Marine Distributions of Chinook Salmon from the West Coast of North America Determined by Coded Wire Tag Recoveries

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Abstract.—The coded wire tag (CWT) database contains detailed information on millions of Pacific salmon *Oncorhynchus* spp. released from hatcheries or smolt traps and recovered in the north Pacific Ocean and its tributaries. I used this data set to examine the spatial and temporal variation in the marine distributions of 77 hatchery and 16 wild populations of Chinook salmon *O. tshawytscha* based on recoveries of an estimated 632,000 tagged salmon in coastal waters from southern California to the Bering Sea during 1979–1994 (and 1995–2004 for select hatcheries). Chinook salmon showed 12 distinct region-specific recovery patterns. Chinook salmon originating in a common freshwater region had similar marine distributions, which were distinct from those of adjacent regions. Different run types (e.g., spring, summer, and fall runs) originating in the same region exhibited variation in their marine distributions consistent with recovery at different stages of their ocean residence period. Recovery patterns were surprisingly stable across years, despite high interannual variation in ocean conditions. By contrast, ocean age influenced recovery patterns, as older fish were recovered further from their natal stream than younger fish. Although most of the CWT data used in the analysis came from hatchery fish, recoveries of tagged wild populations indicate patterns similar to those of fish from nearby hatcheries. The consistency in these findings across broad geographic areas suggests that they apply to Chinook salmon across the entire Pacific Rim. Similar findings for tagged coho salmon *O. kisutch* indicate that the observed patterns may apply to Pacific salmon as a whole and provide a model for other highly migratory fishes that have not benefited from such intensive tagging programs. The results also have implications for the genetic control of migration and salmon's ability to respond to climate change.

Knowing the spatial dynamics of an organism—where it is located during each stage of its life—is crucial to understanding the factors affecting its survival and reproductive success (Leggett 1985). This is particularly true for anadromous Pacific salmon *Oncorhynchus* spp. because of their use of both freshwater and marine environments. Although Pacific salmon spend most of their life in marine waters, relatively little is know about their location during marine residence or the factors affecting their distribution or survival (Pearcy 1992; Quinn 2005). Better knowledge of these factors is critical for effective management but is also necessary to understand the basic biology and, therefore, long-term survival of these culturally and commercially important species.

Chinook salmon *O. tshawytscha* have long been the focus of tagging studies used to determine oceanic distributions and origins of particular stocks (Neave 1964; Major et al. 1978). Early work determined that salmon from different freshwater regions had different marine distributions, although there was considerable spatial and temporal overlap in distributions (Milne 1957; Wright 1968). Studies in large river basins such

as the Columbia River determined that Chinook salmon from different parts of the basin or with different run types also had different marine distributions (Wahle and Vreeland 1978; Wahle et al. 1981). (Chinook salmon display variation in the timing when returning adults enter rivers to spawn [termed "run type"]. These run types typically consist of spring, summer, or fall runs, based on when they reenter freshwater.) Using ocean distribution information for Chinook salmon from North America, Healey (1983) suggested that stream-type Chinook salmon (those with yearling smolts, typically spring and some summer run populations) have a much more offshore distribution than do ocean-type Chinook salmon (those with subyearling smolts, typically fall and some summer run populations), which are largely restricted to "onshore" (coastal) waters. He proposed that these distributional differences (in addition to other life history traits) were sufficient to classify the two groups as separate races, rather than phenotypic variants.

Coded wire tags (CWTs), 1-mm-long pieces of metal wire etched with a code (Jefferts et al. 1963), have been used extensively to tag Pacific salmon since the late 1960s. This program is probably the world's largest fish tagging program with respect to the number of tags deployed and retrieved each year (Guy et al. 1996), and has greatly increased our knowledge of

salmon distributions. In recent years (late 1990s to early 2000s), 50 million Pacific salmon (39 million Chinook salmon) bearing CWTs have been released annually, while 275,000 tagged salmon are recovered annually from fisheries, at hatcheries or weirs, and on spawning grounds (J. K. Johnson, Regional Mark Processing Center, Portland, Oregon, unpublished report; available: www.rmis.org). Coded wire tags are inserted in the nasal cartilage of juvenile salmon prior to release from the hatchery or in wild fish captured during out-migration. Each tag code is associated with both fish type (e.g., stock, size, age) and release information (e.g., location, date, number tagged); fish bearing the same code (termed a "release group") typically number in the thousands of tagged individuals. Information on each release group and recovered tag is contained in an online database (Regional Mark Information System [RMIS]; http://www.rmpc.org).

The CWT program is designed specifically for, and primarily used by, salmon managers to determine the distributions as well as harvest and survival rates of salmon stocks. Salmon managers effectively use these CWT-derived, stock-specific distribution patterns to design fisheries that specifically target particular stocks, while avoiding those that have conservation concerns (PSC 2007; PFMC 2009). In its most wide-ranging management application, the Pacific Salmon Commission (PSC) uses CWT data in its Chinook salmon cohort analysis model, which estimates exploitation histories for 39 indicator stocks from Southeast Alaska to Oregon (PSC 2007). Despite its widespread use by managers, however, it is difficult to construct a coastwide picture of marine distributions from these studies because of their often limited geographic range, use of recovery areas based on fishery type rather than geographic area, and lack of a common methodology (e.g., release group selection criteria, years, or recovery areas used).

Owing to the enormous amount of information it contains and increasingly user-friendly Web access, the CWT database has also been used to address a number of salmon-related topics outside of the management arena. These studies include investigation of the factors affecting salmon marine survival (Coronado and Hilborn 1998; Ryding and Skalski 1999; Magnusson and Hilborn 2003; Quinn et al. 2005; Wells et al. 2006), movements of both juveniles (Morris et al. 2007; Trudel et al. 2009) and adults (Norris et al. 2000; Weitkamp and Neely 2002), and homing fidelity (Pascual and Quinn 1994; Hard and Heard 1999; Candy and Beacham 2000).

Here, I use the CWT database to explore the spatial and temporal variation of marine distributions of Chinook salmon from the West Coast of North America, once they become vulnerable to fisheries (typically after a year in the ocean). This analysis follows the methodology used in our earlier analysis of marine distributions of coho salmon *O. kisutch* (Weitkamp and Neely 2002); it effectively uses thousands of coastal fishers from southern California to the Bering Sea as samplers of the marine environment to detect the presence and abundance of millions of tagged salmon. The information presented here forms a comprehensive assessment of Chinook salmon marine distribution patterns along the West Coast of North America and provides new insight into the marine residence period for this species. These distribution patterns may also serve as an important model for Pacific salmon and other migratory fishes.

Methods

The objective of this study was to investigate ocean distribution patterns of Chinook salmon by using coastal marine fisheries as samplers of coded-wire-tagged Chinook salmon, employing the RMIS CWT database. Because Chinook salmon hatcheries often release tagged fish with more than one run type and both run type and hatchery location may influence marine distribution patterns, the basis of this analysis is the hatchery run type group (HRG), or the specific hatchery and run type for which marine recovery patterns were determined. Each HRG was assigned to a particular freshwater release region based on the general geographic location or conservation unit (Myers et al. 1998) of the hatchery; HRGs and release regions used in the analysis are provided in Table A.1 in the appendix. By contrast, the recovery location of each tagged salmon was assigned to a marine recovery area, which has very specific boundaries (see Methods below). Accordingly, hatcheries were located in freshwater release regions and their tagged fish were recovered in marine recovery areas.

In using this database, I assume that the CWT database is "correct" (i.e., that fisheries were sampled consistently, adjustments to account for sampling were appropriate, all recovered tags were read and reported, and there was no bias due to year or location, etc.). Given that the CWT program exists for management purposes, which needs the most complete and accurate data possible, I expect this assumption is sufficiently valid and that bias did not unduly influence my results.

Selection of hatcheries, release groups, recoveries, and recovery areas.—The primary goal of this analysis was to describe the marine recovery patterns of tagged Chinook salmon coastwide and examine the effects of hatchery location and run type on recovery patterns using similar objectives and methodology as our coho salmon analysis (Weitkamp and Neely 2002). Because

the CWT database contains information on millions of tagged Chinook salmon released and recovered over the last four decades, I was able to select particular hatcheries, release groups, recoveries, and recovery areas in order to have large numbers of both HRGs and recoveries, while discarding data that might introduce bias or "noise" into the analysis. Specifically, hatcheries used in the analysis were selected to represent Chinook salmon populations along the West Coast of North America and had a minimum of 1,000 estimated recoveries (after adjusting for sampling effort—see below) distributed over at least 3 years. Exceptions to these criteria occurred in release regions in which too few hatcheries were available that either met the recovery criteria (e.g., Cook Inlet, Upper Fraser River) or when hatcheries were within 10 km of each other (e.g., Quinault Lake and National Fish Hatcheries, and Wells Hatchery and Spawning Channel, Washington); in these situations, hatchery data were combined (Table A.1).

To minimize potentially confounding factors due to the use of exotic stocks or transportation of fish prior to release (e.g., Reisenbichler 1988), release groups were excluded from the analysis if releases (1) contained experimental fish (release type E or B in the database); (2) used stocks with names other than the hatchery, stream, or local river basin name; or (3) occurred anywhere other than the hatchery or hatchery stream. By using these criteria, release groups effectively served as replicates for each HRG. Exceptions to this last rule included the use of fish released at multiple locations in Cook Inlet, Queen Charlotte Islands, and Upper Fraser River due to a shortage of release groups meeting the criteria.

Recoveries of CWT release groups were selected to determine the typical distribution of Chinook salmon in coastal waters. Marine (as defined in the CWT database) recoveries during 1979–1994 were used in this analysis because both sampling for CWTs and fishing effort were more or less constant (RMIS; PSC 2005; PFMC 2009). In particular, prior to 1979 sampling for CWTs was incomplete, while after 1994 the large west coast Vancouver Island troll fishery was greatly curtailed. Recoveries during 1995–2004 were also included in the analysis for hatcheries located in Alaska, northern British Columbia, and the Central Valley (Sacramento and San Joaquin rivers), California, because few recoveries were available from these hatcheries prior to 1995 and few ($<5\%$) of their fish were caught by West Coast Vancouver Island fisheries. Recovery patterns for these hatcheries between the two time periods (1979–1994 and 1995–2004) were quite similar (Bray–Curtis similarity $>90\%$; see next section for definition), indicating the inclusion of recoveries in

the latter period did not unduly influence recovery patterns.

All recoveries were adjusted to account for sampling effort but not the unmarked fish associated with each CWT release group (both fields are provided in the database). The adjustment (expansion) factor used to account for sampling effort was capped at 20 (i.e., recovery of a single tag represented a maximum of 20 estimated recoveries) because of the considerable uncertainty associated with larger adjustment factors. This had little effect on recovery patterns, however, because the vast majority ($>95\%$) of expansion factors were less than 20 and, of those that exceeded 20, over half concerned less than five recovered tags. Like the coho analysis, Chinook salmon recoveries were also restricted to the dominant ocean ages (the age at which most Chinook salmon from each HRG were caught, either 1–3 or 2–4 years) to limit variation in recovery patterns due to ocean age. This age restriction represents a tradeoff between controlling for the effects of age versus having enough recoveries for statistically meaningful analyses.

Hatchery location and marine distribution patterns.—To determine where each tag was recovered, each of the approximately 7,770 coastal marine recovery location codes in the CWT database were assigned to one of 21 marine recovery areas used in the coho analysis (Figure 1; Weitkamp and Neely 2002). These recovery areas were selected to be approximately the same size coastwide, to represent geographically distinct areas where possible, and to have boundaries that correspond to fisheries management statistical areas to minimize overlap between recovery areas. Recoveries with location codes that overlapped multiple recovery areas were evenly divided between overlapped areas, while those that could not be assigned to a particular recovery area (e.g., covered an entire state or province) were discarded; these recoveries made up less than 0.5% of all recoveries. Likewise, recoveries with high seas location codes (those beginning with the number 7) represented less than 1% of all recoveries and were deliberately excluded from the analysis.

Once all recoveries were assigned to recovery areas, I estimated marine distributions from the proportion of recoveries (R_{ij}) by HRG j in recovery area i over all years as

$$R_{ij} = \frac{\sum\limits_{k} r_{ijk}}{\sum\limits_{i} \sum\limits_{k} r_{ijk}},$$

where r_{ijk} is the estimated number of recoveries from HRG j in recovery area i in year k. This formulation
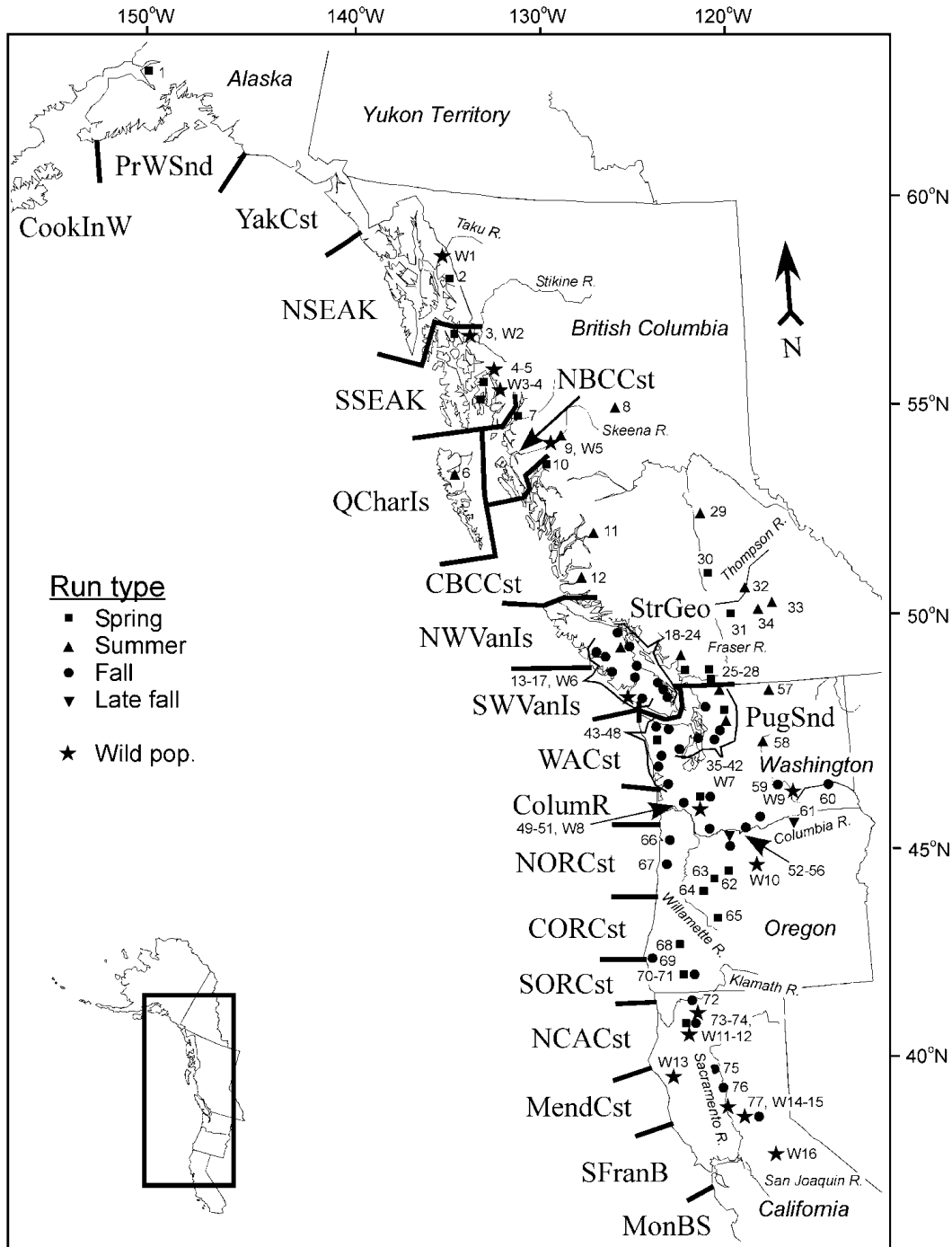
FIGURE 1.—Locations of the 77 hatchery run type groups (HRGs [1–77]), 16 tagged wild populations (W1–W16), and 21 marine recovery areas (indicated by dark lines) used in the analysis. Different symbols represent the different HRG run types; the names of and recovery statistics for the HRGs and wild populations are provided in Tables A.1 and A.2, respectively. The abbreviations of the marine recovery areas are as follows: CookInW = Cook Inlet west; PrWSound = Prince William Sound; YakCst = Yakutat Coast; NSEAK = northern Southeast Alaska; SSEAK = southern Southeast Alaska; QCharIs = Queen Charlotte Islands; NBCCst = northern British Columbia coast; CBCCst = central British Columbia coast; NWVanIs = northwest Vancouver Island; SWVanIs = southwest Vancouver Island; StrGeo = Strait of Georgia; PugSnd = Puget Sound; WACst = Washington coast; ColumR = Columbia River; NORCst = north Oregon coast; CORCst: central Oregon coast; SORCst = southern Oregon coast; NCACst = northern California coast; MendCst = Mendocino coast; SFranB = San Francisco Bay; MonBS = Monterey Bay south.

gives equal weight to all recoveries, regardless of the year in which fish were recovered. This provided the primary data set for the analysis: the proportion (or percent by multiplying portions by 100) of recoveries in each of the 21 recovery areas for each HRG.

I also estimated the weighted average marine distance of recovery (D; travel by water only) for each HRG j between all recovery areas in which Chinook salmon were recovered and the recovery area j in which their home stream enters the ocean ("home recovery area") as

$$D = \sum_i d_i R_{ij},$$

where d_i is marine distance (using great-circle distance) between the geographic center of recovery area i and the center of the home recovery area j, and R_{ij} is the proportion of recoveries by HRG j in recovery area i, defined above. Because recovery area was the smallest spatial scale used in this analysis, all recoveries occurring within the home recovery area had a distance of zero. Untransformed mean distances were compared by release region or run type using either Mann–Whitney test of medians (MW) followed by Bonferroni test between pairwise groups or Kruskal Wallace (KW) one-way analysis of variance (ANOVA) on ranks followed by a KW multiple-comparison test (Zar 1984).

Statistical analysis of marine distributions.—I employed three complementary multivariate techniques to explore variation in marine distributions: (1) nonmetric multidimensional scaling (MDS), (2) analysis of similarities (ANOSIM; a multivariate analog to ANOVA) to test for the influence of specific factors on ocean distributions, and (3) cluster analysis. All analyses were run using PRIMER-E software (Clarke and Gorley 2006). These analyses all employed resemblance matrices constructed using pairwise Bray–Curtis similarities (S) between each pair of HRGs (i and j) as

$$S_{ij} = \frac{\sum_k 2\min(r_{ik}, r_{jk})}{\sum_k (r_{ik} + r_{jk})},$$

where r_{ik} and r_{jk} are the proportion of recoveries in recovery area k by HRGs i and j, respectively. In this application, Bray–Curtis similarity ranges from 0 (no recoveries in common) to 1 (identical recovery patterns). Bray–Curtis similarity coefficients are widely used in ecological studies because they are unaffected by changes in scale (e.g., using percent or proportions) or the number of variables (recovery areas) used, and produces a value of zero when both values being compared are zero (joint absence problem; Clarke 1993; Legendre and Legendre 1998). Proportions were deliberately not transformed so that variation in the original data were retained, although analyses conducted with log or square root transformations produced similar results.

The MDS is a ranking technique based on a set of similarity coefficients that places points in two- (2-D) or three-dimensional (3-D) MDS space in relation to their similarity (i.e., points farther apart are less similar than those closer together). Unlike multivariate AN-OVA, MDS does not require data to be normally distributed and is better suited for the large number of variables employed here (21 recovery areas; Clarke 1993). The MDS uses an iterative process to find the best (minimum) solution; therefore, each run used 25 iterations with random starting locations. Minimum stress (a measure of agreement between the ranks of similarities and distances in 2-D [or 3-D] MDS space) was attained in multiple iterations of each run, while multiple runs of each data set produced similar configurations, suggesting true minimum solutions were attained with this method.

As applied here, the ANOSIM is a permutation procedure used to test whether particular groups of HRGs were more similar to each other with respect to recovery patterns than would be expected strictly by chance (Clarke 1993). The groups of interest were those based on release region and run type. The procedure produces a global R-statistic that typically ranges from 0 (no separation of groups) to 1 (complete separation of groups), although negative values (indicating no separation) are possible (Clarke 1993).

Finally, to evaluate how release region influences recovery patterns without the added influence of run type, I analyzed only fall run type HRGs using hierarchical agglomerative clustering based on group-averaging linkages. The cluster analysis included the similarity profile (SIMPROF) test, which determines the significance of each node of the cluster by permutation (Clarke 1993).

Comparison of hatchery and wild marine distributions.—Because most salmon tagged with CWTs are hatchery reared, yet hatchery-reared fish are known to vary from their wild counterparts in many important ways (NRC 1996; Quinn 2005), I explored whether recovery patterns for HRGs were similar to wild salmon from the same release region. This evaluation used the methods described above for HRGs (e.g., same recovery areas, years of interest, release criteria, marine recovery metrics). However, because relatively few wild Chinook salmon have been tagged and recovered, I included populations that had fewer than 1,000 recoveries and included wild fish that were

trapped, tagged, and released from multiple tributaries within each river basin (Table A.2).

Marine distributions of wild populations were compared to HRGs at two spatial scales. At fine spatial scales, I calculated Bray–Curtis similarity coefficients between each wild population and the nearest HRG with the same run type to quantify the similarity between the two. At large spatial scales, all wild populations were included with all HRGs in an MDS plot to determine whether wild populations were similar to hatchery populations from the same release region, regardless of exact geographic location or run type.

Marine distributions by year and ocean age.—I conducted two secondary analyses to explore how marine distributions varied by year and by ocean age (ocean age = recovery year − release year). These analyses were restricted to HRGs used in the main analysis that had at least 100 estimated recoveries in each of 10 years (1979–1994 only) or at least four ocean ages (1–5); too few tagged Chinook salmon were recovered at ocean age 0 to analyze. For each HRG used in these analyses, I calculated the proportion of recoveries in each recovery area and mean distance of recovery (both described previously) for each year or ocean age that had a minimum of 100 estimated recoveries.

Bray–Curtis similarity coefficients were calculated between years or ocean ages, both within and between HRGs. Differences in similarity coefficients between years or ocean ages within HRGs were evaluated using either nonparametric (KW tests) or parametric one-way ANOVAs on untransformed data, as appropriate (Zar 1984). This analysis included examination of whether particular years may have influenced recovery patterns coastwide (as might be expected from ocean-scale El Niño or La Niña events), leading to consistently low mean similarities with other years. These analyses only considered similarities calculated within HRGs between years (i.e., no between-HRG similarities were included). I also used pairwise Bray–Curtis similarities as a basis for MDS, ANOSIM, and cluster analyses to explore variation associated with year or age, using the methods described for the primary analysis above.

Variation in mean distance by year was evaluated using coefficient of variation (CV = 100 × SD/mean) corrected for small sample sizes (Sokal and Rohlf 1995). Variation in CV by run type was evaluated by one-way ANOVA on untransformed data, which met all normality and variance assumptions (Zar 1984). The effects of ocean age on mean distance of recovery was explored by converting distance at each age into standardized anomalies so that mean distances by age for each HRG had a mean of zero and SD equal to 1.

These were compared across HRGs by ocean age using KW tests (Zar 1984).

Results

Recovery Statistics

This analysis was based on an estimated 620,275 hatchery Chinook salmon recovered in coastal waters of the eastern North Pacific. These tagged salmon represented 3,375 CWT release groups and 77 HRGs from Alaska (5), British Columbia (29), Washington (25), Oregon (12), and California (6; Figure 1). Over half of the HRGs consisted of fall run types (42), with lesser numbers of spring (19), summer (14), and late fall (upriver bright) (2) run types (Table A.1). The analysis also employed recoveries of an estimated 11,982 wild Chinook salmon that were tagged as smolts in 16 rivers in Alaska (4), British Columbia (2), Washington (3), Oregon (1) and California (6; Figure 1; Table A.2). Like hatchery Chinook salmon, most wild release groups consisted of fall run types (56%), followed by spring (31%) and summer (13%) run types. On average, each recovery area recovered an estimated 29,537 hatchery and 569 wild tagged fish, representing 47 HRGs and 7 wild populations, respectively (Table A.3).

Hatchery Location and Marine Distribution Patterns

Marine distribution patterns for the 77 HRGs indicate a clear latitudinal cline: tagged Chinook salmon released from northern hatcheries had more northern distributions than those from southern hatcheries (Figures 2, 3). However, the distribution of fish across recovery areas followed three broad patterns based on release region: (1) Chinook salmon from Alaskan hatcheries (HRGs 1–5) were largely recovered in Alaska, few recoveries occurring south of Alaska; (2) salmon originating from hatcheries in northern British Columbia to the Oregon coast (HRGs 6–69) were widely dispersed and recovered from the home recovery area (in which the natal stream enters the ocean) north to Southeast Alaska; and (3) Chinook salmon from hatcheries in southern Oregon and California (HRGs 70–77) were rarely caught north of the Columbia River (ColumR) recovery area. These southern hatcheries also had the highest number of recoveries south of the home recovery area (Figures 2, 3).

Within this second group, recovery patterns were also apparent at finer spatial scales such that Chinook salmon released from a particular geographic region generally shared a common recovery pattern which was distinct from that of adjacent regions. For example, most Chinook salmon released from Puget Sound hatcheries (e.g., Samish River [Figure 3]) were
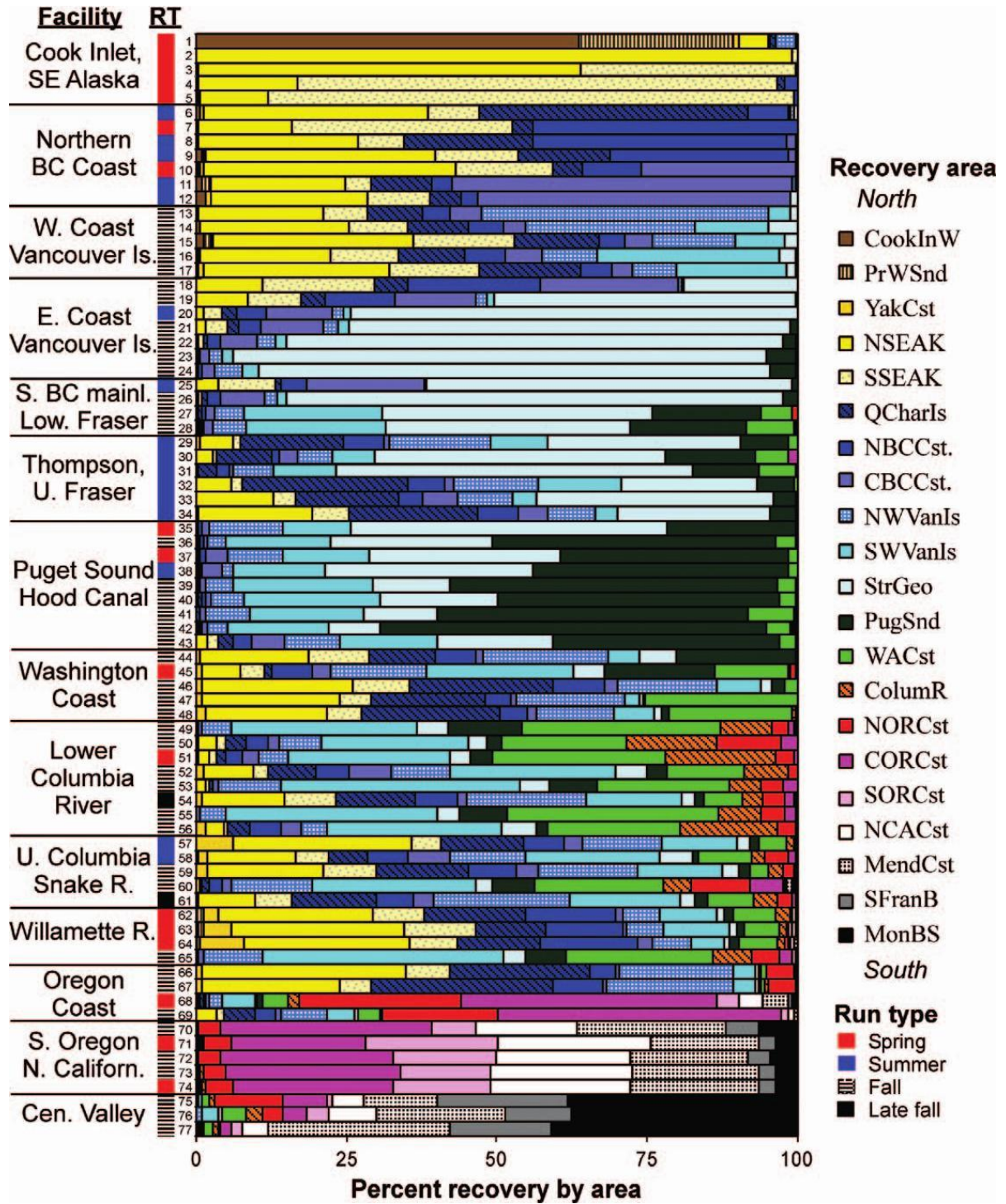
FIGURE 2.—Recovery patterns for coded-wire-tagged Chinook salmon by HRG, arranged by geographic region from north (top) to south (bottom). Each horizontal bar represents the percentages of recoveries in the 21 marine recovery areas for a single HRG; recovery area abbreviations and boundaries are provided in Figure 1. Run timing (RT) and HRG numbers are indicated to the left of the bar chart. See Figure 1 for HRG locations and Table A.1 for HRG names and recovery statistics.
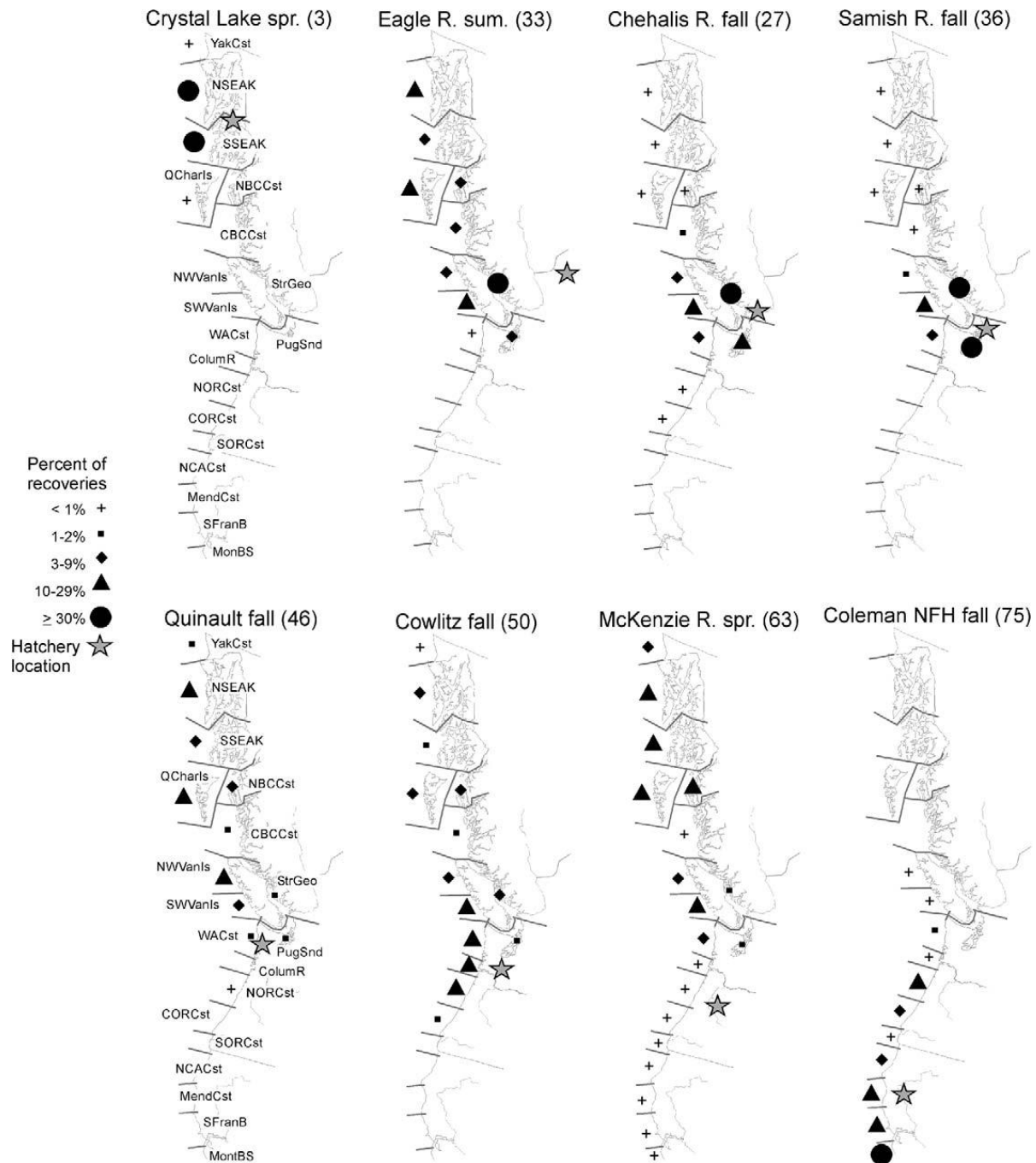
FIGURE 3.—Maps illustrating the percentages of recoveries by marine recovery area from the Yakutat coast to Monterey Bay south for select HRGs. Recoveries in recovery areas with less than 0.1% are not shown; recoveries in the Cook Inlet West and Prince William Sound recovery areas are included with Yakutat recoveries. The stars indicate the approximate locations of the different hatcheries.

primarily recovered in Puget Sound (PugSnd), Strait of Georgia (StrGeo), and west coast of Vancouver Island (WCVanIs) recovery areas (Figure 2). By contrast, tagged Chinook salmon released from nearby Washington coast hatcheries (e.g., Quinault [Figure 3]) had very different recovery patterns and were primarily

recovered in northern and southern Southeast Alaska (NSEAK and SSEAK, respectively), Queen Charlotte Islands (QCharIs), and WCVanIs recovery areas. Other abrupt changes in recovery patterns between hatcheries in adjacent freshwater release regions apparent in Figure 2 occurred between Chinook salmon originating

from (1) southeast Alaska and northern British Columbia; (2) upper Fraser River, Puget Sound, and the Washington coast, and (3) the Oregon coast, southern Oregon–northern California, and the Central Valley.

Salmon from the same release region but with different run types also had different marine distributions in many cases (Figures 2, 3). For example, the three spring Chinook salmon HRGs from the Willamette River (62–64; McKenzie River [Figure 3]) had similar recovery patterns and were largely caught in NSEAK, SSEAK, QCharIs, and northern British Columbia coast (NBCCst) recovery areas. By contrast, the only fall Chinook salmon from the Willamette River (Stayton Pond, 65) was largely restricted to WCVanIs and Washington coast (WACst) recovery areas (Figure 2). Similarly, most recoveries of fall Chinook salmon from the lower Fraser River (HRGs 27–28; Chehalis River [Figure 3]) were in or near the home recovery area (StrGeo, PugSnd, WCVanIs), while Upper Fraser River summer Chinook salmon (HRGs 29, 32–34; Eagle River [Figure 3]) also included recoveries in NSEAK, SSEAK, and NBCCst recovery areas.

This tendency for spring or summer run types to be recovered farther from the home recovery area than fall run types from the same region is also apparent in mean recovery distance, which was significantly lower in fall-type HRGs (mean = 225 km) than either spring (380 km) or summer (342 km) run types from the same region (KW $H \geq 6.7$; $P < 0.05$). In other cases, there was little variation in recovery patterns for different run types within common release regions; recovery patterns for spring and summer Chinook salmon from northern British Columbia were quite similar, as were those for spring, summer, and fall Chinook salmon from Puget Sound, and spring and fall Chinook salmon from southern Oregon–northern California (Figure 2).

Several HRGs also appeared to have distribution patterns that differed from the region-specific pattern (Figure 2), perhaps reflecting transitional distributions. In particular, both the Elwha (43) and Elk River (69) had recovery patterns that were intermediate between the release region in which they are located (Puget Sound [35–43] and Oregon coast [66–69], respectively) and adjacent regions (Washington coast and southern Oregon, respectively). Chinook salmon released from Columbia River hatcheries (including the Snake and Willamette rivers; HRGs 49–65) also showed considerable variation in recovery patterns, mainly due to the proportion of recoveries in NSEAK and SSEAK recovery areas. However, this variation appeared to be largely independent of either run type or hatchery location within the basin (Figure 2).

Statistical Analysis of Hatchery Marine Distributions

Variation in recovery patterns between HRGs was explored using MDS, ANOSIM, and comparisons of pairwise Bray–Curtis similarities and confirmed many of the patterns observed in Figures 2 and 3, discussed above. For example, the MDS analysis of recovery patterns represented the data fairly well in two dimensions (2-D stress = 0.12) and resulted in numerous nonoverlapping clusters of HRGs from common release regions (Figure 4). For instance, Chinook salmon HRGs originating from Alaska (1–5), northern British Columbia (6–12), west coast of Vancouver Island (13–17), Oregon coast (66–69), southern Oregon–northern California (70–74), and the Central Valley (75–77) formed discrete groups that were consistent with release region (Figure 4).

Chinook salmon from the center of the range—the east coast of Vancouver Island to the Columbia River (including the Snake and Willamette rivers)—also clustered by release region, although there was considerable overlap between these regions in MDS space (Figure 4), indicating considerable resemblance in recovery patterns. Despite the overlap, however, region-specific recovery patterns could be discerned: Chinook salmon from the east coast of Vancouver Island (18–24), upper Fraser River (29–34), and Puget Sound (35–43) each formed discrete clusters, which were overlain by southern British Columbia mainland–lower Fraser River HRGs (25–28), half (HRGs 25, 26) grouping with east coast of Vancouver Island HRGs and the other half (HRGs 27, 28) grouping with Puget Sound HRGs. Similarly, Chinook salmon from the Washington coast (44–48), lower Columbia (49–56), upper Columbia–Snake (57–61), and Willamette (62–65) rivers overlapped each other in MDS space. In this case, the only fall run type from the Willamette River (Stayton Pond, 65) and Lyons Ferry (60) from the upper Columbia–Snake rivers were outliers within their respective regions, as were two Washington coast HRGs (44, 45; Figure 4).

The ANOSIM was used to test for differences in recovery patterns based on release region and run type. Using the 15 release regions (Table A.1), both factors formed better groups than would be expected by chance, release region creating better separated groups (global $R = 0.85$; $P < 0.01$) than run type (global $R = 0.36$; $P < 0.01$). Pairwise comparisons of recovery patterns by release region indicate that most regions were well separated from each other (global $R > 0.7$; Table 1), although the statistical significance of many comparisons was low due to limited numbers of possible permutations. Two exceptions where little separation between release regions was indicated
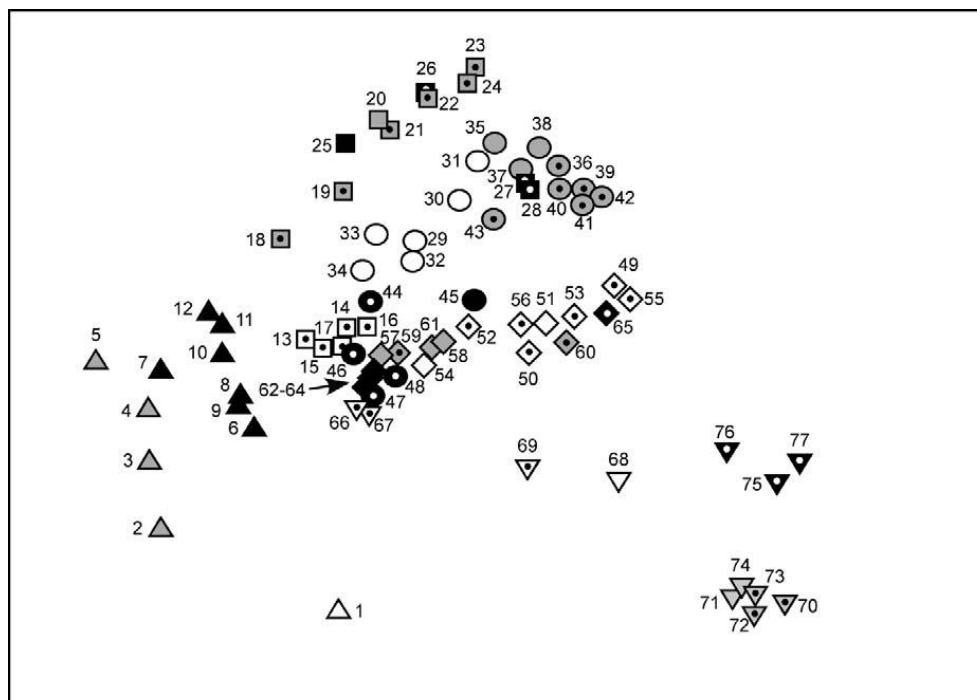
FIGURE 4.—Nonmetric multidimensional scaling for the 77 HRGs, estimated from Bray–Curtis similarities calculated from the recoveries in the 21 recovery areas. This analysis arranges all HRGs in two-dimensional space, so that points that are closer together denote greater similarity than those that are further apart.

TABLE 1.—Global R-values between freshwater release regions estimated by analysis of similarities (ANOSIM). The value of R ranges from -1 (no separation) to $+1$ (complete separation). Values that are statistically significant at $P < 0.05$ are in bold italics; instances in which there were too few hatcheries to estimate R are indicated by dashes. The HRGs located within each release region are listed in Table A.1.

Release region	Cook Inlet	Southeast Alaska	North British Columbia coast	West coast Vancouver Island	East coast Vancouver Island	South British Columbia–Lower Fraser River
Southeast Alaska	1.00					
North British Columbia coast	1.00	0.11				
West coast Vancouver Island	–	–	–			
East coast Vancouver Island	–	–	1.00	*0.90*		
South British Columbia–Lower Fraser River	–	–	1.00	*1.00*	0.19	
Upper Fraser River	1.00	1.00	*0.88*	–	1.00	1.00
Puget Sound	1.00	1.00	1.00	*1.00*	*0.90*	*0.84*
Washington coast	–	0.92	1.00	*0.42*	*0.90*	*1.00*
Lower Columbia River	–	1.00	1.00	*0.98*	*0.97*	*0.98*
Upper Columbia–Snake	–	–	*0.53*	0.42	*0.93*	*0.80*
Willamette rivers	1.00	0.56	0.75	1.00	1.00	1.00
Oregon coast	–	1.00	1.00	*0.50*	*0.93*	1.00
South Oregon–North California coasts	1.00	1.00	1.00	*1.00*	*1.00*	1.00
Central Valley	–	–	–	*1.00*	*1.00*	1.00

TABLE 2.—Mean Bray–Curtis similarities calculated between all pairwise hatchery run type groups (HRGs) within each freshwater release region. Similarities were estimated between (1) all HRGs regardless of run type, (2) HRGs with the same run type, and (3) those with different run types. The total number of comparisons between all HRGs within each region is provided (*n*); a dash indicates that only one run type was available for that region. Similarity ranges from 0% (no recoveries in common) to 100% (identical recoveries).

Release region	*n*	All run types	Same run types	Different run types
Southeast Alaska	6	47.7	47.7	–
North British Columbia coast	21	54.7	55.5	53.8
West coast Vancouver Island	10	73.0	73.0	–
East coast Vancouver Island	21	67.9	64.3	77.0
South British Columbia–Lower Fraser River	6	60.9	66.1	55.8
Upper Fraser River	15	68.2	78.2	59.5
Puget Sound	36	77.2	81.7	70.9
Washington coast	10	65.6	73.1	54.5
Lower Columbia River	28	69.3	74.5	63.2
Upper Columbia–Snake rivers	10	67.2	58.8	69.3
Willamette River	6	58.1	88.5	27.6
Oregon coast	6	42.7	49.9	35.7
South Oregon–North California coasts	7	86.6	88.3	87.2
Central Valley	3	78.9	78.9	–

despite high statistical power were between the east coast of Vancouver Island and southern British Columbia mainland–lower Fraser River ($R = 0.19$), and upper Fraser River and Puget Sound regions ($R = 0.26$; Table 1); this is consistent with overlap between these HRGs in the MDS plot (Figure 4).

By run type, ANOSIM indicated that spring runs had distinct recovery patterns from both summer and fall runs ($R = 0.38$; $P < 0.05$), while summer and fall run types did not form well-separated groups ($R = 0.10$; $P > 0.10$). I also used Bray–Curtis similarities calculated between all pairs of HRGs ($n = 2{,}926$) to explore variation in recovery patterns by run type within regions (Table 2). Within regions with multiple run types, pairwise similarities between HRGs with

common run types (mean = 71.8%) exceeded those with different run types (mean = 60.5%; MW: $U = 1.7$, $P < 0.05$; Table 2). However, the recovery patterns for the five hatcheries releasing more than one run type (Puntledge [19–20]; Cowlitz [50–51], Cole Rivers [70–71], and Trinity River [73–74]; Table A.1) were quite similar between fall and summer or spring run types (mean similarity = 82.5%). By contrast, recovery patterns were divergent (48.4%) for the only hatchery releasing both fall and late fall (upriver bright) runs (Bonneville [53–54]), although recovery patterns for the two late fall HRGs (54, 61) were alike (89.1%).

Finally, to explore the effects of release region on recovery patterns while limiting variation due to run type, I performed cluster analysis on only those HRGs

TABLE 1.—Extended.

Upper Fraser River	Puget Sound	Washington Coast	Lower Columbia River	Upper Columbia–Snake rivers	Willamette River	Oregon Coast	South Oregon–North California coasts
0.88							
1.00	*1.00*						
1.00	*1.00*	*1.00*					
1.00	*1.00*	0.36	0.41				
1.00	*1.00*	*1.00*	0.01	0.00			
1.00	*1.00*	0.26	*0.95*	0.17	1.00		
1.00	*1.00*	*1.00*	*1.00*	1.00	*1.00*	*0.81*	
–	*1.00*	*1.00*	*1.00*	1.00	*1.00*	1.00	1.00
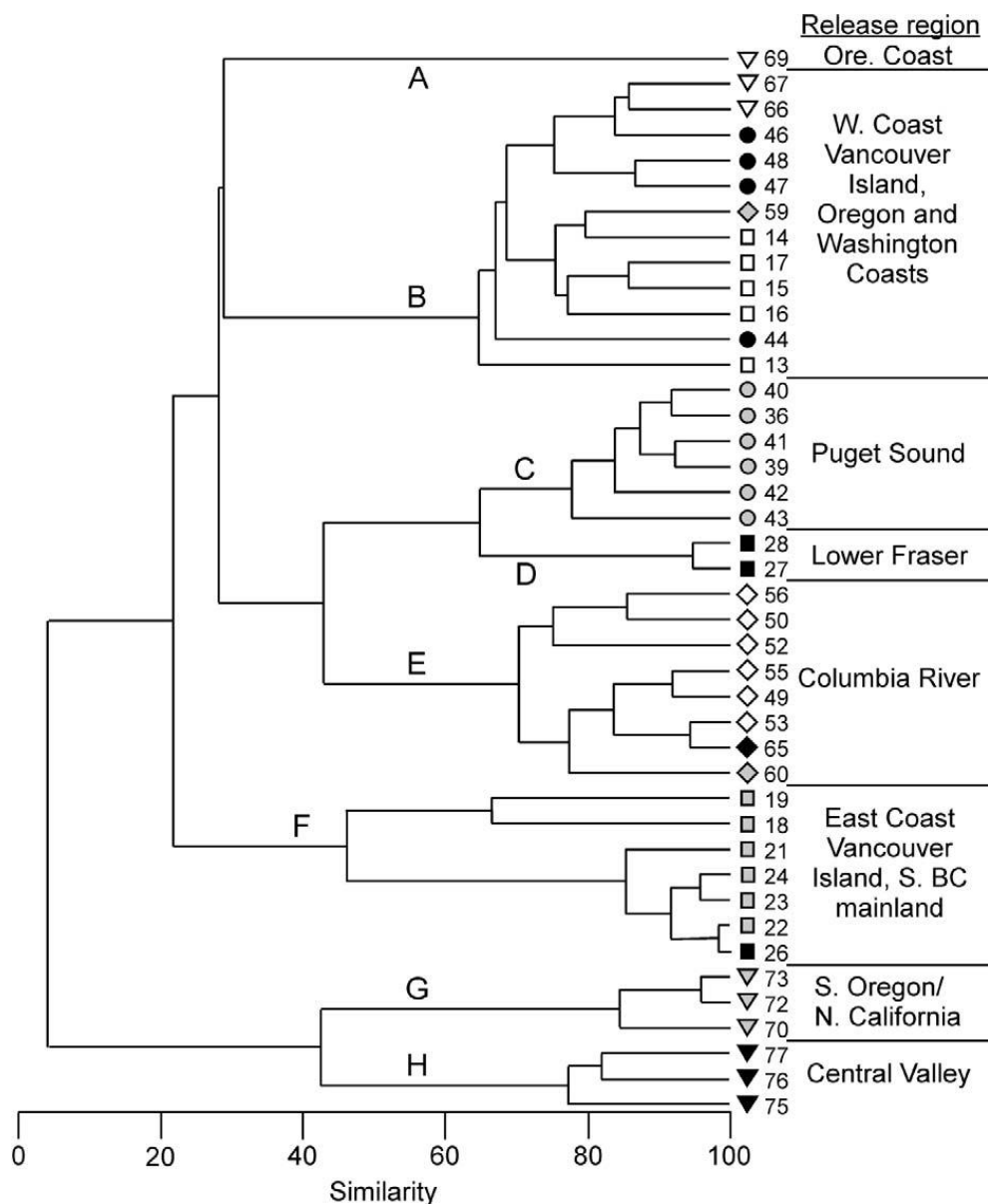
FIGURE 5.—Dendrogram resulting from a cluster analysis of 42 fall Chinook salmon HRGs based on CWT recovery patterns, using Bray–Curtis similarities and group-average linkage. The similarity profile permutation test was used to determine that eight clusters (A–H) were statistically valid. The region of each HRG is provided by name and symbol as in Figure 4.

that contained fall Chinook salmon. The resulting dendrogram contains eight distinct clusters (labeled A–H in Figure 5) with strong correspondence to release location. With only two exceptions, all clusters contained fall Chinook salmon from a single geographic area, such as Puget Sound (cluster C), Columbia River (cluster E), or the Central Valley (cluster H). The two exceptions included HRGs that were either from coastal areas (cluster B) or HRGs from adjacent regions (cluster F). In addition, one HRG identified as transitional in Figure 2 (Elk River [69]) formed its own cluster (A), while another transitional

HRG (Elwha [43]) grouped with other Puget Sound hatcheries (Figure 5). Like the MDS and ANOSIM analyses, this analysis confirms that release region dominates distribution patterns with generally abrupt transitions between regions.

Comparison of Hatchery and Wild Marine Distributions

Bray–Curtis similarities were calculated between the 16 tagged wild Chinook salmon populations and the nearest hatchery with the same run type. High mean Bray–Curtis similarity (average = 75.3%; Table 3)

TABLE 3.—Bray–Curtis similarities calculated between tagged wild populations and the nearest hatchery run type group (HRG) with the same run timing, based on recovery patterns across the 21 recovery areas. The location of each wild population and HRG is provided in Figure 1; recovery statistics are provided in Tables A.1 and A.2.

Run type	Wild population	HRG	Similarity (%)
Spring	W1. Taku River	2. Snettisham	98.7
Spring	W2. Stikine River	3. Crystal Lake	80.9
Spring	W3. Unuk River	5. Neets Bay	79.2
Spring	W4. Chickamin River	4. Deer Mountain	79.7
Summer	W5. Kitsumkalum River	9. Terrace	84.6
Fall	W6. Nitinat River	17. Nitinat River	69.4
Summer	W7. Skagit River	38. Wallace River	71.8
Fall	W8. Lewis River	50. Cowlitz	66.3
Fall	W9. Hanford Reach	59. Priest Rapids	75.9
Fall	W10. Deschutes River	56. Klickitat	71.4
Fall	W11. Shasta River	72. Iron Gate	66.8
Fall	W12. Trinity River	73. Trinity River	58.6
Fall	W13. South Fork Eel river	73. Trinity River	61.7
Spring	W14. Butte Creek	75. Coleman National Fish Hatchery[a]	92.9
Fall	W15. Feather River	77. Feather River	75.1
Fall	W16. Mokelumne River	77. Feather River	71.9

[a] No hatcheries releasing spring Chinook salmon from the Central Valley were used in the analysis; the nearest such spring run (Trinity River [74]) on the north California coast has a similarity of 38.3% with Butte Creek.

between these pairs indicated common marine distributions at local scales. Wild recovery patterns were also analyzed together with all HRGs using a MDS analysis (Figure 6). The MDS represented variation in recovery patterns fairly well (2-D stress = 0.11) and produced a spatial arrangement of HRGs that was very similar to that constructed without wild populations (Figure 4). In the hatchery and wild MDS plot (Figure 6), all wild populations were located near HRGs from the same geographic region, indicating that wild populations share marine distribution patterns with hatcheries from the same region but not with geographically distant hatcheries.

Marine Distributions by Year

Thirty HRGs with at least 100 estimated recoveries in each of 10 or more years were used to explore how recovery patterns varied by year via mean similarities and distances of recovery, ANOSIM, and MDS. These analyses all indicated that recovery patterns were surprisingly stable over time and no year(s) stood out as having unusual recovery patterns. Although there was clearly some variation in mean distance of recovery between years (mean CV = 29.5%), few HRGs had significant trends in mean distance and similarity between years was high (mean = 73.0%; Table 4). However, interannual variability was influenced by run type: CVs of mean distance for HRGs with either spring (37.2%) or summer (42.5%) run type were higher than those with fall run types (26.3%), and mean similarity between years tended to be lower for spring run HRGs (64.6%) than either fall (74.7%) or summer (76.6%) run HRGs (Table 4; ANOVA: $F \geq$

3.0, $P < 0.07$). In addition, ANOSIM analysis of marine distributions by year indicated that either HRG ($R = 0.89$; $P < 0.01$) or release region ($R = 0.83$; $P < 0.01$) produced well-defined groups, but year did not ($R = 0.00$; $P > 0.10$).

The MDS analysis (2-D stress = 0.13) indicated that HRGs from each release region formed reasonably discrete groups regardless of year (Figure 7), suggesting geographically based recovery patterns with little interannual influence. Like the MDS for the 77 HRGs (Figure 4), HRGs from some release regions were completely isolated from others (e.g., southeast Alaska, northern British Columbia, Oregon coast, southern Oregon–northern California), while HRGs from other regions overlapped each other (e.g., Washington coast, upper Columbia–Snake rivers, Willamette River, east coast Vancouver Island, and southern British Columbia mainland–lower Fraser River). Those HRGs from the same region and same year (not illustrated in Figure 7) failed to group together in the MDS plot, suggesting interannual variation in recovery patterns was not consistent at smaller spatial scales (i.e., release regions). Similarly, the cluster analysis (data not shown) produced clusters based largely on common geographic region and run type; each contained multiple years. These results indicate that marine distribution patterns were fairly robust to interannual variation.

An additional analysis was used to determine whether any particular year(s) may have resulted in coastwide changes in distributions (i.e., have exceptionally low similarities with other years), such as might be expected from the strong El Niño (1982,
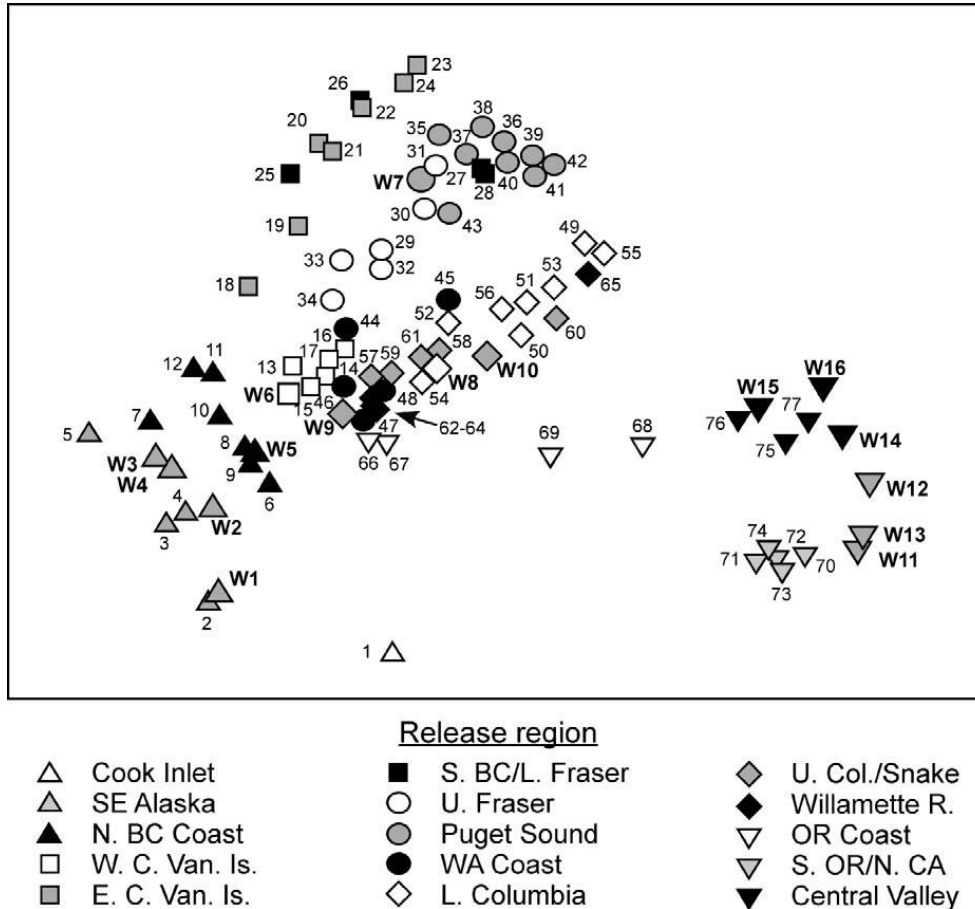
FIGURE 6.—Nonmetric multidimensional scaling for the 77 HRGs and 16 wild populations based on the recoveries in the 21 recovery areas.

1983) or La Niña (1988, 1989) events. The results indicated that although mean similarities between years 1979–1994 were statistically different (KW: $H = 40.7$, $P < 0.01$), the difference was caused by 1991 having higher mean similarity with other years (average = 76.9%) than the years 1980, 1981, 1983, 1984, and 1993 (70.5–72.2%). Apparently, 1991 was a particularly "normal" year coastwide with respect to Chinook salmon marine distributions (and ocean conditions in general; Beamish et al. 2000; Chavez et al. 2003; Lehodey et al. 2006), while other years (1980, 1981, 1983, 1984, 1993) were less so, but were not consistently different from other years.

Two region-specific trends in distance over time (Table 4) can be explained by changes in fishing effort. The positive trend in distance for southern Oregon–northern California HRGs (70–74) was consistent with decreased Chinook salmon landings in northern California and extreme southern Oregon during the late 1980s and early 1990s (PFMC 2009), leading to proportionally higher catches in Oregon recovery areas

and, therefore, greater mean distances for these HRGs. In the second case, mean distances for west coast Vancouver Island HRGs (13, 16, 17) decreased due to increasing proportional recoveries in WCVanIs and decreasing recoveries in recovery areas north of Vancouver Island (NSEAK, SSEAK, NBCCst). Although this trend occurred while total landings off Vancouver Island declined by 30%, west coast Vancouver Island tidal sport landings increased fivefold from 1979 to 1994 (PSC 2005), suggesting these local stocks may have been particularly vulnerable to these "inshore" fisheries.

Marine Distributions by Ocean Age

Differences in marine recovery patterns by ocean age were evaluated for 29 HRGs (Table 5) using comparisons of Bray–Curtis similarities and mean distances, and ANOSIM and MDS. All analyses indicate that recovery patterns varied by ocean age, younger fish generally being caught closer to the home stream than older fish. For example, mean distance of

TABLE 4.—Summary statistics for recovery patterns for select hatchery run type groups (HRGs) across years. Provided are the mean number of recoveries per year, the number of years available, the mean distance to the recovery area, the coefficient of variation (CV), and the regression coefficient (r^2) and slope from regressing distance on year (values significant at $P < 0.05$ are in bold italics). Also provided are mean Bray–Curtis similarities between all pairwise comparisons for each HRG by year.

HRG (run type)	Mean recoveries per year	Number of years	Mean distance (km)	CV (%)	r^2	Slope	Similarity (%)
3. Crystal Lake (spring)	642	10	132	28.8	*0.41*	−7.3	79.0
10. Kitimat River (spring)	337	15	289	26.0	0.26	8.0	75.2
11. Snootli Creek (summer)	359	10	175	25.2	0.15	−5.1	77.3
13. Conuma River (fall)	1,211	13	307	30.1	*0.72*	−18.7	72.1
16. Robertson Creek (fall)	3,148	16	313	18.9	*0.54*	−8.6	76.6
17. Nitinat River (fall)	522	11	437	17.5	0.26	−10.8	73.7
18. Quinsam River (fall)	703	16	403	14.1	0.01	−1.0	76.7
19. Puntledge River (fall)	491	10	278	41.1	0.04	4.3	69.8
20. Puntledge River (summer)	397	11	137	59.8	0.11	6.2	75.9
21. Big Qualicum River (fall)	878	16	114	29.9	0.05	1.5	86.1
23. Chemainus River (fall)	1,616	11	19	22.9	0.14	0.4	93.8
24. Cowichan River (fall)	1,453	12	28	37.3	0.19	0.9	90.1
26. Capilano River (fall)	1,415	12	56	49.8	0.02	0.8	88.4
27. Chehalis River (fall)	932	11	88	40.2	*0.57*	7.5	73.7
36. Samish (fall)	1,665	11	64	24.8	0.00	0.0	78.7
40. Soos Creek (fall)	553	10	74	32.8	0.04	−0.9	78.4
41. Grovers Creek (fall)	518	10	78	20.9	0.21	2.2	78.9
46. Quinault Lake–NFH (fall)	433	15	493	13.4	0.01	1.4	70.9
50. Cowlitz (fall)	386	12	214	29.8	0.05	−3.5	65.6
51. Cowlitz (spring)	3,295	14	225	28.6	0.05	−3.5	65.9
55. Spring Creek NFH (fall)	1,887	13	173	14.2	0.03	0.7	71.7
59. Priest Rapids (fall)	405	14	541	19.6	0.00	0.1	65.4
65. Stayton Pond (fall)	769	14	186	17.4	0.18	−3.1	67.2
67. Salmon River (fall)	568	10	643	16.2	0.18	−10.9	70.2
68. Rock Creek (spring)	396	12	150	67.5	0.20	−11.7	48.8
69. Elk River (fall)	888	12	268	39.0	0.13	−8.8	65.3
71. Cole Rivers (spring)	1,888	13	135	42.6	*0.68*	8.4	54.7
72. Iron Gate (fall)	1,321	13	130	22.8	*0.72*	5.6	61.8
73. Trinity River (fall)	2,870	12	117	26.9	0.26	4.1	67.8
74. Trinity River (spring)	1,184	11	113	29.6	*0.47*	5.6	64.3

recovery for Chinook salmon with ocean ages 1 and 2 averaged 187 km, while that for Chinook salmon ages 3–5 averaged 325 km (Table 5). Comparison of mean distance anomalies by ocean age, which controls for HRG-specific differences in mean distance, produced similar results: Chinook salmon caught at ages 1 (mean anomaly $= -0.39$) and 2 (-0.40) had statistically lower mean distance anomalies than those caught at ages 3, 4, and 5 (0.32–0.49; KW: $H = 43.6$, $P < 0.01$).

The MDS analysis showed considerable variation in age-based recovery patterns by release region (data not shown), although the fit was reasonable (2-D stress = 0.15). In the MDS space, points with a common region and ocean age tended to group together, while those of different ages were farther apart. Likewise, the ANOSIM test of recovery patterns using region and ocean age indicated that discrete groups were formed with both region and ocean age, although the influence of region (global $R = 0.77$; $P < 0.01$) was greater than ocean age ($R = 0.16$; $P < 0.01$). The analysis indicated that recovery patterns of ocean age-1 salmon were distinct from those at ages 2, 3 and 4, as were those between ages 2 and 4 (Table 6). These results based on

multivariate techniques are reasonably consistent with those based on the univariate mean distance.

Discussion

I provide a comprehensive analysis of coastal distribution patterns for Chinook salmon from the West Coast of North America. This analysis indicates that Chinook salmon originating from a particular freshwater region shared a common marine distribution pattern, which was distinct from the patterns of adjacent regions. At the broadest spatial scale, three general recovery patterns were apparent representing Chinook salmon originating from (1) Alaska (recovered only in Alaska); (2) British Columbia, Washington, and Oregon (recovered from the home recovery area to southeast Alaska); and (3) southern Oregon and California (recovered in Oregon and California). At finer spatial scales, 12 distinct recovery patterns were identified, representing Chinook salmon from Cook Inlet, southeast Alaska, northern British Columbia, east and west coasts of Vancouver Island, upper Fraser River, Puget Sound, lower Columbia River, upper Columbia–Snake rivers, Willamette River (spring run),
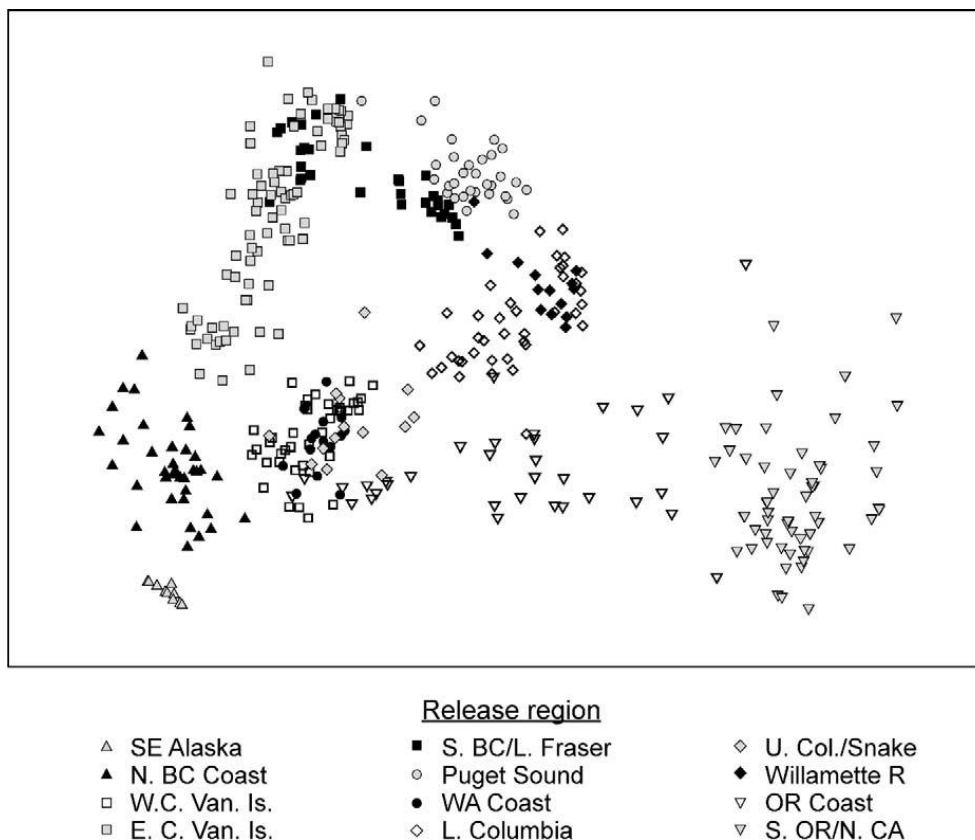
FIGURE 7.—Nonmetric multidimensional scaling by year for select HRGs based on the recoveries in the 21 recovery areas. For clarity, the HRG numbers and years are not shown, but the points are coded by release region.

Oregon coast, southern Oregon–northern California, and the Central Valley (Figures 2, 4). Recovery patterns for Chinook salmon from the southern British Columbia mainland–lower Fraser River and Washington coast were less distinct and displayed considerable overlap with marine distributions of adjacent release regions.

These patterns are familiar to salmon managers who use distributional differences at even finer spatial and temporal scales to target fisheries on particular stocks while avoiding others. For example, in 2008 ocean fisheries for Chinook salmon were closed from Cape Falcon (the dividing line between the north Oregon coast [NORCst] and ColumR recovery areas) to the U.S.–Mexico border to minimize ocean harvest of Central Valley Chinook salmon (PFMC 2009). Not surprisingly, my analysis indicated that 94% of recoveries of Central Valley HRGs (75–77; Coleman NFH [Figure 3]) occurred within this area (NORCst to Monterey Bay South recovery areas), suggesting the closure was highly effective. While managers are typically focused on marine distributions of particular stocks, however, this analysis included populations along the entire West Coast of North America.

Assumptions Underlying the Analysis

This analysis assumes that the number of Chinook salmon with CWTs recovered in a particular recovery area reflects the abundance of tagged fish in that area relative to other recovery areas. However, catch is a function of both salmon abundance and fishing effort, potentially leading to violations of the assumption if effort is unevenly distributed in space or time. Fishing effort was deliberately excluded from calculations of marine recovery patterns in order to simplify the analysis, yet its absence may bias the marine distribution patterns or recovery distances provided here. For example, correspondence between trends in distance by year and changes in landings in northern California and off the west coast of Vancouver Island discussed above point to two examples where fishing effort clearly influenced recovery patterns.

Despite this potentially confounding factor, however, the patterns presented here are thought to largely reflect Chinook salmon abundance in the coastal eastern North Pacific, with relatively minor influence from fishing effort. Studies that have deliberately incorporated fishing effort in estimations of marine distributions or ocean recovery rates have demonstrated

TABLE 5.—Mean distance traveled (km) and Bray–Curtis similarities (means of all pairwise comparisons between ages) by ocean age (recovery year – release year) for select hatchery run type groups (HRGs). Also provided is the mean estimated number of recoveries per ocean age.

HRG (run type)	Mean recoveries per ocean age	Distance by ocean age (years)					Mean similarity (%)
		1	2	3	4	5	
1. Cook Inlet (spring)	305	23	132	174	13		76.2
3. Crystal Lake (spring)	2,523	146	131	136	74	62	75.7
4. Deer Mountain (spring)	861	54	61	30	19		85.1
7. Kincolith River (spring)	529	10	109	146	136		65.2
10. Kitimat River (spring)	2,102	53	288	357	180		58.8
13. Conuma River (fall)	3,223	149	207	240	227	267	83.1
16. Robertson Creek (fall)	10,328	172	265	340	327	348	72.7
18. Quinsam River (fall)	3,588	350	383	445	347	444	71.1
19. Puntledge River (fall)	1,387	91	270	413	396		64.3
21. Big Qualicum River (fall)	3,546	73	90	160	353		70.1
26. Capilano River (fall)	4,328	43	53	76	73		87.5
27. Chehalis River (fall)	2,597	47	94	116	182		62.2
33. Eagle River (summer)	1,797	85	195	325	389		60.2
34. Shuswap River (summer)	1,218	63	252	394	423		61.0
36. Samish (fall)	4,755	52	63	74	58		68.8
39. Issaquah (fall)	1,933	19	73	99	81		72.8
40. Soos Creek (fall)	1,494	33	87	85	90		72.4
43. Elwha (fall)	581	171	113	169	186		75.6
46. Quinault Lake–NFH (fall)	1,405	364	370	503	563	563	69.5
47. Humptulips (fall)	1,560		203	400	417	356	76.2
48. Forks Creek (fall)	1,125		271	406	430	529	71.5
50. Cowlitz (fall)	1,260	252	158	261	466		49.0
54. Bonneville late (fall)	2,154	340	317	460	609	628	51.7
59. Priest Rapids (fall)	1,738	352	395	594	660		57.9
61. Irrigon late (fall)	689	328	314	523	650		55.5
66. Trask River (fall)	539		595	681	710	606	81.1
67. Salmon River (fall)	1,500		475	668	680	597	74.6
69. Elk River (fall)	2,710	430	157	243	292		66.4
73. Trinity River (fall)	8,686	108	117	104	76		75.7

that fishing effort has relatively little influence compared with other factors, such as region, fish age, year, or environmental effects (Norris et al. 2000; Hyun et al. 2007). Similarly, results from the PSC's Chinook salmon cohort analysis model (PSC 2007), which includes fishing effort and stock-specific salmon abundance, indicate marine distributions for indicator stocks that, although not directly comparable, are not dissimilar to those estimated here without fishing effort. Inclusion of fishing effort is critical for salmon management, but it appears to be less so for determining marine distributions of individual populations across large geographic areas.

In addition, the primary years used in this analysis (1979–1994) were specifically selected to encompass a period when fishing effort was more or less constant (or as constant as fishing effort ever is). Although effort clearly was not constant during this period, recovery patterns were surprisingly stable over time (Table 4; Figure 7), regional structure far exceeding that due to year. By using recoveries over multiple years (average of 13 years for each HRG; Table A.1), variation in marine distributions due to changes in fishing effort in a given year was minimized by considering the entire time period as a whole. Furthermore, if fishing effort

was explicitly considered in the analysis, region-specific distribution patterns identified here are expected to become more clear, not less so. Consequently, while fishing effort probably influenced the marine distribution patterns to some degree, the patterns presented here should largely represent the relative abundance of salmon in marine waters and therefore reflect their "true" marine distributions.

Variation in Marine Distributions

The analysis indicated that recovery patterns were surprisingly stable across years despite considerable

TABLE 6.—Global R-values between marine distribution patterns by ocean age estimated by analysis of similarity. The value of R ranges from −1 (no separation) to +1 (complete separation). Values that are statistically separated at $P < 0.05$ are in bold italics.

Ocean age	Ocean age			
	1	2	3	4
1				
2	*0.23*			
3	*0.50*	0.04		
4	*0.59*	*0.29*	−0.10	
5	0.21	0.09	−0.13	−0.08

variation in ocean conditions observed during 1979–1994, including strong El Niño (1982–83) and La Niña (1988–89) events (Trenberth 1997). These variable ocean conditions altered marine ecosystems throughout the northeast Pacific Ocean (e.g., Beamish et al. 2000; Chavez et al. 2003; Lehodey et al. 2006) and influenced Chinook salmon survival and growth directly (Johnson 1988; Magnusson and Hilborn 2003; Wells et al. 2006). Little interannual change in marine distributions suggest that Chinook salmon distributions are driven to a larger degree by genetic control of migration (Brannon and Setter 1989; Kallio-Nyberg and Ikonen 1992) than by either local environmental conditions (Hodgson et al. 2006) or opportunistic foraging opportunities (Kallio-Nyberg et al. 1999; Healey 2000). This high stability may reflect a strategy to "spread the risk" in response to unpredictable ocean conditions (Leggett 1985), resulting in higher survival overall than species which are less dispersed and, therefore, more vulnerable to catastrophic events.

In contrast, marine distribution patterns were influenced by ocean age, and individuals that spent longer in the ocean were recovered farther from the home stream than those that had recently entered the ocean (Table 5). Although this finding has previously been observed (e.g., Wright 1968; Brannon and Setter 1989; Norris et al. 2000), the extent to which it occurs has not been appreciated. Whether this difference results primarily from size-dependent swimming speeds, age-specific habitat choice, or some other factor is not known.

Run type also influenced marine distribution patterns: fall Chinook salmon were typically recovered closer to the home stream than were spring or summer run types. These trends are consistent with Healey's (1983, 1991) proposal that stream-type Chinook salmon have a more oceanic distribution than do ocean-type Chinook salmon. However, these patterns were also consistent with the fact that different run types are caught at different stages of their marine residence, particularly with respect to their time of freshwater entry. Specifically, most tagged salmon used here (88%) were recovered during May–September, while only 12% were recovered during October–April. Consequently, most spring Chinook salmon that were sexually mature had already entered freshwater before these intense marine fisheries began. Therefore, most spring Chinook salmon caught in marine fisheries were individuals who were remaining in marine waters for at least another year, or in the "offshore feeding phase" (Healey 2000). By contrast, a large but unknown proportion of fall Chinook salmon are intercepted by marine fishers during their homeward

migration while making directed movements towards the natal stream (Healey 2000); summer Chinook salmon are probably intermediate between spring and fall Chinook salmon. My results are consistent with these life history differences: spring and summer Chinook salmon were caught both farther from their home stream and had greater temporal variability in recovery patterns than did fall Chinook salmon, suggesting behavioral differences (directed migration versus undirected feeding) associated with run type at time of capture.

Differences in marine distributions between multiple run types entering the ocean at a common location (e.g., Fraser or Columbia rivers) also suggest a strong genetic component to the patterns, although run-specific life history differences discussed above obviously confound the issue. Perhaps the best evidence for a large genetic component to recovery comes from marine distributions of nonlocal stocks, which were deliberately excluded from this analysis. For example, Rogue River (southern Oregon) Chinook salmon have been released from the Columbia River because they are "south migrating" (Nicholas and Hankin 1988) and therefore readily caught off the Oregon coast. Analysis of tagged Rogue River Chinook salmon released from the Columbia River indicates that only 9% of these fish were recovered north of the Columbia River recovery area compared with 87% for native Columbia-origin Chinook salmon (HRGs 49–65; Figure 2). Because the two groups enter the ocean at the same location and time (RMIS), the difference suggests considerable genetic control of marine distributions.

Marine distribution patterns were also similar between tagged wild Chinook salmon and hatchery fish from the same region (Table 3; Figure 6), consistent with similar studies of Chinook (Healey and Groot 1987) and coho salmon (Weitkamp and Neely 2002). Given that most Chinook salmon hatchery stocks were founded from local wild populations (Myers et al. 1998), this suggests that selective forces associated with hatchery rearing (e.g., NRC 1996; Kallio-Nyberg and Koljonen 1997; Quinn 2005) have had little effect on marine distributions. Alternately, similar marine distributions may simply reflect that both hatchery and wild individuals belong to a single homogenized population (e.g., Williamson and May 2005), although the extent to which this occurs coastwide is unclear (e.g., Teel et al. 2000; Withler et al. 2007).

Comparison to Coho Salmon Marine Distributions

Compared with our earlier analysis of coho salmon marine distributions (Weitkamp and Neely 2002), the

patterns provided here for Chinook salmon had several obvious similarities and differences, probably reflecting both species-specific life history differences and common responses to marine environments. For example, Chinook salmon were much more widely distributed in the eastern North Pacific than coho salmon, consistent with their greater marine age at recovery (typically 1–4 years) than coho salmon (1 year) and the tendency for older fish to be caught farther from the home stream, discussed previously. Despite this difference, however, Chinook salmon marine distribution patterns followed the same model as coho salmon: fish from a particular freshwater release region shared a common marine recovery pattern, limited transition in patterns occurring between regions. Although distribution patterns within release regions were not as uniform in Chinook salmon due to variation associated with ocean age and run type, most changes in recovery patterns occurred at the same locations in both species. Consequently, the 12 groups identified here for Chinook salmon were nearly identical to the 12 groups identified for coho salmon (Weitkamp and Neely 2002). In most cases, these groups were also similar to those based strictly on genetics (Teel et al. 2003; Waples et al. 2004; Beacham et al. 2006; Van Doornik et al. 2007).

Finally, both Chinook and coho salmon (L. A. Weitkamp, unpublished data) displayed surprisingly low interannual variability in recovery patterns despite high variability in ocean conditions. The fact that marine distributions of both species were apparently unaffected by extreme ocean conditions, even though survival and growth clearly were (Johnson 1988; Magnusson and Hilborn 2003; Wells et al. 2006), suggests a common response to unpredictable ocean conditions. This implies that widespread and stable marine distributions may exist in other Pacific salmon and other fish species, and may be a universal response to dynamic marine environments.

Implications

The results of this analysis have implications for basic salmon biology and the ability of Chinook salmon to respond to climate change. Above all, it emphasizes the fact that Pacific salmon clearly know where they are in the ocean. Tagged Chinook salmon were recovered in coastal waters hundreds to thousands of kilometers from their natal streams and therefore were in close proximity to thousands of streams which they could have easily entered to spawn. Instead, most (>90%) salmon chose to return to their natal stream (Healey 1991; Myers et al. 1998; Quinn 2005) and apparently know how to get there.

The results can also be used to understand how

salmon will respond to climate change, which will probably increase water temperatures and decrease coastal productivity in much of the northeast Pacific Ocean (Crozier et al. 2008). Limited interannual variation in marine distributions despite variable ocean conditions reported here suggests that salmon's response to deteriorating conditions may result in poor survival rather than alterations in marine distributions. Chinook salmon originating from southern Oregon and California may be particularly susceptible to these changes because of their extreme southern distributions, both as juveniles (Trudel et al. 2009) and adults (Figure 2). Furthermore, recent evidence suggests that these populations are already limited by temperature preferences to a fraction of available marine habitats in this region (Hinke et al. 2005). Current marine distributions must reflect successful strategies in the face of variable ocean conditions (Thorpe 1999); however, it is not clear how—or how quickly—they can adapt to future conditions.

This analysis indicated that Chinook salmon exhibit region-specific marine distributions; salmon originating from a particular freshwater region share common recovery patterns, which differs from that of adjacent regions. Distribution patterns varied by run type, consistent with recovery of fish at different stages of ocean residency; it is less clear why marine distributions vary with ocean age. The results also suggest that some populations may be more vulnerable to climate change due to their restricted marine distributions. Similar region-specific marine distributions with limited interannual variation observed in coho salmon suggest a universal salmon response to dynamic marine environments and provide an important model for migratory fishes which have not benefited from such intensive tagging programs.

Acknowledgments

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Appendix: Recovery Statistics for Hatchery Run Timing Groups

TABLE A.1.—Recovery statistics for the 77 Chinook hatchery run timing groups (HRGs) used in the analysis.

Release region[a]	HRG	Run type	Estimated number of tags recovered	Number of areas from which tags were recovered	Number of years in which tags were recovered[b]	Mean recoveries per year	Distance (km)
Cook Inlet, Alaska	1. Cook Inlet[c]	Spring	976	9	17	57	221
Southeast Alaska	2. Snettisham	Spring	2,020	3	14	144	186
	3. Crystal Lake	Spring	9,841	6	21	469	294
	4. Deer Mountain	Spring	3,301	7	22	150	202
	5. Neets Bay	Spring	3,154	6	8	394	196
North British Columbia coast	6. Masset	Summer	1,214	10	19	64	324
	7. Kincolith River	Spring	1,737	6	16	109	142
	8. Fort Babine	Summer	3,130	9	19	165	136
	9. Terrace	Summer	3,207	11	20	160	185
	10. Kitimat River	Spring	7,331	11	26	282	450
	11. Snootli Creek	Summer	5,787	13	22	263	324
	12. Oweekeno	Summer	1,380	9	10	138	353
West coast Vancouver Island	13. Conuma River	Fall	15,738	12	14	1,124	290
	14. Gold River	Fall	2,061	11	6	344	336
	15. Clayoquot	Fall	2,452	11	5	490	560
	16. Robertson Creek	Fall	50,365	15	16	3,148	435
	17. Nitinat River	Fall	5,781	13	13	445	527
East coast Vancouver Island	18. Quinsam River	Fall	11,248	13	16	703	459
	19. Puntledge River	Fall	5,275	9	16	330	297
	20. Puntledge River	Summer	4,417	8	16	276	155
	21. Big Qualicum River	Fall	14,055	11	16	878	153
	22. Nanaimo River	Fall	6,906	11	12	576	100
	23. Chemainus River	Fall	17,777	11	11	1,616	65
	24. Cowichan River	Fall	17,477	11	15	1,165	75
South British Columbia–lower Fraser River	25. Tenderfoot Creek	Summer	1,065	8	11	97	227
	26. Capilano River	Fall	17,204	11	16	1,075	101
	27. Chehalis River	Fall	10,250	14	11	932	101
	28. Chilliwack River	Fall	9,390	14	9	1,043	104
Upper Fraser–Thompson rivers	29. Quesnel River	Summer	1,379	11	11	125	269
	30. Fraser above Hope[d]	Spring	984	12	10	98	164
	31. Spius Creek	Spring	1,804	10	9	200	109
	32. Clearwater River	Summer	2,509	11	9	279	320
	33. Eagle River	Summer	6,812	10	9	757	322
	34. Shushwap River	Summer	4,647	13	9	516	417
Puget Sound, Washington	35. Kendall Creek	Spring	2,400	9	9	267	221
	36. Samish	Fall	18,345	13	14	1,310	186
	37. Marblemount	Spring	2,518	10	8	315	202
	38. Wallace River	Summer	4,360	10	8	545	201
	39. Issaquah	Fall	7,474	12	11	679	169
	40. Soos Creek	Fall	5,661	12	15	377	179
	41. Grovers Creek	Fall	5,187	13	11	472	163
	42. Hoodsport	Fall	2,313	15	14	165	168
	43. Elwha	Fall	2,063	11	12	172	223
Washington coast	44. Hoko Falls	Fall	1,760	12	7	251	408
	45. Sol Duc	Spring	2,205	15	7	315	332
	46. Quinault Lake– National Fish Hatchery (NFH)	Fall	6,575	14	16	411	589
	47. Humptulips	Fall	5,778	14	10	578	485
	48. Forks Creek	Fall	4,267	14	9	474	494

Table A.1.—Continued.

Release region[a]	HRG	Run type	Estimated number of tags recovered	Number of areas from which tags were recovered	Number of years in which tags were recovered[b]	Mean recoveries per year	Distance (km)
Lower Columbia River, Washington	49. Abernathy	Fall	4,172	14	10	417	248
	50. Cowlitz	Fall	4,791	17	16	299	274
	51. Cowlitz	Spring	46,188	18	16	2,887	265
	52. Washougal	Fall	2,311	14	15	154	420
Lower Columbia River, Oregon	53. Bonneville	Fall	1,867	13	12	156	278
	54. Bonneville	Late	10,015	20	14	715	510
Lower Columbia River, Washington	55. Spring Creek NFH	Fall	24,674	14	16	1,542	237
	56. Klickitat	Fall	1,352	14	5	270	315
Upper Columbia–Snake rivers, Washington	57. Similkameen	Summer	1,333	16	3	444	672
	58. Wells Hatchery–spawning channel	Summer	1,803	16	14	129	492
	59. Priest Rapids	Fall	5,796	19	16	362	587
	60. Lyons Ferry	Fall	5,925	19	9	658	259
Upper Columbia–Snake rivers, Oregon	61. Irrigon	Late	2,528	15	9	281	468
Willamette (Columbia River)	62. Marion Forks	Spring	2,417	16	16	151	668
	63. McKenzie	Spring	1,231	21	15	82	702
	64. Willamette	Spring	1,414	18	15	94	714
	65. Stayton Pond	Fall	10,781	16	15	719	251
Oregon coast	66. Trask River	Fall	1,983	15	10	198	776
	67. Salmon River	Fall	5,829	16	15	389	727
	68. Rock Creek	Spring	4,848	19	14	346	186
	69. Elk River	Fall	10,671	19	14	762	287
South Oregon–north California coasts	70. Cole rivers	Fall	2,646	10	5	529	130
	71. Cole rivers	Spring	24,590	14	15	1,639	108
	72. Iron Gate	Fall	17,185	13	14	1,228	114
	73. Trinity River	Fall	34,637	13	16	2,165	113
	74. Trinity River	Spring	13,219	13	16	826	115
Central Valley, California	75. Coleman NFH	Fall	47,730	16	20	2,387	165
	76. Tehama–Colusa Fish Facility	Fall	3,153	14	9	350	193
	77. Feather River	Fall	1,606	13	10	161	121

[a] The Puget Sound region includes Hood Canal and the eastern Strait of Juan de Fuca. The Washington coast region includes the western Strait of Juan de Fuca. The Oregon coast region extends south of Cape Blanco to include the Elk River.
[b] Recoveries from hatcheries in Alaska (1–12) and the Central Valley (75–77) are from 1979–2004 (26 years total); all others are from 1979–1994.
[c] Includes releases and recoveries from both Fort Richardson and Elemendorf hatcheries.
[d] Includes releases and recoveries of spring Chenook salmon from Deadman River, Eagle River, Penny, and Quesnel River hatcheries.

TABLE A.2.—Recovery statistics for the 16 basins with wild-tagged Chinook salmon used in the analysis.

Region	Population[a]	Run timing	Estimated number of tags recovered	Number of areas from which tags were recovered	Number of years in which tags were recovered[b]	Mean recoveries per year	Distance (km)
Southeast Alaska	W1. Taku River	Spring	837	6	20	42	6
	W2. Stikine River	Spring	109	3	8	14	131
	W3. Unuk River	Spring	1,490	7	18	83	78
	W4. Chickamin River	Spring	415	5	10	42	61
North British Columbia coast	W5. Kitsumkalum River	Summer	209	7	7	30	206
West coast Vancouver Island	W6. Nitinat River	Fall	842	10	7	120	536
Puget Sound	W7. Skagit River	Summer	799	10	4	200	148
Lower Columbia River	W8. Lewis River	Fall	2,967	15	16	185	405
Upper Columbia River–Snake	W9. Hanford Reach	Fall	532	13	5	106	642
Upper Columbia River–Snake	W10. Deschutes River	Fall	345	18	5	69	347
South Oregon–North California coasts	W11. Shasta River	Fall	169	7	4	42	143
	W12. Trinity River	Fall	573	7	11	52	200
	W13. South Fork Eel	Fall	385	7	5	77	128
Central Valley	W14. Butte Creek	Spring	195	8	6	33	159
	W15. Feather River	Fall	1,261	12	14	90	203
	W16. Mokelumne River	Fall	854	10	13	66	135

[a] Includes wild Chinook salmon released from the following tributaries (names given in the CWT database): Butte Creek: Adams Dam, Daldwin Construction Yard, Okie Dam, and Parrot-Phelan Dam; Deschutes: Warm Springs; Feather River: Live Oak, Thermalito Bypass, and Yuba River; Mokelumne: Crockett, Rio Vista, and Woodbridge; Trinity: Horse Linto Creek, Junction City, Steel Bridge, and North Fork Trinity River.
[b] Recoveries in Southeast Alaska (W1–W4) and the Central Valley (W14–16) are from 1979–2004; all others were limited to 1979–1994.

TABLE A.3.—Numbers of fish, hatchery run timing groups (HRGs), and wild population recovered by recovery area across years.

Recovery area	Number of hatchery fish recovered	Number of HRGs represented	Number of wild fish recovered	Number of wild rivers represented
Cook Inlet, west	911	25	11	3
Prince William Sound	569	29	13	4
Yakutat Coast	1,489	47	63	6
Northern Southeast Alaska	50,810	68	2,707	10
Southern Southeast Alaska	29,712	68	1,553	10
Queen Charlotte Islands	27,826	66	479	10
Northern British Columbia coast	20,736	65	488	8
Central British Columbia coast	22,941	64	268	6
Northwest Vancouver Island	37,803	70	644	7
Southwest Vancouver Island	72,247	66	847	7
Strait of Georgia	102,795	69	498	6
Puget Sound	38,231	62	217	5
Washington coast	38,524	63	441	7
Columbia River	14,470	40	221	4
Northern Oregon coast	18,131	44	415	9
Central Oregon coast	37,571	36	349	8
Southern Oregon coast	16,833	21	134	7
Northern California coast	25,149	26	158	7
Mendocino coast	25,961	24	539	7
San Francisco Bay	13,868	13	713	7
Monterey Bay, south	23,700	13	1,186	7