

The Influence of Environmental Variation on the Columbia River Estuarine Fish Community: Implications for Predation on Juvenile Salmonids

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Abstract: Predation is often assumed to be the ultimate cause of mortality for juvenile salmonids in marine waters, but the specific biological or physical factors that influence predation are poorly understood. The Columbia River estuary is a useful model ecosystem to understand the relationship between avian predators, alternative prey, environmental variation, and predation on juvenile Pacific salmonids (*Oncorhynchus* spp.). Here, we explore the influence of a suite of local and ocean basin-scale environmental variables on the composition and abundance of the estuarine fish assemblage, an important determinant of avian predation on juvenile salmon in the Columbia River estuary. Multivariate analyses indicated that variables representing both freshwater (river flow) and marine (ocean temperature, upwelling, plume volume) conditions explained up to half of the variation in the fish assemblage. Many of the same environmental variables were related to the abundances of individual fish species. Our results also suggest that the estuarine fish assemblage in the future will be quite different from the current one, with likely repercussions for predator-prey interactions. Our results from estuarine habitats provide a useful model for understanding the dynamics of predation in marine habitats, which are much more logistically difficult to study.

Keywords: Pacific salmon, avian predation, environmental variation, Columbia River estuary

INTRODUCTION

Our understanding of the marine ecology of juvenile Pacific salmon (*Oncorhynchus* spp.) and steelhead (*O. mykiss*; hereafter collectively referred to as “salmon”) has greatly increased over the last two decades as a result of systematic sampling and study of salmon in coastal ecosystems from California to Alaska (Grimes et al. 2007). This large research effort has resulted in improved understanding of the distribution and migration patterns (e.g., Tucker et al. 2009, 2011; Fisher et al. 2014; Teel et al. 2015), diets (e.g., Brodeur et al. 2007; Daly et al. 2009), and habitat requirements (e.g., Bi et al. 2008; Peterson et al. 2010) of juvenile salmon. Despite these advances, however, one aspect of the marine ecology of juvenile salmon, predation, remains poorly understood (Percy 1992; Percy and McKinnell 2007; Emmett and Krutzikowsky 2008). Many fundamental questions

regarding predation on salmon during the marine phase of the life cycle remain unanswered (Miller et al. 2013; Clai-borne et al. 2014) including: (1) What is the identity of predators by major taxon (i.e., bird, fish, marine mammals)? (2) When does most predation occur? (3) How does predation vary by year or location? (4) Is predation size-selective?

Perhaps the greatest challenge to studying predation is catching predators “in the act” of consuming juvenile salmon—actually finding juvenile salmon in the stomachs of predators. This difficulty is due to rapid digestion rates, extremely large populations of some predators, and relatively low abundance levels of juvenile salmon compared to other prey typically consumed by known salmon predators. For example, Emmett and Krutzikowsky (2008) examined the stomachs of over 5,000 Pacific hake (*Merluccius productus*) and 2,000 jack mackerel (*Trachurus symmetricus*) over six years, in which they observed a total of seven juvenile fall

Chinook salmon (*O. tshawytscha*). Based on the estimated population sizes of the two predators, they estimated that each salmon found in a predator's stomach represented 0.4 million to 3.4 million juvenile salmon consumed by Pacific hake and 0.1 million to 0.4 million salmon consumed by jack mackerel. This level of predation potentially represents up to 20% of the approximately 80 million fall Chinook salmon that emigrate from the Columbia River annually (R. Zabel, Rich.Zabel@noaa.gov, pers. comm.).

The Columbia River estuary presents a unique opportunity to study predation on juvenile salmon because hundreds of millions of juvenile salmon from throughout the Columbia River basin are concentrated in the lower estuary as they migrate to the ocean (Weitkamp et al. 2012, 2015; Teel et al. 2014). The lower estuary also contains two large breeding colonies of piscivorous birds, Caspian terns (*Hydroprogne caspia*) and double-crested cormorants (*Phalacrocorax auritus*), which both consume millions of juvenile salmon each year (Collis et al. 2001; Ryan et al. 2003; Roby et al. 2014). Furthermore, because both bird species forage largely within the estuary (Lyons et al. 2007), and the estuary itself has well defined borders (land to the north and south, a restricted mouth), it can serve as a model ecosystem for the study of predation on juvenile salmon.

As part of a broader study, we are using paired data sets of the estuarine fish assemblage (Weitkamp et al. 2012; Weitkamp, unpublished data) and tern and cormorant diets (Roby et al. 2014; Lyons, unpublished data) to examine prey selectivity by the two avian predators over a six-year study period (2007–2012; Lyons et al. 2014; Good, unpublished data). Results of these analyses point to the critical role that alternative prey plays in determining predation rates on juvenile salmon. Specifically, consumption of juvenile salmon by

both Caspian terns and double-crested cormorants is strongly influenced by the availability of alternative prey, although the level of alternative prey that changes predation behavior is quite different between the two avian predators (Roby et al. 2002, 2014; Lyons et al. 2014). In addition, cormorant diet composition in the Columbia River estuary is related to environmental variation, presumably through environmental influence on the estuarine fish community and alternative prey (Lyons 2010; Lyons et al. 2014).

Here, we examine the environmental factors that likely influence the estuarine fish community in the Columbia River estuary, a critical piece of the salmon-alternative prey-predator puzzle. A previous analysis of the same dataset during 2007–2010, found that salinity, river temperature and flow, and sea surface temperature (SST) were important drivers of the fish community at extremely fine temporal scales (hours to weeks; Weitkamp et al. 2012). We were interested in expanding this analysis to determine whether the same factors remained important when two additional years (2011 and 2012) were added to the analysis at longer time scales (weeks to months) using a more rigorous quantitative method. River flow in 2011 was the highest in over a decade, reaching 17,188 m³/sec (607,000 ft³/sec) on 31 May 2011 (USGS stream flow data, www.usgs.gov); such extremes in parameter values are important to understand the influence of environmental variation.

We also explored how changes in environmental conditions might influence individual fish species abundances. We expected that individual species would respond uniquely to environmental conditions, given the diverse life-history patterns represented by the estuarine fish assemblage. For example, most juvenile salmon display directed downstream migration to the ocean, northern anchovy (*Engraulis mor-*

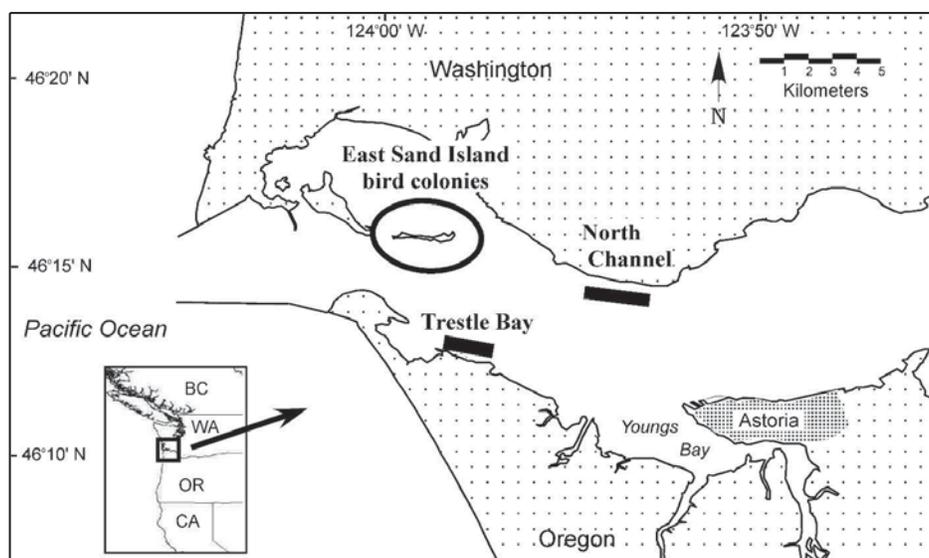


Fig. 1. Map of the lower Columbia River estuary showing the locations of the two purse seine sites, Trestle Bay and North Channel, and the bird colonies on East Sand Island. The inset map shows the location of the Columbia River estuary along the west coast of North America. State (U.S.) or provincial (Canada) abbreviations are: BC: British Columbia; WA: Washington; OR: Oregon; CA: California.

dax) are a marine species that occasionally enters the estuary, while threespine sticklebacks (*Gasterosteus aculeatus*), shiner perch (*Cymatogaster aggregata*), and juvenile American shad (*Alosa sapidissima*) are considered estuarine residents.

Finally, we used the results of this analysis to explore the likely response of the fish assemblage to the effects of climate change. Climate change in this region is expected to increase water temperature in both freshwater and marine habitats, and decrease river discharge due to more precipitation falling as rain rather than snow (Mote et al. 2003; Mote and Salathé 2010; Abatzoglou et al. 2014). How climate change will influence ocean dynamics, specifically upwelling strength and phenology, is an area of active debate (Mote and Mantua 2002; Diffenbaugh 2005; Bograd et al. 2009). Overall, our results indicate a dynamic fish assemblage that is responding to local and basin-scale environmental variation, and will likely change in the future, with implications for predation on juvenile salmon.

MATERIALS AND METHODS

Fish Collection

The estuarine fish assemblage data comes from an ongoing study of juvenile salmon and associated estuarine fishes in the lower Columbia River estuary during 2007–2012. The methodology is described in detail by Weitkamp et al. (2012) and is briefly summarized here. Fish were sampled with a fine mesh purse seine (10.6-m deep × 155-m long) during daylight hours at two stations, North Channel (46° 14.2'N, 123° 54.2'W) and Trestle Bay (46° 12.9'N, 123° 57.7'W), which are within sight of the mouth of the Columbia River, and the large Caspian tern and double-crested cormorant colonies on East Sand Island (Fig. 1). Sampling was conducted every two weeks from mid-April until late June or early July in all years (2007–2012).

During each sampling trip (termed a “cruise”), the net was repeatedly set, retrieved, and the catch processed throughout the incoming tide at each station. The net was deployed in two configurations: during quantitative round hauls it was set in a circle (area = 1,912 m²) and immediately pursed, while during non-quantitative tows the net was towed upstream for 10 minutes before pursing to increase the catch of fish. Mean fish densities were estimated from 3–6 quantitative hauls made at each station during each cruise, while fish sizes were estimated from both round hauls and tows. Regardless of the net configuration, all captured fish were identified to species, enumerated, and up to 50 of each species were measured (fork length (FL) or total length (TL) to the nearest 1 mm). A subset of fish was given a lethal dose of MS-222, labeled and bagged; once on shore, these fish were measured for both length (FL or TL in mm) and weight (g).

Fish Assemblage Data

Our analysis used fish data expressed as both numbers and biomass of each species. We did this because some species (e.g., threespine stickleback) are smaller than others, and the size of most fish of a given species varied by season and year. The biomass of each fish species was estimated for each cruise from all measured lengths of that species converted to weight using a length-weight relationship based on 100s or 1000s of fish measurements (Weitkamp, unpublished data), and averaged for that cruise. These species- and cruise-specific biomass estimates were then multiplied by the mean number of fish caught during that cruise to produce total biomass for each species in each cruise.

We restricted our analysis of the fish community data to 13 species/age classes that are commonly caught in the estuary and comprise > 95% of the fish caught by number and biomass. The 13 species include the six juvenile salmon species/age classes (chum [*O. keta*], coho [*O. kisutch*], sockeye [*O. nerka*], subyearling and yearling Chinook salmon, and steelhead [*O. mykiss*]), American shad, longfin smelt (*Spirinchus thaleichthys*), northern anchovy, Pacific herring (*Clupea pallasii*), shiner perch, surf smelt (*Hypomesus pretiosus*), and threespine stickleback. In these analyses, monthly numeric or biomass data for each species/age class were transformed using square root ($x + 1$). Using fewer or more fish species and different transformations produced similar results as those presented here.

The fish assemblage data were analyzed using two time scales: biweekly (every two weeks when cruises occurred) and monthly (averaged across cruises each month). We did this for several reasons. First, the estuarine fish community is extremely dynamic (Weitkamp et al. 2012) and we wanted to identify environmental variables that likely contributed to variation among cruises. Second, many of the large-scale environmental parameters (e.g., the Pacific Decadal Oscillation (PDO) and the Oceanic Niño Index (ONI)) are only available at monthly time scales, and therefore we used fish data averaged by month to compare against monthly environmental variables. By using two time scales, we also recognize that environmental variation occurs across a range of temporal scales. Accordingly, we expected that environmental parameters associated with biweekly data would likely differ from those associated with monthly data. Our dataset included 33 biweekly and 18 monthly estimates of the estuarine fish assemblage during April–June for the years 2007–2012 (Fig. 2).

Statistical Analysis

Environmental Variables

Our primary goal was to determine which environmental variables, if any, likely influenced the estuarine fish assemblage we observed in the Columbia River estuary. We selected 10 environmental variables that represented both local and

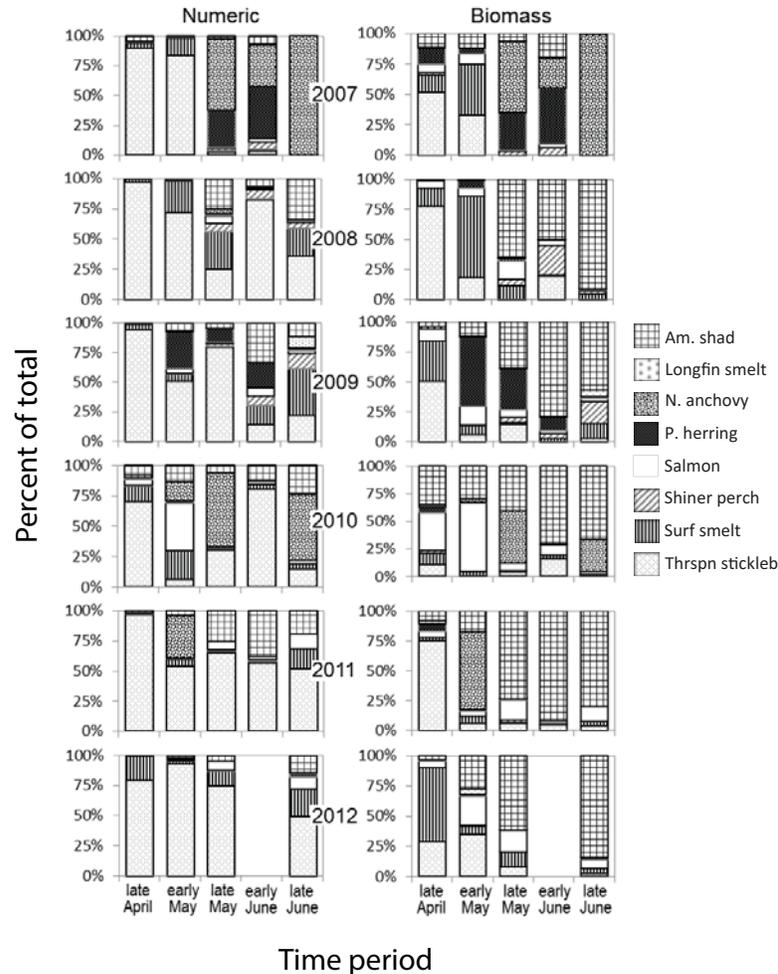


Fig. 2. The estuarine fish assemblage data set used in the analysis, expressed as percent abundance (left column) or biomass (right column) by two-week time periods. To simplify the graph, all juvenile salmon are placed in a single category. Abbreviations are Am.: American; N.: northern; P.: Pacific; Thrspn stickleb.: Threespine stickleback.

ocean basin-scale variables for this analysis (Table 1). Local variables represented both riverine (e.g., river flow), and marine conditions (e.g., sea surface temperature (SST), sea level height (SLH), upwelling strength, plume volume) because the fish assemblage included both estuarine and marine species. Analyses at monthly time scales only used monthly values for these local variables (the month in which fish data were collected), but biweekly analyses included weekly means from the week preceding fish collection, although correlations between monthly and weekly data were generally high ($r > 0.53$).

Ocean basin-scale variables represented oceanic and atmospheric processes and patterns at much larger spatial scales. These variables included the PDO and the North Pacific Gyre Oscillation (NPGO; Table 1), both of which have been shown to drive the dynamics of salmon and invertebrate populations in the California Current (Mantua et al. 1997; DiLorenzo et al. 2008; Lindegren et al. 2013). Because there are often delays between changes in large-scale indices and changes observed in our region (e.g., Peterson and Schwing

2003), our environmental dataset of these indices included lags of 0, -2, and -4 months (i.e., values of the indices 0, 2, or 4 months before the fish data of interest), which are indicated by numbers following the indicator name (e.g., PDO0 has zero lag, NPGO-4 has a 4-month lag).

This analysis was based on the assumption that concurrent changes in environmental variables and the fish assemblage reflect causation (the environment influences the fish assemblage). Because of this assumption, we deliberately omitted river temperature from the analysis. Prior investigations have shown that strong seasonal trends in river temperature (nearly linear increase from April to June with very little interannual variation) was consistently chosen as a strong explanatory variable. However, we believe the selection of this variable by models at least partially reflected seasonal changes in the fish community rather than direct response of the fish community to temperature variation. Because we could not distinguish between these two processes, we chose to exclude river temperature in our analysis.

Many of the environmental variables were correlated with each other at $r > 0.5$, due in large part to the use of lags of ocean basin-scale environmental variables. For example, values of PDO, ONI, NPGO or North Pacific Index (NPI) separated by two months (e.g., PDO0 vs. PDO-2, NPGO-2 vs. NPGO-4) had an average correlation of 0.69, while the PDO0, PDO-2, and PDO-4 were positively correlated with ONI-2 and ONI-4 ($r = 0.61$ – 0.74). In addition, monthly plume volume and river flow were strongly correlated ($r = 0.81$). Environmental variables used in the analysis were found to meet the assumptions of normality, and all were transformed so they had a mean of zero and standard deviation of one for the time period of interest.

Multivariate and Univariate Methods

We used multivariate and univariate methods to explore variation in the fish community data and the influence of environmental variables on fish in the estuary. To explore seasonal and interannual variation in the fish community, we first constructed matrices of pairwise Bray Curtis similarity coefficients calculated from the fish community among 2-week periods or months by year, with separate matrices for numeric and biomass data. These matrices were then used to construct non-metric multiple-dimensional scaling (MDS) plots to graphically explore variation in fish assem-

blage structure. The MDS ordination technique places all points in MDS space in relation to their similarity (i.e., points further apart in MDS space are less similar than those closer together). In all MDS analyses, random starting locations were used for each of 25 iterations to find the best solution. Minimum stress was attained in multiple iterations suggesting a true minimum solution. Stress values from our MDS plots were less than 0.15, indicating spatial representation of data by the MDS plot was consistent with the structure of the original data set (Clarke and Gorley 2006).

We quantitatively evaluated temporal variation on assemblage composition using ANOSIM, a multivariate analog to analysis of variance. This produces Global R values that indicate the degree of separation of groups generated by a particular factor (or pair of factors). These Global R values range from 0 (no separation) to 1 (complete separation); it also generates statistical probabilities by permutation (Clarke and Gorley 2006).

We used two methods to investigate the influence of environmental variables (i.e., = indicators) on fish in the estuary (i.e., = response variable): multivariate techniques were used on the overall fish community and univariate methods on individual fish species. We used multivariate, multiple regression to evaluate the influence of environmental variation on the overall community expressed as numbers of

Table 1. Environmental variables used in the analysis. All values were provided by month (ocean basin-scale variables), or averaged by week or month (local/regional variables) for April–June for the years 2007–2012.

Variable name	Description and data source
Local/regional variables	
River flow	Weekly and monthly means of daily Columbia River flow at Quincy, OR (USGS site 14246900). Units: m ³ /sec. Source: www.usgs.gov
Columbia River plume	Weekly and monthly means of modeled daily volume of the Columbia River plume. Units: km ² . Source: www.stccmop.org/datamart/virtualcolumbiariver .
Sea surface temperature (SST)	Weekly and monthly means of hourly SST recorded at three NOAA buoys: Umpqua offshore (46229), Stonewall Bank (46050), and Grays Harbor (46211). Units: °C. Source: www.wrh.noaa.gov/pqr/buoys.php
Upwelling index	Monthly upwelling at 45°N. Units: m ³ /sec/100 m coastline. Source: www.pfel.noaa.gov/products/PFELData/upwell/monthly/upindex.mon
Upwelling anomaly	Monthly upwelling anomalies at 45°N. Units: m ³ /sec/100 m coastline. Source: www.pfel.noaa.gov/products/PFELData/upwell/monthly/upanoms.mon
Sea level height	Monthly sea level height measured at Astoria, OR (NOAA Tide station 9439040), with seasonal and linear trends removed. Units: m. Source: http://tidesandcurrents.noaa.gov/sltrends/residual.htm?stnid=9439040
Ocean basin-scale variables	
Pacific Decadal Oscillation (PDO)	Leading Principal Component of monthly SST anomalies in the North Pacific Ocean. Source: http://jisao.washington.edu/pdo/PDO.latest
North Pacific Gyre Oscillation (NPGO)	2 nd dominant mode of sea level height for the NE Pacific. Source: www.o3d.org/npgo/
Oceanic Niño Index (ONI)	Anomaly from the Niño 3.4 region. Source: www.cpc.ncep.noaa.gov/data/indices/
North Pacific Index (NPI)	Index of sea level pressure over the region 30°N–65°N, 160°E–140°W. Source: https://climatedataguide.ucar.edu/climate-data/north-pacific-np-index-trenberth-and-hurrell-monthly-and-winter

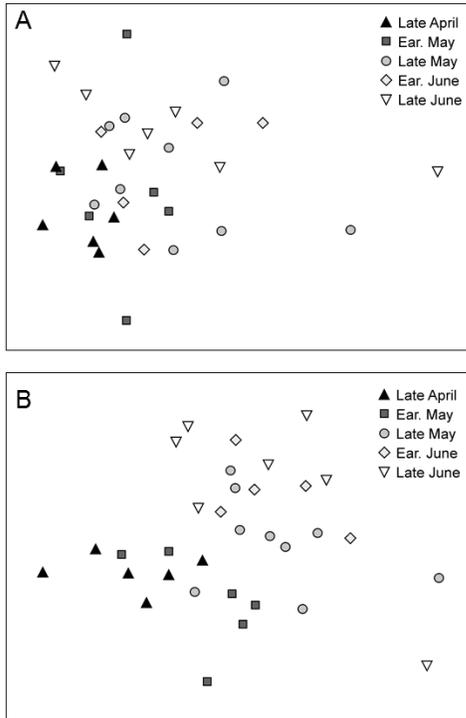


Fig. 3. MDS plots of fish assemblage data at biweekly time scales expressed as numbers of fish (A) or biomass (B).

fish or biomass. This analysis began with matrices of pairwise-Bray Curtis similarity coefficients calculated from the fish community among 2-week periods or months by year. These similarity matrices were then subjected to a principal coordinate analysis to partition the variation. Finally, a multiple regression was conducted on the principal coordinate axes using the specified environmental indicators (Table 1; Legendre and Anderson 1999; Anderson et al. 2008). We used Akaike’s Information Criterion corrected for small sample sizes (AICc) to find the best model from all possible models. This analysis was run using the Distance-based Linear Model (DistLM) function in PERMANOVA+ for PRIMER-E software (Anderson et al. 2008).

We also examined the influence of regional indicators on individual species abundances using the two time scales (bi-weekly, monthly). This was evaluated as series of individual regressions for the species used in the assemblage analysis. We did not conduct regressions on any juvenile salmon or longfin smelt because all have relatively low abundances and the salmon were rapidly migrating through the estuary to the ocean and therefore were unlikely responding to environmental variation. We restricted our results to regression coefficients that were statistically significant at $p < 0.05$ to minimize spurious results associated with running multiple tests.

Table 2. Results of the multivariate multiple regression of Columbia River estuary fish community data expressed as numeric or biomass, evaluated at two time scales (biweekly or monthly) for the months of April, May and June. Included are Akaike’s Information Criterion corrected for small sample sizes (AICc) and regression coefficients (r^2) for the best models.

Fish data type	AICc	r^2	Environmental variables ^a
Biweekly time scale			
Numeric	245.2	0.420	Flow (W), SLH (M), SST (W), PDO0, PDO-4, Upw An
	245.5	0.478	Flow (W), SLH (M), SST (W), NPGO-2, ONI0, ONI-2, ONI-4, Upw An
Biomass	234.6	0.374	Flow (W), NPGO-2, PI Vol (W), SST (W)
	234.6	0.411	Flow (W), NPGO-2, PI Vol (W), Upw In, Upw An
	234.6	0.445	Flow (W), NPGO-2, PI Vol (W), Upw In, Upw An, ONI0
Monthly time scale			
Numeric	124.9	0.478	NPGO-2, SST (M), PI Vol (M)
	125.9	0.555	NPGO-2, SST (M), PI Vol (M), NPGO0
Biomass	128.1	0.508	PDO0, Upw In, Upw An
	128.6	0.391	SST (M), SLH (M)
	128.7	0.492	SST, NPGO-2, PI Vol (M)

^aAbbreviations are SST: Sea surface temperature; SLH: sea level height; Upw In: Upwelling Index, Upw An: Upwelling Anomaly; PI Vol: Plume volume; NPGO: North Pacific Gyre Oscillation; PDO: Pacific Decadal Oscillation; NPI: North Pacific Index. Items in parentheses indicate weekly (W) or monthly (M) values, or lag times of -2 or -4 months (see methods).

RESULTS

Estuarine Fish Assemblage

The estuarine fish assemblage each spring displayed both seasonal and interannual variation, with differing patterns between numeric and biomass data (Fig. 2). In both data sets, threespine sticklebacks had the greatest contributions early in the season and in time periods with high flows (2011, early June in 2008 and 2010) and declined by late June, especially in the biomass data. Other species, including American shad, northern anchovy, Pacific herring, juvenile salmon, and surf smelt, varied by year and date but were generally more prominent in May and June than in April, especially in years with lower flow (e.g., 2007 and 2009). They also had higher relative values by biomass than numeric abundance, likely due to their relatively large body size.

This seasonal variation is a prominent feature of MDS plots of the fish assemblage data expressed as both biomass and numbers of fish at both time scales. Points representing the fish assemblage early in the season were generally on the left side of the graph and those later in the season were farther right (Fig. 3). These patterns were confirmed quantitatively using ANOSIM. Well-separated groups were formed by month (Global $R \geq 0.29, p < 0.05$) but not by year (Global $R \leq 0.1, p > 0.10$) in numeric and biomass data grouped by month. In contrast, separation of groups in fish assemblage

data at biweekly time scales differed by the data type: biomass data formed well separated groups by month (Global $R = 0.35, p < 0.05$) but not year (Global $R \leq 0.1, p > 0.10$), while numeric data formed weak but statistically significant groups by year (Global $R = 0.21, p < 0.05$) but not month (Global $R \leq 0.1, p > 0.10$).

Environmental Influences on the Fish Assemblage

The results of our analyses of environmental influences on the Columbia River estuarine fish community and individual species suggested that multiple environmental factors were likely important, especially those associated with river flow or plume volume, SST, and upwelling (Table 2; Fig. 4). Results varied by the time scale of interest, with less difference between models using the fish assemblage expressed as numbers or biomass of fish. The best models resulting from fish data at biweekly time scales included more variables (≥ 4) than those using monthly time scales (≥ 2) because of the larger number of fish assemblage data points.

When evaluated at biweekly time scales, the variable river flow was included in all top regression models. The best models based on fish biomass also included SLH and SST, and those based on numeric abundance all included plume volume and NPGO-2. For models using biweekly time scales, the AICc values were nearly identical for models containing increasing numbers of variables, but—not

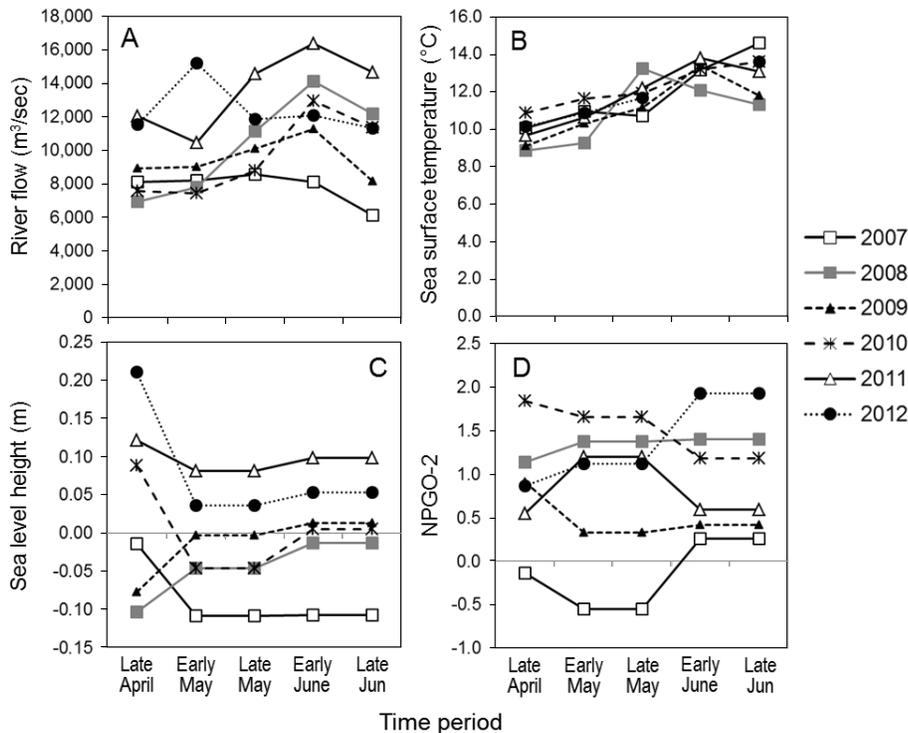


Fig. 4. Graphs illustrating biweekly values of select environmental variables during the years 2007–2012 used in the analysis. The variables are (A) river flow, (B) sea surface temperature, (C) sea level height, and (D) North Pacific Gyre Oscillation at a lag of -2 months (NPGO-2; see text).

surprisingly—coefficients of variation (r^2) increased as the number of variables increased.

For multivariate multiple regressions based on fish assemblage data at monthly time scales, no single variable was found in all of the best models, and none contained the variable river flow (Table 2). Regressions based on numeric data all contained NPGO-2, SST, and plume volume, while those based on biomass had no single variable in common, although SST was included in two of the three best biomass models. The biomass model with the lowest AICc score and explained the most variation ($r^2 = 0.51$) included PDO0 and upwelling index and anomaly (Table 2).

Influence of Environmental Variation on Individual Fish Species

Linear regressions between the numeric abundance of each fish species and each environmental variable (Table 3) indicated that no single variable explained variation across all fish species, consistent with our expectations. Instead, the environmental variables of SST, SLH, and upwelling index each had explanatory power for abundances of three groups. The results were consistent regardless of the time scale used. For example, the abundances of northern anchovy, shiner perch and threespine stickleback were all explained by the

same environmental variables (SLH, upwelling index, and SST, respectively) at both biweekly and monthly time scales.

The signs of the regression coefficients were almost always the same for each environmental variable, whether evaluated at biweekly or monthly time scales (Table 3). For example, relationships to SLH and plume volume were negative and those to upwelling index were positive. The one exception was SST, which was negative for threespine stickleback at biweekly or monthly time scales, but positive for American shad at monthly time scales (Fig. 5).

DISCUSSION

Our analysis of the Columbia River estuary fish assemblage suggests that there are complex interactions between the estuarine fish assemblage and the physical environment, which likely cause even more complicated interactions among the environment, alternative prey, juvenile salmon, and their predators. River flow or plume volume, SST, and several measures of upwelling were identified as important explanatory factors for variation in the fish assemblage as a whole, and also explained variation in the abundances of individual species. However, no single environmental variable was present in all best regression models explaining variation in the fish assemblage, and these best models contained from two to eight environmental variables despite the fact that the criteria we used for model selection (AICc) included a penalty for the numbers of variables selected. This is in contrast to other studies that have demonstrated that single variables, especially the PDO, can have a strong influence on species assemblages, including Pacific salmon, coastal zooplankton, and forage fish (Mantua et al. 1997; Peterson and Schwing 2003; Lindegren et al. 2013). This difference can be at least partially explained by our using biweekly and monthly values of both environmental variables and fish assemblage abundances, in contrast to other studies that used these variables averaged across monthly or annual time scales (e.g. Burke et al. 2013).

Sea surface temperature was an important explanatory variable for the fish assemblage as a whole and the abundance of individual species. Sea surface temperature also showed a strong seasonal patterns, with linear increases in temperature over time with relatively little interannual variability (Fig. 4b). Consequently, its inclusion in many regression models may reflect the strong seasonal pattern in the fish data, rather than their direct response to temperature. Evidence that the fish community may be directly responding to SST comes from the best regression models for numeric data at biweekly time scales (Table 2). Both top regression models included SST, despite the fact that the fish assemblage data did not have a significant seasonal signal, at least at monthly time scales. Inclusion of years with very different seasonal patterns in SST will allow us to determine the extent to which the fish assemblage is directly responding to SST or whether it marks the passage of time. Unfor-

Table 3. Results of regressions between environmental variables and the abundance of fish species at biweekly or monthly time scales. Only regression coefficients that were statistically significant at $p < 0.05$ are shown. The sign of the regression coefficient is also indicated.

Fish species	r^2	Environmental variable (coefficient sign) ^a
Biweekly time scale		
Northern anchovy	0.17	SLH (-)
Northern anchovy	0.13	Flow (-)
Pacific herring	0.18	SLH (-)
Shiner perch	0.27	Upw In (+)
Threespine stickleback	0.35	SST (-)
Monthly time scale		
American shad	0.45	Upw In (+)
American shad	0.38	SST (+)
American shad	0.25	PI vol (-)
Northern anchovy	0.27	SLH (-)
Shiner perch	0.52	Upw In (+)
Shiner perch	0.28	PI vol (-)
Threespine stickleback	0.36	SST (-)

^aAbbreviations are SLH: Sea level height; Upw In: Upwelling index; SST: Sea surface temperature; PI vol: Plume volume.

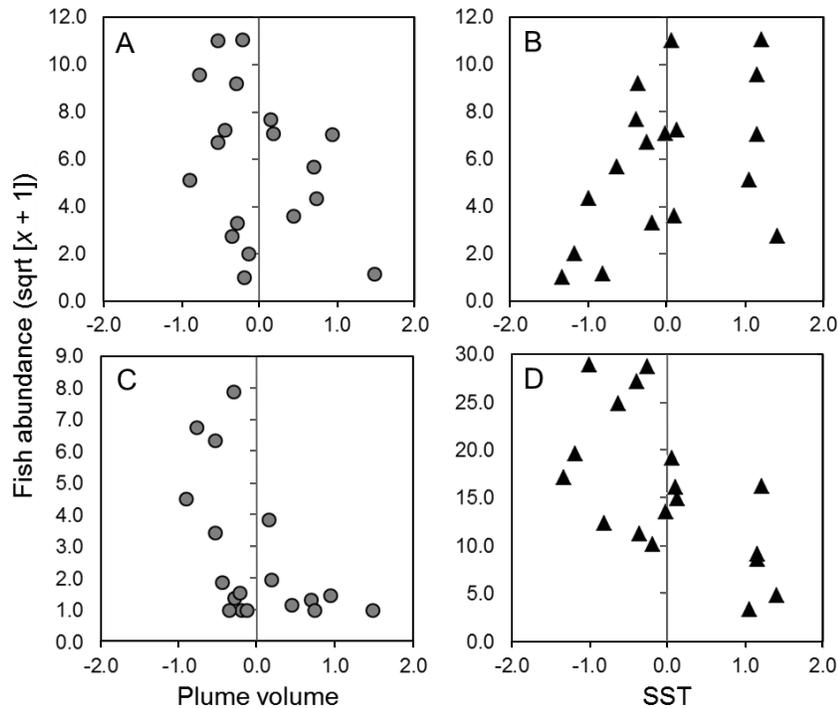


Fig. 5. Scatter plots illustrating the abundance of fish species (transformed using square root of $x + 1$) and normalized environmental variables at monthly time scales. The plots show American shad and plume volume (A) and sea surface temperature (SST; B), shiner perch and plume volume (C) and threespine stickleback and SST (D).

tunately, it is not possible to differentiate between these two scenarios from our data.

Although the environmental variables included in the best regression models varied by the time scale and type of data used, they described many of the same processes. For example, plume volume is a function of both river flow and coastal winds (Burla et al. 2008), and flow and plume volume were highly correlated in our dataset ($r = 0.81$). Similarly, upwelling was represented by four variables: directly by the upwelling index and upwelling anomaly, and indirectly by SLH and the NPGO. The upwelling anomaly differs from the index by excluding the seasonal trend, SLH decreases during upwelling as surface waters move offshore by Ekman transport, while fluctuations in the NPGO are driven by regional and basin-scale variations in wind-driven upwelling (DiLorenzo et al. 2008). The PDO describes the pattern of SSTs across the North Pacific Ocean and has been shown to lead changes in coastal SSTs in our geographic area (Peterson and Schwing 2003). However, correlations between PDO and its lags and SST in our dataset were quite low ($r \leq 0.11$) for reasons that are not clear. Despite the many environmental variables identified as important in our analyses, they reflect just a few physical processes.

Our findings that ocean temperature, river flow, NPGO-2, and upwelling were important explanatory variables for the estuarine fish assemblage at biweekly time scales differs somewhat from a previous analysis using the same data set

but fewer years (4 vs. 6; Weitkamp et al. 2012). The earlier analysis found that river temperature and flow, SST, and the PDO were important, but that NPGO and upwelling were not. Apparent differences in the results of the two studies may reflect differences in the methodology. The earlier analysis used ranks (rather than actual values) to find matrices constructed from environmental variables that best fit the structure of the matrix of fish assemblage similarities, regardless of the number of environmental variables used. In contrast, the current analysis used multiple regression to find the environmental variables that fit the actual variation in the multivariate fish data, using criteria that restrict the number of variables selected. Consequently, the current analysis should be considered more quantitative than the previous one. In addition, the current analysis used two additional years of data—one of which provided extreme flow values—therefore increasing the number of data points and statistical power, with greater contrast in flow.

A similar analysis of the fish and nekton assemblage in the Columbia River plume—just outside the river mouth from our study area—also found multiple local environmental variables were associated with seasonal and interannual variation in the plume assemblage (Litz et al. 2013). As in our study, Litz et al. (2013) demonstrated that environmental conditions including temperature, salinity, and upwelling, were most strongly correlated with variation in the fish and nekton assemblage. However basin-scale parameters (e.g.,

PDO, NPGO, ONI) provided little explanatory power, although time lags for these parameters were not included in the analysis. Given that many individual fish species, including surf smelt, northern anchovy, and Pacific herring, likely move between these two study areas and are therefore responding to the same environmental conditions, parallel findings are to be expected.

One crucial question is how the estuarine fish community will respond to future climate conditions—specifically increased water temperatures and decreased flow—which has important implications for predation on juvenile salmon in the future. Flow and plume volume (which is strongly correlated to river flow) were important explanatory variables in top regression models of the fish assemblage data, as well as in regressions using the abundance of individual species. This suggests that expected future declines in river flow will likely influence the fish community, perhaps resulting in disproportional increases in some species such as northern anchovy, American shad, and shiner perch, which generally increased in abundance as river flow or plume volume decreased (Fig. 5).

Sea surface temperature was also identified as an important explanatory variable. However, while SST was negatively related to the abundance of threespine stickleback, it was positively related to the abundance of American shad (Fig. 5), suggesting future increases in SST may have contradictory effects on the fish community, causing some species to increase and others to decline. Clearly, sorting out the direct effects of current—let alone future—environmental forcing on the estuarine fish assemblage and its consequent influence on salmon predation is complex and extremely difficult to predict.

CONCLUSION

Our analysis suggests that the estuarine fish assemblage as a whole is influenced by environmental variation associated with river flow, ocean temperature, and upwelling. This environmentally-driven variation in the fish assemblage alters the abundance of juvenile salmon relative to other fish species, many of which serve as alternative prey for salmon predators. Most avian (Gladics et al. 2014; Roby et al. 2014), marine mammal (Yurk and Trites 2000; Browne et al. 2002), and piscine (Emmett and Krutzikowsky 2008; Brodeur et al. 2014) predators along the Pacific coast of North America primarily consume forage fishes and invertebrates (squid, krill), with only minor dietary contributions from juvenile salmon. Consequently, fully understanding predation on juvenile salmon from either the salmon or predator standpoint cannot be accomplished in isolation: the abundance and dynamics of alternative prey should be considered.

Unfortunately, with the exception of a few species of fishes (e.g., Pacific sardines, *Sardinops sagax*, northern anchovy), relatively little research has been conducted on the basic biology—population size, recruitment dynamics, dis-

tributions, and habitat requirements—for most forage fish species in coastal waters (Pikitch et al. 2012; Lindegren et al. 2013; Litz et al. 2013). This lack of basic information limits our ability to predict the response of these species to current environmental conditions (Brodeur et al. 2005; Ruzicka et al. 2012), let alone those expected to occur with climate change in the next few decades (Cheung et al. 2015). Given the importance of forage fishes to coastal food webs (Field et al. 2006), and their role as alternative prey for salmon predators (Gladics et al. 2014), greater understanding of forage fish biology is a topic of research that desperately needs more attention.

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