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Hydrologic regime and the conservation of salmon life history diversity

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A B S T R A C T

Life history diversity of imperiled Pacific salmon *Oncorhynchus* spp. substantially contributes to their persistence, and conservation of such diversity is a critical element of recovery efforts. Preserving and restoring diversity of life history traits depends in part on environmental factors affecting their expression. We analyzed relationships between annual hydrograph patterns and life history traits (spawn timing, age at spawning, age at outmigration, and body size) of Puget Sound Chinook salmon (*Oncorhynchus tshawytscha*) to identify environmental indicators of current and historic diversity. Based on mean monthly flow patterns, we identified three hydrologic regimes: snowmelt-dominated, rainfall-dominated, and transitional. Chinook populations in snowmelt-dominated areas contained higher proportions of the stream-type life history (juvenile residence >1 year in freshwater), had older spawners, and tended to spawn earlier in the year than populations in rainfall-dominated areas. There are few extant Puget Sound populations dominated by the stream-type life history, as several populations with high proportions of stream-type fish have been extirpated by construction of dams that prevent migration into snowmelt-dominated reaches. The few extant populations are thus a high priority for conservation. The low level of genetic distinction between stream-type and ocean-type (juvenile residence <1 year in freshwater) life histories suggests that allowing some portion of extant populations to recolonize habitats above dams might allow re-expression of suppressed life history characteristics, creating a broader spatial distribution of the stream-type life history. Climate change ultimately may limit the effectiveness of some conservation efforts, as stream-type Chinook may be dependent on a diminishing snowmelt-dominated habitat.

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1. Introduction

Conservation of life history diversity is important to the persistence of species confronted by habitat change and environmental perturbations (Kendall and Fox, 2002; Watters et al., 2003). This is particularly true among Pacific salmon (Hilborn et al., 2003; Ford, 2004), where conservation of such diversity

has become an important goal of recovery efforts for imperiled stocks (McElhany et al., 2000; Ruckelshaus et al., 2002, 2003). However, two critical challenges for conservation are determining which populations will provide the greatest benefits to species persistence through diversity (Ruckelshaus et al., 2003), and what kinds of habitat management might promote life history diversity (Watters et al., 2003). One

approach to making such determinations is to estimate the likely historical diversity that existed within the species, using environmental attributes as surrogates for life history diversity that has been lost. The logic in this approach is that historical population structure resulted in a persistent species, so historical population structure and diversity provide a useful baseline for determining recovery needs. Once the historical diversity has been characterized, populations and habitats that have high priority for diversity protection can be identified, in conjunction with assessments of how many populations are needed for species persistence (Ruckelshaus et al., 2003, 2004).

We apply this approach to Chinook salmon in Puget Sound, recently listed under the United States Endangered Species Act (Federal Register, 1999). Body morphologies and life history patterns of Pacific salmon vary considerably within species, including variation in body length, upstream migration timing, spawning age and timing, and outmigration age and timing (Ricker, 1972; Taylor, 1991; Groot and Margolis, 1991). Such variation occurs at scales ranging from continental to local (Taylor, 1991), and may reflect adaptive responses to environmental selective pressures such as temperature regime (Brannon, 1987; Beacham and Murray, 1989; Unwin et al., 2000; Hodgson and Quinn, 2002), flow regime (Smith, 1969; Beacham and Murray, 1987; Quinn et al., 2001), predation pressure (Quinn et al., 2001), distance to spawning grounds (Taylor, 1990; Healey, 2001; Kinnison et al., 2001), or location of rearing areas relative to spawning areas (Brannon, 1972; Brannon et al., 1981; Quinn, 1985). Many of these traits appear to be adaptive (Taylor, 1991), but the genetic basis for most is not fully understood and it is possible that both genetic and phenotypic diversity have arisen through other evolutionary mechanisms (Adkison, 1995; Waples et al., 2004). This uncertainty about the underlying causes of life history diversity may affect selection of strategies for maintaining such variation within a salmon. Nevertheless, relating life history diversity to environmental attributes is an important first step toward understanding historical diversity and developing conservation goals.

In this paper, we examine how regional environmental indicators might inform the identification of populations that should be conserved in order to achieve recovery of Puget Sound Chinook salmon. We first relate life history traits to environmental characteristics in order to estimate the historical pattern of life history diversity in Puget Sound. We select environmental variables that are likely to exert long-term selective pressures on Chinook salmon, reasoning that such factors can significantly influence genotypic or phenotypic variation among populations. We focus on relationships between annual hydrograph patterns and spawn timing, age at spawning, outmigration age, and body size – attributes which collectively distinguish ocean-type (juveniles migrate to sea soon after emerging from the gravel) and stream-type (juveniles rear in fresh water for at least one year after emergence) life histories in Chinook salmon (Taylor, 1990; Healey, 1991). Having estimated historical life history diversity, we then examine how and why the current pattern of life history differs from the historical pattern. Finally, we discuss how these analyses inform two important considerations in salmon conservation efforts: (1) identifying populations of critical conservation importance, and (2) recovering lost life history diversity by restoring access to historically available habitats.

2. Study area

The Puget Sound basin encompasses 15 main river systems and many smaller independent streams that drain a total area of 35,500 km^2 (Ebbert et al., 2000). The basin contains three physiographic provinces oriented along its north–south axis: the central Puget Lowland province, the Olympic Mountains to the west, and the Cascade Mountains to the east (Black and Silkey, 1998) (Fig. 1). Uplifted ranges in both the Olympic and Cascade Mountains commonly exceed 1800 m, and volcanic peaks exceed 3000 m in elevation. Mean annual precipitation ranges from less than 50 cm/yr in the Puget Lowland to more than 450 cm/yr in the Cascade Mountains. Much of the higher elevation precipitation falls as snow and melts later in the spring. Lower elevation areas receive most precipitation as rain, and most runoff occurs in fall and winter.

Puget Sound Chinook salmon are typically described as either ocean-type or stream-type, depending upon the length of juvenile residence in fresh water. Ocean-type Chinook salmon are the most numerous, entering Puget Sound rivers between June and September and typically spawning in September and October (Williams et al., 1975; Healey, 1991). Newly emergent fry migrate downstream over a period of one to three months, with most fish reaching salt water between February and June. Stream-type Chinook salmon enter Puget Sound rivers between March and July, and peak spawning occurs in August and September. Juveniles rear in freshwater for approximately one year before migrating to salt water. Adults then rear at sea for three to five years before returning to spawn (Coronado and Hilborn, 1998). The degree of genetic distinctness underlying the stream- and ocean-type life histories varies throughout the range of Chinook salmon (Waples et al., 2004). In the interior Columbia Basin, adults that differ in migration timing (a common difference between stream- and ocean-type Chinook) are genetically distinct (Healey, 1991), with population divergence times estimated at 1000–100,000 years ago (Waples et al., 2004). By contrast, the relatively recent colonization of Puget Sound by Chinook salmon (approximately 16,000 years ago, Pess et al., 2003) and ongoing gene flow among populations have limited genetic divergence between the two life history types. Estimated divergence time between the two life history forms in Puget Sound is between 10 and 1000 years ago (Marshall et al., 1995; Waples et al., 2004).

Puget Sound Chinook have been divided into 22 demographically independent populations based on differences in genetic and life history attributes, geographic distances separating spawning aggregations, estimates of dispersal (straying) among streams, and correlations in abundance time series (Ruckelshaus et al., in press) (Fig. 1). In addition to the 22 extant populations, there are anecdotal and historical reports of several extirpated Chinook populations (Nehlsen et al., 1991; Ruckelshaus et al., in press). Due to sparse
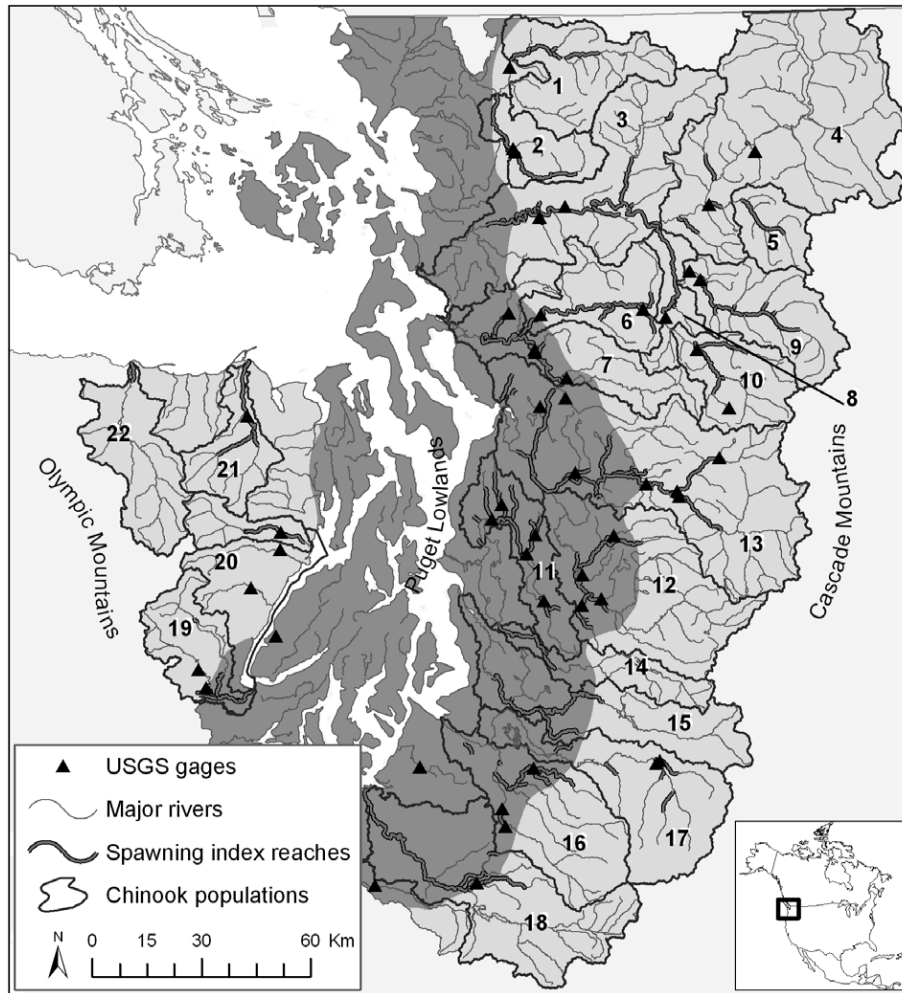
Fig. 1 – Location of Chinook populations, stream gauges, and Chinook spawning index reaches in Puget Sound, Washington. Numbers correspond to populations listed in Table 1 (Map ID column).

historical information, the historical life history diversity of Puget Sound Chinook is not well known.

Chinook hatcheries have operated in the Puget Sound region for over a century, and hatchery fish are ubiquitous in freshwater and marine habitats in the area (Myers et al., 1998). In certain areas of Puget Sound, some or most of the naturally spawning Chinook salmon were born in a hatchery. The fraction of naturally spawning Chinook that are of hatchery origin is can be estimated in only 75% of the populations within Puget Sound (Table 1). Of these, only the six populations in the Skagit River Basin are known to have little or no hatchery influence. Among the remaining six populations for which we have estimates, between 40% and 90% of the natural spawners are hatchery fish (Good et al., 2005). Spawning populations with unknown fractions of hatchery fish occur in the southern and western portions of Puget Sound (Fig. 1, populations 16, 17, 18, 19, and 20) where marking of hatchery fish is intermittent. Due to hatchery management practices in those streams, fractions of hatchery fish in the spawning population are likely to be toward the higher end of the 40–90% range (Good et al., 2005).

3. Methods

To relate life history traits to environmental characteristics, we selected habitat variables that likely exert long-term selective pressure on salmon populations. That is, we avoided variables that vary greatly from year to year (which predominantly affect inter-annual variation in survival), and focused on variables that are spatially variable but temporally relatively consistent. Initially we hoped to examine both stream temperature and hydrograph patterns as correlates of life history diversity because previous studies suggest both are important (Brannon, 1987; Taylor, 1990; Quinn and Adams, 1996; Willson, 1997). However, significant gaps in the spatial array of stream temperature data forced us to limit our analysis to patterns in the hydrograph. With respect to the hydrograph, land uses such as logging and urbanization increase the magnitude of small floods in small streams (Booth and

Population	Hydrologic regime	Mean spawn date (SD, N)[a]	Mean no. years of spawner data[b] (range)	Percent stream-type fish	Mean spawner age (SD, N)[c]	Mean Length (SD, N)[d]	Proportion hatchery fish[e]	Map ID
Table 1 – Hydrologic regime and life history trait values for each of 22 independent populations of Chinook salmon in Puget Sound								
North Fork Stillaguamish	R	242.8 (17.2, 2)	44 (19–69)	4	3.6 (0.7, 12)	69.9 (5.2, 51)	27	6
South Fork Stillaguamish	R	251.8 (40.8, 1)	17	5	3.6 (0.7, 9)	65.1 (5.3, 48)	ND	7
Green/Duwamish	R	261.2 (23.6, 3)	58 (51–61)	0	3.7 (0.7, 11*)	65.8 (5.0, 36)	65	15
Skokomish	R	264.4 (12.7, 2)	41 (26–55)	ND	3.5 (0.7, 3*)	ND	ND	19
Puyallup	R	279.4 (12.8, 3)	43 (32–53)	1	3.8 (0.6, 8)	66.7 (5.2, 35)	ND	16
Cedar	R	280.3 (19.3, 1)	98	0	3.9 (0.6, 1*)	66.3 (5.1, 54)	21	14
Nisqually	R	281.2 (11.7, 3)	40 (39–40)	1	3.4 (0.8, 2)	ND	25	18
Snoqualmie	R	282.5 (4.7, 2)	65 (63–68)	23	3.9 (0.7, 6)	ND	15	12
North Lake Washington	R	288.3 (13.4, 5)	21 (10–33)	3	3.4 (0.7, 1)	ND	79	11
Suiattle	S	229.8 (13.4, 5)	8 (8–8)	59	4.3 (0.9, 8)	67.2 (4.6, 95)	<5	9
North + Middle Fork Nooksack	S	248.3 (16.1, 3)	8 (4–11)	32	3.8 (0.6, 3)	64.6 (4.6, 94)	61	1
Upper Cascade	S	260.0 (14.5, 1)	50	37	4.2 (0.6, 3)	ND	<5	5
Dungeness	T	229.4 (25.6, 2)	67 (67–67)	16	4.3 (0.8, 9*)	ND	ND	21
South Fork Nooksack	T	246.8 (21.5, 1)	45	27	4.0 (0.5, 2)	65.5 (7.5, 36)	34	2
Elwha	T	255.2 (18.9, 1)	82	35	4.1 (0.7, 9)	ND	ND	22
Upper Sauk	T	259.0 (9.1, 1)	72	47	4.2 (0.8, 6*)	ND	<5	10
Upper Skagit	T	263.4 (14.2, 3)	44 (7–81)	7	4.0 (0.7, 8)	72.0 (3.6, 52)	<5	4
Mid Hood Canal	T	265.5 (11.1, 3)	32 (18–59)	ND	3.8 (0.7, 2*)	ND	46	20
White	T	268.7 (9.7, 4)	33 (15–52)	7	3.8 (0.8, 6)	59.8 (5.8, 40)	30	17
Skykomish	T	277.6 (9.5, 4)	53 (36–71)	36	4.1 (0.7, 5)	68.2 (4.9, 63)	29	13
Lower Skagit	T	283.2 (7.6, 1)	72	16	3.9 (0.7, 4)	68.8 (6.8, 26)	<5	3
Lower Sauk	T	ND	16	7	4.0 (0.7, 7)	ND	<5	8

Hydrologic regimes are rainfall dominated (R), snowmelt dominated (S), or transitional (T; see text for explanation and Fig. 2 for illustration). Life history traits are mean spawn date (Julian day), percent stream-type fish (the remainder are ocean-type fish), mean spawner age (years), mean adult male postorbital-hypural length at age 4 (cm), and proportion of hatchery fish. Missing values are indicated by ND. Map ID refers to extant populations in Figs. 1 and 6.

Table 1 – *continued*

a Standard deviation (SD) of spawn date calculated from normalized intra-annual time series of spawner densities in index survey areas; see Section 3 for details. N is the number of index areas sampled for each population.

b Mean number of years of spawner data across all index reaches.

c N, number of years of data; each year includes a sample of at least 40 spawners. Populations with asterisks (') had sampling years with less than 40 spawners per year: Green/Duwamish = 36; Upper Sauk = 25; Dungeness = 10; Cedar = 9; and Skokomish and Mid Hood Canal = 1.

d N, number of individual spawners sampled.

e Mean percentage of naturally spawning fish that are of hatchery origin. Total years of hatchery operations vary among streams. A proportion "<5%" indicates that infrequent samples suggest a low percentage of hatchery fish, but limited sample size precludes a more accurate calculation of percent hatchery fish. "ND" indicates no data were available on the percentage of naturally spawning hatchery Chinook.

Jackson, 1997; Beschta et al., 2000). However, neither activity alters fundamental patterns of runoff (i.e., shifting dominant runoff periods from one season to another), so we focused our analysis on shape of the annual hydrograph rather than on magnitudes of specific flows. The basic steps in our analysis were: (1) classify hydrologic regimes based on relative magnitudes of mean monthly flows, (2) compile life history data for each population, and (3) examine the relationship between hydrologic regimes and life history variables, using populations as the unit of observation.

3.1.   Hydrologic regimes

We classified hydrograph patterns based on time series of mean monthly discharge at 49 United States Geological Survey stream gauges located throughout Puget Sound (http://water-data.usgs.gov/usa/nwis/sw [accessed 18 May 2004]) (Fig. 1). Gauges used in the analysis had at least a 9-year period of record (mean 23 years, maximum 74 years) and little or no artificial regulation of flows. Mean monthly flows were averaged over all years, producing an average annual hydrograph for each gauge. To identify groups of gauges with similar hydrologic regimes, we performed a cluster analysis using the group average distance algorithm with $1 - r_s$ as the distance measure, where r_s is the Spearman rank correlation between average monthly flows at a pair of gauges (Manly, 1994). Using the correlation coefficient to measure similarity between sites emphasizes the timing and relative magnitude of peak and low flows, ignoring the total magnitude of flow. Based on this cluster analysis, we classified hydrograph patterns into three groups: snowmelt-dominated (S), rainfall-dominated (R), or transitional (T). We assessed the temporal consistency of these groupings by repeating the cluster analysis separately for each decade and looking for shifts in classification among decades. Periods of record for 33 gauges contained at least eight years of data within more than one decade.

To determine the hydrologic regime experienced by each Chinook population, we used the subset of gauges located within or adjacent to index areas where spawner surveys are conducted in each population (a total of 24 gauges corresponding to 15 populations). Because representative gauges were not available for all populations, we used parametric classification tree analysis (Venables and Ripley, 1998) to infer hydrograph patterns for the remaining populations based on mean basin elevation and mean annual precipitation (data from Williams et al., 1985). We fitted the classification tree to the full dataset of 49 gauges, using mean elevation and mean annual precipitation in the catchment basin of each gauge as predictors, and hydrograph type (R, S, or T) as the categorical response variable. For prediction, we used the most parsimonious tree that included terminal nodes for all three hydrograph types. We mapped predicted hydrologic regimes using USGS 30-m digital elevation data and mean annual precipitation for the Puget Sound basin (Daly and Taylor, 1998). This map allowed us to assign hydrograph types to the seven populations lacking nearby gauges. Each population was assigned the hydrograph pattern observed or predicted for the majority of its index areas. In eight of the 14 populations represented by >1 index area, the index areas had identical hydrograph patterns.

3.2.   Life history traits

We examined two components of life history trait values, the population mean and within-population variance. Both are potentially responsive to selective environments, and selective pressure on either can result in divergence of life history traits (Stearns, 1992). Comparing trait means among populations indicates whether the central tendency of an attribute varies spatially, and allows exploration of how the trait values themselves might be related to local environmental conditions. Differences in the variance of trait values among populations suggest that environmental or other selective factors affect the range of values exhibited by a trait. To avoid potentially confounding effects of hatchery fish on life history trait values, we removed hatchery-origin fish from samples used in these analyses where possible. Hatchery-origin fish can be identified by external marks or tags, otolith or scale analyses, or, less precisely, by the time at which they return to rivers to spawn. We were able to remove hatchery fish from 17 of the 22 populations. The five populations for which we could not remove hatchery fish are also those most likely to show an influence of hatchery fish (populations 16, 17, 18, 19, and 20). These populations are comprised mainly of ocean-type Chinook.

Spawn timing was estimated from time series of spawner densities (fish/km) obtained from annual visual surveys in 52 index areas representing the 22 Chinook populations (D. O'Connor, Washington Department of Fish and Wildlife, Olympia, Washington, unpublished data). Data for each index area were screened to select years in which at least six surveys were done and densities on the first and last survey dates were at most 20% of the maximum density for the year. These criteria, which ensured that time series captured the majority of the spawning period, yielded from 1 to 17 years of data per index area. The density time series for each area and year was integrated numerically by calculating the area under the curve (AUC), and all densities were divided by the AUC to give a standardized density kernel that reflected

spawning phenology rather than absolute abundance. The standardized kernels were averaged across years to produce a single timing curve for each area. We calculated the mean spawning date as a weighted sum of calendar dates with the standardized densities as weights, in direct analogy to the expectation of a discrete probability distribution (Miller and Miller, 1999). Similarly, we calculated the variance of spawn timing as the weighted sum of squared deviations between each calendar date in the series and the mean date. Finally, we averaged the mean spawning date and standard deviation (square root of the variance) across index areas within each population.

Spawner age and age at outmigration were obtained by analyzing scales from adult Chinook carcasses on spawning grounds (A. Marshall and C. Busack, Washington Department of Fish and Wildlife, Olympia, Washington, unpublished data). Mean spawner age, standard deviation of spawner age, and percent of adults that were stream-type (i.e., that spent their first year in freshwater) were calculated for each population. Fork lengths or postorbital-hypural lengths of carcasses were also measured (A. Marshall and C. Busack, Washington Department of Fish and Wildlife, Olympia, Washington, unpublished data). Only age-4 males had large enough sample sizes ($n > 20$) for length analyses. Linear regression was used to convert fork lengths to postorbital-hypural lengths ($R^2 = 0.93$). Mean and standard deviation of length were then calculated for each population.

3.3. Relationships among life history traits and hydrologic regime

We tested differences in life-history trait means and variances across hydrologic regimes (Table 1) using ANOVA. Pairwise comparisons among trait means were performed using Tukey tests when the main effect was significant. We also examined concordance among traits, or the presence of suites of life history characteristics, with a cluster analysis of populations based on similarity in trait means. Due to substantial gaps in the length data, this analysis was restricted to mean spawn timing, mean spawner age, and percent stream-type spawners. Variables were centered and standardized, and the matrix of Euclidean distances was used to cluster populations by the group average distance method (Manly, 1994).

4. Results

Puget Sound streams fell into three major groups based on the shape of the mean annual hydrograph (Fig. 2): a rainfall-dominated pattern (R) with a winter peak and low flows in August–September, a snowmelt-dominated pattern (S) with a peak in May–July and low flows in late winter or early spring, and a transitional pattern (T) with both rainfall- and snowmelt-driven peaks and low flows in August–September. When we examined inter-decadal variation in hydrograph patterns (using cluster analysis of mean monthly flows by decade), the dendrogram topology was less well-resolved, but the R, S, and T hydrograph patterns were still readily apparent. Only 6 sites changed group membership among decades, and no gauge ever changed from R to S or vice versa.

Parametric classification tree analysis indicated that the hydrograph pattern was associated with both mean basin elevation and mean annual precipitation (Fig. 3). Gauges on streams with mean basin elevation <791 m were predicted to have R-type hydrographs. Gauges with mean basin elevation ⩾791 were predicted to have the T hydrograph pattern unless mean basin elevation exceeded 1306 m and mean annual precipitation in the catchment exceeded 258 cm, in which case the S pattern was predicted (Fig. 3). The tree correctly classified 92% (45/49) of the gauges used to fit the model.

Chinook populations differed significantly across hydrologic regimes in mean spawner age ($F_{2,19} = 10.64$, $P = 0.0008$, Fig. 4C) and percent stream-type adults ($F_{2,17} = 13.93$, $P = 0.0003$, Fig. 4B), but there was no significant difference in the length of age-4 male spawners ($F_{2,9} = 0.064$, $P = 0.939$, Fig. 4D). Post hoc Tukey tests indicated that Chinook returning to spawn in R streams were younger as outmigrating smolts and as adults than those in T or S streams. The difference in outmigration age was particularly striking: only 4.5% (95% CI: 0.1–10.8%) of Chinook in R streams migrated to sea as yearlings, compared to 22.1% (13.5–31.3%) in T streams and 43.0% (32.3–59.4%) in S streams. Spawning date varied from a mean of 4 September (95% CI: 27 July–11 October) in snowmelt-dominated streams to 27 September (15 September–9 October) in rainfall-dominated streams, although these differences were not statistically significant ($P = 0.09$, Fig. 4A). Outmigration age was positively correlated with mean spawner age ($r = 0.74$, $P = 0.0002$) and weakly negatively correlated with mean spawning date ($r = -0.44$, $P = 0.062$), and spawner age and spawn date were negatively correlated ($r = -0.48$, $P = 0.028$). There were no significant effects of hydrograph type on standard deviations or coefficients of variation in spawning date, spawner age, or body length.

A cluster analysis identified two major groups of Chinook populations based on similarity in mean spawning date, mean spawner age, and percent stream-type adults (Fig. 5). Not surprisingly, Group 1 corresponded to populations composed almost entirely of the ocean-type life history, and Group 2 populations contained relatively high proportions of the stream-type life history. Examination of hydrologic regimes associated with each group showed that all eight rainfall-associated populations included in this analysis were in Group 1, whereas all three snowmelt-associated populations were in Group 2.

Snowmelt-dominated systems occur throughout the Cascade Mountain range and Olympic Mountains (Fig. 6), yet extant populations dominated by stream-type Chinook are restricted to a small area in the northern Cascades. Anecdotal and historical accounts of early-spawning life history types (Ruckelshaus et al., in press) indicate that stream-type fish may have inhabited all of the currently uninhabited snowmelt systems. Early-spawning populations that have apparently been extirpated are listed in Table 2, and their locations are shown in Fig. 6.

5. Discussion

Phenotypic diversity (including life history diversity) is a key contributor to population and species persistence for

salmon, as it confers resilience to populations in the face of environmental perturbations (McElhany et al., 2000; Hilborn et al., 2003; Ruckelshaus et al., 2003). Understanding the nature and causes of life history variation is of critical importance to recovery of Pacific salmon (Taylor, 1991; Waples et al., 2001, 2004), relevant both to the conservation of genetic and life history diversity in extant populations and to the possibility of re-establishing extirpated populations (Adkison, 1995). If divergence of the two life histories in Chinook salmon is indeed adaptive, then conservation strategies should have considerable focus on preserving the genetic diversity underlying life history diversity. Moreover, re-establishing extirpated life history types will depend on whether the genetic and environmental conditions exist for these types to re-evolve. By contrast, if life history variation is primarily determined by plasticity in response to environmental conditions, then conservation of both life history types should be possible once salmon are allowed to reoccupy their historical habitats.

5.1.   Adaptive nature of the two life history types

Environmental correlates of life history traits are commonly cited as evidence that habitat conditions are at least partly responsible for the evolution of salmon life history variation (Taylor, 1990; Healey and Prince, 1995; Waples et al., 2001). However, it has been difficult to identify selective mechanisms and their fitness consequences, and therefore to clearly explain why such correlations exist (Adkison, 1995; Marschall et al., 1998; Hendry et al., 2003; Waples et al., 2004). Moreover, there are multiple mechanisms by which both genetic diversity and life history diversity might arise in salmon populations, and not all can be considered adaptive (Adkison, 1995). If we accept Taylor's (1991) definition of adaptive traits, demonstrating that the two life history types are the result of adaptation to environmental conditions requires evidence that: (1) there is a genetic basis for the two life history types, (2) there is a survival advantage for each life history type in its dominant environment, and (3) one
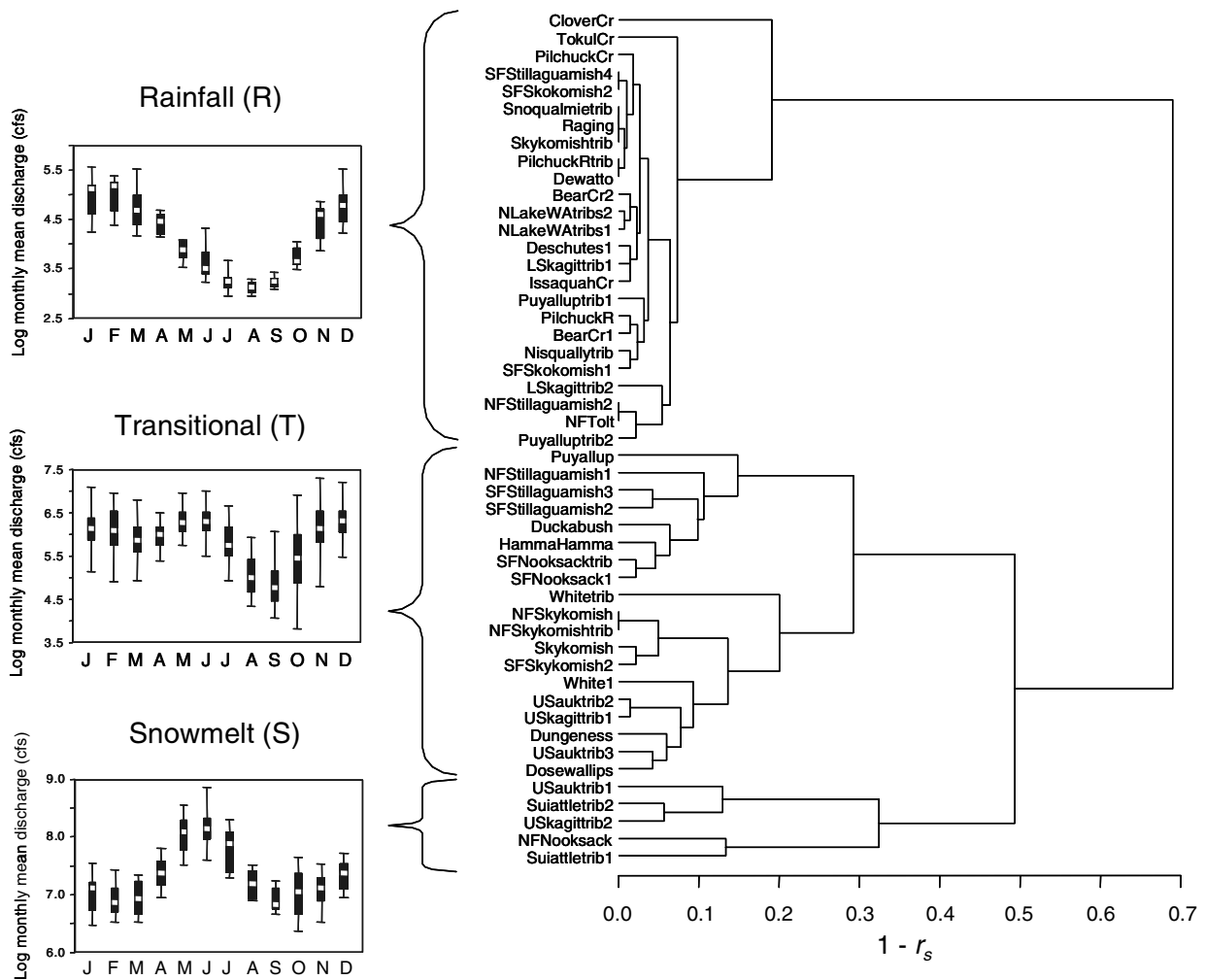

Fig. 2 – Clustering of Puget Sound streams based on correlations in the annual pattern of mean monthly flows measured at stream gauges identified three basic hydrograph patterns: R = rainfall dominated, S = snowmelt dominated, and T = transitional. Insets at left depict typical hydrographs for each hydrologic regime: Issaquah Creek (R), Duckabush River (T), and Suiattle River (S). Note change in y-axis scales among graphs.
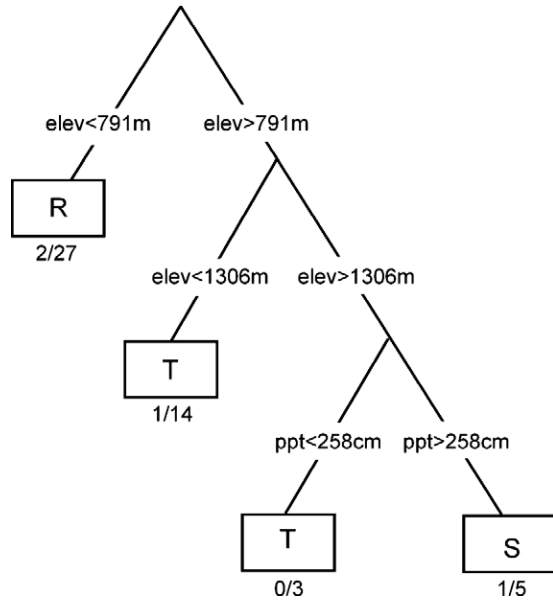
Fig. 3 – Classification tree predicting the hydrologic regime of Puget Sound streams (rainfall dominated, R; snowmelt dominated, S; transitional, T). Classifications are based on mean basin elevation (m) and mean annual basin precipitation (cm). Predicted hydrologic regimes are indicated at terminal nodes, along with the number of observations that are incorrectly classified and the total number of observations (incorrect/total).

or several selective mechanisms maintain the two life histories in the wild.

In Puget Sound Chinook salmon, populations in rainfall-dominated hydrologic regimes have younger spawners and smaller proportions of stream-type fish than populations in snowmelt-dominated regimes. Spawning timing was not statistically different among populations, but spawning timing was correlated with the other two traits. Such suites of traits appear to have a strong genetic basis in at least some Chinook salmon populations in other areas (Unwin et al., 2000; Quinn et al., 2000; Waples et al., 2004). Perhaps more importantly, there is some empirical evidence that these traits are heritable (Hankin et al., 1993; Quinn et al., 2000), and that these traits should respond rapidly to selection (Quinn et al., 2000). Healey (2001) suggested that differences in age and size of spawners between ocean-type and stream-type Chinook salmon in British Columbia were probably adaptive, but that selective mechanisms were not readily apparent. Age and size of North American Chinook were not related to latitude or migration distance, suggesting that local adaptations of body size are probably the result of factors in the freshwater portion of their life cycle (Roni and Quinn, 1995). Other studies suggest that selection on salmon size is related to variation in stream size and flow depth (Beacham and Murray, 1987; Quinn et al., 2001), or to deeper scour of bed material in large rivers (Montgomery et al., 1999). Mean length-at-age did not differ between stream-type and ocean-type fish in North America, despite differing ocean residence time (i.e., stream-type fish spend approximately one year less at sea than ocean-type fish of the same age) (Roni and Quinn, 1995). Puget Sound Chinook showed the same pattern, suggesting that differences in size and age at ocean entry do not ultimately determine adult body size.

Mean spawning date was about three weeks earlier in snowmelt-dominated areas than in rainfall-dominated areas, but the result was not statistically significant ($P = 0.09$) owing in part to the small number of extant snowmelt populations ($n = 3$). Such differences in spawning timing (i.e., upstream populations spawning earlier than downstream populations) have been found in other salmonids (Webb and McLay, 1996;
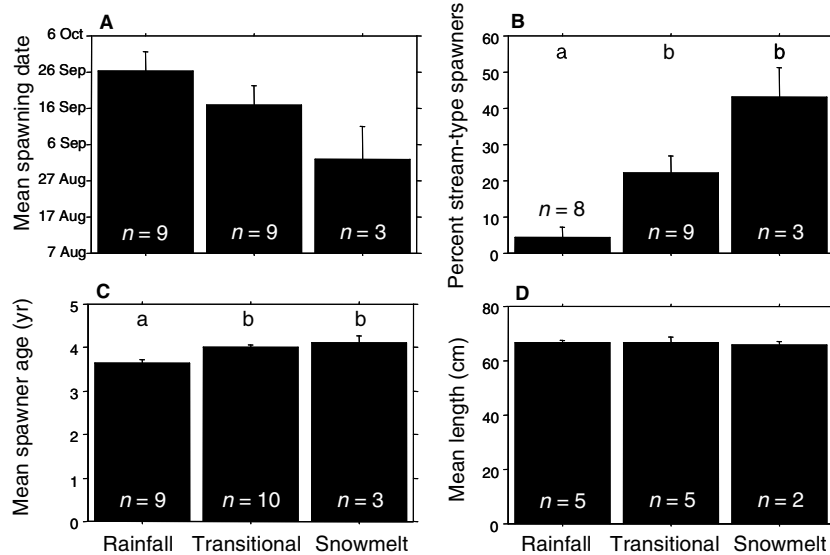
Fig. 4 – Mean (+1 SE) life history phenotypes of Chinook salmon populations spawning in rivers with rainfall-dominated, snowmelt-dominated, or transitional hydrograph patterns. (A) Mean date of spawning. (B) Percent stream-type spawners. (C) Mean age of spawners. (D) Mean postorbital-hypural length of 4-year old male spawners. Sample sizes are shown on bars. Where the main effect of hydrograph type was significant at $\alpha = 0.05$, different letters indicate significant pairwise differences between groups based on Tukey tests for multiple comparisons.
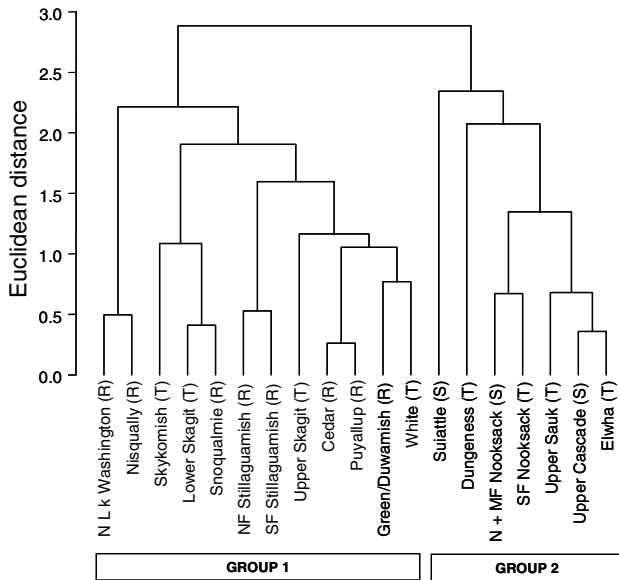
Fig. 5 – Phenetic clustering of Puget Sound Chinook populations based on mean date of spawning, percent of age-1 smolts, and mean age of spawners. Three populations (Lower Sauk, Skokomish, and Mid Hood Canal) were omitted due to incomplete data. The two major phenotypic groups revealed by the cluster analysis correspond to populations with later spawning and mostly ocean-type outmigrants (Group 1) and populations with earlier spawning and a relatively high proportion of stream-type fish (Group 2). The hydrologic regime (R, T, or S) experienced by each population is indicated.

Beer and Anderson, 2001), and some studies suggest adaptive mechanisms driving these differences (Brannon, 1987; Webb and McLay, 1996; Beer and Anderson, 2001). Differences in spawning timing appear to be a balance between stabilizing selection on timing of fry emergence (Brannon, 1987; Webb and McLay, 1996) and avoidance of high stream temperatures during the spawning period (Beer and Anderson, 2001). Colder incubation temperatures in snowmelt-dominated systems may increase incubation time for predominantly stream-type fish, and earlier spawning favors earlier fry emergence in spring that coincides with favorable environmental conditions (Brannon, 1987; Beer and Anderson, 2001). By contrast, fish spawning in lower reaches may face high summer stream temperatures and be forced to spawn later (Beer and Anderson, 2001). For Puget Sound Chinook salmon, such environmental conditions would lead over time to selection of earlier spawning adults in snowmelt systems, and later spawning adults in rainfall-dominated systems.

Outmigration timing is influenced by stream temperature primarily through growth rates and the annual decision of juvenile salmon to smolt or remain in fresh water. In environments with lower stream temperatures (such as the snowmelt-dominated habitats in Puget Sound), juvenile growth rates are low (Taylor, 1990; Unwin et al., 2000) and juveniles may elect to remain in fresh water through their second winter rather than begin their seaward migration at a smaller size (Unwin et al., 2000). This later migration appears to confer a

survival advantage to stream-type juveniles in areas of low growth opportunity (Thorpe, 1987; Taylor, 1990; Metcalfe, 1998).

Aside from factors related to hydrologic regime or temperature, life history types in some areas are correlated with distance from sea to spawning grounds (e.g., Taylor, 1990; Healey, 2001). Where stream-type fish have longer migration distance or longer time in fresh water prior to spawning, they tend to have smaller eggs (Healey, 2001) and juveniles from smaller eggs are smaller at emergence and may not grow large enough to migrate to sea in their first summer (Healey, 2001; Kinnison et al., 1998). While it is possible that migration distance exerts a selective pressure on Chinook salmon in Puget Sound, it is likely very weak as the range of migration distances in Puget Sound is small and both life histories occur within the same reaches (meaning they have the same migration distance). Hence, migration distance is not likely to explain the variation we observe among Puget Sound populations.

The influence of hatcheries on patterns of Puget Sound Chinook life history diversity remains unclear. Hatchery fish can alter the genetic composition of a wild population, and they also experience different selective environments than wild salmon for at least part of their life cycle. Thus, their presence in a population may alter its distribution of life history traits. For example, returns of coho (*Oncorhynchus kisutch*) and Chinook salmon in the Lake Washington basin have become progressively earlier over the past 50 years due to artificial selection, despite increasing water temperatures and the expectation that spawning should be later (Quinn et al., 2002). This suggests that differences in mean spawning date among Puget Sound Chinook populations may be smaller than they were historically. Hatchery fish dominate Chinook populations in southern and western Puget Sound where extant populations are characterized by the ocean-type life history (WDF et al., 1993). The lack of stream-type life history in these populations may be partly a result of hatchery practices, but may also result from loss of salmon access to historical spawning grounds in the snowmelt-dominated hydrologic regime.

5.2. Conservation implications

The maintenance and restoration of phenotypic diversity in salmon populations is a primary goal of efforts to recover the species (McElhany et al., 2000). In Puget Sound Chinook, only two of the extant populations are dominated by the stream-type life history, and both are found within the snowmelt hydrologic regime in the northern Cascades. Given the paucity of stream-type populations relative to their historical range, it is likely that any strategy to conserve life history diversity within Puget Sound Chinook salmon will include a focus on preserving both of the remaining stream-type populations. However, there might still be considerable risk to persistence of the stream-type life history because both populations occupy a small geographic area, and the risk of catastrophic events affecting both populations is greater than if they were more widely separated. Therefore, the likelihood of achieving recovery goals will be greater if management efforts focus on conserving additional populations containing the stream-type life history, or on restoring populations to areas where the stream-type life history occurred historically.
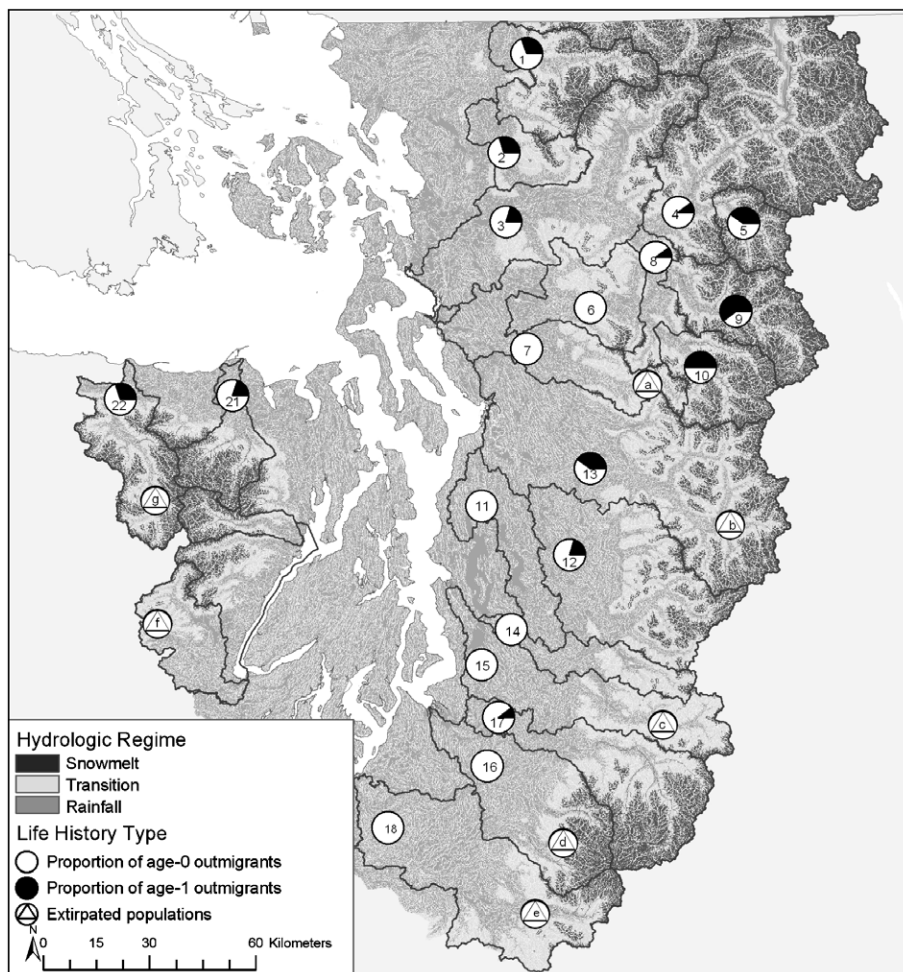
Fig. 6 – Mapped hydrologic regimes and approximate location of spawning populations. Extant populations are shown as pie charts indicating the proportion of ocean-type and stream-type fish. Locations of potential historical populations (described in Table 2) in snowmelt-dominated streams, which reportedly had high proportions of the stream-type life history, are indicated with a circle containing a triangle. Numbers and lowercase letters inside symbols indicate populations identified in Tables 1 and 2, respectively (Map ID column).

Table 2 – Reported early spawning populations of Chinook salmon that may have been extirpated (Ruckelshaus et al., in press), including probable spawning locations based on mapping of snowmelt hydrologic regimes and probable causes of extirpation

Basin	Probable historical spawning location	Probable cause of extirpation	Map ID
Stillaguamish	Squire, Boulder Creeks[a]	Possible loss of permanent snow fields	a
Snohomish	Sultan River[b] North Fork Skykomish[b]	Culmback dam blocked access in 1965 Unknown	b
Green	Upper Green River[b]	Headworks dam blocked access in 1911	c
Puyallup	Upper Puyallup River[c]	Electron dam blocked access in 1903	d
Nisqually	Upper Nisqually River[d]	La Grande dam blocked access in 1910	e
Skokomish	North Fork[b]	Cushman dam blocked access in 1926	f
Elwha	Upper Elwha River[b]	Elwha dam blocked access in 1912	g

Map ID refers to extirpated populations shown in Fig. 6.
a Fransen et al. (1977).
b Probable location based on predicted snowmelt hydrologic regime.
c Kerwin (1999).
d Historical access to upper Nisqually uncertain.

Snowmelt-dominated streams are found throughout Puget Sound, yet stream-type Chinook populations have been extirpated from much of their potential range – primarily by blocking adult migration into those habitats. An important management question is then: what is the likelihood that extirpated stream-type life histories might be re-established? The answer depends upon the degree of genetic basis for these life history differences, and upon how rapidly such trait variation can respond to changing environmental conditions. If these traits are largely environmentally controlled, then the stream type life history should quickly re-emerge once fish are allowed access to the snowmelt-dominated environment. If the opposite is true (i.e., these traits are primarily genetically determined), such efforts could be hindered by the inability of the extant populations to adapt to the snowmelt environment (e.g., Hendry et al., 2003).

Several studies suggest it is possible to re-establish the stream-type life history in areas where it has been extirpated. The relatively recent divergence (10–1000 years) of stream- and ocean-type populations in Puget Sound Chinook (Waples et al., 2004) indicates that predominantly ocean-type populations may retain a genetic composition that will allow re-emergence of the stream-type form. Indeed, dendrograms depicting patterns of genetic relatedness of Puget Sound Chinook indicate that the stream-type fish have evolved independently in all of the watersheds in which they occur (Waples et al., 2004). Perhaps more importantly, studies of Chinook salmon transplanted to New Zealand 90 years ago suggest that divergence of life history traits can occur on decadal time frames (Unwin, 1997; Kinnison et al., 2001; Unwin et al., 2000; Quinn et al., 2000). It is conceivable then that allowing extant ocean-type populations to reoccupy habitats within the snowmelt hydrologic regime might allow re-expression of suppressed life history characteristics.

Given the apparent dependence of stream-type Chinook salmon on snowmelt-dominated flow regimes, it is hard to predict whether efforts to conserve and expand the stream-type life history in Puget Sound Chinook salmon will be hindered by climate change and the potential loss of snowmelt-dominated habitats. Climate and hydrology models project significant reductions in both total snow pack and low-elevation snow pack in the Pacific Northwest over the next 50 years (Mote et al., 2003) – changes that will shrink the extent of the snowmelt-dominated habitat available to salmon. Such changes may restrict our ability to conserve diverse salmon life histories, as the stream-type life history appears to be dependent on a diminishing habitat. Nevertheless, strategies to conserve salmon are more likely to succeed if they focus on preserving genetic and life history options for the species, increasing their ability to adapt to environmental changes in the future (Mantua and Francis, 2004).

Acknowledgements

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