Influence of the Columbia River plume (USA) on the vertical and horizontal distribution of mesozooplankton over the Washington and Oregon shelf

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River plumes extending out over continental shelf waters have distinct frontal boundaries along their leading edges that concentrate highly buoyant particles, including zooplankton. The margin between the base of the plume and the underlying oceanic waters is often much larger in spatial extent than the visible surface front, but the influence of this region of a river plume on the vertical and horizontal distribution of zooplankton is less well understood. Using a laser optical plankton counter (LOPC) and a conductivity–temperature–depth sensor (CTD) mounted to a rapidly undulating tow body, we examined the horizontal and vertical distribution of zooplankton proximate to the Columbia River plume, to study how plume waters affect zooplankton over the continental shelf. Overall, vertically integrated zooplankton abundance and biovolume was elevated close to “aged” plume waters. Zooplankton tended to aggregate near the surface close to river plume waters. When plume waters are present at the surface, zooplankton aggregations tended to be in the upper 10 m of the water column, compared with 25 m when the plume was not present. The presence of river plumes may be ecologically and energetically important to surface feeding planktivores such as larval and juvenile fish.

Keywords: fronts, laser optical plankton counter (LOPC), Northeast Pacific, river plume, zooplankton.

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Introduction

The Columbia River and its tributaries contain run-off from ~415 000 km² of the US and Canada and pump an average of 7300 m³ s⁻¹ of fresh water into the Columbia River estuary. Tidal modulation of discharge from the estuary creates river plumes that vary in volume from 2 × 10¹⁰ to 11 × 10¹⁰ m³ (Hickey et al., 1998) and may extend several hundred kilometres out over the continental shelf (Garcia Berdeal et al., 2002). The river plume moves north and south of the river mouth, depending on a combination of the Coriolis effect and windforcing (Hickey et al., 2005). Strong winds from the north occur primarily during spring and summer, induce upwelling, and move the plume across the shelf and to the southwest. During periods of weak or northward (downwelling) winds, the plume is primarily nearshore and flows northwards.

The impact of these plume waters on the shelf ecosystem is not well understood, especially in terms of how they affect the abundance and distribution of zooplankton. Of the distinctive features of river plumes is the abrupt frontal boundary established between the buoyant fresh water and the surrounding oceanic waters. Along the leading edge of the plume, a near-surface frontal boundary is often quite visible as a result of optical differences between the river water and ocean water, and the presence of “sea foam” and buoyant materials (flotsam and jetsam) that accumulate at convergence zones. The visible surface fronts often attract fish, seabirds, and mammals, and are therefore often utilized by fishers. They have been the subject of many studies investigating how and why these regions accumulate biomass from various trophic levels. For zooplankton, the influence of river plumes on their distribution has been studied across the globe, including in Chesapeake Bay (Roman et al., 2005), the Gulf of Mexico (Grimes and Finucane, 1991), the Japan Sea (Fukuwaka and Suzuki, 1998), and the Bay of Biscay (Albaina and Irigoien, 2004), as well as the Northeast Pacific off Canada (Parsons et al., 1969; Mackas et al., 1980; St John et al., 1992) and around the Columbia River (Small and Cross, 1972; De Robertis et al., 2005; Morgan et al., 2005). These studies primarily focused on the visible surface front where vertical circulation associated with the convergence of river and oceanic water masses concentrates buoyant particles and organisms, including those that “act” buoyant through active vertical swimming (Franks, 1992; Genin et al., 2005).

Plankton typically aggregate near or within density gradients, and a recent study demonstrated that several species of copepods may also be attracted to strong velocity gradients (Woodson et al., 2005). For river plumes, these types of gradients are present both horizontally, along the leading edge of the plume, and vertically, along the base or lower margin interface between the plume and underlying waters. Because most of the interface between plume waters and oceanic waters occurs in the horizontal...
plane beneath the plume, this may be an important region for zooplankton aggregation and retention. The transient nature of river plumes, and difficulties in simultaneously detecting and sampling the base of the plume with traditional net systems, makes it nearly impossible to study these regions using traditional methods. As part of the Co-OP River Influences on Shelf Ecosystems (RISE) project, we collected physical and biological data at a vertical and spatial resolution appropriate for addressing the question: how does the presence of river plume waters impact the distribution (vertical and horizontal) and abundance of mesozooplankton along the continental shelf?

**Methods**

Data were gathered during two broad-scale surveys conducted throughout a region spanning 85 km north and south of the Columbia River mouth and extending out to 90 km from shore (Figure 1). The first survey took place between 31 May and 2 June 2005, and the second between 18 and 20 June 2005. Each survey was conducted by the RV "Pt Sur" towing a suite of instruments attached to a Triaxus tow body (Macartney, Denmark). The instrument suite included a laser optical plankton counter (LOPC; Brooke-Ocean Technology, Nova Scotia), conductivity-temperature-depth sensor (CTD; Applied Microsystems Ltd, Vancouver, BC, USA), and fluorometer (Wetlabs, Philomath, OR, USA). The LOPC gathered abundance and size information for particles with an equivalent spherical diameter (ESD) of 0.09–35 mm (Herman et al., 2004). Data from the LOPC were gathered continuously and recorded by a shipboard computer at a rate of 2 Hz (2 samples s⁻¹). Data from the CTD were recorded at 25 Hz, fluorescence at 2 Hz, and GPS information at 1 Hz. Based on the minimum recording rate of the GPS, all data were binned to 1 s intervals. The Triaxus tow body was towed horizontally at a speed of approximately 3 m s⁻¹ and undulated in a sawtooth pattern through the upper 35–80 m of the water column at a vertical velocity of ~1 m s⁻¹. At these velocities, the 1 s binned data provide a vertical resolution of ~1 m and an average horizontal resolution along the survey path of 100–250 m, depending on the depth of the undulation.

Data from the LOPC provide counts and size estimates for each particle detected. The LOPC uses 35 elements (1 x 1 mm photodiodes) to detect the shadow of each particle passing through the laser sheet of light in the sampling tunnel. Particles that are small enough to be detected by only a single element are automatically placed into 1 of 122 ESD size categories between 0.09 and 1.92 mm ESD, preprogrammed into the electronics of the system. Larger particles (typically >1.5 mm ESD) that cross multiple elements are recorded along with information on their shape and are converted to ESD using a function provided by the manufacturer (Brooke-Ocean Technologies). The vast range of possible particle sizes necessitated binning them into size categories for data storage and analysis (Platt and Denman, 1977; Zhou and Huntley, 1997). In this case, the particles were binned into 20 size categories of equal log₁₀ widths, resulting in a minimum bin width of 0.03 mm and a maximum of 9.04 mm (i.e. Bin 1 spans 0.09–0.12 mm ESD, and Bin 20 spans 25.96–35 mm ESD).

Data from the fluorometer were converted from digital counts to mg Chl a m⁻³ using a scale factor derived from comparisons with extracted chlorophyll values. Water samples from various depths were collected before deployment and after recovery of the Triaxus system using a Niskin bottle rosette. Samples from each bottle were collected and passed through individual Whatman GF/F filters and frozen in centrifuge tubes for later analysis using 90% acetone for extraction and a benchtop fluorometer (Turner Designs 10-AU) analysis.

As a result of the abundance of crab pots (Dungeness crab fishery) and risks involved with towing the Triaxus in water depths <50 m, neither of the surveys was able to sample inshore of the 50 m isobath (~20 km from the coast). During a portion of the June survey, the Triaxus was pulled out of the water, and CTD data were gathered inshore of the 50 m isobath using both the ship’s flow-through system and the profiling CTD on the rosette sampler (SeaBird, Model 911).

For some analyses, the depth of the thermocline and the pycnocline are used to illustrate the distribution of phytoplankton and zooplankton in relation to the plume and physical gradients. For each data point below 2 m depth, the difference in temperature and density between points ~2 m above and below that point was calculated. The difference in depth between the points was divided by the difference in temperature and density to provide...

**Figure 1.** Surface salinity (top), integrated Chl a fluorescence (middle), and integrated zooplankton abundance (bottom) for the upper 35 m of the water column during the May (left) and June (right) surveys. Depth contours represent the 50, 150, and 250 m isobaths. In the bottom panels, the portions of transects with a parallel black line alongside were sampled during the night. Black arrows identify the two transects depicted in Figure 2 (later). The study location is centred offshore of the Columbia River (CR) in the northwestern US.
separate measurement of the linear slope for both parameters. The point with the greatest change (smallest slope) in temperature and density is considered to be the depth of the thermocline and pycnocline, respectively.

Results
For simplicity, the initial survey (31 May–2 June) will be referred to as the May survey and the second survey (18–20 June) will be referred to as the June survey. During the surveys, each complete undulation of the tow body provided two vertical profiles of the sampled water column. There were 3817 vertical profiles obtained along 620 km of cruise track during the May survey and 1290 vertical profiles from 354 km of survey track during the June survey. While near plume waters, the Triaxus operated primarily in the upper 35 m of the water column to maximize the horizontal resolution of physical parameters being used by various groups involved in the RISE project. To eliminate bias introduced by comparing vertically integrated values from profiles of different depths (i.e. 35 m near the plume and 80 m away from the plume), only the data from the upper 35 m across the entire study area are presented in these analyses.

The LOPC does not discriminate between different types of particles, such as detritus and zooplankton. Studies comparing LOPC counts with net-tow zooplankton abundances indicate that the LOPC provides a reasonable, although consistently higher, estimate of zooplankton abundance compared with net samples (Herman and Harvey, 2006; Finlay et al., 2007). Several net samples were collected between the May and June surveys. The mesh size of the net used (0.153 mm) does not retain the full range of particles detected by the LOPC. The abundances of zooplankton within the nets (data not shown) were \( \approx 1.5 \times 10^4 \) zooplankton m\(^{-3}\) and within an order of magnitude range of the counts from the LOPC. The reasonable agreement between net samples and LOPC data led us to believe that a significant proportion of the particles detected were zooplankton, and will therefore be referred to as such hereafter.

The influence of diel vertical migration is taken into consideration as well. When looking at vertical zooplankton distributions, or integrating zooplankton throughout portions of the water column, diel vertical migration of zooplankton needs to be accounted for. Because we are only using data from the upper 35 m of the water column, we focus on the data collected during daytime hours for analyses, using sunrise and sunset as the cut-off. Eliminating the night-time data reduces the number of vertical profiles from 3817 to 2457 during the May survey and from 1290 to 1168 during the June survey. The spatial coverage of the surveys, including the portions of the surveys done during night-time hours, is shown in Figure 1.

Horizontal distribution
Salinity values at 2 m depth reveal the spatial coverage of fresher plume waters across the survey area (Figure 1). During the May survey, the plume was predominantly south- and westward, extending roughly 90 km from the river mouth; note that our southernmost transect was south of the plume. During the June survey, the wind direction was more variable, and the river plume flowed predominantly to the north and close to shore, staying shorewards of the 50 m isobath.

In May, the distribution of Chl \( \alpha \) closely followed the spatial coverage of the plume waters (Figure 1), but was patchier in June. Fluorescence values, integrated through the upper 35 m of the water column, ranged from 10 to 70 mg Chl \( \alpha \) m\(^{-2}\) and tended to track the plume waters during the May survey and the shelf break between the 150 and 250 m isobaths during the June survey.

Figure 2. Salinity (top), Chl \( \alpha \) (middle), and zooplankton abundance (bottom) along cross-shelf transects (indicated by arrows in Figure 1) just south of the Columbia River mouth during the May (left) and June (right) surveys. The pycnocline (solid white line) and thermocline (solid black line) are shown in each panel. See the Methods section for details on how these lines were calculated.
Zooplankton counts from the LOPC, integrated throughout the upper 35 m of the water column, had a variable distribution across the survey area. During both the May and June surveys, values ranged from $1 \times 10^6$ to $>7 \times 10^6$ ind. m$^{-2}$, with the highest concentrations often occurring north of or near the northern edge of the plume (May) between 46°20’N and 46°30’N. High concentrations (red areas in Figure 1) were measured 60 km north of the mouth of the Columbia River during the May survey and along the mid- to outer shelf regions, away from the plume, during the May and June surveys.

**Vertical distribution**

Profiles from two cross-shelf transects, one from each survey, illustrate the variation in the vertical distribution of salinity, Chl $a$, and zooplankton (Figure 2). The transects were sampled during similar times of the day (09:00–15:00 local time) and crossed the shelf at roughly the same latitude and water depths. During the May survey, plume waters were primarily in the upper 15 m of the water column, as evidenced by the low salinities and the location of the pycnocline and thermocline at ~5 and 12-m depth, respectively (Figure 2). In June, when plume waters were primarily to the north, the thermocline and pycnocline were nearly coincident with each other and were around 20 m depth over much of the shelf.

Elevated concentrations of both chlorophyll and zooplankton were associated with the pycnocline and thermocline. During the May survey, a chlorophyll maximum of ~5 mg Chl $a$ m$^{-3}$ was present along the pycnocline at 5 m depth within the plume waters and at 25 m beyond the extent of the plume waters. For June, the maximum Chl $a$ concentration was ~1.5 mg Chl $a$ m$^{-3}$ and at a depth of 15–20 m. Zooplankton concentrations ranged from $1 \times 10^5$ to $4 \times 10^5$ ind. m$^{-3}$ during both the May and June surveys. The densest aggregations of zooplankton tended to occur around the thermocline. During the May survey, zooplankton were primarily between 5 and 15-m depth near the base of the plume, near the surface at the western extent of the plume, and then concentrated around 15–25 m depth beyond the extent of the plume (Figure 2). During the June survey, the densest aggregations of zooplankton were found along the thermocline near 25 m depth, away from the plume. When fresher surface waters (salinity <29) were present, the highest zooplankton concentration was just beneath these waters around 5–10-m depth, similar to the May survey.

**Regional trends**

Variations in the mean integrated (upper 35 m) Chl $a$ abundance, zooplankton abundance, and zooplankton biovolume are plotted against surface salinity values, averaged by 0.5 salinity bins for the 2457 and 1168 vertical profiles in May and June, respectively (Figure 3). During the May survey, there was a peak in integrated Chl $a$ fluorescence between salinity values of 27–29. In June, peak values were found beneath plume waters with salinities of 18–20. In both surveys, Chl $a$ fluorescence tended to decrease with increasing salinity, with the lowest values found in more offshore oligotrophic waters.

Zooplankton abundance did not follow the same trend between surveys. During the May survey, abundances ranged from $3.5 \times 10^6$ to $~7 \times 10^6$ ind. m$^{-2}$, with the peak in abundance associated with surface salinities around 27–30. During the June survey, there was a greater range in zooplankton abundance, with a peak in mean abundance around $6.5 \times 10^6$ ind. m$^{-2}$ at a salinity of 24.5, and a minimum of $~1 \times 10^6$ ind. m$^{-2}$ at a salinity of 32.

Zooplankton biovolume, calculated as a spherical volume from the ESD data, followed a similar trend to that of abundance data. During the May survey, the peaks in biovolume were at salinities of 19 and 28. The June survey had a peak in zooplankton biovolume across a narrow range of salinity from 23 to 25, but overall tended to decrease with salinity values of 25–32.

The biovolume data were divided into three size categories to determine if one particular portion of the size spectrum of particles is contributing the most to the biovolume trend (Figure 4). The three size categories (<0.4, 0.4–2.4, and >2.4 mm ESD) were based primarily on an equal distribution of the 20 size bins. No direct correlation between particle size and zooplankton species was done during this study. However, some idea of where particular taxonomic groups and developmental stages may occur in various ranges of ESD can be extrapolated from previous studies (Edvardsen et al., 2002; Baumgartner, 2003; Herman and Harvey, 2006). Based on data from the Northwest Atlantic (Herman and Harvey, 2006), copepod eggs and nauplii would occupy the <0.4 mm ESD size range; copepodids, adult copepods, and early stage krill would be in the middle range (0.4–2.4 mm ESD), and larger zooplankton species, including later stages of krill, in the upper range (>2.4 mm ESD).

During the May survey, particles <0.4 mm ESD were relatively consistent in biovolume across much of the salinity range, but had a distinct peak between a salinity of 27–29. Biovolume in the 0.4–2.4 mm ESD range had two peaks, one centred on a salinity of 21, and the other on 28. For the largest particles (>2.4 mm ESD), variability was quite high, but the trend was for biovolume to decrease with salinity, from highs of $2 \times 10^3$ mm$^3$ m$^{-2}$ at salinities of 18, 20, and 24 to lows <0.5 $10^3$ mm$^3$ m$^{-2}$ at salinities of 28–31.5. During the June survey, the <0.4 mm ESD particles were

![Figure 3. Mean integrated values of Chl $a$ fluorescence (top), zooplankton abundance (middle), and zooplankton biovolume (bottom), relative to surface salinity values for the May and June surveys. Integrated values are for the upper 35 m of the water column. Error bars represent the 95% confidence interval.](https://academic.oup.com/icesjms/article-abstract/65/3/477/785383)
similar in total biovolume m$^{-2}$ across the range of surface salinities, but there was much greater variance for salinities lower than 26. For the size range of 0.4–2.4 mm ESD, there was no clear pattern; highest volumes were seen at salinities of 31.5 and the lowest at salinities of 22.5 and 32. For the largest particles (>2.4 mm ESD), biovolumes were lower than in May, again with no clear pattern in relation to surface salinity.

**Depth variation with salinity and latitude**

The impact of plume waters on the vertical distribution of zooplankton is evident when comparing the mean depth of the zooplankton centre of biovolume (COB) in the water column with surface salinity (Figure 5). The zooplankton COB, analogous to the centre of mass of an object, was calculated for each vertical profile using the equation $\text{COB} = \sum (b_i d_i) / \sum b_i$, where $b_i$ is the biovolume m$^{-3}$ at depth $d_i$ for the sampling range of $i = 1$ to 35 m. There was a distinct deepening of the COB from 14 m down to 20 m with increasing surface salinity during the May survey. During the June survey, when the plume was weak and directed northwards, the mean depth of the COB was relatively constant, between depths of 17 and 18 m. Geographically, this shift in the depth of the COB results in a strong latitudinal gradient in the depth of the zooplankton, when plume waters are present (Figure 5). In May, the mean depth of the COB north and south of the river mouth differed by as much as 6 m. In June, when plume waters were not as prevalent in the survey area, there was very little apparent latitudinal difference in the depth of the COB.

**Discussion**

During the May survey, most of the water coming out of the Columbia River was flowing to the southwest, driven by winds blowing from the north. During the June survey, wind velocities were reduced, and the wind direction shifted from southerly to northerly several times during the 40 h of surveying. The lower velocity and variable winds do not support strong upwelling and, in this scenario, plume waters primarily flowed to the north and close to shore. Sampling a similar geographic region during both the presence and absence of the plume provides an opportunity to investigate how the plume impacts the regional shelf ecosystem.

From the horizontal maps (Figure 1), vertical profiles (Figure 2), and the generally negative relationship between surface salinity and integrated Chl $a$ abundance (highest in low to intermediate values of salinity for both cruises; Figure 3), phytoplankton standing stock is enhanced within the plume waters. Columbia River water tends to have low levels of both nitrate and iron, but incorporates higher levels of nitrate and iron from deep waters that upwell onto the shelf and are entrained into the plume either within the estuary or near the river mouth (Lohan and Bruland, 2006). The gradual decrease in Chl $a$ standing stock with increasing salinity may be a function of the plume waters being diluted by surrounding shelf waters that are low in Chl $a$, as well as increased grazing pressure by micro- and mesozooplankton that may be attracted to and/or retained within the plume waters. Assuming a mean velocity of 10–20 cm s$^{-1}$ for currents over the shelf, plume waters could have remained in the 80 km of study region for 4–10 d, which would be ample time for rapid growth of microzooplankton grazers (Landry and Hassett, 1982; Landry and Lorenzen, 1989).

As the plume waters age and increase in salinity by mixing with ocean water, the decrease in phytoplankton standing stock is accompanied by a slight increase in zooplankton abundance. Although timescales of 4–10 d are not sufficient for substantial
population growth in mesozooplankton for this region (Peterson, 2001), it would be sufficient for motile zooplankton to encounter the plume during random swimming or directed vertical migrations and become concentrated in phytoplankton-rich layers, as suggested in Figure 2, by choosing to remain there to feed. Alternatively, strong density and velocity gradients are known to attract and retain many species of zooplankton (Harder, 1968; Lougee et al., 2002; Woodson et al., 2005), which could also contribute to the aggregations of zooplankton along the base of the plume (Figure 2). Interestingly, the zooplankton appeared to aggregate more heavily close to the thermocline than close to the pycnocline, within the plume waters. Outside the extent of the plume, and when plume waters were not present, the thermocline and pycnocline were nearly coincident with each other, and zooplankton aggregated along the relatively weak gradients but were also found throughout a greater portion of the upper water column.

Across the three size classes of zooplankton, during the May cruise, the highest biovolume generally occurred at salinities between 26 and 30, characteristic of aged plume waters and surface fronts. The intermediate size class (0.4–2.4 mm ESD) and largest size class (>2.4 mm ESD) also exhibited a peak in biovolume beneath surface salinities of 19–21. From the horizontal map (Figure 1), it appears that most of these high biovolume—low salinity values come from plume waters that were beyond the shelf at the furthest extent of the plume, nearly 80 km from the river mouth. Because the surface salinities were far lower than upwelled water (salinities >33.5), we suggest that the presence of aged plume waters, especially in areas south of the river mouth, can be a good indicator of regions of high zooplankton abundance and biovolume.

The June cruise did not reveal a clear pattern in the biovolume vs. salinity charts, perhaps the result of the near-absence of a plume in the area sampled. Note also that the biovolume in each of the three size classes during the June cruise (Figure 4) was, on average, about half the value observed 19 d earlier in May. The presence of a large, sustained, southwesterly directed plume (such as occurs under conditions of upwelling) results in larger zooplankton biovolumes south of the Columbia River than when there is a northwards-directed plume during downwelling. It is likely that interactions between plume waters and upwelled waters, evident in the nutrient regime (Lohan and Bruland, 2006), create favourable conditions for other trophic levels.

One of the more important influences of the river plume on zooplankton over the shelf is probably the establishment of shallow and strong gradients in temperature and density that help to concentrate zooplankton in the upper 15 m of the water column. From the plot of the mean depth of the COB (Figure 5), there is a significant difference in the depth of zooplankton near, and to the south of, the Columbia River mouth when plume waters are present out over the shelf, as during active upwelling conditions. The difference in the mean depth of the COB in the presence and absence of plume waters is ~3–6 m. However, when looking at the depth of the highest concentration of zooplankton (Figure 2), the difference can be ~15–20 m. For adult planktivorous fish, such as the northern anchovy (Engraulis mordax) and Pacific sardine (Sardinops sagax), vertical variations of 20 m are not likely to be significant, especially because they often migrate vertically throughout much of the water column and typically only come to the surface during twilight hours to feed (R. Emmett, unpublished data). For larval fish, however, many species along the Oregon and Washington coast are found almost entirely in the upper 20 m of the water column (Boehlert et al., 1985; Auth and Brodeur, 2006). For these stages, and possibly for the juvenile stages of other fish including salmonids, layers of high densities of zooplankton prey closer to the surface may be physiologically and ecologically beneficial. The juvenile salmonids have not been shown to utilize the surface fronts along the plume boundaries (De Robertis et al., 2005), but because bottom margins of plumes greatly exceed the spatial extent of vertical surface fronts along the perimeter of the plume, these regions may be an important, but little studied resource for the intermediate life-history stages of these species.

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