Early Ocean Dispersal Patterns of Columbia River Chinook and Coho Salmon

Citation	Fisher, J. P., Weitkamp, L. A., Teel, D. J., Hinton, S. A., Orsi, J. A., Farley Jr, E. V., ... & Trudel, M. (2014). Early Ocean Dispersal Patterns of Columbia River Chinook and Coho Salmon. Transactions of the American Fisheries Society, 143 (1), 252-272. doi:10.1080/00028487.2013.847862
DOI	10.1080/00028487.2013.847862
Publisher	Taylor & Francis
Version	Version of Record
Citable Link	http://hdl.handle.net/1957/47058
Terms of Use	http://cdss.library.oregonstate.edu/sa-termsofuse

Transactions of the American Fisheries Society 143:252–272, 2014

ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1080/00028487.2013.847862

ARTICLE

Early Ocean Dispersal Patterns of Columbia River Chinook and Coho Salmon

J. P. Fisher*[1]
Cooperative Institute for Marine Resources Studies, Oregon State University, 2030 Marine Science Drive, Newport, Oregon 97365, USA

L. A. Weitkamp
National Oceanic and Atmospheric Administration Fisheries, Northwest Fisheries Science Center, 2032 Southeast Marine Science Drive, Newport, Oregon 97365, USA

D. J. Teel
National Oceanic and Atmospheric Administration Fisheries, Northwest Fisheries Science Center, Manchester Research Laboratory, Post Office Box 130, Manchester, Washington 98353, USA

S. A. Hinton
National Oceanic and Atmospheric Administration Fisheries, Northwest Fisheries Science Center, Point Adams Field Station, 520 Heceta Place, Hammond, Oregon 97121, USA

J. A. Orsi and E. V. Farley Jr.
National Oceanic and Atmospheric Administration Fisheries, Alaska Fisheries Science Center, Auke Bay Laboratories, Ted Stevens Marine Research Institute, 17109 Point Lena Loop Road, Juneau, Alaska 99801, USA

J. F. T. Morris, M. E. Thiess, R. M. Sweeting, and M. Trudel
Fisheries and Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, British Columbia V9T 6N7, Canada

Abstract
Several evolutionarily significant units (ESUs) of Columbia River asin Chinook Salmon *Oncorhynchus tshawytscha* and Coho Salmon *O. kisutch* are listed as threatened or endangered under the U.S. Endangered Species Act. Yet little is known about the spatial and temporal distributions of these ESUs immediately following ocean entry, when year-class success may be determined. We documented differences in dispersal patterns during the early ocean period among groups defined by ESU, adult run timing, and smolt age. Between 1995 and 2006, 1,896 coded-wire-tagged juvenile fish from the Columbia River basin were recovered during 6,142 research trawl events along the West Coast of North America. Three distinct ocean dispersal patterns were observed: (1) age-1 (yearling) mid and upper Columbia River spring-run and Snake River spring–summer-run Chinook Salmon migrated rapidly northward and by late summer were not found south of Vancouver Island; (2) age-0 (subyearling) lower Columbia River fall, upper Columbia River summer, upper Columbia River fall, and Snake River fall Chinook Salmon dispersed slowly, remaining mainly south of Vancouver Island through autumn; and (3) age-1 lower Columbia River spring, upper Columbia River summer, and upper Willamette River spring Chinook Salmon and Coho Salmon were widespread along the coast from summer through fall, indicating a diversity of dispersal rates. Generally, the ocean dispersal of age-1 fish was faster and more extensive than that of age-0 fish, with some age-1 fish migrating as fast as 10–40 km/d (0.5–3.0 body lengths/s).

*Corresponding author: jmcfisher@minetfiber.com
[1]Present address: 879 Monmouth Avenue North, Monmouth, Oregon 97361, USA.
Received March 25, 2013; accepted September 6, 2013
Published online January 6, 2014

Within groups, interannual variation in dispersal was moderate. Identification of the distinct temporal and spatial ocean distribution patterns of juvenile salmon from Columbia River basin ESUs is important in order to evaluate the potential influence of changing ocean conditions on the survival and long term sustainability of these fish populations.

During the 20th century, many Columbia River salmon spawning populations were greatly reduced or extirpated (Nehlsen et al. 1991; Kope and Wainwright 1998; Gustafson et al. 2007). Currently, five Chinook Salmon *Oncorhynchus tshawytscha* evolutionarily significant units (ESUs) and one Coho Salmon *O. kisutch* ESU in the basin are considered threatened or endangered under the U.S. Endangered Species Act (Ford 2011). Evolutionarily significant units are groups of populations that are substantially isolated from other populations reproductively and contribute significantly to the ecological and genetic diversity of the species (Weitkamp et al. 1995; Myers et al. 1998). Although anthropogenic changes to freshwater habitats have been major contributors to the decline of Columbia River salmon, conditions during the period of seaward migration and the first few months following ocean entry may influence much of the interannual or interdecadal variability in salmon abundance (Fisher and Pearcy 1988; Pearcy 1992; Bradford 1995; Logerwell et al. 2003; Mueter et al. 2005; Miller et al. 2013). Understanding where and how ocean conditions affect the survival of juvenile salmon depends on knowing the initial marine dispersal and migration patterns of these fish (Pearcy 1992).

Mass-marking of juvenile salmon with coded wire tags (CWTs; Jefferts et al. 1963) provides a unique opportunity to study the dispersal and migration patterns of salmon during their marine life. These small wires are inserted into the nose cartilage of juvenile salmon in freshwater before their seaward migration, with a different numeric code for each release group (Nandor et al. 2010). About 50 million Pacific salmon with CWTs are released annually from Alaska to California (Nandor et al. 2010). Recoveries of salmon with CWTs are primarily used by managers to estimate stock-specific harvest and survival rates, but they can also be used to determine juvenile and adult distribution patterns during their marine phase (Nandor et al. 2010; Weitkamp 2010). Marine recoveries of juvenile salmon with CWTs form the basis for this paper.

The initial ocean migrations of juvenile Chinook and Coho Salmon originating from Oregon to Alaska have been documented in several early studies using small-mesh purse seines, modified commercial salmon trolling gear, and surface trawls. Juveniles were either captured and tagged at sea and subsequently recovered as adults (e.g., Hartt and Dell 1986) or had a CWT implanted prior to leaving freshwater and were recovered in ocean sampling (e.g., Miller et al. 1983; Pearcy and Fisher 1988, 1990; Fisher and Pearcy 1995; Orsi and Jaenicke 1996; Morris et al. 2007; Trudel et al. 2009). Collectively, the tag studies revealed that age-1 (yearling) Chinook Salmon juveniles from spring-run (season of adult return to rivers) populations in the Columbia River basin have very different distributions than age-0 (subyearling) fish from fall-run populations. Spring-run juveniles migrate rapidly north away from the river and may reach coastal areas in Southeast Alaska by early summer and the northeastern Gulf of Alaska by late summer (Miller et al. 1983; Hartt and Dell 1986; Fisher and Pearcy 1995; Orsi et al. 2000; Trudel et al. 2009). More recently, genetic data have been used to estimate the stock origins of juveniles sampled in ocean trawl surveys conducted along the British Columbia and Southeast Alaska coasts, also documenting the rapid northward migration of Columbia River spring-run fish (Trudel et al. 2004; Tucker et al. 2011, 2012). In contrast to the findings for spring-run juveniles, both CWT and genetic data show that Columbia River fall-run Chinook Salmon remain along coastal areas from Oregon to southern British Columbia throughout the summer and are not caught north of Vancouver Island (Fisher and Pearcy 1995; Teel 2004; Trudel et al. 2009; Tucker et al. 2011).

Ocean sampling studies depict a distribution pattern for Coho Salmon from the Columbia River that differs from those of both spring- and fall-run Chinook Salmon. Analyses of tagged fish and genetic data show that throughout the summer Columbia River Coho Salmon juveniles are broadly distributed along coastal areas north of the river, including as far as the Gulf of Alaska (Hartt and Dell 1986; Pearcy and Fisher 1988; Orsi et al. 2000; Trudel et al. 2004; Morris et al. 2007). However, sampling in southern areas reveals that some juveniles migrate south of the Columbia River along the Oregon and northern California coast (Pearcy and Fisher 1988; Brodeur et al. 2004; Morris et al. 2007; Van Doornik et al. 2007).

Previous studies did not differentiate the early ocean dispersal patterns of the different Columbia River ESUs. However, because Columbia River salmon are managed in order to maintain or restore populations of specific ESUs, and since ocean conditions during the early marine phase may be a determinant of year-class success, it is important to know whether and how the early ocean distributions of the different ESUs differ spatially and temporally. This is a necessary first step to understanding when and where ocean conditions may impact the survival of the different ESUs.

In this paper we reexamine a decade of CWT recoveries of juvenile Columbia River Chinook and Coho Salmon caught along the shelf waters from Oregon to Alaska (Morris et al. 2007; Trudel et al. 2009). The objectives of the study were to (1) evaluate, for the first time, the early ocean dispersal patterns of different groups defined by ESU, adult run timing, and smolt age; (2) examine dispersal in finer temporal and spatial scales than was done in the previous studies; and (3) estimate dates of ocean entry in order to better estimate ocean dispersal rates.

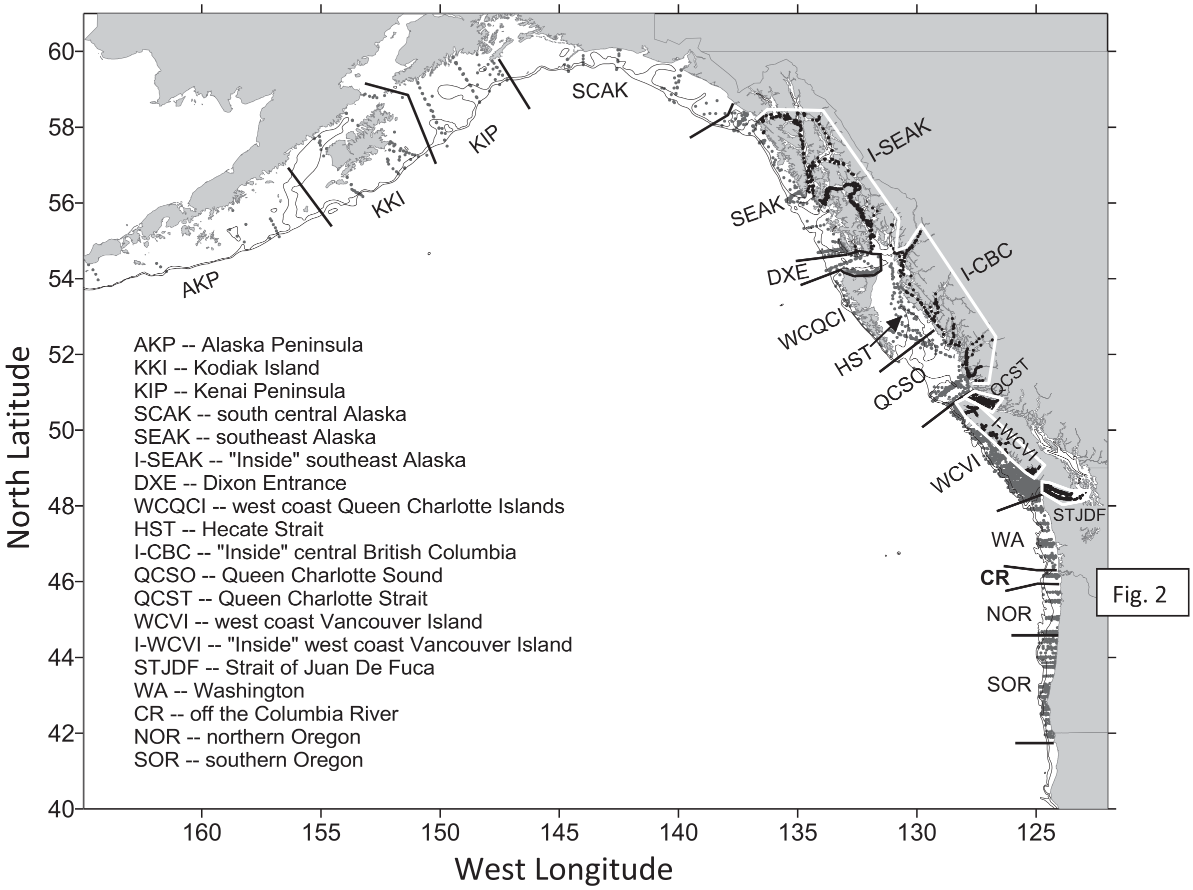

FIGURE 1. Regions sampled with surface rope trawls, 1995–2006. Sampling stations in 14 regions on the open shelf are indicated by gray dots; stations in five regions in protected waters (fjords, inlets, etc. in Southeast Alaska, central British Columbia, Queen Charlotte Strait, Vancouver Island, and the Strait of Juan de Fuca) are indicated by black dots. The 200-m and 500-m isobaths also are shown.

METHODS

Study area and sampling.—Between 1995 and 2006, juvenile salmon originating from the Columbia River basin were collected over the continental shelf (inshore of the 500-m isobath but including deeper fjords, straits, and inlets) of the West Coast of North America from southern Oregon to the Alaska Peninsula by six different research programs (Figure 1; Table 1). We summarized the sampling effort by 19 catch regions: 14 on the open shelf and five in inlets, straits, and fjords (Figure 1). One region was just off the mouth of the Columbia River, 16 were to the north and west of the river, and 2 were to the south of the river. Although sampling also occurred offshore of the continental shelf, too few Columbia River juvenile Chinook or Coho Salmon were caught there (six), so we restricted our analyses to the sampling conducted on the continental shelf (Figure 1).

Sampling was performed with modified midwater rope trawls towed at 5.2–9.3 km/h either at the surface or below the surface (headrope 0–5 m deep or >5 m deep, respectively), and with vertical mouth openings from 10 to 30 m. More detailed methods are found in Farley et al. (2001), Sweeting et al. (2003), Morris et al. (2004), Fisher et al. (2007), and Orsi et al. (2007).

For each month and catch region, we calculated total effort (km^2 swept by the net) by summing across all years of sampling for both the surface and subsurface tows (Table 2). Most of the effort (as well as most of the catch) was in surface tows that sampled approximately the upper 20–25 m of the water column (Table 2). Previous studies had shown that the density of juvenile salmon is higher in the upper 20–30 m of the water column than in deeper water (Orsi et al. 1995; Beamish et al. 2000; Emmett et al. 2004), although juvenile Chinook Salmon may move deeper as they grow (Orsi et al. 1995). Effort varied significantly by month and region, with the greatest effort in Southeast Alaska, off the west coast of Vancouver Island, off the Washington coast, and off the northern and southern Oregon coasts (Table 2).

CWT data.—All juvenile Chinook and Coho Salmon were measured (FL; mm), weighed (g), identified to species, and checked for the presence of a CWT. Release data for each CWT numeric code, including species, run, stock, fish age, average fish size (FL or weight), date, location, the number of tagged fish, and the number of associated untagged fish were obtained from the Regional Mark Information System online database

TABLE 1. Trawl sampling over the continental shelf (≤500 m bottom depth or in "inside" waters), by research program, years, and regions. See Figure 1 for region locations. Abbreviations are as follows: NOAA = U.S. National Oceanic and Atmospheric Administration, DFO = Canadian Department of Fisheries and Oceans, and NEP-GLOBEC = Northeast Pacific Global Ocean Ecosystems Dynamics.

Center and project	Years	Surface tows	Subsurface tows	Regions sampled[a]
NOAA, Auke Bay Laboratories,				
ocean carrying capacity	1998–2002	182	0	AKP, KIP, KKI, SCAK, SEAK
Southeast Alaska coastal monitoring	1997–2006	938	0	SEAK, I-SEAK
DFO Pacific Biological Laboratory				
High-seas salmon	1995–2006	1,695	368	All except KIP, NOR, CR, SOR
Salmon interactions	1995–2004, 2006	724	851	I-CBC, QCSO, WCVI, I-WCVI, QCST, I-STJDF, WA
NOAA, Northwest Fisheries Science Center and Oregon State University				
Columbia River plume study	1998–2006	1,081	0	WA, CR, NOR
NEP-GLOBEC	2000, 2002	303	0	NOR, SOR
All sampling		4,923	1,219	

[a]Ten or more hauls in each region.

(Regional Mark Processing Center, Pacific States Marine Fisheries Commission; available: www.rmpc.org). The release locations of the tagged fish in the Columbia River basin that we recovered in the ocean are shown in Figure 2.

ESU, run, and age-groups.—Juvenile Chinook Salmon from seven of eight Columbia River ESUs (Good et al. 2005; Ford 2011) were identified in our ocean catches of tagged fish (Table 3). No juvenile salmon were recovered from an eighth ESU (the Deschutes River summer–fall run) in our ocean sampling. Of the seven ESUs, we subdivided two (the lower Columbia River ESU and the upper Columbia River summer–fall-run ESU) by adult run timing (Table 3). Additionally, the upper Columbia River summer-run subgroup and the Snake River fall-run ESU included substantial proportions of both small age-0 and large age-1 smolts (Table 3). Since the ocean entry timing and early marine dispersal of the two size- and age-classes may differ, they were analyzed separately. In all, 11 Chinook Salmon groups defined by ESU, adult run timing, and smolt age were analyzed.

Currently only the lower Columbia River Coho Salmon ESU is extant, and for most analyses all Columbia River Coho Salmon were placed together in this ESU (Table 3). However, we also examined the early ocean dispersal rates of early fall-run (type S) and late fall-run (type N) Coho Salmon released in different basins.

The five Columbia River basins in which the different ESUs originate along with their approximate boundaries are shown in Figure 2. The hatcheries, local stocks, or release basins contributing to each of the nine Chinook and Coho Salmon groups defined by ESU and adult run timing are listed in Table A.1 in the appendix.

Temporal and spatial ocean distribution—For each month and catch region we calculated the catch per unit effort (CPUE) of the different ESUs/runs/age-groups for all years combined by dividing the total catch by the total effort (from Table 2). When calculating CPUE, the catch of each tagged fish was expanded for the untagged fish associated with its release group. For example, if a hatchery release group consisted of 50,000 fish with CWTs and 200,000 untagged fish (250,000 fish total), then each recovery of a tagged fish from that group was multiplied by five. We assumed that the dispersal behavior of tagged and untagged fish from a release group was similar and that each recovery of a tagged fish indicated potential additional recoveries of associated untagged fish.

We qualitatively and quantitatively evaluated the group-specific variation in marine distribution. For the qualitative analyses, we described the dispersal pattern of each ESU/run/age-group by constructing bubble plots of CPUE in each month and catch area for all years combined. We restricted the quantitative analyses to univariate and multivariate techniques on the catch data expanded for both sampling effort and the untagged fish associated with each tag group (as outlined above), although analyses using actual raw tag numbers produced very similar results. Our univariate method consisted of calculating the mean distance of recovery (D) from the Columbia River mouth for each group as

$$D = \sum_i d_i R_i,$$

where d_i is marine distance (km) between each recovery location i and the mouth of the Columbia River and R_i is the proportion of tagged Salmon recovered at location i for that group, regardless of month of recovery. The distance traveled in the ocean by each tagged fish was estimated by summing great circle distances between the Columbia River mouth and

TABLE 2. Total effort (km^2 swept out by the net, i.e., the width of the net mouth times the distance towed) during surface (headrope within 5 m of the surface) and subsurface tows over the continental shelf in different regions and months, 1995–2006. The greatest efforts (>8 km^2) are denoted by bold italics. See Figure 1 for regions.

Region	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Surface tows										
AKP							3.1			1.6
KKI		0.9					***10.2***			1.2
KIP						***11.5***	5.4		0.4	
SCAK		0.3				***8.3***			0.9	
SEAK	1.9	4.2			7.0	6.9	7.4		***11.8***	2.6
I-SEAK		***14.5***		3.1	***8.6***	***10.8***	***9.9***		***14.1***	***11.4***
DXE		5.2			5.7	2.6	1.5		5.0	1.8
WCQCI		0.3			1.6				1.5	
HST		6.0			2.1	1.4	1.7		4.2	0.4
I-CBC		6.2			2.1		0.2	1.1	5.4	***8.1***
QCSO		5.6		1.1	***9.8***	4.6	6.3	1.1	**9.4**	1.4
I-QCST			1.0		2.2	2.1		3.3		1.9
WCVI	6.9	***13.6***	***15.2***	1.8	***11.4***	***14.4***	7.6	**8.1**	***24.4***	3.8
I-WCVI	3.5	***9.2***		1.1	1.5	1.2			***12.0***	3.0
SJDF	4.2	1.2	7.9	2.2	1.4	7.4		6.9	4.6	2.9
WA		0.8	4.0	6.7	***19.7***		0.9	***19.7***		1.2
CR				4.5	6.4		0.7	5.3		0.6
NOR				6.7	***15.2***		2.6	***14.4***		0.8
SOR					***12.5***		***10.2***		1.6	
Subsurface tows										
KKI		0.4								1.8
KIP									0.6	
SCAK		0.1							0.9	
SEAK		1.0			0.1	0.3			4.5	0.4
I-SEAK		1.9							4.6	4.8
DXE		0.1			1.3				0.3	
WCQCI							0.4			
HST		0.1			1.2	0.4	0.1		2.8	
I-CBC		1.3			2.5			0.3	1.7	
QCSO		0.3		0.4	2.6	0.1	0.4	1.6	1.3	
I-QCST			0.9		0.7	0.5		3.2	0.3	2.1
WCVI	4.4	***11.5***	***18.5***		***10.0***	***9.1***	5.2	***11.1***	***9.4***	5.2
I-WCVI	0.4	0.9		0.8		0.6			0.1	0.6
SJDF	5.0	1.5	***8.7***	3.5	1.5	***8.4***		***9.7***	5.6	5.5
WA		1.0	6.1		4.2			2.4		

the ocean capture location, using up to 16 way-points situated to confine the hypothetical migration path to the continental shelf (Table A.2). Fish caught north of Vancouver Island were routed through Queen Charlotte Sound, Hecate Strait, and Dixon Entrance, with the exception of those caught off the west coast of the Queen Charlotte Islands (now known as Haida Gwaii; Figure 1). Recoveries that occurred south of the Columbia River where given negative distance values, so that D is measured as distance north of the Columbia River. We evaluated differences in D among the ESUs/runs/age-groups described earlier (Table 3) using a Mann–Whitney test for differences in medians or Kruskal–Wallis one-way ANOVA on ranks (Zar 1984).

Our multivariate techniques were based on pairwise Bray–Curtis similarity coefficients among all groups, which were calculated from the proportion of recoveries in each of the 19 recovery areas (Figure 1) independent of the month or year of recovery. Bray–Curtis similarity coefficients are widely used in ecological studies because they are unaffected by changes in scale (e.g., using percents or proportions) or the number of variables used and produce a value of zero when both values being

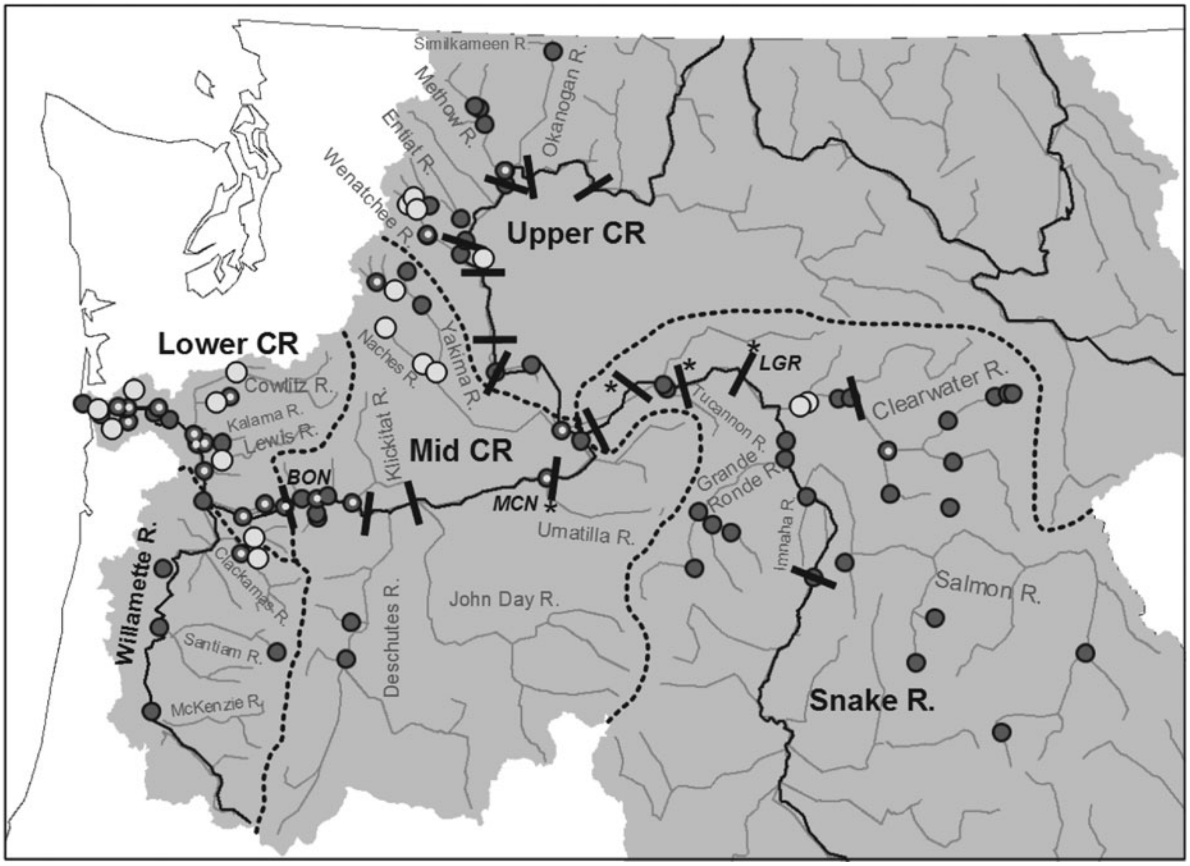

FIGURE 2. Map of the Columbia River (CR) basin showing the release sites of coded-wire-tagged Chinook Salmon (dark circles), Coho Salmon (light circles), and both species (light dots in dark circles) as well as major dams (bars). The abbreviations LGR, MCN, and BON stand for the Lower Granite, McNary, and Bonneville dams, respectively. The four dams at which the collection and downstream transport of smolts occur are marked with asterisks. The dotted lines delineate the approximate boundaries of the Chinook Salmon ESU and adult run timing groups used in our analysis. The groups are lower Columbia River fall and spring (Lower CR), upper Willamette River spring (Willamette R), mid–Columbia River spring (Mid CR), upper Columbia River summer (Upper CR), and fall and spring–summer Snake River (Snake R). The upper Columbia River fall ESU/run group includes fall Chinook Salmon juveniles released both in the upper Columbia River (Upper CR) and mid–Columbia River (Mid CR).

compared are zero (the joint absence problem; Clarke 1993; Legendre and Legendre 1998). In this application, similarities ranged from 0 (dissimilar recovery patterns) to 100 (identical recovery patterns). All multivariate analyses were run with PRIMER-E software (www.primer-e.com).

We qualitatively compared pairwise Bray–Curtis similarity coefficients estimated among all groups. We also quantitatively compared these coefficients using ANOSIM (a multivariate analog to ANOVA) to test for the influence of species, subbasin (i.e., Willamette River, Snake River, or upper, mid, and lower Columbia River), run timing (using the same groups described for distance analysis above), and age at release (0 or 1) on recovery patterns. The ANOSIM analysis produces global R values that indicate the degree of separation of groups generated by a particular factor or pair of factors. These global R values range from 0 (no separation) to 1 (complete separation); the procedure also generates statistical probabilities by permutation.

To evaluate the interannual variation in recovery patterns, we used a subset of groups and years to calculate annual mean travel distances and Bray–Curtis similarity coefficients as described above. We selected this subset by only including years in which at least 15 actual CWTs were recovered for a group. This criterion was selected as the minimum number of tags that would represent true distribution patterns; greater tag recoveries ($>$100/year) are desirable for this type of analysis. We also restricted the analysis to groups for which the 15-tag criterion was met for at least 3 years. Variation across fewer than 3 years was difficult to evaluate. Although the criterion was determined from actual tag recoveries, distances and similarities were estimated using recoveries corrected for effort.

We evaluated the interannual variation in recovery patterns using both travel distances and pairwise Bray–Curtis similarities estimated for each year and each group. We evaluated the variation in mean distances by estimating coefficients of variation and calculated mean similarity between years from the

TABLE 3. Evolutionarily significant unit (ESU), adult run timing, and age at hatchery release of coded-wire-tagged Columbia River basin Chinook and Coho Salmon recovered in trawl sampling from 1995 through 2006. The ESU status under the U.S. Endangered Species Act (E = endangered, T = threatened, N = not listed) is also shown.

ESU	Status	Adult run timing	Dominant age(s) at release[a]
Chinook Salmon			
Lower Columbia River	T	Fall	0
		Spring	1
Upper Columbia River summer–fall	N	Fall[b]	0
		Summer	1 and 0
Snake River fall	T	Fall	1 and 0
Upper Willamette River	T	Spring	1
Mid–Columbia River spring	N	Spring	1
Upper Columbia River spring	E	Spring	1
Snake River spring–summer	T	Spring–summer	1
Coho Salmon			
Lower Columbia River[c]	T	Fall	1

[a]Age refers to the number of winters spent in freshwater once the fish have hatched. Hence, age-0 fish migrate to sea during the year they hatch, whereas age-1 fish have spent a full year in freshwater prior to migrating to sea.

[b]The fall-run component of the upper Columbia River summer–fall-run ESU includes several stocks released in the mid–Columbia River basin (i.e., the Bonneville Pool, mid–Columbia River, Little White Salmon National Fish Hatchery, and Umatilla River stocks; Table A.1). To avoid confusion, the entire fall-run component of this ESU is referred to throughout as the upper Columbia River fall run to more closely match the name of the ESU.

[c]Includes fish released in the upper Columbia and Snake rivers not technically part of the lower Columbia River Coho Salmon ESU (HSRG 2009).

same groups. We also used ANOSIM to quantitatively evaluate the variation in marine recovery patterns due to the influence of year, ESU, run timing (i.e., spring, summer, or fall) and subbasin (i.e., Willamette, Snake, and upper and mid–Columbia River) as factors.

Ocean dispersal rates.—We estimated the ocean dispersal rate for each tagged juvenile salmon both in absolute terms (km/d, where km = the distance traveled in the ocean and d = the estimated number of days between ocean entry and capture) and in size-specific terms (body lengths [bl]/s, where bl = [FL at recovery + average FL at release]/2 and s = the estimated number of seconds between ocean entry and capture). For this analysis, distances both north and south of the Columbia River mouth were positive. Sometimes, only the average weight at release was given for a release group; to calculate bl in such cases, the average FL at release was estimated by regression from release groups for which both average FL and weight were reported, i.e.,

$$\text{FL (mm)} = 45.8992 \cdot \text{Wt (g)}^{0.322587}, \quad n = 3{,}676 \text{ groups}, \quad r^2 = 0.98 \text{ for Chinook salmon}$$

and

$$\text{FL (mm)} = 45.9901 \cdot \text{Wt (g)}^{0.328823}, \quad n = 2{,}249 \text{ groups}, \quad r^2 = 0.98 \text{ for Coho Salmon.}^2$$

The ocean entry date of each tagged fish was estimated as release date + rkm/(rkm/d), where rkm = the distance from the release site to the mouth of the Columbia River and rkm/d = the estimated downstream migration rate. Distances between release locations and the mouth of the Columbia River were obtained from various sources, including (1) StreamNet data exchange format version 2005.1 downloadable database (www.streamnet.org/downloaddatabase.html/ [September 2008]); (2) the Fish Passage Center (www.fpc.org [June 2011]); (3) Columbia River Data Access in Real Time, School of Aquatic and Fisheries Sciences, University of Washington, Seattle (www.cbr.washington.edu/dart [June 2011]); and (4) chapter 4, section K of PSMFC 2009). When the exact release site along a tributary was not indicated in the CWT database, the release was assumed to have occurred at the rearing hatchery if the hatchery was on the same tributary as the release; otherwise, it was assumed to have occurred halfway up the tributary in the case of long tributaries (>135 km in length) or at the mouth of the tributary in the case of short tributaries (<135 km in length).

Estimates of the downstream migration rates of the different ESUs/runs/age-groups were provided by recoveries of tagged fish in purse seine sampling in the lower Columbia River estuary between mid-April and mid-October 2006–2011 (Weitkamp et al. 2012; L. Weitkamp, unpublished data) (Table 4). When estimating ocean entry date, we used the 75th rather than the 50th percentile of the downstream migration rate (Table 4) because it resulted in a higher percentage of ocean entry dates that were earlier than the actual ocean recovery date (94% versus 82%). Fish were excluded from the estimation of ocean dispersal rates when their estimated ocean entry date occurred after their actual ocean capture date. Fish from a single CWT release are often found in the Columbia River estuary over a period of several days to several weeks (Dawley et al. 1985; Weitkamp, unpublished data), and therefore our estimate of the ocean entry date of any individual fish may be in error by a similar time period. Because errors in estimated ocean dispersal rates may be especially large for very recent ocean entrants, we used only data from fish estimated to have been in the ocean for at least 5 d (n = 1,687, which represents 89% of the CWT fish caught as part of this study) when comparing dispersal rates among groups. Differences in dispersal rates (km/d) among groups were compared by Kruskal–Wallis rank-sum

[2]The regressions were constructed from data available in the Regional Mark Information System online database (www.rmpc.org [September 2008])

TABLE 4. Downstream migration rates of coded-wire-tagged juvenile Chinook and Coho Salmon from release to subsequent capture during purse seining operations in the lower Columbia River estuary (rkm 15) from mid-April to mid-October, 2006–2011 (L. Weitkamp, unpublished data). The data for Chinook Salmon are grouped by ESU, adult run timing, and age at release (0 or 1), those for Coho Salmon by release area and age. The ocean entry dates of each tagged release were estimated using these data (see Methods).

		Downstream migration rates (km/d)			
Group	*n*	25th percentile	Median	75th percentile	Mean
Chinook Salmon					
Lower Columbia, fall, 0	101	2.4	5.3	7.3	7.3
Lower Columbia, spring, 1	19	1.9	2.4	3.5	2.5
Upper Willamette, spring, 1	19	6.0	8.7	16.7	22.7
Mid Columbia, spring, 1	44	7.6	10.5	21.3	15.1
Upper Columbia, fall, 0	59	8.2	14.9	24.6	18.4
Upper Columbia, summer, 1 and 0	91	18.7	21.9	29.1	27.1
Upper Columbia, spring, 1	67	15.8	18.6	24.6	20.6
Snake, fall and spring–summer, 1	121	15.7	20.7	25.4	22.0
Snake, fall, 0	54	22.8	34.5	45.6	36.1
Coho Salmon					
Lower–mid Columbia, 1	68	6.3	9.3	25.1	25.3
Upper Columbia–Snake, 1	48	15.3	19.2	26.5	23.4

tests (Statistical package R, version 2.14.0; www.r-project.org/foundation).

RESULTS

Catch Summary

A total of 1,896 Chinook and Coho Salmon with CWTs were caught in the ocean the same year that they were released (Table 5). Most fish (1,792) were caught in surface tows, and most were caught between northern Oregon and the west coast of Vancouver Island within about 600 km of the Columbia River, where the total effort was also high (Tables 2, 5). No fish were caught as far north and west as the Alaskan Peninsula. In the year of ocean entry, about nine times as many freshwater age-1 ($n = 1{,}703$) as age-0 ($n = 193$) tagged Salmon were caught in the ocean. However, because of differences in tagging rates between age-1 fish (higher rates) and age-0 fish (lower rates) and differences in the vulnerability to capture of these two age-classes (see Discussion), these raw catch numbers do not reflect the relative abundances of the two ages in the ocean.

Spatial and Temporal Distribution Patterns

Plots of the CPUE of tagged fish (expanded for associated untagged fish) by recovery month and region during their first year in the ocean indicate a variety of dispersal patterns among the groups defined by ESU, run timing, and smolt age, ranging from very rapid northward dispersal to slower, seemingly less directed dispersal (Figure 3A–J). Several groups exhibited a "mixed" dispersal pattern, with some fish migrating rapidly northward, others moving more slowly northward, and still others moving to the south. The lower Columbia River fall and spring runs, upper Columbia River summer and fall runs, and Snake River fall run of Chinook Salmon were found throughout the summer and fall and for an extended period following ocean entry in the region from the west coast of Vancouver Island south to southern Oregon (Figure 3A–E). During their first ocean summer, age-0 fish from these groups were never found north of Vancouver Island and were most common in the sampling regions along the Washington and Oregon coast. Although some age-1 fish from the upper Columbia River summer run (Figure 3E) and the lower Columbia River spring run (Figure 3B) migrated as far north as Alaska by summer, other age-1 fish from these same groups remained in southern sampling areas into the late summer or fall, suggesting considerable within-group variation in dispersal following ocean entry.

The upper Willamette River spring-run Chinook Salmon group entered the ocean as early as March. By June it was widely dispersed latitudinally from southern Oregon to Southeast Alaska. However, by August it was rarely found south of Vancouver Island, although a few fish were present in the sampling regions off Washington and the Columbia River in September (Figure 3F).

The clearest examples of rapid, northward-directed dispersal were for the mid and upper Columbia River spring run and the Snake River spring–summer run of Chinook Salmon. The distributions of these groups shifted northward every month after ocean entry in May, so that from midsummer to fall they were extremely rare on the shelf south of Alaska (Figure 3G–I).

Columbia River Coho Salmon were concentrated off of the Columbia River and Washington coast in May and by June were widely dispersed from northern Oregon to Southeast Alaska. Columbia River Coho Salmon continued to be found in

TABLE 5. Recoveries ($n = 1{,}896$) by region of tagged juvenile Columbia River basin Chinook and Coho Salmon during their first several months in the ocean, grouped by ESU, adult run timing, and age at release (0 or 1). These are actual recoveries, i.e., not expanded for associated untagged fish or corrected for effort. Included are six recoveries over deep water (>500 m deep) and 104 recoveries in subsurface tows (headrope below 5 m deep). Sampling was conducted from 1995 through 2006. See Figure 1 for region locations. No tagged juvenile salmon were recovered in region AKP.

	ESU, run, release age															
	Lower Columbia		Upper Columbia Fall		Upper Columbia Summer		Snake Fall		Upper Willamette Spring		Mid Columbia Spring		Upper Columbia Spring	Snake Spring–summer		Coho Salmon Fall
Recovery region	Fall 0	Spring 1	0	1	0	1	0	1	0	1	0	1	1	0	1	1
KKI												1				2
KIP												2				7
SCAK										5					3	0
SEAK		2								3		7	4		6	12
I-SEAK		2				2				3		1				2
DXE		2				1						1	1		1	1
WCQCI						1										0
HST		1				2				2		1	1		4	1
I-CBC						5										0
QCSO		1				7		3		4		11	3		9	6
WCVI	2	13	1	1	1	82	1	32	4	34	1	13	26		26	103
I-WCVI						1		2		2						3
SJDF		2				13		10		3		2				5
WA	24	36	36	2	7	279	41	53		43		44	67	2	42	154
CR	2	28	19		8	92	20	45		26		28	41		43	45
NOR		14	16		4	13	3	29		4		1	2			39
SOR		13	1			3		5		3		1				2
Total	28	114	73	3	20	501	65	179	4	132	1	113	145	2	134	382

moderate abundance throughout the summer and fall along the west coast of Vancouver Island south to the northern Oregon coast (Figure 3J). The great latitudinal range in the distribution of juvenile Coho Salmon from June through September suggests that their early ocean dispersal varies considerably (Figure 3J). Early fall-run Coho Salmon (type S fish) were more widely dispersed latitudinally than late fall-run Coho Salmon (type N fish), with 10% of the raw catch of the type S fish occurring off northern British Columbia or Alaska but only 2% of the catch of type N fish occurring that far north. Although some early fall-run Coho Salmon migrate rapidly to the north, others do not. For example, of the 41 Coho Salmon caught in September and October from the west coast of Vancouver Island south to Oregon, 22 were early fall-run fish and 19 were late fall-run fish. Of the highly migratory juvenile Coho Salmon recovered in Alaskan waters, 87% originated in the lower and mid Columbia River and 13% in the upper Columbia and Snake rivers. These last are part of efforts to reestablish populations of Coho Salmon in the upper Columbia River basin, where it is thought that as many as three historical ESUs have been extirpated (Gustafson et al. 2007).

Marine Dispersal Rates

The estimated marine dispersal rates of age-1 Chinook and Coho Salmon ranged from less than 2.5 km/d to almost 40 km/d (Figure 4A). The dispersal rates of age-0 Chinook Salmon generally were low, usually less than 2.5 km/d (Figure 4A). Fish migrating north of Vancouver Island during their first summer or fall in the ocean (>619 km) traveled between about 5 and 40 km/d, and those reaching south-central Alaska and farther north (~1,850 km) traveled between about 15 and 30 km/d. In terms of bl/s, the fastest estimated dispersal rate was slightly more than 3.0 bl/s, and many of the fish migrating the greatest distances traveled between 0.5 and 2.0 bl/s (Figure 4B). Most age-0 fish, however, traveled more slowly than 0.25 bl/s (Figure 4B).

Kruskal–Wallis rank-sum tests ($P < 0.05$) identified six dispersal rate patterns (a–f) among the 12 groups defined by ESU, run, and age, with little overlap between age-0 and age-1 fish (Figure 5). Only the age-1 lower Columbia River spring-run group had a dispersal rate pattern (e) similar to those of some age-0 groups. The three fastest dispersal rate patterns (a–c) were for the mid and upper Columbia River spring run, the Snake River spring–summer run, the upper Willamette River spring run, and the age-1 upper Columbia River summer-run Chinook Salmon groups, along with Coho Salmon (Figure 5).

It is noteworthy that within the two Chinook Salmon groups with both age-1 and age-0 smolts (upper Columbia River summer and Snake River fall runs), the age-1 smolts dispersed more rapidly. Additionally, within the Lower Columbia River ESU,

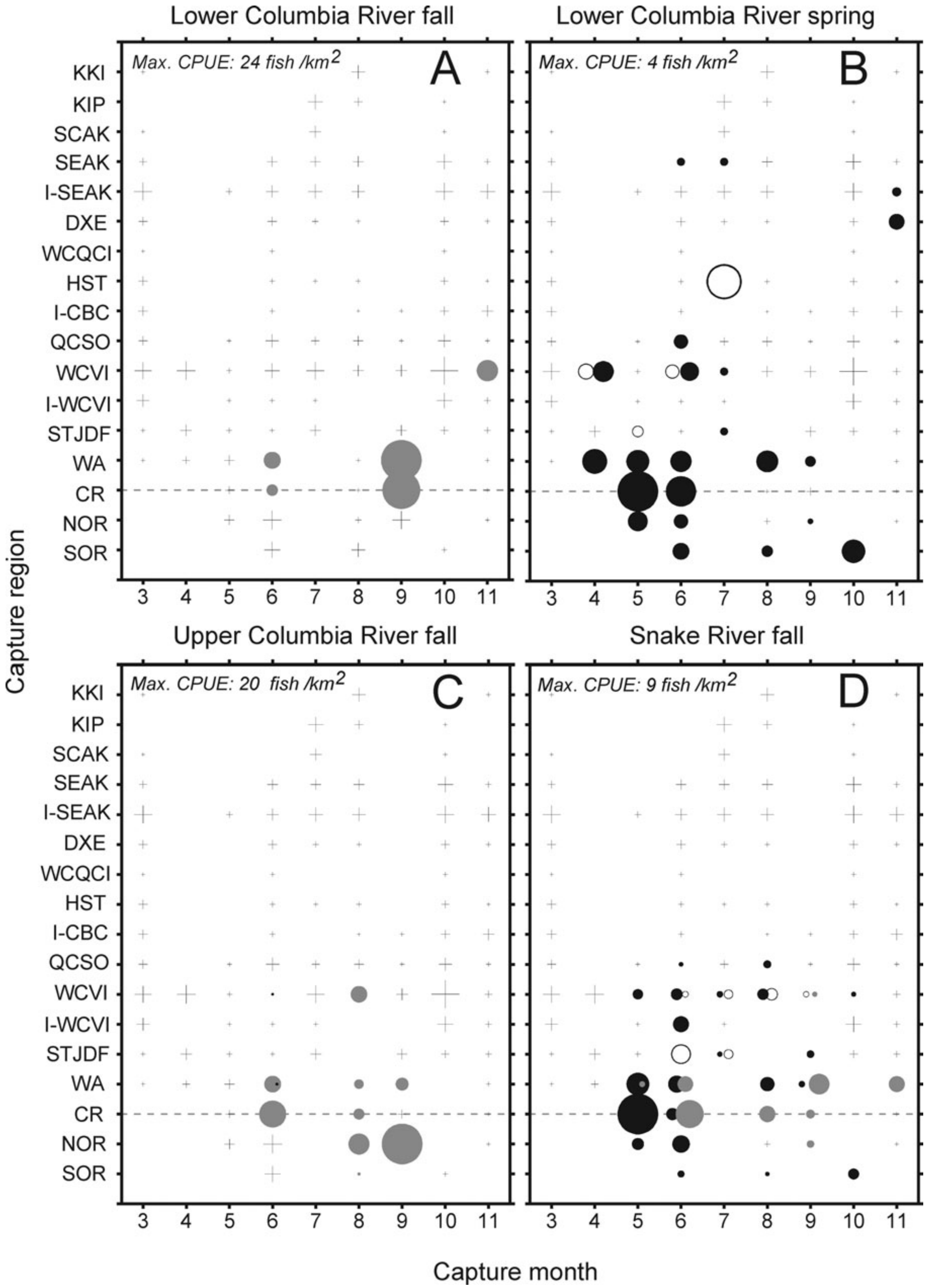

FIGURE 3. Catch per unit effort during the first ocean year of tagged age-0 fish (gray circles) and age-1 fish (black circles for surface catches, open circles for subsurface catches) by ESU and adult run timing, capture region (see Figure 1), and month. The values are actual catches expanded for associated untagged fish (see Methods). The area of each circle is directly proportional to CPUE, with the largest circle in each panel indicating the maximum CPUE for that segment. The size of each cross (shown only when CPUE = 0) indicates the total surface trawl effort in each region and month. No tagged juvenile salmon were recovered in region AKP (Figure 1), so this region is not shown here.

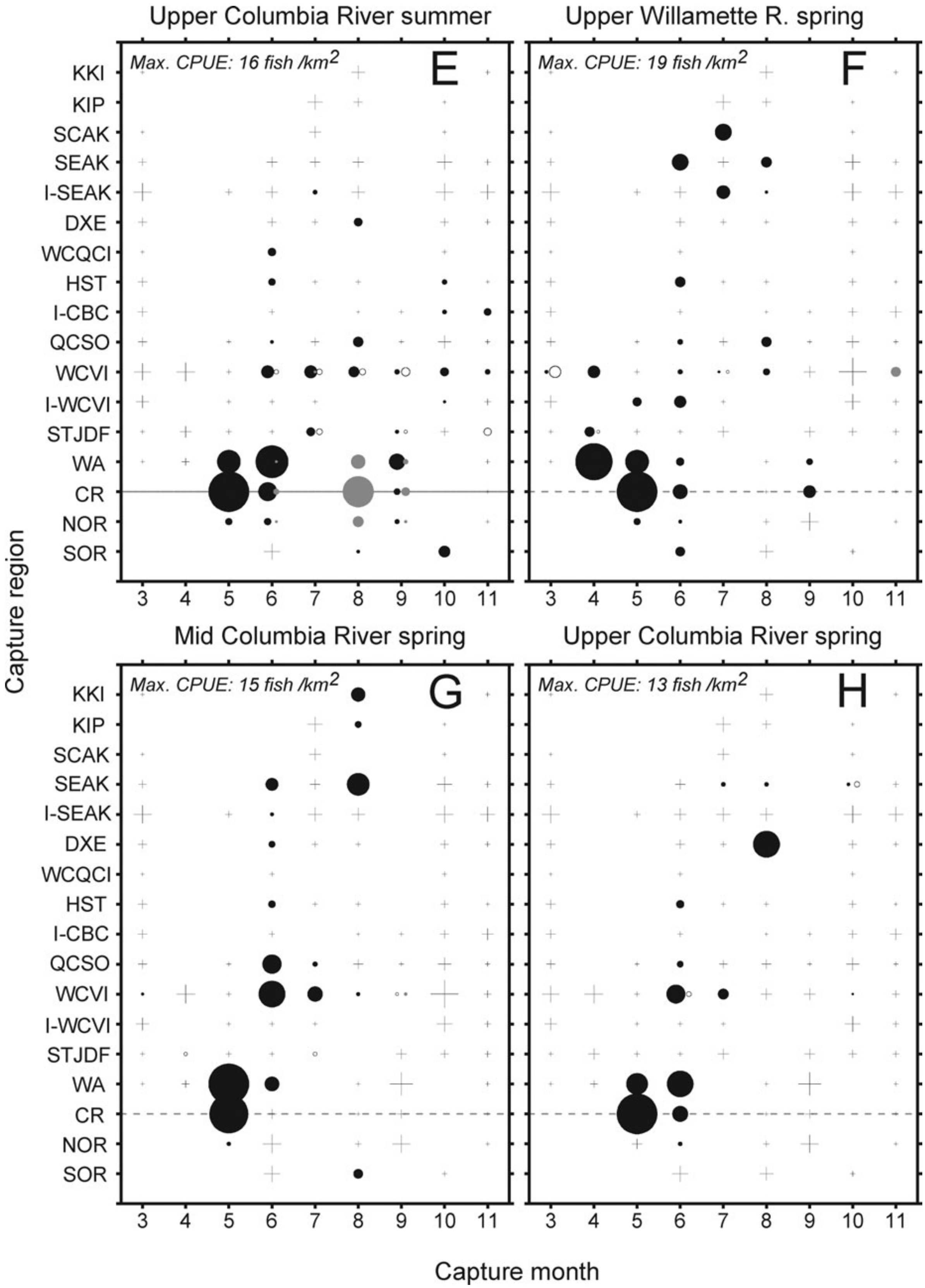

FIGURE 3. Continued.

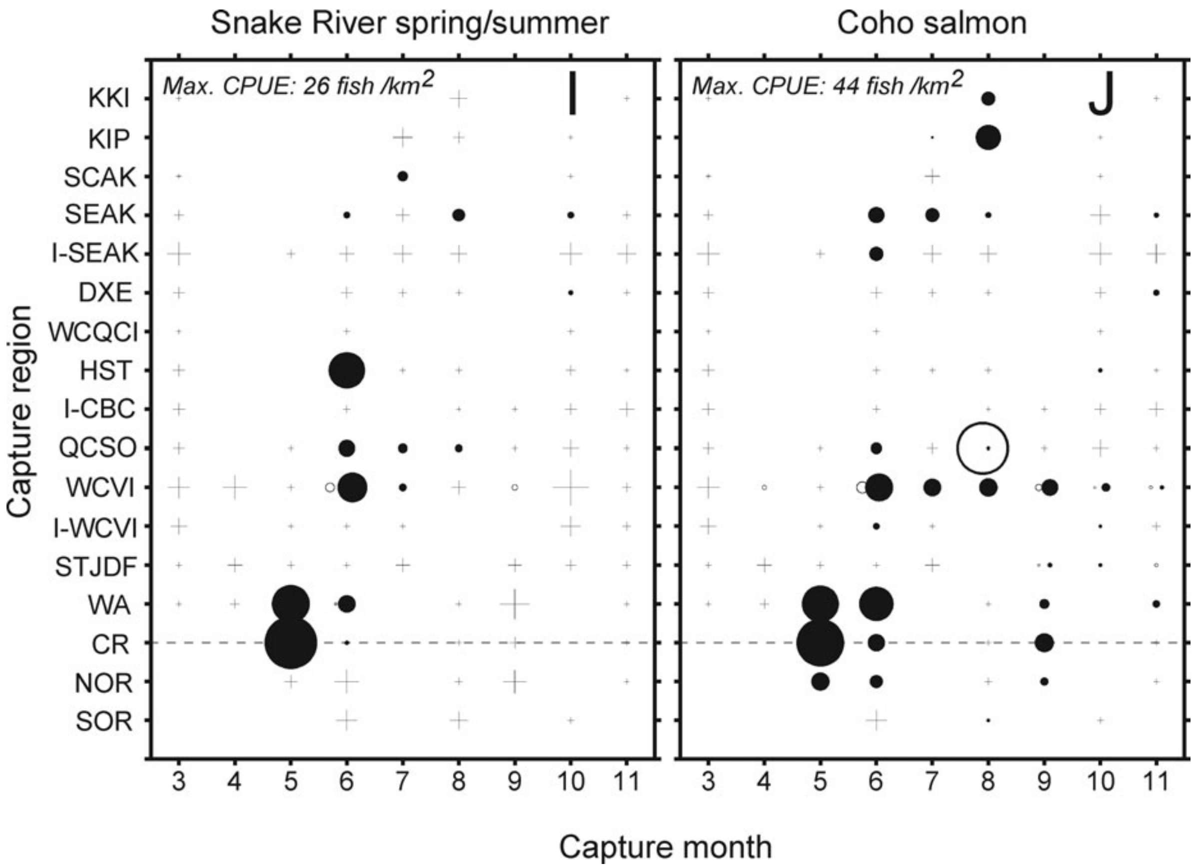

FIGURE 3. Continued.

the age-1 spring-run fish generally dispersed more rapidly than the age-0 fall-run fish (Figure 5).

Dispersal rates were positively skewed, with substantially higher means than medians and 75th, 90th, and 95th percentiles that were displaced far to the right (Figure 5). Much of this skewing in dispersal rate was related to the distance traveled by fish from the Columbia River prior to capture. Large numbers of slowly dispersing fish were caught close to the Columbia River, and smaller numbers of more rapidly migrating fish were caught at more distant locations. For example, for the upper Columbia River spring, Snake River spring–summer, and upper Willamette River spring runs of Chinook Salmon combined (a and b; Figure 5), the dispersal rate was lowest ($n = 287$; median = 3.6 km/d) for fish caught off Oregon and Washington, intermediate ($n = 76$; median = 10.0 km/d) for fish caught off Vancouver Island, and highest ($n = 73$; median = 14.7 km/d) for fish caught north of Vancouver Island.

Within the single Coho Salmon ESU, early fall-run stocks dispersed more rapidly after ocean entry than did the late fall-run stocks (Table 6). Late fall-run fish were released exclusively in the lower or mid Columbia River, whereas early fall-run fish were released throughout the Columbia and Snake River basins. For fish released in the lower Columbia River basin, the average ocean dispersal rate of early fall-run fish was twice that of late fall-run fish (Table 6).

The variation in dispersal patterns among groups (Figures 3, 5) is also reflected in both the mean distance traveled between ocean entry and recovery and pairwise Bray–Curtis similarity coefficients (Table 7), neither of which considers month of recovery. For example, the upper Columbia River fall run (Figure 3C), the only group recovered largely along the Oregon coast, was also the only group with a negative (south of the Columbia River) recovery distance (–40.0 km). The other Chinook Salmon fall-run groups (i.e., age-0 lower Columbia River

TABLE 6. Median and mean ocean dispersal rates of age-1 Columbia River Coho Salmon by adult run timing (early fall run [type S] and late fall run [type N]) and release basin.

			Ocean dispersal rates (km/d)	
Release basin	Run timing	n	Median	Mean
Lower Columbia	Early fall	139	4.2	6.6
Lower Columbia	Late fall	82	2.7	3.3
Mid Columbia	Early fall	14	3.0	4.6
Mid Columbia	Late fall	8	2.0	3.2
Upper Columbia	Early fall	111	4.8	6.5
Snake	Early fall	12	4.6	5.3

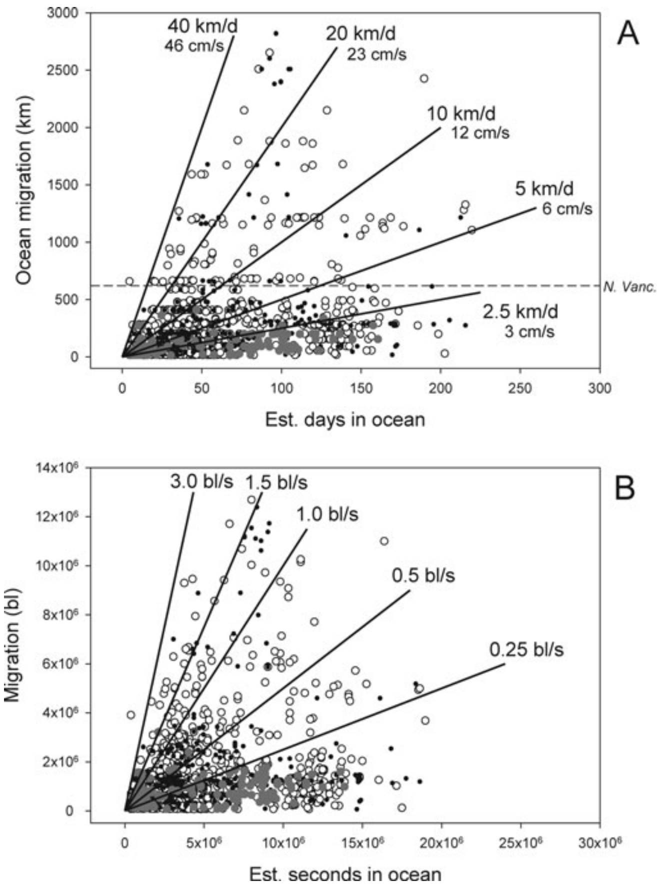

FIGURE 4. Scatterplots of **(A)** minimum ocean migration (km) versus estimated days in the ocean and **(B)** minimum ocean migration in body lengths (bl) versus estimated seconds in the ocean for age-0 Chinook Salmon (gray circles), age-1 Chinook Salmon (open circles), and age-1 Coho Salmon (black dots). Selected lines of equal migration rates are labeled. Only fish estimated to have been in the ocean ≥5 d are shown. Dispersal within 400 km of the Columbia River mouth was either to the north or to the south, whereas that >400 km from the river's mouth was to the north. In panel (A) the northern extent of sampling off Vancouver Island is indicated by the dashed line at 619 km.

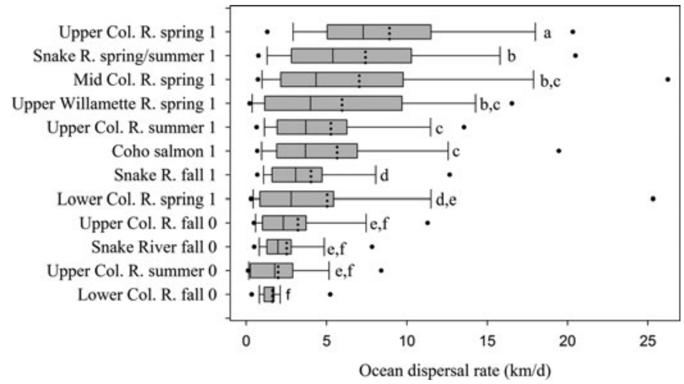

FIGURE 5. Box plots of the dispersal rates of Columbia River basin Chinook and Coho Salmon estimated to have been in the ocean for at least 5 d by ESU, adult run timing, and smolt age. The median, interquartile range, 10th and 90th percentiles and 5th and 95th percentiles are shown by boxes, whiskers, and dots, respectively. The median and mean rates are indicated by the solid and dotted lines, respectively. Six groups of similar dispersal rates are indicated by lowercase letters (Kruskal–Wallis rank-sum tests; $P > 0.05$).

fall and age-0 and -1 Snake River fall) also had relatively low mean distances traveled (47.7–99.7 km), as indicated by their high recovery rates between Vancouver Island and the Oregon coast (Table 5; Figure 3). By contrast, the mean distances traveled by the mid and upper Columbia River spring runs, the Snake River spring–summer run, and the upper Willamette River spring run were large (>200 km) due to relatively high recoveries from Southeast Alaska, the Kenai Peninsula, and even Kodiak Island. The mean distances traveled by Columbia River spring-run fish (the lower, mid, and upper Columbia River spring, upper Willamette River spring, and Snake River spring–summer runs), which had a grand mean of 307 km, were significantly higher than the distances traveled by the fall runs (lower Columbia River fall, Snake River fall [ages 0 and 1], and upper Columbia River fall), which had a grand mean of 46 km (Mann–Whitney $U = 2.4$, $P < 0.05$). However, when ESU, run timing, and smolt age were not considered, there were no differences in the mean ocean distance traveled for fish between basins (i.e., lower Columbia River, mid–upper Columbia River, Snake River, and Willamette River; Kruskal–Wallis $H = 1.2$, $P > 0.10$). The mean distance traveled by lower Columbia River Coho Salmon (393 km) was about equal to that traveled by the Snake River spring–summer Chinook Salmon (395 km) and was exceeded only by mid–Columbia River spring Chinook Salmon (504 km), reflecting relatively high recoveries in Alaskan waters for these groups.

Pairwise Bray–Curtis similarity coefficients (Table 7) revealed similar patterns. For example, three interior basin spring Chinook Salmon groups (the mid–Columbia River spring, upper Columbia River spring, and Snake River spring–summer runs), which all displayed rapid northward movements, also had high pairwise similarity coefficients (mean = 71.5). By contrast, the groups which showed more variation in pattern (the upper Columbia River fall, upper Columbia River summer, and Snake River fall runs) were also less similar to each other (mean = 59.7), as were the fall and spring runs of the lower Columbia River Chinook Salmon ESU (57.2). Upper Columbia River fall Chinook Salmon, the only group with a negative (southward) distance traveled since ocean entry, also had the lowest similarity coefficients (mean = 42.8), reflecting their distinctive dispersal around the mouth of the Columbia River. Coho Salmon had higher similarity to spring or summer Chinook Salmon runs (mean = 73.0) than fall Chinook Salmon runs (mean = 61.2), regardless of basin.

Given these patterns, it was not surprising that ANOSIM analyses restricted to Chinook Salmon indicated well-defined groups based on age at release (global $R = 0.50$, $P < 0.05$) and both age (0.76) and run (0.75) when basin was included, although neither age nor run were statistically significant at $P < 0.10$. When Coho Salmon were included in the ANOSIM, the best-formed groups were produced by age at release (global

TABLE 7. Mean distance (km, underlined along the diagonal) and pairwise Bray–Curtis similarity coefficients estimated among Chinook and Coho Salmon groups based on the proportion of juvenile salmon tagged with coded wire tags that were recovered in each of the 19 recovery areas (averaged across years). Release age (0 or 1) is indicated. Tag recoveries were expanded for both sampling effort and unmarked fish. The similarity coefficients range from 0 (no recoveries in common) to 100 (identical recovery patterns).

Group	Lower Columbia, fall, 0	Lower Columbia, spring, 1	Mid Columbia, spring, 1	Snake, fall, 0	Snake, fall, 1	Snake, spring–summer, 1	Upper Columbia, fall, 0	Upper Columbia, spring, 1	Upper Columbia, summer, 1	Upper Willamette, spring, 1	Coho Salmon, 1
Lower Columbia, fall, 0	99.7										
Lower Columbia, spring, 1	57.2	112.9									
Mid Columbia, spring, 1	59.4	70.3	503.8								
Snake, fall, 0	80.2	71.3	59.8	74.6							
Snake, fall, 1	57.7	90.8	62.6	71.9	47.7						
Snake, spring–summer, 1	54.4	71.1	73.1	59.8	63.2	395.2					
Upper Columbia, fall, 0	38.9	46.8	39.7	42.7	53.3	39.2	−40.0				
Upper Columbia, spring, 1	67.9	77.6	70.9	83.2	72.4	70.7	39.2	201.9			
Upper Columbia, summer, 1	78.1	74.8	68.7	86.9	73.5	67.0	42.1	81.6	132.5		
Upper Willamette, spring, 1	57.5	77.1	70.1	70.7	75.8	77.5	40.3	78.8	78.8	323.4	
Coho Salmon	64.3	73.3	80.6	68.1	66.9	67.1	45.5	74.7	73.8	68.6	393.0

$R = 0.55$, $P < 0.05$) or run (0.81, $P < 0.05$) when basin was accounted for.

Interannual Variation in Dispersal Patterns

We were able to assess interannual variation for seven groups defined by ESU and run. These groups had an average of 5.1 years during which 31.8 raw CWTs were recovered (Table 8). The magnitude of interannual variation in recovery patterns was similar regardless of the metrics used (i.e., CV or pairwise similarity coefficients) and was generally moderate. For example, the variation in mean distance between years was fairly low (CV = 0.31–0.66), as was the mean pairwise similarity among years (mean = 55.4). While most Chinook Salmon groups with low similarity among years had high CVs (both indicating high interannual variation) and vice versa, the Snake River spring–summer run group was unusual in having a low CV (0.31, suggesting low interannual variation) but also relatively low similarity between years (49.5, suggesting high interannual variation). This likely resulted from recoveries that were variable between years yet produced similar mean travel distances. The ANOSIM analyses conducted with or without Coho Salmon indicated that the year variable produced only moderately cohesive groups (global $R < 0.25$, $P < 0.05$), but no other variable(s) (i.e., run, species, basin, or age at release) produced better-defined groups. Despite the relatively high CV among years for Coho Salmon (0.66), they were recovered in Alaska during the summer and fall in 9 out of 12 years and off Oregon in 7 of 9 years, indicating that the latitudinally diverse dispersal pattern of these fish (Figure 3J) was consistent among years. (Expanded catch per square kilometer in each of five catch areas is shown for each ESU/run and age-group by year in Table A.3).

DISCUSSION

Ocean Distribution Patterns and Genetic Relatedness

The ocean dispersal patterns of the Columbia River Chinook Salmon ESUs that we describe in this paper are largely concordant with the four major genetic lineages in the basin. The most genetically divergent lineage (Waples et al. 2004; Narum et al. 2010) is found in the interior basin and comprises the mid–Columbia River spring-run, upper Columbia River

TABLE 8. Mean distances, CV (SD/mean), and pairwise Bray–Curtis similarities across years for selected groups of juvenile Chinook and Coho Salmon. The analysis was restricted to cases in which at least 15 actual recoveries occurred in each of at least three years.

Group	Years	Mean raw tags/year	Mean distance (km)	CV	Mean pairwise similarity
Mid Columbia, spring, 1	4	18.8	392.4	0.65	50.8
Snake, fall, 1	5	25.0	59.0	0.56	72.7
Snake, spring–summer, 1	4	25.3	332.3	0.31	49.5
Upper Columbia, spring, 1	5	25.2	153.0	0.56	61.2
Upper Columbia, summer, 1	8	58.5	156.7	0.54	65.1
Upper Willamette, spring, 1	3	21.3	342.8	0.59	35.4
Coho Salmon, 1	7	48.6	291.0	0.66	53.3

spring-run, and Snake River spring–summer-run ESUs. This interior spring-run lineage is also the most distinctive with respect to ocean dispersal. Juveniles are nearly entirely age 1, migrate rapidly to the north during the first 4 months following ocean entry, and are very rarely caught on the continental shelf in the fall. High mean distances traveled in the ocean and high pairwise similarity among the three ESUs of this lineage are consistent with their uniformly rapid northwards migration. Genetic data also show this temporal and spatial pattern of abundance (Tucker et al. 2011), which is consistent with a hypothesized off-shelf movement into deeper water by many of these fish sometime during their first summer or fall in the ocean or with movement into deeper water on the shelf that is below the depth of the sampling gear (e.g., Orsi and Wertheimer 1995). Additionally, very few subadult or adult fish from this lineage are caught in the coastal fisheries (Myers et al. 1998; Waples et al. 2004; Weitkamp 2010), suggesting a mainly offshore ocean existence after the first few months at sea.

Two more closely related Chinook Salmon genetic lineages are the interior summer–fall lineage (comprising the upper Columbia River summer–fall and the Snake River fall ESUs) and the lower Columbia River lineage (comprising the fall and spring runs of the lower Columbia River ESU) (Waples et al. 2004; Narum et al. 2010). Age-0 juveniles from these two lineages disperse slowly and remain mainly south of Vancouver Island through autumn. These two genetic lineages also share largely coastal distributions both as juveniles and maturing fish. However, the latitudinal ocean ranges between individual ESUs vary greatly, which is reflected in their relatively low pairwise similarity coefficients. The Snake River fall-run ESU and the lower Columbia River fall-run group have the most southern distributions both as juvenile fish and as maturing and adult fish in the coastal ocean fisheries (Weitkamp 2010). For example, 94% of the catch of maturing and adult Snake River fall Chinook Salmon occurred from Vancouver Island south (Weitkamp 2010). Conversely, although age-0 juveniles from the upper Columbia River summer–fall ESU are also found mainly south of Vancouver Island during their first few months in the ocean, age-1 juveniles were found as far north as Southeast Alaska and as adults or subadults in the coastal fisheries they are widespread along the coast, with half of the catch occurring north of Vancouver Island (Weitkamp 2010).

The distribution patterns outlined above are concordant with previous studies describing rapid northward ocean dispersal of interior Columbia River basin spring-run age-1 juveniles and slow and mainly southern distribution of the basin's fall-run age-0 fish (Miller et al. 1983; Hartt and Dell 1986; Fisher and Pearcy 1995; Orsi et al. 2000; Trudel et al. 2009; Tucker et al. 2011). These two patterns closely fit the generalized marine migration patterns that Healey (1983, 1991) described as the "stream-type" and "ocean-type" races of Chinook Salmon. However, our data demonstrate that at least two groups do not neatly fit either of the two life history classifications. For example, many age-1 spring-run juveniles from the genetically distinct upper Willamette River ESU (the fourth genetic lineage; Waples et al. 2004; Narum et al. 2010) migrate rapidly to the north following ocean entry and are seldom found on the shelf during the fall of their first ocean year, suggesting a stream-type pattern. Some age-1 spring-run fish from the lower Columbia River ESU also migrate rapidly northward following ocean entry, but others (e.g., those from the Cowlitz River; Trudel et al. 2009) move south along the coast of Oregon and are found on the shelf in the fall. However, both of these groups of age-1 spring Chinook Salmon subsequently appear to be ocean-type as maturing and adult fish, contributing significantly to coastal ocean fisheries at multiple ages (Waples et al. 2004; Weitkamp 2010); the Willamette River spring run is mainly caught in northern British Columbian and Alaskan waters, while the lower Columbia River spring run is mainly intercepted from Vancouver Island south (Weitkamp 2010). Our findings of diverse and complex distributions for several ESUs from the Columbia River are consistent with those of Trudel et al. (2009), who concluded that the migrations of Chinook Salmon juveniles originating in the region from Oregon to Southeast Alaska did not conform to those hypothesized for the stream-type and ocean-type classifications.

Diversity of Coho Salmon Dispersal

There is only a single extant Columbia River Coho Salmon ESU (Weitkamp et al. 1995; Gustafson et al. 2007), and therefore the Coho Salmon in the basin are not as genetically diverse as Chinook Salmon. Despite this, these Coho Salmon show great diversity in their early ocean migrations, with both faster- and slower-migrating fish. We were able to detect differences in the early ocean dispersal of early and late fall-run fish, with the early fall run generally dispersing more rapidly than the late fall run. However, although some juvenile Coho Salmon undertake extensive northerly migrations before returning as maturing fish to the coastal fisheries off Vancouver Island, Washington, and Oregon (Weitkamp and Neely 2002), other juvenile Coho Salmon from both runs remain in the region from Vancouver Island south to Oregon into September and October of their first ocean year. This mixture of slow- and fast-dispersing fish, which exposes the juvenile fish to ocean conditions over a wide latitudinal range, was hypothesized by Morris et al. (2007) to be a strategy that evolved to increase the probability that some fish survive to reproduce even when the conditions for survival are bad in certain areas of the coastal ocean.

Depth Distribution

Some caution is appropriate when interpreting the dispersal patterns of juvenile salmon from the near-surface samples (mainly the upper 20 m) reported here. Using modified trolling gear in Southeast Alaska, Orsi and Wertheimer (1995) found that the size of Chinook Salmon increased with depth and that by September about 45% of Chinook Salmon and about 30% of Coho Salmon were found at depths greater than 22 m. Therefore, ontogenetic shifts in depth distribution may complicate the interpretation of the dispersal patterns from surface tows.

Additionally, small age-0 Chinook Salmon are most abundant at shallow inshore stations (Miller et al. 1983; Fisher et al. 2007; Orsi et al. 2007), often in water depths of less than 9 m (where other salmon species are rare) and well outside our sampling over water depths of greater than 30 m (Miller et al. 1983; Marin Jarrin et al. 2009; L. Weitkamp, unpublished data). The inshore distribution of age-0 Chinook Salmon, along with a low tagging rate, probably accounts for our relatively low catches of tagged fish in this age-class. As they grow, age-0 Chinook Salmon move offshore (Miller et al. 1983). Additional sampling of the nearshore and surf region for age-0 Chinook Salmon would likely be informative (Marin Jarrin et al. 2009), but it is technically difficult.

Ocean Dispersal Rate

The range in estimated ocean dispersal rates that we found for Columbia River Chinook and Coho Salmon was similar to the range directly observed from detections of acoustically tagged fish (Chittenden et al. 2009; Rechisky et al. 2009; Melnychuk et al. 2010). Rechisky et al. (2009) observed an average rate of ~17 km/d for six acoustically tagged age-1 interior Columbia River basin spring Chinook Salmon traveling between Willapa Bay and northern Vancouver Island, and we estimated a similar average rate of 15 km/d for age-1 fish between the mouth of the Columbia River and their point of capture north of Vancouver Island. However, our estimates of the average rates for age-1 salmon caught nearer to the mouth of the Columbia River off Oregon and Washington were considerably lower (mean = 4.5 km/d). The slower dispersal rates for fish caught near the mouth of the Columbia River may reflect a period of foraging, saltwater acclimation, or searching for directional cues before directed, active migration commences, as has been hypothesized and demonstrated for some juvenile salmon stocks in the Strait of Georgia (Chittenden et al. 2009; Melnychuk et al. 2010). For salmon exiting the Columbia River, a delay in directed migration may be particularly long for age-0 fish.

Interannual Variability

Our analysis of interannual variability was limited by the number of groups and years for which we had minimally adequate data and likely includes variation due to spatial differences in sampling effort among years. Despite this, we were able to show that interannual variation was modest based on the variation in mean travel distances and pairwise similarity coefficients estimated among years. These findings are consistent with those of other recent studies based on much larger sample sizes showing that the marine distribution patterns of both juvenile and adult Chinook Salmon are stable between years despite considerable variation in marine environments (Weitkamp 2010; Tucker et al. 2012).

Potential Ocean Impacts on Survival

In this study, we have demonstrated that there is great diversity of early ocean dispersal among the different Columbia River Chinook and Coho Salmon ESUs. Although large-scale changes in ocean climate (e.g., the Pacific Decadal Oscillation; Mantua et al. 1997) could affect survival during the early ocean phase of all ESUs similarly, the survival of certain ESUs (especially the age-0 fish) may be particularly sensitive to changes in local ocean conditions near the mouth of the Columbia River. Because of their slow dispersal and restricted ocean distribution along the Washington and Oregon coasts, we expect that age-0 fish from the lower Columbia River, upper Columbia River summer–fall, and Snake River fall Chinook Salmon ESUs would be particularly sensitive to changes in ocean conditions near the mouth of the Columbia River that might affect survival (e.g., the strength of upwelling and the size and position of the river's plume). For example, Miller et al. (2013) found that the survival of upper Columbia River summer–fall Chinook Salmon was related to the volume of the plume during the emigration of age-0 fish. In addition, because of the great variability in early ocean dispersal of age-1 lower Columbia River spring, upper Columbia River summer, and upper Willamette River spring Chinook Salmon and lower Columbia River Coho Salmon**,** we would expect the average survival of these groups to be impacted by local ocean conditions off Oregon and Washington as well as ocean conditions over a wide latitudinal range. Ocean conditions along the coasts of British Columbia and Alaska may be particularly important for the early marine survival of age-1 fish from the mid–Columbia River spring, upper Columbia River spring, and Snake River spring–summer ESUs, which migrate rapidly northward out of local waters following ocean entry. Nonetheless, local environmental conditions experienced soon after out-migration may also affect the distributions of these fish (Burke et al. 2013) as well as their subsequent adult abundance (Tomaro et al. 2012). It is important that studies investigating potential anthropogenic impacts in freshwater on survival of the different Columbia River ESUs (e.g., Schaller et al. 1999) also take into account the possibility of different ocean survival rates among the different ESUs due to differences in their early ocean dispersal. Otherwise, separating freshwater impacts from ocean impacts on survival would be impossible (see also the discussion in Trudel et al. 2009).

Future Work

Our knowledge of the early ocean dispersal of juvenile salmonids is still relatively incomplete. We do not know, for instance, where they are during the winter months between their first and second ocean years. Additional sampling during the winter at appropriate depths (e.g., Trudel et al. 2004; Tucker et al. 2011; Trudel and Tucker 2013) along a broader region of the coast could reveal more about the distribution of stocks between their first and second years in the ocean. Further study of the early ocean dispersal of juvenile salmon using a diversity of tagging technologies (e.g., CWT, passive integrated transponder, archival, and acoustic tags) as well as genetic identification of untagged fish (e.g., Van Doornik et al. 2007; Tucker et al. 2011) will greatly improve our understanding of the locations and timing of ocean events affecting the survival of the different ESUs of Columbia River salmon.

ACKNOWLEDGMENTS

We thank the crews of the fishing vessels *Frosti*, *Sea Eagle*, *Viking Storm*, and *Ocean Selector*, the Canadian Coast Guard ship *W. E. Ricker*, and NOAA ships *David Starr Jordon*, *John N. Cobb*, and *Miller Freeman* as well as the numerous technicians who assisted with field work and laboratory analysis. Jim Myers, Sean Hayes, and several anonymous reviewers provided very helpful suggestions for improving the manuscript. Funding was provided by NOAA Fisheries, Fisheries and Oceans Canada, the Bonneville Power Administration, and the U.S. GLOBEC Northeast Pacific program.

REFERENCES

Beamish, R. J., D. McCaughran, J. R. King, R. M. Sweeting, and G. A. McFarlane. 2000. Estimating the abundance of juvenile Coho Salmon in the Strait of Georgia by means of surface trawls. North American Journal of Fisheries Management 20:369–375.

Bradford, M. J. 1995. Comparative review of Pacific salmon survival rates. Canadian Journal of Fisheries and Aquatic Sciences 52:1327–1338.

Brodeur, R. D., J. P. Fisher, D. J. Teel, R. L. Emmett, E. Casillas, and T. W. Miller. 2004. Juvenile salmonid distribution, growth, condition, origin, and environmental and species associations in the northern California Current. U.S. National Marine Fisheries Service Fishery Bulletin 102:25–46.

Burke, B. J., M. C. Liermann, D. J. Teel, and J. J. Anderson. 2013. Environmental and geospatial factors drive juvenile Chinook Salmon distribution during early ocean migration. Canadian Journal of Fisheries and Aquatic Sciences 70:1167–1177.

Chittenden, C. M., R. J. Beamish, C. M. Neville, R. M. Sweeting, and R. S. McKinley. 2009. The use of acoustic tags to determine the timing and location of the juvenile Coho Salmon migration out of the Strait of Georgia, Canada. Transactions of the American Fisheries Society 138:1220–1225.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117–143.

Dawley, E. M., R. D. Ledgerwood, and A. L. Jensen. 1985. Beach and purse seine sampling of juvenile salmonids in the Columbia River estuary and ocean plume, 1977–1983, volume II: data on marked fish recoveries. NOAA Technical Memorandum NMFS F/NWC-75.

Emmett, R. L., R. D. Brodeur, and P. M. Orton. 2004. The vertical distribution of juvenile salmon (*Oncorhynchus* spp.) and associated fishes in the Columbia River plume. Fisheries Oceanography 13:392–402.

Farley, E. V., Jr., B. L. Wing, E. D. Cokelet, C. M. Kondzela, E. C. Martinson, N. Weemes, J. H. Moss, M. Auburn-Cook, and C. Fitch. 2001. Gulf of Alaska coastal research (July and August 2001) on juvenile salmon. Alaska Fisheries Science Center, North Pacific Anadromous Fish Commission Document 559, Juneau. Available: www.pmel.noaa.gov/foci/operations/2001/Instructions/Great_Pacific/npafc559goacr2001.pdf. (February 2013).

Fisher, J. P., and W. G. Pearcy. 1988. Growth of juvenile Coho Salmon (*Oncorhynchus kisutch*) off Oregon and Washington, USA, in years of differing coastal upwelling. Canadian Journal of Fisheries and Aquatic Sciences 45:1036–1044.

Fisher, J. P., and W. G. Pearcy. 1995. Distribution, migration, and growth of juvenile Chinook Salmon, *Oncorhynchus tshawytscha,* off Oregon and Washington. U.S. National Marine Fisheries Service Fishery Bulletin 93:274–289.

Fisher, J. P., M. Trudel, A. Ammann, J. A. Orsi, J. Piccolo, C. Bucher, E. Casillas, J. A. Harding, R. B. MacFarlane, R. D. Brodeur, J. F. T. Morris, and D. W. Welch. 2007. Comparisons of the coastal distributions and abundances of juvenile Pacific salmon from central California to the northern Gulf of Alaska. Pages 31–80 *in* C. B. Grimes, R. D. Brodeur, L. J. Haldorson, and S. M. McKinnell, editors. The ecology of juvenile salmon in the northeast Pacific Ocean: regional comparisons. American Fisheries Society, Symposium 57, Bethesda, Maryland.

Ford, M. J., editor. 2011. Status review update for Pacific salmon and steelhead listed under the Endangered Species Act: Pacific Northwest. NOAA Technical Memorandum NMFS-NWFSC-113.

Good, T. P., R. S. Waples, and P. Adams, editors. 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. NOAA Technical Memorandum NMFS-NWFSC-66.

Gustafson, R. G., R. S. Waples, J. M. Myers, L. A. Weitkamp, G. J. Bryant, O. W. Johnson, and J. J. Hard. 2007. Pacific salmon extinctions: quantifying lost and remaining diversity. Conservation Biology 21:1009–1020.

Hartt, A. C., and M. B. Dell. 1986. Early oceanic migrations and growth of juvenile Pacific salmon and steelhead trout. International North Pacific Fisheries Commission Bulletin 46.

Healey, M. C. 1983. Coastwide distribution and ocean migration patterns of stream- and ocean-type Chinook Salmon, *Oncorhynchus tshawytscha*. Canadian Field-Naturalist 97:427–433.

Healey, M. C. 1991. Life history of Chinook Salmon (*Oncorhynchus tshawytscha*). Pages 311–393 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

HSRG (Hatchery Scientific Review Group). 2009. Columbia River hatchery reform project, final system-wide report, appendix E. HSRG, Pacific Northwest Hatchery Reform Project. Available: www.hatcheryreform.us/hrp/reports/system/welcome_show.action. (February 2013).

Jefferts, K. B., P. K. Bergman, and H. F. Fiscus. 1963. A coded wire identification system for macro-organisms. Nature 198:460–462.

Kope, R., and T. Wainwright. 1998. Trends in the status of Pacific salmon populations in Washington, Oregon, California, and Idaho. North Pacific Anadromous Fish Commission Bulletin 1:1–12.

Legendre, P., and L. Legendre. 1998. Numerical ecology, 2nd English edition. Elsevier Science, Amsterdam.

Logerwell, E. A., N. Mantua, P. W. Lawson, R. C. Francis, and V. N. Agostini. 2003. Tracking environmental processes in the coastal zone for understanding and predicting Oregon Coho (*Oncorhynchus kisutch*) marine survival. Fisheries Oceanography 12:554–568.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78:1069–1079.

Marin Jarrin, J. R., A. L. Shanks, and M. A. Banks. 2009. Confirmation of the presence and use of sandy beach surf-zones by juvenile Chinook Salmon. Environmental Biology of Fishes 85:119–125.

Melnychuk, M. C., D. W. Welch, and C. J. Walters. 2010. Spatio-temporal migration patterns of Pacific salmon smolts in rivers and coastal marine waters. PLoS (Public Library of Science) ONE [online serial] 5(9):e12916.

Miller, D. R., J. G. Williams, and C. W. Sims. 1983. Distribution, abundance and growth of juvenile salmonids off the coast of Oregon and Washington, summer (1980). Fisheries Research 2:1–17.

Miller, J. A., D. J. Teel, A. Baptista, and C. A. Morgan. 2013. Disentangling bottom-up and top-down effects on survival during early ocean residence in a population of Chinook Salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 70:617–629.

Morris, J. F. T., M. Trudel, M. E. Thiess, R. M. Sweeting, J. Fisher, S. A. Hinton, E. A. Fergusson, J. A. Orsi, E. V. Farley Jr., and D. W. Welch. 2007. Stock-specific migrations of juvenile Coho Salmon derived from coded-wire tag recoveries on the continental shelf of western North America. Pages 81–104 *in* C. B. Grimes, R. D. Brodeur, L. J. Haldorson, and S. M. McKinnell, editors. The ecology of juvenile salmon in the northeast Pacific Ocean: regional comparisons. American Fisheries Society, Symposium 57, Bethesda, Maryland.

Morris, J. F. T., M. Trudel, D. W. Welch, M. E. Thiess, T. B. Zubkowski, and H. R. C. MacLean. 2004. Canadian highseas salmon surveys in the fall of 2003 and the winter of 2004: seasonal changes in the distributions of juvenile salmon on the continental shelf off British Columbia and Southeast Alaska. Fisheries and Oceans Canada, North Pacific Anadromous Fish Commission Document 780, Nanaimo. Available: www.npafc.org/new/publications/Documents/PDF%202004/780%28Canada%29.pdf. (February 2013).

Mueter, F. J., B. J. Pyper, and R. M. Peterman. 2005. Relationships between coastal ocean conditions and survival rates of northeast Pacific salmon at multiple lags. Transactions of the American Fisheries Society 134:105–119.

Myers, J. M., R. G. Kope, G. J. Bryant, D. Teel, L. J. Lierheimer, T. C. Wainwright, W. S. Grant, F. W. Waknitz, K. Neely, S. T. Lindley, and R. S. Waples. 1998. Status review of Chinook Salmon from Washington, Idaho, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-35.

Nandor, G. F., J. R. Longwill, and D. L. Webb. 2010. Overview of the coded wire tag program in the greater Pacific region of North America. Pages 5–46 *in* K. S. Wolf and J. S. O'Neal, editors. Tagging, telemetry, and marking measures for monitoring fish populations. Pacific Northwest Aquatic Monitoring Partnership, Special Publication 2010-002. Available: www.pnamp.org/document/2888. (November 2013).

Narum, S. R., J. E. Hess, and A. P. Matala. 2010. Examining genetic lineages of Chinook Salmon in the Columbia River basin. Transactions of the American Fisheries Society 139:1465–1477.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4–21.

Orsi, J. A., J. A. Harding, S. S. Pool, R. D. Brodeur, L. J. Haldorson, J. M. Murphy, J. H. Moss, E. V. Farley Jr., R. M. Sweeting, J. F. T. Morris, M. Trudel, R. J. Beamish, R. L. Emmett, and E. A. Fergusson. 2007. Epipelagic fish assemblages associated with juvenile Pacific salmon in neritic waters of the California Current and the Alaska Current. Pages 105–155 *in* G. Churchill, R. Brodeur, L. Haldorson, and S. McKinnell, editors. The ecology of juvenile salmon in the northeast Pacific Ocean: regional comparisons. American Fisheries Society, Symposium 57, Bethesda, Maryland.

Orsi, J. A., and H. W. Jaenicke. 1996. Marine distribution and origin of prerecruit Chinook Salmon, *Oncorhynchus tshawytscha,* in southeastern Alaska. U.S. National Marine Fisheries Service Fishery Bulletin 94:482–497.

Orsi, J. A., M. V. Sturdevant, J. M. Murphy, D. G. Mortensen, and B. L. Wing. 2000. Seasonal habitat use and early marine ecology of juvenile Pacific salmon in southeastern Alaska. North Pacific Anadromous Fish Commission Bulletin 2:111–122.

Orsi, J. A., and A. C. Wertheimer. 1995. Marine vertical distribution of juvenile Chinook and Coho salmon in southeastern Alaska. Transactions of the American Fisheries Society 124:159–169.

Pearcy, W. G. 1992. Ocean ecology of North Pacific salmonids. University of Washington Press, Seattle.

Pearcy, W. G., and J. P. Fisher. 1988. Migrations of Coho Salmon, *Oncorhynchus kisutch,* during their first summer in the ocean. U.S. National Marine Fisheries Service Fishery Bulletin 86:173–195.

Pearcy, W. G., and J. P. Fisher. 1990. Distribution and abundance of juvenile salmonids off Oregon and Washington, 1981–1985. NOAA Technical Report NMFS 93.

PSMFC (Pacific States Marine Fisheries Commission). 2009. 2009 PIT tag specification document. PSMFC, Portland, Oregon. Available: www.ptagis.org./ (March 2011).

Rechisky, E. L., D. W. Welch, A. D. Porter, M. C. Jacobs, and A. Ladouceur. 2009. Experimental measurement of hydrosystem-induced delayed mortality in juvenile Snake River spring Chinook Salmon (*Oncorhynchus tshawytscha*) using a large-scale acoustic array. Canadian Journal of Fisheries and Aquatic Sciences 66:1019–1024.

Schaller, H. A., C. E. Petrosky, and O. P. Langness. 1999. Contrasting patterns of productivity and survival rates for stream-type Chinook Salmon (*Oncorhynchus tshawytscha*) populations of the Snake and Columbia rivers. Canadian Journal of Fisheries and Aquatic Sciences 56:1031–1045.

Sweeting, R. M., R. J. Beamish, D. J. Noakes, and C. M. Neville. 2003. Replacement of wild Coho Salmon by hatchery-reared Coho Salmon in the Strait of Georgia over the past three decades. North American Journal of Fisheries Management 23:492–502.

Teel, D. J. 2004. Genetic mixed stock analysis of juvenile Chinook Salmon in coastal areas of western North America. North Pacific Anadromous Fish Commission Technical Report 5:47–48. Available: www.npafc.org/new/pub_technical5.html. (February 2013).

Tomaro, L. M., D. J. Teel, W. T. Peterson, and J. A. Miller. 2012. When is bigger better? early marine residence of middle and upper Columbia River spring Chinook Salmon. Marine Ecology Progress Series 452:237–252.

Trudel, M., J. Fisher, J. A. Orsi, J. F. T. Morris, M. E. Thiess, R. M. Sweeting, S. Hinton, E. A. Fergusson, and D. W. Welch. 2009. Distribution and migration of juvenile Chinook Salmon derived from coded wire tag recoveries along the continental shelf of western North America. Transactions of the American Fisheries Society 138:1369–1391.

Trudel, M., and S. Tucker. 2013. Depth distribution of 1SW Chinook Salmon in Quatsino Sound, British Columbia, during winter. North Pacific Anadromous Fish Commission, Document 1453, Vancouver. Available: www.npafc.org. (March 2013).

Trudel, M., D. W. Welch, J. F. T. Morris, J. R. Candy, and T. D. Beacham. 2004. Using genetic markers to understand the coastal migration of juvenile Coho (*Oncorhynchus kisutch*) and Chinook Salmon (*O. tshawytscha*). North Pacific Anadromous Fish Commission Technical Report 5:52–54.

Tucker, S., M. Trudel, D. W. Welch, J. R. Candy, J. F. T. Morris, M. E. Thiess, C. Wallace, and T. D. Beacham. 2011. Life history and seasonal stock-specific ocean migration of juvenile Chinook Salmon. Transactions of the American Fisheries Society 140:1101–1119.

Tucker, S., M. Trudel, D. W. Welch, J. R. Candy, J. F. T. Morris, M. E. Thiess, C. Wallace, and T. D. Beacham. 2012. Annual coastal migration of juvenile Chinook Salmon: static stock-specific patterns in a highly dynamic ocean. Marine Ecology Progress Series 449:245–262.

Van Doornik, D. M., D. J. Teel, D. R. Kuligowski, C. A. Morgan, and E. Casillas. 2007. Genetic analyses provide insight into the early ocean stock distribution and survival of juvenile Coho Salmon off the coasts of Washington and Oregon. North American Journal of Fisheries Management 27:220–237.

Waples, R. S., D. J. Teel, J. M. Myers, and A. R. Marshall. 2004. Life-history divergence in Chinook Salmon: historic contingency and parallel evolution. Evolution 58:386–403.

Weitkamp, L. A. 2010. Marine distributions of Chinook Salmon from the West Coast of North America determined by coded wire tag recoveries. Transactions of the American Fisheries Society 139:147–170.

Weitkamp, L. A., P. J. Bentley, and M. N. C. Litz. 2012. Seasonal and interannual variation in juvenile salmonids and associated fish assemblage in open waters of the lower Columbia River estuary. U.S. National Marine Fisheries Service Fishery Bulletin 110:426–450.

Weitkamp, L. A., and K. Neely. 2002. Coho Salmon (*Oncorhynchus kisutch*) ocean migration patterns: insight from marine coded-wire tag recoveries. Canadian Journal of Fisheries and Aquatic Sciences 59:1100–1115.

Weitkamp, L. A., T. C. Wainwright, G. J. Bryant, G. B. Milner, D. J. Teel, R. G. Kope, and R. S. Waples. 1995. Status review of Coho Salmon from Washington, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-24.

Zar, J. H. 1984. Biostatistical analysis, 2nd edition. Prentice-Hall, Englewood Cliffs, New Jersey.

Appendix: Detailed Data

TABLE A.1. Origins of the fish in the nine groups of Columbia and Snake River Chinook Salmon by ESU and adult run timing and the Columbia River Coho Salmon group analyzed in this study.

Group	Contributing hatcheries, stocks, or release basins[a]
Lower Columbia, fall	Big Cr., Elochaman R., Cowlitz R., Lewis R., Wind R. (Spring Cr.)
Lower Columbia, spring	Cowlitz R., Lewis R., Kalama R., Sandy R.
Upper Columbia, fall	Bonneville Pool, mid–Columbia River, Little White Salmon NFH, Umatilla R., Priest Rapids, upper Columbia River, Washington brights
Upper Columbia, summer	Wenatchee R., Wells Hatchery, Methow R.–Okanogan R., Turtle Rock Hatchery
Snake, fall	Lyons Ferry Hatchery, Snake R., mixed Snake R., lower Snake R.
Upper Willamette, spring	Clackamas R., North Fork Santiam R., South Fork Santiam R., McKenzie Hatchery, Mid Fork Willamette R.
Mid Columbia, spring	Carson NFH, Wind R., Little White Salmon NFH, Hood R., Klickitat R., Deschutes R., Warm Springs R., Round Butte Hatchery, Umatilla R., Yakima R.
Upper Columbia, spring	Leavenworth Hatchery, Chiwawa R., Entiat R., Methow R., Twisp R., Chewuch R.
Snake, spring–summer	Palouse R.–Tucannon R., Clearwater R., Grande Ronde R.–Imnaha R., Salmon R.
Coho Salmon	Youngs Bay–Claskanie R., Grays R.–Elochaman R., Cowlitz R., Tilton R., Kalama R., Lewis R., Willamette R., Clackamas R., Washougal R., Sandy R., Wind R.–White Salmon R., Hood R., Oregon general, Wenatchee R., Methow R.–Okanogan R., Clearwater R.

[a]Abbreviations are as follows: R. = River, Cr. = Creek, and NFH = National Fish Hatchery.

TABLE A.2. Waypoints used along with capture locations to estimate minimum ocean migration distances of Columbia River basin Chinook and Coho Salmon. See Figure 1 for area locations.

Latitude (°N)	Longitude (°W)	Area	Distance (km) from Columbia River
46.244	124.058	Mouth	0
44.662	124.339	NOR	178
48.304	125.034	WCVI	241
48.457	124.742	STJDF	268
50.051	127.911	WCVI	527
50.396	128.179	WCVI	570
50.764	128.789	QCSO	629
54.383	131.178	HST	1,063
54.566	133.007	DXE	1,183
55.555	134.274	SEAK	1,320
56.935	134.616	SEAK	1,475
58.131	134.969	SEAK	1,609
58.338	137.407	SEAK	1,683
59.933	142.783	SCAK	2,037
59.534	147.318	KIP	2,296
58.821	151.048	KIP	2,523
58.706	153.328	KKI	2,655

TABLE A.3. Recoveries of tagged fish by group, year, and recovery region. Values are tag recoveries expanded for associated untagged fish per square kilometer. For simplicity, the northern tag recovery areas (Figure 1) were grouped into the following recovery regions: north of Vancouver Island (NVI, including Queen Charlotte Sound) and Vancouver Island–Strait of Juan de Fuca (VI–SJF).

	Recovery region					Recovery region				
Year	NVI	VI–SJF	Washington coast	Columbia River	Oregon coast	NVI	VI–SJF	Washington coast	Columbia River	Oregon coast
	Lower Columbia River fall Chinook Salmon					**Lower Columbia River spring Chinook Salmon**				
1996	0	0	0			0	1.4	0		
1997	0	0	0			0	0.3	0		
1998	0	1	0	8.2	0	0.1	0	0.6	3.3	0
1999	0	0	3.6	0	0	0	0.1	0.3	3.2	0.5
2000	0	0.1	0	0	0	0	0.2	0.6	0.6	0.1
2001	0	0	56.8	0	0	0	0	0.5	1.4	0
2002	0	0	22.6	0	0	0	0	4.6	8.9	1.2
2003	0	0	12.8	0	0	0	0	0.5	0.4	0
2004	0	0	0	0	0	0.1	0	0.7	1	0
2005	0	0	0	47.6	0	0	0.1	0.4	0	0
2006	0	0	11.2	0	0	0.1	0.5	0.1	0	0
	Upper Columbia River fall Chinook Salmon					**Snake River fall Chinook Salmon (age 0)**				
1996	0	0	0			0	0	0		
1997	0	0	0			0	0	0		
1998	0	0	0	19.4	2.8	0	0	0	0	0
1999	0	1.1	0.3	0	2	0	0	0.7	0	0.1
2000	0	0	0.3	0	0.8	0	0	0	1.2	0.2
2001	0	0	1.1	0.7	0	0	0	0.2	0	0
2002	0	0	1.9	0.6	5.6	0	0	3.6	0	0.1
2003	0	0	7.3	0	0	0	0	0.7	2.9	0
2004	0	0	1.1	1.5	0	0	0	1.2	0.5	0
2005	0	0	0.6	0.5	40.5	0	0	0.8	0.4	0
2006	0	0	3.9	9.4	3	0	0.1	3.9	7.1	0
	Snake River fall Chinook Salmon (age 1)					**Upper Columbia River summer Chinook Salmon (age 1)**				
1996	0	0	0			0	0	0		
1997	0	0.3	0			0	0.2	0		
1998	0	0	0	0	0.9	0	0.2	0.2	0	0
1999	0	0.5	1.3	11.7	1.8	0.1	1.3	5.4	14	0.7
2000	0	0.1	2.6	2.9	0.1	0	0.7	8.4	16.4	0
2001	0	0.2	0.9	0.7	0	0	0.3	4	3.5	0.3
2002	0	0	1.6	1.3	0.3	0.1	0.2	12.5	4.5	0.1
2003	0.1	0	1	2.9	1.2	0.3	0	5.6	4.1	1
2004	0	0.2	0.9	0.5	0.7	0	0.1	8	3.9	0.7
2005	0	0	0.6	0	0	0.1	0.3	2.1	0	0
2006	0	0.1	1.4	2.4	0.5	0.2	0.9	6.3	3.2	0.2
	Mid–Columbia River spring Chinook Salmon					**Upper Columbia River spring Chinook Salmon**				
1996	0	0	0			0	0	0		
1997	0.3	0	0			0	0	0		
1998	1	0	0	0	0	0	0	0	0	0
1999	0.1	2.4	5.2	16.3	0	0.2	0.6	7	9	0
2000	0.2	1.6	3	1.2	0	0.1	0.7	4.1	6.9	0
2001	0.4	0.1	0.2	7.6	0	0	0.1	0.2	0	0
2002	0	0.1	0.8	4.3	0.4	0.3	0	4.4	2.2	0

(Continued on next page)

TABLE A.3. Continued.

Year	Recovery region: NVI	VI–SJF	Washington coast	Columbia River	Oregon coast	Recovery region: NVI	VI–SJF	Washington coast	Columbia River	Oregon coast
2003	1.9	2.2	7.8	0.8	0.2	0.1	0.2	1.7	4.2	0.5
2004	0.1	0	0	0.5	0	0	0	1.1	11.4	0
2005	0	0	0.9	0	0	0	0	0.6	0	0
2006	0.3	0	4	2.8	0	0.1	1.3	3.7	1	0
	Snake River spring–summer Chinook Salmon					**Lower Columbia River Coho Salmon**				
1996	0	0	0			0	0	0		
1997	0	0	0			1.4	0.4	0		
1998	0.7	0	0	0	0	0.5	0.7	0	0	0.9
1999	1.9	0.9	4.5	23.3	0	0.3	1.8	0.5	4	2
2000	0.5	0.4	7.8	16.2	0	3.4	4.2	21.8	17.7	0.3
2001	0	0	1.8	1.5	0	0	3	6.5	14.8	0.3
2002	0	0	2.5	6.2	0	0.8	1.9	33.7	56.5	0
2003	0.7	1.8	4	3.3	0	0.2	0	22.6	4.1	2.9
2004	0.3	0	0	9.2	0	0.6	0.4	8.2	19	5.6
2005	0.1	0	0	0	0	0.9	0.2	0.4	0	0
2006	0	5.1	5.7	2.9	0	1.3	6.8	11.2	8.7	7.7