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ABSTRACT

Freshwater discharge from large rivers into the coastal ocean creates tidally-driven frontal systems known to enhance mixing, primary production, and secondary production. Many authors suggest that tidal plume fronts increase energy flow to fish-eating predators by attracting planktivorous fishes to feed on plankton aggregated by the fronts. However, few studies of plume fronts directly examine piscivorous predator response to plume fronts. Our work examined densities of piscivorous seabirds relative to the plume region and plume fronts of the Columbia River, USA. Common murres (*Uria aalge*) and sooty shearwaters (*Puffinus griseus*) composed 83% of all birds detected on mesoscale surveys of the Washington and Oregon coasts (June 2003–2006), and 91.3% of all birds detected on fine scale surveys of the plume region less than 40 km from the river mouth (May 2003 and 2006). Mesoscale comparisons showed consistently more predators in the central plume area compared to the surrounding marine area (murres: 10.1–21.5 vs. 3.4–8.2 birds km^{-2}; shearwaters: 24.2–75.1 vs. 11.8–25.9 birds km^{-2}). Fine scale comparisons showed that murre density in 2003 and shearwater density in both 2003 and 2006 were significantly elevated in the tidal plume region composed of the most recently discharged river water. Murres tended to be more abundant on the north face of the plume. In May 2003, more murres and shearwaters were found within 3 km of the front on any given transect, although maximum bird density was not necessarily found in the same location as the front itself. Predator density on a given transect was not correlated with frontal strength in either year. The high bird densities we observed associated with the tidal plume demonstrate that the turbid Columbia River plume does not necessarily provide fish with refuge from visual predators. Bird predation in the plume region may therefore impact early marine survival of Pacific salmon (*Oncorhynchus* spp.), which must migrate through the tidal plume and plume front to enter the ocean. Because murres and shearwaters eat primarily planktivorous fish such as the northern anchovy (*Engraulis mordax*), aggregation of these birds in the plume supports the hypothesis that it is the plume region as a whole, and not just the plume fronts, which enhances trophic transfer to piscivorous predators via planktivorous fishes.

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1. Introduction

The tidal discharge of freshwater from large rivers into the sea creates convergent river plume fronts that structure physical and biological properties of the nearshore ocean. Convergent fronts at the leading edge of river plumes aggregate planktonic organisms in coastal ecosystems and therefore provide a predictable food source that may attract schools of planktivorous fishes to the frontal region (Govoni and Grimes, 1992; Grimes and Finucane, 1991; Le Fevre, 1986; Morgan et al., 2005). Increased concentrations of planktivorous fishes such as anchovy (*Engraulis* spp.) and herring (*Clupea* spp.) are then thought to create feeding "hot spots" that lead to elevated densities of piscivorous predators including fishes, birds, and mammals. Many authors suggest that these multi-trophic level responses to fronts, frontal mixing, and coastal water masses created by river discharge are important to energy flow and fish recruitment in coastal ecosystems (e.g. De Robertis et al., 2005; Grimes and Kingsford, 1996; Kudela et al., 2010; Morgan et al., 2005). Examples of systems where responses to river plume fronts are known in lower trophic levels and suspected for upper trophic levels include – but are not limited to – the Elbe and the Rhône rivers in Europe (Skov and Prins, 2001), the Amazon River in South America (Grimes and Kingsford, 1996), and the Mississippi (Govoni and Grimes, 1992), Columbia (De Robertis et al., 2005; Morgan et al., 2005), and Fraser

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(St. John et al., 1992) rivers in North America. However, only one of these studies specifically examined the spatial response of fish predators (loons) to river discharge and its associated frontal system (Skov and Prins, 2001). Skov and Prins (2001) found that the winter density of loons was consistently and significantly higher within 5 km of the estuarine front of the Jutland Coastal Current in the southwestern North Sea. These authors could find only two additional published studies which mention bird response to plume fronts (Briggs et al., 1987; Uspenskvi, 1956); neither of those studies presented quantitative analyses of predator distributions.

The Columbia River is the fourth largest river in North America by volume, with an average flow of 7300 m^3 s^{-1} (Bottom et al., 2005). The river plume is a dominant feature along the coasts of Oregon and Washington throughout the year (Hickey et al., 2010). Recent multi-disciplinary studies examined the physical, chemical, and biological structure of the Columbia River plume and plume front (e.g. Hickey et al. (2010) and the references therein). Inter-disciplinary studies of ocean salmon ecology have also independently examined biological responses to the plume front (De Robertis et al., 2005; Morgan et al., 2005). Investigators from both research efforts frequently infer that energy transfer to piscivorous predators is enhanced in the region of the Columbia River plume (De Robertis et al., 2005; Hickey et al., 2010; Morgan et al., 2005 and references therein), yet we could find no published data which test that specific hypothesis.

The purpose of our work was to examine the distribution and abundance of piscivorous seabirds compared to the Columbia River plume and the strength and position of tidal fronts associated with the plume region. Seabirds are some of the most abundant predators found in this area. The response of seabirds to the plume and plume front is of interest to fisheries oceanographers not only for understanding the plume's role in trophic transfer through the food web, but also because seaward-migrating juvenile salmon must pass through the plume front to enter the ocean, and ocean avian predation at the front may account for some of the as-yet unexplained variation in salmon marine survival (Pearcy, 1992; Scheuerell et al., 2009). Understanding the mechanisms behind variation in early marine survival of salmon is of concern to regional fisheries managers legally responsible for restoring threatened salmon populations (NMFS, 2008, 2010).

We investigated four basic aspects of predator response to the Columbia River plume and the strength and location of plume fronts. First, we determined whether fish-eating birds were more abundant in the central plume area compared with other areas of the Washington and Oregon shelf. Second, we examined whether birds near the river mouth were equally distributed among the three coastal water masses derived from frontal mixing of river discharge with coastal waters (c.f. Horner-Devine et al., 2009). Third, we examined the relationship between bird density and the strength of salinity gradients across the frontal zone of the plume. Finally, we investigated bird abundance relative to the position of the plume front to determine whether maximum bird densities were seen at or near the frontal zone itself. The answers to these questions will begin to address the hypothesis that plumes or plume fronts facilitate energy flow through planktivorous fishes to piscivorous predators.

2. Methods

2.1. Mesoscale surveys: June 2003–2006

We began collecting at-sea survey data for marine birds in 2003 as part of a long-term effort by NOAA Fisheries, Oregon State University, and the Bonneville Power Administration to understand biological and physical processes impacting marine survival of juvenile salmon in the Pacific Northwest. During late June of 2003–2006, we recorded counts of marine birds along each of nine cross-shelf transects from the northern border of Washington State to Newport, Oregon, USA (Fig. 1). Transect locations allowed general comparison of bird density between two coastal areas: the central plume area, including the three transects bracketing the river mouth (Willapa Bay-WB, Columbia River-CR, Cape Meares-CM); and the marine area, including all other shelf transects influenced primarily by ambient marine waters (from north to south: Father and Son-FS, La Push-LP, Queets River-QR, Grays Harbor-GH, Cascade Head-CH, and Newport Hydrographic-NH). We recorded bird counts continuously for approximately 2 hours while traveling due east from 33–43 km offshore and proceeding as far inshore as the survey vessel could safely navigate (typically between 2–9 km from the beach). We maintained a speed of 4.1–4.6 m/s (8–9 knots) during data collection.

2.2. Fine scale surveys: May 2003, May 2006

To examine relationships between bird density, the plume region itself, and tidally-driven plume fronts, we completed a series of fine scale radial transects during 24–27 May 2003 and 02–04 May 2006 (Fig. 2). Transects originated ~10 km north of the river mouth and varied in length from 18–31 km long. The radial design was necessary to maximize the probability of encountering and crossing a visible surface tidal front (Morgan et al., 2005). The radial design also allowed us to sample water in the three major water masses found in the plume: the tidal plume (surface salinities < 21), containing the most recent river discharge released onto the coast; the recirculating plume (surface salinities 21–26), created by 3–4 days of mixing at tidal fronts; and the far-field plume (surface salinities 26–32.5), where ultimate mixing of river water and ambient ocean water occurs (c.f. Horner-Devine et al., 2009). Surveys began at dawn and continued until dusk. We recorded bird and salinity data continuously along each transect.

2.3. Bird observations

For both meso- and fine scale surveys, we used standard, 300-m wide strip-transect methods to collect continuous observations of marine bird abundance and distribution (Tasker et al., 1984). A primary observer used $8 \times$ binoculars to identify and count all flying or sitting birds within a strip extending 300-m out from the bow to the beam of the ship in a 90-degree arc on the side of the vessel with the best viewing conditions. Every bird sighting was recorded by a secondary observer who immediately entered the data into a laptop computer running either WinFlock (2003–2004, G.L. Hunt, Jr., University of California, Irvine, CA) or SeeBird (2005–2006, L. Ballance, Southwest Fisheries Science Center, La Jolla, CA) data acquisition programs. The computer automatically stamped each observation in WinFlock with the date and time to the nearest second. These time stamps were subsequently converted to latitude and longitude based on interpolation from latitude and longitude positions entered manually on a regular basis throughout the survey. Observations in SeeBird were automatically stamped with date, time, latitude, and longitude via a direct NMEA data stream from a global positioning satellite (GPS) antenna to the computer. The secondary observer also assisted with sightings or identifications (Spear et al., 2004). During the fine-scale surveys, observer and recorder duties rotated every 2 h to minimize fatigue. Observers were 7.1-m above sea level on the bridge of the F/V *Frosti* (May 2003, June 2003, 2004, and 2006); 12.6-m above sea level on the flying bridge of the NOAA R/V *McArthur II* (May 2006); and 3.0-m above sea level on
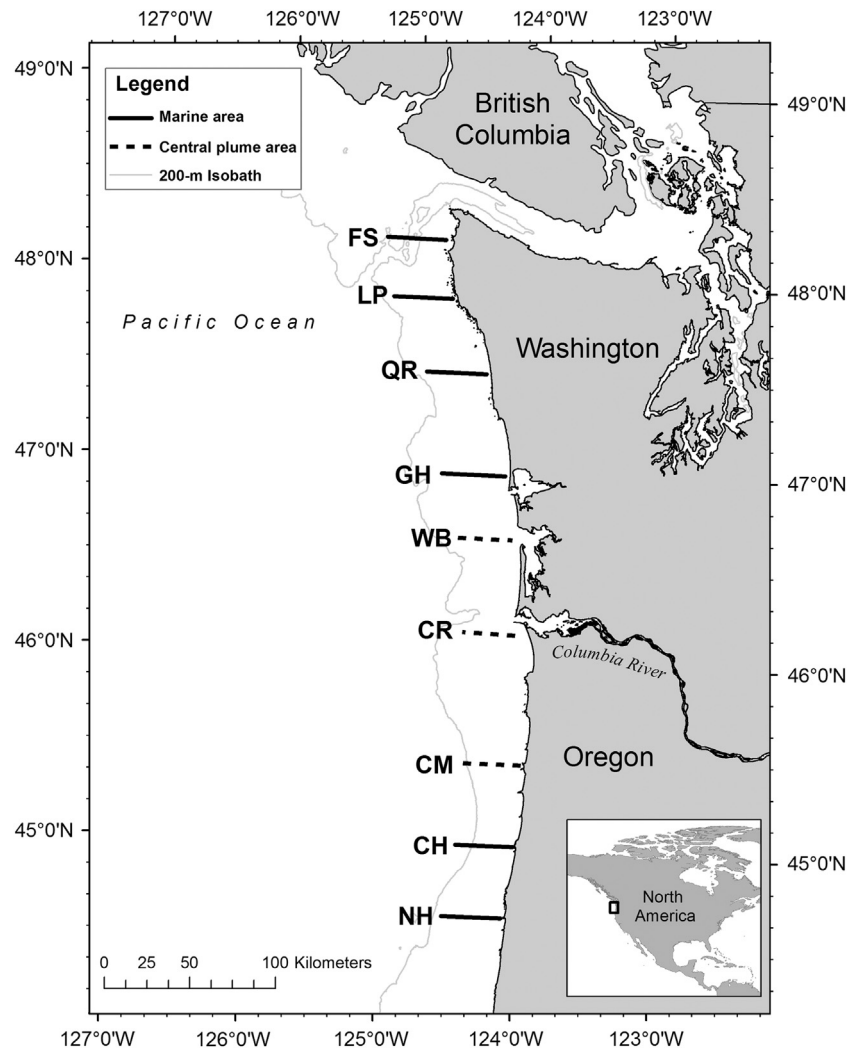
Fig. 1. Mesoscale survey lines from the Oregon and Washington coasts, USA. Each transect line is named for a geographic feature in proximity to the inshore end of the line as follows: FS=Father and Son, LP=La Push, QR=Queets River, GH=Grays Harbor, WB=Willapa Bay, CR=Columbia River, CM=Cape Meares, CH=Cascade Head, and NH=Newport Hydrographic.

the bridge of the F/V *Pacific Fury* (June 2005). We calibrated strip-widths for each survey vessel according to methods of Heinemann (1981). Data collected included species identification, species counts, and standard behaviors (e.g. sitting, flying, feeding, and ship-following). Observers also recorded the latitude and longitude of any visible surface boundary/convergence that was crossed by the ship. Visual observations were recorded independently of knowledge of surface salinity data.

2.4. Sea surface temperature and salinity

We used a deck-mounted portable water bath system to continuously record sea surface temperature and salinity on each vessel. Seawater from ~3 m depth was pumped via the shortest route from the ship's hull intake directly into the sensor port of a calibrated SeaBird Electronics SBE 19 conductivity-temperature-depth unit. To isolate the instrument sensors from effects of changing air temperature on deck, the SBE 19 was completely submerged in a large PVC tube supplied with a continuously flowing water bath of the same water which was fed to the sensors. The instrument recorded the time, date, latitude, longitude, temperature, and conductivity every four seconds to a data file on a laptop computer. We processed raw data files with Seabird's SeaSoft software and converted conductivity to salinity.

2.5. Data analysis

For mesoscale surveys in June, we calculated bird density (birds km^{-2}) for each individual transect in each year. We used a two-way ANOVA to examine the effect of year (2003, 2004, 2005, and 2006) and area (Central plume area: WB, CR, and CM; Marine area: FS, LP, QR, GH, CH, and NH) on bird density. We $\log_{10}(x+1)$-transformed bird density data to normalize data and to homogenize sample variances. The test was performed on total birds seen, whether birds were first detected on the water or flying. We excluded birds that were following the ship from the analysis.

For fine scale surveys in May, we wanted to avoid counting birds transiting through the survey area, therefore we included only birds sitting on the water or actively feeding in our analyses. We created a MATLAB software routine (MathWorks, Inc., R2010a) to calculate mean temperature and salinity within 1-km segments of each transect from the high-resolution sea surface temperature and salinity data. A 1-km bin size allowed us to spatially resolve salinity in the tidal plume (<21), the recirculating plume (21–26), and the far-field plume regions (26–32.5) as well as to identify the frontal zone of greatest salinity change. The 1-km bin size was also necessary to distinguish the plume front per se from salinity variation at very small spatial scales due to other physical features such as internal wave packets (Nash and Moum, 2005).
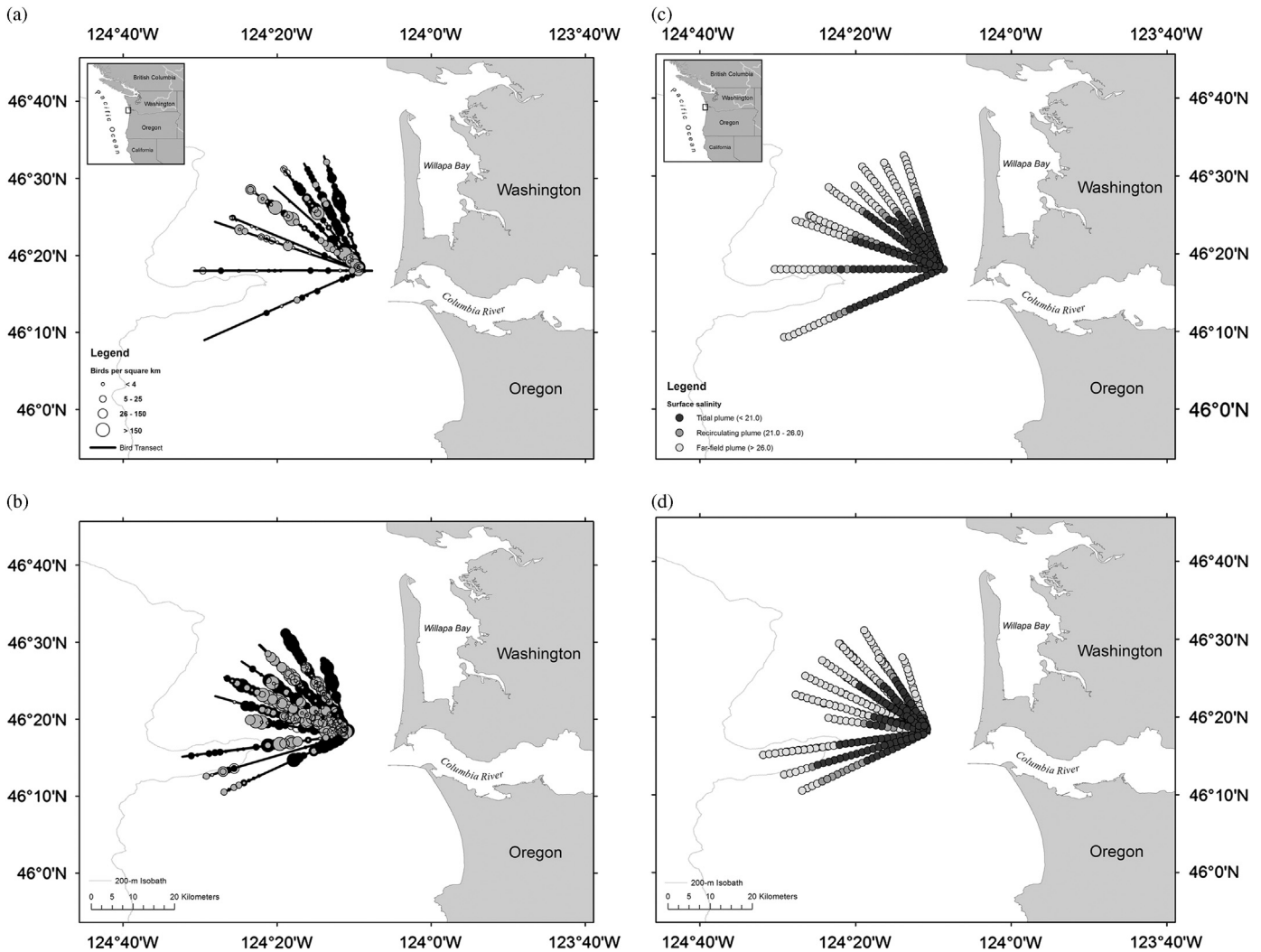
Fig. 2. Fine scale radial survey lines around the mouth of the Columbia River, USA. Counterclockwise from left: (a) bird density in May 2003 (b) bird density in May 2006 (c) surface salinity in May 2003 and (d) surface salinity in May 2006. In (a) and (b), common murres are shown as black circles, sooty shearwaters as gray circles, and all other birds as white circles.

We calculated differences between mean temperature and mean salinity in each 1-km bin for every pair of adjacent bins on a radial transect, beginning with the offshore-most bin and proceeding inshore. The maximum salinity difference observed in these pairwise comparisons was assumed to define the location (bin, #) and strength ($\Delta S \cdot km^{-1}$) of the frontal zone on each transect. We assumed the latitude and longitude of the midpoint in the bin exhibiting the maximum salinity difference indicated the geographic location of the front.

To examine whether birds were equally distributed across all three coastal plume regions as defined in Horner-Devine et al. (2009), we assigned each 1-km bin in a given year to a plume region based on the observed mean salinity in that bin (tidal plume: S < 21, recirculating plume: 21–26, far-field plume: 26–32.5). We then used a χ^2 goodness-of-fit test to compare observed, total count of birds in each region with the expected count under the assumption of equal distribution of birds across each plume region. We also used a χ^2 goodness-of-fit test to determine whether or not there was an association between sightings of visible surface fronts and frontal strength, where frontal strength was categorized as either weak ($\Delta S < 5\ km^{-1}$), moderate ($5\ km^{-1} < \Delta S < 8\ km^{-1}$), or strong ($\Delta S > 8\ km^{-1}$).

We used Spearman rank correlation to examine the correlation between bird density on each radial transect and transect orientation. Radial transect orientation was measured by the inshore-to-offshore true compass bearing of an individual transect. For example, a radial transect oriented directly east-west would be assigned a bearing of 270°, one oriented northwest–southeast would have a bearing of 315°, and one oriented north-south would have a bearing of 000.° Similar to our treatment of temperature and salinity, we used a MATLAB routine to calculate bird density in 1-km segments along each radial transect. Partial bins of < 1 km length at the end of each transect accounted for less than 5% of bird counts in 27 of 30 cases, so we did not use these "leftover" partial segments in our analysis. No discarded partial bin would have changed analysis results. Density for a given radial transect was calculated as the mean of all 1-km density bins for that transect.

To determine whether or not bird abundance was correlated with the strength of the plume front, we also used Spearman rank correlations to compare the maximum observed salinity difference to bird density on individual transects. Finally, to determine whether or not maximum bird density within a radial transect was spatially associated with the frontal zone on that transect, we

used Spearman rank correlation to compare the 1-km bin containing the maximum observed salinity difference (frontal zone location) to (1) the bin containing maximum bird density, and (2) the proportion of total birds detected within 3 km on either side of the midpoint of the frontal zone.

3. Results

3.1. Mesoscale surveys: June 2003–2006

We completed 12 transects bracketing the river mouth (central plume area: WB, CR, and CM) and 21 transects away from the river mouth (marine area: FS, LP, QR, GH, CH, and NH) during June in 2003–2006. We recorded a total of 13,412 birds on the water or flying during the meso-survey effort. The most commonly observed bird species were two diving predators, common murres (*Uria aalge*, 22.6%) and sooty shearwaters (*Puffinus griseus*, 60.4%). These two species accounted for 83% of all birds recorded during June meso-surveys. Common murres breed during the summer on the Oregon and Washington coasts, whereas sooty shearwaters are non-breeding migrants from Chile and New Zealand (Wiens and Scott, 1976). Both species are thought to eat primarily fish in the survey area, although they may occasionally consume krill or other crustaceans (Varoujean and Matthews, 1983; Wiens and Scott, 1976). Other species accounted for only 17% of sightings, and included gulls (Laridae), alcids aside from murres (Alcidae), tubenoses aside from sooty shearwaters (Procellariformes), and loons (Gaviiformes).

Densities (birds km^{-2}) of murres, shearwaters, and other species from the mesoscale survey in each area and year are reported in Table 1. For purposes of direct comparison with densities reported in the fine scale surveys, where we excluded flying birds from the analysis, we also report mesoscale results excluding flying birds. Common murres were 2.3–4.5 times more abundant on the three transects in the central plume area compared with densities observed on transects in the marine area (Table 1). There was a significant effect of area on mean murre

density ($p < 0.001$), but there were no significant effects of year or area x year interactions on murre density (Table 2, two-way ANOVA on $\log_{10}(x+1)$-transformed data). Although sooty shearwaters tended to be 1.3 to 4.6 times more abundant in the central plume area, these differences were not statistically significant for area, year, or region x year interaction (Table 2, $p=0.21$ 0.96, and 0.82 respectively). There was no consistent pattern in the abundance of other species between areas, although the ANOVA results did reveal significant year and area × year effects (Table 2, $p=0.98$, 0.03, and 0.04 respectively).

3.2. Fine scale surveys: May 2003, May 2006

We completed nine radial transects in May 2003 and 21 radial transects in May 2006. Radial transect length varied from 18–31 km, depending on whether or not a visible front was detected, and if so, how far away from the river mouth it was located. When clearly visible, actively convergent surface fronts were closer to the river mouth, and shorter track lines were sufficient to cross the front and proceed beyond the front for several kilometers. In May 2003, seas were calm with no swell, and winds were light (< 2 m s^{-1}) during the entire survey period. In May 2006, swell was from the NW at 1.5–3-m, and winds were primarily from the north and northwest. Wind speed was 4–12 m s^{-1} during 02–03 May 2006 and 2.5–10 m s^{-1} on 04 May 2006.

A visible surface front was present on 20 of 30 transects (Fig. 3). Typically, the surface boundary exhibited an abrupt, distinct, actively convergent foam line separating the most recently

Table 1
Bird densities compared among central plume and marine areas of the mesoscale survey, given as mean±standard error of the mean.

Flying, sitting, or feeding				
	June 2003	**June 2004**	**June 2005**	**June 2006**
Common murre				
Central plume area	19.1±7.6	10.1±0.6	21.5±8.5	15.3±7.0
Marine area	8.2±1.3	3.8±0.8	7.5±2.7	3.4±1.3
Sooty shearwater				
Central plume area	75.1±60.9	26.6±19.1	24.2±11.7	35.7±14.4
Marine area	16.3±8.4	20.0±4.8	11.8±5.1	25.9±12.4
Other				
Central plume area	4.2±1.5	19.1±6.9	5.3±1.2	4.2±2.5
Marine area	7.9±1.4	6.9±1.4	5.3±1.2	5.5±1.2

Sitting or feeding only				
	June 2003	**June 2004**	**June 2005**	**June 2006**
Common murre				
Central plume area	11.5±3.3	5.8±1.6	2.0±0.9	4.9±3.1
Marine area	4.7±0.4	2.8±0.8	5.4±2.0	1.0±0.3
Sooty shearwater				
Central plume area	67.4±60.8	11.8±18.3	19.5±10.5	26.3±14.6
Marine area	10.5±7.7	11.0±4.6	9.6±5.0	3.8±2.9
Other				
Central plume area	0.6±0.4	6.5±2.4	0.9±0.4	0.6±0.2
Marine area	2.1±1.1	1.3±0.4	1.2±0.3	1.3±0.3

Table 2
Two-way ANOVA results comparing mean densities from mesoscale surveys. Statistically significant differences are highlighted in bold type.

		Degrees of freedom	*F*	*p*
Common murre	**Area**	**1**	**14.2**	**< 0.001**
	Year	3	1.7	0.19
	Area × year	3	0.2	0.89
Sooty shearwater	Area	1	1.69	0.21
	Year	3	0.11	0.96
	Area × year	3	0.31	0.82
Other birds	Area	1	< 0.001	0.98
	Year	**3**	**3.69**	**0.03**
	Area × year	**3**	**3.18**	**0.04**

Fig. 3. Example of visible tidal plume front from fine scale surveys < 30 km from the mouth of the Columbia River, 02 May 2006. River water is on the left, coastal ocean water on the right; and the foam line between the two is 1–2 m wide. The dozens of small, black-and-white objects visible on the water surface are common murres; gulls can be seen flying along the foam line.

discharged river water from coastal waters. River water most frequently showed greater surface roughness, brown color, and high turbidity compared to coastal water which was less rough and more blue-green or gray in appearance. The presence of a distinct, visible surface front was significantly associated with moderate and strong salinity gradients, but not with weak gradients (Table 3, χ^2 test for observed vs. expected frequencies, $p=0.005$).

Twenty-seven transects sampled the tidal plume (salinity < 21), through the recirculating plume (salinities 21–26), and into the far-field plume (salinities > 26) (Fig. 2a and b). Three transects on 02 May 2006 had surface salinities > 30 over their entire length, and thus these only sampled the far-field plume. Salinity change across the frontal zone varied from weak ($\Delta S < 5$ km^{-1}, $n=12$), to moderate (5 km^{-1} < $\Delta S \leq 8$ km^{-1}, $n=9$), to strong (8 km^{-1} < ΔS, $n=9$). Mean surface salinity in 1-km bins varied from 9.9–31.5 in 2003 and from 12.9–32.3 in 2006. Summary data for each radial transect are presented in Table 4.

Comparison of mean sea surface temperatures from our portable system with the closest hourly readings from the forward temperature sensor in the shipboard system aboard the NOAA R/V McArthur II in May 2006 showed good agreement. The ship's forward sensor sampled water immediately after it entered the flow-through system, before warming of the water in the pipes leading to the portable system took place. Differences between the portable and shipboard systems ranged from 0.009–1.019 °C, with a mean difference of 0.290 °C. The temperature difference between instruments exceeded 0.5 °C in only three instances. Mean temperatures in 1-km bins ranged from 12.8–17.5 °C in late May 2003 and 10.0–13.1 °C in early May 2006. Sea surface temperature was relatively homogeneous within individual transects. Temperature gradients km^{-1} of survey track were less than 1 °C in 28 of 30 cases, and the full range of temperatures encountered was less than 2 °C in 29 of 30 cases. We therefore considered the effects of temperature to have negligible impacts on frontal strength or location with any given radial transect.

During our fine scale surveys, we recorded a total of 3320 birds on the water from nine radial transects during May 2003 and 10,363 birds from 21 radial transects in May 2006 (Fig. 3c and d). The most commonly observed bird species on radial transects were common murres (61.1% in 2003, 49.5% in 2006) and sooty shearwaters (31.4% in 2003, 41.5% in 2006). In total, murres and shearwaters accounted for 91.3% of all sightings on radial transects. Birds were significantly more abundant in May 2006 than in May 2003 (murres: 36.4±6.2 vs. 15.4±5.2 birds km^{-2}, shearwaters: 38.4±10.7 vs. 10.8±5.9 birds km^{-2}; other species 6.9±1.9 vs. 0.7 ±0.3 birds km^{-2}; t-test on log$_{10}$ (x+1)-transformed data, < 0.01 in all cases).

Radial transects successfully sampled birds in the tidal plume, the recirculating plume, and the far-field plume in both 2003 and 2006 (Fig. 2c and d). Bird counts were not equally distributed across the three plume regions defined by Horner-Devine et al. (2009), Table 5. During 2003, murres and shearwaters occurred in

the tidal plume region more often than would be expected if they were distributed equally across the three plume regions (goodness-of-fit test, χ^2 for murres=134.9, χ^2 for shearwaters=130.6; d. f.=2, $p < 0.0001$ for both species). Other species, however, were found more often in the recirculating and far-field plumes that expected ($\chi^2=218$, d.f.=2, $p < 0.0001$). During 2006, murres were equally distributed across all three plume regions (goodness-of-fit test, $\chi^2=1.1$, d.f.=2, $p=0.29$), but shearwaters were more common in the tidal plume region than in the other two regions ($\chi^2=191.3$, d.f.=2, $p < 0.0001$). Other species were more common in the recirculating plume region than in the tidal or far-field region ($\chi^2=807.5$, d.f.=2, $p < 0.0001$).

Because of the observed difference in bird densities between 2003 and 2006, we initially ran all Spearman rank correlation statistics of bird density vs. fronts separately for each year. Two factors exhibited significant year-specific effects: radial transect orientation and proportion of sightings ≤3 km of the front (Table 6). For the other two factors that did not exhibit year effects (front strength, front location), we pooled data from 2003 and 2006 to increase the statistical power of the tests.

The mean density of common murres was significantly correlated with radial transect orientation in 2003 (Table 6; Spearman rank correlation, $p=0.03$). Although this relationship was not significant in 2006, there were three outlier data points in 2006, where we defined an outlier x to be values greater than 63.0, according to the formula:

$$(\text{mean}+\text{standard error})+[3 \times (\text{mean}+\text{standard error})-(\text{mean}-\text{standard error})]$$

If we excluded three outlier data points with densities of > 63 birds km^{-2} (Fig. 4), the correlation became much stronger (Spearman rank correlation, $R=0.45$, $p=0.06$). Murres were therefore more abundant on the north and northwest face of the plume than on the western face. The densities of shearwaters and other species were not significantly related to transect orientation (Table 6).

At the scale of individual radial transects, murre density was not related to the strength of the front. Shearwater densities had a tendency to be more abundant on transects with stronger fronts, but this was not statistically significant (Fig. 5, Table 6; Spearman rank correlation, $p=0.16$). Other birds also had a tendency to be more abundant on transects with stronger fronts; however, this was not significant either (Table 6; Spearman rank correlation, $p=0.08$). There was no statistical correlation between the 1-km segment of maximum bird density and the 1-km segment of the maximum salinity gradient (Table 6). Front strength was positively correlated with the proportion of bird sightings within 3 km of the front for both murres and shearwaters in 2003 (Table 6, Spearman rank correlation, $p=0.02$ and 0.01, respectively), but not in 2006 (Table 6, Spearman rank correlation, $p=0.64$ and $p=0.90$, respectively).

4. Discussion

In our mesoscale coastal surveys, common murre density was significantly higher in the central plume area near the Columbia River mouth than in other marine areas of Washington and Oregon coasts. Shearwater density was also consistently higher in the central plume area, although this pattern was not statistically significant. In our fine scale surveys at the river mouth, murres and shearwaters were both significantly associated with the tidal plume in 2003. Murre and shearwater abundance within 3 km of the frontal zone was positively correlated with frontal strength, although there was no correlation between the 1-km segment containing the front and the 1-km segment containing maximum

Table 3
Goodness-of-fit contingency table for the occurrence of visible fronts on fine scale radial transects.

Frontal strength	Visible surface front	No visible surface front
Weak ($\Delta S < 5$ km^{-1})	4	8
Moderate (5 km^{-1} < $\Delta S \leq 8$ km^{-1})	7	2
Strong ($\Delta S > 8$ km^{-1})	9	0
Totals	20	10

Table 4

Summary data for fine scale radial transects in May 2003 and May 2006.

Date	Start time	Radial transect bearing	Tide height (m)	Hours after previous high tide	Mean temp (°C)	Min. salinity	Max. salinity	Front strength (ΔS/km)	Distance: max. salinity gradient to visible front (km)	Common murre density (birds km^{-2})	Sooty shearwater density (birds km^{-2})	Other species density (birds km^{-2})	Distance: front to max. bird density (km)
24-May-03	10:36	270	1.63	2.2	14.0	16.1	31.5	2.3	No visible front	1.72	1.72	0.58	17
24-May-03	12:51	240	1.63	4.5	14.1	9.9	31.2	3.8	No visible front	2.69	0.32	0.00	8
25-May-03	6:01	310	2.10	8.5	13.5	14.3	31.3	5.5	1.0	10.83	30.12	1.55	2
25-May-03	12:43	295	1.61	3.2	14.7	13.9	31.4	2.8	7.1	0.74	4.19	0.86	6
25-May-03	18:05	345	1.61	8.6	15.1	16.4	28.6	4.7	0.5	32.50	1.19	0.12	1
26-May-03	5:54	337	2.11	7.7	13.7	12.1	30.3	8.3	0.9	25.71	6.91	2.62	2
26-May-03	15:27	300	1.64	4.9	15.0	14.5	30.2	1.7	No visible front	1.87	0.53	0.27	15
26-May-03	17:49	330	1.64	7.3	14.7	15.3	30.5	3.8	No visible front	19.29	1.31	0.24	2
27-May-03	16:04	325	1.71	4.6	16.1	16.9	31.0	2.8	No visible front	43.08	50.64	0.38	13
2-May-06	6:28	330	2.33	2.7	10.2	31.2	32.0	0.3	No visible front	46.17	7.04	5.06	0
2-May-06	8:24	320	2.33	4.7	10.4	30.4	32.0	0.3	18.8	98.85	17.31	8.72	19
2-May-06	9:46	300	2.33	6.0	10.6	20.1	31.9	6.1	No visible front	45.50	27.08	1.80	13
2-May-06	11:34	290	2.33	7.8	11.2	15.3	31.6	8.7	1.2	10.29	8.12	3.19	1
2-May-06	12:55	310	2.33	9.2	11.3	16.7	31.7	11.9	1	43.07	1.07	0.80	8
2-May-06	14:52	320	2.33	11.1	11.3	19.1	32.1	5.2	0.9	100.51	81.03	7.69	2
2-May-06	16:19	340	2.33	12.6	10.8	19.2	32.3	5.1	No visible front	52.22	0.00	1.48	10
2-May-06	17:42	330	2.33	14.0	10.5	31.1	32.3	0.7	12.9	11.05	3.68	1.05	1
3-May-06	7:16	240	2.12	2.8	10.5	16.6	31.4	3.5	No visible front	83.20	2.27	7.47	18
3-May-06	8:45	320	2.12	4.3	10.4	18.1	32.3	5.9	0.7	21.48	6.11	5.00	12
3-May-06	10:06	330	2.12	5.6	10.4	13.9	32.1	15.4	0.2	29.82	1.40	6.84	8
3-May-06	11:04	260	2.12	6.6	11.3	14.5	31.3	14.1	3.6	11.45	12.46	6.67	5
3-May-06	12:36	250	2.12	8.1	11.6	12.9	30.6	7.8	0.8	3.72	2.82	5.00	1
3-May-06	14:11	310	2.12	9.7	11.3	14.6	32.0	12.6	1.4	17.19	52.10	9.47	5
3-May-06	15:31	300	2.12	11.0	11.4	16.0	32.0	8.3	1.8	50.88	93.68	41.05	1
3-May-06	16:31	290	2.12	12.0	11.6	16.2	31.3	5.5	0.5	25.88	96.67	14.90	5
3-May-06	17:51	280	2.12	13.4	11.5	18.0	30.6	5.2	6.2	38.07	114.39	8.07	10
4-May-06	6:38	260	1.90	1.2	11.0	15.8	31.4	2.6	No visible front	10.37	11.11	0.12	8
4-May-06	14:53	330	1.90	9.4	12.0	16.6	31.7	5.8	0.1	25.26	33.68	7.90	2
4-May-06	16:07	320	1.90	10.7	12.4	16.5	31.5	8.2	1.6	20.20	50.98	0.59	3
4-May-06	17:05	310	1.90	11.6	12.4	15.8	31.0	9.7	0.1	20.00	183.33	1.05	2

Table 5
Goodness-of-fit contingency table for bird counts vs. plume region, fine scale surveys, May 2003 and May 2006.

	Plume region	Salinity range	Total 1-km bins	Observed bird count	Expected bird count
May 2003					
	Tidal	< 21	138	746	603.9
Common murre	Recirculating	21–26	23	33	99.7
	Far field	26–32.5	88	308	383.5
	Tidal	< 21	138	579	423.3
Sooty shearwater	Recirculating	21–26	23	51	72.4
	Far field	26–32.5	88	153	278.3
	Tidal	< 21	138	11	30.6
Other species	Recirculating	21–26	23	13	5.1
	Far field	26–32.5	88	31	19.3
May 2006					
	Tidal	< 21	140	1478	1504.3
Common murre	Recirculating	21–26	24	271	256.2
	Far field	26–32.5	286	3078	3066.5
	Tidal	< 21	140	1742	1338.7
Sooty shearwater	Recirculating	21–26	24	158	227
	Far field	26–32.5	286	2378	2172.3
	Tidal	< 21	140	205	257.4
Other species	Recirculating	21–26	24	231	45.2
	Far field	26–32.5	286	411	544.4

Table 6
Spearman rank correlations for bird densities vs. frontal characteristics, fine scale surveys, May 2003 and May 2006. Statistically significant values are indicated in bold type.

	Year	Spearman *R*	*p* value
Density vs. radial transect orientation			
Common murre	**2003**	**0.78**	**0.01**
	2006	0.29	0.20
	2006[**]	0.45	0.06
Sooty shearwater	2003	0.78	0.46
	2006	−0.19	0.41
	2006[**]	−0.05	0.78
Other species	2003	0.10	0.80
	2006	−0.09	0.69
Density vs. front strength			
Common murre		0.01	0.96
Sooty shearwater		0.26	0.16
Other species		0.33	0.08
Maximum density vs. front location			
Common murre		−0.02	0.90
Sooty shearwater		0.06	0.75
Other species		−0.01	0.97
Proportion at front vs. front strength			
Common murre	**2003**	**0.77**	**0.02**
	2006	−0.11	0.64
Sooty shearwater	**2003**	**0.80**	**0.01**
	2006	0.03	0.90
Other species	2003	0.24	0.57
	2006	0.13	0.57

[**] Three outliers > 63 bird km^{-2} excluded.

Fig. 4. Density of common murres vs. transect bearing, fine scale surveys. The solid line is the best linear fit to the 2003 data; the dotted line represents the best linear fit to the 2006 data after three outliers of > 63 murres km^{-2} were removed.

Fig. 5. Bird density vs. front strength, fine scale surveys. Front strength is defined as the maximum salinity gradient observed between adjacent pairs of 1 km bins on a given transect.

bird density. Murre density in both 2003 and 2006 was higher on the northern face of the plume than on the western and southwestern faces. In 2006, fine scale results were somewhat different. Higher shearwater densities were significantly associated with the tidal plume, as they were in 2003. In contrast, murres were equally distributed among all three fine-scale plume regions in 2006. Neither murre nor shearwater density showed a significant relationship between front strength, front location, or proximity to the front at the fine scale in 2006.

Similar patterns of interannual variation in mesoscale vs. fine scale associations of piscivorous birds with upwelling fronts and frontal regions of the California Current were observed by
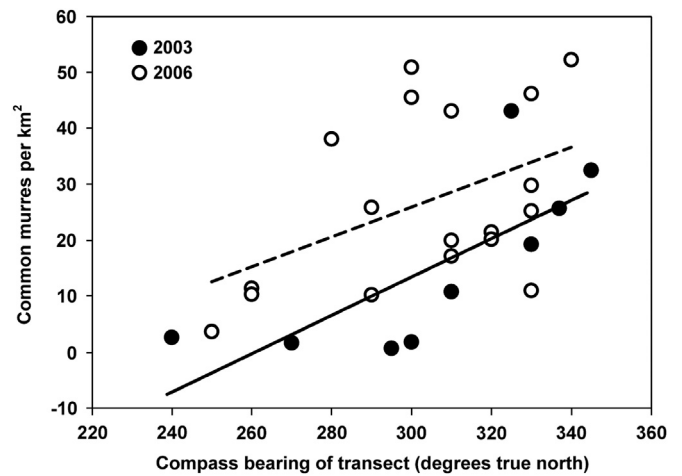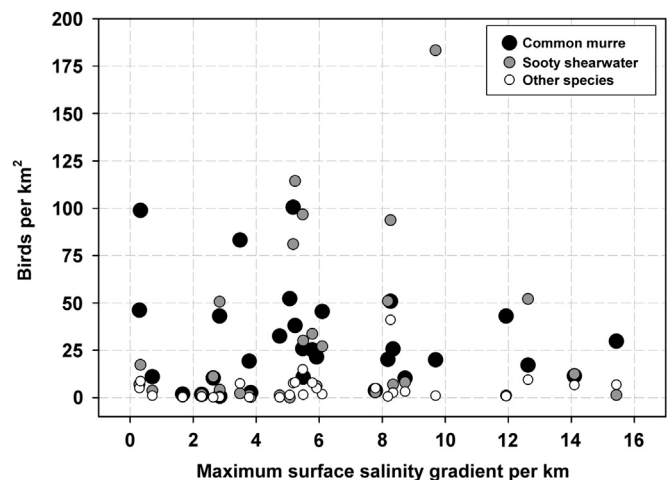
Ainley et al. (2009). On the central and southern coast of Oregon, murres and shearwaters were less strongly associated with physical measures of fronts during a year of higher prey availability than in a year with less prey availability. The distribution and abundance of prey may therefore modulate the response of predators to the plume and plume fronts among years.

Elevated densities of murres and shearwaters in the central plume region of our mesoscale surveys (Table 1) were similar in magnitude to elevated densities observed by Ainley et al. (2005) at summer upwelling fronts in the northern California Current (12 murres km^{-2}, 39 shearwaters km^{-2}). Densities of murres during both years of fine scale surveys in the plume itself (15.4 birds km^{-2} in 2003 and 36.4 birds km^{-2}) were higher than those observed by Ainley et al. (2005) and by us in the mesoscale surveys (Table 6). Unlike Ainley et al. (2009), who noted it seemed murres and shearwaters did not co-occur in mixed flocks in central and southern Oregon, we observed murres and shearwaters on the water or foraging in mixed groups in the plume region. We could find only one other published study reporting May/June murre and shearwater densities near the Columbia River plume (Varoujean and Matthews, 1983). During 1982, Varoujean and Matthews (1983) recorded densities of common murres (sitting only) between 18–123 birds km^{-2}, with a mean density of 51 birds km^{-2}. Densities of sooty shearwaters (sitting and flying) varied between 0–866 birds km^{-2}, with a mean density of 25 birds km^{-2}.

It has been proposed that the entire plume region affected by tidal fronts in an area of elevated production (Kudela et al., 2010). When compared to other marine areas on the Washington and Oregon coasts, our results support the hypothesis that it is the plume region as a whole, rather than only the plume fronts per se, that attracts piscivorous bird predators. Our comparison of bird distribution among tidal, recirculating, and far-field plume regions showed more birds were often associated with the tidal plume compared to other regions of the plume. Horner-Devine et al. (2009) observed this region of the plume is bounded by strong fronts. We found the visual manifestation of the surface front can persist for several hours even though the front is non-stationary and propagating rapidly offshore. In addition, our results documented that visible surface convergences were consistently associated with moderate to strong salinity gradients across the front. These observations indicate visual cues from the surface front are a reliable way for avian predators (or research scientists) to locate the tidal plume region as well as the active tidal fronts themselves, even when plume morphology and plume fronts are highly dynamic. Our observation that bird predators are associated with the tidal plume region is consistent with the elevated regional productivity hypothesis.

Because planktivorous fish such as the northern anchovy are attracted to the Columbia River plume region for feeding and reproduction (Litz et al., 2008; Parnel et al., 2008), the tidal plume region may be an area where predator encounter rates with planktivorous fishes are higher than elsewhere on the Washington or Oregon coasts. If this is the case, then neither planktivorous fishes nor fish predators may need to remain at the actively convergent front to experience high encounter rates with their respective prey. For example, Peterson and Peterson (2008) provide evidence that elevated zooplankton biomass is found not only at the Columbia River tidal plume perimeter – the tidal front – but also below the surface along the entire base of the plume. Therefore, plankton aggregations occur in extensive subsurface patches in the tidal plume away from the front as well as in the narrow frontal boundary itself. This provides a much larger spatial footprint of foraging opportunities for planktivores than the surface front alone.

Although turbidity in the tidal plume would certainly affect the distance at which murres and shearwaters could visually detect planktivorous fishes or juvenile salmon, these predators were clearly not deterred from foraging in the plume region, as has been suggested by De Robertis et al. (2003, 2005). We found higher murre and shearwater density in tidal plume during 2003, and higher shearwater density in the tidal plume in 2006. Results are in contrast to what would be expected if these visual predators avoided or were consistently less abundant in turbid waters, and are consistent with Ainley's (1977) hypothesis that turbid water actually permits diving predators to make a closer approach to prey before prey detect the predator. Because all juvenile salmon must pass from the Columbia River through the tidal plume and plume front to successfully enter the ocean, avian predation in the tidal plume region could directly affect early marine survival of outmigrating juvenile salmon. The mortality effect of bird predators on salmon is probably modulated by variation in the abundance of alternative prey such as anchovy or smelt (Kaltenberg et al., 2010). Kudela et al. (2010) postulate that in times of poor ocean productivity, trophic activity may become concentrated in the Columbia River plume region. If this is so, then salmon mortality due to ocean avian predation may be especially high in poor ocean years if seabird foraging becomes even more concentrated in the tidal plume region. The Columbia River is similar to the Fraser River in that both of these systems produce significant runs of Pacific salmon, and the plume regions attract both planktivores and visual predators (c.f. St. John et al., 1992). It would be interesting to compare seabird foraging patterns between the Columbia, the Fraser, and other salmon-producing rivers in North America.

We observed that murre density was higher on transects crossing the northwest and north face of the plume front when compared to the western face. Similarly, the proportion of murres and shearwaters seen within 3 km of the front was positively related to the strength of the front in 2003. These results support the hypothesis that murres and shearwaters aggregate in regions of stronger fronts and near the front itself. The reasons for differential use of the north face could be due to asymmetry in plume front properties that affect the distribution of plankton and planktivorous fishes. For example, stronger plume fronts have been shown to form on the northern face of the plume, compared to the southern face (Jay et al., 2009). In addition, the breakdown of the plume front proceeds from south to north as the release of internal waves drains kinetic energy from the front (Jay et al., 2009). Elevated zooplankton abundance associated with frontal structure is therefore likely to be more predictable and more persistent in the north than to the west or the south, possibly increasing the use of that area by planktivorous fishes and fish predators.

We did not find strong support for the hypothesis that mean bird density on any given radial transect was related to strength of the plume front in either 2003 or 2006, nor did we find support for the idea that maximum bird density was co-located with the maximum salinity gradient across the front. These results are similar to those of St. John et al. (1992) and De Robertis et al. (2005) for juvenile salmon, who found higher salmon abundance in the plume/front region compared to surrounding coastal water, but who were unable to detect aggregations of juvenile salmon at the tidal front itself. De Robertis et al. (2005) speculated that the dynamic nature of plume fronts made it difficult for salmon to detect and remain aggregated with the front. We offer another possible explanation for the ephemeral nature of spatial associations between fronts, fish, and predators. Even if planktivorous fish schools spend more time at the front, and are initially detected by predators there, those fish will not remain stationary if attacked by predators, and hungry predators will likely pursue fleeing prey. The cycle of encounter–evasion–pursuit would create highly dynamic predator-prey interactions at the front itself. It is

interesting that stronger associations of predators with the front itself were seen in 2003, when predators were less abundant, than in 2006, when predators were more abundant. Perhaps fish-front associations in this area are more stable when fewer predators are in the environment.

The lack of correlation between bird density and front location at the fine scale may also have been influenced by a sampling bias inherent in allocated ship time. Data were collected on seven different days at sea, and hence we only truly sampled seven different, independent iterations of tidal front/plume formation. Our data set is therefore unable to resolve any time-of-day effects independent of tidal effects which may confound the ability to resolve tide effects (c.f. Zamon, 2003), nor was it able to resolve effects of seasonal or inter-annual variation in river discharge affecting the size of the tidal plume and strength of the fronts. We captured front evolution over an entire tidal cycle on two sampling days (02–03 May 2006, Table 4). It appears that in both cases shearwater and murre density peaked 10–11 h after the previous high tide. Direct land-based observations indicate this is approximately the time when the front on the north face of the plume separates from the North Jetty of the Columbia River and propagates northward away from the river mouth (Zamon, unpublished data). A more robust test of associations of predators with the tidal front would require time series observations over many tidal cycles to fully examine the relationship between bird density and different phases of front evolution.

Predator aggregations in the plume region most likely occur due to foraging habitat selection, rather than constraints imposed by breeding or other behaviors. Sooty shearwaters are the most abundant bird in the California Current ecosystem during summer months, but they do not breed in the northern hemisphere (Ainley et al. 2005; Briggs and Chu, 1986). Therefore, they have no reproductive constraint which restricts them to foraging in the plume region. Although common murre colonies are located on both the Washington and Oregon coasts, no known breeding colonies are near the river mouth; the nearest murre colony is located 35 km to the south off Tillamook Head in Oregon (Naughton et al., 2007; Speich and Wahl, 1989). While birds from this colony are most likely commuting to the plume to feed, a colony effect alone is an unlikely explanation for murre aggregations in the plume. Seabird diet data in May-June for the region occupied by the Columbia River plume is lacking except for one study of common murre diet by Varoujean and Matthews (1983). The most frequently occurring fish species in murre diets were northern anchovy (*Engraulis mordax*, 74% of samples), Pacific tomcod (*Microgadus proximus*, 44.2%), whitebait smelt (*Allosmerus elongatus*, 24.7%), and coho salmon (*Oncorhynchus kisutch*, 10.4%). Only five of 77 birds had empty stomachs, indicating a high proportion of murres were actively and successfully foraging (93.5%).

Understanding how planktivorous fish distributions, especially those of northern anchovy, vary with the creation, propagation, and dissipation of the tidal plume and plume fronts will be key to understanding trophic transfer to fish-eating predators near the Columbia River. Northern anchovy, Pacific herring (*Clupea pallasi*), whitebait smelt, and Pacific sardine (*Sardinops sagax*) are the ecologically dominant planktivores in the nearshore plume (Emmett et al., 2006). Because northern anchovy spawn in the Columbia River plume and are the most common prey item found in murres and shearwaters, anchovy are likely to be the dominant fish interacting with the plume and fish predators using the plume (Litz et al., 2008; Parnel et al., 2008; Richardson, 1980). Preliminary work by Kaltenberg et al. (2010) with fixed acoustic moorings confirms that variation in schooling fish abundance in the plume region is influenced by plume parameters such as temperature, salinity, and river flow. A process-oriented study combining fixed and mobile acoustic surveys of fish distribution with diet and

behavioral studies of murres and shearwaters would be the next logical step towards a better understanding of the role of the Columbia River plume front and subsequent energy flow in the food web. Such a study would also provide fisheries managers with important information on ocean avian predation as a factor affecting the early marine survival of juvenile salmon.

Our results confirm that river plumes are oceanographic features which are likely to structure predator–prey interactions in coastal ecosystems where there are large river discharges. To test this hypothesis across systems, we recommend that future oceanographic work studying river plumes and plume fronts include surveys of seabird predators and planktivorous fishes as part of the sampling routine.

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