

Selective occupancy of a persistent yet variable coastal river plume by two seabird species

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ABSTRACT: Advances in telemetry and modeling of physical processes expand opportunities to assess relationships between marine predators and their dynamic habitat. The Columbia River plume (CRP) attracts sooty shearwaters *Ardenna grisea* and common murres *Uria aalge*, but how seabirds respond to variability in plume waters is unknown. We characterized seabird distributions in relation to hourly, daily, monthly, and seasonal variation in CRP location and surface area by attaching satellite telemetry tags to shearwaters in 2008 and 2009, and to murres in 2012 and 2013. We matched seabird locations to surface salinity from a high-resolution hydrodynamic model of the CRP and adjacent waters. Utilization distributions indicated high-use areas north of the Columbia River mouth and in continental shelf waters. Shearwater and murre occupancy of tidal (<21 psu), recirculating (21–26 psu), and boundary (26–31 psu) plume waters was on average 31 % greater than expected and positively correlated with CRP surface area. Seabird latitude was positively correlated with latitude of the geographic center of the CRP, indicating that birds move in phase with the plume. We detected a threshold response of seabirds to plume size, and birds were closer to the convergent CRP boundary (28 psu isohaline) after a surface area threshold between 1500 and 4000 km² was exceeded. We conclude that shearwaters and murres selectively occupy and track plume waters, particularly dynamic boundary waters where foraging opportunities may be enhanced by increases in surface area and associated biophysical coupling that aggregates zooplankton and attracts prey fishes.

KEY WORDS: Bio-physical coupling · Columbia River plume · Frontal regions · Hydrodynamic modelling · Satellite telemetry · Seabird foraging · Shearwater · Murre

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INTRODUCTION

Mobile marine predators often forage in regions of the world's oceans where the predictability of marine productivity can maximize energetic intake (Weimerskirch 2007). In these regions, elevated primary and secondary production is generated by dynamic physical oceanographic processes, which aggregate passive or weakly-swimming organisms to create patches of plankton, and facilitate biophysical coupling (Franks 1992, Dower & Brodeur 2004). Planktivorous fishes are attracted to areas of concentrated plankton, including density fronts (Olson et al. 1994), which in

turn attract piscivorous fishes and other predators (Fiedler & Bernard 1987, Bost et al. 2009). Relationships among mobile marine predators to large-scale (>1000 km; Hunt & Schneider 1987) areas of enhanced productivity, such as shelf edges and upwelling zones, are well established (e.g. Block et al. 2011). In comparison, associations with dynamic features that vary spatially and temporally at finer scales (1–100 km, hours to days) remain less understood, even though marine predators have been shown to respond at these scales (Hunt et al. 1999, Zamon 2003, Ainley et al. 2005).

Relationships of marine predators to fine-scale oceanographic features associated with foraging

areas have been difficult to quantify because temporal averaging of satellite-derived, environmental data over multiple days can mask processes that generate variability in ocean features at finer temporal scales (Mannocci et al. 2017, Scales et al. 2017). Recent advances in satellite telemetry used to track mobile marine predators and numerical modeling of dynamic, coastal processes now enable assessment of predators and their foraging environment at matching spatial and temporal resolutions (Hart & Hyrenbach 2009). Satellite-linked, Argos Doppler tags (i.e. platform terminal transmitters; PTTs) allow high-resolution (i.e. hours, kilometers) tracking of mobile predators for long periods (i.e. months) through large and

remote areas of the open ocean. When coupled with high-resolution oceanographic data, relationships between tagged predators and dynamic physical features, including circulation of water masses and associated density fronts, can be resolved.

Areas where fresh and saltwater interface (e.g. estuaries, river plumes, tidewater glaciers) form dynamic oceanographic features that are important for marine predators including seabirds (Skov & Prins 2001, Kowalczyk et al. 2015, Arimitsu et al. 2016). Mixing of buoyant freshwater discharge with saltwater near the mouth of the Columbia River in the northern California Current Ecosystem (CCE) forms a mesoscale (100–1000 km) plume and associated convergent mixing fronts at the boundaries

between water masses (Burla et al. 2010, Hickey et al. 2010). Although the Columbia River plume (CRP) is present along the Oregon and Washington coasts year round, the geographic location and size (i.e. surface area) vary seasonally with changes in river discharge, tidal and coastal currents, and wind direction (Fig. 1; Hickey et al. 2005, 2010, Horner-Devine et al. 2009). Changes in plume location and morphology can occur at temporal scales of 2–24 h and spatial scales of 1–100 km (Hickey et al. 1998, Jay et al. 2009). The plume is generally oriented southward and offshore of the Oregon coast during late spring and summer, when river discharge is at a seasonal high and northwest winds create upwelling conditions and offshore transport increases (Fig. 1; Thomas & Weatherbee 2006, Horner-Devine et al. 2009). The plume shifts northward and close to the Washington coast during fall, winter, and periodically during spring and summer when southwest winds create downwelling conditions (Hickey et al. 2005, Thomas & Weatherbee 2006). Areas where convergent fronts mix freshwater and saltwater near the plume edge are particularly dynamic compared with the plume center, and fronts along the boundary can vary in location and strength with hourly shifts in tidal currents and local winds (Jay et al. 2009). In comparison, the plume center is relatively persistent offshore of the Columbia River mouth, where a

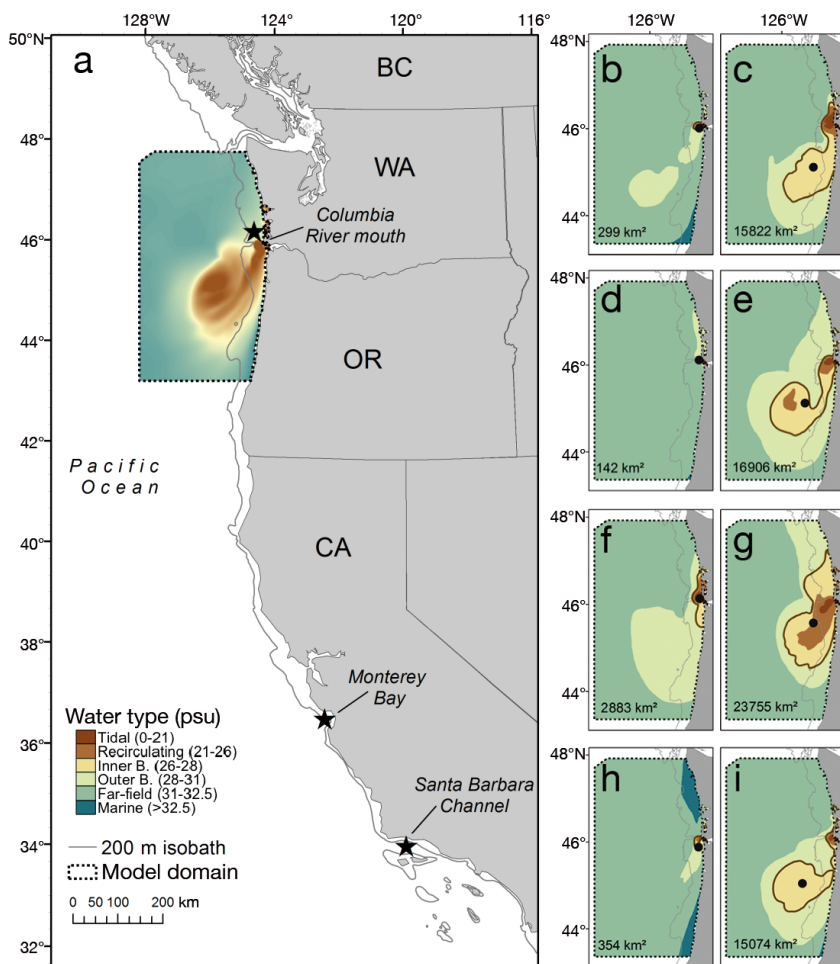


Fig. 1. Study site on US west coast showing the Columbia River plume hydrodynamic model domain and (a) an example of the hydrodynamic model output for 20 June 2013. Black stars indicate approximate locations where seabirds were captured and tagged. Subset maps show the minimum and maximum plume surface areas during the study period for each year. Minimum plume surface areas occurred on (b) 15 September 2008, (d) 17 October 2009, (f) 8 June 2012, and (h) 27 July 2013. Maximum plume surface areas during the study period occurred on (c) 21 June 2008, (e) 27 May 2009, (g) 8 May 2012, and (i) 12 June 2013. Dark brown line represents the plume boundary (28 psu isohaline); black dots represent the location of the mean center of the plume

pulse of low-salinity river discharge is generated with each tidal cycle. In addition to geographic variability, plume surface area fluctuates over 2 orders of magnitude, from $\sim 150 \text{ km}^2$ during periods of low river discharge (e.g. late summer) to $\sim 24\,000 \text{ km}^2$ in spring during peak river discharge and strong, persistent upwelling winds (Horner-Devine et al. 2009).

The CRP influences stratification and recirculates terrigenous and marine-derived nutrients near the surface, fueling primary and secondary productivity (Kudela et al. 2010). Biophysical coupling near the plume edge aggregates zooplankton (Morgan et al. 2005), which attracts small schooling coastal pelagic fishes including northern anchovy *Engraulis mordax* that feed on zooplankton and larval fish (Miller & Brodeur 2007). The CRP is also an important foraging area for sooty shearwaters *Ardenna grisea* and common murre *Uria aalge* (Zamon et al. 2014) that consume anchovy, juvenile Pacific tomcod *Microgadus proximus*, smelts (Family Osmeridae), and juvenile salmon *Oncorhynchus* spp. (Wiens & Scott 1975, Varoujean & Matthews 1983). Zamon et al. (2014) demonstrated that shearwater and murre distributions are greatest near the northern face of the plume, where density fronts are often strongest (Jay et al. 2009). Phillips et al. (2017) subsequently demonstrated that shearwaters near the CRP were consistently $\sim 100 \text{ km}$ north of the geographic center of the plume near high densities of forage fishes, which contrasted to murre distributions that were within $\sim 20 \text{ km}$ of the plume center. Phillips et al. (2017) also found that juvenile salmon and forage fish densities did not vary with CRP size, but both shearwater and murre densities were highest when plume surface area was low, indicating that seabirds concentrate in plume waters to maximize prey encounter rates. Both studies relied on ship-based transect data during relatively short survey periods (3–10 d) in late spring, which limits inferences about CRP effects on seabird distributions. Whether seabirds track fine-scale variation in CRP size and location through spring and summer, and at a finer spatio-temporal resolution, remains unknown.

The ability of seabirds to track physical changes in foraging areas may be influenced by species-specific differences in foraging constraints. Sooty shearwaters breed in the southern hemisphere but are one of the most abundant marine predators found in the CCE from May through September (Briggs & Chu 1986). They are highly mobile, aggregating in large flocks near areas of enhanced prey availability (Shaffer et al. 2006). Shearwaters use local enhancement, visual cues, and possibly olfaction to locate foraging

areas (Hutchinson et al. 1984, Van Buskirk & Nevitt 2008, Mitkus et al. 2016). In contrast, common murre *breed* on small coastal islands in the CCE from May through August, and breeding birds are typically constrained to foraging trips within 100 km of their colonies in continental shelf waters (Cairns et al. 1987). Murre *may* rely on memory to re-locate predictable foraging areas within the 100 km radius of their colony (Davoren et al. 2003, Regular et al. 2013), including low salinity CRP waters (Phillips et al. 2017). Therefore, we predicted that shearwaters and murre *would* contrast in their responses to the CRP at hourly, daily, monthly, and seasonal time periods. Specifically, we hypothesized that shearwaters *would* track the plume edge and occur in mixed salinity waters near productive plume boundaries. Murre *were* predicted to track the location of the plume center and occur in lower salinity waters near the river mouth.

This study examined the spatial and temporal dynamics of seabird distributions associated with the CRP in the northern CCE. We used satellite telemetry collected during spring and summer in 2008 and 2009 from sooty shearwaters and in 2012 and 2013 from common murre *and* data from a high-resolution hydrodynamic model to relate movements of seabirds to hourly, daily, monthly, and seasonal changes in the location and size of the CRP. We also characterized and compared species-specific distributions to determine if shearwaters tracked different areas of the plume than murre *s.*

MATERIALS AND METHODS

Data acquisition and processing

Defining the CRP using surface salinity

To assess the size (i.e. surface area) and location of the CRP, we used surface salinity predicted from a hydrodynamic model developed specifically to capture the dynamic nature of the CRP region (Zhang & Baptista 2008). Estimates of 1 h and 24 h gridded (1 km^2 horizontal resolution) surface salinities were obtained from a skill-assessed 4D (space-time) semi-implicit, Eulerian-Lagrangian finite-element/volume (SELFE) hindcast simulation model of baroclinic circulation (Zhang & Baptista 2008) developed by the Center for Coastal Margin Observation and Prediction (CMOP; www.stccmop.org/datamart/virtualcolumbia river). The circulation model produces hourly surface salinity estimates (range: 0–33.6 practical salinity units [psu]) at the midpoint of each 1 km^2 cell extending

from 43.4° to 48.0° N and from shore to 127.8° W, covering a model domain of approximately 147 900 km² (Fig. 1). The model domain encompasses an area large enough to include variability in river discharge, seasonal winds along the coast, the influence of the Strait of Juan de Fuca freshwater discharge, and circulation of adjacent ocean waters (A. M. Baptista pers. comm.).

To evaluate relationships among seabirds and the range of salinities within and surrounding the CRP, we categorized surface salinities from the hydrodynamic model using plume water definitions adapted from Horner-Devine et al. (2009) and Burla et al. (2010). Categories include: tidal (<21 psu), recirculating (21–26 psu), inner boundary (26–28 psu), outer boundary (28–31 psu), and far-field (31–32.5 psu) water types. Waters with salinities ≤31 psu (i.e. tidal, recirculating, inner, and outer boundary waters) were collectively termed 'plume waters.' Far-field waters were treated separately in analyses. Surface salinities >32.5 psu were considered marine waters. The daily geographic mean center of the plume was tabulated using output from the 24 h circulation model and used as an index of plume location. The daily 28 psu isohaline contour, which corresponds to the median salinity of the inner and outer plume boundary categories, was estimated from the 24 h circulation model raster output using the 'contour' command in Geospatial Modeling Environment (Beyer 2015) and used as an index of the plume boundary (Burla et al. 2010). The area of water within the 28 psu isohaline contour was tabulated using output from the 24 h circulation model and used as an index of plume surface area. To evaluate relationships between length of the 28 psu isohaline (i.e. perimeter) and plume surface area, we calculated the ratio of daily surface area to perimeter. We then estimated the inflection point and asymptote of the data using the nonlinear least squares logistic model functions 'nls' and 'SSlogis' in R stats package (R Core Team 2015).

Seabird locations

Seabird locations were collected using satellite transmitters attached to shearwaters in 2008 (n = 13) and 2009 (n = 17; Telonics TAV-2630 PTTs; see Adams et al. 2012) and common murrelets in 2012 (n = 12) and 2013 (n = 14; Telonics TAV-2617 PTTs). All murrelets and some shearwaters (n = 7 in 2008, n = 5 in 2009) were captured and released near the mouth of the Columbia River, Washington (Table 1). Data from 18 (n = 6 in 2008, n = 12 in 2009) additional shearwa-

ters that were captured and tagged in California (Monterey Bay [MB] and Santa Barbara Channel [SBC]), and migrated north to the study area were included in analyses when the birds were located within the model domain (Table 1). All seabirds were captured at night from the water using a handheld spotlight and dipnet (Ronconi et al. 2010) from a 5 m Boston Whaler deployed from shore (California) or a 4 m Zodiac inflatable deployed from a support vessel (Washington). PTTs were attached mid-dorsum using a suture-glue-tape combination (Macleod et al. 2008), and programmed to transmit every 60 s from late morning through early evening (11:00–21:00 h PST) for shearwaters, and every 60 s for 4 h in the morning (08:00–12:00 h) and 4 h in the evening (14:00–18:00 h) for murrelets. These duty cycles were chosen to maximize daily regional satellite availability, the number of transmissions (i.e. total tracking period), and day through evening foraging movements.

Locations of individual birds were estimated using the ARGOS system, which measures the Doppler Effect on transmission frequency (www.argos-system.org; CLS 2013), and archived via the Satellite Tracking and Analysis Tool (STAT; Coyne & Godley 2005). STAT was used to flag and manually correct 'mirror' locations and remove duplicate records (Adams et al. 2012). To resolve tag attachment or instrument failure, we removed data from tags that did not transmit for more than 2 wk, had intermittent transmissions (e.g. 5 d gap in transmissions), or showed evidence of halted movement (i.e. when median daily movements fell below the 95% confidence interval of average movement of birds for the sampling year; S. Loreda pers. comm.). All ARGOS location class data (LC-3 through LC-B, excluding LC-Z) were filtered using a speed-distance-angle filter (Freitas et al. 2008), resulting in a nominal spatial accuracy of 3 km. Speed thresholds of 16.7 m s⁻¹ for shearwaters and 24.3 m s⁻¹ for murrelets were specified, and default settings for distances and angles were used (Adams et al. 2012). Speed thresholds were based on calculated maximum sustained flight speed plus 3 standard deviations in a 5 m s⁻¹ tailwind (cf. Spear & Ainley 1997). To analyze spatial use in areas influenced by the CRP, we limited seabird locations to those between 43.0° and 48.8° N, and between 127.9° and 123.4° W to encompass movements near the edge of the model domain and to exclude movements beyond 100 km of the domain boundary. This 100 km buffer allowed us to examine movements of birds that exited and returned to the model domain, and to exclude birds that exited the domain and did not

Table 1. Summary of satellite telemetry data for sooty shearwaters *Ardenna grisea* in 2008 and 2009, and common murre *Uria aalge* in 2012 and 2013. Capture locations include: Columbia River plume, WA (CRP), Monterey Bay, CA (MB), and Santa Barbara Channel, CA (SBC). Blood was not collected to determine sex of shearwaters, and body mass was not recorded for murre in 2012 due to suboptimal weather conditions. Start and end dates (given as mo/d/yr) are for the time each individual was within the model domain. PTT: platform terminal transmitter; U: undetermined

Year	Capture location	PTT	Body mass (g)	Sex	Start date	End date	Days in model domain	Locations used for analysis		
Sooty shearwater										
2008	CRP	84209	720	U	6/19/08	7/7/08	19	231		
		84210	870	U	6/20/08	7/5/08	16	219		
		84211	850	U	6/20/08	7/8/08	19	157		
		84212	770	U	6/19/08	7/25/08	36	273		
		84215	920	U	6/20/08	9/28/08	101	1205		
		84217	920	U	6/19/08	7/8/08	20	233		
		84218	780	U	6/19/08	7/9/08	21	243		
		84220	750	U	9/30/08	10/13/08	13	104		
	MB	84224	880	U	9/20/08	10/9/08	19	232		
		84230	890	U	8/24/08	8/27/08	3	40		
	SBC	84231	930	U	9/11/08	10/1/08	20	260		
		84232	830	U	9/19/08	9/26/08	7	12		
		84235	880	U	9/18/08	9/19/08	1	6		
		2009	CRP	94556	900	U	5/15/09	9/4/09	112	1137
94557				900	U	6/7/09	10/1/09	117	1311	
94558	870			U	6/7/09	11/30/09	177	1749		
94559	840			U	6/7/09	6/26/09	20	222		
94560	870			U	6/7/09	11/23/09	170	640		
MB	94565		780	U	11/5/09	12/10/09	35	451		
	94566		810	U	10/13/09	10/26/09	13	167		
	94567		810	U	10/3/09	10/17/09	14	146		
	94570		830	U	10/7/09	11/6/09	30	290		
	94571		810	U	9/15/09	10/27/09	42	501		
SBC	94572	890	U	9/28/09	10/23/09	25	282			
	94574	860	U	8/12/09	10/23/09	72	698			
	94576	820	U	10/14/09	10/23/09	10	85			
	94582	810	U	10/20/09	11/10/09	21	126			
	94584	700	U	9/14/09	10/26/09	42	461			
2009	SBC	94585	825	U	10/15/09	12/6/09	52	628		
		84236	730	U	10/18/09	11/18/09	31	382		
		Common murre								
2012	CRP	110331	NA	M	5/5/12	6/11/12	37	182		
		110332	NA	U	5/4/12	5/23/12	19	112		
		110333	NA	F	5/6/12	6/6/12	31	136		
		110334	NA	M	5/5/12	6/3/12	29	156		
		110335	NA	F	5/5/12	7/10/12	66	281		
		110336	NA	F	5/5/12	6/28/12	54	289		
		110337	NA	F	5/5/12	7/6/12	62	287		
		110338	NA	M	5/5/12	7/9/12	64	225		
		110339	NA	F	5/6/12	7/4/12	60	295		
		110342	NA	F	5/5/12	5/23/12	18	100		
		110343	NA	F	5/6/12	6/28/12	54	267		
		110345	NA	M	5/5/12	5/14/12	9	50		
		2013	CRP	129159	1030	F	6/17/13	7/6/13	20	228
				129160	1000	F	6/11/13	7/2/13	21	222
				129161	980	M	6/11/13	8/1/13	51	281
129162	1000			F	6/10/13	7/28/13	48	501		
129163	1120			F	6/17/13	6/28/13	12	133		
129164	1080			M	6/11/13	7/29/13	48	449		
129165	920			M	6/17/13	8/6/13	50	367		
129166	940			F	6/11/13	7/25/13	44	446		
129168	980			F	6/16/13	8/23/13	68	611		
129169	1080			M	6/12/13	6/30/13	18	171		
129170	860			M	6/17/13	7/2/13	15	160		
129171	1020			M	6/16/13	6/30/13	13	160		
129172	1140			F	6/16/13	7/6/13	20	170		
129173	1100	M	6/11/13	7/15/13	33	314				

return. We also excluded the first 5 d of tracking data for birds tagged near the mouth of the Columbia River to avoid using positions that may have been affected by capture.

Data analysis

Spatial distributions

To examine spatial distributions of seabirds in the model domain, 99% Brownian bridge utilization distributions (99UDs; Horne et al. 2007) were calculated for each sampling year and species using the 'kernelbb' function in R package *adehabitat* (Calenge 2006). The Brownian bridge approach provides a better estimate of time spent in each area compared to fixed kernel density estimators because it estimates space-use from animal trajectories with serial autocorrelation of relocations (Horne et al. 2007). We calculated 99UDs for each seabird by specifying the first (speed) and second (cell size) smoothing parameters, which relate to species-specific flight speed (see preceding subsection) and our estimated nominal ARGOS location accuracy (3 km). To calculate an overall 99UD raster for all birds tagged in each year, we first calculated 99UDs for each individual within the model domain. Each individual's 99UD was then proportionately weighted by the individual's duration (i.e. tracking days per individual divided by total tracking days for all individuals) and summed again to represent the population 99UD for each year.

Occupancy of plume waters

To examine seabird use of the CRP at the finest spatio-temporal resolution possible, we further limited seabird location data to those with best ARGOS location classes (LC-3, LC-2, and LC-1 [error range ≤ 1 km]), to match the resolution of the plume model (1 km² grid cells). Seabird locations were projected in a Lambert Conformal Conic coordinate system (WGS 1984 datum) to match the salinity model output. The salinity value at each seabird location was extracted from the matched 1 h plume model output raster at a spatial resolution of 1 km². Each location was then assigned a salinity category (tidal, recirculating, inner/outer boundary, far-field, or marine) based on the extracted salinity value. To estimate occupancy of each water type by individual birds, locations in each category were summed and divided by the total number of locations in the model domain. Expected

occupancy was proportional to the availability of each water type in the model domain during the temporal period of the study, and was calculated using the proportion of each category represented in the sum of the 1 h salinity model outputs that matched seabird locations. We then compared observed seabird occupancy of each water type to expected using chi-square analyses (Zar 1999). Species-specific occupancy of each water type was compared between years using Welch's *t*-test (Zar 1999). We also examined variability in occupancy by individual seabirds within each year by calculating coefficients of variation (CVs). To determine if tracking duration (i.e. total number of locations obtained from each tagged seabird) influenced observed occupancy of the CRP, we compared plume occupancy with number of locations obtained from each individual seabird using Pearson correlations.

Seabird response to plume dynamics

To quantify seabird movements associated with CRP dynamics, we used multiple metrics. First, to evaluate spatial shifts of the CRP and seabirds through time, we calculated Pearson correlation coefficients between the daily mean latitude of the plume center and individual seabirds, and evaluated mean daily latitude of seabirds in relation to the latitude of the river mouth. Next, daily occupancy (averaged hourly occupancy) of plume waters through time by individual seabirds was compared with CRP surface area using Pearson correlation. Then, to quantify associations between seabirds and the CRP center and edge, we measured the Euclidean distance from each seabird location to the daily location of the plume center and plume boundary (i.e. 28 psu isohaline). We tested for differences between shearwater and murre distance measurements using Mann-Whitney tests (Zar 1999). To determine if murre or shearwaters exhibited greater variability in distances to the plume center or boundary, we calculated the CV of each species-specific metric for each year. To quantify relationships between seabird distances to the plume center and boundary and plume surface area, we calculated Spearman's correlation coefficients because distance measurements were not normally distributed (Zar 1999). We hypothesized that shearwater distances to the plume center would be similar to previous findings (~100 km; Phillips et al. 2017), and that distances to the plume edge would be less and not correlated with surface area, indicating that the shearwaters were able to locate and remain near the

plume boundary under varying CRP sizes. In contrast, we expected that murre distances to the plume center would be less (~20 km; Phillips et al. 2017) and not vary with surface area, and distances to the plume edge would positively correlate with surface area, as the plume boundary was expected to expand farther from the center with increased surface area (Fig. 1). We also compared patterns of seabird distances to the plume center, boundary and plume occupancy before and after the estimated inflection point of the surface area to perimeter ratio for each year using Mann-Whitney tests (Zar 1999) to determine if shearwaters or murre showed a threshold foraging response to the physical dynamics of the CRP. Unless otherwise stated, all statistics were analyzed using 2-tailed distributions and an alpha of 0.05.

RESULTS

We determined locations for shearwaters between late June and mid-October in 2008 (average tracking duration: 23 ± 25 d, SD), and from mid-May to mid-December in 2009 (58 ± 54 d). The period of locations determined for murre was shorter than that of shearwaters, and ranged from early May to mid-July in 2012 (42 ± 87 d), and from mid-June to early August in 2013 (33 ± 18 d; Table 1). After tabulating and filtering PTT location data, subsetting locations within 100 km of the model domain, and removing the first 5 d of transmissions, we retained 3215 locations (247 ± 303 locations bird^{-1}) for shearwaters in 2008, 9276 locations (546 ± 461 locations bird^{-1}) for shearwaters in 2009, 2380 locations (198 ± 87 locations bird^{-1}) for murre in 2012, and 4213 locations (301 ± 151 locations bird^{-1}) for murre in 2013 for analyses (Table 1).

Spatial distributions

Highest general use areas based on 99UDs for shearwaters and murre

were near the mouth of the Columbia River and extended north along the Washington coast, near Willapa Bay and Grays Harbor. Species-specific distribution patterns were also observed (Fig. 2). Shearwaters were distributed widely throughout the model domain (longitudinal extent: 123.47° to 127.80° W),

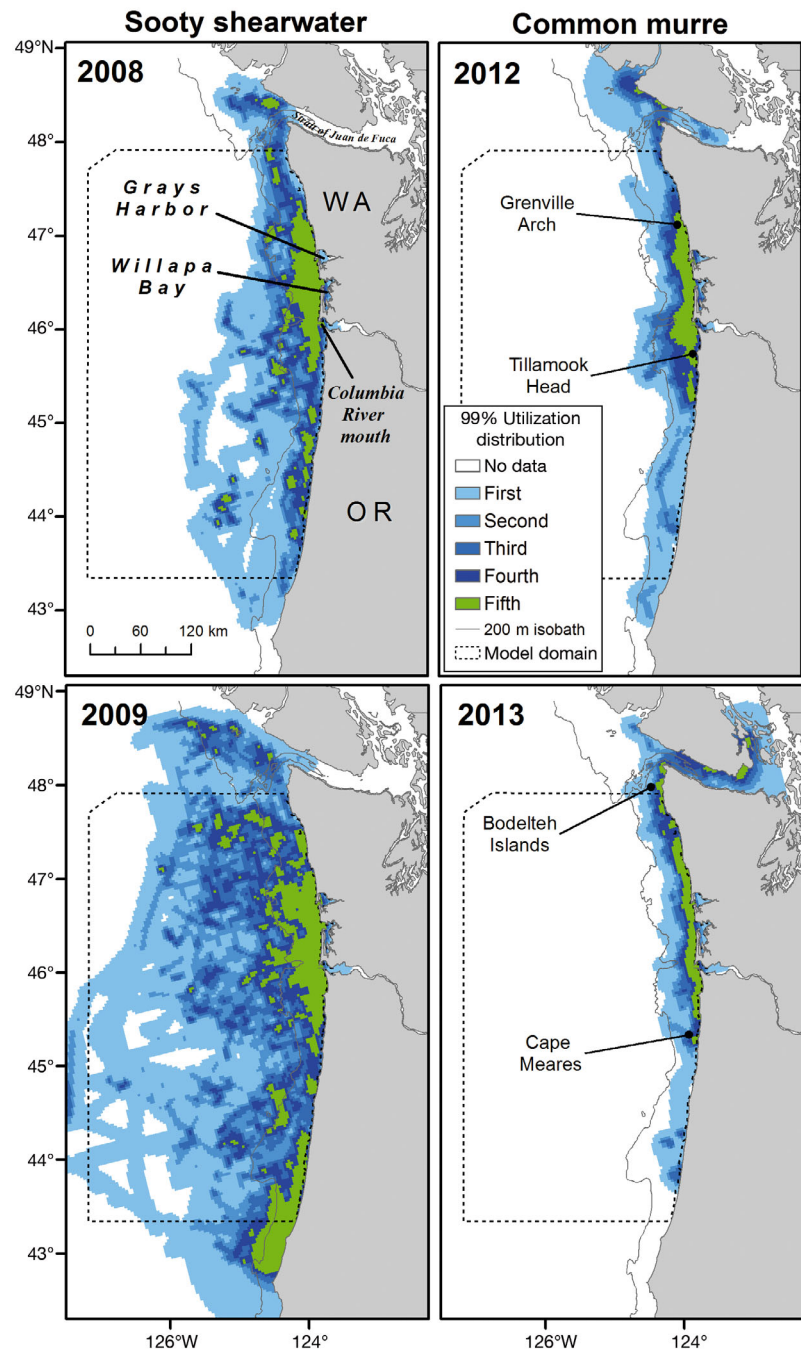


Fig. 2. Sooty shearwater *Ardenna grisea* and common murre *Uria aalge* 99% utilization distributions in the Columbia River plume model domain. Data are displayed by quintiles, with the fifth quintile showing highest use areas (80th–100th percentile)

including continental shelf (<200 m depth) and slope (200–2000 m depth) waters off Washington and Oregon. However, highest-use areas of shearwaters were generally within 40 km of shore in 2008, and 50 km in 2009 (Fig. 2). Shearwater latitudinal extent was also broad, and included the movements of shearwaters tagged in California into the model domain, and the use of waters near the mouth of the Strait of Juan de Fuca, north of the model boundary (Fig. 2). Despite their vagility, shearwaters that were tagged near the CRP spent the majority of time (95.0%) within the model domain in both 2008 and 2009.

Murres were distributed in a narrower band closer to the coast in continental shelf waters, with a longitudinal extent ranging from 123.35° to 125.35° W (Fig. 2). Highest-use areas were within 40 km of shore in 2012, and 20 km in 2013. Utilization distributions indicated some use of waters near small colonies along the central and northern Washington coast in both 2012 and 2013, particularly the Bodelteh Islands and Grenville Arch, as well as Tillamook Head and Cape Meares in northern Oregon (Fig. 2), but obvious central place foraging behavior, such as repeated trips to land, was not observed. Murres tagged near the CRP spent most of their time within the model domain in 2012 (72.8%) and 2013 (62.2%), but residence time was less than that of shearwaters. Mobility of tagged murres was greater than expected, and the latitudinal range encompassed the full model domain. Similar to shearwaters, some murres used waters near the mouth of the Strait of Juan de Fuca and, in 2013, 7 murres used waters near the southeast side of Vancouver Island, British Columbia (Canada), before returning to the model domain.

Occupancy of plume waters

Occupancy of plume waters by both shearwaters and murres was greater than expected based on the proportion of available water types in the model domain (2008: $\chi^2_5 = 105.4$, $p < 0.001$; 2009: $\chi^2_5 = 34.6$, $p < 0.001$; 2012: $\chi^2_5 = 542.6$, $p < 0.001$; 2013: $\chi^2_5 = 724.3$, $p < 0.001$). The percentage of shearwaters in plume waters (i.e. tidal, recirculating, inner, and outer plume boundary waters, combined) was 26.8% greater than what was available in 2008, and 8.9% greater than what was available in 2009 (Fig. 3). The median salinity occupied by shearwaters in both 2008 and 2009 was 31.5 psu (i.e. far-field plume waters). Even though most shearwaters occurred in far-field waters (2008: 59.6%, 2009: 72.9%), the ob-

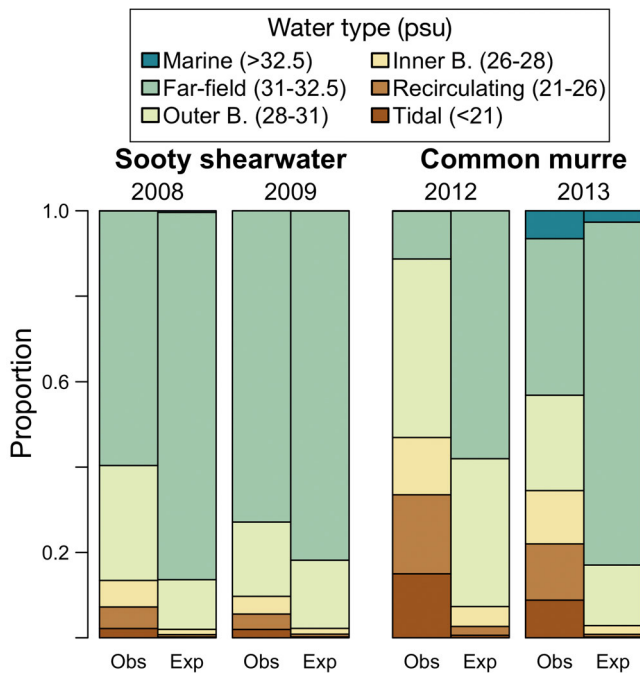


Fig. 3. Proportion of sooty shearwater *Ardenna grisea* and common murre *Uria aalge* observed occupancy of different water types in each year (Obs) compared to expected (Exp) availability of each water type from the hydrodynamic model output

served disproportionate plume occupancy was due to increased use of tidal, recirculating, and boundary waters (Fig. 3). In 2008, the greatest difference in observed versus expected occupancy occurred in outer boundary waters ($\Delta_{\text{obs-exp}} = 15.3\%$). In 2009, the greatest difference in observed versus expected occupancy occurred in recirculating and inner boundary waters (combined $\Delta_{\text{obs-exp}} = 5.8\%$).

In comparison, the percentage of murres occurring in plume waters was 46.7% greater than what was available in 2012, and 39.8% greater than what was available in 2013 (Fig. 3). The median salinity occupied by murres in 2012 was 28.3 psu (i.e. outer boundary waters), and most murre locations occurred in outer boundary waters (41.8%). Considerable numbers of murre locations also occurred in inner boundary (13.4%), recirculating (18.5%), and tidal (15.0%) waters. Murres occupied far-field waters 11.2% of the time in 2012. The median salinity occupied by murres in 2013 was 30.3 psu (i.e. outer boundary waters), and most murre locations occurred in far-field waters (36.6%), followed by outer boundary (22.4%), inner boundary (12.5%), and recirculating (13.2%) plume waters. Disproportionate plume occupancy was primarily due to increased use of tidal and recirculating waters compared with other water

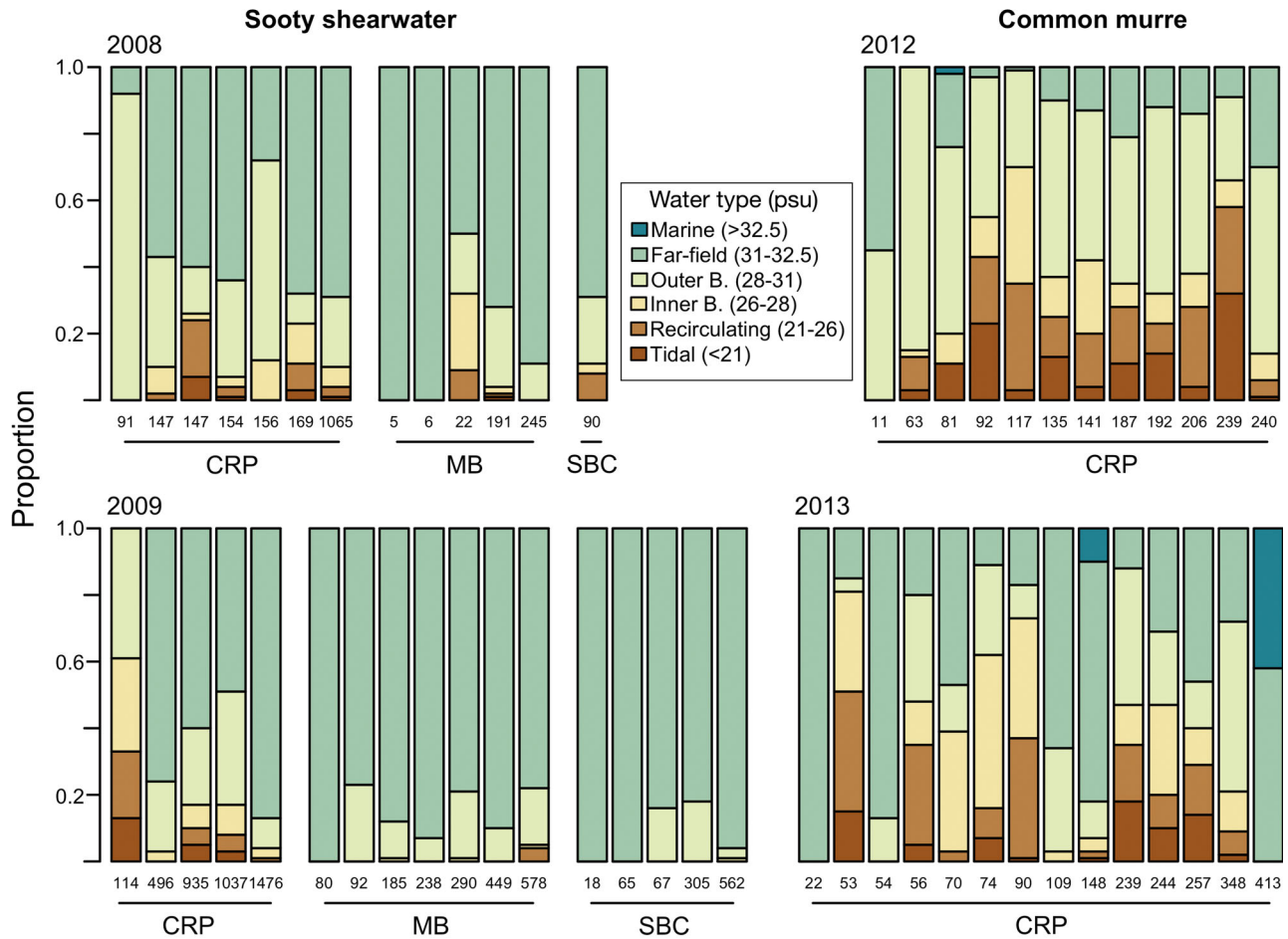


Fig. 4. Proportion of time individual seabirds occupied different water types during the time they were in the model domain. Each bar represents an individual bird. Capture locations are indicated on the x-axis (CRP: Columbia River plume; MB: Monterey Bay; SBC: Santa Barbara Channel). The number of locations used in each analysis is shown below each bar

types, and the difference between observed and expected occupancy ($\Delta_{\text{obs-exp}}$) of these 2 water types combined was 30.9% in 2012 and 21.2% in 2013.

Despite persistent residency in the model domain by shearwaters (average = 95.0%) and murre (average = 67.5%), use of plume waters varied with tagging location and by individual birds (Fig. 4). Shearwaters tagged in the CRP were located more frequently in plume waters (average: 49.4%) than birds that were tagged in MB and SBC (average: 24.4%), although a few individuals from California used tidal and recirculating waters, in addition to boundary and far-field waters (Fig. 4). Occupancy of plume waters by shearwaters did not differ between years (average: 27.6%; $t_{25.2} = -1.57$, $p = 0.130$), but variability among individuals was high (2008, CV = 72%; 2009, CV = 115%). Murre occupancy of plume waters was greater than that of shearwaters, and significantly greater in 2012 (87.2%) than during 2013 (55.9%; $t_{19.2} = 3.22$, $p = 0.004$; Fig. 4). Individual variability in

plume occupancy among murre was less than that of shearwaters in 2012 (CV = 17%) and 2013 (CV = 62%). Sample size (i.e. number of locations per individual bird) was not correlated with occupancy of plume waters among shearwaters ($r = -0.009$, $t_{28} = -0.05$, $p = 0.96$) or murre ($r = -0.21$, $t_{24} = -1.11$, $p = 0.27$).

Seabird response to plume dynamics

Daily latitudes of plume centers and seabirds were positively correlated in all years (2008: $r = 0.22$, $t_{113} = 2.43$, $p = 0.017$; 2009: $r = 0.14$, $t_{196} = 1.93$, $p = 0.050$, and 2013: $r = 0.565$, $t_{72} = 5.58$, $p < 0.001$), with the exception of 2012 ($r = -0.03$, $t_{64} = -0.26$, $p = 0.795$), when murre moved north in June and July and the plume center remained south of the river mouth. The latitude of the plume center reached maximum southerly extent in May or June in all years, and shifted northward, adjacent to the river mouth after

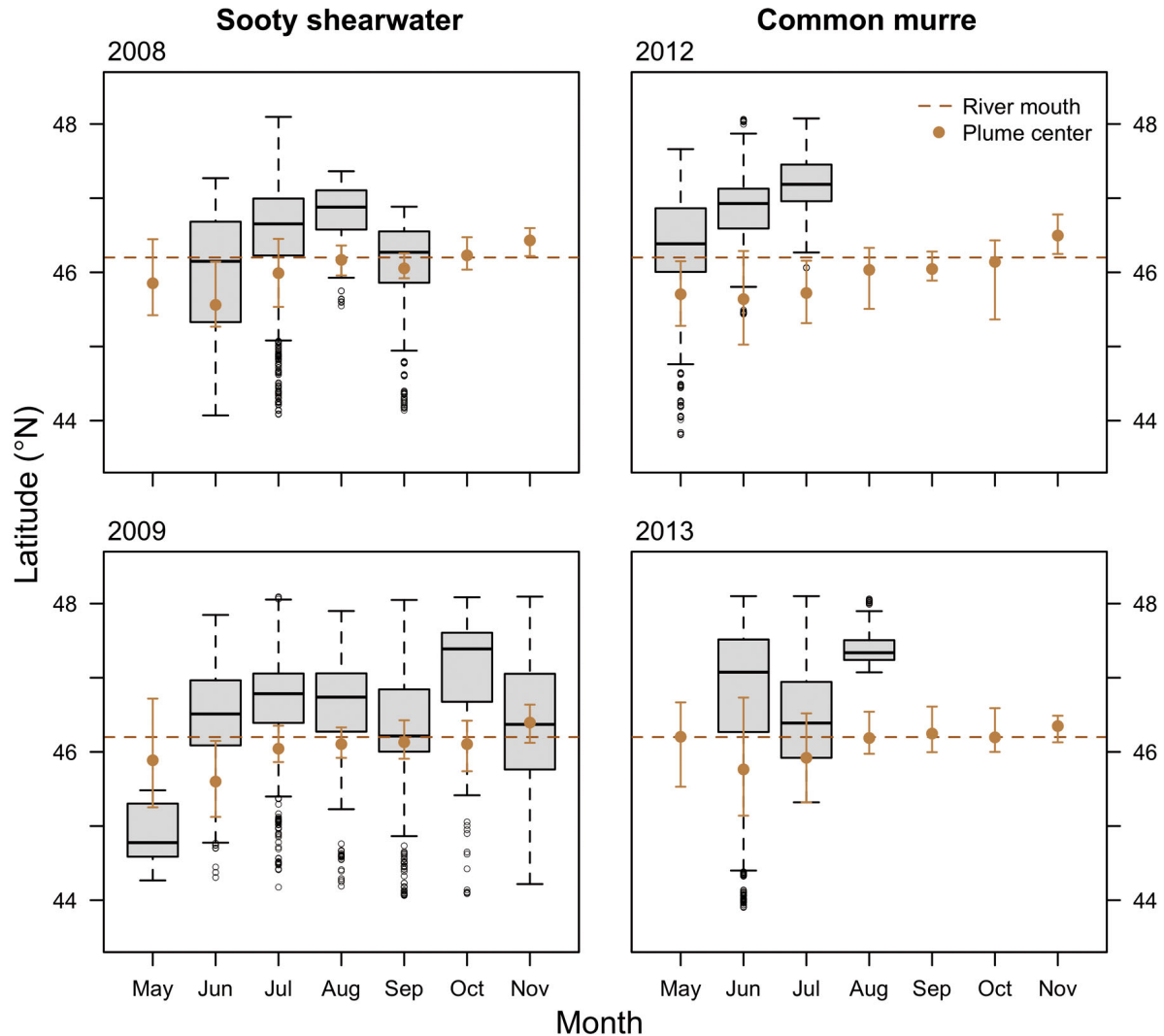


Fig. 5. Monthly latitudes of seabirds relative to the location of the mouth of the Columbia River (dashed line). Dark line: median; box: interquartile range (IQR); error bars: max./min. within $1.5 \times$ IQR above/below IQR; black dots: outliers. Mean latitude of the plume center shown as brown points (\pm range)

July (Fig. 5). The distribution of mean latitudes through time among shearwaters and murres was comparable (Fig. 5). The mean latitude of both shearwaters and murres was north of the river mouth and plume center, except during May 2009 when the plume center was north of shearwaters, and during September and November 2009 when latitudes of shearwaters and the plume centers were equivalent (difference of less than 0.05° latitude).

Occupancy of plume waters was similar for shearwaters and murres, and was positively correlated with plume surface area in all years (2008: $r = 0.32$, $p < 0.001$; 2009: $r = 0.63$, $p < 0.001$; 2013: $r = 0.73$, $p < 0.001$) except 2012 ($r = 0.20$, $p = 0.114$). Although variability was high, especially in 2008, occupancy

by shearwaters was greatest in May and June, and decreased during July through November (Fig. 6). Occupancy by murres was also greatest in May (data only available in 2012) and June, and declined through July and August (data only available in 2013). Plume surface areas also were greatest in May and June of all years, and declined through November (Fig. 6). The median salinity of occupied waters by both shearwaters and murres was between 28.8 and 29.4 psu in May (data only available in 2009 and 2012), increased to between 29.9 and 30.1 psu in June, and between 30.8 and 31.6 psu in July. After July, median salinities of occupied waters were greater than 31.0 psu, indicating low occupancy of plume waters.

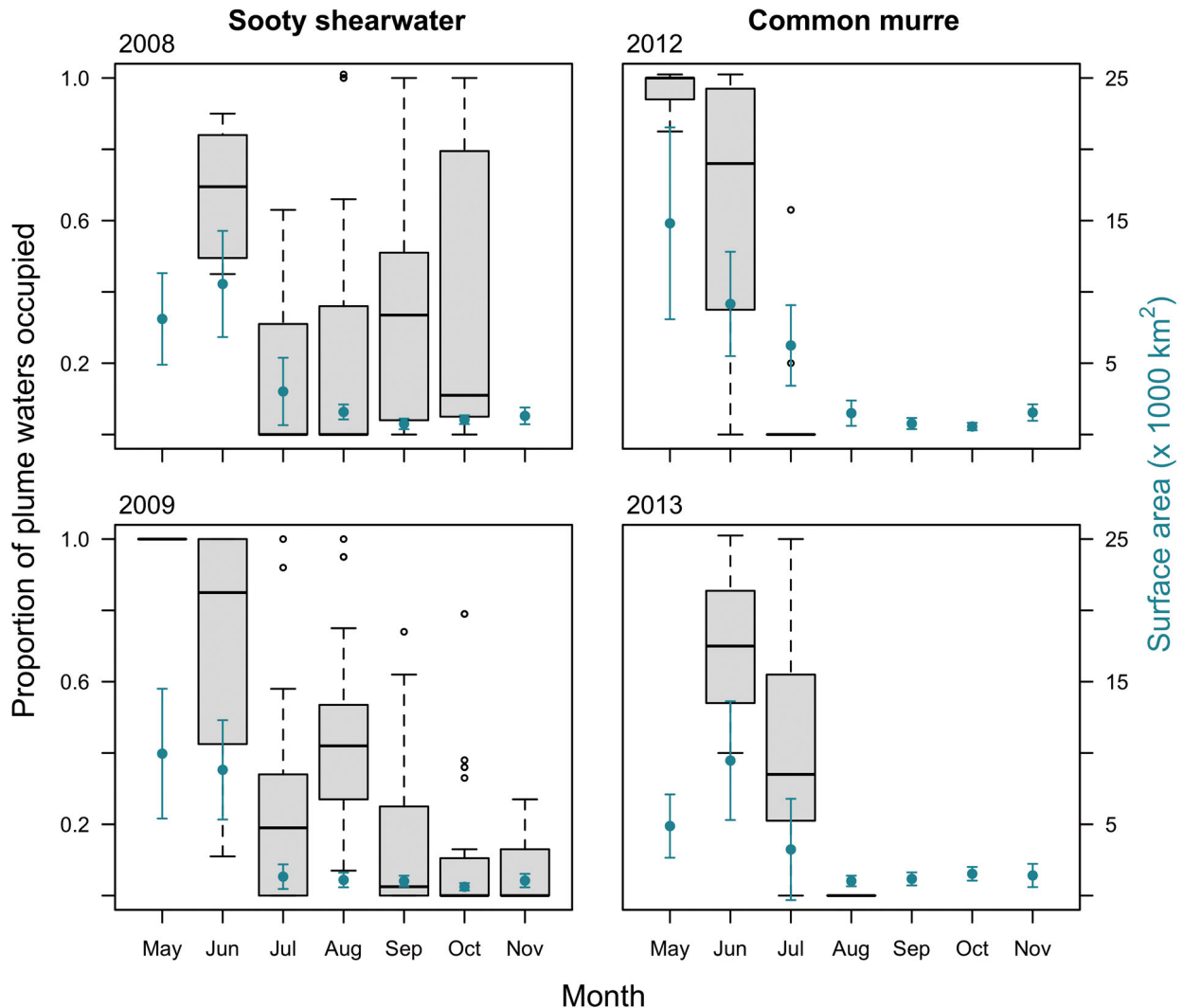


Fig. 6. Occupancy of plume waters (≤ 31 psu) by seabirds. Dark line: median; box: interquartile range; error bars: max./min. within $1.5 \times$ IQR above/below IQR; black dots: outliers. Mean plume surface areas (\pm SD) are shown as blue points

Both shearwaters and murre occurred significantly closer to the plume boundary than the plume center (shearwaters: $U = 661\,960$, $p < 0.001$; murre: $U = 682\,820$, $p < 0.001$). Median distances of shearwaters to the plume boundary (50 km) were greater than distances of murre (15 km; $U = 479\,060$, $p < 0.001$). Median distances of shearwaters to the plume center (107 km) were slightly less than distances of murre (115 km; $U = 392\,470$, $p = 0.017$). The median distance of shearwaters to the plume center was slightly less in 2008 (104 km) compared to 2009 (108 km; $U = 87\,254$, $p = 0.011$). In comparison, the median distance of shearwaters to the plume boundary was less in 2008 (24 km) than in 2009 (64 km; $U = 65\,316$, $p < 0.001$). The median distance of murre to the plume center did not differ between 2012

(111 km) and 2013 (125 km; $U = 83\,238$, $p = 0.051$), whereas the median distance of murre to the plume boundary was less in 2012 (12 km) than in 2013 (20 km; $U = 65\,788$, $p < 0.001$).

Individual variability among shearwater and murre distances to the plume center and boundary were high. Distances of individual shearwaters to the plume center ranged from 3–287 km, and from 6–345 km for murre. Variability in distances to the plume center was similar for shearwaters (CV = 55%) and murre (CV = 54%). Distances of individual shearwaters to the plume boundary ranged from <3–263 km, and from <3–180 km for murre. Variability in distances to the plume boundary was high for shearwaters (CV = 91%) and murre (CV = 117%).

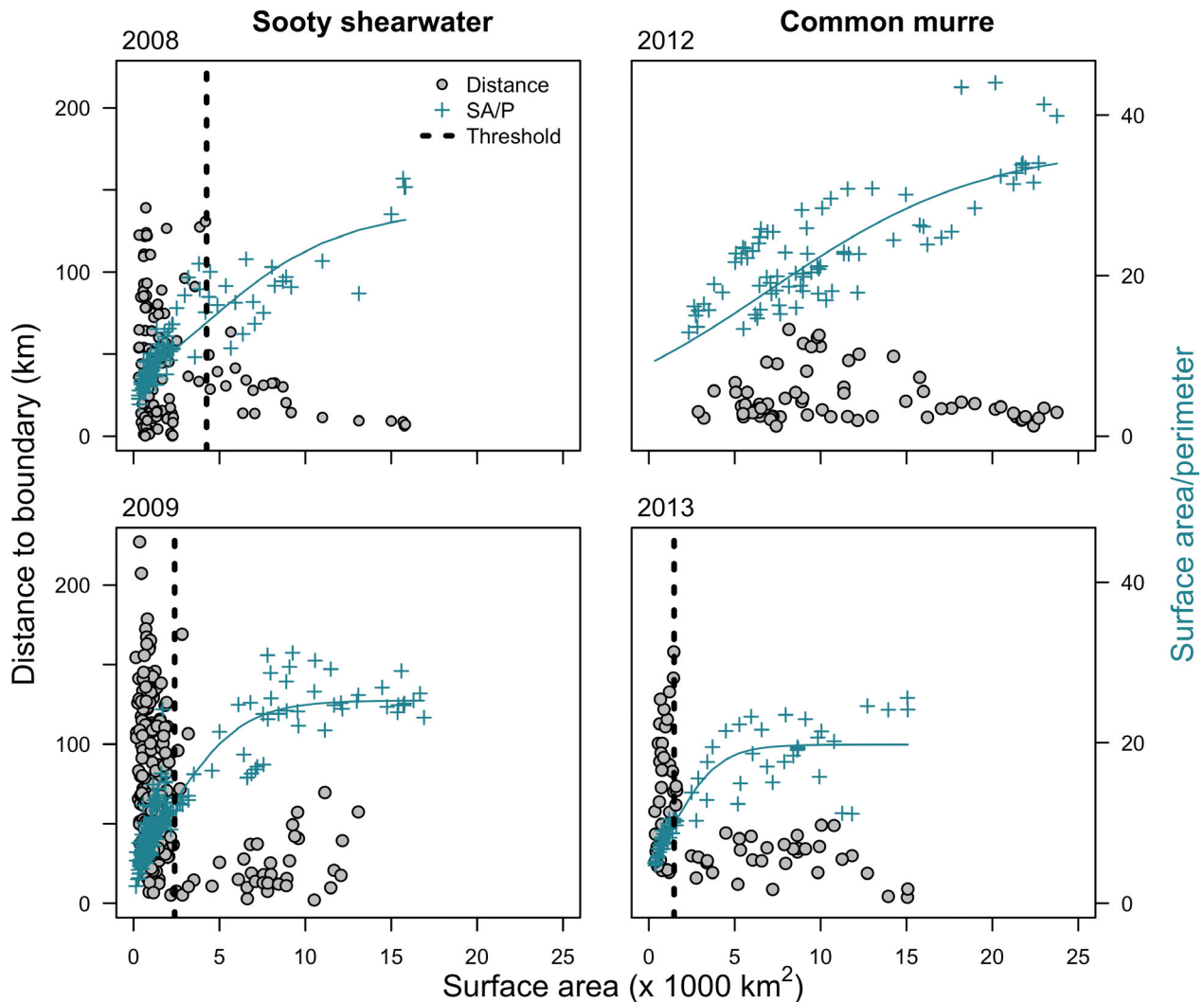


Fig. 7. Relationship between plume surface area and seabird distance to the plume boundary (gray dots), and plume surface area and the surface area to perimeter ratio (SA/P; plus signs). Solid blue lines are nonlinear least squares model fits, and dashed vertical line marks the inflection point (i.e. threshold) of the curve from the model fit. No inflection point was estimated in 2012

We did not find clear relationships between plume surface area and distances of seabirds to the plume center. Distances of shearwaters to the plume center were positively correlated with plume surface area in 2008 ($\rho = 0.197$, $p < 0.001$), but negatively correlated in 2009 ($\rho = -0.123$, $p = 0.001$). Distances of murres to the plume center were positively correlated with plume surface area in 2013 ($\rho = 0.480$, $p < 0.001$), but uncorrelated in 2012 ($\rho = -0.024$, $p = 0.606$). In contrast, relationships between surface area and distances of shearwaters and murres to the plume boundary showed remarkable similarity (Fig. 7). Shearwater and murre distances to the plume boundary were negatively correlated with plume surface area in all years (2008: $\rho = -0.381$, $p < 0.001$; 2009:

$\rho = -0.396$, $p < 0.001$; 2012: $\rho = -0.162$, $p < 0.001$; and 2013: $\rho = -0.240$, $p < 0.001$). However, the relationship was not linear, and logistic regressions indicated a threshold between surface area and seabird distances to the plume boundary (Fig. 7). The estimated inflection point of the fitted surface area to perimeter ratio corresponded to the surface area at which seabird distances to the plume boundary showed a threshold response in 3 of 4 yr. The threshold value ranged from surface areas of ~1500–4000 km². Mean distance of shearwaters to the plume boundary was 50.1 ± 40.6 km in 2008 before the surface area threshold (4252 km²) was exceeded, and declined by half (to 25.3 ± 15.2 km) after the surface area increased beyond the threshold ($U = 1339$, $p = 0.025$). Similarly,

mean distance of shearwaters to the plume boundary was 86.0 ± 46.1 km in 2009 before the surface area threshold (2392 km^2) was exceeded, and declined significantly to 32.0 ± 33.5 km after the surface area increased beyond the threshold ($U = 5228$, $p < 0.001$). Mean distance of murrelets to the plume boundary was 70.2 ± 36.9 km in 2013 before the surface area threshold (1472 km^2) was exceeded, and declined to 30.7 ± 15.9 km after the surface area increased beyond the threshold ($U = 1115$, $p < 0.001$). In 2012, plume surface areas $< 2800 \text{ km}^2$ did not occur during the study period, and an inflection point in the surface area to perimeter curve could not be estimated. However, all distance measurements of murrelets to the plume boundary were low (23.4 ± 15.3 km), and comparable to distances of murrelets observed in 2013 after the surface area threshold was exceeded (Fig. 7). Corresponding with the decline in seabird distances to the plume boundary, we also found significant declines in the salinity of occupied waters after the surface area thresholds were exceeded. In 2008, mean salinity of waters used by shearwaters declined from 31.0 ± 1.2 psu to 29.8 ± 1.8 psu ($U = 1438$, $p = 0.003$). In 2009, mean salinity of waters used by shearwaters declined from 31.1 ± 1.0 psu to 27.5 ± 4.3 psu ($U = 5415$, $p < 0.001$). In 2013, mean salinity of waters used by murrelets declined from 31.8 ± 1.2 psu to a mean of 27.7 ± 2.7 psu ($U = 1185$, $p < 0.001$). The mean salinity of waters used by murrelets in 2012 was consistently low (27.4 ± 2.8 psu).

DISCUSSION

By combining seabird telemetry data with a high-resolution model of sea surface salinity, we demonstrated that shearwaters and murrelets selectively occupy and track CRP waters, particularly dynamic boundary waters where foraging opportunities likely were enhanced by seasonal increases in plume surface area and biophysical coupling. In addition to quantifying high occupancy of plume waters by shearwaters and murrelets, the telemetry data allowed us to identify species-specific spatial distributions and relationships with distinct water types. Although shearwaters ranged farther offshore (especially in 2009) and used far-field plume waters more often than murrelets, we observed disproportionate use of recirculating and boundary waters closer to the coast. Murrelets occupied a narrower nearshore area closer to the coast (especially in 2013), and disproportionately used recirculating and tidal waters. Telemetry also revealed that murrelets and shearwaters

moved in phase with the plume (i.e. there were positive correlations between seabirds and plume center latitudes), and exhibited threshold responses to increases in surface area by moving towards plume boundaries.

Based on our observation of disproportionate occupancy of plume waters by both shearwaters and murrelets, and movement towards plume boundary waters during periods of increased plume size, we suggest that seabirds actively target plume-enhanced production and biophysical coupling at plume edges. We observed greatest spatial use by both species near the Columbia River mouth, and north along the Washington coast near Willapa Bay and Grays Harbor. Strong convergent fronts form on the north or upwind side of the river plume as freshwater flowing out of the river interacts with coastal upwelling winds and southward current velocities (Jay et al. 2009). Convergent plume fronts may present a visual or olfactory cue for seabirds, with visible foam lines, color discontinuities, and changes in surface roughness that mark the boundary between water masses (Ainley & Jacobs 1981, Hunt et al. 1998, Zamon et al. 2014). This likely is an area of enhanced prey availability, particularly during periods of increased surface areas, because zooplankton become aggregated (Morgan et al. 2005), and forage fishes and juvenile salmon densities north of the river mouth are high (Phillips et al. 2017) and positively correlated with river discharge (Emmett et al. 2004, Kaltenberg et al. 2010).

We observed threshold responses among seabirds to plume surface area, where seabird distances to the plume boundary declined significantly after thresholds between 1500 and 4000 km^2 were exceeded. Seabird distances to the plume boundary showed no obvious patterns before the surface area thresholds were exceeded, and seabirds were equally likely to occur near a plume boundary as far away. After the surface area threshold was exceeded, shearwaters and murrelets were located within 25 – 30 km of the plume boundary. This is consistent with the finding of Phillips et al. (2017) that seabird density in waters < 28 psu declined as plume surface area increased, and indicates that seabirds moved to boundary waters. Considering that foraging shearwaters and non-breeding murrelets are highly mobile (Hatch et al. 2000a, Adams et al. 2012), rely on local enhancement (Davoren et al. 2003), and forage in mixed-species flocks (Hoffman et al. 1981), the observed threshold responses indicate an important relationship between seabird foraging and dynamic frontal processes near the CRP. Surface areas less than ob-

served thresholds are typical during early spring and late summer, but less frequent during late spring and summer when river discharge and plume surface area peaks (Burla et al. 2010). The productivity and biophysical coupling generated by greater river discharge and increasing plume surface area, possibly coupled with visual cues near convergent fronts, may cause seabirds to track the location of plume boundaries. Our observed relationship between seabirds and plume surface area may serve as a useful predictor of seabird distributions near the CRP and inform other studies of threshold responses of seabirds to physical oceanographic features.

Positive correlations between seabird latitudes and the plume center in 3 of 4 study years indicated that shearwaters and murre tracked north–south plume movements. The plume center serves as a useful index of plume location, but overall median distances of seabirds to the plume center were 4 times greater than overall median distances to the plume boundary, indicating that the observed correlations were related more to the ability of seabirds to track shifts in the entire river plume and associated boundary waters, rather than just the center. This observation is corroborated by the lack of a relationship between distances of shearwaters or murre to the plume center and surface area. The observed latitudinal range of shearwaters was extensive and is consistent with observations that this species exploits productivity throughout the greater CCE (Shaffer et al. 2006, Adams et al. 2012). In contrast to our predictions, latitudinal movements of murre were also extensive along the coast, and were of similar range to shearwaters. Tagged murre were more closely associated with the plume boundary than the plume center, indicating that murre are just as capable of tracking and responding to changes in plume size and location as shearwaters.

The relatively high mobility of murre in this study indicated that we either tagged non-breeding birds or that tagging caused the birds to abandon colony attendance. There was no evidence of returns to or exits from breeding colonies by tagged murre, although utilization distributions indicated that some murre occupied waters near small colonies along the central and northern Washington coast (including Grenville Arch and the Bodelteh Islands), and the northern Oregon coast (Tillamook Head). If breeding birds were commuting to nests outside of the duty cycle of tag transmissions (e.g. during the middle of the day or night), a portion of colony attendance may have been undetected. However, given that murre pairs alternate nest duties (Verspoor et al. 1987), we

would have expected that some of the location data would occur at colonies if tagged birds were actively breeding. Although a similar tagging study (with slightly smaller VHF radio tags) on the northern Washington coast found no evidence of altered breeding behavior in murre (Hamel et al. 2004), the stress of capture and timing of tag deployments may have caused birds to skip breeding efforts or abandon colony attendance for the season. Tagging effects, tag loss, and potential bird mortality may all bias location data (Hatch et al. 2000b, Wilson & McMahon 2006), and there was some evidence of murre tag attachment and failure in 2012 and 2013. The cessation of movement by 2 birds in 2013 after 20 d of tag transmission was interpreted as bird mortality (S. Loredano pers. comm.).

Differences in occupancy of specific water types by shearwaters and murre may be related to spatial segregation resulting from different foraging capabilities, prey selectivity, or interspecific competition. We suggest that the disproportionate use of tidal and recirculating waters by murre indicated that this species relied on memory or coastal landmarks to find and occupy persistent and predictable plume waters near the river mouth (Davoren et al. 2003, Regular et al. 2013). Lower water clarity, either from sediment-laden plume water or increased concentrations of phytoplankton near the surface, was associated with greater murre and shearwater densities at the spatial scale of the model domain (Phillips et al. 2017). Tidal and recirculating waters may be more turbid, and murre may be better adapted for foraging in turbid waters than shearwaters (Lovvorn et al. 2001, Regular et al. 2011, Grémillet et al. 2012). Shearwaters disproportionately occupied inner and outer boundary waters, which may be less turbid than the lower salinity waters occupied by murre. Although food habits of shearwaters and murre were not quantified in this study, there is no published evidence indicating that either species selectively consumes different prey (Chu 1984, Ainley et al. 1996). Both species are wing-propelled pursuit divers, but maximum dive depths of sooty shearwaters (~70 m; Weimerskirch & Sagar 1996) are less than those of murre (~180 m; Piatt & Nettleship 1985). A range of prey species occupy depths that are accessible to these avian predators. For example, northern anchovy typically aggregate deeper in the water column (10–70 m) near plume boundaries (Kaltenberg et al. 2010, Phillips et al. 2017), while juvenile salmon are more evenly distributed in surface plume waters (0–20 m; De Robertis et al. 2005). Interference competition, thought to occur in other parts of the northern CCE (Ainley et al.

2009), may also be important near the CRP. Differences in occupancy of plume water types, and the more nearshore distribution of murres, may have resulted from spatial segregation between the 2 species. Without data on spatial distributions of shearwaters and murres during the same year, and corresponding prey fields and diets of both species, we are not able to resolve the potential for different foraging capabilities, prey selectivity, or interference competition.

Relationships among seabirds and the CRP observed in this study appear to be relatively consistent between species and across years. Although we did not track shearwaters and murres during the same years, our observations indicate that oceanographic conditions are a stronger influence on seabird–plume relationships than differences between species. For example, both shearwaters and murres shifted their locations in phase with the plume center, demonstrating their ability to track its location. Further, the threshold response of seabirds to plume surface area occurred regardless of year or range of surface areas observed. Patterns observed in 2012 were consistently different from 2008, 2009, and 2013, indicating that environmental conditions were different for murres tracked during 2012. River discharge during May through July 2012 was the second greatest during the 10 yr period between 2005 and 2015 (US Geological Survey surface water station 14 246 900; <http://waterdata.usgs.gov/usa/nwis/>), and was 24 % greater than discharges in 2008, 2009, and 2013. Plume surface areas in 2012 were never less than the observed surface area threshold ($\sim 1500 \text{ km}^2$) that elicited a response of murres in 2013. Above average plume surface area and enhanced southerly extent of the plume in 2012 may explain the high occupancy of tidal and recirculating waters (and low occupancy of boundary waters) by murres, lack of clear relationships with surface area, farther offshore distribution, and poor correlation to plume center latitude. Interestingly, the median distance of murres to the plume boundary in 2012 was the shortest of any year, and murres occupied less saline waters (0–26 psu) proportionately more (33.5%) in 2012 compared to 2013 (21.9%). We speculate that the surface area threshold was already exceeded when tags were deployed in 2012, that murres were able to locate and track plume boundaries nearshore, and that they moved farther offshore to occupy the inside edge of the plume in relatively lower salinity waters. Even though our interannual comparisons provided insights on shearwater and murre relationships to the CRP, to fully understand species-specific responses of seabirds to river plume

dynamics, we suggest comparative studies that incorporate telemetry data on both species during the same year.

Our results demonstrate that seabirds respond to a highly dynamic river plume, and we suggest that other large river plume ecosystems around the world may have similar influences on mobile marine predators. For example, González Carman et al. (2016) found that distributions of sea turtles, pinnipeds, and seabirds in the southwestern Atlantic Ocean were most abundant near the Río de la Plata plume. River plumes and associated convergent fronts can be very productive habitats, and may represent priority conservation areas for multiple marine vertebrate taxa (Scales et al. 2014). Other areas where freshwater and saltwater interface, including glaciated fjords, are also important habitats for mobile predators (Arimitsu et al. 2016), and may become more important as climate change impacts the volume and timing of freshwater flux to the ocean. We suggest that our approach linking a hydrodynamic model with telemetry data may be applicable to other studies evaluating relationships between marine predators and ecosystems influenced by freshwater plumes.

Acknowledgements. This research was supported in part by Bonneville Power Administration, Bureau of Ocean Energy Management (Intra-agency Agreement Number M10PG00081/0003, NSL PC-10-05), Moss Landing Marine Laboratories (MLML), NOAA Fisheries Northwest Fisheries Science Center, and the US Geological Survey's Western Ecological Research Center. The captains and crew of the R/V 'Magister' (operated by NOAA Fisheries) and M/V 'Forerunner' (operated by Clatsop Community College Marine and Environmental Research and Training Station) were vital in satellite tag deployments in Washington, along with the assistance from expert bird and boat handlers P. Bentley, T. Cross, J. Felis, A. Gladics, T. Guy, L. Kerr, J. Mason, J. Mannas, H. Nevins, and numerous volunteers from Oregon State University and the Astoria-Warrenton community. We also thank numerous MLML graduate students, L. Harvey, and D. Mazurkiewicz for assistance with tag deployments in California. Institutional Animal Care and Use Committee review and approval for this study were provided by San Jose State University Research Foundation (J.A.: nos. 807 and 929). *Author contributions.* E.M.P. conducted fieldwork, led analysis, and wrote the paper, J.A. developed tracking/movement methodology, conducted fieldwork, and assisted with writing, J.E.Z. conducted fieldwork, and assisted with concept and writing, and J.K.H. advised oceanographic approaches and assisted with analyses/writing. Authority for satellite telemetry was provided by USGS Bird Banding Laboratory Auxiliary Marking Authority no. 22911 (J.A.) and no. 23682 (J.E.Z.), California Department of Fish and Game Scientific Collecting Permit no. 6443 (J.A.), and State of Washington Scientific Collection Permit no. 05-500 (J.E.Z.). We thank A. M. Baptista and C. Seaton (Center for Model Observation and Prediction) for the hydrodynamic model outputs. J. Felis, R. W. Henry, and R. Hytinen assisted with data processing. Previous drafts of this paper benefited

from comments and suggestions provided by L. A. Hall, G. L. Hunt Jr., and 2 anonymous reviewers. The use of trade, product, or firm names in this publication is for descriptive purposes and does not imply endorsement by the US Government.

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