Coho salmon (*Oncorhynchus kisutch*) ocean migration patterns: insight from marine coded-wire tag recoveries

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Abstract: We investigated geographic variation in the ocean migration of coho salmon (*Oncorhynchus kisutch*) by examining recovery locations of 1.77 million coded-wire tagged fish from 90 hatcheries and 36 wild populations along the west coast of North America. Principal component, cluster, and similarity analyses were used to reveal both large- and small-scale variation in marine recovery patterns. We identified 12 distinct ocean distribution patterns, each associated with a particular geographic region. Despite these distinct patterns, however, fish from a given population were widely dispersed in the coastal ocean. Recovery patterns for tagged wild populations were consistent with those of hatchery populations from the same region, suggesting that marine distributions based on hatchery populations are reasonable proxies for distributions of wild populations. These region-specific distribution patterns suggest unappreciated life history diversity for coho salmon in the marine environment. When combined with region-specific adult size variation, they suggest migratory differences earlier in the ocean residence period as well. These results provide a novel framework with which to view geographic variation in salmon ocean ecology, conservation, and management.

Résumé : L'examen des sites de récupération de 1,77 million poissons marqués à l'aide de fils de fer codés et provenant de 90 piscicultures et de 36 populations sauvages le long de la côte occidentale de l'Amérique du Nord a permis d'étudier la variation géographique de la migration en mer du saumon coho (*Oncorhynchus kisutch*). Des analyses en composantes principales et des analyses de regroupement et de similarité ont servi à mettre en évidence la variation à petite et à grande échelles des patterns de récupération en mer. Douze patterns distincts de distribution en mer ont pu être identifiés, chacun associé à une région géographique particulière. Malgré l'existence de tels patterns, cependant, les poissons d'une même population se dispersent considérablement dans l'océan côtier. Les patterns de récupération des poissons marqués de populations sauvages correspondent à ceux des poissons d'élevage de la même région, ce qui laisse croire que les répartitions en mer déterminées à partir de poissons de pisciculture sont d'assez fidèles représentations des répartitions des populations sauvages. L'existence de patterns de répartition spécifiques à chaque région révèle une diversité dans la biologie du saumon coho en mer que l'on ne soupçonnait pas. Si on considère de plus la variation d'une région à une autre de la taille des adultes, il semble qu'il existe aussi des différences migratoires tôt dans la période de résidence en mer. Ces résultats fournissent donc un nouveau cadre pour l'examen de la variation géographique en écologie, conservation et gestion des saumons en mer.

[Traduit par la Rédaction]

Introduction

Ocean residence is a critical component of the Pacific salmon (*Oncorhynchus* spp.) life cycle. While salmon are in the ocean, they migrate hundreds or thousands of kilometres, greatly increase in size, and acquire the energy reserves necessary for reproduction. Yet our understanding of where salmon go in the ocean is extremely limited (Pearcy 1992), especially for coho salmon (*Oncorhynchus kisutch*). In part, this is due to coho salmon's lesser overall abundance compared with other Pacific salmon species (Sandercock 1991) and relatively infrequent capture on the high seas (Manzer et al. 1965; Godfrey et al. 1975). Although the general location in the North Pacific for coho salmon from large freshwater regions is known (e.g., Pacific Northwest, Alaska, Asia; Godfrey et al. 1975; Myers et al. 1996), until now, there has been no evidence to indicate migrational differences at finer geographic scales.

Coded-wire tags (CWTs), 1 mm-long pieces of uniquely encoded wire inserted into the nasal cartilage of juvenile salmon, have been widely used by fisheries agencies as a management tool for Pacific salmon since the early 1970s. Over seven million tagged coho salmon representing 400 separate tag groups have been released annually in recent years (Pacific States Marine Fisheries Commission (PSMFC) 1993). Most CWTs are used on hatchery-reared fish, although some wild populations are also tagged. Tagged fish are recovered from commercial, sport, and tribal fisheries, at hatcheries, and

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during escapement surveys. Because of the enormous amount of information it contains, the CWT database is increasingly being used to address questions regarding salmon movements (Norris et al. 2000), homing fidelity (Hard and Heard 1999; Candy and Beacham 2000), and marine survival (e.g., Coronado and Hilborn 1998; Ryding and Skalski 1999; Hobday and Boehlert 2001).

In this paper, we report the use of marine recoveries of coho salmon marked with CWTs (hereafter referred to as CWTed salmon) to gain insight into coho salmon ocean migrations. Ocean research programs that sample salmon in marine environments traditionally use a single research vessel sequentially fishing at a series of fixed sampling stations (e.g., Godfrey et al. 1975; Pearcy 1992), which limits both the geographic and temporal extent of the sampling effort. By using the CWT database, we effectively used thousands of coastal fishers from central California to the Bering Sea as samplers of the marine environment to detect the presence and abundance of millions of tagged hatchery and wild coho salmon. This sampling effort was fairly consistent for 25 years (Pacific Fishery Management Council (PFMC) 1999). Because of the geographic extent of this sampling effort and the number of tagged fish recovered, we were able to quantitatively explore regional differences in coho salmon presence and abundance in the ocean at spatial scales that would have been impossible with data from traditional marine research methods. Our investigation has yielded exciting new insight about life history diversity in marine environments for coho salmon. This unappreciated marine diversity may also exist for other species of Pacific salmon but is only detectable with mass tagging and sampling programs like those used for CWTs.

Materials and methods

Our objective was to use coastal marine fisheries as samplers of CWTed coho salmon to investigate ocean distribution patterns, using PSMFC's CWT database (PSMFC 1993). In using this database, we assume that all appropriate fisheries were consistently sampled for tagged fish, expansions for sampling effort were correct, all recovered tags were read and reported, and there was no bias in these factors between regions or years of interest. Because the database is maintained for management purposes, which presumably requires the most complete and accurate data possible, we believe that the above assumptions are sufficiently valid and did not unduly influence our results.

Hatchery and CWT release group selection

Coho salmon hatcheries and CWT release groups were selected to provide releases arranged approximately evenly over a wide geographic area and large numbers of marine recoveries over multiple years. Hatcheries selected for the analysis had a minimum of 1000 marine recoveries (expanded for sampling effort) distributed over at least 3 years and were distributed from central Alaska to central California. Exceptions to these general criteria occurred in regions in which few hatcheries were available that either met the criteria or had releases in many years (e.g., central California and northern British Columbia). In some moderate-sized basins with two hatcheries (e.g., Elwha and Quinault basins (Washington)), data for both hatcheries were combined.

To minimize potentially confounding factors, release groups were generally excluded if releases (*i*) contained experimental fish (release type *E* or *B* in the database), (*ii*) used stocks with names other than the hatchery, stream, or local river basin name, or (*iii*) occurred anywhere other than the hatchery or hatchery stream. Exceptions to this rule included the use of experimental release groups from California hatcheries because nonexperimental releases that met our criteria (e.g., years of interest) were not available and the inclusion of two Oregon Coast hatcheries (Salmon River, Rock Creek (Rogue River)) for geographic coverage. These Oregon facilities raise coho salmon from, and release them back into, the Siletz and Umpqua basins, respectively (M. Lewis, Oregon Department of Fish and Wildlife, 28655 Hwy. 34, Corvallis, OR 97333, U.S.A., personal communication).

Recoveries and recovery areas

Recoveries of CWT release groups were selected to determine the typical movements of adult coho salmon in coastal areas as they returned to their natal streams. Marine (as specified in the PSMFC database) recoveries were used from return years 1979–1993, during which time fishing effort was reasonably constant (PFMC 1999) and comprehensive sampling for tags was conducted by all appropriate agencies. Recoveries were restricted to the dominant adult age, typically 3 years for populations from central British Columbia southwards and 4 years for those from northern British Columbia and Alaska. Recovery numbers were expanded for sampling effort (required because many catches are subsampled for the presence of CWTs) as provided in the PSMFC database.

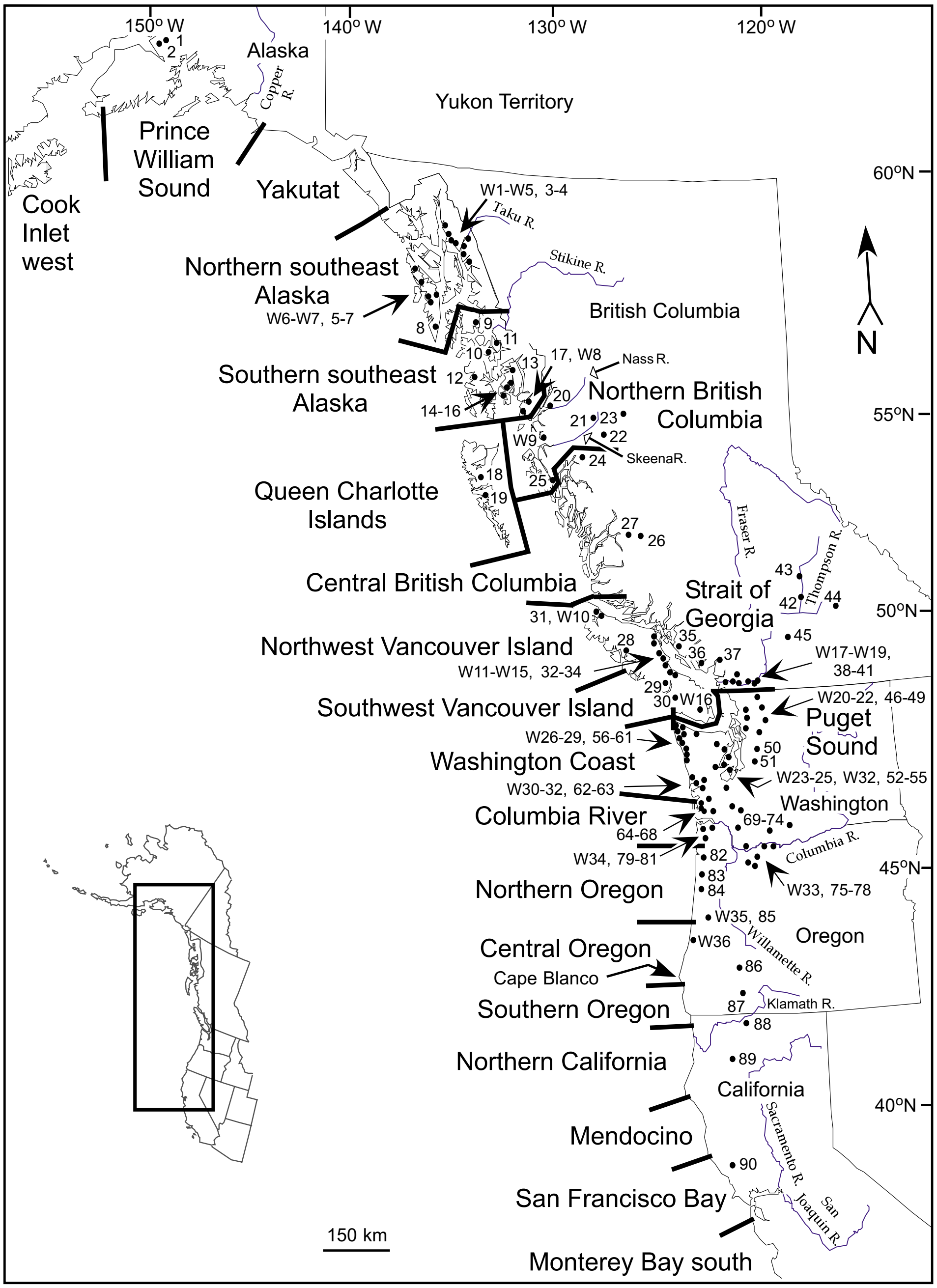
Each of the approximately 4400 coho salmon marine recovery location codes in the database was assigned to 1 of 21 recovery areas (Fig. 1). These recovery areas were selected to be approximately the same size coastwide, to represent geographically distinct areas where possible, and to have boundaries that corresponded to fishing management units to minimize overlap between recovery areas. Recoveries with location codes that overlapped multiple recovery areas (e.g., several older recovery location codes in northern California) were evenly divided between the overlapped areas.

The proportion of recoveries (R_{ij}) by hatchery j in area i over all years was calculated as

$$R_{ij} = \frac{\sum_k r_{ijk}}{\sum_i \sum_k r_{ijk}}$$

where r_{ijk} is the number of recoveries from hatchery j in recovery area i in year k. Because the data showed relatively low interannual variation in recovery patterns compared to the number of fish recovered, we selected a formula that gives equal weight to all fish, regardless of year recovered. Further exploration of interannual and seasonal variation in recovery patterns will be the subject of forthcoming work (L. Weitkamp, unpublished data).

Fig. 1. Locations of the 90 hatcheries (labeled 1–90), 21 recovery areas (indicated by dark lines), and 36 wild populations (labeled W1–W36) used in the analysis. Hatchery names and recovery statistics are provided in Appendix A, Table A1, and wild population names and recovery statistics are provided in Appendix A, Table A3.



We estimated the average marine (travel by water only) distance (D_j) between areas in which coho salmon were recovered and the river mouth of hatchery j as

$$D_j = \sum_i d_{ij} R_{ij}$$

where d_{ij} is marine distance between the geographic center of recovery area i and river mouth of hatchery j, and R_{ij} is the proportion of recoveries by hatchery j in area i, defined above.

Wild coho salmon

To investigate whether CWT recovery patterns from hatchery fish were similar to those for wild fish, marine recoveries of wild tagged groups were analyzed using methods for hatchery fish described above (e.g., same recovery areas, years of interest, dominant ocean age). Because relatively few wild coho salmon have been tagged and recovered, recoveries from basins recovering less than 1000 fish and in fewer than 3 years were included in the analysis. Recoveries of fish with wild parents released from Oregon coast hatcheries were used as a surrogate for wild fish because of the lack of wild tagging programs in the area. Releases and recoveries in basins in which wild fish were tagged at multiple locations were pooled.

Data analysis

We sought to determine if the locations of CWT recoveries in the ocean were grouped in distinct patterns associated with the geographic origin of the fish, using two complementary techniques. The foundation for this analysis was each hatchery's 21-coordinate vector of the percent recoveries in each of the 21 recovery areas. We performed a principal component (PC) analysis on the CWT dataset (percent recovered by area) to produce a few key PCs that explained a large fraction of the variance of the larger dataset. We also used this CWT dataset in a hierarchical agglomerative clustering algorithm, using Euclidean distance and unweighted arithmetic average clustering (UPGMA; Legendre and Legendre 1998). Other distances (Manhattan, percent overlap) and methods of agglomerative clustering (e.g., Wards, single linkage) produced clusters similar to those defined at a distance of 10 using UPGMA and Euclidean distances. Accordingly, these other methods are not discussed further, and the distance of 10 was selected as our distance of interest. We examined the geographic coherence of groupings resulting from both PC and clustering analyses.

We expected similarity in CWT recovery patterns to decline as distance between hatcheries increased. To investigate the spatial scale at which this change occurred, we compared proportional similarity (Whittaker 1952) between populations to their marine distance (travel by water only). Proportional similarity (PS) of recovery patterns between hatcheries j and l was calculated as

$$\mathrm{PS}_{jl} \equiv 2\sum_{i=1} \min\left[\frac{x_{ij}}{z}, \frac{x_{il}}{z}\right]$$

where x_{ij} is the percent of recoveries of hatchery j in recovery area i, and z is the sum of the percentage of recoveries for hatcheries k and l over all recovery areas. This index varies from 1 (identical) to 0 (no recoveries in common). Proportional similarity was also used to compare recovery patterns between wild populations and nearest hatchery populations.

Results

Recovery statistics

Ninety hatcheries from Alaska (hatcheries 1–17), British Columbia (18–45), Washington (46–74), Oregon (75–87), and California (88–90) were used in the analysis (Fig. 1), representing 1.47 million marine recoveries (Appendix A, Table A1). On average, a total of 16 344 recoveries were available per hatchery, representing 8.7 years of recoveries (Appendix A, Table A1). Coho salmon from a given hatchery were surprisingly widespread and were recovered from an average of 11.4 of 21 possible recovery areas. Mean distance between hatchery river mouth and recovery locations (D), averaged over all hatcheries, was 251 km (standard deviation (SD) = 118; Appendix A, Table A1). To investigate how this distance was affected by recoveries of a few fish far from the hatchery river mouth, we recalculated D for each hatchery using only recovery areas in which the percentage of fish recovered exceeded 5%. The mean of this modified D was 201.8 km (SD = 97.0), a 20% decline. Hatcheries with the greatest proportional change in D were those that required the most recovery areas combined to achieve 90% of total recoveries (slope = 3.65, $R^2 = 0.271$, $p < 0.001$) and those with the lowest river mouth latitude (slope = –1.42, $R^2 = 0.299$, $p < 0.001$).

An average of 70 045 coho salmon were recovered in each recovery area, but the six areas with the most and six areas with the least recoveries accounted for 74% (1.09 million) and 2% (23 586 fish) of all recoveries, respectively (Appendix A, Table A2). Despite this variability, coho salmon from 49 hatcheries were recovered in each recovery area on average (Appendix A, Table A2). The relationship between the number of coho salmon and number of hatcheries recovered per recovery area was weak when the six recovery areas with fewer than 10 000 recoveries were removed from the analysis (slope = 4.8×10^{-5}, $R^2 = 0.19$, $p = 0.10$). This suggests that for most recovery areas, the number of coho salmon captured was largely independent of the number of hatcheries represented.

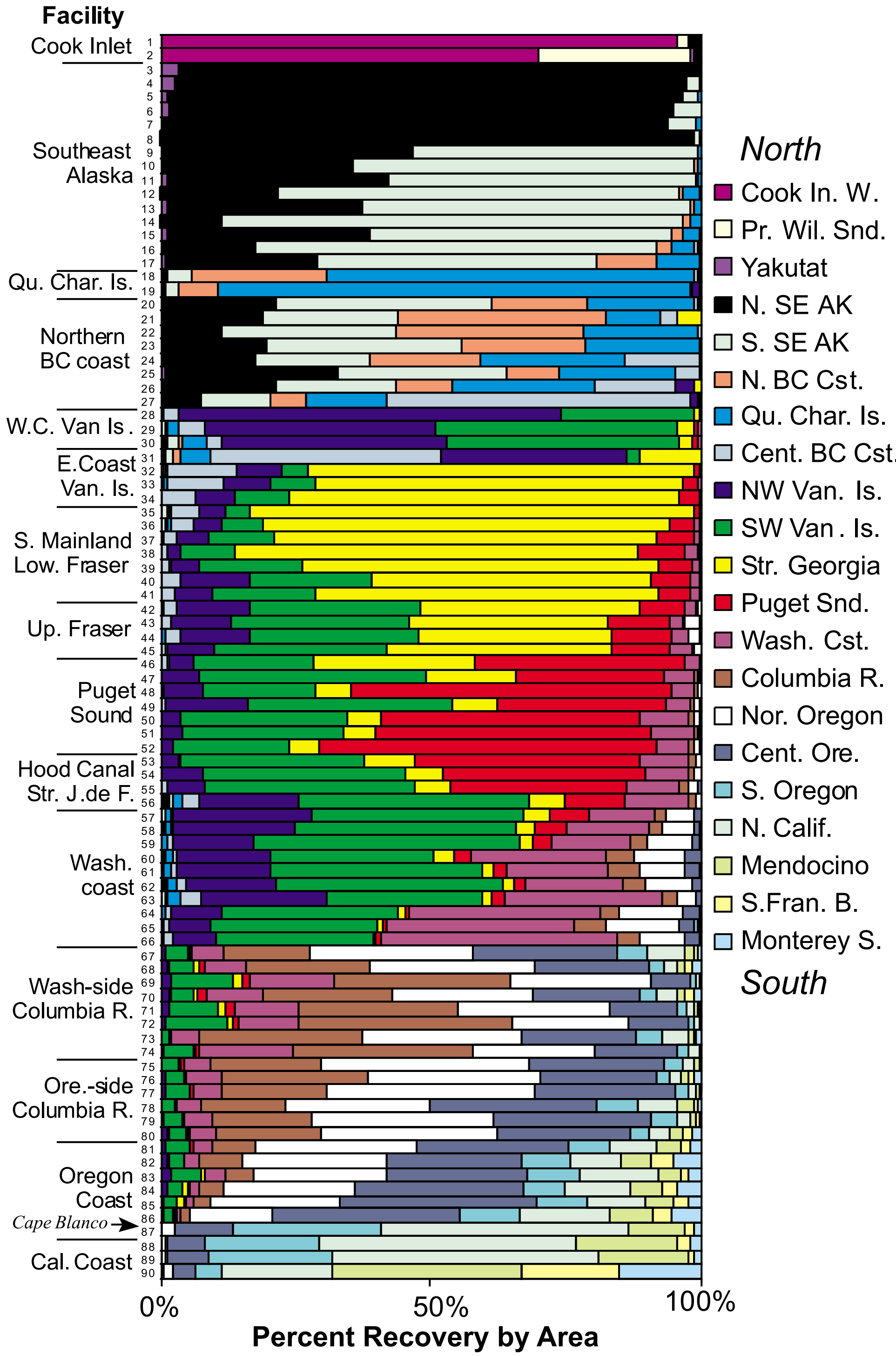
Data were available for wild tagged fish from 36 basins from Alaska (basins W1–W8), British Columbia (W9–W19), Washington (W20–W32), and Oregon (W33–W36) (Fig. 1), representing a total of 295 000 wild-tagged coho salmon recovered in marine fisheries (Appendix A, Table A3). On average, each wild release basin had 7.4 years of recoveries, 959 recoveries per year, and recoveries from seven recovery areas. Mean distance between basin river mouth and recovery locations (D), averaged over all basins, was 238 km (SD = 123; Appendix A, Table A3).

Hatchery location and recovery pattern

Recovery patterns for each of the 90 hatcheries indicate that most recoveries tended to occur in local waters, and neighboring hatcheries typically had similar recovery patterns (Fig. 2). For example, releases from Cook Inlet (Alaska) hatcheries (1–2) were collected primarily in Cook Inlet, and releases from Oregon Coast hatcheries (81–85) were likewise recovered along the Oregon Coast.

However, there are several striking departures from this pattern. In particular, in a few cases, neighboring hatcheries exhibit very discordant recovery patterns. For instance, the Naselle Hatchery (66 in Fig. 2) and Grays River Hatchery (67 in Fig. 2) are only 20 km apart, and their fish enter the ocean approximately 40 km apart at Willapa Bay (Washington) and the Columbia River, respectively. Yet their CWT recoveries reflect very different ocean migration patterns. Coho salmon from the Naselle were largely recovered north of their river of origin, from the Washington coast as far north as central British Columbia, whereas Grays River coho salmon were largely recovered from the Columbia River southwards (Fig. 2). Furthermore, Naselle recovery patterns were typical of other Washington coast populations (57–65), whereas Grays River patterns were typical of lower Columbia River hatcheries (68–80) (Fig. 2). Other abrupt transitions occurred between hatcheries in Cook Inlet (1–2) and southeast Alaska (3–17), Queen Charlotte Islands (18–19) and northern British Columbia (20–27) or Alaska, west (28–

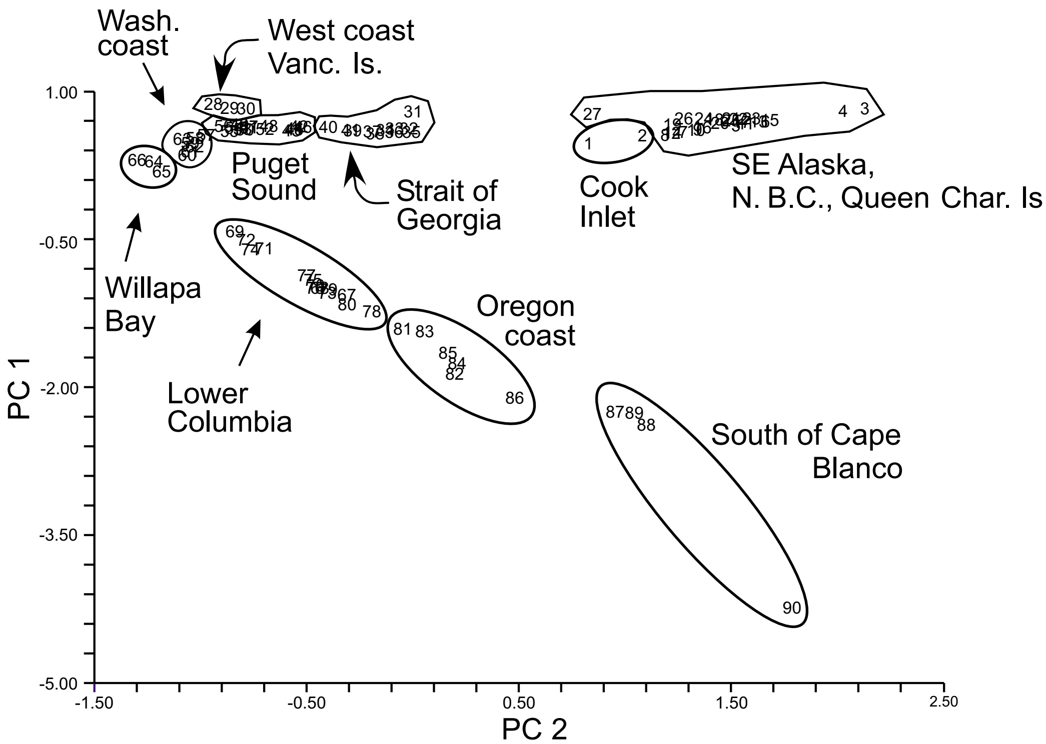
Fig. 2. Recovery patterns of coded-wire tagged coho salmon (*Oncorhynchus kisutch*) by hatchery. Each bar provides the percent of recoveries in the 21 recovery areas for a single hatchery (see Fig. 1 for hatchery locations and Appendix A, Table A1, for hatchery names). The geographic region of hatcheries is indicated.



30) and east (31–34) coasts of Vancouver Island, Puget Sound (46–54), and the Washington coast (57–66), and north (81–86) and south (87–90) of Cape Blanco (Oregon coast) (Fig. 2). These acute changes in recovery patterns suggest that fish from a particular region may share a region-specific response to the ocean environment, resulting in distributions that are fundamentally different from the distributions of neighboring regions, while clearly exhibiting a latitudinal influence. Such fine-scale differences in ocean location have not been documented across such large geographic areas before for any species of Pacific salmon.

Three hatcheries (Bella Bella (27), Port Hardy (31), and Warm Springs (90)) exhibited distribution patterns that were distinctive from those of adjacent hatcheries. These may be

Fig. 3. Hatchery loadings for principal components 1 and 2. See Appendix A, Table A1, for hatchery names and Fig. 1 for hatchery locations.



interpreted as either transitional recovery patterns or the sole representatives of additional recovery pattern types.

Statistical analyses of hatchery recovery patterns

Principal component analysis

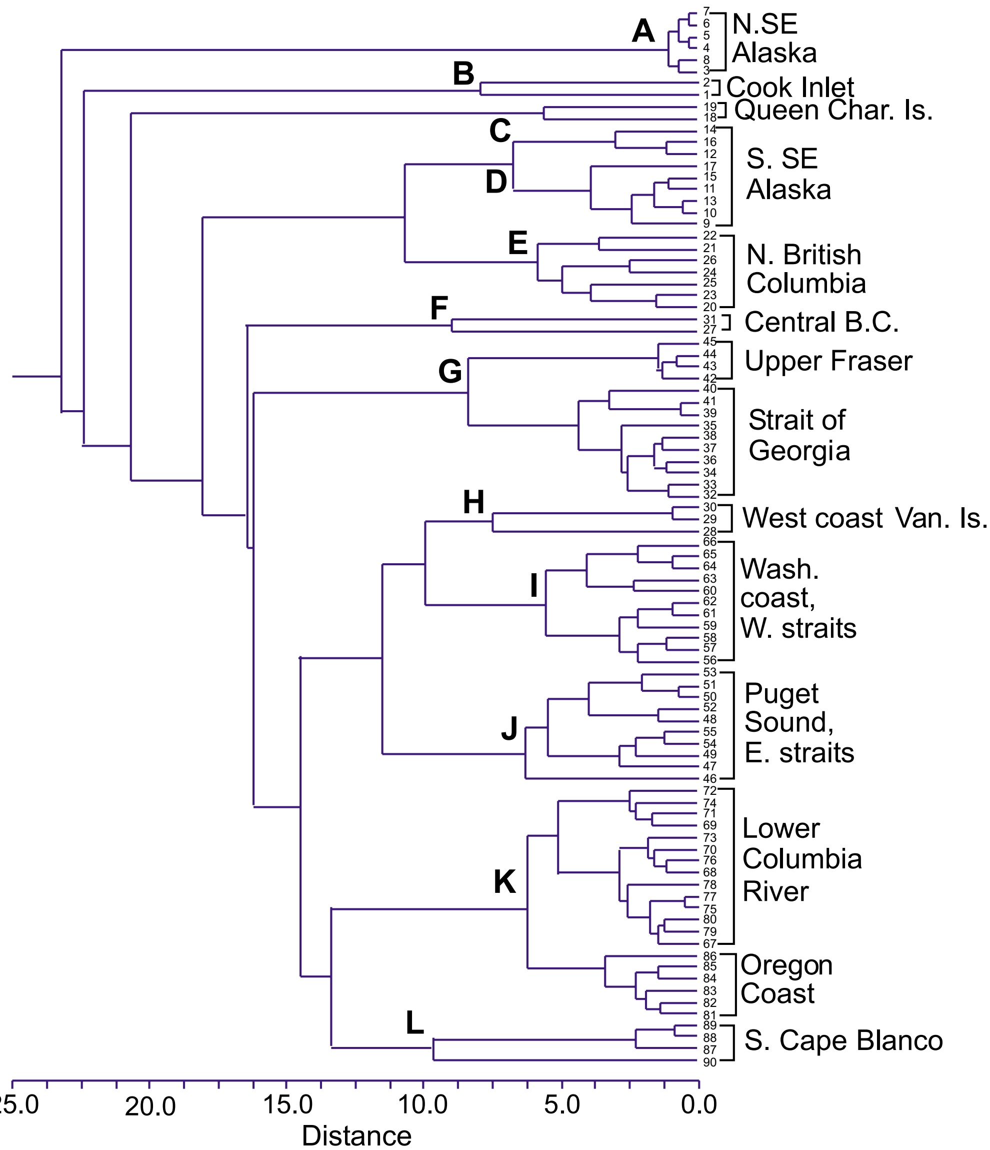
Principal component analysis (PCA) of the matrix of pairwise Euclidean distances between hatcheries was used to further examine the obviously strong geographic signal observed in CWT recoveries. The first four PCs, with eigenvalues ranging from 4.71 to 1.79, individually explained 23% to 9% (sum = 59%) of the total variance in the recovery-by-area dataset and produced groupings associated with geographic location of the hatcheries, even though no geographic-specific information was used in the analysis. For example, the first PC (PC1) was associated with the large change in recovery patterns at the Columbia River; hatcheries from the Columbia River southwards (67–90) had increasingly negative PC1 scores, whereas those north of the Columbia River (1–66) were positive (Fig. 3). The second PC (PC2) separated hatcheries by their geographic distance from the center of the range—hatcheries near the center had strongly negative scores, whereas those at the ends had strongly positive scores (Fig. 3). Together, PC1 and PC2 grouped hatcheries from geographically close areas, such as Cook Inlet, Strait of Georgia, Puget Sound, Washington coast, Columbia River, and south of Cape Blanco (Fig. 3). The third (PC3) and fourth (PC4) PCs (not shown) provided further separation between hatcheries north of the Columbia River. For example, PC4 clearly differentiated between hatcheries in Cook Inlet (average loading –4.7), southeast Alaska (–0.3), Queen Charlotte Islands (+2.5), northern B.C. (+1.5), and the west coast of Vancouver Island (WCVI) (0.0).

Cluster analysis

Cluster analysis, using the matrix of pairwise Euclidean distances between hatchery populations based on CWT recovery patterns, produced well-separated groups with clear geographic congruity (Fig. 4). At a distance of 10, 12 distinct clusters were apparent (labeled *A* to *L* in Fig. 4), each representing hatcheries in a particular geographic region. Many of these clusters were consistent with the groups identified by the PCAs described above, e.g., Cook Inlet, Strait of Georgia, Puget Sound, WCVI, Washington coast, and south of Cape Blanco (clusters *B*, *G* to *J*, and *L*, respectively; Fig. 4).

Several of these dominant clusters also exhibited smaller groupings that corresponded to finer-scale geographic patterns. For example, cluster *G* can be further divided into subclusters consisting of upper (hatcheries 42–45) and lower (39–41) Fraser River and Strait of Georgia (32–38) hatcheries, whereas cluster *K* includes lower Columbia River (67–80) and Oregon coast (81–86) subclusters (Fig. 4). The Columbia River subcluster of cluster *K* exhibited further fine-scale structure based on management practices. Washington State uses two hatchery stocks in its Columbia River coho salmon production: type S (South), which is an early-returning coho salmon having a "southern" distribution, and type N (North), which is a late-returning fish with a "northern" distribution. Oregon uses hatchery stocks similar to the type S stock in the Columbia River. The top branch of this subcluster contains all Washington hatcheries that exclusively release type N stock (hatcheries 69, 72, and 74) and

Fig. 4. Dendrogram resulting from cluster analysis of coho salmon (*Oncorhynchus kisutch*) coded-wire tag recovery patterns from 90 hatcheries, based on Euclidean distance and unweighted arithmetic average clustering. Twelve clusters formed at a distance of 10 are indicated (*A*–*L*). The geographic region of hatcheries is indicated. Refer to Appendix A, Table A1, for hatchery names and Fig. 1 for hatchery locations.



one that releases both stocks (hatchery 71), whereas the remaining branches are composed of Washington hatcheries that release type S stock exclusively (67, 70), mixtures of types N and S stocks (68, 73), or Oregon hatcheries (75–80).

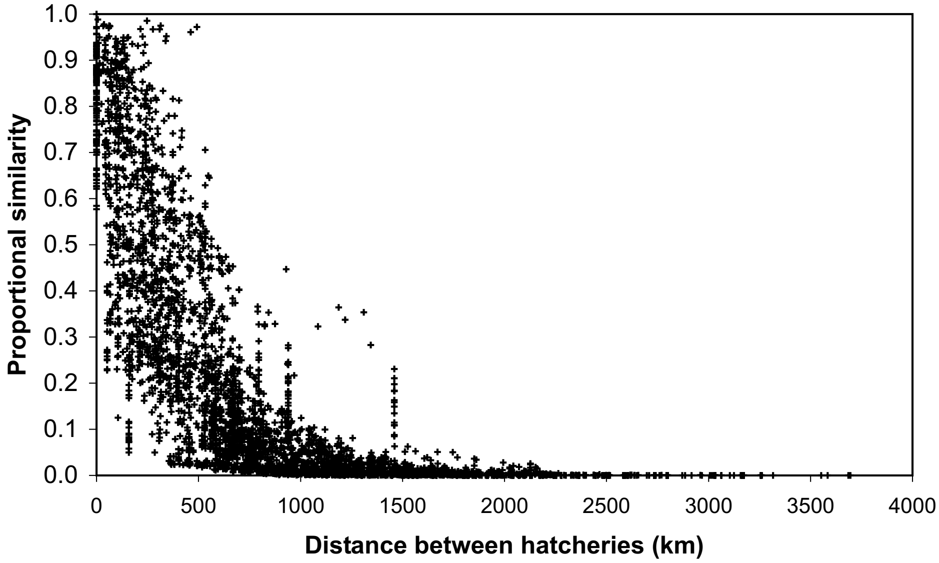
Recovery patterns and geographic distance between hatcheries

A comparison of proportional similarity versus distance between hatcheries (Fig. 5) indicated a clear decline in similarity with increasing distance. Although the average similarity between the 4005 pairwise comparisons was 0.204, hatcheries within 500 km of each other had a mean similarity of 0.51, whereas those at distances greater than 500 km had a mean similarity of 0.06. These results were consistent with the spatial scales indicated by both the PC and cluster analyses described above, neither of which included geographic information: hatcheries within 300–500 km of each other exhibited the greatest similarity in recovery patterns.

Comparison of hatchery and wild recovery patterns

Proportional similarities were calculated between the 36 wild tagged populations and the nearest hatchery. Mean similarity was 0.873 (SD = 0.107) (Table 1), indicating high similarity in recovery patterns between wild and nearby hatchery populations. Wild recovery patterns were also analyzed together with all hatcheries in a cluster analysis, using methods identical with those described earlier. The dendrogram resulting from this analysis grouped all wild populations with hatcheries from the same region (Fig. 6), although not necessarily from the same basin. With the addition of 36 wild populations, the wild and hatchery den-

Fig. 5. Proportional similarity (Whittaker 1952) versus distance for all 4005 pairwise comparisons between hatcheries. The similarity index varies from 1 (identical) to 0 (no recoveries in common).



drogram differed from the hatchery-only dendrogram in its fine-scale structure, but it produced the same large clusters.

Discussion

We provide the first comprehensive evidence for variation in marine distributions of west coast coho salmon at a variety of geographic scales. It has long been recognized that coho salmon from different areas of the Pacific Rim (e.g., Pacific Northwest, Alaska, Asia) tend to be located in different parts of the ocean (Godfrey et al. 1975; Myers et al. 1996), and managers structure marine fisheries according to known differences in migratory patterns between populations at smaller spatial scales (PFMC 1999). In addition, population-specific differences in marine distribution patterns based on CWT or similar tag recoveries have been observed in coho (Weitkamp et al. 1995), chinook (*O. tshawytscha*; Myers et al. 1998; Norris et al. 2000), and Atlantic salmon (*Salmo salar*; Kallio-Nyberg et al. 1999). Our study is unique in its geographic scope, the large number of release groups and hatcheries used, and the relatively small recovery areas employed. Because of these factors, we were able to demonstrate that at small geographic scales, fish released from a particular freshwater region share a unique recovery pattern, which can be quite different from that of adjacent regions, with minimal transition between the two patterns. These abrupt changes in recovery patterns occurred repeatedly between west coast coho salmon hatcheries, resulting in at least 12 distinct recovery patterns. We also observed patterns at larger geographic scales, such as the fundamental change in ocean distribution patterns north and south of the Columbia River.

Our results suggest that the high diversity observed in Pacific salmon for life history traits commonly measured in freshwater (e.g., age at smoltification or maturity, run timing; e.g., Ricker 1972; Groot and Margolis 1991) may be equaled by a diversity of ocean migration patterns. This fine-scale life history diversity can only be detected by using thousands of fishers from Alaska to California as samplers of millions of tagged fish. Furthermore, it is likely that other Pacific salmon species exhibit comparable levels of fine-scale diversity in ocean migration patterns, but traditional ocean research methods do not recover enough fish of known origin across a large enough area to detect this potential variation.

Analysis assumptions

Our analysis used coastal fisheries as "samplers" of the ocean to recover tagged coho salmon and therefore infer "true" ocean distributions. This assumes that fisheries sample all areas equally and fish are equally susceptible to a fishery occurring in a particular area. Although ocean fisheries were abundant, widespread, and relatively constant during the years of interest, 1979–1993 (PFMC 1999), neither of the above assumptions are entirely true—some areas had greater fishing effort than others and not all fish inhabiting particular areas may have been sampled. However, three lines of evidence indicate that our results provided an accurate general picture of the marine distribution of coho salmon in the last months of their marine residence.

First, although fisheries that intercept coho salmon do not occur evenly in all coastal waters, we believe the sampling effort was sufficient such that observed recovery patterns reflect coho salmon distributions rather than fishing effort. For example, the relationship between number of coho salmon captured and number of hatcheries recovered in a particular recovery area were largely independent, especially when considering only recovery areas with greater than 10 000 recoveries. However, even recovery areas with fewer than 10 000 total recoveries were represented by a surprisingly large number of hatcheries (mean = 21). Observed recovery patterns also relied largely on the presence or absence of fish from a particular recovery area: on average, 75% of all fish from a given hatchery were recovered in only two recovery areas, whereas 95% were captured in five recovery areas. Consequently, although coho salmon from a given hatchery could be found in most recovery areas, they were either abundant or effectively absent in a given recovery area regardless of the fishing intensity. This suggests that differen-

Table 1. Proportional similarlity (Whittaker 1952) between wild tagged populations and the nearest hatchery population based on coded-wire tag recovery patterns.

Wild population	Hatchery population	Proportional similarity
W1 Berners River	3 Gastineau	0.985
W2 Auke Creek	3 Gastineau	0.995
W3 Taku River	3 Gastineau	0.964
W4 Tatsamenie Lake	4 Snettisham	0.982
W5 Speel Lake	4 Snettisham	0.987
W6 Ford Arm Lake	6 Sheldon Jackson	0.962
W7 Salmon Lake	8 Port Armstrong	0.967
W8 H. Smith Lake	20 Kincolith	0.741
W9 Lachmach River	20 Kincolith	0.902
W10 Keogh River	31 Port Hardy	0.677
W11 Quinsam River	32 Quinsam River	0.895
W12 Black Creek	32 Quinsam River	0.873
W13 Trent River	33 Puntledge River	0.872
W14 Little Qualicum River	34 Big Qualicum River	0.948
W15 French Creek	34 Big Qualicum River	0.843
W16 Mesachie Creek	34 Big Qualicum River	0.441
W17 Salmon River	39 Inch Creek	0.973
W18 Pitt River	40 Chehalis River	0.738
W19 Chilliwack River	41 Chilliwack River	0.811
W20 Skagit River	47 Marblemount	0.906
W21 Stillaguamish River	47 Marblemount	0.892
W22 Snohomish River	49 Wallace River	0.843
W23 Deschutes River	52 Minter Creek	0.821
W24 South Hood Canal	53 George Adams	0.937
W25 Big Beef Creek	54 Quilcene NFH	0.872
W26 Hoko River	56 Elwha H/SCh	0.846
W27 Dickey River	59 Sol Duc	0.892
W28 Hoh River	60 Chalaat Creek	0.835
W29 Queets River	61 Quinault NFH/Lake	0.921
W30 Stevens Creek	62 Humptulips	0.893
W31 Lower Chehalis River	63 Bingham Creek	0.972
W32 Upper Chehalis River	63 Bingham Creek	0.859
W33 Clackamas River	78 Eagle Creek NFH	0.757
W34 Fish Hawk Lake	81 Nehalem	0.908
W35 Alsea River	85 Fall Creek	0.834
W36 Eel Lake	86 Rock Creek	0.899

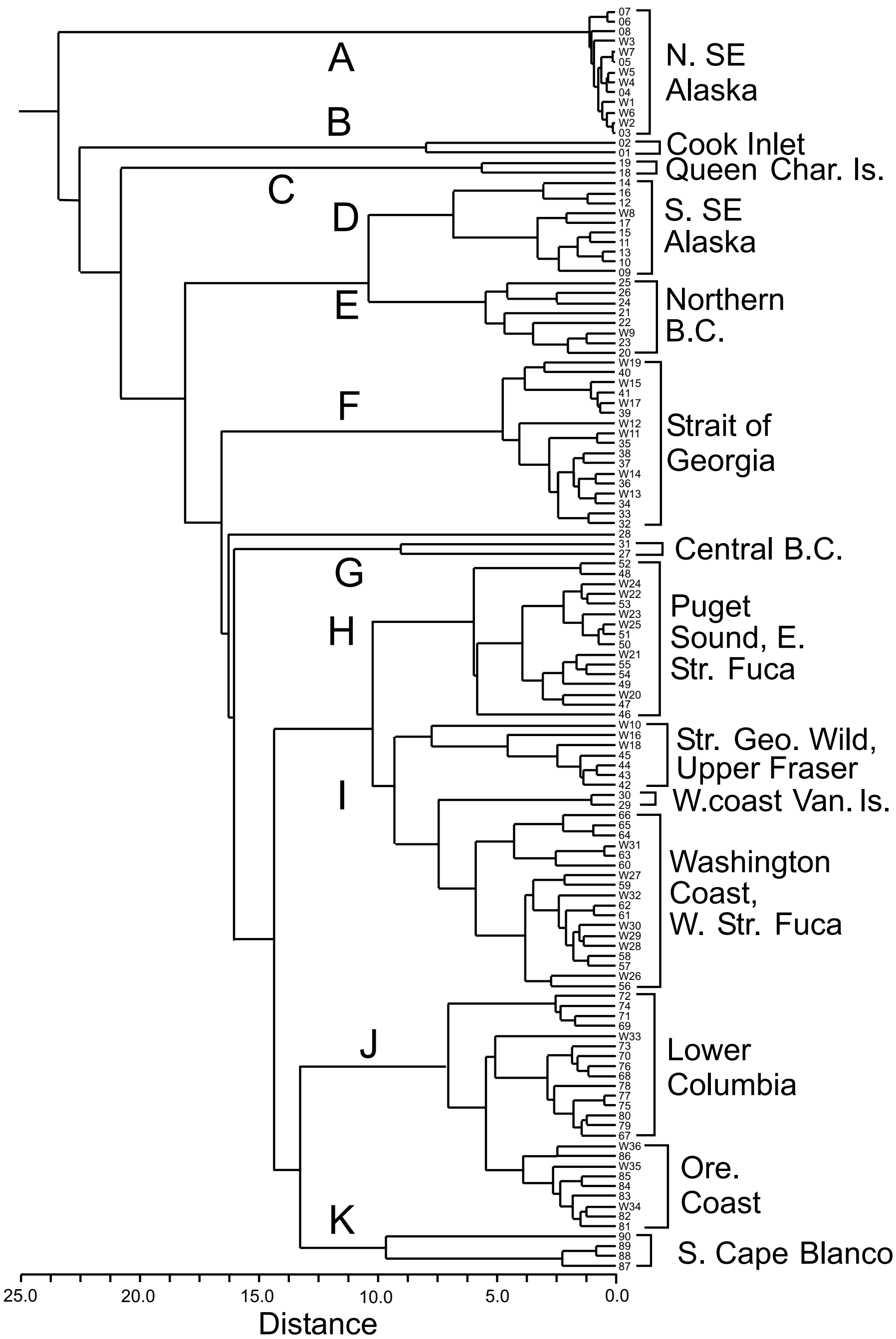
Note: The similarity index varies from 1 (identical) to 0 (no recoveries in common). Basin and hatchery locations are provided in Fig. 1.

tial fishing effort was not the primary source of the patterns we observed. Furthermore, if removal of this confounding factor from the analysis were possible, it should increase, rather than decrease, region-specific differences in recovery patterns. In an analysis of CWT marine recovery patterns for chinook salmon, Norris et al. (2000) determined that fishing effort had relatively little influence compared with region, fish age, or year effects.

Second, fisheries generally target salmon when and where they are aggregated and therefore easily caught. Accordingly, most CWTs are recovered in fisheries targeting concentrations of coho salmon. However, tagged coho salmon are also recovered in fisheries targeting other Pacific salmon species. These fisheries, which are abundant and widespread, may not catch coho salmon as effectively as coho-specific fisheries because of gear differences. Nonetheless, they serve as samplers of areas with relatively low coho salmon abundance, providing greater sampling coverage than otherwise might occur.

Finally, there is the question of whether observed recovery patterns were largely due to release location or an inherent property of the fish themselves (i.e., genetics). Strong evidence for a large genetic component to recovery patterns comes from the Columbia River, where Washington State uses type S (South) and type N (North) stocks, as discussed earlier. Hatcheries exclusively releasing type S (hatcheries 67 and 70) had a more southern distribution than those exclusively releasing type N (69, 72, and 74), with 39% of recoveries occurring from central Oregon southwards (vs. 12% for type N). Type N hatcheries had correspondingly higher recoveries from Washington coast northwards (27% for type N, 13% for type S). These differences occurred despite the fact that both groups entered the ocean at the same location—the Columbia River. Additional evidence for a genetic influence on migra-

Fig. 6. Dendrogram resulting from cluster analysis of coho salmon (*Oncorhynchus kisutch*) coded-wire tag recovery patterns from 36 wild tagged populations (W1–W36) and 90 hatcheries (1–90), based on Euclidean distance and unweighted arithmetic average clustering. Wild populations are in bold type. Eleven clusters formed at a distance of 10 are indicated (*A*–*K*). The geographic region of hatcheries is indicated. Hatchery and wild names are provided in Appendix A, Table A1 and Table A3, respectively, and locations are indicated in Fig. 1.



tion pattern may be found in stock transfer experiments (e.g., Weitkamp et al. 1995).

Hatchery vs. wild recovery patterns

The vast majority of CWT salmon originate from hatcheries, which may alter the behavior or genetic makeup of salmon populations through rearing conditions and breeding practices (NRC 1996). Variable time of domestication may also cause some hatchery populations to have changed more than others. Consequently, there is concern that marine distribution patterns based principally on hatchery fish may not be representative of wild populations.

Recovery patterns for 36 wild populations clearly indicate that regional hatchery recovery patterns are typical of wild recovery patterns from the same region. This suggests that patterns derived from recoveries of millions of hatchery fish are a reasonable surrogate for wild populations. Although similarities in wild and hatchery recovery patterns have been observed for adjacent coho (Labelle et al. 1997) and chinook (Healey and Groot 1987) salmon populations, our results suggest similarities across much larger spatial scales than previously appreciated. Furthermore, the strength of region-specific CWT recovery patterns in most regions, which have hatchery populations of various ages up to several decades, suggest that time of domestication has relatively little influence on these patterns compared with other factors (e.g., hatchery location, release year). This agrees with the observations by Coronado and Hilborn (1998) for hatchery age and marine survival based on CWTs. Given that most west coast coho salmon hatchery populations were originally derived from local wild populations (Weitkamp et al. 1995), similarities between hatchery and wild populations are not unexpected. Apparently, selective forces associated with hatchery practices that have resulted in changes in other life history traits (e.g., Flagg et al. 1995; NRC 1996) have not similarly affected ocean distributions.

Implications of region-specific CWT recovery patterns

Based on interceptions in coastal fisheries, we have shown that coho salmon from different freshwater regions inhabit different areas of the coastal ocean, where they potentially experience unique oceanic conditions. Although these fisheries occur during the last few months of a 1½-year ocean residence, we suggest that these differences begin earlier in the ocean residence period. This is because variation in adult size is largely caused by variation in growth rates during the last year in the ocean (van den Berghe and Gross 1989; Rogers and Ruggerone 1993). In 1983, returning adult Oregon Coast coho salmon were exceptionally small (Johnson 1988), thought to be caused by poor feeding conditions during the strong El Niño that year (Brodeur et al. 1985; Pearcy 1992). In contrast, maturing adult coho salmon returning to the Washington coast during the same year exhibited no perceptible decrease in size (J. Packer, Washington Department of Fish and Wildlife, 600 Capitol Way N., Olympia, Wash., U.S.A., unpublished data). Our analysis indicates that Oregon and Washington coast coho salmon were largely recovered exclusively south or north of the Columbia River, respectively, in late summer with little overlap in distributions. The large size difference observed in 1983, however, suggests that Oregon and Washington coast coho salmon were experiencing different conditions for more than just a month or two and therefore were inhabiting different parts of the ocean over a longer period. Our results suggest that these differences in ocean location are typical; however, they may be detectable only when conditions for one group are particularly poor, such as those associated with the 1983 El Niño.

Our findings also have implications for coho salmon management, conservation, and ecology because they shed new light on the murky world of salmon ocean ecology. For example, fisheries managers may be able to use ocean distribution information to determine the effects of particular ocean conditions on adult size and therefore increase predictive ability of catch size and value. In addition, the suspected genetic component to these patterns provides further incentive for caution in the use of non-native stocks for hatchery production or conservation programs (NRC 1996).

These results also suggest several avenues to pursue with further research that should increase our understanding of salmon ocean ecology. For example, examining trends in coho salmon adult size over time (e.g., Ricker 1981; Bigler et al. 1996) using the geographic regions indicated by these CWT recovery patterns may indicate region-specific differences in adult size in some years that may correspond to particularly poor local ocean conditions. Similarly, there may be unappreciated associations between geographic patterns in marine survival (e.g., Coronado and Hillborn 1998; Ryding and Skalski 1999) and both fine- and large-scale differences in ocean migration patterns. Our results also provide a novel framework with which to evaluate the coastwide impacts of extreme climatic conditions such as El Niño and La Niña events (Mysak 1986; Johnson 1988) or decadal-scale changes (Hare et al. 1999) on coho salmon survival and growth. We are presently analyzing marine CWT recovery patterns using week, month, and year of recovery to provide even greater insight into region-specific differences in coho salmon ocean migration patterns (L. Weitkamp, unpublished data). Finally, similar analyses can and should be conducted for chinook salmon, another species commonly tagged with CWTs, to examine how these two species behave in the common oceanic environment.

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Appendix A

Table A1. Recovery statistics for the 90 hatcheries used in the analysis.

State or province	Region	Hatchery no.	Hatchery name	Estimated no. tags recovered	No. areas recovered from	No. years released	Mean recoveries per year	Distance (*D*) (km)
AK	Cook Inlet	1	Ft. Richardson	2 531	7	8	316	552
AK	Cook Inlet	2	Elmendorf	3 206	5	6	534	482
AK	N. SE AK	3	Gastineau	28 698	5	4	7175	195
AK	N. SE AK	4	Snettisham	8 706	5	6	1451	180
AK	N. SE AK	5	Hidden Falls	4 165	7	3	1388	105
AK	N. SE AK	6	Sheld. Jackson	2 563	4	8	320	159
AK	N. SE AK	7	Medvejie	5 612	5	7	802	161
AK	N. SE AK	8	Pt. Armstrong	16 760	5	3	5587	302
AK	Central SE AK	9	Crystal Lake	3 835	5	7	548	201
AK	Central SE AK	10	Burnett Inlet	3 487	6	7	498	180
AK	S. SE AK	11	E. West Cove	12 792	7	7	1827	210

Table A1 (*continued*).

State or province	Region	Hatchery no.	Hatchery name	Estimated no. tags recovered	No. areas recovered from	No. years released	Mean recoveries per year	Distance (*D*) (km)
AK	S. SE AK	12	Klawock	19 611	7	8	2451	130
AK	S. SE AK	13	Neets Bay	27 253	7	8	3407	187
AK	S. SE AK	14	Deer Mountain	12 401	5	5	2480	99
AK	S. SE AK	15	Whitman Lake	13 971	8	8	1746	204
AK	S. SE AK	16	Tamgas Creek	40 594	14	7	5799	179
AK	S. SE AK	17	Nakat Inlet	17 377	7	7	2482	247
B.C.	Queen Char. Is.	18	Masset	1 646	7	6	274	174
B.C.	Queen Char. Is.	19	Pallant Creek	7 305	8	9	812	68
B.C.	N. B.C. coast	20	Kincolith	4 533	9	5	907	302
B.C.	N. B.C. coast	21	Kispiox River	444	6	3	148	289
B.C.	N. B.C. coast	22	Toboggan Creek	2 637	6	5	527	252
B.C.	N. B.C. coast	23	Fort Babine	3 895	9	7	556	298
B.C.	N. B.C. coast	24	Kitimat River	12 209	11	8	1526	357
B.C.	N. B.C. coast	25	Hartley Bay	4 215	8	4	1054	408
B.C.	N. B.C. coast	26	Snootli Creek	9 515	10	6	1586	411
B.C.	N. B.C. coast	27	Bella Bella	5 064	8	6	844	243
B.C.	West coast Van. Is.	28	Conuma River	16 561	10	9	1840	76
B.C.	West coast Van. Is.	29	Robertson Creek	29 176	12	15	1945	144
B.C.	West coast Van. Is.	30	Nitinat River	5 467	11	6	911	182
B.C.	East coast Van. Is.	31	Port Hardy	5 473	10	4	1368	191
B.C.	East coast Van. Is.	32	Quinsam River	99 229	16	15	6615	88
B.C.	East coast Van. Is.	33	Puntledge River	47 467	13	15	3164	85
B.C.	East coast Van. Is.	34	Big Qualicum River	43 953	12	15	2930	101
B.C.	S. B.C. coast	35	Sliammon River	6 326	11	5	1265	98
B.C.	S. B.C. coast	36	Sechelt	10 355	12	10	1036	143
B.C.	S. B.C. coast	37	Tenderfoot Creek	30 943	13	9	3438	186
B.C.	S. B.C. coast	38	Capilano River	107 498	12	15	7167	125
B.C.	Lower Fraser	39	Inch Creek	25 350	12	10	2535	125
B.C.	Lower Fraser	40	Chehalis River	23 442	13	9	2605	144
B.C.	Lower Fraser	41	Chilliwack River	65 335	13	11	5940	131
B.C.	Upper Fraser/Thompson	42	Thompson River	13 927	13	9	1547	161
B.C.	Upper Fraser/Thompson	43	Clearwater River	2 695	11	3	898	181
B.C.	Upper Fraser/Thompson	44	Eagle River	16 856	15	8	2107	180
B.C.	Upper Fraser/Thompson	45	Spius Creek	11 332	12	7	1619	164
WA	N. Puget	46	Kendall Creek	18 603	12	6	3101	151
WA	N. Puget Sound	47	Marblemount	11 966	12	5	2393	146
WA	N. Puget Sound	48	Tulalip	73 454	12	12	6121	88
WA	N. Puget Sound	49	Wallace River	42 080	14	10	4208	145
WA	Central Puget Sound	50	Soos Creek	47 325	14	9	5258	178
WA	Central Puget Sound	51	Voights Creek	45 692	12	9	5077	223
WA	Central Puget Sound	52	Minter Creek	20 881	12	6	3480	225
WA	Hood Canal	53	Geo. Adams	18 522	10	9	2058	257
WA	Hood Canal	54	Quilcene NFH	16 166	11	8	2021	158
WA	Strait of Juan de Fuca	55	Dungeness	7 794	13	5	1559	141
WA	Strait of Juan de Fuca	56	Elwha H/SCh	3 227	12	9	359	204

Table A1 (*concluded*).

State or province	Region	Hatchery no.	Hatchery name	Estimated no. tags recovered	No. areas recovered from	No. years released	Mean recoveries per year	Distance (*D*) (km)
WA	Olympic Pen.	57	Educket Creek	5 742	15	3	1914	210
WA	Olympic Pen.	58	Makah NFH	10 454	16	4	2614	209
WA	Olympic Pen.	59	Sol Duc	11 512	16	10	1151	242
WA	Olympic Pen.	60	Chalaat Creek	2 264	14	6	377	265
WA	Olympic Pen.	61	Quinault NFH/Lake	14 969	17	10	1497	297
WA	SW Wash. coast	62	Humptulips	13 065	14	10	1307	341
WA	SW Wash. coast	63	Bingham Creek	5 748	14	9	639	336
WA	SW Wash. coast	64	Forks Creek	13 865	17	7	1981	314
WA	SW Wash. coast	65	Nemah	4 706	16	4	1177	334
WA	SW Wash. coast	66	Naselle	10 636	16	4	2659	330
WA	WA Columbia River	67	Grays River	11 524	13	14	823	447
WA	WA Columbia River	68	Elochoman	4 542	14	6	757	385
WA	WA Columbia River	69	Cowlitz Salmon	26 264	17	11	2388	255
WA	WA Columbia River	70	Toutle River	4 695	13	4	1174	392
WA	WA Columbia River	71	Lewis River	10 219	14	8	1277	295
WA	WA Columbia River	72	Washougal	10 226	13	8	1278	245
WA	WA Columbia River	73	Willard NFH	4 202	13	8	525	355
WA	WA Columbia River	74	Klickitat	5 172	14	8	647	273
OR	OR Columbia River	75	Oxbow	3 004	14	4	751	353
OR	OR Columbia River	76	Bonneville	5 949	14	10	595	352
OR	OR Columbia River	77	Sandy	35 424	16	10	3542	349
OR	OR Columbia River	78	Eagle Creek NFH	16 917	14	7	2417	485
OR	OR Columbia River	79	Big Creek	15 418	15	12	1285	393
OR	OR Columbia River	80	Klaskanine NF/Pond	9 436	15	10	944	429
OR	N. Oregon coast	81	Nehalem	6 006	15	10	601	485
OR	N. Oregon coast	82	Trask River	8 057	15	13	620	543
OR	N. Oregon coast	83	Salmon River	2 818	14	13	217	465
OR	Central Oregon coast	84	Siletz	4 254	13	12	355	462
OR	Central Oregon coast	85	Fall Creek	8 319	14	13	640	396
OR	S. Oregon coast	86	Rock Creek	6 937	15	11	631	389
OR	S. Oregon coast	87	Cole River	6 703	10	13	516	249
CA	N. Calif. coast	88	Iron Gate	9 015	11	12	751	214
CA	N. Calif. coast	89	Trinity River	20 019	11	12	1668	200
CA	Central Calif. coast	90	Warm Springs	748	9	4	187	288

Note: Hatchery locations are indicated in Fig. 1. Values provided are across all years. AK, Alaska; B.C., British Columbia; WA, Washington; OR, Oregon; CA, California.

Table A2. Hatchery and wild population recoveries by recovery area across all years.

Recovery Area	No. hatchery fish recovered	No. hatcheries represented	No. wild fish recovered	No. wild populations represented
Cook Inlet Westward	4 646	2	2	2
Prince William Sound	1 027	12	54	4
Yakutat	2 431	23	1 163	9
Northern southeast AK	113 318	57	33 276	19
Southern southeast AK	113 325	60	6 466	22
Northern B.C. coast	12 773	60	2 119	22
Queen Charlotte Islands	26 290	69	2 652	24
Central B.C. coast	40 263	67	7 650	27
Northwest Vancouver Island	100 410	74	22 411	28
Southwest Vancouver Island	221 041	66	60 921	27
Strait of Georgia	368 844	71	66 200	27
Puget Sound	174 736	62	59 942	26
Washington coast	63 167	63	13 658	27
Columbia River	48 195	62	2 980	23
Northern Oregon	70 523	61	5 681	23
Central Oregon	51 407	56	4 685	20
Southern Oregon	16 959	38	1 179	12
Northern California	26 113	37	1 395	8
Mendocino	9 806	32	876	5
San Francisco Bay	2 631	28	595	3
Monterey Bay South	3 045	27	666	3

Note: See Fig. 1 for recovery area locations. AK, Alaska; B.C., British Columbia.

Table A3. Recovery statistics for the 36 basins with wild-tagged coho salmon used in the analysis.

State or province	Region	Basin No.	Basin name[a]	Estimated no. tags recovered	No. areas recovered from	No. years released	Mean recoveries per year	Distance (D) (km)
AK	NE SE AK	W-1	Berners River	17 132	5	11	1557	305
AK	NE SE AK	W-2	Auke Creek	857	4	5	171	216
AK/B.C.	NE SE AK	W-3	Taku River	1 944	6	6	324	271
AK	NE SE AK	W-4	Tatsamenie Lake	787	5	6	131	340
AK	NE SE AK	W-5	Speel Lake	2 013	4	6	335	266
AK	NW SE AK	W-6	Ford Arm Lake	6 242	5	11	567	66
AK	NW SE AK	W-7	Salmon Lake	1 434	5	4	359	172
AK	S. SE AK	W-8	H. Smith Lake	8 464	6	10	846	239
B.C.	N. B.C. coast	W-9	Lachmach River	5 355	7	6	893	301
B.C.	East coast Van. Is.	W-10	Keogh River	3 860	11	3	1287	173
B.C.	East coast Van. Is.	W-11	Quinsam River	2 404	9	3	801	45
B.C.	East coast Van. Is.	W-12	Black Creek	41 636	13	10	4164	103
B.C.	East coast Van. Is.	W-13	Trent River	6 873	10	6	1146	102
B.C.	East coast Van. Is.	W-14	L. Qualicum River	2 567	9	3	856	95
B.C.	East coast Van. Is.	W-15	French Creek	5 256	8	5	1051	139
B.C.	East coast Van. Is.	W-16	Mesachie Creek	1 216	8	6	203	177
B.C.	Lower Fraser	W-17	Salmon River	20 797	12	10	2080	108
B.C.	Lower Fraser	W-18	Pitt River	2 412	8	3	804	183
B.C.	Lower Fraser	W-19	Chilliwack River	1 255	7	3	418	152
WA	N. Puget Sound	W-20	Skagit River	14 741	13	9	1638	150
WA	N. Puget Sound	W-21	Stillaguamish River	11 535	11	7	1648	129
WA	N. Puget Sound	W-22	Snohomish River	31 609	14	9	3512	142
WA	S. Puget Sound	W-23	Deschutes River	16 538	11	14	1181	376
WA	Hood Canal	W-24	S. Hood Canal	17 358	9	8	2170	275
WA	Hood Canal	W-25	Big Beef Creek	40 330	15	15	2689	173
WA	Strait of Juan de Fuca	W-26	Hoko River	2 330	13	4	582	165
WA	Olympic Pen.	W-27	Dickey River	2 251	13	6	375	251

Table A3 (*concluded*).

State or province	Region	Basin No.	Basin name[a]	Estimated no. tags recovered	No. areas recovered from	No. years released	Mean recoveries per year	Distance (*D*) (km)
WA	Olympic Pen.	W-28	Hoh River	657	11	4	164	276
WA	Olympic Pen.	W-29	Queets River	3 284	12	12	274	277
WA	SW WA coast	W-30	Stevens Creek	2 958	15	11	269	387
WA	SW WA coast	W-31	Lower Chehalis River	3 085	14	11	280	342
WA	SW WA coast	W-32	Upper Chehalis River	2 187	14	8	273	352
OR	OR Columbia	W-33	Clackamas River	525	10	3	175	440
OR	N. OR coast	W-34	Fish Hawk Lake	4 697	17	11	427	538
OR	Central OR coast	W-35	Alsea River	4 412	14	8	552	538
OR	Central OR coast	W-36	Eel Lake	3 566	13	11	324	323

Note: Basin locations are provided in Fig. 1. Values provided are across all years. AK, Alaska; B.C., British Columbia; WA, Washington; OR, Oregon.
[a]Basins listed include wild coho salmon released from the following tributaries (names given in the CWT database): Taku (in both Canadian and American waters); Skagit (Baker River, Etach, Nookachamps, and Mannser creeks, and Skagit River tributaries); Stillaguamish River (Stillaguamish River, Canyon and Fortson creeks); Snohomish (Griffin, Harris, and Little Pilchuck creeks and SF Skykomish); S. Hood Canal (Mill Creek, Skokomish, Tahuya, and Union rivers); Queets (Hurst, Miller, and North creeks, Snahapish and Clearwater rivers); Lower Chehalis (Bingham Creek and Chehalis River); Upper Chehalis (Beaver and Scatter creeks, Black River, and Upper Chehalis River).