

Experimental evidence of population-specific marine spatial distributions of Chinook salmon, *Oncorhynchus tshawytscha*

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Abstract Migratory behavior can be affected by attributes of the animals themselves such as size and growth rate, external factors such as biotic and abiotic features of the environment, and also genetic tendencies. To better understand the role of genetics in the migratory behavior of Chinook salmon, *Oncorhynchus tshawytscha*, we report the results of an experiment in which two populations (University of Washington (UW) hatchery and Elwha River) and their hybrid offspring were reared at, tagged, and released from a single site, the UW hatchery, at a common size and date. The patterns of recoveries in fisheries differed markedly with respect to spatial distribution and also age of the fish. A larger proportion of the Elwha River fish were recovered in Puget Sound in their first year of marine life than

the other groups (40.7% vs. 11.2% for UW and 7.0% for the hybrids). The Elwha River fish also showed a higher proportion of northerly recoveries (21.9%) than UW fish (1.7%), and hybrids showed an intermediate value (8.1%). In contrast, no Elwha River fish were recovered south along the Washington coast compared to 1.3% of the hybrids and 7.7% of the UW fish. The specific mechanisms controlling the migration patterns of the populations remain unclear but the results strongly indicated a genetic influence on distribution patterns.

Keywords *Oncorhynchus tshawytscha* · Chinook salmon · Marine migration · Genetics

Introduction

The mechanisms guiding the migrations of animals are among the great mysteries of biology. A variety of sensory systems are apparently involved in the animal's ability to find its way home from distant locations (e.g., in ocean environments: Lohmann et al. 2008) but the direction taken by individuals on their first migration away from the natal area is also fascinating. In the case of Pacific salmon (*Oncorhynchus* species), decades of tagging maturing salmon at sea and recovering them in the natal areas, and tagging of juveniles in their natal areas and recovering them at sea, have indicated the population-specific distribution patterns of fish from different natal locations (e.g., Nicholas and Hankin

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1989; Weitkamp and Neely 2002; Weitkamp 2010; reviewed by Quinn and Myers 2004; Quinn 2005). These different distribution patterns presumably result from a combination of factors, including the areas where the fish enter the marine environment, the conditions that they experience upon entry (e.g., currents, temperature, prey, etc.), and internal factors such as size and physiology.

In addition to influences of local conditions and state of the fish on early marine distribution, genetic factors may also affect distribution. Some populations enter the ocean at the same place (e.g., the mouth of the Columbia River) but show different distributions, as inferred from patterns of recovery in fisheries (Waples et al. 2004; Weitkamp 2010). Two populations of Atlantic salmon, *Salmo salar*, differed in migratory behavior upon entering seawater, as indicated by ultrasonic tracking (Plantalech manel-la et al. 2011). Coded wire tagging experiments with Atlantic salmon in the Baltic Sea also indicated population-specific distribution patterns, though fish size and prey abundance affected movements as well (Kallio-Nyberg and Ikonen 1992; Kallio-Nyberg et al. 1999). Similar experiments on Pacific salmon have been limited, but Chinook salmon from the Rogue River, Oregon that were transplanted to the Columbia River showed a marine distribution that differed from that of fish from the hatchery in the Columbia River system where they were released (Pascual and Quinn 1994).

The purpose of this paper is to report the results of an experiment in which two populations of Chinook salmon, *O. tshawytscha*, and their hybrids were reared to a common size and released on the same day from a hatchery in central Puget Sound, Washington. The progeny were all marked with coded wire tags and their recoveries recorded. We tested the null hypothesis that the spatial distributions of recoveries would be similar, against the predicted alternative that the pure populations would differ and the hybrids would be intermediate. In addition to differences in overall distribution between the groups, we were especially interested in their tendency to remain within Puget Sound. Chinook (and coho, *O. kisutch*) salmon characteristically migrate to feed along the Pacific Ocean coast but it has long been known that sub-adults feed in Puget Sound all year (Pressey 1953; Haw et al. 1967) as well as those feeding along the coast. The factors that affect residency in Puget Sound are complex and incompletely known, but the

location of release and body size seem to influence the tendency to remain (Moring 1976; Chamberlin et al. 2011). However, genetic influences on migration in general and Puget Sound resident behavior in particular are also plausible. Preliminary assessments of the results of this experiment were reported by Brannon (1984) and Brannon and Hershberger (1984) but here we present a more complete analysis of the recoveries, which have been updated in the coded wire tagging database. We include in our analysis an explicit examination of interactions between age and distribution patterns because differences in age composition among populations (e.g., Roni and Quinn 1995) might confound comparisons between spatial distributions.

Methods

Three experimental groups of Chinook salmon were produced in brood year 1973 and released in spring 1974: one from the University of Washington (UW) hatchery population, one from the Elwha River, and a hybrid group with Elwha River males and UW females (Fig. 1). The UW hatchery population was founded in the late 1940s with fish primarily derived from the Green River system (Soos Creek Hatchery) in Puget Sound. In subsequent years, exchanges with other Puget Sound hatchery populations took place so the hatchery did not produce a pure population but rather one that was generally representative of Puget Sound hatchery Chinook salmon. The juveniles are ocean-type (i.e., sub-yearling smolts) and the adults return in summer and early fall, and spawn in fall. The Elwha River drains into the Strait of Juan de Fuca, west of Puget Sound and closer to the Pacific Ocean. Two dams on the river constructed early in the 20th century reduced habitat available to the salmon and in 1976 a hatchery was constructed on the lower river to supplement natural spawning in the 5 km of river below the lower dam. Prior to that the Elwha Chinook salmon were spawned artificially and transferred to the Dungeness River hatchery 30 km east of the Elwha River for incubation and rearing, and then returned to the Elwha River for release as smolts. Like the UW populations, the Elwha River Chinook salmon display an ocean-type juvenile life history and return in the late summer and fall to spawn.

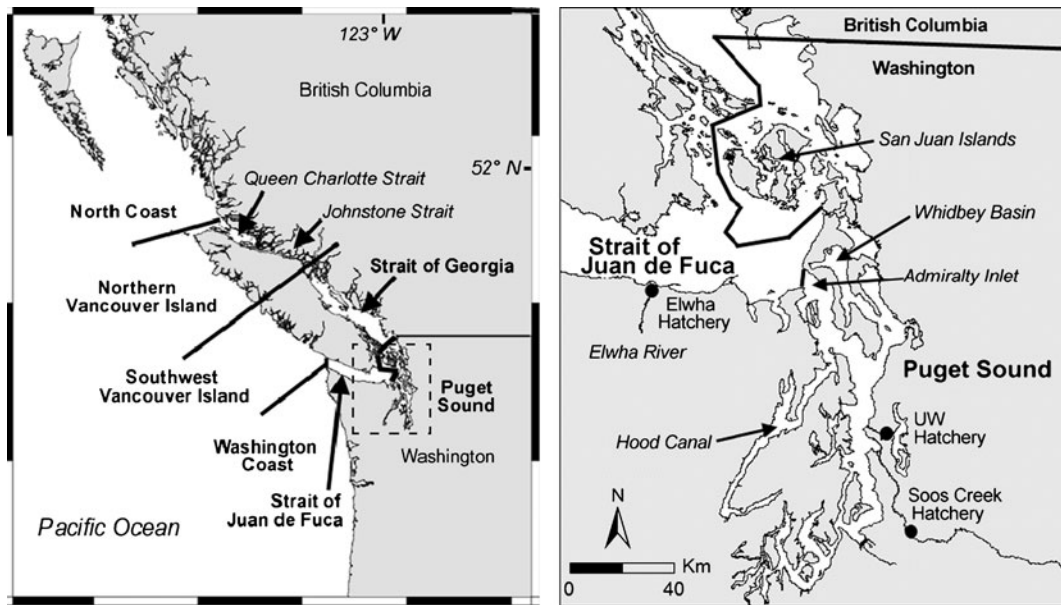


Fig. 1 Map of the seven recovery areas used to describe distributions of tagged Chinook salmon: the North Coast of British Columbia and southeastern Alaska, Northern Vancouver Island on the east and west coasts, Southwest Vancouver Island, the Strait of Juan de Fuca, the Strait of Georgia, Puget Sound,

and the Washington Coast. The insert shows Puget Sound, including the boundaries (see [Methods](#) for details), the release location (UW Hatchery) and the ancestral origins of the fish (Elwha River and Soos Creek)

Both the UW and Elwha River populations of Chinook salmon are included in the Puget Sound Evolutionarily Significant Unit (ESU) as designated by NOAA-Fisheries (Myers et al. 1998). However, the Elwha River population is intermediate between the Puget Sound ESU and Washington Coast ESU in location, marine distribution, and other features (Myers et al. 1998). Specifically, Elwha River Chinook salmon are more often recovered in northern British Columbia and Alaska fisheries, and less often recovered in Puget Sound than are Soos Creek Chinook salmon (Weitkamp 2010). Records indicated virtually no straying between the Elwha River and Lake Washington basins, and significant genetic differentiation between the Chinook salmon from Elwha River and those in central Puget Sound (Ruckelshaus et al. 2006).

In 1973 gametes were taken artificially and transferred to the UW where three experimental groups were formed. Each group was produced by four males, each spawned with one of four females. The first group consisted of UW fish, spawned on site in a manner typical of this population. The second group consisted of Elwha River fish, and the third group consisted of eggs from UW females, fertilized

with milt from Elwha River males at the UW hatchery. The experimental groups were all incubated at the UW hatchery and released on 16 May 1974.

All embryos were incubated until they hatched, transferred to troughs for feeding when their yolk had been fully absorbed, and reared in separate but identical raceways until they were marked with coded wire tags (CWT) unique to each group. After marking, they were combined for final rearing in an outdoor holding pond at the hatchery prior to release. The average sizes of fish at release, based on bulk weights and counts of the fish, were similar among the groups (UW: 12.7 g, hybrids: 12.1 g, Elwha: 12.2 g), and were normal for the UW population (long term average release date = 13 May, average weight = 12.9 g; Quinn et al. 2005). From the UW hatchery the route is westward ~8 km through the Lake Washington Ship Canal, the Hiram M. Chittenden Locks, and into Puget Sound.

The adipose fin was excised from each fish at the time of tagging (UW: $n=12\,957$, hybrids: $n=18\,940$, Elwha: $n=11\,199$). This external mark facilitated recoveries of the internal tags from salmon taken in fisheries; the heads were brought to central processing sites where the tags were removed, the codes read,

and the information shared among the management agencies (Johnson 1990). CWT recovery data were acquired from the Regional Mark Processing Center database (www.rmhc.org). All recoveries occurred between 1974 and 1978. The number of tags recovered at a given time and location was expanded to account for sampling effort within a particular area and fishery. Expanded recoveries represent the estimated number of fish with a specific tag code caught in a given area, and our analyses were conducted using these estimates. For analysis purposes we only considered recoveries in marine fisheries; neither those of maturing salmon in freshwater, nor those in the hatchery itself, were included because we were interested in the marine distribution patterns.

To compare distributions, the location codes for all individual recoveries in the database were grouped into one of seven regions (Fig. 1). These areas incorporate the statistical areas by which the data are aggregated by the management agencies (Department of Fisheries and Oceans, Canada (DFO) and the Washington Department of Fish and Wildlife (WDFW)), following other studies that examined CWT recovery data for salmonids along the west coast of North America (Weitkamp and Neely 2002; Weitkamp 2010). The areas also correspond to prominent features of the region, in terms of geography and oceanography. The North Coast included all recoveries in Alaska and the coast of British Columbia north of Cape Caution, including the DFO statistical areas 1–10, 101–110, 130, 142 (Pacific Fishery Management Area Regulations 2007). Northern Vancouver Island included Queen Charlotte Strait and Johnstone Strait south through Discovery Passage (DFO areas 11, 12 and 13) on the northeast coast of the island, and the northwest coast of the island south to and including Nootka Sound (DFO areas 111, 125, 126 and 127, and 25, 26 and 27). Southwest Vancouver Island included areas 121–124 and 21–24 to Bonilla Point Lighthouse. The Strait of Juan de Fuca included DFO area 20 subareas 19–1:4 to Cadboro Point, and WDFW area 4 east of the line from Bonilla, B.C. to Tatoosh, WA, and areas 5 and 6. The Strait of Georgia extended southward from just south of Quadra Island and included DFO areas 14–19 and 28 and 29. The Washington coast extended from Neah Bay southward (WDFW area 4). Puget Sound was defined as the waters from Admiralty Inlet southward, including Hood Canal and Whidbey Basin

(WDFW area 8) and also the San Juan Islands (WDFW area 7). Fishing effort was not assumed to be constant among all regions and years, thus the recoveries were used for presenting general distribution patterns and particularly for comparisons among the experimental groups because all groups were released in the same year and were exposed to the same fisheries.

Analysis of distribution patterns must consider monthly and annual time scales, especially for salmon feeding within Puget Sound. At the time of the study there was no size limit for Chinook salmon and fishing was open all year in Puget Sound. Sub-adults entered fisheries in their first fall and winter of life at sea and remained vulnerable in Puget Sound during their entire lives. However, not all Puget Sound recoveries indicated residence because salmon that migrated to feed along the coast for several years might be caught in Puget Sound as they returned to their natal stream. Thus if a fish was caught in the summer or early fall (e.g., July through October) in Puget Sound it is not possible to determine whether it had been feeding off the coast or in Puget Sound earlier in the year. By November essentially all the fish are in the hatchery and most have already been spawned (Quinn et al. 2002), so recoveries in Puget Sound from November through June were classified as residents. Fish recovered outside Puget Sound were classified as migrants regardless of the date. Those caught in Puget Sound from July through the end of October were classified as uncertain in terms of residency.

In addition to the seasonal patterns, it was important to examine the data with respect to the age at which the fish were recovered. Because the fish were released on 16 May 1974, we considered all recoveries until 16 May 1975 to be in the fish's first year of life, and so on for the subsequent years. The expanded numbers of recoveries for the release groups were compared both spatially (by region) and temporally (by month and year) using contingency tables to test for independence. The null hypothesis for all tests was that there was no difference in the distribution of tag recoveries among groups, regions, or years. All tests of significance were computed based upon Pearson's chi-square statistic at $\alpha=0.05$.

In addition to the univariate methods, multivariate methods were used to detect and visualize differences

in distributions among populations and age groups using PRIMER v6 software (Clarke and Gorley 2006). Recovery data were standardized to the total number of recoveries in all regions for each population/age combination and the Bray-Curtis coefficient (Bray and Curtis 1957) was used to create a resemblance matrix from the standardized data for subsequent analysis of similarity (ANOSIM) among recovery distributions. A non-metric Multi-Dimensional Scaling (MDS) plot was created from the resemblance matrix to depict differences associated with both factors based on recovery location. Differences were tested using a two-way crossed ANOSIM without replication (Clarke 1993) because only one data point existed for each population/age combination (i.e., the standardized number of recoveries).

Results

In total, 2266 fish from the three release groups were recovered from 1974–1978 in marine waters, with 1113 from the UW group, 604 hybrids, and 549 Elwha fish. The spatial distributions differed among groups ($\chi^2=523.5$, $P<0.001$, Table 1). For all release groups, more fish were caught in Puget Sound than any other region (Elwha=59.7%, hybrid=44.4%, UW=41.1%). A higher percent of Elwha fish (19.5%) were recovered north of Vancouver Island than either UW (0.3%) or hybrid fish (2.5%). Other than Puget Sound, the north coast, and SW Vancouver Island, where 11.8% of the Elwha fish were recovered, few Elwha River fish were recovered, and none was

recovered along the Washington coast. After Puget Sound, the greatest proportion of UW and hybrid recoveries came from SW Vancouver Island (26.0% and 34.3% respectively). In general, the distribution of hybrid recoveries fell between those of the UW and Elwha groups (e.g., Washington coast, Puget Sound, Strait of Georgia, Strait of Juan de Fuca, and north coast).

There were marked differences in age at recovery among groups ($\chi^2=438.7$, $P<0.001$, Fig. 2), and this complicated analysis of spatial patterns of recovery. More Elwha fish were recovered in the first year after release than any other age, or than the other groups. However, a relatively large number of Elwha fish were recovered at age 4, and four of six age 5 recoveries were Elwha fish, with the other two being hybrids. UW fish were mostly recovered at ages 2 and 3 (85% combined), and the hybrids primarily at age 3 after release (51%). The distribution of recoveries also showed an interaction between age and region. Specifically, 99.2% of all recoveries of age 1 fish were in Puget Sound (compared to 59.3% at age 2 and 17.4% at age 3). Older fish were recovered at a wider range of locations. Recoveries during the third year post-release for the UW and hybrid groups had the greatest variation in locations but were primarily off SW Vancouver Island (48% and 53%, respectively). Of the 549 Elwha fish recovered, 222 were age 1 fish in Puget Sound. This exceeded the recovery counts from the other two groups combined (167) and skewed all calculations of the recoveries of Elwha fish as percents of all recoveries. When the age 1 recoveries in Puget Sound were excluded, 32.7% of the remaining recoveries were along the north coast, compared to 2.7% for the hybrids and 0.3% for the UW fish.

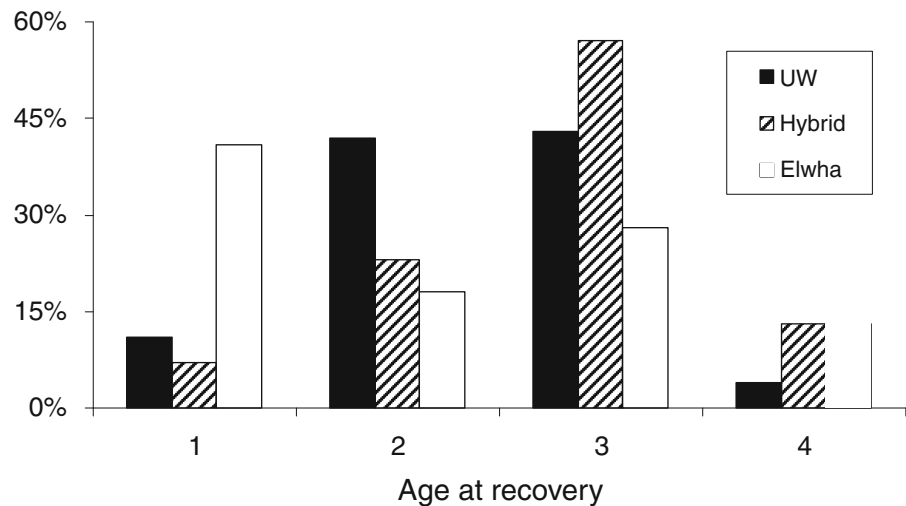
The two-way crossed ANOSIM test revealed that recovery location varied with age at recovery ($R=0.695$, $P=0.026$) and population ($R=0.622$, $P=0.062$; Fig. 3). All but 3 of the 395 recoveries of age-1 fish among all groups were in Puget Sound (the others being in the Strait of Juan de Fuca). This limited spatial distribution of this age group affected the ability to detect differences among populations, and tended to exaggerate the differences in recovery patterns attributable to age.

Puget Sound had the highest number of recoveries among regions, with year-round recoveries from all groups totaling 1053 fish (Fig. 4). These included 378 salmon (35.9%) caught from July through October

Table 1 Spatial distribution (% of all recoveries within each group) of Chinook salmon from UW, Elwha River, and hybrid groups, released from the UW hatchery

Region	UW	Hybrids	Elwha
North coast	0.3	2.5	19.5
Northern Vancouver Island	1.4	5.6	2.4
Southwest Vancouver Island	26.0	34.3	11.8
Strait of Georgia	10.3	7.3	2.9
Strait of Juan de Fuca	13.2	4.6	3.6
Puget Sound	41.1	44.4	59.7
Washington coast	7.7	1.3	0.0
Total	1113	604	549

Fig. 2 Percent of recoveries of UW (black), hybrid (striped), and Elwha (white) Chinook salmon as a function of age since they were released (e.g., within the first year post-release, second year, etc.). Percentages are cumulative within release groups, not age groups. Age-5 recoveries (4 Elwha fish and 2 hybrids) were omitted from the graph



that were of uncertain distribution because at this time of year salmon from the coast tend to migrate through Puget Sound to enter the Lake Washington Ship Canal. There were also 675 (64.1%) salmon that were classified as residents, mostly caught from November through February. These residents were compared to the fish whose recovery locations indicated that they were not residents (i.e., any location outside Puget Sound, $n=1213$ for all groups combined). The proportion of Puget Sound residents differed dramatically among groups ($\chi^2=87.2$, $P<0.001$), with a much higher proportion of Elwha fish (53.5%) than UW (30.4%) and hybrids (28.7%). In addition, the majority (77.4%) of all Elwha fish recovered in Puget

Sound were during the resident period whereas the recoveries of UW (62.6%) and hybrid fish (50.4%) were more evenly distributed between residents and non-residents. The percent of Puget Sound recoveries classified as residents was similar and high for the Elwha fish of all ages (Table 2). In contrast, the UW and hybrid fish recovered in Puget Sound early in life were primarily in the resident period but older fish were primarily during the period when maturing fish were expected to return from the ocean.

Discussion

The patterns of coded wire tag recoveries indicated that marine distribution, age at recovery, and interactions between distribution and age all differed between Chinook salmon groups (UW, Elwha River, and hybrids) released at the same site, date, and size. In general the Elwha and UW fish showed the most different patterns (i.e., overall opposite trends of northerly and southerly distributions respectively) and the distribution of hybrids was intermediate between the pure populations.

The distribution of UW recoveries observed for our study was similar to the general pattern of this population (Quinn et al. 2005). More broadly, Weitkamp (2010) found that most Puget Sound Chinook salmon (e.g., those from the Soos Creek hatchery and also the Issaquah Creek hatchery, located in the Lake Washington basin and propagating fish largely derived from Soos Creek) were caught

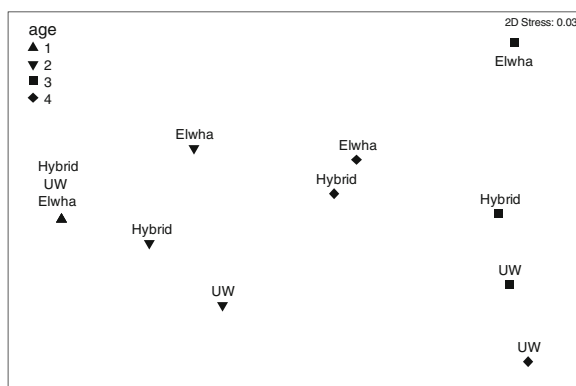
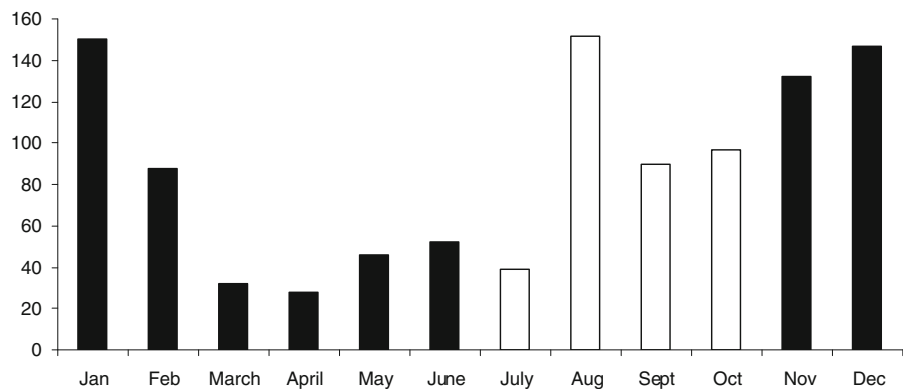


Fig. 3 Two dimensional MDS ordinations of CWT recovery distributions by population (UW, Elwha, Hybrid) and age groups: 1=triangles, 2=upside down triangles, 3=squares, 4=diamonds). Stress value indicates a goodness of fit measure for multivariate compression into two dimensions (see Clarke 1993)

Fig. 4 Number of recoveries of Chinook salmon by month within Puget Sound for all groups (UW, hybrid, and Elwha) combined ($n=1053$). Black bars indicate salmon classified as residents; white bars indicate salmon of uncertain distribution because they were recovered during the period when salmon return to Puget Sound from the ocean



relatively close to the release location (e.g., Strait of Georgia, southwest Vancouver Island) and few traveled north of Vancouver Island. However, fish from the Elwha River were more similar to populations from the Washington coast than were other Puget Sound populations, displaying a more northerly migration (Weitkamp 2010; see also Trudel et al. 2009). Our results showed a greater tendency to migrate northward by the Elwha fish, even though they were released far from their normal point of entry into the marine environment. Such consistency in the distributions of the Elwha fish regardless of release location, and the intermediate distribution pattern of the hybrid group suggested a significant genetic component to the marine distributions. However, the Elwha River group also showed a much higher proportion of fish recovered within Puget Sound in their first year after release, and this suggests some incompatibility between their innate migratory behavior and the environment where they entered marine waters. The Strait of Juan de Fuca differs dramatically from central Puget Sound in

many respects including but not limited to geographic orientation and physical properties such as currents, tidal flow and exchange, nutrient upwelling, etc. (Mofjeld and Larsen 1984; Babson et al. 2005; Thomson et al. 2007). The results are consistent with the hypothesis that some of the Elwha River fish exited Puget Sound and displayed a distribution similar to their native population but a large fraction did not exit Puget Sound and were caught as residents, especially in their first year at sea but in subsequent years as well.

The mechanisms that guide these and other juvenile salmon from the locations where they enter marine waters to their population-specific feeding grounds are not well known. Field sampling indicates that the early marine migrations are directed rather than random (e.g., Jaenicke et al. 1984; Groot et al. 1989) and experiments indicated the salmon can use Earth's magnetic field for orientation (Quinn 1980; Quinn and Brannon 1982). These orientation patterns are presumably under genetic control, and there is ample evidence for genetic control over other aspects of migration such as rheotaxis of juveniles (Brannon 1972; Bowler 1975), the timing of downstream migration by smolts (Orciari and Leonard 1996), adult migration and spawning timing (Quinn et al. 2000). However, the interactions between directional preferences, proximate environmental conditions that the fish encounter (e.g., temperature, salinity, prey), and their internal condition (physiological capacity for osmoregulation, growth, etc.) are not known.

The recovery patterns of the experimental groups may have reflected differences in patterns of return migration as well as differences in orientation during the outward journey. Homing mechanisms at sea are poorly understood but there appears to be a transition

Table 2 Percentages of the recoveries of University of Washington (UW), Elwha River, and hybrid Chinook salmon in Puget Sound ($n=1053$) that took place between November and June, inclusive, and thus were classified as resident fish ($n=675$). Age refers to the year of recovery, relative to the date of release (i.e., within the 1st, 2nd, 3rd and 4th year of life at sea)

Age	UW	Hybrid	Elwha
1	95.2	92.9	85.1
2	60.5	66.0	70.0
3	16.9	33.7	86.7
4	0.0	0.0	32.3
Total	62.6	50.4	77.4

from open-water mechanisms to the olfactory orientation that guides salmon to their natal stream (Hasler and Scholz 1983; Dittman and Quinn 1996). Olfactory imprinting should have been sufficient to guide the maturing adults back to the UW hatchery once they were in central Puget Sound and could detect the odors from the Lake Washington basin. There is some genetic basis for homing (Bams 1976; McIsaac and Quinn 1988) but this influence is subtle compared to the role of odors imprinted by juveniles (e.g., Donaldson and Allen 1957; Quinn 1993). It is unclear to what extent disorientation at earlier phases of the return migration, beyond the direct influence of odors learned on the outward journey, might have caused the distribution of Elwha River recoveries to differ from those of UW fish, but such an effect is plausible.

Chinook salmon are present in Puget Sound in every month of the year (Pressey 1953; Haw et al. 1967) and contribute to a significant recreational fishery in the region. We were interested in the contribution of each release group to the resident population within Puget Sound because this appears to be an alternative migration pattern, with links to growth and contaminant accumulation (O'Neill and West 2009). All groups were recovered in Puget Sound during the entire year but the temporal pattern of recoveries within Puget Sound differed markedly. All groups showed a peak in recoveries in Puget Sound from July to October, likely representing maturing adults returning to spawn. However, the peak was much more pronounced for the UW and hybrid release groups. In addition to this seasonal difference, the UW and hybrid groups were represented by progressively fewer resident recoveries among the older age groups (Table 2), consistent with analysis reported by O'Neill and West (2009). In contrast, a large proportion of the Elwha group was recovered as residents, even among the older fish, although only 30% of the 106 Elwha fish recovered in Puget Sound occurred after the first year. As with the other findings, the precise mechanism controlling the interactions between season, age, and area of recovery are unclear but the data indicate a substantial degree of genetic control. In general, life history transitions of salmon seem to be controlled by norms of reaction, whereby grow rate is linked to smolt transformation and seaward migration of juveniles, and maturation and return migration of adults (Quinn et al. 2009). It seems likely that the UW and Elwha populations

differed in migratory orientation as smolts entering Puget Sound, and they also differed in some interaction between age or maturity state and distribution that caused the differences between the pure forms and the hybrids.

Notwithstanding the differences between groups in spatial and temporal patterns of recovery, it is also important to note the problems of studying fish behavior based upon the date and place of capture. One cannot determine where a fish was before it was caught, nor where it would have subsequently gone had it not been caught. Nevertheless, the large number of Elwha fish recovered in Puget Sound during the first year indicated a very different pattern from the other groups, and the tendency for the hybrids to be intermediate between the two populations in most aspects of distribution also indicated a genetic basis for the differences, whatever the specific mechanisms.

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