

Columbia River plume fronts. II. Distribution, abundance, and feeding ecology of juvenile salmon

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ABSTRACT: Well-defined fronts develop at the seaward edge of riverine plumes where suspended materials and planktonic organisms are concentrated by convergent water flows. Riverine plume fronts have been hypothesized to be favorable fish habitats because they can lead to localized prey aggregations. We examined the spatial distribution of juvenile Pacific salmonids *Oncorhynchus* spp. in and around plankton-rich frontal regions of the Columbia River plume to test the hypothesis that juvenile salmonids aggregate at riverine plume fronts to feed. Juvenile salmonids tended to be abundant in the frontal and plume regions compared to the more marine shelf waters, but this pattern differed among species and was not consistent across the 2 study years. Stomach fullness tended to be higher in the more marine shelf waters than either the front or plume areas, which does not support the hypothesis that salmonids consistently ingest more prey at frontal regions. Many prey organisms were disproportionately abundant at these fronts, but salmon stomach-content analysis did not reveal higher stomach contents at fronts or identify prey groups indicative of feeding in the frontal areas. Although our results indicate that the Columbia River plume influences the distributions of juvenile salmon, our observations do not support the hypothesis that juvenile salmonids congregate to feed at fronts at the leading edge of the Columbia River plume. The short persistence time of these fronts may prevent juvenile salmon from exploiting these food-rich, but ephemeral, features.

KEY WORDS: Frontal regions · Juvenile salmon · Distribution · Feeding habits · Columbia River plume

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INTRODUCTION

River discharge into the coastal ocean establishes well-developed river plumes, which have the potential to influence the distribution, abundance and growth of planktivorous fishes. Freshwater input by major rivers results in buoyant, low-salinity plumes extending into the coastal ocean and well out onto the continental shelf (e.g. Grimes & Finucane 1991, Hickey et al. 1998, Gillanders & Kingsford 2002). Well-defined fronts de-

velop at the seaward edge of riverine plumes, where suspended materials and planktonic organisms are concentrated by convergent flow (Le Févre 1986, Grimes & Finucane 1991, Franks 1992, Govoni & Grimes 1992). Riverine plume fronts are often hypothesized to be favorable habitats for planktivorous fishes because of their elevated concentrations of planktonic prey, particularly near-surface neustonic species (Le Févre 1986, St. John et al. 1992, Grimes & Kingsford 1996, Morgan et al. 2005, this volume).

Coastal waters of the Pacific Northwest are heavily influenced by freshwater discharge (Barnes et al. 1972, Hickey & Banas 2003). The Columbia River is the largest river on the Pacific Coast of North America, and accounts for 60 to 90 % of total drainage along the coast between San Francisco and the Strait of Juan de Fuca, with this fraction highest in late summer (Barnes et al. 1972). This freshwater input produces a shallow, low-salinity, buoyant plume, which extends over a large area off the Oregon–Washington coast (Owen 1968, Hickey et al. 1998).

The largest runs of Pacific salmon (*Oncorhynchus* spp.) in the continental USA occur in the Columbia River basin. This river basin is heavily influenced by human activities and is actively managed for navigation, hydroelectric power generation, irrigation and flood control (Sherwood et al. 1990). Many naturally spawning populations of salmonids in the region have declined (National Research Council 1996, Bisson et al. 2000), despite large-scale propagation of salmonids in hatcheries. Estimates of the number of salmon smolts outmigrating from the Columbia River basin are in excess of 100 million annually, the majority of which originate from hatcheries (Bisson et al. 2000).

The timing of ocean entry of many Columbia River salmonids (e.g. yearling coho salmon *Oncorhynchus kisutch*, Chinook salmon *O. tshawytscha*, chum salmon *O. keta*, and steelhead trout *O. mykiss*) coincides with high river flows during late spring and early summer, when the low-salinity coastal plume is well developed. Juvenile salmon enter the low-salinity plume when they exit the estuary, and remain abundant in coastal waters during their first summer at sea (Pearcy & Fisher 1990). Given that the plume is the first area salmon encounter during ocean entry, changes in plume structure may significantly influence the distribution, growth and survival of salmon.

Columbia River outflow establishes 3 distinct regions in the coastal ocean: a low-salinity plume, higher salinity coastal shelf waters, and fronts separating these 2 water masses. Fronts develop at the boundary between the low-salinity plume water, which has recently advected out of the estuary, and the more saline coastal marine water. The strength of these fronts fluctuates with freshwater outflow and tidal period. These fronts are transient but recurrent features, forming near the river mouth with the ebb tide as low-salinity water exits out of the estuary, and persisting for several hours as they propagate out to sea with the tide (Morgan et al. 2005). As with other river plumes (Grimes & Finucane 1991, Kingsford & Suthers 1994), the front can be clearly identified by sharp horizontal gradients in salinity and water clarity, as well as by accumulations of foam and flotsam.

River plume fronts concentrate fish eggs, larvae and zooplankton (Grimes & Finucane 1991, Grimes &

Kingsford 1996), but the effect of these fronts on larger, more mobile fishes such as juvenile salmon is poorly understood (Largier 1993). In the frontal areas of the Columbia River plume, planktonic organisms are concentrated by convergent flow, particularly in near-surface waters, where the biomass of plankton is 4 to 47 times higher than in adjacent waters (Morgan et al. 2005). If juvenile salmon, which are surface-oriented feeders (Brodeur 1989), are able to locate and maintain themselves within these food-rich fronts, they will encounter higher prey densities in frontal regions, which could increase ingestion rates. Increased feeding leads to increased growth (Brandt 1993), which in turn may affect marine survival. Mortality of juvenile salmon in the ocean is highly size-dependent (Healy 1982, Pearcy 1992, McGurk 1996), and elevated growth during the critical first summer at sea should decrease mortality by reducing the amount of time spent in small, vulnerable size-classes.

Fronts at the leading edge of the Columbia River plume are areas of strong environmental gradients, which may serve as mechanisms of prey concentration and habitat demarcation for pelagic fish populations (Largier 1993). In this study, we performed field sampling of juvenile salmon distributions and stomach content analysis to test the hypothesis that juvenile salmonids aggregate in and around frontal regions of the Columbia River plume in order to feed.

MATERIALS AND METHODS

Field sampling. In order to assess whether fronts are favorable habitats for juvenile salmon, we examined the spatial distribution of zooplankton and juvenile salmonids in and around the fronts at the leading edge of the Columbia River plume. Sampling was conducted during daylight hours on the FV 'Frosti' on May 23 to 27 of 2001, and May 23 to 29 of 2002. To minimize the influence of spatial and temporal sampling effects, a blocked sampling design was used. We sampled fishes with a surface trawl, made conductivity, temperature and depth (CTD) casts, collected water samples, and collected zooplankton with plankton and neuston nets at a series of blocked triplicate stations (hereafter 'station block'). Methods were comparable in both years, but due to interannual differences in river flows the distance between the habitats sampled in each station block was larger in 2002 (~14 km compared to ~8.5 km in 2001; see Morgan et al. 2005 for details). Each station block consisted of 1 station in each of the 3 distinct habitats: the low-salinity plume, along the surface front at the leading edge of the plume, and in the adjacent more saline coastal marine water (hereafter referred to as plume, front, and ocean habitats, respec-

tively). Sampling design, physical measurements, and prey sampling are reported in Morgan et al. (2005), and are only briefly described here.

Juvenile salmonids were sampled by towing a Nordic 264 rope trawl (Nor'Eastern Trawl Systems) at the surface for 15 min at $\sim 6 \text{ km h}^{-1}$. This pelagic trawl has an $\sim 30 \text{ m}$ wide by $\sim 18 \text{ m}$ deep mouth opening, and is made of graded mesh (162.3 cm at the mouth to 8.9 cm in the cod end). A 0.8 cm liner was used to retain small fishes in the cod end. Buoys were attached to the headrope to keep the top of the trawl near the surface. Trawl catches were standardized to areal density (fishes km^{-2}) by normalizing by the trawl width (30 m), and the distance between the start- and end-points of the tow as determined by a global positioning system receiver ($\bar{x} \pm \text{SD}$, $1.8 \pm 0.2 \text{ km}$).

Juvenile salmon captured in trawls were identified, measured, and frozen for further analysis. In the laboratory, the fishes were thawed, identifications were confirmed, and individuals were weighed. Salmonids were examined for marks of hatchery origin such as coded wire or passive integrated transponder tags, latex markings, or adipose fin clips. Juvenile salmon were assigned to length-based age classes modified from those of Pearcy & Fisher (1990) based on ongoing sampling of fishes from coastal Oregon and Washington (J. Fisher pers. comm.). Chinook salmon captured during this May study that were $\leq 120 \text{ mm}$ in fork length (FL) were considered subyearlings, and Chinook between 121 and 250 mm FL were considered yearlings. Coho salmon $\leq 275 \text{ mm}$ FL were considered yearlings, and chum salmon and steelhead $\leq 350 \text{ mm}$ FL were considered juveniles.

We computed a morphometric condition factor based on deviations from a length–weight relationship computed for all the fish of a given species captured in this study (Jakob et al. 1996). A linear regression of \log_{10} transformed length (mm) versus \log_{10} weight (g) measurements was used to predict weight at a given size. The residuals between the log-transformed observed and expected weights for the observed fish length were multiplied by 100. This condition factor is a measure of weight at a given size: if it is negative, the fish is comparatively underweight relative to others in the sample, and if it is positive, the individual is comparatively heavy.

Stomach-content analysis. Stomach-content analysis was performed on all fishes captured up to a maximum of 30 from a given haul. Stomachs were removed and preserved individually in 10% buffered formaldehyde. After 2 wk in this fixative, the stomachs were removed, rinsed 3 times in water and transferred to 70% ethanol. After 2 wk in ethanol the stomachs were again rinsed 3 times and transferred to water. The stomachs and their contents were blotted and weighed, the contents were

removed, and the empty stomachs were weighed in order to determine stomach content weight (Schabetsberger et al. 2003). To compare the feeding intensity of individuals of different sizes, stomach content weight (SCW) was standardized to percent fish body weight (%BW) using the following relation:

$$\% \text{BW} = \frac{\text{SCW}}{\text{BW} - \text{SCW}} \times 100 \quad (1)$$

where all weights are in grams. The %BW index was not correlated with fish weight for any of the species considered in either year of this study (Student's *t*-test of correlation coefficient, $p > 0.05$ in all cases).

Detailed stomach-content analysis was conducted in cases where an adequate number of salmonids were captured to allow comparison among habitats. For yearling coho and Chinook salmon, fishes were analyzed from station blocks in which at least 5 individuals were captured in each of the 3 habitats (ocean, front, plume) of a given station block. This resulted in 5 blocks in which yearling coho salmon could be compared across habitats (4 in 2001, 1 in 2002), and 6 blocks from 2002 in which yearling Chinook salmon could be compared across habitats. Juvenile chum salmon, which were generally absent from the plume habitat, were analyzed from 3 station blocks in which > 5 individuals were captured in the ocean and front habitats. Prey items were counted and identified to the lowest possible taxonomic level.

For further analysis, prey species were pooled into major prey categories based on frequency of occurrence and taxonomic similarity. For yearling coho and Chinook salmon the following prey groups were used: pteropods, gammarid amphipods, hyperiid amphipods, adult euphausiids, *Cancer magister* (Dungeness crab) megalopae, other crab megalopae (i.e. megalopae other than *C. magister*), fishes of the family Cottidae (sculpins), Pacific sandlance *Ammodytes hexapterus*, other fishes, and unidentifiable fish remains. These categories accounted for 98.9% of ingested prey by number. For juvenile chum salmon, the following groups were used: large copepods ($> 2.5 \text{ mm}$), small copepods ($< 2.5 \text{ mm}$), hyperiid amphipods, euphausiid calyptopis stages, euphausiid furcilia stages, insects, chaetognaths, larvaceans, northern anchovy (*Engraulis mordax*) eggs, and sanddab (*Citharichthys* spp.) eggs. These categories accounted for 99.8% of ingested prey by number.

Statistical analysis. We analyzed differences in salmon abundance, feeding intensity, length and condition factor with respect to the ocean, front and plume habitats using generalized linear models (GLM) (McCullough & Nelder 1989). In all cases, we blocked the statistical analysis by station to reflect the experimental design, and utilized an α of 0.05 as a criterion

for statistical significance. When the GLM indicated significant differences, we performed post-hoc multiple comparisons with Tukey's HSD test (Zar 1984).

Salmon length and feeding intensity are continuous variables with skewed distributions, and we thus modeled these variables with a normal error structure following suitable transformations. Lengths were \log_{10} -transformed, and stomach contents were $\log_{10}(x + 1)$ -transformed since some of these values were 0. Statistical tests were conducted on stomach contents in cases where sufficient individuals were captured.

The underlying data for salmon abundance were numbers of individuals captured per trawl. Since the trawls were towed over different distances, we normalized the counts as density per unit area sampled. This is analogous to having varying exposure to count-based distributions (e.g. Lawless 1987), and count-based generalized linear models are still appropriate in this application. We used a negative binomial error model to account for over-dispersion in the data (Welch & Ishida 1993, Power & Moser 1999).

A sequential approach was used to identify if diets of juvenile salmon were consistently different among the sampled habitats. Non-metric multidimensional scaling (NMDS) (Kruskal 1964, Mather 1976) was used to ordinate stomach contents based on the prey groups described above to compare the diets in the ocean, front and plume habitats. Because juvenile chum salmon stomachs contained large numbers of prey ($\bar{x} = 342.6$) compared to coho and Chinook salmon ($\bar{x} = 7.5, 7.2$, respectively), chum salmon were analyzed as individual fish, while yearling coho and Chinook salmon from a given haul were pooled to describe the overall diet. The NMDS and its associated statistical analyses are sensitive to large numbers of zeros (McCune & Grace 2002), and pooling coho and Chinook stomach contents from a given trawl was necessary to fulfill the assumptions of the statistical tests. Prey taxa occurring in less than 5% of samples were excluded from the analyses. Proportions of the pooled prey groups were calculated for further analysis. Details of the NMDS analysis including parameter values are the same as described by Morgan et al. (2003). In this application, NMDS arranges the analyzed fish (or pooled fish from a trawl) onto k dimensions (axes) by quantifying similarity based on groups of ingested prey. The closer 2 samples are in prey species space, the more similar the diet. Calculations were made using the Sørensen distance measure (Bray & Curtis 1957), using PC-Ord Version 4.27 software (McCune & Mefford 1999). A 3-dimensional solution was computed for all ordinations based on the results of Monte Carlo tests (McCune & Grace 2002); however, most of the original variance is explained by 2 of the axes (2001 coho: 85%; 2001 chum: 52%; 2002 Chinook:

86%), and graphical presentations of NMDS results are based on the dominant 2 axes to facilitate visualization. The orientation of axes derived from NMDS is arbitrary (McCune & Mefford 1999, McCune & Grace 2002), and therefore we rotated the ordinations such that the maximum separation among habitats was aligned with axis 1 so that the ordinations were in a similar orientation and could be more easily compared. The species matrix was overlaid on the ordination plots to help examine which prey groups contributed to the differences in prey composition (McCune & Grace 2002, Pickering & Veneman 2004).

The blocked multi-response permutation procedure (blocked MRPP, McCune & Grace 2002) was used to test the hypothesis of no difference in prey composition among habitats. This blocked non-parametric test generates a p -value to evaluate the probability of an observed difference between groups occurring by chance, and a within-group agreement statistic, A , which describes within-group homogeneity compared to random expectation. If heterogeneity within a group equals that expected by chance, $A = 0$, while if all items in a group are identical, $A = 1$. In order to examine the effects of habitat on diet, stomach contents were blocked by station. To evaluate the relative similarity of diets of fishes captured at a station, this analysis was repeated, blocking by habitat. The value of A from these 2 tests can be used to assess the relative importance of habitat versus station block in determining the diet of juvenile salmon. In the case of chum salmon, where analysis of individual fish precluded blocked analyses, unblocked MRPP grouping either by habitat or by station block was conducted in an analogous fashion. The Euclidean distance measure was employed in all cases to allow for median alignment in blocked tests (which cannot be done with the Sørensen distance measure), and to maintain consistency among tests. In cases where MRPP analysis revealed statistically significant differences in overall diet, indicator species analysis (ISA, Dufrene & Legendre 1997) was used to identify the prey species that were disproportionately consumed in a given habitat.

RESULTS

We completed 8 triplicate ocean, front and plume station blocks in 2001 and 9 in 2002. A total of 1395 juvenile salmonids were captured in 2001 and 1744 in 2002. Species composition was dominated by 4 species and differed between years. Yearling coho salmon were abundant in both years and accounted for 54.1 and 45.1% of juvenile salmonids in 2001 and 2002, respectively, while yearling Chinook salmon were less abun-

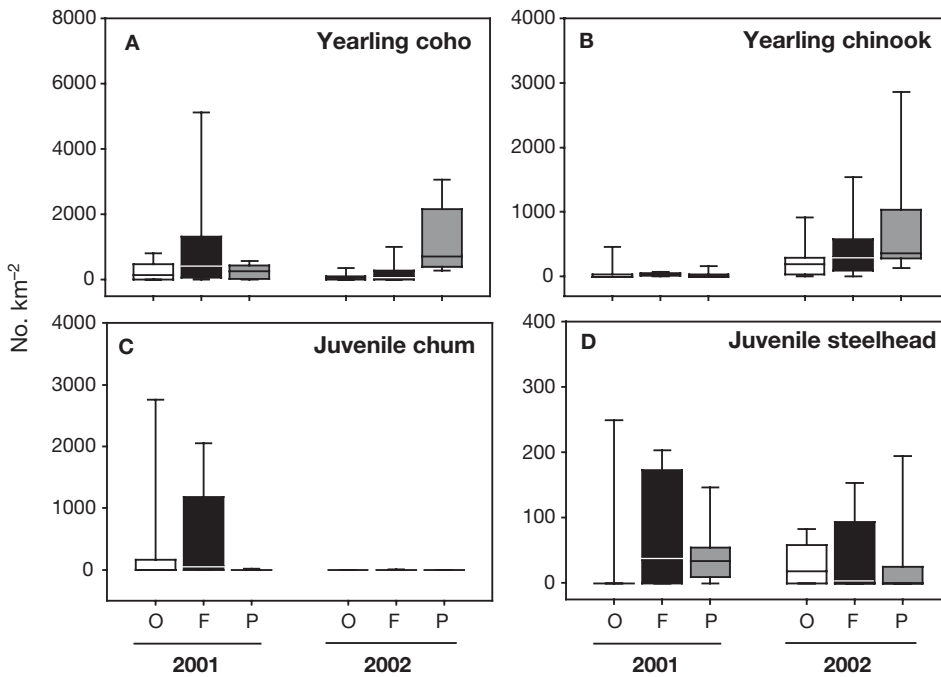


Fig. 1. *Oncorhynchus* spp. Abundance of (A) *O. kisutch*, (B) *O. tshawytscha*, (C) *O. keta* and (D) *O. mykiss* captured in ocean (O), front (F) and plume (P) habitats off Columbia River using surface trawl. Box plots demarcate 10th, 25th, 50th, 75th and 90th percentiles of densities

dant in 2001 compared to 2002 (5.0 versus 46.5%). Juvenile chum salmon were abundant in 2001 (35.4% of total), but only a single individual was captured in 2002. Juvenile steelhead were present at lower abundances during 2001 and 2002 (5.2 and 3.4%, respectively).

Catches of juvenile salmonids were highly variable, with frequent zero catches (Fig. 1). We observed significant differences in salmon abundance in the ocean, front and plume habitats both among species and between years. However, the trends were not consistent between years (Table 1). In 2001, juvenile chum and yearling coho salmon were more abundant in the vicinity of the front, while juvenile steelhead were more abundant in the front and plume habitats. In 2002, both yearling coho and Chinook salmon were more abundant in the plume habitat, whereas juvenile steelhead were more abundant at the front. No significant differences in abundance among habitats were observed for yearling Chinook salmon in 2001, when abundances were low and there were frequent (42%) zero catches. Insufficient chum salmon were captured in 2002 to merit statistical analysis.

In both 2001 and 2002, the majority of yearling coho (82.8 and 80.9%, respectively), yearling Chinook salmon (59.5 and 86.7%), and juvenile steelhead (72.6 and 71.2%) were marked, indicating that the majority of salmonids captured were of hatchery origin. Since not all hatchery salmon are marked prior to release, these proportions represent an underestimate of hatchery fishes. No marks were found on juvenile chum. There were no significant differences in the fraction of marked fishes among ocean, front and plume habitats (χ^2 test, $p > 0.2$ in all cases).

Habitat-specific patterns in body size differed among species and between years (Fig. 2). When significant differences in size were identified by the GLM analysis (coho 2002, chum 2001, steelhead 2001), fishes captured in the ocean habitat tended to be larger than those captured in the frontal regions (Table 2). Differences in

condition factor were less pronounced, as there was only a single case (coho salmon yearlings in 2002) in which condition factor differed significantly among habitats (Table 3). In this case, individuals in the ocean and plume habitats were significantly heavier for their length than those in the frontal region. However, there were marked interannual differences in the condition factor of juvenile salmon in the study area. Yearling coho and Chinook salmon, as well as juvenile steel-

Table 1. *Oncorhynchus* spp. Generalized linear model (GLM) analysis of salmonid catches in ocean, front and plume habitats. p-value reflects probability of overall differences among habitats identified by GLM, and differences in shading demarcate significant differences in abundance between habitats identified by pairwise post-hoc tests. Juvenile chum salmon were not sufficiently abundant in 2002 to merit statistical analysis. ns: not significant; intermed.: intermediate

Species	Year	Ocean	Front	Plume	p-value
Coho yearling (<i>O. kisutch</i>)	2001	lower	higher	no diff.	<0.05
	2002	lower		higher	<0.001
Chinook yearling (<i>O. tshawytscha</i>)	2001	no differences			ns
	2002	lower		higher	<0.005
Chum juvenile (<i>O. keta</i>)	2001	intermed.	higher	lower	<0.001
Steelhead juvenile (<i>O. mykiss</i>)	2001	lower	higher		<0.001
	2002	no diff.	higher	lower	<0.05

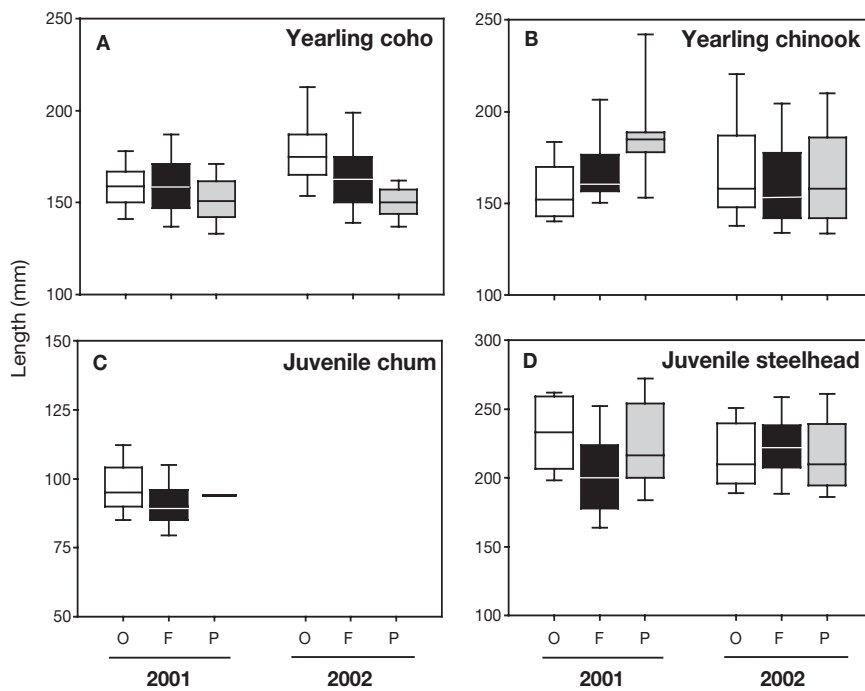


Fig. 2. *Oncorhynchus* spp. Fork lengths of (A) *O. kisutch*, (B) *O. tshawytscha*, (C) *O. keta* and (D) *O. mykiss* captured in ocean (O), front (F) and plume (P) habitats. Box plots as in Fig. 1

Table 2. *Oncorhynchus* spp. Generalized linear model (GLM) analysis of salmonid body length in ocean, front and plume habitats. Further details as in Table 1

Species	Year	Ocean	Front	Plume	p-value
Coho yearling (<i>O. kisutch</i>)	2001	no differences			ns
	2002	higher	lower		<0.001
Chinook yearling (<i>O. tshawytscha</i>)	2001	no differences			ns
	2002	no differences			ns
Chum juvenile (<i>O. keta</i>)	2001	higher	lower	higher	<0.001
Steelhead juvenile (<i>O. mykiss</i>)	2001	higher	lower	no diff.	<0.01
	2002	no differences			ns

Table 3. *Oncorhynchus* spp. Generalized linear model (GLM) analysis of salmonid condition factor in ocean, front and plume habitats. Further details as in Table 1

Species	Year	Ocean	Front	Plume	p-value
Coho yearling (<i>O. kisutch</i>)	2001	no differences			ns
	2002	higher	lower	higher	<0.005
Chinook yearling (<i>O. tshawytscha</i>)	2001	no differences			ns
	2002	no differences			ns
Chum juvenile (<i>O. keta</i>)	2001	no differences			ns
Steelhead juvenile (<i>O. mykiss</i>)	2001	no differences			ns
	2002	no differences			ns

head, were on average heavier for their length in 2002 than in 2001 (Fig. 3, GLM analysis, $p < 0.001$ for each species).

Juvenile chum salmon fed exclusively on planktonic prey. In 2001, their diet was dominated by small copepods <2.5 mm total length (98.8% *Centropages abdominalis*), northern anchovy (*Engraulis mordax*) and sanddab (*Citharichthys* spp.) eggs, larval euphausiids, and larvaceans (Fig. 4). In 2001 the diet of yearling coho salmon was numerically dominated by crab megalopae (primarily *Cancer magister*), adult euphausiids and hyperiid amphipods, and was only 16.2% fishes by number (Fig. 5). In 2002, the diet of yearling coho salmon was numerically dominated by fishes (72.5%), with fewer planktonic prey (Fig. 5). Prey consumed by yearling Chinook salmon captured in 2002 were similar to prey of yearling coho salmon in 2002 (Fig. 5), but comprised more crab megalopae (other than *C. magister*), hyperiid amphipods and pteropods and fewer fishes (60.4% by number) and euphausiids.

Analysis of feeding intensity (Fig. 6) indicated that juvenile salmon in the ocean habitat tended to have fuller stomachs than those in the front and plume habitats. In both 2001 and 2002, yearling coho salmon had higher stomach content weights in the ocean than in the front and plume habitats, as did juvenile chum salmon in 2001 (Table 4). Yearling Chinook salmon in 2002 did not exhibit significant differences in stomach fullness among habitats. Stomach-content weights for yearling coho salmon, which was the only species abundant enough in both years to allow interannual comparisons, were approximately twice as high in 2002 than in 2001 (Fig. 7, GLM, $p < 0.001$).

The NMDS ordination of the diets of yearling coho salmon in 2001 indicated that diet differed among habitats. Coho salmon diets tended to group by the habitat in which they were captured (Fig. 8A). MRPP analysis blocked by station indicated that taxonomic composition of coho stom-

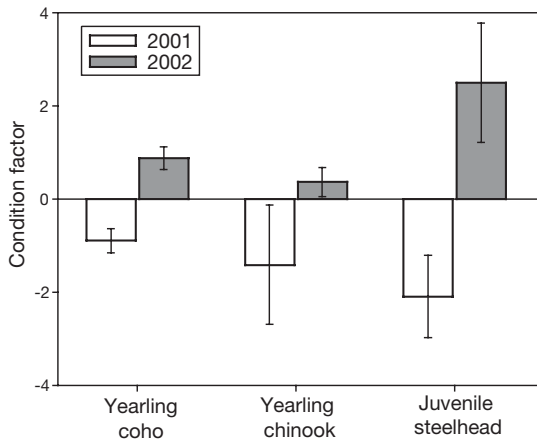


Fig. 3. *Oncorhynchus* spp. Mean (± 2 SE) condition factor of *O. kisutch*, *O. tshawytscha* and *O. mykiss* during 2001 and 2002

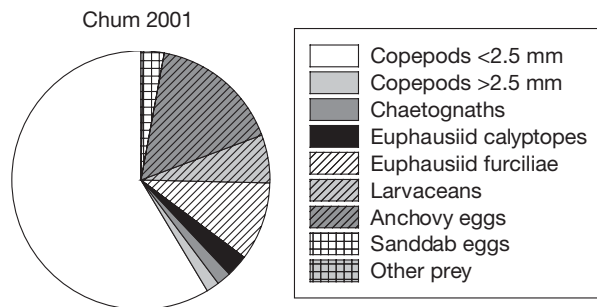


Fig. 4. *Oncorhynchus keta*. Percent, by number, of major prey categories consumed by juvenile chum salmon ($n = 112$) in 2001. Prey categories in key are depicted counterclockwise from vertical

ach contents was significantly different among habitats ($p < 0.001$), and that the diet within a habitat was more similar than would be expected by chance ($A = 0.31$). MRPP analyses blocked by habitat were not significant ($p = 0.58$, $A = -0.02$), indicating that diet did not differ among stations. Indicator species analysis (ISA) and an overlay of the prey species matrix on the NMDS ordination (Fig. 8A) revealed that *Cancer magister* megalopae comprised a larger fraction of the diet in the plume, while hyperiid amphipods and other crab megalopae were indicative of diets of individuals captured in the ocean habitat.

NMDS ordination showed that overall, the diet of juvenile chum salmon in 2001 was similar between habitats, but differed among station block (Fig. 8B). MRPP analysis grouping by station block did not identify differences in prey composition between ocean and front habitats ($p = 0.30$), and within-group agreement was similar to that expected by chance ($A = 0.0001$). MRPP analysis grouping by habitat showed significant differences ($p < 0.0001$) among stations and high

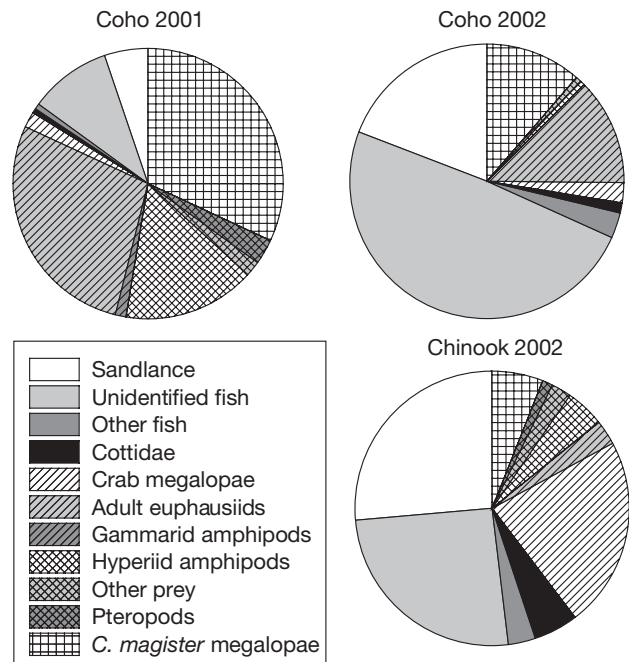


Fig. 5. *Oncorhynchus* spp. Percent, by number, of major prey categories consumed by yearling *O. kisutch* in 2001 ($n = 246$) and 2002 ($n = 83$) and by yearling *O. tshawytscha* in 2002 ($n = 344$). Unpatterned prey categories correspond to fish prey. Prey categories in key are depicted counterclockwise from vertical

within-group agreement ($A = 0.97$), which indicates that diets differed substantially among stations.

NMDS ordination of yearling Chinook salmon in 2002 revealed that stomach contents tended to cluster more strongly by station block than by ocean or front habitat (Fig. 8C). MRPP analysis blocked by station indicated that taxonomic composition of stomach contents differed among habitats ($p < 0.01$). However, within-group agreement was only slightly higher than would be expected by chance ($A = 0.09$), indicating that the difference in diet among habitats was not very consistent among stations in the same habitat. MRPP analysis blocked by habitat was significant ($p < 0.01$) and had higher within-group agreement ($A = 0.20$), indicating that yearling Chinook diets were more similar among stations than habitats. ISA revealed that crab megalopae other than *Cancer magister* were indicative of the diets of fish captured in the plume, while adult euphausiids reflected the diets of fish captured in the ocean habitat.

DISCUSSION

Our observations of the distribution of juvenile salmonids show that densities of juvenile salmonids were generally higher in either the plume and/or front

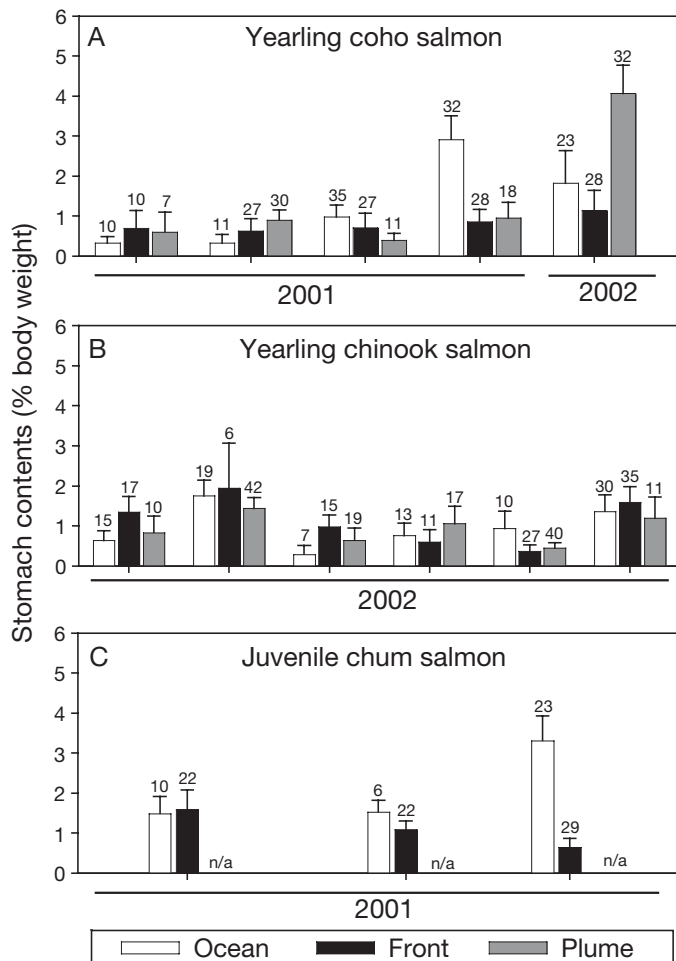


Fig. 6. *Oncorhynchus* spp. Mean (+2 SE) stomach fullness of (A) *O. kisutch*, (B) *O. tshawytscha* and (C) *O. keta*. Each group of bars represents a triplicate station block in which ocean, front and plume habitats were sampled. Year of capture is given below abscissa; number of fish is given above error bars

waters compared to the higher salinity ocean waters. Juvenile coho and chum salmon were more abundant at fronts compared to surrounding waters in 2001, and steelhead were more abundant at fronts in 2002, but the trends in distribution among habitats were not consistent across the study years. Thus, although we did observe juvenile salmon to be more abundant at fronts at times, our results are inconsistent with the hypothesis that salmonids, like their zooplankton prey, are consistently more abundant in the vicinity of the plankton-rich Columbia River Plume fronts. Rather, we observed that juvenile salmon are generally more abundant in the front and plume regions

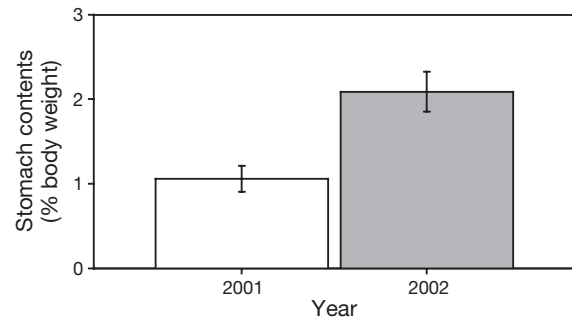


Fig. 7. *Oncorhynchus kisutch*. Mean (± 2 SE) stomach fullness of yearlings in 2001 and 2002

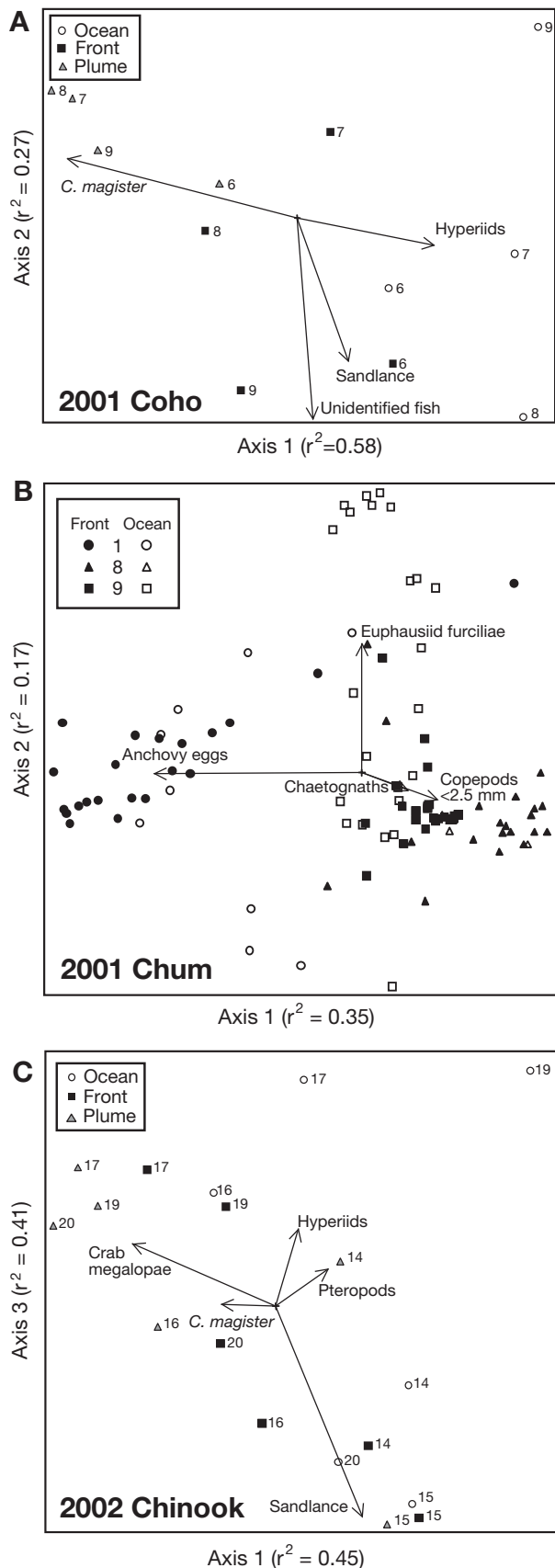
compared to more marine waters. This distribution pattern may reflect the outmigration of large numbers of juvenile salmon from the Columbia River estuary into coastal waters during the study period, and is consistent with previous reports of higher abundances of recent ocean-entry salmon in river plumes (Pearcy & Fisher 1990, St. John et al. 1992, Fukuwaka & Suzuki 1998).

Chum salmon differed from other salmonids in that they were rare in the plume. They are more likely to have originated from coastal streams and estuaries on the Washington Coast, since in the Columbia River populations of chum salmon have been at low levels in recent years (Joint Columbia River Management Staff 2002). Given that these fish have adapted to the more saline coastal water, they may have actively avoided entering the low-salinity plume to minimize osmotic stress.

Stomach-content analysis did not support the hypothesis that juvenile salmonids benefit from increased feeding rates when they associate with river plume fronts. In no case were stomach contents of fishes captured at fronts higher than in other habitats. When differences in feeding intensity were significant, coho and chum salmon captured in the ocean had higher stomach fullness. Given the lack of a correlation between feeding intensity and body length, differences in fish size among habitats are unlikely to account for our observations of elevated stomach contents of chum and coho salmon captured in the ocean.

Table 4. *Oncorhynchus* spp. Generalized linear model (GLM) analysis of salmon feeding intensity in ocean, front and plume habitats. Further details as in Table 1. na: insufficient fish captured to allow analysis; intermed.: intermediate

Species	Year	Ocean	Front	Plume	p-value
Coho yearling (<i>O. kisutch</i>)	2001	higher	lower		<0.001
	2002	higher	lower	intermed.	<0.001
Chinook yearl. (<i>O. tshawytscha</i>)	2002	no differences			ns
Chum juvenile (<i>O. keta</i>)	2002	higher	lower	na	<0.001



NMDS ordinations indicated that coho salmon diet in 2001 differed among habitats, but the diet of chum salmon in 2001 and Chinook salmon in 2001 were related primarily to station blocks. MRPP analysis indicated that diets of yearling coho and Chinook salmon differed significantly among the ocean, front and plume habitats. Although the composition of the plankton in the vicinity of fronts differed substantially from that of the ocean and plume habitats (Morgan et al. 2005), ISA did not identify any species that were characteristic of feeding at fronts.

When significant differences in the body size of juvenile salmonids among the ocean, front and plume habitats were documented (coho salmon 2002, chum salmon 2001, steelhead 2001), fishes captured in the ocean were larger. In addition, there were no differences in the proportion of hatchery-marked fishes among habitats, indicating that wild and hatchery fishes do not differentially occupy the ocean, front and plume habitats. Few differences were observed in condition factor among the different habitats. Given their larger size, salmonids captured in the ocean habitat probably emigrated from the estuary prior to those captured in the more nearshore front and plume habitats.

Taken together, our observations of the distribution and feeding of salmonids in the Columbia River plume are consistent with reports from other regions (St. John et al. 1992, Fukuwaka & Suzuki 1998) that out-migrating juvenile salmonids utilize low-salinity plumes as nursery areas as they adjust their physiology to the more saline environment, where opportunities for feeding and growth are higher. Residence in the more turbid plume waters (Morgan et al. 2005) may also be advantageous for salmon early after ocean-entry, as moderate turbidity is likely to decrease vulnerability to visually hunting predators, but is unlikely to affect planktivorous feeding by salmon smolts (De Robertis et al. 2003).

Fig. 8. *Oncorhynchus* spp. Results of nonmetric multidimensional scaling ordination for (A) yearling *O. kisutch* in 2001, (B) juvenile *O. keta* in 2001 and (C) yearling *O. tshawytscha* in 2002, based on composition of ingested prey. The closer 2 data points are, the more similar the ingested prey. Symbol shading represents samples from different habitats, and clusters of similarly shaded symbols indicate that diets differ among habitats. For coho and Chinook salmon, each data point represents pooled diet for fish from a given trawl; for juvenile chum, each data point represents the stomach contents of individual fish. Station block is annotated by a number next to data points in (A) and (C) and by symbol shape in (B). r^2 : percent of variance explained along each axis; the total of the 2 axes = percent of original variance explained by 2-dimensional representation of ordination shown. Joint plots depict prey species correlation with ordination in species space; length and direction of vectors indicate relationship of prey species to axes

The relatively small spatial scale and limited persistence times of fronts at the leading edge of the Columbia River plume may limit the degree to which juvenile salmon are able to take advantage of these plankton-rich features. The fronts are narrow in the cross-frontal dimension, and although they are recurrent, their duration is on the order of hours, as (like other river plume fronts) they form on the ebb tide and relax as the tide changes (Kingsford & Suthers 1994, Morgan et al. 2005). The timing and extent of tides was similar in both study years, and it unlikely that there were any major changes in the persistence of the fronts between study years. As discussed by Olson (2002), the time scales over which fronts persist may limit the degree to which fishes can locate and exploit the fronts. This is consistent with our observation that a substantial amount of variability in the distribution of and feeding by juvenile salmonids can be attributed to the station blocks, which account for the spatial and temporal arrangement of trawl samples. This indicates that events occurring over short temporal and spatial scales influence juvenile salmon in this dynamic environment and emphasize the importance of a blocked sampling design. More persistent fronts such as topographically controlled fronts or upwelling fronts (e.g. Wolanski & Hamner 1988, Largier 1993, Olson 2002) are more likely to have consistently elevated densities of fishes because the longer time scales over which these features persist will allow fishes to locate and congregate at these more stable features.

The short time scales over which a river plume front persists may limit the degree to which it is possible to observe differences in feeding intensity with stomach-content analysis. For example, approximately 6 to 9 h are required for coho salmon to clear 50% of their stomach volumes at the temperatures encountered in this study (Brodeur & Pearcy 1987). Stomach contents may reflect feeding history over time scales longer than the persistence time of the fronts, and this may mask elevated feeding over short time periods. However, if juvenile salmonids were able to consistently locate and maintain themselves within fronts, and consumed sufficient prey in food-rich frontal regions to result in a biologically meaningful increase in growth rate, an effect of this magnitude should have been detectable in the stomach contents of individuals captured at the fronts.

Occupying frontal regions may also have a negative effect on juvenile salmonids due to increased predation pressure. Fronts often attract highly mobile predators such as piscivorous fishes and seabirds (Owen 1968, Skov & Prins 2001, Olson 2002), and juvenile salmonids in the vicinity of fronts may face a higher probability of predation. Juvenile salmon near fronts at the leading edge of the Columbia River plume may be

particularly vulnerable to avian predators, which from an aerial vantage point are able to rapidly locate transient fronts and focus their feeding on these locations. Many piscivorous seabirds, including the common murre *Uria aalge*, aggregated in and were observed to be actively feeding in frontal regions of the Columbia River plume (Morgan et al. 2005, their Fig. 1c).

We observed strong interannual differences in condition and feeding intensity of juvenile salmon in the coastal ocean over the 2 yr of our study. Environmental conditions in 2002 appeared to be more favorable for outmigrating juvenile salmon than in 2001. In 2002, condition indices revealed that juvenile coho and Chinook salmon and steelhead were significantly heavier for their length than in 2001. For juvenile coho salmon, it was possible to compare feeding intensity between years, and stomach contents were approximately 2-fold higher in 2002 than in 2001. This suggests that better feeding conditions in the coastal ocean contributed to the increased body weight at size observed in 2002. In addition, there was a higher proportion of fishes in the diet of coho salmon in 2002. Fishes are energetically dense compared to planktonic prey (Davis et al. 1998), and increased availability of fish prey may have contributed to elevated growth. In addition, concurrent plankton sampling documented elevated biomass of organisms consumed by juvenile salmon, and higher standing stocks of chlorophyll *a* in 2002 compared to 2001 (Morgan et al. 2005).

As discussed by Morgan et al. (2005), the 2 study years differed in that the plume was larger in 2002 than 2001 due to higher Columbia River flows, and it is possible that the observed differences in the distribution, feeding and growth of juvenile salmon are related to plume structure. Although our study was designed to test the hypothesis that juvenile salmon aggregate to feed at fronts, our observations document substantial interannual variability in the distribution patterns, growth and feeding of juvenile salmon in the vicinity of the Columbia River plume. Higher prey availability, elevated feeding and higher condition of juvenile salmon co-occurred with higher river flows and a larger plume in 2002 compared to 2001. Coho smolt-to-adult survivorship in the 'Oregon production index area' (which is dominated by Columbia River stocks) was substantially higher for coho entering the ocean in 2002 (3.75%), than in 2001 (2.46%) (Salmon Technical Team 2005). This is consistent with our observation that conditions during ocean entry in 2002 were more favorable for outmigrating coho salmon than in 2001, and the notion (Pearcy 1992) that events during early ocean residence influence overall salmon survivorship. Focused long-term studies should be designed to determine if this is a consistent pattern by testing the hypothesis that growth and survivorship of juvenile

salmonids is related to changes in the timing and intensity of freshwater discharge into the coastal ocean. This relationship is of particular interest given that management and diversion of the Columbia River has substantially altered both the timing and magnitude of Columbia River discharge (Sherwood et al. 1990).

In summary, our study indicates that juvenile Pacific salmon in the coastal waters off the Columbia River tend to be more abundant in the low-salinity plume and frontal regions than in the more saline coastal waters in the early summer as they make the transition from the estuary to the coastal ocean. In some cases, juvenile salmon were aggregated at fronts, but there was substantial interannual variability in distribution, and no species was consistently abundant at fronts in both study years compared to the surrounding ocean and plume waters. Individuals captured in the more marine waters tended to be larger in body size and had fuller stomachs, suggesting that larger juveniles moved to more marine waters, where feeding opportunities were better, after making the physiological transition to a marine habitat. Although planktonic organisms consumed by juvenile salmon were substantially concentrated by convergent water flow at fronts at the leading edge of the plume, we did not detect increased salmon feeding intensity in the vicinity of these fronts compared to adjacent ocean and plume waters. This may be due to the short persistence time and rapid propagation of river plume fronts, which may make it difficult for fishes to locate and exploit these ephemeral, but food-rich, features.

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