



Ocean distribution and habitat associations of yearling coho (*Oncorhynchus kisutch*) and Chinook (*O. tshawytscha*) salmon in the northern California Current

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ABSTRACT

Yearling juvenile coho and Chinook salmon were sampled on 28 cruises in June and September 1981–85 and 1998–07 in continental shelf and oceanic waters off the Pacific Northwest. Oceanographic variables measured included temperature, salinity, water depth, and chlorophyll concentration (all cruises) and copepod biomass during the cruises from 1998–07. Juvenile salmonids were found almost exclusively in continental shelf waters, and showed a patchy distribution: half were collected in ~5% of the collections and none were collected in ~40% of the collections. Variance-to-mean ratios of the catches were high, also indicating patchy spatial distributions for both species. The salmon were most abundant in the vicinity of the Columbia River and the Washington coast in June; by September, both were less abundant, although still found mainly off Washington. In June, the geographic center-of-mass of the distribution for each species was located off Grays Harbor, WA, near the northern end of our sampling grid, but in September, it shifted southward and inshore. Coho salmon ranged further offshore than Chinook salmon: in June, the average

median depth where they were caught was 85.6 and 55.0 m, respectively, and in September it was 65.5 and 43.7 m, respectively. Abundances of both species were significantly correlated with water depth (negatively), chlorophyll (positively) and copepod biomass (positively). Abundances of yearling Chinook salmon, but not of yearling coho salmon, were correlated with temperature (negatively). We discuss the potential role of coastal upwelling, submarine canyons and krill in determining the spatial distributions of the salmon.

Key words: Chinook salmon, coho salmon, northern California Current, patchiness, pelagic habitat

INTRODUCTION

Recruitment of many Pacific salmonid populations in the California Current has fluctuated by more than an order of magnitude over the past 40 yr. For example, smolt-to-adult survival of hatchery-raised coho salmon (*Oncorhynchus kisutch*) for the period 1960–77 ranged from 5 to 10%, for 1978–91 from 2 to 7%, but then plummeted to <1% from 1992–97 (Logerwell *et al.*, 2003). These interannual variations in survival appear to be linked to decadal scale variability in climate and ocean conditions (Mantua *et al.*, 1997). Ocean conditions during the period of high coho salmon marine survival before 1977 were characterized by relatively cool ocean temperatures and high productivity in the northeast Pacific Ocean. In 1978, a 20-yr period of warmer ocean conditions and low productivity began (Roemmich and McGowan, 1995), and poor salmon marine survival ensued (Logerwell *et al.*, 2003).

Following the strong 1997–98 El Niño event, the climate of the eastern North Pacific underwent a rapid and striking transition, suggesting that a climate shift occurred (Peterson and Schwing, 2003). Upwelling-favorable winds strengthened, coastal waters cooled by several degrees Celsius, and many Pacific Northwest salmon stocks began to recover. This recent climate shift, starting in autumn 1998, may be a major factor in the increases in ocean survival of both coho and Chinook salmon observed from 2000–03 in the Pacific

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Northwest (Logerwell *et al.*, 2003; Peterson and Schwing, 2003).

It is now widely accepted that salmon survival is strongly linked to ocean conditions (Percy, 1992). Furthermore, survival is believed to be set during a salmonid's first summer at sea (Percy, 1992). However, research has yet to establish the nature of the mechanisms and linkages between ocean conditions and salmon growth and survival. To study this problem, we need to establish where these salmonids live as juveniles during their first few months in the ocean and we need to describe the characteristics of these habitats. It is only after we have determined where salmon live during the first summer at sea that we can begin to explore physical and biological variables that might affect salmon growth and survival.

Even though much research has been directed at studying the ecology and habitats occupied by juvenile salmon in the sea (reviewed by Brodeur *et al.*, 2000; Percy, 1992), our understanding of the distribution and movement patterns of juvenile salmon in the ocean remains rudimentary. Scientists with the U.S. GLOBEC program studied the distribution and abundance of juvenile salmonids off central and southern Oregon in June and August 2000 and 2002 (Brodeur *et al.*, 2004). Significant associations were found between sea surface temperature (T), salinity (S), chlorophyll (CHL) and bottom depth (D), and the abundance of coho or Chinook salmon in August but not June. While many correlations between juvenile salmon fish abundance and environmental variables were weak, Brodeur *et al.* (2004) and Percy and Fisher (1990) noted one consistent pattern: the distribution of juvenile salmonids was restricted to shelf waters.

Bi *et al.* (2007) compared the presence/absence of yearling Chinook and coho salmon in trawl surveys in 1998–05 with D, T, S, and CHL, using logistic regression to determine the probability of not catching (and catching) juvenile salmon at a given station. For all life history stages, the probability of a zero-catch decreased as chlorophyll concentration increased and depth decreased; decreasing temperature also significantly predicted the presence of yearling Chinook salmon. Environmental variables that were not significant predictors included nutrients and salinity. Bi *et al.* (2007) concluded that a larger area of juvenile salmon habitat occurred off Washington and the mouth of the Columbia River than off Oregon. As chlorophyll-*a* was a good indicator of juvenile salmonid habitat, Bi *et al.* (2008) used the distribution of chlorophyll-*a* from the SeaWiFS satellite to map potential salmon habitat. During warm ocean years (e.g., 1998 and 2005), juvenile salmon habitat was more

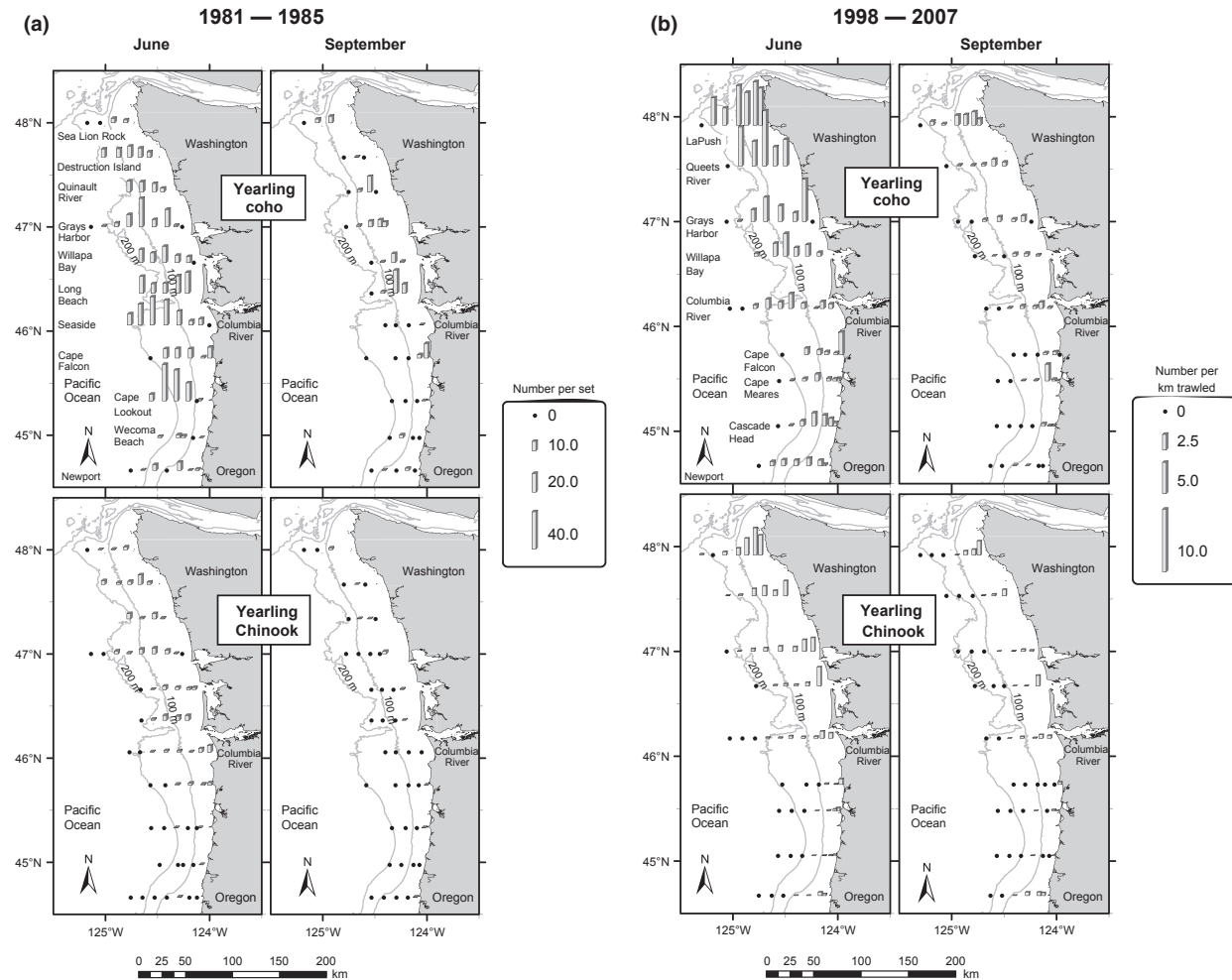
fragmented and less connected than during cold years (such as 1999–02). During cold years, habitat was continuous along the entire inner-middle shelf, and had a far greater area than during the warm years.

The purposes of this paper are (i) to define and describe *seasonal and interannual* patterns in the distribution, abundance, and habitat associations of yearling coho and Chinook salmon in relation to water depth, temperature, salinity, chlorophyll, and copepod biomass, and (ii) to compare patterns in these variables from two different studies: a purse seine data set in 1981–85 (Percy and Fisher, 1990), and a 10-yr trawl survey from cruises in the same region in 1998–07. This study differs from those of Bi *et al.* (2007, 2008) in that it considers interannual variations in habitat usage, and makes use of the catch per unit effort data (rather than presence/absence data used in Bi *et al.*, 2007, 2008) in relation to habitat parameters. We include data from the 1980s that have not been analyzed previously in terms of habitat parameters. In this paper we also elaborate on new results concerning (i) patchiness of salmon distributions, (ii) relationships between habitat size and upwelling strength, and (iii) the coincidence of the distributions of euphausiids with salmon, as indexed by the distribution of euphausiid eggs. We discuss how the cross-shelf distributions of salmonids relate to cross-shelf zonation of zooplankton and consider the role that submarine canyons along the Washington shelf might play in establishing large areas of suitable habitat for juvenile salmon.

MATERIALS AND METHODS

From 1981 to 1985, juvenile salmon were collected off Oregon and Washington with a herring purse seine. Here we reanalyzed catches from the June and September cruises (Percy and Fisher, 1990). We refer to these efforts as the OSU survey (OSU = Oregon State University). From 1998 to the present, juvenile salmon were collected with a pelagic rope trawl during June and September. We refer to these efforts as the BPA survey (BPA = Bonneville Power Administration, the source of funds for this project). Figure 1 shows transect and station location (as well as the average catches) for sampling in 1981–85 (eight cruises) and 1998–07 (20 cruises). The purse seine was 32-mm mesh, 457–495 m long, 20–60 m deep, and was set in a circle with a diameter of 146–158 m and an area of 16 600–19 500 m² (Percy and Fisher, 1990). The rope trawl was a Nordic 264 manufactured by Nor'Eastern Trawl Systems (Bainbridge Island, WA, USA), with a mouth opening

Figure 1. Catches of juvenile (yearling) coho and Chinook salmon in June and September averaged over the years 1981–85 during the OSU study (a) and 1998–07 during the BPA study (b).



~30 m wide by ~20 m high and 200 m long, with a cod-end liner of 0.8-cm mesh. Tows sampled the upper 20 m of the water column, were usually of 30 min duration, sampling approximately 3+ km or 90 000+ m² of water. This value is about five times the surface area sampled by the purse seine. Results are reported separately for these two gear types because their relative efficiencies for catching juvenile salmon are unknown. Our interest was in investigating whether salmon distributions in both inshore–offshore and north–south directions were similar or different between the two decades (1980s versus 2000s). Both studies sampled along transects perpendicular to the coastline, at five to seven stations from as close to shore as possible (~30 m depth), and offshore to just beyond the shelf break. Table 1 lists cruise dates, number of hauls, and the depth range of stations sampled.

During the OSU survey, the sea surface temperature was measured with a mercury thermometer. A water sample was collected with a 1-L Niskin bottle from a depth of 1 m for later analysis of salinity with a laboratory bench-top salinometer and chlorophyll-*a* collected on GF/F filters, extracted in 90% acetone, then fluorescence measured with a calibrated Model-10 Turner Designs fluorometer. During the BPA surveys, a water sample was collected with a 1-L Niskin bottle from a depth of 3 m for later analysis of chlorophyll (GF/F filters) extracted with 90% acetone then run on a calibrated Turner 10-AU fluorometer (845 W. Maude Ave, Sunnyvale, CA, USA). In addition, during the BPA surveys, a vertical profile of temperature and salinity was made using a Sea-Bird SBE-19plus CTD (Sea-Bird Electronics, 13431 N 20th Street, Bellevue, WA, USA). Zooplankton was collected during the BPA surveys with a 0.5-m diameter

Table 1. Summary of data sources for juvenile salmon caught in purse seines (1981–85) and in the Nordic trawl (1998–07).

Cruise	Total # of hauls	Depth range (m)
Jun 81	38	26–366
Jun 82	41	11–560
Sep 82	27	53–571
Jun 83	36	33–549
Sep 83	32	40–192
Jun 84	42	40–345
Sep 84	42	43–549
Jun 85	54	27–920
Jun 98	31	18–329
Sep 98	39	27–457
Jun 99	43	24–1097
Sep 99	45	21–531
Jun 00	27	31–856
Sep 00	27	31–245
Jun 01	45	29–622
Sep 01	42	28–330
Jun 02	45	25–1,080
Sep 02	43	28–203
Jun 03	53	22–1078
Sep 03	37	24–307
Jun 04	49	27–547
Sep 04	45	25–271
Jun 05	39	28–343
Sep 05	42	23–336
Jun 06	51	25–1465
Sep 06	44	25–512
Jun 07	43	23–588
Sep 07	34	27–176

200- μ m mesh net hauled vertically from a maximum depth of 100 m to the surface. The OSU surveys included only a few zooplankton samples and thus are not part of the analyses in this paper.

Juvenile salmon captured in trawls were identified, measured, and frozen for further analysis. Juvenile salmon were assigned to length-based age classes modified from those of Percy and Fisher (1990) and Fisher and Percy (1995) based on ongoing sampling of fishes from coastal Oregon and Washington (J. Fisher, Oregon State University, USA, pers. comm.). Chinook salmon captured during June with fork lengths (FL) between 141 and 280 mm FL and coho salmon ≤ 330 mm FL were considered yearlings. In September, Chinook salmon between 251 and 400 mm FL and coho salmon ≤ 450 mm FL were considered yearlings. Coho salmon in the 1980s were a mix of 'normal' yearlings and smaller 'accelerated growth' sub-yearling fish released from commercial salmon ranches throughout the summer. In June, most

coho salmon were yearlings (Percy and Fisher, 1988). In September, the two ages of coho salmon were distinguished using fork length, and those of 230–450 mm FL were classified as yearling fish. Only the yearling coho salmon are included in this study.

Catch data were standardized to effort [catch per unit effort (CPUE): numbers per set (1981–85)] or numbers per km towed (1998–07). The catch data from 1981 were multiplied by 1.17 to correct for the slightly smaller purse seine used that year. In the text, all references to 'catch' refer to the standardized catch (CPUE).

Chlorophyll concentration was analyzed fluorometrically, following extraction in 90% acetone. Zooplankton was enumerated by removing two 1.1-mL piston pipette subsamples from the sample, then counting both with the aid of a binocular dissecting microscope. All copepods were identified to species and enumerated by adult and juvenile stages. Total copepod biomass was calculated by multiplying taxon abundance (number per cubic meter) by the dry weight of each taxon (obtained from literature values), summing across all taxa, and then multiplying by 0.4 to convert dry weight to carbon weight. Euphausiid eggs were not enumerated to species; data are reported as number of eggs per cubic meter.

Spatial distributions of juvenile salmonids from the June and September 1981–85 and 1998–07 cruises were summarized by calculating the average catches at each station over all years (Fig. 1). Patchiness was evaluated for each cruise from the ratios of the variance to mean (coefficient of dispersion), with ratios >1 indicating a contagious or patchy distribution of fish, and ratios <1 indicating that the fish were more evenly distributed. To describe the distribution of patches, we defined 'patch stations' as those stations where at least 10% of the fish during each cruise were collected. There were usually only two or three patch stations per cruise.

We describe the alongshore variations in distribution patterns of juvenile salmon by calculating the geographic center or 'center of mass' (fish catch at stations weighted by both latitude and longitude) for each cruise (US Bureau of the Census, 2001). Associations between the catches of yearling coho and Chinook salmon and habitat variables at each station (water depth, sea surface temperature, sea surface salinity, chlorophyll-*a*, and copepod biomass) were examined using Spearman's rank correlations.

Habitat associations were also analyzed using principal components analysis of environmental variables and correlations with salmon abundance. For these analyses we used PC-ORD software (MJM Software Design, Gleneden Beach, OR, USA). All environ-

Figure 2. Interannual variations in the center-of-mass for yearling coho and Chinook salmon in June and September, 1982–85 (top) and 1999–07 (bottom). Location of the center-of-mass in each year is indicated by a single digit which refers to the year (for example, in the upper graph: 1982 = 2; 1983 = 3, etc., and in the bottom graph, 2001 = 1, 1999 = 9, etc.). Data from 1981 and June 1998 were not included because the northernmost transects were not sampled on those cruises.

mental variables listed above were first log-transformed due to their non-normal distributions; data were analyzed for the OSU and BPA efforts for June and September separately. We only included the first two principal components, as together they accounted for 73.3–78.8% of the variance. Using those variables with strong loadings (>0.5) we described the factors that best describe habitat associations. Subsequent to the PCA analysis, potential links between eigenvectors and salmon abundances was investigated using Spearman's rank correlations.

We also characterized the distribution of the salmon catches versus habitat variables (water depth, salinity, temperature, chlorophyll-*a*, and copepod biomass) by constructing for each variable a cumulative-percent frequency curve (CFC). CFCs were constructed by plotting on the x-axis the stations ranked by habitat variable, from lowest to highest value (for depth, temperature, and salinity) or highest to lowest (for chlorophyll-*a* and copepod biomass), then plotting on the y-axis for each station the cumulative percentage of the total catch of salmon during the cruise. This analysis generated hundreds of CFC plots, which were summarized by comparing the value of a given habitat variable at which the cumulative percentage of fish catch equaled 80%, then 80% values among cruises and life history type were compared using Student's *t*-tests or geometric mean linear regression. We also compared the 80% depths with strength of upwelling cumulated over the 10 days prior to visiting the Grays Harbor transect (location shown in Fig. 1) to test the hypothesis that strong upwelling results in larger habitat area or volume. This transect was chosen because it is at or near the center of the distribution of the juvenile salmonids.

RESULTS

Alongshore variations in distribution patterns of juvenile salmonids

Averages of salmon catches in June and September for the OSU and BPA surveys are shown in Fig. 1. In June, yearling coho and Chinook salmon were found exclusively in continental shelf waters. During the BPA study (1998–07) the highest numbers of both species were found off La Push, Queets River, and Grays Harbor, WA, whereas during the OSU study (1981–85) the

highest numbers of coho salmon were found further south, from Grays Harbor south to Cape Lookout. Coho salmon were more broadly distributed than yearling Chinook salmon, being collected at least once at all but 11 stations during the period June 1981–85 and all but 10 stations over the period June 1998–07.

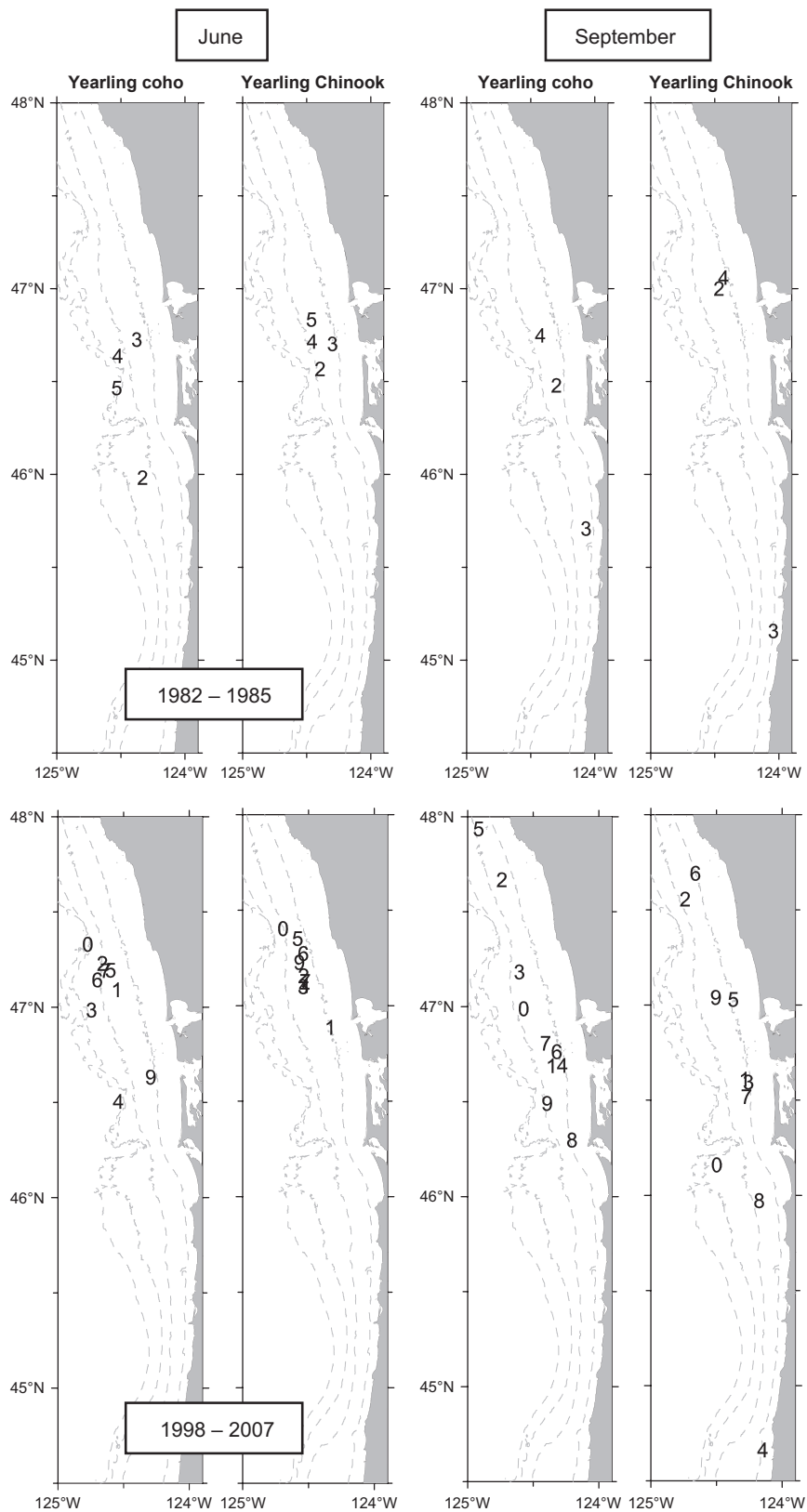
In contrast, yearling Chinook salmon were collected most frequently only off Washington State, were always closer to shore than coho salmon, had a lower average abundance, and were caught at least once at all but 24 stations in 1981–85 and at all but 18 stations in 1998–07. By September, both coho and yearling Chinook salmon had moved closer to shore as compared to June. Yearling Chinook salmon were seldom taken in any trawl offshore of the 100-m isobath in September.

Alongshore differences in the center of CPUE of the spatial distributions of salmonids

Interannual variability in the geographic centers of distribution of yearling coho and Chinook salmon was less in June than September (Fig. 2). During June 1982–85, the center of mass of juvenile salmonids spanned a distance of ~ 90 km, ranging from Cape Falcon (46°N) northwards to Grays Harbor (46.8°N), whereas in September 1982–84, the center of mass spanned a distance of ~ 210 km, ranging from about 45.2°N , northward to Grays Harbor, 47.1°N (Fig. 2). A similar pattern was seen during 1998–07: the center of mass spanned a distance of ~ 100 and ~ 215 km (360 km if September 2004 is included) in June and September, respectively. Furthermore, with the exception of yearling Chinook salmon caught in September, the geographical location of the center of mass was much farther south in 1982–85 than in 1998–07.

Patchiness

The frequency distribution of catch per unit effort resembled a Poisson distribution (Fig. 3) but was zero-inflated with a greater number of zero-catches than expected (assuming a Poisson distribution). The variance-to-mean ratios (coefficients of dispersion) were often greater than unity, indicating that the distribution of juvenile salmonids is patchy. This was the case for both the OSU purse seine studies and the BPA trawl surveys.



Among cruises, the proportion of samples that contained salmon was correlated with the average catch (Fig. 4). When salmon were abundant, they were found at a greater number of stations and tended to occupy a greater area of the continental shelf, but in only two cruises were salmon found at >75% of the stations sampled. When salmon were found in low abundances (such as during the 1983 and 1998 El Niño events, and during the summer of 2005) the proportion of stations where salmonids were caught was <10%.

The coefficients of dispersion of catch during each cruise averaged 41.4 for coho salmon (median = 19.2) and 20.3 for Chinook salmon (median = 3.0) for the OSU surveys, but 5.5 for coho salmon (median = 3.5) and 2.8 for Chinook salmon (median = 2.4) for the BPA cruises. A plot of the coefficient of dispersion

versus the mean catch per cruise shows a clear pattern of increased patchiness with increased fish catch, although patchiness tended to level off at the highest mean catches (Fig. 5). Thus the greater the numbers of fish that are present in shelf waters, the greater the patchiness.

During the June and September BPA cruises, we found that half of the catch of juvenile coho salmon was taken in only 3.5 and 3.7 trawls, respectively, and half of the yearling Chinook salmon in only 3.2 and 2.3 trawls, respectively. Similarly, during the June and September OSU cruises, we found that half of the catch of juvenile coho salmon was taken in only 4.6 and 2.3 sets, respectively, and half of the yearling Chinook salmon were taken in only 4.0 and 1.7 sets, respectively.

During BPA trawl surveys, we found patches at a total of 124 of 824 stations (or 15.1%). Most patches were off the Washington coast. Half of the patches

Figure 3. Frequency distribution of catches of yearling coho and yearling Chinook salmon during the 1981–85 (top) and 1998–07 (bottom) cruises. The x-axis is scaled as a percentage of the total catch during each cruise. The vertical line separates those samples making up less than or greater than 10% of the total catch during each cruise.

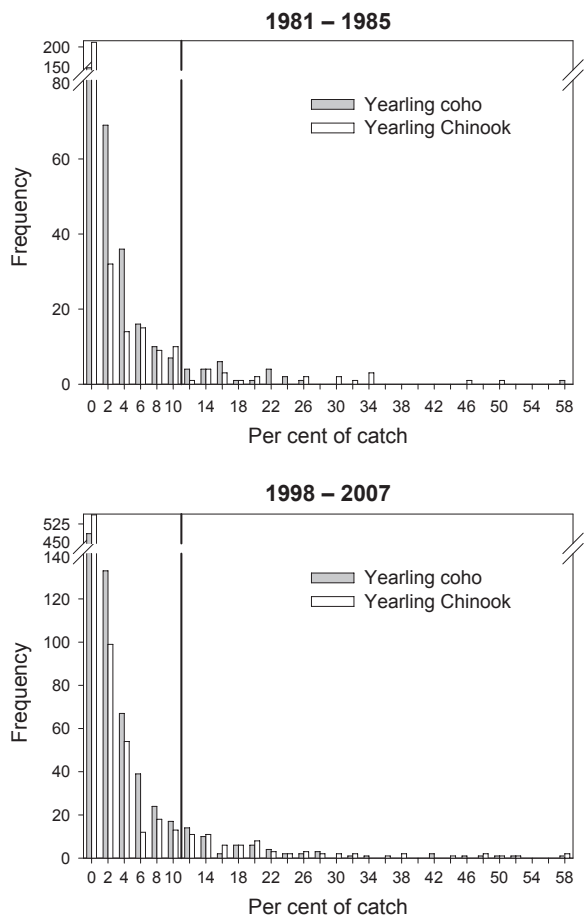


Figure 4. Relationship between number of yearling salmonids caught (top) in a purse seine set in 1981–85, and the proportion of sets that contained salmonids, and (bottom) in a rope trawl in 1998–07 and the proportion of trawls that contained salmonids.

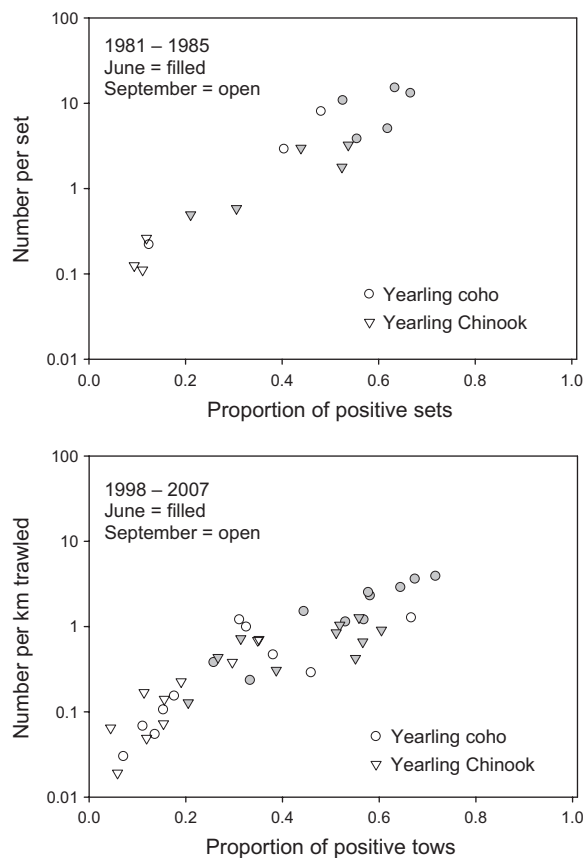
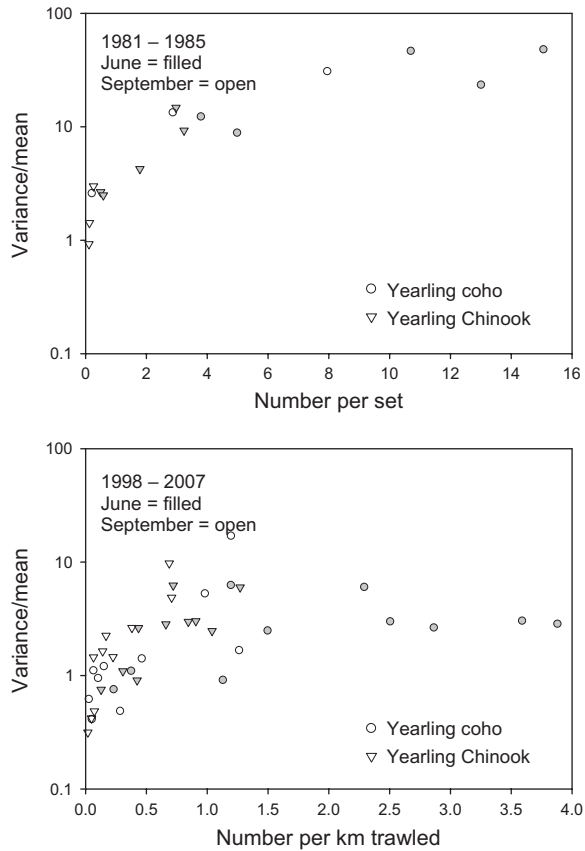


Figure 5. Relationship between the variance/mean ratio and number of fish caught in purse seine sets (top) and rope trawl (bottom). Values >1 indicate a patchy distribution of fish, values = 1 a random distribution and values <1 indicate an even distribution.



recurred at only seven stations: WB05 [five nautical miles (nmi; 1 nmi = 1.852 km) off Willapa Bay], CR07 (7 nmi off the Columbia River), QR06 (6 nmi off the Queets River), GH06 (6 nmi off Grays Harbor) and LP04, LP06, and LP09 (4, 6, and 9 nmi off La Push, WA) (Table 2). The average water depth at stations where patches were found was 87.8 ± 15.5 m (95% confidence intervals) for yearling coho salmon and 50.4 ± 13.3 m for yearling Chinook salmon (June) and 59.0 ± 8.3 m and 46.8 ± 7.1 m, respectively (September).

A similar result was found for the OSU purse seine cruises, with patches occurring in June and September at a total of 46 of 312 stations (or 14.7%). In June and September, most patches occurred off the Washington coast between 46.3°N to just south of Cape Flattery at 48°N . The average water depth of patches for juvenile salmon was 109.2 ± 40.2 m (coho) versus 67 ± 24.6 m (Chinook) in June and 59.8 ± 8.5 m and

56.2 ± 15.7 m, respectively, for coho and Chinook salmon in September.

Cross-shelf differences in the distribution of salmon and environmental variables

During BPA trawl surveys, an average of 1.5 yearling coho salmon were caught per km towed and 0.58 yearling Chinook salmon per km towed. The maximum catches were 44.1 and 16.6 fish km^{-1} , respectively. During the OSU purse seine study, yearling coho salmon also were more abundant than yearling Chinook salmon, averaging 7.8 and 1.4 fish per purse seine set, respectively, with a maximum catch of 127 and 35 fish per set, respectively.

During both studies, yearling coho and Chinook salmon were found in moderate numbers throughout continental shelf waters, mainly in water with sea surface temperatures (SST) of $9\text{--}16^\circ\text{C}$ (Fig. 6). The largest catches were in water with temperatures between 11 and 16°C . Juvenile salmonids were found over a wide range of sea surface salinities (SSS), ranging from values of 18 to 33.8, but very few juvenile salmon were found in waters having SSS values <24 or 25 (Fig. 6), and the largest catches were in water with salinity >30. Both species were found over a wide range of chlorophyll concentrations and copepod biomass, although many of the highest salmon catches were in waters where both chlorophyll concentration and copepod biomass were low to moderate (Fig. 6).

Spearman's rank correlations of salmonid abundance versus habitat variables are summarized in Table 3. For yearling Chinook salmon, correlations were negative between abundance and water depth and temperature, and positive between abundance and chlorophyll-*a* (and significant at the $P < 0.05$ level) as were most of the correlations with salinity. For yearling coho salmon, abundance was most strongly correlated with chlorophyll-*a*. We found significant positive correlations between copepod biomass and both yearling Chinook and coho salmon abundance (Table 3) for the BPA period (1998–07).

Results of the principal components analysis suggest that PC1 represents the effect of coastal upwelling on temperature, salinity, and productivity in a zonal (inshore–offshore or cross-shelf direction), as in both decades and for both June and September, the loadings of temperature and depth are always negative and of salinity and chlorophyll-*a* are always positive for this component (Table 4). The loadings on the second axis (PC 2) were positive for salinity for all four comparisons, and depth for three comparisons. This suggests that PC 2 may represent alongshore

Station	June			September			Total patches
	June patches	Patch by species CO,YC	Times sampled	Sept patches	Patch by species CO,YC	Times sampled	
LP04	5	1,4	9	6	2,4	10	11
LP06	7	2,5	9	5	2,3	10	12
LP09	7	3,4	8	4	3,1	10	12
LP12	4	3,1	8	2	2,0	10	6
QR06	3	1,2	7	4	1,3	7	7
QR10	0	0,0	7	3	2,1	7	3
QR14	4	3,1	7	0	0,0	7	4
GH03	1	0,1	3	1	0,1	5	2
GH06	3	1,2	9	4	2,2	9	7
GH16	4	3,1	10	1	0,1	10	5
WB05	4	0,4	9	6	2,4	8	10
WB09	0	0,0	9	3	2,1	9	3
CR04	2	0,2	10	2	0,2	9	4
CR07	3	1,2	10	7	5,2	10	10
CM03	0	0,0	9	3	1,2	10	3
NH03	0	0,0	5	2	0,2	6	2
NH05	2	1,1	10	3	0,3	9	5

Table 2. Stations with highest frequency of occurrence of salmonid patches during the 1998–07 BPA cruises. Stations with patches were defined as those where for any given cruise, 10% or more of the total fish of that species were caught. Figure 1 shows stations locations. CO, yearling coho salmon; YC, yearling Chinook salmon. Based on this definition, for example, patches of salmonids were encountered at the station 4 nautical miles off of La Push on five occasions in June (one for coho salmon and four for Chinook salmon) of a total of nine samples. Stations are arranged by transect from north to south and within a transect from inshore to offshore.

variability, first because the PC2 axis is orthogonal to the PC1 axis, but also because salinity is higher at the southern end of the sampling grid. An alongshore gradient occurs because of greater upwelling (of high salinity water) off central Oregon than off northern Washington, which has lower salinity due to both the Columbia River plume and water exiting from the Strait of Juan de Fuca.

The Spearman correlations of the PCA analysis with salmon abundance suggest that yearling Chinook salmon are more strongly and positively associated with upwelling (PC1; Table 4) compared with yearling coho salmon. Further, yearling Chinook salmon were more strongly and negatively associated with PC2 than were yearling coho salmon in June of both studies, indicating the tendency for Chinook salmon to be more abundant at the northern end of the sampling grid. Coho salmon were correlated with PC1 only once (positively, June 1998–07) but negatively (although weakly) with PC2 for three comparisons (Table 4). Coho salmon were less well correlated with PC2 than were yearling Chinook salmon, an expected result because coho salmon are more evenly distributed along the coast.

Cross-shelf distribution patterns: 80th percentile values for environmental variables

Another way to illustrate the distribution of the two salmon species in relation to habitat descriptors is

through use of cumulative frequency curves (Table 5) of water depth, temperature, salinity, chlorophyll-*a*, and copepod biomass, using the 80th percentile of the cumulative percentage of the total catch of salmon during the cruise for each habitat variable. Averaged over all cruises in June, 80% of the yearling coho and Chinook salmon were found in the nearshore zone (~30 m water depth) out to depths of 124 and 83 m, respectively. A similar pattern was seen in September, when 80% of the yearling coho and Chinook salmon were found out to depths of 84 and 60 m, respectively (Table 5). The differences in depth distribution between the two species in both months were significant ($P < 0.001$). Thus, yearling coho salmon are found farther out at sea, and they occupy a broader habitat in continental shelf waters than yearling Chinook salmon. For the other habitat variables, each taxon usually shared similar averaged 80% values (see Table 5): temperatures of ~13.3–14.5°C, salinity ~29.0–32.6, chlorophyll-*a* ~1.3–3.7 $\mu\text{g CHL-}a \text{ L}^{-1}$ and copepod biomass 7.8–11.4 mg carbon m^{-3} . There were some differences: Chinook salmon in September were found in significantly more saline water ($P < 0.001$) and Chinook salmon in June were found in waters with significantly greater chlorophyll-*a* concentration than were coho salmon (Table 5).

A comparison of the water depths at stations out to which 80% of the yearling coho and Chinook salmon were found in each of the June through September

Figure 6. Scattergrams showing relationships between the number of salmon caught in the purse seine sets (top) and rope trawl (bottom) at each sampling station versus depth of the water, sea surface salinity, sea surface temperature, chlorophyll a concentration, and copepod biomass at each station sampled.

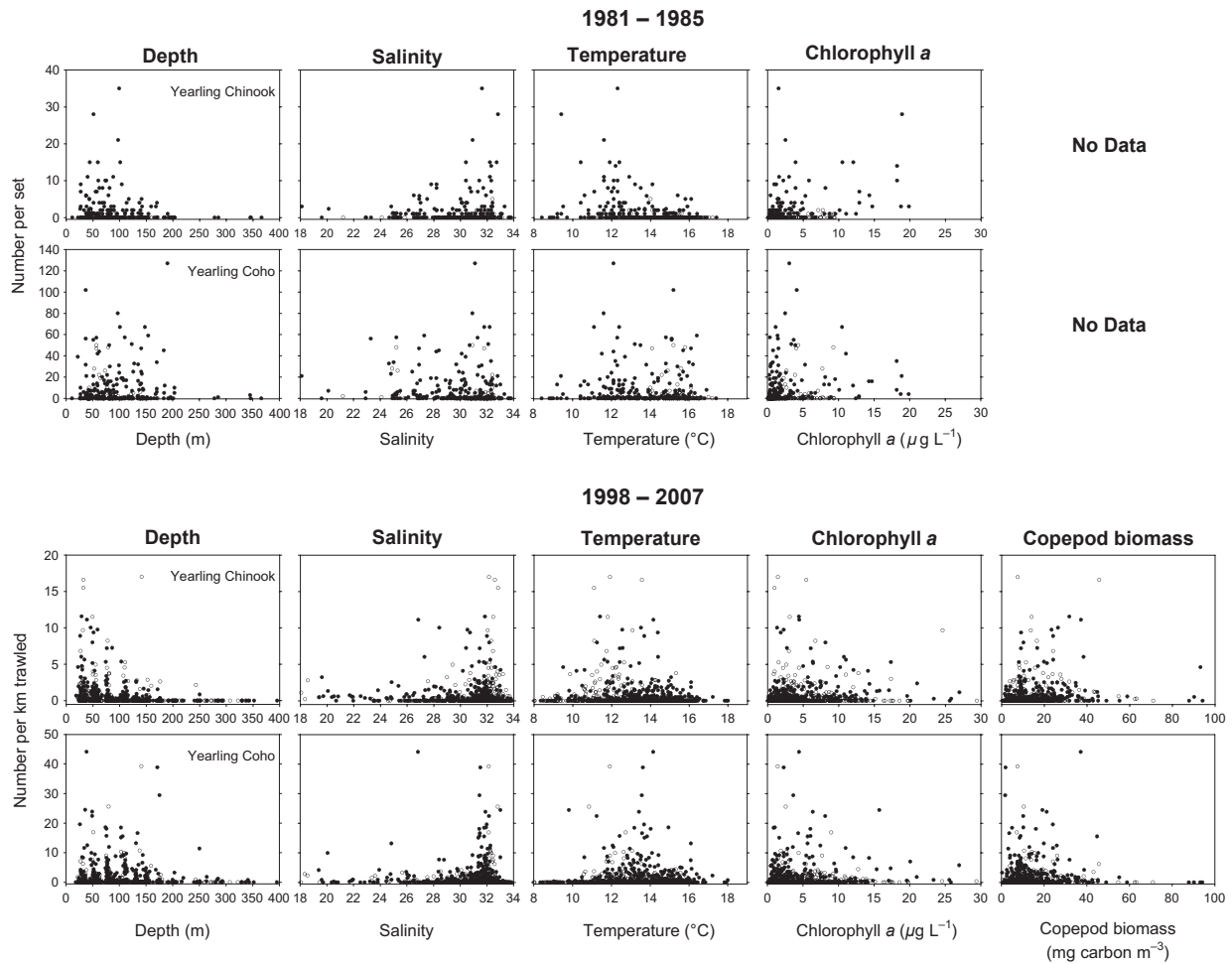


Table 3. June and September 1981–85 and 1998–07 Spearman rank correlations and (n, n copepod biomass) for depth, temperature (Temp), salinity (Sal) and chlorophyll-a (Chl a) with catch per unit effort of yearling coho and Chinook and coho salmon. Bold number with shading indicates value is significant at $P < 0.05$. NA indicates that no fish were caught during that cruise or no samples were counted for copepod biomass. Superscripted numbers indicate that many fewer samples for that variable.

Cruise (N)	Yearling Chinook					Yearling coho				
	Depth	Temp	Sal	Chl a	Copepod biomass	Depth	Temp	Sal	Chl a	Copepod biomass
June 1981–85 (211)	-0.28	-0.29	0.08	0.50	NA	-0.005	0.01	-0.12	0.32	NA
Sept 1982–84 (101)	-0.29	-0.24	0.05	0.27	NA	-0.19	-0.02	-0.04	0.24	NA
June 1998–07 (426, 420)	-0.50	-0.19²	-0.04²	0.48⁶	0.29	-0.12	-0.08²	0.04²	0.26⁶	0.09
Sept 1998–07 (398, 281)	-0.39	-0.17¹	0.13¹	0.20²	0.30	-0.20	0.09¹	-0.15¹	0.27²	0.30

cruises is shown in Fig. 7. Seasonal changes in depth distribution are clearly seen, with the salmon found out to deeper depths in June (circles) as compared to September (triangles). The differences in depth

distribution between the two species are also clearly seen by the GM regression of yearling Chinook salmon 80% depths with yearling coho salmon 80% depths – regardless of season, yearling coho salmon were on

Table 4. Principle component (PC) analysis loadings of log of depth, temperature (Temp), salinity (Sal) and chlorophyll-*a* (Chl-*a*) for cruises in June and September 1981–85 and 1998–07 and significant ($P < 0.05$) Spearman rank correlations of PC axes with catch per unit effort of yearling Chinook and coho salmon. The percentage of the total variance explained by each component is shown.

Environmental variables	June 1981–85		June 1998–07		Sept 1982–84		Sept 1998–07	
	PC1 (42.0%)	PC2 (31.5%)	PC1 (46.5%)	PC2 (32.3%)	PC1 (49.3%)	PC2 (28.5%)	PC1 (40.1%)	PC2 (33.2%)
Depth	-0.27	0.66	-0.59	0.25	-0.51	-0.08	-0.56	0.42
Temp	-0.68	-0.16	-0.55	-0.43	-0.63	-0.20	-0.66	-0.25
Sal	0.35	0.67	0.11	0.81	0.04	0.91	0.42	0.58
Chl <i>a</i>	0.59	-0.29	0.58	-0.31	0.59	-0.34	0.27	-0.65
Spearman correlations								
Yearling Chinook	0.36	-0.28	0.47	-0.27	0.31	–	0.33	-0.23
Yearling coho	–	-0.16	0.19	-0.11	–	–	–	-0.32

Table 5. Values (average and 95% confidence intervals) for the 80th percentile from cumulative percent frequency curves of depth, temperature, salinity, chlorophyll, and copepod biomass for yearling coho and Chinook salmon captured in June and September, averaged over all cruises in June and September. An 'S' indicates that values of *t*-test for differences between yearling coho and yearling Chinook salmon were significant at the $P < 0.05$ level. An 'E' indicates that values of *t*-test for differences between the salmon and the environment sampled were significantly different at the $P < 0.05$ level.

	June		Yearling Chinook	September		Yearling Chinook
	Environment	Yearling coho		Environment	Yearling coho	
Depth (m)	151.2 ± 10.7	123.7 ± 20.2 ^{SE}	82.7 ± 12.7 ^{SE}	134.2 ± 8.9	84.2 ± 11.7 ^{SE}	60.4 ± 7.9 ^{SE}
Temperature (°C)	14.8 ± 0.6	14.5 ± 0.6	14.1 ± 0.6	14.5 ± 0.7	14.0 ± 0.8	13.3 ± 0.7 ^E
Salinity	31.7 ± 0.4	29.0 ± 4.5	31.5 ± 0.7	32.4 ± 0.2	32.0 ± 0.4 ^S	32.6 ± 0.3 ^S
Chlorophyll ($\mu\text{g L}^{-1}$)	0.8 ± 0.2	1.3 ± 0.4 ^{SE}	2.8 ± 1.2 ^{SE}	1.6 ± 0.4	3.1 ± 0.7 ^E	3.7 ± 1.2 ^E
Copepod biomass (mg m^{-3})	6.5 ± 2.0	7.8 ± 3.9	9.2 ± 3.3	5.1 ± 2.8	9.0 ± 4.3 ^E	11.4 ± 5.6 ^E

average found out to water depths that were 20–60 m deeper than water depths occupied by yearling Chinook salmon.

Influence of coastal upwelling on cross-shelf distributions of salmonids

The strength of coastal upwelling in June also influences the offshore extent of salmonid distributions – that is, the stronger the upwelling (as measured by the PFEL upwelling index, Pacific Fisheries Environmental Laboratory, 2008), the greater the distance offshore within which 80% of the fish are found (Fig. 8, upper panel). The relationship between upwelling and offshore distribution was stronger for coho salmon than for Chinook salmon.

The upwelling data in Fig. 8 are cumulative for the 10 days prior to sampling the Grays Harbor transect; however, correlations were run for cumulative upwelling conditions ranging from 5 to 20 days prior to sampling and in every case, significant correlations

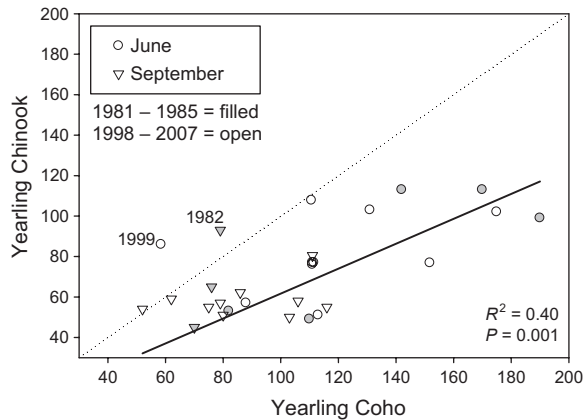
were found for coho salmon. Lags of 10–13 days prior gave slightly higher correlations than did other time periods.

No significant correlation was found between upwelling strength and 80% water depth in September (Fig. 8, lower panel), likely due to the fact that upwelling is weak-to-nonexistent at this time of the year off Washington State. A careful comparison of the two panels shows that when upwelling is 0–20 units, salmon are distributed over the same depth intervals (50–100 m) in June and September.

Cross-shelf distributions of chlorophyll, copepod biomass, and euphausiid eggs

Considering the cross-shelf differences in salmonid distribution (yearling Chinook salmon found out to mid-shelf depths and yearling coho salmon ranging to outer shelf waters), in what ways might the inshore waters differ from offshore waters? Three environmental variables are closely related to salmon distributions: depth, phytoplankton biomass (as indexed by

Figure 7. Scattergrams showing the relationship between water depth out to which 80% of the yearling Chinook salmon were caught versus water depth out to which 80% of the yearling coho salmon were caught, in June and September for both the 1981–85 and 1998–07 data sets. The dotted line is the 1 : 1 line. The equation for the geometric mean regression (solid line) is $Chin_{80\%} = 6.833 + 0.60381\ coho_{80\%}$.



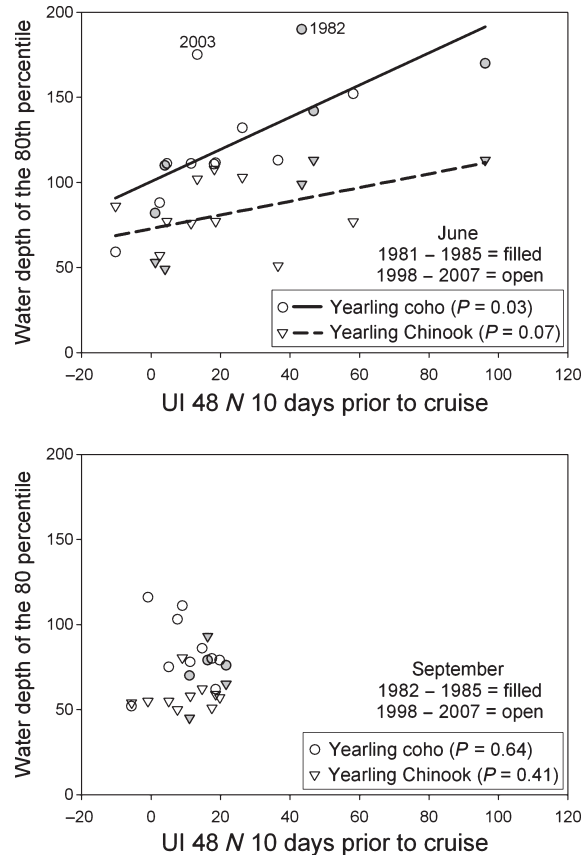
chlorophyll concentrations), and copepod biomass (Tables 3 and 5). Plankton biomass (Fig. 9) shows strong cross-shelf patterns, with highest phytoplankton and copepod biomass near shore in water depths <50 m, intermediate biomass values in inner and mid-shelf waters out to 50–100 m water depth (the approximate offshore limit for yearling Chinook salmon), and lowest values in outer-shelf waters of 100–150 m depth. Biomass of both phytoplankton and copepods declined exponentially in the cross-shelf direction, and approached values at the continental shelf break (200 m) that were only 10% of those in inner shelf waters.

Similarly, the distribution and abundance of euphausiid eggs in our zooplankton samples in June resembles the distribution of salmonids (compare Figs 1 and 10); euphausiid eggs are far more abundant in samples collected off Washington than off Oregon, particularly along the more northerly transects (La Push, Grays Harbor, and Willapa Bay). Maximum abundances of eggs were seen in inner and mid-shelf waters off northern Washington, and in outer-shelf waters off central and southern Washington, but at and beyond the shelf break (200 m water depth) off Oregon. Euphausiids do not usually spawn in September and thus no data are shown for that month.

DISCUSSION

Pearcy and Fisher (1990) and Pearcy (1992) were among the first to describe the distribution and

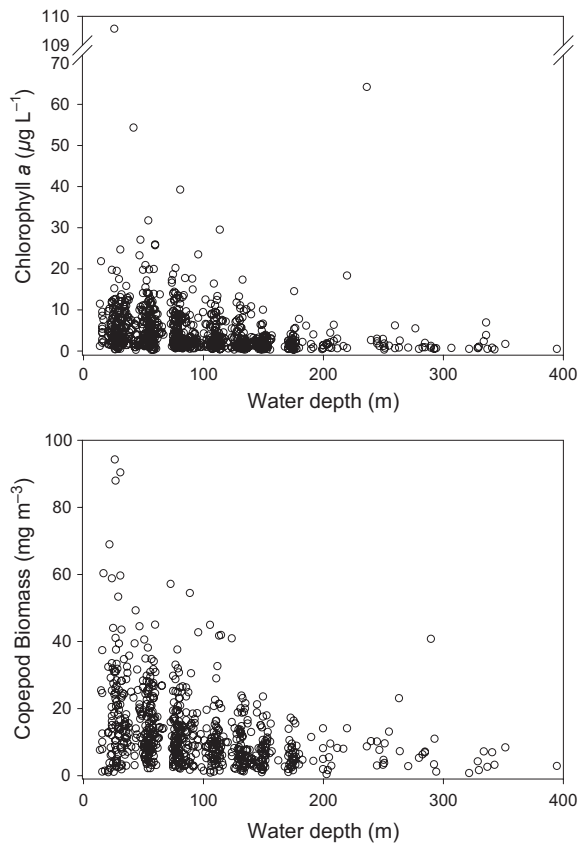
Figure 8. Relationship between water depth out to which 80% of the yearling coho and Chinook salmon were collected in June (top) and September (bottom) versus cumulative upwelling 10 days prior to a cruise. Correlations between water depth and cumulative upwelling were run for lags of 5–20 days and all were significant in June, but not in September.



abundance of juvenile salmonids off the Pacific Northwest. They captured more juvenile coho than Chinook salmon, and their surveys usually produced larger catches in coastal waters off Washington State than northern or central Oregon (see also Fig. 1). In both this earlier (OSU) and later (BPA) study, juvenile salmon in June were found chiefly at stations where water depths ranged from 30 to ~125 m, but by September, yearling coho salmon habitat area was reduced in size to an area defined by the 30- to ~80-m isobath.

Both the OSU and BPA studies found that yearling Chinook salmon habitat overlaps with yearling coho salmon in inner shelf waters, but that yearling Chinook salmon did not range as far out to sea as yearling coho salmon, suggesting that yearling Chinook salmon habitat preferences are associated with shallower nearshore waters. Unfortunately, neither the OSU

Figure 9. Relationship between chlorophyll *a* concentration (top) and copepod biomass (bottom) and water depth for all samples collected in 1998–07.



purse seine nor our trawl allowed us to take samples in waters shallower than ~ 30 m, therefore we have no direct information on how close to shore yearling coho or Chinook salmon might range. However, previous sampling in the surf zone in water < 9 m depth just north and south of the Columbia River mouth (Miller *et al.*, 1983) and south of Coos Bay, OR (Jarrin *et al.*, 2009), indicated that nearly all salmonids caught in that very shallow nearshore zone were small, mainly *sub-yearling* Chinook salmon < 130 mm FL. Therefore, the onshore distribution of the larger yearling Chinook and coho salmon likely ends somewhere between 30 and 9 m depth.

Fisher *et al.* (2007) compared alongshore distributions of juvenile coho, Chinook, sockeye, pink and chum salmon from samples collected from California north to southeast Alaska, in June and September in 2000, 2002, and 2004. They found that in June, yearling coho and Chinook salmon were most abundant off the coasts of Washington State and Vancouver Island; however, by September most yearling Chinook salmon had left the area, whereas year-

ling coho salmon were found in the same regions as in June. They also reported yearling Chinook salmon were found over shallower water than coho salmon and the other salmon taxa.

In the BPA study in June, most of the juvenile salmonids were collected in coastal waters off Washington and in the vicinity of the Columbia River plume. The division point between high and low catches appears to be near $45^{\circ}30'N$ (Cape Meares, OR), with most of the salmon being found to the north (see Fig. 1). This distribution pattern reflects both their point of origin (the Columbia River) and their tendency to swim towards the north, against the prevailing coastal currents (Percy and Fisher, 1988; Groot and Margolis, 1991; Fisher and Percy, 1995; Fisher *et al.*, 2007; Morris *et al.*, 2007; Trudel *et al.*, 2009). In September, the yearling coho salmon were most abundant off Washington, thus the continued presence of high numbers of coho salmon in late summer off the Columbia River, Washington coast, and Vancouver Island (and the low abundance of yearling Chinook salmon in September) suggests that many coho salmon are less migratory than yearling Chinook salmon during their first summer at sea. This result is consistent with analysis of coded-wire tag data that shows that yearling Chinook salmon move rapidly toward the north and can appear in the northern Gulf of Alaska waters by August (Hartt and Dell, 1986; Fisher and Percy, 1995; Orsi and Jaenicke, 1996; Trudel *et al.*, 2009). However, there are both slow and fast migrating coho salmon (Morris *et al.*, 2007).

An unresolved issue is what appears to be a more northerly distribution of juvenile salmon from the BPA study (1998–07) as compared with the OSU study (1981–85). Population genetic analysis of the coho captured in the BPA study from 1998 to 2005 (using microsatellites; Van Doornik *et al.*, 2007) showed that the fish collected off the northern Washington coast (La Push, Queets, and Grays Harbor) were primarily fish originating from the Columbia River ($\sim 50\%$), coastal rivers of Washington State ($\sim 25\%$), and coastal rivers of Oregon State ($\sim 12\%$). Approximately 75% of fish collected near the Columbia River originated from the Columbia River. We do not know the origin of fish collected during the OSU study as accurately. However, although many coded wire-tagged coho salmon caught during the OSU study originated in the Columbia River, a substantial proportion also originated in coastal Oregon public and private hatcheries (Percy and Fisher, 1988). Releases of yearling coho salmon from these coastal hatcheries were much greater during the OSU sampling period than during the BPA sampling

period, dropping between the two periods from 24.8% to only 3.9% of the numbers released in the Columbia River (P.F.M.C, 2008, calculated from Appendix Table BI). In addition, in 1981–85, very large numbers of sub-yearling coho salmon smolts were released from Yaquina Bay, OR (44°39'N) (R.M.P.C, 2008). Although we excluded most of the sub-yearling fish from the OSU analyses for September, we were unable to separate the two age classes for June (see Materials and Methods). Thus, it is very likely that coastal Oregon fish were a larger fraction of the catch during the OSU study than during the BPA study, which may have contributed to the more southerly distribution of yearling coho salmon observed during the former study. An alternate explanation is that the OSU cruises in June were all completed during the second and third weeks of the month, whereas the BPA cruises were always during the final third of the month. Thus, the OSU-collected salmonids had spent slightly less time at sea before capture than the BPA salmonids and thus may not have migrated as far north.

In our study, half of the fish collected on any cruise was usually taken at three or four stations (typically 5–8% of the stations sampled), and these stations were always in continental shelf waters off Washington State. Certain stations repeatedly produced high catches, in particular, one station off Willapa Bay (WB05) and the Columbia River (CR07), and several stations off La Push (LP04, 06, and 09). We do not know if these patch distributions reflect a tendency for yearling coho and Chinook salmon to travel in schools in the ocean. In fresh water, schooling behavior is most strongly developed among pink salmon (*Oncorhynchus gorbuscha*), sockeye salmon (*Oncorhynchus nerka*), and to a lesser extent, chum salmon (*Oncorhynchus keta*), and large schools of pink salmon have been observed in shallow marine waters (Groot and Margolis, 1991; Hoar, 1958). Schooling of coho and Chinook salmon in fresh water has been observed occasionally (Mesa, 1994; Swain and Holtby, 1989). Whether juvenile Chinook and coho salmon form schools in the ocean remains unstudied. The highest catch of yearling coho salmon was 44 per km trawled and of yearling Chinook salmon, 17 per km trawled, but this represents an integral over a distance of 3–5 km. Given that we cannot know when the fish were caught during a trawl, we do not know if they were evenly distributed along the 3+ km distance, or grouped at one or several geographical points, and thus we have no evidence for or against schooling behavior, or their tendency to form aggregations. However, the data from the OSU Purse

Seines study had variance-to-mean ratios that were usually greater than the BPA Trawl Study, indicating that patches can be at the same scale as a purse seine (diameter of ~160 m). The causes of these small-scale aggregations are not known; however, they could be the result of salmonids feeding on prey that are themselves distributed in patches.

The pattern of cross-shelf distribution of salmonids appears to be related to certain aspects of the physical oceanography of continental shelf waters in that salmonid distributions are similar to cross-shelf variations in hydrography and upwelling. The inner and mid-shelf waters, out to a depth of approximately 50–80 m (the 'habitat' of yearling Chinook salmon) is the zone of most active upwelling in the Pacific Northwest, and is where cold upwelled waters can reach the sea surface (Hickey, 1989). The water column in this region is frequently well-mixed and has the coldest temperatures and highest salinity. This region also has strong temporal variability in temperatures. Huyer (1977) showed that sea surface temperatures during the upwelling season off the central Oregon coast usually ranged from 8 to 11°C at a location 5 miles offshore of Newport (water depth 60 m), whereas at outer shelf stations off Newport, the SST can range from 10 to 17°C. Furthermore, the water column at mid-shelf and offshore stations is always stratified. Upwelling off Oregon and Washington is strongest in June and July, but weak to non-existent by the end of September. We hypothesize that the tendency for juvenile salmonid to reside farther offshore in June than September is a direct result of the strength of the upwelling and of the resulting expansion of the upwelling zone and the upwelling ecosystem. The entire shelf can be influenced by upwelling when winds are strong (such as in June and July); however, in September, only the inner shelf is influenced by the upwelling and the area (or volume) influenced by upwelling is greatly reduced. Correlations with upwelling and cross-shelf distribution of salmon shown in Fig. 8 support this idea. Furthermore, Hinke *et al.* (2005) showed the same result for sub-adult fall Chinook salmon – for this life history type, habitat availability was high when upwelling was strong in summer, but became more localized in the fall towards the end of the upwelling season.

There is also strong ecological zonation of zooplankton and euphausiids that may influence the distribution patterns of salmon (Peterson *et al.*, 1979; Landry and Lorenzen, 1989; Morgan *et al.*, 2003; Lamb and Peterson, 2005). The dominant zooplankton species nearshore (water depths <50 m) are the copepods *Acartia hudsonica*, *Centropages abdominalis*, cladocerans, and larvae of benthic invertebrates. The nearshore

zone is also the domain of osmeriids (smelts) (Mundy, 1984; Richardson and Percy, 1977), known to be key prey items of juvenile salmon (Peterson *et al.*, 1982; Brodeur and Percy, 1990; Schabetsberger *et al.*, 2003). In mid-shelf waters, zooplankton community structure changes and the dominant copepod species are the larger *Pseudocalanus mimus* and *Calanus marshallae*. Mid-shelf waters are where the euphausiid *Thysanoessa spinifera* can become a dominant taxon (Gomez-Gutierrez *et al.*, 2005). Outer shelf waters are the domain of large copepods (*Calanus marshallae*, *Neocalanus plumchrus* and *Neocalanus cristatus* and the euphausiid *Euphausia pacifica*). In outer shelf waters, euphausiid biomass often equals and/or exceeds copepod biomass (C.T. Shaw, Oregon State University, Newport, OR, USA, pers. comm.). All of these species are typical of cool subarctic waters. However, beyond the continental shelf, the zooplankton community changes rapidly to one dominated by warm-water species from the North Pacific Transition Zone (Keister and Peterson, 2003; Morgan *et al.*, 2003). The observation that juvenile salmonids do not appear to venture off the continental shelf suggests they associate with subarctic coastal waters and the zooplankton and nekton assemblages that they contain. Support for this hypothesis is that there are good correlations between coho salmonid survival and the biomass of lipid-rich boreal neritic copepod species in coastal waters (Peterson and Schwing, 2003; Hooff and Peterson, 2006;). Therefore, we suggest that cross-shelf variations in copepod distribution and abundance may be a good proxy descriptor of favorable habitats of foraging salmonids.

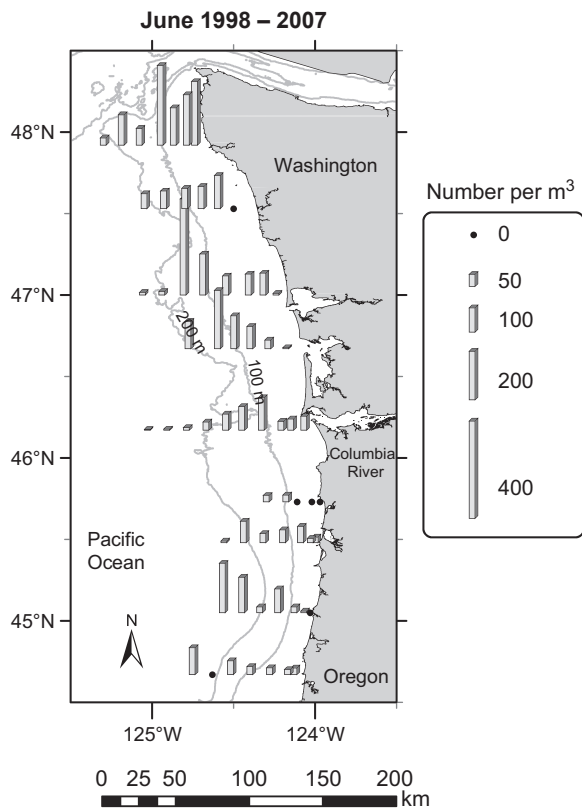
Cross-shelf variations in habitat characteristics do not necessarily explain the alongshore differences. Our data (and that shown in Brodeur *et al.*, 2004) certainly suggest that large differences exist between the habitat characteristics of the Oregon and Washington continental shelves, with what appears to be 'less-preferred habitat' off Oregon but 'good habitat' off Washington (Bi *et al.*, 2007, 2008). Thus we ask: 'Are there special attributes of the Washington shelf that suggest that continental shelf waters there may offer a better habitat for juvenile salmonids, particularly for yearling coho and Chinook salmon?' First, shelf waters off Washington experience less upwelling than off Oregon due to lighter northerly winds in summer and a shorter upwelling season (Hickey, 1979). Secondly, the Washington shelf is a reduced salinity environment with shelf waters that are a mixture of water originating from the relatively fresh Strait of Juan de Fuca to the north, fresher waters from the Columbia River plume, and upwelled water of subarctic origin

(Hickey and Banas, 2003). Thirdly, for many months of the year, the shelf waters off Washington are under the influence of the Columbia River plume (Hickey *et al.*, 2005), a situation which will lead to strong stratification, reduced wind mixing and less turbulence in shelf waters off Washington as compared to Oregon. Finally, the Washington shelf may well be more productive than the Oregon shelf because nutrients are constantly being re-supplied from the Strait of Juan de Fuca (Hickey and Banas, 2008) as well as by intermittent coastal upwelling. Also, iron concentrations are extremely high, being replenished each winter through sediment deposition by the Columbia River plume; high iron concentrations are believed to be a requisite for high productivity (Chase *et al.*, 2007).

We have developed four alternative hypotheses that may account for the observation that salmon are more abundant off Washington than Oregon. The first hypothesis relates to the fact that the Washington shelf is very wide as compared to Oregon, has relatively sluggish circulation, high productivity and longer retention of water as compared to the Oregon shelf, an attribute that may be favored by juvenile salmon (Hickey and Banas, 2008). Chlorophyll levels off Washington as determined from the SeaWiFS satellite, are on average three times higher than off Oregon (Thomas *et al.*, 2003). Given the higher chlorophyll levels, the upper waters are probably more turbid and may offer some protection for juvenile salmonids from visual predators. Although copepod biomass is no higher off Washington than Oregon, euphausiid biomass may be higher, as indicated by a larger number of euphausiid eggs off WA than OR (Fig. 10). As euphausiid eggs hatch 38 h after being laid (Gómez-Gutiérrez *et al.*, 2005), the presence of eggs in the water column indicates the presence of adult female euphausiids in the same region. Egg abundances could be higher either because there are more adult female euphausiids there or because the per capita egg production is higher as compared to Oregon due to high phytoplankton biomass. Given that euphausiids are often one of the most abundant prey items in stomachs of juvenile salmonids (Peterson *et al.*, 1982; Brodeur and Percy, 1990) it may not be a coincidence that regions with high abundances of euphausiid eggs are also regions of high abundances of juvenile salmonids in June.

A second alternative hypothesis relates to the presence of submarine canyons which are present along the Washington coast (but not off Oregon). These canyons may be a conduit for transport of euphausiids from deep waters up onto the shelf. The shelf off Washington is penetrated by the Juan de

Figure 10. Abundances of euphausiid eggs averaged for each station sampled in June, 1998–07.



Fuca, Queets, Grays Harbor, Willapa, and Astoria canyons. Each extends shoreward, penetrating the shelf to about the 100-m isobath. Each canyon may be a conduit for the transport of euphausiids onto the continental shelf due to increased upwelling flux in continental shelf canyons (e.g., Kämpf, 2007). Adult euphausiids which are present in the deep waters of the canyons perform their normal diel vertical migration each night to feed on rich phytoplankton resources in surface waters. During the night, while in surface waters, they would be transported towards the south (or north depending on winds and coastal currents), away from the canyon walls, and with the dawn they would find themselves trapped over shallow shelf waters where they would be subject to predation by juvenile salmon (which only feed during daytime). Thus adult euphausiid biomass could be maintained at high levels in shelf waters through this canyon–diel migration transport/trapping pathway (Pereyra *et al.*, 1969; Allen *et al.*, 2003). Furthermore, this could be a mechanism that leads to patchiness of both salmonids and euphausiids. Given that euphausiids are an important prey for juvenile salmonids (Peterson *et al.*, 1982; Brodeur and Pearcy, 1990; Schabetsberger *et al.*,

2003) this canyon-trapping mechanism would assure rich feeding grounds in the vicinity of canyons during the upwelling season.

A third hypothesis is based on the idea that cyclonic-gyre features associated with the heads of canyons could concentrate salmonid prey (euphausiids and juvenile fish), making canyon heads prime feeding grounds. Noting that salmon patches were almost always found only along Washington transects, off Astoria, Willapa Bay, Grays Harbor, Queets River, and La Push, and near the heads of canyons, we hypothesize that gyres associated with canyons could concentrate salmonid prey (euphausiids and juvenile fishes), making canyon heads prime feeding grounds, as suggested by others (Mackas *et al.*, 1997; Allen *et al.*, 2001). Furthermore, such gyres could also be a cause of the patchiness we observed in salmon distributions.

A fourth alternate hypothesis that may explain the differential in latitudinal distribution of salmon is related to their inherent migratory characteristics. In this regard, their distributions may be solely the result of the tendency of juvenile salmon to swim north from their river-of-origin, and any relationships with productivity, canyons or krill are purely coincidental. Given that the Columbia River is the source of the majority of yearling coho and Chinook salmon in our study area, this hypothesis has some credence. Thus high catch rates of juveniles at stations off La Push, Queets River, Grays Harbor, and Willapa Bay may only be related to the proximity of these locations to the Columbia River and any general relationships between the spatial distribution of salmonids and the location of submarine canyons or the distribution of their euphausiid prey are purely coincidental.

In conclusion, we have established several relationships:

- 1 juvenile yearling coho salmon can occupy waters across most of the continental shelf, whereas the yearling Chinook salmon are, for whatever reasons, restricted to the inner-to-mid shelf waters;
- 2 both species were collected farther from shore in June than in September, suggesting a response to strong upwelling in June and weak-to-nonexistent upwelling in September—strong upwelling increases the volume of the pelagic habitat available to salmonids;
- 3 both species had patchy distributions;
- 4 all salmonids were most abundant off Washington State in June whereas by September, most of the yearling Chinook salmon had left the area. Relatively larger numbers of juvenile coho salmon remained, but mainly along the coast of Washington.

A combination of four hypotheses remain to be evaluated that may explain the observation that the center of distribution was off Washington.

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