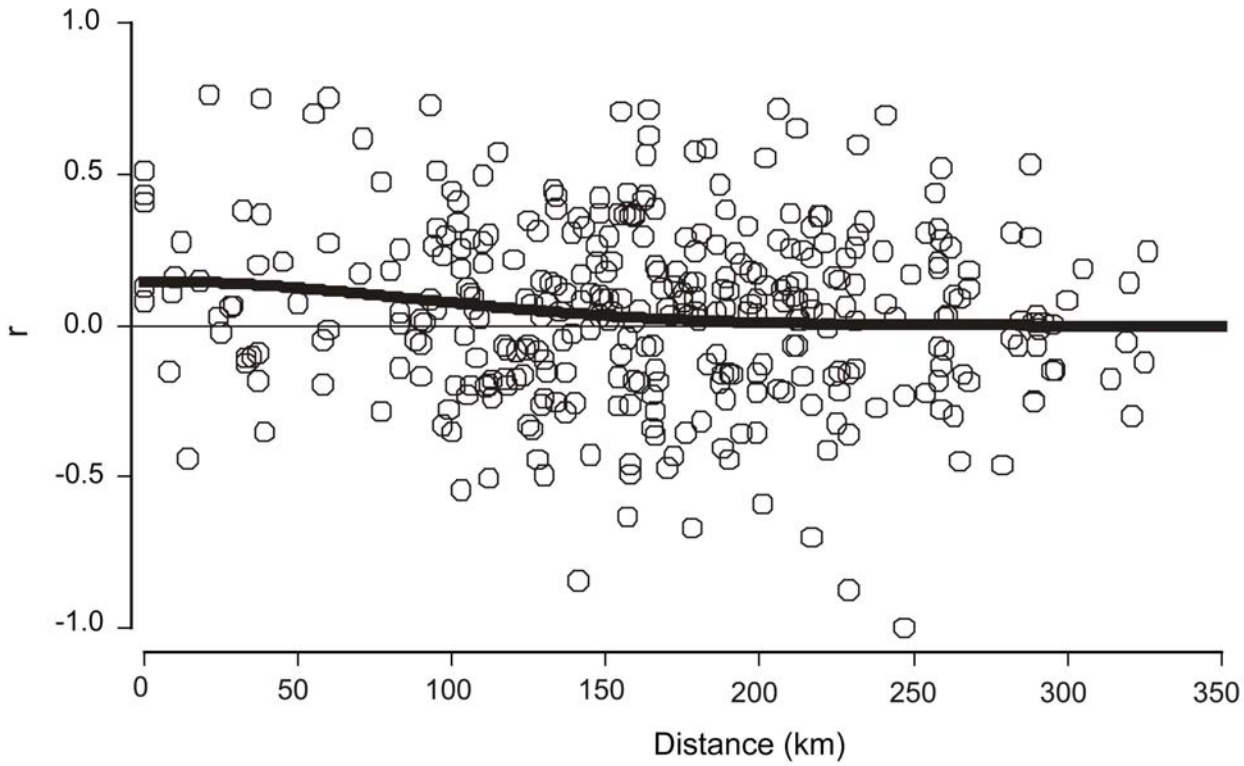

Figure A-6. Spatial correlogram for spawner abundance in Puget Sound Chinook salmon stocks. The correlation in abundance between each pair of stocks (based on trend-AR model residuals) is plotted against the geographic distance separating their spawning areas. The solid line is the Gaussian decay model fit to the correlation and distance data.

The TRT chose to focus on two hydrologic variables, peak discharge during the incubation period and low flow during the upriver spawning migration, because previous studies indicated that these variables have strong effects on salmonid vital rates that may be detectable in spawner escapement data (Beamer and Pess 1999). Time series of discharge measured at stream gauges on or near Puget Sound Chinook salmon spawning grounds were obtained from the U.S. Geological Survey (USGS 2005). Gauge data were available for 22 of the 31 stocks. Peak flow during incubation was defined as the maximum instantaneous discharge observed between 1 September and 31 March of each broodyear. Low flow during spawning migration was defined as the minimum 7-day mean flow observed between 1 May and 31 October of each return year. Scatter plots of abundance (the raw number of spawners and the residuals from the time-series models) against peak and low flow were used to check visually for effects of the hydrologic variables. Because peak discharge is hypothesized to affect egg-to-fry survival and most Chinook salmon in Puget Sound spawn between the ages of 3 and 5 (WDF 1993, Beamer and Pess 1999), the team used lagged scatter plots with the peak flow time series lagged by 3, 4, or 5 years. Low flows during summer and early fall may delay migrating spawners, increase stress-related mortality, or prevent access to spawning grounds, so abundance in each year was plotted against low flow observed in the same year.

Results

Lagged scatter plots do not suggest a systematic relationship between spawner abundance and instantaneous peak flow at a time lag of 3, 4, or 5 years in any stock. This conclusion is not altered when residuals from the time-series models, rather than raw or log-transformed escapement estimates, are used as the index of abundance. Similarly scatter plots of spawner abundance against 7-day summer low flow provide no evidence of any relationship between these variables. It is clear from inspection of the scatter plots that attempting to statistically model the relationship between peak flow and abundance would not be informative for the question the TRT was addressing. In summary, in interpreting correlations in time series of abundance data, the team could not distinguish between correlations due to environmental conditions experienced by groups of fish and those due to migrants between two groups. For this reason we feel that the level of inference from population synchrony analyses is relatively low.

Habitat Characteristics

Identifying Hydrologic Regions in Puget Sound

Methods

The TRT performed a set of analyses intended to classify all the rivers and streams in Puget Sound into hydrologic regions based on hydrologic patterns, mean basin elevation, and mean annual precipitation. An understanding of regional hydrologic regimes can provide insights into the selective environment fish experience and therefore illuminate a potential influence on population structure. These analyses are especially useful in areas where genetic, abundance, and life history data are not informative. For example winter hydrologic conditions, such as low flow and cold temperatures in high elevations, influence the intra-gravel environment and the success of overwintering of eggs and alevins (Blachut 1988), which could in turn affect spawn timing.

The TRT used a two-step process to identify hydrologic regions. First the team identified distinct groups of streams based on the overall hydrograph pattern observed at a sample of stream gauges. Second the team used a classification tree analysis to identify broad hydrologic regions across Puget Sound to describe hydrographs in areas where gauge data were not available. These are the two steps:

Identifying stream-flow patterns based on annual hydrograph—The TRT obtained time series of monthly mean discharge (cubic feet per second) at 52 USGS stream gauges located throughout Puget Sound from the Washington Department of Ecology (USGS 2005). The time series included 8–74 years of data, depending on the gauge. The USGS gauges included in this analysis had at least a 10-year period of record, little to no artificial regulation, and were located within or adjacent to Chinook salmon spawning habitat.

The log-transformed monthly means were averaged over all years for the gauge, producing an average annual hydrograph. The average hydrographs were treated as variables with 12 observations (one observation per month), and rank correlation coefficients between these variables were computed for all pairs of gauges. Using correlation coefficients to measure

similarity between gauges emphasizes the timing and relative magnitude of peak and low flows, ignoring differences in the total magnitude of flow. The correlation matrix was used in a UPGMA cluster analysis with $1 - r_s$ as the distance measure.

Identifying hydrologic regions using predictive models—Because gauge data were not available for all stream reaches where Chinook salmon are known to spawn, the TRT developed empirical models to predict hydrograph patterns using known, easily measured variables. The team chose average basin elevation, defined as the average elevation of all points upslope of a given point, and average annual precipitation as predictors for several reasons. First previous studies in Puget Sound (Beechie 1992, Amerman and Orsborn 1987) found predictive relationships between these variables and a variety of hydrologic characteristics. Measurements of elevation and precipitation were then easily obtained for the entire region. Because the models were fitted using data on gauge characteristics reported by the USGS, rather than geographic information system (GIS) data layers, three gauges were omitted from the analysis because elevation and precipitation measurements were not available.

The TRT developed models using a parametric version of classification tree analysis (Venables and Ripley 1994). Classification tree analysis predicts group membership based on known variables, enabling us to predict hydrograph patterns for all of Puget Sound based on patterns at a set of stream-flow gauges. These classification tree models use a recursive partitioning algorithm to construct a binary decision tree, similar to a taxonomic key, in which observations are classified into predefined categories (in this case the four hydrograph types—R, RS, SR, and S—identified in the previous subsection on stream-flow patterns) based on their scores on one or more predictor variables (elevation and precipitation). Data for mean basin elevation and mean annual precipitation were obtained for each USGS gauge from Williams et al. (1985).

In the classification tree analysis the observations in each tree node are partitioned into two daughter nodes by choosing the split along the range of a single predictor that maximizes the log-likelihood over all possible splits of all predictors, where the likelihood is based on a multinomial model for the frequencies of the categories (Venables and Ripley 1994). The splitting continues until a stopping criterion is reached (in this case nodes were not split when they contained two or fewer observations). The tree can then be "pruned" by sequentially eliminating terminal nodes and computing AIC for each nested subtree (Burnham and Anderson 1998, Venables and Ripley 1994). The subtree with the lowest AIC score is selected as the most parsimonious model for the data. Because the sample size was small relative to the number of estimated parameters in the fully fitted tree, the TRT used the small-sample correction AIC_c in addition to AIC (Burnham and Anderson 1998), and compared the results of pruning on the two criteria.

Based on those break points the TRT mapped the resulting hydrologic regions using GIS analysis. The team used 30-m digital elevation model data from USGS to calculate mean basin elevation across Puget Sound. We combined the mean basin elevation data with mean annual precipitation data for 1961–1990 (Daly and Taylor 1998) to produce a hydroregion map.

Results

Identifying stream-flow patterns based on annual hydrographs—Hydrographs of mean monthly flow showed three basic patterns:

1. A rainfall-dominated pattern (hereafter R) with a winter peak and low flows in August–September (e.g., Issaquah Creek).
2. A snowmelt-dominated pattern (S) with a peak in May–July and low flows in late winter or early spring (e.g., Suiattle River).
3. An intermediate pattern with both rainfall- and snowmelt-driven peaks and low flows typically in August–September (Figure A-7).

The intermediate category was further subdivided into streams (e.g., Duckabush River) whose highest peaks are driven by rainfall (RS) and those (e.g., White River) whose highest peaks are due to snowmelt (SR). This classification was supported by the UPGMA dendrogram (not shown), which showed four main clusters of streams based on hydrograph pattern.

Identifying hydrologic regions using predictive models—The classification tree analysis resulted in an AIC-selected classification tree with six terminal nodes. (The terminal nodes represent the predictive classification scheme defined by the tree, with predicted values equal to the most common category in the node.) This tree had an overall misclassification rate of 6/49. That is, the predicted hydrograph category was incorrect for six of the 49 gauges in the sample, whereas the tree with the lowest value of AIC_c had only two terminal nodes and an overall misclassification rate of 13/49. Because the AIC-selected tree seemed clearly overfitted, but the two-node, AIC_c-selected tree was not predicatively useful, the TRT chose a tree of intermediate complexity to use for prediction. This tree had five terminal nodes and an overall misclassification rate of 7/49 (Figure A-7). For this tree, delta (Δ)AIC = 0.5 and $\Delta AIC_c = 8.65$, where $\Delta AIC_i = AIC_i - \min\{AIC_j \text{ for all candidate models } j\}$. Thus it was not the most parsimonious model, but it represented a reasonable compromise between the two criteria.

In the final tree the discriminations among hydrograph types were based primarily on average basin elevation (Figure A-7). Streams with an average elevation of below 2,595 feet generally had type R hydrographs. Between 2,595 and 3,110 feet elevation, most streams were type RS. Streams between 3,110 and 4,285 feet elevation were generally type SR, as were streams higher than 4,285 feet that experience less than 101.5 inches of precipitation annually. Only streams higher than 4,285 feet with greater than 101.5 inches of precipitation were predicted to be type S. Figure A-8 shows the resulting four hydroregions mapped across Puget Sound, together with the SASSI Chinook salmon populations.

Comparisons of Stream Temperature among Puget Sound Chinook Salmon Spawning Areas

Methods

Time series of monthly temperature at 47 river and stream monitoring stations were obtained from the Washington Department of Ecology. The data consist of temperatures taken once to several times a month, for portions of the year only or for all months. The TRT conducted two analyses of stream temperature. First the team examined the pattern of stream

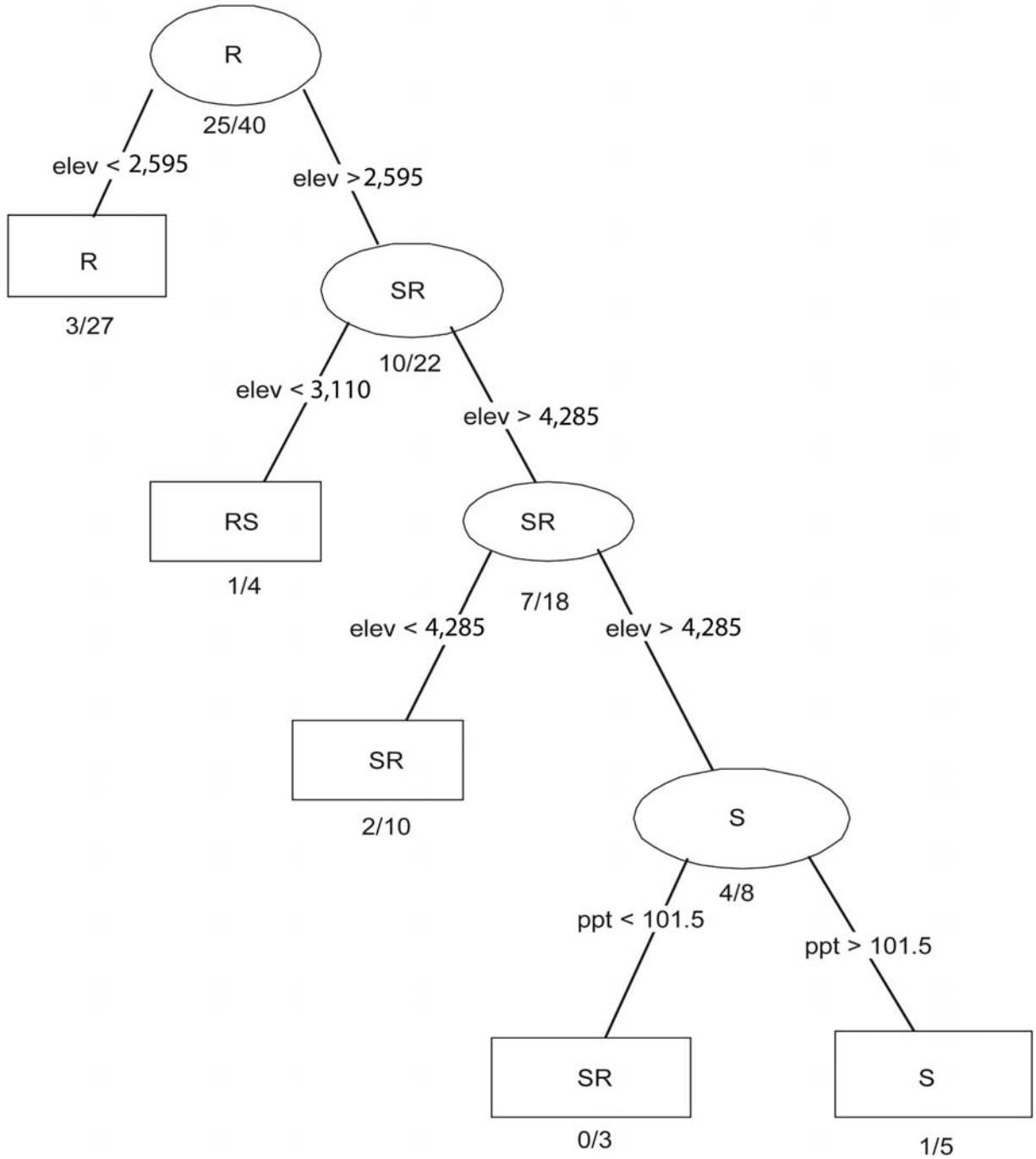

Figure A-7. Classification tree used to predict hydrograph type from average basin elevation (ft) and average annual precipitation (in). The hydrograph categories (R = rainfall dominated, RS = rainfall/snowmelt dominated, SR = snowmelt/rainfall dominated, S = snowmelt dominated) correspond to the clusters identified by UPGMA cluster analysis; typical examples of each category are shown. The category indicated on each terminal node (rectangles) is the predicted hydrograph type for the observations in that node. The fraction of observations in each node (ovals) that are incorrectly classified is indicated under the node.

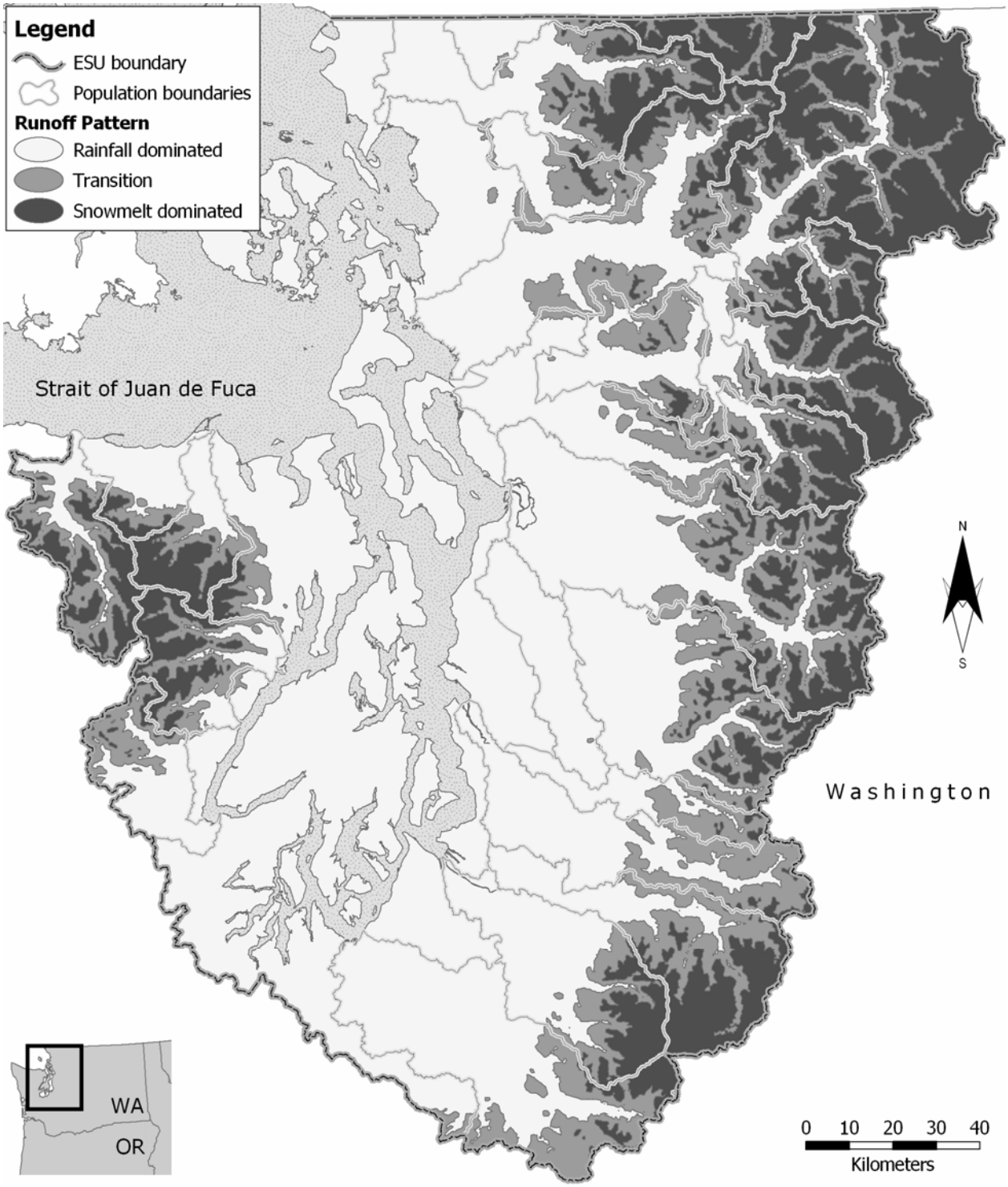

Figure A-8. Runoff-pattern regions in Puget Sound derived from mean basin elevation and mean annual precipitation using classification tree analysis.

temperatures throughout all months of the year (contingent on available data). For this analysis, we calculated monthly mean temperatures for each station across all years, producing an average annual stream temperature profile. Then similar to the stream hydrograph pattern analysis, the team treated mean annual temperature profiles as variables and calculated rank correlation coefficients for pairwise combinations of variables. We used the resulting correlation matrix in UPGMA cluster analysis.

In the second analysis the TRT evaluated differences between the average stream temperatures during the incubation period of the various Chinook populations. The team restricted data to temperatures during the three-month period following the median spawning date for each index area where Chinook are surveyed. Note that Chinook spawning surveys were not conducted in the vicinity of 11 of the 47 temperature monitoring stations. In these cases we used the median spawn date for the nearest index area to choose the beginning of the 3-month incubation period. We averaged stream temperatures over the 3-month incubation period for each station and across all years to produce an average monthly stream temperature. We calculated differences between average monthly stream temperatures for pairwise combinations of all stations. We used the resulting matrix for UPGMA cluster analysis.

Results

In the first analysis, annual stream temperature profiles, all stations demonstrated a similar pattern; temperatures are cool in the winter, rise to a peak in summer, and decline again during fall. The primary differences in temperature profiles were apparent in the incline and decline and range of temperatures. These differences, however, were not well resolved through UPGMA cluster analysis. The UPGMA dendrogram did not show any distinct stream groupings based on similar temperature profiles. Similarly differences in stream temperature during the Chinook salmon incubation period were not found with UPGMA cluster analysis. The resulting dendrogram (Figure A-9) did not show any notable groupings between temperature stations.

EPA Ecoregions

The U.S. Environmental Protection Agency (EPA) defines ecoregions based on a number of characteristics—geology, physiography, soils, land-use patterns, vegetation, climate, wildlife, and hydrology. The ecoregion definitions are based on scales over which the characteristics are relatively homogeneous. These ecoregions may partly describe differences in the selective environments that Chinook salmon experience throughout Puget Sound. The EPA defines ecoregions on a number of different spatial scales—the TRT summarized two of the EPA scales (or levels) for evaluating habitat characteristics and their possible relation to population structure. The EPA divides the North American continent into 78 regions at level III. Four main level III ecoregions occur within Puget Sound; North Cascades, Puget Lowland, Cascades, and the Coast Range. The EPA also developed finer scale level IV ecoregions for portions of the United States, including Puget Sound (Figures A-10 and A-11): 15 main level IV ecoregions occur within Puget Sound.

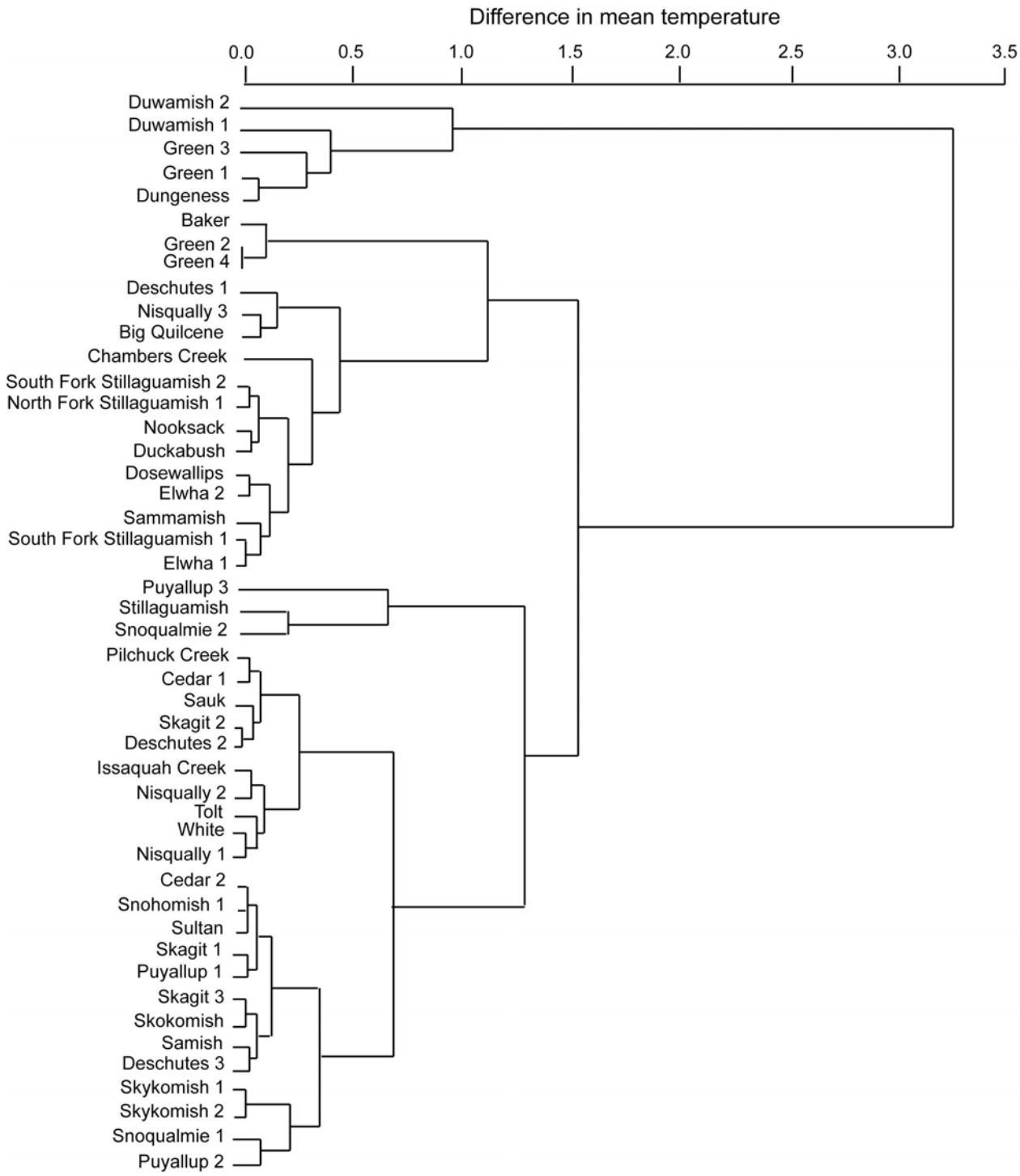

Figure A-9. Clustering of Puget Sound Chinook salmon spawning areas based on differences in mean temperature during Chinook salmon egg incubation. Mean incubation temperature in each area is based on an assumed three-month incubation period beginning on the median date of Chinook salmon spawning in the nearest index survey area. Absolute difference in mean temperature was the dissimilarity measure used in the UPGMA cluster analysis. Locations signify rivers unless otherwise noted.

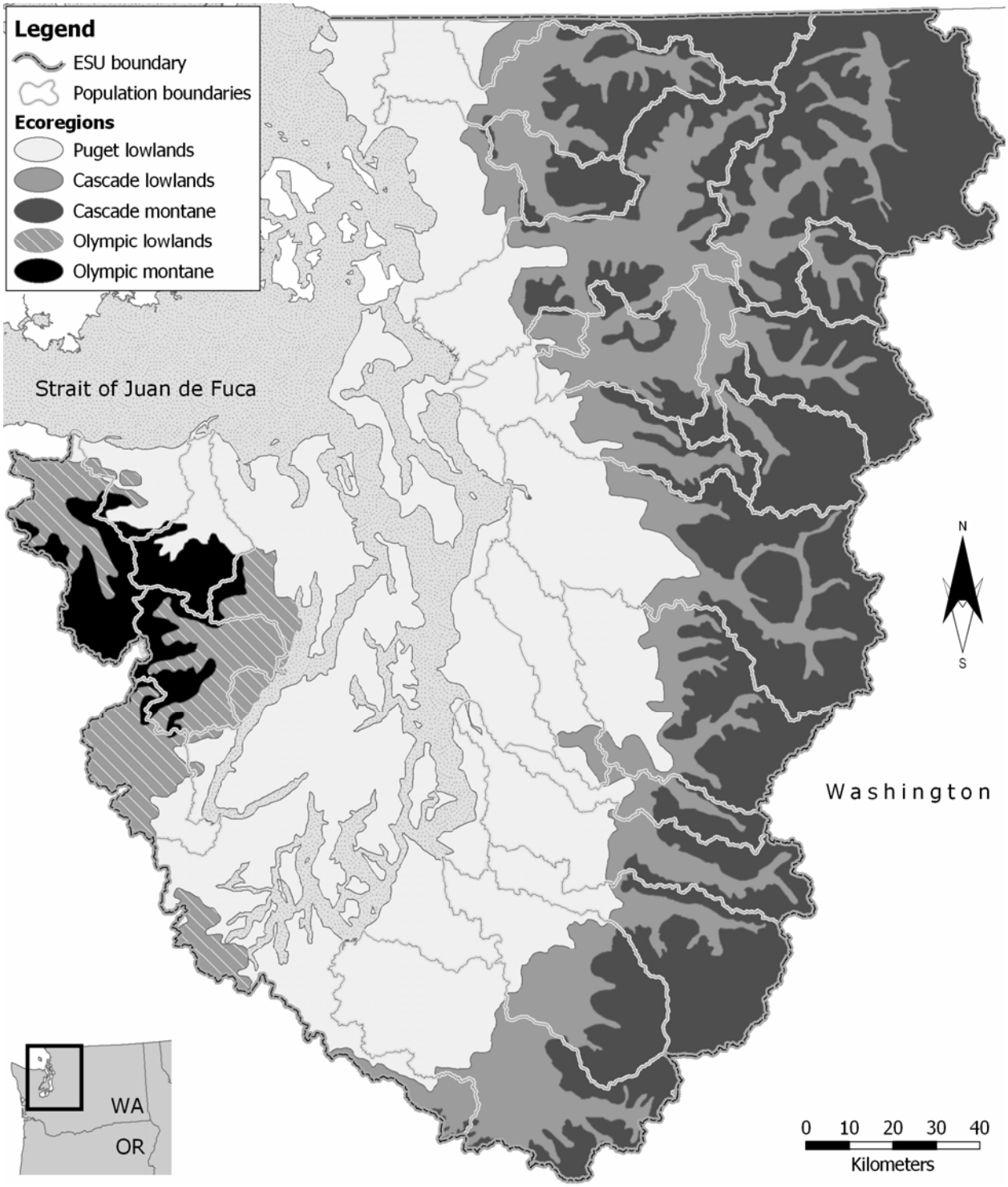

Figure A-10. U.S. Environmental Protection Agency level IV ecoregions in Puget Sound. Ecoregions represent areas of general similarity in an ecosystem, and in quality and quantity of environmental resources. Source: EPA 2006.

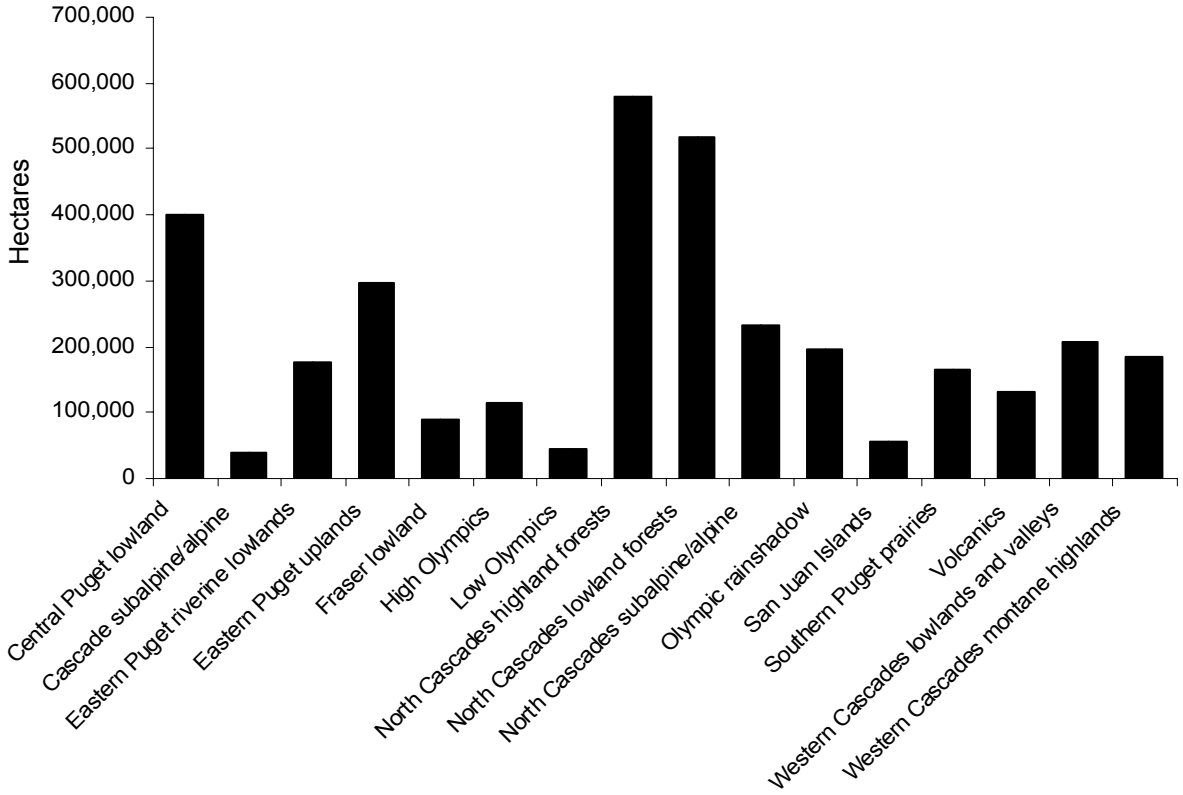

Figure A-11. Sum of areas (in hectares) for the level IV ecoregions occurring in the Puget Sound ESU (including areas outside of population boundaries and the islands). Source: EPA 2006.

Geology

The USGS developed geologic maps for various western states using 40 different classifications. Distinct geological characteristics may partly describe differences in the selective environments that Chinook salmon experience throughout Puget Sound. The Interior Columbia Basin Ecosystem Management Project digitized and combined these state maps into one map (ICBEMP 2006). The TRT simplified the 40 geologic classifications into 10 main categories: alluvium, calc-alkaline igneous, carbonate, glacial drift, gneiss, mafic igneous, meta-sandstone, phyllite and schist, sedimentary, and ultramafic (Figure A-12, Table A-3).

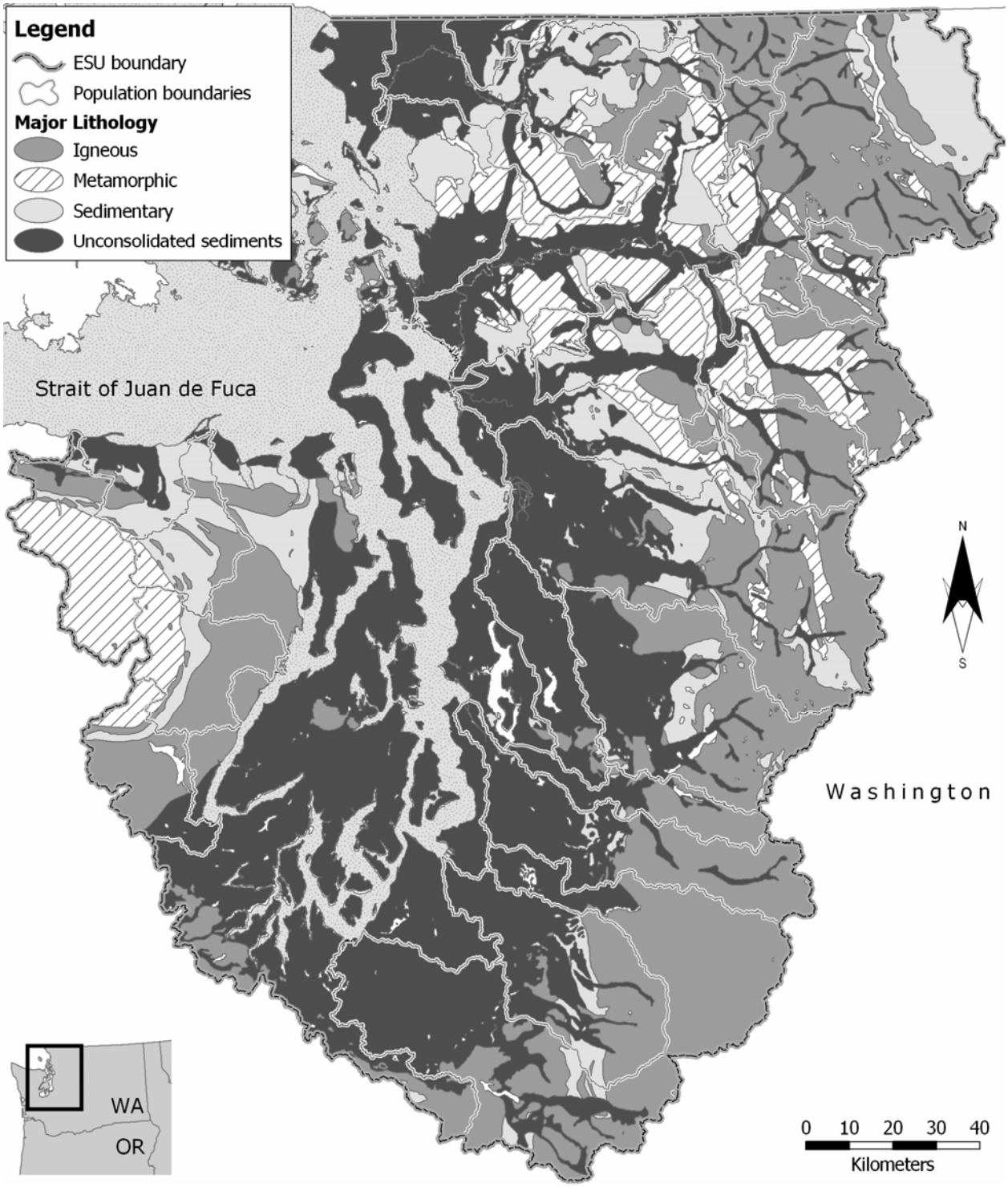

Figure A-12. Geology of Puget Sound region using 10 major lithologies from U.S. Geological Survey data. Source: ICBEMP 2006.

Table A-3. Sum of acres (in hectares) for the lithology classes occurring in the Puget Sound ESU (including areas outside of population boundaries and the islands). Source: ICBEMP 2006.

Broad geological type	**Lithology**	**ha**
Igneous		
	Calc-alkaline intrusive	283,265.31
	Calc-alkaline meta-volcanic	3,072.52
	Calc-alkaline volcanoclastic	395,386.76
	Granitic gneiss	166,816.93
	Mafic gneiss	2,963.09
	Mafic intrusive	6,141.56
	Mafic meta-volcanic	373.22
	Mafic volcanic flow	260,110.24
	Ultramafic	14,507.79
Igneous totals		1,132,637.40
Metamorphic		
	Interlayered meta-sedimentary	61,837.42
	Mafic schist and greenstone	36,196.50
	Meta-sandstone	200,468.04
	Meta-sedimentary phyllite and schist	112,879.32
Metamorphic totals		411,381.29
Sedimentary		
	Carbonate	5,211.31
	Conglomerate	19,121.28
	Sandstone	302,058.78
	Siltstone	108,088.38
Sedimentary totals		434,479.75
Unconsolidated sediments		
	Alluvium	405,755.29
	Glacial drift	1,009,597.13
	Landslide	13,604.26
Unconsolidated sediments totals		1,428,956.69
Total ha in Puget Sound ESU region		3,407,455.14

Appendix B: Data Tables

Appendix B includes results from data analyses conducted as part of the Technical Recovery Team's (TRT's) efforts to identify demographically independent populations of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound. Not all data were explicitly considered by the TRT for each indicator—they are included in this technical memorandum for completeness and to spur collection of additional data. The data are summarized in a matrix format for each watershed. Values in each cell represent some measure of distance or difference between the two sites being considered. Methods for calculating differences between sites for each data type are described in the body of this technical memorandum or in this appendix. The tables in Appendix B are:

- B-1—Estimates of theta (θ) and Nm
- B-2—Estimates of time since divergence between sites
- B-3—Cavalli-Sforza and Edwards' chord distance
- B-4—Nei's genetic distance
- B-5—P values from pairwise G-tests for heterogeneity in allele frequencies at 29 loci
- B-6—Absolute differences in the overall mean of yearly weighted mean spawning dates
- B-7—Dissimilarity matrix for smolt-spawner age distributions
- B-8—Absolute differences in mean spawner length of Puget Sound Chinook salmon
- B-9—Correlation coefficients on residuals from autoregressive trend model: product-moment correlations and Spearman's rank correlations
- B-10—Correlation matrix for mean monthly discharge at USGS stream gauges in Puget Sound
- B-11—Absolute difference in mean temperature during incubation for Chinook salmon in Puget Sound

Table B-1 Estimates of θ (above dashes) and Nm (below dashes). There is no comparison for the Strait of Juan de Fuca due to a lack of data. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Nooksack River basin

	South Fork Nooksack	North Fork Nooksack
South Fork Nooksack	—	0.024
North Fork Nooksack	10.321	—

Skagit River basin

	Lower Skagit	Upper Skagit	Lower Sauk	Upper Sauk	Suiattle	Cascade
Lower Skagit	—	0.016	0.157	0.013	0.025	0.089
Upper Skagit	15.605	—	0.111	0.015	0.046	0.110
Lower Sauk	1.342	2.011	—	0.091	0.237	0.376
Upper Sauk	19.076	15.942	2.499	—	0.057	0.145
Suiattle	9.899	5.207	0.807	4.157	—	0.028
Cascade	2.558	2.031	0.416	1.477	8.635	—

Stillaguamish River basin

	North Fork Stillaguamish	South Fork Stillaguamish
North Fork Stillaguamish	—	0.051
South Fork Stillaguamish	4.679	—

Snohomish River basin

	Skykomish	Sultan	Wallace	Bridal Veil Creek	Snoqualmie
Skykomish	—	0.012	0.003	0.000	0.007
Sultan	19.999	—	0.008	0.010	0.013
Wallace	82.641	30.216	—	0.000	0.005
Bridal Veil Creek	–753.262	23.712	–521.083	—	0.006
Snoqualmie	35.317	19.582	52.084	40.707	—

Table B-1 continued. Estimates of θ (above dashes) and Nm (below dashes). There is no comparison for the Strait of Juan de Fuca due to a lack of data. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Lake Washington

	Cedar	Sammamish	Issaquah Creek
Cedar	—	0.008	0.012
Sammamish	32.520	—	0.012
Issaquah Creek	21.328	20.488	—

South Puget Sound

	Duwamish/Green	Newaukum Creek	Puyallup	White	Nisqually	Deschutes
Duwamish/Green	—		0.004	0.024	0.005	0.001
Newaukum Creek	–295.061	—	0.007	0.021	0.002	0.002
Puyallup	59.688	36.151	—	0.019	0.016	0.008
White	10.009	11.559	12.663	—	0.019	0.026
Nisqually	50.275	135.916	15.223	13.156	—	0.012
Deschutes	416.417	103.787	29.424	9.524	20.160	—

Hood Canal

	Skokomish	Hamma Hamma
Skokomish	—	0.012
Hamma Hamma	20.935	—

Table B-2. Estimates of time since divergence between sites (*t*, in generations). There are no comparisons for Lake Washington, Hood Canal, or the Strait of Juan de Fuca due to a lack of data. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Nooksack River basin

	South Fork Nooksack	North Fork Nooksack
South Fork Nooksack	—	
North Fork Nooksack	7.10	—

Skagit River basin

	Lower Skagit	Upper Skagit	Lower Sauk	Upper Sauk	Suiattle	Cascade
Lower Skagit	—					
Upper Skagit	98.40	—				
Lower Sauk	324.80	274.30	—			
Upper Sauk	17.90	24.70	96.00	—		
Suiattle	41.90	94.40	313.40	55.00	—	
Cascade	67.30	90.10	285.10	84.40	16.60	—

Stillaguamish River basin

	North Fork Stillaguamish	South Fork Stillaguamish
North Fork Stillaguamish	—	
South Fork Stillaguamish	25.70	—

Snohomish River basin

	Skykomish	Wallace	Bridal Veil Creek	Snoqualmie
Skykomish	—			
Wallace	5.10	—		
Bridal Veil Creek	–0.60	–0.60	—	
Snoqualmie	19.30	7.20	10.30	—

Table B-2 continued. Estimates of time since divergence between sites (*t*, in generations). There are no comparisons for Lake Washington, Hood Canal, or the Strait of Juan de Fuca due to a lack of data. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

South Puget Sound				
	Duwamish/Green	Puyallup	White	Nisqually
Duwamish/Green	—			
Puyallup	19.90	—		
White			—	
Nisqually	7.20	20.40		—

Table B-3. Cavalli-Sforza and Edwards' chord distance. There is no comparison for the Strait of Juan de Fuca due to a lack of data. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Nooksack River basin

	South Fork Nooksack	North Fork Nooksack
South Fork Nooksack	—	
North Fork Nooksack	0.0748	—

Skagit River basin

	Lower Skagit	Upper Skagit	Lower Sauk	Upper Sauk	Suiattle	Cascade
Lower Skagit	—					
Upper Skagit	0.0382	—				
Lower Sauk	0.0573	0.0514	—			
Upper Sauk	0.0528	0.0385	0.0560	—		
Suiattle	0.0523	0.0317	0.0543	0.0418	—	
Cascade	0.0575	0.0439	0.0669	0.0491	0.0439	—

Stillaguamish River basin

	North Fork Stillaguamish	South Fork Stillaguamish
North Fork Stillaguamish	—	
South Fork Stillaguamish	0.0713	—

Snohomish River basin

	Skykomish	Sultan	Wallace	Bridal Veil Creek	Snoqualmie
Skykomish	—				
Sultan	0.0518	—			
Wallace	0.0418	0.0451	—		
Bridal Veil Creek	0.0433	0.0513	0.0437	—	
Snoqualmie	0.0486	0.0566	0.0536	0.0573	—

Table B-3 continued. Cavalli-Sforza and Edwards' chord distance. There is no comparison for the Strait of Juan de Fuca due to a lack of data. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Lake Washington

	Cedar	Sammamish	Issaquah Creek
Cedar	—		
Sammamish	0.0573	—	
Issaquah Creek	0.0472	0.0478	—

South Puget Sound

	Duwamish/Green	Newaukum Creek	Puyallup	White	Nisqually	Deschutes
Duwamish/Green	—					
Newaukum Creek	0.0244	—				
Puyallup	0.0394	0.0461	—			
White	0.0511	0.0531	0.0614	—		
Nisqually	0.0533	0.0499	0.0627	0.0677	—	
Deschutes	0.0356	0.0361	0.0480	0.0595	0.0596	—

Hood Canal

	Skokomish	Hamma Hamma
Skokomish	—	
Hamma Hamma	0.0488	—

Table B-4. Nei's (1978) genetic distance. There are no comparisons for Hood Canal or the Strait of Juan de Fuca due to a lack of data. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Nooksack River basin

	South Fork Nooksack	North Fork Nooksack
South Fork Nooksack	—	
North Fork Nooksack	0.003	—

Skagit River basin

	Lower Skagit	Upper Skagit	Lower Sauk	Upper Sauk	Suiattle	Cascade
Lower Skagit	—					
Upper Skagit	0.0007	—				
Lower Sauk	0.0005	0.0002	—			
Upper Sauk	0.0009	0.0007	0.0004	—		
Suiattle	0.0016	0.0006	0.0009	0.0007	—	
Cascade	0.0012	0.0004	0.0011	0.0008	0.0009	—

Stillaguamish River basin

	North Fork Stillaguamish	South Fork Stillaguamish
North Fork Stillaguamish	—	
South Fork Stillaguamish	0.0043	—

Snohomish River basin

	Skykomish	Sultan	Wallace	Bridal Veil Creek	Snoqualmie
Skykomish	—				
Sultan	0.0018	—			
Wallace	0.0000	0.0010	—		
Bridal Veil Creek	0.0000	0.0018	0.0000	—	
Snoqualmie	0.0008	0.0024	0.0009	0.0015	—

Table B-4 continued. Nei's (1978) genetic distance. There are no comparisons for Hood Canal or the Strait of Juan de Fuca due to a lack of data. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Lake Washington

	Cedar	Sammamish	Issaquah Creek
Cedar	—		
Sammamish	0.0013	—	
Issaquah Creek	0.0007	0.0008	—

South Puget Sound

	Duwamish/Green	Newaukum Creek	Puyallup	White	Nisqually	Deschutes
Duwamish/Green	—					
Newaukum Creek	0.0000	—				
Puyallup	0.0005	0.0007	—			
White	0.0010	0.0008	0.0008	—		
Nisqually	0.0004	0.0000	0.0010	0.0015	—	
Deschutes	0.0002	0.0004	0.0003	0.0014	0.0007	—

Table B-5. P values from pairwise G-tests for heterogeneity in allele frequencies at 29 loci. There is no comparison for the Strait of Juan de Fuca due to a lack of data. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Nooksack River basin

	South Fork Nooksack	North Fork Nooksack
South Fork Nooksack	—	
North Fork Nooksack	0.0000	—

Skagit River basin

	Lower Skagit	Upper Skagit	Lower Sauk	Upper Sauk	Suiattle	Cascade
Lower Skagit	—					
Upper Skagit	0.0086	—				
Lower Sauk	0.0006	0.0042	—			
Upper Sauk	0.0000	0.0032	0.0009	—		
Suiattle	0.0000	0.0000	0.0000	0.0000	—	
Cascade	0.0000	0.0043	0.0000	0.0011	0.0002	—

Stillaguamish River basin

	North Fork Stillaguamish	South Fork Stillaguamish
North Fork Stillaguamish	—	
South Fork Stillaguamish	0.0000	—

Snohomish River basin

	Skykomish	Sultan	Wallace	Bridal Veil Creek	Snoqualmie
Skykomish	—				
Sultan	0.0001	—			
Wallace	0.2673	0.0273	—		
Bridal Veil Creek	0.2276	0.0011	0.3247	—	
Snoqualmie	0.0009	0.0000	0.0002	0.0000	—

Table B-5 continued. P values from pairwise G-tests for heterogeneity in allele frequencies at 29 loci. There is no comparison for the Strait of Juan de Fuca due to a lack of data. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Lake Washington

	Cedar	Sammamish	Issaquah Creek
Cedar	—		
Sammamish	0.0000	—	
Issaquah Creek	0.0029	0.0384	—

South Puget Sound

	Duwamish/Green	Newaukum Creek	Puyallup	White	Nisqually	Deschutes
Duwamish/Green	—					
Newaukum Creek	0.6926	—				
Puyallup	0.0111	0.0013	—			
White	0.0000	0.0000	0.0000	—		
Nisqually	0.0071	0.0263	0.0006	0.0000	—	
Deschutes	0.1283	0.1593	0.0073	0.0000	0.0013	—

Hood Canal

	Skokomish	Hamma Hamma
Skokomish	—	
Hamma Hamma	0.1359	—

Table B-6. Absolute differences (d) in the overall mean of yearly weighted mean spawning dates. Bold = significant differences in two-sample t-tests using a basinwide Bonferroni-adjusted alpha level. Italics = no test could be performed because fewer than three annual means were available. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Nooksack River basin

				North Fork Nooksack	
	Nooksack	South Fork Nooksack	Middle Fork Nooksack	Kendall Creek	Canyon Creek
Nooksack	—				
South Fork Nooksack	9.20	—			
Middle Fork Nooksack	*11.10*	*1.90*	—		
North Fork Nooksack					
Kendall Creek	**17.20**	8.00	*6.10*	—	
Canyon Creek	4.40	13.60	*15.50*	**21.60**	—

Skagit River basin

					Suiattle							
	Lower Skagit	Upper Skagit	Lower Sauk	Upper Sauk	Big Creek	Tenas Creek	Buck Creek	Lime Creek	Sulphur Creek	Upper Skagit Illabot Creek	Cascade	Upper Skagit Bacon Creek
Lower Skagit	—											
Upper Skagit	*17.90*	—										
Lower Sauk	*16.00*	*1.90*	—									
Upper Sauk	*27.20*	*9.30*	*11.20*	—								
Suiattle												
Big Creek	*61.40*	**43.60**	*45.50*	*34.30*	—							
Tenas Creek	*65.00*	**47.10**	*49.00*	*37.80*	3.60	—						
Buck Creek	*56.30*	**38.40**	*40.30*	*29.10*	5.20	8.70	—					
Lime Creek	*55.70*	**37.90**	*39.80*	*28.60*	5.70	**9.30**	0.50	—				
Sulphur Creek	*53.30*	**35.40**	*37.30*	*26.10*	**8.20**	**11.70**	3.00	2.50	—			
Upper Skagit Illabot Creek	*15.60*	2.30	*0.40*	*11.60*	**45.90**	**49.40**	**40.70**	**40.20**	**37.70**	—		
Cascade	*24.90*	7.10	*8.90*	*2.30*	**36.50**	**40.10**	**31.40**	**30.80**	**28.30**	9.40	—	
Upper Skagit Bacon Creek	*21.70*	3.80	*5.70*	*5.50*	**39.70**	**43.30**	**34.60**	**34.00**	**31.60**	6.10	3.20	—

Table B-6 continued. Absolute differences (d) in the overall mean of yearly weighted mean spawning dates. Bold = significant differences in two-sample t-tests using a basin-wide Bonferroni-adjusted alpha level. Italics = no test could be performed because fewer than three annual means were available. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Stillaguamish River basin

	North Fork Stillaguamish	North Fork Stillaguamish Squire Creek	South Fork Stillaguamish Jim Creek
North Fork Stillaguamish	—		
North Fork Stillaguamish Squire Creek	5.30	—	
South Fork Stillaguamish Jim Creek	*20.90*	*15.60*	—

Snohomish River basin

	Snohomish	Sultan	Wallace	Bridal Veil Creek	Snoqualmie	Snoqualmie-Tolt
Snohomish	—					
Sultan	*9.30*	—				
Wallace	11.80	*2.50*	—			
Bridal Veil Creek	*2.70*	*6.60*	9.10	—		
Snoqualmie	*3.00*	*6.30*	*8.80*	*0.30*	—	
Snoqualmie-Tolt	*2.70*	*12.00*	*14.50*	*5.40*	*5.70*	—

Lake Washington

	North Lake Washington					
	Swamp Creek	North Creek	Big Bear Creek	Cottage Lake Creek	Issaquah-Holder creeks	Cedar
North Lake Washington						
Swamp Creek	—					
North Creek	*13.60*	—				
Big Bear Creek	*19.50*	*5.90*	—			
Cottage Lake Creek	*18.30*	*4.60*	*1.20*	—		
Issaquah-Holder creeks	*19.80*	*6.20*	*0.30*	*1.50*	—	
Cedar	*21.70*	*8.10*	*2.20*	*3.50*	*1.90*	—

Table B-6 continued. Absolute differences (d) in the overall mean of yearly weighted mean spawning dates. Bold = significant differences in two-sample t-tests using a basin-wide Bonferroni-adjusted alpha level. Italics = no test could be performed because fewer than three annual means were available. Locations are rivers unless otherwise noted. Data source: WDFW no date.

South Puget Sound

		Green			White				Puyallup		Nisqually			South Sound						
	Duwamish/Green	Crisp Creek	Newaukum Creek	Puyallup-Clarks Creek	Stuck	Boise Creek	Clearwater	Greenwater	Carbon	South Prairie Creek	Kapowsin Creek	Nisqually	Ohop Creek	Skookum Creek	Coulter Creek	Burley Creek	Blackjack Creek	Gorst Creek	Clear Creek	Dogfish Creek
Duwamish/Green	—																			
Green																				
Crisp Creek	*8.30*	—																		
Newaukum Creek	2.40	*5.80*	—																	
Puyallup-Clarks Creek	3.70	*12.00*	6.20	—																
White River																				
Stuck River	3.30	*4.90*	0.90	7.10	—															
Boise Creek	4.40	*3.90*	2.00	8.10	1.10	—														
Clearwater River	10.10	*1.90*	7.70	13.80	6.80	5.70	—													
Greenwater River	14.20	*6.00*	11.80	18.00	10.90	9.80	4.10	—												
Puyallup																				
Carbon River	*1.10*	*7.10*	*1.30*	*4.90*	*2.20*	*3.30*	*9.00*	*13.10*	—											
South Prairie Creek	5.20	*3.00*	2.80	8.90	1.90	0.80	4.90	9.00	*4.10*	—										
Nisqually River																				
Kapowsin Creek	1.40	*9.60*	3.80	2.30	4.70	5.80	11.50	15.60	*2.50*	6.60	—									
Nisqually	6.50	*14.70*	8.90	2.70	9.80	10.90	16.60	20.70	*7.60*	11.70	5.10	—								
Ohop Creek	9.10	*17.40*	11.60	5.40	12.50	13.60	19.30	23.40	*10.30*	14.40	7.80	2.70	—							
South Sound																				
Skookum Creek	10.90	*19.20*	13.30	7.20	14.20	15.30	21.00	25.10	*12.00*	**16.10**	9.50	4.40	1.70	—						
Coulter Creek	*2.10*	*10.30*	*4.50*	*1.70*	*5.40*	*6.50*	*12.20*	*16.30*	*3.20*	*7.30*	*0.70*	*4.40*	*7.10*	*8.80*	—					
Burley Creek	6.10	*14.40*	8.50	2.40	9.40	10.50	16.20	20.30	*7.20*	11.30	4.70	0.40	3.10	4.80	*4.00*	—				
Blackjack Creek	*21.70*	*30.00*	*24.20*	*18.00*	*25.10*	*26.10*	*31.80*	*36.00*	*22.90*	27.00	*20.40*	*15.30*	*12.60*	*10.80*	*19.70*	*15.60*	—			
Gorst Creek	0.60	*8.90*	3.10	3.10	4.00	5.00	10.70	14.90	*1.70*	5.80	0.80	5.90	8.50	10.30	*1.40*	5.50	*21.10*	—		
Clear Creek	*1.00*	*7.30*	*1.50*	*4.70*	*2.40*	*3.50*	*9.20*	*13.30*	*0.20*	*4.30*	*2.30*	*7.40*	*10.10*	*11.90*	*3.00*	*7.00*	*22.70*	*1.60*	—	
Dogfish Creek	4.70	*12.90*	7.10	0.90	8.00	9.10	14.80	18.90	*5.80*	9.90	3.30	1.80	4.50	6.20	*2.60*	1.40	*17.10*	4.00	*5.60*	—

Table B-6 continued. Absolute differences (d) in the overall mean of yearly weighted mean spawning dates. Bold = significant differences in two-sample t-tests using a basin-wide Bonferroni-adjusted alpha level. Italics = no test could be performed because fewer than three annual means were available. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Hood Canal

	Skokomish	South Fork Skokomish	Hamma Hamma	Duckabush	Dosewallips
Skokomish	—				
South Fork Skokomish	**17.8**	—			
Hamma Hamma	*8.9*	*9.0*	—		
Duckabush	*14.7*	*3.1*	*5.8*	—	
Dosewallips	*1.5*	*19.3*	*10.4*	16.2	—

Strait of Juan de Fuca

	Dungeness	Grey Wolf	Elwha
Dungeness	—		
Grey Wolf	**21.1**	—	
Elwha	4.1	25.2	—

Table B-7. Dissimilarity matrix (1 − % overlap) for smolt-spawner age distributions. Bold = significant differences in two-sample t-tests using a basin-wide Bonferroni-adjusted alpha level. There is no comparison for Lake Washington due to a lack of data. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Nooksack River basin

	South Fork Nooksack	North Fork Nooksack
South Fork Nooksack	—	
North Fork Nooksack	**0.32**	—

Skagit River basin

			Suiattle			Upper Skagit		
	Skagit	Sauk	Buck Creek	Lime Creek	Sulphur Creek	Illabot Creek	Cascade	Clark Creek
Skagit	—							
Sauk	**0.32**	—						
Suiattle								
Buck Creek	**0.38**	0.19	—					
Lime Creek	**0.48**	0.27	0.12	—				
Sulphur Creek	**0.69**	**0.46**	**0.31**	0.27	—			
Upper Skagit								
Illabot Creek	**0.45**	**0.42**	**0.36**	0.37	**0.48**	—		
Cascade	**0.40**	**0.27**	**0.18**	0.28	**0.37**	0.19	—	
Clark Creek	**0.64**	**0.59**	**0.52**	**0.54**	**0.48**	**0.26**	**0.38**	—

Stillaguamish River basin

	North Fork Stillaguamish	South Fork Stillaguamish
North Fork Stillaguamish	—	
South Fork Stillaguamish	**0.11**	—

Table B-7 continued. Dissimilarity matrix (1 − % overlap) for smolt-spawner age distributions. Bold = significant differences in two-sample t-tests using a basin-wide Bonferroni-adjusted alpha level. There is no comparison for Lake Washington due to a lack of data. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Snohomish River basin

	Snoqualmie	Tokul Creek	Wallace	May Creek
Snoqualmie	—			
Tokul Creek	0.33	—		
Wallace	**0.54**	**0.62**	—	
May Creek	**0.54**	**0.64**	**0.62**	—

South Puget Sound

		Green		Puyallup		
	Duwamish/Green	Big Soos Creek	Newaukum Creek	Voight Creek	South Prairie Creek	Deschutes
Duwamish/Green	—					
Green						
Big Soos Creek	**0.14**	—				
Newaukum Creek	**0.16**	**0.25**	—			
Puyallup						
Voight Creek	**0.18**	**0.09**	**0.32**	—		
South Prairie Creek	**0.28**	0.14	**0.31**	0.18	—	
Deschutes	**0.17**	**0.13**	**0.28**	**0.11**	0.22	—

Table B-7 continued. Dissimilarity matrix (1 − % overlap) for smolt-spawner age distributions. Bold = significant differences in two-sample t-tests using a basin-wide Bonferroni-adjusted alpha level. There is no comparison for Lake Washington due to a lack of data. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Hood Canal

	Skokomish	Skokomish Purdy Creek	Finch Creek
Skokomish	—		
Skokomish Purdy Creek	0.09	—	
Finch Creek	0.13	**0.19**	—

Strait of Juan de Fuca

	Dungeness	Elwha
Dungeness	—	
Elwha	**0.41**	—

Table B-8. Absolute differences in mean spawner length (post-orbital hypural length of age-4 fish, cm) of Puget Sound Chinook salmon. Sexes and broodyears for each stock are pooled. There are no comparisons for Nooksack River basin, Lake Washington, Hood Canal, or Strait of Juan de Fuca due to lack of data. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Skagit River basin

	Lower Skagit	Upper Skagit	Suiattle
Lower Skagit	—		
Upper Skagit	4.58	—	
Suiattle	4.61	9.19	—

Stillaguamish River basin

	North Fork Stillaguamish	South Fork Stillaguamish
North Fork Stillaguamish	—	
South Fork Stillaguamish	4.75	—

Snohomish River basin

	Skykomish	Sultan	Bridal Veil Creek	Snoqualmie
Skykomish	—			
Sultan	–1.53	—		
Bridal Veil Creek	8.85	10.37	—	
Snoqualmie	6.79	8.32	–2.05	—

South Puget Sound

	Green-Newaukum Creek	Puyallup-South Prairie Creek	White
Green-Newaukum Creek	—		
Puyallup-South Prairie Creek	0.91	—	
White	6.01	6.92	—

Table B-9. Correlation coefficients on residuals from autoregressive trend model: product-moment correlations below diagonal (1.00), Spearman's rank correlations above. Bold = significant differences in two-sample t-tests using a basin-wide Bonferroni-adjusted alpha level. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Nooksack River basin

	South Fork Nooksack	North Fork Nooksack
South Fork Nooksack	1.00	
North Fork Nooksack		1.00

Skagit River basin

	Lower Skagit	Upper Skagit	Lower Sauk	Upper Sauk	Suiattle	Cascade
Lower Skagit	1.00	0.26	**0.75**	0.27	0.11	
Upper Skagit	0.37	1.00	0.35	0.22	0.34	
Lower Sauk	**0.75**	0.41	1.00	0.30	0.21	
Upper Sauk	0.07	0.20	0.16	1.00	0.12	
Suiattle	0.21	0.38	0.28	0.07	1.00	
Cascade						1.00

Stillaguamish River basin

	North Fork Stillaguamish	South Fork Stillaguamish
North Fork Stillaguamish	1.00	0.35
South Fork Stillaguamish	0.51	1.00

Snohomish River basin

	Lower Snohomish	Skykomish	Sultan	Wallace	Bridal Veil Creek	Snoqualmie
Lower Snohomish	1.00			0.46		0.07
Skykomish		1.00				
Sultan			1.00			
Wallace	0.43			1.00		0.08
Bridal Veil Creek					1.00	
Snoqualmie	0.08			0.11		1.00

Table B-9 continued. Correlation coefficients on residuals from autoregressive trend model: product-moment correlations below diagonal (1.00), Spearman's rank correlations above. Bold = significant differences in two-sample t-tests using a basin-wide Bonferroni-adjusted alpha level. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Lake Washington

	Cedar	North Lake Washington	Sammamish	Issaquah Creek
Cedar	1.00	0.19		
North Lake Washington	**0.62**	1.00		
Sammamish			1.00	
Issaquah Creek				1.00

South Puget Sound

	Duwamish/ Green	Puyallup	White	Nisqually	Deschutes	Miscellaneous 13	Miscellaneous 13A	Miscellaneous 13B
Duwamish/Green	1.00	0.21	–0.02	0.29	–0.10	0.02	–0.19	0.22
Puyallup	0.25	1.00	0.08	0.41	0.65	0.18	–0.08	–0.22
White	0.01	0.13	1.00	–0.09	0.07	0.46	–0.10	0.08
Nisqually	0.17	0.27	–0.01	1.00	–0.10	0.31	–0.20	0.06
Deschutes	–0.11	0.73	0.09	–0.10	1.00	–0.03	–0.39	0.06
Miscellaneous 13	0.02	0.25	0.59	0.41	0.02	1.00	0.00	–0.03
Miscellaneous 13A	–0.20	0.02	–0.06	–0.11	–0.35	0.13	1.00	–0.20
Miscellaneous 13B	0.06	–0.14	0.04	0.06	0.15	–0.03	–0.13	1.00

Hood Canal

	Skokomish	Hamma Hamma	Duckabush	Dosewallips
Skokomish	1.00	0.18	0.09	–0.13
Hamma Hamma	–0.03	1.00	–0.33	0.67
Duckabush	0.03	–0.44	1.00	–0.02
Dosewallips	–0.09	0.76	–0.15	1.00

Table B-9 continued. Correlation coefficients on residuals from autoregressive trend model: product-moment correlations below diagonal (1.00), Spearman's rank correlations above. Bold = significant differences in two-sample t-tests using a basin-wide Bonferroni-adjusted alpha level. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Strait of Juan de Fuca		
	Dungeness	Elwha
Dungeness	1.00	–0.04
Elwha	–0.18	1.00

Table B-10. Correlation matrix (Spearman's rank correlations r) for mean monthly discharge at USGS stream gauges in Puget Sound. Bold = significant correlations using a basin-wide Bonferroni-adjusted alpha level. There is no correlation matrix for Strait of Juan de Fuca due to lack of data. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Nooksack River basin

		South Fork Nooksack	
	North Fork Nooksack	1	2
North Fork Nooksack	1.00		
South Fork Nooksack			
1	0.49	1.00	
2	0.52	**0.98**	1.00

Skagit River basin

	Upper Skagit		Upper Sauk			Suiattle		Lower Skagit	
	1	2	1	2	3	1	2	1	2
Upper Skagit									
1	1.00								
2	0.76	1.00							
Upper Sauk									
1	0.85	0.87	1.00						
2	**0.99**	0.71	0.78	1.00					
3	0.90	0.64	0.65	0.94	1.00				
Suiattle									
1	0.64	0.78	0.58	0.62	0.52	1.00			
2	0.83	0.94	0.87	0.82	0.80	0.66	1.00		
Lower Skagit									
1	0.04	–0.50	–0.34	0.12	0.23	–0.38	–0.27	1.00	
2	0.18	–0.35	–0.19	0.23	0.32	–0.36	–0.14	0.89	1.00

Table B-10 continued. Correlation matrix (Spearman's rank correlations r) for mean monthly discharge at USGS stream gauges in Puget Sound. Bold = significant correlations using a basin-wide Bonferroni-adjusted alpha level. There is no correlation matrix for Strait of Juan de Fuca due to lack of data. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Stillaguamish River basin

	South Fork Stillaguamish				North Fork Stillaguamish		Mainstem Stillaguamish
	1	2	3	4	1	2	Pilchuck Creek
South Fork Stillaguamish							
1	1.00						
2	0.85	1.00					
3	0.74	**0.96**	1.00				
4	**0.99**	0.89	0.78	1.00			
North Fork Stillaguamish							
1	0.72	0.92	0.87	0.74	1.00		
2	**0.94**	**0.97**	0.90	**0.97**	0.84	1.00	
Mainstem Stillaguamish							1.00
Pilchuck Creek	**0.97**	0.83	0.71	**0.98**	0.70	**0.93**	

Table B-10 continued. Correlation matrix (Spearman's rank correlations r) for mean monthly discharge at USGS stream gauges in Puget Sound. Bold = significant correlations using a basin-wide Bonferroni-adjusted alpha level. There is no correlation matrix for Strait of Juan de Fuca due to lack of data. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Snohomish River basin

	Skykomish						Snoqualmie				Lower Snohomish	
	South fork 1	South fork 2	North fork tributary	North fork	Skykomish	Woods Creek	Tokul Creek	Raging Creek	Tributary	North Fork Tolt	Pilchuck	Pilchuck tributaries
Skykomish												
South fork 1	1.00											
South fork 2	0.84	1.00										
North fork tributary	0.83	0.97	1.00									
North fork	0.83	0.97	1.00	1.00								
Skykomish	0.82	0.98	0.94	0.94	1.00							
Woods Creek	0.13	0.39	0.29	0.29	0.47	1.00						
Snoqualmie												
Tokul Creek	0.20	0.36	0.26	0.26	0.45	0.95	1.00					
Raging Creek	0.13	0.39	0.26	0.29	0.47	1.00	0.95	1.00				
Tributary	0.13	0.39	0.29	0.29	0.47	1.00	0.95	1.00	1.00			
North Fork Tolt	0.29	0.58	0.48	0.48	0.65	0.96	0.89	0.96	0.96	1.00		
Lower Snohomish												
Pilchuck	0.08	0.31	0.22	0.22	0.40	0.97	0.90	0.97	0.97	0.92	1.00	
Pilchuck tributaries	0.10	0.36	0.27	0.27	0.43	0.99	0.94	0.99	0.99	0.93	0.96	1.00

Table B-10 continued. Correlation matrix (Spearman's rank correlations r) for mean monthly discharge at USGS stream gauges in Puget Sound. Bold = significant correlations using a basin-wide Bonferroni-adjusted alpha level. There is no correlation matrix for Strait of Juan de Fuca due to lack of data. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Lake Washington

		North Lake Washington			
	Issaquah Creek	Bear Creek 1	Bear Creek 2	Tributary 1	Tributary 2
Issaquah Creek	1.00				
North Lake Washington					
Bear Creek 1	**0.96**	1.00			
Bear Creek 2	**0.96**	**0.98**	1.00		
Tributary 1	**0.97**	**0.97**	**0.99**	1.00	
Tributary 2	**0.98**	**0.98**	**0.98**	**0.99**	1.00

South Puget Sound

	Deschutes		Nisqually	South Sound	Puyallup			White	
	1	2	tributary	Clover Creek	Tributary 1	Puyallup	Tributary 2	White	Tributary
Deschutes									
1	1.00								
2	**0.99**	1.00							
Nisqually tributary	0.97	0.97	1.00						
South Sound Clover Creek	0.89	0.91	0.82	1.00					
Puyallup									
Tributary 1	0.97	0.97	**0.98**	0.89	1.00				
Puyallup	0.66	0.64	0.71	0.49	0.64	1.00			
Tributary 2	**0.97**	0.95	**0.97**	0.80	0.95	0.73	1.00		
White									
White	0.08	0.08	0.13	0.15	0.12	0.69	0.17	1.00	
Tributary	0.52	0.52	0.53	0.63	0.57	0.70	0.56	0.73	1.00

Table B-10 continued. Correlation matrix (Spearman's rank correlations r) for mean monthly discharge at USGS stream gauges in Puget Sound. Bold = significant correlations using a basin-wide Bonferroni-adjusted alpha level. There is no correlation matrix for Strait of Juan de Fuca due to lack of data. Locations signify rivers unless otherwise noted. Data source: WDFW no date.

Hood Canal

				South Fork Skokomish		
	Dosewallips	Duckabush	Hamma Hamma	1	2	Dewatto
Dosewallips	1.00					
Duckabush	0.84	1.00				
Hamma Hamma	0.78	**0.95**	1.00			
South Fork Skokomish						
1	0.27	0.61	0.71	1.00		
2	0.32	0.65	0.76	**0.98**	1.00	
Dewatto	0.29	0.59	0.72	**0.97**	**0.99**	1.00

Table B-11. Absolute difference in mean temperature (°C) during incubation for Chinook salmon in Puget Sound. Temperature was measured at USGS stations over variable time intervals. Annual incubation temperature is estimated as the mean temperature during the three-month period beginning on the median date of spawning in the nearest Chinook index survey area. Differences presented in the table are based on means over all years of available data. Bold = significant differences in two-sample t tests using a basin-wide Bonferroni-adjusted alpha level. Italics = no test could be performed because fewer than three annual means were available. Locations signify rivers unless otherwise noted. There is no chart for the Nooksack River basin due to lack of data. Data source: WDFW no date.

Skagit River basin

	Lower Skagit	Upper Skagit 1	Upper Skagit 2	Upper Skagit Baker	Lower Sauk
Lower Skagit	—				
Upper Skagit 1	0.40	—			
Upper Skagit 2	0.15	0.55	—		
Upper Skagit Baker	**2.31**	**1.91**	**2.46**	—	
Lower Sauk	0.35	0.05	0.50	**1.96**	—

Stillaguamish River basin

	Main stem	South fork 1	South fork 2	North fork 1
Main stem	—			
South fork 1	**2.32**	—		
South fork 2	2.05	0.27	—	
North fork 1	**2.08**	0.24	0.03	—

Table B-11 continued. Absolute difference in mean temperature (°C) during incubation for Chinook salmon in Puget Sound. Temperature was measured at USGS stations over variable time intervals. Annual incubation temperature is estimated as the mean temperature during the three-month period beginning on the median date of spawning in the nearest Chinook index survey area. Differences presented in the table are based on means over all years of available data. Bold = significant differences in two-sample t tests using a basin-wide Bonferroni-adjusted alpha level. Italics = no test could be performed because fewer than three annual means were available. Locations signify rivers unless otherwise noted. There is no chart for the Nooksack River basin due to lack of data. Data source: WDFW no date.

Snohomish River basin

			Skyomish		Snoqualmie			
	Snohomish	Lower Snohomish-Pilchuck	1	2	1	2	Sultan	Snoqualmie-Tolt
Snohomish	—							
Lower Snohomish-Pilchuck	0.38	—						
Skykomish								
1	0.50	0.88	—					
2	0.52	0.90	0.02	—				
Snoqualmie								
1	0.33	0.72	0.17	0.19	—			
2	**1.02**	**1.40**	0.52	0.50	0.69	—		
Sultan	*0.01*	*0.39*	*0.49*	*0.51*	*0.32*	*1.01*	—	
Snoqualmie-Tolt	*0.58*	*0.19*	*1.08*	*1.10*	*0.91*	*1.60*	*0.59*	—

Lake Washington

	Sammamish	Issaquah Creek	Cedar 1	Cedar 2
Sammamish	—			
Issaquah Creek	*0.84*	—		
Cedar 1	**1.24**	*0.40*	—	
Cedar 2	**1.62**	*0.78*	0.38	—

Table B-11 continued. Absolute difference in mean temperature (°C) during incubation for Chinook salmon in Puget Sound. Temperature was measured at USGS stations over variable time intervals. Annual incubation temperature is estimated as the mean temperature during the three-month period beginning on the median date of spawning in the nearest Chinook index survey area. Differences presented in the table are based on means over all years of available data. Bold = significant differences in two-sample t tests using a basin-wide Bonferroni-adjusted alpha level. Italics = no test could be performed because fewer than three annual means were available. Locations signify rivers unless otherwise noted. There is no chart for the Nooksack River basin due to lack of data. Data source: WDFW no date.

South Puget Sound

	Duwamish		Green				Puyallup				Nisqually			Chambers	Deschutes		
	1	2	1	Big Soos	2	3	1	2	3	White	1	2	3	Creek	1	2	3
Duwamish																	
1	—																
2	*0.67*	—															
Green																	
1	0.34	*1.01*	—														
Big Soos	1.46	*2.13*	1.12	—													
2	0.59	*1.26*	0.26	0.86	—												
3	1.46	*2.13*	1.12	0.00	0.86	—											
Puyallup																	
1	**3.92**	*4.59*	**3.58**	2.46	3.32	**2.46**	—										
2	**4.20**	*4.87*	**3.86**	2.74	**3.60**	**2.74**	0.28	—									
3	**5.53**	*6.20*	**5.19**	**4.07**	**4.94**	**4.07**	1.61	1.33	—								
White	**3.29**	*3.96*	**2.95**	1.83	**2.69**	**1.83**	0.63	0.91	**2.24**	—							
Nisqually																	
1	**3.30**	*3.98*	**2.97**	1.85	**2.71**	**1.85**	0.61	0.89	**2.23**	0.02	—						
2	**3.24**	*3.91*	**2.90**	1.78	2.64	1.78	0.68	0.96	2.29	0.05	0.07	—					
3	**2.94**	*3.61*	**2.60**	1.48	**2.35**	1.48	0.98	**1.26**	**2.59**	0.35	0.36	0.30	—				
Chambers Creek	**2.22**	*2.89*	**1.89**	0.77	1.63	0.76	1.69	**1.97**	**3.31**	1.06	1.08	1.01	0.72	—			
Deschutes																	
1	*3.06*	*3.73*	*2.72*	*1.60*	*2.46*	*1.60*	*0.86*	*1.14*	*2.47*	*0.23*	*0.25*	*0.18*	*0.12*	*0.84*	—		
2	**3.49**	*4.16*	**3.15**	2.03	**2.89**	**2.03**	0.43	0.71	**2.04**	0.20	0.18	0.25	0.55	1.27	*0.43*	—	
3	4.09	*4.76*	**3.75**	2.63	**3.50**	**2.63**	0.17	0.11	1.44	0.80	0.78	0.85	1.15	**1.87**	*1.03*	0.60	—

Table B-11 continued. Absolute difference in mean temperature (°C) during incubation for Chinook salmon in Puget Sound. Temperature was measured at USGS stations over variable time intervals. Annual incubation temperature is estimated as the mean temperature during the three-month period beginning on the median date of spawning in the nearest Chinook index survey area. Differences presented in the table are based on means over all years of available data. Bold = significant differences in two-sample t tests using a basin-wide Bonferroni-adjusted alpha level. Italics = no test could be performed because fewer than three annual means were available. Locations signify rivers unless otherwise noted. There is no chart for the Nooksack River basin due to lack of data. Data source: WDFW no date.

Hood Canal

	Skokomish	Duckabush	Dosewallips	Big Quilcene
Skokomish	—			
Duckabush	*1.44*	—		
Dosewallips	*1.53*	*0.09*	—	
Big Quilcene	*1.18*	*0.26*	*0.35*	—

Strait of Juan de Fuca

	Dungeness	Elwha 1	Elwha 2
Dungeness	—		
Elwha 1	*2.16*	—	
Elwha 2	*2.28*	0.12	—

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