



Biotic and abiotic factors influencing forage fish and pelagic nekton community in the Columbia River plume (USA) throughout the upwelling season 1999–2009

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Litz, M. N. C., Emmett, R. L., Bentley, P. J., Claiborne, A. M., and Barceló, C. Biotic and abiotic factors influencing forage fish and pelagic nekton community in the Columbia River plume (USA) throughout the upwelling season 1999–2009. – ICES Journal of Marine Science, 71: 5–18.

Received 14 December 2012; accepted 6 May 2013; advance access publication 19 June 2013.

Large river plumes modify coastal environments and can impact production across multiple trophic levels. From 1999 to 2009, the assemblages of forage fish, predator fish, and other pelagic nekton were monitored in coastal waters associated with the Columbia River plume. Surveys were conducted at night to target vertically migrating species, and community structure evaluated to better understand ecological interactions. Distinct inshore and offshore communities were identified during spring and summer that were correlated with ocean temperature, salinity, plume volume, and upwelling intensity. Resident euryhaline forage fish species, such as smelts, anchovy, herring, market squid, juvenile salmon, and spiny dogfish, showed a high affinity for inshore habitat and the lower salinity plume during spring. Highly migratory species, such as sardine, piscivorous hake, sharks, and mackerels, were associated with warmer, saltier waters offshore, during strong upwelling periods in summer. Overall, our study of pelagic nekton revealed that temporal dynamics in abundance and community composition were associated with seasonal abiotic phenomenon, but not interannual, large-scale oceanographic processes. Forage fish assemblages differed seasonally and spatially from the assemblages of major piscivorous predators. This finding suggests a potential role of the plume as refuge for forage fish from predation by piscivorous fish in the northern California Current.

Keywords: California current, Columbia River plume, community analysis, forage fish, predator fish.

Introduction

Determining nekton community structure in response to anthropogenic and oceanographic processes within coastal marine ecosystems is important for understanding ecological interactions. For example, understanding which species associate with each other, and why, or how they respond to environmental variability may improve the capacity of foodweb models used for ecological forecasting, bioenergetics modelling, and ecosystem management (Hunsicker *et al.*, 2011; Ruzicka *et al.*, 2012). Differences in nekton community structure in response to environmental variability may provide insight into the effects of climate change (Walther *et al.*, 2002), and changes in the nekton community composition as a direct result of fishery exploitation can inform stock assessments

(Link *et al.*, 2011). In the Northeast Pacific, the pelagic nekton community is made up of forage fish—small schooling species, whose major role in marine foodwebs is to transfer primary production to higher trophic levels (Pikitch *et al.*, 2012), and piscivorous predators, including large fish and invertebrates. Typical of eastern boundary upwelling ecosystems, the abundance of pelagic nekton in the northern California Current is dominated by a few species whose biomass fluctuates depending on species-specific biological and physical relationships (Emmett and Brodeur, 2000; Chavez *et al.*, 2003; Brodeur *et al.*, 2005; Emmett *et al.*, 2006).

In coastal systems worldwide, where there are rivers, highly productive, low-density plumes extend out into the ocean. The size of the plume varies with the size of the river, the strength of the

annual flood, and properties of the coastal current system (Wiseman and Garvine, 1995). Large riverine plumes formed by rivers such as the Amazon in Brazil, the Changjiang (Yantze) in China, the Rhine in the Netherlands, and the Columbia in the United States, may extend several hundred kilometres across the shelf or along the coast (Grimes and Kingsford, 1996). The mixing zones between low-salinity plume water and ocean water have a characteristic structure based on differences in water mass densities (Kudela et al., 2010). The lighter plume water overrides heavy ocean water, creating a frontal zone of convergence at the leading edge where large aggregations of zooplankton, larval fish, and their predators accumulate (Grimes and Kingsford, 1996).

The Columbia River is the largest source of freshwater entering coastal waters off the western United States (Hickey et al., 2005). The mean monthly discharge from the Columbia River peaks in spring when the snowpack is released, and during our study period (1999–2009), flow rates ranged from 2551 to 12 762 m³ s⁻¹ [United States Geological Survey (USGS), <http://waterdata.usgs.gov/or/nwis>]. The freshwater plume formed by the Columbia River is characterized by low salinity (<28 psu), high turbidity due to inputs of terrigenous sediment and nutrients, enhanced stratification, and eddies (Hickey et al., 2005; Burla et al., 2010a; Kudela et al., 2010). During high flow, the Columbia River plume modifies regional coastal circulation patterns and is frequently bidirectional throughout the upwelling season (April–August) in response to prevailing windstress and Ekman transport (Hickey and Banas, 2003; Hickey et al., 2005). The plume moves across the shelf and southwest during southward (upwelling) winds or nearshore and to the north during weak or northward (downwelling) winds.

Physical properties associated with the Columbia River, such as flow rate, location of the plume front, plume depth, and plume volume, have been shown to influence the distribution and abundance of several taxa, including phytoplankton (Kudela et al., 2010), zooplankton (De Robertis et al., 2005; Morgan et al., 2005; Peterson and Peterson, 2008), ichthyoplankton (Parnel et al., 2008; Auth, 2011), forage fish (Richardson, 1973; Kaltenberg et al., 2010), juvenile Pacific salmon (*Oncorhynchus* spp., Emmett et al., 2004; Burla et al., 2010b), and fish predators (Emmett et al., 2006). Understanding how variability in the physical and biological properties of the Columbia River plume influences pelagic community structure is critical for understanding trophic dynamics and energy flow, is important for determining essential fish habitat, and is useful for assessing how future climate changes will impact the pelagic ecosystem of the Northeast Pacific (Mote and Salathé, 2010).

Pelagic nekton which utilize the Columbia River plume and adjacent habitat include a variety of invertebrate and fish populations, many of which are commercially important, including local populations of Pacific salmon, Pacific herring (*Clupea pallasii*), northern anchovy (*Engraulis mordax*), California market squid (*Doryteuthis opalescens*), and spiny dogfish (*Squalus acanthias*). In addition, there are seasonally migratory coastal pelagic species that move north in summer, including the forage fish species Pacific sardine (*Sardinops sagax*), piscivorous predators like Pacific hake (*Merluccius productus*), Pacific mackerel (*Scomber japonicas*), jack mackerel (*Trachurus symmetricus*), and more recently, Humboldt squid (*Dosidicus gigas*). These migratory species generally arrive in the study area beginning in June and are more abundant during warmer, *El Niño* periods (Pearcy, 2002; Brodeur et al., 2005). Off the Columbia River, there are currently directed commercial

fisheries for Pacific salmon, hake, and sardine. Jack mackerel and Pacific mackerel are captured incidentally in the hake fishery, and there is a small bait fishery targeting northern anchovy (Emmett et al., 2006; Litz et al., 2008).

Since 1999, the community composition of pelagic nekton in the northern California Current System has changed significantly, synchronous with periods of positive (i.e. warmer sea surface temperature, SST) and negative (i.e. cooler SSTs) Pacific Decadal Oscillation (PDO) values (Mantua et al., 1997; Emmett and Brodeur, 2000), *El Niño* and *La Niña* events (Pearcy, 2002), variations in the intensity of coastal upwelling (Brodeur et al., 2006; Barth et al., 2007), and periods of high and low Columbia River flow and plume volume (Burla et al., 2010a). In this study, we examined the role of the Columbia River plume on changes in forage fish and pelagic nekton community structure relative to overall physical and biological variability. The Columbia River plume has been shown to influence forage fish recruitment and foraging success (Richardson, 1973), but detailed analyses on how the plume affects pelagic community structure is lacking. If community structure is driven by the plume, we expected variations in community to be associated with local and regional environmental factors. If differences are driven by basin-scale variability, we expected processes such as *El Niño* to be associated with changes in community structure.

Not all pelagic nekton species are tolerant of low salinity (i.e. <28 psu). Despite this, some pelagic nekton species (e.g. salmon and Pacific lamprey *Lampetra tridentata*) are anadromous, meaning that they spend most of their lives at sea and migrate to freshwater to spawn. Other pelagic nekton species, including Pacific herring, can be classified as euryhaline, meaning that they can effectively osmoregulate across a range of salinities. Previous research (Emmett et al., 2006; Litz et al., 2008) determined that many forage fish species showed a high affinity for inshore, low-salinity habitat, so we hypothesized that station depth would factor strongly in determining community structure. We also expected forage fish to display strong seasonal phenology within the plume, co-occurring with the spring transition from downwelling to upwelling conditions. That expectation was based on acoustic time-series results of schooling forage fish within the Columbia River plume (Kaltenberg et al., 2010). To test these hypotheses, we employed multivariate statistical techniques to evaluate the associations of pelagic nekton community structure along environmental gradients. The objectives of this study were to (i) identify and describe seasonal, annual, and cross-shelf variability in pelagic nekton assemblages within the Columbia River plume, (ii) identify taxa indicative of each temporal and spatial assemblage, and (iii) identify the scale at which environmental factors influence changes both to specific species and to community structure. The dataset analysed by this study represents the longest continuous time-series of pelagic nekton from night-time sampling in the Northeast Pacific.

Methods

Sampling

From 1999 to 2009, we collected data on pelagic forage fish and other pelagic nekton associated with the Columbia River plume along with physical oceanographic data to understand the relationships between oceanographic conditions and pelagic nekton catch fluctuations. The study area was located off the mouth of the Columbia River (Figure 1) and consisted of sampling at 12 stations along two transect lines (six stations per transect) north and south of the mouth of the Columbia River (46°15'N and 124°05'W). Stations

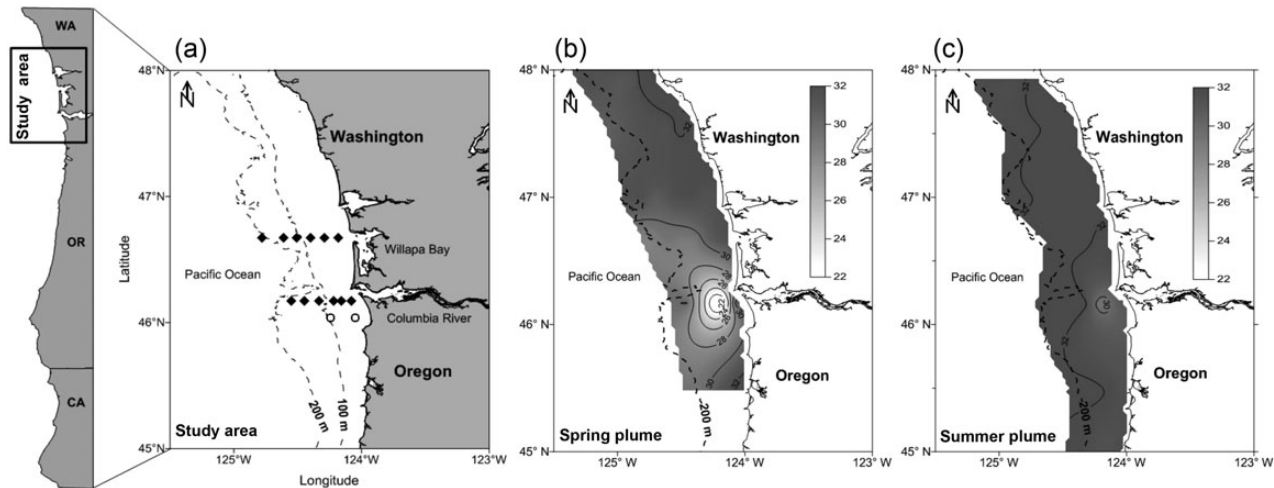


Figure 1. Maps showing (a) location of stations sampled during Predator Study cruises 1999–2009, and salinity contour plots generated from repeated CTD casts in the study area representing typical Columbia River plume structure in (b) spring and (c) summer. Station locations are represented by a filled diamond. Water samples collected at stations designated by an open circle were measured for Chl *a* concentration ($\mu\text{g l}^{-1}$) during each cruise. The 100- and 200-m isobaths overlaid on the study area map in dashed lines represent the mid-shelf and shelf break, respectively. A dashed line representing the shelf break only is overlaid on the salinity contour maps.

ranged from 7.4 to 55.6 km offshore along the continental shelf. Sampling occurred at night to take advantage of the diel vertically migrating behaviour of pelagic predators and prey (Bailey *et al.*, 1982; Emmett *et al.*, 2004, 2006; Krutzikowsky and Emmett, 2005; Emmett and Krutzikowsky, 2008). In all, 1080 surface trawls were conducted over 11 years approximately every 10 d from May to July (all years), with additional sampling in April (1999–2005) and August (2002 and 2004–2009). All surface trawls were accomplished using a 264-rope trawl (Nor’Eastern Trawl Systems, Inc., Bainbridge Island, WA, USA) towed directly behind a chartered commercial fishing vessel at an average speed of 1.5 m s^{-1} for durations of 15–30 min. For complete details, see Emmett *et al.* (2006). In brief, the trawl measured 100 m long and had an effective fishing mouth of 28 m wide by 12 m deep (336 m^2), with variable mesh sizes (9–163 cm), and a 6.1-m knotless liner (8.0 mm mesh) sewn into the codend. All individuals caught by the trawl were identified to the lowest possible taxon and counted, except for a large haul (>1000 individuals), when the total catch was estimated by sub-sampling. The location of the start and the end of each trawl was recorded using the ship’s GPS, and the distance trawled confirmed by deploying a General Oceanics™ Mechanical Flowmeter alongside the ship during trawling. Catch numbers from each haul were standardized by dividing the number of individuals by the total distance trawled (number per kilometre trawled).

In addition to collecting catch data, physical environmental information was collected at each station by deploying a SeaBird SBE 19 conductivity, temperature, and depth (CTD) profiler, which recorded temperature ($^{\circ}\text{C}$) and salinity measurements from the surface down to 100 m or within 5 m of the bottom. Chlorophyll *a* (Chl *a*; $\mu\text{g l}^{-1}$) was also collected from water at 3-m depth on Whatman GF/C glass microfiber filters at two locations during each cruise (Figure 1). Samples of Chl *a* were treated with acetone and measured with a Turner Designs 10-AU Fluorometer. Regional oceanographic data incorporated into our analysis were the monthly mean upwelling index for 45°N and 125°W , a measure of wind-driven coastal upwelling (and a proxy for primary and secondary production) from the Pacific Fisheries

Environmental Laboratory (<http://www.pfeg.noaa.gov>), monthly mean values for Columbia River discharge from the USGS, and Columbia River plume volume (m^3), determined from multiyear retrospective simulations by the Center for Coastal Margin, Observation, and Prediction (<http://www.stccmop.org/>). As an index, plume volume incorporates variability in Columbia River discharge and coastal wind patterns and is strongly related to salmon survival (Burla *et al.*, 2010b; Miller *et al.*, 2013). Basin-scale oceanographic variability was assessed using monthly values for the PDO from the Joint Institute for the Study of the Atmosphere and Ocean (Mantua *et al.*, 1997; <http://jisao.washington.edu>) and monthly values for the North Pacific Gyre Oscillation (NPGO; Di Lorenzo *et al.*, 2008) from the California Current Ecosystem Long Term Ecological Research Site (<http://www.o3d.org/npgo>). The PDO and the NPGO are independent and unrelated values emerging from analyses of SST and sea surface height anomalies over the Northeast Pacific, respectively. The PDO is associated with variations in temperature, and the NPGO is associated with changes relating to salinity, nutrients, and Chl *a* (Di Lorenzo *et al.*, 2008). Monthly multivariate *El Niño* Southern Oscillation Index (MEI) values from the NOAA Earth System Research Laboratory (<http://www.esrl.noaa.gov/psd/enso/mei>) were also used to describe ocean-atmospheric variability. The MEI represents the first principal component of variability related to six main observed variables over the tropical Pacific, which are sea-level pressure, zonal and meridional components of surface wind, surface air and sea temperatures, and cloudiness. Based on the scale of physical variability imposed by the Columbia River plume, we expected local and regional environmental variables (i.e. salinity and plume volume) to be more closely associated with variations in community structure than basin-scale variables (i.e. PDO, NPGO, and MEI).

Data structure and reduction

To perform this analysis, all standardized catch data (number km^{-1}) were averaged across both transects inshore and offshore of the mid-shelf break (100 m). Data were aggregated such that the

species matrix (96 sample units \times 106 taxa) represented the average catch from either an inshore or a offshore sampling location during a particular month (April–August) and year (1999–2009). Pelagic nekton in the species matrix consisted of invertebrates (crustaceans and cephalopods) and fish. Some fish species were separated by size class because large fish may utilize different habitats during different life-history phases, or ontogenetic stages, and can be alternatively prey or predator depending on size. For example, we classified Pacific hake 0–99 mm in total length (TL) as young-of-the-year (YOY), 100–299 mm TL as juveniles, and >300 mm TL as adults. We also classified a number of YOY species as pelagic species, although as adults they are bottom dwellers (e.g. Pleuronectidae and Scorpaenidae). Mesopelagic species (e.g. Myctophidae) were also included in the pelagic species matrix if they were caught in surface tows. To address the zero truncation problem and reduce the effect of overly abundant species, the data were transformed using the generalized logarithmic procedure $[\log(x + x_{\min}) - \log(x_{\min})]$. Before analysis, two sample units were identified as outliers. The outliers had an average distance >3.0 s.d. from the overall mean distance and were deleted from the species matrix. One of the outliers contained a rare species, brown Irish lord (*Hemilepidotus spinosus*), not present in any other sample units. Therefore, the final species matrix used in the analysis consisted of 94 sample units \times 105 taxa.

The environmental matrix (94 sample units \times 23 parameters) contained 17 quantitative and 6 categorical environmental variables that corresponded to each sample unit. There were eight quantitative variables that consisted of binary values for station depth (inshore = 0–100 m and offshore >100 m), season (spring = April–May and summer = June–August), presence of the plume (fresh ≤ 28 psu and salty >28 psu), and ocean temperature (cool $\leq 12^\circ\text{C}$ and warm $>12^\circ\text{C}$). There were also three quantitative *in situ* measurements, which included mean SST (1 m), sea surface salinity (SSS), and Chl *a*, collected at 3 m. In addition, there were six quantitative variables that represented monthly values for regional and basin-scale environmental variability and included upwelling intensity, Columbia River discharge, Columbia River plume volume, PDO, NPGO, and MEI. The six categorical variables in the environmental matrix were station depth (inshore/offshore), season (spring/summer), presence of the plume (fresh/salty), ocean temperature (cool/warm), month (April–August), and year (1999–2009).

Statistical analysis

We analysed all catch data (Table 1) using PC-ORD v.6.07 (McCune and Mefford, 2011). As a first step, non-parametric multiresponse permutation procedures (Mielke and Berry, 2001) were used to test the hypothesis of no difference between pelagic communities based on station depth, season, presence of the plume, ocean temperature, month, and year. For this analysis, we used a Sørensen (Bray–Curtis) distance measure. Multiresponse permutation procedures calculate an A-statistic ranging from 0 to 1. The A-statistic is a measure of effect size and reflects within-group homogeneity, with the maximum value (1) indicating complete agreement within a group. The *p*-value represents how likely an observed difference is due to chance based on the effect size (McCune and Grace, 2002). For these tests, statistical significance was determined at the $\alpha = 0.05$ level. For pairwise comparisons between months, the level of significance was adjusted for the number of comparisons ($n = 5$) to the $\alpha = 0.01$ level.

Next, non-metric multidimensional scaling (Kruskal, 1964; McCune and Grace, 2002) was used to ordinate sample units in species space to identify sample unit clusters with similar nekton communities. Non-metric multidimensional scaling has proven useful in analysing marine communities in the Northeast Pacific (e.g. Morgan *et al.*, 2003; Brodeur *et al.*, 2005) and is considered one of the most robust ordination methods for non-normal, zero-truncated data. In non-metric multidimensional scaling, the distance of sampled communities to each other reflects their underlying dissimilarity in multivariate space. The goal is to generate a plot of sample points such that the rank order of the dissimilarity values between all pairs of samples is preserved in the spatial arrangement of points in the final plot: the most dissimilar samples are farthest apart and the most similar samples are closest together. A “stress” value measures the success of the ordination at preserving the relationship between rank orders and plotted distances. In PC-ORD, stress is scaled from 0 to 100 (Mather, 1976) with low stress (2–5) considered an excellent representation of community structure, medium stress (5–20) considered good to fair with no risk of drawing false inferences, and high stress (>20) considered poor and dangerous to interpret (McCune and Grace, 2002). We performed an ordination on the species matrix using the Sørensen (Bray–Curtis) distance measure. Random starting configurations were used for the analysis with 250 runs of real data. Monte Carlo simulations were conducted with an additional 250 runs of randomized data which were then compared with the real data to determine the dimensionality of a final solution. The *p*-values were calculated as the proportion of randomized runs with stress less than or equal to the observed stress. Correlation coefficients (*r*) were used to describe the strength and direction of linear relationships between non-metric multidimensional scaling axis scores and individual species and environmental parameters. This approach provided a method to describe the ordination, but was not used to test the hypotheses of relationships between axis scores and individual species and environmental parameters; thus, *p*-values were not generated (McCune and Grace, 2002). For this analysis, an $r^2 > 0.15$ was considered ecologically meaningful. Finally, the ordination was rotated so that the first axis corresponded to the axis of maximum environmental variability.

To robustly examine the fidelity of individual species to *a priori* groups (station depth, season, presence of the plume, ocean temperature, and year), we performed indicator species analysis (Dufrêne and Legendre, 1997). For this analysis, indicator values were calculated for each species in a group, based on the proportional abundance and frequency of a species in that group, with values ranging from 0 to 100. Indicator values were tested for statistical significance using 4999 runs of a Monte Carlo randomization, and statistical significance determined at the $\alpha = 0.05$ level. Lastly, to assess interannual variability, we plotted the mean annual catch (number km trawled⁻¹) of the most abundant forage fish and predator fish, along with the mean annual values for indices representing large-scale oceanographic variability within the North Pacific Ocean (i.e. PDO, NPGO, and MEI), and tested for linear dependence between each pair using the Pearson correlation coefficient (*r*). For these tests, the level of significance was set at the $\alpha = 0.05$ level.

Results

Species richness was highest in 2002 and 2006 (58 species) and lowest in 2003 and 2005 (45 species; Table 1). Results from multiresponse permutation procedures (Table 2) indicated that differences

Table 1. A list of the 106 pelagic nekton taxa examined in this study.

Scientific name	1999 (109)	2000 (96)	2001 (113)	2002 (112)	2003 (115)	2004 (106)	2005 (118)	2006 (95)	2007 (73)	2008 (59)	2009 (83)
Decapoda (unid.)							0.023	0.460	0.008	0.028	0.092
<i>Pandalus</i> spp. (unid.)		0.172									
<i>Pandalus jordani</i>		10.85	0.005	0.865	0.174					0.375	0.016
Teuthida (unid.)			0.006	0.063		0.014	0.070	0.211	0.028		0.009
<i>Doryteuthis opalescens</i>	4.160	0.330	13.25	20.24	15.59	2.120	5.542	3.664	0.951	0.086	0.173
<i>Onychoteuthis borealijaponica</i>				0.006						0.021	0.227
<i>Ommastrephes bartramii</i>			0.047	0.543	0.018	0.083					
<i>Dosidicus gigas</i>								0.020			9.218
<i>Octopus dofleini</i>					0.011						
<i>Octopus rubescens</i>									0.005		
<i>Lampetra ayresii</i>	0.003									0.019	0.010
<i>Lampetra tridentata</i>	0.012	0.060	0.006	0.034	0.023	0.007	0.025	0.041	0.006	0.030	0.014
<i>Lamna ditropis</i>											0.005
<i>Alopias vulpinus</i>	0.006			0.006				0.007	0.011		0.004
<i>Galeorhinus zyopterus</i>	0.017	0.018	0.008	0.069	0.058	0.041	0.021	0.032	0.053	0.074	0.109
<i>Prionace glauca</i>	0.016		0.005	0.022	0.011	0.060	0.067	0.020		0.014	0.018
<i>Squalus acanthius</i> (juv.)	0.064	0.233	0.313	0.244	0.011	0.217	0.235	0.465	0.214	0.674	0.026
<i>Squalus acanthias</i> (ad.)	0.302	11.13	12.31	0.730	0.305	2.771	0.902	3.638	0.867	0.587	0.146
<i>Raja binoculata</i>	0.040	0.006	0.014	0.010			0.006	0.035		0.021	0.004
<i>Torpedo californica</i>					0.005	0.007					
Osteichthyes (unid.)	0.017			0.006				0.183			0.007
Anguilliformes (unid.)		0.003			0.007						
<i>Alosa sapidissima</i>	0.594	0.086	0.334	1.103	5.155	0.608	0.960	0.431	0.885	1.250	1.118
<i>Clupea pallasii</i>	18.86	154.2	473.9	117.1	295.9	34.49	35.50	16.76	46.38	21.69	31.18
<i>Sardinops sagax</i>	33.65	176.4	225.3	171.6	245.6	76.47	156.2	73.98	138.8	77.50	61.09
<i>Engraulis mordax</i>	4.013	154.1	527.8	634.6	1 100	487.4	618.2	54.21	67.12	69.11	178.1
<i>Oncorhynchus gorboscha</i>			0.020	0.005							
<i>Oncorhynchus keta</i>	0.003	0.034	2.116	0.035	0.028		0.008	0.188	0.145	0.028	0.077
<i>Oncorhynchus kisutch</i>	0.112	0.945	1.061	0.425	0.372	0.356	0.093	0.010	0.395	0.092	0.289
<i>Oncorhynchus nerka</i>			0.020	0.011					0.014		0.005
<i>Oncorhynchus tshawytscha</i>	1.271	2.734	2.467	1.865	2.067	1.311	0.430	0.335	0.468	0.695	1.159
<i>Oncorhynchus clarki</i>			0.019	0.006	0.005				0.012		0.005
<i>Oncorhynchus mykiss</i>	0.003	0.029	0.037	0.023	0.094	0.007	0.017	0.015	0.033	0.007	0.019
Osmeridae (YOY)	0.288	0.174	0.000	0.207				0.821		0.494	0.053
<i>Hypomesus pretiosus</i>	0.031		0.169	0.843	0.323	0.015	0.133		0.020	0.100	0.004
<i>Spirinchus starksi</i>	0.013	0.003	0.033	0.023	0.006		0.006			0.013	
<i>Spirinchus thaleichthys</i>	0.186	0.903	3.967	0.388				1.389	0.132	0.623	0.787
<i>Thaleichthys pacificus</i>	0.100	0.236	0.397	4.495	21.01	1.544			0.039	0.085	0.037
<i>Allosmerus elongatus</i>	2.394	641.7	1 413	507.1	876.3	336.7	87.04	41.261	84.13	49.80	266.4
<i>Bathylagus ochotensis</i>									0.007		
Myctophidae (unid.)		0.066	1.463	0.010			0.655	0.698			
<i>Stenobranchius leucopsarus</i>						0.282		0.178			
<i>Tarletonbeania crenularis</i>								1.046		0.111	0.279
<i>Gadus macrocephalus</i>							0.005	0.009			
<i>Microgadus proximus</i> (YOY)	2.753	5.200	1.154	8.454	0.272	0.097		0.008	0.863	1.171	40.40
<i>Merluccius productus</i> (YOY)						3.011	0.291	113.2	0.251	0.290	0.018
<i>Merluccius productus</i> (juv.)	0.170					0.008	7.485	0.107	1 046	6.877	108.8
<i>Merluccius productus</i> (ad.)	6.988	0.547	1.574	12.06	39.53	46.17	6.700	5.263	3.195	0.878	0.817
<i>Porichthys notatus</i>	0.080		0.017		0.025	0.000		0.036	0.015		0.069
<i>Cololabis saira</i>				0.005						0.008	0.012
Trachipteridae (unid.)							0.008				
<i>Trachipterus altivelis</i>							0.039	0.016			
<i>Gasterosteus aculeatus</i>		0.003		0.081			0.014	0.030			0.004
<i>Sebastes</i> spp. (YOY)	0.043	0.218	0.018	0.356	0.165	1.178	1.598	2.761	0.169	1.944	0.143
<i>Sebastes alutus</i> (YOY)						2.266					
<i>Sebastes crameri</i> (YOY)		0.206			0.063	0.052					
<i>Sebastes entomelas</i> (YOY)		0.006									
<i>Sebastes flavidus</i> (YOY)						0.216					
<i>Sebastes flavidus</i> (ad.)	0.003		0.003							0.006	

Continued

Table 1. Continued

Scientific name	1999 (109)	2000 (96)	2001 (113)	2002 (112)	2003 (115)	2004 (106)	2005 (118)	2006 (95)	2007 (73)	2008 (59)	2009 (83)
<i>Sebastes jordani</i> (YOY)						0.736					
<i>Sebastes melanops</i> (YOY)	0.099	0.717		0.020	0.006	0.007					
<i>Sebastes melanops</i> (ad.)	0.020	0.006	0.018	0.008	0.006		0.014		0.059		
<i>Sebastes pinniger</i> (YOY)						0.029					
<i>Sebastes saxicola</i> (YOY)						0.043					
<i>Anoplopoma fimbria</i>	0.008	0.127		0.146	0.006	0.109	0.020	0.064		0.130	
Hexagrammidae (YOY)										0.007	
Hexagrammidae (juv.)			0.005								
<i>Ophiodon elongatus</i> (YOY)		0.003	0.000	0.012		0.007			0.124	0.769	0.084
<i>Ophiodon elongatus</i> (ad.)			0.005					0.010			
Cottidae (unid.)											0.013
<i>Leptocottus armatus</i>	0.011	0.007	0.040	0.005	0.018	0.016		0.025	0.101	0.077	0.021
<i>Hemilepidotus spinosus</i>			0.003								
Agonidae (unid.)			0.007	0.005			0.037	0.018	0.010		
<i>Bathyagonus</i> spp. (unid.)				0.006							
<i>Agonopsis vulsa</i>					0.009	0.007		0.010			
<i>Ocella verrucosa</i>			0.006	0.011	0.006			0.021	0.020	0.077	0.040
<i>Liparis</i> spp. (unid.)	0.002		0.006							0.009	0.004
<i>Aptocyclus ventricosus</i>			0.013								
<i>Trachurus symmetricus</i>	5.696	3.350	7.928	2.199	1.499	1.391	0.358	0.267	0.715	0.042	0.409
<i>Cymatogaster aggregate</i>											0.004
<i>Trichodon trichodon</i>				0.005	0.010	0.005		0.009			
<i>Pholis ornate</i>								0.008			
<i>Anarrhichthys ocellatus</i>	0.033	0.032	0.029	0.011	0.016	0.022	0.007	0.018		0.013	0.012
<i>Ammodytes hexapterus</i> (YOY)	0.014	0.011		0.062							
<i>Scomber japonicas</i>	1.900	0.673	2.251	0.034	1.109	0.141	1.065	2.441	5.405	0.163	0.191
<i>Peprilus simillimus</i>			0.018	0.730	0.011	0.054	0.056	0.025			
<i>Icichthys lockingtoni</i>							0.020	0.017			0.005
<i>Icosteus aenigmaticus</i>	0.002						0.008	0.010			
Pleuronectiformes (YOY)		0.154	0.003	0.023	0.007		0.354	0.043		0.028	0.012
Bothidae (unid.)		0.016		0.005					0.006		
<i>Citharichthys</i> spp. (YOY)			0.054								
<i>Citharichthys sordidus</i>	0.717	0.849	10.23	4.546	28.88	2.683	1.803	4.689	4.481	0.669	3.320
<i>Citharichthys stigmaeus</i>				0.017					0.006		
Pleuronectidae (unid.)		0.008	0.003	0.008							0.005
<i>Glyptocephalus zachirus</i> (YOY)		0.547	0.014	0.063		0.007	0.059	0.366	0.005		
<i>Glyptocephalus zachirus</i> (ad.)	0.006										
<i>Hippoglossoides elassodon</i>							0.007				
<i>Isopsetta isolepis</i>	0.025	0.005	0.008								
<i>Lyopsetta exilis</i> (YOY)		0.032							0.008		
<i>Lyopsetta exilis</i> (ad.)	0.008		0.006					0.065	0.009		
<i>Microstomus pacificus</i>			0.004		0.015			0.086	0.016		0.005
<i>Parophrys vetulus</i>	0.022	0.006			0.012	0.014	0.007	0.009	0.040	0.006	
<i>Platichthys stellatus</i>	0.399	0.113	0.715	0.415	0.172	0.049	0.022	0.042	0.044	0.422	0.037
<i>Pleuronichthys ceanosus</i>						0.037					
<i>Psettichthys melanostictus</i>	0.002	0.003	0.008	0.005				0.009		0.044	
<i>Mola mola</i>							0.020	0.010	0.011		0.006
Total Number of Species	47	48	55	58	45	46	45	58	47	47	56

Values given are annual mean catch (number per km trawled). The numbers in parentheses are the number of valid hauls per year. The abbreviations stand for unidentified (unid.), young-of-the-year (YOY), juvenile (juv.), and adult (ad.).

in the pelagic nekton community were related to many factors: station depth, season, presence of the plume, ocean temperature, month, and year (all with A-statistic > 0.03 and $p < 0.01$). Pairwise comparisons of individual months (Table 2) revealed that there was no difference in the pelagic community between April and May over the entire sampling period or between June and July, June and August, or July and August (all with

A-statistic < 0.02 and $p > 0.01$). Similarity in community structure determined by pairwise comparisons between months justified combining months into two seasons (spring = April–May and summer = June–August) for all further analyses.

The non-metric multidimensional scaling ordination that best described this dataset had a three-dimensional ordination, Monte Carlo $p = 0.020$, and medium stress (14.9), which we considered

Table 2. Results of multiresponse permutation procedures testing for community differences in the following sample unit groups: station depth (inshore = 0–100 m and offshore > 100 m), season (spring = April–May and summer = June–August), presence of the plume (fresh = salinity \leq 28 psu and salty = salinity > 28 psu), ocean temperature (cool \leq 12°C and warm > 12°C), year (1998–2009), and month (April–August).

Factor	Pairwise	A-Statistic	p-value
Depth (inshore/offshore)		0.085	<0.001
Season (spring/summer)		0.060	<0.001
Presence of the plume (fresh/salty)		0.032	<0.001
Ocean temperature (cool/warm)		0.031	<0.001
Year (1999–2009)		0.084	<0.001
Month (April–August)		0.073	<0.001
	April–May	0.018	0.016
	April–June	0.089	<0.001
	April–July	0.119	<0.001
	April–August	0.093	<0.001
	May–June	0.037	<0.001
	May–July	0.064	<0.001
	May–August	0.057	<0.001
	June–July	<0.001	0.362
	June–August	0.017	0.020
	July–August	0.010	0.090

Pairwise comparisons between months in bold differ significantly from each other (level of significance = 0.010).

to be fair but interpretable and typical of ecological community data (Kruskal, 1964). The final instability was <0.001 and based on a final solution resulting from 131 iterations. The ordination represented 86.3% of the variation in pelagic nekton community structure. In the ordination shown, axis 1 represented 34.8%, axis 2 represented 37.8%, and axis 3 represented 13.7% of the variation (Figure 2). The strongest environmental variables associated with differences in pelagic nekton community structure for this solution were station depth, season, presence of the plume, ocean temperature, *in situ* SST, Columbia River plume volume, upwelling intensity, and *in situ* SSS (Table 3). Axis 1 was negatively associated with inshore stations (0–100 m depth) and positively associated with offshore stations (>100 m depth) and higher values of *in situ* SST. Axis 2 was positively associated with stations sampled in spring (April–May), when the plume was present (SSS \leq 28 psu), ocean temperatures cool (SST \leq 12°C), and Columbia River plume volume values were highest (mean = 1.92×10^{10} m³). Axis 2 was negatively associated with stations sampled in summer (June–August), during warm (SST > 12°C), salty (SSS > 28 psu), and upwelling conditions. No environmental variables were associated with axis 3 at the level of $r^2 > 0.15$, but axis 3 was negatively associated with piscivorous fish and positively associated with forage fish (Figure 2, Table 4). Neither Chl *a*, Columbia River flow, nor the basin-wide environmental variables (i.e. PDO, NPGO, or MEI) were correlated with any of the axes at $r^2 > 0.15$.

There were 17 species strongly associated with the environmental gradients based on their correlations with the distance matrix (Figure 2, Table 4). Species negatively associated with axis 1 (the inshore group) were whitebait smelt (*Allosmerus elongatus*), Pacific sanddab (*Citharichthys sordidus*), juvenile spiny dogfish, Pacific herring, starry flounder (*Platichthys stellatus*), longfin smelt (*Spirinchus thaleichthys*), juvenile Chinook salmon (*Oncorhynchus tshawytscha*), and California market squid. Whitebait smelt and

Pacific herring were also positively associated with axis 2 (the spring group during cool, fresh conditions, when plume volume was greatest). Species positively associated with axis 1 (the offshore group with high SST) were blue shark (*Prionace glauca*) and jack mackerel. Jack mackerel was also negatively associated with axis 2 (the summer group during warm, salty, upwelling conditions), along with Pacific sardine, Pacific mackerel, juvenile Pacific hake, soupfin shark (*Galeorhinus zyopterus*), and Pacific hake YOY. Species negatively associated with axis 3 (the predator group) were adult jack mackerel, Pacific mackerel, and Pacific hake. The only species positively associated with axis 3 (the forage fish group) was northern anchovy.

There was good agreement between indicator species determined from *a priori* categorical groupings (inshore/offshore, spring/summer, fresh/salty, and cool/warm) using indicator species analysis (Figure 3) and individual species correlations with environmental variables determined by non-metric multidimensional scaling (Figure 2; Table 4). In all, 20 species were identified as significant ($p < 0.05$) inshore indicators and included the eight species negatively correlated with axis 1 (the inshore group) from non-metric multidimensional scaling analysis. There were also 11 species identified as significant offshore indicator species and included the two species (blue shark and jack mackerel) positively correlated with axis 1 (the offshore group with high SST). In contrast, six species were identified as significant spring indicator species, and 15 species significant summer indicator species. In the ordination, Pacific herring and whitebait smelt were positively associated with axis 2 (the spring group during cool, fresh conditions, when plume volume was greatest), but only whitebait smelt was included as a significant spring indicator species using indicator species analysis. However, four of the five significant freshwater indicator species [whitebait smelt, lingcod YOY (*Ophiodon elongatus*), surf smelt (*Hypomesus pretiosus*), and juvenile Chinook salmon] were also significant spring indicators. The six species negatively correlated with axis 2 (the summer group during warm, salty, upwelling conditions), which included soupfin shark, Pacific mackerel, jack mackerel, Pacific hake (juvenile and YOY), and Pacific sardine, were all individually classified as significant summer indicator species, warm water indicator species, and saltwater indicator species. The only exception was juvenile hake, which was not a warm water indicator species.

Pelagic nekton identified as indicators for individual years (Table 5) included anomalous species not usually encountered in the Northeast Pacific. For example, the predator Humboldt squid, which appeared in the northern California Current following the 1997 *El Niño* (Pearcy, 2002) and occurred in high abundance during summer 2009 (Litz *et al.*, 2011), was identified as a significant ($p > 0.05$) indicator in 2009. Pelagic nekton identified as indicators for year also included YOY species during years of exceptional recruitment. For example, the northern shift in spawning distribution by Pacific hake described by Phillips *et al.* (2007) was confirmed by indicator species analysis, with Pacific hake identified as a significant indicator species in 2004 (adult), 2006 (YOY), and 2007 (juvenile).

Many species and environmental factors varied annually throughout the study (Figure 4). There were cool *La Niña* conditions prevalent during 1999 and in 2007 through 2008, followed by a warm *El Niño* period in 2009. There was also a weak *El Niño* during 2004, whereas 2005 was characterized by delayed upwelling conditions, which was unrelated to *El Niño*. The Columbia River flow rate during the sampling period in 2001 ($4073 \text{ m}^3 \text{ s}^{-1}$) was about half what it averaged in other years. Annual values for MEI and PDO

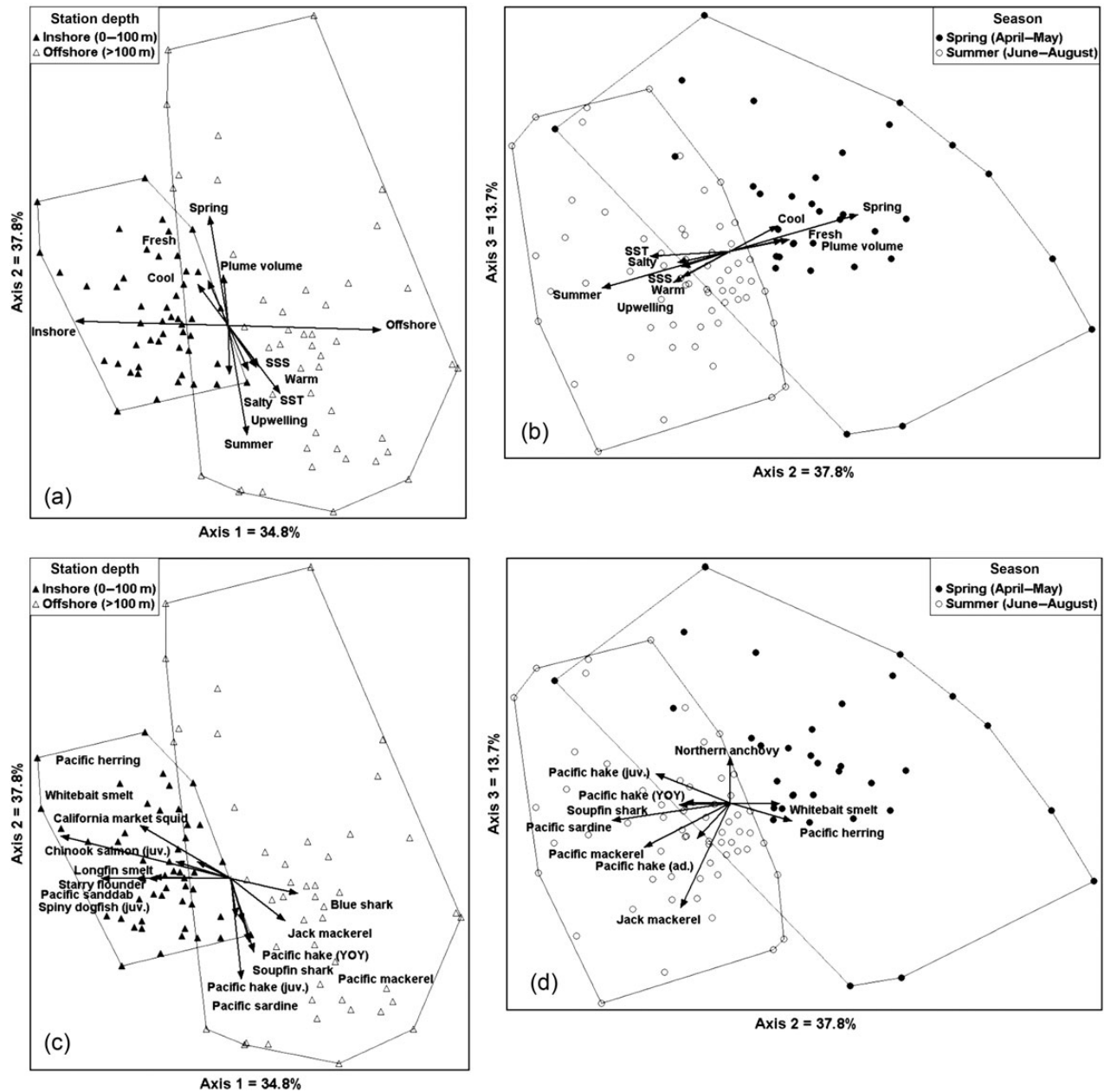


Figure 2. Results of non-metric multidimensional scaling analysis where each point represents the log-transformed catch (number km trawled⁻¹) of pelagic nekton sampled either inshore (0–100 m) or offshore (>100 m) by month (April–August) and year (1998–2009) plotted in species space. Top plots show joint plots of environmental variables (cut-off $r^2 = 0.15$ for inclusion) for axes 1–2 (a) and axes 2–3 (b). The bottom plots show joint plots of species (cut-off $r^2 = 0.15$ for inclusion) for axes 1–2 (c) and axes 2–3 (d). The length of each joint plot line is proportional to the strength of the correlation. Symbols are based on categorical groupings for station depth (inshore 0–100 m, denoted by a filled triangle, and offshore >100 m, denoted by an open triangle); or season (spring = April–May, denoted by a filled circle, and summer = June–August, denoted by an open circle). Abbreviations for environmental variables are SST (1 m) and SSS. Abbreviations for species are adult (ad.), juvenile (juv.), and young-of-the-year (YOY).

during our study period were positively correlated with each other ($r = 0.81$, $p = 0.03$), and both MEI and PDO were negatively correlated with NPGO, but not significantly. Northern anchovy and Pacific hake were both positively correlated with PDO ($r = 0.76$ for anchovy and 0.67 for hake, both with $p < 0.05$), and northern anchovy was also correlated with MEI ($r = 0.64$, $p = 0.03$). However, of the most abundant species, only jack mackerel was significantly correlated with NPGO ($r = 0.62$, $p = 0.41$).

Discussion

We compared the community structure of pelagic nekton, including forage fish and piscivorous predators, over 11 years of sampling along the continental shelf associated with the Columbia River plume. Our results show distinct inshore/offshore and spring/summer forage fish and predator fish communities, but also an overall high level of annual variability. Forage fish (smelts, northern anchovy, Pacific herring, California market squid, and juvenile

Table 3. Pearson's correlation coefficients *r* between non-metric multidimensional scaling ordination axes and quantitative environmental variables correlated with one or more axes (correlations with $r^2 > 0.15$ in bold).

Factor	Axis 1	Axis 2	Axis 3
Depth (inshore/offshore)	-0.784/0.784	0.134/-0.134	-0.166/0.166
Season (spring/summer)	-0.274/0.274	0.665/-0.665	0.355/-0.355
Presence of the plume (fresh/salty)	-0.282/0.282	0.425/-0.425	0.197/-0.197
Ocean temperature (cool/warm)	-0.351/0.351	0.406/-0.406	0.296/-0.296
Sea surface temperature (SST)	0.457	-0.525	-0.130
Plume volume	-0.143	0.453	0.205
Upwelling intensity	0.066	-0.442	-0.328
SSS	0.335	-0.410	-0.233

Table 4. Pearson's correlation coefficients *r* between non-metric multidimensional scaling ordination axes and species correlated with one or more axes (correlations with $r^2 > 0.15$ in bold).

Common name	Scientific name	Axis 1	Axis 2	Axis 3
Blue shark	<i>Prionace glauca</i>	0.517	-0.253	-0.177
California market squid	<i>Doryteuthis opalescens</i>	-0.366	0.267	-0.189
Chinook salmon	<i>Oncorhynchus tshawytscha</i>	-0.469	0.269	-0.071
Pacific mackerel	<i>Scomber japonicus</i>	0.298	-0.548	-0.392
Jack mackerel	<i>Trachurus symmetricus</i>	0.463	-0.419	-0.602
Longfin smelt	<i>Spirinchus thaleichthys</i>	-0.560	0.085	0.101
Northern anchovy	<i>Engraulis mordax</i>	-0.166	-0.008	0.400
Pacific hake (YOY)	<i>Merluccius productus</i>	0.143	-0.393	0.050
Pacific hake (juv.)	<i>Merluccius productus</i>	0.267	-0.509	-0.248
Pacific hake (ad.)	<i>Merluccius productus</i>	0.251	-0.342	-0.351
Pacific herring	<i>Clupea pallasii</i>	-0.600	0.470	-0.248
Pacific sanddab	<i>Citharichthys sordidus</i>	-0.726	-0.008	-0.134
Pacific sardine	<i>Sardinops sagax</i>	0.194	-0.637	-0.244
Southern shark	<i>Galeorhinus zyopterus</i>	0.220	-0.422	-0.081
Spiny dogfish (juv.)	<i>Squalus acanthias</i>	-0.620	0.003	-0.195
Starry flounder	<i>Platichthys stellatus</i>	-0.577	0.038	-0.256
Whitebait smelt	<i>Allosmerus elongatus</i>	-0.824	0.425	-0.035

Abbreviations for distinct age classes are as follows: young-of-the-year (YOY), juvenile (juv.), and adult (ad.).

salmon) were more frequently captured inshore (≤ 100 m depth) during spring (April–May), within the low-salinity plume (≤ 28 psu) where ocean temperatures were cool ($\leq 12^\circ\text{C}$). Predatory migratory fish (Pacific hake, jack mackerel, Pacific mackerel, and sharks) were generally absent in spring, but were caught primarily offshore (> 100 m depth) in summer during upwelling, where ocean salinities were high (> 28 psu) and temperatures

warm ($> 12^\circ\text{C}$). There were notable exceptions: spiny dogfish co-occurred with resident forage fish as part of the inshore, fresh, cool, spring community, whereas Pacific sardine (a forage fish) co-occurred with piscivorous, migratory coastal pelagics as part of the offshore, salty, warm, summer community. Overall, there appeared to be strong spatial and temporal distinctions between resident forage fish and migratory predator fish assemblages, suggesting that the Columbia River plume is a refuge for forage fish from predation. This finding was supported by a diet study (Emmett and Krutzikowsky, 2008) which found Pacific hake and jack mackerel predation rates on forage fish to be low compared with other plume systems. In contrast, high predation rates on juvenile salmon and herring by spiny dogfish, Pacific hake, and lamprey associated with the Fraser River plume in Canada led researchers to reject the notion of the plume as a refuge from predation (St John *et al.*, 1992). Expanding our knowledge of interactions between forage fish and their predators within other large plume systems seems a worthwhile goal.

Throughout the Pacific, populations of anchovy and sardine oscillate out of phase with each other over decadal periods (Chavez *et al.*, 2003). These so-called biological regime shifts are associated with large-scale changes in ocean temperature and primary productivity. It has been hypothesized that population oscillations occur because sardine and anchovy exploit their environments differently, based on differences in gillraker morphology (Van der Lingen *et al.*, 2006). These differences can influence habitat utilization, foraging success, and population sizes, particularly during periods of poor productivity, when it is thought that sardine benefit from the phytoplankton assemblages that bloom offshore in response to wind stress curl upwelling (Rybczewski and Checkley, 2008). The northern anchovy population in our study area has an inshore distribution and does not migrate (Litz *et al.*, 2008). Moreover, strong evidence shows that this species utilizes the frontal zone of the Columbia River plume to spawn (Richardson, 1973). Results of our study provide support for separate foraging habitats for Pacific sardine and northern anchovy with Pacific sardine co-occurring with highly migratory coastal pelagic species offshore and northern anchovy co-occurring with other forage fish inshore. Curiously, abundance patterns of anchovy and sardine in our study region appeared to be synchronous (Figure 4), suggesting that other mechanisms may be regulating population sizes.

Forage fish and predators may utilize different habitats associated with the Columbia River plume for several reasons. For one, forage fish are euryhaline compared with larger fish predators, and as year-long residents, also appear to be more tolerant of lower temperatures (Moyle and Davis, 2000). Thermal tolerance of lower temperatures and the ability to osmoregulate at lower salinities (Burger and Hess, 1960) may also explain why piscivorous spiny dogfish co-occurred inshore, within the cool, fresh plume environment along with most forage fish species. High catches of juvenile forage fish and spiny dogfish indicated that the plume may be an important spawning area in spring (Richardson, 1973; Emmett *et al.*, 2006). Second, in a laboratory study, De Robertis *et al.* (2003) showed that turbid environments, like those characteristic of the Columbia River plume, may be advantageous for planktivorous forage fish because they are less vulnerable to predation in this habitat, but do not experience a substantial decrease in feeding efficiency. However, neither that laboratory study nor our study considered the influence of other predators within the Columbia River plume, like seabirds or marine mammals. The influence of

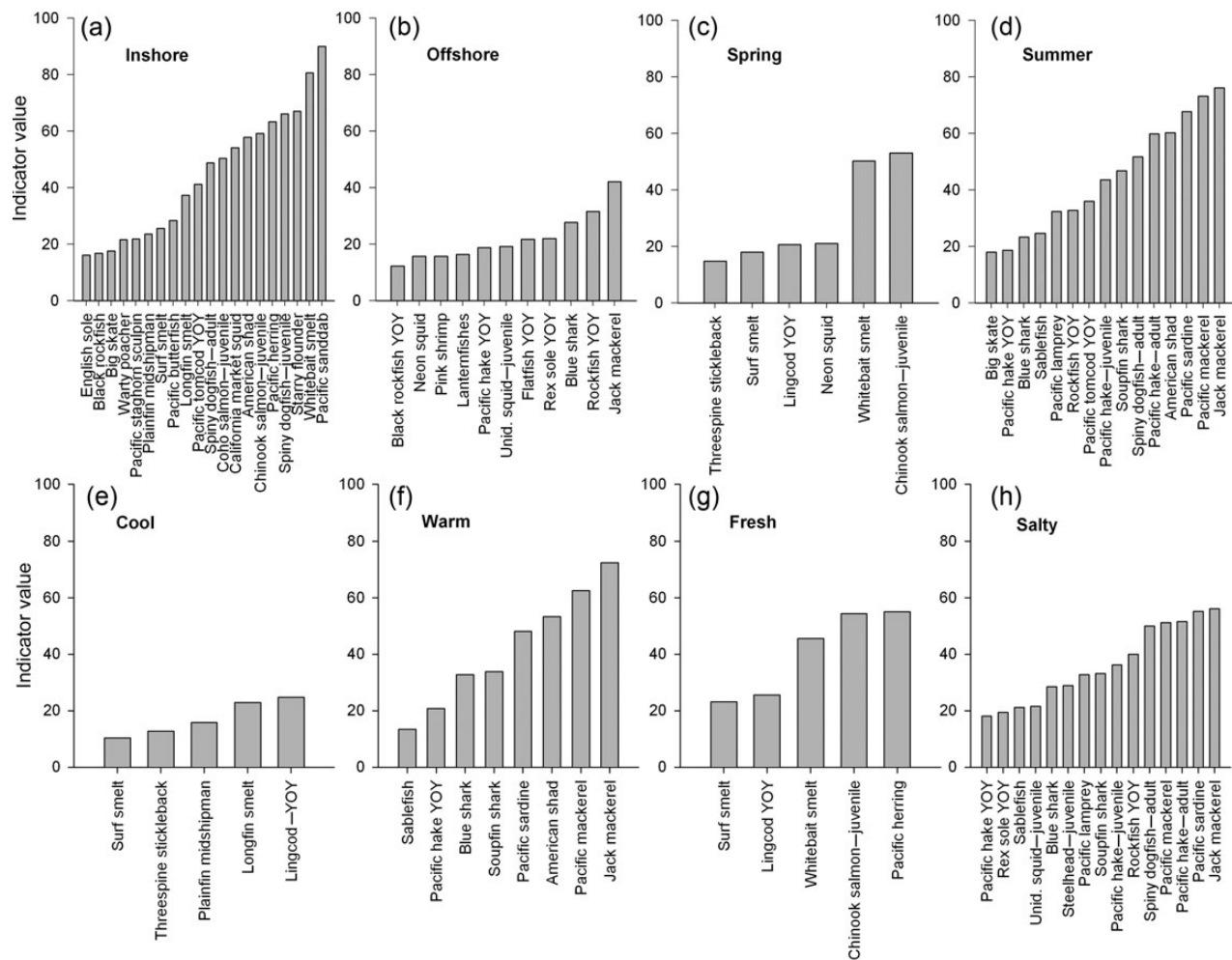


Figure 3. Paired plots showing significant ($p < 0.05$) indicator values in increasing order for pelagic nekton species identified as either (A) inshore (station depth 0–100 m) or (b) offshore (station depth ≤ 100 m), (c) spring (April–May) or (d) summer (June–August), (e) cool (1 m ocean temperature $\leq 12^\circ\text{C}$) or (f) warm (1 m surface water temperature $> 12^\circ\text{C}$), or (g) fresh (1 m water salinity ≤ 28 psu) or (h) salty (1 m surface water salinity > 28 psu) indicator species determined by indicator species analysis. Species that are 0-age are listed as YOY. Unidentified species are abbreviated as unid.

seabird predation on forage fish and juvenile salmon populations in the Columbia River plume can be quite large (Roby *et al.*, 2002).

Hypothesized causes for variability in forage fish year-class success in and around the Columbia River plume include changes in food availability (De Robertis *et al.*, 2005), predation (Emmett and Krutzikowsky, 2008), and advection during early life stages (Auth, 2011). Offshore advection due to high river flow probably contributed to the identification of five YOY species as offshore indicators using indicator species analysis (Figure 3b), including rockfish (*Sebastes* spp.), Pacific hake, rex sole (*Glyptocephalus zachirus*), and other unidentified YOY flatfish (Pleuronectiformes); these fish only spend a short phase as juveniles in the pelagic zone (typically in spring); thus, they are susceptible to offshore transportation by the plume and by coastal upwelling in spring when Columbia River flows are greatest. During our study period, Auth (2011) consistently found higher concentrations of all dominant taxa and total larvae in the offshore Columbia River plume region compared with the inshore plume.

Several environmental variables were weakly ($r^2 < 0.15$) associated with non-metric multidimensional scaling ordination

scores, including Columbia River flow, Chl *a*, and the basin-scale indices of oceanographic conditions (i.e. PDO, NPGO, and MEI). This was very surprising for several reasons. First, we were surprised that Columbia River flow was not correlated with pelagic community structure because the Columbia River plume volume and the presence of the plume both appeared to be related to community differences in our non-metric multidimensional scaling analysis (Figure 2, Table 3) and because the Columbia River flow has been hypothesized as a transport mechanism that influences larval fish distributions in the study area (Parnel *et al.*, 2008; Auth, 2011). Moreover, variations in flow were shown to account for more than 40% of the variation in plume volume (Burla *et al.*, 2010a). Clearly, more work needs to be done evaluating how mesoscale processes, like tidal exchange, wind stress, upwelling jets, and currents, influence Columbia River plume dynamics both horizontally and vertically (e.g. Banas *et al.*, 2009; Hickey *et al.*, 2009; Burla *et al.*, 2010a). By understanding the physical processes, we will better understand the mechanisms by which plume volume influences biological community structure. It would also be useful to examine all the connections between plume dynamics and

Table 5. Pelagic nekton species identified as significant ($p < 0.05$) annual indicators for pelagic nekton catches 1999–2009 associated with the Columbia River plume according to indicator species analysis.

Year	Common name	Scientific name	FO	IV	p-value
2001	Pink salmon	<i>Oncorhynchus gorbuscha</i>	0.03	26.5	0.009
2002	California market squid	<i>Doryteuthis opalescens</i>	0.59	14.9	0.007
2003	Eulachon	<i>Thaleichthys pacificus</i>	0.33	30.5	<0.001
	Giant Pacific octopus (juv.)	<i>Octopus dofleini</i>	0.02	25.0	0.041
	Pacific herring	<i>Clupea pallasii</i>	0.81	11.9	0.010
2004	Pacific hake (ad.)	<i>Merluccius productus</i>	0.43	14.3	0.030
	Northern anchovy	<i>Engraulis mordax</i>	0.81	12.4	0.017
2006	Pacific hake (YOY)	<i>Merluccius productus</i>	0.33	22.9	0.010
	Dover sole	<i>Microstomus pacificus</i>	0.11	22.2	0.009
	Squid (unid. juv.)	Teuthida	0.10	20.2	0.013
	Rex sole (YOY)	<i>Glyptocephalus zachirus zachirus</i>	0.15	19.8	0.021
	Pacific sanddab	<i>Citharichthys sordidus</i>	0.36	15.9	0.045
2007	Pacific hake (juv.)	<i>Merluccius productus</i>	0.41	38.1	0.002
2008	Lingcod (YOY)	<i>Ophiodon elongatus</i>	0.12	31.0	0.001
	Pacific staghorn sculpin	<i>Leptocottus armatus</i>	0.12	17.9	0.027
	Pacific tomcod (YOY)	<i>Microgadus proximus</i>	0.34	16.7	0.048
2009	Humboldt squid	<i>Dosidicus gigas</i>	0.13	31.9	0.004
	Clubhook squid	<i>Onychoteuthis borealijaponica</i>	0.06	24.6	0.010

Annual frequency of occurrence (FO) scaled from 0 to 1 for each species is displayed in decreasing order of the indicator value (IV). Abbreviations for distinct age classes are as follows: unidentified (unid.), young-of-the-year (YOY), juvenile (juv.), and adult (ad.).

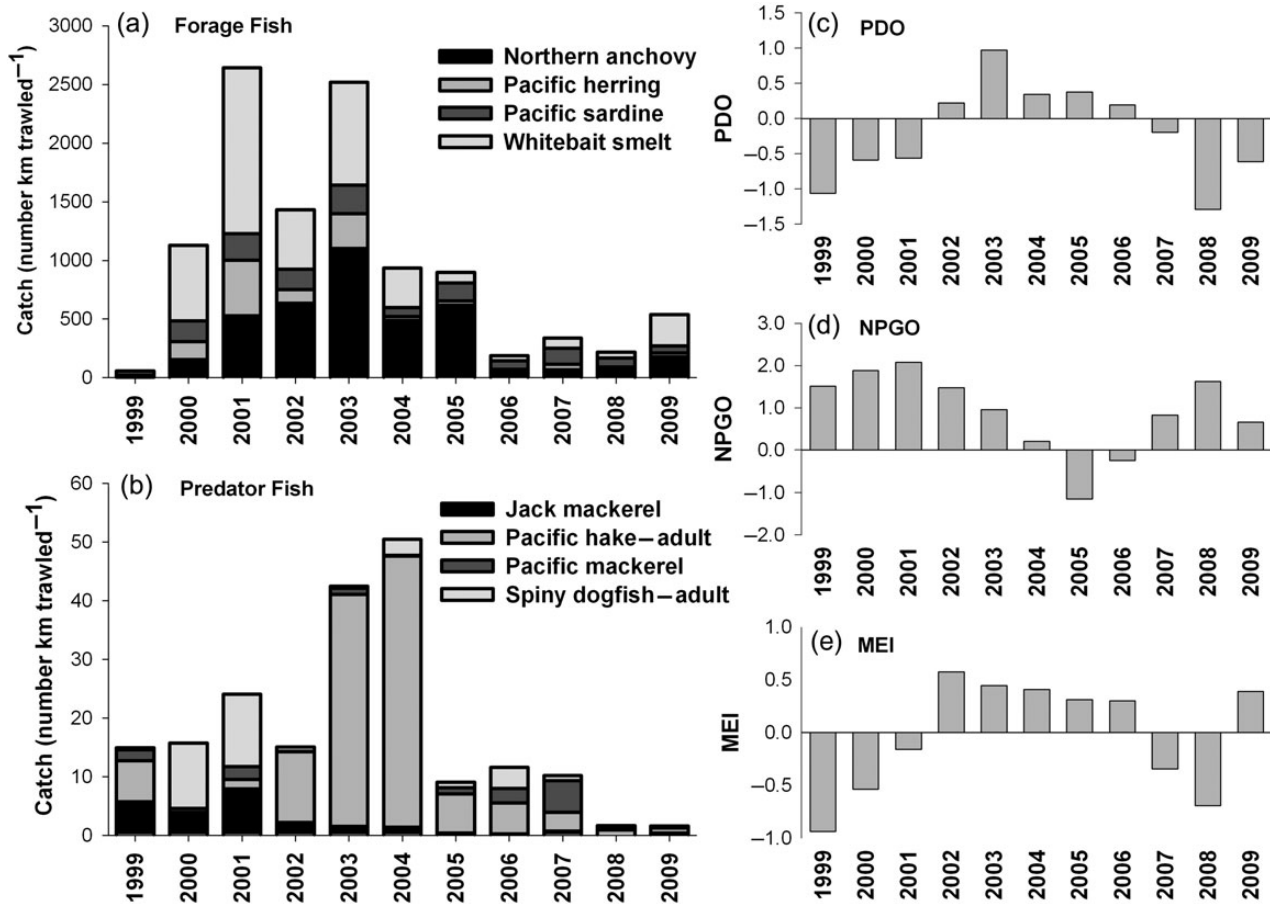


Figure 4. Annual mean catch (number km trawled⁻¹) for the most abundant (a) forage fish and (b) predator fish during night-time sampling of pelagic nekton off the Columbia River 1999–2009 during the upwelling season (April–August). Also shown are the mean annual values for the following large-scale oceanographic indices during our study period: (c) the PDO index, (d) the North Pacific Gyre Oscillation (NPGO) index, and (e) the Multivariate *El Niño* Southern Oscillation index (MEI).

primary productivity (e.g. Kudela *et al.*, 2010), zooplankton aggregations (e.g. De Robertis *et al.*, 2005; Morgan *et al.*, 2005; Peterson and Peterson, 2008), and planktivorous fish distributions (e.g. Emmett *et al.*, 2006).

Second, we were surprised that Chl *a* was not correlated with pelagic community structure, mainly because forage fish are planktivorous. We expected patterns in Chl *a* to be correlated with forage fish abundance. Interestingly, Parnel *et al.* (2008) found that Chl *a* did not provide explanatory power for variations in ichthyoplankton species composition associated with the Columbia River plume using the same Chl *a* dataset. This lack of association may be driven by lag times needed between primary production and zooplankton populations. However, we did not have zooplankton samples from each station to test this hypothesis. It is also possible that the location of our Chl *a* sample stations were inadequate to measure the patchiness of phytoplankton resources within the plume. Finer-scaled sampling or remotely sensed phytoplankton data could resolve this problem.

Third, we were surprised that none of the basin-scale variables were related to pelagic community structure over our study period, particularly given the large annual variability in forage fish and predator fish abundance observed (Figure 4), as well as significant correlations between annual catch values and PDO, NPGO, and MEI. These large-scale oceanographic indices have been shown to capture variability in phytoplankton (Di Lorenzo *et al.*, 2008), zooplankton (Peterson and Schwing, 2003), forage fish (Chavez *et al.*, 2003), and salmon populations (Mantua *et al.*, 1997) throughout the Northeast Pacific. However, the Columbia River plume is a unique environment, and as we suspected, the pelagic community responded to local and regional environmental differences more than to basin-wide oceanographic variability. The lack of association between pelagic nekton and basin-scale environmental variables may be a reflection of the scale that the community was evaluated. Age structure of the forage fish may also have complicated the analysis, as there are lag times between large-scale oceanographic forcing and forage fish recruitment (e.g. Litz *et al.*, 2008). Future analysis of forage fish communities may want to consider age structure as another parameter.

Forage fish are important prey for a wide suite of marine predators (Pikitch *et al.*, 2012). In addition, forage fish might serve as an alternative prey for predators that would otherwise consume juvenile salmon during their ocean migration (Pearcy, 1992; Weitkamp *et al.*, 2012). Over 95% of the salmon we captured were juveniles, and they were associated with forage fish in spring when ocean temperatures were cool ($\leq 12^{\circ}\text{C}$) and salinities fresh (≤ 28 psu). In particular, juvenile Chinook salmon were most strongly associated with California market squid, Pacific herring, whitebait smelt, and longfin smelt in the inshore environment (Figure 2c, Table 4). This suggests that increased abundances of these forage fish species within the Columbia River plume may mitigate the effects of predation on salmon smolts and lead to higher rates of marine survival. However, this finding may only be limited to Chinook and coho (*O. kisutch*) salmon, as juvenile steelhead (*O. mykiss*) was a significant saltwater indicator species ($p < 0.05$, Figure 4h). In a study on steelhead survival, Burla *et al.* (2010b) found that steelhead benefited from the Columbia River plume environment at a narrow window during their ocean entry and speculated that they did so by utilizing the plume to move quickly away from coastal habitats.

In conclusion, the results of this study show strong inshore–offshore, seasonal, temperature, salinity, and upwelling-driven

gradients in pelagic nekton community structure associated with the Columbia River plume. The Columbia River plume is a productive habitat for many commercially important species and is characterized by highly dynamic physical and biological conditions operating on various spatio-temporal scales. Our research indicates that forage fish and predator fish utilize significantly different habitats associated with the Columbia River plume and supports the hypothesis that the plume acts as a refuge for forage fish from predation. However, since the maximum depth of the plume determined by CTD casts during our study period was 16 m, better understanding of the spatial extent of the plume is needed. We recommend that future work on pelagic nekton and river plumes should focus on the associations between vertical and horizontal plume structure and forage fish distributions, age structure, and spawning success, with particular emphasis on coordinated zooplankton and forage fish collections.

Acknowledgements

We would like to thank all the field staff, especially G. Krutzikowsky, C. Johnson, and P. Peterson, for their assistance collecting data for this study. We would also like to thank C. Morgan for help creating and managing the catch database and for processing data used to create the maps. A. Baptista provided helpful information on the “Virtual Columbia River” modelling system (<http://www.stccmop.org/datamart/virtualcolumbiariver>), and B. McCune provided valuable statistical advice. This work would not have been possible without the tremendous knowledge and expertise of the captains and crew of the chartered fishing vessels used for this study. The authors are grateful to L. Weitkamp, J. Peterson, T. Auth, and two anonymous reviewers whose comments on earlier drafts made this a stronger paper. Conversations with J. Miller and T. Hurst were particularly insightful. The study was supported by NOAA Fisheries, Oregon State University Cooperative Institute for Marine Resources Studies (CIMRS), and a Mamie Markham Research Scholarship.

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Handling editor: Marta Coll