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ARTICLE

Genetic Identification of Chinook Salmon: Stock-Specific Distributions of Juveniles along the Washington and Oregon Coasts

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Abstract

We used microsatellite DNA data and genetic stock identification methods to delineate the temporal and spatial distributions of juvenile Chinook Salmon *Oncorhynchus tshawytscha* occupying coastal habitats extending from central Oregon to northern Washington. Juveniles were collected in trawl surveys conducted during spring, summer, and autumn over 15 years. Distributions (mean latitude and distance from shore) differed between yearling and subyearling life history types and between stocks; many of these differences were consistent across years. Yearlings were nearly all (98%) from Columbia River sources, and only 6% were naturally produced. In late May, yearlings from the lower Columbia and Willamette rivers were farther north than other yearlings, likely due to the early spring timing of their releases from hatcheries and subsequent out-migration from the Columbia River.

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However, yearling distributions in late June reflected known migration behaviors. Yearlings from interior Columbia and Snake River sources were farthest north by June, whereas yearlings from other stocks were more spread out in latitude. Subyearlings sampled in early summer were also largely from the Columbia River (98%), but greater percentages of subyearlings from coastal rivers were present during the fall (24%). In contrast to yearlings, natural production accounted for nearly one-third of subyearlings. Subyearlings of most stocks tended to remain relatively near their point of sea entry throughout the summer. Subyearlings from the Snake River fall-run stock and upper Columbia River summer-fall-run stock exhibited diverse distributions that included both southward and northward dispersal. Overall, distributions of Chinook Salmon stocks and life history types reflected differences in migration behavior but also reflected the influence of environmental factors and hatchery practices.

A long-held tenet of discerning fish biologists is that effective management and conservation of Pacific salmon *Oncorhynchus* spp. require knowledge of stock-specific migration and dispersal patterns (Rich 1939; Simon and Larkin 1972; Hartt 1980; Walters 1996). This requirement presents a challenge because salmon exhibit a great diversity of movement patterns, particularly during their ocean phase. Nonetheless, for many populations, the marine pathways of migrating adult fish are well known by fishery managers because adults are routinely sampled in fisheries conducted along much of the West Coast of North America (Cleaver 1969; Utter et al. 1987; Shalee et al. 1999; Weitkamp and Neely 2002; Beacham et al. 2008; Weitkamp 2010). In many areas, the marine migrations of juvenile salmon have also been studied intensively as part of efforts to understand variability in salmon production and to determine why populations respond to environmental conditions in different ways. Most studies of juvenile Pacific salmon have focused on the distributions of fish during the first weeks and months after ocean entry because this period is characterized by highly variable growth and survival (Godfrey 1958; Hartt 1980; Mortensen et al. 2000; Miller et al. 2014). Knowledge of where fish are during this critical period is important since the physical and biological ocean conditions that are thought to determine year-class strength vary with latitude and also across the continental shelf (Pearcy 1992; Brodeur et al. 2000; Percy and McKinnell 2007).

Salmon tagging has long been the primary means for studying marine distributions during this early critical period. During initial research efforts, juvenile fish were captured and tagged at sea, and some were later recovered as adults when returning to spawn in their natal streams (Foerster 1955; Godfrey et al. 1975; Hartt and Dell 1986). Later, numerous ocean research surveys captured juveniles that had been coded-wire-tagged during hatchery rearing (Miller et al. 1983; Percy and Fisher 1988; Orsi and Jaenicke 1996; Morris et al. 2007; Trudel et al. 2009; Fisher et al. 2014). More recently, genetic stock identification methods have been applied to samples from many coastal areas to delineate the early marine distributions of both naturally and hatchery-produced juvenile salmon (Teel et al. 2003; Van Doornik et al. 2007; Tucker et al. 2009; Seeb et al. 2011; Beacham et al. 2012, 2014). The migrations of juvenile Chinook Salmon *O. tshawytscha* have

been examined using genetic techniques, most extensively along the continental shelf off British Columbia and southeastern Alaska (Tucker et al. 2011, 2012) but also in Puget Sound, Washington (Rice et al. 2011), and off the southern Oregon and northern California coasts (Brodeur et al. 2004). Genetic data have also been used to study the distributions of juvenile Chinook Salmon in coastal areas along Oregon and Washington; however, those analyses were limited to a few selected genetic stocks (Teel 2004; Burke et al. 2013a).

Additional study of stock-specific distributions off the coasts of Oregon and Washington is warranted because those coastal areas are major rearing and migration habitats for juvenile Chinook Salmon (Miller et al. 1983; Percy and Fisher 1990; Peterson et al. 2010; Daly et al. 2012; Burke et al. 2013a). In an analysis of juvenile abundances along the coast from central California to the northern Gulf of Alaska, Fisher et al. (2007) found that the greatest catches of juvenile Chinook Salmon occurred from central Oregon to northern Washington. The region's Chinook Salmon productivity is centered in the Columbia River, which historically supported the largest runs in the world (Van Hyning 1973). Although widespread habitat losses, dam construction, and periods of sustained overfishing have greatly reduced the abundance of naturally produced Chinook Salmon in the Columbia River (Myers et al. 1998; Ford 2011), artificial production of this species is currently enormous, with more than 100 million juveniles released from the basin's hatcheries each year (Paquet et al. 2011).

In addition to their great abundance, Chinook Salmon in the region are characterized by high genetic, ecological, and life history diversity (Waples et al. 2001). Juvenile life histories are highly variable among and within populations, particularly with regard to the timing of downstream migration and the age at ocean entry. Two general ocean entry life history types of Chinook Salmon have been identified (Healey 1991): subyearlings and yearlings. Subyearlings enter the ocean during their first year (age 0) and have highly diverse downstream movement patterns (Rich 1920). In many areas, subyearlings move into estuaries and marine areas throughout the year, with temporally broad migratory peaks typically occurring in summer (Rich 1920; Reimers 1973; McCabe et al. 1986). Yearlings reside for a year in freshwater before moving seaward (at age 1) and typically

migrate to the ocean as larger smolts during spring (Rich 1920; Weitkamp et al. 2012). Although the age of ocean entry is variable in most naturally spawning populations, yearling life histories are most common in populations with adults that return to freshwater in the spring (i.e., spring run; Waples et al. 2004). In contrast, subyearling types predominate in fall-run populations. Columbia River hatcheries focus on subyearling releases for fall-run populations and yearling culture strategies for spring runs. However, hatchery propagation of fall-run populations in the Snake River and summer-run populations in the upper Columbia River includes substantial production of both subyearlings and yearlings (Fisher et al. 2014).

Previous studies have shown that the marine migrations of the region's juvenile Chinook Salmon also differ between yearling and subyearling life history types (Miller et al. 1983; Fisher and Pearcy 1995; Trudel et al. 2009; Tucker et al. 2011). Yearlings disperse rapidly after entering the ocean. For example, yearlings from spring-run populations in the interior headwater tributaries of the Columbia and Snake rivers make very rapid northward migrations, and by late summer they are primarily found off the Alaska coast (Tucker et al. 2011; Fisher et al. 2014). However, the migrations of yearlings from spring-run populations in the lower Columbia and Willamette rivers and from summer-run sources in the upper Columbia River are much more variable; by the end of summer, yearlings from these stocks are widely distributed along the coast (Fisher et al. 2014). In contrast to the two yearling dispersal patterns, subyearlings from the Columbia River and adjacent coastal streams mostly remain south of Vancouver Island through autumn (Trudel et al. 2009; Tucker et al. 2011; Fisher et al. 2014). Although these three distinct migration types have been well documented, a genetic assessment of stock-specific juvenile distributions is lacking for marine areas immediately north and south of the Columbia River. This information gap is particularly notable for the region's subyearlings, which occupy coastal habitats in the area during their first summer at sea.

The objective of our study was to use genetic stock identification to delineate the temporal and spatial distributions of juvenile Chinook Salmon occupying coastal habitats from central Oregon to northern Washington. Juveniles were collected during 15 years of trawl surveys conducted in spring, summer, and autumn along a fixed grid that included both nearshore and offshore sampling stations. We report the first stock composition estimates for subyearling and yearling juveniles off Oregon and Washington, and we also present the proportions of naturally and hatchery-produced juveniles from specific stocks. Furthermore, we assessed whether the initial spatial distributions of yearlings (latitude and distance from shore) in spring and summer differed between stocks that are known to migrate rapidly northward and those that display more variable migrations.

Samples collected in summer and autumn were used to examine the seasonal and spatial distributions of the region's more resident subyearlings and to search for stock-specific differences in habitat use.

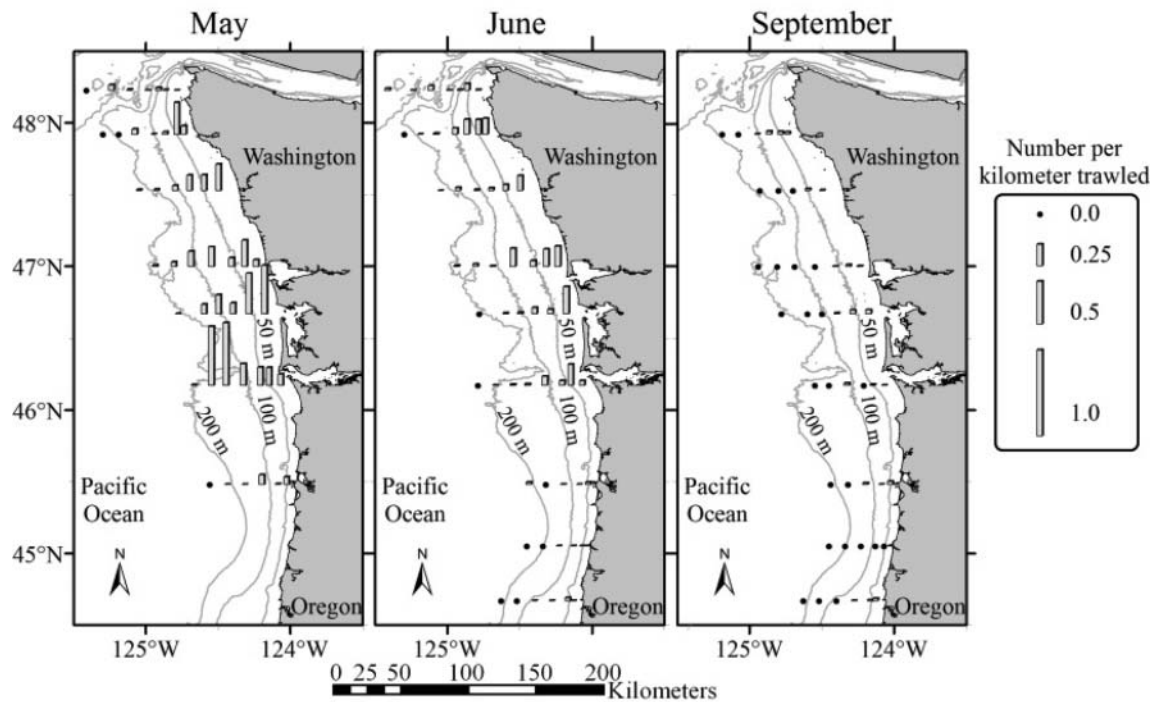
METHODS

Ocean sampling and juvenile life history classification.—Juvenile Chinook Salmon were collected during annual juvenile salmon trawl surveys that were conducted along the Washington and Oregon coasts by National Ocean and Atmospheric Administration Fisheries (Figure 1; Brodeur et al. 2005; Peterson et al. 2010). Data used in the present study were from surveys conducted in late May of 2006–2012 and in late June and late September of 1998–2012. Trawls consisted of 30-min-long surface tows with a 264 Nordic rope trawl (see Krutzikowski and Emmett 2005 for a detailed description). Trawling occurred along seven to nine transects situated perpendicular to shore, ranging from northern Washington (48.2°N) to central Oregon (44.7°N; Figure 1). Sampling stations began as close to shore as possible (1–5 nautical miles offshore [1 nautical mile = 1.852 km]; ~30-m depth) and continued offshore (in about 5-nautical-mile increments) to just beyond the shelf.

Onboard the sampling vessel, juvenile Chinook Salmon were identified, measured (FL, mm), and frozen. In the laboratory, fish were remeasured and examined for markings indicative of hatchery origin (e.g., clipped adipose fin, coded wire tag [CWT], or other tag). Samples of fin tissue were taken for genetic analysis and were stored in 100% ethanol. For most trawls, tissues were collected from all fish captured. However, for several large catches (>100 fish), juveniles from all size-classes were subsampled to comprise the genetic sample. We used FL and month of ocean capture to classify juvenile life history type as either subyearling or yearling; size cutoffs were derived from known ages based on scale analysis and from tagged fish (Percy and Fisher 1990; Fisher and Pearcy 1995; Weitkamp et al. 2012). Fish larger than the yearling size category were assumed to be older (i.e., sea entry in earlier years) and were not included in analyses. Among fish that were captured in May, those ranging from 121 to 250 mm were classified as yearlings, and smaller individuals were considered subyearlings. Size cutoffs used to designate yearling fish were 141–280 mm for June captures and 251–400 mm for September captures. Subyearling and yearling CPUEs for each station were computed by dividing the number of captured subyearlings or yearlings by the number of kilometers that were towed to obtain the sample.

Genetic data collection.—Genomic DNA was isolated from fin tissue samples by using Wizard Genomic DNA Purification Kits (Promega Corp.) in accordance with the manufacturer's protocols. Polymerase chain reactions (PCRs) were then conducted to amplify 13 microsatellite DNA loci

A: West Cascade spring yearlings



B: Willamette River spring yearlings

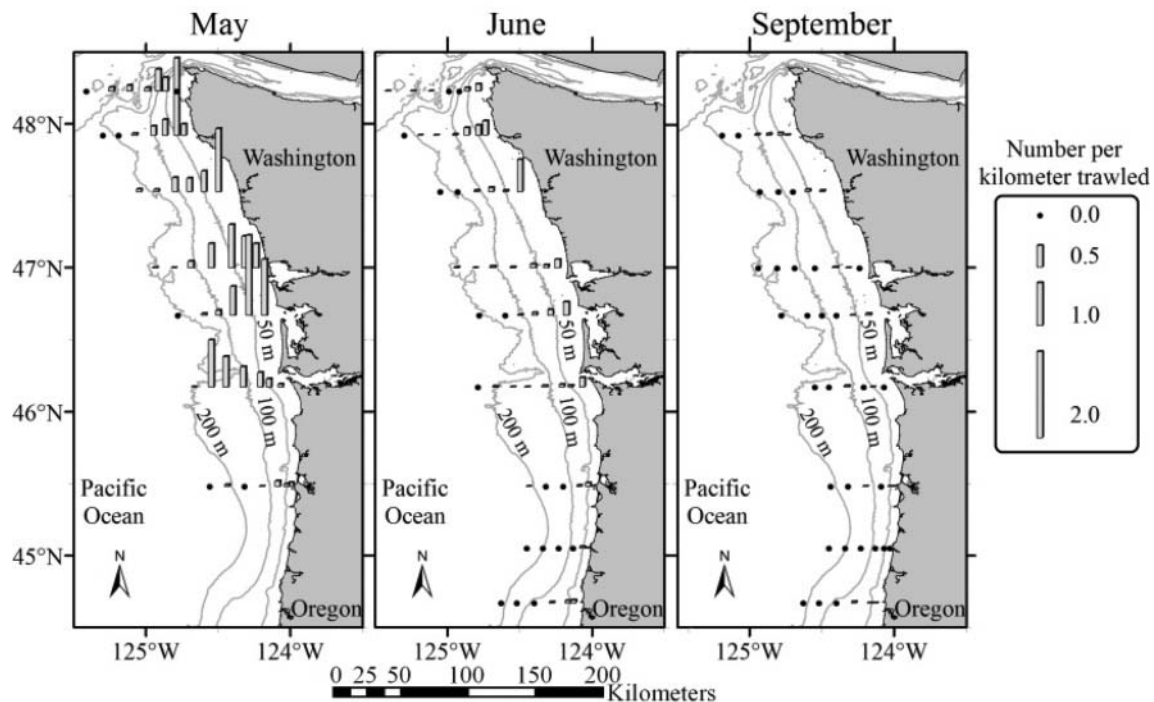
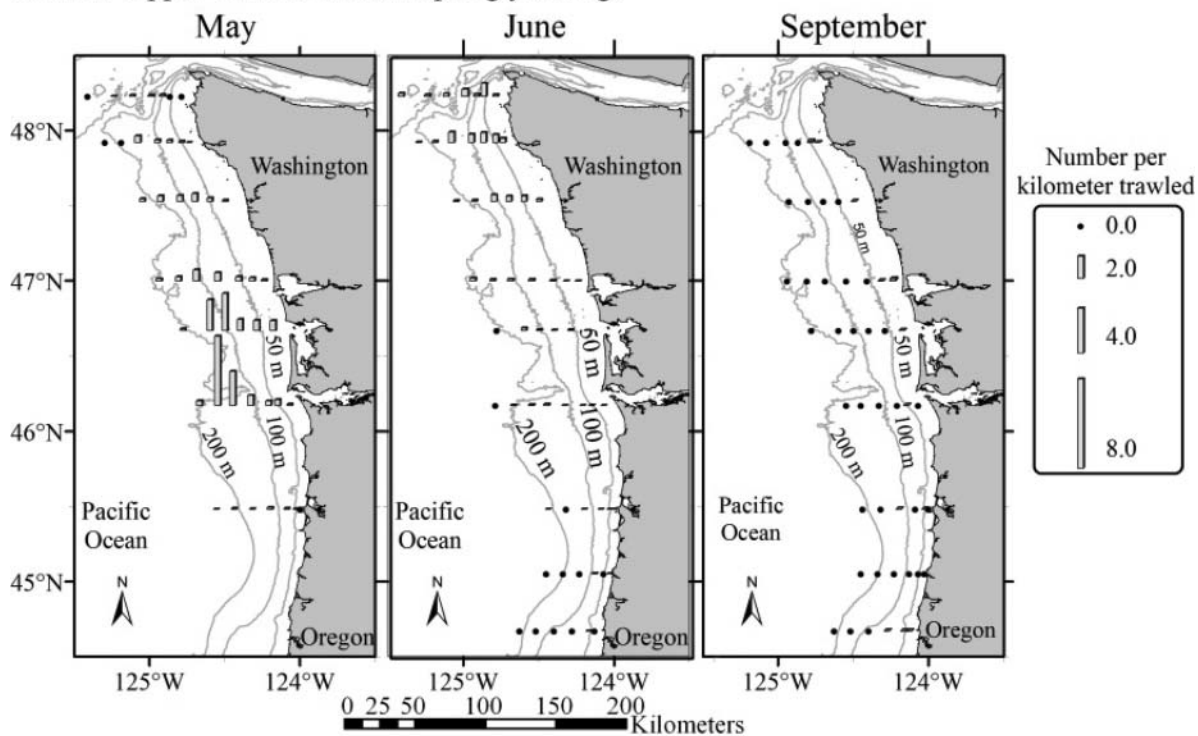


FIGURE 1. Maps showing the sampling transects and stock-specific CPUEs (fish/km trawled) for juvenile Chinook Salmon of each life history type sampled in May (2006–2012), June (1998–2012), and September (1998–2012): (A) West Cascade spring-run yearlings, (B) Willamette River spring-run yearlings, (C) mid-/upper Columbia River spring-run yearlings, (D) Snake River spring-run yearlings, (E) upper Columbia River summer–fall-run yearlings, (F) Snake River fall-run yearlings, (G) Washington coast subyearlings, (H) West Cascade fall-run subyearlings, (I) Spring Creek group fall-run subyearlings, (J) upper Columbia River summer–fall-run subyearlings, (K) Snake River fall-run subyearlings, and (L) Oregon coast subyearlings.

C: Mid / Upper Columbia River spring yearlings



D: Snake River spring yearlings

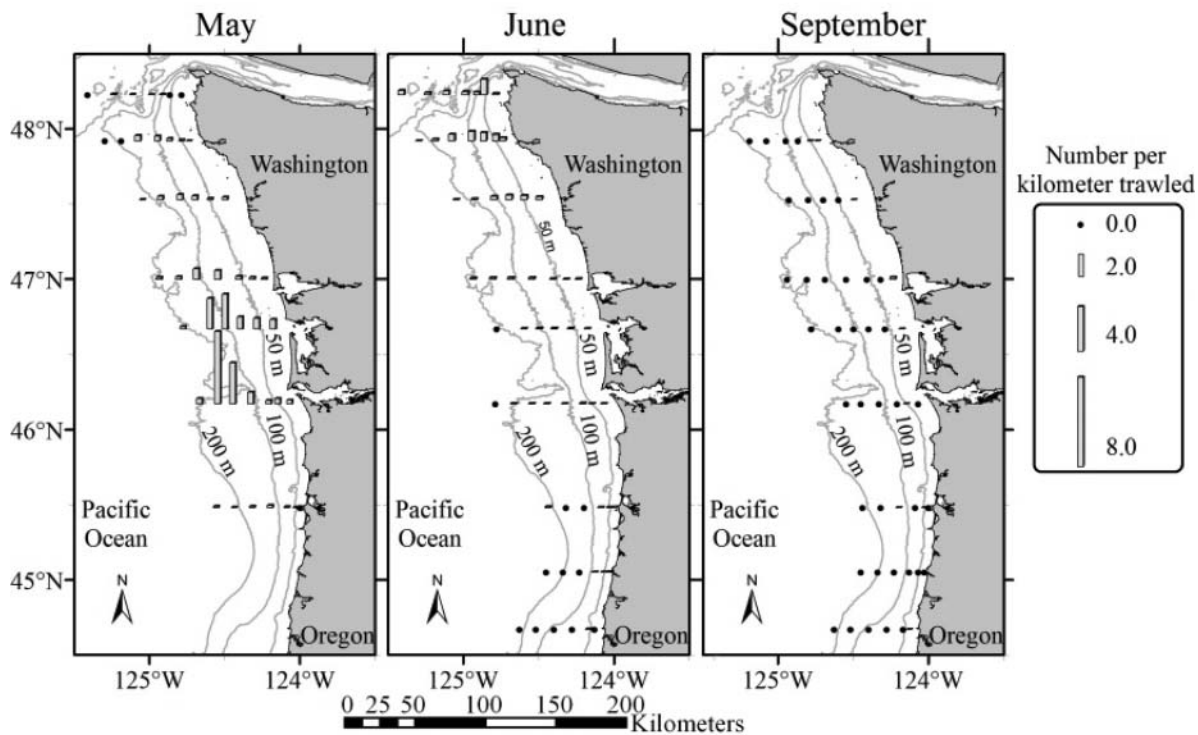
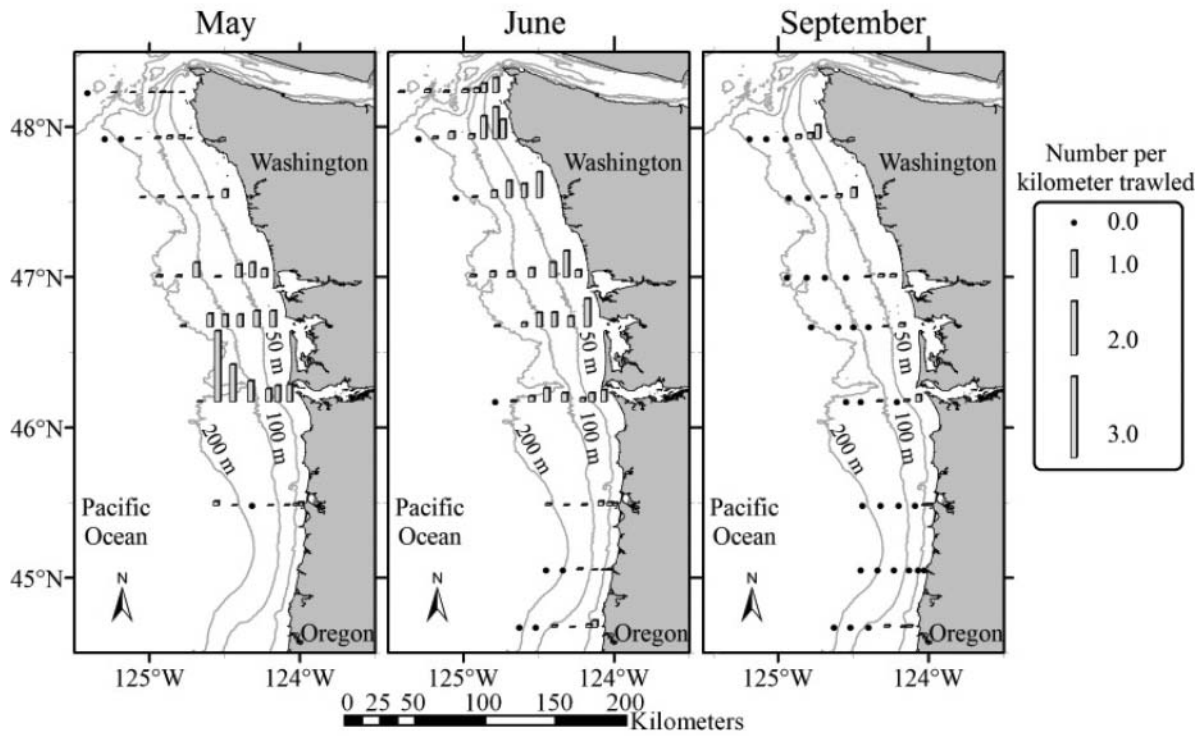


FIGURE 1. Continued.

E: Upper Columbia River summer/fall yearlings



F: Snake River fall yearlings

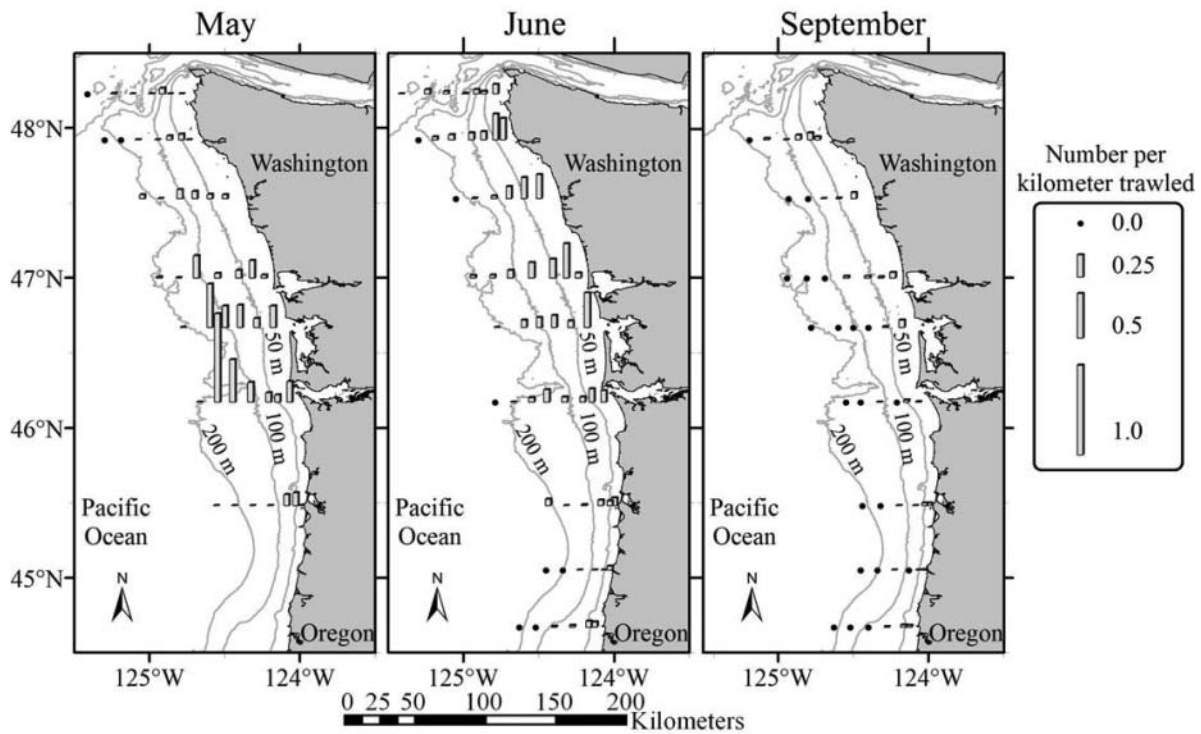
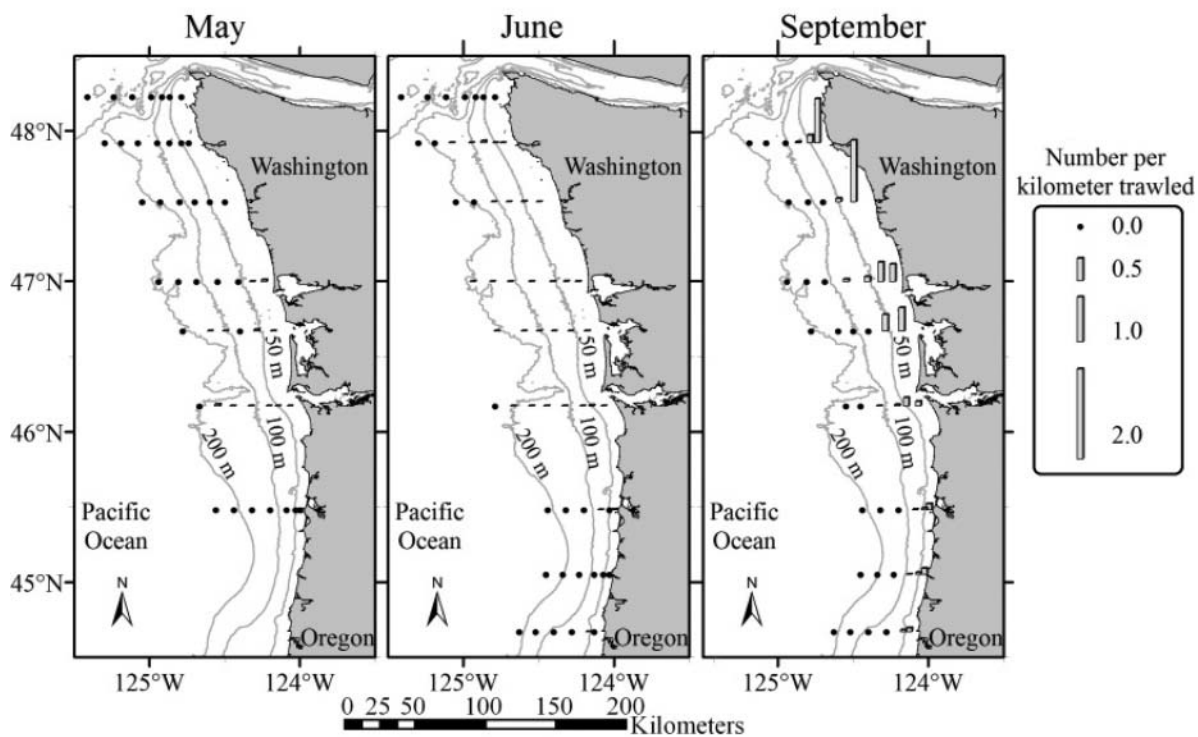


FIGURE 1. Continued.

G: Washington coast subyearlings



H: West Cascade fall subyearlings

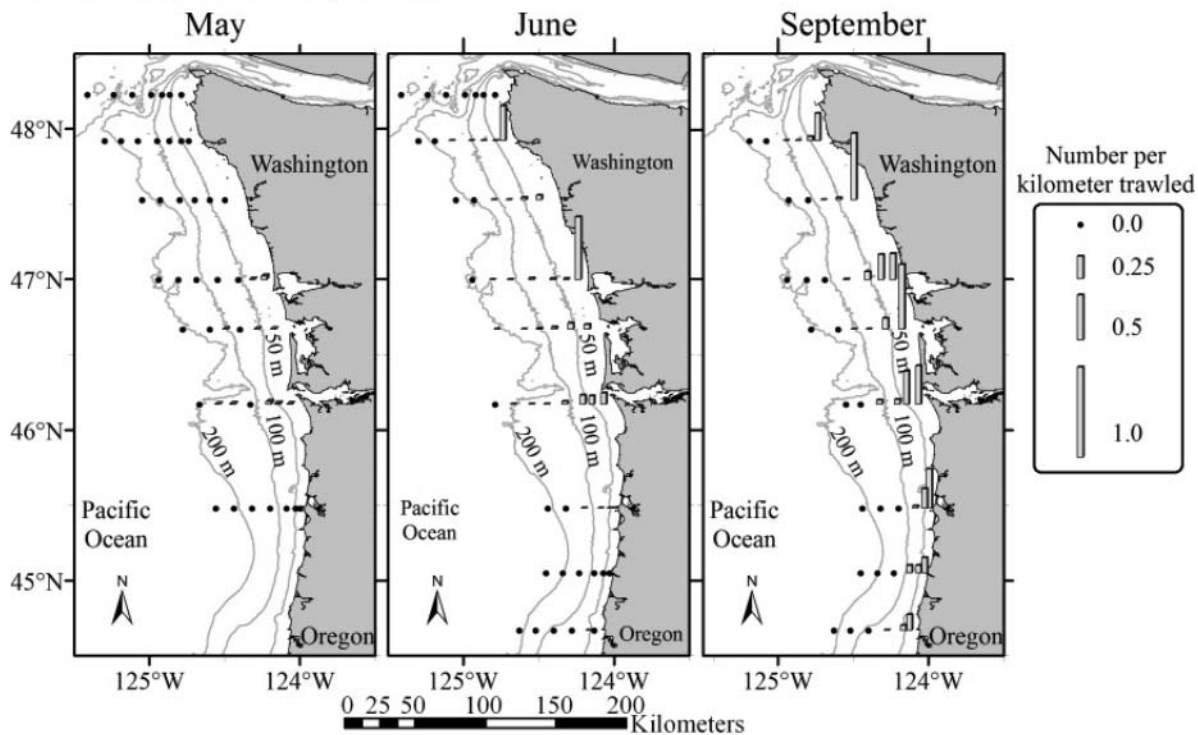
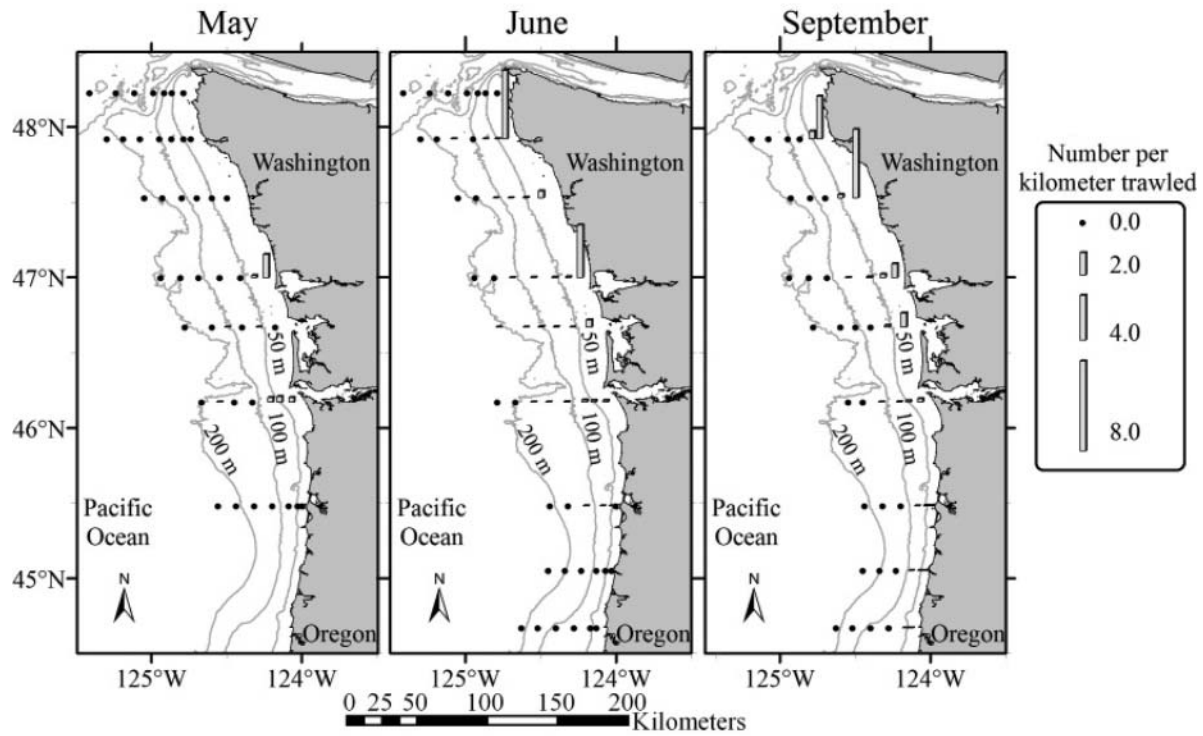


FIGURE 1. Continued.

I: Spring Creek group fall subyearlings



J: Upper Columbia River summer/fall subyearlings

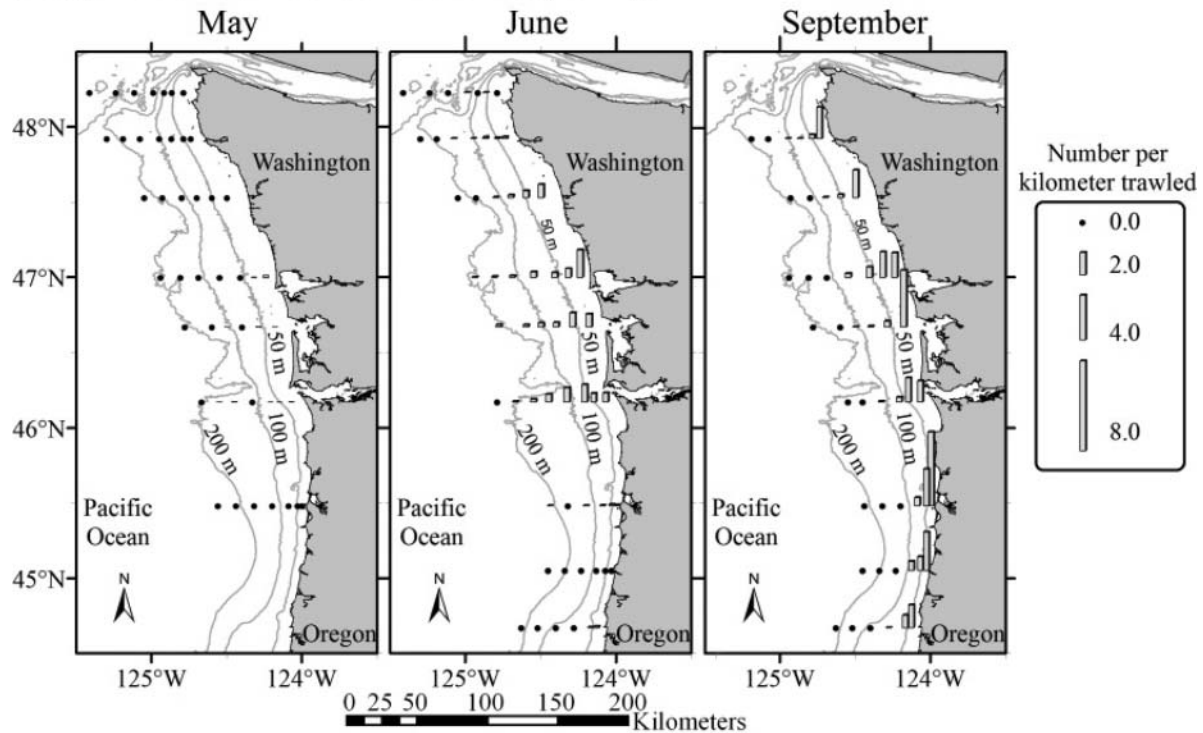
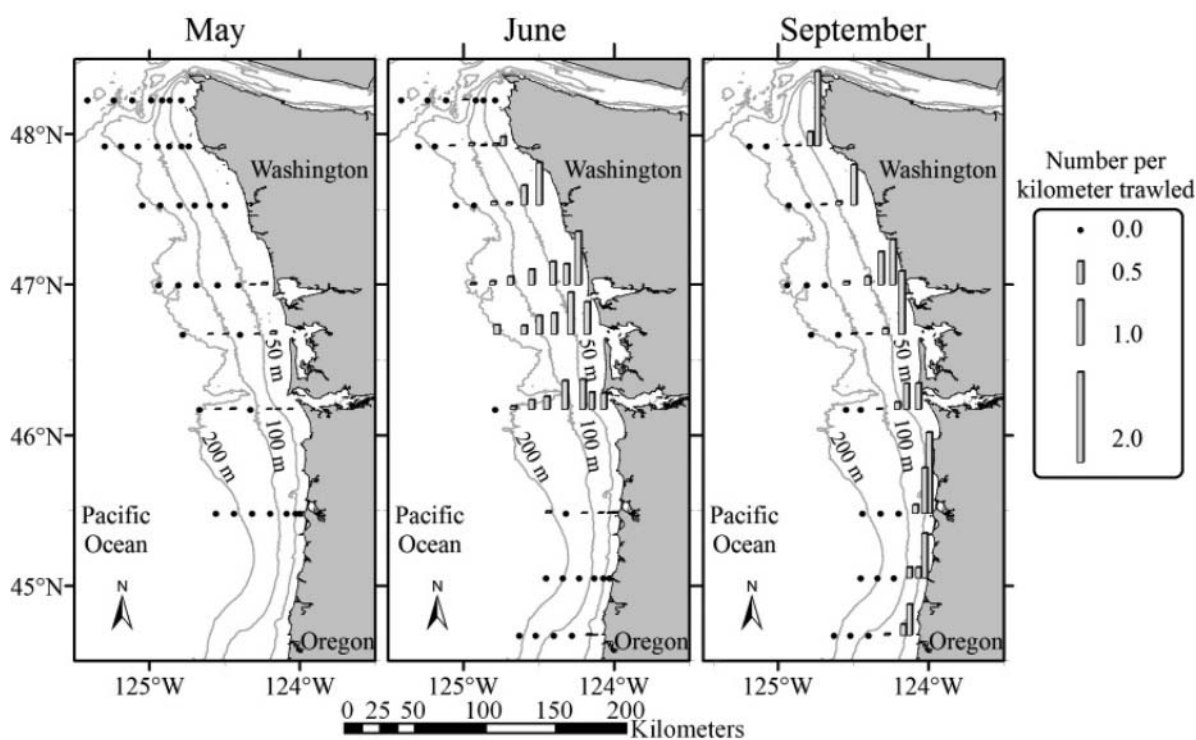


FIGURE 1. Continued.

K: Snake River fall subyearlings



L: Oregon coast subyearlings

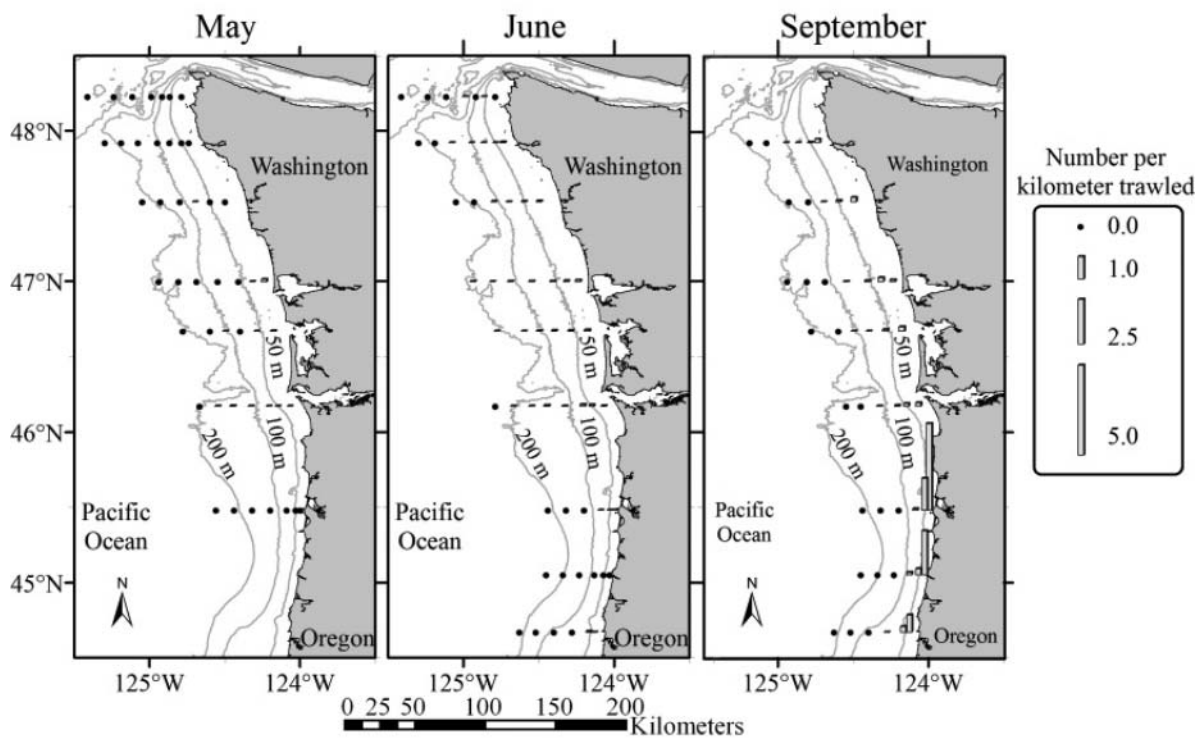


FIGURE 1. Continued.

that have been standardized for Chinook Salmon by several West Coast genetics laboratories (Seeb et al. 2007). The resulting PCR products were analyzed with Applied Biosystems, Inc. (ABI), 3100 and 3730 Genetic Analyzers, and genotypes were determined using ABI GeneScan and ABI Genotyper software.

Stock composition analysis.—Genetic stock identification analyses were conducted using the likelihood model of Rannala and Mountain (1997) as implemented by the genetic stock identification program ONCOR (Kalinowski et al. 2007). Two types of stock identification analysis were implemented to address different questions. First, ONCOR and a standard approach to genetic stock identification mixture modeling (Manel et al. 2005) were used to estimate the overall proportional stock compositions of samples grouped by month and by length-based juvenile life history type (i.e., subyearlings and yearlings). This approach uses a “baseline” of genotypic data from potential source populations (Milner et al. 1985) to estimate the most likely proportional composition of the set of mixture genotypes. The precision of stock composition results was estimated by bootstrapping baseline and mixture data 100 times (Kalinowski et al. 2007). Second, we used ONCOR and the

genetic baseline to estimate the stock origins of individual fish. The individual fish stock assignments were used to estimate stock-specific CPUE per station for the analysis of spatial distributions and to estimate percentages of natural-origin fish (see below).

Genetic stock identification analyses were conducted by using a Chinook Salmon microsatellite DNA baseline that was compiled from the multi-agency databases described by Seeb et al. (2007), Moran et al. (2013), and Hess et al. (2014). Stock allocations were made to 141 individual Columbia River basin and coastal baseline populations and were summed to estimate the proportional contributions of 14 regional stocks (Table 1). The 14 stocks were generally congruent with the Chinook Salmon evolutionarily significant units (ESUs) identified under the U.S. Endangered Species Act (ESA; Myers et al. 1998; Table 1). However, due to a lack of appreciable genetic differentiation between several ESUs, estimates for juveniles from those areas were combined into larger reporting units. Results for the three Central Valley (California) ESUs were combined into a single reporting unit, as were results for the Mid-Columbia River ESU and Upper Columbia River ESU. In addition, preliminary results showed that the three southern Oregon and California coastal ESUs south of the study area were very minor contributors to our

TABLE 1. Chinook Salmon genetic baseline used for stock identification analysis in this study. Genetic stock or region, primary juvenile life history type, evolutionarily significant unit (ESU), number of baseline populations, and sample size are given (ESU status: 1 = endangered; 2 = threatened; 3 = species of concern; 4 = listing not warranted). Geographic areas for baseline populations in British Columbia (BC) are indicated. Genetic data are from Seeb et al. (2007), Moran et al. (2013), and Hess et al. (2014).

Genetic stock/region	Juvenile life history type	ESU (status)	Baseline populations	Sample size
Southern BC/Salish Sea	Subyearling ^a	South BC mainland, east Vancouver Island, Fraser River, and west Vancouver Island; and Puget Sound ESU (2)	60	8,169
Washington coast	Subyearling ^a	Washington Coast ESU (4)	7	767
West Cascade fall	Subyearling	Lower Columbia River ESU (2)	3	357
West Cascade spring	Yearling	Lower Columbia River ESU (2)	3	428
Spring Creek group fall	Subyearling	Lower Columbia River ESU (2)	4	384
Willamette River spring	Yearling	Upper Willamette River ESU (2)	5	559
Deschutes River fall	Subyearling	Deschutes River Summer–Fall ESU (4)	2	288
Upper Columbia River summer–fall	Subyearling ^b	Upper Columbia River Summer–Fall ESU (4)	4	706
Mid-/upper Columbia River spring	Yearling	Mid-Columbia River Spring ESU (4); and Upper Columbia River Spring ESU (1)	6	740
Snake River spring	Yearling	Snake River Spring–Summer ESU (2)	8	909
Snake River fall	Subyearling ^b	Snake River Fall ESU (2)	3	474
Oregon coast	Subyearling ^a	Oregon Coast ESU (4)	19	2,345
Southern Oregon/California coast	Subyearling ^a	Southern Oregon and Northern California Coastal ESU (4); Upper Klamath and Trinity Rivers ESU (3); and California Coast ESU (2)	8	1,119
Central Valley, California	Subyearling	Central Valley Fall ESU (3); Central Valley Spring ESU (2); and Sacramento River Winter ESU (1)	9	1,000
Total			141	18,245

^aSpring-run populations in these regions primarily exhibit the yearling life history type.

^bSome hatchery programs release yearlings from these stocks.

samples; we therefore combined estimates for those ESUs into a single regional stock. Similarly, results for the Puget Sound ESU were combined with results for the British Columbia sources north of the study area.

For the Lower Columbia River ESU, genetic estimates were made for three genetically distinct stocks (Myers et al. 2006; Seeb et al. 2007; Moran et al. 2013). Spring-run and fall-run populations originating in tributaries of the western Cascade Mountains were differentiated from each other and from a fall-run stock native to the Columbia River gorge (Table 1). Hereafter, we refer to the Columbia River gorge native fall-run stock as the “Spring Creek group” because the current distribution of the stock reflects the use (since 1901) of fish and eggs from Spring Creek National Fish Hatchery (NFH) to stock hatcheries and rivers throughout the lower Columbia River (Myers et al. 2006).

Some fish ($N = 319$) from our trawl surveys were initially classified as yearlings based on FL but were later reclassified as subyearlings. The reclassification of these fish ($\sim 3\%$ of our total sample) was based on their individual genetic stock assignments (described below). The reclassified individuals were large fish that were assigned to the Central Valley stock and to the Spring Creek group fall-run stock in the lower Columbia River. Chinook Salmon from the Sacramento and San Joaquin rivers of California are thought to enter the ocean primarily as subyearlings, with out-migrations occurring throughout much of the year (Fisher 1994; Waples et al. 2004). Central Valley subyearlings that entered the ocean during winter or spring likely exceeded our size cutoffs after several months of marine growth. Spring Creek NFH releases large subyearling smolts in May of each year (Regional Mark Information System [RMIS]; www.rmmpc.org), and these fish can exceed the subyearling size cutoffs when captured in ocean surveys. A few individuals that were reclassified (2 fish from the Central Valley; 48 fish from the Spring Creek group) were confirmed to be subyearlings based on hatchery release information from the CWTs.

Stock-specific catch per unit effort.—ONCOR was used to compute the relative probability of regional stock membership for each individual ocean-caught fish. In this procedure, an individual is “carved up” and allocated to each source in proportion to these relative probabilities (Manel et al. 2005). For each sampling station during a given survey, we summed the full individual assignment probability values for all subyearlings and for all yearlings to estimate the proportions of each stock in the catch. The resulting proportions were then applied to the total number of each life history type caught at the station to estimate stock-specific CPUEs.

Distribution maps.—Stock-specific and life-history-specific CPUEs for each station were averaged across years for each survey month to examine the average distributions. Only stations that were sampled during at least 25% of the years for each month were included (i.e., at least 2 of the 7 surveys

conducted in May; at least 4 of the 15 surveys conducted in June; and at least 4 of the 15 surveys conducted in September). Charts were made using ArcMap 10.0 for each life history type and stock sampled in each month.

Spatial statistics.—Our sampling regime used fixed-location sampling sites that were partially designed to capture the full spatial distribution of particular stocks. Therefore, many trawls resulted in a CPUE of zero for select stocks (e.g., we sampled close to shore to catch certain stocks, knowing that other stocks might not be that close). Therefore, calculation of a simple mean for latitude or distance from shore would have resulted in biased estimates of location. Instead, we calculated the mean location (latitude or distance from shore) by weighting each sample by the CPUE for a given stock caught in that trawl. By design, trawls with zero catch of a given stock had no influence on the mean location for that stock. For this analysis of stock-specific spatial distributions by month and life history type, data were combined across all survey years.

For many of the Chinook Salmon stocks, the spatial distribution of juveniles was nonnormal, making traditional statistical tests inappropriate. We therefore chose to use permutation-based methods for all statistical tests. We first calculated the weighted mean latitude and weighted mean distance from shore for each stock individually (with subyearlings and yearlings considered separately) as described above. For each pair of stocks to be compared, we then calculated the difference in weighted mean latitude and distance from shore. To determine whether these differences were greater than one would expect if the two stocks’ distributions had been drawn from the same underlying spatial distribution (i.e., our null hypothesis), we compared them to the differences generated from 5,000 permutations of the data. For each permutation, we randomly reassigned the two CPUE values to the two stocks (one value for each stock in the comparison) and recalculated the difference in weighted mean latitude and distance from shore between the two stocks. All P -values reported here represent the proportion of permutations for which the difference in weighted means was more extreme than the observed difference. Because we made multiple pairwise comparisons, significance was determined using Bonferroni-corrected probabilities. All stocks with sample sizes of 75 or more fish for a given month and life history type were included in the statistical tests.

For each stock and life history type included in statistical tests, we also characterized the interannual variability in spatial distributions. To estimate interannual variability in latitude or distance from shore during a given month, we calculated the weighted mean value for each year separately; interannual variability was then represented as the SD of the annual weighted means.

Estimates of natural-origin fish and coded-wire-tagged fish.—We used ONCOR to assign each individual fish to a most likely stock of origin (i.e., the stock with the highest relative probability). The numbers of marked fish (those with

adipose fin clips or CWTs) and unmarked fish in the resulting set of fish for each stock were used to estimate the proportions of natural-origin fish. Not all hatchery fish are marked, and marking rates vary among hatcheries. Marking rates for juvenile Chinook Salmon released from hatcheries were compiled from the RMIS database (Table 2). To calculate the potential number of naturally produced fish in the catches, we (1) estimated the total number of hatchery fish (calculated as [number of marked fish assigned to a stock]/[marking rate for the stock]) and then (2) subtracted the estimated number of hatchery fish from the total number of fish in the sample. Estimation of the numbers of naturally produced fish was restricted to the most recent study years (2006–2012), when marking rates for several stocks were relatively high (>90%). To improve the overall accuracy of the estimates of natural-origin fish, estimates were not made for sample sizes smaller than 50 fish.

To assess the accuracy of our genetic estimates, we identified a subset of the juvenile Chinook Salmon that had received CWTs. Release data for each CWT numeric code, including species, run, fish age, date, hatchery, stock, and location, were

obtained from the RMIS database. Based on this information, we classified each juvenile as originating from 1 of the 14 regional genetic stocks in our analysis. The CWT classification of each fish was then compared with the stock of origin (i.e., the stock with the highest relative probability) that was estimated using ONCOR and the fish's genotypic data. We also used the entire subset of fish with CWTs to create a mixed-stock sample of "known" origin to evaluate the accuracy of stock composition estimates produced by ONCOR.

RESULTS

Seasonal Abundance Trends in Catches

The CPUE varied among years, among seasons, and between life history types (Figure 2). For all years that included May sampling, the yearling CPUE was greatest in May, with a mean of 2.4 fish/km trawled. In all years, yearling CPUE in June was intermediate (mean = 0.9 fish/km), and September CPUE of yearlings was lowest (0.2 fish/km). The

TABLE 2. Average annual number of Chinook Salmon released from hatcheries in 2006–2012, months of releases, and percentages of hatchery fish that were marked at release (from the Regional Mark Information System; www.rmipc.org); numbers of unmarked and marked juveniles assigned to regional genetic stocks from sampling along the Washington and Oregon coasts (2006–2012); and estimated number of natural-origin juveniles, number of hatchery-origin juveniles, and percentage of natural-origin juveniles in samples based on marking rates of released fish.

Genetic stock/region	Hatchery releases			Juveniles in ocean catch				
	Average release (millions)	Peak month(s)	Percent marked	Unmarked	Hatchery marked	Estimated natural origin	Estimated hatchery origin	Percentage of catch estimated to be of natural origin
Yearlings								
West Cascade spring	3.1	Feb–Mar	89.9	11	173	0 ^a	184	0.0
Willamette River spring	5.5	Feb–Mar	98.5	48	405	42	411	9.3
Upper Columbia River summer–fall	2.8	Apr	92.9	13	570	0 ^a	583	0.0
Mid-/upper Columbia River spring	8.3	Mar–Apr	97.5	95	706	77	724	9.6
Snake River spring	11.3	Mar–Apr	99.6	71	689	68	692	8.9
Snake River fall	0.9	Apr	97.9	8	205	4	209	1.9
Total yearlings	31.9			246	2,748	191	2,803	6.4
Subyearlings								
Washington coast	10.7	May–Jun	89.1	69	62	61	70	46.6
West Cascade fall	16.1	Jun–Jul	90.1	56	45	51	50	50.5
Willamette River spring	1.8	Oct–Nov	95.6	53	6	53	6	89.8
Spring Creek group fall	24.2	Apr–May	89.1	58	476	0 ^a	534	0.0
Deschutes River fall	<0.1	May	100.0	60	26	60	26	69.8
Upper Columbia River summer–fall	21.5	Jun–Jul	60.5	883	429	603	709	46.0
Snake River fall	4.1	May–Jun	65.2	315	268	172	411	29.5
Oregon coast	4.0	Jun–Jul	55.5	148	79	85	142	37.4
Total subyearlings	82.5			1,642	1,391	1,085	1,948	35.8

^aThe percentage of marked ocean-caught fish equaled or exceeded the hatchery marking rate; therefore, the estimated number of natural-origin juveniles was zero.

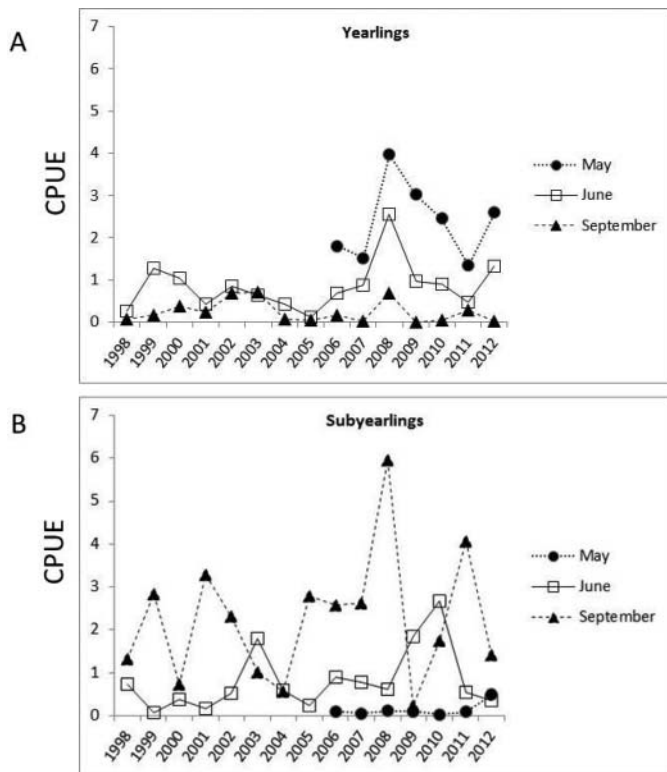


FIGURE 2. Chinook Salmon CPUE (fish/km trawled) for (A) yearlings and (B) subyearlings sampled along the Washington and Oregon coasts in May (2006–2012), June (1998–2012), and September (1998–2012).

CPUE pattern for subyearlings was opposite the yearling CPUE pattern in most years, with the lowest value observed in May (0.1 fish/km), an intermediate value in June (0.8 fish/km), and the highest value in September (2.2 fish/km). However, in 4 of the 15 sampling years, subyearling CPUE was greater in June than in September.

Comparison of Genetic Estimates and Stock Origins based on Coded Wire Tags

Genetic and CWT data were obtained for 2,223 sampled fish (Table 3). Overall, genetic assignments and CWT origins agreed for 82% of the individuals. Genetic assignment accuracy for the 14 genetic stocks ranged from 65% for the Snake River spring-run stock to 100% for the southern British Columbia/Salish Sea stock and the West Cascade (lower Columbia River) fall-run stock. Approximately 80% of the genetic allocations that did not agree with the CWT data were between two pairs of stocks from the interior Columbia River basin: (1) the upper Columbia River summer–fall run and Snake River fall run (54% of the misallocations); and (2) the mid-/upper Columbia River spring run and Snake River spring run (25% of the misallocations). The differences between genetic stock composition estimates and the composition

based on CWT data averaged 0.3%. The greatest differences were observed for the Deschutes River fall run (0.8%) and the upper Columbia River summer–fall run (0.7%).

Stock Composition of Juveniles

Genetic data from a total of 9,703 sampled fish were used to estimate proportional stock composition of juvenile Chinook Salmon captured during coastal trawl surveys (Table 4; Figure 3). Overall, approximately 98% of the yearlings sampled in May were estimated to originate from Columbia River basin sources. The May yearlings were 82% spring-run fish from the basin, primarily from the mid-/upper Columbia River (28%), Snake River (27%), and Willamette River (19%) stocks. May yearlings included smaller percentages of upper Columbia River summer–fall-run (10%), West Cascade spring-run (8%), and Snake River fall-run (5%) fish. The contribution of all other stocks combined was approximately 3%.

Yearlings sampled in June were also predominately from the Columbia River basin (98%), but only 54% were from the basin's spring-run stocks. June percentages for the mid-/upper Columbia River spring run (21%), Snake River spring run (20%), Willamette River spring run (7%), and West Cascade spring run (7%) were lower than the corresponding May percentages. The greatest contributor to June yearlings was the upper Columbia River summer–fall stock (31%). The Snake River fall-run stock comprised 10% of the June sample of yearlings.

In addition to being the largest contributor to June yearling samples, the upper Columbia River summer–fall-run stock comprised the greatest percentage of June subyearlings (33%). Other stocks represented at high percentages in the subyearling samples included the Snake River fall run (30%) and Spring Creek group fall run (18%). Overall, greater than 98% of the subyearlings sampled in June were from Columbia River basin stocks.

Approximately 77% of September subyearlings were from Columbia River basin sources, with the largest percentages contributed by the upper Columbia River summer–fall-run (42%), Spring Creek group fall-run (15%), and Snake River fall-run (11%) stocks. Subyearlings from coastal Oregon (12%) and Washington (5%) were also present, as were smaller percentages of fish originating from systems south and north of the study area (1–3%).

Relatively few ($n = 115$) subyearlings were captured during 7 years of May sampling, and the majority (57%) of those fish belonged to the Spring Creek group fall stock. May subyearlings also included Columbia River basin spring-run fish (~40%). Yearlings were rare in September surveys; 161 samples were analyzed from 15 survey years. The greatest percentage contributions to September yearlings were from the upper Columbia River summer–fall run (44%), Snake River fall run (15%), West Cascade spring run (12%), and West Cascade fall run (9%).

TABLE 3. Number of juvenile Chinook Salmon with coded wire tags (CWTs) indicating origin, compared with genetic stock assignments to 14 stocks in samples collected along the Washington and Oregon coasts. Actual and genetic estimates of percentage stock composition for the 2,223 fish with CWTs are also shown (stocks: BCS = southern British Columbia/Salish Sea; WA = Washington coast; WCF = West Cascade fall run; WCS = West Cascade spring run; WS = Willamette River spring run; SCG = Spring Creek group fall run; DES = Deschutes River fall run; USF = upper Columbia River summer–fall run; MUS = mid-/upper Columbia River spring run; SS = Snake River spring run; SF = Snake River fall run; OR = Oregon coast; SOCA = southern Oregon/California coast; CV = Central Valley, California). Values in bold italics represent the numbers of individuals for which CWT origin and genetic stock assignment were in agreement.

Genetic stock assignment	CWT origin													
	BCS	WA	WCF	WCS	WS	SCG	DES	USF	MUS	SS	SF	OR	SOCA	CV
BCS	3	1						4	2		1		1	
WA		47						2	1			3		
WCF			2	2	1	1		1		1	1	2		
WCS				57	2				5			1		
WS				2	80			1		4				
SCG				1		43					3			
DES							0	5			6			
USF					3	1		788			104	4	2	1
MUS				4					246	59				
SS									42	121				
SF						2		112			379			
OR		6		1				1				49		
SOCA								1				2	7	
CV														2
Total	3	54	2	67	86	47	0	915	296	185	494	61	10	3
Actual %	0.1	2.4	0.1	3.0	3.9	2.1	0.0	41.2	13.3	8.3	22.2	2.7	0.4	0.1
Genetic %	0.1	2.3	0.5	3.4	3.6	2.0	0.8	40.5	13.7	7.5	22.0	2.6	0.5	0.1

Hatchery- and Natural-Origin Fish

Hatchery fish were predominant among juveniles sampled off the Washington and Oregon coasts from 2006 through 2012 (Table 2). Approximately 92% of yearlings and 46% of subyearlings were marked hatchery fish. For all stocks included in this analysis, hatchery releases of yearlings were marked at high rates (90–100%). The marked percentage of West Cascade spring-run yearlings in our ocean catches (94%) was higher than the hatchery release marking rate for the stock (90%). Similarly, 98% of the ocean-caught upper Columbia River summer–fall-run yearlings were marked, thus exceeding the stock's hatchery marking rate (93%). For these two stocks, the estimated percentage of hatchery fish was over 100%; we therefore concluded that the entire catch of these stocks was likely of hatchery origin. When catches of unmarked yearlings from other stocks were adjusted for hatchery releases of unmarked fish, the total estimated percentage of natural-origin yearlings in the study area was 6%. The highest percentages of natural-origin yearlings were contributed by the Willamette River, mid-/upper Columbia River, and Snake River spring-run stocks (9–10%).

Hatchery releases of subyearlings were marked at lower and more variable rates (56–100%) during the 7 years, making it more difficult to accurately assess the percentage of natural-

origin subyearlings in our catches. After adjustment for hatchery marking rates, approximately 36% of the subyearlings sampled in our surveys were estimated to be of natural origin. Among the major contributors to subyearling catches, the percentages of natural-origin fish were 46% for subyearlings from the upper Columbia River summer–fall stock and 30% for subyearlings from the Snake River fall stock. However, for the Spring Creek group fall-run stock, the percentage of captured subyearlings that had marks was the same as the hatchery marking rate (89%); we therefore considered these fish to be entirely of hatchery origin.

Seasonal and Spatial Distributions of Stocks

Yearlings.—In May, yearlings from all of the stocks analyzed were primarily distributed off the mouth of the Columbia River and northward along the Washington coast (Table 5; Figure 1). Spring-run fish from the Willamette River stock were farther north than yearlings from interior basin stocks during May ($P \leq 0.01$; see Supplementary Table S.1 available online). The mean latitude of yearlings increased from May to June for all stocks, and the northward shift was most evident for spring-run yearlings from the mid-/upper Columbia River and Snake River ($P < 0.001$; Figure 4). By June, the interior

TABLE 4. Estimated percentage composition of 14 regional genetic stocks observed in samples of juvenile Chinook Salmon collected along the Washington and Oregon coasts (n = number of sampled fish). May samples were collected in 2006–2012; June and September samples were collected in 1998–2012. The range in parentheses below each estimate is the 95% confidence interval derived from 100 bootstrap resamplings of baseline and mixed-stock genotypes. Estimated composition values greater than 10% are shown in bold italics.

Stock	May		June		September	
	Yearlings ($n = 1,896$)	Subyearlings ($n = 115$)	Yearlings ($n = 1,814$)	Subyearlings ($n = 1,752$)	Yearlings ($n = 161$)	Subyearlings ($n = 3,965$)
Southern British Columbia/Salish Sea	0.7(0.5–1.8)	0.4(0.0–5.5)	0.3(0.3–1.2)	0.5(0.3–1.3)	2.5(0.6–7.2)	1.1(0.9–1.9)
Washington coast	0.6(0.2–0.9)	0.0(0.0–1.7)	0.1(0.0–0.4)	0.2(0.1–0.4)	1.2(0.0–3.5)	5.3(4.2–5.8)
West Cascade fall	1.0(0.6–1.9)	0.0(0.0–12.4)	1.7(1.1–2.5)	1.5(1.7–4.0)	9.3(2.5–14.3)	5.1(4.5–6.9)
West Cascade spring	7.6(6.3–9.5)	2.9(0.0–9.4)	6.5(5.4–8.2)	0.8(0.5–1.8)	11.8 (6.8–19.5)	0.4(0.2–1.1)
Willamette River spring	19.2 (16.4–20.4)	0.9(0.0–2.6)	6.8(5.4–7.6)	4.8(3.7–5.6)	7.3(1.9–11.6)	0.7(0.4–0.9)
Spring Creek group fall	0.0(0.0–0.0)	57.4 (42.2–60.4)	0.0(0.0–0.1)	17.8 (14.4–18.4)	0.0(0.0–2.0)	15.0 (12.5–15.2)
Deschutes River fall	0.6(0.2–1.4)	0.0(0.0–0.0)	0.5(0.2–1.5)	5.0(3.0–6.7)	2.0(0.0–6.8)	2.8(2.1–4.1)
Upper Columbia River summer–fall	9.5(8.1–11.0)	0.9(0.0–5.1)	31.0 (27.7–33.3)	32.8 (29.1–36.6)	43.8 (34.1–52.3)	41.8 (36.4–42.8)
Mid-/upper Columbia River spring	28.3 (23.8–29.9)	13.5 (5.3–21.0)	20.8 (17.1–21.7)	2.3(1.3–2.9)	1.4(0.0–3.5)	0.0(0.0–0.1)
Snake River spring	27.3 (25.4–31.7)	22.3 (11.0–27.8)	20.2 (17.0–22.9)	3.0(2.1–3.9)	1.1(0.0–3.7)	0.1(0.0–0.1)
Snake River fall	4.8(3.3–5.7)	1.8(0.0–4.5)	10.2 (8.6–12.7)	30.4 (25.9–34.4)	14.8 (8.7–22.4)	10.6 (9.5–15.1)
Oregon coast	0.5(0.2–1.4)	0.0(0.0–1.3)	1.9(1.2–2.6)	0.6(0.1–1.5)	5.1(1.0–8.8)	11.9 (10.8–13.6)
Southern Oregon/California coast	0.0(0.0–0.2)	0.0(0.0–0.0)	0.0(0.0–0.4)	0.2(0.0–0.6)	0.0(0.0–2.2)	2.2(1.7–2.7)
Central Valley	0.0(0.0–0.1)	0.0(0.0–0.9)	0.0(0.0–0.1)	0.0(0.0–0.5)	0.0(0.0–3.1)	3.1(2.6–3.8)

spring-run stocks were farther north than other yearlings ($P < 0.001$; Table S.2). Upper Columbia River summer–fall-run and Snake River fall-run yearlings also shifted to the north from May to June ($P < 0.001$). For all yearlings, the spread in latitude was greater during June than during May, and this increase in variability was most evident for the upper Columbia River summer–fall stock and the Snake River fall stock ($P < 0.001$).

Yearlings were also closer to shore in June than in May (Table 5; Figure 1). The shift toward shore was most apparent for the interior basin stocks that were located farthest offshore in May ($P < 0.03$). Willamette River and West Cascade spring-run yearlings were also captured closer to shore, but the May-to-June comparisons were not significant for these stocks ($P = 0.29$ and 0.39 , respectively).

By June, Willamette River spring-run yearlings were closer to shore than yearlings of the other stocks ($P < 0.01$), and the mid-/upper Columbia River spring-run stock was the farthest offshore, although the distance from shore was not significantly different from that of the Snake River spring-run yearlings ($P = 0.44$). Yearlings of the West Cascade spring run, upper Columbia River summer–fall run, and Snake River fall run were intermediate in location between the more-offshore interior basin spring-run stocks and the nearer-shore Willamette River spring-run stock during both May and June.

Subyearlings.—In June, subyearlings from the upper Columbia River summer–fall-run and Snake River fall-run stocks were primarily dispersed along the Washington coast (Table 5; Figure 1). By September, subyearlings from the two stocks were distributed farther south, and the fish were distributed broadly across the entire latitudinal range of the study area. The change in mean latitude was not significant for the upper Columbia River summer–fall ($P = 0.08$) or Snake River fall ($P = 0.18$) subyearlings. In contrast, June and September distributions were relatively similar for the Spring Creek group fall-run subyearlings; these subyearlings were farther north than upper Columbia River summer–fall-run and Snake River fall-run stocks during June ($P < 0.01$; Table S.3). Subyearlings of the Spring Creek group fall stock also had the most northerly distribution of any stock in September when coastal stocks contributed to our catches ($P \leq 0.01$; Table S.4). Subyearlings from the Oregon coast stock were primarily distributed off the Oregon coast, whereas Washington coast subyearlings were situated farther north ($P < 0.001$) and largely caught off the coast of Washington.

During the summer, the distributions of subyearlings shifted strongly toward shore, and the variability in distance from shore also decreased. The shift inshore from June to September was evident for subyearlings of the upper Columbia River summer–fall-run stock and the Snake River fall-run

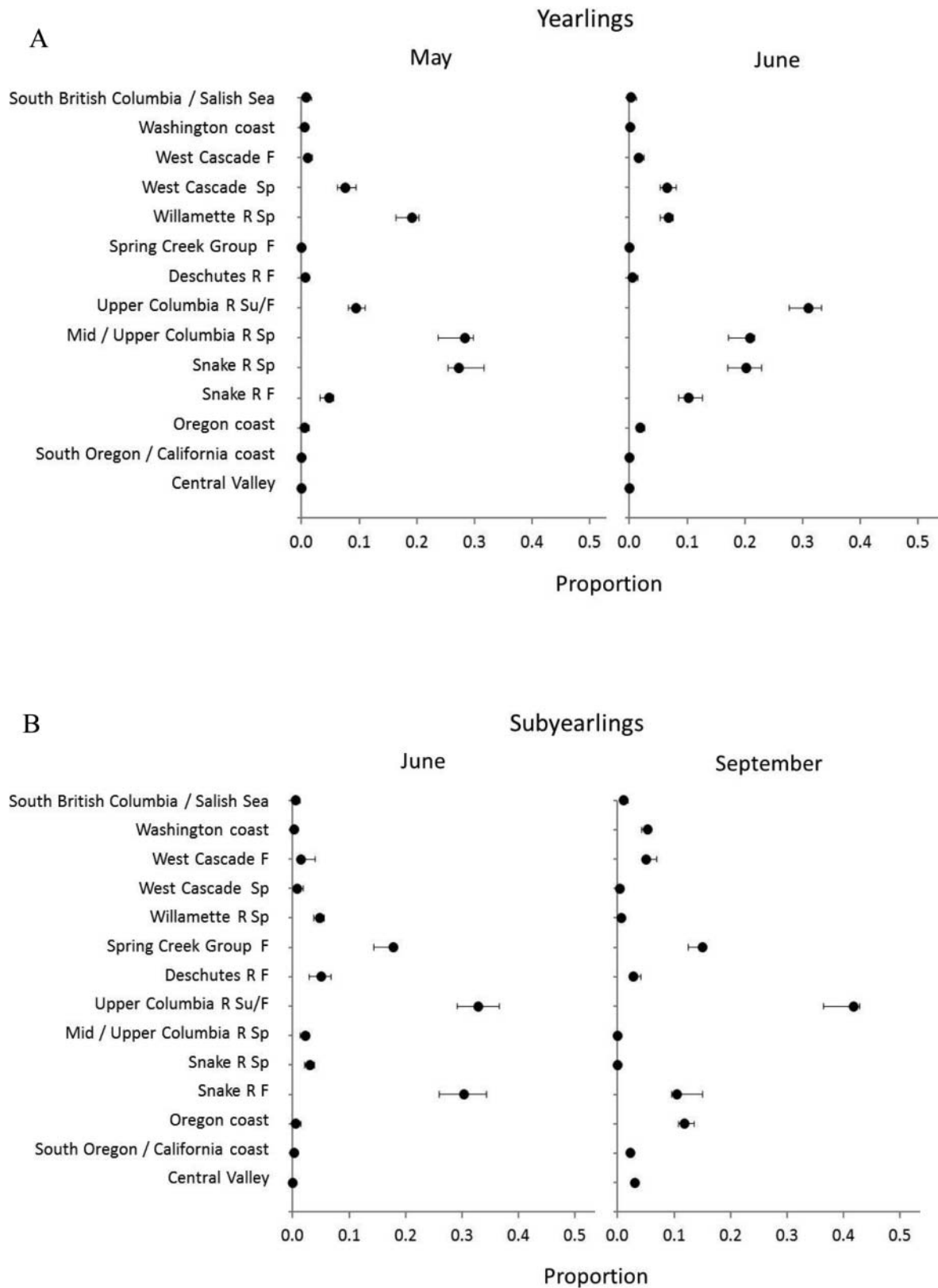


FIGURE 3. Estimated proportional stock composition (14 regional stocks) of (A) yearling and (B) subyearling Chinook Salmon sampled along the Washington and Oregon coasts in May (2006–2012), June (1998–2012), and September (1998–2012). Solid circles are the mean estimated proportions; horizontal lines are 95% confidence intervals derived from 100 bootstrap resamplings of baseline and mixed-stock genotypes (R = River, Sp = spring run, Su = summer run, F = fall run; May yearlings: $n = 1,896$; June yearlings: $n = 1,814$; June subyearlings: $n = 1,752$; September subyearlings: $n = 3,965$).

TABLE 5. Weighted mean latitude ($^{\circ}$ N) and distance from shore (nautical miles [nm]; 1 nautical mile = 1.852 km) for juvenile Chinook Salmon in samples collected along the Washington and Oregon coasts, presented for each life history type, stock, and sampling month. The variability metric is the weighted SD (spread) among annual means. For yearlings, bold italic values for a stock in June indicate a significant difference from the comparable May value. Similarly, for subyearlings, bold italic values for a stock in September indicate a significant difference from the comparable June value.

Stock	Latitude ($^{\circ}$ N)		Distance from shore (nm)	
	Mean	Spread	Mean	Spread
May yearlings				
West Cascade spring	46.72	0.40	13.25	53.58
Willamette River spring	47.03	0.45	10.74	38.10
Mid-/upper Columbia River spring	46.61	0.28	18.85	40.02
Snake River spring	46.55	0.24	18.92	39.11
Upper Columbia River summer–fall	46.49	0.21	15.62	62.07
Snake River fall	46.53	0.27	16.45	59.26
June yearlings				
West Cascade spring	47.02	0.54	8.72	27.13
Willamette River spring	47.12	0.73	6.78	15.50
Mid-/upper Columbia River spring	47.68	0.28	13.45	46.91
Snake River spring	47.68	0.37	12.52	42.88
Upper Columbia River summer–fall	47.06	0.66	10.24	39.82
Snake River fall	46.92	0.71	9.78	39.17
June subyearlings				
Willamette River spring	47.07	0.39	8.86	26.20
Spring Creek group fall	47.44	0.33	4.42	3.24
Upper Columbia River summer–fall	46.65	0.30	10.04	35.76
Snake River fall	46.76	0.27	10.92	42.32
September subyearlings				
Washington coast	47.10	0.71	5.40	5.07
West Cascade fall	46.44	0.84	4.75	6.02
Spring Creek group fall	47.53	0.26	5.14	1.94
Deschutes River fall	46.02	0.87	3.53	6.71
Upper Columbia River summer–fall	46.11	0.94	4.04	7.39
Snake River fall	46.31	1.14	4.03	6.13
Oregon coast	45.50	0.41	2.21	3.57
Southern Oregon/California coast	45.80	0.66	4.29	11.82
Central Valley	45.75	0.93	5.78	11.85

stock ($P < 0.001$). Overall, September subyearlings were primarily caught at the most inshore trawled station on each transect, and mean distances from shore ranged from 5.8 nautical miles for the Central Valley stock to 2.2 nautical miles for the Oregon coast stock.

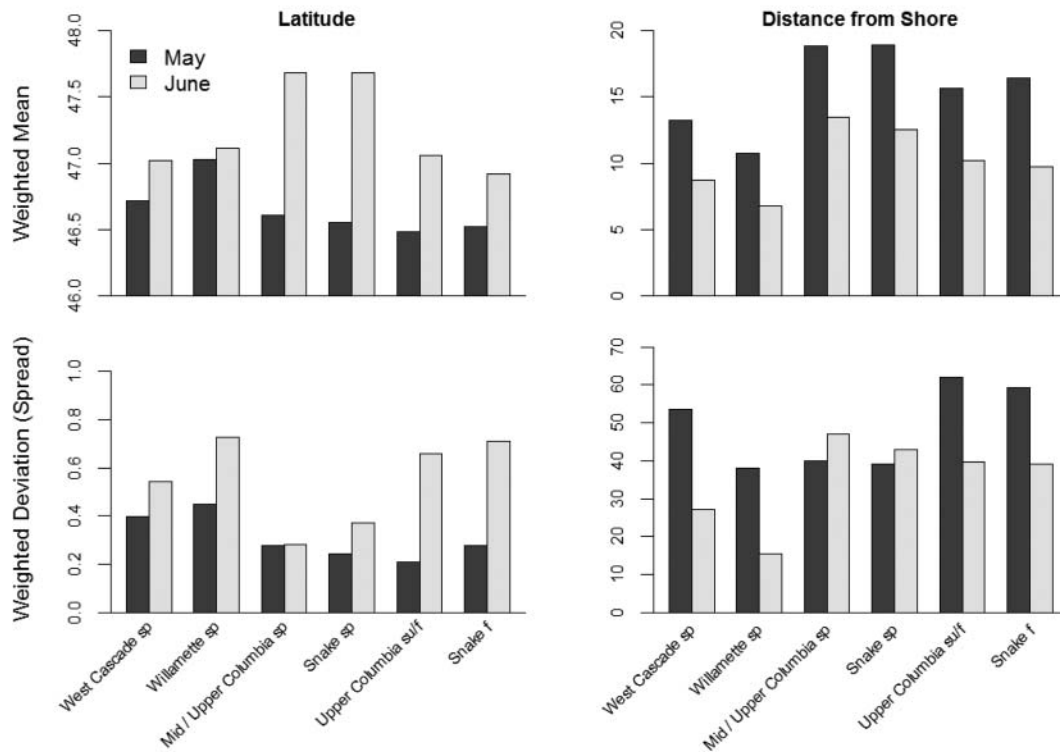
Interannual variation.—Juvenile Chinook Salmon distributions varied among years, and several patterns were consistent among stocks (Tables 6, 7). Overall, the lowest levels of interannual variability in latitude were observed for yearlings sampled in May (range of SD among years = 0.19–0.27). Variability in latitude for yearlings was greater in June (SD = 0.37–0.77). For yearlings of spring-run stocks, the variability in distance from shore also increased from May (SD = 2.3–3.7) to June (SD = 3.1–4.1). However, interannual variability in distance from shore for summer–fall-run and fall-run

yearlings was lower in June (SD = 2.4 and 2.8, respectively) than in May (SD = 4.8 and 3.8).

Among subyearlings, interannual variability in latitude increased from June to September for the Spring Creek group fall-run (SD = 0.59–0.76), upper Columbia River summer–fall-run (SD = 0.34–0.44), and Snake River fall-run (SD = 0.30–0.44) stocks (Table 7). In contrast, for those same three stocks, interannual variability in distance from shore decreased from June (SD = 2.4–6.3) to September (SD = 0.9–1.1).

Many of the patterns in mean latitude and distance from shore described above for yearlings and subyearlings were consistent among years (Figures 5, 6). For example, Willamette River spring-run yearlings were farther north and closer to shore in May than other stocks for all 6 years in which that

Yearlings



Subyearlings

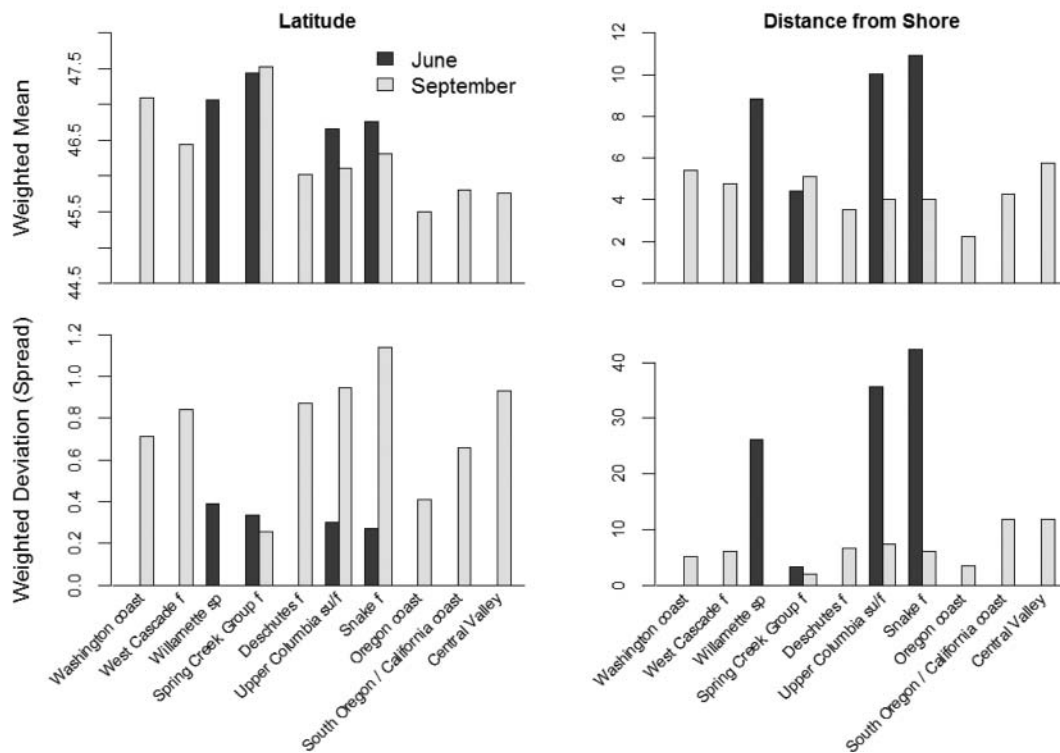


FIGURE 4. Weighted mean latitude ($^{\circ}$ N) and distance from shore (nautical miles [nm]; 1 nautical mile = 1.852 km) for yearling and subyearling Chinook Salmon of each stock sampled along the Washington and Oregon coasts in May, June, and September (sp = spring run; su = summer run; f = fall run). Variability is expressed as the weighted deviation (spread).

TABLE 6. Interannual variability in latitude (°N) and distance from shore (nautical miles [nm]; 1 nautical mile = 1.852 km) for yearling Chinook Salmon by sampling month and stock. Values were calculated by first estimating the weighted mean latitude or distance from shore for each year separately and then determining the SD of the annual values.

Stock	May		June	
	Latitude (°N)	Distance from shore (nm)	Latitude (°N)	Distance from shore (nm)
West Cascade spring	0.21	2.3	0.37	3.1
Willamette River spring	0.25	2.7	0.77	3.2
Mid-/upper Columbia River spring	0.27	3.5	0.45	3.7
Snake River spring	0.27	3.7	0.45	4.1
Upper Columbia River summer–fall	0.21	4.8	0.41	2.4
Snake River fall	0.19	3.8	0.47	2.8

stock was captured. During June, the mid-/upper Columbia River and Snake River spring-run yearlings were farther from shore than other stocks in 10 of 11 annual comparisons and were farther north than other stocks in all 11 years. However, although the mean latitude of spring-run yearlings increased from May to June in all 18 annual comparisons, this shift northward was observed in only 6 of 10 comparisons for yearlings of the upper Columbia River summer–fall and Snake River fall stocks.

Several distribution patterns were also consistent among years for subyearlings (Figure 6). The Spring Creek group fall-run stock was located farther north than the upper Columbia River summer–fall-run and Snake River fall-run stocks during both June and September in 14 of 15 annual comparisons. Upper Columbia River summer–fall-run and Snake River fall-run subyearlings shifted closer to shore in all 19 annual comparisons.

Yearlings and subyearlings from the same stock—Mean latitude and distance from shore were compared between

yearlings and subyearlings from the same stock (Table 5; Figure 4). We were able to make this comparison for three of the stocks sampled in June. For the upper Columbia River summer–fall stock, yearlings were farther north than subyearlings ($P < 0.001$). Yearlings of the Snake River fall-run stock were also farther north than subyearlings of that stock, but the comparison was not significant ($P = 0.20$). Mean latitude was not significantly different between yearlings and subyearlings of the Willamette River spring-run stock ($P = 0.99$). For all three stocks, yearlings had a greater latitudinal spread than subyearlings (upper Columbia River summer–fall: $P < 0.001$; Snake River fall: $P < 0.001$; Willamette River spring: $P = 0.04$). In addition, Willamette River subyearlings were further offshore ($P = 0.01$) and more spread out in distance from shore ($P = 0.01$) than were the stock's yearlings.

Marked and unmarked juveniles from the same stock.—In September, marked Snake River fall subyearlings had a more northerly distribution than the stock's unmarked subyearlings

TABLE 7. Interannual variability in latitude (°N) and distance from shore (nautical miles [nm]; 1 nautical mile = 1.852 km) for subyearling Chinook Salmon by sampling month and stock. Values were calculated by first estimating the weighted mean latitude or distance from shore for each year separately and then determining the SD of the annual values. Stocks or months with no value had sample sizes less than 75 fish.

Stock	June		September	
	Latitude (°N)	Distance from shore (nm)	Latitude (°N)	Distance from shore (nm)
Washington coast			0.57	1.6
West Cascade fall			0.56	1.2
Willamette River spring	0.48	2.9		
Spring Creek group fall	0.59	6.3	0.76	0.9
Deschutes River fall			0.45	1.5
Upper Columbia River summer–fall	0.34	2.4	0.44	1.1
Snake River fall	0.30	2.9	0.44	1.0
Oregon coast			0.29	1.1
Southern Oregon/California coast			0.58	1.8
Central Valley			0.85	3.0

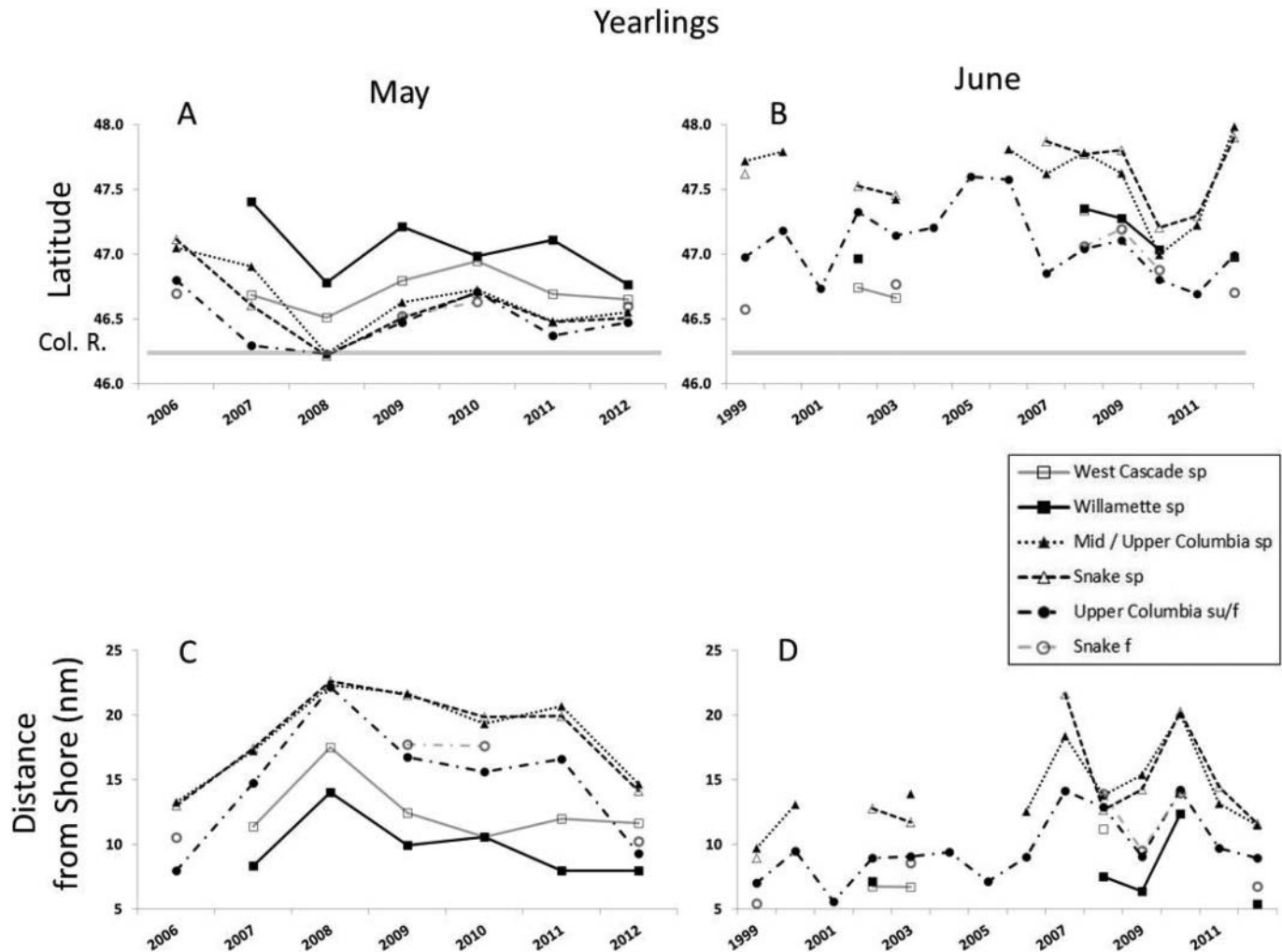


FIGURE 5. Annual weighted mean (A) latitude (°N) in May, (B) latitude in June, (C) distance from shore (nautical miles [nm]; 1 nautical mile = 1.852 km) in May, and (D) distance from shore in June for yearling Chinook Salmon representing various stocks sampled along the Washington and Oregon coasts (sp = spring run; su = summer run; f = fall run). Sampling months with fewer than 10 fish for a given stock were excluded from this analysis; none of the stocks sampled in June 1998 met the minimum sample size criterion. The gray horizontal line indicates the latitude of the Columbia River mouth.

($P = 0.03$). Latitude in June, distance from shore in June, and distance from shore in September did not significantly differ between the two groups. Similar comparisons for marked and unmarked upper Columbia River summer–fall subyearlings indicated no significant differences.

DISCUSSION

Chinook Salmon Stock Composition

Genetic estimates based on 15 years of sampling in coastal habitats off Washington and Oregon revealed that fish from Columbia River sources comprise approximately 98% of yearlings present during late spring and early summer. This finding is consistent with previous studies showing that most tagged yearlings within our sampling area are from hatcheries located

in the Columbia River basin (Miller et al. 1983; Fisher and Percy 1995; Trudel et al. 2009; Fisher et al. 2014). In addition, we estimated that only 6% of yearlings in these marine habitats are naturally produced. In the seven most recent years of sampling, our catches included fewer than 200 naturally produced yearlings. Thus, our findings reflect the massive scale of contemporary yearling Chinook Salmon production by Columbia River hatcheries (Table 2) but also indicate the diminished abundance of natural populations in the Columbia and Snake rivers (Myers et al. 1998; Ford 2011). Moreover, taken together with the rarity of naturally produced Coho Salmon *O. kisutch* in the coastal ocean (Teel et al. 2003) and the patchy marine spatial distribution of Chinook Salmon and Coho Salmon yearlings (Peterson et al. 2010), our results highlight the difficulty of sampling ESA-protected Columbia River salmon populations in coastal habitats—yet those

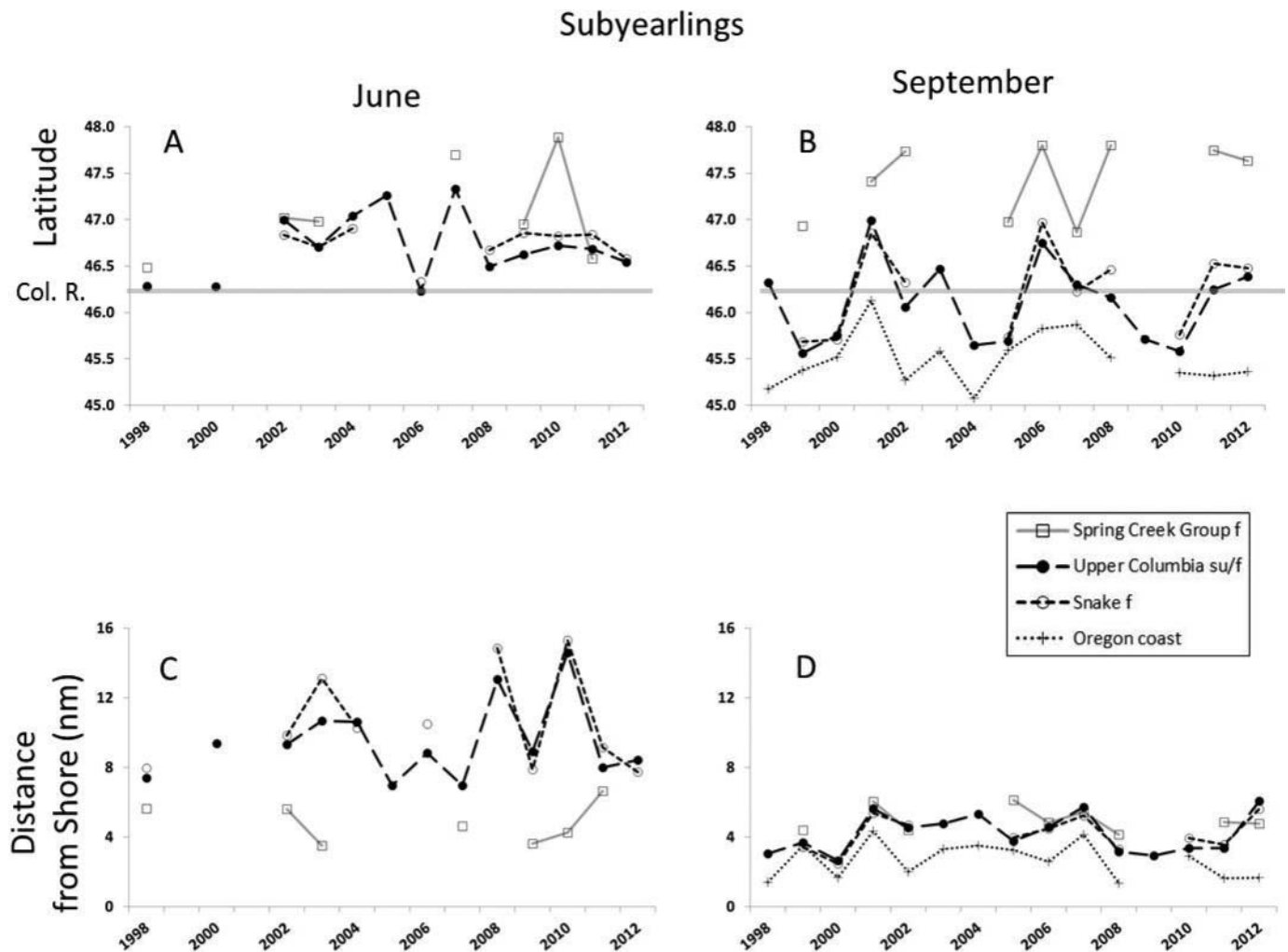


FIGURE 6. Annual weighted mean (A) latitude in June ($^{\circ}$ N), (B) latitude in September, (C) distance from shore (nautical miles [nm]; 1 nautical mile = 1.852 km) in June, and (D) distance from shore in September for subyearling Chinook Salmon of the four stocks that were most abundant in samples collected along the Washington and Oregon coasts (su = summer run; f = fall run). Sampling months with fewer than 10 fish for a given stock were excluded from this analysis; none of the stocks sampled in June 1999 or June 2001 met the minimum sample size criterion. The gray horizontal line indicates the latitude of the Columbia River mouth.

populations are frequently of greatest concern in marine growth and survival studies conducted in the region (Jacobson et al. 2008; Burla et al. 2010; Daly et al. 2012; Miller et al. 2014).

In contrast to the yearling composition, Chinook Salmon subyearlings sampled off the Oregon and Washington coasts comprised greater proportions of fish from coastal rivers and also included more fish that were naturally produced. In early summer, subyearlings were nearly all from the Columbia River, with substantial proportions from the upper Columbia River summer–fall-run (33%) and Snake River fall-run (30%) stocks. However, in autumn, when subyearlings were most abundant, nearly 25% of the subyearlings were from coastal sources and nearly half of those fish originated from northern and central Oregon coastal rivers. Small proportions of subyearlings from populations in coastal Washington, southern

Oregon, and California also occupied the nearshore habitats. Unlike the sparseness of naturally produced yearlings off Oregon and Washington, we estimated that natural production accounted for more than one-third of the subyearlings. By far, the largest contribution of natural subyearlings was from the upper Columbia River summer–fall stock; this is likely due to the robust natural spawning of fall-run fish in the Hanford Reach, located upstream of the Snake River confluence (Dauble and Watson 1997).

It is worthwhile to note that although yearling life histories are predominant in spring-run populations of Chinook Salmon, substantial proportions of the fish that we classified as subyearlings were allocated to spring-run stocks. This result is not surprising with regard to lower Columbia River spring-run stocks (i.e., Willamette River and West Cascade), for which subyearling downstream movements and subsequent estuarine

rearing are well documented (Craig and Townsend 1946; Hymer et al. 1992; Roegner et al. 2012; Teel et al. 2014). Less expected were our estimates of subyearling life histories for the Snake River and mid-/upper Columbia River spring runs, since their freshwater-returning adults almost all enter the ocean as yearlings (Waples et al. 2004; Hess et al. 2014). Among the interior basin spring-run fish that were smaller than our size-based thresholds for yearlings in May (>120 mm) and June (>140 mm), nearly all were without hatchery marks (data not shown), suggesting that they were naturally produced. Further study should include age determinations (e.g., analysis of scales or otoliths) to verify our life history classification of small, naturally produced fish from these stocks. Although we have verified our cut-offs for hatchery fish, additional data may show that our size-at-capture delineations are not appropriate for use with yearlings reared in low-growth environments of the interior Columbia and Snake rivers.

The lack of West Cascade fall-run subyearlings in our catches is intriguing and may be explained by an insufficiency of inshore sampling. Despite constituting nearly 25% of the subyearling hatchery production in the Columbia River basin, releases of the West Cascade fall stock contributed only 3% to our catches of hatchery subyearlings. Moreover, during summer, naturally produced fry and fingerlings of the West Cascade fall-run stock are predominant in shallow rearing areas throughout the lower Columbia River estuary (Roegner et al. 2012; Teel et al. 2014), yet the stock comprised only 5% of our ocean-caught subyearlings in September. Previous studies off the coasts of Oregon and Washington have documented the presence of small Chinook Salmon subyearlings (<130 mm) inshore of 4 km (Miller et al. 1983; Fisher and Percy 1995), including in shallow, sandy beach surf-zone habitats (Marin Jarrin et al. 2009). Stock-specific analyses were not conducted in those earlier studies. Nonetheless, we conjecture that small, naturally produced subyearlings of the West Cascade fall run are more abundant inshore of our sampling grid and likely north of the Columbia River, where our stations began 3–6 nautical miles offshore.

Seasonal Density Patterns

Although the densities of Chinook Salmon yearlings along the Washington and Oregon coasts fluctuated annually, strong seasonal shifts were apparent each year (Figure 2). The peak densities that we observed at the end of May occurred relatively soon after the spring emigration of yearlings from the Columbia River and adjacent coastal rivers (Rich 1920; Healey 1991; Weitkamp et al. 2012). At the end of June, the decreased yearling densities in the area likely reflected both mortality, which remains largely unquantified (Emmett and Krutzikowski 2008; Burke et al. 2013b), and the well-known migration of yearlings into more northerly regions (Orsi et al. 2000; Trudel et al. 2009; Tucker et al. 2011; Fisher et al.

2014). Although migration patterns and rates differed among stocks (Figure 1; Fisher et al. 2014), by autumn the density of yearlings in the region was low (Figure 2; Peterson et al. 2010). However, it is important to note that although many yearlings reside in coastal areas off Washington and Oregon rather briefly, it is a critical period of feeding and growth and is essential for determining the year-class strength of Columbia River spring-run Chinook Salmon (Tomaro et al. 2012; Burke et al. 2013b; Miller et al. 2014).

Subyearlings were prevalent in coastal areas during early summer and—in contrast to yearlings—they were also abundant off the Oregon and Washington coasts during autumn. In most years, subyearling densities increased during the summer, in part because the timing of ocean entry for subyearlings is very protracted and out-migration from the region's rivers is substantial throughout the summer (Rich 1920; Reimers 1973; Howell et al. 1985; McCabe et al. 1986; Roegner et al. 2012). Unlike yearlings, relatively few of the region's subyearlings migrate north of Washington during their first ocean summer (Tucker et al. 2011; Fisher et al. 2014). Interestingly, in 4 of the 15 years of sampling, subyearling densities were lower in September than in June, suggesting fluctuations in either recruitment or survival. However, a recent analysis of upper Columbia River summer–fall Chinook Salmon indicated that neither June subyearling density nor September subyearling density is a strong predictor of subsequent adult abundance (Miller et al. 2013). Nonetheless, Miller et al. (2013) found that survival is positively related to river plume size and also to the coastal ocean conditions experienced by subyearlings off Oregon and Washington during the summer.

Yearling Distributions

In late spring, differences in the initial distributions of yearlings from different stocks did not conform to the generalized migration patterns that have been previously documented for Columbia River stocks (Trudel et al. 2009; Fisher et al. 2014). We found that Willamette River and West Cascade spring-run juveniles, which comprised more than 25% of May yearlings, were farther north than yearlings from the interior basin spring-run stocks, which exhibit more rapid northward migrations. Clearly, distributions and stock abundances in the spring are influenced by (1) the timing of large hatchery releases of juveniles and (2) the timing of ocean entry. Large releases of Willamette River and West Cascade spring-run juveniles begin in February, well before the peak releases of yearlings from other parts of the basin (Table 2). The lower Columbia River yearlings enter the ocean primarily in April, earlier than yearlings from the interior Columbia River (Weitkamp et al., in press). Lower-river yearlings are also larger than interior basin yearlings after ocean entry (Burke et al. 2013a); as a result, they may be capable of faster swim speeds, which could also contribute to the more northward location of Willamette

River and West Cascade spring-run yearlings during the initial marine period.

Physical and environmental factors affect the marine migrations of Columbia River yearlings (Peterson et al. 2010; Burke et al. 2013a; McMichael et al. 2013) and likely influenced the distributions observed in our study. Our large catches along the Columbia River transect in May were mostly at stations farther offshore than our catches along the Washington coast. This pattern was very apparent for yearlings from the mid-/upper Columbia River and Snake River spring-run stocks, which were more offshore than other yearlings. By June, yearlings of these stocks as well as other stocks were distributed closer to shore. One explanation for these patterns is that currents associated with the Columbia River affect the early spatial distribution of yearlings by sweeping them offshore, which is followed by “corrective” movements toward shore as the fish swim northward. A change in movement direction associated with ocean currents was also recently documented by McMichael et al. (2013), who used acoustic telemetry to track yearling Chinook Salmon in marine habitats near the Columbia River mouth. In that study, yearlings initially migrated south in the river plume before reversing direction and moving northward. Behavioral compensation for ocean currents and other external factors is also supported by multiple recent modeling studies of salmon movements in the marine environment (Burke et al. 2014; Putman et al. 2014), which demonstrated that salmon alter their swim speed and direction to account for ocean currents. Moreover, the analysis by Burke et al. (2013a) showed that during their early ocean migration, Chinook Salmon yearlings from the Columbia River display stock-specific behavioral responses to local environmental factors (chlorophyll-*a* concentration and temperature) in addition to broad-scale geospatial cues (latitude and distance from shore).

By June, yearling distributions along the coast of Washington clearly reflected behavioral differences that characterized subsequent stock-specific migrations along the coastal shelf. Consistent with the CWT analysis of Fisher et al. (2014), we found that yearlings from the mid-/upper Columbia River and Snake River spring-run stocks were farthest north and also had the smallest latitudinal spread. After leaving our study area, yearlings from these stocks continue to migrate rapidly northward; they reach Alaska in the summer and move off the continental shelf by autumn (Orsi et al. 2000; Trudel et al. 2009; Tucker et al. 2011; Fisher et al. 2014). Our June data revealed a much different distributional pattern for lower Columbia River spring-run, upper Columbia River summer–fall-run, and Snake River fall-run yearlings. These stocks were significantly more spread out along the coast than the interior basin spring-run yearlings, and they included fish that migrated southward to habitats off the coast of Oregon. Moreover, although yearling densities off Oregon and Washington were low in autumn, the predominant sources of yearlings that remained in the region during autumn were the interior basin summer–fall-run

and lower-river spring-run stocks. These findings are consistent with those of Fisher et al. (2014), who reported that coded-wire-tagged hatchery yearlings from these stocks dispersed in coastal areas from Oregon to Alaska.

Subyearling Distributions

Although subyearlings were concentrated near shore along the Oregon and Washington coasts at the end of summer, stock-specific distributions differed in latitude and inshore distance. For some stocks, these spatial differences were consistent with previous observations that Chinook Salmon subyearlings tend to remain relatively close to the point of sea entry throughout their first ocean summer (Tucker et al. 2011). For example, the movements of subyearlings from coastal rivers adjacent to the Columbia River were very limited: at the end of September, subyearlings from Washington coastal rivers were found along the Washington coast, and those from Oregon coastal rivers were mostly distributed along the Oregon shoreline. In addition, juveniles from Oregon coastal rivers remained much closer to shore than subyearlings from other stocks, including those from southern Oregon and California, which were also distributed along the Oregon coast in September.

However, other latitudinal differences among stocks are due to differing movement patterns, even between fall-run stocks with the same ocean entry location. The diverse marine migrations that have evolved in upper Columbia River summer–fall-run and Snake River fall-run Chinook Salmon include large proportions of subyearlings that migrate southward along the Oregon coast during their first summer at sea. By autumn, subyearlings from the two interior basin stocks were broadly distributed in nearshore habitats from central Oregon to northern Washington. Subyearlings of these stocks were the only groups in our analysis that had a mean shift to the south during the summer, exhibiting a distribution pattern very different from those of some other stocks. For example, among the subyearlings we studied, those of the Spring Creek group had the most northern mean latitude, with relatively little change throughout the summer. By September, Spring Creek group subyearlings had the smallest spread both in latitude and in distance from shore.

The distinctive marine distribution is one of several distinguishing life history characteristics of interior Columbia River fall-run Chinook Salmon (Howell et al. 1985; Myers et al. 1998). Unlike the Spring Creek group fall-run subyearlings, whose freshwater out-migration is concentrated in spring, fish from the upper river occupy estuarine habitats throughout the summer and have very protracted movements to the ocean (Roegner et al. 2012; Teel et al. 2014). However, the difference in ocean entry timing alone does not appear to explain the more southerly marine distribution of the upper-river fish during autumn. Claiborne et al. (2014) used otolith chemistry and structure to study a subset of the upper Columbia River

summer–fall subyearlings from our study; those authors found that the latitudinal distribution in late September was not related to how long the fish had occupied marine habitats (i.e., even some of the early migrants were south of the Columbia River in September). Interestingly, the more southern early marine distribution of upper-river subyearlings does not provide insight into their subsequent coastal distributions as adults. For example, substantial proportions of upper Columbia River fall-run fish are intercepted in fisheries conducted off Alaska and northern British Columbia, whereas Spring Creek group fall-run fish are rarely caught north of Vancouver Island in southern British Columbia (Norris et al. 2000; Weitkamp 2010).

Accurate assessments of stock-specific marine distributions rely on accurate assignments of ocean-caught juveniles to their source stocks. A recent study concluded that reasonably accurate estimates of Chinook Salmon stock identities can be obtained with the microsatellite DNA loci and baseline database used in our study (Hess et al. 2014). Our allocations of fish with CWTs produced results that were consistent with the findings of Hess et al. (2014), who used a leave-one-out method to evaluate assignment accuracies. The accuracy of our assignments to the Columbia River (99%) was also similar to the 97% accuracy obtained by Tucker et al. (2011), who analyzed known-origin Chinook Salmon juveniles by using a different set of microsatellites and a different baseline of populations. However, within the Columbia River, assignment accuracy rates are diminished by a legacy of extensive hatchery stock transfers between regions (Myers et al. 1998, 2006; Hess et al. 2014). In our study, misallocations within interior basin genetic lineages likely inhibited our ability to detect potential differences in distribution (1) between Snake River spring-run yearlings and mid/upper Columbia River spring-run yearlings and also (2) between Snake River fall-run and upper Columbia River summer–fall-run juveniles. This lack of power may have contributed to the near absence of significant differences in our comparisons of these two pairs of stocks. We anticipate that greater resolution for these stocks will be obtained through the identification of high-resolution single-nucleotide polymorphisms (Larson et al. 2014) and through recent efforts to implement parentage-based tagging at Columbia River hatcheries (Steele et al. 2013).

Conclusions

The juvenile Chinook Salmon distribution patterns we identified, many of which are consistent across years, illustrate inherent differences in migration behavior between life history types (age at sea entry) and among stocks. Our findings are in agreement with those of Fisher et al. (2014), who recently documented the differing dispersal of yearling Chinook Salmon from interior spring-run ESUs relative to yearlings from other Columbia River ESUs. Importantly, our study revealed that early marine distributions of subyearlings also

differed among stocks, particularly between interior basin and lower-river stocks.

Distributions also appear to be influenced by extrinsic factors, such as currents or plume conditions, and by hatchery practices. For example, differences in the timing of hatchery releases may determine the sequence with which specific hatchery stocks occupy plume and coastal habitats, possibly influencing the match–mismatch between salmon and their ephemeral prey base (Scheuerell et al. 2009; Miller et al. 2014). Moreover, age at release is also under hatchery control, and we showed that yearlings and subyearlings from the same stock can have differing distributions. Of the stocks included in our analysis, the upper Columbia River summer–fall, Snake River fall, and Willamette River spring stocks have hatchery programs with large releases of both subyearlings and yearlings. The marine distributions of these stocks are therefore most affected by contemporary age-at-release management strategies.

It is hoped that the early marine distributions we have documented will be viewed in the context of ongoing efforts for Chinook Salmon conservation in the Pacific Northwest. Overall, the distribution patterns were largely consistent with the region's Chinook Salmon ESUs, which were delineated by using a synthesis of genetic, ecological, and life history data (Myers et al. 1998; Ford 2011). Moreover, age at ocean entry and ocean distribution patterns are among the variable traits that are considered important for the recovery of endangered and threatened salmon ESUs (Waples et al. 2001, 2004; Good et al. 2007). Such phenotypic and spatial diversity allows species and ESUs to access an array of marine habitats and therefore respond to both short-term and long-term environmental change. The framework developed under the ESA to evaluate salmonid population viability therefore includes trait diversity as a key parameter (McElhany et al. 2000). We recommend broadening those evaluations to incorporate metrics that describe among- and within-ESU variability in early marine distributions.

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