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Influence of a Coastal Riverine Plume on the Cross-shelf Variability in Hydrography, Zooplankton, and Juvenile Salmon Diets

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Abstract Riverine plumes in nearshore coastal waters are areas of enhanced production and accumulation of prey and may increase availability of food during a critical period of juvenile salmon survival and hence serve as a nursery area for these juveniles. Physical and biological sampling was conducted along a cross-shelf transect through the Columbia River plume during May 1999. Based on cluster analyses of physical variables, stations considered to be within the core of the plume, at 27.8–46.3 km from shore, were distinct from inshore (7.4–18.5 km) and offshore (55.6–92.7 km) stations. Five variables (temperature at 10 m, salinity at 3 and 10 m, silicate, and chlorophyll) accounted for 92 % of this difference. Both surface neuston and subsurface plankton tows revealed differences in plankton composition at the plume core stations compared to non-plume stations. However, stomach contents of juvenile Chinook salmon were not significantly different inside and outside the plume core. Comparison of similarity indices showed that the stomach composition was more similar to the catch composition in the neuston than the meter net. Fishes, decapod larvae, and hyperiid amphipods occurred in greater proportions and copepods and euphausiids in lesser proportions in the stomachs than in the plankton. There appeared to be a distinctive plume signal, evident in both the physical environment and zooplankton resources sampled inside and outside the plume core, but the plume signature was not as evident in the salmon diets, possibly due to their higher mobility and shorter residence time within the plume.

Keywords Oceanography · Zooplankton · Habitat · Riverine plume · Feeding habits · Juvenile salmon

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Introduction

The recognition that certain coastal marine habitats contribute disproportionally to the survival of anadromous and marine fishes has led to increased scientific attention to document their value (Beck et al. 2001; Dahlgren et al. 2006; Sheaves et al. 2015). These studies have traditionally focused on nearshore seagrass, mangrove, or rocky reef habitats as many species are known to utilize these areas for feeding and/or shelter from predators during their critical early life stages. For anadromous species, such as salmonids, that move between freshwater and marine habitats, estuaries can provide a transition zone to allow them to adapt to more marine waters (Healey 1982; Bottom et al. 2005). However, due to the tidal flushing dynamics of the estuaries, they may not fully adapt to the new environment in the limited time that they occupy estuarine environments. For large river systems, the presence of a nearshore, surface freshwater plume may facilitate the physiological and behavioral transition to a marine environment that the animal has never experienced before and may serve a critical role as a nearshore extension of the estuarine nursery area for these fish. Thus, the estuarine-nearshore ocean ecotone can be viewed as a continuum in terms of habitat usage (Able 2005).

The Columbia River is a major source of freshwater input to the Eastern Pacific Ocean and accounts for about 77 % on average of the coastal drainage of the US West Coast (Hickey

et al. 1998). This river injects a substantial amount of nutrients into the coastal environment, particularly during peak seasonal flows in late spring (May–June), and these inflows affect the production and transport of phytoplankton and zooplankton in coastal waters (Hill and Wheeler 2002; Peterson and Peterson 2009). At its greatest extent, the Columbia River plume extends hundreds of kilometers offshore and alongshore (Barnes et al. 1972) and impacts large areas of the California Current ecosystem (Hickey and Banas 2003). The river is a source of silicates in coastal waters, and its plume contains the highest levels of total organic carbon in the region (Hill and Wheeler 2002), forming one of the most productive habitats in the northern California Current (Juan-Jordá et al. 2009). Studies in other areas have suggested that riverine plumes enhance productivity of coastal ecosystems through increased nutrient input and water column stability (Kingsford and Suthers 1994; Grimes and Finucane 1991; Grimes 2001; Gillanders and Kingsford 2002; Gillson 2011).

Previous studies on the marine distribution of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in this area indicated that large numbers of these fish are caught inside the Columbia River plume over a period of several months in early summer (Fisher and Pearcy 1995; Fisher et al. 2007). Other studies have examined the importance and impact of riverine plumes to salmon survival (Beamish et al. 1994; Casillas 1999; Burla et al. 2010a) and the mechanisms by which plumes may affect survival (Miller et al. 2013). These include the provision of food resources, refuge from predation due to high turbidity levels in the plume, and/or rapid transport of fish offshore and away from nearshore coastal predators (St. John et al. 1992; Fukuwaka and Suzuki 1998). The predation refuge and transport mechanisms are difficult to test in the field, given the dynamic nature of these systems. However, examination of the prey availability for and feeding intensity of juvenile salmon is relatively straightforward and can yield valuable insight into the utilization patterns of the plume by salmon.

The feeding ecology of juvenile salmon has been the focus of numerous studies along the West Coast of the USA over the past few decades. These studies have examined the seasonal (Emmett et al. 1986; Brodeur and Pearcy 1990), interannual (Brodeur and Pearcy 1990; Brodeur et al. 2007a; Daly et al. 2012), large-scale geographic (Brodeur and Pearcy 1990; Brodeur et al. 2007b; Hertz et al. 2015), and size-related variability (Peterson et al. 1982; Brodeur 1991; Daly et al. 2009) in juvenile salmon diets. Although some studies examined smaller-scale (between station) variability in salmon food habits in relation to oceanographic features such as fronts (DeRobertis et al. 2005) and eddies (Pool et al. 2008), to date, no such attempts have been made to look at variation in diets and corresponding prey availability with respect to the Columbia River plume.

Specific objectives of this study were to (1) determine spatial variations in prey availability by examining cross-shelf patterns in the physical environment, distribution of major zooplankton taxa, and diet of juvenile Chinook salmon in a transect bisecting the plume, (2) compare salmon stomach fullness and zooplankton biomass at stations inside and outside the plume, and (3) undertake detailed quantitative comparisons of the prey taxa consumed by juvenile salmon relative to prey available in the water column (neuston and plankton) at the same time. An overall goal is to test that hypothesis that the plume is a unique environment and whether a distinct benefit from occupying this habitat exists for juvenile salmon with respect to availability of food resources during a critical period in their life history (Pearcy 1992).

Materials and Methods

Field Sampling

Data examined in this study came from a research cruise conducted on 18–25 May 1999 aboard a chartered commercial fishing vessel, the F/V *Sea Eagle*. Five predetermined transect lines were sampled, with stations extending from northern Washington to central Oregon (Fig. 1a, b). We examine data collected along a single transect line known as the Columbia River transect (CR) and located directly offshore from the river mouth, where a majority of fish were caught (see Fig. 1b). Along the CR transect (Table 1), stations began 7.4 km offshore (station CR4) and progressed to 13 and 18.5 km offshore (CR7, CR10). Progressing offshore from CR10, stations were located at intervals of approximately 9 km until CR30, and beyond CR30 at intervals of 18 km until salmon were absent from the trawl samples (at CR50). All samples were taken during the daytime between 0600 and 1900 h with the exception of a repeat sampling at the CR30 station (Table 1), where a full suite of sampling was conducted during nighttime (0317 h) to examine within-station diel variability in biological and physical parameters.

Zooplankton collections were made using two different nets. The first, a 1-m-diameter ring net (hereafter called meter net) with 335-μm mesh, was deployed by letting out 60 m of cable and retrieving it immediately at 30 m min^{-1} while the vessel was underway at 3.6 km h^{-1}. The angle of the wire was maintained so that this net fished obliquely to a total depth of approximately 20 m. The second was a 0.97- by 0.3-m manta neuston net, also with 335-μm mesh (Brown and Cheng 1981). The neuston net was towed for 5 min at the same speed as the meter net, but was towed at the surface but approximately 60 m behind the vessel, to avoid disturbance from its wake. A calibrated General Oceanics flowmeter (General Oceanics Inc., Miami, FL) located inside the mouth of each

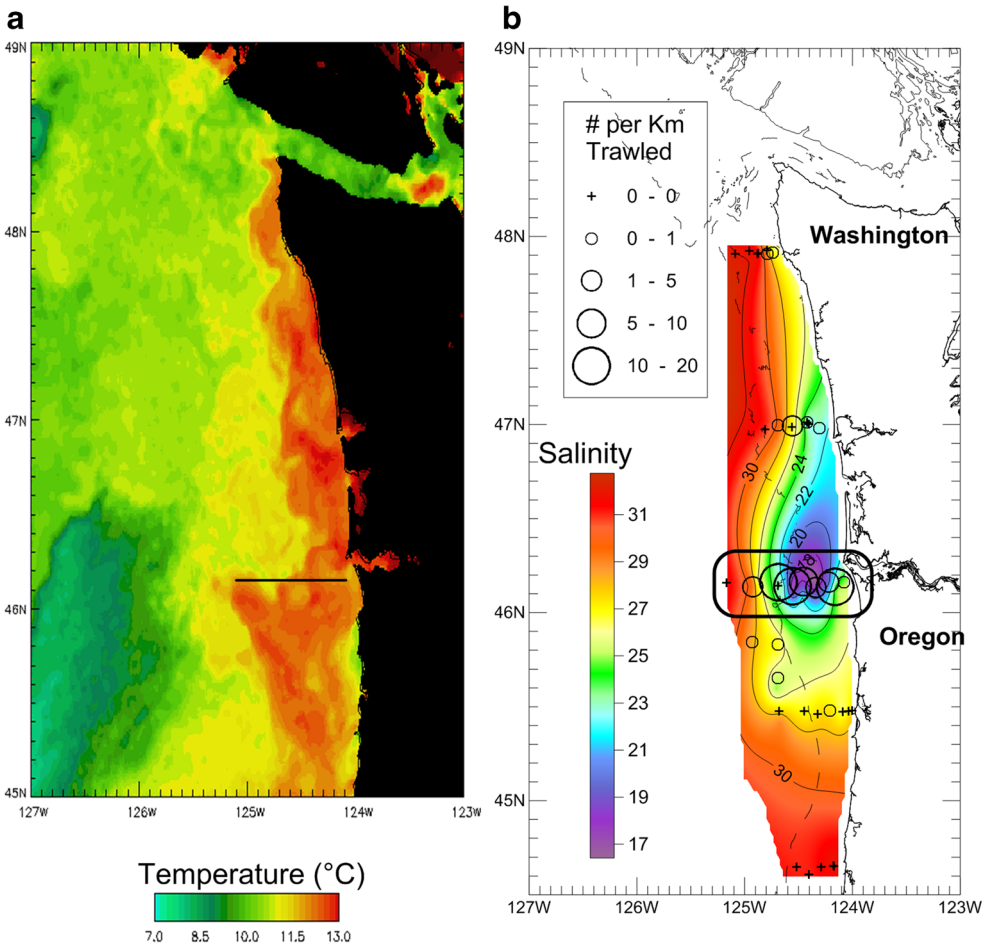

Fig. 1 **a** Sea surface temperature (AVHRR) image collected on May 21, 1999 showing the coast of Washington and Oregon and the transect examined in this study (*black line*) and **b** distribution of sea surface salinity (*contours*) from May 1999 survey and standardized catch of juvenile Chinook salmon (*symbols*) at the sampled stations. The stations examined in this study are enclosed by the *black line*

net was used to estimate the amount of water filtered. Samples were preserved in 5 % buffered formalin.

Juvenile salmon were sampled using a Nordic 264-rope trawl (Net Systems, Bainbridge Island, WA) fished directly astern the vessel at the surface. The mouth opening of the trawl was 18 m deep and 30 m wide, and it was spread apart by a pair of 3.0-m trawl doors (Emmett et al. 2004). The trawl was fished fully open with about 300 m of warp for 30 min at a

Table 1 Station information for trawl and plankton collections made during May 20–21, 1999

Station	Date	Time	Distance offshore (nautical miles)	Distance offshore (km)	Station depth (m)	Latitude (decimal degrees north)	Longitude (decimal degrees west)
CR4	May 20	7:51	4	7.4	29.3	46.16	124.08
CR7	May 20	9:32	7	13.0	67.7	46.14	124.16
CR10	May 20	11:20	10	18.5	78.6	46.16	124.22
CR15	May 20	12:43	15	27.8	113.4	46.13	124.34
CR20	May 20	15:23	20	37.1	133.5	46.16	124.45
CR25	May 20	17:28	25	46.3	148.1	46.14	124.55
CR30D	May 20	19:00	30	55.6	438.9	46.16	124.68
CR30N	May 21	3:17	30	55.6	493.8	46.14	124.69
CR40	May 21	6:03	40	74.1	1024.1	46.14	124.92
CR50	May 21	9:17	50	92.7	848.6	46.16	125.17

Station 30 was sampled during both the daytime (30D) and nighttime (30N)

speed of 1.5 m s^{-1}. To fish the headrope of the trawl close the surface, a cluster of two meshed A-4 Polyform floats were tethered to each wing tip, and two additional A-3 Polyform floats were clipped near the center of the headrope. Data collected with depth sensors document that the headrope generally remains in the upper 2 m of the water column when fished with this configuration (Krutzikowski and Emmett 2005), so the trawl effectively sampled the upper 20 m of the water column. Mesh sizes ranged from 162.6 cm in the throat of the trawl near the jib lines to 8.9 cm in the cod end. To maintain catches of small fish and squid, a 6.1-m-long knotless liner with 0.8-cm mesh was sewn into the cod end.

The physical and biological environment was monitored and sampled at each station immediately prior to or after each trawl effort. A conductivity/temperature/depth (CTD) cast was made with a Sea-Bird SBE 19 Seacat profiler to a depth of 100 m or within 5 m of the bottom. Chlorophyll and nutrient samples were collected with a Niskin bottle from a depth of 3 m. Chlorophyll samples were filtered at sea and analyzed in the laboratory using standard acetone extraction and fluorometric techniques (Arar and Collins 1997). Pigments were extracted in 90 % HPLC grade acetone in deionized water for at least 12 h in a dark freezer before measuring sample fluorescence with a fluorometer (Turner Designs, 10-AU). Chlorophyll *a* was calculated from these fluorescence measurements. Concentrations of phosphate (PO_4), silicate ($Si(OH)_4$), nitrate (NO_3), nitrite (NO_2), and ammonium (NH_4) were determined in nutrient samples by the University of Washington Marine Chemistry Lab using standard methods adapted for an autoanalyzer (UNESCO 1994).

Zooplankton Analysis

In the laboratory, samples were rinsed, and all organisms over an average length of 2.5 mm were counted, as well as all developmental stages of fish, euphausiids, shrimp, crabs, amphipods, isopods, mysids, cumaceans, barnacles, and pteropods. This size criterion was based upon previous analyses of juvenile salmon diets (Brodeur 1991; Schabetsberger et al. 2003), which have indicated that 2.5 mm is the minimum size of prey consumed and that these prey are effectively retained by 335-μm mesh. Using a light table, the entire sample was initially scanned for rare large organisms, which were removed and enumerated. Next, the sample was split using a Folsom splitter, and more common large organisms were removed and enumerated. Finally, a subsample of the split was taken using a Hensen stempel pipette (5–20 ml) to count smaller organisms. A dissecting microscope was used to identify all organisms to the lowest possible taxonomic level and developmental stage.

After extrapolating catch sizes from subsample counts, the data were normalized using flowmeter data to calculate concentrations (individuals m^{-3}). Plankton were then grouped into seven categories: fish, decapods, euphausiids, hyperiid amphipods, pteropods, copepods, and other. These categories were used for ease of comparison with stomach samples, since stomachs contain plankton in a range of states of digestion, which renders them difficult to resolve to the same taxonomic level as plankton that is sampled whole. Biomass of a given taxa was calculated by multiplying the concentration by the carbon weight of individuals of a given developmental stage and summing all species groups to yield milligram per cubic meter. Estimates of zooplankton carbon content were derived from literature values or from our own estimates of dry weight (Morgan et al. 2005).

Stomach Analysis

Stomachs of frozen Chinook salmon were excised in the laboratory and fixed in 5 % formalin before being transferred to 70 % ethanol. Stomachs were opened under a dissection microscope, and the prey contents were removed and identified to the lowest possible taxonomic level (Schabetsberger et al. 2003). Counts and weights of individual taxa were taken, and total length measurements were made on the important fish prey taxa using an ocular or stage micrometer. To examine station differences in overall amount of food eaten, we used an index of feeding intensity (%BW) using the following formula:

$$\%\mathrm{BW} = \frac{\text{Stomach content weight}}{\text{Total fish weight} - \text{Stomach content weight}} \times 100.$$

Statistical Analyses of Environmental Variables

Our aim was to examine among-station variability in different environmental variables that could objectively distinguish sampling sites and characterize them as being inside or outside the plume. We initially examined 13 variables, but two of these (total N and density at 3 m) were highly correlated with other variables and subsequently excluded, leaving 11 variables to use in the analysis (temperature at 3 and 10 m, salinity at 3 and 10 m, PO_4, $Si(OH)_4$, NO_3, NO_2, NH_4, stability, and chlorophyll *a* at 1 m). For this analysis, stability was defined as the difference between density at 20 and 1 m, divided by their difference in depth (19 m). Frequency distributions of the remaining variables were examined, and several of them were highly skewed, necessitating the use of a log $(x + 1)$ transformation and all data were relativized to allow comparison among them. These data were next analyzed using routines from the multivariate analysis package PRIMER-E version 6 (Clarke and Gorley 2006). An environmental similarity matrix was calculated (Euclidean distance measure), and then agglomerative cluster analysis was used to examine correspondence among stations. Distinct clusters were determined using the similarity

profile (SIMPROF) test routine which uses a permutation algorithm to test the null hypothesis that specified groupings are not significant ($p = 0.05$) from each other (Clarke et al. 2008). The groupings determined were then compared using one-way ANOSIM to test the null hypotheses (H_o) of no difference in environmental variables between groupings or water masses (plume vs non-plume). The Similarities Percentages (SIMPER) routine was then applied to identify those variables which were characteristic of each of the water masses and were most responsible for the differences among water mass groupings (Clarke and Gorley 2006).

Statistical Analysis of Diet and Zooplankton Variability

As for the environmental variables, we constructed similarity matrices (Bray-Curtis distance measure) of the numerical composition of major taxonomic categories in catches from the neuston and meter nets and pooled (by station) stomach data. All data were fourth-root transformed to minimize the effects of extreme values and standardized to sample totals. We used cluster analysis (hierarchical group-average sorting strategy) to examine the relationships among stations to compare with the environmental clusters. We again tested for differences using ANOSIM and the characteristic taxa that accounted from the differences when found using SIMPER for the same station groupings we determined from the environmental data. Finally, we used the PRIMER package RELATE to compare the matched similarity matrices among stomachs, neuston net samples, and meter net samples to determine whether there was any similarity between diets and available zooplankton (Clarke and Warwick 2001).

Feeding Selectivity

Feeding selectivity was quantified using the "log of the odds ratio" (LOR), which has the desirable properties of being symmetrical around 0 (no selection) and ranges from 0 to + ∞, in the case of positive prey selection, and from 0 to −∞, in the case of negative prey selection (Gabriel 1978), and would be comparable to previous studies on selection of prey by juvenile Chinook salmon (Schabetsberger et al. 2003):

$$\mathrm{LOR} = \ln\left(\frac{d_i(100-e_i)}{e_i(100-d_i)}\right)$$

where d_i and e_i are the percentages of taxon i in the diet and environment, respectively.

To describe the prey field, we pooled zooplankton into major prey taxa and calculated average densities for each station for both the meter and neuston nets. Some taxonomic groups (chaetognaths, cnidarians) were never represented in the diet (selection = −∞) and were therefore excluded from the selectivity analysis.

Results

Physical and Biological Conditions

The Columbia River plume was well developed during this cruise period due to above-normal river discharge during May 1999 (Fig. 2). The plume was visible trailing offshore and slightly to the north along the Washington coast in both satellite temperature images and our in situ surface salinity data (Fig. 1). The CR transect we sampled bisected the entire plume as it progressed off the shelf. Vertical profile sections clearly showed the subsurface manifestation of the plume in the occurrence of low salinity and density water extending down to at least 5 m at approximately 36 km offshore (Fig. 3).

Nutrient concentrations and chlorophyll standing stocks were quite variable across the plume (Fig. 4). Chlorophyll concentrations peaked 27.8–37.1 km from shore at stations (CR15 and CR20) with the lowest surface salinities. Silicate and total N peaked slightly farther offshore (37.1–46.3 km; CR20–CR25) and decreased dramatically with increased distance from shore (Fig. 4).

Although there were four other transects sampled both north and south of the Columbia River transect during this cruise, the vast majority (86 %) of juvenile Chinook salmon were caught along the CR transect (Fig. 1b). With the exception of a moderately large ($n = 72$) catch of Pacific herring (*Clupea pallasii*), at the inshore station (7.4 km; CR4) where only two juvenile Chinook salmon were caught, there were few other pelagic marine fishes caught along this entire transect, especially within the plume. The highest Chinook salmon catches per haul were found at the 55.6-km (CR30) station, followed by the 46.3 km (CR25) station (Fig. 5a). However, the juvenile Chinook salmon were largest in length at the 27.8- (CR15) and 37.1- (CR20) km stations (Fig. 5b). Since very few salmon were caught at the 7.4-km (CR4) station, and none were caught at the 92.7-km (CR50) station, these two end stations were excluded from the biological analyses.

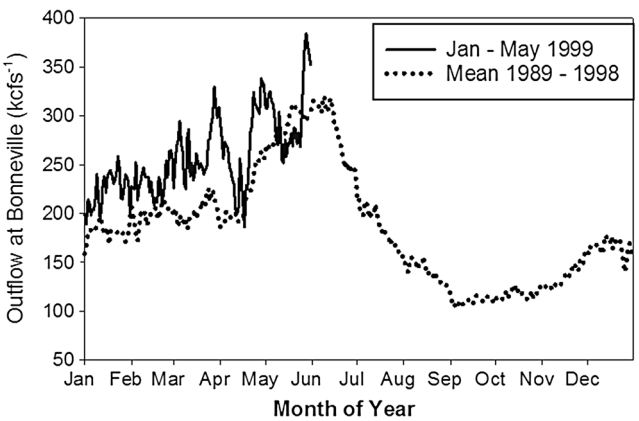

Fig. 2 Comparison of 10-year average (*solid line*) and May 1999 (*dotted line*) flow at the Bonneville Dam on the Columbia River

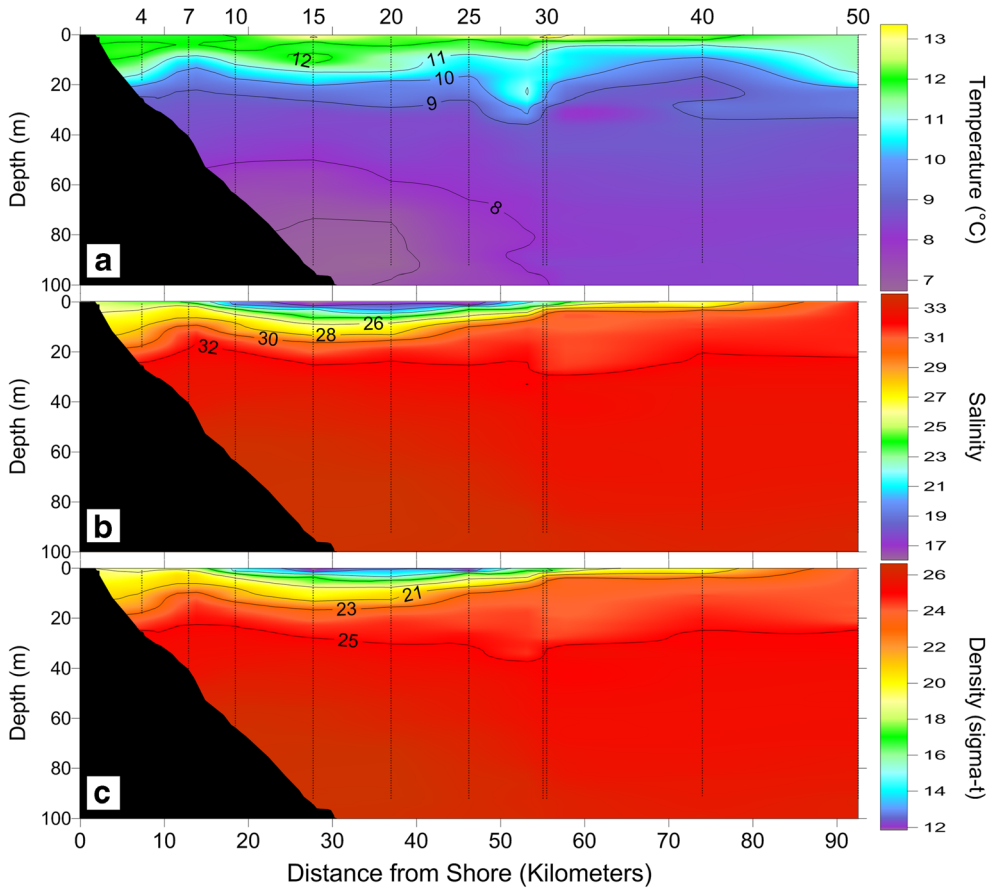

Fig. 3 Cross-shelf sections of the **a** temperature, **b** salinity, and **c** density taken along the Columbia River transect. The station names are listed above the *top panel* of the graph. The *dotted lines* indicate the location of CTD casts with two casts taken at CR30. See Fig. 1 for the location of the sampling transect

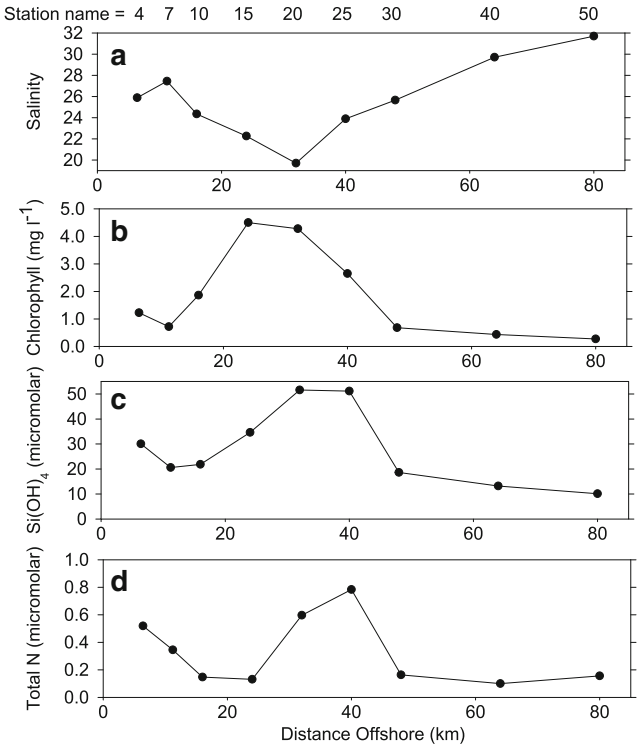

Fig. 4 Cross-shelf distribution of **a** salinity, **b** chlorophyll, **c** silicate, and **d** total nitrogen found during May 20–21, 1999 along the Columbia River transect

Variability in Plankton and Stomach Contents

The neuston net captured a high percentage of the "other" category from CR7 to CR25 (Fig. 6a). This was made up primarily of barnacle (Infraclass Cirripedia) cyprid larvae at the CR7 and CR15 stations, with the addition of the isopod (*Idotea fewkesi*) at the CR20 and CR25 stations. At the

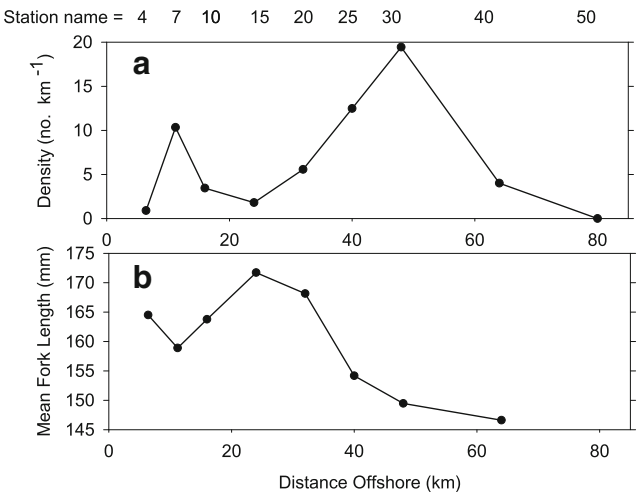

Fig. 5 **a** Density and **b** mean fork length of juvenile Chinook salmon collected at each station. No salmon were collected at CR50

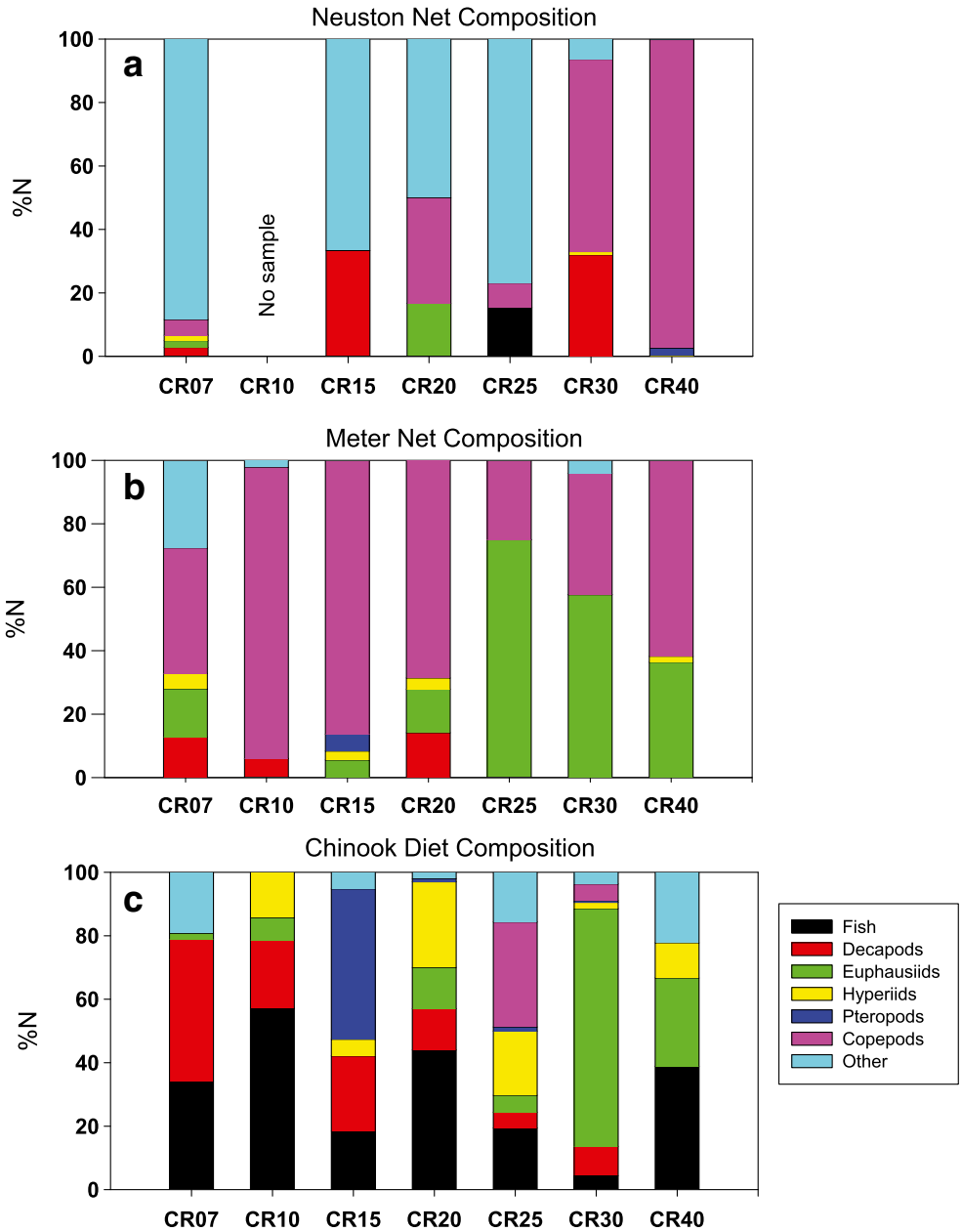

Fig. 6 Numerical composition by major taxonomic categories of **a** neuston and **b** meter net tows and of **c** Chinook stomach contents by station as a percent of total. See "Results" section for a description of "other"

offshore stations, neuston catches were primarily large copepods (*Calanus* spp. and *Epilabidocera longipedata*) and larval-stage crabs (*Cancer* spp.). Pteropods and hyperiid amphipods were rarely captured in the neuston net (Fig. 6a).

The meter net also showed a shift of plankton caught going from inshore to offshore (Fig. 6b). This catch was composed of high numbers of large copepods (*Calanus* spp. and *E. longipedata*) at all stations but more so inshore. At offshore stations CR25, CR30, and CR40, the meter net also captured high numbers of larval euphausiids (*Euphausia pacifica* and *Thysanoessa spinifera* (Fig. 6b). Hyperiid amphipods (mainly *Themisto pacifica* and *Hyperoche medusarum*) were caught in lower numbers but at all stations. Catches of fish in the meter net were rare, and pteropods were abundant only at station CR15.

Chinook salmon captured at any given station generally had a wider variety of prey items in their stomachs than were available from either plankton net at the same station (Fig. 6c), although salmon diets also showed some inshore-to-offshore trends. For example, decapods (Crangonidae, Pandalidae, and *Cancer* spp. larvae) comprised a higher percentage of the diet in stomachs from inshore stations, whereas euphausiids (*T. spinifera* and *E. pacifica*) were more abundant in stomachs from offshore stations. Other prey categories, such as hyperiid amphipods (mainly *H. medusarum*) and fish (*Ammodytes hexapterus* and Pleuronectidae) were found in stomachs from

all stations. Similar to the meter net catch, pteropods were found in stomachs in high numbers at only one station, CR15.

Cluster analyses revealed slightly different patterns of aggregation between the physical environment, plankton, and Chinook salmon diets with respect to position along the transect (Fig. 7). With regards to the environmental data, the inshore stations (CR7 and CR10) more closely resembled the two offshore stations (CR30 and CR40), while the remaining stations, CR15–25, represented the core of the plume in terms of their physical conditions (Fig. 7a). ANOSIM revealed significant differences between these two clusters (global $R = 0.889$, $p = 0.019$). Five variables (salinity at 3 and 10 m, chlorophyll *a*, temperature at 10 m, and silicate) accounted for 92 % of this difference in the SIMPER analysis (Table 2). The same three stations that were distinct for the environmental data (CR15, CR20, and CR25) had a significantly different ($R = 0.812$, $p = 0.029$) composition than the rest of the neuston net collections (Fig. 7b—no sample was collected at CR10). Euphausiid calyptopis and anchovy eggs were substantially more abundant in the plume, whereas the reverse was true for barnacle nauplii, *Pleurobrachia* (ctenophore), and insects (Table 2). For the meter net data, CR15 and CR20 again formed a cluster, with the remaining inshore and offshore stations associated in a larger cluster including CR 25 (Fig. 7c). However, when we tested the composition of the plume vs non-plume stations determined by the physical data, the differences were significant despite CR25 being in a different grouping ($R = 0.631$, $p = 0.036$). In this case, anchovy eggs and the copepod *Calanus marshallae* were indicative of the plume stations and euphausiid furcilia were characteristic of the non-plume water (Table 2). Finally, among the diet compositions at each station, CR15 was most distinct, followed by CR40, but the remaining stations inshore from CR25 clustered apart from the offshore stations (Fig. 7d). However, the similarity level at which these clusters split was much lower for Chinook salmon diets than for either the environmental data or the two plankton gears, suggesting substantially less-defined groupings, and the salmon caught in the plume and non-plume water masses did not consume different prey ($R = 0.385$, $p = 0.071$). Interestingly, in both plankton gears and Chinook salmon stomachs, the day sample composition at CR30 was more similar to the night composition at that station than to any of the other daytime stations, even for adjacent stations sampled only a few hours apart from the daytime sampling (Fig. 7b–d).

In terms of stomach fullness, CR20 and CR30 were well above the transect average, and CR15 and CR40 were below

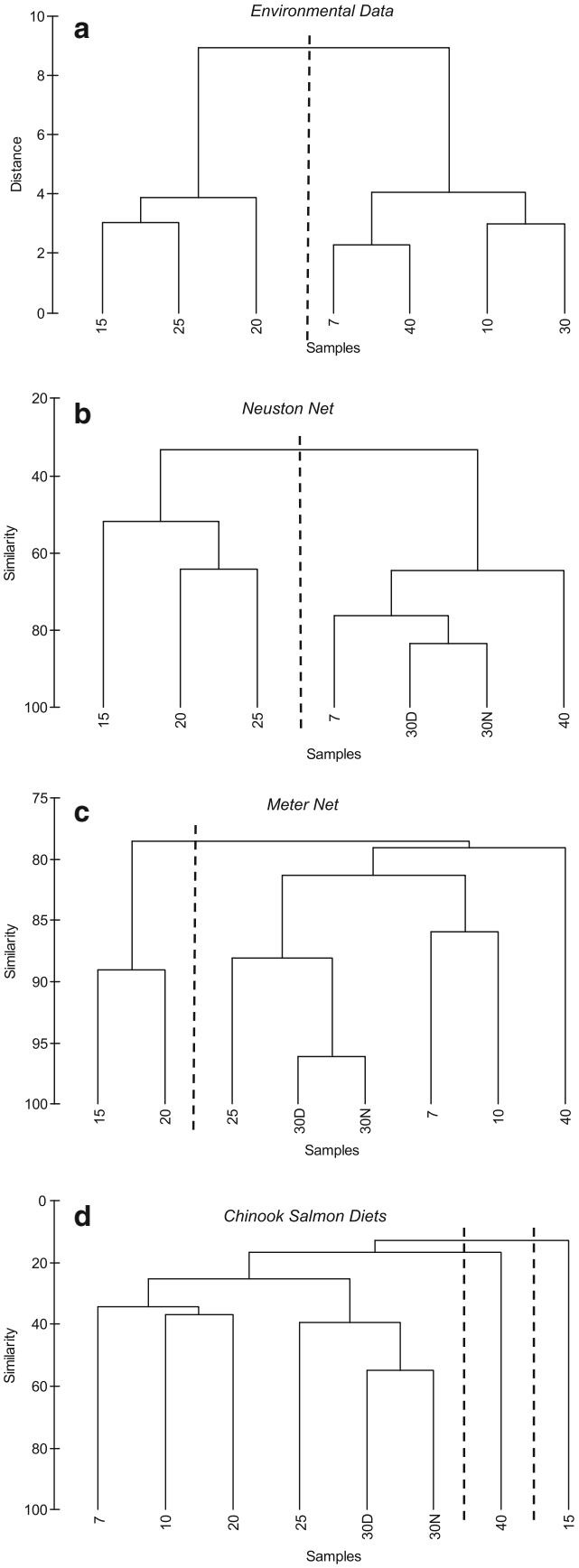

Fig. 7 Cluster analysis of the **a** environmental data, **b** neuston net, **c** meter net, and **d** stomach content data by station. *D* and *N* represent the day and night collections, respectively, at NH30. *Dotted lines* indicate significant ($p < 0.05$) levels of separation of cluster groups based on a similarity profile (SIMPROF) test

Table 2 Results of Similarities Percentages (SIMPER) analyses showing the mean values and percentage contributions of the five most important (a) environmental variables, (b) neuston taxa, and (c) meter net taxa examined

	Plume	Non-plume	Cumulative % contribution
a. Environmental variables			
Salinity (3 m)	21.29	26.70	34.01
Salinity (10 m)	26.42	30.39	58.53
Chlorophyll *a*	4.48	0.96	80.28
Temperature (10 m)	11.67	10.62	86.79
Si (OH)4	3.83	2.99	91.97
b. Neuston net			
Cirripede nauplii	0.87	30.02	15.34
Euphausiid calyptopis	28.25	0.00	30.25
Pleurobrachia spp.	0.00	25.93	44.08
Insecta	0.00	25.64	55.00
Engraulis mordax eggs	17.53	0.00	63.37
c. Meter net			
Thysanoessa spinifera furcilia	11.97	20.98	13.25
Engraulis mordax eggs	19.21	0.00	24.86
Euphausiid furcilia	0.00	20.03	35.43
Calanus marshallae	17.45	0.00	45.44
Euphausia pacifica furcilia	0.50	16.68	55.14

Stations were grouped into plume and non-plume based on cluster analysis of environmental variables

the average (Fig. 8a). This pattern did not correspond with the distribution of biomass found in both plankton nets, which peaked at the two offshore stations mainly due to the high biomass of euphausiid furcilia and adults caught in the meter net (Fig. 8b) and decapods in the neuston net (Fig. 8c). The offshore neuston net was dominated by copepods which were not utilized by juvenile Chinook salmon (Fig. 6).

Comparisons Between Ingested Prey and Available Zooplankton

Fishes, decapod larvae, and hyperiid amphipods were, in general, positively selected at most stations, whereas and copepods were negatively selected by juvenile Chinook salmon relative to their estimated abundance in the plankton (Fig. 9). Euphausiids (adults and juveniles) were mostly negatively selected inshore but were consumed in similar proportions to their estimated abundance at the offshore stations. The sign of the selection was similar for both gear types, but the values for the meter net were substantially skewed to more positive selection (Fig. 9), indicating that this gear was less likely to catch the prey of juvenile Chinook salmon than the neuston net. Rank correlations of similarities among the various matrices showed that overall, the meter net catch was not significantly correlated with either the neuston catch ($\rho = 0.37$; $p = 0.07$) or the stomach contents ($\rho = 0.33$; $p = 0.12$). However, the neuston catch and stomach contents did show a significant correlation ($\rho = 0.57$; $p = 0.003$) in taxonomic composition when all stations were combined.

In terms of the size of fish prey, plankton caught in the neuston net were more similar to those found in the stomachs of juvenile Chinook salmon than to those caught in the meter net (Fig. 10). The distribution of fish sizes from the meter net catch was unimodal, with most prey fish <20 mm in length. The median size of fish prey in the meter net (12 mm) was significantly smaller than that in the neuston sample (45 mm) or stomach contents (40 mm; Kolmogorov-Smirnov test, $p < 0.001$ for both). In contrast, the size range of prey fish from the neuston catch was similar to that of prey fish from stomach contents

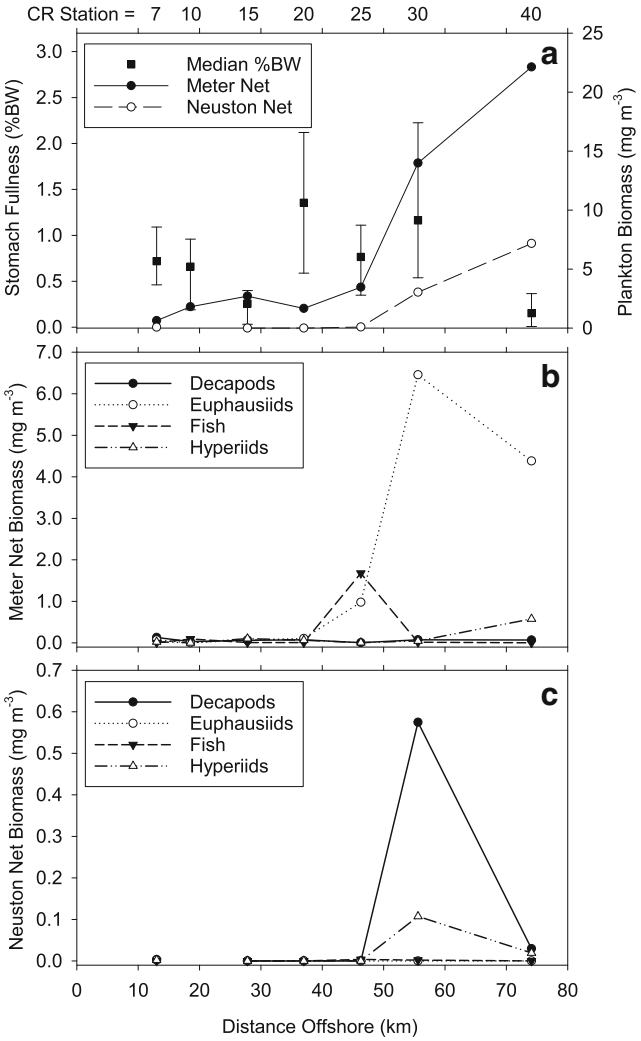

Fig. 8 **a** Median and 95 % (*upper error bar*) and 5 % (*lower error bar*) values of the stomach contents as a proportion of body weight. Also shown are the total wet weight biomass of plankton found in the meter and neuston net (*right axis*), **b** biomass by meter net, and **c** by neuston collections of the major taxa consumed by juvenile Chinook salmon in this study

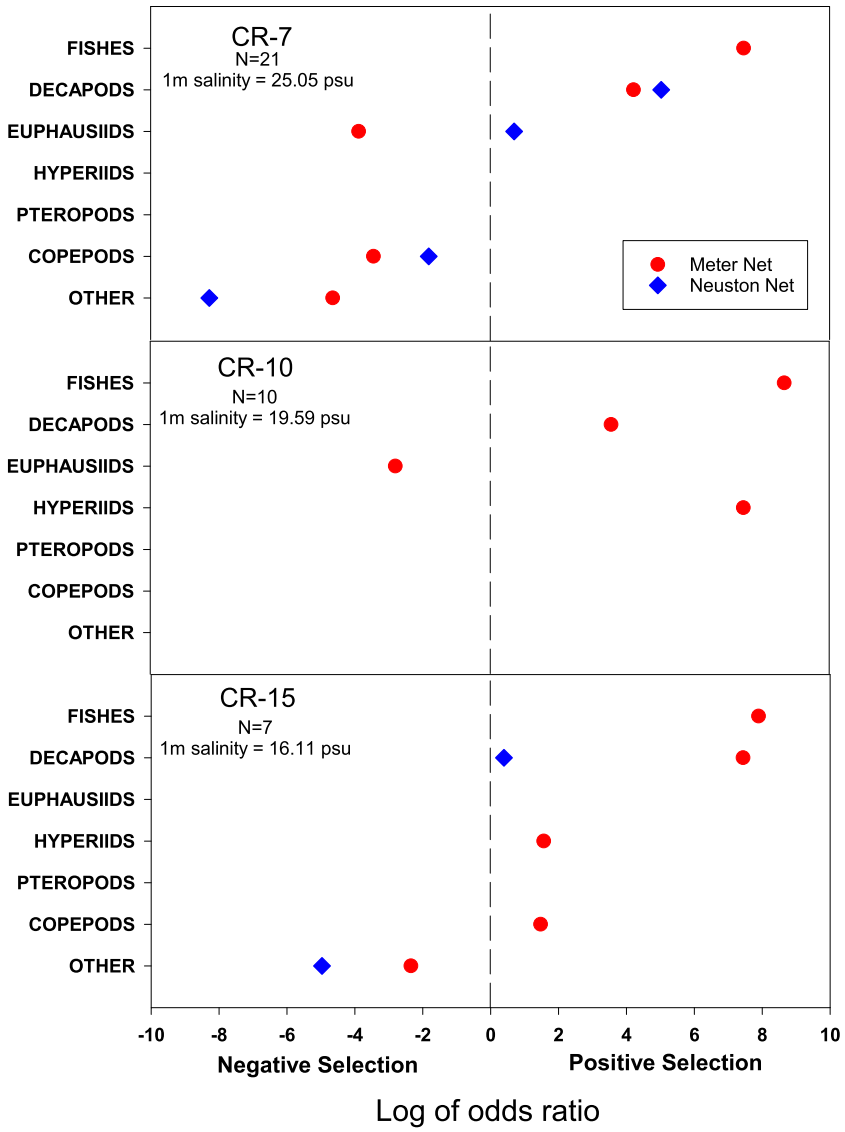

Fig. 9 Log of the odds ratios showing selectivity indices for major prey items by juvenile Chinook salmon for each station where a sufficient number of stomachs were available (*N*). Also shown are the surface salinity measures at each station. No neuston sample was taken at CR10

(Fig. 8), and the size distributions were not significantly different (Kolmogorov-Smirnov test, $p = 0.092$).

Discussion

Our sampling along a transect that bisected the Columbia River plume indicated that chlorophyll concentrations and salmon densities were higher inside the plume core than outside of it, although we did not see a corresponding higher level of surface or subsurface zooplankton biomass in the plume. However, we did observe differences in zooplankton composition in both nets between what was in the plume core vs what was both inshore and offshore of the plume. Juvenile salmon stomach fullness was not significantly higher inside the plume than outside. Based on data from a single transect sampled during 1 year, we cannot say unequivocally whether the plume represents a critical nursery area for salmon in their early period of ocean residence compared with more oceanic waters, but our study does show clear indications that the plume represents a unique environment compared to the surrounding shelf waters.

The Columbia River plume is highly dynamic in space and time, with much of the modulation in its size and direction depending on outflow, semidiurnal tides, seasonal currents, and local wind forcing (Hickey et al. 1998; Hickey and Banas 2003). An empirical orthogonal function analysis of multi-year simulations of plume dynamics (Burla et al. 2010b) suggests that river discharge (over 40 %) and shelf winds (over 20 %) explain nearly 65 % of the plume variability. During summer, the plume generally extends south and away from the

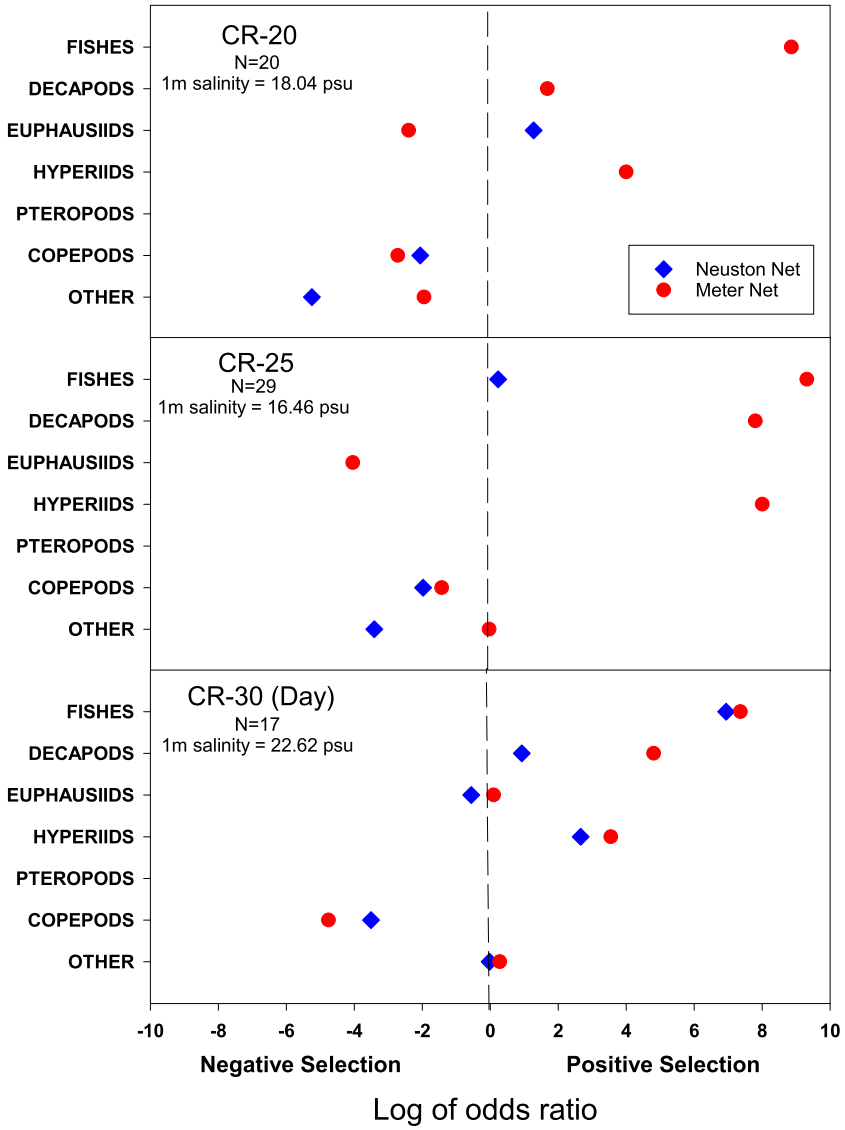

Fig. 9 continued.

coast as it is influenced by southward winds leading to offshore Ekman transport (Thomas and Weatherbee 2006). However, observations and modeling results suggest that plume flow is bidirectional, with both northward- and southward-flowing branches (Garcia-Berdeal et al. 2002; Hickey et al. 2005; Burla et al. 2010b). What is considered the "bulk plume" is actually a complicated admixture of subcomponents and is dependent on the time since the freshwater entered the ocean and the prevailing physical wind and current conditions (Horner-Devine et al. 2009; Jay et al. 2009). These factors make plume characterization problematic. Roegner et al. (2003) conducted a mesoscale survey in the Columbia River plume slightly north of our study area but during the same time period in late May 1999. They found that changes in wind intensity over a period of a few days can dramatically alter both water properties and phytoplankton distributions, with corresponding changes in plankton biomass.

Thomas and Weatherbee (2006) examined 6 years (1998–2003) of multispectral satellite data and found that the plume was relatively extensive in May 1999 compared to all other years except 1998. They found the 1999 plume core generally orientated directly offshore with a secondary plume of fresh water hugging the Washington coast. Columbia River discharge was exceptionally high, and model simulations also suggested an above-average plume volume in May 1999, based on the 28.0 isohaline (Burla et al. 2010b; see also the Columbia River Climatological Atlas at: http://www.stccmop.org/datamart/virtualcolumbiariver/simulationdatabases/climatologicalatlas). This indicates that if the plume does have a biophysical effect on plankton and juvenile salmon distribution, it would most likely have been manifested in the year we examined.

Although all stations along the CR transect in our study may be influenced in varying degrees by outflow of the Columbia

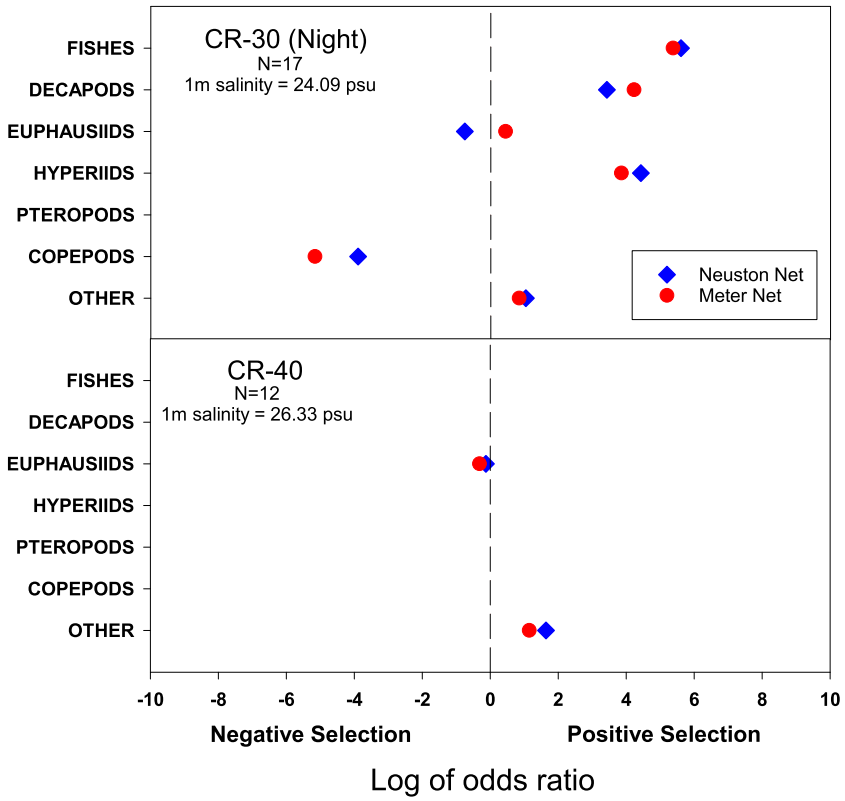

Fig. 9 continued.

River, the region referred to as the plume core was shown to be a somewhat unique environment differing significantly from stations inshore and offshore of the plume core. This is based not only on its physical and chemical characteristics but also based upon its plankton composition (Fig. 7). However, the level of differentiation between water masses was not the same with each measure we examined. The physical and chemical environment was the most conservative in that it was dependent mostly on advection and diffusion, which are relatively slow processes. Neustonic taxa are somewhat limited in their mobility and appear to be advected with the plume for the most part and showed substantial dissimilarity in community composition between plume and non-plume stations. The taxa which showed the greatest differences were either weak swimmers (barnacle nauplii, euphausiid larvae, or gelatinous zooplankton) or completely lack swimming ability (fish eggs and dead insects). In contrast, subsurface zooplankton have some limited mobility in that they can migrate vertically in the water column and thus experience multi-directional currents at different depths (Morgan 2014). Thus, the water masses showed less differentiation in meter net catches than the neuston net, and the species driving these differences were not likely to vertically migrate great distances (euphausiid larvae, small copepods, and fish eggs). The salmon stomach contents showed the fewest differences between the plume core and the stations outside the plume. Salmon are by far the most mobile of the taxa examined, and considering that the stomach evacuation time for juvenile Chinook salmon was on the order of 24 h at the temperatures we observed (Benkwitt et al. 2009), the prey found in stomachs may have been consumed at locations other than where they were caught. This added spatial and temporal variability may account for the decreased coherence between diet and physical parameters compared to that between these same physical parameters and zooplankton.

Chinook salmon were caught at all stations except for the farthest offshore (80 km), but peak catches were just offshore from the plume core. Substantial inshore–offshore variability in diet composition and overall stomach fullness was observed, with a change occurring beyond CR20. Overall plankton biomass in both nets was substantially higher at the offshore stations along this transect, but this trend was not reflected in stomach fullness.

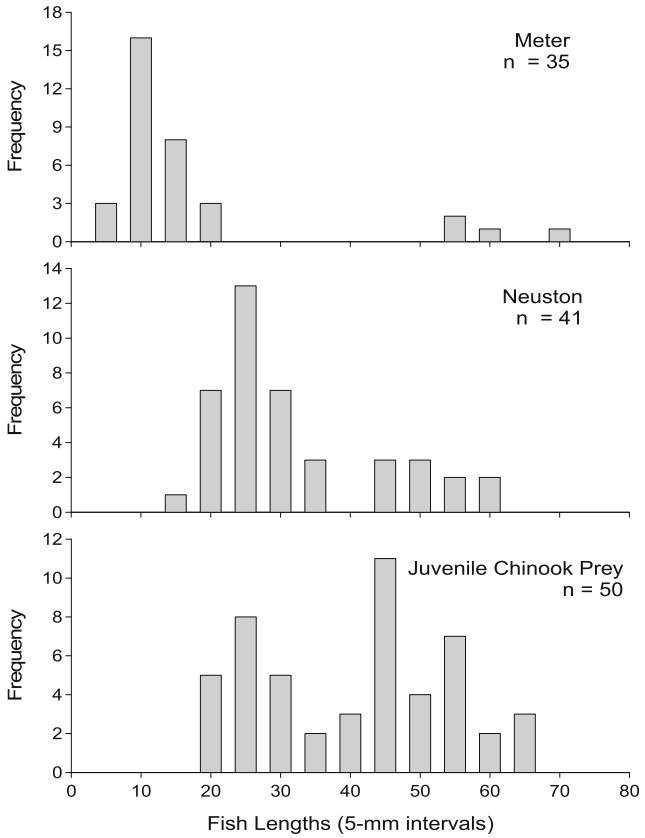

Fig. 10 Frequency distributions of all fish total lengths found in the meter net, neuston net, and stomach contents from this study

This could be related to the inability of salmon caught inshore to adapt to a new prey spectrum upon first arriving in the ocean (Daly et al. 2009; 2010). Most of the fish sampled had originated in the Columbia River (74 % of the 119 fish that were run for genetics were from the Snake and Mid-to-Upper Columbia River stocks; D. Teel, NWFSC, personal communication) and had likely been in the ocean for less than 1 month when they were caught, based on coded-wire-tag recoveries (n = 116) and otolith analysis. Of the 13 Snake River Chinook salmon that had their otolith microchemistry examined (Tomaro et al. 2012; Miller et al. 2013), four had been in brackish or ocean water just 1 day at the time of capture, with the rest from 10 to 43 days, part of which was spent in the estuary. However, the low biomass in these stomachs was more likely the consequence of timing of the samples: stations at which the highest stomach fullness occurred (CR20–CR30) were sampled in late afternoon, which may correspond to a diel period of maximum feeding (Benkwitt et al. 2009). Biomass at station CR30 from nighttime sampling with both the meter and neuston nets was substantially higher than biomass from daytime sampling conducted 8 h earlier at the same station (data not shown). However, taxonomic composition based on cluster analysis between day and night at CR30 was fairly similar—even more similar than that between CR30 and adjacent daytime stations sampled only 6.4 km and 1 or 2 h apart. This suggests that cross-shelf transport of plankton was relatively minimal at this location along this transect.

Chinook salmon diets were more similar to samples from the neuston net, in terms of type of prey eaten and the size of prey fish consumed, than to those from the meter net. It is uncertain whether this was due to the location in the water column where salmon fed or whether there was greater selectivity by the meter net than the neuston net. However, it should be noted that diets of juvenile Chinook salmon in the ocean quickly shift from zooplankton to juvenile fishes (Daly et al. 2009), which are of a size not easily captured in small plankton nets. Quantitative assessment of actual juvenile salmon prey may require small micronekton trawls with fine mesh liners (Brodeur et al. 2011). However, the neuston net appears to sample a more appropriate size range of juvenile fishes than the meter net, better overlapping the range of prey types and sizes found in salmon stomachs (Brodeur 1989; Pool et al. 2008; Brodeur et al. 2013).

Among the prey caught by these plankton gears, it was readily apparent that salmon selected the larger and more visible (i.e., heavily pigmented) prey groups such as juvenile fishes, crab larvae, and hyperiid amphipods (Peterson et al. 1982; Brodeur and Pearcy 1990; Schabetsberger et al. 2003). Many of these prey items of juvenile salmon, especially those that are surface-oriented, have been found in higher abundance in the neuston at Columbia River plume fronts, suggesting a potential concentration in and around these convergence zones (Morgan et al. 2005; Peterson and Peterson 2009). Zooplankton-sized particles tend to concentrate near the bottom boundary of the plume as well (Peterson and Peterson 2008; 2009); however, it is not known if the species favored by juvenile salmon are concentrated in these regions. Finer-scale sampling of both plankton and salmon may reveal the importance of frontal and plume dynamics in structuring salmon distributions in the Columbia River plume region (Roegner et al. 2003, 2013; DeRobertis et al. 2005; Morgan et al. 2005). Similar water mass separation of meroplankton and ichthyoplankton distributions has been observed in the Chesapeake Bay plume off the east coast of the USA (Reiss and McConaugha 1999; Shanks et al. 2002).

A potential confounding factor in our comparisons between the taxa collected in the two plankton gears and those found in the Chinook salmon stomachs is that some prey, and perhaps the predators themselves, may undergo diel vertical migration. The only information available presently on the

diel vertical distribution of juvenile Chinook salmon comes from a series of depth-stratified hauls made in May and June 2000 within the plume at a station close to our CR7 station (Emmett et al. 2004). This study found significantly higher densities of age 0.0 and 1.0 Chinook salmon in the surface (0–12 m) than in the subsurface tows (12–18 m) during both day and night, which suggests that the predators were residing mainly in the surface area that we sampled.

Information on the diel vertical distribution of zooplankton within and around the Columbia River plume is also very limited. Many crustacean zooplankton (Jamieson and Phillips 1993; Morgan 2014) and larval fish (Auth et al. 2007) that are prey of juvenile salmon are known to undergo diel vertical migrations and are generally found deeper in the water column during the day than at night. However, many larval fish species reside mostly in the upper 20 m of the water column throughout the diel period off the central Oregon coast (Boehlert et al. 1985; Auth and Brodeur 2006). Morgan et al. (2009) found that cirripede and many decapod larvae had a center of mass in the upper 20 m off the central California Coast. The only study of diel depth distribution relative to the Columbia River Plume involved sampling with an Optical Particle Counter towed throughout the upper 35 m on cross-shelf transects in near proximity to our study area (Peterson and Peterson 2008). This study found that the center of biomass of the detectable plankton was always in the upper 20 m and in the plume was often <10 m in depth. Since juvenile Chinook salmon feed primarily during diurnal or crepuscular periods (Schabetsberger et al. 2003), it is likely that they were foraging at similar depth levels as many of their prey, particularly in the plume core, but diel vertical migration of some larger prey such as euphausiids and juvenile fishes may have led to a mismatch in daytime feeding and prey availability that we were not able to account for with our sampling.

Whether salmon benefit from being in the plume environment depends not only on their feeding success but also upon their relative growth rates compared to other habitats, as well as their vulnerability to predators, which may aggregate in the plume especially at plume fronts (DeRobertis et al. 2005; Zamon et al. 2014), relative to the non-plume regions. Other fish species (e.g., northern anchovy, *Engraulis mordax*) are known to use the Columbia River plume as spawning and nursery habitat (Litz et al. 2008; Parnel et al. 2008) due to its high productivity and relative stability, and these features may also make it attractive as a nursery area for other marine and anadromous species. Clearly, more intensive study is warranted examining the residency time of juvenile salmon in the plume and the benefits they receive in this region versus any potential costs incurred.

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