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Determination of Independent Populations and Viability Criteria for the Hood Canal Summer Chum Salmon Evolutionarily Significant Unit

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Determination of Independent Populations and Viability Criteria for the Hood Canal Summer Chum Salmon Evolutionarily Significant Unit

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Executive Summary

The Puget Sound Technical Recovery Team identified two independent populations of summer chum salmon (*Oncorhynchus keta*) within the Hood Canal Summer Chum Salmon evolutionarily significant unit (ESU), which is listed as threatened under the U.S. Endangered Species Act. Our analysis was based on allozyme and microsatellite DNA variation, straying patterns, historical and present geographical distribution, and life history and ecological variations. Based on multiple lines of evidence, we concluded that the ESU contains two independent populations. The Strait of Juan de Fuca population spawns in rivers and streams entering the eastern Strait of Juan de Fuca and Admiralty Inlet. The Hood Canal population includes all spawning aggregations within the Hood Canal watershed. An analysis by state and tribal biologists in 2000 identified three extant stocks associated with the Strait of Juan de Fuca population and six extant stocks associated with Hood Canal population. However, we considered spawning aggregations to be independent populations only if the aggregations were isolated to such an extent that exchanges of individuals among the aggregations would not be expected to substantially affect the population dynamics or extinction risk of the different groups over a 100-year time frame.

Genetic analyses showed that genetic differences among spawning aggregations followed a pattern of isolation by distance, where the amount of exchange between spawning aggregations was greatest among streams that were geographically close; independence among spawning aggregations increased as geographical distances increased. Independent populations most likely occurred when adjacent spawning aggregations were separated by at least 30 km. Given historical distributions and ecological conditions that presumably sustained a persistent ESU, these distances separate the ESU into two groups: the Strait of Juan de Fuca and the Hood Canal aggregations. Additionally, our analyses indicate that stocks identified by earlier analyses—as well as spawning aggregations that have disappeared from some streams—are important for the viability of these populations through their effects on spatial structure and diversity.

For populations within salmon ESUs, the National Marine Fisheries Service defines viability as a 0.95 probability of population persistence over a 100-year time frame. Four main population parameters—abundance, productivity, spatial structure, and diversity—describe the attributes of a viable population. The abundance and productivity attributes are estimated through quantitative population models; spatial structure and diversity of viable populations are described more qualitatively.

Population viability has been determined using two methods: one assuming density-independent returns from spawners and the other using density-dependent functions. In order to have a less than 0.05 probability of extinction, the Strait of Juan de Fuca summer chum salmon population requires an escapement level of 12,500 fish, assuming density independence. Assuming density dependence and no harvest, a viable Strait of Juan de Fuca population would need escapements between 4,500 and 5,100 spawners, depending on the population's corresponding intrinsic productivity (α) and capacity (β), two parameters that describe a population viability curve using a Beverton-Holt stock recruit function. To support harvest, the population viability curves should have higher values of α and β than without harvest. Other solutions for a viable Strait of Juan de Fuca population are given in this report.

The Hood Canal summer chum salmon population would have a less than 0.05 probability of extinction if it had an escapement level of 24,700 fish, assuming density independence. Assuming density dependence and no harvest, a viable Hood Canal population would need escapements between 18,300 and 19,100 spawners, depending on assumptions about α and β of the population. To support harvest, the population viability curves should have higher values of α and β than without harvest. Other solutions for a viable Hood Canal summer chum population are given in this report.

To maintain diversity and spatial structure to support population viability, the Hood Canal and Strait of Juan de Fuca populations will have persistent spawning aggregations in each of the major ecological diversity groups delineated within their boundaries. In addition, spawning aggregations need to be distributed across the historical range of the population and at less than specified maximum distances. Such a distribution of subpopulations within each population will enhance diversity, increasing the chances that each population will be resilient to future environmental and anthropogenic changes.

Since the Hood Canal Summer Chum Salmon ESU has only two independent populations, both the Strait of Juan de Fuca population and the Hood Canal population would need to be viable to have a viable ESU at low risk of extinction. Viability is defined by all four viability parameters: abundance, productivity, spatial distribution (structure), and diversity.

Background

In the 1980s, the abundance of summer chum salmon (*Oncorhynchus keta*) returning to the Hood Canal and the Strait of Juan de Fuca regions of Puget Sound began to decline precipitously. Several spawning aggregations within these areas were extirpated during this period (Johnson et al. 1997). By 1992, state and tribal natural resource comanagers had increased protection for the fish and soon began to develop conservation strategies to restore summer chum salmon abundance and distribution. This planning led to completion of an implementation plan for recovery actions—the Summer Chum Salmon Conservation Initiative (WDFW and PNPTT 2000).

In the meantime, the federal government had listed the Hood Canal Summer Chum Salmon evolutionarily significant unit (ESU) as threatened with extinction under the U.S. Endangered Species Act (ESA) (NMFS 1999). To help guide the ESA recovery response for the listed ESU, the Puget Sound Technical Recovery Team (PSTRT) was charged with 1) identifying conservation units within the species that would be the focus of recovery activities under the ESA and 2) developing population and ESU viability criteria. This paper describes the conservation units (independent populations) and viability criteria for the Hood Canal Summer Chum Salmon ESU and populations identified by the PSTRT.

Identification of Independent Populations within the Hood Canal Summer Chum Salmon ESU

Introduction

Chum salmon have the widest natural geographic distribution of all salmon species, but are most abundant in North America from Kotzebue Sound in northwest Alaska to Tillamook Bay, Oregon (Salo 1991). The early spawning type or "summer" chum salmon have a much more limited distribution that extends from the Yukon River in the north to British Columbia and Washington in the south. In the Puget Sound region of Washington, some runs of chum salmon display this summer adult migratory timing. Entering freshwater as spawning adults in late summer, these salmon are uniquely adapted to exploit spawning habitat when river and stream levels are typically low and before most other populations and species of salmon return to spawn.

The conservation units for recovery identified by the PSTRT are based on the concept of a viable salmonid population (VSP), defined by McElhany et al. (2000) as:

> an independent population of any Pacific salmonid (genus *Oncorhynchus*) that has a negligible risk of extinction due to threats from demographic variation (random or directional), local environmental variation, and genetic diversity changes (random or directional) over a 100-year time frame.

In this context, the conservation units of interest are independent populations, which are spawning aggregations that are isolated to such an extent that exchanges of individuals among the aggregations do not substantially affect the population dynamics or extinction risk of the different groups (independent populations) over a 100-year time frame.

Demographic independence of salmon varies over time and geography. Identification of different stocks of salmon implies a degree of reproductive independence that is useful for management (Moulton 1939, Larkin 1972, Ricker 1972), but no single standard exists for all stocks. To avoid confusion, we use "stock" to refer to any geographical spawning aggregations used for management; "population" refers specifically to an aggregation meeting the independent population criteria; and "subpopulation" refers to unique aggregations of salmon that may be independent for periods less than 100 years or whose likelihood of persistence depends on limited exchanges with other such groups.

The definitive information needed to characterize the independence of different spawning aggregations is long-term migration rates between different aggregations and the demographic consequences of that migration. In practice, such information is rare. Consequently, we use different kinds of information that are proxies for understanding the degree of reproductive isolation between spawning aggregations within the Hood Canal Summer Chum Salmon ESU. Each type of information contributes to our understanding of population boundaries and structure, but none alone provides us complete confidence in our answer. In the following subsections, the PSTRT discusses these information types in order of the strength of inference about population structure, everything else being equal, beginning with the most powerful.

1. Geography. Reproductive independence will be defined in part by the spatial distribution of 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 exchange between groups (such as distance between streams) can provide a useful starting point from which to look more closely at the attributes of groups of fish within geographic areas, but will not generally support strong inferences at finer scales (e.g., distinguishing separate populations within a small river basin.) In addition, biogeographical characteristics and historical connections between river basins on geological time scales can also be informative in defining population boundaries.
2. Migration rates. The extent to which adults return to spawn in nonnatal streams (straying) will affect the degree of reproductive isolation and, therefore, demographic independence between groups. Straying estimates are the primary indicators available of the amount of connectivity between spawning aggregations. Stray rate estimates are particular to a group of fish and the season and streams in which they are made. Thus they provide useful information about straying under current conditions. Data are usually not available to obtain estimates of the magnitude of their variation over long time periods (e.g., 100 years).
3. Genetic attributes. In contrast to direct estimates of migration, indirect estimates based on the genetic differences among groups for neutral genetic traits can be used to estimate long-term average rates of straying. These should be interpreted with caution, because they may reflect recent anthropogenic sources of migration (e.g., hatchery practices or altered hydrological connections) or unknown extinctions and recolonizations, and they describe average straying rates at a single point in time when the rates may actually be changing. Adaptive genetic differences among groups of fish, as indicated by quantitative traits or molecular markers, are more difficult to document than neutral genetic traits, but they provide support for independence because they suggest that the groups have responded to local selection pressures or have maintained unique traits in spite of unknown amounts of straying.
4. Patterns of life history and phenotypic characteristics. Although most life history and phenotypic traits may be influenced by environmental variation, they may also reflect genetic variation, or genetic-by-environmental interactions. Phenotypic variation may be useful as a proxy for genetic variation. It may also indicate similarities or differences in the selective environments experienced by salmon in different streams that could lead to adaptive genetic differences.
5. Population dynamics. Abundance data can be used to explore the degree to which demographic trajectories of two groups of fish are independent of one another. All else being equal, the less correlated that time series of abundance is between two groups, the more likely it is that they are independent. Interpretation of these patterns can be confounded by correlated environmental characteristics that affect abundance. When trends in abundance of groups that are in close proximity (i.e., share similar

environmental influence) are not correlated, it may indicate demographic independence. The reverse is not always the case—when correlations in abundance between groups of fish are detected, more work is needed to rule out confounding sources of correlation.

6. Environmental and habitat characteristics. The biotic and abiotic characteristics of occupied salmonid habitat may also help identify potentially independent groups if these ecological characteristics are associated with different selective environments. The relative strength of inference for this kind of information is weak, because we generally do not know which environmental variables affect selection or whether those effects will be observed at the population level. Differences in adaptive traits or phenotypes may help support these inferences.

Methods and Results

Geographical Distribution

Previous Analyses

The freshwater and estuarine distribution of the Hood Canal Summer Chum Salmon ESU is restricted to the eastern Strait of Juan de Fuca, Admiralty Inlet, and Hood Canal marine subbasins of western Washington (Figure 1). In the eastern Strait of Juan de Fuca, state and tribal biologists assessing the status of summer chum salmon in the early 1990s identified small but persistent natural spawning aggregations in three streams (Salmon, Snow, and Jimmycomelately). Spawning also was noted in the Dungeness River, although the size of the aggregation was unknown. Adult salmon had been observed in Chimacum Creek through the early 1980s, but that spawning aggregation became extirpated near the middle 1980s. In Hood Canal, spawning aggregations persist in most of the major rivers draining the Olympic Mountains on the western edge of the canal, including Big and Little Quilcene, Dosewallips, Duckabush, and Hamma Hamma rivers and Lilliwaup Creek. On the eastern side of Hood Canal, persistent spawning was restricted to the Union River (WDFW and PNPTT 2000).

Historical information and habitat characteristics of other streams indicated summer chum salmon were once more broadly distributed within this region, especially in the streams draining the eastern shore of Hood Canal (Figure 1). Based on the historical size of the river and historical tribal fishing records, a major spawning aggregation may once have occurred in the Skokomish River. State and tribal biologists also identified recent extirpations in Big Beef Creek, Anderson Creek, Dewatto River, Tahuya River, and Finch Creek. Although state and tribal biologists could not identify the magnitude or frequency of spawning in other streams such as Seabeck, Stavis, and Big and Little Mission creeks, these smaller streams were likely historically used by summer chum salmon (WDFW and PNPTT 2000).

New Analyses—Methods and Results

To examine the potential change in spatial structure between historical spawning and extant spawning aggregations, we compared the distribution of geographical distances between all pairs of spawning aggregations. We measured pair-wise geographical distances (kilometers) as the shoreline distance between mouths of streams using the most direct passage over open

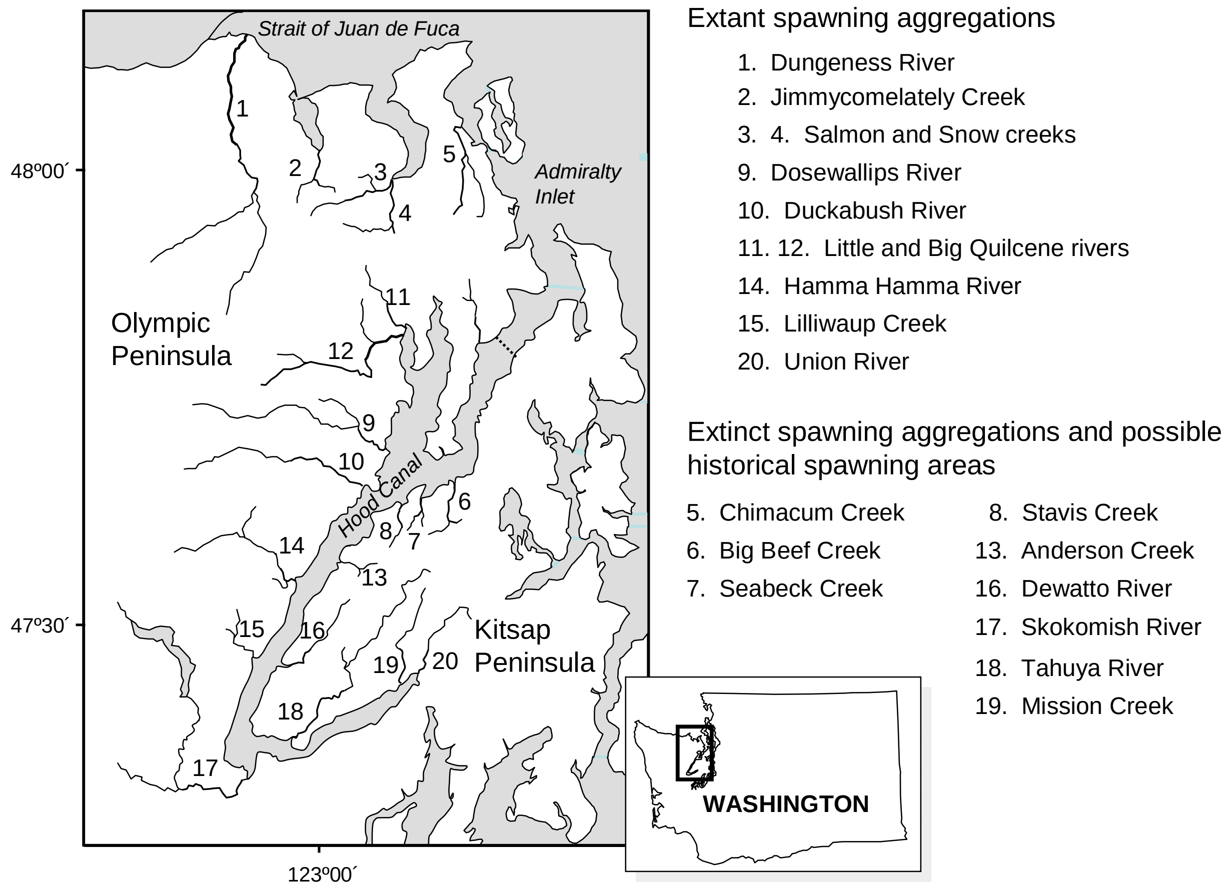

Figure 1. Extant and historical distribution of Hood Canal summer chum salmon. Recent recovery efforts are reintroducing summer chum to Chimacum Creek, Big Beef Creek, and Tahuya River, where they have been recently extirpated.

water at a scale of 1:200,000 using DeLorme Topo 4.0 digital maps. We tested for differences between historical and extant distributions using log-likelihood ratio tests (G-test, Sokal and Rolf 1995) after collapsing distance classes into short (0–80 km), moderate (80–160 km), and long (>160 km) distances.

Our results show that extant aggregations of summer chum salmon currently are more isolated by geographical distance than under historical conditions. Historically, most summer chum aggregations were less than 80 km apart with the greatest proportion separated by 20–40 km (Table 1, Figure 2). The mean and median distances separating historical spawning aggregations were 17 km and 13 km, respectively. Under historical conditions, the proportion of summer chum salmon populations separated by distances ranging from 80 to 220 km were less than those separated by 0–40 km, but the proportions were fairly evenly distributed among larger distance classes.

In contrast, most extant summer chum salmon spawning aggregations still occur within 20–40 km of each other, but extinctions of some spawning aggregations have led to a significant

Table 1. Geographical distance (km) between likely historical spawning locations of summer chum salmon in Strait of Juan de Fuca and Hood Canal areas. Shaded cells indicate distances that are less than 38 km apart, which is the most likely minimum distance over which independent populations occur. Locations are keyed to Figure 1.

Location	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
1. Dungeness R	0																			
2. Jimmycomelately Cr	19	0																		
3. Salmon Cr	52	33	0																	
4. Snow Cr	53	34	1	0																
5. Chimacum Cr	98	79	46	45	0															
6. Big Beef Cr	159	140	107	106	61	0														
7. Seabeck Cr	163	144	111	110	65	5	0													
8. Stavis Cr	166	147	114	113	68	12	7	0												
9. Dosewallips R	165	146	113	112	67	9	8	8	0											
10. Duckabush R	168	149	116	115	70	12	10	6	8	0										
11. Little Quilcene R	177	158	125	124	79	21	23	16	22	30	0									
12. Big Quilcene R	176	157	124	123	78	22	22	15	21	29	1	0								
13. Anderson Cr	180	161	128	127	82	26	21	14	18	10	30	29	0							
14. Hamma Hamma R	184	165	132	131	86	40	27	31	24	16	46	45	6	0						
15. Lilliwaup Cr	197	178	145	144	99	53	40	44	37	29	59	58	19	13	0					
16. Dewatto R	197	178	145	144	99	43	38	31	35	27	47	46	17	12	5	0				
17. Skokomish R	210	191	158	157	112	56	53	47	50	42	72	71	32	26	13	16	0			
18. Tahuya R	218	199	166	165	120	61	56	49	58	50	80	79	40	34	15	18	8	0		
19. Mission Cr	236	217	184	183	138	79	74	67	76	68	98	97	58	52	33	36	26	18	0	
20. Union R	239	220	187	186	141	82	77	70	79	71	101	100	61	55	36	39	29	21	3	0

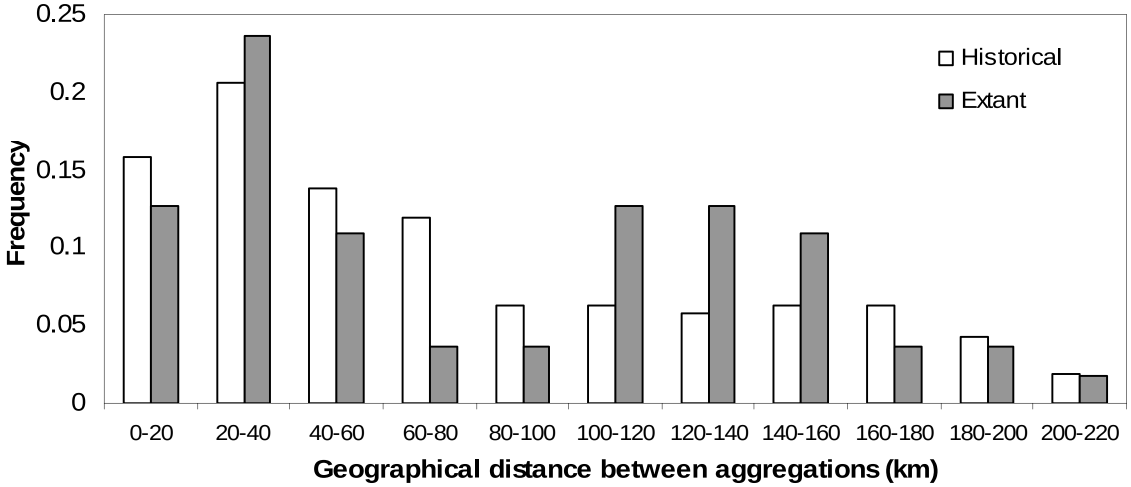

Figure 2. Geographical distribution of historical and extant spawning aggregations of summer chum salmon based on frequency of pair-wise distances.

increase in the proportion of aggregations isolated by 80–160 km (G = 39.58, df = 2, $p < 0.001$). Geographically, these extinctions occurred primarily on the Kitsap Peninsula (eastern Hood Canal), in the Admiralty Inlet catchment at the center of the geographic range of the ESU, and in the Skokomish River (Figure 1). This reduced by 60% the proportion of spawning aggregations separated by 60–100 km and doubled the proportion of spawning locations isolated by more than 100 km. Practically, this increased the geographical isolation between the remaining aggregations in the Strait of Juan de Fuca, northern Hood Canal, and Union River at the southern edge of the spawning distribution.

Migration

No information exists for straying of natural-origin adult summer chum salmon to nonnatal streams within the Hood Canal Summer Chum Salmon ESU. Since 1992, however, when state and tribal biologists began using artificial propagation to rebuild threatened stocks and reintroduce summer chum to historical areas, they have monitored the returns of uniquely marked salmon to streams draining into the Strait of Juan de Fuca and Hood Canal. Analysis of expanded recoveries of otolith-marked and adipose-clipped adult salmon in 2001 and 2002 (WDFW and PNPTT 2003) showed that straying was a nonlinear function of distance from the release location (Figure 3).

Most summer chum salmon (≈70–95%) returned to the stream from which they were released. Of those fish not returning to release locations, most returned to a location within 50 km of their release. This resulted in very little straying between the Hood Canal and the Strait of Juan de Fuca aggregations, although straying was greater from Strait of Juan de Fuca hatchery releases than from Hood Canal releases. Approximately 0.07% of releases in Hood Canal streams were recovered in Strait of Juan de Fuca streams, whereas approximately 1.5% of releases into Strait of Juan de Fuca streams were found in Hood Canal streams. Analysis of the earlier data (WDFW and PNPTT 2003) and recoveries from 2003 through 2005 (WDFW and

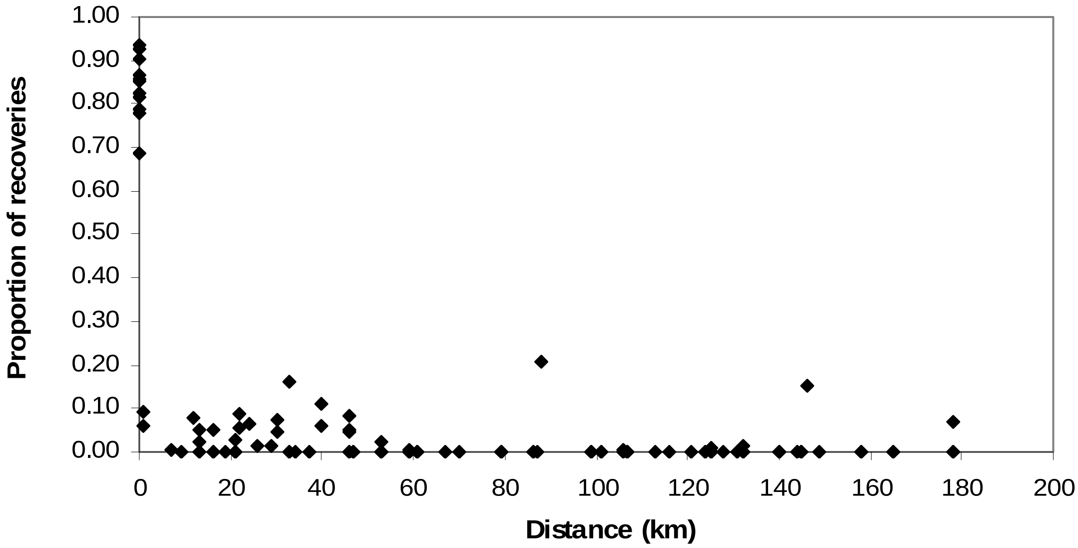

Figure 3. Relationship between proportions of marked hatchery summer chum salmon recovered as adults and distance from original release location.

PNPTC 2006) suggest that the locations to which summer chum salmon return remain constant from year to year, but the proportions vary.

Genetic Attributes

Previous Analyses

The lack of genetically distinct geographical groups of summer chum salmon has confounded past efforts to identify independent stocks. In 1993 state and tribal biologists identified four stocks of summer chum salmon based primarily on geographical location and a few samples with statistically different allozyme frequencies (WDFW and WWTIT 1994). Two stocks—Discovery Bay and Sequim Bay—were associated with streams flowing into the eastern Strait of Juan de Fuca. They identified two additional stocks in Hood Canal: a Union River stock and a west side Hood Canal stock that included the remaining spawning aggregations.

Using expanded allozyme data, Phelps et al. (1995) reexamined the genetic differences among chum salmon throughout Puget Sound. They documented major divergence of nine samples of summer chum salmon of Hood Canal and the Strait of Juan de Fuca from other aggregations of chum salmon. Within the summer chum salmon lineage, Phelps et al. (1995) suggested there were two major groups, a Strait of Juan de Fuca group and a Hood Canal group, based on significantly different allele frequencies. Discovery Bay and Sequim Bay stocks comprised the Strait of Juan de Fuca group. Within the Hood Canal group, they proposed three stocks: a Union River stock, which had significantly different allele frequencies from the western Hood Canal (Olympic Peninsula) stock, and an eastern Hood Canal (Kitsap Peninsula) stock, which they believed was distinct and independent because it had been extirpated when other stocks had not. Johnson et al. (1997) reanalyzed data from Phelps et al. (1995) and confirmed the divergence of summer chum salmon, which they designated an ESU (Waples 1991) under the

ESA. Although both studies detected allele frequency differences among summer chum salmon, cluster analyses did not show geographically distinct groups of spawning aggregations.

To provide the foundation for the Summer Chum Salmon Conservation Initiative, state and tribal comanagers identified nine extant stocks of summer chum salmon, seven recently extirpated stocks, and additional geographical areas where summer chum may have occurred (Figure 1) (WDFW and PNPTT 2000). The nine extant stocks were delineated based primarily on geographical separation of spawning aggregations and apparent allozyme frequency differences between some samples. These differences were defined based on pair-wise tests of allelic heterogeneity that were uncorrected for the increase in Type I error from multiple comparisons (see Kassler and Shaklee 2003).

Kassler and Shaklee (2003) expanded the number of samples and reanalyzed the pair-wise comparisons after correcting for multiple comparisons. They concluded the data showed two stocks in the eastern Strait of Juan de Fuca—Discovery Bay and Sequim Bay—and three stocks in Hood Canal associated with Union River, Lilliwaup Creek, and the remaining aggregations in western Hood Canal tributaries. Most recently, Small and Young (2003) analyzed variations at 18 microsatellite loci in a similar group of samples from the Hood Canal Summer Chum Salmon ESU. They found significant genotypic differences between Hood Canal region and Strait of Juan de Fuca region aggregations and among Union, Lilliwaup, and Strait of Juan de Fuca aggregations, but the remaining aggregations did not show genotypic differences. Union River, Discovery Bay, and Sequim Bay fish could be precisely assigned to their collection locations based on individual genotypes, but classification of fish from other locations had greater error.

These analyses provide only limited insight into demographic relationships of spawning aggregations of summer chum salmon. Analyses relying on pair-wise tests of allelic heterogeneity among different spawning aggregations showed some statistical differences in allele frequencies. *P*-values from pair-wise tests of allelic heterogeneity that WDFW used to infer stock structure were largely dependent on sample size and variability of the loci used and do not necessarily reflect demographic relationships among spawning aggregations. Cluster analyses, which group samples based on their genetic similarity, also failed to identify genetically discrete groups that might correspond to independent populations. Although nearly all dendrograms of genetic similarity in summer chum salmon showed a cluster formed by Sequim Bay aggregations, most displayed "chaining," a pattern where the dendrogram forms by successive additions of branches associated with individual aggregations rather than distinct clusters (Figure 4).

Interestingly, although Kassler and Shaklee (2003) did not comment on it, the differences in their data suggest a geographical pattern of isolation of subpopulations by geographical distance rather than geographical clustering of similar spawning aggregations. Although Kassler and Shaklee's (2003) cluster analysis did not show distinct differences within Hood Canal because of chaining, the most genetically divergent aggregation—the Union River—was geographically most distant. Ignoring the Little Quilcene sample, which was small and not statistically different from Quilcene Bay samples, subsequent divergence followed the same geographical pattern (Figure 4). Chaining in dendrograms often reflects an underlying linear

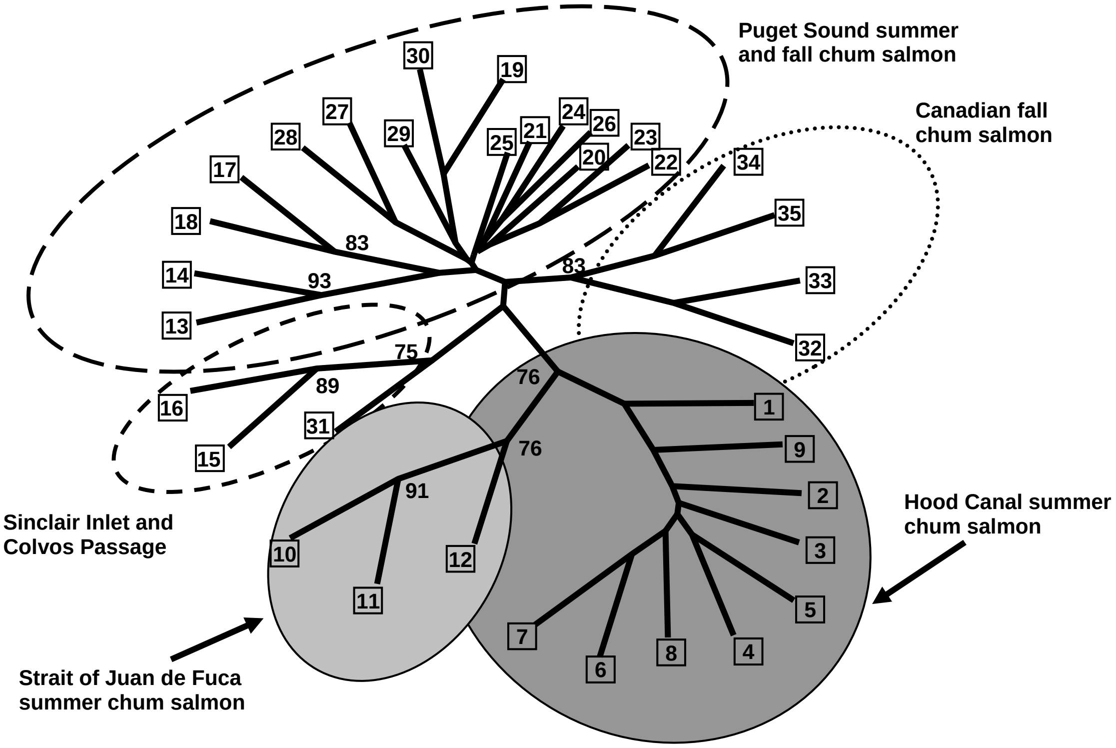

Figure 4. Relationship of 35 summer and fall chum salmon populations using Cavalli-Sforza and Edwards (1967) chord distance and neighbor-joining clustering (modified from Kassler and Shaklee 2003). Dendrogram shows chaining of Hood Canal summer chum salmon samples. Key to summer chum samples: 1 Union River, 2 Lilliwaup Creek, 3 Hamma Hamma River, 4 Duckabush River, 5 Dosewallips River, 6 Big Beef Creek (introduced from Quilcene National Fish Hatchery), 7 Quilcene Bay, 8 Quilcene National Fish Hatchery (introduced from Quilcene Bay), 9 Little Quilcene River, 10 Snow Creek, 11 Salmon Creek, and 12 Jimmycomelately Creek.

rather than hierarchical structure in the data, although it is also characteristic of clustering algorithms that use low levels of genetic similarity to define clusters (Dunn and Everitt 1982).

New Analyses—Methods

If little hierarchical structure exists among spawning aggregations of summer chum salmon from Hood Canal and Strait of Juan de Fuca streams, at what geographical scale do independent populations occur? Because there appeared to be few genetically discrete groups of summer chum associated with the major river systems, the PSTRT hypothesized that genetic exchange and independence might be related due to geographical proximity of many different subpopulations to each other, rather than due to homing to major river systems or environmental differences. When subpopulations occur geographically in line, for example, a one-dimensional stepping-stone pattern of straying (where most genetic exchange is between neighboring subpopulations) can lead to genetic differences between subpopulations that are several subpopulations apart, even though there are few or no differences between adjacent subpopulations. The stepping-stone process of migration leads to patterns of genetic isolation by distance that can be detected with empirical data (Wright 1943).

We examined allozyme and microsatellite DNA data of summer chum salmon for evidence of isolation by distance. Allozyme data were from 28 loci and 43 collections in streams within the Hood Canal Summer Chum Salmon ESU (Kassler and Shaklee 2003). Microsatellite DNA data were from Small and Young (2003). After finding no significant differences among years within sample locations using Bonferroni adjusted log-likelihood ratio tests, data from different years within streams were combined for subsequent analyses. Pair-wise *Fst* values were calculated using GENEPOP (Raymond and Rousset 1995). Migrants per generation, *Nm*, were calculated from *Fst* values, using $Nm = (1 - Fst)/4\ Fst$. *Nm* values for *Fst* near zero were arbitrarily set to 250 to avoid undefined or unrealistically high values. Geographical distances (km) were measured as the shoreline distance between mouths of streams using the most direct passage over open water at a scale of 1:200,000 using DeLorme Topo 4.0 digital maps (Table 1).

Under isolation by distance, independence between groups—as measured by estimates of genetically effective *Nm*—increases with increasing geographical distance. Genetic theory predicts that more than one migrant per generation can prevent substantial genetic divergence and that rates between 1 and 10 may be necessary to prevent extinction of fragmented populations (Mills and Allendorf 1996, Wang 2004). To statistically describe the relationship between genetic connectivity and geographic distance, Mantel tests for association between *Nm* and distance and reduced major axis regressions were performed using IBD 1.4 (Bohonak 2002). Regression confidence limits were constructed from 1,000 bootstrap regressions over all points.

No empirical analyses indicate the maximum rates of genetic exchange that we might expect to find between independent populations. To inform decisions about the geographical scale of independent populations formed by isolation by distance, we analyzed expert conclusions for Chinook salmon (*O. tshawytscha*) in Puget Sound where geneticists have identified independent populations based on genetic information as well as knowledge of migration rates, life history and phenotypic differences, population dynamics, and habitat differences. Chinook salmon in Puget Sound show evidence of isolation by distance and eight geneticists representing different institutions examined patterns of genetic differentiation among 21 spawning aggregations of Chinook salmon (Ruckelshaus et al. 2006). They independently scored 34 pair-wise comparisons for independence on a scale of +4 (very independent) to –4 (no independence).

Because *Nm* provides a genetic estimate of long-term, demographic exchange that is independent of species differences, we used the distribution of independence scores greater than one relative to the analysis of *Nm* to characterize scientific opinion about the largest rate of genetic exchange between independent populations. Under an isolation-by-distance relationship, this corresponds to the smallest spatial scale at which independent populations might occur, which would be conservative in protecting ESU population structure. To describe the uncertainty in the maximum *Nm*, we generated a mean and 95% confidence interval by randomly resampling a triangular distribution 1,000 times where the minimum of the distribution was the smallest *Nm* expert score that always reflected independence and the maximum was the largest *Nm* score associated with independence.

New Analyses—Results

We concluded that isolation by distance best explains the genetic structure in summer chum salmon. Using allozyme data collected from 1985 to 2001 from Kassler and Shaklee (2003) and microsatellite DNA data from Small and Young (2003), we found a strong relationship between *Nm* and geographical distance (Figure 5 and Figure 6). As geographical distances increased between aggregations, they exchanged fewer migrants. The isolation-by-distance relationships were indistinguishable between allozyme and microsatellite DNA data. Exchange of migrants ranged from approximately 250 per generation to 4 per generation over distances of 1 to 219 km. The greatest genetic exchange was between aggregations in the Hamma Hamma, Dosewallips, Duckabush, and Quilcene rivers of the west central Hood Canal region and between Discovery Bay (Salmon and Snow creeks) and Sequim Bay (Jimmycomelately Creek) aggregations in the Strait of Juan de Fuca.

An interesting feature of this relationship is the apparent clustering of most Strait of Juan de Fuca comparisons at greater distances and fewer migrants per generation (Figure 5). This kind of pattern sometimes suggests greater demographic isolation and more rapid genetic

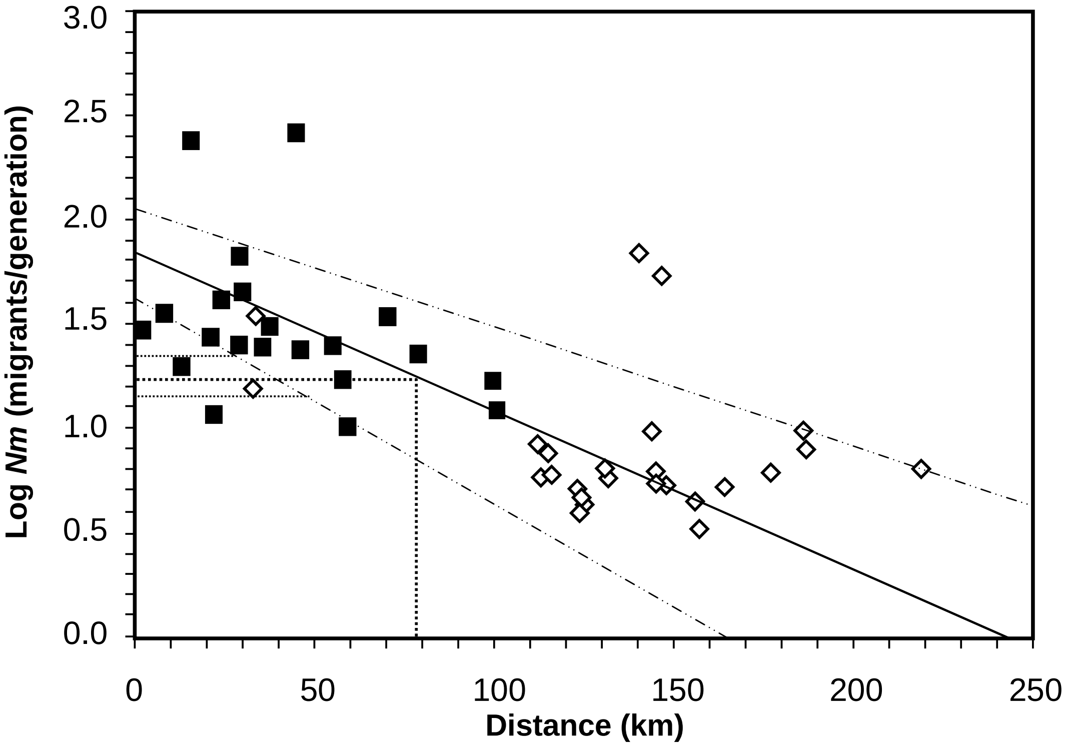

Figure 5. Relationship between *Nm* and distance based on allozyme data. Open diamonds include Strait of Juan de Fuca samples; solid squares represent Hood Canal samples. Mantel test indicates significant association between *Nm* and distance (Z = 3747.08, $p \leq 0.0000$). The regression line (solid line) using reduced major axis regression is log(*Nm*) = 1.85 – 0.0076 km. $R^2 = 0.60$. Dash-dotted lines show 95% confidence limits based on 1,000 bootstrap regressions over all points. Dotted lines show distribution of scientific opinion for maximum *Nm* indicating population independence; light dotted lines show 95% confidence limits, the heavy dotted line is the mean.

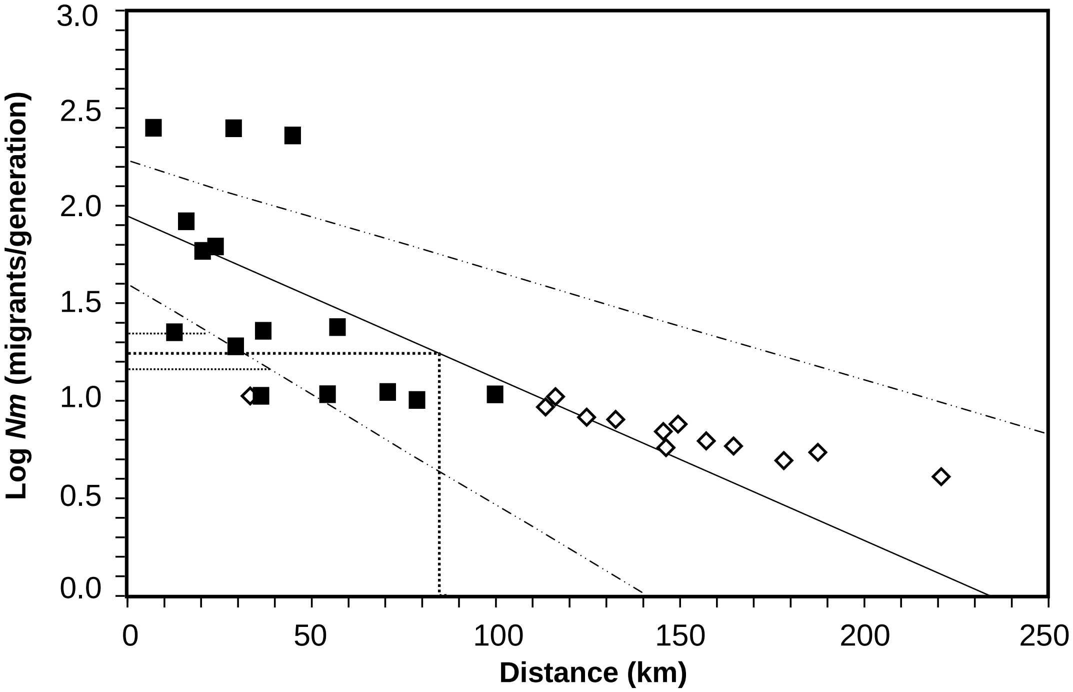

Figure 6. Relationship between *Nm* and distance based on microsatellite DNA data. Open diamonds include Strait of Juan de Fuca samples, solid squares represent Hood Canal samples. Mantel test indicates significant association between *Nm* and distance (Z = 2357.84, $p \leq 0.0000$). The regression line (solid line) using reduced major axis regression is log(*Nm*) = 1.96 – 0.0084km. $R^2 = 0.57$. Dash-dotted lines show 95% confidence limits based on 1,000 bootstrap regressions over all points. Dotted lines show distribution of scientific opinion for maximum *Nm* indicating population independence; light dotted lines show 95% confidence limits, the heavy dotted line is the mean.

differentiation than would be expected if there were equilibrium between gene flow and genetic drift (Slatkin 1993). In this case, however, the pattern appears to reflect an absence of sample comparisons between 60 and 100 km apart (Figure 5 and Figure 6), rather than a lack of gene flow–genetic drift equilibrium. Extirpation of summer chum salmon aggregations from streams along the northeastern Olympic Peninsula and the northwestern Kitsap Peninsula may explain this absence.

As noted, the effect of these extinctions was to increase geographical isolation of the Strait of Juan de Fuca aggregations from central Hood Canal aggregations and the Union River aggregation. This isolation would have increased genetic drift and promoted allele frequency differences, which were detected by earlier genetic studies, among these aggregations. Consequently, the observation that Strait of Juan de Fuca, central Hood Canal, Lilliwaup Creek, and Union River aggregations are evolving more or less independently may be an artifact of recent extinctions rather than a reflection of long-term, viable population structure.

The isolation-by-distance relationship we found in summer chum salmon suggests that the aggregations represent a single metapopulation. Figure 5 shows that the isolation-by-distance relationship for all Strait of Juan de Fuca comparisons including those at short distances (i.e., between Discovery Bay [Salmon and Snow creeks] and Sequim Bay [Jimmycomelately Creek] samples) is similar to the relationship for summer chum overall.

Historically, all summer chum salmon spawning aggregations may have been more connected by migration and gene flow occurring through stepping-stone spawning aggregations in streams such as Chimacum, Big Beef, Seabeck, and Stavis creeks in northern Hood Canal and the Skokomish, Dewatto, and Tahuya rivers in southern Hood Canal. The mean and median distances separating historical spawning aggregations, for example, were 17 km and 13 km, respectively. Under historical conditions, demographic isolation between Salmon and Snow creeks (Strait of Juan de Fuca) and Dosewallips River (Hood Canal) summer chum salmon may have occurred in three steps of approximately 40 km, which is typical of the isolation of the largest proportion of historical spawning aggregations, rather than one step of 112 km, which exists now (Table 1). Under stepping-stone migration, gene flow would have limited the genetic differentiation that otherwise would have occurred under greater geographical isolation. Geographically intermediate populations may also have been genetically intermediate because of the increased opportunity for gene flow, which would have limited the clustering observed in recent analyses.

Genetic Independence

When genetic differences among populations reflect isolation by distance with no clear geographical or genetic discontinuities, identifying discrete, independent populations is problematic. Although at some geographic distance, spawning aggregations may be genetically different at a level that suggests demographic independence between two pairs of aggregations, if the distance is much larger than that separating the two pairs, they may exist independently only because of intermediate aggregations that are not independent.

Based on an independent survey of geneticists asked to identify independent populations from measures of genetic differentiation, however, aggregations with $Nm = 15$ were always considered independent, aggregations with Nm equal to or less than 25 were sometimes independent, and aggregations with Nm values greater than 25 were never independent (Figure 7). Considering the uncertainty in scientific opinion over the magnitude of Nm that would reflect independence and the uncertainty in the isolation-by-distance relationship of Nm to distance, the average distance over which independence might occur for summer chum salmon was 77–83 km, based on allozyme and microsatellite DNA data, respectively (Figure 5 and Figure 6). At this scale, none of the aggregations of summer chum salmon in the Strait of Juan de Fuca and Hood Canal can be considered truly independent, although significant differences exist among aggregations.

The most likely minimum distance separating two spawning aggregations that could be considered independent was 30–38 km, based on microsatellite DNA and allozyme data, respectively (Figure 5 and Figure 6). Within this distance, most adjacent historical spawning aggregations would not be independent populations (Table 1). Aggregations separated by several streams might be considered independent if there were no spawning aggregations acting as stepping-stones between them, but this is generally not the case. Strictly applying only the most likely minimum distance as a criterion, three independent populations might have occurred historically for summer chum salmon: Strait of Juan de Fuca aggregations, Chimacum Creek,

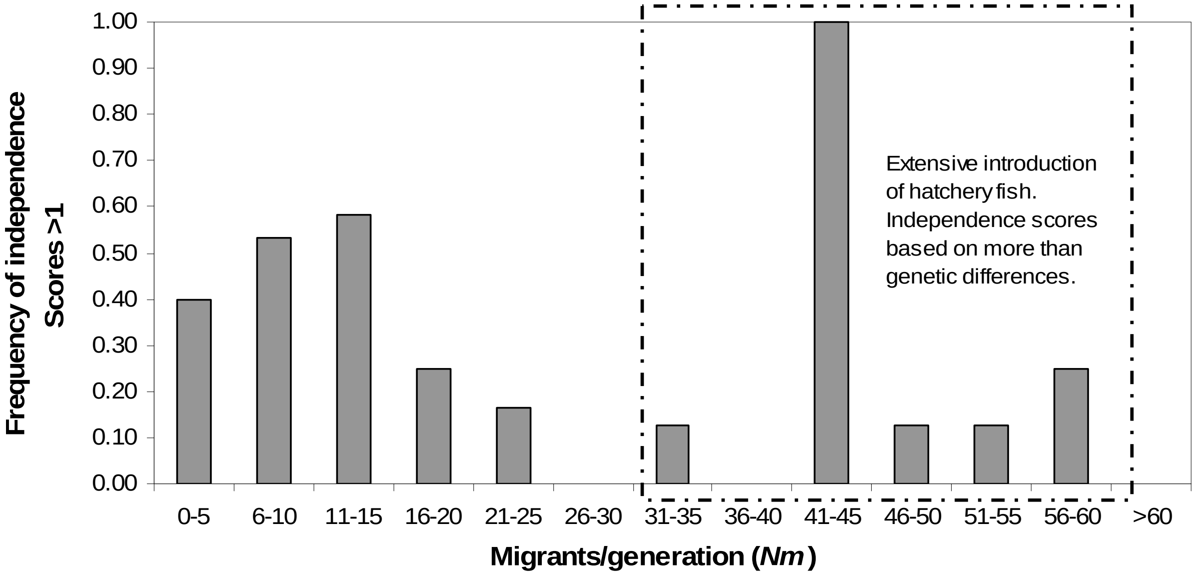

Figure 7. Distribution of population independence scores from experts judging Puget Sound Chinook salmon for different levels of genetic exchange (*Nm*). For geographically distinct spawning aggregations with evidence of gene flow from introductions of nonindigenous hatchery fish, estimates of historical independence were not associated with *Nm* and were based on other indicators.

and Hood Canal aggregations (Table 1). This scenario, however, ignores the capacity of available, stable historical habitat in these locations to support a viable, independent population. This is an important consideration for Chimacum Creek, which occupies a much smaller geographical area than either the Strait of Juan de Fuca (without Chimacum) or the Hood Canal aggregation.

Life History and Phenotypic Characteristics

Little information exists on stock-specific life history variation in summer chum salmon. Much of the available information is summarized in the Summer Chum Salmon Conservation Initiative and its appendices (WDFW and PNPTT 2000). Many life history traits of summer chum that have been studied tend to be similar among aggregations and may reflect a common adaptation to the demands of spawning in streams with low flows and early migration of juveniles from freshwater to estuarine areas.

Some life history traits in Hood Canal summer chum salmon do vary among streams. Adults returning to Strait of Juan de Fuca streams may enter the strait earlier than Hood Canal aggregations. Entry of adults into freshwater, which occurs between late August and mid-October, however, is approximately a week earlier for the southernmost Hood Canal aggregation (Union River) than the northern Strait of Juan de Fuca populations (WDFW and PNPTT 2000). Adults spawn soon after entering freshwater, but development rates of juveniles may be different. Geographical variation in time to emergence of juveniles after incubation may reflect environmental differences (Bakkala 1970, Salo 1991) and genetic traits (Robison et al. 2001). Strait of Juan de Fuca aggregations, which occupy colder streams than Hood Canal aggregations, generally produce fry that emerge later than fry from Hood Canal aggregations (Tynan 1997). Likewise, summer chum salmon originating from the colder, mainly snow melt–fed west side Hood Canal watersheds emerge later than summer chum from warmer, rainfall-fed streams on the Kitsap Peninsula (WDFW and PNPTT 2000).

A unique life history attribute is the substantial proportion of the Sequim Bay subpopulation that returns to spawn as small, 2-year-old fish in some years (WDFW and PNPTT 2000, 2003, WDFW and PNPTC 2006). Such a distinct life history trait may be related to the significantly different genetic characteristics of summer chum salmon from Sequim Bay. Other subpopulations included in the ESU do not exhibit this early age at return.

Population Dynamics

Exploring population dynamics was not informative for identifying independent populations in the Hood Canal Summer Chum Salmon ESU, in part because of hatchery supplementation programs, which have contributed to returns since 1995. More details on population dynamics can be found in the Viability Criteria section of this report.

Environmental and Habitat Characteristics

To determine whether potential environmental differences exist between summer chum salmon habitats that might give rise to locally adapted, independent populations, we examined the distribution of summer chum across freshwater ecoregions and marine subbasins. Although differences in habitat characteristics among Puget Sound streams and marine subbasins are apparent, the biological significance of those differences to summer chum salmon is not yet well understood.

The literature on Pacific salmonids suggests that population structure and diversity of the fish are closely linked to patterns of ecological diversity (Healey and Prince 1995, Hanski and Gilpin 1996, McElhany et al. 2000, Rieman and Dunham 2000, Waples et al. 2001, Beechie et al. 2006, Fresh et al. in press). The argument is that geographic differences in habitat characteristics within and among watersheds may provide insights into the different selective environments fish experience, and thus indicate the degree of selectively driven isolation that might arise among spawning groups. In this subsection, we discuss the relationships between patterns of environmental and habitat characteristics and the historically independent population delineations. This information is also useful for examining diversity and spatial structure attributes for the corresponding independent populations.

Ecoregional boundaries can be a useful way to describe habitat differences that may be of selective relevance to salmon. Streams within an ecoregion share similar biotic and abiotic characteristics, including geology, physiography, vegetation, climate, soils, land use, hydrology, and fauna that affect instream environmental conditions (Omernik 1987, 1995, 2003). In addition, including larger-scale ecoregional patterns helps to integrate landscape and riverine processes and their affects on potential selective environments experienced by salmon (Berman 2002). We examined the patterns of overlays between ecoregions identified by the Environmental Protection Agency (EPA) and each of the watersheds that contain the identified historical spawning aggregations. Ecological diversity at the EPA level III geographic scale corresponds to genetic and life history diversity of salmonid ESUs (McElhany et al. 2000, Waples et al. 2001). Level IV ecoregions, which are further subdivisions of level III units, are thus an appropriate level of ecological diversity to consider for discriminating potentially different selective environments among populations within an ESU. We have applied data sets relating the EPA level IV ecoregional units and sixth level hydrologic units (EPA 2004).

We identified five distinct groupings of watersheds occurring in distinct combinations of ecoregions encompassed by the Hood Canal Summer Chum Salmon ESU boundaries. The Dungeness, Big Quilcene and Little Quilcene rivers have headwaters in the High Olympics, Low Olympics, and Coast Range Volcanics ecoregions and lower reaches in the Olympic Rainshadow ecoregion. A group consisting of Discovery Bay (Salmon and Snow creeks), Sequim Bay (Jimmycomelately Creek), Admiralty Inlet (Chimacum Creek), and Western Upper Hood Canal tributaries are all fully contained within the Olympic Rainshadow ecoregion. The Duckabush and Dosewallips rivers are fully contained within the High Olympics, Low Olympics, and Coast Range Volcanics ecoregions. The Hamma Hamma and Skokomish rivers and Lilliwaup Creek have headwaters in the High Olympics, Low Olympics, and Coast Range Volcanics ecoregions and lower reaches in the Central Puget Sound Lowlands ecoregion. The final group, encompassing the West Kitsap tributaries to Hood Canal and Admiralty Inlet, is fully contained within the Central Puget Sound Lowlands ecoregion.

In addition to ecological diversity in spawning environments, watersheds containing spawning aggregations flow into distinct regions within the marine environment (Figure 8). We therefore postulate that outmigrants and returning adults from spawning aggregations experiencing different marine subregions represent additional increments of ecological diversity for the population structure of the ESU. The variety of regimes experienced by the spawning aggregations may influence the expression of freshwater and marine life history characteristics of summer chum salmon, resulting in significant local variation within a population, a result consistent with findings from studies on chum salmon in Russia and British Columbia and with the variations reported for Chinook salmon in the Puget Sound Salmon Recovery Plan (Kulikova 1972, Beacham and Murray 1987, Shared Strategy 2007). Boundaries of biogeographically distinct marine subbasins within Puget Sound previously have been identified (PSWQAT 2002, Shared Strategy 2007). Other groupings that were also considered may be appropriate and warrant further investigation as more information becomes available relating to what marine and freshwater habitat attributes best predict summer chum diversity.

The watersheds were thus binned into similar groupings of ecoregions nested within their respective marine catchments to fully capture the potentially distinct ecological conditions experienced by summer chum salmon in each group. Overlaying the watershed units grouped by similar ecoregions and the marine subbasins into which the streams flow results in seven ecological diversity groups (Table 2). Table 2 provides a listing of the ecological composition of each stratum and the associated historical and extant spawning aggregations of summer chum each contains. These are also mapped in Figure 8.

Remaining Uncertainties in Population Structure

We presently lack sufficient metapopulation structure data in proximity to the proposed boundary between the two populations to resolve whether the boundary may nest within the

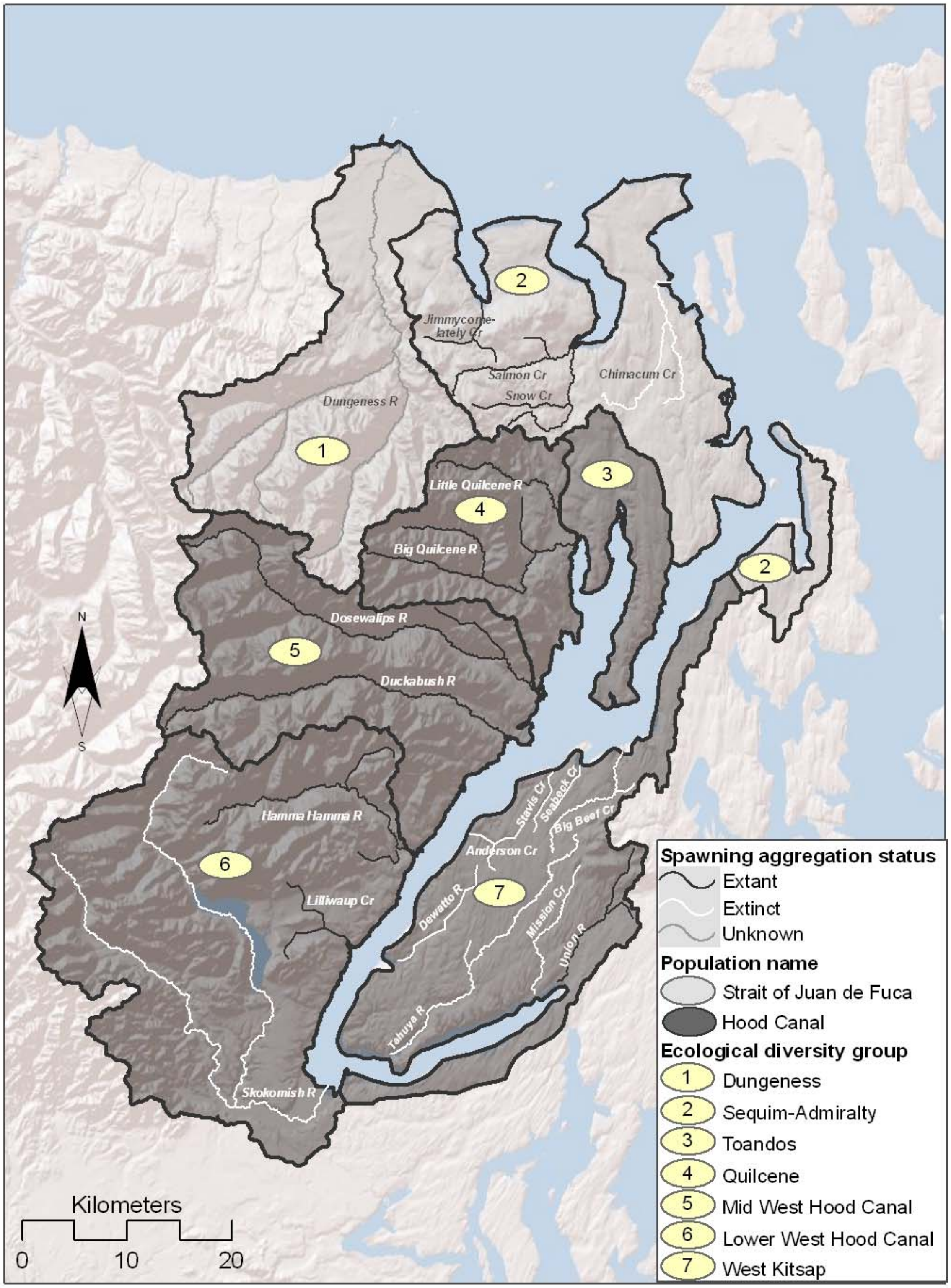

Figure 8. The two populations of the Hood Canal Summer Chum Salmon ESU, including the streams with spawning aggregations and seven ecological diversity groups.

Table 2. Seven proposed ecological diversity groups of the Hood Canal Summer Chum Salmon ESU by geographic regions and associated spawning aggregations.

Geographic region (population)	Proposed ecological diversity groups (names)	Freshwater ecoregions (headwaters)	Freshwater ecoregions (lower reaches)	Spawning aggregations: Extant* and extinct**
Eastern Strait of Juan de Fuca	Dungeness	High Olympics Low Olympics Coast Range Volcanics	Olympic Rainshadow	Dungeness River (unknown)
	Sequim-Admiralty	Olympic Rainshadow	Olympic Rainshadow	Jimmycomelately Creek* Salmon Creek* Snow Creek* Chimacum Creek**
		Central Puget Sound Lowlands	Central Puget Sound Lowlands	Unknown
Hood Canal	Toandos	Olympic Rainshadow	Olympic Rainshadow	Unknown
	Quilcene	High Olympics Low Olympics Coast Range Volcanics	Coast Range Volcanics	Big Quilcene River* Little Quilcene River*
	Mid West Hood Canal	High Olympics Low Olympics Coast Range Volcanics	Coast Range Volcanics	Dosewallips River* Duckabush River*
	West Kitsap	Central Puget Sound Lowlands	Central Puget Sound Lowlands	Big Beef Creek** Seabeck Creek** Stavis Creek** Anderson Creek** Dewatto River** Tahuya River** Mission Creek** Union River*
	Lower West Hood Canal	High Olympics Low Olympics Coast Range Volcanics	Central Puget Sound Lowlands	Hamma Hamma River* Lilliwaup Creek* Skokomish River*

geographic regions as proposed or may instead follow ecoregional unit boundaries. Also, it appears unlikely that ecological conditions within the small independent watersheds adjacent to the proposed boundary line could have supported any persistent spawning aggregations that would merit equal consideration to the other ecological diversity groups comprising the ESU. Nevertheless, it appears plausible that even intermittent spawning within these areas may contribute to the connectivity between the populations and to ESU persistence. Therefore, we conclude that the above delineation will be adequate to guide current recovery planning needs. Further investigation of population characteristics is warranted as recovery planning and implementation proceeds to more confidently delineate the boundary between the populations and how that may relate to ecological diversity delineations in this transitional area.

There is uncertainty about whether the Dungeness River represents a subpopulation or a minor spawning aggregation within the Strait of Juan de Fuca population. This could have consequences in setting viability criteria for the population (see the Viability Criteria section of this report).

Conclusions

Independent Populations

For the Hood Canal Summer Chum Salmon ESU, migration rates and genetic attributes offer moderate to strong support for two independent populations: one in the Hood Canal and a second in the Strait of Juan de Fuca. A key finding from our analyses is that the historical interdependence of subpopulations was directly related to how far apart they were geographically. The greatest level of exchange and interdependence likely was between subpopulations that were geographically close to one another. The likelihood of exchanging migrants decreased and genetic differences increased as greater distances separated subpopulations.

Data on current patterns of migration suggest little demographic exchange of fish between these two regions in recent years. Fuss and Hopley (1991) noted that hatchery-raised fall chum salmon in Hood Canal also have a high fidelity to their stream of origin. Although the data that we used were from artificially propagated fish derived from native broodstocks, exchange between wild aggregations may be even less than the estimated rates for hatchery summer chum salmon. Straying rates are a function of complex environmental and population-specific characteristics (Hard and Heard 1999). Rearing and release strategies of hatchery-raised fish, for example, may interfere with homing of salmon to natal areas (Quinn 1993, Pasqual et al. 1995) and elevate straying rates above natural levels. Likewise, appropriate broodstock selection strategies such as those used for Hood Canal and Strait of Juan de Fuca summer chum salmon have been shown to decrease straying of chum salmon over time (Tallman and Healey 1994).

Genetic Characteristics

Genetic characteristics of summer chum salmon support the evidence from migration rate estimates. The estimates of genetic exchange, which integrate the effects of straying among spawning aggregations over many generations, decreased predictably as geographical distance between spawning aggregations increased. One hundred and twelve km separate the geographically closest major spawning aggregations in Hood Canal (Dosewallips River) and the Strait of Juan de Fuca (Salmon and Snow creeks) (Table 1), and these aggregations were associated with a level of *Nm* that most geneticists concluded was too low to affect the demographics and persistence of these two groups. Chimacum Creek, which lies between these major spawning aggregations, may provide additional production to the Hood Canal and the Strait of Juan de Fuca populations, but the likely historical capacity in these locations most likely could not support a distinct independent population, because of their much smaller basin size.

Although the genetic data allow excellent estimates of genetic exchange, we considered the overall strength of inference to be moderate. Precise theoretical or empirical relationships between *Nm* and demographic population independence are not available and thus we relied on expert knowledge to make such judgments. Evidence from other potential indicators of population structure—such as life history variation, population dynamics, and habitat characteristics—was consistent with our identification of two independent populations, but the strength of inference from these data was weak (Table 3). Figure 8 presents the proposed two historically independent populations together with the associated spawning streams and seven proposed ecological diversity units.

The Summer Chum Salmon Conservation Initiative (WDFW and PNPTT 2000), developed by the comanagers, identified nine extant stocks of summer chum salmon and seven recently extirpated stocks as management units for the conservation and recovery of the ESU. Our analyses indicate that these are subpopulations, which contribute to either the Hood Canal or Strait of Juan de Fuca population depending on their geographical location. Furthermore, our analyses strongly support the use of these local stocks as management units for recovering the ESU.

Table 3. Evidence and strength of inference for different indicators of independent populations of summer chum salmon.

		Strength of inference	
Indicator	**Evidence**	**Population**	**Subpopulation**
Geography	No geographical barriers; distances between historical spawning aggregations are small but have increased because of local extirpations. Despite small distances, natural recolonization of areas where extirpations have occurred has not been observed.	Weak	Weak, but lack of recolonization is consistent with subpopulation structure
Migration rates	Marked summer chum raised in hatcheries show 0.07–1.5% straying rates between Hood Canal and Strait of Juan de Fuca; 70–95% of fish return to natal streams and most of the rest return to streams within 50 km.	Strong support of independence between Hood Canal and Strait of Juan de Fuca fish	Moderate; shows isolation-by-distance subpopulation structure
Genetic attributes	Sequim Bay fish (in Strait of Juan de Fuca) consistently different from other summer chum in genetic studies; PSTRT analyses show strong isolation by distance suggesting aggregations separated by more than 30–38 km.	Moderate support of independence between Hood Canal and Strait of Juan de Fuca fish	Strong support of isolation-by-distance subpopulation structure
Life history characteristics	Possible differences in entry timing, emergence timing, and juvenile migration timing between summer chum streams in Hood Canal and Strait of Juan de Fuca.	Weak, but possible	Weak
Population dynamics	No correlation in trends of adult returns between Hood Canal and Strait of Juan de Fuca.	Not informative	Not informative
Habitat characteristics	Hood Canal and Strait of Juan de Fuca summer chum habitat characterized by different freshwater ecoregions and marine conditions.	Weak, but possible	Weak

Viability Criteria for the Hood Canal Summer Chum Salmon ESU and Populations

Introduction

The PSTRT is charged with identifying the biological characteristics of a recovered ESU in support of developing delisting and recovery criteria. These biological characteristics are based on the collective viability of individual populations, their characteristics, and their distributions throughout the ESU. A viable ESU is defined as one that is naturally self-sustaining and has a negligible risk of extinction over a long period of time, likely time periods greater than 100 years (McElhany et al. 2000). Using ESU-wide characteristics, the PSTRT provides technical assistance as the comanagers and the Hood Canal Coordinating Council, in cooperation with the National Marine Fisheries Service (NMFS), implement a recovery plan to meet broad regional goals for recovery.

As the PSTRT concluded in the previous section of this report, the Hood Canal Summer Chum Salmon ESU consists of two historically independent populations: the Strait of Juan de Fuca and the Hood Canal populations.

The Strait of Juan de Fuca population spawns in rivers and streams entering the Eastern Strait of Juan de Fuca Geographical Region of Puget Sound and includes extant spawning aggregations of summer chum in the Dungeness River and in Salmon, Snow and Jimmycomelately creeks. The historical spawning aggregation in Chimacum Creek has been locally extirpated, but summer chum have been reintroduced through a now-terminated hatchery supplementation program (see the Identification of Independent Populations section, Figure 8 and Table 2).

The Hood Canal population includes all spawning aggregations in streams entering the Hood Canal Geographic Region of Puget Sound. Summer chum salmon spawning aggregations within the Hood Canal population historically persisted in most of the major rivers draining the Olympic Mountains on the western edge of the canal, including the Big and Little Quilcene, Dosewallips, Duckabush, Hamma Hamma, and Skokomish rivers and Lilliwaup and Finch creeks. On the eastern side of Hood Canal, summer chum spawned in the Big Beef and Anderson creeks and Union, Dewatto, and Tahuya rivers. Seabeck, Stavis, Big and Little Mission creeks, and others were likely historically used by summer chum (WDFW and PNPTT 2000). Currently, sizable summer chum salmon spawning aggregations are found only in the Big and Little Quilcene, Dosewallips, Duckabush, and Hamma Hamma rivers and Lilliwaup Creek on the western side of Hood Canal, and in the Union River on the southeastern portion of the canal (See the Identification of Independent Populations section, Figure 8 and Table 2). Small numbers (<25 annually) are found in the Skokomish and Dewatto rivers. Summer chum in Big Beef Creek and Tahuya River are being reintroduced through hatchery supplementation programs.

For the ESU to be viable, both populations must to be viable. Quantitative analyses have been conducted to estimate the abundance and productivity criteria for both Hood Canal Summer Chum Salmon ESU populations and to evaluate spatial structure and diversity. The PSTRT has developed a set of recommendations that describe guidelines for incorporating viability criteria in planning for a viable population; these are found at the end of this document.

Population Viability

The PSTRT evaluates population viability using four key characteristics as described in the VSP document (McElhany et al. 2000): abundance, productivity, spatial structure, and diversity. Abundance is the number of individuals in the population at a given life stage or time. Productivity (or growth rate), as used here, is the actual or expected ratio of abundance in the next generation to current abundance. Spatial structure refers to how the abundance at any life stage is distributed among available or potentially available habitats. Diversity is the variety of life histories, sizes, and other characteristics expressed by individuals within a population. These characteristics together describe a viable population.

Population viability is estimated as a probability of population persistence over a defined period of time (McElhany et al 2000). “Viable” in this sense refers to a naturally self-sustaining population that has a negligible risk of extinction over a 100-year time frame. The acceptable level of risk of extinction is a policy decision informed by available technical guidance and analyses. In this case, the population viability criteria we have developed describe the abundance, productivity, and diversity of summer chum salmon required for a naturally self-sustaining population to have either a 0.95 or 0.99 probability of persistence over a 100-year time period.

For Hood Canal Summer Chum Salmon ESU populations, we used two methods of population viability analyses (PVAs) for estimating minimum abundance levels associated with population persistence. The two methods we used incorporate uncertainty in the data (estimated returns per spawner) to determine minimum target levels of abundance and productivity such that the population does not go extinct in the face of environmental variation and anthropogenic factors.

One method uses variability around replacement recruits per spawner (R/S = 1) to derive minimum target escapement levels needed to maintain the population above a quasi-extinction threshold (QET), assuming that the population time series approximates a Brownian motion (Dennis et al. 1991). The other method assumes that the R/S relationship is density dependent and uses a R/S function to estimate R/S for different spawning levels. The variability around the predicted recruits is used to generate a productivity curve (defined by intrinsic productivity and capacity) that results in the population remaining above a specified QET given a fixed exploitation rate (ER, fraction of return taken by fishery). Separate productivity curves are estimated for the Hood Canal and Strait of Juan de Fuca populations over an ER range of 0–0.3.

The abundance and productivity targets for population viability assume that the populations maintain or, preferably, improve their spatial distribution and diversity. We used two diversity indices to measure spatial distribution of spawning aggregations within the populations; these indices take into account the number of streams used for spawning and the relative abundance of adults between spawning sites. We have no direct measures for life history diversity; but for the purposes of defining population viability, we assume that if spatial distribution remains diverse, then so will life history.

Source Data for Viability Analyses

For each of the spawning aggregations in the two populations in the Hood Canal Summer Chum Salmon ESU, the PSTRT compiled annual estimates of the number of summer chum spawning naturally (i.e., spawning escapement), broodstock take, and catch for the 1974–2005 period (Figure 9 and Figure 10). Spawning aggregation refers to the level at which spawning

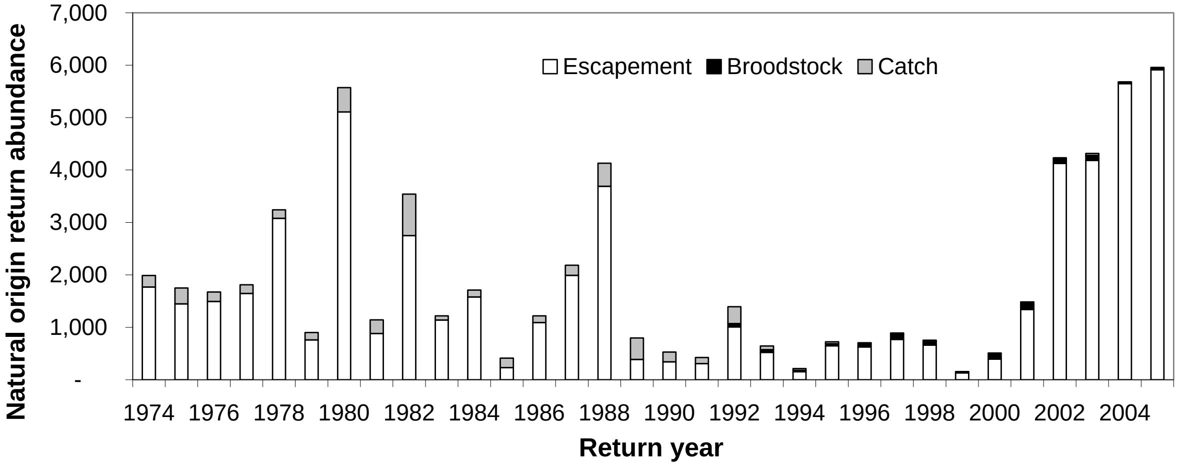

Figure 9. Annual return abundance of natural-origin summer chum salmon of the Strait of Juan de Fuca region from 1974 to 2005 (from PSTRT abundance and productivity tables using data from WDFW and PNPTT 2000, 2003, WDFW and PNPTC 2004, 2005, 2006).

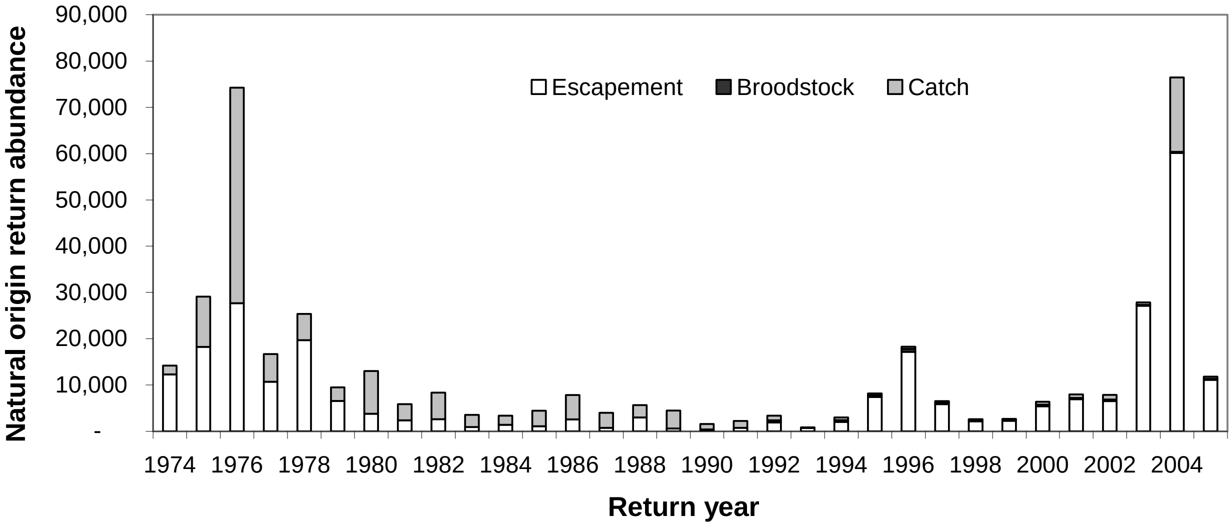

Figure 10. Annual return abundance of natural-origin summer chum salmon aggregations of the Hood Canal region from 1974 to 2005 (from PSTRT abundance and productivity tables using data from WDFW and PNPTT 2000, 2003, WDFW and PNPTC 2004, 2005, 2006).

escapement is reported by the comanagers and includes, for the Strait of Juan de Fuca population, Jimmycomelately, Snow, Salmon, and Chimacum creeks. For the Hood Canal population, the spawning aggregations include Big and Little Quilcene, Dosewallips, Duckabush, Hamma Hamma, Union, Dewatto, and Tahuya rivers and Anderson, Big Beef, and Lilliwaup creeks. Escapement estimates are not available for this period for the Dungeness River in the Strait of Juan de Fuca population or the Skokomish River in the Hood Canal population, so they have not been included in analyses at the spawning aggregation level.

Natural spawning escapement estimates, broodstock take, and catch per fishing area were provided by the comanagers (see WDFW and PNPTT 2000 for escapement estimation methods). Total recruitment includes, for the purposes of these analyses, the number of adult summer chum salmon caught in Canadian and U.S. fisheries, fish that spawn naturally, and fish removed for broodstock take. Observed predation, normally by marine mammals, was not included since observations were sporadic. Recruitment is calculated from run reconstruction analyses after the method used by the comanagers (see WDFW and PNPTT 2000 for run reconstruction methods).

Some of the naturally spawning summer chum salmon aggregations in Hood Canal and the Strait of Juan de Fuca include hatchery-reared spawners in addition to those that originated from natural habitats. Including such hatchery-origin fish in counts of natural spawning can mask the true status of the natural-origin population. However, all hatchery-origin summer chum in the two regions are now mass marked, allowing for their differentiation from co-occurring natural-origin fish (WDFW and PNPTT 2000). Based on estimates of the numbers of natural-origin fish and hatchery-origin fish to natural spawning populations provided by the comanagers, we used only natural-origin fish in viability modeling. Broodstock removals to sustain the supplementation programs began in 1992 and the first 3-year-old, hatchery–origin chum returned to the region in 1995. Hatchery contributions to total adult recruitment between 1995 and 2005 have ranged 38–74% in the Strait of Juan de Fuca population and 16–49% in the Hood Canal population.

For the years 1999 to 2005, summer chum salmon from most of the spawning aggregations within each population were sampled for age, mark, and genetic composition. Sample sizes are good each year, with generally well over 100 fish per aggregation and from 300 to 1,000 fish for the Strait of Juan de Fuca population and from 300 to 3,000 for the Hood Canal population (WDFW and PNPTT 2000, 2001, 2003, WDFW and PNPTC 2004, 2005, 2006). Age is reported separately for natural-origin and hatchery-origin fish. Adults return as age 2 to 5 years; age-2 fish returning to the spawning grounds are considered mature fish. Age distribution estimates are available for each spawning aggregation. A weighted age distribution for each population is estimated based on the relative proportion of each spawning aggregation in the population each year. The estimated average age of returning adults is 3.4 years for the Strait of Juan de Fuca population and 3.6 years for the Hood Canal population. The annual age composition on the spawning grounds is used for cohort run reconstruction that is used in developing spawner-recruit functions. For years with age data, those data are used; for years without age data, the average age composition over available years is used for cohorts and is weighted by the relative total abundance for each contribution year to the cohort (Sands in prep*a*.).

Productivity is measured as the number of natural-origin adult returns per natural spawner. Productivity has been estimated from the cohort run reconstruction and is shown in Figure 11 and Figure 12. While average R/S over the 1974 to 2001 cohort is 2.6 for the Strait of Juan de Fuca population and 3.1 for the Hood Canal population, variability around these averages is great.

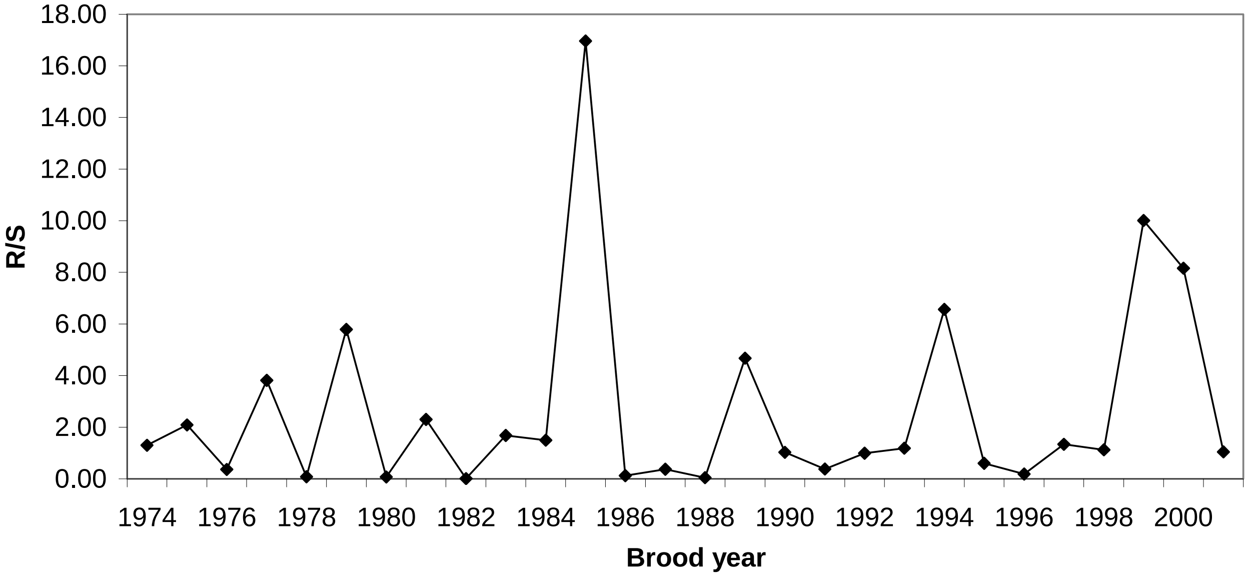

Figure 11. Strait of Juan de Fuca summer chum salmon population R/S for 1974–2001 brood years. The average R/S is 2.6 with a SD of 3.8.

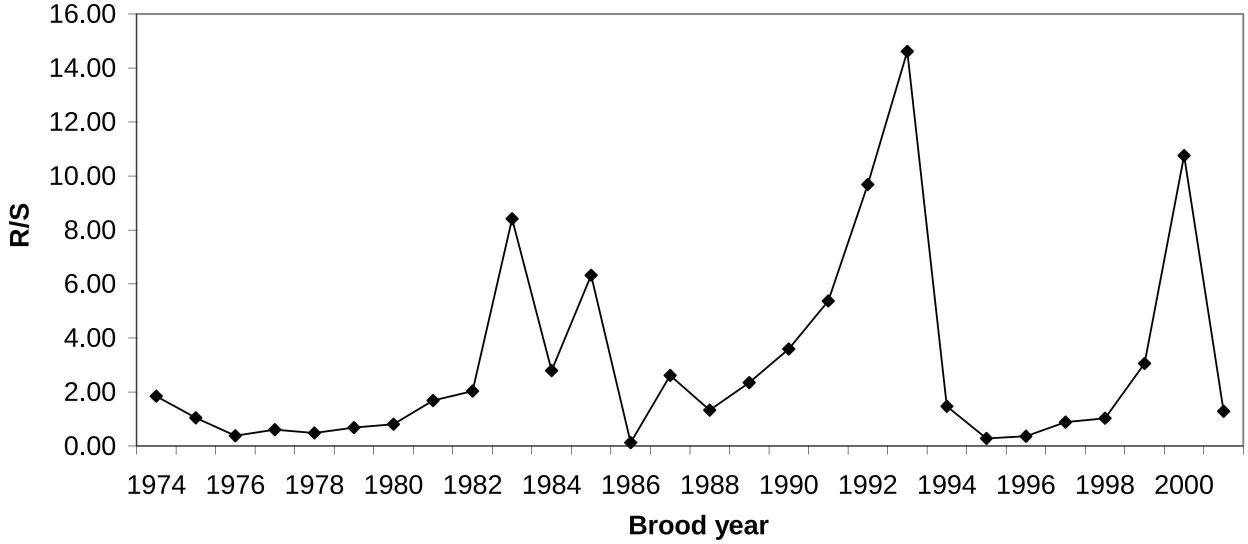

Figure 12. Hood Canal summer chum salmon population R/S for 1974–2001 brood years. The average R/S is 3.1 with a SD of 3.6.

Estimating Quasi-extinction for Summer Chum Salmon

The quasi-extinction threshold, N_{QET}, is the population size below which extinction risk is mostly determined by depensatory effects and other factors not included in estimates of the variance of potential population growth rate (σ^2) derived from populations at higher abundances. Several processes are important in setting N_{QET} (Lande 1998) and there is no single accepted way to determine this parameter, but the outcome of PVA analysis is highly sensitive to its value. We used the potential loss of genetic diversity associated with small population size as a guide to setting N_{QET}, because it addresses risks to three VSP criteria: abundance, spatial structure, and diversity. Conservation guidelines usually assume that populations cannot tolerate genetic effective sizes (N_e) less than 50 for more than short periods of time without significant risk (Soule 1980, Allendorf et al. 1997). Genetic drift begins to dominate natural selection in determining the genetic characteristics of populations smaller than 50 to 100 fish effective size (Gall 1987). Allendorf et al. (1997) recommended that Pacific salmon population effective sizes be above 500 to guard against long-term deleterious genetic change due to genetic drift and above 50 to guard against short-term change.

Methods

Because of the historical population genetic structure identified for summer chum salmon (see results of the population identification analyses, Figure 5 and Figure 6), maintaining genetic diversity requires that spawning aggregations be sustainable across the population's range. The overall N_e for the whole population, which is used to determine a census number, N_{QET}, for PVA analyses, depends on the sizes of the subpopulations and the amount of genetic migration among them. Consequently, we calculated the total population N_e by assuming a minimum subpopulation genetic effective size, N_e, of 50 for each of 5 persistent spawning aggregations in the Hood Canal population and 4 persistent spawning aggregations in the Strait of Juan de Fuca population. The number of spawning aggregations per population was based on the spawning area covered by the population and the distance between spawning aggregations so that it was consistent with the viability criteria for spatial structure.

In the Strait of Juan de Fuca population, we considered two scenarios: 1) all 4 aggregations are major spawning aggregations each with a minimum N_e of 50 and 2) 3 are major spawning aggregations and the fourth, the Dungeness River, is a satellite spawning aggregation with an N_e of 10. To estimate the degree of exchange, we assumed straying patterns for the natural spawning fish to be that observed from artificially propagated, otolith-marked, or adipose-clipped summer chum salmon in 2001 and 2002 (WDFW and PNPTT 2003). These observations showed that most hatchery fish homed to their natal streams and straying rates declined rapidly with distance from the natal stream. Based on these data, the proportion of adults, P, that return to their stream of origin or another stream was approximately

$$P_{\mathrm{ADULTS}} = 0.66 - 0.35\log(\mathrm{km});\ R^2 = 0.73 \qquad (1)$$

Assuming migration probabilities are similar to the observed straying patterns, we estimated the nonnatal migration probabilities using the above relationship and calculated homing probability as one minus the total nonnatal migration probability. We used the Tufto-Hindar algorithm (Tufto and Hindar 2003) to solve for an overall N_e for the population given the different subpopulations and migration rates. We converted N_e to N_{QET} using the relationships in Waples (1990):

$$N_{QET} = N_e \div \frac{N_e}{N_c} \div B \tag{2}$$

where N_e was the total effective population size as calculated above based on the number of regions and distance between aggregates, $N_e{:}N_c$ was the effective size to census size ratio of 0.2, and B was an average generation length (3.6 years for the Hood Canal population and 3.4 years for the Juan de Fuca population).

Results

Based on this approach, total N_e for the Hood Canal population should be 254; this converts to $N_{QET} \approx 350$. Likewise, assuming four major aggregations in the Strait of Juan de Fuca population, total N_e for the Strait of Juan de Fuca population should be 205, which converts to $N_{QET} \approx 300$. Alternatively, assuming under recovered conditions that spawning in the Dungeness is persistent but small, N_e for the Strait of Juan de Fuca population would be 109, which converts to $N_{QET} \approx 160$.

PVA for Abundance and Productivity Criteria

Two analyses were used for PVA to determine criteria for abundance and productivity. The first, based on a density-independent model based on work of Dennis et al. (1991) and Holmes (2001), assumes a stable growth rate and no harvest. We refer to this approach as SimSalmon, after the name of the computer program we used to implement this method (online at http://www.nwfsc.noaa.gov/trt/wlc/viability_simsalmon.cfm). The second analysis is based on density-dependent spawner–recruit curves and uses the simulation model Viability and Risk Assessment Procedure (VRAP, Sands in prep*b*.). VRAP also allows the incorporation of different exploitation rates in determining viable criteria.

SimSalmon Methods

The first PVA was based on the assumption that population dynamics are density independent, fluctuating only based on the variability of the population growth rate (Dennis et al. 1991). The results from this method strongly rely on the estimated variance of the population growth rate. We applied the methods of Holmes (2001), Holmes and Fagen (2002), and McElhany and Payne (in prep.) to available Hood Canal Summer Chum Salmon ESU data to derive variance estimates, as was done for Puget Sound Chinook salmon (Rawson et al. in prep.). Given an observed time series of abundances, one can estimate the population growth rate (λ) and the variance (σ^2) of the natural logarithm of the growth rate (μ). A stable population, neither increasing nor decreasing over time, would have a $\lambda = 1$ and a $\mu = 0$. Assuming that the population dynamics will be restored in the future such that 1) the growth rate is stable or increasing ($\lambda \geq 1$), and 2) the variance of the growth rate will remain the same as in the period of the observed time series, one can estimate the minimum initial population size necessary to maintain the probability or risk of extinction at or below a given level over a given number of years. Using this method, the viability criterion is for the population abundance to exceed the minimum size and for the growth rate to exceed $\lambda = 1$ over the specified time period.

There are two steps in this analysis. The first is to estimate σ^2 from the observed data, for which we used the slope method (Holmes 2001). The second step is to project extinction risk assuming that the time course of the population approximates a Brownian motion (Dennis et al. 1991).

As used in this PVA analysis, recruitment means the number of summer chum salmon that would have spawned naturally in the absence of any harvest.[1] The PSTRT worked with the comanagers to develop estimates of the numbers of natural-origin and hatchery-origin recruits and spawners for the 1974–2005 period. All natural spawners are used for the parent spawner estimates and natural-origin spawners and harvest are used for the recruits in viability modeling.

Parameter estimation—The slope method (Holmes 2001) was developed to separate process error (the parameter of interest) from measurement error in salmon time series. This method has been shown to produce reliable estimates of process error in the face of large measurement error when the population dynamics follow the assumptions of the model and also when the population dynamics follow other forms, including some of the density-dependent, spawner–recruit relationships commonly found in salmon (Holmes and Fagan 2002). The slope method, as we applied it, uses the 4-year running sums of abundance, expressed either as natural spawning escapement or total recruitment (average age at return is 3.4 years for the Strait of Juan de Fuca and 3.6 years for Hood Canal).

We used estimated σ^2 two ways for each population: using the time series of estimated natural spawning escapements and using the time series of total recruitment. The first estimate uses the Holmes (2001) method directly to compute the variance of $\log(N_{t+1}/N_t)$ for a time series, where N_t is the running sum of natural-origin spawning escapement at time t. The second estimate uses the estimate of total recruitment as N_t. In all cases we used 4-year-long unweighted running sums of the appropriate time series as the basic input data and lags (τ) of 1 through 4 years ($\tau = 4$ in Holmes' notation) for the slope estimates.

The length of the time series used for estimating σ^2 is positively correlated with the parameter estimate. This is true even when the underlying process can be assumed to be Markovian (McElhany and Payne in prep.), as is the case for the simple model for which this technique was first developed. Given the well-known longer-term cycles and regime shifts that govern Pacific salmon population dynamics (Pearcy 1992, 1997, Mantua et al. 1997), this tendency is exacerbated, at least as time series length increases from very short to 30–40 years. The time periods chosen (see Table 4) were based on finding a stable period with respect to population abundance.

Testing the assumptions of the model—To determine whether the assumptions underlying the slope method held for the Hood Canal Summer Chum Salmon ESU data, we chose time series from time periods with relatively stable population sizes, and tested for the linearity of the relationship between σ^2 and τ using the square of the Pearson correlation coefficient (r^2) and fit of the $\log(N_{t+1}/N_t)$ to the normal distribution with the Shapiro-Wilk test.

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[1] Used here, recruitment refers to calendar year recruitment, meaning fish of all ages returning in a single year. Other applications, such as our second PVA, use brood year recruitment, which counts all the fish in a single cohort returning over several years.

Table 4. Estimated values of the variance (σ^2) and the natural logarithm of the growth rate (μ) for Hood Canal and Strait of Juan de Fuca summer chum salmon populations computed on natural escapement and total recruitment time series for the indicated time periods. The stability notes refer to population abundance. Values in bold face are recommended for use in determining minimum viable population sizes.

		Natural escapement		Total return	
Population: time period	**Years**	σ^2	μ	σ^2	μ
Hood Canal–all years	1974–2003	0.416	–0.015	0.204	–0.035
Hood Canal–stable, high	1974–1978	a*	a	a	a
Hood Canal–stable, low	1981–1994	0.020	–0.029	**0.042**	–0.076
Hood Canal–decreasing	1978–1990	0.127	–0.213	0.056	–0.137
Hood Canal–increasing	1990–2003	0.442	0.250	0.268	0.185
Strait–all years	1974–2003	0.220	0.024	0.209	0.021
Strait–stable, high	1974–1984	0.041	0.000	**0.032**	0.007
Strait–stable, low	1989–2000	0.005	–0.056	0.013	–0.089
Strait–decreasing	1982–1994	0.415	–0.117	0.136	–0.103
Strait–increasing	1994–2003	0.096	0.387	0.092	0.372

* a = insufficient number of years available to estimate σ^2.

Population projection—To project a population's extinction probability, we assumed that a population grows at a lognormally distributed growth rate with a mean of $\lambda = 1$ and variance around μ being σ^2. We also simulated populations at several positive growth rates ($\lambda > 1$) in order to investigate the effect of positive growth rate on the required minimum population size. The straightforward approach we used is described by McElhany and Payne (in prep.) and we used their SimSalmon computer program to compute the results. This program repeatedly simulates population trajectories for Y years, starting with a population size of N. The trajectory is assumed to go extinct if the population size over a 4-year average ever falls below N_{QET} during the Y years. Otherwise it is not extinct. This projection method includes the additional constraint that the population size can never exceed the initial population value. This provides a high estimate of extinction probability since, if this constraint is removed, extinction probabilities are much lower than with the constraint in place.[2]

SimSalmon Results

Parameter estimation—Estimates of σ^2 for the Hood Canal and Strait of Juan de Fuca summer chum salmon populations ranged from 0.005 to 0.442, depending on the time period chosen and whether the analysis was on the time series of natural escapement or total recruitment (Table 4). Based on visual examination of the data, we divided the time series into periods of increasing, decreasing, or stable population sizes. The rate of population increase or decrease is measured by μ, the natural logarithm of the average annual growth rate. We used estimates of σ^2 from the time segment for each population with the lowest value of μ (Table 4). Between using the time series of natural escapement or the total recruitment for σ^2, we chose total recruitment because it is independent of the effect of harvest, which has been variable over the years.

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[2] P. McElhany, Northwest Fisheries Science Center, Seattle, WA. Pers. commun., January 2005.

Visual examination of the relationship between σ^2 and τ for the time series used suggests that the assumption of linearity is well founded. Analysis of these time series for normality of the distribution of $\log(N_{t+1}/N)$ showed both Shapiro-Wilk coefficients with *p*-values consistent with the assumption of a normal distribution (Hood Canal, $p = 0.45$; Strait of Juan de Fuca, $p = 0.85$).

Population projection—Determining minimum population sizes needed to ensure viability using the SimSalmon program requires the following input variables to be specified: potential population growth rate (λ or its natural logarithm μ), σ^2, time period for the simulation in years (Y), extinction probability, and N_{QET}. We assumed a stable population by setting $\mu = 0$ and simulated values of σ^2 from 0.005 to 0.05 in increments of 0.005. We used 100 years for Y and 0.05 and 0.01 for the extinction probability following McElhany et al. (2000).

With this input, one can produce a table of viable spawning populations sizes for a range of σ^2 values, assuming $\mu = 0$ (Table 5). Given $\mu = 0$ and the recommended σ^2 value of 0.03 for the Strait of Juan de Fuca population (Table 4), the viable spawning population size range (reflecting extinction probabilities of 1–5%) is about 13,000 to 31,000, assuming that the Dungeness River can support a major spawning aggregation, and about 6,000 to 20,000, assuming the Dungeness River supports a minor satellite spawning aggregation. For the Hood Canal population with a σ^2 value of 0.04, the corresponding viability range is about 25,000 to 85,000 summer chum spawners.

VRAP Methods

The second PVA analysis used is the VRAP model (Sands in prep*b*.). VRAP adds the dimensions of productivity, capacity, and exploitation rate over the single numeric estimate of spawning size from SimSalmon and assumes that population dynamics are density dependent. With the VRAP method, there is not an estimate for a viable escapement level independent of other considerations. Viability is expressed as the parameters of a spawner-recruit curve given a

Table 5. Results of population projections using SimSalmon model for σ^2 ranging from 0.005 to 0.05, $\mu = 0$, extinction probabilities of 0.05 and 0.01, and N_{QET} of 350 for Hood Canal and both 300 and 160 for the Strait of Juan de Fuca. Based on the recommended values of σ^2 (Table 4) and other assumptions (see text), the recommended ranges for the minimum viable annual population sizes for the Hood Canal and Strait populations are shown in bold face.

	Hood Canal, N_{QET} = 350		**Strait, N_{QET} = 300**		**Strait, N_{QET} = 160**	
σ^2	***p* = 0.05**	***p* = 0.01**	***p* = 0.05**	***p* = 0.01**	***p* = 0.05**	***p* = 0.01**
0.005	1,600	2,600	1,400	2,100	700	1,100
0.010	2,900	5,000	2,400	4,400	1,400	2,400
0.015	4,700	10,600	4,200	7,900	2,000	4,100
0.020	7,500	16,700	6,100	13,200	3,200	7,600
0.025	10,000	27,200	9,100	21,700	4,600	11,300
0.030	15,900	35,300	**12,500**	**30,800**	**5,600**	**20,200**
0.035	19,200	47,000	16,300	51,000	7,900	27,700
0.040	**24,700**	**84,500**	21,300	61,600	12,000	39,700
0.045	30,900	127,100	26,300	86,900	13,800	62,700
0.050	40,200	156,400	43,200	142,900	17,500	67,700

desired harvest level; the resulting escapement can be estimated from these parameters. VRAP is the same model that has been used to determine rebuilding exploitation rates (RER, i.e., the highest level of harvest that allows rebuilding of the population) for jeopardy determinations for Puget Sound Chinook salmon (NMFS 2001). The model has two modes of operation.

- Harvest mode: Given a spawner-recruit function with parameters fit to available data, the model determines the RER that results in the population not going below a lower escapement threshold more than a chosen percent of the time and ends, at the end of the modeled time spawn of years, above an upper escapement threshold a chosen percent of the time.
- Population mode: Given a fixed ER, the model allows one to determine from output risk tables the intrinsic productivity and capacity parameters of a chosen spawner-recruit function that results in the population not going extinct more than a chosen percent of the time over a given time period (e.g., 5% probability or risk of extinction over 100 years).

This analysis of population viability for the Hood Canal Summer Chum Salmon ESU used the population mode of VRAP.

VRAP is a stochastic simulation model that projects recruits and spawners over a period of years based on a spawner-recruit relationship chosen from Ricker (1975), Beverton-Holt (Ricker 1975), and hockey stick (Barrowman and Meyers 2000) functions, given a starting population size and a target exploitation rate. In VRAP, harvest mortality may be estimated by age for two fishery types: mixed maturity stock fishery and mature stock fishery. Input values for average simple harvest rates and average maturation rates by age are used to partition the target exploitation rate by age and fishery. Simple harvest rates are the portion of the cohort by age taken by the fishery. Maturation rates are the proportion of the cohort after the mixed maturity fishery that mature and migrate back to the spawning grounds. The magnitude of the harvest rates is adjusted until the desired total exploitation rate is reached while maintaining the age and fishery distribution of the harvest. All of the Hood Canal summer chum harvest is assumed to be taken on fish returning to the spawning grounds, that is, there is only a mature stock fishery on Hood Canal summer chum salmon.

In this analysis, uncertainty in the projected number of recruits is introduced as process error and management error. The average ratio of estimated recruits (from cohort run reconstruction) to the predicted recruits from the spawner-recruit curve and the variance of that ratio (i.e., process error recruits) σ^2 are used to stochastically determine recruits from the predicted R/S. These error terms are determined during the parameter estimation stage explained below. To address uncertainty about the ability to achieve a target exploitation rate (i.e., management error), we used data in comanager reports (WDFW and PNPTT 2001, 2003, WDFW and PNPTC 2004, 2005, 2006) to estimate the variability in the forecasted exploitation rate under the comanagers' Base Conservation Regime compared to the actual exploitation rate achieved. However, the Base Conservation Regime exploitation rate "targets" are actually ceilings and the comanagers strive not to exceed those levels. Therefore, the coefficient of variance (with a mean value of one) around the actual versus forecasted levels is used in VRAP; this assumes that the comanagers will target an ER as summer chum populations become viable.

Both these sources of variability—process error and management error—are expressed as gamma distributions around the predicted recruits, and the target ER as the distribution of these errors is skewed rather than normal. The two parameters of the gamma distribution are the shape parameter (gamma1) and the scale parameter (gamma2). The gamma distribution is a skewed distribution; the two parameters may be calculated from the mean and standard deviation of the data with gamma1 = mean-squared/variance and gamma2 = variance/mean.

Parameter estimation—Prior to running VRAP, the population data is run through the Dynamics Model to determine the spawner-recruit relationship for the time span of data being used; this gives us the variability estimate of observed versus predicted recruits that will be used in the viability analyses. For summer chum salmon, no covariates for the environment have been found that are useful for explaining the variance, although an exhaustive search has not been made. By excluding environmental variables for now, the process error incorporates variability due to environmental factors as well as sampling and observation error.

To estimate the parameters of the spawner-recruit function, a Microsoft Excel spreadsheet model developed by Jim Scott (WDFW) and adapted by Norma Sands (NMFS) was used. This model is referred to as the Dynamic Model and utilizes the solver function in Excel to iteratively solve for parameters that minimize the error between predicted calendar year escapement and the observed calendar year escapement. This approach allows one to solve for nonlinear functions, such as when covariates are appended to the spawner-recruit functions and to minimize error on escapement rather than on recruits.

Process error—Minimizing the error between predicted and estimated calendar year escapement is used since the escapements are closer to being observed data than recruits, which are based on proportioning catch estimates according to relative escapement or terminal size for each spawning aggregation. In other words, there is undoubtedly greater error in our estimates of recruits than escapement, since the error for recruits includes the error inherent in escapement plus the error introduced from catch estimates and age estimates. The process error in estimating recruits is larger when minimizing on escapement than if we minimized on recruits, reflecting the fact that we are less certain in our estimates of recruits than escapement.

The Dynamic Model uses the existing data of natural spawners, natural-origin spawners, and harvest rates as recorded in the PSTRT abundance and productivity tables, as well as maturation rates and recruits estimated from the cohort run reconstruction done within the abundance and productivity tables. Three spawner-recruit functions are run and compared: hockey stick, Ricker, and Beverton-Holt. For each function, the model iteratively picks spawner-recruit function parameters, predicts the cohort size at age 2 years (adult equivalent [AEQ] recruits divided by age-2 AEQ), and uses the age-specific harvest rates and maturation rates to conduct a cohort run reconstruction. From the run reconstruction, predicted calendar year escapements are constructed and tested against the observed escapements for minimizing error. Predicted AEQ recruits are compared with the AEQ recruits estimated in the abundance and productivity tables to determine the process error to supply the VRAP model.

All three spawner-recruit functions were run using the Dynamic Model. The Dynamic Model calculates the F-statistic that can be used to test if the independent variable—spawners—explains a significant amount of the variation in recruits and the probability from the

F-distribution that the fit could happen from chance using methods from Kleinbaum and Kupper (1978).

$$F = \text{mean square regression/mean square residual} = (N\text{-}2) \times R^2 / (1\text{-}R^2) \qquad (3)$$

where R^2 is the square of the Pearson correlation of the predicted and estimated escapement or recruits. The F-statistic and associated probability can tell us if the independent variable—spawners—significantly explains the variation in escapement or recruits, but cannot tell us which function to use if they all do a good job of explaining the variability.

The Beverton-Holt function was chosen for both the Strait of Juan de Fuca and Hood Canal summer chum populations. The Beverton-Holt function is generally written as

$$R = S / (c \times S + p) \qquad (4)$$

where p is the intrinsic productivity parameter (recruits per spawner approaches 1/p as spawners approach zero) and c is the capacity parameter (maximum recruits = 1/c) (Ricker 1975). In order to express them as recognizable values, VRAP uses the form

$$R = S / (S/\beta + 1/\alpha) \qquad (5)$$

such that α presents the productivity at the origin and β represents maximum recruits. Returns per spawner are modified by the QET and depensation values provided to the model. Spawning levels less than the QET return no recruits and spawning levels between the QET and the depensation level return spawners according to a line between the recruits at depensation and no recruits at QET.

A summary of the output data from the Dynamic Model that are used as input for the VRAP model is given in Table 6. The α and β parameters given in Table 6 represent values estimated over 1974–2001 brood year data. For the VRAP simulation runs, α was set to a fixed number and the model determined the probability of extinction for a range of β values.

VRAP Results

Parameter estimation—Management error was estimated as a gamma distribution with gamma1 = 4.082 and gamma2 = 0.245 (mean = 1, SD = 0.245 with a skewed rather than normal distribution).

For the Strait of Juan de Fuca population, all three spawner-recruit functions determined from the Dynamic Model and estimated over 1974–2001 brood years resulted in parent natural spawners, significantly explaining the variability seen in progeny annual natural-origin spawners at the 1% level of error. The fit of the estimated recruits to the predicted recruit curve was less precise, as was expected since we were not minimizing on recruit error. None of the three spawner-recruit functions showed that the spawners significantly explained the variation seen in recruits. All three spawner-recruit functions indicated low productivity for the population as evidenced by the closeness of the left-hand portion of the curve to the replacement line (Figure 13). The resulting estimate of variability of estimated recruits compared to predicted recruits

Table 6. Summary of output results from the Dynamic Model used as input to the VRAP model for the Strait of Juan de Fuca (Strait) and Hood Canal (Canal) summer chum salmon populations. For each VRAP simulation run, intrinsic productivity (α) and ER were set to fixed values and the model output gave the probability of extinction for a range of capacity (β) parameter values.

Parameter	**Strait**	**Canal**
Function (Beverton-Holt)		
α productivity	4.61	7.24
β capacity	1,590	8,340
Process error		
Gamma1	0.876	0.557
Gamma2	1.982	2.931
QET	300	350
Depensation	310	710
Management error		
Gamma1	4.082	4.082
Gamma2	0.245	0.245
Starting population size		
Age 1	27,072	207,808
Age 2	13,536	103,904
Age 3	8,082	62,289
Age 4	2,721	30,171
Age 5	35	603
Maturation rate		
Age 2	0.0244	0.0015
Age 3	0.5755	0.3857
Age 4	0.9757	0.9505
Age 5	1.0000	1.0000
Harvest rate (all considered mature catch)		
Age 2	0.0000	0.0000
Age 3	0.1281	0.3680
Age 4	0.1291	0.3683
Age 5	0.1271	0.3604
Recent average ER	0.0040	0.1420

was expressed as a gamma distribution with, for the Beverton-Holt function, parameters 0.876 and 1.982 for gamma1 and gamma2. Expressed as a mean and SD, although the distribution is not normal, the values are mean = 1.74, SD =1.85. Note that with a mean of 1.74, the deviations greater than the predicted curve are greater than the deviations less than the curve (Figure 13).

For the Hood Canal population, all three spawner-recruit functions, estimated over 1974–2001 brood years, resulted in parent natural spawners significantly explaining the variability seen in progeny annual natural-origin spawners at the 1% level of error. The fit of the estimated recruits to predicted recruits, using the spawner-recruit parameters based on minimizing on return spawners, was better for the Hood Canal population than the Strait of Juan de Fuca population. The parent spawners significantly explained the variability in recruits at a 5% level for the Beverton-Holt and Ricker functions and at a 10% level for the hockey stick function. We chose the Beverton-Holt function for the analysis of the Hood Canal population to be compatible with the analysis for the Strait of Juan de Fuca population.

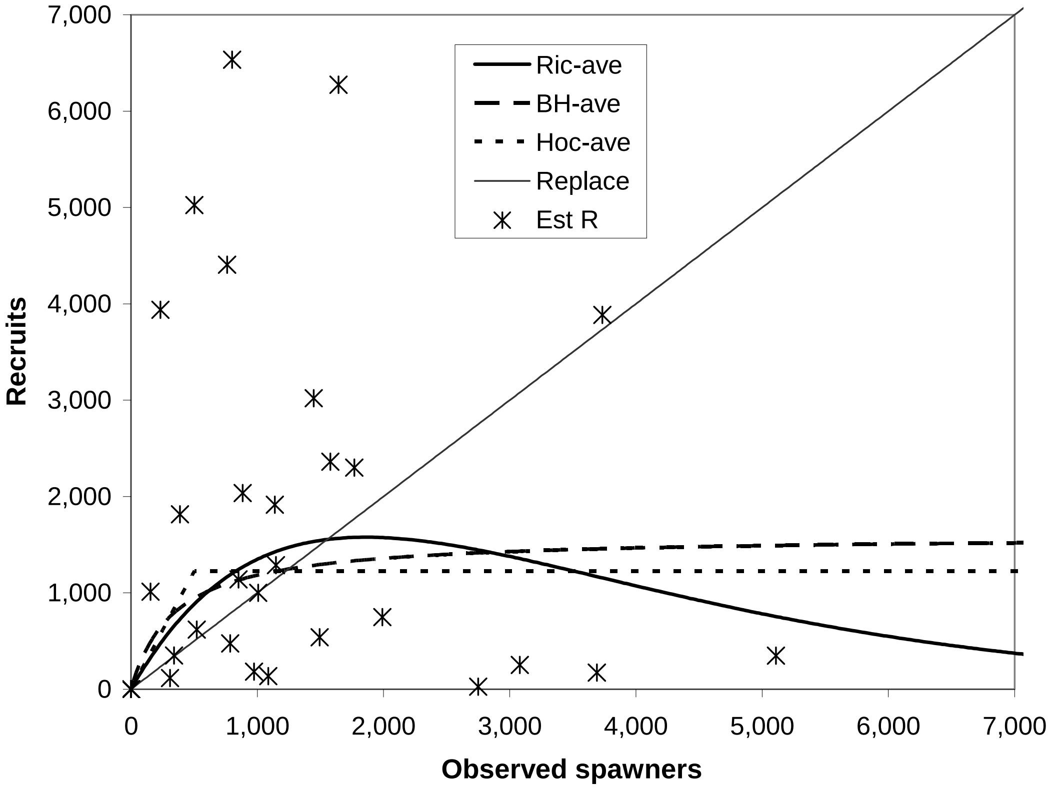

Figure 13. Results from the Dynamic Model for estimation of spawner-recruit functions for the Strait of Juan de Fuca summer chum salmon population. The stars represent actual estimated recruits from the cohort run reconstruction in the abundance and productivity tables.

The Hood Canal population is more productive than the Strait of Juan de Fuca population as evidenced by the spawner-recruit graphs (Figure 13 and Figure 14). The resulting estimate of variability of estimated recruits to predicted recruits for the Hood Canal population expressed as a gamma distribution was 0.557 and 2.931 for the gamma1 and gamma2 parameters, respectively. Expressed as mean and SD, although the distribution is not normal, the values are mean =1.63, SD = 2.19 for the Hood Canal population. Again note that with a mean of 1.63, the deviations greater than the predicted curve are greater than the deviations less than the curve (Figure 14).

Viability criteria—Viability criteria are presented as spawner-recruit functions and there is a family of curves that represent viable population conditions. The parameter α, as estimated by the Dynamic Model for the Beverton-Holt relationship over the 1974–2005 data set, was 4.6 for the Strait of Juan de Fuca and 7.2 for the Hood Canal population. Therefore, we used a range for α of 3–6 and 5–9 for the Strait of Juan de Fuca and Hood Canal populations, respectively, for running the viability simulations. ERs of 0, 0.1, 0.2, and 0.3 were used in the model.

Each VRAP run, with given α and ER levels, estimated extinction probability over a range of β values set by the user. The minimum value of β for viability was then chosen as the smallest level that consistently gave an extinction probability of 5% or less over 100 years. The condition of viability is thus defined by three parameters: α, β, and ER. The associated number

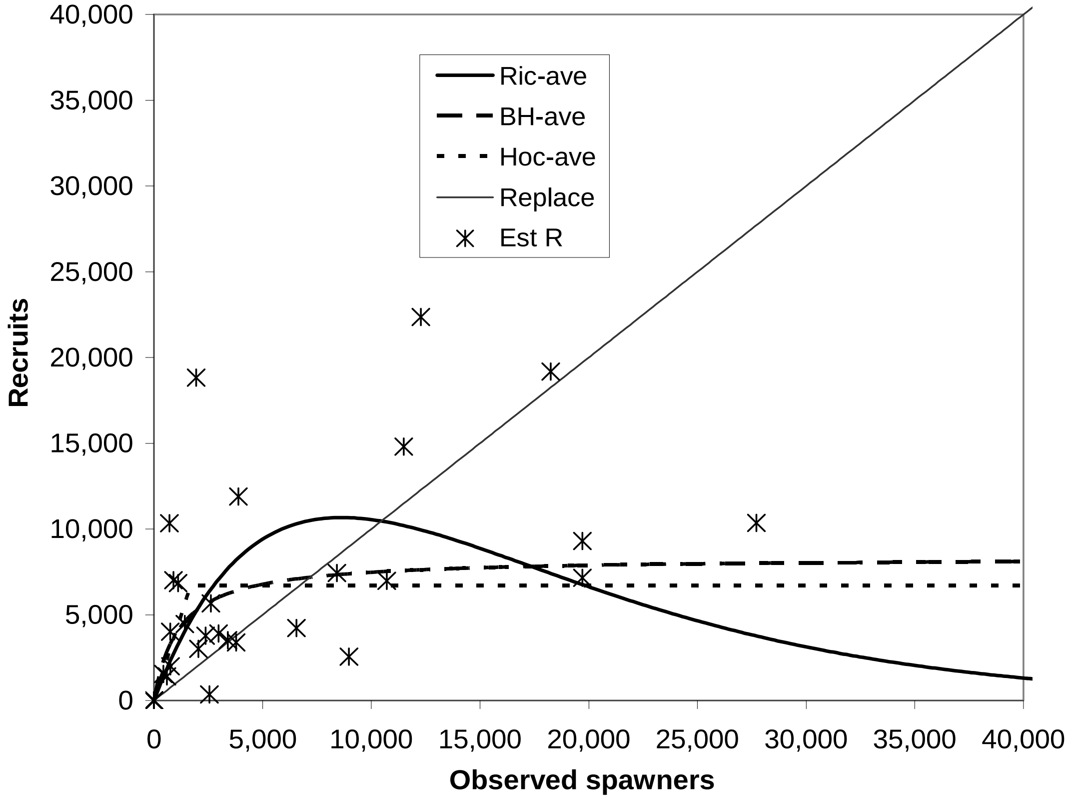

Figure 14. Results from the Dynamic Model for estimation of spawner-recruit functions for the Hood Canal summer chum salmon population. The stars represent actual estimated recruits from the cohort run reconstruction in the abundance and productivity tables. The data point 2000 is off the chart, being 73,500 recruits from a spawning of 8,000 spawners.

of spawners (i.e., the resulting viable escapement level) needed to sustain an equilibrium rate of exploitation, given the α and β parameters, was calculated as the average annual escapement realized over the 100-year run. Each annual escapement is the average of 3,000 simulations. This viable escapement is termed resulting viable escapement since, on its own, the escapement level is not viable unless the function parameters α and β are met and the target ER is not exceeded.

Several combinations of viable population parameters for the two populations in the Hood Canal Summer Chum Salmon ESU are shown in Table 7 and Table 8 and graphed in Figure 15 and Figure 16. In interpreting the results of the VRAP viability analyses, the viability level is a curve defined by the α and β parameters that supports a given ER; the viable escapement level is the average escapement that would result from the given ER. The population could be managed for a target ER from which one would expect the corresponding escapement level on average, or one could manage for the escapement level and, on average, obtain the corresponding ER.

For the 1974–2005 period, α is 4.6, β is about 1,600, and average escapement is about 2,000 summer chum salmon for the Strait of Juan de Fuca population; so the population is not currently viable. It appears that the recent 5-year average escapement of about 4,300 spawners

Table 7. A selection of viable spawner-recruit functions as defined by the intrinsic productivity (α) and capacity (β) parameters for specific exploitation rates (ERs) for the Strait of Juan de Fuca summer chum salmon population (QET = 300). The simulation model, VRAP, estimates the resulting average escapement (Esc) for each combination of α, β, and ER value. VRAP runs were made using both a 1% and a 5% risk of extinction over 100 years.

	$\alpha = 3$		**$\alpha = 4$**		**$\alpha = 5$**		**$\alpha = 6$**	
	β	**Esc**	**β**	**Esc**	**β**	**Esc**	**β**	**Esc**
≤5% risk								
ER = 0.0	4,300	5,100	3,700	4,800	3,300	4,500	3,300	4,700
ER = 0.1	5,300	5,400	4,500	5,100	3,900	4,700	3,700	4,600
ER = 0.2	6,500	5,500	5,300	5,100	4,700	4,800	4,500	4,800
ER = 0.3	9,500	6,400	7,100	5,600	6,300	5,400	5,500	5,000
≤1% risk								
ER = 0.0	8,300	9,700	6,500	8,400	6,300	8,600	5,700	8,000
ER = 0.1	9,100	9,200	7,900	8,800	6,900	8,200	6,300	7,800
ER = 0.2	13,000	10,900	10,000	9,500	8,300	8,500	7,900	8,500
ER = 0.3	18,500	12,300	13,000	10,500	10,500	8,900	9,500	8,500

Table 8. A selection of viable spawner-recruit functions as defined by the intrinsic productivity (α) and capacity (β) parameters for specific exploitation rates (ERs) for the Hood Canal summer chum salmon population (QET = 350). The simulation model, VRAP, estimates the resulting average Esc for each combination of α, β, and ER value. VRAP runs were made using both a 1% and a 5% risk of extinction over 100 years.

	$\alpha = 5$		**$\alpha = 6$**		**$\alpha = 7$**		**$\alpha = 8$**		**$\alpha = 9$**	
	β	**Esc**	**β**	**Esc**	**β**	**Esc**	**β**	**Esc**	**β**	**Esc**
≤5% risk										
ER = 0.0	17,000	20,600	15,000	19,100	14,000	18,400	13,500	18,300	13,000	17,900
ER = 0.1	20,500	21,500	18,500	20,400	17,500	20,000	15,500	18,300	15,500	18,600
ER = 0.2	27,000	23,900	23,500	22,000	21,000	20,700	20,000	20,200	17,500	18,200
ER = 0.3	35,000	25,300	29,000	22,500	27,500	22,300	25,500	21,500	24,000	20,800
≤1% risk										
ER = 0.0	41,500	48,500	37,000	45,500	32,500	41,300	30,500	39,700	29,500	39,200
ER = 0.1	53,500	54,200	42,000	45,100	38,500	43,000	33,000	38,100	33,000	38,800
ER = 0.2	66,500	57,100	55,000	50,200	51,000	48,800	43,500	43,000	42,000	42,500
ER = 0.3	97,500	68,000	77,500	58,500	66,000	52,300	61,000	50,400	57,000	48,300

(upper circle in Figure 15) is close to the escapement needed for a viable population and that the viable escapement levels do not vary widely over the ranges of productivity values modeled (Table 7, Figure 15). However, escapement or productivity or both alone do not define population viability. In particular, higher capacity values are needed for the Strait of Juan de Fuca population to maintain no more than a 5% probability of extinction over a 100-year time frame.

Similar statements can be made for the Hood Canal summer chum population, that is, with current capacity ($\beta = 8{,}300$) and current productivity ($\alpha = 7.2$), the population is not viable (Table 8, Figure 16) even though the recent 5-year average escapement is about 23,000 spawners

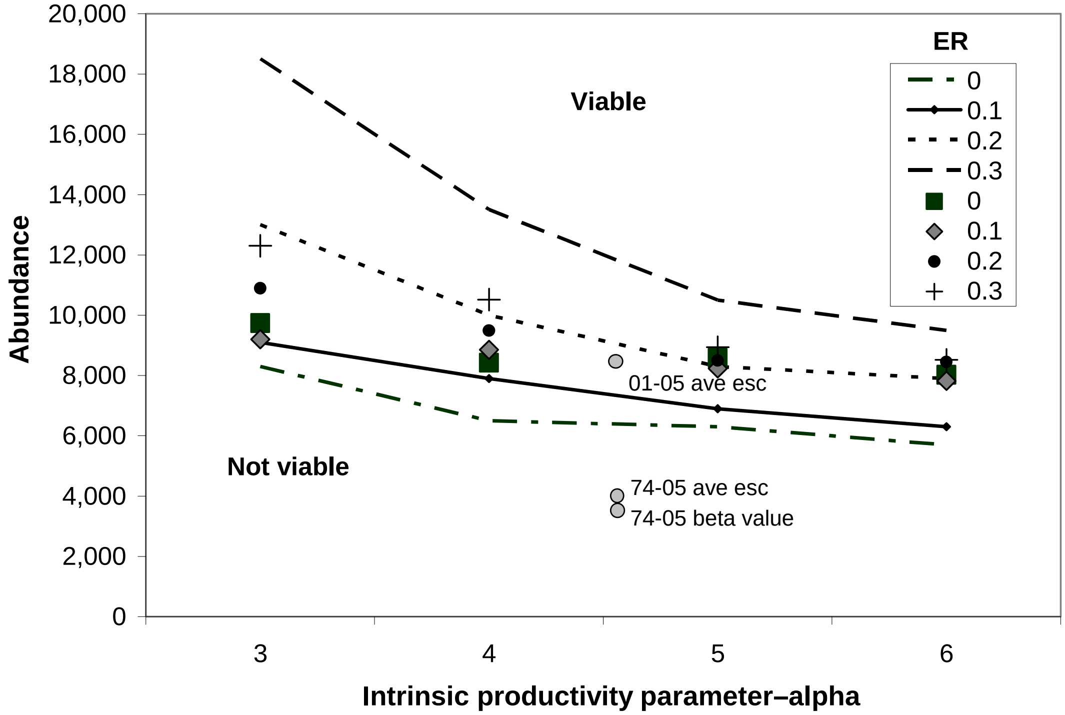

Figure 15. Viability curves for the Strait of Juan de Fuca summer chum salmon population for no harvest, expressed as ER, and three levels of ER (lines) and associated realized escapement levels (symbols) using the 5% probability of extinction over 100 years. Viability curves are defined by function parameters (intrinsic productivity on the x-axis and capacity on the y-axis), not by escapement abundance. Also indicated on the graph, by circles, are the capacity (abundance = 1,600) and average escapement (abundance = 1,800) at average productivity (4.6 on x-axis) determined over the period of the analysis (1974–2005). The recent (2001–2005) average escapement (abundance = 4,300, plotted at average 1974–2005 intrinsic productivity) is also shown. The population is not viable despite recent escapements of about 4,300 spawners as the capacity is too low for the associated productivity.

(upper circle in Figure 16). Again, in particular, higher capacity values are needed to maintain no more than a 5% probability of extinction over a 100-year time frame.

The difference in viable abundance for the two populations is—like the SimSalmon estimates—due to the greater QET and variability for the Hood Canal population. In the VRAP analysis, differences in depensation levels and maturation rate (Table 7 and Table 8) also contribute to the differences in viability levels; however, it is the process error (variability around predicted recruits) that attributes to most of the difference.

Comparison of SimSalmon and VRAP results

Results from the PVAs for no harvest are compared in Table 9 using the 5% and 1% risk of extinction criteria, respectively. As SimSalmon results are for no harvest, only the no harvest case for VRAP is compared here. Viability curves for various levels of harvest are in Table 7 and Table 8. It is not surprising that VRAP viability escapements are much less than SimSalmon

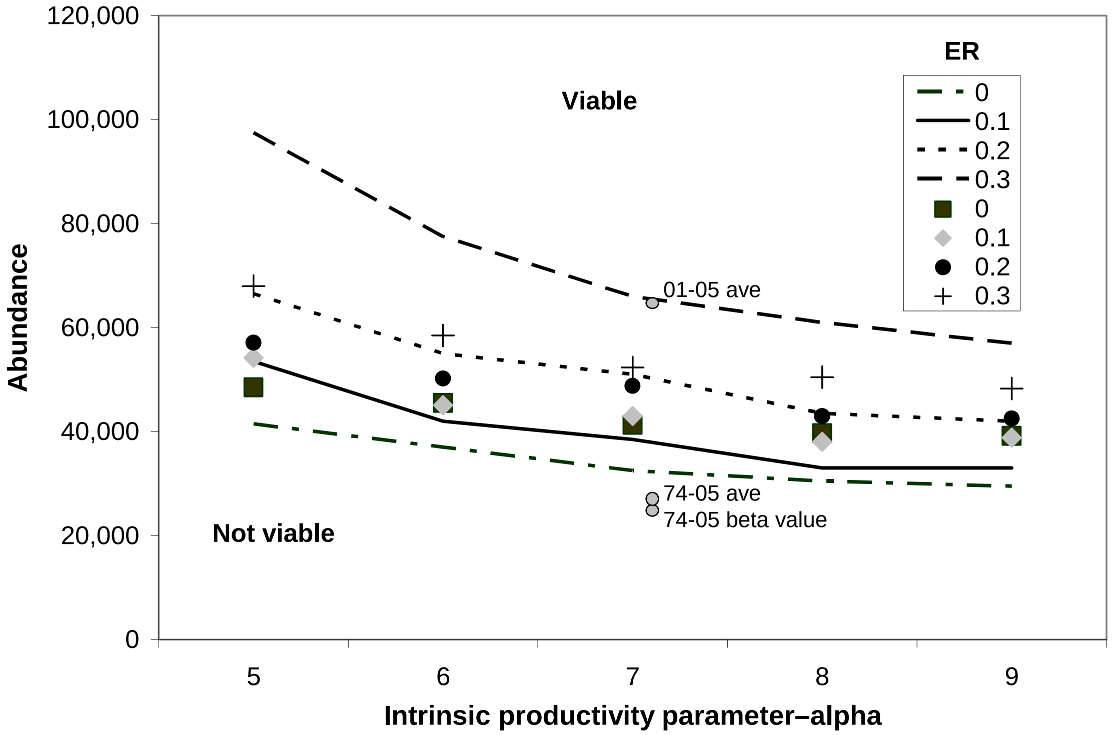

Figure 16. Viability curves for the Hood Canal summer chum salmon population for no harvest, expressed as ER, and three levels of ER (lines) and associated realized escapement levels (symbols) using the 5% probability of extinction over 100 years. Viability curves are defined by function parameters (intrinsic productivity on the x-axis and capacity on the y-axis), not by escapement abundance. Also indicated on the graph, by circles, are the capacity (abundance = 8,300) and average escapement (abundance = 8,600) at average productivity (7.2 on x-axis) determined over the period of the analysis (1974–2005). The recent (2001–2005) average escapement (abundance = 23,000, plotted at average 1974–2005 intrinsic productivity) is also shown. The population is not viable despite recent escapements of about 23,000 spawners as the capacity is too low for the associated productivity.

estimates, since VRAP assumes the robustness of the population to return more recruits per spawner at lower spawning levels than at higher spawning levels.

From the SimSalmon analysis, higher escapement abundance levels are needed for viability, since the method assumes density independence and the relatively conservative population condition that productivity is at a level where one spawner produces only one adult fish in the subsequent generation (i.e., the population is just replacing itself). There are no positive density-dependent effects at low population sizes. From the VRAP analysis, lower escapement levels are possible for viability if the viable α and β can be estimated and met. This requires that data is sufficient to estimate and understand the population dynamics and that density dependence can be shown or assumed.

Incorporating Spatial Distribution Characteristics into Evaluation of Viability

All four VSP parameters are critical to the viability of salmon populations; all are interrelated, and levels of all four attributes in aggregate characterize extinction risk (Fresh et al.

Table 9. Viability estimates of escapement from the two PVA analyses for 5% risk and 1% risk of extinction and no harvest for the Strait of Juan de Fuca and Hood Canal populations. Note that the VRAP viable escapement levels are only valid if the associated productivity (α) and capacity (β) parameters are also achieved. Other viable productivity and capacity pairs are possible; those given here are for intrinsic productivity equal or close to current intrinsic productivity for comparison with SimSalmon.

Risk	**QET**	**SimSalmon Esc**	**VRAP**					
Strait of Juan de Fuca								
			α = 3		α = 4		α = 5	
			β	Esc	β	Esc	β	Esc
5%	300	12,500	4,300	5,100	3,700	4,800	3,300	4,500
1%	300	30,800	8,300	9,700	6,500	8,400	6,300	8,600
Hood Canal								
			α = 6		α = 7		α = 8	
			β	Esc	β	Esc	β	Esc
5%	350	24,700	15,000	19,100	14,000	18,400	13,500	18,300
1%	350	84,500	37,000	45,500	32,500	41,300	30,500	39,700

in press). Developing approaches to evaluate spatial structure and diversity in recovery planning and implementation are needed so that recovery options can be completely assessed and possible outcomes of suites of actions fully evaluated (McElhany et al. 2000). A quantitative analysis of spatial distribution was conducted here to help further guide evaluations of the viability of the populations in terms of all four VSP characteristics and their interacting effects. The following analysis and results are presented not as a prescriptive solution but as quantitative information to help illustrate the relationships to be considered in evaluations of viability relative to the above described criteria. We have no direct measures for life history diversity, but for the purposes of defining population viability, we assume that if spatial distribution remains diverse, then so will life history diversity.

Methods

The diversity index is a single statistic that describes the number of components in a group and their relative abundance or evenness. Diversity is high when there are many components and their abundances are fairly even. Our components are spawning aggregations and their abundances are spawning numbers. Since spawning aggregations are spatially separated units, we are looking at the spatial structure of the population as well as relative abundances. We used both Simpson (1949) and Shannon (Shannon and Weaver 1949) measures of diversity. The latter has the advantage of being able to measure diversity of the ESU hierarchically by characterizing diversity of spawning aggregations within a population and populations within the ESU (Pielou 1969).

The Simpson index (D) is formulated as

$$D = 1-1/(N(N-1)) \sum_j N_j(N_j-1) \tag{6}$$

where N is the total population (natural escapement) or sample from the population and N_j is the total number of N that belong to spawning aggregation j. If the probability of two individuals chosen at random belonging to the same spawning aggregation is high, then diversity is low. For a given set (number) of spawning aggregations, diversity is at a maximum when all spawning aggregations have the same abundance.

The Shannon index (H) for a population is formulated as

$$H = -\sum_j (N_j/N) \ln(N_j/N) \tag{7}$$

For the ESU the multigroup index is formulated as

$$H = H(ESU) + H(P) \tag{8}$$

where H(ESU) is the diversity based on the populations within the ESU and H(P) is the average of the diversities within each population.

Data

The annual spawning escapement for the Strait of Juan de Fuca summer chum salmon population has been monitored for four component spawning aggregations since 1974: Jimmycomelately, Salmon, Snow, and Chimacum creeks. Over the period 1974–2005, 60% of the natural spawners and 66% of the total return (spawners + broodstock + catch) were observed as returns to Salmon Creek. More extensive monitoring of returns to the Dungeness River, where summer chum are known to occur at very low levels (WDFW and PNPTT 2000), has been done during August through October since at least 1986 (i.e., at the same time as spawner surveys for Chinook salmon in the system). Estimated Dungeness River escapement represented 1.5% of the total spawning for the Juan de Fuca population in 2004 and 0.02% in 2005. The Chimacum Creek stock was extirpated in the early 1980s and a hatchery-based reintroduction program using Salmon Creek spawning aggregation began in 1996 to reestablish summer chum spawning.

The annual escapement for the Hood Canal summer chum salmon population has been monitored for 11 spawning aggregations: Little Quilcene, Big Quilcene, Dosewallips, Duckabush, Hamma Hamma, Dewatto, Tahuya, and Union rivers and Lilliwaup, Anderson, and Big Beef creeks. Over the period 1974–2005, 86% of the natural spawners and 80% of the total return (spawners + broodstock + catch) were from five spawning aggregations: Big Quilcene, Dosewallips, Duckabush, Hamma Hamma, and Union rivers. Returns to Big Beef and Anderson creeks declined to no fish in the 1980s; a hatchery reintroduction program was initiated on Big Beef Creek in 1996. Returns to the Dewatto and Tahuya rivers diminished to very low levels (<9 annually for Dewatto and 1 annually for the Tahuya) in the 1990s and both native stocks are considered functionally extirpated (WDFW and PNPTT 2000); a hatchery reintroduction program was initiated on Tahuya River in 2003. Focused monitoring of annual summer chum escapements to the Skokomish River, where the native summer chum population was extirpated, began in 2004.

The total number of fish escaping to spawn naturally is used as the measure of annual abundance for diversity estimation.

Results

The relative total abundance of spawning by the component spawning aggregations has changed over time. For the Strait of Juan de Fuca population, this has reduced the diversity of the population (Figure 17). In the early years of our data availability (1974–1978), there were relatively equal proportions spawning in Jimmycomelately, Snow, and Salmon creeks; in recent years the majority of the escapement for the population has been observed in Salmon Creek. Returns to Chimacum Creek were reestablished beginning in 1999 with a hatchery supplementation program using Salmon and Snow creek stock. Surveys of salmon on the Dungeness River suggest that this system during this time had few to no summer chum spawners; it represented only 1% of the total spawning in 2004.

For the Hood Canal population, from 1974 to 1978 three spawning aggregations—the Dosewallips, Duckabush, and Hamma Hamma rivers—had more than 50% of the escapement (Figure 18). In most recent years, the Big Quilcene River has had on average 42% of the escapement followed by the Dosewallips and Union rivers.

Results from the two diversity indices are very similar for both populations (Figure 19 and Figure 20). For the Strait of Juan de Fuca population, the average over the early period of 1974–1978, when the diversity was relative constant, is 63% for the Simpson index and 1.05 for the Shannon index. The diversity index, which reflects spatial distribution and relative abundance, declined during the 1980s and 1990s and now shows a recent increase. A good initial target level for viability would be the early year (1974–1978) average, as we know this is attainable by this population. The maximum values for a population with five components, all being equally abundant, are 80% and 1.61, respectively for the Simpson and Shannon indices. The averages for recent years (2001–2005), where an increase is observed, are 45% and 0.86, respectively, and appear to indicate a trajectory towards the earlier levels (Figure 19). As returns to Chimacum Creek and Dungeness River increase, diversity can surpass that of the earlier years when returns to these two systems were low to none.

For the Hood Canal population, relatively high stable indices of diversity extended from 1974 through 1985. Starting with data from 1974, the average over this relatively stable period is 80% for the Simpson index and 1.86 for the Shannon index. The diversity values declined during the 1980s and 1990s and show recent increases since about 2000. Again, a good initial target level for viability would be the early year (1968–1985) average. The averages for recent years (2001–2005), where an increase is observed, are 74% and 1.6, respectively, and appear to indicate a trajectory towards the early period averages. The maximum values for a population with 12 components, all being equally abundant, are 92% and 2.48, respectively for the Simpson and Shannon indices.

ESU Viability

The ESU viability criterion for the Hood Canal Summer Chum Salmon ESU is relatively simple: in order for the ESU to have a negligible risk of extinction, both the Strait of Juan de Fuca and Hood Canal populations need to be viable. Summer chum salmon exist today in each of these two historical populations in several spawning aggregations located in various rivers and creeks (Identification of Independent Populations section, Figure 8).

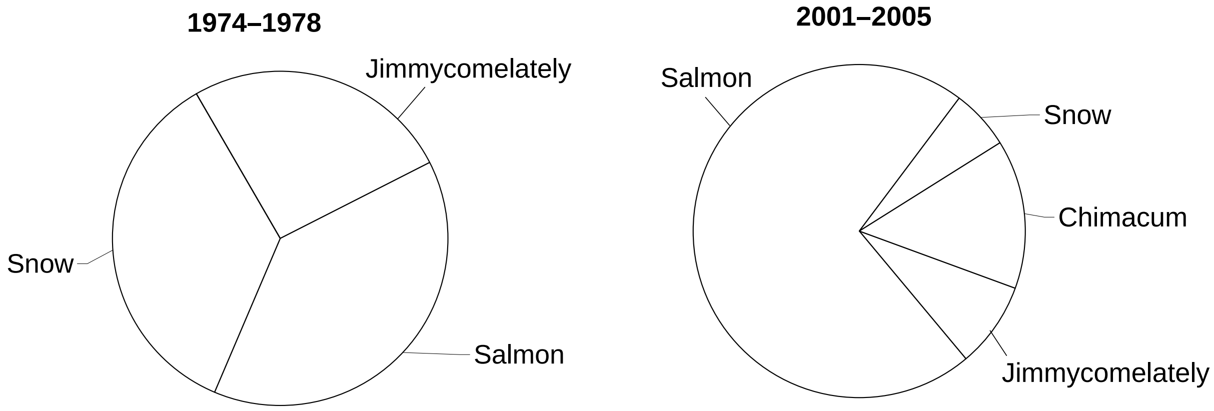

Figure 17. Distribution of escapement for spawning aggregations within the Strait of Juan de Fuca summer chum salmon population for 1974–1978 and 2001–2005. The pie sections represent the average annual percentage of total population escapement represented by each spawning aggregation over the given time period. The Simpson Index associated with 1974–1978 is 0.63 compared with 0.45 for 2001–2005. The comparable Shannon indices are 1.05 and 0.86 as of 20 December 2006.

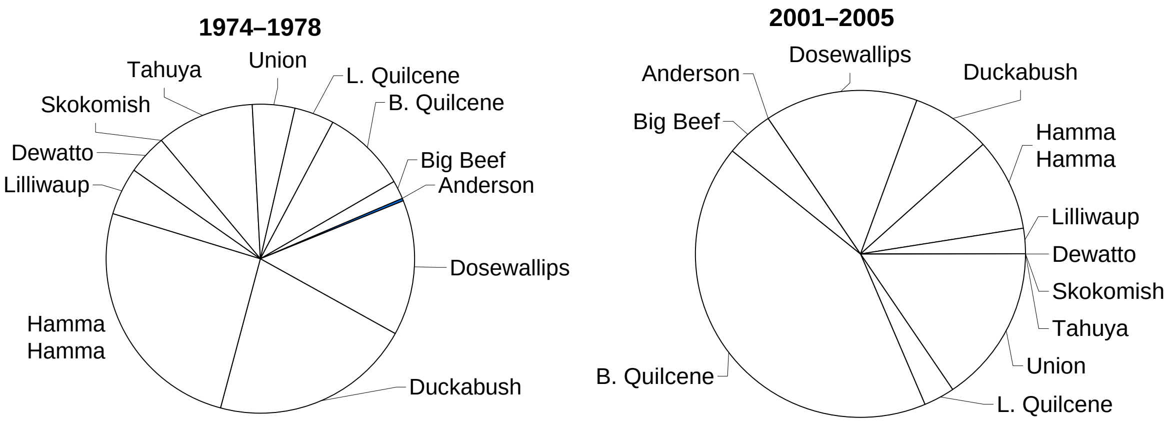

Figure 18. Distribution of escapement for spawning aggregations within the Hood Canal summer chum salmon population for 1974–1978 and 2001–2005. The pie sections represent the average annual percentage of total population escapement represented by each spawning aggregation over the given time period. The Simpson Index associated with 1974–1978 is 0.80 compared with 0.74 for 2001–2005. The comparable Shannon indices are 1.86 and 1.60 as of 29 December 2006.

Discussion and Recommendations

Abundance and Productivity

The range in viable population spawning abundances as determined from SimSalmon represents the range of the risk of extinction from 5 to 1 percent and gives a single escapement value assuming no density dependence in recruits per spawner, although the method of predicting returns does incorporate a maximum return. The VRAP method incorporates density dependence, assumes a function with productivity that changes with spawning level, and has an

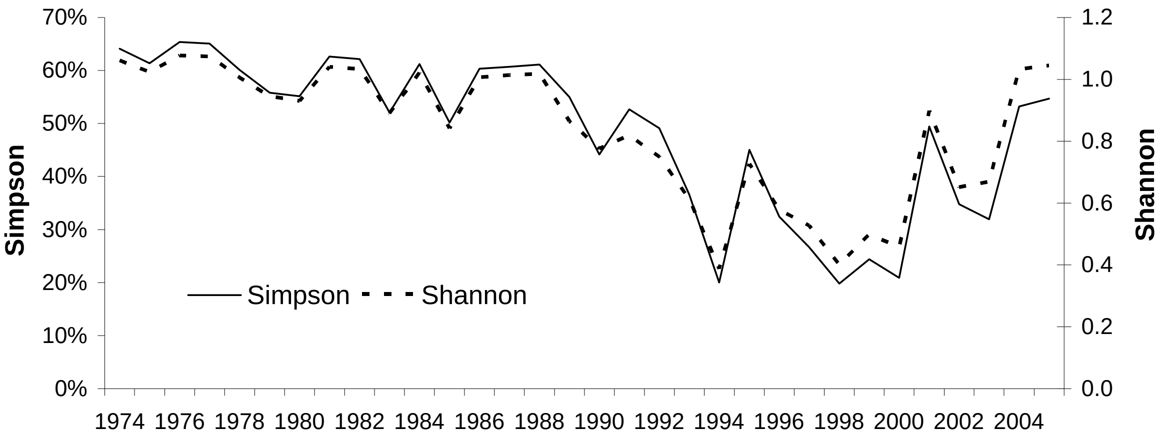

Figure 19. Diversity indices for the Strait of Juan de Fuca summer chum salmon population, 1974–2005. The indices are estimated over the five spawning aggregations in this population.

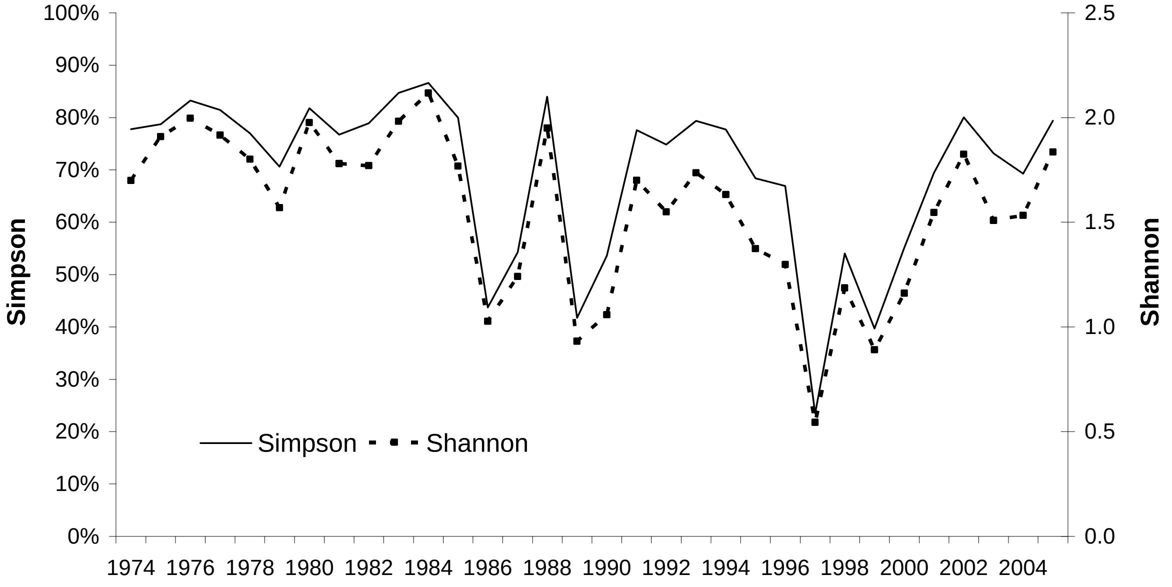

Figure 20. Diversity indices for the Hood Canal summer chum salmon population, 1974–2005. The indices are estimated over the 12 spawning aggregations in this population.

average maximum recruit value (i.e., capacity). This second approach allows us to determine the productivity and capacity needed for different levels of harvest. The viable escapement level as estimated using VRAP is dependent on the population achieving the associated intrinsic productivity and capacity parameters of the viable spawner-recruit curve.

The SimSalmon viability goals are simply escapement levels for a given level of risk and do not address the question of how much harvest the population can sustain and remain viable. Also, because the SimSalmon method does not incorporate density dependence, abundance levels resulting from this approach are generally higher than those resulting from models that assume that productivity increases as abundance decreases. This difference is apparent when comparing the SimSalmon and VRAP results (Table 9).

Another method of examining viable escapement levels is to estimate population capacity and productivity under habitat conditions defined as properly functioning by NMFS (1996). This method was used for Puget Sound Chinook salmon populations using ecosystem diagnosis and treatment (EDT) (Rawson et al. in prep.). The Hood Canal Coordinating Council and the comanagers are conducting EDT analyses for stocks within the Hood Canal Summer Chum Salmon ESU; they are expected to be available in late 2009.[3]

Spatial Structure and Diversity

The relative total abundance of spawning by the component spawning aggregations has changed over time for both populations, with one spawning aggregation in each population now contributing most of the total abundance (Figure 17 and Figure 18). This has reduced the diversity index for both populations, although the declines in the diversity measure seen in the late 1980s and 1990s have been reversed since around 2000 (Figure 19 and Figure 20). As formally extinct stocks are being reintroduced through hatchery supplementation programs, both populations have the opportunity to increase the number of spawning aggregations and, with time, increase the relative contribution of currently low abundance spawning aggregations. Both of these events would increase the diversity index and, by improving spatial structure, allow for a fuller expression of life history diversity types.

The subpopulation structure of summer chum salmon has important implications for designing successful strategies to recover the spatial structure and diversity attributes necessary for viable salmon populations. Efforts to rebuild sustainable populations by recovering habitat and reintroducing summer chum salmon to tributaries where they have been extirpated will be most successful if they focus on streams with major spawning aggregations, which can act as core natural production areas, and the smaller tributaries that are needed to reestablish the connections among these larger groups.

Although we found little information on adaptive differences among stocks across the range of summer chum differences that might guide reintroduction efforts, our analyses of spatial patterns of neutral genetic variation suggest that sources of broodstock for reintroductions should come from nearby spawning aggregations, as previously described in the Summer Chum Salmon Conservation Initiative (WDFW and PNPTT 2000) and implemented for the three reintroduction programs in the region. This would simulate the natural patterns of gene flow in summer chum salmon that we believe are most likely to promote successful reestablishment.

Recommendations

Recommendation 1: Abundance and productivity

A viable population of summer chum salmon in the Strait of Juan de Fuca population has 12,500 spawners, assuming a 1:1 replacement rate and density-independent dynamics at low population sizes. Spawner escapement numbers for a viable Strait of Juan de Fuca population

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[3] L. Lestelle, Biostream Environmental, Poulsbo, WA. Pers. commun., 20 August 2009.

could be as low as 4,500 adults if we can assume that the population is driven by density-dependent dynamics and the intrinsic α and β parameters of the population's viable spawner-recruit curve can be estimated and achieved (i.e., for escapement = 4,500, then $\alpha = 5$ and $\beta = 3{,}300$). Similarly, a viable population of summer chum in the Hood Canal population has 24,700 spawners, assuming a 1:1 replacement rate and density-independent dynamics at low population sizes. Spawner escapement numbers for a viable Hood Canal population could be as low as 18,300 adults if we can assume that the population is driven by density-dependent dynamics and the corresponding intrinsic α and β parameters of the population's viable spawner-recruit curve can be estimated and achieved (i.e., for escapement = 18,300, then $\alpha = 5$ and $\beta = 13{,}500$). Estimates of spawner escapement consistent with viable summer chum populations under different assumptions of intrinsic productivity, capacity, and persistence probability are presented in Table 5 and Tables 7–9.

Before the population achieves its viable state (where the population abundance is stable, or $\lambda = 1$), a useful benchmark for tracking progress in recovery is for the population growth rate for spawners (λ) to be greater than 1.

Rationale: A population will have a low risk of extinction if it has sufficient abundance and productivity to withstand the natural variability in returns due to environmental and anthropogenic factors. Viability estimates are based on natural variation observed in returns per spawner or population growth rate, and specifying in a population projection that the population not go below a quasi-extinction level more than a small proportion of the time. The relationship between abundance and productivity for a particular population can be represented as a curve along which productivity required for viability decreases as abundance increases.

In contrast, the higher viable abundance numbers that we present assume density independence and relatively conservative population conditions; that is, the productivity is at a level where one spawner produces only one adult fish in the subsequent generation (the population is just replacing itself) and there are no positive density-dependent effects at low population sizes. On the other hand, the lower viable escapement numbers we present are possible if we know more about the population dynamics and can assume density dependence; that is, if the population realized productivity is greater than replacement, the capacity of the population is known, and there are positive impacts of density dependence at low population sizes. Under conditions of higher productivity, the resilience of the population to environmental changes is increased, and fewer spawners than the equilibrium level are required to assure the viability of the population.

Uncertainty: Significant scientific uncertainty exists in our ability to describe the characteristics of a viable summer chum salmon population. This uncertainty results from 1) our limited understanding of the interacting factors controlling population dynamics, 2) the quality and quantity of data available, and 3) our inability to predict the environmental and anthropogenic conditions that will affect each population in the future. The structure and parameters included in the viability models used by the PSTRT may result in underestimates or overestimates of the abundance and productivity criteria. Qualitatively evaluating the net bias of the models is difficult due to the large number of confounding factors that must be considered. Ecological interactions, the spatial distribution of the population, life history diversity, and variance of the estimate of the variability in the population growth rate were not incorporated into the analyses and are likely to result in underestimates in the abundance criteria. Therefore, depending on the biological conditions in an individual population, the accuracy of the estimated probability of persistence for a population at a given level of abundance is uncertain.

A key uncertainty in the recovery abundance criteria for the Strait of Juan de Fuca population focuses on the role of the Dungeness River spawning aggregation. Although currently summer chum salmon are observed in small numbers in the Dungeness River, the historical size of this spawning aggregation is unknown. Likewise, although spawning in the Dungeness River is important to maintain the spatial distribution and diversity of the population, the potential contribution of summer chum spawning to abundance under recovered habitat conditions is unknown. This has important implications in determining recovery criteria for abundance for the Strait of Juan de Fuca population as shown by the different results of our PVA modeling.

Given the uncertainty, we recommend using abundance criteria assuming that the Dungeness River would contain one of the major spawning aggregations for this population because it minimizes the likelihood that, at the recommended abundance levels, the population would go extinct. In keeping with the approach we used for other ESUs, such as Puget Sound Chinook salmon and Lake Ozette sockeye salmon (*O. Nerka*), we also recommend that when analyses of potential habitat capacity and information about the response of the Strait of Juan de Fuca population—including the Dungeness River—recovery actions become available, they be used to verify the recommended abundance criteria. For populations in other ESUs, we have used this information as part of a series of decision rules to moderate against setting abundance criteria unrealistically high.

As with all viability goals for abundance and productivity, those presented in this document are based on observed variability in the returns of salmon related to the escapement. This estimate of variability will likely change over time as environmental conditions change and recovery actions are taken. As such, viability goals should be reevaluated on a regular basis. New analyses and methods should also be incorporated as they become available.

Recommendation 2: Spatial structure

A viable population contains multiple persistent spawning aggregations. The number of persistent aggregations needed for viability depends on the historical biological characteristics of the population and the historical distribution of spawning aggregations of the population. A population that meets the criteria below is likely to have a negligible risk of extinction over a 100-year period (i.e., be viable):

- Spawning aggregations are distributed across the historical range of the population.
- Most spawning aggregations are within 20 km of adjacent aggregations.
- Major spawning aggregations (spawning aggregations in rivers and creeks that have historically provided the most persistent habitat) are distributed across the historical range of the population and are not more than approximately 40 km apart.

Rationale: A population with well-distributed spawning aggregations is less likely to go extinct than one with a severely limited distribution. Within populations that have a considerable range of distances between the most widely separated aggregations (such as those in the Hood Canal Summer Chum Salmon ESU), well-distributed spawning aggregations can "spread the risk" from disturbances, lending the population more resistance to severe local disturbances and catastrophes. Furthermore, should an aggregation suffer decline or extirpation, nearby aggregations can act as sources for rescue or recolonization, provided they are not too distant. In particular, major spawning aggregations in relative proximity throughout the population help to further maintain a balance between the benefits of connectivity and broad distribution. Finally, geographically well-distributed aggregations also provide important ecological contributions to freshwater and marine ecosystems.

Although it may not be necessary to reestablish spawning aggregations in all rivers and streams where they historically occurred, meeting spatial structure population viability criteria in the Hood Canal and Strait of Juan de Fuca populations will require reestablishing spawning aggregations in many of the major rivers and the smaller streams and creeks where they have been extirpated. The loss of these intermediate stepping-stone spawning aggregations can increase the demographic isolation of subpopulations, which increases the likelihood of these subpopulations becoming extinct, and which in turn reduces the likelihood of population and ESU persistence.

Based on the genetic analyses and historical distribution of summer chum salmon in the ESU, our analyses suggest that most spawning aggregations should be within 20 km of each other and that major spawning aggregations (e.g., in larger river systems) should not be separated by more than approximately 40 km. Particularly in the early stages of population and ESU recovery, production of summer chum from smaller streams may provide important contributions to the health of freshwater, estuarine, and marine ecosystems and to the maintenance of the viability of the populations. The presence of salmon in these habitats can provide stopgaps for ecological services and may provide temporary but significant cumulative production while degraded habitats in other rivers and creeks recover.

The loss of the Skokomish River, the largest tributary to the geographic region, to the collection of spawning aggregations in the southwestern area of the Hood Canal catchment may represent a loss of both major historical ecological diversity and spatial connectivity to the remainder of the ESU.

Recommendation 3: Diversity

Depending on the geographic extent and ecological context of the population, a viable population includes one or more persistent spawning aggregations from each of the two to four major ecological diversity groups historically present within the two populations.

Rationale: This recommendation is meant to help maintain the genetic and phenotypic diversity of the population. For any population, maintaining genetic and phenotypic diversity is critical for responding to future environmental variability and change. Such diversity also allows the population to occupy, and thus potentially adapt to, a wider range of environmental conditions and to colonize or recolonize newly available habitats. The conservation of this diversity is particularly important for recovery of a population that occupies a large area of diverse habitats as do the populations within the Hood Canal Summer Chum Salmon ESU.

Maintaining and reestablishing functional subpopulations across the range of ecological diversity historically experienced by summer chum salmon may help promote the above diversity. Therefore, a viable distribution of spawning aggregations will contain persistent spawning aggregations within each of the major ecological diversity groups described below (see Table 2 and Figure 8). We specifically exclude the Toandos group from this criterion until we have evidence that spawning aggregations within the unit may significantly contribute to ESU spatial structure.

The spawning and early rearing range of the Strait of Juan de Fuca population is comprised of two ecological diversity groups with historical spawning aggregations in rivers and streams entering the Eastern Strait of Juan de Fuca Geographic Region of Puget Sound. The Dungeness unit has headwaters in the High Olympics, Low Olympics, and Coast Range Volcanics ecoregions and lower reaches in the Olympic Rainshadow ecoregion and constitutes the first ecological diversity group within the Eastern Strait of Juan de Fuca Geographic Region. The second unit is comprised mostly of the Sequim Bay, Discovery Bay, and Admiralty Inlet watersheds, which are all fully contained within the Olympic Rainshadow ecoregion. It is referred to as the Sequim-Admiralty ecological diversity group. Those West Kitsap watersheds that drain into Admiralty Inlet are also part of this second unit (Figure 8); they are all fully contained within the Central Puget Sound Lowlands ecoregion.

Similarly, the early life history range of the Hood Canal population is comprised of five ecological diversity groups, four of which contain historical spawning in rivers and streams entering the Hood Canal Geographic Region of Puget Sound. The watersheds within the Quilcene unit have headwaters in the High Olympics, Low Olympics, and Coast Range Volcanics ecoregions and lower reaches in the Olympic Rainshadow ecoregion. The watersheds within the Mid West Hood Canal unit are fully contained within the High Olympics, Low Olympics, and Coast Range Volcanics ecoregions. The watersheds within the West Kitsap unit are fully contained within the Central Puget Sound Lowlands ecoregion. The watersheds within the Lower West Hood Canal unit have headwaters in the High Olympics, Low Olympics, and Coast Range Volcanics ecoregions and lower reaches in the Central Puget Sound Lowlands ecoregion. The Toandos unit has watersheds fully contained within the Olympic Rainshadow ecoregion. See Table 2 for a listing of the ecological composition of each stratum and the associated historical and extant spawning aggregations of summer chum salmon each contains.

Some uncertainty remains regarding the appropriate geographic scale for delineation of ecological diversity as it relates to biological diversity of the ESU and the population units, particularly understanding the significance of marine biogeographic and ecoregional diversity to summer chum diversity. Regardless of the way ecological diversity is divided, the loss of spawning aggregations within three or four of the major ecological diversity groups demonstrates losses in spatial connectivity and distribution and the potential for selective differences within the ESU.

Recommendation 4: Viable population

A viable population has spawning, rearing, and migratory habitats that function in a manner that is consistent with population persistence.

Rationale: In addition to providing spawning and freshwater rearing habitat, the biological characteristics and distribution of summer chum salmon suggest that rivers, streams, estuaries, and nearshore habitats within the Hood Canal Summer Chum Salmon ESU can be important for viability in other ways.

- Conditions in freshwater tributaries will affect the estuarine and nearshore environments into which they empty. Poor water quality and other habitat degradation can create inhospitable or stressful local conditions for summer chum salmon utilizing the estuaries and nearshore.
- Estuarine habitats associated with both spawning and nonspawning tributaries act as stepping-stone habitats for early marine outmigrants and returning migrants, thus potentially affecting the probability of successful dispersal and recolonization.

Recommendation 5: ESU viability

The Hood Canal Summer Chum Salmon ESU would have a negligible risk of extinction if both of the historical populations of summer chum achieve a low risk (i.e., viable) status.

Rationale: Criteria for a viable ESU focus on minimizing risk and maximizing resiliency of the ESU to catastrophic events or to environmental changes that occur too rapidly for population adaptation. The VSP document (McElhany et al. 2000) suggests using historical patterns of population abundance, distribution, and diversity as a reference against which to evaluate ESU viability, since an historical ESU was very likely viable. The aim of the ESU viability guidelines is to describe the viability characteristics of the component populations that are necessary to ensure a high probability of ESU persistence. “Viable” in this sense refers to a naturally self-sustaining population that has a negligible risk of extinction over a 100-year time frame.

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