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Predator-prey interactions influenced by a dynamic river plume

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Complete List of Authors:	Phillips, Elizabeth M.; University of Washington School of Aquatic and Fishery Sciences Horne, John K.; University of Washington, Zamon, Jeannette E.; National Marine Fisheries Service - NOAA
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- 1 i. Title:
- 2 Predator-prey interactions influenced by a dynamic river plume
- 3 ii. Authors:
- 4 Elizabeth M. Phillips, John K. Horne, Jeannette E. Zamon
- 5 iii. Affiliation and address:
- 6 E.M. Phillips and J.K. Horne: University of Washington, School of Aquatic and Fishery
- 7 Sciences, Seattle, WA 98195, USA; emp11@uw.edu and jhorne@uw.edu
- 8 J.E. Zamon: NOAA Fisheries, Point Adams Research Station, Hammond, OR 97121,
- 9 USA; jen.zamon@noaa.gov
- 10 iv. Corresponding author:
- 11 Elizabeth M. Phillips
- 12 University of Washington, School of Aquatic and Fishery Sciences, Seattle, WA 98195,
- 13 USA
- 14 Phone: 206-221-5459
- 15 Email: emp11@uw.edu

16 Abstract: Marine predator-prey interactions are often influenced by oceanographic processes
17 that aggregate prey. We examined density distributions of seabirds and prey fish associated with
18 the Columbia River plume to determine if variation in plume size (i.e., volume or surface area)
19 or location influences predator-prey interactions. Common murre (*Uria aalge*), sooty shearwater
20 (*Ardenna grisea*), and forage fish including northern anchovy (*Engraulis mordax*) and juvenile
21 salmon (*Oncorhynchus* spp.) occurred disproportionately in plume waters relative to adjacent
22 marine waters. Water clarity, an indicator of plume-influenced waters, was a significant
23 predictor of seabird and prey densities throughout the survey area. Murres occurred within 20
24 km of the plume center of gravity (CG) whereas shearwaters occurred ~100 km north of the
25 plume CG, concurrent with highest densities of prey fish. Global indices of collocation (GIC)
26 were relatively low between murres and prey, compared to high values between shearwaters and
27 prey. Seabird densities were negatively correlated with plume size, suggesting that seabirds
28 concentrate in the plume to maximize foraging effort. We conclude that variation in Columbia
29 River plume size and location influences predator distributions, which increases predation
30 pressure on prey, including threatened salmonid species.

Introduction

Predator-prey interactions are influenced by environmental conditions that affect a predator's ability to locate and capture prey (Wiens 1976). In the marine environment, predators often utilize physical features such as density fronts between water masses to locate prey in a relatively featureless environment (Decker and Hunt 1996; Hunt 1997; Ainley et al. 2009). Density fronts formed by freshwater flow into the ocean are important areas of biophysical coupling that aggregate zooplankton and larval fish (Govoni et al. 1989; Govoni and Grimes 1992; Morgan et al. 2005), making them available to planktivorous and piscivorous predators. Increased abundances of predators near river plumes (Ashford et al. 2013; Zamon et al. 2014; Kowalczyk et al. 2015) suggests that these physical features may be hotspots for predator-prey interactions.

Freshwater discharge from the Columbia River into marine waters of the northern California Current creates a large brackish plume (Hickey et al. 2010). During peak river flows, the plume can extend hundreds of kilometers along the Oregon and Washington coasts (Hickey et al. 2005). Its size (i.e., volume and surface area), location, and depth are primarily influenced by river flow (Burla et al. 2010), but seasonal winds, currents, and the semi-diurnal tidal cycle also contribute to variability in plume volume, surface area, and orientation relative to the coast (Hickey et al. 2005; Horner-Devine et al. 2009; Jay et al. 2009).

Columbia River flow and plume size typically peak during spring (April – June), which coincides with the downstream movement of approximately 133–143 million hatchery-reared and an unknown, but substantially smaller number of naturally-produced juvenile salmon (i.e., smolts) including coho (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*) (FPC 2015). Small schooling pelagic fishes including northern anchovy (*Engraulis mordax*), Pacific

herring (*Clupea pallasii*), Pacific sardine (*Sardinops sagax*), and smelts (Osmeridae), collectively called forage fish, also occur near the plume during spring and summer (Litz et al. 2013). In particular, anchovy aggregate and spawn in association with the plume (Richardson 1980; Litz et al. 2008), and are an important component of the prey community (Wiens and Scott 1975). Smolts are considered part of the forage fish community during their early marine residence, as they are similar in length and appearance to many forage fish species (Hoar 1976), overlap in space and time (Emmett et al. 2004, 2006; Orsi et al. 2007), and occur in the diets of many predators (Lance and Thompson 2005; Gladics et al. 2014; Szoboszlai et al. 2015).

Recirculation of nutrients within the plume stimulates primary productivity and zooplankton growth (Kudela et al. 2010), which supports fish and seabird populations (Hickey and Banas 2008). Plume waters can often be visually identified by color discontinuities across boundaries, and avian predators may orient to this contrast when searching for prey (Ainley 1977; Haney and Stone 1988; Cyrus 1991). Two seabird species, common murre (*Uria aalge*) and sooty shearwater (*Ardenna grisea*), are the most visible and numerous piscivores near the Columbia River plume, suggesting that these two species may be important predators in the area (Zamon et al. 2014). Approximately 532 000 individual murrees breed colonially along the Oregon and Washington coasts (Speich and Wahl 1989; Naughton et al. 2007; Fig. 1). Sooty shearwaters migrate annually from New Zealand during their non-breeding season (Shaffer et al. 2006), and a significant portion (~10 million individuals) occur in U.S. west coast shelf waters during boreal spring and summer (Ainley 1976; Briggs et al. 1987). Both avian species use pursuit-diving to capture and consume a variety of prey fish near the plume including northern anchovy, smelts, California market squid (*Doryteuthis opalescens*), and several species of juvenile salmon (Matthews 1983; Varoujean and Matthews 1983).

High mortality of juvenile salmon during early marine residence is likely due to predation (Pearcy 1992; Beamish and Mahnken 2001), but only a few studies have quantitatively examined predator-prey interactions during this period (Beamish et al. 1992; Beamish and Neville 1995; Emmett and Krutzikowsky 2008; Berejikian et al. 2016). Observations of elevated early marine mortality of smolts during periods of low forage fish abundance (Fisher and Pearcy 1988; Pearcy 1992) prompted Emmett and Sampson (2007) to hypothesize that high abundances of forage fishes would reduce predator encounter rates with juvenile salmonids, thereby reducing predation on smolts. Both shearwaters and murre are opportunistic foragers (Matthews 1983; Chu 1984), and the consumption of salmon by these two predators may be correlated with the availability of other prey fish (Holling 1959; Angelstam et al. 1984). Higher densities of juvenile salmon occur in the Columbia River plume during high river flows (Emmett et al. 2004), which also corresponds to increasing densities of northern anchovy (Kaltenberg et al. 2010). Recent research has linked river flow and plume volume to salmon survival (Miller et al. 2013; Brosnan et al. 2014), but evidence to identify mechanisms of survival, including the influence of plume dynamics on predators and prey, is not complete. Objectives of this study were to characterize the avian predator and prey fish community associated with the Columbia River plume, to determine spatial relationships between predators, prey, and the plume, and to assess the relative importance of environmental and biological variables influencing potential seabird and prey interactions.

Materials and methods

Data were collected during an ongoing ecosystem research program examining the ocean ecology of juvenile salmon off the Washington and Oregon coasts (Brodeur et al. 2003).

Hydrographic, trawl, acoustic, and seabird data were collected during daylight hours in May and June 2010 to 2012 on three chartered commercial fishing vessels sampling along transects and at fixed stations from northern Washington State to Newport, Oregon (Table 1).

Transect Sampling

Transects began 35–42 km offshore at dawn with the vessel traveling due east for 2 h at $\sim 5 \text{ m s}^{-1}$ (Fig. 1). Seabird counts were made using standard strip transect survey methods (Tasker et al. 1984), where a single observer counted and identified all flying or sitting birds within 300 m of the vessel on the starboard side, from the bow to the beam of the ship in a 90° arc, using a fixed-interval range finder (Heinemann 1981). Each bird sighting was called out to a recorder who entered the data into a computer linked with GPS to associate a time stamp and position to the bird sighting using SeeBird software (v 4.1.5.0; NOAA Fisheries Southwest Fisheries Science Center, La Jolla, California, USA). Salinity and temperature of seawater was sampled every 2 s from a through-hull port at 3 m depth using a deck-mounted, flow-through, conductivity-temperature-depth instrument (hereafter, CTD; SBE 19, Sea-Bird Electronics Inc.¹, Bellevue, Washington, USA; <http://www.seabird.com/>). To measure prey densities throughout the water column, continuous measurements of mean volume backscattering strength (S_v ; dB re 1 m^{-1} ; MacLennan et al. 2002) were collected using EK60 or ES60 echosounders (Simrad, Kongsberg, Norway; <http://www.simrad.com/>) equipped with hull-mounted, split-beam transducers (7° beamwidths measured at half power points) operating at 38 kHz (Table 1). A pulse duration of 1.024 ms was transmitted at 2000 W at a sampling rate of 0.5 Hz. With the

¹ Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

exception of the May 2012 survey, echosounders were calibrated annually using a 38.1 mm tungsten carbide reference sphere following Foote et al. (1987).

Station Sampling

After transect sampling was completed, 5 to 8 fixed stations along the same transect were sampled, working from east to west (Fig. 1). The first sampling station was located at the 30 m depth contour, between 2 and 9 km offshore. Subsequent stations continued offshore at ~9 km increments until the shelf break was reached (200 m depth), generally less than 55 km offshore. At each station, a profiling CTD (SBE 19plus; Sea-Bird Electronics Inc.) equipped with a transmissometer (C-Star; WET Labs, Philomath, Oregon, USA; <http://www.wetlabs.com/>) was deployed to a maximum depth of 100 m to record temperature, salinity, and transmissivity through the water column. Zooplankton were sampled with a 0.60 m diameter Bongo net, fitted with two black 335 µm mesh nets and a flowmeter (General Oceanics or Tsurumi Seiki Co., Ltd), towed obliquely from approximately 20–30 m deep to the surface. After the CTD and zooplankton net were recovered at the surface, a 108 m long Nordic 264 rope trawl equipped with 3.0 m Lite® trawl doors (NET Systems Inc., Bainbridge Island, Washington, USA; <http://www.net-sys.com/>) was fished at the surface for 30 min at a rate of 1.5 m s⁻¹ to collect pelagic organisms in the upper 15–20 m of the water column. The net opening was ~30x20 m (width x depth) when fishing, and contained variable mesh sizes ranging from 162.6 cm at the net mouth to 8.9 cm at the cod-end, with a 6.1 m long, 0.8 cm mesh knotless liner sewn into the cod-end. All items caught in the trawl were identified and recorded. Small catches were counted in their entirety. For large catches, the total number of each species caught was counted or estimated by weighing and counting a random subsample of individuals and scaling to the total

weight of the catch. All juvenile salmonids were measured to the nearest millimeter (fork length, FL) and preserved for later analysis. Up to 50 non-salmonids were measured, including fish (FL or standard length, SL), squid (dorsal mantle length, DML) and large gelatinous species (bell diameter for medusa, BD). To measure prey densities in the water column during trawling, continuous S_v measurements were collected using the same settings as during transect sampling.

In addition to ship-based sampling, we obtained predicted daily values of plume volume, surface area, depth, and east-west/north-south orientation from the Center for Coastal Margin Observation and Prediction (CMOP; db14 climatological atlas; <http://www.stccmop.org/datamart/virtualcolumbiariver>). We also obtained average Columbia River daily discharge records from Quincy, Oregon (river km 87; U.S. Geological Survey surface water station 14246900; <http://waterdata.usgs.gov/nwis>).

Data Processing

Acoustic Data Processing

Acoustic data were processed using Echoview v 5.4 (<http://www.echoview.com/>). We included the uncalibrated May 2012 acoustic data after comparing S_v measurements from May 2012 to the calibrated data in 2010 and 2011 and finding no evidence of differing patterns in amplitude. For data collected using an ES60 echosounder, the triangle wave error was removed prior to data processing following Keith et al. (2005). Noise spikes and empty pings, where a bottom signal was not received due to vessel motion, were manually removed. Ambient noise levels were estimated using passive data collections in June 2012 (-138.21 dB re 1 m⁻¹ [hereafter dB]) and removed by linear subtraction (Nunnallee 1990; Watkins and Brierley 1996). Data cells that did not meet a 6 dB signal-to-noise ratio threshold were excluded from analyses. Data

from within 10 m of the surface were also excluded to account for transducer depth (4.25 m) and twice the near-field range of the transducers (5.44 m).

Acoustic data were processed as an index of prey available to seabirds, as species identification of acoustic targets was not possible. To determine the volume backscatter threshold (i.e., minimum S_v value), we calculated the expected target strength of an anchovy at 38 kHz based on the expected minimum and maximum fork length of anchovy caught in our trawl (50 and 200 mm) using the target strength to length conversion equation from Demer et al. (2011). The corresponding target strength range (-62.1 dB to -50.1 dB) was used to calculate expected S_v values of a single anchovy occurring in 1 m³ of water from 10 to 70 m depth. The estimated S_v for a 200 mm anchovy ranged from -39.27 dB to -60.61 dB, with a median S_v value of -55.31 dB. The estimated S_v value for a 50 mm anchovy ranged from -51.27 dB to -72.61 dB, with a median value of -67.31 dB. Based on these calculations, the minimum S_v value was set to -60 dB throughout the water column. The -60 dB threshold allowed us to remove backscatter attributed to non-fish organisms such as krill, and is corroborated by previous studies of forage fish in the region that used similar thresholds: -60 dB at 38 kHz (Kaltenberg and Benoit-Bird 2009), -58.5 dB at 38 kHz when “considerable quantities of small, non-hake scatterers were encountered” (Wilson et al. 2000; Fleischer et al. 2005). A maximum S_v value was not set as we were interested in large aggregations of forage fish that may be near the surface and available to piscivorous seabirds. To exclude backscatter from adult hake, we limited our analyses to observations in the upper 70 m of the water column, similar to other acoustic surveys of forage fish in the region (Demer et al. 2011; Zwolinski et al. 2012). This depth also matches the general diving range of sooty shearwaters and common murre (Piatt and Nettleship 1985; Weimerskirch and Sagar 1996; Shaffer et al. 2009). Using the -60 dB threshold, all S_v measurements were

vertically integrated from 10 m below the surface to 70 m depth, and horizontally either in 300 m intervals for the transect data, or along the full length of the trawling distance for station sampling. Acoustic data were then scaled and reported as nautical area scattering coefficients (s_A ; $\text{m}^2 \text{ nmi}^{-2}$; MacLennan et al. 2002), indexed in space and time.

Transect Data Processing

Counts of birds sitting on the water surface were categorized as common murre, sooty shearwater, or other seabird species. To estimate seabird associations with the plume and potential prey, we analyzed seabirds that were sitting on the water surface or observed feeding and excluded birds flying through the area, as birds in flight are not directly associated with the location sampled (van Franeker 1994). Because strip transect census methods assume that all sitting seabirds are detected within the area surveyed (Gaston and Smith 1984; van Franeker 1994), unaltered counts were used to estimate densities in 300 m^2 increments along the survey track. Continuous measures of surface salinity, surface temperature, and s_A were matched by time and location to seabird data using ArcMap 10.1 (ESRI, Redlands, California, USA).

Station Data Processing

To examine patterns in temperature, salinity, and density, we estimated thermocline, halocline, and pycnocline depths by finding the largest point-to-point difference in 1 m averaged CTD downcast values. Zooplankton data were summarized by total biomass at each station (organisms m^{-3}), because species-specific identifications are difficult to make for all plankton species (C.A. Morgan, Oregon State University, Newport, Oregon, personal communication, 2015). Species-specific trawl catches were standardized to fish km^{-1} by dividing the number of

213 fish caught by the distance between the start- and endpoints of the tow as determined by GPS
214 (mean: 3.3 ± 0.7 km, SD). In instances where a trawl was repeated at the same station ($n = 13$),
215 the average catch of the two samples was used for analyses. To delineate potential prey of
216 seabirds, catches were partitioned using known species and species groups consumed by
217 common murre (Varoujean and Matthews 1983; Nevins 2004) and sooty shearwaters (Baltz and
218 Morejohn 1977; Chu 1984). To ensure that appropriate size fish were included as prey and to
219 allow for variation in prey shapes (e.g., body depth versus length), we used a maximum of 250
220 mm FL or DML for all potential prey species, corresponding to twice the standard deviation of
221 FL reported by Nevins (2004) for Pacific sardine consumed by common murre. We did not use
222 a minimum prey length as murre and shearwaters consume a range of prey sizes including larval
223 and juvenile life stages of marine organisms (Lance and Thompson 2005; Szoboszlai et al.
224 2015). All potential non-salmonid prey were categorized as alternative prey, and all salmon
225 ≤ 250 mm FL were categorized as juvenile salmon. To account for life history variation in length
226 at ocean entry for Chinook salmon, we used FL and month of capture to classify juveniles as
227 either subyearling or yearling based on known length-based age classes from scale analysis and
228 tagging studies (Pearcy and Fisher 1990; Fisher and Pearcy 1995). In May, subyearling fish had
229 $FL \leq 120$ mm, and yearlings had FL between 121–250 mm. In June, subyearling fish had FL
230 ≤ 140 mm, and yearlings had FL between 141–250 mm. To assess co-occurrence of different
231 prey groups, trawl catch data were categorized to determine the number of trawls that contained
232 only alternative prey, only juvenile salmon, or both prey groups in the same sample. We also
233 calculated the ratio of juvenile salmon to total prey caught in each trawl. Species that were not
234 considered seabird prey items (e.g., jellyfish, adult salmon) were categorized as non-prey and
235 used to quantify total biomass sampled by the trawl. Shannon's diversity index (Magurran 1988)

was calculated for the catch in each trawl. Catch (fish km⁻¹) estimated from the surface trawl and density estimates from acoustic backscatter were treated as separate variables for all analyses, as there was no relationship between these two measures of fish abundance (Spearman's correlation, $\rho = -0.012$, $p = 0.857$).

To facilitate comparisons of seabird densities with station samples of prey, seabird counts were summed and assigned to the nearest station, using one half the distance between stations as the breakpoint. We addressed the time mismatch between transect seabird counts and subsequent station trawl sampling (average: 4 h; range: 30 min to 13 h) by calculating Spearman's correlation values between the aggregated seabird count data and seabird counts collected opportunistically during station sampling in 2011 and 2012. There was a significant relationship between murre ($\rho = 0.70$, $p = 1.102 \times 10^{-13}$) and shearwater ($\rho = 0.40$, $p = 0.0002$) density estimates, indicating no apparent bias in relative seabird abundance between transect surveys and station sampling.

Data Analysis

To characterize seabird and prey communities associated with the Columbia River plume, we examined intra- and inter-annual variation in river discharge, plume volume, plume surface area, and seabird and fish abundance (fish km⁻¹ and s_A) using Kruskal-Wallis tests and Dunn's multiple comparison test when differences were detected (Zar 1999). Spatial pattern analyses were accomplished by plotting all geospatial data in ArcMap using North America Albers equal-area conic projection. CMOP data was converted from Oregon State Plane coordinates to latitude and longitude. We horizontally interpolated 3 m salinity values measured at each station using ordinary kriging (Cressie 1993). The mixing of low-salinity recirculating plume waters

and high-salinity coastal water creates multiple vertical and horizontal gradients (Horner-Devine et al. 2009; Jay et al. 2009), making plume boundaries difficult to define. We used a 28 practical salinity unit (psu) maximum following Burla et al. (2010) for analyses, but depict the plume surface area using halopycnals of tidal (<21 psu), recirculating (21–26 psu), and far-field plume waters (26–32.5 psu; Horner-Devine et al. 2009) to illustrate the complexity of the plume's horizontal structure.

The total survey area was defined by the northern and southernmost transects, and the eastern and westernmost stations sampled in each survey. Interpolated surface salinity values were used to calculate plume area within the total survey area. To validate our methods, we compared the calculated plume area values from interpolated data to the average predicted surface area values from CMOP model outputs for each survey and found an overall deviance of only 17 km² between the two methods, confirming that our calculations were consistent.

To determine if predators or prey use the plume disproportionately to available area, we categorized each observation as inside (3 m salinity $\leq$ 28 psu at the time of observation) or outside ($>$ 28 psu) the plume, and calculated proportions of seabirds and prey in each area. We focused on the horizontal surface plume as an indicator of overall areal extent, although subsurface ($>$ 3 m) structure of the river plume may be much more complex (Horner-Devine et al. 2009). Observed proportions of predators and prey in the plume were subtracted from expected proportions, defined as the proportion of plume area in the total calculated survey area during each cruise. If seabirds and prey were using the plume proportionate to available area, then differences between observed and expected values would be zero. We also calculated average density of seabirds, juvenile salmon, alternative prey, and acoustic backscatter inside and outside

the plume based on . We compared the distribution of densities inside and outside the plume using Mann-Whitney U tests with an alpha value of 0.05 for significance tests.

Relationships between log-transformed seabird density estimates, log-transformed fish catch, s_A , and plume size were explored using linear regression. We calculated the average plume volume and surface area for each survey from daily values obtained from CMOP model outputs. Because plume volume and surface area are correlated ($\rho = 0.90$, $p = 0.015$), we used average surface area as the explanatory variable in regression models of seabird density, as we hypothesized that air-borne seabirds show a stronger response to areal extent of the plume. We used plume volume in regression models for in-water prey. We also used predicted daily locations of the plume centroid from CMOP model outputs to estimate the overall geographic center of gravity (CG) and inertia (defined as dispersion around the CG) of the plume for each survey (Bez and Rivoirard 2001; Woillez et al. 2007, 2009). We verified our analyses by confirming visually that the estimated plume CG fell within the interpolated plume surface area calculated from CTD casts. We also calculated CG and inertia of seabirds, juvenile salmon, and alternative prey, and compared these to the size and location of the river plume for each survey. The Euclidean distance between the plume CG and each seabird species was compared among surveys using ANOVA (Zar 1999). We also measured the Euclidean distance between each predator and prey CG to estimate ΔCG and calculate a global index of collocation (GIC; Woillez et al. 2007) for each survey using the R package RGeostats (Renard et al. 2015). The GIC calculates the extent to which two populations are geographically distinct, by comparing the distance between their CGs and respective inertias (Woillez et al. 2007). GIC values range between 0, where each population is concentrated at a single but different location, and 1, where the two CGs coincide and the inertias are non-negative. For this study, a GIC value greater than

or equal to the 75th percentile of calculated GIC values (0.888) was considered indicative of high spatial overlap between predator and prey.

To assess the relative importance of environmental and biological variables influencing seabird and prey density distributions, we fit murre and shearwater density, alternative prey, and juvenile salmon catches to generalized linear models (GLM; McCullagh and Nelder 1989), using individual stations as the sampling unit. We used *a priori* model development to generate individual GLMs based on hypothesized relationships between seabirds, prey, and the environment (Burnham and Anderson 2002; Kutner et al. 2004). Six sets of GLMs were used to evaluate: murre density throughout the survey area (Model 1), shearwater density throughout the survey area (Model 2), alternative prey density throughout the survey area (Model 3), juvenile salmon density throughout the survey area (Model 4), murre density within the plume (Model 5), and shearwater density within the plume (Model 6). Each model set included combinations of environmental and biological covariates, and we tested candidate models for each GLM (Table 5). Covariates were evaluated for collinearity using variance inflation factors (VIF) and removed when VIF values exceeded 2 (Burnham and Anderson 2002). For Models 1 and 2, halocline depth, rather than pycnocline, was used because these covariates were collinear and we were primarily interested in the direct influence of plume depth on seabirds. For Models 3 and 4, we included temperature and zooplankton density in addition to salinity and water clarity, as these variables were hypothesized to influence forage fish and juvenile salmon distributions. Models 5 and 6 included only biological covariates, as we hypothesized that once seabirds had located the plume, their densities would no longer relate to environmental characteristics describing plume habitat. To account for interspecific attraction among seabirds, we included an estimate of other seabird species densities at each station in all seabird models. To account for documented

patterns of increased abundances of seabirds nearshore (Menza et al. 2016), we included the distance to shore of each station, measured as the straight-line distance along transect to land, as a geospatial covariate. We used a negative binomial error distribution and log link with the R package MASS (Venables and Ripley 2002) for all GLMs. This allowed us to model overdispersed data without transformation, and accounted for high variability observed in trawl and acoustic covariate data (McCullagh and Nelder 1989). We assumed no spatial autocorrelation among bird densities, as the minimum distance between any two stations was 3.7 km, which is greater than the distance below which autocorrelation has been observed in seabirds (Yen et al. 2006). Values of Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002; Kutner et al. 2004) were tabulated and compared among intermediate models for each model set. The number of intermediate models evaluated for each model set ranged from 5 to 15, and are not presented here. Candidate models with the lowest ΔAICc score and highest weight were chosen as the final model. Final model selection was validated by visually inspecting deviance residual error structure (Zuur et al. 2009), and calculating chi-squared statistics on the null and final model deviance (Burnham and Anderson 2002).

Results

A total of 17 357 birds were counted along 1 381 km of survey transects, and 303 stations were sampled in May and June 2010, 2011, and 2012 (Table 1). Fifty-one percent of all sitting or feeding birds counted were sooty shearwaters, and 34% were common murres (Table 2). While 22 other avian species were observed, murres and shearwaters dominated counts in all surveys. Density estimates were not significantly different between May and June for murres (U

350 = 4588, $p = 0.737$) or shearwaters ($U = 4450$, $p = 0.478$). Density estimates of murre were
351 significantly higher in 2010 (20.6 ± 75.4 birds km^{-2} , $H = 9.298$, $p = 0.010$), compared to 2011
352 (7.0 ± 22.1 birds km^{-2}) and 2012 (5.4 ± 12.0 birds km^{-2}). Shearwater densities were higher in
353 2010 as well (17.3 ± 40.9 birds km^{-2}), but not significantly different than any other year (overall
354 mean: 10.9 ± 32.7 birds km^{-2} ; $H = 1.015$, $p = 0.602$). While murre and shearwaters were
355 observed on all transects, average densities of murre were highest on the Columbia River
356 transect (13.9 ± 27.4 birds km^{-2}), near the nesting colony closest to the river mouth (Cape Meares
357 transect: 34.6 ± 106.3 birds km^{-2}), and near the Yaquina Head, OR nesting colony (Newport
358 Hydrographic transect: 20.5 ± 36.8 birds km^{-2}). Average densities of shearwaters were highest
359 on transects north of the river mouth including Willapa Bay (19.8 ± 42.2 birds km^{-2}), Grays
360 Harbor (25.5 ± 54.2 birds km^{-2}), and Queets River (15.8 ± 43.3 birds km^{-2}).

361 Catch composition by number of prey fish caught in surface trawls included 79%
362 northern anchovy, 16% other alternative prey species, and 5% juvenile salmon. Frequency of
363 occurrence (FO) of yearling Chinook salmon (62.5%) and juvenile coho salmon (52.5%) were
364 the highest of all prey species, but average catch was low for yearling Chinook salmon (2.1 ± 2.9
365 fish km^{-1}) and coho (4.5 ± 11.2 fish km^{-1}) relative to alternative prey catches (Table 3). Average
366 FO of the top six alternative prey species was low (12.7%), but mean catch was higher and more
367 variable than any juvenile salmon species (129.6 ± 248.9 fish km^{-1}). Juvenile salmon catch did
368 not vary significantly among years ($H = 5.917$, $p = 0.052$) or between May and June surveys
369 within the same year ($U = 4426.5$, $p = 0.458$). Juvenile salmon abundance was highest on
370 transects adjacent to, or north of, the river mouth (Columbia River, Willapa Bay, Grays Harbor),
371 and lowest on transects in the south of the survey area. Alternative prey abundance measured by
372 surface trawls did not vary annually ($H = 5.089$, $p = 0.079$), but was significantly greater in June

compared to May ($U = 3841$, $p = 0.024$). Highest forage fish catches occurred on the Grays Harbor and Newport Hydrographic transects. Most (63%; $n = 146$) trawl catches contained a mix of both forage fish and juvenile salmon. In 54% of mixed-prey species trawl catches, a single forage fish species dominated the catch, typically northern anchovy, whereas salmon catch composition ranged from a single species up to six salmonid species caught in the same trawl. Prey fish density measured by acoustic backscatter (s_A) did not vary annually ($U = 5.229$, $p = 0.073$), but was greater in May compared to June ($U = 2187$, $p = 0.009$). Highest s_A values occurred on the Columbia River, Willapa Bay, Grays Harbor, and La Push transects.

Mean river discharge was similar to the 10 year (2002–2012) average for the same May – June period ($10\,058\text{ m}^3\text{ s}^{-1}$) in 2010 ($9\,831\text{ m}^3\text{ s}^{-1}$), but significantly greater than the average ($H = 149.8$, $p < 0.001$) in 2011 ($15\,636\text{ m}^3\text{ s}^{-1}$) and in 2012 ($11\,336\text{ m}^3\text{ s}^{-1}$; Fig. 2). In May 2010, average river discharge ($8\,664\text{ m}^3\text{ s}^{-1}$), estimated plume volume (10.8 km^3), and surface area ($1\,877\text{ km}^2$) were lowest, whereas estimated plume volume was highest in May 2011 (51.9 km^3), when average discharge was highest ($16\,277\text{ m}^3\text{ s}^{-1}$). Highest surface area ($8\,738\text{ km}^2$) occurred in June 2011, when discharge was second highest ($14\,992\text{ m}^3\text{ s}^{-1}$). Overall, the plume area ranged between 0.5 to 26% (mean: 17%) of the total survey area.

Occupation of plume waters compared to adjacent marine waters was disproportionately higher for murre, shearwaters, and all prey fish (Fig. 3). Overall mean densities of murre and shearwaters were higher inside plume waters (murre: $16.1 \pm 21.0\text{ birds km}^{-2}$; shearwaters: $16.6 \pm 16.7\text{ birds km}^{-2}$) compared to mean densities in non-plume waters (murre: $9.8 \pm 8.7\text{ birds km}^{-2}$; shearwaters: $10.4 \pm 6.0\text{ birds km}^{-2}$). We detected differences between plume and non-plume density distributions for murre ($U = 2069.5$, $p = 0.002$), but not for shearwaters ($U = 2794.5$, $p = 0.421$). Similarly, mean densities of all prey fish were higher inside the plume (alternative prey

396 fish: 284.4 ± 613.2 fish trawl⁻¹; juvenile salmon: 6.9 ± 7.6 fish trawl⁻¹; acoustic prey: $380.7 \pm$
 397 408.2 m² nmi⁻²) than outside the plume (alternative prey fish: 74.3 ± 82.8 fish trawl⁻¹; juvenile
 398 salmon: 4.9 ± 3.9 fish trawl⁻¹; acoustic prey: 192.9 ± 121.1 m² nmi⁻²). However, we did not
 399 detect statistically significant differences between plume and non-plume prey distributions
 400 (Mann-Whitney U tests; $p > 0.05$).

401 The density of murres and shearwaters occupying plume waters declined with plume
 402 surface area, although the pattern was significant only for murres ($F = 13.6$, $p = 0.021$, $R^2 = 0.72$;
 403 Fig. 4a) and not shearwaters ($F = 5.0$, $p = 0.090$, $R^2 = 0.44$; Fig. 4b). The density of forage fish
 404 and juvenile salmon caught in surface trawls, and acoustically detected prey, did not show a
 405 relationship to plume volume ($p > 0.05$, $R^2 < 0.20$; Fig. 4c,d). Highest bird densities (murres:
 406 74.2 birds km⁻², shearwaters: 68.1 birds km⁻²) in the plume were observed during the May 2010
 407 survey, when plume surface area and volume were lowest. Lowest densities of murres (3.9 birds
 408 km⁻²) in the plume were observed in the May 2012 survey, when surface area was relatively high
 409 ($6\,219$ km²). Lowest densities of shearwaters (7.3 birds km⁻²) were observed in the June 2011
 410 survey, when plume area was highest ($8\,738$ km²), and no shearwaters were observed in the
 411 plume during the May 2011 survey, when plume area was second highest.

412 The Δ CG between plume locations observed during each survey was low (40.2 ± 29.0
 413 km) and not significantly different between any of the surveys ($F = 2.47$, $p = 0.14$), indicating
 414 that the location of the plume CG was relatively stable. The mean Δ CG between murres and the
 415 plume CG was 20.8 ± 11.7 km, compared to 99.8 ± 35.5 km for shearwaters. Δ CG values
 416 between murres and the plume were not significantly different between surveys ($F = 0.41$, $p =$
 417 0.56), but were, on average, less in May (14.1 km) than in June (27.5 km). Similarly, Δ CG
 418 values between shearwaters and the plume were not significantly different between surveys ($F =$

0.15, $p = 0.72$), but were on average less in May (85.3 km) than in June (114.3 km). The spatial distribution of CGs indicates that murre were consistently within the defined plume surface (≤ 28 psu), with the exception of the June 2011 survey when they were in waters between 29 and 30 psu (Fig. 5). In comparison, shearwater CGs were primarily outside the defined plume surface (> 28 psu), near the northern edge of the plume boundary in waters between 28 and 30 psu, with the exception of May 2012 when they were located within recirculating plume waters (21–26 psu) off the river mouth. The spatial distribution of juvenile salmonids as measured by CG showed shifts in location between May and June surveys. Coho and Chinook salmon CGs were primarily centered to the north of the plume in far-field waters, particularly during June surveys when the pattern was more apparent (Fig. 5). Most alternative prey CGs were centered near the northern portion of the plume, off Grays Harbor, except for northern anchovy, which were often located near recirculating plume waters. The spatial distribution of anchovy shifted from north-central of the river mouth in May, to the south and within plume waters in June.

The extent and size of the river plume also shifted between May and June, indicating shifting oceanographic conditions (Fig. 5). In May 2010, the river plume was oriented to the north of the river mouth, typical of downwelling conditions (Horner-Devine et al. 2009; Hickey et al. 2010). In May 2012 the river plume was bidirectional, which occurs when winds switch from downwelling to upwelling-favorable during a survey (Hickey et al. 2005). When river discharge and upwelling-favorable conditions increased in June, and during May 2011 when discharge was the highest observed, the plume was oriented to the south and offshore of the river mouth.

GIC values between individual prey species and murre ranged between 0.11 and 0.99, and at least one GIC value was ≥ 0.888 for each survey except June 2010 and May 2012 (Table

442 4). Highest GIC values occurred in May 2010 (mean: 0.85 ± 0.16), including multiple species of
443 juvenile salmon and forage fish. Average GIC values were slightly higher for murre in May
444 (0.67 ± 0.24) compared to June (0.57 ± 0.27). However, GIC values between anchovy, herring,
445 and murre were typically greater in June. In comparison, GIC values between shearwaters and
446 prey ranged between 0.10 and 0.99, and at least three GIC values were ≥ 0.888 on every survey,
447 with the exception of May 2012. GIC values were highest between shearwaters and prey
448 including juvenile coho and Chinook salmon, market squid, and surf smelt (*Hypomesus*
449 *pretiosus*). GIC values were highest in June 2010 (mean: 0.84 ± 0.17), followed by May 2010
450 (mean: 0.79 ± 0.22). GIC values between shearwaters and coho and yearling Chinook salmon
451 were high in nearly all surveys, whereas GIC values were only ≥ 0.888 in June for subyearling
452 Chinook salmon (Table 4).

453 Murre and shearwater densities throughout the survey region were related to both
454 environmental and biological variables (Table 6). No candidate model with only biological or
455 environmental variables performed better than models with a combination of covariates. The
456 final model explaining murre density throughout the survey area (Model 1) demonstrated that
457 increases in murre densities were related to decreases in latitude, distance from shore, water
458 clarity, and acoustic backscatter, and increasing densities of other seabirds (i.e., local
459 enhancement; Table 6). The final model explaining shearwater density throughout the survey
460 area (Model 2) indicated that increases in shearwater densities were related to decreases in water
461 clarity and acoustic backscatter, and an increase in the density of other seabirds. Alternative
462 prey densities (Model 3) were related to decreases in water clarity and zooplankton density.
463 Similarly, juvenile salmon densities (Model 4) were related to decreases in water clarity,
464 zooplankton density, and temperature. Murre densities in the plume (Model 5) were related to

Running page head: Predator-prey interactions river plume

increases in the density of other seabirds, acoustic backscatter, trawl diversity, and non-prey density, and decreases in alternative prey and smolt density and the ratio of salmon to total prey. Densities of shearwaters in the plume (Model 6) were related to decreases in acoustic backscatter and alternative prey, and increases in smolt density and the ratio of salmon to total prey in trawl catches.

Discussion

We demonstrate that variation in Columbia River plume size and location influences spatial distributions of predators and prey. Seabirds and prey fish occurred disproportionately in plume waters relative to adjacent waters. Decreased water clarity was a significant predictor of predators and prey, confirming that enhanced plume-driven productivity supports upper trophic levels. Shearwater and murre densities increased in the plume when plume size declined, suggesting that seabirds concentrate in the plume to maximize foraging effort. Forage fish and juvenile salmon catches did not vary with plume size, indicating that prey associated with the plume are available to predators under varying plume conditions. Indices of collocation between prey fish and seabirds were highest when plume volume and surface area were lowest, demonstrating that reduced plume size increases prey encounter rates for foraging seabirds. Prey occupying plume waters when volumes are low or surface areas are small may experience increased predation pressure, which may be especially important for salmon residing in or migrating through the plume during their transition from freshwater to the ocean.

Murre and shearwater spatial densities were structured by the river plume, but distributions and relationships to biological variables differed between species. Despite similar energetic demands during spring and summer (Wiens and Scott 1975), distances that each

species can move along the coast in search of food may explain differences in results. Murres are central place foragers (Orlans and Pearson 1979) during spring and summer (April – August) and the range over which breeding adult murres can forage is restricted to approximately 100 km radius of their colony to successfully incubate eggs, rear chicks, and fledge young (Decker and Hunt 1996; Hatch et al. 2000; Davoren et al. 2003b). Although the colonies of origin and proportion of actively breeding murres are unknown, high densities of breeding murres would be expected, and were observed, near dense colonies on the Newport Hydrographic transect and on the Cape Meares transect. However, similar densities were observed on the Columbia River transect, suggesting that birds are transiting at least 80 km from colonies to the north or south of the river mouth to forage in the plume. Memory and local enhancement are important for visually foraging seabirds constrained to a colony (Davoren et al. 2003a, 2010; Regular et al. 2013; Tremblay et al. 2014), and turbid plume waters nearshore may be a predictable and persistent feature that murres use to locate prey. This is supported by our finding that the murre distributional center of gravity was within 20 km of the plume center, and greater murre densities were related to decreasing water clarity. Murre densities were not, however, related to increased prey densities in surface trawls, and indices of collocation with prey were relatively low. Murre densities in the plume were related to acoustic backscatter deeper in the water column (10-70 m), catches of non-prey items, and the diversity of organisms caught in surface trawls, including adult salmon, sharks, and jellyfish. Once murres have located the plume, they may be cueing on large organisms near the water surface as visual indicators of increased local prey densities (i.e., patches). Many large organisms also consume forage fish (Brodeur et al. 2014), so the association of murres with non-prey and diverse trawl catches may indicate facilitation or competition (Ainley et al. 2009; Toge et al. 2011; Sato et al. 2015). Given the disproportionately

high occurrence of alternative prey and juvenile salmon in the plume, the relatively high prey densities available under a variety of plume conditions and throughout the water column, and the ability of murres to dive below the area sampled by the surface trawl to access prey, we propose that murres employ a hierarchical foraging strategy by first detecting the turbid water of the river plume or local aggregations of other seabirds, then locating large organisms near the surface of the water, and finally initiating foraging on smaller pelagic prey. Increasing murre densities in the plume as surface area declined further supports the idea that murres utilize the surface manifestation of the plume as a predictable cue for locating prey, regardless of variability in relative plume size or location of the plume.

Sooty shearwaters in the northern hemisphere are not constrained to colonies and are expected to be more associated with areas of high prey availability (Ainley et al. 2009; Adams et al. 2012; Lyday et al. 2015) compared to breeding murres. Yet even for unconstrained foragers, the plume influences shearwater distributions, as demonstrated by the relationship between increasing shearwater densities with declining water clarity and the consistent occurrence of shearwaters ~100 km to the north of the plume center. Global indices of collocation between multiple species of alternative prey and shearwaters were high in the survey region, suggesting that shearwaters occupying these waters have increased encounter rates with forage fish. This result may be dependent on the scale of observation, as shearwater densities were not related to local densities of forage fish measured acoustically or by the surface trawl. This may be due to unresolved patchiness in forage fish distributions, availability to sampling gear during the day (e.g., net avoidance), or survey design that did not adapt to dynamic plume conditions. Shearwaters may be able to visually identify and track tidal fronts that form the northern plume boundary (Zamon et al. 2014), which typically propagate northward and roughly perpendicular

to the Washington coast (Horner-Devine et al. 2009; Jay et al. 2009). Tidal fronts are areas of high productivity throughout the season (Hickey and Banas 2008; Jay et al. 2009), which explains why so many forage fish species were located in the northern plume area. As river discharge increases, plume volume and surface area also typically increase, and the plume orientation shifts to the south (Burla et al. 2010). Thus, the relationship between declining shearwater densities and plume area may relate to the shifting geographic location of the plume. The location of shearwater CGs in waters between 28 and 32 psu also indicates that these predators utilize a range of mixed plume waters.

Northern anchovy were the most abundant forage fish caught in our surface trawls, and their distributions may be an important factor influencing predator-prey interactions associated with the plume. Anchovy are a significant component of seabird diets in the northern California Current (Wiens and Scott 1975; Varoujean and Matthews 1983), particularly during spawning (mid-June – mid-August; Richardson 1980), when abundances are linked to increasing river discharge and upwelling-favorable ocean conditions (Litz et al. 2008; Kaltenberg et al. 2010). We observed a shift in anchovy density distributions between May and June surveys, with increased densities and more southerly distributions in June, which may increase availability to murre foraging in central plume waters. While estimates of collocation between murre and anchovy were relatively low across all surveys, highest values were observed during June surveys and in May 2011, when river flow was the highest observed. Declines observed in murre density with increased plume surface area may indicate an interaction between river flow and the location of spawning aggregations of anchovy, which may be closer to the productive frontal boundaries of the plume. In comparison, shearwaters were only collocated with anchovy in May 2010, when plume volume and surface area were the lowest observed and indices of

collocation were high for numerous prey species. In most surveys, shearwaters were collocated with other forage fish species (e.g., herring, squid, smelt), in addition to coho and Chinook salmon that all occurred in high densities north of the river mouth. While anchovy are probably an important factor influencing murre distributions in the plume, other forage fish species including herring and smelt may also influence shearwater distributions.

Yearling coho and Chinook salmon were more evenly distributed in trawl catch samples compared to forage fish, suggesting that these salmonid species are available to predators under a variety of plume conditions. The constant availability may sustain avian and other predators during periods of proportionately lower abundances of forage fish. The relatively even distribution of smolts may also explain the negative relationship of juvenile salmon and zooplankton densities, which are concentrated at convergent zones in frontal regions of the plume (Morgan et al. 2005). Variable marine migration rates of salmon stocks (Fisher et al. 2014; Teel et al. 2015) may influence the location and timing that smolts are vulnerable to predators. Once in the ocean, yearling coho and Chinook salmon migrating along the Washington coast were consistently collocated with shearwaters. Subyearling smolts that migrate to the ocean later than yearlings were collocated with murre in May, and shearwaters only in June after they began their migration north. The positive relationship between smolt catches, the ratio of smolts to alternative prey, and shearwater densities indicates that the area north of the river mouth may be an important “predator gauntlet” that juvenile salmon must pass through during their northern migration.

Exposure to avian predators in the Columbia River plume, particularly during periods of low river flow, could be a mechanism explaining variation in returns of adult salmon. Juvenile salmon are thought to use river plumes as transitional habitats for osmoregulation, feeding, and

580 refuge (Quinn 2005). Our results suggest that elevated predation mortality may also occur in
581 river plumes. Only 1–4% of smolts entering the ocean are estimated to spawn as adults
582 (Bradford 1995; Coronado and Hilborn 1998), with the majority of this mortality occurring
583 within weeks to months of entry into marine waters (Parker 1968; Beamish and Mahnken 2001).
584 The relationship between increasing plume volume and salmon survival documented by Miller et
585 al. (2013) may be partially explained by the decline in seabird densities we documented with
586 increasing plume size. Although Emmett et al. (2004) found that higher river flows resulted in
587 increased numbers of juvenile salmon in plume waters, a larger plume may reduce smolt
588 predation by increasing the total search area for shearwaters and murre foraging in the plume.
589 Avian predation of smolts in the lower Columbia River estuary by Caspian terns (*Hydroprogne*
590 *caspia*) and double-crested cormorants (*Phalacrocorax auritus*) is estimated at between 3 and 21
591 million smolts per year (Collis et al. 2001; Evans et al. 2012). Given that there is at least an
592 order of magnitude more murre (~131 000; Speich and Wahl 1989; Suryan et al. 2012) and
593 shearwaters (~2.2 million; Wiens and Scott 1975; Adams et al. 2012) than terns (12 500) and
594 cormorants (27 000; Roby et al. 2015), and that murre and shearwaters consume salmon in
595 similar proportions to terns and cormorants (Matthews 1983; Varoujean and Matthews 1983; J.E.
596 Zamon, NOAA Fisheries, Hammond, Oregon, unpublished data), juvenile salmonid mortality by
597 seabirds is certainly higher than currently estimated. To definitively address the impact of
598 seabird predation on salmonids associated with the Columbia River plume and to estimate avian
599 predation rates, data on smolt and alternative prey species composition, depth distribution,
600 abundance, and availability, concurrent with seabird diet samples over a range of plume
601 conditions are needed.

Freshwater inputs to coastal ecosystems occur across land-sea interfaces around the world (Dai and Trenberth 2002). Plume patterns influencing predators and prey observed during this study may inform future research on the influence of a changing climate on ecological interactions in other river plumes (e.g., Fraser River, Canada), including increasing predation pressure during juvenile salmon outmigration (*sensu* Mote et al. 2003). Hydropower and storage dams have stabilized seasonal river flows and reduced annual discharge (Dai et al. 2009), and modified the size and orientation of the Columbia River plume (Ebbesmeyer and Tangborn 1992). As climate change impacts snowpack and subsequent freshwater runoff (Hamlet et al. 2007; Palmer et al. 2008), plume volumes may be further reduced. In the Pacific Northwest, earlier spring peak flows, and reduced spring and summer runoff volumes are expected in the Columbia River Basin (Hamlet and Lettenmaier 1999; Payne et al. 2004; Palmer et al. 2008). The lowest flows observed during our study occurred in 2010, but were greater than average daily flows in 2013–2015 (U.S. Geological Survey surface water station 14246900; <http://waterdata.usgs.gov/nwis>). Because of the enhanced productivity generated by nutrient input and recirculation, river plumes have been identified as potential refugia for juvenile and adult fish during periods of low ocean productivity (Litz et al. 2013). Our results show that river plumes are important areas for predator-prey interactions, and that changing environmental conditions have the potential to affect trophic interactions and energy flow in coastal food webs influenced by river plumes.

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1004

1005 Table 1. Summary of survey effort including year, month, fishing vessel, and date range, acoustic data collection settings, sampling
 1006 effort, and mean river flow and plume volume during each survey.

1007

Year	Month	Vessel	Date range	Echosounder	Sound speed (m s ⁻¹)	Absorption coefficient (dB m ⁻¹)	Total stations sampled	Total surface trawls	Km survey effort ^a	Mean river flow (1000 m ³ s ⁻¹)	Mean plume volume (km ³)
2010	May	Chellissa	5/21 - 5/27	-	-	-	41	39	201.3	8.7	10.8
	June	Frosti	6/21 - 6/28	ES60	1493.89	0.008047	57	55	275.5	11.0	11.3
2011	May	Frosti	5/21 - 5/27	ES60	1480.49	0.008302	50	48	223.1	16.3	51.9
	June	Frosti	6/20 - 6/27	ES60	1480.49	0.008302	57	56	272.7	15.0	38.7
2012	May	Miss Sue	5/30 - 6/3	EK60	1482.94	0.009835	45	32	145.8	10.2	33.1
	June	Frosti	6/21 - 6/28	ES60	1479.80	0.009101	53	50	262.1	12.4	16.0

^aline transect survey effort only; excludes trawl distances

1008

1009 Table 2. Summary of sitting and/or feeding seabird species observed on line transect surveys in May and June 2010-2012, including
1010 number of individual birds observed, percent of total, and frequency of occurrence.

Common Name	Scientific Name	Total	% of Total	FO	2010		2011		2012	
					May	June	May	June	May	June
Sooty shearwater	<i>Ardenna grisea</i>	5181	50.62	1.0	606	3108	449	353	282	383
Common murre	<i>Uria aalge</i>	3526	34.45	1.0	629	1632	267	441	255	302
Pink-footed shearwater	<i>Ardenna creatopus</i>	815	7.96	1.0	16	242	15	324	3	215
Dark shearwater (unid.)	<i>Ardenna</i> spp.	189	1.85	0.5	87	93	-	-	-	9
Rhinoceros auklet	<i>Cerorhinca monocerata</i>	141	1.38	1.0	12	63	52	8	4	2
Black-footed albatross	<i>Phoebastria nigripes</i>	77	0.75	0.7	-	14	-	61	1	1
Phalarope (unid.)	<i>Phalaropus</i> spp.	73	0.71	0.2	-	-	73	-	-	-
Cassin's auklet	<i>Ptychoramphus aleuticus</i>	51	0.50	0.8	5	-	15	2	6	23
Western x glaucous-winged gull	<i>Larus occidentalis x glaucescens</i>	47	0.46	0.8	1	35	1	5	-	5
Gull (unid.)	<i>Larus</i> spp.	37	0.36	0.8	12	3	18	3	1	-
Pacific loon	<i>Gavia pacifica</i>	23	0.22	0.7	5	2	12	4	-	-
Ancient murrelet	<i>Synthliboramphus antiquus</i>	10	0.10	0.5	3	-	4	-	3	-
Northern fulmar	<i>Fulmarus glacialis</i>	10	0.10	0.5	-	3	1	6	-	-
Marbled murrelet	<i>Brachyramphus marmoratus</i>	8	0.08	0.5	-	4	-	2	-	2
Alcid (unid.)	Alcidae	7	0.07	0.3	1	-	6	-	-	-
Red-necked phalarope	<i>Phalaropus lobatus</i>	6	0.06	0.2	6	-	-	-	-	-
Immature gull (unid.)	<i>Larus</i> spp.	6	0.06	0.5	1	-	3	2	-	-
Double-crested cormorant	<i>Phalacrocorax auritus</i>	5	0.05	0.7	-	1	1	2	-	1
Western gull	<i>Larus occidentalis</i>	4	0.04	0.2	-	-	-	-	-	4
Brown pelican	<i>Pelecanus occidentalis</i>	3	0.03	0.2	-	-	-	-	-	3
Tufted puffin	<i>Fratercula cirrhata</i>	3	0.03	0.3	-	1	2	-	-	-
Scoter (unid.)	<i>Melanitta</i> spp.	3	0.03	0.2	-	-	3	-	-	-
Pelagic cormorant	<i>Phalacrocorax pelagicus</i>	2	0.02	0.3	-	1	-	1	-	-
Cormorant (unid.)	<i>Phalacrocorax</i> spp.	2	0.02	0.2	-	2	-	-	-	-

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Brandt's cormorant	<i>Phalacrocorax penicillatus</i>	1	0.01	0.2	-	-	-	-	1	-
Common loon	<i>Gavia immer</i>	1	0.01	0.2	-	-	1	-	-	-
Glaucous-winged gull	<i>Larus glaucescens</i>	1	0.01	0.2	-	1	-	-	-	-
Red-throated loon	<i>Gavia stellata</i>	1	0.01	0.2	-	-	1	-	-	-
Ring-billed gull	<i>Larus delawarensis</i>	1	0.01	0.2	-	-	-	1	-	-
South Polar skua	<i>Catharacta maccormicki</i>	1	0.01	0.2	-	-	-	1	-	-
Western grebe	<i>Aechmophorus occidentalis</i>	1	0.01	0.2	-	-	1	-	-	-
Total		10236	100.0		1384	5205	925	1216	556	950

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1013 Table 3. Summary of organisms collected in surface trawl surveys in May and June 2010-2012, including category used for data
1014 analyses, catch per unit effort (CPUE), frequency of occurrence (FO) and size range observed.

Category	Common name	Scientific name	CPUE	FO	Size range (mm)
Juvenile Salmon Prey	Coho salmon	<i>Oncorhynchus kisutch</i>	4.50	52.50	97-250
	Chinook salmon (subyearling)	<i>Oncorhynchus tshawytscha</i>	3.04	24.64	82-120 (M); 77-140 (J)
	Chinook salmon (yearling)	<i>Oncorhynchus tshawytscha</i>	2.12	62.50	121-250 (M); 141-250 (J)
	Chum salmon	<i>Oncorhynchus keta</i>	1.82	21.79	66-250
	Sockeye salmon	<i>Oncorhynchus nerka</i>	1.69	22.14	95-250
	Steelhead	<i>Oncorhynchus mykiss</i>	0.44	9.64	165-250
	Cutthroat trout	<i>Oncorhynchus clarkii</i>	0.31	1.07	213-250
Alternative Prey	Northern anchovy	<i>Engraulis mordax</i>	636.87	14.29	32-170
	Pacific sardine	<i>Sardinops sagax</i>	50.38	13.21	96-250
	Surf smelt	<i>Hypomesus pretiosus</i>	37.22	8.57	72-186
	California market squid	<i>Doryteuthis opalescens</i>	22.00	24.64	15-184
	Whitebait smelt	<i>Allosmerus elongatus</i>	18.31	4.29	70-127
	Pacific herring	<i>Clupea pallasii</i>	13.04	12.14	55-240
	Sablefish (juv.)	<i>Anoplopoma fimbria</i>	11.80	2.50	63-218
	Widow rockfish	<i>Sebastes entomelas</i>	11.23	0.36	32-72
	Slender barracudina	<i>Lestidiops ringens</i>	5.47	2.14	59-106
	Yellowtail rockfish	<i>Sebastes flavidus</i>	4.48	0.36	15-68
	Darkblotched rockfish	<i>Sebastes crameri</i>	3.46	1.79	16-46
	Squid (unid.)	Teuthida	3.20	1.79	25-59
	Smelt (unid.)	<i>Osmeridae</i> spp.	2.92	9.29	28-98
	Rock greenling	<i>Hexagrammos lagocephalus</i>	1.53	1.07	54-61
	Pacific saury	<i>Cololabis saira</i>	1.53	0.36	88-250
	Pacific mackerel	<i>Scomber japonicus</i>	1.48	1.79	200-250
	Speckled sanddab	<i>Citharichthys stigmaeus</i>	1.18	1.43	28-42

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	Pacific sand lance	<i>Ammodytes hexapterus</i>	1.01	3.93	34-61
	Shortbelly rockfish	<i>Sebastes jordani</i>	0.91	0.71	35-41
	Canary rockfish	<i>Sebastes pinniger</i>	0.85	1.07	21-35
	Rex sole	<i>Glyptocephalus zachirus</i>	0.76	0.36	62-68
	Lingcod	<i>Ophiodon elongatus</i>	0.53	0.71	43-58
	Sanddab (unid.)	<i>Citharichthys</i> spp.	0.32	0.36	45
	Pacific sandfish	<i>Trichodon trichodon</i>	0.32	0.36	212
	Pacific tomcod	<i>Microgadus proximus</i>	0.29	1.79	37-51
	American shad	<i>Alosa sapidissima</i>	0.29	0.71	179-205
	Medusafish	<i>Icichthys lockingtoni</i>	0.28	0.71	13-100
	Shiner perch	<i>Cymatogaster aggregata</i>	0.28	0.36	98
	Northern ronquil	<i>Ronquilus jordani</i>	0.27	0.36	30
	Threespine stickleback	<i>Gasterosteus aculeatus</i>	0.27	0.36	76
	Herring family	<i>Clupeidae</i>	0.27	0.36	30
Non-prey Biomass	Sea nettle	<i>Chrysaora fuscescens</i>	36.92	30.00	15-350
	Spiny dogfish	<i>Squalus acanthias</i>	32.71	8.21	50-1150
	Water jelly	<i>Aequorea</i> spp.	22.63	32.86	10-210
	Pacific hake	<i>Merluccius productus</i>	3.76	2.14	320-390
	Cross jelly	<i>Mitrocoma cellularia</i>	1.61	1.43	20-78
	Steelhead	<i>Oncorhynchus mykiss</i>	1.40	2.86	251-598
	Comb jellies	<i>Ctenophora</i>	0.89	34.29	-
	Black rockfish	<i>Sebastes melanops</i>	0.88	1.43	272-470
	Pink salmon	<i>Oncorhynchus gorbuscha</i>	0.82	0.71	465-489
	Chinook salmon	<i>Oncorhynchus tshawytscha</i>	0.80	52.14	251-870
	Pacific sardine (>250 mm)	<i>Sardinops sagax</i>	0.78	3.21	251-273
	Pacific saury (>250 mm)	<i>Cololabis saira</i>	0.70	0.71	251-305
	Starry flounder	<i>Platichthys stellatus</i>	0.54	4.64	230-560
	Egg yolk jelly	<i>Phacellophora camtschatica</i>	0.52	12.86	70-380
	Coho salmon	<i>Oncorhynchus kisutch</i>	0.52	38.21	251-712
	Pacific staghorn sculpin	<i>Leptocottus armatus</i>	0.50	2.14	170-265
	Jack mackerel	<i>Trachurus symmetricus</i>	0.50	1.79	523-690

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Moon jelly	<i>Aurelia spp.</i>	0.45	8.21	65-355
Wolf-eel	<i>Anarrhichthys ocellatus</i>	0.44	12.50	260-605
Blue shark	<i>Prionace glauca</i>	0.38	1.79	520-1800
Lion's mane jelly	<i>Cyanea capillata</i>	0.36	1.43	120-300
Soupfin shark	<i>Galeorhinus zyopterus</i>	0.35	2.86	780-1758
English sole	<i>Parophrys vetulus</i>	0.34	0.36	300
Chum salmon	<i>Oncorhynchus keta</i>	0.33	3.93	251-695
Cutthroat trout	<i>Oncorhynchus clarkii</i>	0.32	1.07	251-400
Salmon shark	<i>Lamna ditropis</i>	0.30	0.36	1950
Pacific lamprey	<i>Lampetra tridentata</i>	0.30	0.71	308-720
Pacific mackerel (>250 mm)	<i>Scomber japonicus</i>	0.29	0.71	251-282
Butter sole	<i>Isopsetta isolepis</i>	0.29	0.36	25
River lamprey	<i>Lampetra ayresii</i>	0.28	2.14	258-330
Yellowtail rockfish	<i>Sebastes flavidus</i>	0.28	0.36	415
Widow rockfish	<i>Sebastes entomelas</i>	0.28	0.36	386
Sockeye salmon	<i>Oncorhynchus nerka</i>	0.28	0.71	251-465
Jellyfish (unid.)	<i>Scyphozoa spp.</i>	0.32	0.71	155
Penicillate jelly	<i>Polyorchis penicillatus</i>	0.29	0.36	30-70
Sea butterfly	<i>Corolla spectabilis</i>	0.34	3.21	-
Salp (unid.)	<i>Salpidae</i>	0.34	0.71	-
Beroe (unid.)	<i>Beroe spp.</i>	0.33	0.71	-
Carinaria japonica	<i>Carinaria japonica</i>	0.32	4.64	-
Hormiphora cucumis	<i>Hormiphora cucumis</i>	0.32	26.79	-
Umbrella jelly	<i>Eutonina indicans</i>	0.29	0.36	-
Sea gooseberry	<i>Pleurobrachia spp.</i>	0.28	7.14	-
Clio pyramidata	<i>Clio pyramidata</i>	0.28	0.36	-
Sea angel	<i>Clione limacina</i>	0.26	0.36	-

1015 Table 4. Global index of collocation values between murre and shearwaters and the three most frequently caught juvenile salmon,
1016 and the six most abundant alternative prey fish species; darker shading indicates higher value of GIC and values ≥ 0.888 were
1017 considered indicative of a relationship between predator and prey.

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Predator	Prey Species	2010		2011		2012	
		May	June	May	June	May	June
Common murre	Chinook salmon (SY)	0.879	0.361	0.940	0.423	0.418	0.876
	Chinook salmon (Y)	0.954	0.411	0.748	0.364	0.575	0.728
	Coho salmon	0.988	0.387	0.713	0.429	0.663	0.805
	Northern anchovy	0.670	0.856	0.847	0.809	0.196	0.939
	Pacific herring	0.919	0.202	0.719	0.924	0.406	0.882
	Pacific sardine	0.919	0.425	0.679	0.342	0.669	0.377
	Market squid	0.933	0.567	0.579	0.629	0.488	0.906
	Surf smelt	0.887	0.198	0.838	0.521	0.196	0.281
	Whitebait smelt	0.484	0.106	0.182	0.609	0.484	0.983
Sooty shearwater	Chinook salmon (SY)	0.777	0.982	0.400	0.996	0.815	0.972
	Chinook salmon (Y)	0.918	0.990	0.972	0.858	0.887	0.921
	Coho salmon	0.771	0.977	0.977	0.891	0.937	0.973
	Northern anchovy	0.971	0.511	0.220	0.605	0.468	0.651
	Pacific herring	0.966	0.793	0.998	0.679	0.696	0.675
	Pacific sardine	0.899	0.932	0.590	0.723	0.364	0.468
	Market squid	0.659	0.889	0.940	0.928	0.776	0.611
	Surf smelt	0.887	0.902	0.939	0.988	0.469	0.088
	Whitebait smelt	0.270	0.604	0.348	0.066	0.880	0.881

Table 5. Variables used in generalized linear models, including variable type and measurement, abbreviation used to describe covariates in the final models, the models in which each variable was included, and median, range, mean and standard deviation of the measurements.

Variable Type	Measurement	Abbreviation	Model	Median	Range	Mean	SD
Environmental	3 m salinity (psu)	SSS	1,2,3,4	30.9	19.9 - 33.3	29.7	2.4
	3m Water clarity (%)	Clar	1,2,3,4	85.9	50.5 - 96.9	85.2	7.3
	3 m temperature (°C)	SST	3,4	12.7	9.1 - 16.0	12.7	1.5
	Halocline depth (m)	Halo	1,2	9.0	1 - 117	13.9	16.6
	Plume surface area (km ²)	PIArea	1,2	5106.6	927.3 - 9,320.9	5,318.4	2,555.8
Biological	Juvenile Salmon (fish trawl ⁻¹)	Sal	1,2,5,6	1.9	0 - 122.0	5.4	11.4
	Alternative Prey (fish trawl ⁻¹)	Alt	1,2,5,6	0.8	0 - 9,136.6	111.2	682.4
	Salmon:Total Prey	SalRatio	1,2,5,6	0.6	0 - 1	0.5	0.4
	Non-prey (organisms trawl ⁻¹)	Non-prey	1,2,5,6	1.6	0 - 919.1	22.5	92.5
	Trawl Diversity	Div	1,2,5,6	0.9	0 - 1.99	0.9	0.5
	S _A between 10-70 m (m ² nmi ⁻²)	NASC	1,2,5,6	1.3	0.00029 - 1,802.3	23.1	133.1
	Other seabirds (birds km ⁻²)	LocEnh	1,2,5,6	4.3	0 - 601.2	14.0	40.8
	Zooplankton (organisms m ⁻³)	Zoop	3,4	0.9	0.0047 - 3,476.6	22.3	254.2
Geospatial	Distance from shore (km)	Dist	1,2	25.9	1.9 - 57.4	25.9	15.7
	Latitude (dd)	Lat	1,2,3,4	46.99	44.66 - 48.23	46.80	1.03

1028 Table 6. Generalized linear model results for predator (murre and shearwater) and prey (juvenile salmon and alternative prey)
 1029 densities throughout the survey region, and predators within the river plume. Final models presented include slope and parameter
 1030 estimates for significant covariates, AICc, and model weight.

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Model	Final Model Equation	Weight
1: Murre density throughout region	$44.7 + -0.03(\text{Clar}) + 0.0081(\text{LocEnh}) + -0.000037(\text{NASC}) + -0.10(\text{Dist}) + -0.83(\text{Lat})$	1.00
2: Shearwater density throughout region	$7.5 + -0.063(\text{Clar}) + 0.001(\text{LocEnh}) + -0.0031(\text{NASC})$	0.94
3: Alternative prey throughout region	$12.3 + -0.084(\text{Clar}) + -0.11(\text{Zoop})$	0.38
4: Smolt density throughout region	$10.0 + -0.060(\text{Clar}) + -0.25(\text{SST}) + -0.061(\text{Zoop})$	0.64
5: Murre density in plume	$1.6 + -1.36(\text{SalRatio}) + 0.0062(\text{Non-prey}) + 1.01(\text{Div})$	0.95
6: Shearwater density in plume	$1.3 + + 0.025(\text{Sal}) + -0.0022(\text{Alt}) + 1.54(\text{SalRatio}) + -0.025(\text{NASC})$	0.93

Figure Captions

Figure 1. Map of study area, including line transects and oceanographic sampling stations along the Oregon and Washington coasts. Each transect line is named for a geographic feature in proximity to the inshore end of the line as follows: FS = Father and Son, LP = La Push, QR = Queets River, GH = Grays Harbor, WB = Willapa Bay, CR = Columbia River, CM = Cape Meares, and NH = Newport Hydrographic. Murre colonies along the coast are shown as yellow circles with circle size representing estimated colony size based on count data from U.S. Fish and Wildlife Service. Map created using ArcGIS® software by Esri.

Figure 2. Average daily Columbia River flow in 2010, 2011, 2012, and 10 y average (2002 – 2012) measured at U.S. Geological Survey surface water station 14246900.

Figure 3. Area use of the Columbia River plume by seabirds and prey fish in each survey. Use was calculated by subtracting the observed proportions of seabirds and prey in the plume from expected proportions, defined as the proportion of plume area in the total calculated survey area during each cruise. If seabirds and prey were using the plume proportionate to available area, then differences between observed and expected values would be zero. Values greater than zero indicate disproportionate occurrence in the plume.

Figure 4. The relationship between a) mean plume surface area ($\pm$ SE) and density of common murrelets in the plume, and mean plume volume ($\pm$ SE) and b) shearwaters in the plume, c) prey fish densities in the plume measured by surface trawl and d) acoustic backscatter in the plume.

1055 Figure 5. Distribution of the interpolated plume surface area, centers of gravity, and axes of
1056 inertia of predators and prey in 2010, 2011, and 2012 in May (top panels) and June (bottom
1057 panels). Maps created using ArcGIS® software by Esri.

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Figure 1. Map of study area, including line transects and oceanographic sampling stations along the Oregon and Washington coasts. Each transect line is named for a geographic feature in

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1075 Figure 4. The relationship between mean plume surface area or volume ($\pm$ SE) and density of a) common murre, b) shearwaters, c)
1076 prey fish densities measured by surface trawl, and d) acoustic backscatter in the plume.

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1080 inertia of predators and prey in 2010, 2011, and 2012 in May (top panels) and June (bottom
1081 panels). Maps created using ArcGIS® software by Esri.

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