The influence of the Columbia River plume on predator-prey interactions

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Abstract

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Oceanographic processes that aggregate prey and facilitate the transfer of energy to higher trophic levels often influence marine predator-prey interactions. Buoyant discharge from the Columbia River forms a large freshwater plume bounded by convergent fronts in the northern California Current. These oceanographic features aggregate zooplankton and attract coastal pelagic fish species (CPS) including northern anchovy (*Engraulis mordax*). Juvenile salmon (*Oncorhynchus* spp.) use the Columbia River plume as they migrate to sea and experience elevated mortality during early marine residence. Seabirds including sooty shearwaters (*Ardenna grisea*) and common murres (*Uria aalge*) use the plume to forage, consuming CPS and juvenile salmon, and the Columbia River plume may influence predator-prey interactions and juvenile salmon survival. This dissertation examined the influence of the Columbia River plume on distributions of seabirds and fish prey, and characterized conditions that influence juvenile

salmon predation risk. Chapter 1 provides a general introduction to the Columbia River plume ecosystem. Chapter 2 demonstrates the disproportionate occurrence of murres, shearwaters, CPS, and juvenile salmon in plume waters, the positive relationship between turbid plume waters and seabird densities, and the aggregation of seabirds in the plume when surface area is low. Chapter 3 used satellite telemetry and a high resolution hydrodynamic model of plume circulation to demonstrate the ability of murres and shearwaters to track the north-south movements of the plume, and the movement of seabirds towards biophysically active plume boundaries when surface areas exceed a threshold of ~1,500–4,000 km^2. Chapter 4 compared murre distributions observed from ship, plane, and satellite telemetry data perspectives, and identified similarities and differences in seabird spatiotemporal distributions that can inform species distribution models. Chapter 5 documented a relationship between low plume surface areas and increased juvenile coho and Chinook salmon predation risk from seabirds, and the mediating role of CPS in predator-prey interactions near the plume. Taken together, the results of this dissertation demonstrate that variation in Columbia River plume surface area and river discharge influences predator-prey interactions and juvenile salmonid predation risk. Chapter 6 offers a synthesis of the results and recommendations for future research aimed at informing Pacific salmon ocean ecology, management, and conservation.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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DEDICATION

For my mother, Judith Rae Phillips (1946-2006) – Look mom, I did it!

Eventually, all things merge into one,
and a river runs through it

Norman Maclean

Chapter 1. INTRODUCTION

Predator-prey interactions are often influenced by oceanographic processes that aggregate prey and facilitate the transfer of energy from primary producers to higher trophic levels. This process, called biophysical coupling, creates patches of productivity (Steele 1976, Haury et al. 1978, Mackas et al. 1985) and increases habitat complexity (Cairns & Schneider 1990, Steele et al. 1994, Hunt 1997). Biophysical coupling occurs directly at lower trophic levels, where water circulation aggregates passive or weakly swimming planktonic organisms (Franks 1992). Planktivorous fishes are attracted to areas of concentrated plankton, including density fronts (Olson et al. 1994, Acha et al. 2015), which in turn attract piscivorous fishes, seabirds, and marine mammals (Fiedler & Bernard 1987, Bost et al. 2009, Godø et al. 2012). Observations of predator foraging 'hotspots' are often in areas of enhanced productivity and high densities of zooplankton and fish (Nur et al. 2011, Davoren 2013, Bouchet et al. 2015).

Oceanographic processes operate across multiple spatiotemporal scales, from upwelling in eastern boundary currents at seasonal and interannual scales (>1000 km, months–years) to zooplankton accumulation near estuarine fronts at meso- and fine scales (<1000 km, hours–days; Stommel 1963, Haury et al. 1978, Hunt & Schneider 1987). Relationships of mobile marine predators to large-scale oceanographic processes are well-established (e.g., Weimerskirch 2007, Block et al. 2011). In comparison, predator associations with dynamic processes that vary at meso- and fine scales remain less understood. Scale-dependent relationships of apex marine predators to oceanographic processes that increase productivity and aggregate prey are often examined using direct observations during at-sea surveys. This type of data typifies a Eulerian perspective, where sampling occurs at fixed locations within a grid so that species composition and abundance can be estimated. In comparison, a Lagrangian perspective tracks animal

movements through space and time, with the sampling area defined by the animal's range (Rutz & Hays 2009, Tremblay et al. 2009, Watanuki et al. 2016). Locations of marine predators recorded by animal-borne tracking devices are an example of a Lagrangian sampling approach, and offer another way to examine scale-dependent distribution patterns (Costa et al. 2012, Block et al. 2016, Sequeira et al. 2018). Species distributions obtained from either a Eulerian or Lagrangian perspective can be linked to oceanographic processes by obtaining and examining biotic and abiotic data at matching spatiotemporal resolutions.

Areas with large freshwater inputs to the ocean (e.g., estuaries, river mouths, tidewater glaciers) often form mesoscale plumes with sharp density gradients separating buoyant freshwater from denser marine waters (Skreslet 1986, Yankovsky & Chapman 1997). Convergent fronts formed by the discharge of low salinity water enhance biophysical coupling, aggregate prey (Mackas & Louttit 1988, St. John et al. 1992), and attract marine predators (Skov & Prins 2001, Kowalczyk et al. 2015, Arimitsu et al. 2016). For example, the Columbia River is the fourth largest river in North America by volume, with high freshwater discharges that form a broad and relatively deep plume in the northern California Current (Barnes et al. 1972, Hickey et al. 1998). The physical properties of the Columbia River plume (CRP) include low salinity buoyant river water that floats above dense, cold marine waters on the shelf (Hickey et al. 2010). Tidally-generated pulses of freshwater from the most recent tidal exchange and older re-circulating plume water interact vertically and horizontally, creating internal waves and convergent mixing fronts at plume edges adjacent to marine waters (Horner-Devine et al. 2009, Burla et al. 2010, Hickey et al. 2010). The recirculating CRP influences stratification and retains terrigenous and marine-derived, nutrient-enriched water near the surface that increases productivity across three trophic levels (Kudela et al. 2010). Suspended sediment loads and

phytoplankton growth in plume waters also increase turbidity (Frame & Lessard 2009), making the plume a visually distinct oceanographic feature in the northern California Current (Fiedler & Laurs 1990).

The CRP is present along the Oregon and Washington coasts year round, with its spatial area extending hundreds of kilometers, shaped by surrounding dense oceanic waters, variation in wind direction, tidal and coastal currents, and seasonal patterns of river flow (Hickey et al. 2005, 2010, Horner-Devine et al. 2009). Despite its persistence, the CRP is very dynamic. Changes in plume location and morphology can occur at spatial scales of 1–100 km and temporal scales of 2–24 h (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, northwest winds create upwelling conditions, and offshore transport increases (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 that push the plume northward and inshore (Hickey et al. 2005, Thomas & Weatherbee 2006). In addition to geographic variability, the plume surface area fluctuates over two orders of magnitude, from ~150 km^2 during periods of low river discharge (e.g., late summer) to ~24,000 km^2 in spring during peak river discharge and strong, persistent upwelling winds (Horner-Devine et al. 2009).

Convergent fronts created by the mixing of buoyant freshwater and dense ocean water along the edges of the plume can vary in location and strength with hourly shifts in tidal currents and local winds (Jay et al. 2009). These dynamic fronts are the primary mechanism influencing the biological community near the CRP (Garvine & Monk 1974). Biophysical coupling near the plume edge aggregates zooplankton and larval fish and often creates visible “scum” lines of

foam and flotsam at the surface of the water (Morgan et al. 2005, Zamon et al. 2014). Small schooling coastal pelagic fish species (CPS) including Pacific sardine (*Sardinops sagax*), surf smelt (*Hypomesus pretiosus*), Pacific herring (*Clupea pallasi*), and whitebait smelt (*Allosmerus elongatus*) are attracted to areas of aggregated prey (Acha et al. 2015) and are a major component of the diet of many marine predators in the California Current ecosystem, including piscivorous fish, marine mammals, and seabirds (Pikitch et al. 2014, Szoboszlai et al. 2015). CPS occur in increased abundances near the CRP (Brodeur et al. 2005, Litz et al. 2013), where they consume a variety of copepods, euphausiids, and early life stage fishes (Miller & Brodeur 2007). The northern subpopulation of northern anchovy (*Engraulis mordax*) is the most abundant CPS in the northern California Current, occurring in large, dense schools associated with the edges of the CRP (Richardson 1981, Litz et al. 2008). Northern anchovy spawn in association with the plume (Laroche & Richardson 1980, Litz et al. 2008), with eggs and larvae often found in plume waters during summer (Richardson 1973, Laroche & Richardson 1980, Checkley et al. 2000). Thus, the spatial distribution, temporal abundance, and spawn timing of northern anchovy near the CRP is more variable than other CPS species, and has been linked to variation in the location and size of the CRP and river discharge (Kaltenberg et al. 2010).

Seasonal increases in freshwater discharge and associated coastal productivity near the CRP also influence the migration timing and residence time of endangered Columbia Basin juvenile salmon (*Oncorhynchus* spp.) migrating from freshwater to the ocean (Emmett et al. 2004, De Robertis et al. 2005, Brosnan et al. 2014). As juvenile salmon move through the Columbia River estuary and plume, they alter their physiology, behavior, and morphology to survive in the ocean, a process called smoltification (Hoar 1958, 1976). Smoltification is initiated by external and internal cues including photoperiod, hormones, temperature, and size

(Wedemeyer et al. 1980, Quinn 2005). Smoltification is an evolutionary adaptation by juvenile salmon as they migrate into an unstructured environment where their blue-green backs, silver sides, and white bellies provide camouflage from predators (Quinn 2005). Once smoltification is complete, juvenile salmon, or smolts, become part of the CPS community near the CRP, as they are similar in size (90–250 mm) and appearance to many CPS species (Hoar 1976), and their distributions overlap in space and time (Emmett et al. 2006).

Smolts experience increased mortality during migration and early marine residence (Pearcy 1992), with predation being a hypothesized important mechanism influencing returning adult abundances (Muir et al. 2006, Scheuerell et al. 2009). Marine mammals including harbor seals (*Phoca vitulina*) and California sea lions (*Zalophus californianus*) consume smolts on the Washington and Oregon coasts (Szoboszlai et al. 2015, Adams et al. 2016, Chasco et al. 2017). Predatory marine fishes including Pacific hake (*Merluccius productus*), jack mackerel (*Trachurus symmetricus*), spiny dogfish (*Squalus acanthias*), soupfin sharks (*Galeorhinus galeus*), steelhead (*O. mykiss*), and cutthroat trout (*O. clarki*) have all been documented to consume juvenile salmonids along the coast (Emmett & Krutzikowsky 2008, Brodeur et al. 2014). Data on the consumption of salmon by piscivorous seabirds in the CRP and along the Washington and Oregon coasts is limited, but sampling of sooty shearwaters (*Ardenna grisea*) and common murres (*Uria aalge*) indicate that coho salmon (*O. kisutch*), Chinook salmon (*O. tshawytscha*), and steelhead occur in up to 10% of diet samples (Wiens & Scott 1975, Varoujean & Matthews 1983, Lance & Thompson 2005). In all studies, smolts constituted a fraction of the prey consumed, which consisted primarily of CPS species including anchovy, juvenile rockfish (*Sebastes* spp.), herring, and market squid (*Doryteuthis opalescens*) (Szoboszlai et al. 2015).

Increased consumption of smolts by predators when other CPS species are less available can have potentially negative impacts on the overall survival of salmon (Wells et al. 2017).

The presence of juvenile salmon in predator diets, and observations of low adult salmon returns during periods when CPS abundances were low (Fisher & Pearcy 1988, Pearcy 1992), prompted researchers to hypothesize that the availability of alternative prey (i.e., CPS) for predators influences juvenile salmon survival (Emmett & Sampson 2007). The alternate prey hypothesis suggests that high abundances of CPS during the period that smolts enter the marine environment and reside in the CRP may mediate predation impacts by increasing the total number of prey available, and reducing the proportion of smolts consumed by predators (Emmett & Krutzikowsky 2008). Alternatively, when CPS abundances are low, juvenile salmon may be more at risk of predation and experience elevated early marine mortality (Fisher & Pearcy 1988, Pearcy 1992).

In addition to alternative prey, predation can be influenced by abiotic factors that affect prey densities and detectability. For example, low light levels often reduce prey detectability for visually foraging predators, which may decrease predation rates (Petersen & Gadomski 1994, Vogel & Beauchamp 1999, Hansen et al. 2013). Turbid plume waters have been hypothesized to provide cover for salmon (De Robertis et al. 2003, 2005). However, some seabirds are attracted to turbid waters to forage (Ainley 1977, Haney & Stone 1988, Cyrus 1991), which may negate refugia benefits of the CRP for some prey species (Holsman et al. 2012).

The type and amount of fish consumed by predators is influenced by oceanographic conditions that aggregate prey and influence detectability, prey community composition, the response of predators to the abundance and distribution of prey, and predator energetic demands. Sooty shearwaters and common murres consistently occur in increased abundances in the CRP

and adjacent waters during the period when most smolts first enter the ocean (Zamon et al. 2014), suggesting that the CRP may be an important foraging area for seabirds. Northern anchovy, Pacific tomcod (*Migrogadus proximus*), and smelts are important components of shearwater and murre diets near the CRP (Wiens & Scott 1975, Varoujean & Matthews 1983), but seabirds also consume juvenile salmon. Whether seabirds aggregate in the river plume in response to the structure of the plume, the availability of prey, or a combination of factors, is unknown. Both shearwaters and murres are opportunistic foragers (Matthews 1983, Chu 1984), and the consumption of salmon by these two predators may be correlated with salmon abundance and/or the availability of other prey. High densities of juvenile salmon in the Columbia River plume during high river flows (Emmett et al. 2004) also corresponds to increasing densities of northern anchovy (Kaltenberg et al. 2010). River flow and plume volume has been linked to salmon survival (Miller et al. 2013, Brosnan et al. 2014), but evidence that identifies mortality mechanisms, including the influence of plume dynamics on predators and alternate prey, is not complete. Variation in plume size and location may influence predator and prey distributions, and subsequent predation pressure on salmon. Especially in the absence of alternate prey, seabirds attracted to this habitat may exert significant predation pressure on juvenile salmon.

The CRP and adjacent marine habitat along the Washington and Oregon coasts provides a case study to examine how a mesoscale oceanographic feature may influence predator-prey interactions. To understand predator-prey interactions near the CRP, a multidisciplinary sampling approach including *in situ* sampling from ship surveys, aerial surveys, satellite telemetry of individual shearwaters and murres, and hydrodynamic oceanographic models was used. Project objectives 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. This research is expected to provide a better understanding on the influence of the CRP on juvenile salmon predation risk, the potential for CPS to mediate seabird-smolt interactions, and identify potential CRP metrics that resource managers can use to inform decisions including hatchery releases in relation to river flow.

Chapter 2. PREDATOR-PREY INTERACTIONS INFLUENCED BY A DYNAMIC RIVER PLUME[1]

2.1 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 & 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 & 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

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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 2016). 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 & 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 & 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 & 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 & 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 murres breed colonially along the

Oregon and Washington coasts (Speich & Wahl 1989, Naughton et al. 2007; **Figure 2.1**). 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 & Matthews 1983).

High mortality of juvenile salmon during early marine residence is likely due to predation (Pearcy 1992, Beamish & Mahnken 2001), but only a few studies have quantitatively examined predator-prey interactions during this period (Beamish et al. 1992, Beamish & Neville 1995, Emmett & Krutzikowsky 2008, Berejikian et al. 2016). Observations of elevated early marine mortality of smolts during periods of low forage fish abundance (Fisher & Pearcy 1988, Pearcy 1992) prompted Emmett & 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 murres 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.

2.2 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 2.1**).

2.2.1 *Transect Sampling*

Transects began 35–42 km offshore at dawn with the vessel traveling due east for 2 h at ~5 m s^{-1} (**Figure 2.1**). 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., 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 2.1**). A pulse duration of 1.024 ms was transmitted at 2000 W at a sampling rate of 0.5 Hz. With the exception of the May 2012 survey, echosounders were calibrated annually using a 38.1 mm tungsten carbide reference sphere following Foote et al. (1987).

2.2.2 *Station Sampling*

After transect sampling was completed, 5 to 8 fixed stations along the same transect were sampled, working from east to west (**Figure 2.1**). 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 within 5 m of the bottom or a maximum depth of 200 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, predicted daily values of plume volume, surface area, depth, and east-west/north-south orientation were obtained from the Center for Coastal Margin Observation and Prediction (CMOP; db14 climatological atlas; http://www.stccmop.org/datamart/virtualcolumbiariver). Average Columbia River daily discharge records from Quincy, Oregon were also obtained (river km 87; U.S. Geological Survey surface water station 14246900; http://waterdata.usgs.gov/nwis).

2.2.3 *Data Processing*

2.2.3.1 Acoustic Data Processing

Acoustic data were processed using Echoview v 5.4 (http://www.echoview.com/). Uncalibrated acoustic data from May 2012 were included 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 & 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), the expected target strength of an anchovy at 38 kHz was calculated based on the expected minimum and maximum fork length of anchovy caught in the trawl (50 and 200 mm) using the target strength to length conversion equation from Barange et al. (1996). 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 m^3 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 & 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 large aggregations of forage fish that may be near the surface and available to piscivorous seabirds was of interest. To exclude backscatter from adult hake, analyses were limited 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 murres (Piatt & Nettleship 1985, Weimerskirch & 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; $m^2\,nmi^{-2}$; MacLennan et al. 2002), indexed in space and time.

2.2.3.2 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, only seabirds that were sitting on the water surface or observed feeding were analyzed, and birds flying through the area were excluded, 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 & 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).

2.2.3.3 Station Data Processing

To examine patterns in temperature, salinity, and density, thermocline, halocline, and pycnocline depths were estimated 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 fish caught by the distance between the start- and endpoints of the tow as determined by GPS (mean: 3.3 ± 0.7 km, SD). In instances where a trawl was repeated at the same station (n = 13), the average catch of the two samples was used for analyses. To delineate potential prey of seabirds, catches were partitioned using known species and species groups consumed by common murres (Varoujean & Matthews 1983, Nevins 2004) and sooty shearwaters (Baltz & Morejohn 1977, Chu 1984). To ensure that appropriate size fish were included as prey and to allow for variation in prey shapes (e.g., body depth versus length), a maximum of 250 mm FL or DML for all potential prey species was used, corresponding to twice the standard deviation of FL reported by Nevins (2004) for Pacific sardine consumed by common murres. A minimum prey length was not used, as murres and shearwaters consume a range of prey sizes including larval and juvenile life stages of marine organisms (Lance & Thompson 2005, Szoboszlai et al. 2015). All potential non-salmonid prey were categorized as alternative prey, and all salmon ≤250 mm FL were categorized as juvenile salmon. To account for life history variation in length at ocean entry for Chinook salmon, FL and month of capture were used to classify juveniles as either subyearling or yearling based on known length-based age classes from scale analysis and tagging studies (Pearcy & Fisher 1990, Fisher & Pearcy 1995). In May, subyearling fish had FL ≤120 mm, and yearlings had FL between 121–250 mm. In June, subyearling fish had FL ≤140 mm, and yearlings had FL between 141–250 mm. To assess co-occurrence of different prey groups, trawl catch data were categorized to determine the number of trawls that contained only alternative prey, only juvenile salmon, or both prey groups in the same sample. The ratio of juvenile salmon to total prey caught in each trawl was also

calculated. Species that were not considered seabird prey items (e.g., jellyfish, adult salmon) were categorized as non-prey and 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. The time mismatch between transect seabird counts and subsequent station trawl sampling (average: 4 h; range: 30 min to 13 h) was addressed 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.

2.2.4 *Data Analysis*

To characterize seabird and prey communities associated with the Columbia River plume, intra- and inter-annual variation in river discharge, plume volume, plume surface area, and seabird and fish abundance (fish km^{-1} and s_A) was examined using Kruskall-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. Horizontal interpolation of 3 m salinity values measured at each station was accomplished 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. A 28 practical salinity unit (psu) maximum was used following Burla et al. (2010) for analyses, but the plume surface area was also depicted using haloclines 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 my methods, calculated plume area values from interpolated data were compared to the average predicted surface area values from CMOP model outputs for each survey and found an overall deviance of only 17 km^2 between the two methods, confirming that the calculations were consistent.

To determine if predators or prey use the plume disproportionately to available area, each observation was categorized as inside (3 m salinity ≤ 28 psu at the time of observation) or outside (> 28 psu) the plume, and proportions of seabirds and prey in each area were calculated. The horizontal surface plume was used 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. Average density of seabirds,

juvenile salmon, alternative prey, and acoustic backscatter inside and outside the plume were also calculated. The distribution of densities inside and outside the plume were compared 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. The average plume volume and surface area was calculated for each survey from daily values obtained from CMOP model outputs. Because plume volume and surface area are correlated ($\rho = 0.90$, $p = 0.015$), average surface area was used as the explanatory variable in regression models of seabird density, as air-borne seabirds were hypothesized to show a stronger response to areal extent of the plume. Plume volume was used in regression models for in-water prey. Predicted daily locations of the plume centroid from CMOP model outputs were also used to estimate the overall geographic center of gravity (CG) and inertia (defined as dispersion around the CG) of the plume for each survey (Bez & Rivoirard 2001, Woillez et al. 2007, 2009). These analyses were verified by visually confirming that the estimated plume CG fell within the interpolated plume surface area calculated from CTD casts. CG and inertia of seabirds, juvenile salmon, and alternative prey were also calculated and compared 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). The Euclidean distance between each predator and prey CG was measured 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, murre and shearwater density, alternative prey, and juvenile salmon catches were fit to generalized linear models (GLM; McCullagh & Nelder 1989), using individual stations as the sampling unit. *A priori* model development was used to generate individual GLMs based on hypothesized relationships between seabirds, prey, and the environment (Kutner et al. 2004, Burnham & Anderson 2011). 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 candidate models were tested for each GLM (**Table 2.5**). Covariates were evaluated for collinearity using variance inflation factors (VIF) and removed when VIF values exceeded 2 (Burnham & Anderson 2011). For Models 1 and 2, halocline depth, rather than pycnocline, was used because these covariates were collinear and I was primarily interested in the direct influence of plume depth on seabirds. For Models 3 and 4, temperature and zooplankton density were included 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 it was 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, an estimate of

other seabird species densities at each station in all seabird models was included. To account for documented patterns of increased abundances of seabirds nearshore (Menza et al. 2016), the distance to shore of each station, measured as the straight-line distance along transect to land, was included as a geospatial covariate. A negative binomial error distribution and log link with the R package MASS (Venables & Ripley 2002) was used for all GLMs. This allowed me to model overdispersed data without transformation, and accounted for high variability observed in trawl and acoustic covariate data (McCullagh & Nelder 1989). Spatial autocorrelation among bird densities was assumed to be minimal, 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 & Anderson 2011, 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 & Anderson 2011).

2.3 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 2.1**). Fifty-one percent of all sitting or feeding birds counted were sooty shearwaters, and 34% were common murres (**Table 2.2**). 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 ($U = 4588$, $p = 0.737$) or shearwaters ($U = 4450$, $p = 0.478$). Density estimates of murres were significantly higher in 2010 (20.6 ± 75.4 birds km^{-2}, $H = 9.298$, $p = 0.010$), compared to 2011 (7.0 ± 22.1 birds km^{-2}) and 2012 (5.4 ± 12.0 birds km^{-2}). Shearwater densities were higher in 2010 as well (17.3 ± 40.9 birds km^{-2}), but not significantly different than any other year (overall mean: 10.9 ± 32.7 birds km^{-2}; $H = 1.015$, $p = 0.602$). While murres and shearwaters were observed on all transects, average densities of murres were highest on the Columbia River transect (13.9 ± 27.4 birds km^{-2}), near the nesting colony closest to the river mouth (Cape Meares transect: 34.6 ± 106.3 birds km^{-2}), and near the Yaquina Head, OR nesting colony (Newport Hydrographic transect: 20.5 ± 36.8 birds km^{-2}). Average densities of shearwaters were highest on transects north of the river mouth including Willapa Bay (19.8 ± 42.2 birds km^{-2}), Grays Harbor (25.5 ± 54.2 birds km^{-2}), and Queets River (15.8 ± 43.3 birds km^{-2}).

Catch composition by number of prey fish caught in surface trawls included 79% northern anchovy, 16% other alternative prey species, and 5% juvenile salmon. Frequency of occurrence (FO) of yearling Chinook salmon (62.5%) and juvenile coho salmon (52.5%) were the highest of all prey species, but average catch was low for yearling Chinook salmon (2.1 ± 2.9 fish km^{-1}) and coho (4.5 ± 11.2 fish km^{-1}) relative to alternative prey catches (**Table 2.3**). Average FO of the top six alternative prey species was low (12.7%), but mean catch was higher and more variable than any juvenile salmon species (129.6 ± 248.9 fish km^{-1}). Juvenile salmon catch did not vary significantly among years ($H = 5.917$, $p = 0.052$) or between May and June surveys within the same year ($U = 4426.5$, $p = 0.458$). Juvenile salmon abundance was highest on transects adjacent to, or north of, the river mouth (Columbia River, Willapa Bay, Grays Harbor), and lowest on transects in the south of the survey area. Alternative prey abundance

measured by 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 $m^3 s^{-1}$) in 2010 (9,831 $m^3 s^{-1}$), but significantly greater than the average ($H = 149.8$, $p < 0.001$) in 2011 (15,636 $m^3 s^{-1}$) and in 2012 (11,336 $m^3 s^{-1}$; **Figure 2.2**). In May 2010, average river discharge (8,664 $m^3 s^{-1}$), estimated plume volume (10.8 km^3), and surface area (1,877 km^2) were lowest, whereas estimated plume volume was highest in May 2011 (51.9 km^3), when average discharge was highest (16,277 $m^3 s^{-1}$). Highest surface area (8,738 km^2) occurred in June 2011, when discharge was second highest (14,992 $m^3 s^{-1}$). 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 murres, shearwaters, and all prey fish (**Figure 2.3**). Overall mean densities of murres and shearwaters were higher inside plume waters (murres: 16.1 ± 21.0 birds km^{-2}; shearwaters: 16.6 ± 16.7 birds km^{-2}) compared to mean densities in non-plume waters (murres: 9.8 ± 8.7 birds km^{-2}; shearwaters: 10.4 ± 6.0 birds km^{-2}). Differences between plume and non-plume density distributions were detected for murres ($U = 2069.5$, $p = 0.002$), but not for shearwaters ($U =$

2794.5, p = 0.421). Similarly, mean densities of all prey fish were higher inside the plume (alternative prey fish: 284.4 ± 613.2 fish trawl^{-1}; juvenile salmon: 6.9 ± 7.6 fish trawl^{-1}; acoustic prey: 380.7 ± 408.2 m^2 nmi $^{-2}$) than outside the plume (alternative prey fish: 74.3 ± 82.8 fish trawl^{-1}; juvenile salmon: 4.9 ± 3.9 fish trawl^{-1}; acoustic prey: 192.9 ± 121.1 m^2 nmi $^{-2}$). However, there was no statistically significant differences between plume and non-plume prey distributions (Mann-Whitney U tests; $p > 0.05$).

The density of murres and shearwaters occupying plume waters declined with plume surface area, although the pattern was significant only for murres ($F = 13.6$, $p = 0.021$, $R^2 = 0.72$; **Figure 2.4**a) and not shearwaters ($F = 5.0$, $p = 0.090$, $R^2 = 0.44$; **Figure 2.4**b). The density of forage fish and juvenile salmon caught in surface trawls, and acoustically detected prey, did not show a relationship to plume volume ($p > 0.05$, $R^2 < 0.20$; **Figure 2.4**c,d). Highest bird densities (murres: 74.2 birds km^{-2}, shearwaters: 68.1 birds km^{-2}) in the plume were observed during the May 2010 survey, when plume surface area and volume were lowest. Lowest densities of murres (3.9 birds km^{-2}) in the plume were observed in the May 2012 survey, when surface area was relatively high (6,219 km^2). Lowest densities of shearwaters (7.3 birds km^{-2}) were observed in the June 2011 survey, when plume area was highest (8,738 km^2), and no shearwaters were observed in the plume during the May 2011 survey, when plume area was second highest.

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

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 murres 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 (**Figure 2.5**). 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 (**Figure 2.5**). 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 (**Figure 2.5**). 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 murres 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 2.4**). Highest GIC values occurred in May 2010 (mean: 0.85 ± 0.16), including multiple species of juvenile salmon and forage fish. Average GIC values were slightly higher for murres in May (0.67 ± 0.24) compared to June (0.57 ± 0.27). However, GIC values between anchovy, herring, and murres were typically greater in June. In comparison, GIC values between shearwaters and prey ranged between 0.10 and 0.99, and at least three GIC values were ≥0.888 on every survey, with the exception of May 2012. GIC values were highest between shearwaters and prey including juvenile coho and Chinook salmon, market squid, and surf smelt (*Hypomesus pretiosus*). GIC values were highest in June 2010 (mean: 0.84 ± 0.17), followed by May 2010 (mean: 0.79 ± 0.22). GIC values between shearwaters and coho and yearling Chinook salmon were high in nearly all surveys, whereas GIC values were only ≥0.888 in June for subyearling Chinook salmon (**Table 2.4**).

Murre and shearwater densities throughout the survey region were related to both environmental and biological variables (**Table 2.6**). No candidate model with only biological or environmental variables performed better than models with a combination of covariates. The final model explaining murre density throughout the survey area (Model 1) demonstrated that increases in murre densities were related to decreases in latitude, distance from shore, water clarity, and acoustic backscatter, and increasing densities of other seabirds (i.e., local enhancement; **Table 2.6**). The final model explaining shearwater density throughout the survey area (Model 2) indicated that increases in shearwater densities were related to decreases in water clarity and acoustic backscatter, and an increase in the density of other seabirds. Alternative prey densities (Model 3) were related to decreases in water clarity and zooplankton density. Similarly,

juvenile salmon densities (Model 4) were related to decreases in water clarity, zooplankton density, and temperature. Murre densities in the plume (Model 5) were related to 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.

2.4 DISCUSSION

This chapter demonstrates 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 & 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 (Orians & 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 & Hunt 1996, Hatch et al. 2000a, Davoren et al. 2003a). 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. 2003b, 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 the 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, I 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 mures. 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 & 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 the 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 & Scott 1975, Varoujean & 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). A shift in anchovy density distributions was observed between May and June surveys, with increased densities and more southerly distributions in June, which may increase availability to murres foraging in central plume waters. While estimates of collocation between murres 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 infleunce 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 murres in May, and with shearwaters only in June after the salmon 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 refuge (Quinn 2005). These results suggest that elevated predation mortality may also occur in river plumes. Only 1–4% of smolts entering the ocean are estimated to spawn as adults (Bradford 1995, Coronado & Hilborn 1998), with the majority of this mortality occurring within weeks to months of entry into marine waters (Parker 1968, Beamish & Mahnken 2001). The relationship between increasing plume volume and salmon survival documented by Miller et al. (2013) may be partially explained by the decline in seabird densities that were documented with increasing plume size. Although Emmett et al. (2004) found that higher river flows resulted in increased numbers of juvenile salmon in plume waters, a larger plume may reduce smolt predation by increasing the total search area for shearwaters and murres foraging in the plume. Avian predation of smolts in the lower Columbia River estuary by Caspian terns (*Hydroprogne caspia*) and double-crested cormorants (*Phalacrocorax auritus*) is estimated at between 3 and 21 million smolts per year (Collis et al. 2001, Evans et al. 2012). Given that there is at least an order of magnitude more murres (~131,000; Speich & Wahl 1989, Suryan et al. 2012) and shearwaters (~2.2 million; Wiens & Scott 1975, Adams et al. 2012) than terns (12,500) and cormorants (27,000; Roby et al. 2015), and that murres and shearwaters consume salmon in similar proportions to terns and cormorants (Matthews 1983, Varoujean & Matthews 1983, J.E. Zamon, NOAA Fisheries, Hammond, Oregon, unpublished data), juvenile salmonid mortality by seabirds is certainly higher than currently estimated. To definitively address the impact of seabird predation on salmonids associated with the Columbia River plume and to estimate avian predation rates, data on smolt and alternative prey species composition, depth distribution,

abundance, and availability, concurrent with seabird diet samples over a range of plume conditions are needed.

Freshwater inputs to coastal ecosystems occur across land-sea interfaces around the world (Dai & 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 & 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 & Lettenmaier 1999, Payne et al. 2004, Palmer et al. 2008). The lowest flows observed during the 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). These 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.

2.5 TABLES

Table 2.1 – Summary of survey effort including year, month, fishing vessel, and date range, acoustic data collection settings, sampling effort, and mean river flow and plume volume during each survey.

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	EK60	1493.89	0.008047	57	55	275.5	11.0	11.3
2011	May	Frosti	5/21 - 5/27	EK60	1480.49	0.008302	50	48	223.1	16.3	51.9
	June	Frosti	6/20 - 6/27	EK60	1480.49	0.008302	57	56	272.7	15.0	38.7
2012	May	Miss Sue	5/30 - 6/3	ES60	1482.94	0.009835	45	32	145.8	10.2	33.1
	June	Frosti	6/21 - 6/28	EK60	1479.80	0.009101	53	50	262.1	12.4	16.0

[a]line transect survey effort only; excludes trawl distances

Table 2.2 – Summary of sitting and/or feeding seabird species observed on line transect surveys in May and June 2010-2012, including number of individual birds observed, percent of total, and percent frequency of occurrence.

					2010		2011		2012	
Common Name	**Scientific Name**	**Total**	**% of Total**	**% FO**	**May**	**June**	**May**	**June**	**May**	**June**
Sooty shearwater	*Ardenna grisea*	5181	50.6	100.0	606	3108	449	353	282	383
Common murre	*Uria aalge*	3526	34.5	100.0	629	1632	267	441	255	302
Pink-footed shearwater	*Ardenna creatopus*	815	7.9	100.0	16	242	15	324	3	215
Dark shearwater (unid.)	*Ardenna* spp.	189	1.9	50.0	87	93	-	-	-	9
Rhinoceros auklet	*Cerorhinca monocerata*	141	1.4	100.0	12	63	52	8	4	2
Black-footed albatross	*Phoebastria nigripes*	77	0.8	66.7	-	14	-	61	1	1
Phalarope (unid.)	*Phalaropus* spp.	73	0.7	16.7	-	-	73	-	-	-
Cassin's auklet	*Ptychoramphus aleuticus*	51	0.5	83.3	5	-	15	2	6	23
Western x glaucous-winged gull	*Larus occidentalis x glaucescens*	47	0.5	83.3	1	35	1	5	-	5
Gull (unid.)	*Larus* spp.	37	0.4	83.3	12	3	18	3	1	-
Pacific loon	*Gavia pacifica*	23	0.2	66.7	5	2	12	4	-	-
Ancient murrelet	*Synthliboramphus antiquus*	10	0.1	50.0	3	-	4	-	3	-
Northern fulmar	*Fulmarus glacialis*	10	0.1	50.0	-	3	1	6	-	-
Marbled murrelet	*Brachyramphus marmoratus*	8	0.1	50.0	-	4	-	2	-	2
Alcid (unid.)	Alcidae	7	0.1	33.3	1	-	6	-	-	-
Red-necked phalarope	*Phalaropus lobatus*	6	0.1	16.7	6	-	-	-	-	-
Immature gull (unid.)	*Larus* spp.	6	0.1	50.0	1	-	3	2	-	-
Double-crested cormorant	*Phalacrocorax auritus*	5	0.1	66.7	-	1	1	2	-	1
Western gull	*Larus occidentalis*	4	0.04	16.7	-	-	-	-	-	4
Brown pelican	*Pelecanus occidentalis*	3	0.03	16.7	-	-	-	-	-	3
Tufted puffin	*Fratercula cirrhata*	3	0.03	33.3	-	1	2	-	-	-
Scoter (unid.)	*Melanitta* spp.	3	0.03	16.7	-	-	3	-	-	-

Pelagic cormorant	*Phalacrocorax pelagicus*	2	0.02	33.3	-	1	-	1	-	-
Cormorant (unid.)	*Phalacrocorax* spp.	2	0.02	16.7	-	2	-	-	-	-
Brandt's cormorant	*Phalacrocorax penicillatus*	1	0.01	16.7	-	-	-	-	1	-
Common loon	*Gavia immer*	1	0.01	16.7	-	-	1	-	-	-
Glaucous-winged gull	*Larus glaucescens*	1	0.01	16.7	-	1	-	-	-	-
Red-throated loon	*Gavia stellata*	1	0.01	16.7	-	-	1	-	-	-
Ring-billed gull	*Larus delawarensis*	1	0.01	16.7	-	-	-	1	-	-
South Polar skua	*Catharacta maccormicki*	1	0.01	16.7	-	-	-	1	-	-
Western grebe	*Aechmophorus occidentalis*	1	0.01	16.7	-	-	1	-	-	-
Total		**10236**	**100.0**		**1384**	**5205**	**925**	**1216**	**556**	**950**

Table 2.3 – Summary of organisms collected in surface trawl surveys in May and June 2010–2012, including category used for data analyses, catch per unit effort (CPUE), percent frequency of occurrence (FO) and size range observed. For Chinook salmon, size range of fish caught in May (M) and June (J) are shown separately.

Category	Common name	Scientific name	CPUE	% FO	Size range (mm)
Juvenile Salmon Prey	Coho salmon	*Oncorhynchus kisutch*	4.5	52.5	97-250
	Chinook salmon (subyearling)	*Oncorhynchus tshawytscha*	3.0	24.6	82-120 (M); 77-140 (J)
	Chinook salmon (yearling)	*Oncorhynchus tshawytscha*	2.1	62.5	121-250 (M); 141-250 (J)
	Chum salmon	*Oncorhynchus keta*	1.8	21.8	66-250
	Sockeye salmon	*Oncorhynchus nerka*	1.7	22.1	95-250
	Steelhead	*Oncorhynchus mykiss*	0.4	9.6	165-250
	Cutthroat trout	*Oncorhynchus clarkii*	0.3	1.1	213-250
Alternative Prey	Northern anchovy	*Engraulis mordax*	636.9	14.3	32-170
	Pacific sardine	*Sardinops sagax*	50.4	13.2	96-250
	Surf smelt	*Hypomesus pretiosus*	37.2	8.6	72-186
	California market squid	*Doryteuthis opalescens*	22.0	24.6	15-184
	Whitebait smelt	*Allosmerus elongatus*	18.3	4.3	70-127
	Pacific herring	*Clupea pallasii*	13.0	12.1	55-240
	Sablefish (juv.)	*Anoplopoma fimbria*	11.8	2.5	63-218
	Widow rockfish	*Sebastes entomelas*	11.2	0.4	32-72
	Slender barracudina	*Lestidiops ringens*	5.5	2.1	59-106
	Yellowtail rockfish	*Sebastes flavidus*	4.5	0.4	15-68
	Darkblotched rockfish	*Sebastes crameri*	3.5	1.8	16-46
	Squid (unid.)	Teuthida	3.2	1.8	25-59
	Smelt (unid.)	*Osmeridae* spp.	2.9	9.3	28-98
	Rock greenling	*Hexagrammos lagocephalus*	1.5	1.2	54-61
	Pacific saury	*Cololabis saira*	1.5	0.7	88-250

	Pacific mackerel	*Scomber japonicus*	1.5	1.8	200-250
	Speckled sanddab	*Citharichthys stigmaeus*	1.2	1.4	28-42
	Pacific sand lance	*Ammodytes hexapterus*	1.0	3.9	34-61
	Shortbelly rockfish	*Sebastes jordani*	0.9	0.7	35-41
	Canary rockfish	*Sebastes pinniger*	0.9	1.1	21-35
	Rex sole	*Glyptocephalus zachirus*	0.8	0.4	62-68
	Lingcod	*Ophiodon elongatus*	0.5	0.7	43-58
	Sanddab (unid.)	*Citharichthys* spp.	0.3	0.4	45
	Pacific sandfish	*Trichodon trichodon*	0.3	0.4	212
	Pacific tomcod	*Microgadus proximus*	0.3	1.8	37-51
	American shad	*Alosa sapidissima*	0.3	0.7	179-205
	Medusafish	*Icichthys lockingtoni*	0.3	0.7	13-100
	Shiner perch	*Cymatogaster aggregata*	0.3	0.4	98
	Northern ronquil	*Ronquilus jordani*	0.3	0.4	30
	Threespine stickleback	*Gasterosteus aculeatus*	0.3	0.4	76
	Herring family	*Clupeidae*	0.3	0.4	30
Non-prey Biomass	Sea nettle	*Chrysaora fuscescens*	36.9	30.0	15-350
	Spiny dogfish	*Squalus acanthias*	32.7	8.2	50-1150
	Water jelly	*Aequorea spp.*	22.6	32.9	10-210
	Pacific hake	*Merluccius productus*	3.8	2.1	320-390
	Cross jelly	*Mitrocoma cellularia*	1.6	1.4	20-78
	Steelhead	*Oncorhynchus mykiss*	1.4	2.9	251-598
	Comb jellies	*Ctenophora*	0.9	34.3	-
	Black rockfish	*Sebastes melanops*	0.9	1.4	272-470
	Pink salmon	*Oncorhynchus gorbuscha*	0.8	0.7	465-489
	Chinook salmon	*Oncorhynchus tshawytscha*	0.8	52.1	251-870
	Pacific sardine (>250 mm)	*Sardinops sagax*	0.8	3.2	251-273
	Pacific saury (>250 mm)	*Cololabis saira*	0.7	0.7	251-305
	Starry flounder	*Platichthys stellatus*	0.5	4.6	230-560
	Eggyolk jelly	*Phacellophora camtschatica*	0.5	12.9	70-380
	Coho salmon	*Oncorhynchus kisutch*	0.5	38.2	251-712

Pacific staghorn sculpin	*Leptocottus armatus*	0.5	2.1	170-265
Jack mackerel	*Trachurus symmetricus*	0.5	1.8	523-690
Moon jelly	*Aurelia spp.*	0.5	8.28	65-355
Wolf-eel	*Anarrhichthys ocellatus*	0.4	12.5	260-605
Blue shark	*Prionace glauca*	0.4	1.8	520-1800
Lion's mane jelly	*Cyanea capillata*	0.4	1.4	120-300
Soupfin shark	*Galeorhinus zyopterus*	0.4	2.9	780-1758
English sole	*Parophrys vetulus*	0.4	0.4	300
Chum salmon	*Oncorhynchus keta*	0.3	3.9	251-695
Cutthroat trout	*Oncorhynchus clarkii*	0.3	1.1	251-400
Salmon shark	*Lamna ditropis*	0.3	0.4	1950
Pacific lamprey	*Lampetra tridentata*	0.3	0.7	308-720
Pacific mackerel (>250 mm)	*Scomber japonicus*	0.3	0.7	251-282
Butter sole	*Isopsetta isolepis*	0.3	0.4	25
River lamprey	*Lampetra ayresii*	0.3	2.1	258-330
Yellowtail rockfish	*Sebastes flavidus*	0.3	0.4	415
Widow rockfish	*Sebastes entomelas*	0.3	0.4	386
Sockeye salmon	*Oncorhynchus nerka*	0.3	0.7	251-465
Jellyfish (unid.)	*Scyphozoa spp.*	0.3	0.7	155
Penicillate jelly	*Polyorchis penicillatus*	0.3	0.4	30-70
Sea butterfly	*Corolla spectabilis*	0.3	3.2	-
Salp (unid.)	*Salpidae*	0.3	0.7	-
Beroe (unid.)	*Beroe spp.*	0.3	0.7	-
Carinaria japonica	*Carinaria japonica*	0.3	4.6	-
Hormiphora cucumis	*Hormiphora cucumis*	0.3	26.8	-
Umbrella jelly	*Eutonina indicans*	0.3	0.4	-
Sea gooseberry	*Pleurobrachia* spp.	0.3	7.1	-
Clio pyramidata	*Clio pyramidata*	0.3	0.4	-
Sea angel	*Clione limacina*	0.3	0.4	-

Table 2.4 – Global index of collocation values between common murres (*Uria aalge*) and sooty shearwaters (*Ardenna grisea*) and the three most frequently caught juvenile salmon (*Oncorhynchus* spp.), and the six most abundant alternative prey fish species; darker shading indicates higher value of GIC. Values greater than the 75th percentile (0.888) were considered indicative of a relationship between predator and prey.

		2010		2011		2012	
Predator	**Prey Species**	**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 2.5 – Variables used in generalized linear models, including type and measurement, abbreviation used to describe covariates in the final models, the models in which each variable was included, and the median, range, mean and standard deviation of each measurement.

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)	PlArea	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

Table 2.6 – Generalized linear model results for predator (murre and shearwater) and prey (alternative prey and juvenile salmon) densities throughout the survey region, and predators within the river plume. Final models presented include slope and parameter estimates for significant covariates and model weight.

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

2.6 FIGURES

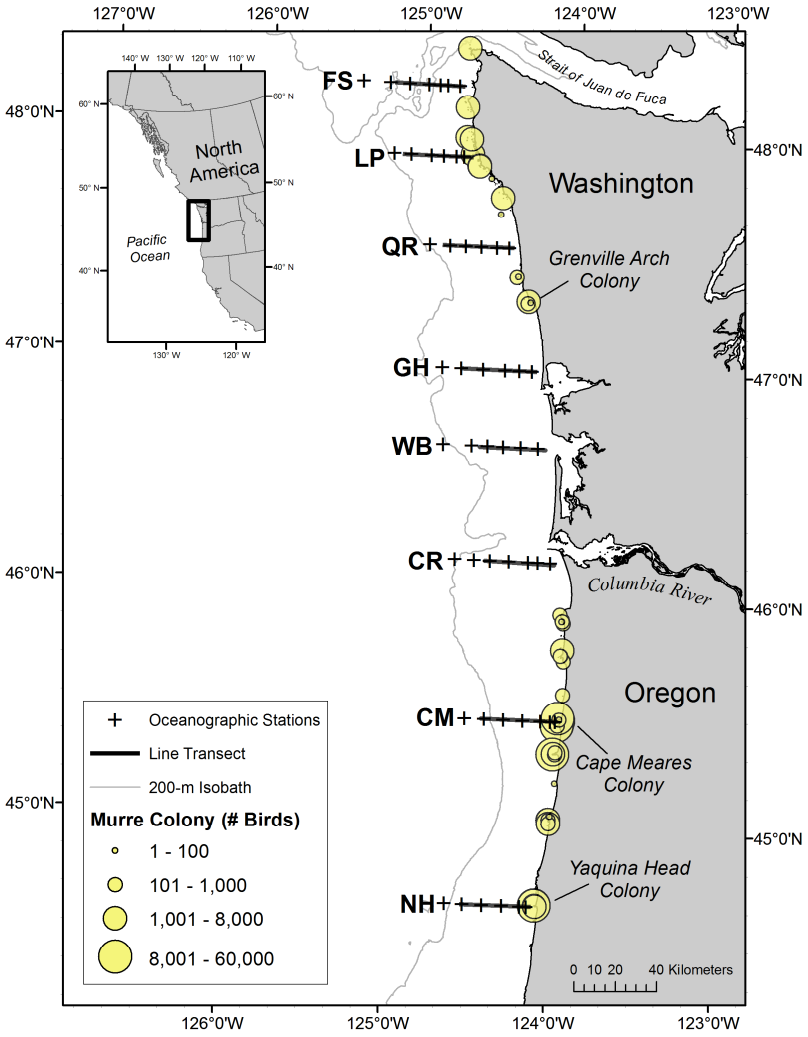

Figure 2.1 – Map of study area, including line transects and oceanographic sampling stations along the Oregon and Washington coasts. Each transect line is named for a geographic feature in proximity to the inshore end of the line as follows: FS = Father and Son, LP = La Push, QR = Queets River, GH = Grays Harbor, WB = Willapa Bay, CR = Columbia River, CM = Cape Meares, and NH = Newport Hydrographic. Common murre (*Uria aalge*) 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.

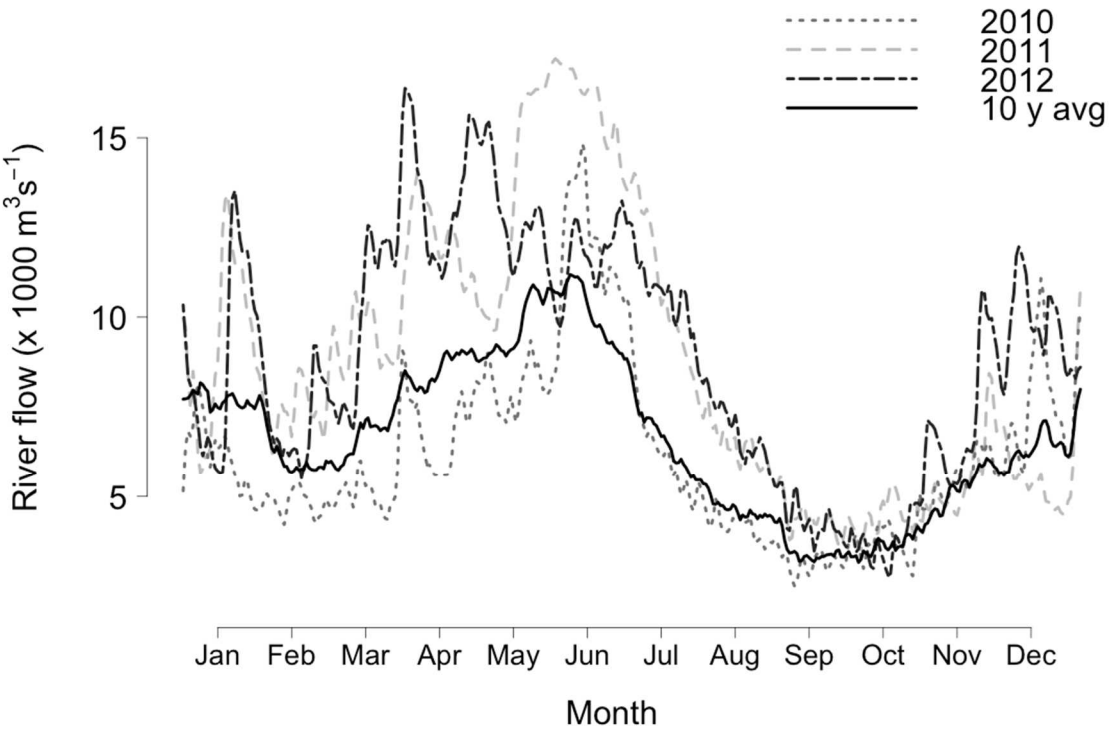

Figure 2.2 – Average daily Columbia River flow in 2010, 2011, 2012, and 10 y average (2002–2012) measured at U.S. Geological Survey surface water station 14246900.

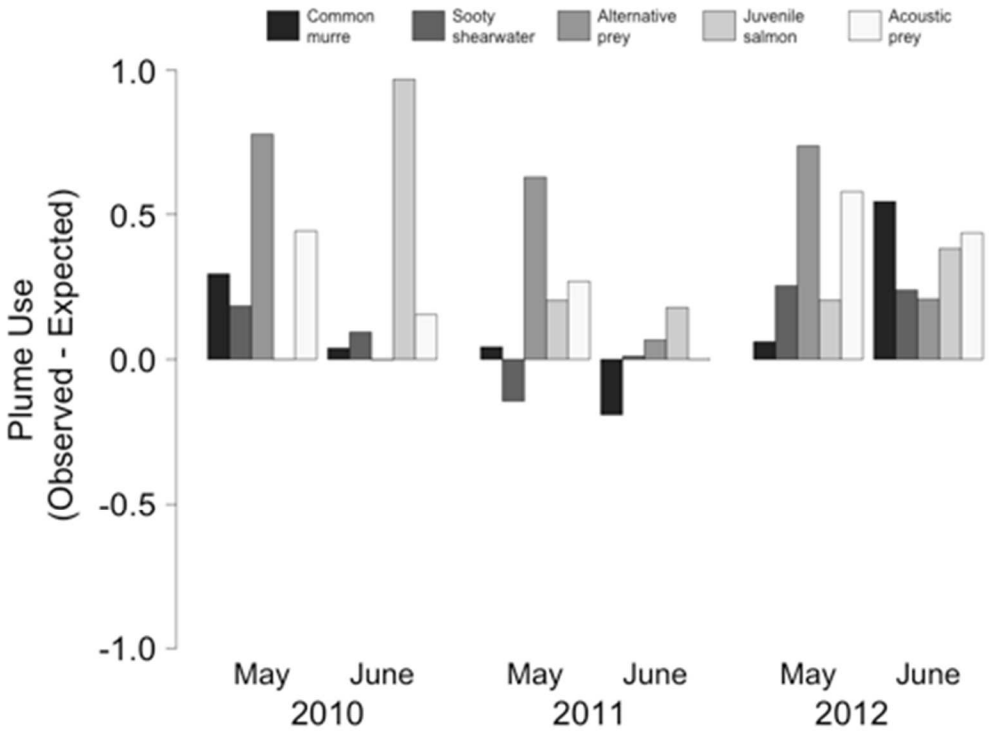

Figure 2.3 – Area use of the Columbia River plume by seabirds and prey in each survey. Use was calculated by subtracting the observed proportions of seabirds and prey in the plume from expected proportions, defined as the proportion of plume area in the total calculated survey area during each cruise. 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.

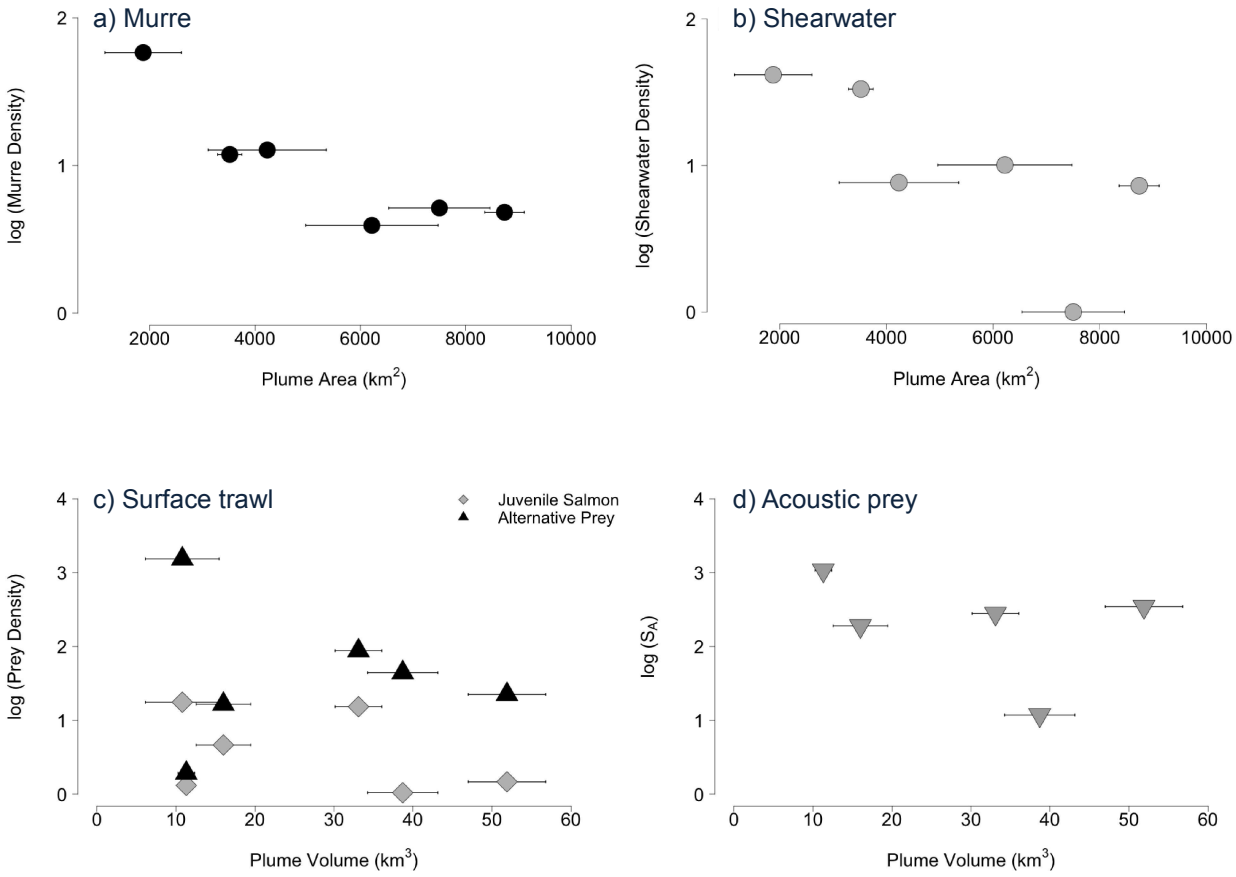

Figure 2.4 – The relationship between mean plume surface area or volume (±SE) and density of a) common murres (*Uria aalge*), b) sooty shearwaters (*Ardenna grisea*), c) prey fish densities measured by surface trawl, and d) acoustic backscatter in the plume.

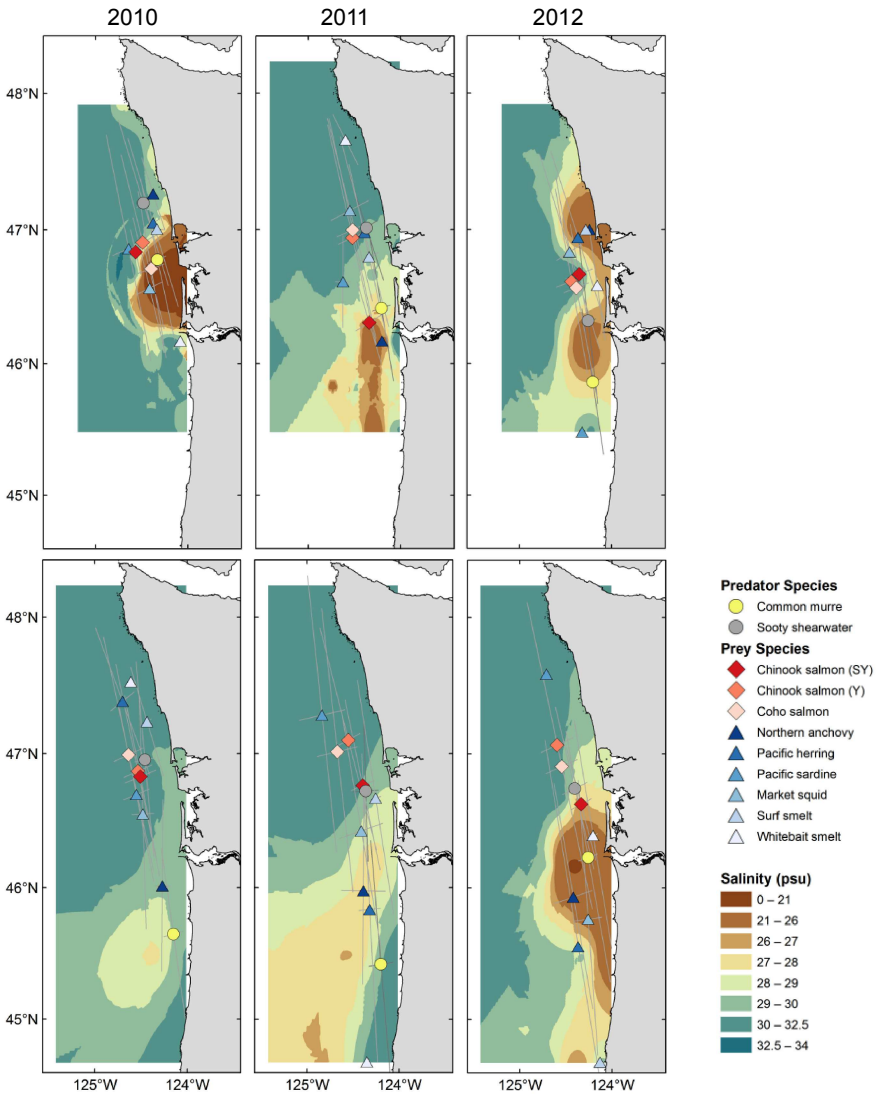

Figure 2.5 – Distribution of the interpolated plume surface area, centers of gravity, and axes of inertia of predators and prey in 2010, 2011, and 2012 in May (top panels) and June (bottom panels).

Chapter 3. SELECTIVE OCCUPANCY OF A PERSISTENT YET VARIABLE COASTAL RIVER PLUME BY TWO SEABIRD SPECIES[2]

3.1 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

[2] This work has been published:
Phillips EM, Horne JK, Adams J, Zamon JE (2018) Selective occupancy of a persistent yet variable coastal river plume by two seabird species. Mar Ecol Prog Ser 594:245–261

features at finer temporal scales (Scales et al. 2017, Mannocci 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 (**Figure 3.1**; 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 (**Figure 3.1**; 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 pulse of low-salinity river discharge is generated with each tidal cycle. In addition to geographic variability, plume surface area fluctuates over two orders of magnitude, from ~150 km^2 during periods of low river discharge (e.g., late summer) to ~24,000 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 murres (*Uria aalge*) (Zamon et al. 2014) that consume anchovy, juvenile Pacific tomcod (*Microgadus proximus*), smelts (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). Chapter 2 of this dissertation subsequently demonstrated that shearwaters near the CRP were consistently ~100 km north of the geographic center of the plume near high densities of

forage fishes, which contrasted to murre distributions that were within ~20 km of the plume center. Chapter 2 also demonstrated 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 murres 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). Murres may rely on memory to re-locate predictable foraging areas within the 100 km radius of their colony (Davoren et al. 2003b, Regular et al. 2013), including low salinity CRP waters (Chapter 2). Therefore, I predicted that shearwaters and murres would contrast in their responses to the CRP at hourly, daily, monthly, and seasonal time periods. Specifically, I hypothesized that shearwaters would track the plume edge and occur in mixed salinity waters

near productive plume boundaries. Murres 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. I used satellite telemetry collected during spring and summer in 2008 and 2009 from sooty shearwaters and in 2012 and 2013 from common murres 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. Species-specific distributions were also characterized and compared to determine if shearwaters tracked different areas of the plume than murres.

3.2 METHODS

3.2.1 *Data acquisition and processing*

3.2.1.1 Defining the Columbia River plume using surface salinity

To assess the size (i.e., surface area) and location of the CRP, I 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; http://www.stccmop.org/datamart/virtualcolumbiariver). 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 km^2 (**Figure 3.1**). 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, CMOP, pers. comm.).

To evaluate relationships among seabirds and the range of salinities within and surrounding the CRP, I 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 I calculated the ratio of daily surface area to perimeter. I 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 2016).

3.2.1.2 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 murres in 2012 (n = 12) and 2013 (n = 14; Telonics TAV-2617 PTTs). All murres and some shearwaters (n = 7 in 2008, n = 5 in 2009) were captured and released near the mouth of the Columbia River, Washington (**Table 3.1**). Data from 18 (n = 6 in 2008, n = 12 in 2009) additional shearwaters 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 3.1**). 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 (1100–2100 PST) for shearwaters, and every 60 s for 4 h in the morning (0800–1200 PST) and 4 h in the evening (1400–1800 PST) for murres. 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, data from tags that did not transmit for more than two weeks, had intermittent transmissions (e.g., 5 d gap in transmissions), or showed

evidence of halted movement were removed (i.e., when median daily movements fell below the 95% confidence interval of average movement of birds for the sampling year; S. Loredo, Oregon State University, 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 ms^{-1} for shearwaters, and 24.3 ms^{-1} for murres 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 three standard deviations in a 5 ms^{-1} tailwind (cf. Spear & Ainley 1997). To analyze spatial use in areas influenced by the CRP, seabird locations were limited 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 return. The first 5 d of tracking data for birds tagged near the mouth of the Columbia River were also excluded to avoid using positions that may have been affected by capture.

3.2.2 *Data analysis*

3.2.2.1 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). I 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 paragraph) and our estimated nominal ARGOS location accuracy (3 km). To calculate an overall 99UD raster for all birds tagged in each year, 99UDs were first calculated 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.

3.2.2.2 Occupancy of plume waters

To examine seabird use of the CRP at the finest spatio-temporal resolution possible, seabird location data were further limited 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 km^2 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 km^2. 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. Observed seabird occupancy of each water type was then compared to expected occupancy using chi-square analyses (Zar 1999). Species-specific occupancy of each water type was compared between years using Welch's t-test (Zar 1999).

Variability in occupancy by individual seabirds within each year was also examined by calculating coefficients of variation (CV). To determine if tracking duration (i.e., total number of locations obtained from each tagged seabird) influenced observed occupancy of the CRP, I compared plume waters with number of locations obtained from each individual seabird using Pearson correlations.

3.2.2.3 Seabird response to plume dynamics

To quantify seabird movements associated with CRP dynamics, multiple metrics were used. First, to evaluate spatial shifts of the CRP and seabirds through time, Pearson correlation coefficients were calculated 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, the Euclidean distance from each seabird location to the daily location of the plume center and plume boundary (i.e., 28 psu isohaline) was measured. I tested for differences between shearwater and murre distance measurements using Mann-Whitney tests (Zar 1999). To determine if murres or shearwaters exhibited greater variability in distances to the plume center or boundary, I 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, Spearman's correlation coefficients were calculated because distance measurements were not normally distributed (Zar 1999). I hypothesized that shearwater distances to the plume center would be similar to previous findings (~100 km; Chapter 2), 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, I expected that murre distances to the plume center would be less (~20 km; Chapter 2) 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 (**Figure 3.1**). Patterns of seabird distances to the plume center, boundary and plume occupancy were also compared 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 murres showed a threshold foraging response to the physical dynamics of the CRP. Unless otherwise stated, all statistics were analyzed using two-tailed distributions and an alpha of 0.05.

3.3 RESULTS

Locations for shearwaters were determined between late June to 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 murres 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 3.1**). After tabulating and filtering PTT location data, subsetting locations within 100 km of the model domain, and removing the first 5 d of transmissions, I 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 murres in 2012, and 4213 locations (301 ± 151 locations $bird^{-1}$) for murres in 2013 for analyses (**Table 3.1**).

3.3.1 *Spatial distributions*

Highest general use areas based on 99UDs for shearwaters and murres 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 (**Figure 3.2**). Shearwaters were distributed widely throughout the model domain (longitudinal extent: -123.47° to -127.80°W), 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 (**Figure 3.2**). 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 domain boundary (**Figure 3.2**). 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 (**Figure 3.2**). 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 (**Figure 3.2**), 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 before returning to the model domain.

3.3.2 *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 (**Figure 3.3**). 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 observed disproportionate plume occupancy was due to increased use of tidal, recirculating, and boundary waters (**Figure 3.3**). In 2008, the greatest difference in observed versus expected occupancy occurred in outer boundary waters ($\Delta_{obs-exp}$=15.3%). In 2009, the greatest difference in observed versus expected occupancy occurred in recirculating and inner boundary waters (combined $\Delta_{obs-exp}$=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 (**Figure 3.3**). 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 types, and the difference between observed and expected occupancy ($\Delta_{obs-exp}$) of these two 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 murres (average = 67.5%), use of plume waters varied with tagging location and by individual birds (**Figure 3.4**). 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 (**Figure 3.4**). 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%; $t_{19.2} = 3.22$, $p = 0.004$; **Figure 3.4**). Individual variability in plume occupancy among murres 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 murres ($r = -0.21$, $t_{24} = -1.11$, $p = 0.27$).

3.3.3 *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 murres 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 July (**Figure 3.5**). The distribution of mean latitudes through time among shearwaters and murres was comparable (**Figure 3.5**). 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 (**Figure 3.6**). 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 (**Figure 3.6**). 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.

Both shearwaters and murres occurred significantly closer to the plume boundary than the plume center (shearwaters: $U = 661960$, $p < 0.001$; murres: $U = 682820$, $p < 0.001$). Median distances of shearwaters to the plume boundary (50 km) were greater than distances of murres (15 km; $U = 479060$, $p < 0.001$). Median distances of shearwaters to the plume center (107 km)

were slightly less than distances of murres (115 km; U = 392470, 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 = 87254, 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 = 65316, p < 0.001). The median distance of murres to the plume center did not differ between 2012 (111 km) and 2013 (125 km; U = 83238, p = 0.051), whereas the median distance of murres to the plume boundary was less in 2012 (12 km) than in 2013 (20 km; U = 65788, 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 murres. Variability in distances to the plume center was similar for shearwaters (CV = 55%) and murres (CV = 54%). Distances of individual shearwaters to the plume boundary ranged from < 3 km to 263 km, and from < 3 km to 180 km for murres. Variability in distances to the plume boundary was high for shearwaters (CV = 91%) and murres (CV = 117%).

I 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 (ρ = 0.197, p < 0.001), but negative in 2009 (ρ = -0.123, p = 0.001). Distances of murres to the plume center were positively correlated with plume surface area in 2013 (ρ = 0.480, p < 0.001), but uncorrelated in 2012 (ρ = -0.024, p = 0.606). In contrast, relationships between surface area and distances of shearwaters and murres to the plume boundary showed remarkable similarity (**Figure 3.7**). Shearwater and murre distances to the plume boundary were negatively correlated with plume surface area in all years (2008: ρ = -0.381, p < 0.001, 2009: ρ = -0.396, p < 0.001, 2012: ρ = -0.162, p < 0.001, and 2013: ρ = -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 (**Figure 3.7**). 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 years. The threshold value ranged from surface areas of ~1500–4000 km^2. Mean distance of shearwaters to the plume boundary was 50.1 ± 40.6 km in 2008 before the surface area threshold (4252 km^2) 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 murres 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 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 murres to the plume boundary were low (23.4 ± 15.3 km), and comparable to distances of murres observed in 2013 after the surface area threshold was exceeded (**Figure 3.7**). Corresponding with the decline in seabird distances to the plume boundary, I 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 murres 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 murres in 2012 was consistently low (27.4 ± 2.8 psu).

3.4 DISCUSSION

By combining seabird telemetry data with a high-resolution model of sea surface salinity, this chapter demonstrated that shearwaters and murres selectively occupy and track Columbia River plume 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 murres, 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 murres, disproportionate use of recirculating and boundary waters closer to the coast was observed. Murres occupied a narrower nearshore area closer to the coast (especially in 2013), and disproportionately used recirculating and tidal waters. Telemetry also revealed that murres 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 the observation of disproportionate occupancy of plume waters by both shearwaters and murres, and movement towards plume boundary waters during periods of increased plume size (i.e., surface area), I suggest that seabirds actively target plume-enhanced production and biophysical coupling at plume edges. Greatest spatial use by both species was observed 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 (Chapter 2) and positively correlated with river discharge (Emmett et al. 2004, Kaltenberg et al. 2010).

Threshold responses were observed among seabirds to plume surface area, where seabird distances to the plume boundary declined significantly after thresholds between 1500–400 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 murres were located within 25–30 km of the plume boundary. This is consistent with the finding in Chapter 2 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 murres are highly mobile (Hatch et al. 2000a, Adams et al. 2012), rely on local enhancement (Davoren et al. 2003a), 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 observed 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. The 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 three of four years indicated that shearwaters and murres 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 four 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 murres 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 California Current Ecosystem (Shaffer et al. 2006, Adams et al. 2012). In contrast to my predictions, latitudinal movements of murres were also extensive along the coast, and were of similar range to shearwaters. Tagged murres were more closely associated with the plume boundary than the plume center, indicating that murres are just as capable of tracking and responding to changes in plume size and location as shearwaters.

The relatively high mobility of murres in this study indicated that either non-breeding birds were tagged or that tagging caused the birds to abandon colony attendance. There was no evidence of returns to or exits from breeding colonies by tagged murres, although utilization distributions indicated that some murres 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), I 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 murres (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. 2000a, b, Wilson & McMahon 2006), and there was some evidence of murre tag attachment and failure in 2012 and 2013. The cessation of movement by two birds in 2013 after 20 days of tag transmission was interpreted as bird mortality (S. Loredo, Oregon State University, pers. comm.).

Differences in occupancy of specific water types by shearwaters and murres may be related to spatial segregation resulting from different foraging capabilities, prey selectivity, or interspecific competition. I suggest that the disproportionate use of tidal and recirculating waters by murres 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. 2003b, 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 (Chapter 2). Tidal and recirculating waters may be more turbid, and murres 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 murres. Although prey habits of shearwaters and murres were not quantified in this study, there is no published evidence indicating that either species selectively consume 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 murres (~180 m; Piatt & Nettleship 1985). A range of prey species occupy depths that are accessible to these avian predators. Forage fish species, including northern anchovy, typically aggregate deeper in the water column (10–70 m) near plume boundaries (Kaltenberg et al. 2010), 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 two species. Without data on spatial distributions of shearwaters and murres during the same year, and corresponding prey fields and diets of both species, the potential for different foraging capabilities, prey selectivity, or interference competition cannot be resolved.

Relationships among seabirds and the CRP observed in this study appear to be relatively consistent between species and across years. Although shearwaters and murres were not tracked during the same years, these 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 ten-year-period between 2005 and 2015 (U.S. Geological Survey surface water station 14246900; http://www.cbr.washington.edu/dart), 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 (~1500 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%). The surface area threshold may have already been exceeded when tags were deployed in 2012, and I speculate that murres were able to locate and track plume boundaries nearshore, and they moved farther offshore to occupy the inside edge of the plume in relatively lower salinity waters. Even though the interannual comparisons provided insights on shearwater and murre relationships to the CRP, to fully understand species-specific responses of seabirds to river plume dynamics, comparative studies that incorporate telemetry data on both species during the same year are merited.

These results demonstrated that seabirds responded to a highly dynamic river plume, and 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. My approach that linked a hydrodynamic model with telemetry data may be applicable to other studies evaluating relationships between marine predators and ecosystems influenced by freshwater plumes.

3.5 TABLES

Table 3.1 – Summary of satellite telemetry data for sooty shearwaters (*Ardenna grisea*) in 2008 and 2009, and common murres (*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 murres in 2012 due to suboptimal weather conditions.

Species	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
		SBC	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
			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
			94572	890	U	9/28/09	10/23/09	25	282
			94574	860	U	8/12/09	10/23/09	72	698
		SBC	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
			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

*Start and End Dates are for time each individual was within the model domain

3.6 FIGURES

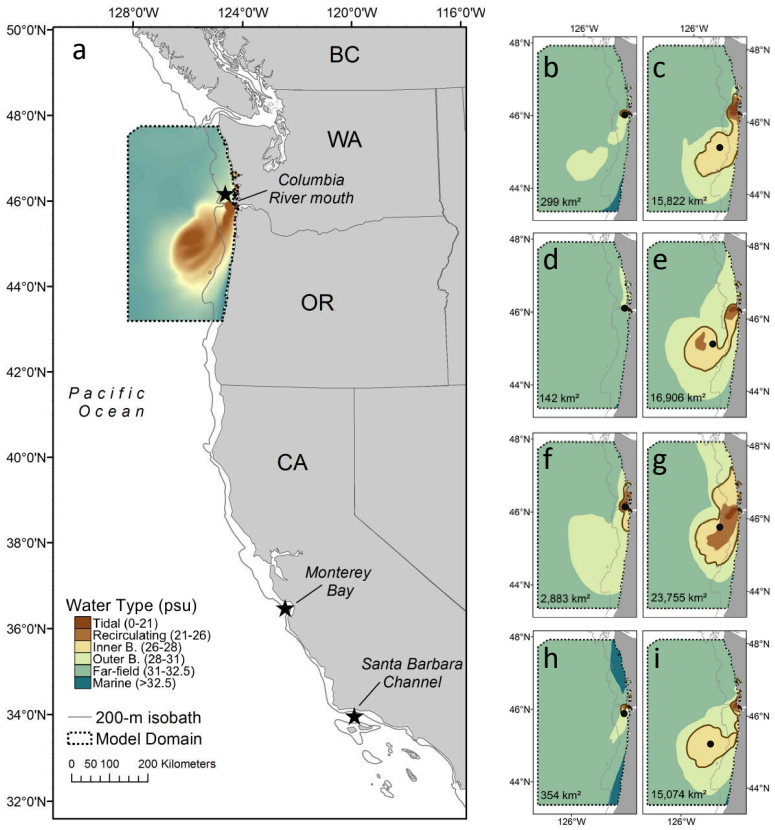

Figure 3.1 – Study site on US west coast showing the Columbia River plume hydrodynamic model domain and a) an example of the hydrodynamic model output for 20 June 2013. Black stars indicate approximate locations where seabirds were captured and tagged. Subset maps show the minimum (left) and maximum (right) 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.

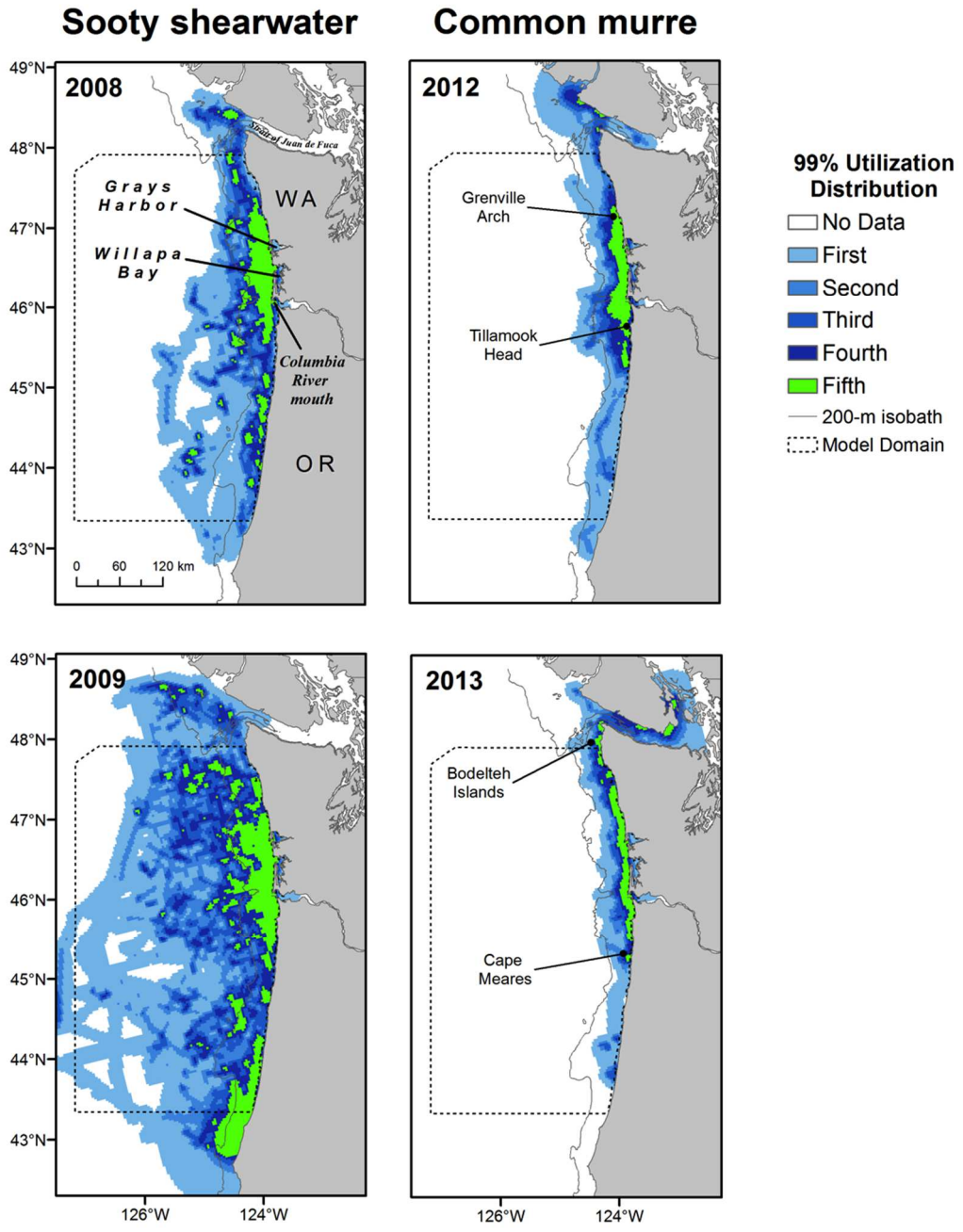

Figure 3.2 – Sooty shearwater (*Ardenna grisea*) and common murre (*Uria aalge*) 99% utilization distributions in the Columbia River plume model domain. Data are displayed by quintiles, with the fifth quintile showing highest use areas (80^{th}–100^{th} percentile).

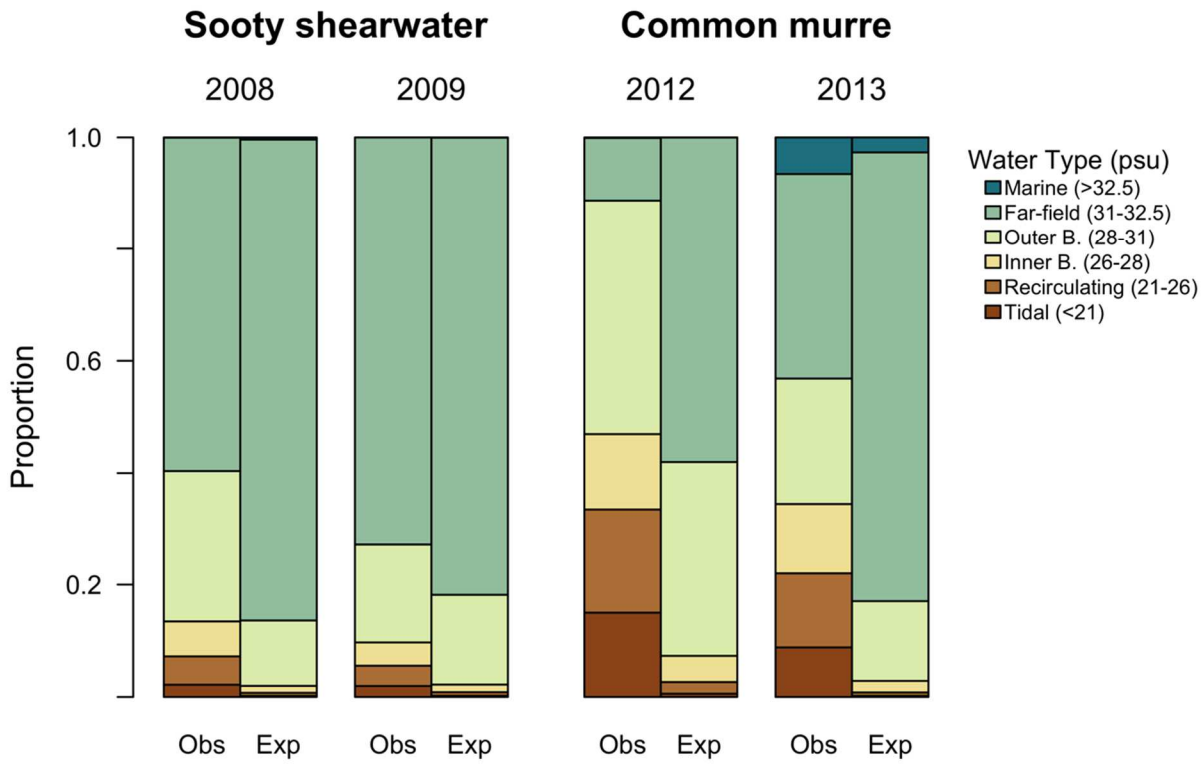

Figure 3.3 – Proportion of sooty shearwater (*Ardenna grisea*) and common murre (*Uria aalge*) observed occupancy of different water types in each year (Obs) compared to expected (Exp) availability of each water type from the hydrodynamic model output.

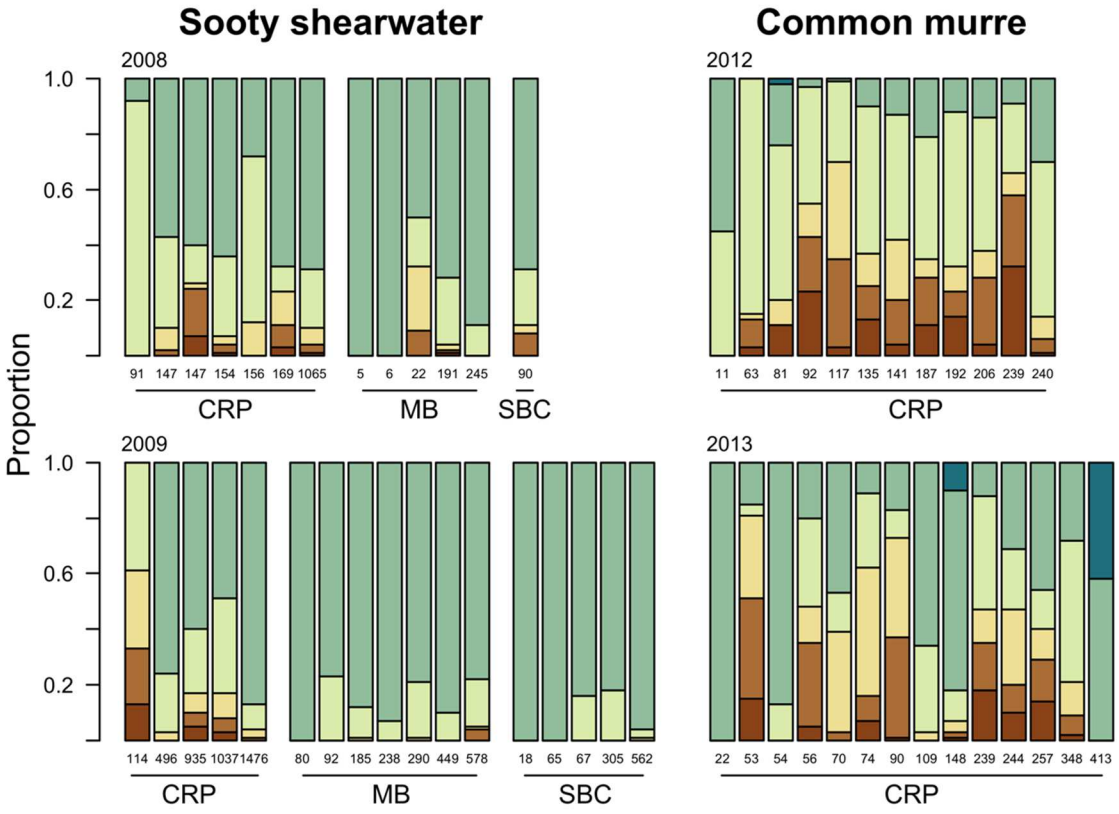

Figure 3.4 – Proportion of time individual seabirds occupied different water types during the time they were in the model domain. Each bar represents an individual bird. Capture locations are indicated on the x-axis (CRP: Columbia River plume; MB: Monterey Bay; SBC: Santa Barbara Channel). The number of locations used in each analysis is shown below each bar.

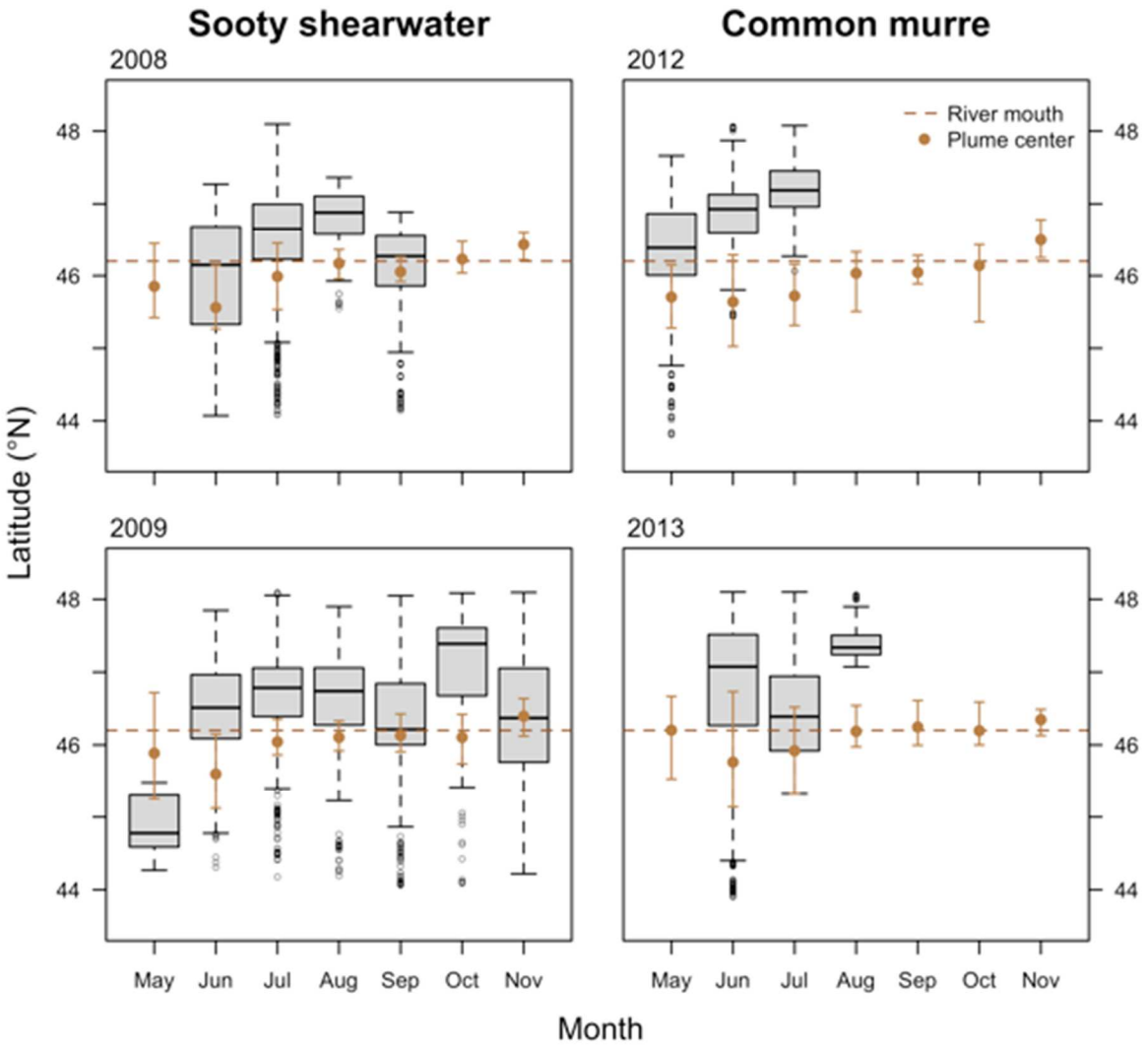

Figure 3.5 – Monthly latitudes of seabirds relative to the location of the mouth of the Columbia River. Dark line: median; box: interquartile range (IQR); error bars: max./min. within 1.5×IQR above/below IQR; black dots: outliers. Mean latitude of the plume center shown as brown points (± range).

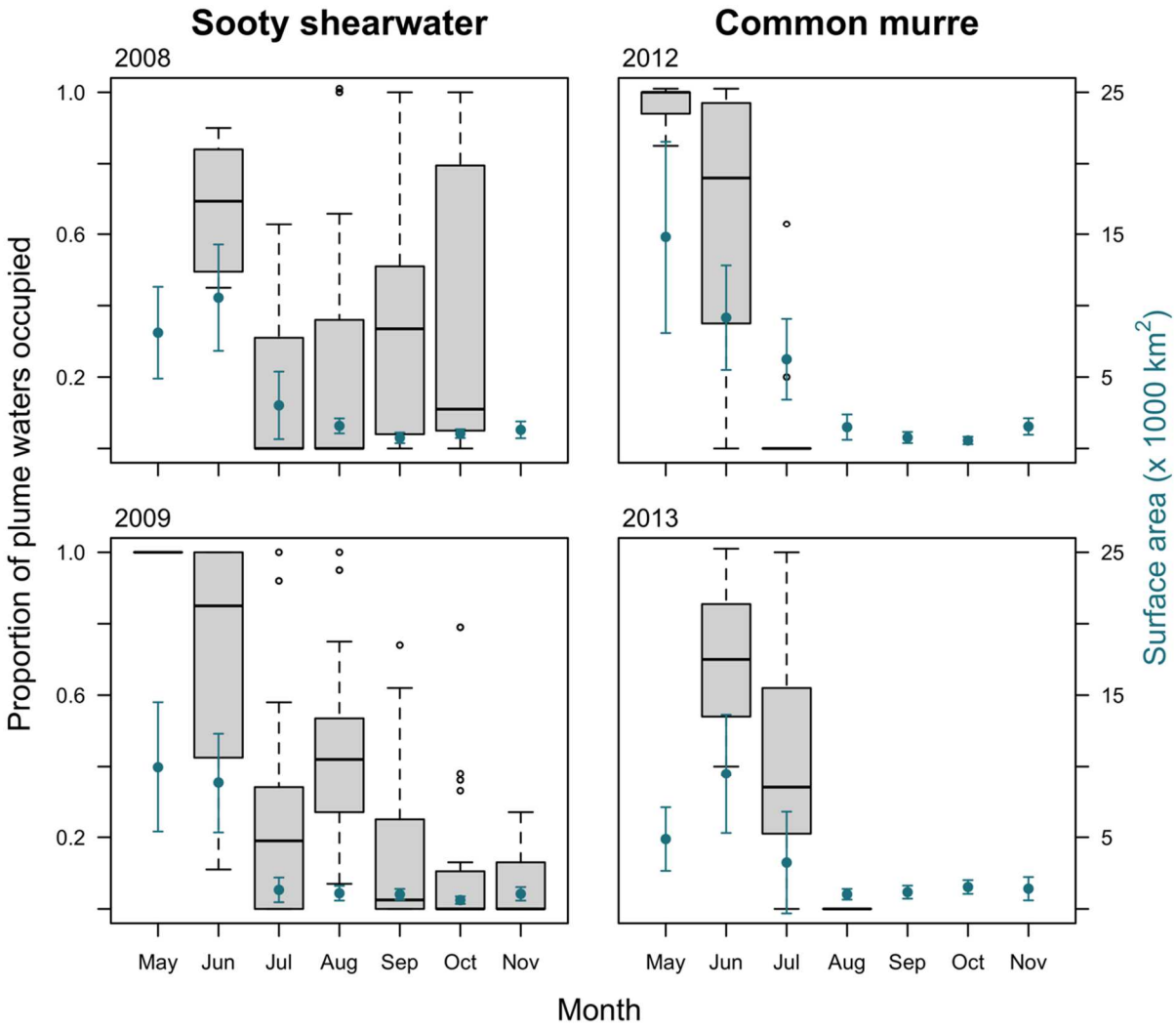

Figure 3.6 – Occupancy of plume waters (≤31 psu) by seabirds. Dark line: median; box: interquartile range; error bars: max./min. within 1.5×IQR above/below IQR; black dots: outliers. Mean plume surface areas (±SD) are shown as blue points.

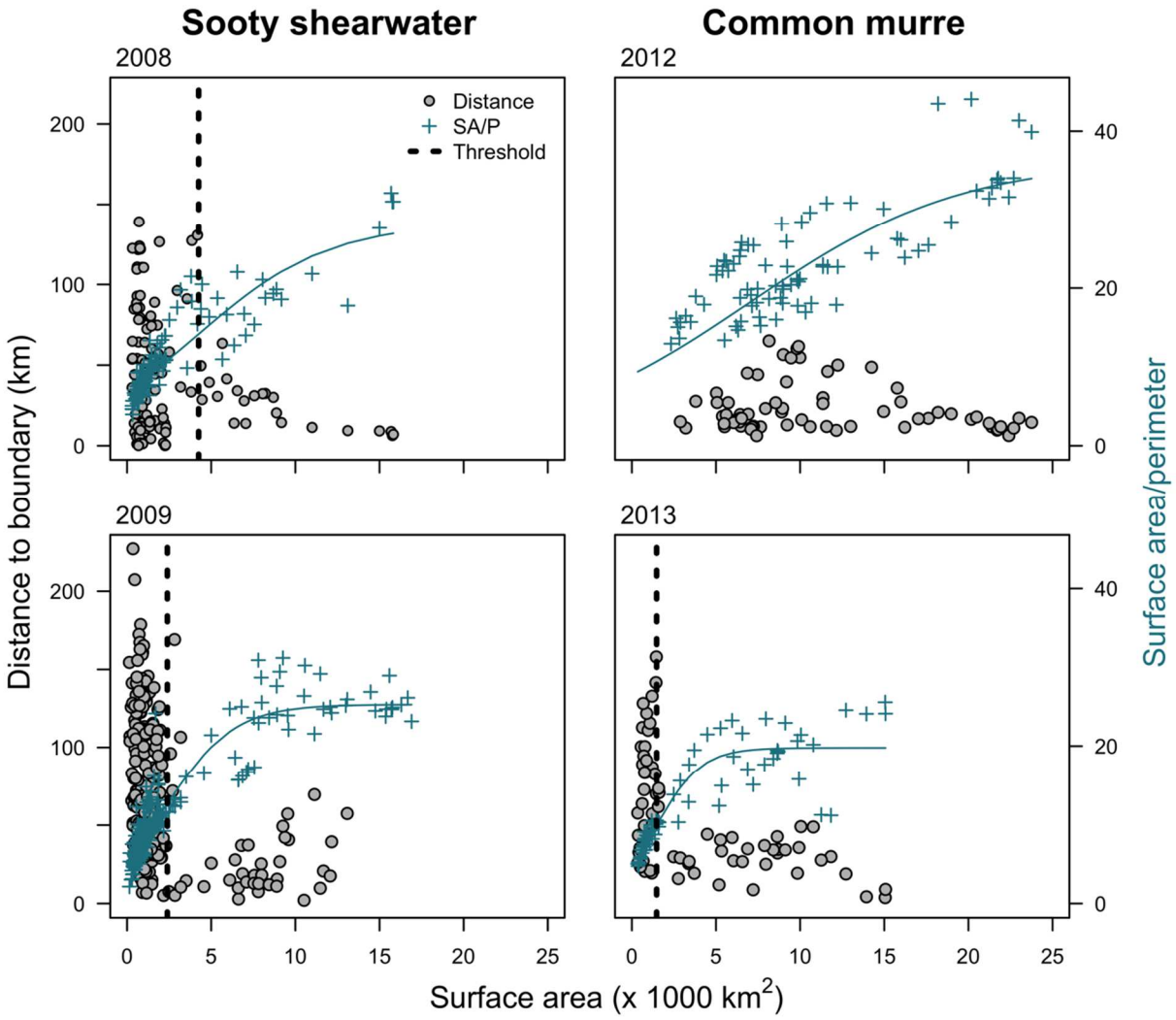

Figure 3.7 – Relationship between plume surface area and seabird distance to the plume boundary (gray dots), and plume surface area and the surface area to perimeter ratio (SA/P; plus signs). Solid blue lines are nonlinear least squares model fits, and dashed vertical line marks the inflection point (i.e. threshold) of the curve from the model fit. No inflection point was estimated in 2012.

Chapter 4. PLANES, BOATS, AND SATELLITE TAGS: COMPARING COMMON MURRE (*URIA AALGE*) DISTRIBUTIONS FROM EULERIAN AND LAGRANGIAN PERSPECTIVES IN THE NORTHERN CALIFORNIA CURRENT

4.1 INTRODUCTION

Distribution and abundance data of mobile species are useful for identifying important foraging, migration, and breeding habitats (MacArthur 1972, Elith & Leathwick 2009). Data can be collected using direct sightings during fixed-grid surveys (i.e., Eulerian sampling) or from locations recorded by animal-borne tracking devices (i.e., Lagrangian sampling; Rutz and Hays 2009, Tremblay et al. 2009). An Eulerian perspective has a long tradition in studies of species distributions, and is an important contributor to research on habitat associations and species interactions (Ainley et al. 2012). A Lagrangian perspective is increasingly used in species distribution studies as innovations in telemetry have accelerated the use of tracking devices (Hart & Hyrenbach 2009, Block et al. 2011).

An Eulerian study design samples at x-y coordinates in a fixed grid through time. Sample locations include predetermined quadrats, counts along transects, or stratified sampling stations. The primary objective of Eulerian sampling is to obtain unbiased information about animal distribution and abundance in a survey area. Observations of multiple species also enable estimates of community composition, diversity, and species interactions (Worm et al. 2003, Hyrenbach et al. 2007, Bennison & Jessopp 2015). In the ocean, Eulerian studies have quantified the distributions of mobile species including piscivorous fish and sharks (Au 1991, Worm et al.

2003, Carlisle et al. 2015), marine mammals (Croll et al. 2005, Bost et al. 2009), and seabirds (Ballance et al. 1997, Ainley et al. 2005). Ship-based transect surveys were an early and significant contributor to studies of pelagic seabird distributions (Wynne-Edwards 1935, Murphy 1936, Brown 1980), and continue to be an important component of at-sea research efforts (Ainley et al. 2009, 2012, Hunt et al. 2018). Ships can survey coastal and pelagic ecosystems along transects for relatively long (i.e., weeks to months) periods across hundreds to thousands of kilometers, and simultaneously sample *in situ* abiotic and biotic factors including temperature, chlorophyll concentration, and prey species, which allows for high-resolution examinations of seabird-habitat relationships (Ainley et al. 2012). However, ships are slow relative to seabird movements, and the flux of seabirds in or out of an area, as well as ship avoidance or attraction, may bias distribution and abundance estimates by convolving spatial patterns with the passage of time (Wahl & Heinemann 1979, van Franeker 1994). Aerial survey methods (e.g., airplanes, drones) can sample an area in a relatively short (i.e., hours to days) period and, because the movement of seabirds is slow relative to an aircraft, a synoptic estimate of species' distributions and abundances may be obtained (Briggs et al. 1985a, Buckland et al. 2001, Certain & Bretagnolle 2008). Aircraft can also survey areas inaccessible to ships (e.g., nearshore shallow habitats, ice fields), but may not be able to transit as far offshore (Henkel et al. 2007, Hodgson et al. 2016). Inferences about seabird distributions using Eulerian data are limited by the spatial extent of the survey, and gaps between survey lines can obscure spatial patterns (Watanuki et al. 2016). Direct sightings of focal seabird species can also be limited by species detectability (Ryan & Cooper 1989, Ronconi & Burger 2009). Further, the resolution of the data constrains analyses to the population level, as breeding status, sex, or age of individual seabirds typically cannot be discerned from sighting data.

In comparison, Lagrangian studies track individual seabirds through space and time. Depending on a species' mobility, a Lagrangian sampling design may increase the spatial extent of the study area compared to an Eulerian perspective (Burger & Shaffer 2008). Lagrangian sampling includes the deployment of tracking devices such as satellite-linked, global positioning system (GPS) tags that provide near real-time, continuous, and independent sampling under all environmental conditions (Burger & Shaffer 2008). Fine-scale (i.e., meters to kilometers) movements can be measured with GPS tags and then matched as closely as possible to remotely-sensed, modeled, or *in situ* environmental data to gain insights on correlations between movement, foraging, and the environment (e.g., Chapter 3). A Lagrangian approach provides high-resolution data at an individual level, but transmitter cost and logistical challenges can limit the number of tags deployed (i.e., sample size; Lindberg & Walker 2007). Further, high individual variability complicates population-level inferences (Gutowsky et al. 2015, Krietsch et al. 2017), and information about species interactions, including local densities of competitors and facilitators, is unknown (Hays et al. 2016). Despite sampling and analytic constraints, significant advances in satellite telemetry technology over the last two decades have resulted in important insights into seabird movement and distribution (Shaffer et al. 2006, Votier et al. 2013, Weimerskirch et al. 2016). As a result, satellite telemetry tags are now a primary component of studies on many wide-ranging marine bird species (Tremblay et al. 2009, Hart & Hyrenbach 2009).

As Lagrangian and Eulerian studies on marine animals accumulate (Drew et al. 2015, Block et al. 2016), integration of data from these two perspectives can enhance studies of species' distributions and inform conservation efforts such as the design and management of marine protected areas (Hyrenbach et al. 2006, Ballard et al. 2012). Vessel-based surveys and

tracking data have been used in statistical models to identify important marine areas for seabirds (Louzao et al. 2009). Species distribution models that relate locations of animals to environmental parameters can provide useful ecological insights and strong predictive capability to facilitate dynamic ocean management (Hazen et al. 2012, 2016). However, if inadequate (i.e., inaccurate or incomplete) data are used, significant bias can increase variability in model results and decrease accuracy of model predictions (Elith & Leathwick 2009). Qualitative comparisons of species distributions observed from Eulerian and Lagrangian perspectives demonstrate that observations are not always equivalent (Watanuki et al. 2016). For example, a comparison between a ship-based (Santora et al. 2011) and a telemetry-based (Adams et al. 2012) study of sooty shearwaters (*Ardenna grisea*) in central California demonstrated that shearwaters observed from either perspective use the same general habitat, but that tagged birds were concentrated nearshore where larger vessels could not survey (Watanuki et al. 2016). Whether observed differences in spatial distributions were related to a spatiotemporal mismatch in sampling coverage, or whether the distributions of shearwaters observed from tag locations and ship surveys were truly different, remains unknown. Contemporaneous data from Eulerian and Lagrangian perspectives are rare, making it difficult to attribute variability in observed distributions to true differences in distributions, mismatches in temporal and/or spatial sampling, or differences in sampling perspectives.

This study evaluated whether interpretations of contemporaneous data on common murre (*Uria aalge*) densities collected during May, June, and July 2012 using ship-based surveys, aerial surveys, and satellite telemetry in the northern California Current resulted in the same estimated distribution patterns. Murres are one of the most numerous seabird species in the northern California Current (Zamon et al. 2014), with approximately 532,000 individual murres breeding

along the Oregon and Washington coasts during spring and summer (April – August; Speich and Wahl 1989; Naughton et al. 2007; **Figure 2.1**). During the breeding season, nesting adult murres are central place foragers that search for prey within an approximately 100 km radius of their colony (Decker & Hunt 1996, Hatch et al. 2000a, Davoren et al. 2003b). Thus, spatial constraints of breeding murres and the availability of concurrent Eulerian and Lagrangian datasets presented an opportunity to test the hypothesis that spatial patterns observed during surveys conducted at the same time and place using different perspectives are comparable. Objectives of this study were to quantify and compare spatiotemporal variability in murre distributions observed within each dataset to examine how survey perspective and sampling methodology potentially influences observed patterns in species' distributions.

4.2 METHODS

4.2.1 *Eulerian sampling*

4.2.1.1 Ship-based surveys

Ship-based data from an ongoing ecosystem research program examining the ocean ecology of juvenile salmon off the Washington and Oregon coasts were used to estimate murre distributions (Brodeur et al. 2003; see Chapter 2 for full details). Direct sightings of flying or sitting murres within 300 m of a chartered commercial fishing vessel were collected using standard strip transect survey methods (Tasker et al. 1984) during daylight hours in May and June 2012. Each bird sighting location was spatially and temporally indexed with Global Positioning System (GPS) coordinates using SeeBird software (v 4.1.5.0; NOAA Fisheries Southwest Fisheries Science Center, La Jolla, California, USA). Each transect was approximately 40 km in length, with survey efforts beginning offshore and the ship traveling due

east (shoreward) for 2 h at ~5 m s^{-1} (**Figure 4.1**). To enable sampling of the large latitudinal range (44.7–48.2°N) of the northern California Current that juvenile salmon occupy during their marine migration, the distance between transects ranged from 35 to 90 km. Data were collected on 5 transects during a survey in late May to early June 2012 (S-1), and on 8 transects during late June 2012 (S-2).

4.2.1.2 Aerial surveys

Aerial data were collected during surveys of the northern California Current by the U.S. Geological Survey (Adams et al. 2014). Sightings of murres were recorded from twin-engine, high wing aircraft (Partenavia P-68, Aspen Helicopters, Oxnard, CA, or Commander AC-500, GoldAero, Arlington, WA) along pre-determined, systematic east-west-oriented transects flown at 160 km h^{-1} from the 2000 m isobath to shore (~90 km; **Figure 4.1**). Using aerial survey methods modified slightly from Mason et al. (2007), two observers counted all birds observed in 150 m strip transects (75 m per side) from 60 m above sea level. The number and location of individual murres were linked with a GPS unit to a laptop computer that allowed simultaneous collection of coordinates (WGS-84 map datum). To sample between 45.2–47.0°N, the latitudinal distance between surveys was 27.8 km. Data were collected on 10 transects on May 19, 2012 (A-1), and on 24 transects on July 1 and 4, 2012 (A-2), which included survey transects and additional focal-area surveys (Adams et al. 2014). The focal-area survey was nested within the overall survey area in shelf waters, consisting of ten, 25 km parallel transect lines spaced 6 km apart (north-south; **Figure 4.1**). For this study, counts of murres obtained during the July 1 and July 4 surveys were treated as one survey for analyses (i.e., all transects were analyzed together).

4.2.2 *Lagrangian sampling*

4.2.2.1 Satellite telemetry

Locations of murres were collected using satellite tags (Telonics TAV-2617 platform terminal transmitters [PTTs]) deployed on 12 murres that were captured, tagged, and released near the mouth of the Columbia River, Washington on May 4 and 5, 2012 (**Figure 4.1**). Positions of individual birds were determined using the ARGOS system (www.argos-system.org; CLS 2013) and archived via the Satellite Tracking and Analysis Tool (STAT; Coyne & Godley 2005). To ensure position accuracy, 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. Full details of the instrument deployments and data processing can be found in Chapter 3, section 3.2.

4.2.3 *Data analysis*

Overall density distributions of murres were first compared between the two Eulerian perspective data sets. Densities of murres observed on ship-based surveys were estimated by dividing the total number of murres observed in 3 km bins (approximately 10 min increments) by the strip area searched (0.9 km^2) to obtain estimates of birds km^{-2}. Densities of murres observed during aerial surveys were estimated by dividing the total number of murres observed in 2.4 km bins (approximately 1 min increments) by the strip area (either 0.18 km^2 [one observer] or 0.36 km^2 [two observers]) to obtain density estimates. To determine if mean densities differed within and between data sets, densities observed during S-1 and S-2, and A-1 and A-2 were compared using *t*-tests (Zar 1999) and then overall mean densities between ship and aerial surveys were

compared. To determine if distribution patterns varied in relation to distance from shore, histograms of murres observed on transects were plotted.

Absolute densities cannot be estimated from locations of individually-tagged murres. Instead, Brownian Bridge utilization distributions (Horne et al. 2007) were calculated to estimate each tagged murre's probability of occurrence using the 'kernelbb' function in R package adehabitat (Calenge 2006). A utilization distribution (UD) is a probability distribution that gives the probability density that an animal is found at a given point in space. It is estimated from sampling the location of individuals in space over a period of time. The Brownian bridge UD approach provides an estimate of space-use from animal trajectories with serial autocorrelation of relocations (Horne et al. 2007). An overall 99% utilization distribution (99UD) for all 12 birds was created by first calculating 99UDs for each individual murre, and then proportionately weighting the 99UD by each tag's duration (i.e., tracking days per individual divided by total tracking days for all individuals) and summed with the rest of the individual 99UDs. The overall 99UD represents an interpolated surface of tagged murre 99% probability density distributions during the full duration of tag transmissions, with a resolution of 3 km^2. To estimated tagged murre distributions during each ship or plane survey, separate 99UDs of tagged murres during each Eulerian survey were calculated. For the ship surveys, this included a 99UD during May 30–June 3 (S-1; n = 10 tagged birds, n = 233 locations) and June 21–June 28 (S-2; n = 8 tagged birds, n = 298 locations). For the aerial surveys, a 99UD on May 19 was calculated (A-1; n = 12 tagged birds, n = 60 locations) and on July 1–4 (A-2; n = 8 tagged birds, n = 157 locations). Because PTT data were available for the periods before, between, and after each Eulerian survey, separate 99UDs were calculated during these periods to determine if tagged murre distributions were different earlier or later in the season. Finally, the distances of tagged murres from shore

were tabulated and plotted to compare with offshore distributions of murres observed on ship or plane transects.

To facilitate direct Eulerian-Lagrangian density distribution comparisons, interpolated, continuous surfaces of murre density distributions from each Eulerian dataset were created. The 'kernel smoothing with barriers' tool in ArcMap 10.3 was used with a first order polynomial kernel function and kernel bandwidths set to the minimum north-south distance between transects to create a smooth prediction surface from observed densities (Worton 1989). Kernel smoothing is a statistical technique to estimate a real valued function as the weighted average of neighboring observed data. The weight is defined by the kernel, such that closer points are given higher weights. The estimated function is smooth, and the level of smoothness is set by the kernel bandwidth. To examine similarities in spatial distributions observed from each perspective, kernel density and 99UD surfaces during each survey were plotted, and the percent overlap between the surfaces was calculated using the 'tabulate intersection' tool in ArcMap 10.3. The geographic center of gravity (CG) of murres observed during each Eulerian survey was also calculated (see Chapter 2 Methods section), and compared to the CG of tagged murre locations. The Euclidean distance between the CGs was measured to determine if geographic locations of murres observed from each perspective differed.

4.3 RESULTS

4.3.1 *Eulerian sampling*

4.3.1.1 Ship-based surveys

A total of 428 murres were observed during 43.4 km^2 of survey effort during S-1, and 749 murres were observed during 78.8 km^2 of survey effort during S-2 (**Table 4.1**). Birds were

observed 4.7–44.8 km from shore in shelf waters, with the majority of murres occurring within 15–40 km of shore (**Figure 4.2**). Mean densities were not significantly different between S-1 (9.9 birds km^{-2}) and S-2 (9.5 birds km^{-2}; $t_{72.3} = -0.076$, $p = 0.940$). Murre densities were consistently highest on the Cape Meares (CM) transect, adjacent to a large murre colony, and on the Columbia River (CR) transect (**Figure 4.3**). During S-1, a mean density of 26.0 birds km^{-2} was observed on the CM transect, and a mean density of 14.1 birds km^{-2} was observed on the CR transect. During S-2, a mean density of 28.4 birds km^{-2} was observed on the CM transect, and a mean density of 23.0 birds km^{-2} was observed on the CR transect. Lowest mean density (0.4 birds km^{-2}) was observed on the La Push (LP) transect during S-1, which contrasted to the higher mean density observed during S-2 on LP (10.2 birds km^{-2}; **Figure 4.3**). Intermediate densities were observed off the central Washington coast during both surveys, including a mean of 3.3–4.2 birds km^{-2} on the Grays Harbor transect and a mean of 2.5–3.9 birds km^{-2} on the Willapa Bay transect. During S-2, low murre densities (mean < 3.0 birds km^{-2}) were observed both in the northern portion of the survey (Father and Son, Queets River transects), and in the southernmost portion of the survey (Newport Hydrographic transect; **Figure 4.3**).

4.3.1.2 Aerial surveys

A total of 618 murres were observed during 45.1 km^2 of survey effort during A-1, and 880 murres during 162.5 km^2 of survey effort during A-2 (**Table 4.1**). Birds were observed across a wider range of distances from shore than in the ship surveys (0.3–93.6 km), although the greatest numbers were observed between 1–25 km from shore, similar to ship surveys (**Figure 4.2**). Mean densities did not differ between A-1 (13.7 birds km^{-2}) and A-2 (5.4 birds km^{-2}; $t_{1.54} = 370.7$, $p = 0.125$). Overall mean densities were not significantly different from ship surveys ($t_{635.1} = 0.631$, $p = 0.528$). During A-1, densities of murres were greatest on the three southernmost

transects (mean: 35.1 birds km^{-2}) on the northern Oregon coast adjacent to a murre colony (Tillamook Head) and near the mouth of the Columbia River (**Figure 4.3**). Lower densities were observed on the southern Washington coast, although relatively high densities (4.4 birds km^{-2}) were observed near Grays Harbor during A-1. During A-2, highest densities (mean: 9.6 birds km^{-2}) were also observed on the northern Oregon coast near murre colonies at Cape Meares and Tillamook Head, and low densities (mean: 0.48 birds km^{-2}) were observed on the southern Washington coast off Willapa Bay and Grays Harbor (**Figure 4.3**).

4.3.2 *Lagrangian sampling*

Satellite-tagged murres were tracked for an average of 54.2 ± 21.9 d (mean ± SD) between early May and early July, covering 114,900,000 km^2. Tag duration ranged between 18–73 d, with 50% (n = 7 tags) transmitting for over 63 d (**Table 4.1**). Overall 99UDs indicated a broad latitudinal use of nearshore coastal waters between British Columbia and California, with most locations within 10 km of the coast (range: 3–76 km; **Figure 4.2**). Overall, highest use areas were located along the northern Oregon and southern Washington coasts (**Figure 4.4**), as well as on the west side of Vancouver Island, British Columbia. One murre flew ~1500 km to California and spent most of its time between Monterey Bay and the Santa Barbara Channel. An additional two birds moved ~950 km north to the Pacific coast of Canada and Haida Gwaii (**Figure 4.4**).

The 99% utilization distribution (UD) calculated for the period before the first vessel survey (i.e., S-1) indicated that tagged murres concentrated along the northern Oregon and southern Washington coast, with high use areas near Grays Harbor and Willapa Bay. One murre flew south into southern Oregon and northern California waters during this time. With the exception of the murre in California waters, the UD calculated during S-1 indicated that most

tagged murres were still concentrated off Grays Harbor and Willapa Bay, and near the mouth of the Columbia River, similar to the location of high densities observed from the ship (**Figure 4.5**). Spatial overlap between the ship kernel density surface (KD) and the tag UD was 34.7%, and the centers of gravity (CGs) of murres observed from the two sampling perspectives were 37.2 km apart. The tag UD indicated a similar spatial distribution of murres for the 16 days between surveys S-1 and S-2, although some tagged murres shifted north into Canadian waters along the west coast of Vancouver Island. During S-2, tagged murres were more broadly distributed throughout Washington coastal waters, with high use areas similar to those observed during S-1 and highest spatial use occurring near Grays Harbor. Overlap between the ship KD and the tag UD during S-2 was 30.1%, and CGs were 22.1 km apart. The spatial distribution of murres observed during both ship surveys were similar, with most murres observed in northern Oregon waters near Cape Meares and the CGs located 43.6 km apart. After the ship surveys, tagged murres continued moving north into Canadian waters, with two birds moving as far north as Haida Gwaii on the Canadian Pacific coast. Some murres also continued to occupy Washington coastal waters, but the UD indicated low spatial use of this area.

The UD calculated for the period before the first aerial survey (i.e., A-1), indicated that tagged murres exhibited high spatial use of waters along the southern Washington and northern Oregon coast, with a high use area off the Long Beach Peninsula just north of the mouth of the Columbia River. The UD calculated during A-1 indicated that the majority of tagged murres used waters near Grays Harbor, Willapa Bay, and off the mouth of the Columbia River (**Figure 4.6**). During A-1, 55.6% of the aerial KD overlapped with the tag UD, and the CGs of murres observed from each perspective were separated by 20.8 km. Spatial distributions of tagged murres were similar to A-1 during the 41 days between aerial surveys. During A-2, tagged

murres showed high use of waters near Grays Harbor, and along the British Columbia coast. The highest murre densities observed from the plane were further south in Oregon coastal waters than the 99UD of tagged murres, and the overlap between the kernel density and the 99UD was only 11.7% during A-2. The location of the CG from telemetry during A-2 reflected the northward movement of tagged murres, which was 301.7 km north of the CG of murres observed during the aerial survey. In comparison, the location of the CGs of murres observed during A-1 and A-2 were only 33.3 km apart, and located off northern Oregon, similar to where the CGs observed during ship surveys were located. After aerial surveys were completed, locations of tagged murres were widespread in coastal Washington and Canadian waters, primarily along the west coast of Vancouver Island and further north in Haida Gwaii.

4.4 DISCUSSION

This chapter used data from two Eulerian-based surveys and one Lagrangian study to illustrate that while seabird distributions inferred from independent, contemporaneous data sets can indicate similar high use areas, survey perspective and methodology can influence observations. At the spatiotemporal scale of the northern California Current during May–July, distributions of murres observed from ship, plane, and satellite tags were similar and indicated high use of waters along the Washington and Oregon coasts. Regardless of latitudinal range, murres occurred in greatest densities within ~20 km of the coast, with higher densities of tagged murres occurring closer (3–5 km) to shore than those observed from a ship or plane. Consistently similar Eulerian density estimates from ship and aerial surveys during May, June, and July demonstrates that large numbers of murres occupy the northern California Current during spring and summer, and that both Eulerian methods can effectively survey this coastal, large-bodied

seabird (Briggs et al. 1985b, Henkel et al. 2007). Although the slower speed of a research vessel can convolve seabird spatial patterns with temporal flux (Ryan & Cooper 1989, van Franeker 1994, Ronconi & Burger 2009), within the period (days to weeks) that ship and aerial surveys were conducted no differences were observed.

Comparisons of murre distributions observed through an Eulerian perspective indicate that geographic centers of gravity and highest mean densities were observed primarily on transects adjacent to large murre colonies on the northern Oregon coast, which is not surprising given that the breeding season for common murres is April–August, and that murres aggregate on the water near colonies before and after foraging bouts (Zador & Piatt 1999, Ainley et al. 2002). The aerial surveys were more limited in their overall latitudinal extent, but a greater number of more closely-spaced transects were surveyed compared to the ship transects. This provided higher resolution data on murre distributions from aerial surveys, which demonstrated lower relative densities near Willapa Bay and Grays Harbor compared to ship surveys. This difference may have been related to daily variation in circulation of the Columbia River plume and the associated convergent fronts that form on the north side of the river plume, which influence murre distributions (Chapter 3). Variation in plume circulation occurs at temporal periods of hours to days (Jay et al. 2009, 2010), which is not detectable at the sampling resolution of the Eulerian surveys. Ship surveys also documented increased densities of murres further north than the aerial surveys sampled, demonstrating that murres occupy much of the nearshore waters along the northern Oregon and Washington coasts, and that their at-sea distributions are likely related to adjacent colonies located along the coast (Parrish et al. 1998, Zador et al. 2009).

The Lagrangian perspective based on satellite tagging offers the opportunity to expand the spatial sampling extent because continuous information about individual locations can be recorded throughout the animal's range, which eliminates the sampling limitations imposed by an Eulerian grid (Hart & Hyrenbach 2009). In this study, telemetry locations demonstrated that the spatial extent of tagged murres encompassed nearshore waters of California, Oregon, Washington, and most of British Columbia. The tags also transmitted continuously for an average of two months between May and July, providing more frequent sampling compared to the discrete Eulerian surveys. During May, the spatial extent and high use areas observed from tag locations were similar to those observed during Eulerian surveys. Most of the tagged birds remained near the Washington coast in May and June, particularly near the mouth of the Columbia River, and overlap between the kernel density surfaces from Eulerian surveys and utilization distributions from the Lagrangian survey was relatively high (~40%). The geographic centers of gravity were also close (<40 km) to each other, indicating similar spatial distributions of tagged and untagged murres in northern Oregon. During July, tagged murres moved away from the Washington and Oregon coasts, primarily flying north into Canadian waters. Thus, during the aerial survey in July, the distributions observed from tagged murres were substantially different than those made from the plane. Only 11% of the kernel density surface from the aerial survey overlapped the tag utilization distribution, and the centers of gravity were ~300 km apart, demonstrating that spatial distributions observed from a Lagrangian perspective can diverge from Eulerian observations, particularly as the time since initial tag deployment increased. Thus, even within a relatively small period of three months, observed spatial patterns can vary depending on perspective.

This study occurred during the breeding season when most murres act as central place foragers, and density distributions were therefore expected to be highest near local colonies. Eulerian results support this hypothesis, and high densities of murres were observed near two large colonies in northern Oregon (Cape Meares and Tillamook Head), as well as colonies on the northern Washington coast including Flattery Rocks. However, high densities of murres were also consistently observed near the mouth of the Columbia River, Willapa Bay, and Grays Harbor, which are at least 40–50 km from the nearest colony. The telemetry data also indicated that waters near the Columbia River were a high use area where tag utilization distributions frequently overlapped ship and aerial kernel density surfaces. This suggests that some murres were commuting from colonies to forage in the Columbia River plume (Chapter 2), or that some of the murres observed during ship, aerial, and telemetry surveys were non-breeding birds that remained at-sea to rest between foraging bouts (i.e., loafers). The Lagrangian results from this study support the latter. Telemetry data demonstrated unexpectedly high mobility of tagged murres, with some individuals moving at least 1,000 km during the temporal period of the Eulerian surveys and utilizing a much greater spatial area than was surveyed by ships or planes. Further, the utilization distributions indicated a northward dispersal into Canadian waters by most of the tagged murres in July, which could not be observed in Eulerian observations. The 12 murres that were captured and tagged near the mouth of the Columbia River had adult plumage and were assumed to be representative of murres observed on the water during ship or aerial surveys. These results suggest that the population of murres occupying the northern California Current consists of a mixed group of central place foraging adults and vagile, non-breeding adults and subadults that differ in their occupancy of the Washington coast. The tagged murres in this study may have been younger birds or non-breeding adults, as these groups exhibit longer

dispersals away from colonies (Hatch et al. 2000a). Alternatively, the relatively high mobility of tagged murres could indicate that tagging caused breeding murres to abandon colony attendance (see Chapter 3 for a discussion). Sample size may have also influenced the observed results (Lindberg & Walker 2007). Of the 12 tagged murres, one flew to California, and ~8 flew into Canadian waters. Individual variability in plume habitat use by the same tagged birds was high (Chapter 3), which can result from tracking a small number of individuals (Fossette et al. 2014, Hays et al. 2016). To better understand the spatial and temporal extent of tagged animal distributions, Lindberg and Walker (2007) estimated that, as a rule of thumb, at least 20–30 tagged individuals are required to reveal population patterns.

Study objectives, accessibility of the area, sampling logistics, and available resources can all influence the choice of survey perspective and methodology (Ainley et al. 2012). This research demonstrates that for Eulerian-based studies where objectives include obtaining accurate population abundance estimates and spatial use of coastal areas by seabirds, ship and aerial survey methods produce similar results, although spatial extent of the transects can limit inferences (see also Briggs et al. 1985b, Henkel et al. 2007). Ships are ideal platforms to sample concurrent abiotic and/or biotic parameters such as sea surface temperature and prey density (Ainley et al. 2012), and therefore offer more opportunities for ecological studies. In comparison, a Lagrangian perspective enables a much larger spatiotemporal sampling range compared to Eulerian surveys, but the ability to quantify densities and examine species interactions is limited (Ainley et al. 2012).

Ship-based, aerial, and telemetry surveys can provide complementary information on species distributions, but the results of this study suggest that a thorough assessment of the spatial extent and synopticity of relevant data is an important first step before integrating

methodological perspectives. Depending on the objective, the spatial extent and temporal mismatch between or among independent data sets (e.g., transect-based and tag-based) may bias observed species' distributions. Efforts to integrate Eulerian and Lagrangian perspectives using quantitative models exist (Hyrenbach et al. 2006, Louzao et al. 2009, Yamamoto et al. 2015), and are continuing to be refined (Watanuki et al. 2016). Given the expected growth of telemetry studies (Hart & Hyrenbach 2009) and efforts to integrate independent data sets, these results serve as a case study on how methodological perspective can influence spatiotemporal observations of species distributions.

4.5 TABLES

Table 4.1 – Description of ship, aerial and telemetry-based data collections for common murres (*Uria aalge*) in 2012 including date range, total duration (days), track length, and total sightings or tag locations used for analyses.

Perspective	Platform	Sample	Date Range	Duration (d)	Track length (km)	Total sightings /locs
Eulerian	Ship	S-1	5/30 – 6/3	5	145.8	428
		S-2	6/21 – 6/28	8	262.1	749
	Aerial	A-1	5/19	1	600.6	618
		A-2	7/1, 7/4	2	1160.2	880
Lagrangian	PTT	T-1	5/5 – 6/11	37	1541.6	182
		T-2	5/5 – 5/23	19	859.3	112
		T-3	5/6 – 7/15	70	4649.3	317
		T-4	5/5 – 6/3	29	1478.3	156
		T-5	5/5 – 7/10	66	2677.6	281
		T-6	5/5 – 7/17	72	3323.5	348
		T-7	5/5 – 7/9	65	2501.0	301
		T-8	5/5 –7/13	68	3290.1	337
		T-9	5/6 – 7/4	60	2162.9	295
		T-12	5/5 – 5/23	18	670.4	100
		T-13	5/6 – 7/23	79	4409.6	341
		T-15	5/5 – 7/11	67	2890.4	317

4.6 FIGURES

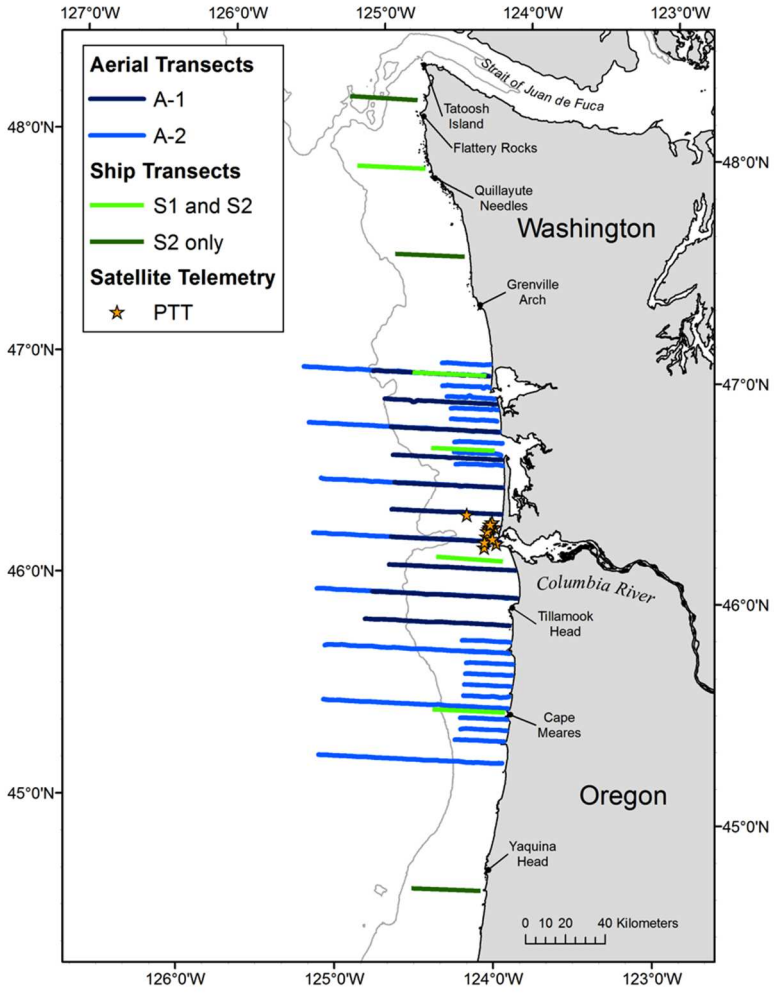

Figure 4.1 – Study area off the Oregon and Washington coast. Ship transects surveyed during May 30 – June 3, 2012 (S-1) and June 21 – June 28, 2012 (S-2) are shown in light green, and transects surveyed only during S-2 are shown in dark green. Aerial transects flown on May 19, 2012 (A-1) are shown in dark blue, and transects flown on July 1 and July 4, 2012 (A-2) are shown in light blue. Locations of PTT deployments for each tagged murre released near the mouth of the Columbia River on May 4 – 5, 2012 are shown as orange stars. Large murre colonies are labeled on the map.

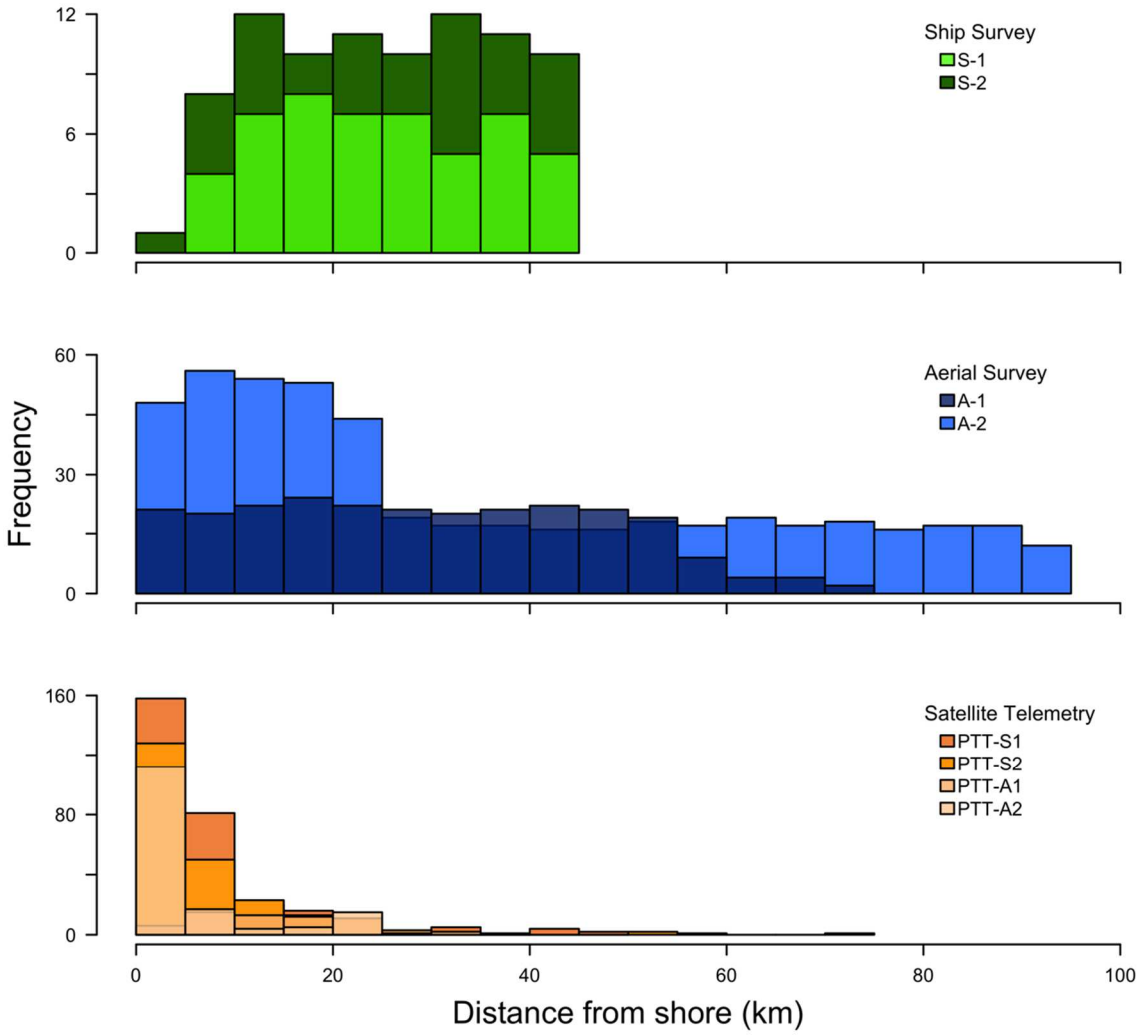

Figure 4.2 – Distribution of common murre (*Uria aalge*) distances from shore during ship-based (S-1, S-2), aerial (A-1, A-2), and satellite telemetry (PTT) observations during ship and aerial surveys.

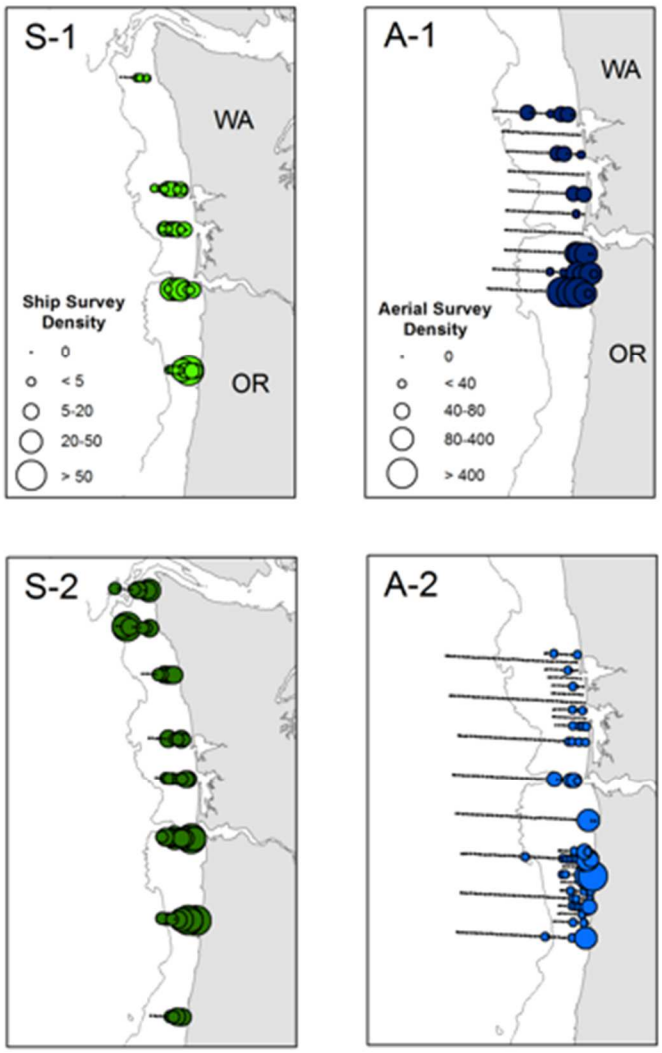

Figure 4.3 – Density distributions of common murres (*Uria aalge*) observed during ship surveys on May 30 – June 3, 2012 (S-1) and June 21 – June 28, 2012 (S-2), and aerial surveys on May 19, 2012 (A-1) and July 1 and July 4, 2012 (A-2) in the northern California Current.

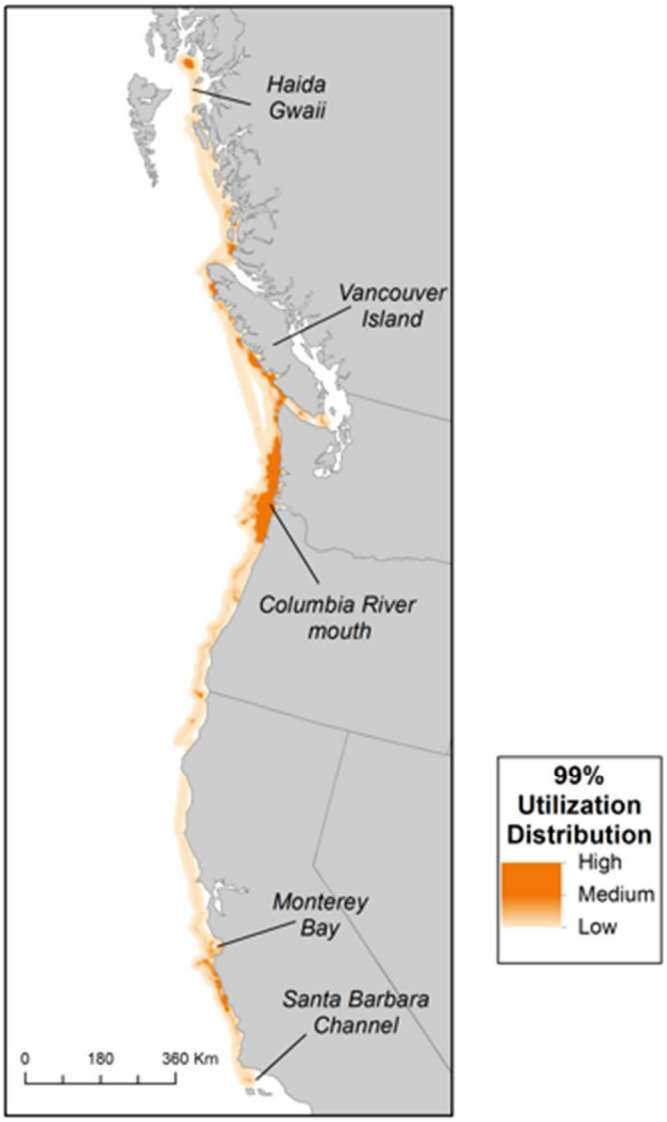

Figure 4.4 – Distribution (99UD) of 12 tagged common murres (*Uria aalge*) during May 4 – July 24, 2012. Locations of high use areas are labeled.

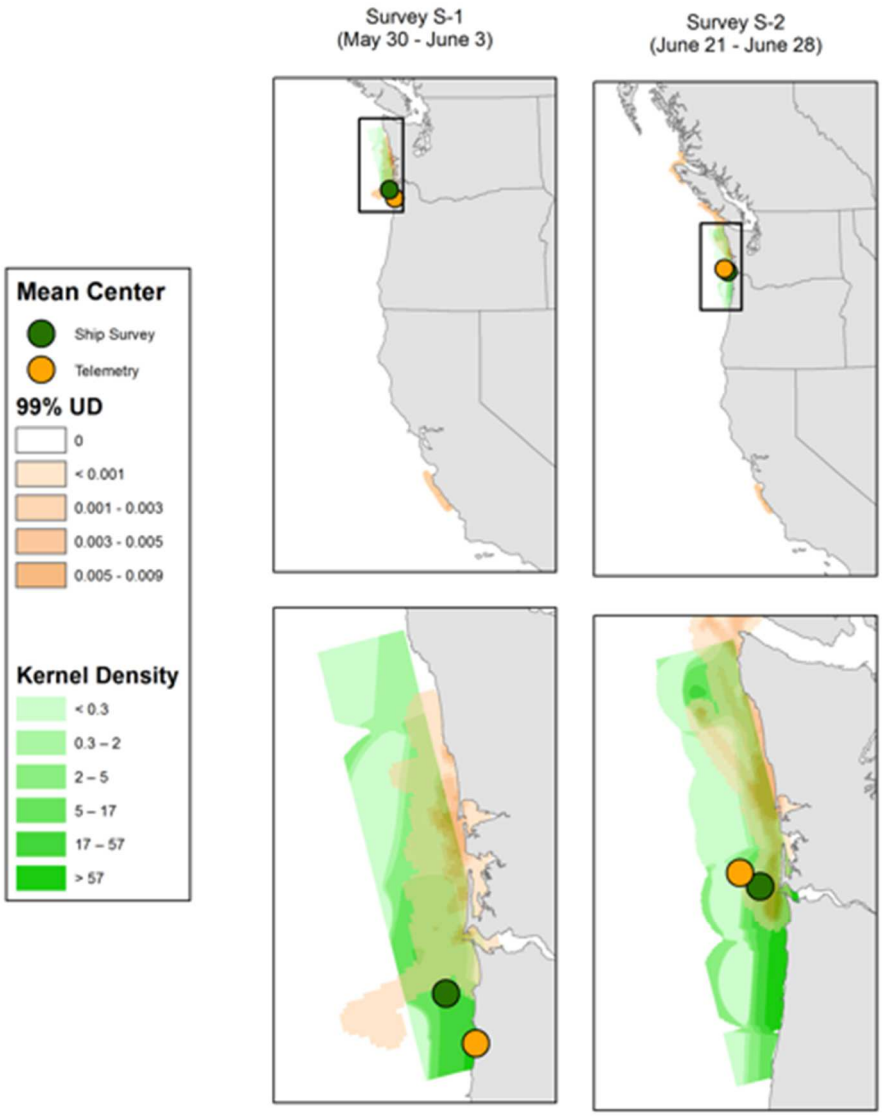

Figure 4.5 – Distribution of tagged common murres (*Uria aalge*; orange shaded area) overlaid with kernel density estimates of murres (green shaded area) observed during surveys S-1 and S-2. Black box shows the inset figure area. The geographic mean centers of murre distribution observed during each ship survey (green point) and from PTT locations (orange point) are also shown.

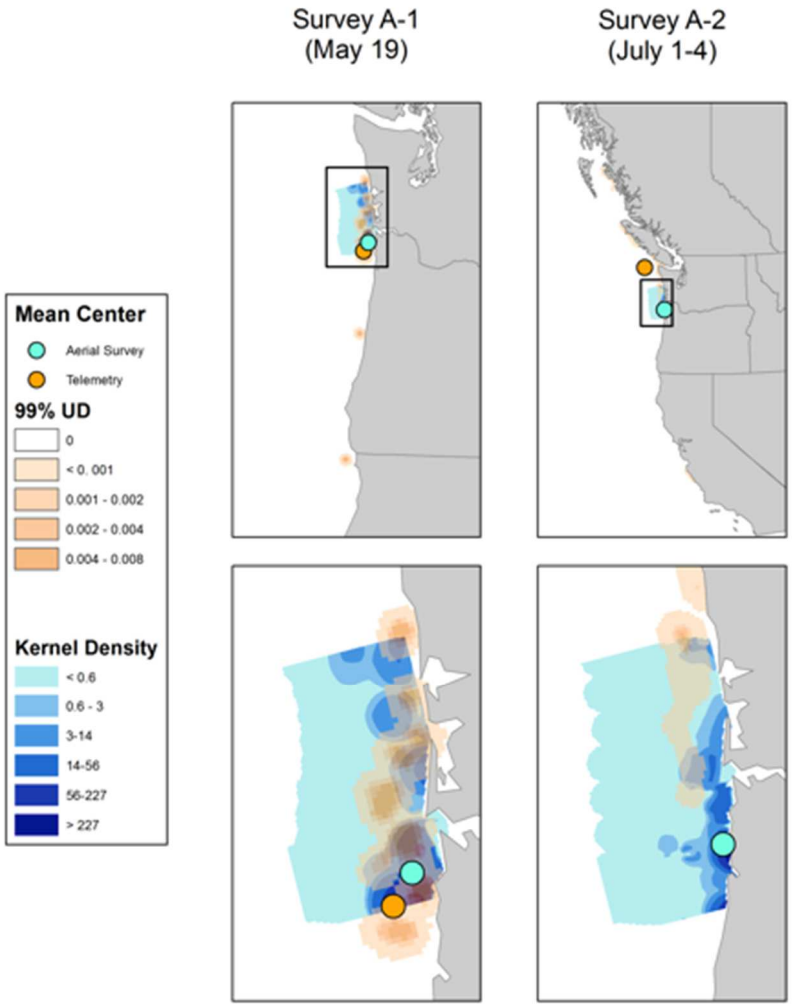

Figure 4.6 – Distribution of tagged common murres (*Uria aalge*; orange shaded area) overlaid with kernel density estimates of murres (blue shaded area) observed during surveys A-1 and A-2. Black box shows the inset figure area. The geographic mean centers of murre distribution observed during each aerial survey (turquoise point) and from PTT locations during A-1 (orange point) are also shown. The mean center of tagged murres was 301.7 km north of the mean center of murres observed during A-2 and therefore only shown on the broader scale map.

Chapter 5. CHARACTERIZING JUVENILE SALMON PREDATION RISK IN THE NORTHERN CALIFORNIA CURRENT

5.1 INTRODUCTION

Interactions between predators and prey influence ecological relationships including trends in population abundance, spatial distributions, and behavior (Lima & Dill 1990, Abrams 2000, Hebblewhite et al. 2005). Predator-prey interactions are contingent on the co-occurrence of predators with prey at a specific time and place, which increases the probability of a predator encountering, attacking, and consuming a prey (Fauchald 2009, Ahrens et al. 2012). Predation can be influenced by abiotic and biotic factors that affect prey densities and detectability. For example, low light levels often reduce prey detectability for visually foraging predators, which may decrease predation rates (Petersen & Gadomski 1994, Vogel & Beauchamp 1999, Mazur and Beauchamp 2003). Migration concentrates animals in a relatively small area, increasing local densities and potential prey encounters with co-occurring predators (Petersen & DeAngelis 2000, Alerstam et al. 2003). The response of predators to prey can be characterized by functional response models, which estimate predator consumption as a function of prey density (Holling 1959). The Holling type II functional response describes predator consumption as a function of increasing prey density, predator attack rate, and prey handling time, representing an asymptotic relationship between consumption rate and prey density (Holling 1959). As the asymptote is reached, the predator's ability to attack and consume prey is saturated by increasing prey density.

In systems where predators switch between different types of prey in proportion to their density (i.e., generalist predator), the availability of other prey species (i.e., alternate prey) may influence foraging behavior of a predator, and reduce overall consumption of any individual prey

species (Abrams & Ginzburg 2000, Tschanz et al. 2007, Prokopenko et al. 2017). For example, many seabird species are generalist predators that exhibit a type II functional response (Piatt et al. 2007, Cury et al. 2011). Piscivorous seabirds including sooty shearwaters (*Ardenna grisea*) and common murres (*Uria aalge*) consume a wide variety of coastal pelagic fish species (CPS; Chu 1984, Ainley et al. 1996, Ballance et al. 2001), and regularly switch between different prey species depending on their availability (Burger & Piatt 1990, Montevecchi et al. 2009). This ability to switch prey consumption to the most abundant species available can reduce consumption of endangered species, and has been a significant component of research on estuarine avian predation of juvenile Pacific salmonids (Collis et al. 2002, Roby et al. 2002).

Predation is considered a significant factor impacting juvenile salmonid survival during estuarine and early marine residence (Pearcy 1992, Beamish & Mahnken 2001), but a thorough understanding of the conditions under which predator encounter and prey consumption occurs remains incomplete. Juvenile salmon from the Columbia River Basin in western North America migrate annually from freshwater and estuarine habitats to the ocean in high densities during spring migration in May and June (Weitkamp et al. 2012). Juvenile salmon, often called smolts during their seaward migration, must pass through the freshwater plume that forms near the mouth of the Columbia River. The Columbia River plume (CRP) attracts high numbers of two piscivorous avian predators, sooty shearwaters (*Ardenna grisea*) and common murres (*Uria aalge;* Zamon et al. 2014). These predators consume smolts and other CPS (Wiens & Scott 1975, Varoujean & Matthews 1983), suggesting that the presence of alternate prey may influence juvenile salmon predation rates in the Columbia River plume (Fisher & Pearcy 1988, Pearcy 1992, Emmett & Sampson 2007). Smolts and CPS are similar in appearance and size, and occur disproportionately in the CRP (Chapter 2). However, spatial aggregation patterns of these two

prey groups differ. Smolts are evenly distributed near the surface in the CRP and do not aggregate near plume boundaries (Chapter 2; De Robertis et al. 2005), whereas CPS often occur near plume boundary areas in dense aggregations deeper in the water column during the day (~10–70 m depth; Chapter 2). Thus, the response of shearwaters and murres to horizontal and vertical distributions of alternate prey may influence predation risk to juvenile salmon.

In addition to alternate prey, factors including plume size, smolt migration timing, turbidity, and temperature have been linked to the marine survival of juvenile salmon, which is often measured by the number of returning adults from a cohort (Bradford 1995, Emmett & Schiewe 1997). For example, survival of interior Columbia River Basin subyearling Chinook salmon (*Oncorhynchus tshawytscha*), represented as adult summer and fall Chinook salmon passing Priest Rapids Dam on the Columbia River, was positively correlated to plume volume (Miller et al. 2013). Yearling Chinook salmon survival was negatively correlated to the amount of time salmon spent in the plume, suggesting that residence in the plume and concurrent exposure to predation was an important factor determining mortality (Brosnan et al. 2014). Shearwater and murre densities in the plume are negatively correlated with CRP surface area (Chapter 2), and satellite-tagged seabirds move towards the plume edge as surface areas increase beyond a threshold of ~1500–4000 km^2 (Chapter 3), indicating that the physical dynamics of the CRP may influence seabird-smolt interactions. Larger smolts and earlier migrating individuals tend to have greater survival (Zabel & Achord 2004, Anderson et al. 2005, Claiborne et al. 2014). Yearling Chinook salmon, which migrate to the ocean after spending one year in freshwater along with juvenile coho salmon (*Oncorhynchus kisutch*), have higher survival rates when they enter the ocean during early to mid-May compared to fish migrating in mid-June, which may be related to springtime river flows (Scheuerell et al. 2009). Turbidity increases with

river flow (Leopold & Langbein 1960, Mulder & Syvitski 1995) and may also reduce predation risk of migrating smolts (Gregory & Levings 1998, De Robertis et al. 2003) due to a reduced visual foraging range for piscivorous fish (Hansen et al. 2013, Hansen & Beauchamp 2015). However, turbid CRP waters also attract shearwaters and murres (Chapter 2) and therefore may not protect smolts from being encountered and consumed by visually-foraging seabirds. The occurrence of seabirds in nearshore coastal Washington waters (Chapter 3, 4), where many juvenile salmon also occur (Fisher et al. 2014, Teel et al. 2015), may increase the vulnerability of smolts to predators. Vulnerability to predators may also be influenced by water temperature, as some stocks of juvenile salmon select coastal habitat based on a narrow range of water temperatures (Burke et al. 2013a).

Seabird predation impacts on juvenile salmon have previously been estimated using diet samples obtained at sea and from colonies (Emmett & Sampson 2007, Roby et al. 2015, Wells et al. 2017). However, recent data on smolt consumption by seabirds in the northern California Current are limited. In the absence of seabird diet data, an index of predation risk can be estimated using observations of co-occurrence among seabirds, smolts, CPS, and hypothesized relationships between predators and prey. Once predation risk is characterized, then the influence of abiotic factors including plume size, turbidity, and temperature on risk magnitudes can be evaluated. Objectives of this chapter were to characterize juvenile salmon predation risk during early marine residence by quantifying seabird and smolt co-occurrence, estimating predation risk, evaluating predation risk in relation to abiotic environmental factors, and correlating risk estimates to adult salmon returns.

5.2 METHODS

To estimate co-occurrence and predation risk, data from an ongoing ecosystem research program examining the ocean ecology of juvenile salmon off the Washington and Oregon coasts were used (Brodeur et al. 2003). Data were collected during daylight hours in May and June 2010–2012 on chartered commercial fishing vessels sampling along transects and at fixed stations from northern Washington State to Newport, Oregon (see Chapter 2 for full details).

5.2.1 *Predator and prey sampling*

Shearwaters and murres were counted along transects that began 35–42 km offshore at dawn with the vessel traveling due east for 2 h at ~5 m s^{-1} using standard strip transect survey methods (Tasker et al. 1984; **Figure 2.1**). Only seabirds that were sitting on the water surface or observed feeding were used to estimate densities in 300 m^2 increments along the survey track.

Immediately after seabird transect sampling was completed, environment and prey samples were collected from 5 to 8 fixed stations along the same transect by running back along the transect in the reverse direction. At each station, a profiling conductivity-temperature-depth instrument (hereafter, CTD; SBE 19plus; Sea-Bird Electronics Inc., Bellevue, Washington, USA; http://www.seabird.com/) was deployed to within 5 m of the bottom, or to a maximum depth of 200 m, to record temperature, salinity, and transmissivity. 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 ~30 x 20 m (width x depth) when fishing. All items caught in the trawl were identified and recorded. All juvenile salmonids were measured to the nearest millimeter (fork length, FL). Up to 50 non-

salmonid organisms were measured, including fish (FL or standard length, SL) and squid (dorsal mantle length, DML). To delineate potential prey of seabirds, individuals greater than 250 mm FL or DML were excluded (c.f., Chapter 2). All non-salmonids were categorized as alternate prey, and all salmon ≤250 mm FL were categorized as juvenile salmon. To account for life history variation in length at ocean entry for Chinook salmon, FL and month of capture were used to classify juvenile Chinook salmon as either subyearling or yearling fish based on length-at-age from scale analysis and tagging studies (Pearcy and Fisher 1990; Fisher and Pearcy 1995; see Chapter 2 for details).

To measure potential seabird prey densities in the water column during trawling, continuous acoustic measurements of mean volume backscattering strength (S_v; dB re 1 m^{-1} [hereafter dB]; 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 2.1**). Acoustic data were processed using Echoview v 5.4 (http://www.echoview.com/), with the S_v threshold set to -60 dB. To develop an index of prey available to seabirds, all S_v measurements were vertically integrated from 10 m below the surface to 70 m depth, the approximate diving range of sooty shearwaters and common murres (Piatt and Nettleship 1985; Weimerskirch and Sagar 1996; Shaffer et al. 2009). Acoustic densities were reported as nautical area scattering coefficients (s_A; m^2 nmi^{-2}; MacLennan et al. 2002), indexed in space and time.

To convert fish sampled by the trawl and fish observed acoustically to equivalent densities (i.e., fish km^{-2}), trawl catches were standardized by dividing the number of fish caught by the area fished. Area fished was calculated as the distance between the start- and endpoints of the tow using GPS coordinates (mean: 3.3 ± 0.7 km, SD), multiplied by the width of the trawl

(0.03 km). Acoustic backscatter was converted from s_A to fish density (ρ_a) using the equation from Parker-Stetter et al. (2009):

$$\rho_a = \frac{\left(\frac{s_A}{4\pi*(1852^2)}\right)}{\sigma_{bs}} * 1x10^6 \quad (5.1)$$

Where σ_{bs} (9.82 x 10^{-6} m^2) is the estimated backscattering cross section of a 200 mm (FL) northern anchovy at 38 kHz with a target strength (TS) of -50.1 dB. The 200 mm FL was based on the average fork length of anchovy caught in the surface trawl, and TS was calculated using the target-strength to length equation from Barange et al. (1996):

$$TS = 20 * \log(FL_{cm}) - 76.10 \quad (5.2)$$

To estimate the density of alternative prey (fish km^{-2}) at each station, non-salmonid prey densities from trawl sampling were summed with acoustically detected prey densities. Juvenile salmonids were excluded from acoustic samples because they typically occur in the upper 10 meters of the water column during the day (Emmett et al. 2004, Smith et al. 2015), and backscatter was integrated below 10 meters.

5.2.2 *Predator-prey co-occurrence*

Co-occurrence was defined as either shearwaters or murres being present at a station where juvenile salmon were caught in the surface trawl. Shearwaters and murres consume similar prey and exhibit similar foraging habits (Varoujean & Matthews 1983, Chu 1984, Ainley et al. 1996), so shearwater and murre densities were combined to create a single predator group for estimates of predation risk. To quantify co-occurrence, shearwater and murre densities were summed and assigned to the nearest trawl station, using one half the distance between stations as the breakpoint. Mean co-occurrence of seabirds with all juvenile salmon was calculated for each

station across all six surveys to determine areas of persistent predator-prey co-location. Co-occurrence of seabirds with the three most commonly caught salmon: juvenile coho, yearling, and subyearling Chinook salmon (see **Table 2.3** in Chapter 2 for details), was also calculated.

5.2.3 *Estimating encounter and predation risk*

Co-occurrence of seabirds and salmon was assumed to be proportional to encounter rate. Therefore, juvenile salmon predation risk given an encounter was hypothesized to be proportional to the density of predators and co-occurring alternate prey at each station, defined as overall predation pressure, *P*. To quantify *P*, I adapted the original Type II functional response model (Holling 1959), which estimates potential prey consumption (*C*) using the equation:

$$C = \frac{aN}{1+ahN} \tag{5.3}$$

where *N* is prey density, *a* is the combined predator attack and consumption rate (i.e., rate of successful predation), and *h* is prey handling time.

To adapt Equation 5.4 to estimate *P*, I first sought to distinguish juvenile salmon and alternate prey as separate components of prey density. Juvenile salmon density (ρ_S) was multiplied by the proportion of juvenile salmon at each station relative to total prey, which included juvenile salmon and alternate prey densities ($\rho_S + \rho_A$). This allowed salmon density to vary as a function of overall prey density available to predators. If there were equal densities of alternate prey and juvenile salmon, the overall salmon density was reduced by 0.5. If no alternate prey were present at the station, the overall salmon density was equal to total salmon density at the station. Seabird attack and capture rate, *a*, was set at 0.6, based on *in situ* observations of seabird-fish interactions (Enstipp et al. 2007, Crook & Davoren 2014). Handling time (*h*) was assumed to be minimal and removed from calculations, as seabirds typically consume fish within

seconds of capture (Enstipp et al. 2007, Crook & Davoren 2014). Seabird density at each station (B) was included to estimate overall predation pressure. These modifications to Equation 5.4 resulted in the equation:

$$P = \frac{a \times \left(\rho_S \times \frac{\rho_S}{\rho_S + \rho_A}\right) \times B}{1 + a \times \left(\rho_S \times \frac{\rho_S}{\rho_S + \rho_A}\right)} \quad (5.4)$$

To estimate the change in relative predation pressure when alternate prey co-occurred with juvenile salmon, P was calculated using only juvenile salmon density at each sampling station, and using juvenile salmon modified by the proportion of alternate prey. Differences in predation pressure with and without alternate prey included in the model were examined using a paired Wilcoxon signed-rank test (Zar 1999).

Finally, to estimate per capita salmon predation risk (R), which is expected to decline with increasing smolt densities, predation pressure (P) was divided by salmon density (ρ_S) at each station:

$$R = \frac{P}{\rho_S} \quad (5.5)$$

Predation pressure P and per capita predation risk R were calculated at each sampling station across all six surveys, resulting in unique, spatially-explicit risk estimates for each month, year, and station. Species- and age class-specific predation risk for juvenile coho, yearling, and subyearling Chinook salmon were also calculated. Risk estimates for May 2010 only include alternate prey density estimates from surface trawl catches because acoustic backscatter was not collected.

5.2.4 *Risk analysis*

To determine if predation risk varied among surveys, risk estimates were log-transformed and compared using a two-way ANOVA with an interaction between month and year (Zar 1999). Coefficients of variation were also calculated for each year to compare interannual variability in predation risk. To determine persistent high risk areas (i.e., risk hotspots), estimates of risk were plotted using ArcGIS 10.3 to examine spatial distributions of risk. Overall estimates of mean predation risk at each station were calculated and plotted, in addition to a grand mean of risk for all stations during each survey. Mean predation risk for coho, yearling, and subyearling Chinook salmon were plotted to examine species- and age class-specific spatial patterns. To compare interannual variability in predation risk for coho, yearling Chinook, and subyearling Chinook salmon, coefficients of variation were calculated.

To evaluate the influence of abiotic factors on predation risk, generalized additive mixed models (GAMMs) with a Poisson error structure and log link function were calculated using the 'mgcv' package (Wood 2016) in R version 3.3.2 (R Core Team 2016). GAMMs are nonparametric regression techniques useful for investigating non-linear relationships between response variables and covariates by using smoothing terms to fit the model (Wood & Augustin 2002, Wood 2006). A GAMM was developed with predation risk as the response variable and covariates including *in situ* measures of salinity (psu), transmissivity (i.e., water clarity; %), and temperature (°C) at 3-m depth sampled during the survey, distance from shore (km), and daily plume surface area (km^2) estimated by a hydrodynamic model of CRP circulation (Center for Coastal Margin Observation and Prediction; db33 climatological atlas; http://www.stccmop.org/datamart/virtualcolumbiariver). Thin plate regression splines were used as smoothing functions, and spline shrinkage was used to perform automatic smoothness

selection of covariates (Wood 2006). To account for spatial autocorrelation, station was included as a random effect. Each explanatory variable was retained in the model if it had a p-value < 0.05. Percent deviance explained and adjusted r^2 was calculated as an indicator of model performance. Models were evaluated by plotting normalized residuals to check for any patterns indicative of a violation of model assumptions (Zuur et al. 2009). The effect of each covariate retained in the final GAMM on predation risk was visually inspected to examine the relationship between risk and abiotic factors. Separate GAMMs were parameterized for coho, yearling, and subyearling Chinook salmon.

To evaluate the relationship between predation risk during early marine residence and salmon survival, the annual return of adult coho, spring Chinook, and fall Chinook salmon, represented by counts of returning fish from the corresponding juvenile year class at Bonneville Dam (the first dam on the Columbia River that interior basin salmon must pass during their return migration) were obtained from Columbia Basin Research (www.cbr.washington.edu/dart/adultruns.html). Juvenile coho and yearling Chinook salmon typically spend two years in the ocean prior to returning to natal rivers in the spring, so adult coho and spring Chinook run counts were lagged by two years (i.e., adult spring Chinook salmon return date of 2012 was assumed to represent outmigration during 2010). Subyearling Chinook salmon typically spend three years at sea and return during the fall (Myers et al. 1998), so fall Chinook salmon run counts were lagged by three years. To determine if predation risk experienced during early marine residence correlated to an index of salmon survival, overall median predation risk for coho, spring Chinook, and fall Chinook salmon during 2010–2012 was compared to adult returns using Pearson correlation.

5.3 RESULTS

Shearwater and murre co-occurrence with juvenile salmon averaged 0.79 ± 0.41 (SD) across the six surveys. Mean co-occurrence was consistently high (mean > 0.75) on all transects except the southernmost transect, Newport Hydrographic (**Figure 5.1**). Mean co-occurrence was greater than 0.75 at all sampling stations along the Columbia River transect, and the majority of stations sampled on transects along the Washington coast (**Figure 5.1**).

Predation risk was not significantly different between months ($F_1 = 0.09$, $p = 0.766$), years ($F_2 = 2.95$, $p = 0.056$), or the interaction of month and year ($F_2 = 1.61$, $p = 0.204$; **Figure 5.2**). Variability was almost twice as high in 2010 (CV = 323.7%) compared to 2011 (CV = 194.1%) and 2012 (CV = 196.8%). Predation risk declined by an average of 26% (range: 0–99%) when densities of alternative prey were included in risk calculations ($V = 11175$, $p < 0.001$).

The spatiotemporal distribution of predation varied by month and year (**Figure 5.3**). Overall predation risk estimates were greatest on the Cape Meares and Columbia River transects, particularly during June surveys (**Figure 5.3**). Risk estimates were also high on the Willapa Bay transect, particularly during 2010. Risk was also relatively high, especially in May 2010 and June 2012, on transects in the northern portion of the survey area (La Push, Father & Son transects). In general, risk was greater closer to shore and highest on transects that bracket the mouth of the Columbia River. Lowest risk estimates occurred on the Newport Hydrographic transect.

Overall predation risk for coho salmon was highest on the Cape Meares transect, but also at stations near the mouth of the Columbia River and nearshore on the Queets River transect (**Figure 5.4**). Predation risk for yearling Chinook salmon was widespread along the coast, with greatest risk nearshore on the Cape Meares, Columbia River, Willapa Bay, Grays Harbor, Queets

River, and La Push transects (**Figure 5.4**). Subyearling Chinook salmon predation risk was greatest nearshore on the Cape Meares transect, and off the mouth of the Columbia River (**Figure 5.4**).

GAMMs for overall predation risk indicated that sea surface temperature, distance from shore, water clarity, and plume surface area had significant effects on risk (**Figure 5.5**). As temperatures increased, predation risk decreased to a low near ~13.5°C, and then increased as temperatures surpassed ~14°C. Predation risk was greatest close to shore, and declined linearly with distance from shore across the range of distances sampled (1.9–46.3 km). Predation risk was higher in waters with water clarity <80%, and then decreased as water clarity increased above 80%. Predation risk was greatest when plume surface areas were the lowest, and declined linearly across the range of surface areas observed (1,535–35,840 km^2).

Increasing water clarity and plume surface area reduced juvenile coho predation risk across the range of observations (**Figure 5.6**). In contrast, coho predation risk increased slightly as sea surface temperature increased, particularly between 11–14°C. GAMM results for yearling Chinook salmon predation risk were similar to results for overall risk, and included greatest predation risk nearshore (<20 km), in turbid waters (<80%), and during periods of low plume surface areas (<10,000 km^2; **Figure 5.7**). GAMMs evaluating subyearling Chinook salmon predation risk indicated different relationships between risk and environmental covariates compared with yearlings. In particular, subyearling Chinook salmon predation risk increased with salinity and plume surface area (**Figure 5.8**). Predation risk was greatest for subyearling Chinook salmon when salinities were between ~29-32 psu, and plume surface area was greater than ~15000 km^2. Similar to coho, subyearling Chinook salmon predation risk increased with sea surface temperatures between 11–14°C, and then declined under warmer temperatures.

Relationships of subyearling Chinook salmon predation risk to water clarity and distance from shore were similar to other results, and indicated greatest predation risk nearshore and in turbid waters (**Figure 5.8**).

Variability in salmon predation risk varied by species and age class, and adult returns were also variable (**Figure 5.9**). Yearling Chinook salmon predation risk was slightly higher in 2010 (CV = 315.3%) compared to 2011 (CV = 258.9%) and 2012 (**Figure 5.9**; CV = 218.9%). In comparison, coho salmon predation risk was high in both 2010 and 2012, and subyearling Chinook salmon predation risk was highest in 2011 (Figure 5.9). Annual spring Chinook salmon adult counts at Bonneville Dam were negatively correlated to yearling Chinook salmon predation risk (**Figure 5.10**; $r = -0.999$, $t_1 = -22.98$, $p = 0.028$). Correlations between coho ($r = 0.935$, $t_1 = 2.64$, $p = 0.230$) and subyearling Chinook salmon ($r = -0.974$, $t_1 = -4.31$, $p = 0.145$) were not significant.

5.4 Discussion

Juvenile salmon predation risk was characterized using co-occurrence of smolts with two seabird species, which enabled quantification of the influence of alternate prey densities and the Columbia River plume on risk estimates. Increases in alternate prey and water clarity significantly reduced predation risk estimates. By examining predation risk of juvenile coho, yearling, and subyearling Chinook salmon, differences between species- and age class-specific relationships to abiotic factors were determined that provide insight to smolt survival. For example, when plume surface area was low, predation risk for coho and yearling Chinook salmon was high, but the opposite relationship was observed for subyearling Chinook salmon. These results could also potentially be used to predict predation risk using river discharge, which

increases plume surface area (Burla et al. 2010), and could aid management decisions aimed at maximizing survival of juvenile salmon in the Columbia Basin.

Mean co-occurrence of juvenile salmon with seabirds was high at the majority of sampling stations in the survey, suggesting that the 'predation gauntlet' that smolts pass through during their migration extends beyond the boundaries of the Columbia River plume. Co-occurrence was greatest near the mouth of the Columbia River, which is not surprising given that juvenile salmon emigrate out of the Columbia River into an area where seabirds consistently occur (Adams et al. 2012, Zamon et al. 2014, Menza et al. 2016). However, co-occurrence at stations in the northern portion of the survey area (La Push, Father & Son transects) was also high, indicating that juvenile salmon are subject to high seabird encounter rates throughout most of their northward migration along the Washington coast.

Co-occurrence was assumed to be proportional to encounter rate, but actual encounter rates of seabirds and juvenile salmon is unknown and may be influenced by a range of biotic and abiotic factors (Ropert-Coudert et al. 2006, Grémillet et al. 2012). For example, large, dense schools of CPS may be more visible to an airborne, visually-foraging seabird than individual salmon. Shearwaters and murres use a hierarchical foraging strategy (Fauchald et al. 2000) near the CRP, where they first respond to turbid water, then associate with large non-prey organisms near the surface (e.g., jellyfish, sharks), and then locate prey fish (Chapter 2). Thus, encounter rates of seabirds and smolts may not be directly proportional to co-occurrence. However, salmon are relatively evenly distributed near the surface and may be more likely to be encountered by seabirds because foraging is initiated from the water surface (Ballance et al. 2001). Steelhead and Chinook salmon near the surface in the Columbia River estuary are more likely to be consumed by avian predators than prey deeper in the water column (Collis et al. 2001, Hostetter et al.

2012), suggesting that these same fish may be vulnerable to predators in plume and nearshore coastal waters, especially in the absence of alternate prey. Alternate prey densities observed as acoustic backscatter in the upper 70 meters of the water column were combined with surface trawl catches, which may obscure relationships between prey located deeper in the water column and salmon near the surface. Additional research on seabird encounter rates under varying prey depth distributions and aggregation sizes will increase understanding of predator-prey co-occurrence and encounter rate probabilities of salmon with seabirds.

The presence of alternate prey was expected to dilute the overall number of juvenile salmon available to seabirds, and I found that predation risk was reduced by 26% when co-occurring alternate prey densities were included in risk calculations. This supports the alternative prey hypothesis (Fisher & Pearcy 1988, Pearcy 1992, Emmett & Sampson 2007), and suggests that predation risk declines as alternate prey densities increase. It should be noted, however, that the observed relationship may change if a different formulation of predation risk is used to include alternate prey in calculations (Abrams & Ginzburg 2000). For example, prey selectivity was not included in predation risk model specifications (Murdoch 1969, Oaten & Murdoch 1975, Chesson 1984). The spatiotemporal variability observed in predation risk across the six surveys suggests that the horizontal distribution and aggregation patterns of alternate prey leads to an uneven spatial distribution of predation risk. For example, CPS densities are often greatest near Grays Harbor and Willapa Bay (Chapter 2), but risk estimates on these transects varied by a factor of two during the six surveys. This result may have been related to the relative proportion of salmon and alternate prey available during each survey, which is influenced by plume dynamics (Chapter 2). Even when alternate prey densities are high, salmon may still be vulnerable. A recent study in California found that when murres shifted their foraging closer to

shore to consume abundant northern anchovy, incidental consumption of juvenile Chinook salmon increased and negatively impacted their survival (Wells et al. 2017). Thus, high densities of CPS may also attract more predators, which may increase predation risk to co-occurring smolts (i.e., apparent competition; Holt 1977). Because there are no recent data on food habits of seabirds near the CRP, and no concurrent data on prey availability in relation to seabird diet, knowledge of seabird prey selectivity when two or more prey co-occur is unknown. Without concurrent data on consumption of smolts by shearwaters and murres, and the availability of alternate prey, estimates of predation and predation impacts cannot be quantified.

Predation risk was consistently highest when water clarity was low, indicating that the turbid plume waters are a predation hotspot for juvenile salmon. Predation risk was greatest when water clarity was less than ~80%, and declined as water clarity increased. Shearwater and murre densities in the northern California Current are related to lower levels of water clarity (Chapter 2). Both species also selectively occupy plume waters (Chapter 3), indicating that the relationship between water clarity and predation risk for juvenile salmon is related to increasing use of turbid plume waters by seabirds. The relationship between water clarity and predation risk is counter to studies of juvenile salmon predation by piscivorous fish in lakes and rivers, where reduced water clarity reduces predation on salmon (Gregory & Levings 1998, Hansen et al. 2013, Hansen & Beauchamp 2015). Salmon may face a trade-off of reduced predation from seabirds in the CRP as they move into relatively clear water that may be counteracted by increased predation risk from piscivorous fish such as Pacific hake (*Merluccius productus*; Emmett et al. 2006, Emmett & Krutzikowsky 2008). For aerial seabirds, plume waters can be visually identified by color discontinuities across boundaries (Haney & Stone 1988, Cyrus 1991, Zamon et al. 2014), and both shearwaters and murres track the location of plume waters (Chapter

3). Seabirds can effectively forage in turbid waters (Haney & Stone 1988, Lovvorn et al. 2001, Grémillet et al. 2012), and the large footprint of the plume is likely a predictable and persistent foraging landmark for these species. Visually foraging seabirds also cue to other birds in foraging flocks on the water or in the air (Hoffman et al. 1981, Haney et al. 1992, Bairos-Novak et al. 2015), and the presence of conspecifics near the CRP may also act as a positive reinforcement for the formation of seabird aggregations. Shearwaters and murres show a threshold response to plume surface area (Chapter 3), which may be related to the non-linear relationship observed between predation risk and water clarity, especially for yearling Chinook salmon. The peak in predation risk around ~80% water clarity may be related to turbidity levels at which plume waters can no longer be delineated from surrounding marine waters, or to the formation of sharp boundaries between turbid plume waters and surrounding ocean waters as plume surface area increases. An examination of the relationship between turbidity and plume surface area was beyond the scope of this study, but further research on the interactions between these two abiotic factors and predator and prey densities are needed to understand the non-linear relationship between predation risk and water clarity.

Plume surface area was an important component of coho and yearling Chinook salmon predation risk, which declined as surface area increased. Thus, in addition to increasing alternate prey densities, increasing plume surface area may dilute juvenile salmon predation risk by creating a larger foraging area for seabirds. Both shearwaters and murres concentrate in the CRP when surface areas are low (Chapter 2), and move towards plume boundary waters when surface areas exceed approximately 1500–4000 km^2 (Chapter 3). This suggests that variation in the size of the river plume and biophysical coupling at the convergent plume fronts creates foraging opportunities for seabirds (Zamon et al. 2014). Northern anchovy densities are positively

correlated with increases in river discharge (Kaltenberg et al. 2010), which prompts anchovy to aggregate and spawn near CRP boundaries in spring and summer (Richardson 1973, 1981). Seabirds that move to the plume boundary as surface area increases may be responding to increasing alternate prey densities near the plume edge, thereby reducing predation risk to juvenile salmon. Plume fronts on the Columbia River aggregate zooplankton and larval fish (Morgan et al. 2005), but juvenile salmon are not known to congregate near plume boundaries to feed (De Robertis et al. 2005). Salmon may avoid plume boundaries as an adaptive response to avoid avian predators. However, some piscivorous predators including Pacific hake, Pacific mackerel (*Scomber japonicas*), jack mackerel (*Trachurus symmetricus*), and blue shark (*Prionace glauca*) avoid low salinity plume waters, while other predators including spiny dogfish (*Squalus acanthias*) associate with warmer, low salinity plume water nearshore (Litz et al. 2013). Thus, even juvenile salmon that are not associated with the plume boundaries may still experience elevated predation pressure as they migrate out of their freshwater habitat. There is growing evidence of smolt consumption by marine mammals including California sea lions (*Zalophus californianus*), harbor seals (*Phoca vitulina*), and harbor porpoise (*Phocoena phocoena*) (Szoboszlai et al. 2015, Chasco et al. 2017, Thomas et al. 2017), which may also negatively impact juvenile salmon survival (Berejikian et al. 2016, Adams et al. 2016). Without empirical data on salmon and alternate prey consumption by piscivorous fish, marine mammals, and seabirds under varying environmental conditions, a full understanding of the relationship between juvenile salmon predation risk and survival is incomplete.

Predation risk estimates for subyearling Chinook salmon indicated higher risk with greater plume surface area, in contrast to estimates of risk for coho and yearling Chinook salmon that exhibited lower risk as plume surface area increased. Emmett et al. (2004) found greater

densities of subyearling Chinook salmon in the CRP when river flows were high, and suggested that these fish may not be able to swim against strong seaward currents. Plume surface areas typically reach seasonal maxima in May–June (Hickey et al. 2010), which is during the yearling coho and Chinook salmon migration (Weitkamp et al. 2012). Subyearling Chinook salmon migrate out of the estuary later in the summer (Weitkamp et al. 2012), when river discharge is typically lower than in May and June. If river discharge has not declined, subyearling Chinook salmon may arrive in the CRP earlier and be more vulnerable to predators. Only samples from May and June were used in this study, although greatest numbers of subyearling Chinook salmon are usually caught in September surveys from the same study area (De Robertis et al. 2005, Miller et al. 2013). Thus, the unexpected relationships to plume surface area may be related to sample size and timing. Interestingly, salinity was not a significant factor in any of the GAMMs except the model of subyearling Chinook salmon predation risk, where greater risk was related to increasing salinity. Subyearling Chinook salmon occupy nearshore waters near the mouth of the Columbia River longer than juvenile coho and yearling Chinook salmon (Fisher & Pearcy 1995, Teel et al. 2015), and variation in salinity due to shifts in the location of the plume, decreases in river discharge, or localized upwelling events may explain the observed relationship to salinity. An inshore pool of saltier water is often present on the south side of the mouth of the Columbia River in northern Oregon waters (Hickey et al. 2010), which is where subyearling Chinook salmon predation risk was greatest and may explain the relationship between salinity and predation risk.

Yearling Chinook salmon predation risk was high across most of the survey area compared to coho and subyearling Chinook salmon, indicating that this prey group may be more vulnerable to predators at multiple locations along the coast. Spring Chinook salmon adult

returns were also the only group that was significantly correlated with annual predation risk. Although only three years of data were used, this suggests a relationship between greater adult spring Chinook salmon returns when predation risk is lower. Overall variability in predation risk was highest in 2010, when spring Chinook adult returns were the lowest, suggesting that variance in predation risk during May and June, rather than the overall median, may be a better indicator of survival (*sensu* Jentsch et al. 2007). Further work examining a longer time series of predation risk estimates and adult returns may provide better information on the relationship between juvenile predation risk, the plume, and adult survival.

Results of this study suggest that knowledge of plume surface area can provide insight on conditions that affect juvenile salmon predation risk. Plume surface area is correlated to river discharge, and both metrics are available from monitoring stations on the river and from hydrodynamic models, such as the SELFE model developed by Zhang & Baptista (2008). This type of data could be developed into an index of predation risk that may provide hatchery managers with a better understanding of how smolt release timing coincides with variation in plume surface area and adult returns. Similarly, springtime river flows could be coordinated to minimize periods of increased juvenile salmon predation risk, especially when risk is predicted to be high (e.g., small plume surface area).

5.5 FIGURES

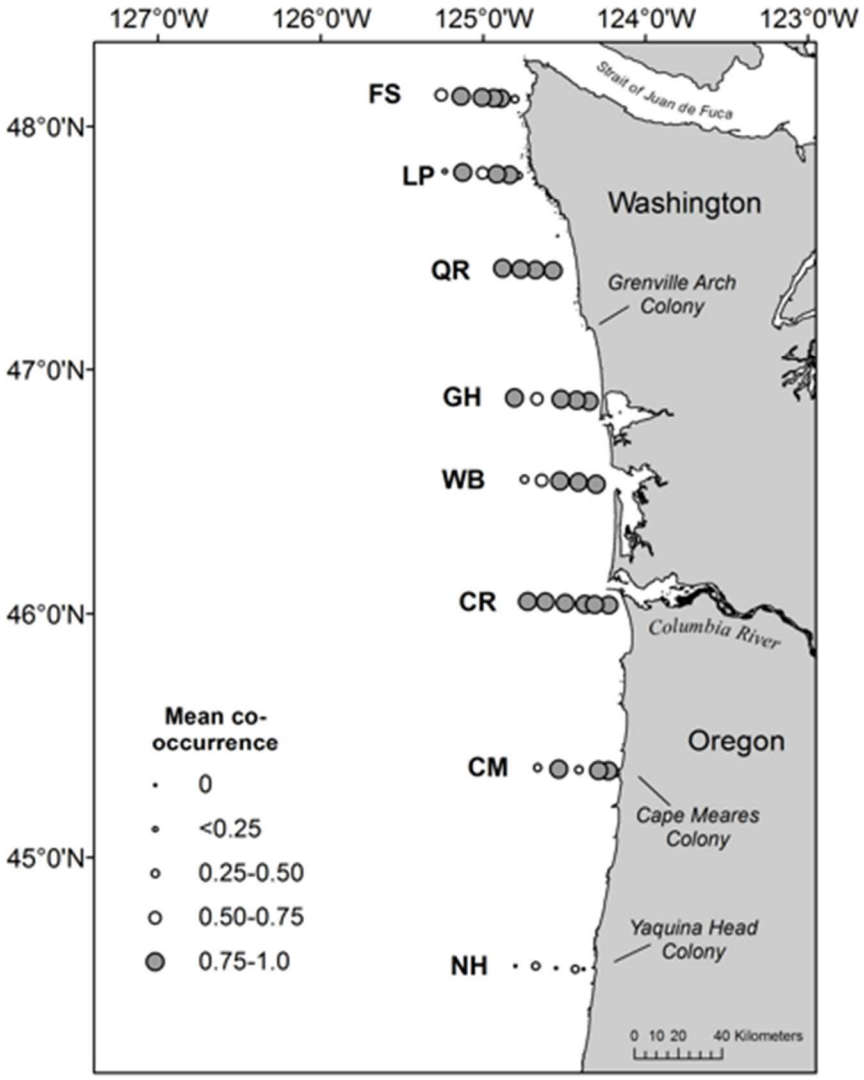

Figure 5.1 – Mean co-occurrence of seabirds and juvenile salmon during six surveys in May and June 2010–2012. Grey dots are stations with mean co-occurrence greater than 0.75. Large murre colonies (Grenville Arch, Cape Meares, and Yaquina Head) are labeled.

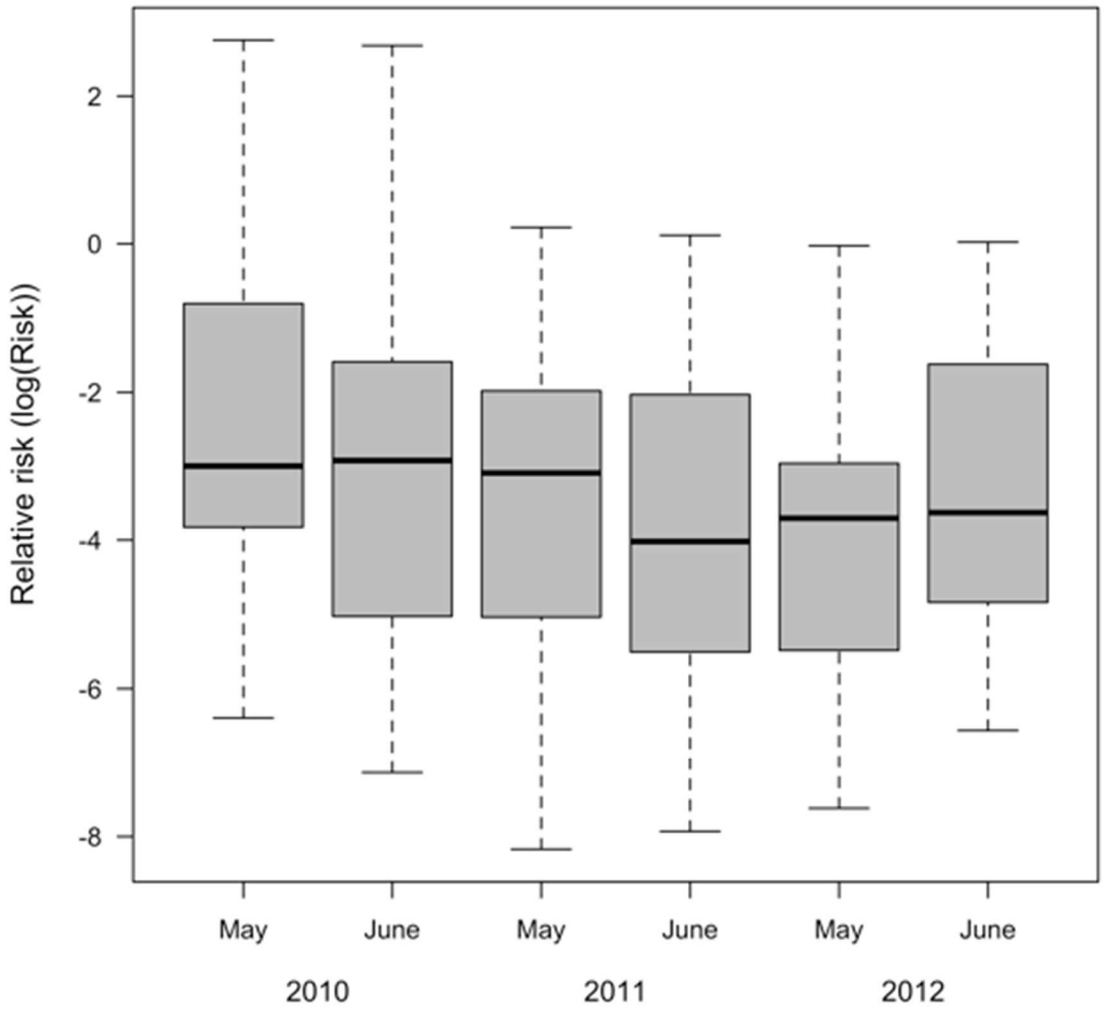

Figure 5.2 – Natural log transformed predation risk for each survey. Dark line: median; box: interquartile range (IQR); error bars: max/min within 1.5 x IQR above/below IQR; outliers not shown.

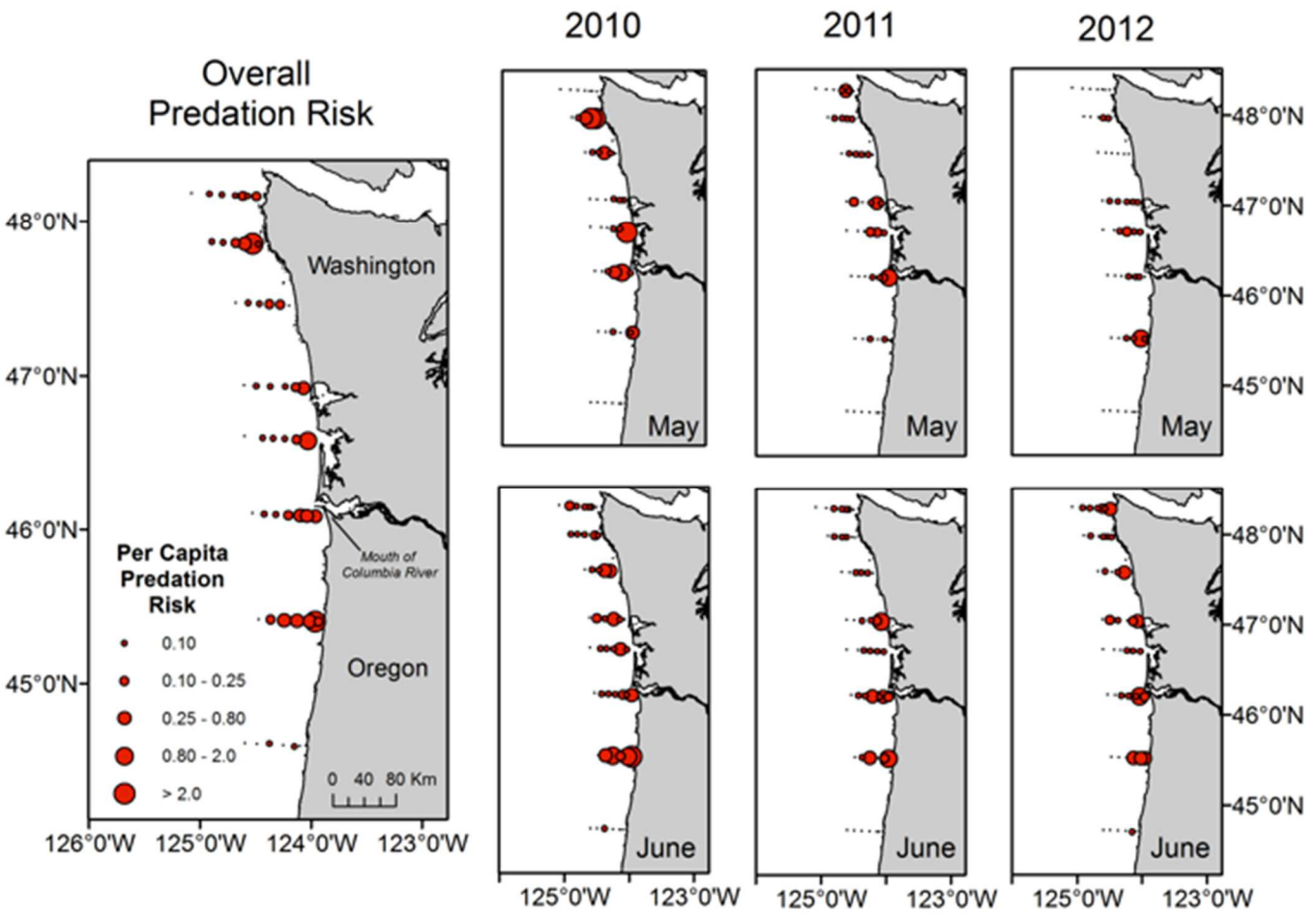

Figure 5.3 – Maps of overall mean per capita predation risk, and predation risk at each sampling station during May and June, 2010–2012.

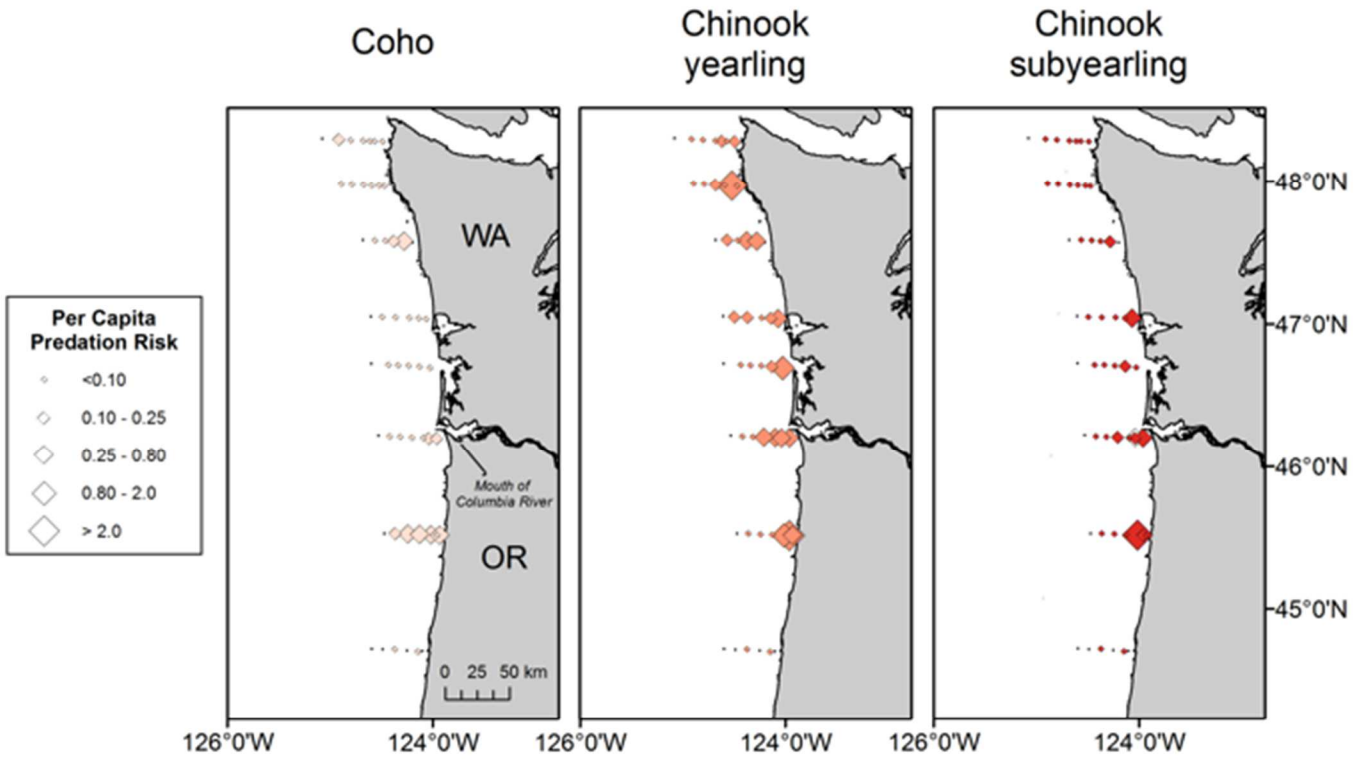

Figure 5.4 – Maps of overall mean per capita predation risk for juvenile coho, yearling, and subyearling Chinook salmon during May and June 2010–2012.

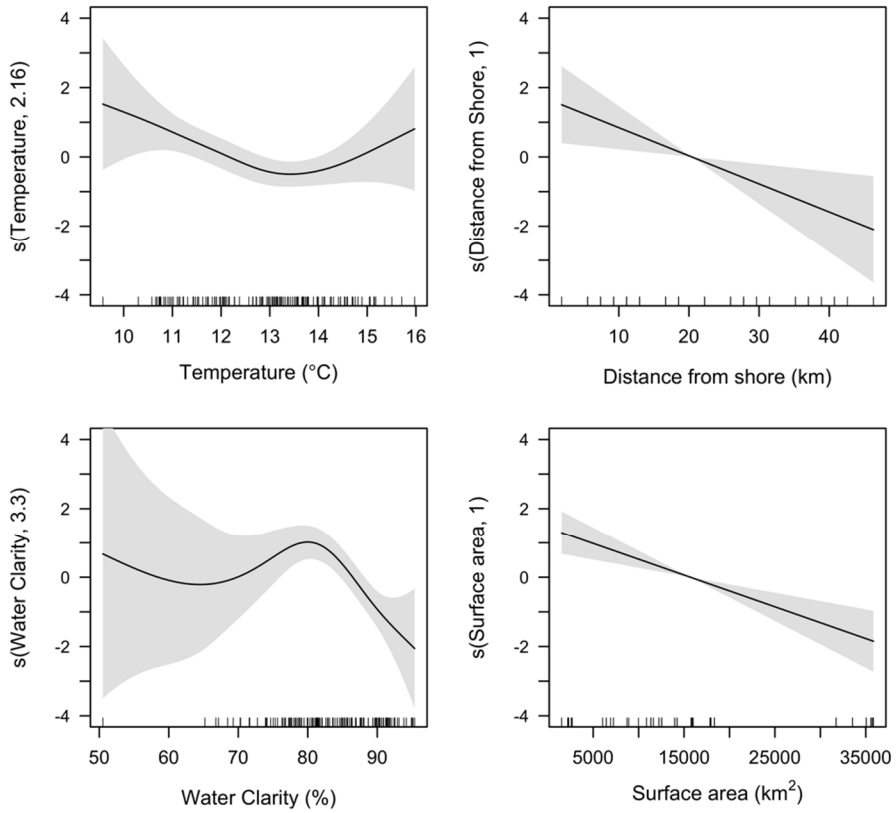

Figure 5.5 – GAMM results for the effects of temperature, distance from shore, water clarity, and plume surface area on per capita predation risk of all juvenile salmon during May and June 2010–2012. Gray shading around smooth fits are 95% confidence intervals, and data availability is indicated by tic marks above x-axis.

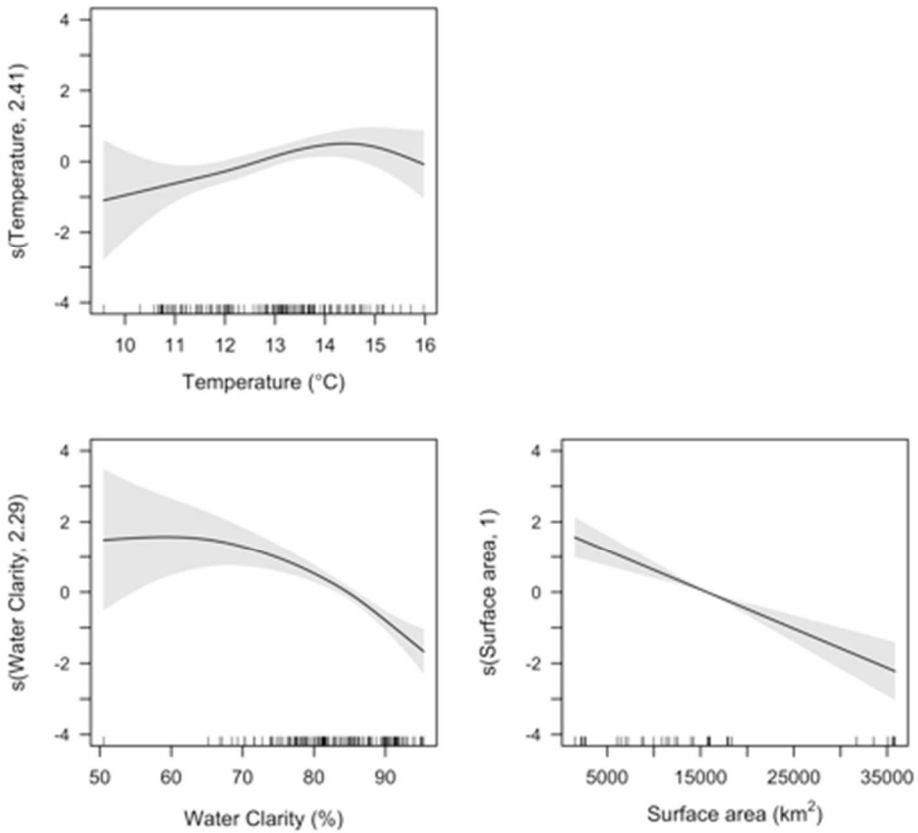

Figure 5.6 – GAMM results for the effects of temperature, water clarity, and plume surface area on per capita predation risk of juvenile coho salmon. Gray shading around smooth fits are 95% confidence intervals, and data availability is indicated by tic marks above x-axis.

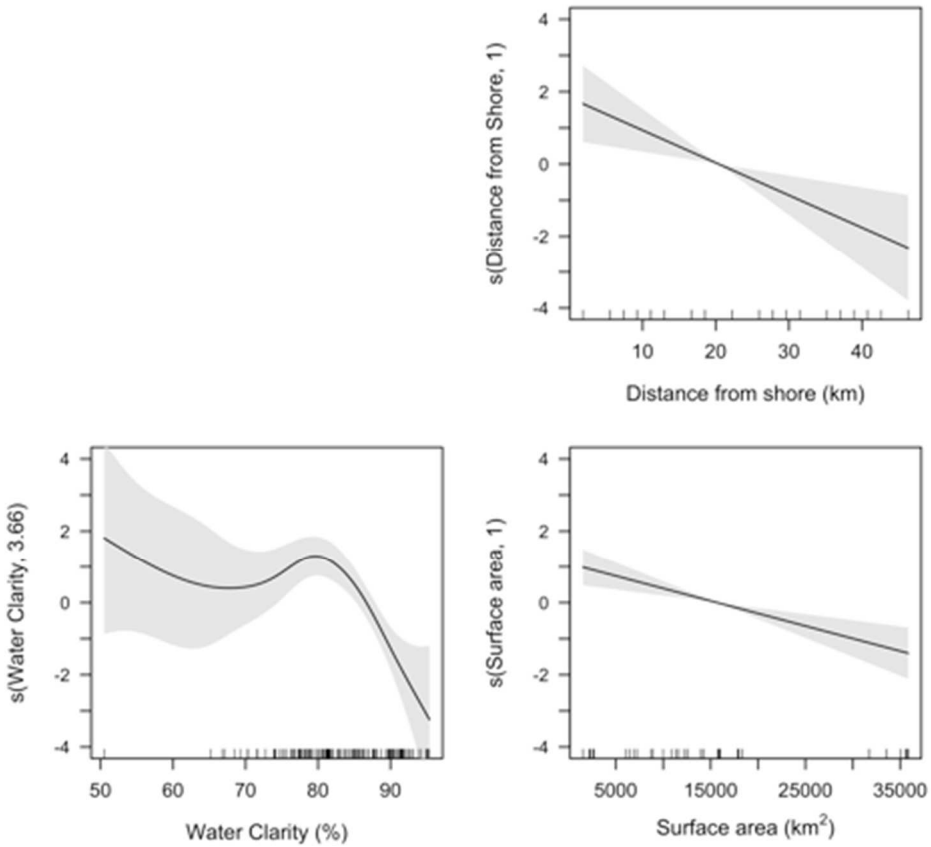

Figure 5.7 – GAMM results for the effects of distance from shore, water clarity, and plume surface area on per capita predation risk of yearling Chinook salmon. Gray shading around smooth fits are 95% confidence intervals, and data availability is indicated by tic marks above x-axis.

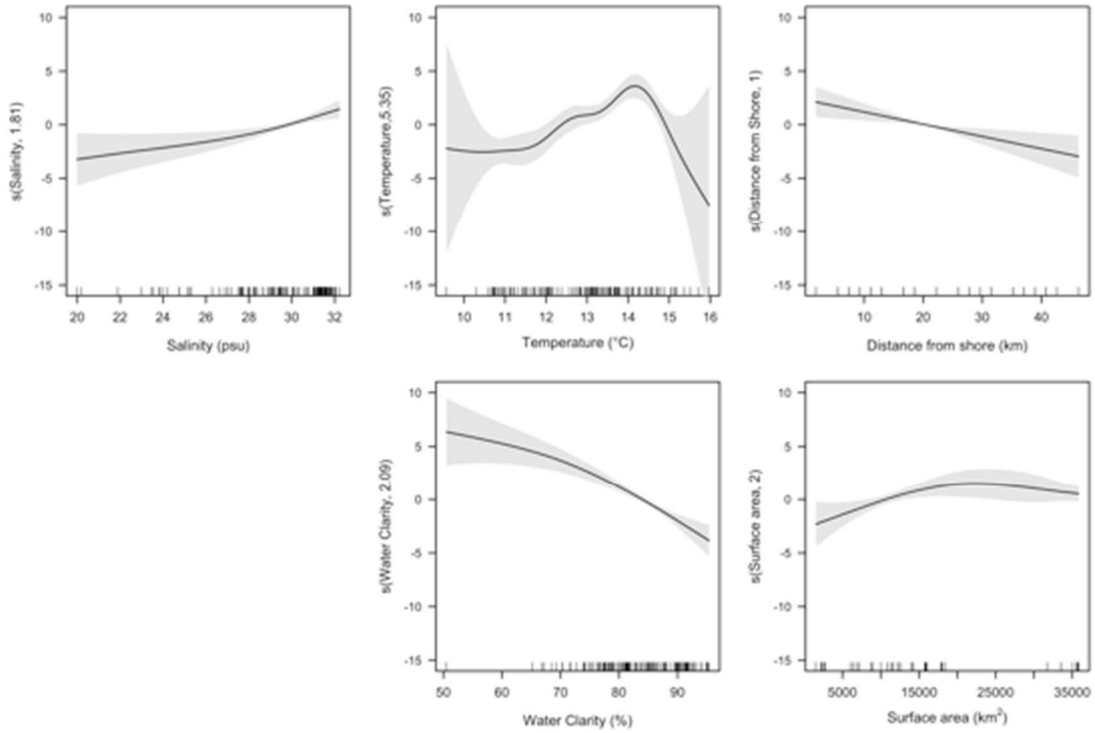

Figure 5.8 – GAMM results for the effects of salinity, temperature, distance from shore, water clarity, and plume surface area on per capita predation risk of subyearling Chinook salmon. Gray shading around smooth fits are 95% confidence intervals, and data availability is indicated by tic marks above x-axis.

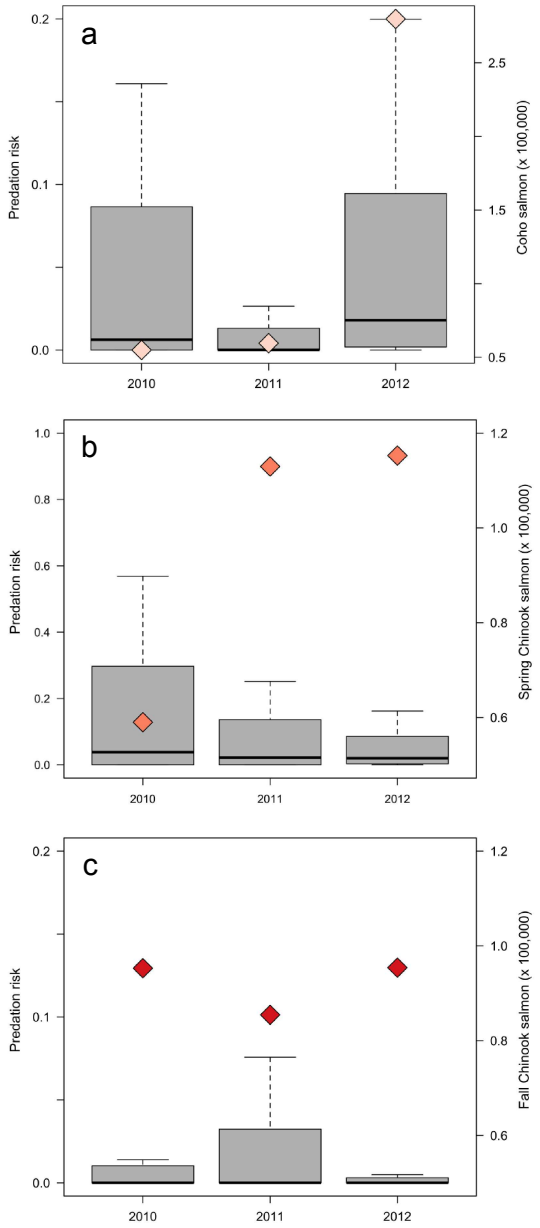

Figure 5.9 – Boxplots of salmon predation risk: a) coho salmon, b) yearling Chinook salmon, c) subyearling Chinook salmon. Dark line: median; box: interquartile range (IQR); error bars: max/min within 1.5 x IQR above/below IQR; outliers not shown. Corresponding salmon counts at Bonneville Dam lagged by two years for coho and yearling Chinook salmon, and three years for subyearling Chinook salmon, are shown as shaded diamonds.

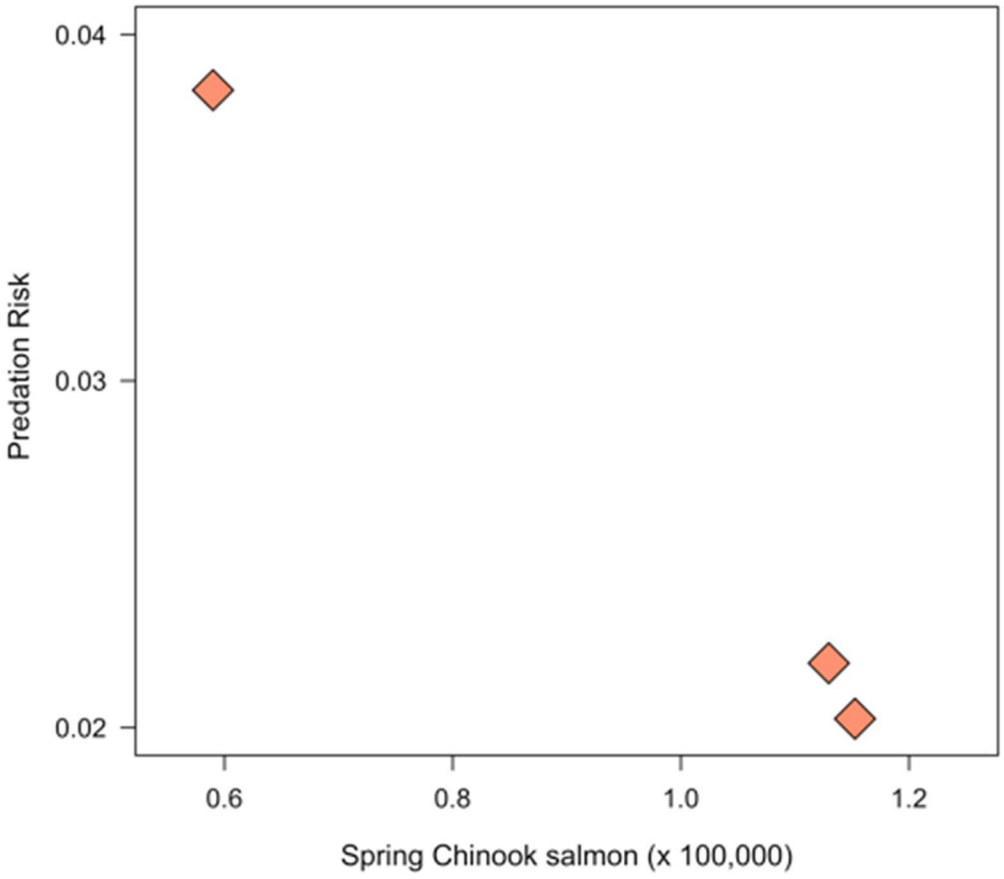

Figure 5.10 – Relationship between spring Chinook salmon adult counts at Bonneville Dam (2-yr lag) and yearling Chinook salmon predation risk (Pearson correlation; $r = -0.999$, $t_1 = -22.98$, $p = 0.028$).

Chapter 6. SYNTHESIS

6.1 THE INFLUENCE OF THE COLUMBIA RIVER PLUME ON PREDATOR-PREY INTERACTIONS

This dissertation provides a quantitative understanding of the Columbia River plume's influence on avian predator and fish prey interactions. River plumes are often areas of enhanced primary and secondary productivity due to increased nutrient input and recirculation of stratified coastal waters (Lohrenz et al. 1999, Kudela et al. 2010, Demidov et al. 2017). Plume-enhanced productivity supports high densities of small coastal pelagic fish species (CPS; St. John et al. 1992, Litz et al. 2013), which attracts upper trophic level piscivorous predators including fish, seabirds, and marine mammals (Owen 1968, Kowalczyk et al. 2015, González Carman et al. 2016). Observations of apex predators occurring in plume habitats are usually attributed to high rates of primary production and biophysical coupling of zooplankton that support high prey fish densities, but direct evidence of these assumed relationships are rare. By using at-sea surveys, satellite telemetry, and a hydrodynamic model, this dissertation demonstrated with direct evidence that the Columbia River plume influences seabird distributions, interactions with prey fish, and juvenile salmon predation risk.

This research is applicable to other parts of the world where river plumes influence seabird distributions. For example, researchers in the Bay of Biscay documented increased densities of common murres (*Uria aalge*) near the confluence of two river plumes, and proposed a relationship between murres and high concentrations of small pelagic fish associated with freshwater discharge from the Gironde and Loire Rivers (Bellier et al. 2010, Le Rest et al. 2016). In the Mediterranean Sea, Cory's shearwaters (*Calonectris diomedea*) and endangered Balearic

shearwaters (*Puffinus mauretanicus*) aggregate near the Ebro River delta, where the input of nutrients from the Ebro River increases productivity during spring and summer (Louzao et al. 2006, 2009). These closely-related species may show parallel foraging patterns of murres and shearwaters observed in this study, including selective occupancy of plume boundary waters where increased densities of CPS occur. Shearwaters and murres use memory (Davoren et al. 2003a, Weimerskirch 2007, Regular et al. 2013), visual cues (Hoffman et al. 1981, Haney et al. 1992, Mitkus et al. 2016), and olfaction (Hutchinson et al. 1984, Van Buskirk & Nevitt 2008) to locate foraging areas. Therefore, increased seabird aggregations near river plumes can be explained by the predictable formation of plumes near river mouths and the surface manifestation of buoyant, turbid waters. The spatial extent of many river plumes may enable detection by seabirds at greater distances than other oceanographic features, such as thermal fronts. Other dynamic river plumes that exhibit seasonal variability in size may also elicit a response by seabirds to increasing plume surface area, similar to the threshold documented in this study.

In addition to seabirds, freshwater discharge from the Columbia River also influences the density and distribution of fish, including species that occupy estuarine and marine waters (Whitfield 2015). For example, stenohaline species including Pacific sardine (*Sardinops sagax*) and Pacific hake (*Merluccius productus*) avoid the low salinity Columbia River plume waters by moving offshore into saltier water (Emmett & Krutzikowsky 2008, Litz et al. 2013). In contrast, some euryhaline species including spiny dogfish (*Squalus acanthias*) and albacore (*Thunnus alalunga*) occur in lower salinity plume waters close to shore (Owen 1968, Richardson 1981, Kaltenberg et al. 2010). Northern anchovy spawn near the Columbia River plume when river discharge increases in spring (Richardson 1981), with the distribution and abundance of eggs,

larvae, and adults positively correlated to river discharge. CPS including northern anchovy, Pacific herring, and smelts occurred disproportionately in plume waters in this study, although species-specific spatial variation was apparent. Pacific herring and Pacific sardine were consistently near the northern edge of the river plume where strong convergent fronts form (Jay et al. 2009), whereas northern anchovy exhibited more variable spatial distributions in relation to the surface area of the plume. In addition to marine fish species, anadromous species including eulachon (*Thaleichthys pacificus*) and Pacific salmonids (*Oncorhynchus* spp.) use the river plume during their movements between fresh- and saltwater habitats (De Robertis et al. 2005, Gustafson et al. 2012), and juvenile salmon smolts were observed disproportionately in plume waters during this study.

6.2 INSIGHTS ON SALMON OCEAN ECOLOGY

The diversity and abundance of CPS near the Columbia River plume played an important role in reducing juvenile salmon predation risk in this study, which supports a previous study that found reduced juvenile salmon predation by hake when CPS were abundant (Emmett & Sampson 2007). Pacific hake, sooty shearwaters, and common murres occupy different habitats along the coast, with shearwaters and murres occurring more frequently nearshore in plume waters (Zamon et al. 2014), and hake in offshore marine waters (Emmett et al. 2006, Litz et al. 2013). Early marine residence is considered a 'critical period' of juvenile salmon life history, because mortality during this time can impact adult recruitment (Hjort 1914, 1926, Beamish & Mahnken 2001). Smolts occupying plume waters may avoid predatory fish such as hake, but experience increased predation from seabirds, highlighting tradeoffs that juvenile salmon face during early marine residence. The abundance and availability of CPS (i.e., alternate prey) to

piscivorous fish, seabirds, and mammalian predators throughout the geographic range of smolt migration is therefore hypothesized to be an important factor in juvenile salmon predation mortality.

Juvenile salmon have to contend with a diverse suite of predators including birds, mammals, and piscivorous fish during their migration through the Columbia River estuary, plume, and coastal marine waters. Collectively, these predators are hypothesized to negatively impact returning adult abundances (Pearcy 1992, Muir et al. 2006, Scheuerell et al. 2009). The best-studied predators are Caspian terns (*Hydroprogne caspia*) and double-crested cormorants (*Phalacrocorax auritus*), which consume between 3 to 21 million smolts per year in the lower Columbia River estuary (Collis et al. 2001, Evans et al. 2012). The total amount of smolts consumed by shearwaters and murres is unknown, but numbers are expected to be similar to estuarine avian predator consumption, based on diet studies, estimated seabird population abundances, and bioenergetics modeling (Wiens & Scott 1975, Varoujean & Matthews 1983). Predatory fish including jack mackerel (*Trachurus symmetricus*), spiny dogfish (*Squalus acanthias*), soupfin sharks (*Galeorhinus galeus*), steelhead (*O. mykiss*), and cutthroat trout (*O. clarki*), in addition to Pacific hake, consume juvenile salmonids (Emmett & Krutzikowsky 2008, Brodeur et al. 2014). Less is known about consumption by marine mammals, but California sea lions (*Zalophus californianus*), harbor seals (*Phoca vitulina*), and possibly harbor porpoise (*Phocoena phocoena*) all consume juvenile salmon (Szoboszlai et al. 2015, Berejikian et al. 2016, Adams et al. 2016). Estimated population abundances of these three apex predator groups vary, with some population estimates ranging into the millions (e.g., hake, shearwaters; Wiens & Scott 1975, Methot & Dorn 1995), indicating potentially significant predation impacts to juvenile salmon populations. A recent study by Wells et al. (2017) demonstrated that even when the

overall proportion of juvenile salmon in a seabird predator's diet is low, incidental consumption when alternate prey are scarce can negatively impact survival of juvenile salmon populations.

In addition to navigating a predation gauntlet, juvenile salmon have evolved to migrate through dynamic and physiologically challenging habitats, where they experience significant changes in abiotic factors including salinity and water clarity. The observed relationship of reduced juvenile salmon predation risk from seabirds with increased plume surface area may indicate an evolutionary strategy that links increased river flows, increased coastal productivity, increased abundance of alternate prey, and increased search area for predators to increased juvenile salmon survival. Plume surface area may be a useful index to track predation risk and survival of juvenile salmon during the early marine period. However, high river flows may also prevent the movement of euryhaline CPS such as northern anchovy into the Columbia River estuary (Weitkamp et al. 2012), which could increase predation pressure on juvenile salmon from foraging terns and cormorants. Relationships between variability of river discharge in the Columbia River estuary, the surface area and volume of the Columbia River plume, the distribution and abundance of CPS, location of foraging predators, and juvenile salmon predation risk are complex. Integrating studies across the continuum of estuarine and plume habitats that juvenile salmon occupy will facilitate a better understanding of the areas and conditions where juvenile salmon predation risk is relatively higher or lower.

6.3 IMPLICATIONS FOR SALMON MANAGEMENT

Salmon are iconic in the Pacific Northwest, vital to the spiritual identity of local Native American tribes, and valued culturally and economically by many communities in the region (NRC 1996). Recovery and conservation of threatened and endangered Pacific salmonid

populations in the Columbia Basin is a science priority for state and federal government agencies and resource managers (NRC 2004). Salmonid conservation and management efforts have focused on spawning habitat restoration to increase survival of eggs and alevins (i.e., yolk-sak larvae), regulation of water flow during downstream migration to reduce impacts of dam passage to fingerlings and smolts, and commercial fishery regulation to allow for adult escapement (NRC 1996). Effective management of salmonid stocks also requires an understanding and quantification of relationships between juvenile salmon population abundance, early marine mortality, and adult returns that can be used to inform harvest guidelines (PFMC 2016).

The influence of variable ocean conditions and the Columbia River plume on juvenile salmon survival is an important issue for Pacific Northwest resource managers (NRC 2004). Including plume and ocean condition metrics in quantitative estimates of adult returns may reduce model uncertainty and improve model performance, which should aid salmon fisheries management and conservation efforts (Burke et al. 2013b). Specifically, fluctuations in plume surface area may account for some of the unexplained variation in adult salmon returns. Further, information on plume surface area may be an informative metric for management of hatchery-reared juvenile salmon releases, as well as water releases at dams to aid juvenile salmon passage and survival through the hydropower system (Scheuerell et al. 2009, Miller et al. 2013, Brosnan et al. 2014). On average, plume surface areas during 1999–2016 exceeded the 1500 km^2 threshold estimated in this study 236 days per year, and exceeded 4000 km^2 114 days per year. Surface areas exceeded 4,000 km^2 72% of the time during the peak smolt migration period of April–June, but also dropped below 1,500 km^2 approximately 5% of the time during the same period. Plume surface area is correlated with river discharge (Burla et al. 2010), and both metrics are available in near real-time from monitoring stations on the river (e.g., discharge, $ft^3\ s^{-1}$; U.S.

Geological Survey surface water station 14246900; http://waterdata.usgs.gov/nwis) or from hydrodynamic model outputs (e.g., surface salinity [psu] forecasts; http://www.stccmop.org/datamart/virtualcolumbiariver/forecasts). These data could be incorporated into scenario analyses to determine if plume surface area will reduce variability in models of adult returns and/or improve salmon survival (Kareiva et al. 2000, Ruckelshaus et al. 2002).

Pacific salmon are an important commercial fishery in Columbia River and the northern California Current, which is one of the first Large Marine Ecosystems (Sherman et al. 1993, Sherman & Duda 1999) where ecosystem-based fisheries management (EBFM) is being implemented (Alexander 1993, Levin et al. 2009, Sydeman & Thompson 2010). EBFM prioritizes management of ecosystems rather than single stocks (Pikitch et al. 2004, Dolan et al. 2016). Using an ecosystem perspective, the Pacific Fishery Management Council (PFMC) recognizes the benefits that CPS provide as forage for other commercially fished species, as well as for seabirds and marine mammals (PFMC 2018). By managing CPS including northern anchovy, CPS will be available as prey for piscivorous predators, which should reduce juvenile salmon predation risk and potentially improve adult salmon return rates.

6.4 IMPLICATIONS FOR CLIMATE CHANGE

The Columbia River Basin has undergone anthropogenic modification for over a century (Sherwood et al. 1990). Hydropower and storage dams have stabilized seasonal river flows, reduced annual discharge, and modified the size and orientation of the Columbia River plume (Ebbesmeyer & Tangborn 1992). Anthropogenic impacts of dams may be exacerbated by climate change, which is expected to significantly alter freshwater resources in the Pacific Northwest

(Hamlet & Lettenmaier 1999, Mote et al. 2003, Payne et al. 2004). For example, diminished snowpack is expected to lower spring and summer freshwater runoff volumes, and cause earlier spring peak flows in the Columbia River Basin (Hamlet & Lettenmaier 1999, Payne et al. 2004, Hamlet et al. 2007). Decreased runoff may further reduce the volume and surface area of plume habitat that juvenile salmon use during early marine residence, and earlier peak flows may result in a mismatch in the timing of smolt arrival to the plume and the peak in ocean productivity (Cushing 1969; Beamish and Mahnken 2001). Further, results from this study demonstrate that seabirds concentrate in the river plume when surface areas are low, which will increase juvenile salmon predation pressure during early marine residence.

Reduced snowpack levels are predicted in part because of warmer air temperatures, which will also increase river, estuary, and ocean temperatures (IPCC 2014) and could alter predator-prey interactions near the Columbia River plume. High temperatures in the Columbia River estuary influence the timing of juvenile salmon migration to sea (Roegner and Teel 2014), which could increase smolt mortality in the plume if salmon prey are unavailable, leading to greater variability in adult returns (Crozier et al. 2008a; Crozier et al. 2008b). Under warm ocean conditions and low river flow, anchovy spawning events may not be as successful, especially because they are dependent on recirculation of the river plume to retain eggs and larvae (Parnel et al. 2008). This lack of egg and larvae retention could lead to reduced abundances of adult CPS as alternate prey for predators, as well as reduced larval CPS prey for juvenile salmon (Daly et al. 2009, 2013, 2017). Fish and seabird populations may also undergo shifts in their range related to ocean temperatures and changing prey availability (Sydeman et al. 2012, Morley et al. 2018), such that predation risk to certain fish species including juvenile salmon may increase, while other prey populations may experience reductions in predation pressure (Durant et al. 2013).

6.5 RECOMMENDATIONS FOR FUTURE RESEARCH

Results of this study can be used to inform management and conservation efforts for Columbia River basin salmonid populations. For example, the surface area of the Columbia River plume is an explanatory factor in two recent studies of juvenile salmon survival, where increased surface areas resulted in greater smolt survival (Miller et al. 2013, Brosnan et al. 2014). This dissertation quantified a link between plume surface area and seabird predators, and identified a threshold surface area between 1500–4000 km^2 that correlates with seabird movement to the plume boundary. Monitoring estimates of plume surface area, or its correlate river discharge, and including this metric in hatchery release and water release decisions may be a useful means to improve juvenile salmon survival. To fully understand the relationship between juvenile salmon survival and the Columbia River plume, it is imperative to quantify consumption of juvenile salmon by piscivorous predators near the Columbia River plume, and to examine conditions under which smolt predation was relatively low or high (e.g., plume surface area < 1500 km^2; low CPS abundance). Without empirical data on salmon and alternate prey consumption by piscivorous fish, seabirds, and marine mammals, the relationship between the Columbia River plume, predation risk, and ultimately salmon survival will remain unresolved.

This dissertation used a combination of *in situ* sampling of physical and biological data from research vessels, remotely-sensed data from boats, aircraft, and satellite telemetry, and hydrodynamic modeling to examine relationships of seabirds and fish near the Columbia River plume. Boat surveys offer unparalleled opportunities to directly measure the environment and associated biological community. Existing NOAA datasets of juvenile salmon, CPS, and seabirds used here were a crucial component of this dissertation. This included net sampling as well as fisheries acoustics data, which allowed for the quantification of CPS throughout the water

column and a better index of alternative prey for predation risk calculations. Data on other aquatic organisms collected in the upper 20 meters of the water column (e.g., jellyfish, sharks) were used to demonstrate the series of cues that shearwaters and murres respond to when foraging near the Columbia River plume. Ecosystem studies such as this one are expensive, but provide invaluable long-term data that can be used to inform ecosystem-based management (Harvey et al. 2016, Hughes et al. 2017). Results of this study also suggest that an expanded analysis of NOAA seabird and juvenile salmon data between 2003–2017 in relation to the Columbia River plume will provide a more comprehensive evaluation of the influence of plume surface area and water clarity on juvenile salmon predation risk, which can then be compared to adult salmon returns across a longer time period.

Comparative studies of river plumes in different regions are needed to validate interpretations from this study, identify generalities, and enhance our understanding of the influence of river plumes on predator-prey interactions. Freshwater influx from other rivers that support large populations of salmon, including the Fraser and Copper Rivers, are probably also areas of increased productivity, biological diversity, and possible hotspots of juvenile salmon predation mortality (St. John et al. 1992, Beamish & Mahnken 2001). Future research comparing patterns of predator and prey distributions within and among large river plumes will help determine if the relationship between plume surface area, seabirds, and juvenile salmon predation risk observed in this study are generic. Similarly, other researchers have identified river plumes as candidates for expanded protections for seabirds (Louzao et al. 2006, 2009). By comparing seabird associations with river plumes in other areas, a better understanding of how plume dynamics influence seabird distributions can be used to inform both fish and seabird conservation efforts.

Finally, results of this study will inform predictions of the influence of climate change on ecological interactions in river plumes, including increasing predation pressure during juvenile salmon early marine residence (*sensu* Mote et al. 2003). Because of the enhanced productivity generated by nutrient input and recirculation, the Columbia River plume has been identified as a potential refuge for juvenile and adult fish during periods of poor ocean productivity, such as delayed upwelling (Litz et al. 2013). Predictions of climate change include more variable upwelling in the California Current (Rykaczewski & Checkley 2008, Rykaczewski et al. 2015), which increases the importance of the Columbia River as a source of localized primary production (Doney et al. 2012, Bakun et al. 2015). However, if seabirds concentrate in river plumes during periods of low ocean productivity, then juvenile salmon predation is expected to intensify, which will compound climate change impacts of lower river discharge, warmer temperatures, and less prey. Responses of predators and prey to variable environmental conditions are difficult to predict, and different species may show unique and contrasting responses. Ongoing research and monitoring of the physical plume habitat, predator populations, CPS stocks, and salmon abundance will enhance our understanding of Columbia River salmon population trends and inform management and conservation efforts aimed at recovering threatened and endangered species.

REFERENCES

Abrams PA (2000) The evolution of predator-prey interactions: Theory and evidence. Annu Rev Ecol Syst 31:79–105

Abrams PA, Ginzburg LR (2000) The nature of predation: Prey dependent, ratio dependent or neither? Trends Ecol Evol 15:337–341

Acha EM, Piola AR, Iribarne O, Mianzan H (2015) Ecological Processes at Marine Fronts: Oases in the Ocean, 2015 edition. Springer

Adams J, Felis J, Mason JW, Takekawa JY (2014) Pacific Continental Shelf Environmental Assessment (PaCSEA): aerial seabird and marine mammal surveys off northern California, Oregon, and Washington, 2011-2012. U.S. Dept. of the Interior, Bureau of Ocean Energy Management, Pacific OCS Region, Camarillo, CA

Adams J, Kaplan IC, Chasco B, Marshall KN, Acevedo-Gutiérrez A, Ward EJ (2016) A century of Chinook salmon consumption by marine mammal predators in the Northeast Pacific Ocean. Ecol Inform 34:44–51

Adams J, MacLeod C, Suryan RM, Hyrenbach KD, Harvey JT (2012) Summer-time use of west coast US National Marine Sanctuaries by migrating sooty shearwaters (*Puffinus griseus*). Biol Conserv 156:105–116

Ahrens R, Walters CJ, Christensen V (2012) Foraging arena theory. Fish Fish 13:41–59

Ainley DG (1976) The occurrence of seabirds in the coastal region of California. West Birds 7:33–68

Ainley DG (1977) Feeding methods in seabirds: a comparison of polar and tropical nesting communities in the eastern Pacific Ocean. In: Llano GA (ed) Adaptations Within Antarctic Ecosystems. Smithsonian Institution, Washington, DC, p 669–685

Ainley DG, Dugger KD, Ford RG, Pierce SD, Reese DC, Brodeur RD, Tynan CT, Barth JA (2009) Association of predators and prey at frontal features in the California Current: competition, facilitation, and co-occurrence. Mar Ecol Prog Ser 389:271–294

Ainley DG, Jacobs SS (1981) Sea-bird affinities for ocean and ice boundaries in the Antarctic. Deep Sea Res Part Oceanogr Res Pap 28:1173–1185

Ainley DG, Nettleship DN, Carter HR, Storey AE (2002) Common Murre (*Uria aalge*) (A Poole and F Gill, Eds.). Birds N Am Online

Ainley DG, Ribic CA, Woehler EJ (2012) Adding the ocean to the study of seabirds: a brief history of at-sea seabird research. Mar Ecol Prog Ser 451:231–243

Ainley DG, Spear LB, Allen SG, Ribic CA (1996) Temporal and spatial patterns in the diet of the common murre in California waters. The Condor 98:691–705

Ainley DG, Spear LB, Tynan CT, Barth JA, Pierce SD, Glenn Ford R, Cowles TJ (2005) Physical and biological variables affecting seabird distributions during the upwelling season of the northern California Current. Deep Sea Res Part II Top Stud Oceanogr 52:123–143

Alerstam T, Hedenström A, Åkesson S (2003) Long□distance migration: evolution and determinants. Oikos 103:247–260

Alexander LM (1993) Large marine ecosystems: A new focus for marine resources management. Mar Policy 17:186–198

Anderson JJ, Gurarie E, Zabel RW (2005) Mean free-path length theory of predator–prey interactions: Application to juvenile salmon migration. Ecol Model 186:196–211

Angelstam P, Lindström E, Widén P (1984) Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. Oecologia 62:199–208

Arimitsu ML, Piatt JF, Mueter F (2016) Influence of glacier runoff on ecosystem structure in Gulf of Alaska fjords. Mar Ecol Prog Ser 560:19–40

Ashford JR, Ezer T, Jones CM (2013) River discharge predicts spatial distributions of beluga whales in the Upper Cook Inlet, Alaska, during early summer. Polar Biol 36:1077–1087

Au DW (1991) Polyspecific nature of tuna schools - shark, dolphin, and seabird associates. Fish Bull 89:343–354

Bairos-Novak KR, Crook KA, Davoren GK (2015) Relative importance of local enhancement as a search strategy for breeding seabirds: an experimental approach. Anim Behav 106:71–78

Bakun A, Black BA, Bograd SJ, García-Reyes M, Miller AJ, Rykaczewski RR, Sydeman WJ (2015) Anticipated effects of climate change on coastal upwelling ecosystems. Curr Clim Change Rep 1:85–93

Ballance LT, Pitman RL, Fiedler PC (2006) Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: A review. Prog Oceanogr 69:360–390

Ballance LT, Pitman RL, Reilly SB (1997) Seabird community structure along a productivity gradient: Importance of competition and energetic constraint. Ecology 78:1502–1518

Ballance LT, Ainley DG, Hunt Jr GL (2001) Seabird Foraging Ecology. In: Steele JH (ed) Encyclopedia of Ocean Sciences. Academic Press, Oxford, p 2636–2644

Ballard G, Jongsomjit D, Veloz SD, Ainley DG (2012) Coexistence of mesopredators in an intact polar ocean ecosystem: The basis for defining a Ross Sea marine protected area. Biol Conserv 156:72–82

Baltz DM, Morejohn GV (1977) Food habits and niche overlap of seabirds wintering on Monterey Bay, California. The Auk 94:526–543

Barange M, Hampton I, Soule M (1996) Empirical determination of *in situ* target strengths of three loosely aggregated pelagic fish species. ICES J Mar Sci J Cons 53:225–232

Barnes CA, Duxbury AC, Morse BA (1972) The circulation and selected properties of the Columbia River effluent at sea. In: Pruter AT, Alverson DL (eds) The Columbia River Estuary and Adjacent Ocean Waters: Bioenvironmental Studies. University of Washington Press, Seattle, WA, p 41–80

Beamish RJ, Mahnken C (2001) A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog Oceanogr 49:423–437

Beamish RJ, Neville C-EM (1995) Pacific salmon and Pacific herring mortalities in the Fraser River plume caused by river lamprey (*Lampetra ayresi*). Can J Fish Aquat Sci 52:644–650

Beamish RJ, Thomson BL, McFarlane GA (1992) Spiny dogfish predation on Chinook and coho salmon and the potential effects on hatchery-produced salmon. Trans Am Fish Soc 121:444–455

Bellier E, Certain G, Planque B, Monestiez P, Bretagnolle V (2010) Modelling habitat selection at multiple scales with multivariate geostatistics: an application to seabirds in open sea. Oikos 119:988–999

Bennison A, Jessopp M (2015) At-sea surveys confirm a North Atlantic biodiversity hotspot. Bird Study 62:262–266

Berejikian BA, Moore ME, Jeffries SJ (2016) Predator-prey interactions between harbor seals and migrating steelhead trout smolts revealed by acoustic telemetry. Mar Ecol Prog Ser 543:21–35

Beyer HL (2015) Geospatial Modelling Environment (Version 0.7.4.0) (software) URL: http://www.spatialecology.com/gme.

Bez N, Rivoirard J (2001) Transitive geostatistics to characterise spatial aggregations with diffuse limits: an application on mackerel ichtyoplankton. Fish Res 50:41–58

Block BA, Holbrook CM, Simmons SE, Holland KN, Ault JS, Costa DP, Mate BR, Seitz AC, Arendt MD, Payne JC, Mahmoudi B, Moore P, Price JM, Levenson JJ, Wilson D, Kochevar RE (2016) Toward a national animal telemetry network for aquatic observations in the United States. Anim Biotelemetry 4:6

Block BA, Jonsen ID, Jorgensen SJ, Winship AJ, Shaffer SA, Bograd SJ, Hazen EL, Foley DG, Breed GA, Harrison A-L, Ganong JE, Swithenbank A, Castleton M, Dewar H, Mate BR, Shillinger GL, Schaefer KM, Benson SR, Weise MJ, Henry RW, Costa DP (2011) Tracking apex marine predator movements in a dynamic ocean. Nature 475:86–90

Bost CA, Cotté C, Bailleul F, Cherel Y, Charrassin JB, Guinet C, Ainley DG, Weimerskirch H (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. J Mar Syst 78:363–376

Bouchet PJ, Meeuwig JJ, Salgado Kent CP, Letessier TB, Jenner CK (2015) Topographic determinants of mobile vertebrate predator hotspots: current knowledge and future directions. Biol Rev 90:699–728

Bradford MJ (1995) Comparative review of Pacific salmon survival rates. Can J Fish Aquat Sci 52:1327–1338

Briggs KT, Chu EW (1986) Sooty shearwaters off California: Distribution, abundance and habitat use. The Condor 88:355–364

Briggs KT, Tyler WB, Lewis DB (1985a) Aerial surveys for seabirds: Methodological experiments. J Wildl Manag 49:412–417

Briggs KT, Tyler WB, Lewis DB (1985b) Comparison of ship and aerial surveys of birds at sea. J Wildl Manag 49:405–411

Briggs KT, Tyler WB, Lewis DB, Carlson DR (1987) Bird communities at sea off California, 1975–1983. Stud Avian Biol 11:1–74

Brodeur RD, Buchanan JC, Emmett RL (2014) Pelagic and demersal fish predators on juvenile and adult forage fishes in the California Current: spatial and temporal variations. CalCOFI Rep 55:96–116

Brodeur RD, Fisher JP, Emmett RL, Casillas E, Morgan CA (2005) Species composition and community structure of pelagic nekton off Oregon and Washington under variable oceanographic conditions. Mar Ecol Prog Ser 298:41–57

Brodeur RD, Myers KW, Helle JH (2003) Research conducted by the United States on the early ocean life history of Pacific salmon. N Pac Anadr Fish Comm Bull 3:89–131

Brosnan IG, Welch DW, Rechisky EL, Porter AD (2014) Evaluating the influence of environmental factors on yearling Chinook salmon survival in the Columbia River plume (USA). Mar Ecol Prog Ser 496:181–196

Brown RGB (1980) Seabirds as Marine Animals. In: Burger J, Olla BL, Winn HE (eds) Behavior of Marine Animals. Springer US, p 1–39

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to Distance Sampling: Estimating Abundance of Biological Populations, 1st edition. Oxford University Press, Oxford; New York

Burger AE, Shaffer SA (2008) Application of tracking and data-logging technology in research and conservation of seabirds. The Auk 125:253–264

Burger AE, Piatt JF (1990) Flexible time budgets in breeding Common Murres: Buffers against variable prey availability. Stud Avian Biol 14:71–83

Burke BJ, Liermann MC, Teel DJ, Anderson JJ (2013a) Environmental and geospatial factors drive juvenile Chinook salmon distribution during early ocean migration. Can J Fish Aquat Sci 70:1167–1177

Burke BJ, Peterson WT, Beckman BR, Morgan C, Daly EA, Litz M (2013b) Multivariate models of adult Pacific salmon returns. PLoS ONE 8:e54134

Burla M, Baptista AM, Zhang YL, Frolov S (2010) Seasonal and interannual variability of the Columbia River plume: A perspective enabled by multiyear simulation databases. J Geophys Res-Oceans 115:C00B16

Burnham KP, Anderson DR (2011) Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach, 2nd edn. Springer-Verlag New York, LLC

Cairns DK, Bredin KA, Montevecchi WA (1987) Activity budgets and foraging ranges of breeding common murres. The Auk 104:218–224

Cairns DK, Schneider DC (1990) Hot spots in cold water: feeding habitat selection by thick-billed murres. Stud Avian Biol No 14:52–60

Calenge C (2006) The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. Ecol Model 197:516–519

Carlisle AB, Litvin SY, Hazen EL, Madigan DJ, Goldman KJ, Lea RN, Block BA (2015) Reconstructing habitat use by juvenile salmon sharks links upwelling to strandings in the California Current. Mar Ecol Prog Ser 525:217–228

Certain G, Bretagnolle V (2008) Monitoring seabirds population in marine ecosystem: The use of strip-transect aerial surveys. Remote Sens Environ 112:3314–3322

Chasco B, Kaplan I, Thomas A, Acevedo-Gutiérrez A, Noren DP, Ford MJ, Hanson MB, Scordino J, Jeffries SJ, Pearson SF, Marshall K, Ward EJ (2017) Estimates of Chinook salmon consumption in Washington State inland waters by four marine mammal predators from 1970 – 2015. Can J Fish Aquat Sci

Checkley Jr. DM, Dotson RC, Griffith DA (2000) Continuous, underway sampling of eggs of Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*) in spring

1996 and 1997 off southern and central California. Deep Sea Res Part II Top Stud Oceanogr 47:1139–1155

Chesson PL (1984) Variable predators and switching behavior. Theor Popul Biol 26:1–26

Chu EW (1984) Sooty shearwaters off California: diet and energy gain. In: Marine Birds: Their feeding ecology and commercial fisheries relationships, Special publication of the Canadian Wildlife Service. Ottawa, p 64–71

Claiborne AM, Miller JA, Weitkamp LA, Teel DJ, Emmett RL (2014) Evidence for selective mortality in marine environments: the role of fish migration size, timing, and production type. Mar Ecol Prog Ser 515:187–202

Collis K, Roby DD, Craig DP, Adamany S, Adkins JY, Lyons DE (2002) Colony size and diet composition of piscivorous waterbirds on the lower Columbia River: Implications for losses of juvenile salmonids to avian predation. Trans Am Fish Soc 131:537–550

Collis K, Roby DD, Craig DP, Ryan BA, Ledgerwood RD (2001) Colonial waterbird predation on juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary: Vulnerability of different salmonid species, stocks, and rearing types. Trans Am Fish Soc 130:385–396

Coronado C, Hilborn R (1998) Spatial and temporal factors affecting survival in coho salmon (*Oncorhynchus kisutch*) in the Pacific Northwest. Can J Fish Aquat Sci 55:2067–2077

Costa DP, Breed GA, Robinson PW (2012) New Insights into Pelagic Migrations: Implications for Ecology and Conservation. Annu Rev Ecol Evol Syst 43:73–96

Coyne MS, Godley BJ (2005) Satellite Tracking and Analysis Tool (STAT): an integrated system for archiving, analyzing and mapping animal tracking data. Mar Ecol Prog Ser 301:1–7

Cressie N (1993) Statistics for spatial data, revised edition, Revised Edition. John Wiley & Sons, Inc., Hoboken, N.J

Croll DA, Marinovic B, Benson S, Chavez FP, Black N, Ternullo R, Tershy BR (2005) From wind to whales: trophic links in a coastal upwelling system. Mar Ecol Prog Ser 289:117–130

Crook KA, Davoren GK (2014) Underwater behaviour of common murres foraging on capelin: influences of prey density and antipredator behaviour. Mar Ecol Prog Ser 501:279–290

Crozier LG, Hendry AP, Lawson PW, Quinn TP, Mantua NJ, Battin J, Shaw RG, Huey RB (2008a) Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon. Evol Appl 1:252–270

Crozier LG, Zabel RW, Hamlet AF (2008b) Predicting differential effects of climate change at the population level with life-cycle models of spring Chinook salmon. Glob Change Biol 14:236–249

Cury PM, Boyd IL, Bonhommeau S, Anker-Nilssen T, Crawford RJM, Furness RW, Mills JA, Murphy EJ, Österblom H, Paleczny M, Piatt JF, Roux J-P, Shannon L, Sydeman WJ (2011) Global seabird response to forage fish depletion—one-third for the birds. Science 334:1703–1706

Cushing DH (1969) The Regularity of the Spawning Season of Some Fishes. J Cons 33:81–92

Cyrus DP (1991) The influence of turbidity on the foraging behavior of Little Terns (*Sterna albifrons*) off the St Lucia Mouth, Zululand, South Africa. Mar Ornithol 19:103–108

Dai A, Qian T, Trenberth KE, Milliman JD (2009) Changes in continental freshwater discharge from 1948 to 2004. J Clim 22:2773–2792

Dai A, Trenberth KE (2002) Estimates of freshwater discharge from continents: Latitudinal and seasonal variations. J Hydrometeorol 3:660–687

Daly EA, Auth TD, Brodeur RD, Peterson WT (2013) Winter ichthyoplankton biomass as a predictor of early summer prey fields and survival of juvenile salmon in the northern California Current. Mar Ecol Prog Ser 484:203–217

Daly EA, Brodeur R, Auth T (2017) Anomalous ocean conditions in 2015: impacts on spring Chinook salmon and their prey field. Mar Ecol Prog Ser 566:169–182

Daly EA, Brodeur RD, Weitkamp LA (2009) Ontogenetic shifts in diets of juvenile and subadult coho and Chinook salmon in coastal marine waters: Important for marine survival? Trans Am Fish Soc 138:1420–1438

Davoren GK (2013) Distribution of marine predator hotspots explained by persistent areas of prey. Mar Biol 160:3043–3058

Davoren GK, Garthe S, Montevecchi WA, Benvenuti S (2010) Influence of prey behaviour and other predators on the foraging activities of a marine avian predator in a Low Arctic ecosystem. Mar Ecol Prog Ser 404:275–287

Davoren GK, Montevecchi WA, Anderson JT (2003a) Distributional patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. Mar Ecol Prog Ser 256:229–242

Davoren GK, Montevecchi WA, Anderson JT (2003b) Search strategies of a pursuit-diving marine bird and the persistence of prey patches. Ecol Monogr 73:463–481

De Robertis A, Morgan CA, Schabetsberger RA, Zabel RW, Brodeur RD, Emmett RL, Knight CM, Krutzikowsky GK, Casillas E (2005) Columbia River plume fronts II. Distribution, abundance, and feeding ecology of juvenile salmon. Mar Ecol Prog Ser 299:33–44

De Robertis A, Ryer CH, Veloza A, Brodeur RD (2003) Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. Can J Fish Aquat Sci 60:1517–1526

Decker MB, Hunt GL (1996) Foraging by murres (*Uria* spp) at tidal fronts surrounding the Pribilof Islands, Alaska, USA. Mar Ecol Prog Ser 139:1–10

Demer DA, Zwolinski JP, Byers KA, Cutter GR, Renfree JS, Sessions TS, Macewicz BJ (2011) Acoustic-trawl surveys of Pacific sardine (*Sardinops sagax*) and other pelagic fishes in the California Current ecosystem: Part 1, Methods and an example application. Pac Fish Manag Counc:37 pp

Demidov AB, Gagarin VI, Vorobieva OV, Makkaveev PN, Artemiev VA, Khrapko AN, Grigoriev AV, Sheberstov SV (2017) Spatial and vertical variability of primary production in the Kara Sea in July and August 2016: the influence of the river plume and subsurface chlorophyll maxima. Polar Biol:1–16

Dolan TE, Patrick WS, Link JS (2016) Delineating the continuum of marine ecosystem-based management: a US fisheries reference point perspective. ICES J Mar Sci 73:1042–1050

Doney SC, Ruckelshaus M, Duffy JE, Barry JP, Chan F, English CA, Galindo HM, Grebmeier JM, Hollowed AB, Knowlton N, Polovina J, Rabalais NN, Sydeman WJ, Talley LD (2012) Climate Change Impacts on Marine Ecosystems. Annu Rev Mar Sci 4:11–37

Dower JF, Brodeur RD (2004) The role of biophysical coupling in concentrating marine organisms around shallow topographies. J Mar Syst 50:1–2

Drew GS, Piatt JF, Renner M (2015) User's guide to the North Pacific Pelagic Seabird Database 2.0. U.S. Geological Survey, Reston, VA

Durant JM, Hjermann D, Falkenhaug T, Gifford DJ, Naustvoll L, Sullivan BK, Beaugrand G, Stenseth NC (2013) Extension of the match-mismatch hypothesis to predator-controlled systems. Mar Ecol Prog Ser 474:43–52

Ebbesmeyer CC, Tangborn W (1992) Linkage of reservoir, coast, and strait dynamics, 1936-1990: Columbia River Basin, Washington Coast, and Juan de Fuca Strait. In: Interdisciplinary Approaches in Hydrology and Hydrogeology. American Institute of Hydrology, St. Paul, MN, p 288–299

Elith J, Leathwick JR (2009) Species distribution models: Ecological explanation and prediction across space and time. Annu Rev Ecol Evol Syst 40:677–697

Emmett RL, Brodeur RD, Orton PM (2004) The vertical distribution of juvenile salmon (*Oncorhynchus* spp.) and associated fishes in the Columbia River plume. Fish Oceanogr 13:392–402

Emmett RL, Krutzikowsky GK (2008) Nocturnal feeding of pacific hake and jack mackerel off the mouth of the Columbia River, 1998-2004: implications for juvenile salmon predation. Trans Am Fish Soc 137:657–676

Emmett RL, Krutzikowsky GK, Bentley P (2006) Abundance and distribution of pelagic piscivorous fishes in the Columbia River plume during spring/early summer 1998–2003: Relationship to oceanographic conditions, forage fishes, and juvenile salmonids. Prog Oceanogr 68:1–26

Emmett RL, Sampson DB (2007) The relationships between predatory fish, forage fishes, and juvenile salmonid marine survival off the Columbia River: A simple trophic model analysis. CalCOFI Rep 48:92–105

Emmett RL, Schiewe MH (1997) Estuarine and ocean survival of Northeastern Pacific salmon: Proceedings of the workshop. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-NWFSC-29

Enstipp MR, Gremillet D, Jones DR (2007) Investigating the functional link between prey abundance and seabird predatory performance. Mar Ecol Prog Ser 331:267–279

Evans AF, Hostetter NJ, Roby DD, Collis K, Lyons DE, Sandford BP, Ledgerwood RD, Sebring S (2012) Systemwide evaluation of avian predation on juvenile salmonids from the Columbia River based on recoveries of passive integrated transponder tags. Trans Am Fish Soc 141:975–989

Fauchald P (2009) Spatial interaction between seabirds and prey: review and synthesis. Mar Ecol Prog Ser 391:139–151

Fauchald P, Erikstad KE, Skarsfjord H (2000) Scale-dependent predator-prey interactions: The hierarchical spatial distribution of seabirds and prey. Ecology 81:773–783

Fiedler PC, Bernard HJ (1987) Tuna aggregation and feeding near fronts observed in satellite imagery. Cont Shelf Res 7:871–881

Fiedler PC, Laurs RM (1990) Variability of the Columbia River plume observed in visible and infrared satellite imagery. Int J Remote Sens 11:999–1010

Fisher JP, Pearcy WG (1988) Growth of juvenile coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington, USA, in years of differing coastal upwelling. Can J Fish Aquat Sci 45:1036–1044

Fisher JP, Pearcy WG (1995) Distribution, migration, and growth of juvenile Chinook salmon, *Oncorhynchus tshawystcha*, off Oregon and Washington. Fish Bull 93:274–289

Fisher JP, Weitkamp LA, Teel DJ, Hinton SA, Orsi JA, Farley EV, Morris JFT, Thiess ME, Sweeting RM, Trudel M (2014) Early ocean dispersal patterns of Columbia River Chinook and coho salmon. Trans Am Fish Soc 143:252–272

Fleischer GW, Cooke KD, Ressler PH, Thomas RE, Blois SK de, Hufnagle LC, Kronlund AR, Holmes JA, Wilson CD (2005) The 2003 integrated acoustic and trawl survey of Pacific hake, *Merluccius productus*, in U.S. and Canadian waters off the Pacific coast. NMFS-NWFSC-NOAA Tech Memo 65:45

Foote KG, Knudsen HP, Vestnes G, MacLennan DN, Simmonds EJ (1987) Calibration of acoustic instruments for fish density estimation: a practical guide. ICES Coop Res Rep 144:69

Fossette S, Witt MJ, Miller P, Nalovic MA, Albareda D, Almeida AP, Broderick AC, Chacón-Chaverri D, Coyne MS, Domingo A, Eckert S, Evans D, Fallabrino A, Ferraroli S, Formia A, Giffoni B, Hays GC, Hughes G, Kelle L, Leslie A, López-Mendilaharsu M, Luschi P, Prosdocimi L, Rodriguez-Heredia S, Turny A, Verhage S, Godley BJ (2014) Pan-Atlantic analysis of the overlap of a highly migratory species, the leatherback turtle, with pelagic longline fisheries. Proc R Soc Lond B Biol Sci 281:20133065

FPC (2016) Fish Passage Center 2015 Annual Report. Fish Passage Center, Portland, OR

Frame ER, Lessard EJ (2009) Does the Columbia River plume influence phytoplankton community structure along the Washington and Oregon coasts? J Geophys Res Oceans 114:1–13

Franeker JA van (1994) A comparison of methods for counting seabirds at sea in the Southern Ocean. J Field Ornithol 65:96–108

Franks PJS (1992) Sink or swim: Accumulation of biomass at fronts. Mar Ecol Prog Ser 82:1–12

Freitas C, Lydersen C, Fedak MA, Kovacs KM (2008) A simple new algorithm to filter marine mammal Argos locations. Mar Mammal Sci 24:315–325

Garvine RW, Monk JD (1974) Frontal structure of a river plume. J Geophys Res 79:2251–2259

Gaston AJ (Anthony J), Smith GEJ (1984) The interpretation of aerial surveys for seabirds: some effects of behaviour. Canadian Wildlife Service, Ottawa

Gladics AJ, Suryan RM, Brodeur RD, Segui LM, Filliger LZ (2014) Constancy and change in marine predator diets across a shift in oceanographic conditions in the Northern California Current. Mar Biol 161:837–851

Godø OR, Samuelsen A, Macaulay GJ, Patel R, Hjøllo SS, Horne J, Kaartvedt S, Johannessen JA (2012) Mesoscale eddies are oases for higher trophic marine life. PLoS ONE 7:e30161

González Carman V, Mandiola A, Alemany D, Dassis M, Pon S, P J, Prosdocimi L, Ponce de León A, Mianzan H, Acha EM, Rodríguez D, Favero M, Copello S (2016) Distribution of megafaunal species in the Southwestern Atlantic: key ecological areas and opportunities for marine conservation. ICES J Mar Sci 73:1579–1588

Govoni JJ, Grimes CB (1992) The surface accumulation of larval fishes by hydrodynamic convergence within the Mississippi River plume front. Cont Shelf Res 12:1265–1276

Govoni JJ, Hoss DE, Colby DR (1989) The spatial distribution of larval fishes about the Mississippi River plume. Limnol Oceanogr 34:178–187

Gregory RS, Levings CD (1998) Turbidity reduces predation on migrating juvenile Pacific salmon. Trans Am Fish Soc 127:275–285

Grémillet D, Nazirides T, Nikolaou H, Crivelli AJ (2012) Fish are not safe from great cormorants in turbid water. Aquat Biol 15:187–194

Gustafson RG, Ford MJ, Adams PB, Drake JS, Emmett RL, Fresh KL, Rowse M, Spangler EAK, Spangler RE, Teel DJ, Wilson MT (2012) Conservation status of eulachon in the California Current. Fish Fish 13:121–138

Gutowsky SE, Leonard ML, Conners MG, Shaffer SA, Jonsen ID (2015) Individual-level variation and higher-level interpretations of space use in wide-ranging species: An albatross case study of sampling effects. Mar Megafauna 2:93

Hamel NJ, Parrish JK, Conquest LL (2004) Effects of tagging on behavior, provisioning, and reproduction in the Common Murre (*Uria aalge*), a diving seabird. Auk 121:1161–1171

Hamlet AF, Lettenmaier DP (1999) Effects of climate change on hydrology and water resources in the Columbia River basin. J Am Water Resour Assoc 35:1597–1623

Hamlet AF, Mote PW, Clark MP, Lettenmaier DP (2007) Twentieth-century trends in runoff, evapotranspiration, and soil moisture in the western United States. J Clim 20:1468–1486

Haney JC, Fristrup KM, Lee DS (1992) Geometry of visual recruitment by seabirds to ephemeral foraging flocks. Ornis Scand Scand J Ornithol 23:49–62

Haney JC, Stone AE (1988) Seabird foraging tactics and water clarity: Are plunge divers really in the clear? Mar Ecol Prog Ser 49:1–9

Hansen AG, Beauchamp DA (2015) Latitudinal and photic effects on diel foraging and predation risk in freshwater pelagic ecosystems. J Anim Ecol 84:532–544

Hansen AG, Beauchamp DA (2014) Effects of prey abundance, distribution, visual contrast and morphology on selection by a pelagic piscivore. Freshw Biol 59:2328–2341

Hansen AG, Beauchamp DA, Schoen ER (2013) Visual prey detection responses of piscivorous trout and salmon: Effects of light, turbidity, and prey size. Trans Am Fish Soc 142:854–867

Hart KM, Hyrenbach KD (2009) Satellite telemetry of marine megavertebrates: the coming of age of an experimental science. Endanger Species Res 10:9–20

Harvey CJ, Reum JCP, Poe MR, Williams GD, Kim SJ (2016) Using conceptual models and qualitative network models to advance integrative assessments of marine ecosystems. Coast Manag 44:486–503

Hatch SA, Meyers PM, Mulcahy DM, Douglas DC (2000a) Seasonal movements and pelagic habitat use of murres and puffins determined by satellite telemetry. The Condor 102:145–154

Hatch SA, Meyers PM, Mulcahy DM, Douglas DC (2000b) Performance of implantable satellite transmitters in diving seabirds. Waterbirds Int J Waterbird Biol 23:84–94

Haury LR, McGowan JA, Wiebe PH (1978) Patterns and processes in the time-space of plankton distributions (JH Steele, Ed.).

Hays GC, Ferreira LC, Sequeira AMM, Meekan MG, Duarte CM, Bailey H, Bailleul F, Bowen WD, Caley MJ, Costa DP, Eguíluz VM, Fossette S, Friedlaender AS, Gales N, Gleiss AC, Gunn J, Harcourt R, Hazen EL, Heithaus MR, Heupel M, Holland K, Horning M, Jonsen I, Kooyman GL, Lowe CG, Madsen PT, Marsh H, Phillips RA, Righton D, Ropert-Coudert Y, Sato K, Shaffer SA, Simpfendorfer CA, Sims DW, Skomal G, Takahashi A, Trathan PN, Wikelski M, Womble JN, Thums M (2016) Key questions in marine megafauna movement ecology. Trends Ecol Evol 31:463–475

Hazen EL, Jorgensen S, Rykaczewski RR, Bograd SJ, Foley DG, Jonsen ID, Shaffer SA, Dunne JP, Costa DP, Crowder LB, Block BA (2012) Predicted habitat shifts of Pacific top predators in a changing climate. Nat Clim Change:10.1038/nclimate1686

Hazen EL, Palacios DM, Forney KA, Howell EA, Becker E, Hoover AL, Irvine L, DeAngelis M, Bograd SJ, Mate BR, Bailey H (2016) WhaleWatch: a dynamic management tool for predicting blue whale density in the California Current. J Appl Ecol:10.1111/1365-2664.12820

Hebblewhite M, Merrill EH, McDonald TL (2005) Spatial decomposition of predation risk using resource selection functions: an example in a wolf–elk predator–prey system. Oikos 111:101–111

Heinemann D (1981) A range finder for pelagic bird censusing. J Wildl Manag 45:489–493

Henkel LA, Ford RG, Tyler WB, Davis JN (2007) Comparison of aerial and boat-based survey methods for marbled murrelets *Brachyramphus marmoratus* and other marine birds. Mar Ornithol 35:145–151

Hickey B, Banas N (2008) Why is the northern end of the California Current system so productive? Oceanography 21:90–107

Hickey B, Geier S, Kachel N, MacFadyen AF (2005) A bi-directional river plume: The Columbia in summer. Cont Shelf Res 25:1631–1656

Hickey BM, Kudela RM, Nash JD, Bruland KW, Peterson WT, MacCready P, Lessard EJ, Jay DA, Banas NS, Baptista AM, Dever EP, Kosro PM, Kilcher LK, Horner-Devine AR, Zaron ED, McCabe RM, Peterson JO, Orton PM, Pan J, Lohan MC (2010) River influences on shelf ecosystems: Introduction and synthesis. J Geophys Res 115:C00B17

Hickey BM, Pietrafesa LJ, Jay DA, Boicourt WC (1998) The Columbia River plume study: Subtidal variability in the velocity and salinity fields. J Geophys Res 103:10339–10368

Hjort J (1914) Fluctuations in the great fisheries of Northern Europe viewed in the light of biological research. Rapp Procès-Verbaux La Réun Cons Int Pour Explor Mer 20:1–228

Hjort J (1926) Fluctuations in the year classes of important food fishes. ICES J Mar Sci 1:5–38

Hoar WS (1958) The evolution of migratory behaviour among juvenile salmon of the genus *Oncorhynchus*. J Fish Res Board Can 15:391–428

Hoar WS (1976) Smolt transformation: evolution, behavior, and physiology. J Fish Res Board Can 33:1233–1252

Hodgson JC, Baylis SM, Mott R, Herrod A, Clarke RH (2016) Precision wildlife monitoring using unmanned aerial vehicles. Sci Rep 6:22574

Hoffman W, Heinemann D, Wiens JA (1981) The ecology of seabird feeding flocks in Alaska. The Auk 98:437–456

Holling CS (1959) The components of predation as revealed by a study of small-mammal predation of the European Pine Sawfly. Can Entomol 91:293–320

Holsman KK, Scheuerell MD, Buhle E, Emmett R (2012) Interacting effects of translocation, artificial propagation, and environmental conditions on the marine survival of Chinook salmon from the Columbia River, Washington, U.S.A. Conserv Biol J Soc Conserv Biol 26:912–922

Holt RD (1977) Predation, apparent competition, and the structure of prey communities. Theor Popul Biol 12:197–229

Hostetter NJ, Evans AF, Roby DD, Collis K (2012) Susceptibility of Juvenile Steelhead to Avian Predation: the Influence of Individual Fish Characteristics and River Conditions. Trans Am Fish Soc 141:1586–1599

Horne JS, Garton EO, Krone SM, Lewis JS (2007) Analyzing animal movements using Brownian bridges. Ecology 88:2354–2363

Horner-Devine AR, Jay DA, Orton PM, Spahn EY (2009) A conceptual model of the strongly tidal Columbia River plume. J Mar Syst 78:460–475

Hughes BB, Beas-Luna R, Barner AK, Brewitt K, Brumbaugh DR, Cerny-Chipman EB, Close SL, Coblentz KE, Nesnera D, L K, Drobnitch ST, Figurski JD, Focht B, Friedman M, Freiwald J, Heady KK, Heady WN, Hettinger A, Johnson A, Karr KA, Mahoney B, Moritsch MM, Osterback A-MK, Reimer J, Robinson J, Rohrer T, Rose JM, Sabal M, Segui LM, Shen C, Sullivan J, Zuercher R, Raimondi PT, Menge BA, Grorud-Colvert K, Novak M, Carr MH (2017) Long-term studies contribute disproportionately to ecology and policy. BioScience 67:271–281

Hunt GL Jr (1997) Physics, zooplankton, and the distribution of least auklets in the Bering Sea — a review. ICES J Mar Sci J Cons 54:600–607

Hunt GL Jr, Mehlum F, Russell RW, Irons DB, Decker MB, Becker PH (1999) Physical processes, prey abundance, and the foraging ecology of seabirds. In: Adams NJ, Slotow RH (eds) Proc. 22 Int. Ornithol. Congr., Durban. Birdlife South Africa, Johannesburg, p 2040–2056

Hunt GL Jr, Renner M, Kuletz KJ, Salo S, Eisner L, Ressler PH, Ladd C, Santora JA (2018) Timing of sea-ice retreat affects the distribution of seabirds and their prey in the southeastern Bering Sea. Mar Ecol Prog Ser 593:209–230

Hunt GL Jr, Russell RW, Coyle KO, Weingartner T (1998) Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. Mar Ecol Prog Ser 167:241–259

Hunt GL Jr, Schneider DC (1987) Scale dependent processes in the physical and biological environment of marine birds. In: Croxall JP (ed) Seabirds: Feeding Ecology and Role in Marine Ecosystems. Cambridge University Press, Cambridge, p 7–41

Hutchinson LV, Wenzel BM, Stager KE, Tedford BL (1984) Further evidence for olfactory foraging by Sooty Shearwaters and Northern Fulmars. In: Marine Birds: Their feeding ecology and commercial fisheries relationships, Special publication of the Canadian Wildlife Service. Ottawa, p 72–77

Hyrenbach KD, Keiper C, Allen SG, Ainley DG, Anderson DJ (2006) Use of marine sanctuaries by far-ranging predators: commuting flights to the California Current System by breeding Hawaiian albatrosses. Fish Oceanogr 15:95–103

Hyrenbach KD, Veit RR, Weimerskirch H, Metzl N, Hunt GL (2007) Community structure across a large-scale ocean productivity gradient: Marine bird assemblages of the Southern Indian Ocean. Deep-Sea Res Part -Oceanogr Res Pap 54:1129–1145

IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland

Jay DA, Pan J, Orton PM, Horner-Devine AR (2009) Asymmetry of Columbia River tidal plume fronts. J Mar Syst 78:442–459

Jay DA, Zaron ED, Pan JY (2010) Initial expansion of the Columbia River tidal plume: Theory and remote sensing observations. J Geophys Res-Oceans 115:C00B15

Jentsch A, Kreyling J, Beierkuhnlein C (2007) A new generation of climate□change experiments: events, not trends. Front Ecol Environ 5:365–374

Kaltenberg AM, Benoit-Bird KJ (2009) Diel behavior of sardine and anchovy schools in the California Current System. Mar Ecol Prog Ser 394:247–262

Kaltenberg A, Emmett R, Benoit-Bird K (2010) Timing of forage fish seasonal appearance in the Columbia River plume and link to ocean conditions. Mar Ecol Prog Ser 419:171–184

Kareiva P, Marvier M, McClure M (2000) Recovery and management options for spring/summer Chinook salmon in the Columbia River Basin. Science 290:977–979

Keith GJ, Ryan TE, Kloser RJ (2005) ES60Adjust.jar Java Software utility to remove a systematic error in Simrad ES60 data. CSIRO Marine and Atmospheric Research, Tasmania, Australia

Kowalczyk ND, Reina RD, Preston TJ, Chiaradia A (2015) Selective foraging within estuarine plume fronts by an inshore resident seabird. Front Mar Sci 2:42

Krietsch J, Hahn S, Kopp M, Phillips R, Peter H, Lisovski S (2017) Consistent variation in individual migration strategies of brown skuas. Mar Ecol Prog Ser AdvanceView:1–13

Kudela RM, Horner-Devine AR, Banas NS, Hickey BM, Peterson TD, McCabe RM, Lessard EJ, Frame E, Bruland KW, Jay DA, Peterson JO, Peterson WT, Kosro PM, Palacios SL, Lohan MC, Dever EP (2010) Multiple trophic levels fueled by recirculation in the Columbia River plume. Geophys Res Lett 37:1–7

Kutner M, Nachtsheim C, Neter J, Li W (2004) Applied linear statistical models, 5th edn. McGraw-Hill/Irwin

Lance MM, Thompson CW (2005) Overlap in diets and foraging of common murres (*Uria aalge*) and rhinoceros auklets (*Cerorhinca monocerata*) after the breeding season. The Auk 122:887–901

Laroche JL, Richardson SL (1980) Reproduction of northern anchovy, *Engraulis mordax*, off Oregon and Washington. Fish Bull 78:603–618

Le Rest K, Certain G, Debétencourt B, Bretagnolle V (2016) Spatio-temporal modelling of auk abundance after the Erika oil spill and implications for conservation. J Appl Ecol:10.1111/1365-2664.12686

Leopold LB, Langbein WB (1960) A primer on water. U.S. Government Printing Office, Washington, D.C.

Levin PS, Fogarty MJ, Murawski SA, Fluharty D (2009) Integrated Ecosystem Assessments: Developing the scientific basis for ecosystem-based management of the ocean. PLOS Biol 7:e1000014

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Lindberg MS, Walker J (2007) Satellite telemetry in avian research and management: Sample size considerations. J Wildl Manag 71:1002–1009

Litz MNC, Emmett RL, Bentley PJ, Claiborne AM, Barceló C (2013) Biotic and abiotic factors influencing forage fish and pelagic nekton community in the Columbia River plume (USA) throughout the upwelling season 1999–2009. ICES J Mar Sci 71:5–18

Litz MNC, Heppell SS, Emmett RL, Brodeur RD (2008) Ecology and distribution of the northern subpopulation of northern anchovy (*Engraulis mordax*) off the US west coast. Calif Coop Ocean Fish Investig Rep 49:167–182

Lohrenz SE, Fahnenstiel GL, Redalje DG, Lang GA, Dagg MJ, Whitledge TE, Dortch Q (1999) Nutrients, irradiance, and mixing as factors regulating primary production in coastal waters impacted by the Mississippi River plume. Cont Shelf Res 19:1113–1141

Louzao M, Bécares J, Rodríguez B, Hyrenbach KD, Ruiz A, Arcos JM (2009) Combining vessel-based surveys and tracking data to identify key marine areas for seabirds. Mar Ecol Prog Ser 391:183–197

Louzao M, Hyrenbach KD, Arcos JM, Abelló P, Sola LG de, Oro D (2006) Oceanographic habitat of an endangered mediterranean Procellariiform: Implications for marine protected areas. Ecol Appl 16:1683–1695

Lovvorn JR, Baduini CL, Hunt GL Jr (2001) Modeling underwater visual and filter feeding by planktivorous shearwaters in unusual sea conditions. Ecology 82:2342–2356

Lyday SE, Ballance LT, Field DB, David Hyrenbach K (2015) Shearwaters as ecosystem indicators: Towards fishery-independent metrics of fish abundance in the California Current. J Mar Syst 146:109–120

MacArthur RH (1972) Geographical ecology: patterns in the distribution of species, 1st edn. Harper & Row, New York

Mackas DL, Denman KL, Abbott MR (1985) Plankton patchiness: biology in the physical vernacular. Bull Mar Sci 37:652–674

Mackas DL, Louttit GC (1988) Aggregation of the copepod *Neocalanus plumchrus* at the margin of the Fraser River plume in the Strait of Georgia. Bull Mar Sci 43:810–824

MacLennan DN, Fernandes PG, Dalen J (2002) A consistent approach to definitions and symbols in fisheries acoustics. ICES J Mar Sci J Cons 59:365–369

Macleod CD, Adams J, Lyver P (2008) At-sea distribution of satellite-tracked Grey-faced petrels, *Pterodroma macroptera gouldi*, captured on the Ruamaahua (Aldermen) Islands, New Zealand. Pap Proc R Soc Tasman 142:73–88

Magurran AE (1988) Ecological diversity and its measurement. Springer Science & Business Media

Mannocci L, Boustany AM, Roberts JJ, Palacios DM, Dunn DC, Halpin PN, Viehman S, Moxley J, Cleary J, Bailey H, Bograd SJ, Becker EA, Gardner B, Hartog JR, Hazen EL,

Ferguson MC, Forney KA, Kinlan BP, Oliver MJ, Perretti CT, Ridoux V, Teo SLH, Winship AJ (2017) Temporal resolutions in species distribution models of highly mobile marine animals: Recommendations for ecologists and managers. Divers Distrib 23:1098–1109

Mason JW, McChesney GJ, McIver WR, Carter HR, Takekawa JY, Golightly RT, Ackerman JT, Orthmeyer D., Perry WM, Yee JL, Pierson MO, McCrary MD (2007) At-Sea Distribution and Abundance of Seabirds Off Southern California: A 20-Year Comparison. Cooper Ornithological Society, Camarillo, CA

Matthews D (1983) Feeding ecology of the common murre, *Uria aalge*, off the Oregon coast. MS Thesis, University of Oregon, Eugene

Mazur MM, Beauchamp DA (2003) A comparison of Visual Prey Detection Among Species of Piscivorous Salmonids: Effects of Light and Low Turbidities. Environ Biol Fishes 67:397–405

McCullagh P, Nelder JA (1989) Generalized linear models, 2nd edn. Chapman and Hall/CRC

Menza C, Leirness J, White T, Winship AJ, Kinlan B, Kracker L, Zamon JE, Ballance LT, Becker E, Forney KA, Barlow J, Adams J, Pereksta D, Pearson S, Pierce J, Jeffries SJ, Calambokidis J, Douglas A, Hanson B, Benson SR, Antrim L (2016) Predictive mapping of seabirds, pinnipeds and cetaceans off the Pacific coast of Washington. NOAA Tech Memo NOS NCCOS 210:96

Methot RD, Dorn MW (1995) Biology and fisheries of North Pacific hake (*M. productus*). In: Alheit J, Pitcher TJ (eds) Hake. Springer Netherlands, p 389–414

Miller TW, Brodeur RD (2007) Diets of and trophic relationships among dominant marine nekton within the northern California Current ecosystem. Fish Bull 105:548–559

Miller JA, Teel DJ, Baptista A, Morgan CA, Bradford M (2013) Disentangling bottom-up and top-down effects on survival during early ocean residence in a population of Chinook salmon (*Oncorhynchus tshawytscha*). Can J Fish Aquat Sci 70:617–629

Mitkus M, Nevitt GA, Danielsen J, Kelber A (2016) Vision on the high seas: spatial resolution and optical sensitivity in two procellariiform seabirds with different foraging strategies. J Exp Biol 219:3329–3338

Montevecchi WA, Benvenuti S, Garthe S, Davoren GK, Fifield D (2009) Flexible foraging tactics by a large opportunistic seabird preying on forage- and large pelagic fishes. Mar Ecol Prog Ser 385:295–306

Morgan CA, De Robertis A, Zabel RW (2005) Columbia River plume fronts. I. Hydrography, zooplankton distribution, and community composition. Mar Ecol Prog Ser 299:19–31

Morley JW, Selden RL, Latour RJ, Frölicher TL, Seagraves RJ, Pinsky ML (2018) Projecting shifts in thermal habitat for 686 species on the North American continental shelf. PLOS ONE 13:e0196127

Mote PW, Parson EA, Hamlet AF, Keeton WS, Lettenmaier D, Mantua N, Miles EL, Peterson DW, Peterson DL, Slaughter R, Snover AK (2003) Preparing for climatic change: The water, salmon, and forests of the Pacific Northwest. Clim Change 61:45–88

Muir WD, Marsh DM, Sandford BP, Smith SG, Williams JG (2006) Post-hydropower system delayed mortality of transported Snake River stream-type Chinook salmon: unraveling the mystery. Trans Am Fish Soc 135:1523–1534

Mulder T, Syvitski JPM (1995) Turbidity Currents Generated at River Mouths during Exceptional Discharges to the World Oceans. J Geol 103:285–299

Murdoch WW (1969) Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol Monogr 39:335–354

Murphy RC (1936) Oceanic birds of South America. American Museum of Natural History, New York

Myers JM, Kope RG, Bryant GJ, Teel D, Lierheimer LJ, Wainwright TC, Grant WS, Waknitz FW, Neely K, Lindley ST, Waples RS (1998) Status review of Chinook salmon from Washington, Idaho, Oregon, and California. NOAA Tech Memo NMFS-NWFSC-35

Naughton MB, Pitkin DJ, Lowe RW, So KJ, Strong CS (2007) Catalog of Oregon seabird colonies. USFWS Biol Tech Publ BTP-R1009-2007

Nevins HM (2004) Diet, demography, and diving behavior of the common murre (*Uria aalge*) in central California. MS Thesis, San Francisco State University, Moss Landing Marine Laboratories

NRC (National Research Council) (1996) Upstream: Salmon and society in the Pacific Northwest. National Academy Press, Washington, DC

NRC (National Research Council) (2004) Managing the Columbia River: Instream flows, water withdrawals, and salmon survival. National Academy Press, Washington, DC

Nunnallee EP (1990) An alternative to thresholding during echo-integration data collection. Rapp Procès-Verbaux La Réun Cons Int Pour Explor Mer 189:92–94

Nur N, Jahncke J, Herzog MP, Howar J, Hyrenbach KD, Zamon JE, Ainley DG, Wiens JA, Morgan K, Ballance LT, Stralberg D (2011) Where the wild things are: Predicting hotspots of seabird aggregations in the California Current System. Ecol Appl 21:2241–2257

Oaten A, Murdoch WW (1975) Switching, functional response, and stability in predator-prey systems. Am Nat 109:299–318

Olson D, Hitchcock G, Mariano A, Ashjian C, Peng G, Nero R, Podesta G (1994) Life on the edge: Marine life and fronts. Oceanography 7:52–60

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs GR (eds) Analysis of Ecological Systems. The Ohio State University Press, Columbus, p 154–177

Orsi JA, Harding JA, Pool SS, Brodeur RD, Haldorson LJ, Murphy JM, Moss JH, Farley EV, Sweeting RM, Morris JFT, Trudel M, Beamish RJ, Emmett RL, Fergusson EA (2007) Epipelagic fish assemblages associated with juvenile Pacific salmon in neritic waters of the California Current and the Alaska Current. Am Fish Soc Symp 57:105–155

Owen RW (1968) Oceanographic conditions in the northeast Pacific Ocean and their relation to the albacore fishery. Fish Bull 66:503–526

Palmer MA, Reidy Liermann CA, Nilsson C, Flörke M, Alcamo J, Lake PS, Bond N (2008) Climate change and the world's river basins: anticipating management options. Front Ecol Environ 6:81–89

Parker RR (1968) Marine mortality schedules of pink salmon of the Bella Coola River, central British Columbia. J Fish Res Board Can 25:757–794

Parker-Stetter SL, Rudstam LG, Sullivan PJ, Warner DM (2009) Standard operating procedures for fisheries acoustic surveys in the Great Lakes. Ann Arbor, MI

Parnel MM, Emmett RL, Brodeur RD (2008) Ichthyoplankton community in the Columbia River plume off Oregon: effects of fluctuating oceanographic conditions. Fish Bull 106:161–173

Parrish J., Lemberg N, South-Oryshchyn L (1998) Effects of colony location and nekton abundance on the at-sea distribution of four seabird species. Fish Oceanogr 7:126–135

Payne JT, Wood AW, Hamlet AF, Palmer RN, Lettenmaier DP (2004) Mitigating the effects of climate change on the water resources of the Columbia River Basin. Clim Change 62:233–256

Pearcy WG (1992) Ocean ecology of north Pacific salmonids. Washington Sea Grant Program: Distributed by the University of Washington Press, Seattle

Pearcy WG, Fisher JP (1990) Distribution and abundance of juvenile salmonids off Oregon and Washington, 1981-1985. NOAA Tech Rep NMFS 93:83

Petersen JH, DeAngelis DL (2000) Dynamics of prey moving through a predator field: a model of migrating juvenile salmon. Math Biosci 165:97–114

Petersen JH, Gadomski DM (1994) Light-mediated predation by northern squawfish on juvenile chinook salmon. J Fish Biol 45:227–242

PFMC (Pacific Fishery Management Council) (2016) Pacific coast salmon fishery management plan for commercial and recreational salmon fisheries off the coasts of Washington, Oregon, and California as amended through Amendment 19. Pacific Fishery Management Council, Portland, OR

PFMC (Pacific Fishery Management Council) (2018) Coastal pelagic species fishery management plan. Pacific Fishery Management Council

Piatt JF, Nettleship DN (1985) Diving depths of four alcids. The Auk 102:293–297

Piatt JF, Harding AMA, Shultz M, Speckman SG, VanPelt TI, Drew GS, Kettle AB (2007) Seabirds as indicators of marine food supplies: Cairns revisited. Mar Ecol Prog Ser 352:221–234

Pikitch EK, Rountos KJ, Essington TE, Santora C, Pauly D, Watson R, Sumaila UR, Boersma PD, Boyd IL, Conover DO, Cury P, Heppell SS, Houde ED, Mangel M, Plagányi É, Sainsbury K, Steneck RS, Geers TM, Gownaris N, Munch SB (2014) The global contribution of forage fish to marine fisheries and ecosystems. Fish Fish 15:43–64

Pikitch EK, Santora C, Babcock EA, Bakun A, Bonfil R, Conover DO, Dayton P, Doukakis P, Fluharty D, Heneman B, Houde ED, Link J, Livingston PA, Mangel M, McAllister MK, Pope J, Sainsbury KJ (2004) Ecosystem-based fishery management. Science 305:346–347

Prokopenko CM, Turgeon K, Fryxell JM (2017) Evaluation of alternative prey-, predator-, and ratio-dependent functional response models in a zooplankton microcosm. Can J Zool 95:177–182

Quinn TP (2005) The behavior and ecology of Pacific salmon and trout. American Fisheries Society; University of Washington Press, Bethesda, MD: Seattle

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Regular PM, Hedd A, Montevecchi WA (2011) Fishing in the dark: A pursuit-diving seabird modifies foraging behaviour in response to nocturnal light levels. PLoS ONE 6:e26763

Regular PM, Hedd A, Montevecchi WA (2013) Must marine predators always follow scaling laws? Memory guides the foraging decisions of a pursuit-diving seabird. Anim Behav 86:545–552

Reif V, Tornberg R, Jungell S, Korpimäki E (2001) Diet variation of common buzzards in Finland supports the alternative prey hypothesis. Ecography 24:267–274

Renard D, Bez N, Desassis N, Beucher H, Ors F, Laporte F (2015) RGeostats: The Geostatistical package [11.0.1]. MINES ParisTech

Richardson SL (1973) Abundance and distribution of larval fishes in waters off Oregon, May-October 1969, with special emphasis on the northern anchovy, *Engraulis mordax*. Fish Bull 71:697–711

Richardson SL (1981) Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern sub-population off Oregon and Washington. Fish Bull 78:855–876

Roby DD, Collis K, Lyons DE, Craig DP, Adkins JY, Myers AM, Suryan RM (2002) Effects of Colony Relocation on Diet and Productivity of Caspian Terns. J Wildl Manag 66:662–673

Roby DD, Collis K, Lyons DE, Suzuki Y, Loschl P, Lawes T, Bixler K, Peck-Richardson A, Piggott A, Bailey O, McKinnon H, Laws A, Mulligan J, Toomey S, Munes A, Schniedermeyer N, Wilson A, Smith G, Saunders K, Hanwacker L, Horton C, Evans AF, Cramer BM, Turecek A, Payton Q, Hawbecker M, Kuligowski DR (2015) Research, monitoring, and evaluation of avian predation on salmonid smolts in the lower and mid-Columbia River. Bonneville Power Adm USACE – Portland Dist Grant Cty PUD Priest Rapids Coord Comm 2014 Annual Report

Roegner GC, Teel DJ (2014) Density and Condition of Subyearling Chinook Salmon in the Lower Columbia River and Estuary in Relation to Water Temperature and Genetic Stock of Origin. Trans Am Fish Soc:1161–1176

Ronconi RA, Burger AE (2009) Estimating seabird densities from vessel transects: Distance sampling and implications for strip transects. Aquat Biol 4:297–309

Ronconi RA, Swaim ZT, Lane HA, Hunnewell RW, Westage AJ, Koopman HN (2010) Modified hoop-net techniques for capturing birds at sea and comparison with other capture methods. Mar Ornithol 38:23–29

Ropert-Coudert Y, Kato A, Wilson RP, Cannell B (2006) Foraging strategies and prey encounter rate of free-ranging Little Penguins. Mar Biol 149:139

Ruckelshaus MH, Levin P, Johnson JB, Kareiva PM (2002) The Pacific Salmon Wars: What science brings to the challenge of recovering species. Annu Rev Ecol Syst 33:665–706

Rutz C, Hays GC (2009) New frontiers in biologging science. Biol Lett:10.1098/rsbl.2009.0089

Ryan PG, Cooper J (1989) Observer precision and bird conspicuousness during counts of birds at sea. South Afr J Mar Sci 8:271–276

Rykaczewski RR, Checkley Jr. DM (2008) Influence of ocean winds on the pelagic ecosystem in upwelling regions. Proc Natl Acad Sci 105:1965–1970

Rykaczewski RR, Dunne JP, Sydeman WJ, García-Reyes M, Black BA, Bograd SJ (2015) Poleward displacement of coastal upwelling-favorable winds in the ocean's eastern boundary currents through the 21st century. Geophys Res Lett 42:2015GL064694

Santora JA, Ralston S, Sydeman WJ (2011) Spatial organization of krill and seabirds in the central California Current. ICES J Mar Sci J Cons 68:1391–1402

Sato NN, Kokubun N, Yamamoto T, Watanuki Y, Kitaysky AS, Takahashi A (2015) The jellyfish buffet: Jellyfish enhance seabird foraging opportunities by concentrating prey. Biol Lett 11:20150358

Scales KL, Hazen EL, Jacox MG, Edwards CA, Boustany AM, Oliver MJ, Bograd SJ (2017) Scale of inference: On the sensitivity of habitat models for wide-ranging marine predators to the resolution of environmental data. Ecography 40:210–220

Scales KL, Miller PI, Hawkes LA, Ingram SN, Sims DW, Votier SC (2014) On the front line: Frontal zones as priority at-sea conservation areas for mobile marine vertebrates. J Appl Ecol 51:1575–1583

Scheuerell MD, Zabel RW, Sandford BP (2009) Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (*Oncorhynchus* spp.). J Appl Ecol 46:983–990

Sequeira AMM, Rodríguez JP, Eguíluz VM, Harcourt R, Hindell M, Sims DW, Duarte CM, Costa DP, Fernández-Gracia J, Ferreira LC, Hays GC, Heupel MR, Meekan MG, Aven A, Bailleul F, Baylis AMM, Berumen ML, Braun CD, Burns J, Caley MJ, Campbell R, Carmichael RH, Clua E, Einoder LD, Friedlaender A, Goebel ME, Goldsworthy SD, Guinet C, Gunn J, Hamer D, Hammerschlag N, Hammill M, Hückstädt LA, Humphries NE, Lea M-A, Lowther A, Mackay A, McHuron E, McKenzie J, McLeay L, McMahon CR, Mengersen K, Muelbert MMC, Pagano AM, Page B, Queiroz N, Robinson PW, Shaffer SA, Shivji M, Skomal GB, Thorrold SR, Villegas-Amtmann S, Weise M, Wells R, Wetherbee B, Wiebkin A, Wienecke B, Thums M (2018) Convergence of marine megafauna movement patterns in coastal and open oceans. Proc Natl Acad Sci:201716137

Shaffer SA, Tremblay Y, Weimerskirch H, Scott D, Thompson DR, Sagar PM, Moller H, Taylor GA, Foley DG, Block BA, Costa DP (2006) Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. Proc Natl Acad Sci 103:12799–12802

Shaffer SA, Weimerskirch H, Scott D, Pinaud D, Thompson DR, Sagar PM, Moller H, Taylor GA, Foley DG, Tremblay Y, Costa DP (2009) Spatiotemporal habitat use by breeding sooty shearwaters *Puffinus griseus*. Mar Ecol Prog Ser 391:209–220

Sherman K, Alexander LM, Gold BD (1993) Large marine ecosystems: Stress, mitigation, and sustainability. Washington, DC, AAAS Press

Sherman K, Duda AM (1999) Large marine ecosystems: An emerging paradigm for fishery sustainability. Fisheries 24:15–26

Sherwood CR, Jay DA, Bradford Harvey R, Hamilton P, Simenstad CA (1990) Historical changes in the Columbia River Estuary. Prog Oceanogr 25:299–352

Skov H, Prins E (2001) Impact of estuarine fronts on the dispersal of piscivorous birds in the German Bight. Mar Ecol Prog Ser 214:279–287

Skreslet S (1986) The role of freshwater outflow in coastal marine ecosystems. Springer-Verlag New York Inc New York, NY

Smith JM, Fresh KL, Kagley AN, Quinn TP (2015) Ultrasonic telemetry reveals seasonal variation in depth distribution and diel vertical migrations of sub-adult Chinook and coho salmon in Puget Sound. Mar Ecol Prog Ser 532:227–242

Spear LB, Ainley DG (1997) Flight speed of seabirds in relation to wind speed and direction. Ibis 139:234–251

Speich SM, Wahl TR (1989) Catalog of Washington seabird colonies. U.S. Fish Wildl. Serv. Biol. Rep. 88 (6). 510 pp

St. John MA, Macdonald JS, Harrison PJ, Beamish RJ, Choromanski E (1992) The Fraser River plume: some preliminary observations on the distribution of juvenile salmon, herring, and their prey. Fish Oceanogr 1:153–162

Steele JH (1976) Patchiness. In: Cushing DH, Walsh JJ (eds) Ecology of the Seas. Blackwell Scientific, Oxford, U.K.

Steele JH, Henderson EW, Mangel M, Clark C (1994) Coupling between Physical and Biological Scales [and Discussion]. Philos Trans Biol Sci 343:5–9

Stommel H (1963) Varieties of oceanographic experience. Science 139:572–576

Suryan RM, Phillips EM, So K, Zamon JE, Lowe RW, Stephensen SW (2012) Marine bird colony and at-sea distributions along the Oregon coast: Implications for marine spatial planning and information gap analysis. Northwest Natl Mar Renew Energy Cent Rep No 2:26

Sydeman WJ, Thompson SA (2010) The California Current Integrated Ecosystem Assessment (IEA), Module II: Trends and variability in climate-ecosystem state. Final Rep NOAA NMFS Environmental Res Div: 59

Sydeman WJ, Thompson SA, Kitaysky A (2012) INTRODUCTION Seabirds and climate change: roadmap for the future. Mar Ecol Prog Ser 454:107–117

Szoboszlai AI, Thayer JA, Wood SA, Sydeman WJ, Koehn LE (2015) Forage species in predator diets: Synthesis of data from the California Current. Ecol Inform 29:45–56

Tasker ML, Jones PH, Dixon T, Blake BF (1984) Counting seabirds at sea from ships: A review of methods employed and a suggestion for a standardized approach. The Auk 101:567–577

Teel DJ, Burke BJ, Kuligowski DR, Morgan CA, Doornik DMV (2015) Genetic identification of Chinook salmon: Stock-specific distributions of juveniles along the Washington and Oregon coasts. Mar Coast Fish 7:274–300

Thomas AC, Nelson BW, Lance MM, Deagle BE, Trites AW (2017) Harbour seals target juvenile salmon of conservation concern. Can J Fish Aquat Sci

Thomas AC, Weatherbee RA (2006) Satellite-measured temporal variability of the Columbia River plume. Remote Sens Environ 100:167–178

Toge K, Yamashita R, Kazama K, Fukuwaka M, Yamamura O, Watanuki Y (2011) The relationship between pink salmon biomass and the body condition of short-tailed shearwaters in the Bering Sea: can fish compete with seabirds? Proc R Soc Lond B Biol Sci 278:2584–2590

Tremblay Y, Bertrand S, Henry RW, Kappes MA, Costa DP, Shaffer SA (2009) Analytical approaches to investigating seabird–environment interactions: a review. Mar Ecol Prog Ser 391:153–163

Tremblay Y, Thiebault A, Mullers R, Pistorius P (2014) Bird-borne video-cameras show that seabird movement patterns relate to previously unrevealed proximate environment, not prey. PLoS ONE 9:e88424

Tschanz B, Bersier L-F, Bacher S (2007) Functional Responses: A Question of Alternative Prey and Predator Density. Ecology 88:1300–1308

Van Buskirk RW, Nevitt GA (2008) The influence of developmental environment on the evolution of olfactory foraging behaviour in procellariiform seabirds. J Evol Biol 21:67–76

van Franeker JA (1994) A comparison of methods for counting seabirds at sea in the Southern Ocean. J Field Ornithol 65:96–108

Varoujean D, Matthews D (1983) Distribution, abundance, and feeding habits of seabirds off the Columbia River, May-June, 1982. University of Oregon Institute of Marine Biology, Charleston, OR

Venables WN, Ripley BD (2002) Modern applied statistics with S, Fourth Edition. Springer, New York

Verspoor E, Birkhead TR, Nettleship DN (1987) Incubation and brooding shift duration in the Common Murre, *Uria aalge*. Can J Zool 65:247–252

Vogel JL, Beauchamp DA (1999) Effects of light, prey size, and turbidity on reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey. Can J Fish Aquat Sci 56:1293–1297

Votier SC, Bicknell A, Cox SL, Scales KL, Patrick SC (2013) A bird's eye view of discard reforms: Bird-borne cameras reveal seabird/fishery interactions. PLoS ONE 8:e57376

Wahl TR, Heinemann D (1979) Seabirds and fishing vessels - co-occurrence and attraction. Condor 81:390–396

Watanuki Y, Suryan RM, Sasaki H, Yamamoto T, Hazen EL, Renner M, Santora JA, O'Hara PD, Sydeman WJ (Eds) (2016) Spatial ecology of marine top predators in the North Pacific: Tools for integrating across datasets and identifying high use areas. PICES Sci Rep No 50:55 pp

Watkins JL, Brierley AS (1996) A post-processing technique to remove background noise from echo integration data. ICES J Mar Sci 53:339–344

Wedemeyer GA, Saunders RL, Clarke WC (1980) Environmental factors affecting smoltification and early marine survival of anadromous salmonids. Mar Fish Rev 42:1–14

Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? Deep Sea Res Part II Top Stud Oceanogr 54:211–223

Weimerskirch H, Bishop C, Jeanniard-du-Dot T, Prudor A, Sachs G (2016) Frigate birds track atmospheric conditions over months-long transoceanic flights. Science 353:74–78

Weimerskirch H, Sagar PM (1996) Diving depths of sooty shearwaters *Puffinus griseus*. Ibis 138:786–788

Weitkamp LA, Bentley PJ, Litz MNC (2012) Seasonal and interannual variation in juvenile salmonids and associated fish assemblage in open waters of the lower Columbia River estuary. Fish Bull 110:426–450

Wells BK, Santora JA, Henderson MJ, Warzybok P, Jahncke J, Bradley RW, Huff DD, Schroeder ID, Nelson P, Field JC, Ainley DG (2017) Environmental conditions and prey-switching by a seabird predator impact juvenile salmon survival. J Mar Syst 174:54–63

Whitfield AK (2015) Why are there so few freshwater fish species in most estuaries? J Fish Biol 86:1227–1250

Wiens JA (1976) Population responses to patchy environments. Annu Rev Ecol Syst 7:81–120

Wiens JA, Scott JM (1975) Model estimation of energy flow in Oregon coastal seabird populations. The Condor 77:439–452

Wilson CD, Guttormsen MA, Cooke K, Saunders MW, Kieser R (2000) Echo integration-trawl survey of Pacific hake, *Merluccius productus*, off the Pacific coast of the United States and Canada during July-August 1998. NOAA Tech Memo NMFS-AFSC-118:103

Wilson RP, McMahon CR (2006) Measuring devices on wild animals: what constitutes acceptable practice? Front Ecol Environ 4:147–154

Woillez M, Poulard J-C, Rivoirard J, Petitgas P, Bez N (2007) Indices for capturing spatial patterns and their evolution in time, with application to European hake (*Merluccius merluccius*) in the Bay of Biscay. ICES J Mar Sci 64:537–550

Woillez M, Rivoirard J, Fernandes PG (2009) Evaluating the uncertainty of abundance estimates from acoustic surveys using geostatistical simulations. ICES J Mar Sci 66:1377–1383

Wood SN (2006) Generalized Additive Models: An Introduction with R. Chapman & Hall/CRC

Wood S (2016) Mixed GAM Computation Vehicle with Automatic Smoothness Estimation.

Wood SN, Augustin NH (2002) GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. Ecol Model 157:157–177

Worm B, Lotze HK, Myers RA (2003) Predator diversity hotspots in the blue ocean. Proc Natl Acad Sci 100:9884–9888

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168

Wynne-Edwards VC (1935) On the habits and distribution of birds on the North Atlantic. Boston Society of Natural History 1935

Yamamoto T, Watanuki Y, Hazen EL, Nishizawa B, Sasaki H, Takahashi A (2015) Statistical integration of tracking and vessel survey data to incorporate life history differences in habitat models. Ecol Appl 25:2394–2406

Yankovsky AE, Chapman DC (1997) A simple theory for the fate of buoyant coastal discharges*. J Phys Oceanogr 27:1386–1401

Yen PPW, Sydeman WJ, Bograd SJ, Hyrenbach KD (2006) Spring-time distributions of migratory marine birds in the southern California Current: Oceanic eddy associations and coastal habitat hotspots over 17 years. Deep Sea Res Part II Top Stud Oceanogr 53:399–418

Zabel RW, Achord S (2004) Relating size of juveniles to survival within and among populations of Chinook salmon. Ecology 85:795–806

Zador SG, Parrish JK, Punt AE (2009) Factors influencing subcolony colonization and persistence in a colonial seabird, the common murre *Uria aalge*. Mar Ecol Prog Ser 376:283–293

Zador SG, Piatt JF (1999) Time-budgets of common murres at a declining and increasing colony in Alaska. The Condor 101:149–152

Zamon JE (2003) Mixed species aggregations feeding upon herring and sandlance schools in a nearshore archipelago depend on flooding tidal currents. Mar Ecol Prog Ser 261:243–255

Zamon JE, Phillips EM, Guy TR (2013) Marine bird aggregations associated with the tidally-driven plume and plume fronts of the Columbia River. Deep Sea Res Part II Top Stud Oceanogr

Zamon JE, Phillips EM, Guy TJ (2014) Marine bird aggregations associated with the tidally-driven plume and plume fronts of the Columbia River. Deep Sea Res Part II Top Stud Oceanogr 107:85–95

Zar JH (1999) Biostatistical analysis, 4th ed. Prentice Hall, Upper Saddle River, N.J

Zhang Y, Baptista AM (2008) SELFE: A semi-implicit Eulerian–Lagrangian finite-element model for cross-scale ocean circulation. Ocean Model 21:71–96

Zuur AF, Ieno EN, Elphick CS (2009) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 9999

Zwolinski JP, Demer DA, Byers KA, Cutter GR, Renfree JS, Sessions TS, Macewicz BJ (2012) Distributions and abundances of Pacific sardine (*Sardinops sagax*) and other pelagic fishes in the California Current Ecosystem during spring 2006, 2008, and 2010, estimated from acoustic–trawl surveys. Fish Bull 110:110–122