

Ultrasonic telemetry reveals seasonal variation in depth distribution and diel vertical migrations of sub-adult Chinook and coho salmon in Puget Sound

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ABSTRACT: Many aquatic organisms display seasonal and diel vertical migration (DVM) patterns, which are influenced by complex combinations of biotic and abiotic factors. Here, we examined the vertical distributions of sub-adult coho *Oncorhynchus kisutch* and Chinook salmon *O. tshawytscha* in Puget Sound, Washington, USA, using acoustic telemetry to (1) compare the depths occupied by each species, (2) determine whether DVM occurred, (3) ascertain if depth distributions changed seasonally, and (4) consider hypotheses regarding abiotic and biotic factors that could affect these behavior patterns. We modeled the data on individual fish depths and detected significant interactions among species, diel period, and season. Coho salmon spent more time near the surface than Chinook salmon overall, and exhibited DVM during the spring, being farther below the surface at night and closer during the day. This reversal of the typical DVM pattern was not evident in other seasons. Chinook salmon showed no evidence of diel movement, only a seasonal shift from being closest to the surface in spring, deeper in summer, deeper yet in fall, and deepest in winter. The proximity of Chinook salmon to the surface coincided with peak productivity measured as chlorophyll *a*, which could affect the salmon through decreased water clarity or some ecological process. The DVM exhibited by coho salmon in spring may be related to water clarity and avoidance of predatory mammals but these hypotheses could not be tested with the available data. Our results emphasize the complexity of diel activity patterns among closely related species, and even among individuals.

KEY WORDS: Salmon · Depth · Diel vertical migration · Telemetry

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INTRODUCTION

For animals occupying lake and ocean habitats, vertical positioning within the water column reflects the pressures of multiple abiotic and biotic factors. Light intensity and phytoplankton density decrease with depth, and low light levels limit the ability of visual predators to see their prey. Temperature, dissolved oxygen and salinity can also vary with depth, which may affect physiological processes and constrain the presence of certain species, depending on their tolerance. It has long been recognized that many organisms make regular vertical movements in

the water column over a 24 h period in order to balance the competing demands of prey capture, predator avoidance, and optimization of physiological performance (Barham 1966, Bary 1967, Lampert 1989). Among fishes, vertical movements are undertaken by many lacustrine (Narver 1970, Mehner et al. 2007, Kahilainen et al. 2009, Probst & Eckmann 2009, Gutowsky et al. 2013) and marine (Dagorn et al. 2000, Gauthier & Rose 2002, Espeland et al. 2010) pelagic species. Moreover, some demersal species move towards and away from shore near the bottom, varying their depth from the surface (Gibson et al. 1998, Andrews & Quinn 2012).

Although diel movements are usually synchronized with light levels, they often reflect complex interactions among biotic and abiotic factors, including the need to capture prey (typically using vision), bioenergetic constraints (e.g. digesting prey efficiently by altering ambient temperature through vertical movement; Sims et al. 2006), and avoidance of visual predators (Clark & Levy 1988, Scheuerell & Schindler 2003). Large pelagic predators tend to be closer to the surface at night and deeper in the day (Dagorn et al. 2000, Kitagawa et al. 2000) as this is commonly the distribution of their prey. However, vertical distribution can also reflect the need to avoid stressful conditions such as low temperatures (Brill et al. 1993, 1999). Not all pelagic predators exhibit diel vertical movement patterns (Coutant & Carroll 1980, Nowak & Quinn 2002); some remain at intermediate depths to intercept vertically migrating prey rather than pursuing them. These complex patterns, combined with seasonal variations (Carey & Scharold 1990) and considerable individual variation (Pade et al. 2009), can make it difficult to interpret changes in vertical distribution.

One approach to studying vertical migration is to compare patterns of migration among species in the same ecosystem. Information on how related (Mehner et al. 2010, Stockwell et al. 2010) or unrelated species (Piet & Guruge 1997, Yatsu et al. 2005, Quinn et al. 2012) respond in the same environment can contribute to a better understanding of behavior patterns. Differences in diel vertical migration (DVM) patterns among species may be due to metabolic benefits (Mehner et al. 2010), life history and predation risk (Quinn et al. 2012), prey distributions (Stockwell et al. 2010) and/or resource partitioning (Piet & Guruge 1997).

Pacific salmon *Oncorhynchus* spp. are a group of closely related species that can have high spatiotemporal overlap, making them suitable for comparative analysis of vertical distribution. The vertical migration of juvenile sockeye salmon *O. nerka* in lakes has been extensively studied with hydroacoustic techniques and towed nets (Narver 1970, Levy 1987, Scheuerell & Schindler 2003), but the vertical migrations of salmon in marine waters are not well known. Mobile tracking of salmon with pressure-sensing transmitters by boat on the high seas (Ogura & Ishida 1995), in coastal waters (Quinn et al. 1989, Ruggerone et al. 1990, Candy & Quinn 1999) and estuaries (Olson & Quinn 1993) is informative, but the tracks are typically a few days at most, and it is difficult to follow more than one fish at a time. As a consequence of the short track duration, any abnormal

behavior (as may result from handling stress) can provide a misleading picture of the species' behavior (Walker & Myers 2009). Data-storage tags can provide longer records of vertical movements and thermal experience of individual fish (Walker et al. 2000, Friedland et al. 2001, Walker & Myers 2009, Nielsen et al. 2011), but the precise locations of the fish are seldom known, few tags are recovered, and it is difficult to compare the behavior of multiple individuals and species.

Although extensive information exists on most aspects of salmon behavior (Quinn 2005), information on the movements of individuals at sea, especially vertical distribution patterns and diel behavior, is notably scarce. There are indications of diel feeding periodicity (Percy et al. 1984) and differences in general depth distribution in steelhead *O. mykiss* close to the surface (Ruggerone et al. 1990, Nielsen et al. 2011, Teo et al. 2013), Chinook *O. tshawytscha* occupying the deepest water, and other species found at more intermediate depths (Ogura & Ishida 1995, Candy & Quinn 1999). However, these conclusions are based on studies of very few individuals, often tracked in different places and seasons.

During their marine life, juvenile and sub-adult coho *O. kistutch* and Chinook salmon overlap broadly in diet and spatial distribution, though there are finer-scale differences between the species (e.g. in southeastern Alaska; Weitkamp et al. 2011). Both species eat a wide range of pelagic invertebrates and fishes, although fishes tend to dominate the diet of Chinook salmon to a greater extent than coho salmon (Prakash 1962, Beacham 1986, Brodeur & Percy 1990, Brodeur et al. 1992, Landingham et al. 1998). This diet overlap suggests that differences in depth distribution might not be related to the behavior of unique prey, but the data are not sufficiently detailed to support comparisons. Daytime trawls at the surface in coastal waters of the Pacific Ocean captured more coho and Chinook salmon than did nighttime trawls (Krutzikowsky & Emmett 2005), suggesting the fish were closer to the surface during the day. However, the authors concluded that the nighttime distributions were so close to the surface that the fish were invulnerable to the gear (Krutzikowsky & Emmett 2005). Other studies in coastal waters have suggested that coho salmon generally remain closer to the surface than Chinook salmon based on catch data (Orsi & Wertheimer 1995), limited telemetry work (Ogura & Ishida 1992, 1995, Candy & Quinn 1999), and by-catch of Chinook salmon in trawl nets in deep water (Erickson & Pikitch 1994).

The purpose of our study was to determine the vertical distribution patterns of sympatric sub-adult coho and Chinook salmon in Puget Sound. Our specific objectives were to (1) compare the mean depths occupied by the 2 species, (2) determine whether either species displayed diel vertical migrations and compare patterns between species, (3) ascertain if there were seasonal changes in the depth distributions, and (4) consider a series of hypotheses regarding abiotic and biotic factors that might affect these behavior patterns. To do so, we modeled fish depth as a function of species, time of day, and time of year, considering both the proximity of the fish to the surface and to the bottom. We then compared fish movements with environmental condition data (temperature, dissolved oxygen [DO], salinity, and chlorophyll *a* [chl *a*]) and studies of the vertical distribution and movements of potential prey species to evaluate possible explanations for the observed behavior of the salmon. We studied fish that were feeding in marine waters rather than those migrating homeward from the North Pacific Ocean, as association with the surface freshwater lens for orientation to odor plumes or osmoregulation by maturing adults might complicate

analysis of vertical distribution (Døving et al. 1985, Olson & Quinn 1993).

MATERIALS AND METHODS

Study site

This study was conducted in Puget Sound, a 2330 km² estuary that is 160 km long, has a maximum width of 40 km, and maximum depth of 283 m (Moore et al. 2008b). Puget Sound consists of several basins, separated by narrow, shallow constrictions: south Puget Sound (south of the Tacoma Narrows), central Puget Sound (from the Tacoma Narrows north to Admiralty Inlet), the Whidbey Basin (east of Whidbey Island), and Hood Canal (Fig. 1). We define Puget Sound proper as ending at Admiralty Inlet, which connects to the Strait of Juan de Fuca in the west, and to the Strait of Georgia and associated waters of the Salish Sea to the north. Puget Sound has shifts in surface temperature and salinity associated with runoff from the rivers flowing into it, and from seasonal and long-term climate patterns (Moore et al. 2008a,b).

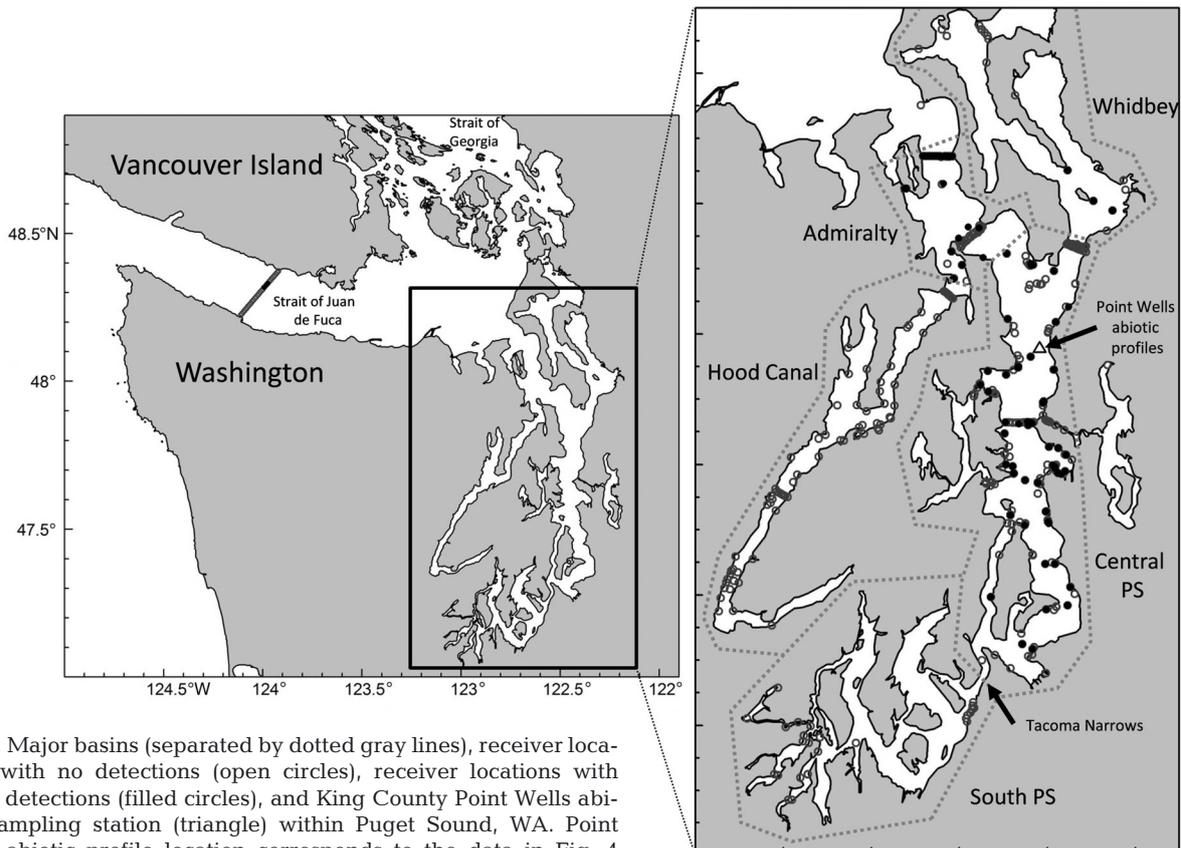


Fig. 1. Major basins (separated by dotted gray lines), receiver locations with no detections (open circles), receiver locations with depth detections (filled circles), and King County Point Wells abiotic sampling station (triangle) within Puget Sound, WA. Point Wells abiotic profile location corresponds to the data in Fig. 4

Field methods

Coho ($n = 11$; fork length [FL] 303 to 346 mm) and Chinook salmon ($n = 24$; FL = 254 to 430 mm [one at 505 mm]) were caught between November 2006 and June 2012 (most during late fall and early spring), using a commercial purse seine vessel or angling using single-point barbless hooks at 10 locations in central Puget Sound. Based on combinations of capture date, capture location, and fish size, these salmon were considered resident at the time of capture. That is, they would have entered Puget Sound during the previous spring or summer and were still in Puget Sound at a time when other members of their cohort would be found along the coast or in offshore waters of the North Pacific Ocean (Trudel et al. 2009). This definition of 'residency' follows Chamberlin et al. (2011). Further details on the phenomenon of resident salmon in Puget Sound are provided by O'Neill & West (2009), Chamberlin et al. (2011) and Rohde et al. (2014). After capture, fish were transferred from the net into a live well containing aerated flow-through seawater. Temperature was maintained at 10 to 12°C and salinity ranged from 28 to 31‰. Fish with visible distress or >10% scale loss were not tagged.

Fish suitable for tagging were transferred to a small cooler with the anesthetic tricaine methanesulfonate (MS-222) at a concentration of 65 mg l⁻¹ to induce loss of equilibrium but still allow opercular movement. Each fish was weighed and measured for FL (for details on individual fish see the Appendix). Fish were checked for the presence of a clipped adipose fin or coded wire tag (either of which would indicate hatchery origin), and a fin clip was taken for subsequent genetic analysis of origin. The fish was then transferred to a surgical table on a closed-cell foam with a cutout that allowed the individual to be positioned on its dorsal side. A supply of ambient temperature water with anesthetic was gravity-fed through a tube and delivered to the gills.

Individually coded VEMCO V9P acoustic transmitters were used for tracking; each transmitter contained a pressure transducer to allow computation of depth. Individuals selected for surgery were >70 g to ensure that the transmitter was <5% of the fish's body weight in air (Hall et al. 2009). Transmission interval of tags varied between 20 and 180 s and battery life ranged from 60 to 910 d. Transmitters were inserted into the peritoneal cavity through a small (15 to 20 mm) incision just off-center of the linea alba of the abdomen and anterior to the pelvic

fins. The incision was closed using a tapered RB-1 needle and Ethicon coated Vicryl 6-0 absorbable suture in 2 interrupted surgeon's knots. Including time in anesthesia and processing time for surgery, each fish was handled for an average of 6 min; actual surgery duration was about 2 min. After surgery, the fish were placed in a recovery tank until they were upright and swimming independently (~15 min), and released near the site of capture. Detections obtained within 24 h of release were not included in the analysis.

Receivers

Since 2004, there has been extensive use of acoustic transmitters in Puget Sound, the Strait of Georgia, and nearby water bodies to study the movements of a variety of fishes (Melnichuk et al. 2007, Welch et al. 2009, Moore et al. 2010, Hayes et al. 2011, Andrews & Quinn 2012). These studies have used a widespread network of receivers maintained by different investigative teams, including over 20 organizations deploying more than 200 receivers, with some in every Puget Sound basin. These studies have coincided with an international monitoring effort (Pacific Ocean Shelf Tracking project) using the same technology along the continental shelf from California to Alaska (Rechisky et al. 2009). The extensive distribution of receivers has allowed researchers to evaluate movements of different species at larger spatial and temporal scales than was previously possible. With numerous receivers deployed, different objectives of individual researchers, and the schedules used for maintaining them, there were inevitable changes in the precise number and location of operational receivers during our study. However, at all times there were many receivers in each of the main basins of Puget Sound and the Strait of Georgia, and an opportunity to detect fish migrating out towards the Pacific Ocean westward via the Strait of Juan de Fuca and northward via Johnstone Strait. Receiver downloads were managed through Hydra (<http://hydra3.sound-data.com/about/>), a data repository designed to help the consortium of researchers share data.

Data analysis

The transmitters were rated for accurate measurement to a maximum depth of 100 m; the maximum transmitted depth was 110 m. Depth detections were

analyzed in 2 ways: absolute depth (distance from the surface to the transmitter) and relative depth. Relative depth was measured as the distance from the surface as a proportion of the maximum depth of the bottom in the transmitter's vicinity—inferred from the maximum bottom depth near the receiver on which the transmitter was detected (fish depth from surface/maximum depth within the receiver detection range). ArcGIS 10 (ESRI™ Desktop GIS software®) was used to calculate 520 m diameter buffers (based on the estimated detection range of the transmitters) around each receiver location. These buffers were clipped with a digital elevation model (PSDEM2005) of Puget Sound obtained from the University of Washington, School of Oceanography (www.ocean.washington.edu/data/pugetsound/ accessed 16 March 2014). The maximum depth within each receiver buffer was used to calculate fish relative depth. In addition, each receiver was categorized based on distance to shore and maximum depth within the range of the receiver as one of the following: (1) onshore–shallow (<1 km to shore and <100 m depth), (2) onshore–deep (<1 km to shore and >100 m depth), and (3) offshore (>1 km to shore and >100 m depth). Chi-squared analyses were used for each species to determine if the number of detections at each type of receiver was independent of season.

The absolute and relative depth detections were summarized for each individual by taking the mean of all detections within each hour of each day of each year. These mean hourly detections were pooled over all years and then categorized by season and diel period. Over the course of the year, the length of day and night periods varies considerably, so analysis by hour of the day does not capture diel activity relative to changing light levels. Consequently, diel periods (day and night) were calculated using sunrise and sunset times obtained from the US Naval Observatory Astronomical Applications Department website (http://aa.usno.navy.mil/data/docs/RS_OneYear.php accessed 16 March 2014). Detections were classified as day if they were between sunrise and sunset; night detections were before sunrise and after sunset.

Linear mixed effects (LME) models, using the individual identity of each fish as a random effect, were used to determine if hourly mean absolute fish depth and hourly mean relative fish depth were different between species (Chinook or coho), diel period (day or night), season (spring, summer, fall, winter) and the 3-way interactions (package 'nlme' in R v.3.1-118; Pinheiro et al. 2014). Models of absolute depth were natural log transformed and relative depth (a proportional variable) were logit

transformed (Warton & Hui 2011). Optimal models were determined using the 10 step protocol for mixed effects models outlined in Zuur et al. (2009). The inclusion of interaction terms was assessed by comparing Akaike's information criterion (AIC) values of the full model to those of reduced models. Autocorrelation of response variables was detected using the 'acf' function in the 'nlme' package. To account for the lack of independence between depth observations, the hourly means of the date–time of detections were used to calculate a correlation structure for each model. All correlation structures available in the 'nlme' package were compared and the structure with the lowest AIC value, which was the exponential correlation structure, was used (Zuur et al. 2009). Homogeneity of variance was assessed by examining boxplots of normalized residuals for each explanatory variable. Heterogeneity of residuals was detected. Therefore, a variance structure that allowed for different standard deviations for each stratum of each independent variable was incorporated into the models ('varIdent' function in the 'nlme' package). Histograms of residuals from the final models confirmed the assumption of normally distributed errors. Post hoc Tukey's multiple comparison tests were performed using the 'multcomp' package (Hothorn et al. 2008). All data analyses were performed in R (R Development Core Team 2013).

To evaluate the possible effects of changes in ambient conditions on fish depth, water quality information was obtained from the King County Puget Sound Marine Monitoring website (<http://green.kingcounty.gov/marine/StationMap.aspx>, accessed 16 March 2014) when fish detections were obtained (2006 to 2012; Fig. 1). King County samples selected locations once a month, collecting profiles of temperature, DO, salinity, and chl *a*. Data from one station in Puget Sound (Point Wells Offshore; 47.77739° N, 122.41761° W) were summarized by monthly mean depth profiles for the surface (0 to 10 m) and the depth of maximum depth detections (90 to 100 m) for the period when fish detections were obtained (2006 to 2012). Three other stations were also examined: West Point Outfall (47.66055° N, 122.44721° W), Fauntleroy-Vashon (47.53333° N, 122.43333° W), and East Passage (47.35861° N, 122.38708° W). The mean value for each 10 m depth bin over 6 yr was calculated and plotted for each month. The abiotic trends were very similar among stations (range in correlations across sites: temperature = 0.96 to 0.99, DO = 0.89 to 0.97, salinity = 0.85 to 0.93, chl *a* = 0.88 to 0.97); therefore, the Point Wells station was

used to indicate conditions in Puget Sound. For each variable, the mean values for 10 and 100 m below the surface were calculated for each month. January to March was considered to be winter, April to June: spring, July to September: summer, and October to December: fall. For each variable, the change in conditions from near the surface to the maximum depth of detections was determined (mean at 10 m – mean at 100 m). ANOVA was used to determine if the difference between 10 and 100 m values for each variable differed among seasons, using months as replicates for season; Tukey’s multiple comparison tests determined which seasons were significantly different. Due to the spatial and temporal limitations of the profile data, the relationship between depth of fish and water quality were not directly tested. We instead discussed how changes in water quality across seasons could influence fish depth.

RESULTS

In total, 55 stationary receivers recorded 5290 detections (823 hourly mean detections) of coho salmon from 1 November 2006 to 24 March 2009, and 57 receivers recorded 14 497 detections (1874 hourly mean detections) of Chinook salmon from 1 November 2006 to 1 October 2012 (Table 1). There was no correlation in the number of receiver detections (log transformed) between species among receiver locations ($r = 0.10$, $p = 0.38$); that is, receivers that often detected one species did not necessarily detect the other.

Detections at each type of receiver (offshore, onshore–deep, and onshore–shallow) depended on season for both Chinook salmon ($\chi^2 = 5341.12$, $p < 0.0001$) and coho salmon ($\chi^2 = 1213.89$, $p < 0.0001$; Fig. 2). There were more detections of Chinook

Table 1. For each season, number of individual Chinook *Oncorhynchus tshawytscha* and coho salmon *O. kisutch* detected (n), number of raw detections, number of hourly mean detections, and model predicted values of absolute depth (from the surface) and relative depth (from the bottom) during the day and night. The model predicted values are presented because they account for temporal autocorrelation among detections

	n	Detections		Hourly mean detections		Model absolute depth (m)		Model relative depth (proportion)	
		Day	Night	Day	Night	Day	Night	Day	Night
Chinook									
Winter	7	1891	1823	209	252	43.65	40.48	0.46	0.38
Spring	11	1426	446	129	55	8.29	11.18	0.10	0.13
Summer	12	3172	1940	502	317	22.67	24.55	0.20	0.24
Fall	12	1732	2067	188	222	33.08	32.29	0.31	0.34
Coho									
Winter	10	449	864	80	93	8.55	12.63	0.12	0.16
Spring	9	1628	1274	319	181	7.23	22.51	0.13	0.27
Summer	7	164	54	53	20	11.71	19.43	0.21	0.25
Fall	3	185	672	29	48	5.31	4.81	0.09	0.08

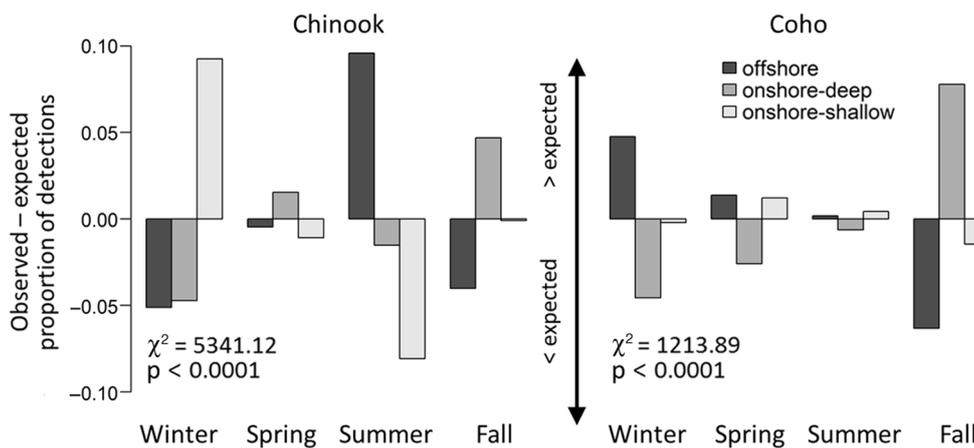


Fig. 2. Proportion of Chinook *Oncorhynchus tshawytscha* and coho salmon *O. kisutch* detections from receivers that were greater than or less than expected at onshore–shallow (<1 km from shore and <100 m depth), onshore–deep (<1 km from shore and >100 m depth), and offshore (>1 km from shore and >100 m depth) for each season. Statistics are for chi-squared analyses indicating lack of independence between receiver type and season

salmon than expected at onshore–shallow receivers in spring and offshore receivers in summer, but fewer detections than expected at offshore and onshore–deep in winter and onshore–shallow in summer. Coho salmon had more detections than expected at offshore receivers in winter (opposite of Chinook salmon) and onshore–deep receivers in fall (similar to Chinook salmon). There were fewer detections than expected of Coho salmon at onshore–deep receivers in winter (similar to Chinook salmon) and offshore receivers in fall (similar to Chinook salmon).

The LME absolute depth and relative depth models indicated that there was a significant 3-way interaction between species, diel period, and season (i.e. depth was different within and between species for some diel periods and seasons; Tables 2 & 3, Fig. 3). The variance associated with the random effects for the absolute depth model were 0.40 (intercept) and 0.88 (residual), and 0.40 (intercept) 0.70 (residual) for the relative depth model. The parameter estimate for the exponential correlation structure was 0.81 for the absolute depth model and 8.41 for the relative depth model.

DVM was not detected for Chinook salmon (i.e. no significant absolute differences between day and

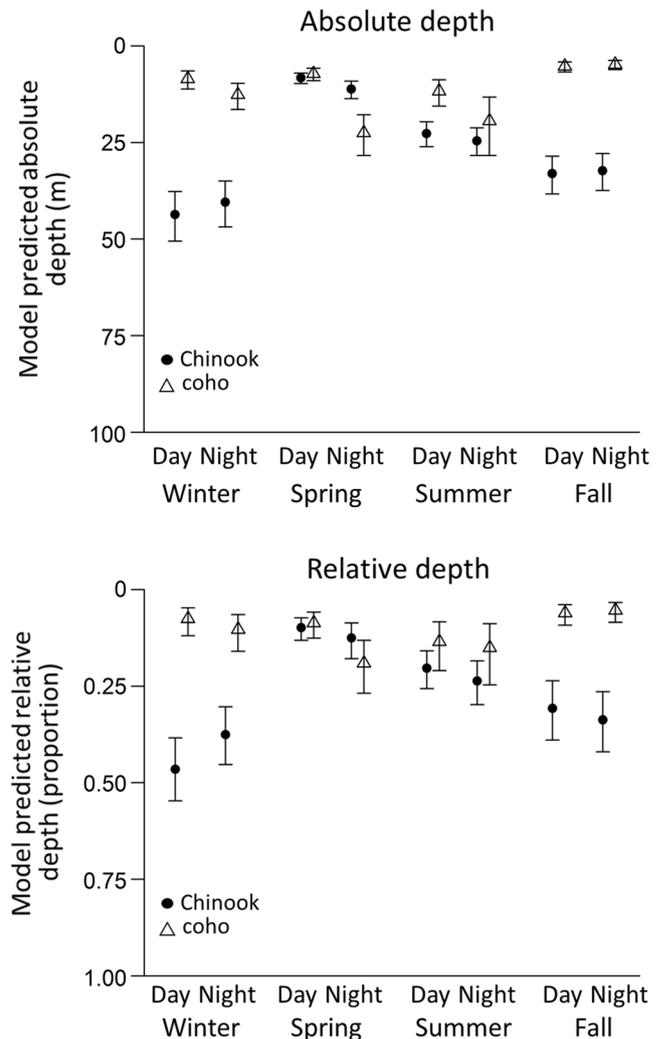


Fig. 3. LME model-predicted absolute depth (from the surface) and relative depth (from the bottom) with ± 2 SE bars for Chinook (circles) and coho (triangles) salmon for each season. See Table 3 for post-hoc multiple comparison tests

night depths within a season; Table 3, Fig. 3). However, there were significant changes in depth among seasons. Chinook salmon were closest to the surface in spring (day = 8.29 m, night = 11.18 m), and were deeper in summer (day = 22.67 m, night = 24.55 m), deeper yet in fall (day = 33.08 m, night = 32.29 m) and deepest in winter (day = 43.65 m, night = 40.48 m; Tables 1 & 3, Fig. 3). The only across-season depth comparison which was not significant within Chinook salmon was fall at day versus winter at night ($p = 0.05$; Table 3).

DVM was detected for coho salmon in spring, i.e. there were significant absolute depth differences between day (7.23 m) and night (22.51 m) but not during the other seasons. Coho salmon were closest to the surface in the fall both during the day (5.31 m)

Table 2. Output from absolute depth (from the surface) and relative depth (from the bottom) linear mixed effects (LME) models including numerator degrees of freedom (df_{num}), denominator degrees of freedom (df_{den}), F -values, and p -values. The fixed effects were species (Chinook *Oncorhynchus tshawytscha* and coho salmon *O. kisutch*), diel period, season and all possible interactions. The identities of individual fish were incorporated as random effects in each model. The mean time of detection (date/time) was used as a correlation structure for each model to account for auto-correlation between time and depth

	df_{num}	df_{den}	F	p
Log-transformed absolute depth				
(Intercept)	1	2648	653.01	<0.0001
Species	1	33	13.55	0.0008
Diel period	1	2648	13.69	0.0002
Season	3	2648	46.25	<0.0001
Species \times Diel period	1	2648	32.69	<0.0001
Species \times Season	3	2648	33.68	<0.0001
Diel period \times Season	3	2648	9.72	<0.0001
Species \times Diel period \times Season	3	2648	3.49	0.015
Logit-transformed relative depth				
(Intercept)	1	2648	182.61	<0.0001
Species	1	33	16.44	0.0003
Diel period	1	2648	46.27	<0.0001
Season	3	2648	21.18	<0.0001
Species \times Diel period	1	2648	10.76	0.0011
Species \times Season	3	2648	46.70	<0.0001
Diel period \times Season	3	2648	11.48	<0.0001
Species \times Diel period \times Season	3	2648	6.00	0.0005

and night (4.81 m), which was significantly closer to the surface than they were at night during the winter (12.63 m), night in spring (22.51 m), and night in summer (19.43 m; Tables 1 & 3, Fig. 3). With one exception (winter \times day = 8.55 m vs. spring \times night = 22.51 m), no other within-species, diel period and season comparisons were significant for coho salmon.

With the exception of a few combinations of diel period and season, Chinook salmon were found significantly farther from the surface than coho salmon (Table 3). Chinook salmon had model predicted values farther from the surface in every season except spring, when coho salmon had depth values farthest from the surface at night (Fig. 3).

Examining depth relative to the bottom revealed similar trends as depth relative to the surface (absolute depth), with some exceptions. Depth relative to the bottom did not differ between fall and winter for Chinook salmon (Table 3, starred values). Depth relative to the bottom was significantly differ-

Table 4. ANOVA table showing the 4 response variables, degrees of freedom (df), sum of squares (SS), mean square (MS), *F*-value and *p*-value from each analysis. The response variables are measured as the difference in abiotic conditions (values at 10 m subtracted from values at 100 m). Each analysis tested for difference across seasons (winter, spring, summer, and fall) for each response variable. See Fig. 4 for post-hoc multiple comparison tests

Response	df	SS	MS	<i>F</i>	<i>p</i>
Temperature difference	3	6.92	2.31	12.20	0.0024
Dissolved oxygen difference	3	9.80	3.27	24.02	0.0002
Salinity difference	3	0.95	0.32	7.10	0.0120
Chlorophyll <i>a</i> difference	3	323.70	107.91	15.36	0.0011

ent in the fall for both day and night compared to summer during the day for coho salmon (Table 3, starred values).

Vertical differences in temperature (ANOVA; *p* = 0.002), DO (ANOVA; *p* = 0.0002), salinity (ANOVA; *p* = 0.012), and chl *a* (ANOVA; *p* = 0.001) varied across seasons and within the water column in Puget Sound (Table 4, Fig. 4). Temperature was higher near the surface in spring and summer, but was similar

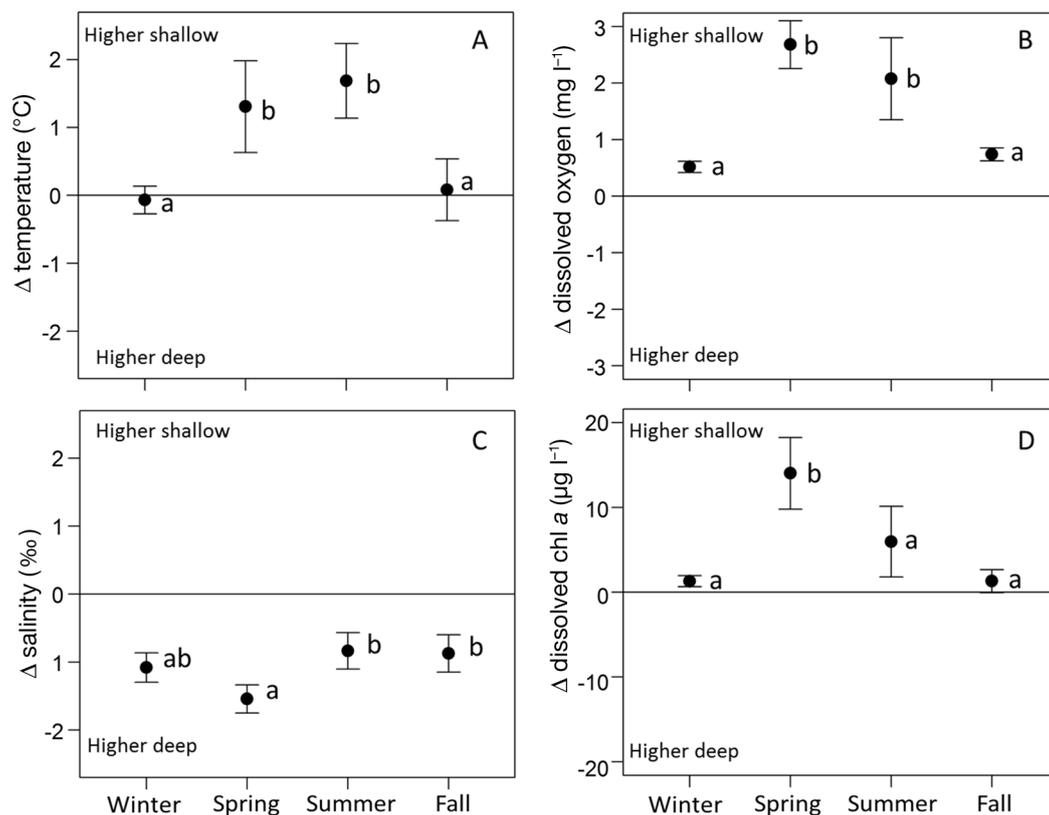


Fig. 4. Difference in (A) temperature, (B) dissolved oxygen (DO), (C) salinity, and (D) chl *a* between 10 and 100 m depths across seasons from the Point Wells (47.77739° N, 122.41761° W), King County monitoring site. Letters indicate significant differences across seasons using Tukey's multiple comparison tests. Data are mean \pm 2SE

within the water column in fall and winter (Fig. 4A). DO showed the same pattern as temperature (Fig. 4B). The water was less saline near the surface in spring compared to summer and fall (Fig. 4C). Chl *a* values were highest near the surface in spring compared to summer, fall and winter (Fig. 4D).

DISCUSSION

Coho salmon were detected close to the surface during the day and farther from the surface at night in the spring, providing evidence of DVM. Depth of coho salmon relative to the bottom confirmed that fish were deeper in the water column at night than during the day. This is the reverse pattern of DVM reported in many other fish species (Mehner 2012). The coho were also farther from the surface at night in winter and summer, but not significantly so. In the fall, coho were very close to the surface during both the day (5.31 m) and night (4.81 m). In spring and summer the number of detections at offshore, onshore–deep, and onshore–shallow receivers were as expected (as determined by chi-squared tests), but during the fall, coho salmon were detected more often than expected at onshore–deep receivers when they were closest to the surface (Fig. 2).

No DVM of Chinook salmon was detected, but they showed clear seasonal changes in depth distribution: closest to the surface in the spring, farther from the surface in summer, farther yet in fall and farthest from the surface in winter. Relative depth from the bottom confirmed these depth patterns. There also seemed to be a shoreward shift in winter, as Chinook salmon were detected almost exclusively at onshore–shallow receivers, far from the surface. The reason for this intriguing pattern (i.e. deeper in the water column nearshore during the winter) requires further

study. Chinook salmon were detected more often than expected at offshore receivers and less than expected at onshore–shallow receivers in the summer, when they were about half as far from the surface (day = 22.67, night = 24.55 m) as they were in the winter (day = 43.65 m, night = 40.48 m).

Despite being similar in trophic level and body size, resident coho and Chinook salmon in Puget Sound displayed different patterns of vertical distribution and movement. With one exception (spring at night), Chinook salmon were found farther from the surface than coho salmon. However, depth distribution differed across seasons (especially for Chinook salmon) and diel period (for coho salmon in spring). Coho salmon showed clear diel patterns (shallow during the day and deeper at night) in spring (Fig. 5: example of diel vertical migration of coho in April). Even though Chinook salmon were more often farther from the surface, coho salmon were also detected 100+ m deep (6.7% of all detections). These results support previous evidence that Chinook salmon occupy deeper water than coho salmon (Ogura & Ishida 1992, 1995, Erickson & Pikitch 1994, Orsi & Wertheimer 1995, Candy & Quinn 1999). However, Chinook salmon tended to occur near onshore–shallow receivers in the winter, while coho tended to use the offshore areas in the winter.

By looking at seasonal and vertical changes in environmental conditions in Puget Sound we sought to consider some of the mechanisms hypothesized to drive seasonal depth distributions and DVM in other systems (Table 5). Mehner (2012) hypothesized that the causal mechanisms of DVM in freshwater systems are bioenergetic efficiency, feeding opportunities, and predator avoidance, and proposed the proximate causes or stimuli to be temperature, hydrostatic pressure, and illumination strength. Mehner (2012) also proposed that the ‘antipredation window’ (Clark & Levy 1988) and the ‘thermal niche (or window)’ (Pörtner & Farrell 2008) likely explain DVM. It is difficult to determine the functional significance of vertical migration in our study because the predator and prey communities were largely unknown, although the physical features of the environment were well characterized by the data obtained.

We might expect fish to be deeper during warm seasons (spring and summer; Fig. 4A) because water temperatures are cooler deeper in the water column, but neither coho nor Chinook salmon showed this pattern. Coho salmon were near the surface in spring and summer (especially during the day), and

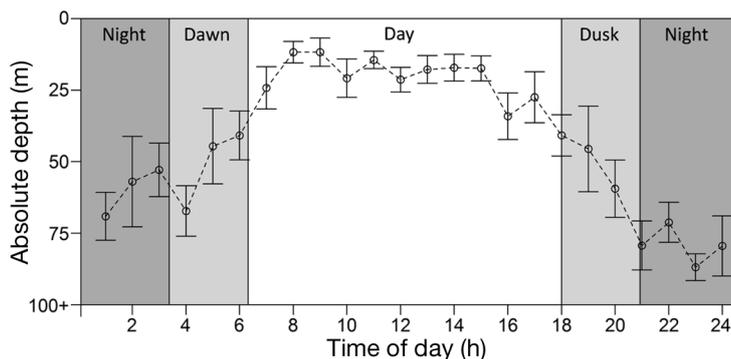


Fig. 5. Mean hourly depths of coho salmon *Oncorhynchus kisutch* (± 2 SE) in April illustrating a clear diel vertical migration

Table 5. Hypotheses, expected response, and species-specific evidence for differences in seasonal and diel depth distributions of Chinook *Oncorhynchus tshawytscha* and coho salmon *O. kisutch*

Hypothesis	Expected response	Chinook evidence	Coho evidence
Depth distribution			
Avoid high temperatures	Farther from the surface in warmer seasons	No avoidance	No avoidance
Avoid low dissolved oxygen (DO)	Close to the surface in seasons with low DO near the bottom.	No avoidance	No avoidance
Avoid freshwater	Farther from the surface in seasons with low salinity at the surface	No avoidance	No avoidance
Seek high chl <i>a</i>	Closer to the surface in seasons with high chl <i>a</i> at the surface.	Closer to the surface during spring when chl <i>a</i> is highest near the surface.	Shallow but no different than other seasons
Diel vertical migration			
Follow prey	Movements and depth mimic distribution of prey	No	No, opposite trend
Avoid nocturnal predators	Movement and depth inverse of predators	No	Harbor seals may be more active (Wright et al. 2007) and dive deeper at night (Lesage et al. 1999). During spring, coho were deeper at night and closer to the surface in the day but this trend is not consistent throughout the year; predators may be influencing the depth of coho in the spring

Chinook salmon were closest to the surface in the spring and then gradually shifted deeper in the water column throughout the summer and beginning of fall and stayed deep during the winter months. Temperatures throughout Puget Sound are well within positive growth ranges (4.5 to 19°C) and do not exceed the optimal growth ranges (10.0 to 15.6°C) of either species of salmon (Brett 1995), so it seems unlikely that their seasonal vertical distributions and movements were strongly related to temperature. Temperature can influence the DVM of fish on smaller time scales (Sims et al. 2006), but our data is not at a sufficiently fine spatiotemporal scale to address this hypothesis.

If DO was limiting depth distribution of fish (Davis 1975), we would expect fish to be closer to the surface in seasons with the lowest DO values at depth (spring and summer; Fig. 4B). Chinook and coho salmon were close to the surface in spring and summer; however, at no depth were DO concentrations at levels that would negatively affect salmon. Therefore, there is no evidence that DO was driving seasonal depth distributions of Chinook salmon or coho salmon.

Considering that these salmon are entering the marine portion of their life history we might expect them to avoid low salinity water, and experimental evidence supports this (McInerney 1964). Salinity was lowest near the surface due to river runoff during the spring. However, Chinook and coho salmon were near the surface in the spring so there was no evidence that they were avoiding freshwater, and salinity is not likely to be driving seasonal depth distribution patterns.

Salmon might be closer to the surface in seasons of high productivity when chl *a* levels are higher near the surface, and Chinook salmon were nearest the surface in spring when chl *a* was highest near the surface. Coho salmon were near the surface in spring but they were also near the surface in other months. It is likely that any connection between chl *a* and salmon depth distributions is indirect, perhaps through decreased water clarity reducing predation risk or necessitating foraging near the surface, or increased prey availability via bottom-up processes.

In some cases, DVM by predators is best explained by the DVM of their prey (e.g. Nichol et al. 2013, but see Mehner et al. 2007). Chinook and coho salmon have considerable diet overlap in Puget Sound (mean = 65%; Kemp 2013) and feed primarily on invertebrates including copepods, crab larvae, euphausiids, gammarids, hyperiids, and fishes in-

cluding Pacific herring *Clupea pallasii*, sand lance *Ammodytes hexapterus*, surf smelt *Hypomesus pretiosus*, and juvenile salmon (Kemp 2013), though coho salmon ingest more invertebrates than do Chinook salmon (Kirkness 1948). Copepods (Bollens et al. 1993, Dagg et al. 1997, Dagg et al. 1998) and Pacific herring (Thorne & Thomas 1990) exhibit diel movements, but in the opposite direction exhibited in our study. These prey organisms tend to be deep during the day and shallower at night, so this is not consistent with the hypothesis that Chinook or coho salmon are following the DVM of their prey.

Salmon may adjust their depth distribution at least in part to avoid predators. Chinook and coho salmon of the size range in this study would be primarily at risk from marine mammals, notably harbor seals *Phoca vitulina*, California sea lions *Zalophus californianus*, Dall's porpoise *Phocoenoides dalli* and harbor porpoise *Phocoena phocoena*. Harbor seals are likely one of the most abundant predators for salmon, especially close to shore. They can hunt for salmon at dusk and at night (Wright et al. 2007, Wilson et al. 2014), and some dive more frequently at night than during the day (Lesage et al. 1999) with dive patterns that have been associated with foraging (Wilson et al. 2014). We found that when DVM occurred, salmon were deeper at night. Although harbor seals can dive to depths >100 m, we assume that capture success would be reduced deeper in the water column due to lower light levels for this visual predator. Thus the DVMs were consistent, at least in part, with predator avoidance, although the complex patterns of salmon vertical distribution and movements were not entirely explained as responses to predation risk and could not be explicitly tested.

It is possible for a fish to be at the same distance from the surface but occupying different areas of the water column. For example, if a fish were 50 m from the surface and in water 100 m deep, that individual would be in the middle of the water column, whereas if the water was 55 m deep the fish would be near the bottom. Examining fish depth relative to the bottom confirmed that Chinook salmon were (in most diel periods and seasons) farther from the surface and closer to the bottom than were coho salmon. Chinook salmon might be farther from the surface than coho salmon because of differences in their ability to see at low light levels; similar ecological segregation has been found along with differences in retinal structure in other salmonid species in lakes (Henderson & Northcote 1988).

The objectives of this study were not to examine the horizontal distributions of the salmon; however, it was

interesting that none of the fish were detected in Hood Canal even though many receivers were deployed throughout that area during the study period. Indeed, the horizontal movements were quite limited, considering the range of locations in Puget Sound where they could have been detected (Rohde et al. 2013). Consequently, our study was largely limited to Central Puget Sound, in addition to the limited number of tagged fish with unequal numbers of detections and an uneven distribution of detections across seasons (limitations common to many telemetry studies). Future studies with larger sample sizes and tagging in multiple basins would be informative. Although this study spanned multiple years, there were not enough data to explicitly test for a year effect. As technology allows for longer battery life and becomes less expensive, future studies will hopefully address yearly variation in depth distribution. Replicating this study could also provide insights into the striking reverse DVM pattern for coho salmon we observed.

In addition to the insights into the behavior of salmon in marine waters, our findings contribute to a growing literature on the complexity of diel activity patterns. The diel activity patterns of stream-dwelling salmonids reflect a mix of predation risk and foraging opportunity, hence may be affected by habitat, hunger, temperature, and food availability, as well as considerable variation among individuals that is not readily explained by biotic or abiotic factors (Railsback et al. 2005, Roy et al. 2013). Similarly, work on upstream migrating salmonids and other anadromous fishes has revealed that diel activity period is context-dependent, varying with hydraulic complexity and predator density (Keefer et al. 2013). At the broadest level, the hypothesis that temporal patterns in activity provide an axis for niche separation among related species has been debated for decades without conclusive evidence (Kronfeld-Schor et al. 2001, Kronfeld-Schor & Dayan 2003). Chinook and coho salmon are each other's closest relatives and their diets overlap broadly, so we might expect them to overlap in space and time. However, our results showed considerable differences in seasonal and diel depth distribution patterns between these species within a rather small geographic region (central Puget Sound). They also showed substantial differences in diel activity patterns in Puget Sound (Rohde et al. 2013, A. N. Kagley et al. unpubl. data). These differences would tend to reduce spatiotemporal overlap and thus reduce competition to a greater extent than might be inferred from diet analysis alone, supporting the hypothesis that temporal patterns can contribute to niche separation.

Acknowledgements. We thank the many people who helped with the field work, including the crew of the fishing vessels and especially Kurt Dobszynski and Jay Field. Dawn Spilbury Pucci and Jennifer Scheuerell provided essential database management assistance. This project depended on the cooperation of the many agencies deploying and retrieving receivers and sharing their data with us, including but not limited to NOAA Northwest Fisheries Science Center, the University of Washington's School of Aquatic and Fishery Sciences, the Washington Department of Fish and Wildlife, the US Army Corps of Engineers, Seattle Aquarium, Seattle City Light, the Nisqually and Squaxin Island tribal fisheries departments, Beam Reach, and the Pacific Ocean Shelf Tracking Project. Funding for this project was provided by the State of Washington's Salmon Recovery Funding Board through the Recreation and Conservation Office, NOAA-Fisheries, and the H. Mason Keeler Endowment at the School of Aquatic and Fishery Sciences, University of Washington. We thank Jessica Rohde and Michael Elam for initial data analysis, Kinsey Frick and Megan Moore for assistance in the field, Kelly Andrews for statistical modeling advice and manuscript comments, Morgan Bond, Mary Moser, and anonymous reviewers for comments on the manuscript, and Fred Goetz and Joshua Chamberlin for their roles in the formation of this project. This research was conducted with permits from the University of Washington's IACUC, the Washington Department of Fish and Wildlife, and NOAA-Fisheries.

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Appendix. Species (Chinook *Oncorhynchus tshawytscha* or coho salmon *O. kisutch*), serial number, tagging date, fork length, weight (NA: not available), origin (H: hatchery; W: wild), number of detections, number of months detected

Species	Tag serial no.	Tagging date (mm/dd/yyyy)	Fork length (mm)	Weight (g)	Origin	No. of detections	No. of months detected
Chinook	3130	06/07/2007	342	457	H	81	1
Chinook	3131	11/01/2006	254	189	W	70	2
Chinook	3133	06/07/2007	369	643	H	354	2
Chinook	3134	11/01/2006	276	237	W	798	1
Chinook	4996	06/07/2007	330	424	H	1246	2
Chinook	4997	06/07/2007	370	616	H	3760	8
Chinook	4998	06/07/2007	255	184	W	24	1
Chinook	5033	11/02/2006	401	821	H	3024	4
Chinook	5034	11/01/2006	505	NA	W	23	1
Chinook	5035	11/01/2006	296	343	W	567	3
Chinook	6038	11/01/2006	260	201	W	151	1
Chinook	1040674	06/07/2007	266	NA	H	852	7
Chinook	1040675	06/08/2007	346	546	W	354	3
Chinook	1040676	06/07/2007	280	276	H	217	2
Chinook	1040677	06/07/2007	330	483	H	18	1
Chinook	1040678	06/07/2007	316	370	W	532	3
Chinook	1045449	12/12/2007	260	207	H	29	1
Chinook	1055537	12/11/2008	273	283	W	64	2
Chinook	1055541	12/11/2008	275	264	W	329	2
Chinook	1082468	05/13/2012	430	NA	H	954	3
Chinook	1082469	06/24/2012	400	NA	H	186	2
Chinook	1082470	06/24/2012	400	NA	H	6	1
Chinook	1082472	06/24/2012	400	NA	W	73	1
Chinook	1082477	04/12/2012	425	NA	H	743	4
Coho	4968	06/07/2007	362	521	W	747	1
Coho	5036	11/01/2006	303	285	W	1488	3
Coho	1045440	02/29/2008	334	NA	H	239	6
Coho	1045441	02/29/2008	320	NA	H	163	6
Coho	1045442	02/29/2008	350	NA	H	69	2
Coho	1045443	02/29/2008	330	NA	H	412	2
Coho	1045444	02/29/2008	344	NA	H	406	4
Coho	1045445	02/29/2008	324	NA	H	336	5
Coho	1045446	02/29/2008	323	NA	H	759	6
Coho	1045447	02/29/2008	341	NA	H	8	1
Coho	1045448	02/29/2008	346	NA	H	661	5

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Submitted: July 14, 2014; Accepted: May 18, 2015
Proofs received from author(s): July 8, 2015