Abstract—The transition between freshwater and marine environments is associated with high mortality for juvenile anadromous salmonids, yet little is known about this critical period in many large rivers. To address this deficiency, we investigated the estuarine ecology of juvenile salmonids and their associated fish assemblage in open-water habitats of the lower Columbia River estuary during spring of 2007–10. For coho (*Oncorhynchus kisutch*), sockeye (*O. nerka*), chum (*O. keta*), and yearling (age 1.0) Chinook (*O. tshawytscha*) salmon, and steelhead (*O. mykiss*), we observed a consistent seasonal pattern characterized by extremely low abundances in mid-April, maximum abundances in May, and near absence by late June. Subyearling (age 0.0) Chinook salmon were most abundant in late June. Although we observed interannual variation in the presence, abundance, and size of juvenile salmonids, no single year was exceptional across all species-and-age classes. We estimated that >90% of juvenile Chinook and coho salmon and steelhead were of hatchery origin, a rate higher than previously reported. In contrast to juvenile salmonids, the abundance and composition of the greater estuarine fish assemblage, of which juvenile salmon were minor members, were extremely variable and likely responding to dynamic physical conditions in the estuary. Comparisons with studies conducted 3 decades earlier suggest striking changes in the estuarine fish assemblage—changes that have unknown but potentially important consequences for juvenile salmon in the Columbia River estuary.

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Seasonal and interannual variation in juvenile salmonids and associated fish assemblage in open waters of the lower Columbia River estuary

Laurie A. Weitkamp (contact author)[1]

Paul J. Bentley[2]

Marisa N. C. Litz[3]

Email address for contact author: laurie.weitkamp@noaa.gov

[1] Conservation Biology Division
Northwest Fisheries Science Center
National Marine Fisheries Service
Newport Research Station
2032 SE Marine Sciences Drive
Newport, Oregon 97365

[2] Fish Ecology Division
Northwest Fisheries Science Center
National Marine Fisheries Service
Point Adams Research Station
520 Heceta Place
Hammond, Oregon 97121-0155

[3] Cooperative Institute for Marine Resources Studies
Hatfield Marine Science Center
Oregon State University
2030 SE Marine Sciences Drive
Newport, Oregon 97365

The Columbia River was historically home to one of the largest Pacific salmon (*Oncorhynchus* spp.) runs in the world, with 10–16 million adult salmon and steelhead (hereafter collectively referred to as *salmon*) returning to the basin annually before European settlement (NRC, 2004). As human population and activities have increased over the last century (Sherwood et al., 1990; NRC, 1996), Columbia River salmon runs have declined to the point that adult returns are typically less than 10% of historical levels (PFMC, 2011). Furthermore, more than half of the salmon populations in the river basin are thought to have become extinct (Gustafson et al., 2007), and most extant wild populations receive protection under the U.S. Endangered Species Act (ESA) as threatened or endangered species (Ford, 2011). This protected species list includes 5 subgroups of steelhead ([*O. mykiss*]; lower, middle, and upper Columbia River and Snake and Willamette rivers) and 1 subgroup each of coho ([*O. kisutch*]; lower Columbia River), chum ([*O. keta*]; Columbia River), and sockeye ([*O. nerka*]; Snake River) salmon (Ford, 2011). Also listed are 5 subgroups of Chinook salmon (*O. tshawytscha*): lower Columbia River, Snake River spring and summer, Snake River fall, upper Columbia River spring, and upper Willamette River (Ford, 2011). These Chinook salmon subgroups display diverse life-history variation, including the timing of adults returning to freshwater (indicated by season [i.e., spring, summer, or fall] in subgroup names (e.g., Snake River fall) and age of ocean entry for juveniles (fall runs have subyearling [age 0.0] smolts, spring runs have yearling [age 1.0] smolts, and smolt age of summer runs vary by group) (Myers et al., 1998). There is no recognized pink salmon (*O. gorbuscha*) population in the Columbia River basin, although individuals often are observed (Hard et al., 1996; Gustafson et al., 2007). Because of these listings, considerable time and resources have been devoted to defining and implementing actions that will help restore salmon populations in the Columbia River.

Hatchery production of anadromous Pacific salmon in the Columbia River basin is extensive; the Fish Passage Center's (FPC) database indicates that ~140 million salmon smolts were released annually during 2007–10 (FPC data available at http://fpc.org/, accessed July 2011). These hatchery fish support commercial, tribal, and recreational fisheries in marine waters from Alaska to California, in addition to fisheries in the Columbia River (PFMC, 2011). Hatchery fish also dominate adult returns and contribute 34–50% of fall Chinook salmon to more than 80% of spring and summer Chinook and coho salmon returns to the Columbia River (NRC, 1996; ISAB[1]). With the emphasis on restoring wild populations, there is increasing concern about potentially negative effects of hatchery fish on wild populations (NRC, 1996; Rand et al., 2012). However, little is known about these interactions in migratory corridors or estuaries, where hatchery and wild populations that are spatially segregated in stream environments have opportunities to interact (Naish et al., 2008; Rand et al., 2012). This gap in knowledge is particularly notable in open-water habitats of the Columbia River estuary, where such basic information, such as the seasonal presence, relative abundance, or potential size differences between hatchery and wild juvenile salmon, is lacking.

As part of the effort to restore Columbia River salmon, attention is increasingly focused on salmon when they are present in the estuary (Fresh et al., 2005; Bottom et al., 2005, 2006). The estuary phase and the initial ocean stage are viewed as "critical periods" of the salmon life cycle because they are periods of high mortality as salmon transition from freshwater to marine habitats (Pearcy, 1992; Schreck et al., 2006; Welch et al., 2008). For example, Kareiva et al. (2000) estimated that even minor (5%) improvements in estuarine and early ocean survival would reverse population declines in Columbia River spring and summer Chinook salmon. However, the causes for the mortality (e.g., predation, starvation, and disease) or the factors that increase or depress mortality in a given year are largely unknown. Furthermore, juvenile salmon are not the only fishes inhabiting estuaries, but rather they are minor members of a larger fish assemblage (Haertel and Osterberg, 1967; McCabe et al., 1983; Bottom and Jones, 1990). Therefore, understanding processes such as predation on juvenile salmon requires understanding the dynamics of the larger fish community (Saunders et al., 2006). A lack of such information has greatly frustrated managers who must identify actions that can be implemented to increase survival during this critical stage.

Although mortality may be high in the estuarine environment, estuaries provide juvenile salmon with productive foraging opportunities, refuge from piscine predation (especially compared with marine waters), and offer intermediate environments during the physiological transition to salt water (Simenstad et al., 1982; Thorpe, 1994; Bottom et al., 2005). However, the degree of benefit likely varies by species and life history type, because some groups (e.g., subyearling Chinook salmon) make prolonged use of estuaries, whereas others (e.g., steelhead) largely pass through estuaries in a few days (Dawley et al.[2]; Schreck et al., 2006; Campbell, 2010; Roegner et al., in press). Extensive research efforts in the Columbia River estuary from the late 1960s (Johnsen and Sims, 1973) to the mid-1980s (McCabe et al., 1983; Dawley et al.[2] ; Bottom and Jones, 1990) clearly established that most juvenile salmon migrating as yearlings (i.e., yearling Chinook and coho salmon and steelhead) passed rapidly through the estuary in the deep channels, bisecting an otherwise broad, flat estuary, where they were effectively caught with a purse seine. By contrast, most subyearling migrants (subyearling Chinook and chum salmon) occupied shallow waters close to shore. Most research efforts conducted since the 1980s have focused primarily on subyearling salmon in shallow-water habitats of the Columbia River estuary (e.g., Bottom et al., 2005; Craig, 2010; Roegner et al., 2010a, in press; Spilseth and Simenstad, 2010).

In 2007, we re-initiated a study the estuarine fish assemblage in deep (~10 m) waters of the Columbia River estuary to address the deficiency of information in these habitats. Specifically, we wanted to characterize the presence and dynamics of juvenile salmon and the greater fish assemblage to which they belong during the spring salmon outmigration (mid-April through late June) and to explore if or how environmental variation may influence the patterns we observed. We were particularly interested in the determination of the following aspects of salmon in the Columbia River estuary: 1) species- or age-class-specific timing and abundance of juvenile salmon and their variation, 2) origins of juvenile salmon, with respect to both hatchery or wild origin, and geographic sources, 3) size distribution and condition of each species or age class of salmon and whether there were size differences between hatchery and wild fish, 4) composition and dynamics of other fishes sharing these open water habitats, and 5) the suitability of nonsalmonids as alternative prey for salmon predators based on overlap in size. Given the multitude of changes that have occurred in the Columbia River basin and estuary over the last 30 years (e.g., Sherwood et al., 1990; NRC, 2004), we also wanted to compare our results with those from studies conducted 3 decades earlier. This comparison allows us to identify how juvenile salmon and the larger estuarine fish community may have changed and begins to provide insight regarding expected changes in the future.

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[1] ISAB (Independent Scientific Advisory Board). 2011. Columbia River Basin food webs: developing a broader scientific foundation for fish and wildlife restoration. Doc. ISAB 2011-1. [Available at http://www.nwcouncil.org.]

[2] Dawley, E. M., R. Ledgerwood, T. H. Blahm, C. W. Sims, J. T. Durkin, R. A. Kirn, A. E. Rankis, G. E. Monan, and F. J. Ossiander. 1986. Migrational characteristics, biological observations, and relative survival of juvenile salmonids entering the Columbia River estuary, 1966–1983. Final report of research funded by Bonneville Power Administration. [Available from Northwest Fisheries Science Center, 2725 Montlake Blvd. E., Seattle, WA 98112].

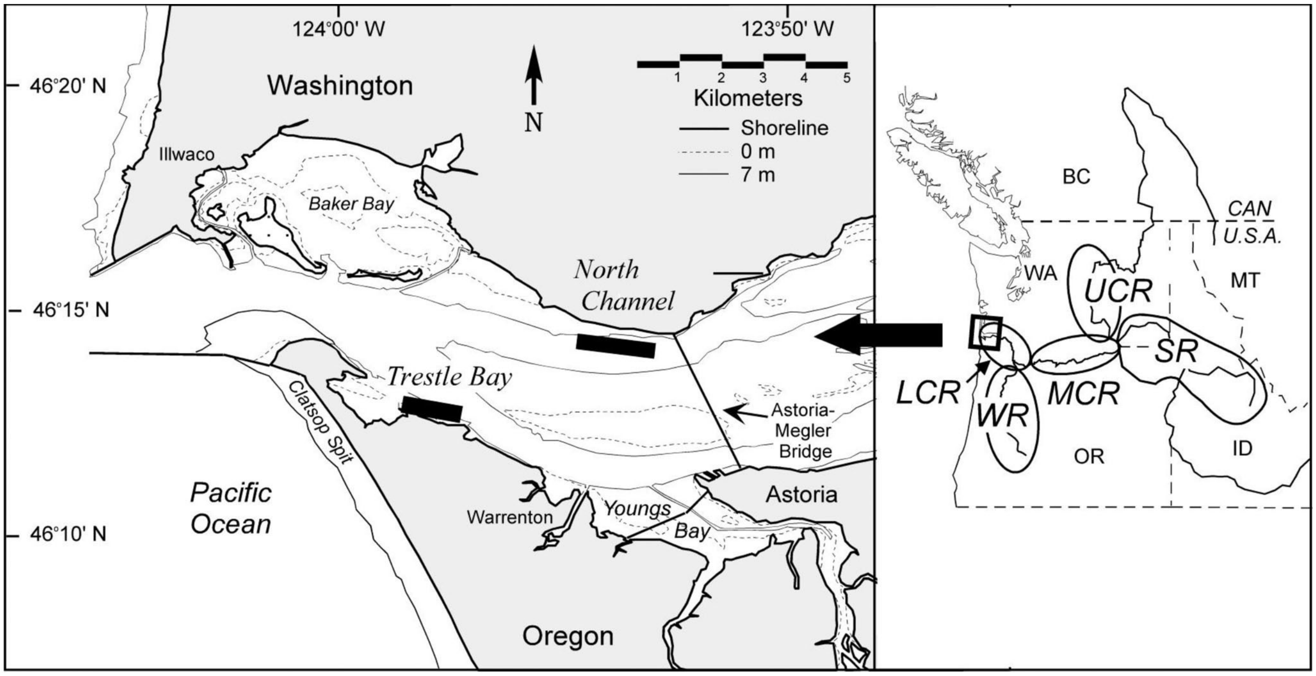

Figure 1

Map of the 2 sampling stations, North Channel and Trestle Bay, used in our study of the estuarine fish assemblage in open-water habitats of the lower Columbia River estuary. Shoreline, 0-m, and 7-m depth contours are indicated, as are major towns. The insert map indicates the location of the study area (black rectangle) and 5 geographic regions within the Columbia River basin from which juvenile salmon originated: lower Columbia River (LCR), Willamette River (WR), mid-Columbia River (MCR), upper Columbia River (UCR), and Snake River (SR). State or province abbreviations: WA=Washington; OR=Oregon; ID=Idaho; MT=Montana; BC=British Columbia.

Materials and methods

Collection of fish

Our sampling was directed toward the spring outmigration of juvenile salmon as they passed through the Columbia River estuary. For each sampling trip or cruise, we had the following objectives: 1) characterize the estuarine fish assemblage by documenting the abundance, size, and condition of fishes (including juvenile salmon) present in the sampling area, and 2) collect 50 individuals of each of 4 juvenile salmon species and age classes (yearling Chinook, subyearling Chinook, and coho salmon, and steelhead) for laboratory analyses; this number reflects a balance between restrictions on lethal sampling of ESA-listed species and the need for sufficient samples for statistical rigor.

To achieve these objectives, fish were sampled during daylight hours every 2 weeks from mid-April to late June or early July during 2007–10 at 2 stations, North Channel (46°14.2′N, 123°54.2′W, river km [rkm 17) and Trestle Bay (46°12.9′N, 123°57.7′W, rkm 13) (Fig. 1). These stations are located in the lower estuary adjacent to the 2 deep channels that bisect the north and south portions of the estuary, respectively, in the "estuarine mixing" region (Bottom and Jones, 1990; Jones et al., 1990). These stations also have historical significance because they have been used as study sites since the late 1960s (Johnsen and Sims, 1973; Dawley et al.[2]).

Sampling was restricted to days with early morning low tides, which typically occur during extreme (minus) tides during springtime; the first set of the net was made at approximately low slack water and sampling continued for the duration of the flood tide. This timetable was adopted because 1) fish are difficult to sample during ebb (outgoing) tides owing to high currents (which often exceed 11 km/h) and 2) strong thermally driven afternoon winds in excess of 48 km/h limited boat maneuverability and, therefore, sampling efficiency. Our timetable left ebb and neap tides and nighttime as times when fish were largely unsampled, but extremely strong downstream currents and close proximity to the hazardous Columbia River bar provide challenging conditions for vessels of any size (Haertel and Osterberg, 1967; Johnsen and Sims, 1973). Nevertheless, in studies of the Columbia River estuary, abundances of juvenile salmon were found to be either greatest during daylight hours (Ledgerwood et al., 1991) or were similar between day and night (Friesen et al., 2007), and therefore we were unlikely to miss large numbers of fish with our sampling schedule.

Fish were sampled with a fine-mesh purse seine (10.6 m deep and 155 m long, with stretched mesh opening 1.7 cm; knotless bunt mesh 1.5 cm); this mesh was sufficiently fine to effectively catch all but a few elongate fishes (e.g., larval smelt [Osmeridae] and small Pacific sand lance [*Ammodytes hexapterus*]). We restricted sampling to depths of 8–10 m; therefore, the net fished the entire water column. We set the net in 1 of 2 configurations (round hauls or towed), depending on our specific objectives (quantitative catches or maximization of the catch of fish); 2 boats were used in both configurations to deploy and retrieve the net. Quantitative round hauls (n=210) involved setting the net in a circle (area=1913 m^2). We define catch per of unit effort (CPUE) as the abundance of fish per 1000 m^2 (round hauls only), and we tried to complete at least 3 round hauls per station per cruise. When densities of juvenile salmon were low (CPUE<2/1000 m^2), we increased the number of fish caught by towing the net for 8–10 min upstream before closing and pursing the net (n=81 sets). We did not attempt to estimate abundances from these nonquantitative sets but did use the salmon collected during these sets to estimate origin and length–weight relationships, and we used length data from all fishes caught.

Regardless of the set configuration, once the net was pursed and fish had been crowded into the knotless bunt, they were transferred to large (190-L) buckets with running river water. All nonsalmonid fishes were identified to species (Eschmeyer et al., 1983; Hart, 1973) and enumerated, and all but 30 of each species were released. The retained fishes were anaesthetized with tricaine methane sulfonate (MS-222), measured (fork length [FL] or total length [TL] to the nearest 1 mm as appropriate), allowed to fully recover, and then released. Fewer individuals (up to 30) of nonsalmonid species were measured from each set than of salmonids (up to 100) because the focus of our study was on juvenile salmon. The measurement of 30 individuals of each nonsalmonid species provided adequate sample sizes (722–3674 length measurements for commonly caught species across the 4 years) without being overly time consuming. We noted the presence of invertebrates in our catch (e.g., California bay shrimp [*Crangon franciscorum*], Dungeness crab [*Cancer magister*], and jellyfishes [*Aequorea* spp., *Aurelia* sp., *Chrysaora fuscescens,* and *Eutonina indicans*]) but did not attempt to quantify their abundances. All invertebrates that we encountered are believed to be native to the Pacific Northwest, with the possible exception of *Aurelia* sp. (Kozloff, 1987; Wrobel and Mills, 1998).

In the case of extremely large catches (>5000 individuals), the total volume of fish in the net was visually estimated: 3 subsamples of known volume (5500 cm^3) were collected and transferred to separate buckets, and the remaining fish were released directly from the net without having been taken on board the vessel. Fish in each subsample were then identified to species, enumerated, and measured as described above. We estimated the total abundance of each species in the haul by taking the average density of each species across the 3 subsamples and multiplying it by the estimated total volume of fish.

Juvenile salmon were anaesthetized, identified to species, checked for the presence of tags (passive integrated transponder [PIT], visible implant elastomer, coded wire tags [CWTs]), or clipped adipose fins, and measured (FL to the nearest 1 mm). Juvenile salmon that were not needed for laboratory analyses were allowed to fully recover and released; tag codes of individuals tagged with PIT tags were "read" electronically before release. Salmon that were retained were given a lethal dose of MS-222, checked for tags and clips, and measured as above; then, they were individually tagged, bagged, and immediately placed on ice. Once on shore, these fish were transferred to a −80°C freezer for later laboratory analysis. In the laboratory, thawed juvenile salmon were remeasured (FL to the nearest 1 mm), weighed (total wet weight in grams), and rechecked for tags and clip marks. Snouts were removed from fish with CWTs for extraction (see the next section *Origins of juvenile salmon*).

Juvenile Chinook salmon were segregated into 2 age categories: subyearling (age 0.0) or yearling (age 1.0) on the basis of fish length (Dawley et al.[2]). The length dividing subyearling from yearling Chinook salmon ranged from 115 mm FL in April to 140 mm on July 1; it was developed from 1) seasonally adjusted length-frequency histograms (Hinton[3]), 2) known ages based on scale analysis (Fisher[4]), and 3) known ages determined from PIT tags or CWTs.

Origins of juvenile salmon

We estimated the hatchery or wild origins and geographic sources of juvenile salmon. Most of the ~140 million hatchery-origin Pacific salmon released in the Columbia River basin annually during the period of 2007–10 were externally marked by clipping (i.e., amputating) the adipose fin before release. These basinwide percentages of hatchery marking ranged from 67.8% (coho salmon) to 91.9% (yearling Chinook salmon) (FPC database). However, because of the large number of hatchery-produced fish that were unmarked (e.g., 16.7 million subyearling Chinook, 7.2 million coho salmon), individuals with intact adipose fins could either be wild or unmarked hatchery fish. We used annual species-specific mark rates from the FPC online database to estimate the percentage of hatchery fish in our catch ($\%H$), as

$$\%H = \frac{\textit{mark rate in catch}}{\textit{mark rate at hatchery}},$$

where the mark rate in catch = the percentage of marked fish that we observed in the estuary for each species-and-age class in each year.

In cases where mark rates in our catch exceeded those levels reported at hatcheries (i.e., $\%H$>100%), we capped $\%H$ at 100% for that year. Because some subyearling

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[3] Hinton, S. 2010. Unpubl. data. Northwest Fisheries Science Center, Hammond, OR 97121.

[4] Fisher, J. 2010. Unpubl. data. Oregon State Univ., Corvallis, OR 97331.

Chinook salmon were released from hatcheries after our study period, we considered only releases occurring at least 10 days before our final cruise of the spring: either June 19 (2007, 2008) or June 14 (2009, 2010). This cutoff is conservative (i.e., may underestimate *%H*) because recovery of subyearling Chinook with CWTs (n=127) in our study took an average of 32 days (range: 2–104 days) from time of release at hatcheries.

Extensive fish-tagging programs active throughout the Columbia River basin also provided information about the geographic origins of many individuals collected in the purse seine. In particular, nearly 30 million juvenile salmon (largely of hatchery origin) are tagged with CWTs (Regional Mark Information System [RMIS], database available at http://www.rmpc.org, accessed June 2011) and 2.5 million hatchery and wild salmon are tagged with PIT tags each year (PIT Tag Information System [PTAGIS], database available at http://www.ptagis.org, accessed June 2011). Both tag types provide information about release location and timing; we used this information to estimate the geographic origins of the salmon we collected.

For fish containing either CWT or PIT tags, we extracted the tags, "read" the tag code visually (CWTs) or electronically (PIT tags), and determined the release location from the appropriate online database. To simplify our analysis, release locations were grouped into 5 geographic regions (Fig. 1): below Bonneville Dam (rkm 235, excluding the Willamette River); mid-Columbia River (between Bonneville Dam and the mouth of the Snake River [rkm 522]); upper Columbia River (accessible waters above the confluence with the Snake River); Snake River (all accessible waters of the Snake River); and Willamette River. We could not determine release locations from the few tags (29 CWTs and 2 PIT) that either had no release information (i.e., agency codes or blank tags) or were not in the databases; some CWTs were lost before they could be read.

Environmental data

To gain insight into the environmentally driven dynamics of the estuarine fish assemblage, we recorded both local and regional environmental data for each purse seine set. These 2 environmental data types were expected to reflect different types of variability: local data would vary at very short time scales (minutes to hours) within the estuary, and regional data would represent longer term variability (days to weeks) at larger spatial scales. Our local data consisted of tidal stage and height information for each set and in situ conductivity, temperature, and depth (CTD) profiles made from the surface to the bottom measured before every set of the net. For purposes of this analysis, we used in situ temperature and salinity measurements at the surface (depth of 1 m) and near-bottom (depth of 7 m) to characterize the local water column. Because of equipment problems, CTD casts were not conducted during 2 of our cruises in 2007 (7-1 and 7-6) and 2 cruises in 2008 (8-1 and 8-7; for dates of these cruises, see Table 1). For these 4 cruises, we substituted modeled temperature and salinity data provided by the Center for Coastal Margin Observation and Prediction (Batista[5]); comparisons between modeled data and in situ temperature and salinity measurements indicated that they were highly correlated (coefficient of correlation [r]≥0.82).

We estimated tidal stage (time relative to low tide) for each set on the basis of low tide predicted for Hammond, Oregon, (NOAA station 9439011; http://tidesandcurrents.noaa.gov), which is within 500 m of our Trestle Bay sampling station. We also used this station to predict low tide at the North Channel site because predicted timing of tidal inundation was similar. We used observed (versus predicted) tidal heights recorded at Astoria, Oregon (NOAA station 9439040) because tidal heights were not available for the Hammond station.

We used regional environmental data that characterized both riverine and marine conditions because estuarine fishes likely were influenced by both freshwater and marine environments. Regional riverine data consisted of daily river flow records from Quincy, Oregon (rkm 87; U.S. Geological Survey [USGS] surface water station 14246900; http://www.usgs.gov, accessed August 2011) and daily temperature measurements at the Dalles Dam (rkm 304; USGS surface water station 14105700), both averaged over the days of the cruise. These stations were the nearest to the estuary among the stations where respective data types were collected.

Marine environmental data reflected conditions both near the mouth of the Columbia River and across the North Pacific Ocean. Local marine data included daily sea-surface temperatures (SST) measured at Stonewall Bank (NOAA Data Buoy 46050; 44°38.3′N, 124°32.0′W; http://www.ndbc.noaa.gov, accessed April 2012), daily Bakun upwelling index (UI) for 45°N, 125°W (http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling, accessed April 2012), and daily sea-level height (SLH) estimated for Astoria (http://ilikai.soest.hawaii.edu/uhslc/htmld, accessed April 2012). We used 2 indices describing the dominant modes of variability across the North Pacific Ocean at monthly intervals: the Pacific Decadal Oscillation (PDO) index (Mantua et al., 1997; http://www.jisao.washington.edu/pdo) and the North Pacific Gyre Oscillation (NPGO) index (Di Lorenzo et al., 2008; http://www.o3d.org/npgo). We estimated pairwise Spearman correlation coefficients between environmental variables to determine how they were related to each other (Sokal and Rohlf, 1995).

Analytical approach

All analyses were designed to explore how juvenile salmon and the estuarine fish assemblage varied at temporal scales ranging from days to years. Because of our focus on juvenile salmon, our analyses of salmon,

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[5] Batista, A. 2012. Unpubl. data. Center for Coastal Margin Observation and Prediction, Oregon Health and Science Univ., Portland, OR 97239.

Table 1

Sampling effort, regional river flow, and river temperature by year and cruise during the 4 years (2007–10) of our study of the estuarine ecology of juvenile salmonids and their associated fish assemblage in open-water habitats of the lower Columbia River estuary. Sampling effort totals, measured as the total number of hauls (round and towed) completed, are provided with dates of each cruise.

Year	Cruise no.	Dates	Total no. of hauls (no. of round hauls)	Mean river flow (1000 m³/sec)	Mean river temperature (°C)
2007	7-1	17–18 April	8 (8)	8.0	9.3
	7-2	1–4 May	24 (16)	8.7	11.3
	7-3	15–17 May	13 (9)	9.0	13.3
	7-4	30–31 May	14 (11)	7.8	15.0
	7-5	12–13 June	13 (10)	7.9	16.0
	7-6	27–28 June	7 (6)	5.7	17.5
		2007 effort	79 (60)		
2008	8-1	10 April	3 (3)	6.1	7.2
	8-2	23–24 April	12 (6)	7.6	9.0
	8-3	6–8 May	18 (12)	8.3	11.0
	8-4	20 May	7 (6)	13.5	13.5
	8-5	3–5 June	15 (9)	13.9	13.5
	8-6	18–19 June	14 (8)	12.5	14.9
	8-7	30 June–1 July	11 (10)	11.1	17.1
		2008 effort	80 (54)		
2009	9-1	15 April	3 (3)	9.3	8.5
	9-2	23–24 April	15 (9)	9.9	9.7
	9-3	7–8 May	13 (10)	11.2	10.3
	9-4	21–22 May	10 (8)	11.1	13.3
	9-5	4–5 June	13 (9)	11.3	15.4
	9-6	23–24 June	8 (7)	8.2	17.1
		2009 effort	62 (46)		
2010	10-1	13–14 April	14 (9)	7.9	9.3
	10-2	28–29 April	12 (6)	7.7	11.5
	10-3	11–12 May	10 (10)	7.4	11.9
	10-4	25–26 May	9 (7)	8.8	13.3
	10-5	8–9 June	12 (6)	13.4	14.4
	10-6	23–24 June	13 (12)	11.6	15.6
		2010 effort	70 (50)		

especially Chinook and coho salmon and steelhead, were more detailed than our analyses of other fishes.

Fish abundance and composition Analysis of temporal and spatial variation of the estuarine fish assemblage was restricted to catch data collected from round hauls (n=210). Seasonal changes in abundance for each of 6 juvenile salmon species-and-age classes (subyearling and yearling Chinook, coho, sockeye, and chum salmon and steelhead) were qualitatively assessed by visually comparing mean CPUE per cruise by year.

For the entire fish assemblage, including juvenile salmon, we calculated the following univariate metrics to assess patterns of abundance: 1) frequency of occurrence of all fish species during each year, 2) mean CPUE and coefficients of variation for the most commonly caught species, and 3) total abundance of all fishes and the relative abundance (as percentage of total) of the most commonly caught fishes, averaged by cruise. Data generated from these analyses were visually compared. These qualitative measures complemented multivariate techniques, specifically: 1) direct comparisons of subsets of Bray-Curtis similarity coefficients among hauls to examine fine-scale temporal and spatial influence, 2) nonmetric multidimensional scaling (MDS) by haul and cruise, and 3) analysis of similarities (ANOSIM, a multivariate analog for analysis of variance, ANOVA) to test for the influence of temporal variation. All multivariate analyses were run with PRIMER-E[6] software (PRIMER-E Ltd., vers. 6, Ivybridge, U.K.).

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[6] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Multivariate analyses were based on pairwise Bray-Curtis similarity coefficients calculated between hauls or cruises. Bray-Curtis similarity coefficients are widely used in ecological studies because they are unaffected by changes in scale (e.g., with percentage or proportions) or the number of variables (e.g., species or hauls) used and produce a value of zero when both values being compared are zero (joint absence problem) (Clarke, 1993; Legendre and Legendre, 1998). In this application, similarity coefficients ranged from 0 (no catches in common) to 1 (identical catches). The fish assemblage used in multivariate analyses was restricted to 13 species-and-age classes of fish that were effectively captured by the purse seine because they were pelagic. We deliberately excluded demersal species from our analyses (e.g., flat fishes [Pleuronectidae], gunnels [Pholidae], and sculpins [Cottidae]) because they were unlikely to be effectively sampled with a purse seine (Bottom and Jones, 1990). The 13 species included the 6 species-and-age classes of juvenile salmon, plus American shad (*Alosa sapidissima*), longfin smelt (*Spirinchus thaleichthys*), northern anchovy (*Engraulis mordax*), Pacific herring (*Clupea pallasii*), shiner perch (*Cymatogaster aggregata*), surf smelt (*Hypomesus pretiosus*), and threespine stickleback (*Gasterosteus aculeatus*). In these analyses, abundances of each species-and-age class in the 210 round hauls were transformed by using $\log(x+1)$. All species are native to the Columbia River and Pacific Northwest, with the exception of American shad (Hart, 1973; Eschmeyer et al., 1983; Hasselman et al., 2012a).

We compared pairwise Bray-Curtis similarity coefficients calculated among subsets of the 210 round hauls to explore fine-scale spatial and temporal variation in catches. Specifically, we examined spatial variation by comparing pairwise similarities among catches at the 2 stations, correcting for tidal stage (i.e., hauls occurred within 1 h of each other, where time 0 is at low tide) within the same cruise; differences were tested with the Mann-Whitney (MW) test for difference in medians. We explored fine-scale temporal variation by testing Bray-Curtis similarity coefficients among hauls made at the same station and within the same cruise but grouped by tidal stage at 1-h increments (i.e., within 1 h of low tide, 2 h, etc.). We used the Kruskal-Wallis (KW) one-way ANOVA on ranks followed by KW multiple-comparison test to determine which groups were different from the others (Zar, 1984).

We also used the matrix of Bray-Curtis similarity coefficients calculated either among hauls or cruises to construct MDS plots to graphically explore variation in fish assemblage structure at the 2 scales (hauls or cruises). The MDS ordination technique places all points in MDS space in relation to their similarity (i.e., points farther apart in MDS space are less similar than those points 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 which suggest a true minimum solution. Stress values of <0.20 indicate that spatial representation of data by the MDS plot is consistent with the structure of the original data set (Clarke and Gorley, 2006). Finally, we quantitatively evaluated temporal variation in assemblage composition by either haul or cruise, using year and biweek (where biweek 1=April 15–30, 2= May 1–15, etc.) for both analyses and Julian date and time after low tide for the matrix based on hauls. For this analysis, we used ANOSIM, which 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); the program also generates statistical probabilities by permutation.

Environmental variation We evaluated the response of the pelagic fish assemblage to environmental variation at 2 scales: haul and cruise. For the former (haul), we used both local (in situ temperature and salinity measured at depths of 1 and 7 m, and tidal stage and height) and regional (river flow and temperature, SST, SLH, UI, PDO, and NPGO) environmental parameters, whereas for the latter (cruise) we used only regional environmental parameters. For both analyses, environmental parameters were normalized, and then Euclidean distances between hauls or cruises were calculated in environmental multivariate space. The relative difference between environmental conditions for each haul or cruise was then compared to haul- or cruise-specific Bray-Curtis similarity coefficients for the fish community (see above) with the BEST function in PRIMER-E (Clarke and Gorley, 2006). This function creates matrices from different combinations of environmental variables and then compares the order (rank) among the fish assemblage with the environmental matrices to determine the environmental matrix with the highest correlation; statistical significance is estimated by permutation.

Size comparisons We compared size distributions of fishes for 2 reasons: 1) to determine which fish species were similar in size to juvenile salmon and, therefore, might serve as alternative prey for salmon predators, and 2) to examine seasonal and interannual variation in juvenile salmon size. We did not compare the sizes of nonsalmonids between years because measurements were made on fish of multiple, undetermined ages; therefore, interpretation of potentially detectable size differences in length would be complex (i.e., could result from changes in growth or age composition).

We evaluated the length of each juvenile salmon species-and-age class in 4 ways: 1) among years, 2) across the season (by date), 3) among years with weight as a covariate, and 4) between marked (known hatchery) and unmarked (hatchery and wild) fish by cruise. Length and weight data were transformed with $\ln(x+1)$ in all comparisons. We used one-way analysis of variance (ANOVA) to evaluate interannual variability in mean length among years, and two-way ANOVA to examine size differences of clipped (hatchery) or unclipped (hatchery+wild) fish by cruise (Zar, 1984). We used analysis of covariance (ANCOVA) to evaluate seasonal changes in length (collection date as a covariate) and length–weight relationships (weight as a covariate).

Results

Environmental conditions

Environmental conditions were extremely variable during our study period (mid-April to late June or early July) among the 4 years, because of both daily tidal inundation and extremely high river-flow events (>14,000 m^3/s) in May 2008 and June 2010 (Table 1); flows during May 2008 were the highest observed in more than a decade (USGS National Water Information System, http://waterdata.usgs.gov, accessed Aug 2011). Both high flow events were characterized by rapid increases in flow, but flows remained elevated much longer in 2008 than they did in 2010, resulting in 3 cruises in 2008 during which mean river flow exceeded 12,500 m^3/s compared with only 1 cruise in 2010 with rates that high (Table 1). By contrast, river flow never exceeded 11,600 m^3/s in either 2007 or 2009. River flow also was negatively correlated with the PDO ($r=-0.48$, $P<0.05$), indicating the influence of large-scale climate forces on terrestrial environments as expressed by river flow (Lawson et al., 2004).

River temperature measured both at the Dalles Dam and at 1-m depth in the estuary were quite similar (Spearman $r=0.98$, $P<0.05$), seasonally increasing from <10°C in mid-April to 15–17°C by late June (Table 1). They also were correlated with coastal SST ($r=0.85$, $P<0.05$), which displayed similar seasonal increases. The snowmelt-driven high flow event in 2008 delayed the seasonal increase in temperature, resulting in temperatures that were somewhat lower in June 2008 than in other years. In situ temperatures measured at 7-m depth also were positively correlated with upstream river temperature ($r=0.88$, $P<0.05$) and coastal SST ($r=0.78$, $P<0.05$), but they were negatively correlated with 7-m salinity ($r=-0.38$, $P<0.05$), indicating intrusion and mixing of consistently cold (8–12°C) marine water at depth.

In contrast to surface temperatures, in situ salinity measured before each haul changed dramatically with tidal stage, such that salinities ranged from essentially fresh (salinity<1 psu) to largely seawater (>25 psu) within the 5–7 h of sampling each day. This tidal variation was greatest at 7-m depth, and time elapsed since low tide was a reasonably good predictor of 7-m salinity (linear regression, coefficient of determination, $r^2=0.7$, $P<0.05$), but river flow was not ($r^2=0.3$, $P<0.05$). However, salinities measured at 1-m depth were influenced both by tidal cycle and river flow, with maximum salinity measured at a depth of 1 m during a cruise being negatively related to flow ($r^2=0.5$, $P<0.05$). In particular, maximum salinities recorded at 1-m depth when flow exceeded 10,987 m^3/s were significantly lower (mean=3.5 psu) than values recorded when river flow was below that level (mean=10.2 psu). This pattern suggests that high flows result in water column stratification with a surface layer of largely fresh water.

Fish catches and composition

We completed a total of 291 purse seine sets (210 round and 81 towed) during spring of 2007–10 (Table 1). During these 4 years, we caught an estimated 248,822 fish in round purse seine sets and an additional 58,194 fish in purse seine tows. These fish represented 27 species (Table 2), including all Pacific salmon species present in the Columbia River: Chinook, coho, chum, and sockeye salmon, steelhead, and sea-run cutthroat trout (*O. clarki*). We also documented the presence of 3 species of smelts (whitebait, longfin, and surf), 3 clupeids (Pacific herring, Pacific sardine [*Sardinops sagax*], and American shad), and 3 flatfishes (English sole, starry flounder [*Platichthys stellatus*], and sand sole [*Psettichthys melanostictus*]). Most fishes were present only in juvenile stages, although several species, including most of the forage fishes (e.g., northern anchovy, Pacific herring, longfin and surf smelts, and American shad), threespine stickleback, Chinook salmon, and steelhead, were present as both juveniles and adults.

Catches of individual species-and-age classes were highly variable both among species and years, as indicated by frequencies of occurrence (FO, Table 2) and coefficients of variation (CVs, Table 3), and likely reflected in part whether species were largely resident in the estuary, transitory, or migratory (anadromous). For example, 2 species—surf smelt (transitory) and threespine stickleback (resident)—were caught in almost every set (FO>80%). Other species caught fairly frequently included shiner perch, longfin smelt, Pacific herring, and American shad. Juvenile salmon exhibited varying levels of occurrence, with Chinook and coho salmon and steelhead caught in roughly half of all sets (FO=34–65%), whereas both chum and sockeye salmon were encountered less frequently (FO<24%). By contrast, many species were infrequently observed in our catches, including 15 species that were completely absent in at least one year (Table 2). Mean annual CVs, estimated for the most commonly caught species ranged from 47% (surf smelt in 2010) to 240% (northern anchovy in 2008), with juvenile salmon generally having lower CVs (range: 46–167%) than most species except surf smelt and threespine stickleback. Accordingly, the abundances of even our most commonly caught fishes were highly variable among sets.

Despite this fine-scale variability in abundances, however, the catch of fish each year generally followed a pattern of increasing abundance and species diversity as the spring advanced (Fig. 2). In all years except 2007 (which had higher overall abundances), mean CPUE (number/1000 m^2) per cruise was <50 in mid-April, increased to roughly 500 in May, and dropped slightly in June to 300. The seasonal change in abundance was accompanied by a change in species composition (Fig. 2B): in all years, the estuarine fish assemblage was dominated by threespine stickleback in April, becoming more diverse and variable in May and June with sporadically high relative abundances of northern

Table 2

Frequency of occurrence (%) for all fish species caught in open waters of the lower Columbia River estuary by year during our study during 2007–10. Life history stages: j=juvenile, a=adult, or subadult, with the "0" and "1" indicating subyearling and yearling Chinook salmon ages, respectively. If no life history stage is indicated, a mixture of ages were observed.

Common name	Scientific name	2007	2008	2009	2010
American shad	*Alosa sapidissima*	66.7	74.5	76.1	70.6
Chinook salmon (j, 0)	*Oncorhynchus tshawytscha*	63.3	58.2	63.0	49.0
Chinook salmon (j, 1)	*Oncorhynchus tshawytscha*	41.7	52.7	58.7	49.0
Chinook salmon (a)	*Oncorhynchus tshawytscha*	3.3	0.0	0.0	0.0
Chum salmon (j)	*Oncorhynchus keta*	15.0	23.6	21.7	23.5
Coho salmon (j)	*Oncorhynchus kisutch*	45.0	40.0	47.8	37.3
Cutthroat trout	*Oncorhynchus clarki*	1.7	1.8	0.0	3.9
English sole (j)	*Parophrys vetulus*	3.3	10.9	6.5	5.9
Kelp greenling (j)	*Hexagrammos decagrammus*	1.7	10.9	4.3	0.0
Lingcod (j)	*Ophiodon elongatus*	1.7	5.5	0.0	0.0
Longfin smelt	*Spirinchus thaleichthys*	16.7	16.4	23.9	7.8
Northern anchovy	*Engraulis mordax*	25.0	10.9	15.2	31.4
Pacific herring	*Clupea pallasii*	61.7	30.9	50.0	31.4
Pacific lamprey (a)	*Lampetra tridentata*	0.0	0.0	4.3	0.0
Pacific sand lance	*Ammodytes hexapterus*	0.0	1.8	0.0	0.0
Pacific sardine	*Sardinops sagax*	3.3	0.0	0.0	9.8
Pacific staghorn sculpin	*Leptocottus armatus*	1.7	0.0	13.0	3.9
Pacific tomcod (j)	*Microgadus proximus*	0.0	5.5	0.0	0.0
River lamprey (j)	*Lampetra ayresii*	3.3	5.5	0.0	11.8
Saddleback gunnel	*Pholis ornata*	1.7	3.6	2.2	2.0
Sand sole (j)	*Psettichthys melanostictus*	1.7	0.0	2.2	0.0
Shiner perch	*Cymatogaster aggregata*	30.0	45.5	47.0	21.6
Snake prickleback	*Lumpenus sagitta*	0.0	0.0	4.3	0.0
Sockeye salmon (j)	*Oncorhynchus nerka*	13.3	5.5	4.3	17.6
Sockeye salmon (a)	*Oncorhynchus nerka*	0.0	0.0	0.0	2.0
Starry flounder	*Platichthys stellatus*	1.7	3.6	0.0	5.9
Steelhead (j)	*Oncorhynchus mykiss*	35.0	34.5	52.2	56.9
Steelhead (a)	*Oncorhynchus mykiss*	3.3	0.0	2.2	2.0
Surf smelt	*Hypomesus pretiosus*	86.7	83.6	82.6	86.3
Threespine stickleback	*Gasterosteus aculeatus*	81.7	87.3	91.3	82.4
Whitebait smelt	*Allosmerus elongatus*	0.0	1.8	0.0	0.0

anchovy (especially in 2007 and 2010), Pacific herring (2007 and 2009), surf smelt (2008 and 2009), American shad (2008), and threespine stickleback (2008–10). This pattern of high relative abundance in particular years was associated with high absolute abundances of northern anchovy, Pacific herring, and surf smelt (Fig. 2), whereas variable abundances of threespine stickleback and American shad occurred despite consistent absolute abundances among years (Table 3). Juvenile salmonids were typically minor members of the estuarine assemblage (contributing <5% numerically), except in early May 2010 (cruise 10-3), when their contribution reached 39% of all fish caught. As with threespine stickleback and American shad, their absolute abundances were quite consistent among years.

Multivariate assemblage analyses Results of the multivariate assemblage analyses were consistent with the patterns described above: they indicated high variability at fine temporal scales (among hauls), and less variability at larger temporal scales (among cruises) or at spatial scales (between stations). For example, comparisons of specific subsets of pairwise Bray-Curtis similarity coefficients based on tidal stage or sampling station indicated that the fish assemblage of the Columbia River estuary was extremely dynamic at fine temporal scales (hours) and less dynamic in space. In particular, pairwise similarities calculated among hauls made at the same station and on the same day (311 comparisons) exhibited nearly as much variation (range: 0– 89.3%) as we saw between any 2 hauls across the entire 4 years of study (range: 0–98.8%). Furthermore, similarity coefficients were highest for hauls made close together in time (relative to low tide) and declined with increasing time between hauls. Specifically, mean pairwise similarities among hauls conducted within 1 h of each other (mean=64.0%), were greater than similarities for hauls occurring 1–2 h apart (61.3%), with the lowest mean

Table 3

Mean catch per unit of effort (CPUE, number/1000 m^2) and coefficients of variation (CV; %) estimated by cruise and averaged by year for the most commonly caught fish species in our study in open-water habitats of the lower Columbia River estuary. Also indicated is the rank of each species based on mean abundances averaged across years (1=most abundant).

		Year							
		2007		2008		2009		2010	
Species-and-age class	Rank	CPUE	CV	CPUE	CV	CPUE	CV	CPUE	CV
American shad	5	28.9	165.1	33.5	153.3	26.3	94.5	31.7	110.4
Chinook salmon									
subyearling	7	4.3	98.1	1.7	128.1	4.0	127.3	3.3	113.7
yearling	9	0.6	45.5	0.8	102.1	1.2	106.0	2.4	132.1
Coho salmon	8	1.1	111.0	1.1	166.8	1.6	142.9	1.3	132.6
Northern anchovy	1	1254.9	157.4	1.1	240.4	0.6	125.2	114.9	165.8
Pacific herring	3	295.2	185.3	1.8	173.8	39.9	118.4	0.8	100.5
Shiner perch	6	19.4	183.1	10.4	137.8	10.2	118.4	0.8	127.1
Steelhead	10	0.6	103.5	0.8	165.6	0.8	130.2	1.6	108.3
Surf smelt	4	14.7	54.5	67.2	162.5	30.6	100.1	10.0	47.0
Threespine stickleback	2	88.6	138.0	230.5	127.1	207.7	115.2	102.6	94.4

similarity among hauls made ≥5 h apart (mean=32.7%; KW H=99.6, P<0.05). In addition, pairwise similarities among sets made during the same cruise within 1 h of each other relative to low tide but at different stations (mean=51.5%) were lower than similarities among sets made at the same station (64.0%; MW U=6.9, P<0.05) and comparable with hauls made at the same station but 3–4 h apart. Taken together, these results suggest a highly dynamic estuarine fish assemblage at fine time scales with modest spatial variation.

We also used MDS plots to graphically evaluate variation in the fish assemblage at 2 scales (haul and cruise). This evaluation indicated that at fine time scales (haul) there was little correspondence between the fish assemblage and any time scale (e.g., time after low tide, cruise, biweek, year) or station (Fig. 3B). For example, hauls occurring within any particular 2-week period failed to form obvious assemblage groups but instead more or less spanned the range of MDS space. By contrast, when considered by cruise, there was a fairly clear pattern with the larger time scale (Fig. 3A). Results from the ANOSIM analysis were consistent with patterns observed in the MDS plots, showing better defined groups (i.e., higher Global R values) by cruise than by haul. When each haul was considered independently, no single or pair of variables produced well-defined groups (R<0.40), consistent with the lack of obvious groups in the MDS plot (Fig. 3B). In this analysis, the variable "biweek" produced the best groups (Global R=0.22), and inclusion of year in a 2-factor analysis increased biweek group separation (Global R=0.35) although year itself did not produce well-defined groups (Global R=0.00). When evaluated by cruise, results were similar to those results produced by haul: the single variable biweek provided the greatest group separation (Global R=0.43), and biweek produced more distinct groups (Global R=0.52) when combined with year.

Environmental forcing of assemblage composition We explored the environmental variables that best fitted the fish assemblage data, either by haul or averaged by cruise. When examined by haul, the environmental model producing the best fit (r=0.40, P<0.05) to the species composition data consisted only of in situ 7-m salinity, and models with fits that were only slightly poorer (0.39≤r≤0.40) included 7-m salinity, 1-m salinity, 1-m temperature, and coastal SST (which was correlated with 1-m temperature). These results suggest the fish assemblage is actively responding to environmental forcing at short temporal scales (hours) associated with tidal inundation and to a lesser extent with seasonal changes. The same analysis for fish assemblage averaged by cruise also indicated that the highest correlation occurred with a single variable, river water temperature (r=0.57, P<0.05), which is largely a seasonal signal. Other models with fairly high correlations (0.46≤r≤0.49) with the fish data included river temperature, coastal SST, PDO, and river flow. Given the strong correlations between river temperature and SST, and between river flow and the PDO, these results suggest the fish community is influenced from both types of climate signals: seasonal and river flow.

Juvenile salmon abundance and timing in the Columbia River estuary

Despite high variability in overall catches, the abundance and timing of juvenile salmon in the estuary was surprisingly consistent among years (Fig. 4). In

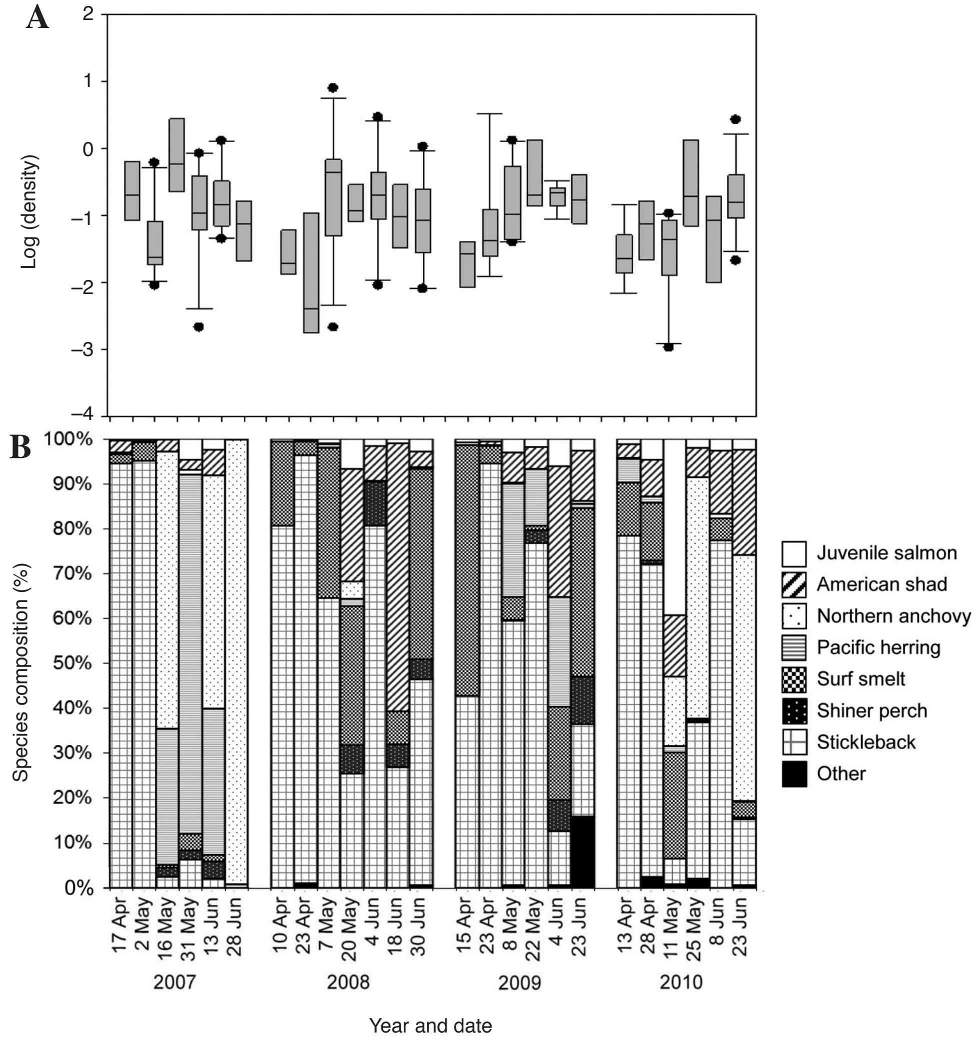

Figure 2

(**A**) Box plots of log-transformed density (number/m^2) and (**B**) percent composition of dominant fish species caught by cruise during spring of 2007–10. These species include American shad (*Alosa sapidissima*), northern anchovy (*Engraulis mordax*), Pacific herring (*Clupea pallasii*), surf smelt (*Hypomesus pretiosus*), shiner perch (*Cymatogaster aggregata*), and threespine stickleback (*Gasterosteus aculeatus*). The category of juvenile salmon includes all species-and-age classes of juvenile salmon combined: yearling and subyearling Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), chum salmon (*O. keta*), sockeye salmon (*O. gorbuscha*), and steelhead (*O. mykiss*). The box plots illustrate 25th and 75th percentiles (lower and upper edges of box, respectively), the median (line within the box), 10th and 90th percentiles (whiskers [error bars] below and above the box, only on cruises when $n \geq 9$), and dots indicate outliers (<10th or >90th percentiles).

mid-April, when sampling began, catches of all juvenile salmon were extremely low (CPUE<1/1000 m^2). As the spring progressed, the abundances of juvenile salmon increased. Maximum abundances occurred in mid-May for yearling Chinook and coho salmon and steelhead, a somewhat earlier peak in abundance occurred in early May for chum salmon, later peaks in abundance occurred in early June for sockeye salmon, and late June or early July for subyearling Chinook salmon. Consequently, when sampling stopped in late June or early July, only subyearling Chinook salmon were still being caught (Fig. 4). The magnitude of peak abundances also exhibited species-specific variation, with the lowest peak abundances observed for chum and sockeye salmon (CPUE<2/1000 m^2), moderate levels seen for yearling Chinook and coho salmon

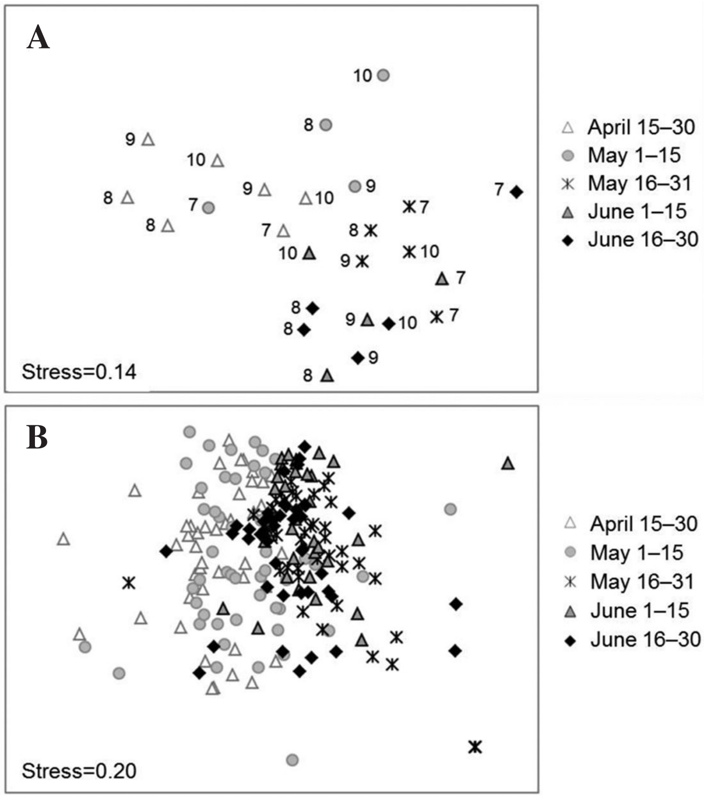

Figure 3

Nonmetric multidimensional scaling (MDS) by (**A**) cruise and (**B**) haul based on the 13 most commonly caught species-and-age classes in the Columbia River fish assemblage during spring of 2007–10. Sampling years in the top graph are abbreviated: 7 for 2007, 8 for 2008, 9 for 2009, and 10 for 2010.

and steelhead (CPUE=2–5/1000 m^2), and the highest abundances estimated for subyearling Chinook salmon (CPUE=8–10/1000 m^2). There was also variation in the length of time that salmon were present in the estuary: both chum and sockeye salmon were caught typically only during a 2–4 week period, yearling Chinook and coho salmon and steelhead were caught readily in the estuary for 6–8 weeks each year, and subyearling Chinook salmon were present for at least 2 months (and presumably longer but sampling was terminated).

We also observed interannual variation in this seasonal abundance pattern, although no single year was associated with exceptional catches for any species-and-age class of juvenile salmon (Fig. 4). For example, the timing of maximum abundances of yearling Chinook and coho salmon and steelhead occurred in late May in 2007 and early May in 2009 and 2010 and subyearling Chinook salmon occurred early in 2009 and 2010 and late in 2008. Similarly, we observed no consistent patterns in the magnitude of maximum abundances; peak abundances for most species, except sockeye salmon, were low in 2007, yet levels were high for chum salmon in 2008, coho salmon in 2009, and steelhead and yearling Chinook salmon in 2010.

Origins of juvenile salmon

We determined the origins of juvenile salmon by both rearing conditions (hatchery vs. wild) and geographic location. From the number of clipped adipose fins we observed in our catches and the number of fish clipped basinwide at hatcheries, we concluded that most juvenile salmon that we collected were of hatchery origin (Table 4); this percentage ranged from 91% for steelhead to 99% for coho salmon, with estimates exceeding 100% for both coho and subyearling Chinook salmon in some years.

We also were able to determine geographic origin for 508 juvenile salmon from which we recovered CWTs and for 38 juveniles with PIT tags (Table 5). These tagged fish originated from locations throughout the Columbia River basin—lower, mid-, and upper Columbia River and the Snake and Willamette rivers. In a notable exception to this pattern, tagged steel-

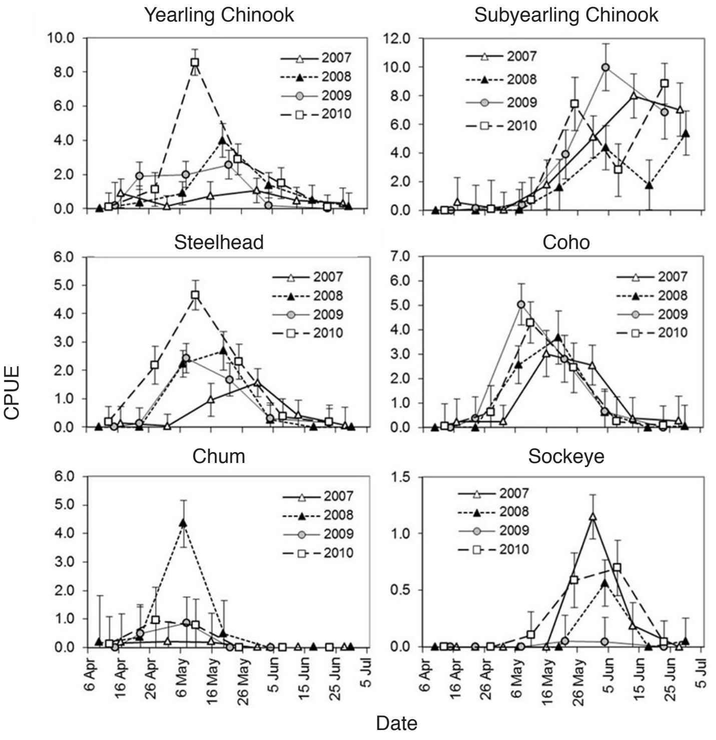

Figure 4

Catch per unit of effort (CPUE) of juvenile salmonids—yearling and subyearling Chinook salmon (*Oncorhynchus tshawytscha*), steelhead (*O. mykiss*), coho salmon (*O. kisutch*), chum salmon (*O. keta*), and sockeye salmon (*O. nerka*)—by date and year in the Columbia River estuary during spring of 2007–10; CPUE values are given as number/1000 m^2 ±1 standard error of the mean (SE).

head originated only from the Snake or mid-Columbia rivers (PIT tag) or Snake and upper Columbia rivers (CWTs).

Fish size

Relative length The length of commonly caught fishes in our study varied considerably, from large (>280 mm) American shad and juvenile steelhead to consistently small (<70 mm) three-spine stickleback (Fig. 5). Because juvenile steelhead were the largest juvenile salmon, only large American shad were of similar size. In contrast, the length range of coho and Chinook salmon overlapped the size of many commonly caught species, including northern anchovy, Pacific herring, shiner perch and surf smelt. The size range for many fishes (e.g., American shad, surf smelt, and Pacific herring) was quite broad because of mixtures of both juvenile and adult ages in our catches.

Juvenile salmon size The size of juvenile salmon generally varied by year and season, although no clear cross-species (i.e., year-specific) patterns were observed in any of the comparisons. For mean length by year, statistically significant differences among years were observed for all species and age classes ($H \geq 11$, $P<0.05$), except for coho salmon ($P>0.10$; Fig. 6). However, these interannual differences were generally small, with absolute mean size differences ranging from 4.7 mm (yearling Chinook) to 11.6 mm (steelhead), which translated to a 3–14% difference in length between years. The mean size of juvenile sockeye salmon showed

Table 4

Estimated percentage of juvenile Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon and steelhead (*O. mykiss*) of hatchery origin caught in open waters of the lower Columbia River estuary. Hatchery percentages were estimated from the percentage of clipped adipose fins observed in the estuary catches divided by the percentage of clipped fish released from hatcheries, averaged over the 4 years of our study, 2007–10. Also included are the mean number of juvenile salmon released annually and the percentage of fish clipped at hatcheries. Hatchery release numbers and information on clipped fish are from the Fish Passage Center (data available at http://fpc.org/, accessed July 2011). Chinook 0 and Chinook 1 refer to subyearling and yearling age classes, respectively.

	Species-and-age class			
	Chinook salmon 0[a]	Chinook salmon 1	Coho salmon	Steelhead
Hatchery release (millions)	49.5	32.4	22.4	15.0
Percentage clipped at hatchery	75.7	91.9	67.8	85.4
Percentage clipped (observed in estuary)	76.0	86.9	76.9	77.6
Estimated percent hatchery	95.7[b]	94.6	99.0[b]	90.9

[a] Includes only hatchery fish released at least 10 days before the final cruise of the season: before June 19 in 2007 and 2008 and June 14 in 2009 and 2010.

[b] Capped at 100% in some years; therefore, estimated percent hatchery does not equal the percent clipped in estuary divided by percent clipped at hatchery.

Table 5

Geographic origins of Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon and steelhead (*O. mykiss*) caught during spring of 2007–10 in the lower Columbia River estuary, determined on the basis of recovery of coded wire tag (CWT) and passive integrated transponder (PIT) tags, shown by major regions of the Columbia River basin. Chinook 0 and Chinook 1 refer to subyearling and yearling age classes, respectively. No tagged steelhead were released in the Willamette and lower Columbia Rivers.

	Species-and-age class							
	Chinook 0		Chinook 1		Coho		Steelhead	
	PIT	CWT	PIT	CWT	PIT	CWT	PIT	CWT
Number of tags recovered	0	127	27	254	2	87	9	33
Release or tagging region[1]	Percentage of tags recovered by region							
Lower Columbia River		29.9	3.7	5.9	0	54.1	0	0
Willamette River		0	0	4.3	0	1.1	0	0
Mid-Columbia River		48.8	14.8	14.6	0	3.4	11.1	0
Upper Columbia River		0.8	29.6	42.1	100	39.1	0	21.2
Snake River		20.5	51.9	33.1	0	2.3	88.9	78.8

[1] Release or tagging regions: lower Columbia River—below river km (rkm) 235 (Bonneville Dam), excluding the Willamette River; Willamette River—all locations in the Willamette River; mid-Columbia River—between Bonneville Dam and confluence with the Snake River (rkm 522); upper Columbia River—accessible waters above the confluence with the Snake River (rkm 522); Snake River—all accessible waters of the Snake River beginning at rkm 522.

the largest variation (annual means ranged from 104 to 135 mm), but the larger size likely reflects that some fish emigrated as 2-year-old smolts (age 2.0) rather than as yearlings (age 1.0). In addition, when mean size was examined across all years, in any given year at least one species-and-age class of juvenile salmon was the largest and one was the smallest, with the exception of 2008, when no species-and-age classes were the smallest. This result suggests that interannual variability in juvenile salmon size was independent for each group (Fig. 6).

We also observed seasonal changes in the size of juvenile salmon; the seasonal size data, like the annual size data, displayed no cross-species patterns. Both coho and yearling Chinook salmon declined in length as the season progressed, whereas steelhead and subyearling Chinook salmon increased in length. Taking into account this seasonal change in length, the mean size of both juvenile subyearling Chinook salmon and steelhead varied by year (ANCOVA test of means, variance ratio [F]>8.0, $P<0.01$), but the size of yearling Chinook and coho salmon did not (ANCOVA test of means, $F\leq1.8$, $P>0.10$). We examined the length–weight relationships of juvenile salmon; common slopes (across all years) between transformed length and weight data ranged from 0.312 for yearling Chinook salmon ($n=658$) to 0.329 for subyearling Chinook salmon ($n=776$), with intermediate slopes for steelhead (0.325, $n=250$) and coho salmon (0.315, $n=637$). Coho salmon and both age classes of Chinook salmon had different slopes between length and weight among years (ANCOVA test of slopes, $F\geq2.3$, $P<0.05$), but, for steelhead, no difference in slope was detected during the 3 years for which data were available (2008–10; $F<1.0$, $P>0.10$).

Finally, we compared the size of clipped (hatchery) and unclipped (wild and hatchery) fish to determine whether clipped hatchery fish were consistently larger than unclipped fish (Fig. 7), as might be the case if most unclipped fish were of wild origin. Examined across all cruises and years, clipped individuals were statistically larger than unclipped fish for coho salmon (mean lengths of 148.7 vs. 140.6 mm, respectively; Two sample $t=6.9$, $P<0.05$) and steelhead (221.6 vs. 198.2 mm, respectively; two sample $t=11.1$, $P<0.05$), but no difference was detected for subyearling or yearling Chinook salmon ($t<1.0$, $P>0.10$). When examined for differences among cruises (to account for seasonal changes in size) the findings were the same: significant differences for coho salmon and steelhead (two-way ANOVA, $F\geq36$, $P<0.05$) but not subyearling or yearling Chinook salmon (two-way ANOVA, $F\leq1.0$, $P>0.10$) (Fig. 7). In addition, we found interaction effects ($F\geq1.8$) for all species at a significance level of $P<0.10$, indicating that although clipped individuals were generally larger than unclipped individuals by cruise, the patterns were not consistent across all cruises.

Discussion

The pelagic fish assemblage we observed in open waters of the lower Columbia River estuary during spring 2007–10 was characteristic of other Pacific Northwest estuaries including those assemblages examined in earlier studies in the Columbia River (e.g., Haertel and Osterberg, 1967; McCabe et al., 1983; Fox et al., 1984; Bottom and Jones, 1990). Many of these species are also commonly caught in marine waters near the mouth of the Columbia River (Brodeur et al., 2005). All species are native to the Columbia River estuary and the Pacific Northwest, with the exception of American shad. This species was introduced into the Columbia basin from the U.S. Atlantic coast (Wydoski and Whitney, 2003) and is currently the single most abundant anadromous fish species in the Columbia River (Hasselman et al., 2012a).

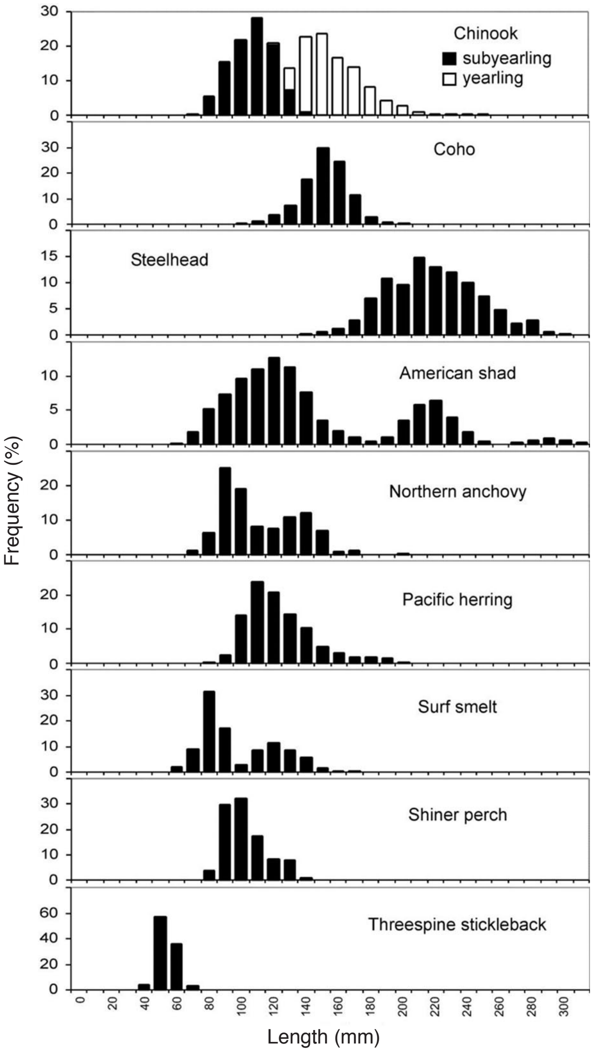

Figure 5

Distributions (%) of length (fork or total; in mm) frequency for selected fish species—Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), steelhead (*O. mykiss*), American shad (*Alosa sapidissima*), northern anchovy (*Engraulis mordax*), Pacific herring (*Clupea pallasii*), shiner perch (*Cymatogaster aggregata*), surf smelt (*Hypomesus pretiosus*), and threespine stickleback (*Gasterosteus aculeatus*)—captured in the Columbia River estuary during 2007–10, all years combined.

The fish assemblage as a whole was extremely dynamic with large variation at daily, seasonal, and interannual time scales. Although there was a general pattern of increasing abundance and species diversity as the season progressed, we often observed nearly as much variation within a single day or cruise as we did within the entire 4 years of our study. Our results indicate that the fish assemblage was responding to environmental forcing at both local (e.g., tide and salinity) and seasonal (e.g., river temperature) time scales. Not surprisingly, this conclusion is similar to the determinations of earlier studies: the fish assemblage was influenced by tides, season, and river flow (Haertel and Osterberg, 1967; Bottom and Jones, 1990; Jones et al., 1990; Simenstad et al., 1990).

Our results are consistent with (and likely in response to) highly dynamic and complex physical circulation in the estuary. Columbia River estuarine circulation is influenced by both riverine processes (e.g., seasonal flow cycles) and ocean processes (e.g., wind-forced upwelling and daily tidal inundation) and their interactions, which result in circulation patterns and water column properties that vary at temporal scales ranging from minutes to years (Jay and Smith, 1990; Chawla et al., 2008; Roegner et al., 2010b). In addition, the north and south channels each have distinct circulation dynamics: strong river flow and a weak salt wedge in the south channel and more salinity intrusion and less river flow in the north channel (Jay and Smith, 1990; Chawla et al., 2008). Given these physical differences between the 2 channels (and, therefore, our study sites), it is surprising that our catches at the 2 stations were not more different than they were.

In addition to physical forcing, variation in the estuarine fish assemblage also reflects use patterns by different species-and-age classes of fish (Bottom and Jones, 1990; Simenstad et al., 1990). For example, many of the species that we caught frequently are typical euryhaline estuarine residents for at least part of their life cycle; this list includes surf smelt, threespine stickleback, shiner perch, longfin smelt, and juvenile Pacific herring and American shad. Primarily marine species (northern anchovy, whitebait smelt, Pacific sardine, lingcod [*Ophiodon elongatus*], and Pacific tomcod [*Microgadus proximus*]) were caught less consistently in the estuary, likely a reflection of seasonal patterns of estuarine use, offshore abundances, and whether conditions in the Columbia River estuary were favorable for occupation (Bottom and Jones, 1990). Finally, many species use the estuary primarily as a migration corridor and were, therefore, consistently caught every year at modest frequencies; downstream migrants include all juvenile salmon and river lamprey (*Lampetra ayresii*), and upstream migrants were adult age classes of American shad, Pacific lamprey (*Lampetra tridentata*), Pacific herring, Chinook salmon, and steelhead.

We observed changes in the fish assemblage in response to high flow events in 2008 and 2010; these

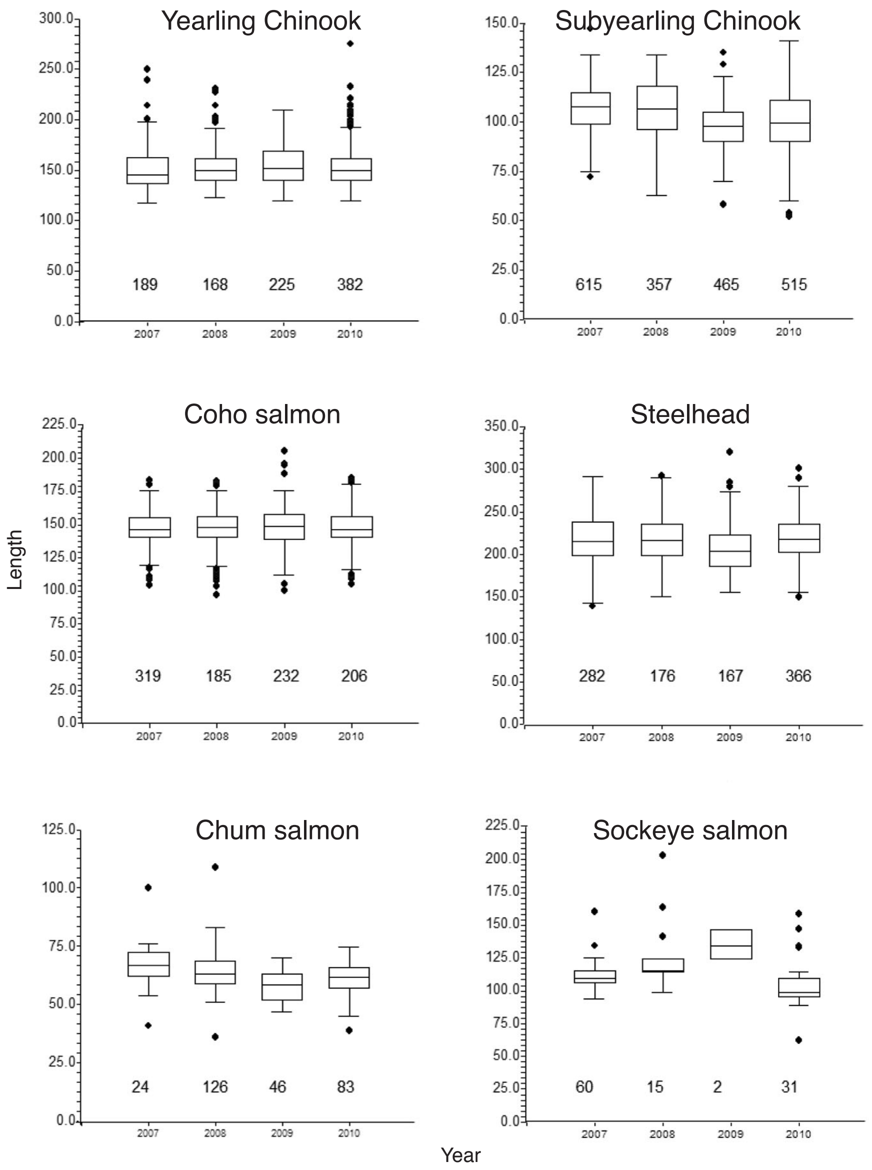

Figure 6

Box plots of fork length (mm) by year for each juvenile salmon species-and-age class: yearling and subyearling Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), steelhead (*O. mykiss*), chum salmon (*O. keta*), and sockeye salmon (*O. nerka*). The box plots illustrate 25th and 75th percentiles (lower and upper edges of box, respectively), the median (line within the box), 10th and 90th percentiles (whiskers [error bars] below and above the box), and dots indicate outliers (<10th or >90th percentiles). Samples sizes are provided below each box. Scales for each graph are different to emphasize species-specific patterns.

events served as natural experiments for the influence of flow. High flow rates influence water column properties and circulation patterns in the estuary (Jay and Smith, 1990; Chawla et al., 2008), including the decline of maximum surface salinity that we observed with increasing flows. Estimated residence time of water in the Columbia River estuary also was much shorter during high flows in 2008 than in 2007, 2009, or 2010 (CCMOP, 2010). High flows also may cause direct, species-specific behavioral responses in fish, including downstream displacement (Dege and Brown, 2004; Purtlebaugh and Allen, 2010). Northern anchovies seem particularly sensitive to high river flows as indicated by their near absence when flows were high in 2008 (cruise 8-4 in

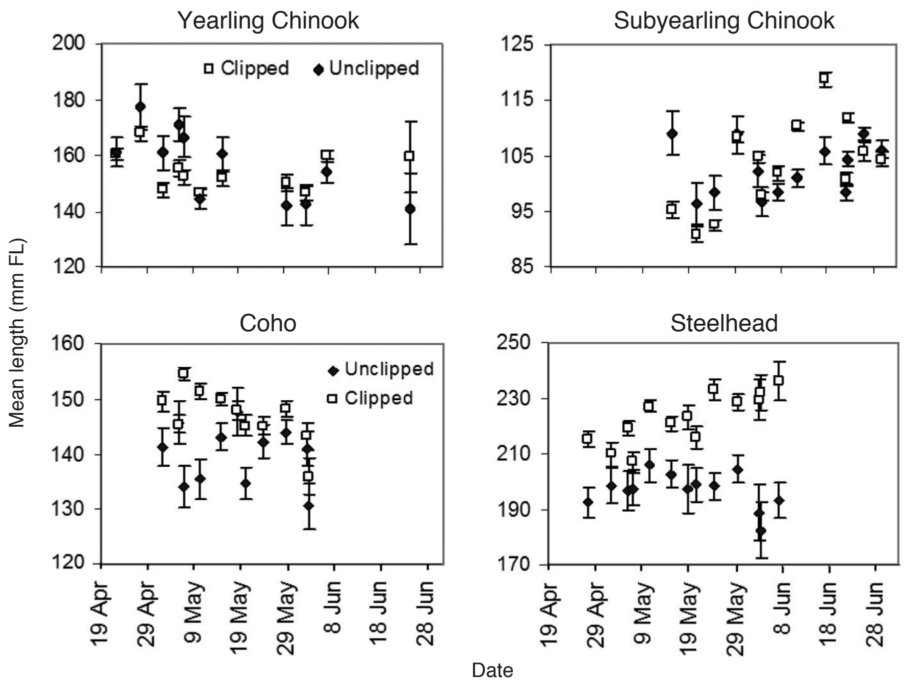

Figure 7

Mean fork length (FL, in millimeters ±1 standard error [SE] of the mean) of clipped (hatchery) and unclipped (wild and hatchery) juvenile salmonids—yearling and subyearling Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), and steelhead (*O. mykiss*)—arranged by sampling date (all years combined).

June onwards) and again on 8 June 2010 (cruise 10-5) during the brief high flow event. Northern anchovy are primarily a marine species but move into estuaries from marine waters in the spring and summer (Fox et al., 1984; Bottom and Jones, 1990). We observed daily movement into the estuary with the flood tide; our largest catches (CPUE>300/1000 m^2) of this species occurred an average of 5 h after low tide when both 1-and 7-m salinities were relatively high (5 and 21 psu, respectively). Given the largely marine nature of northern anchovy, we believe the high flows inhibited their entry into the estuary. In contrast, low abundance of northern anchovy in the estuary in 2009, a year with "normal" flow, was likely a result of their low abundance in marine waters off the mouth of the Columbia River during the spring of 2009 (M. Litz, unpubl. data).

We also suspect that high flows may displace juvenile salmon downstream and transport them rapidly through the Columbia River estuary. For example, in the years with normal flow (2007 and 2009), juvenile Chinook and coho salmon and steelhead reached peak abundances on different dates, and they were at modest abundances (CPUE≥2/1000 m^2) for 6–8 weeks. In contrast, in 2008 all yearling fish reached peak abundances on 20 May (cruise 8-4) as the flow was rapidly increasing, with much lower catch rates on the cruise after (but not before) 20 May. This finding suggests that the fish were being flushed downstream. Other research efforts in the Columbia estuary have shown that juvenile salmon initiate migration in response to increasing flows (Coutant and Whitney, 2006) and that migration rates are highest during high flows (Giorgi et al., 1997; Friesen et al., 2007). It currently is unknown whether juvenile salmon might also respond to high flows by moving laterally into shallower water. Because both migration timing and flow rates influence juvenile salmon behavior and survival (Scheuerell et al., 2009; Petrosky and Schaller, 2010), better understanding of these fine-scale processes is essential for conservation and recovery of at-risk salmon populations.

Predation is a likely source of mortality for juvenile salmon in the Columbia River estuary (ISAB[1]). Therefore, knowing who the predators are is essential. We caught several fishes that can be piscivorous as adults (e.g., lingcod and Pacific tomcod; Love, 2011); however, all individuals were juveniles (and often smaller than juvenile salmon) and therefore unlikely predators of juvenile salmon in the estuary. Three potential piscine predators were cutthroat trout and adults of both spring Chinook salmon and steelhead, all of which are highly piscivorous (Quinn, 2005; Duffy and Beauchamp 2008). Whereas cutthroat trout have relatively small populations in the Columbia River (ISAB[1]), both spring Chinook salmon and steelhead have large populations:

during 2007–10, the estimated in-river run size of adult spring Chinook salmon averaged 400,000 fish (PFMC, 2011), and an average of 21,000 steelhead were counted crossing Bonneville Dam between April 15 and June 30 (FPC database). Although adult salmon generally are believed to cease feeding once they enter freshwater (Groot and Margolis, 1991; Quinn, 2005), if they continue to feed while in the Columbia River estuary, their predation effect on juvenile salmon may be considerable. Unfortunately, we were unable to examine adult salmon diets because of restrictions on ESA-listed species. Despite considerable focus on other piscine predators in freshwater regions of the Columbia River (ISAB[1]), this potential predation source has been largely overlooked but clearly deserves further attention.

Several highly visible predators in the Columbia River estuary (e.g., harbor seals [*Phoca vitulina*], California [*Zalophus californianus*] and Stellar [*Eumetopias jubatus*] sea lions, Caspian Terns [*Hydroprogne caspia*], and Double-crested Cormorants [*Phalacrocorax auritus*]) consume many of the fish species we caught in our study (e.g., anchovy, smelt, clupeids, and shiner perch), including juvenile salmon (Collis et al., 2001; Browne et al., 2002; Anderson et al., 2004, Anderson et al., 2007; Lyons et al., 2007). A primary objective of research on avian predators in the Columbia River estuary is to identify factors influencing predation rates on juvenile salmon, including the abundance of alternative prey (Anderson et al., 2007; Lyons et al., 2007). However, these studies have been hampered by a lack of direct measurements of the fish assemblage or information regarding how it varies at seasonal or annual time scales. Our results provide this critical information and even simple comparisons offer unique insight. For example, the size distribution of forage fishes in our study fully overlaps the size distribution of juvenile salmon (Fig. 5), suggesting that forage fishes are appropriate prey for predators focused on fish that are the size of salmon. In addition, the proportions of salmon in the diets of both Caspian Terns and Double-crested Cormorants are consistently highest in early May (Bird Research Northwest [BRN], http://www.birdresearchnw.org, accessed August 2011), at a time when yearling salmon abundance is rapidly increasing (Fig. 4), yet densities of forage fish are still relatively low (Fig. 2). Furthermore, our findings that river flow influences the estuarine fish assemblage were successfully used to relate flow to the diets of Caspian Terns (Lyons, 2010). Future analyses will include comparisons of the abundance and size of fish (both salmon and nonsalmonids) in the environment and in predator diets to gain further understanding of the dynamics of this important predator–prey relationship.

Juvenile salmon in the Columbia River estuary

Compared with high variation in the overall fish assemblage, the seasonal pattern of juvenile salmon abundance was quite consistent between years (Fig. 4, Table 3). These seasonal patterns are similar to the patterns reported in studies conducted in the Columbia River estuary in the late 1970s and early 1980s (Dawley et al.[2]; McCabe et al., 1983; Bottom and Jones, 1990) and typical of other Northwest estuaries (Bottom and Jones, 1990; Groot and Margolis, 1991; Quinn, 2005). We also observed consistency between contemporary migration patterns and those patterns determined before the advent of large-scale hatchery production and other anthropogenic changes in the Columbia River basin and estuary (Sherwood et al., 1990; NRC, 1996). In particular, Burke (2004) analyzed migration patterns of juvenile Chinook salmon through the Columbia River estuary in 1914–16 using data provided by Rich (1920). This early study found that yearling Chinook salmon migrated through the estuary at approximately the same time that we find (peak in mid-May and low in late June), although they (Rich, 1920; Burke, 2004) also observed an earlier abundance peak in March. We did not sample during March; however, we did not observe elevated abundances in mid-April (suggestive of an earlier abundance peak), nor was one apparent in the daily smolt counts at Bonneville Dam that commence each spring in early March (FPC database). The size of these historical yearling migrants (80–125 mm FL; Burke, 2004) also was much smaller than the size we currently observe (Fig. 6), although part of the size difference may result from a different sampling location. Juvenile salmon collected near shore (where Rich [1920] likely collected his fish) tend to be smaller than the ones collected in open waters (senior author, unpubl. data). Our trends for subyearling salmon most closely mirror the “fingerling-estuarine rearing” group described by Burke (2004) that was at low abundance in mid-May, reached peak abundance in mid-July, and continued to be present in the estuary through fall. Like yearling migrants, these historical fish (mean size ~85 mm FL) were smaller than the fish we currently catch, but they also were caught near shore where we expect they would have been smaller.

Similar to our findings, Dawley et al.[7] observed a similar composition of juvenile salmon by species-and age-class by month during 1978–80, with approximately equal abundances of subyearling and yearling Chinook and coho salmon and steelhead in May and mainly subyearling Chinook salmon in June (Fig. 8B). However, in April, we caught more subyearling Chinook salmon and chum salmon than the earlier catches, which had higher levels of yearling Chinook and coho salmon. The higher chum catches that we observed likely reflect a modest increase in the Columbia River chum populations (Ford, 2011). It is not apparent why we observed higher proportions of subyearling Chinook salmon in

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[7] Dawley, E. M., R. Ledgerwood, and A. L. Jensen. 1985. Beach and purse seine sampling of juvenile salmonids in the Columbia River estuary and ocean plume, 1977–1983: vol. I: Procedures, sampling effort, and catch data. Final report of research funded by Bonneville Power Administration. [Available from Northwest Fisheries Science Center, 2725 Montlake Blvd. E., Seattle, WA 98112.]

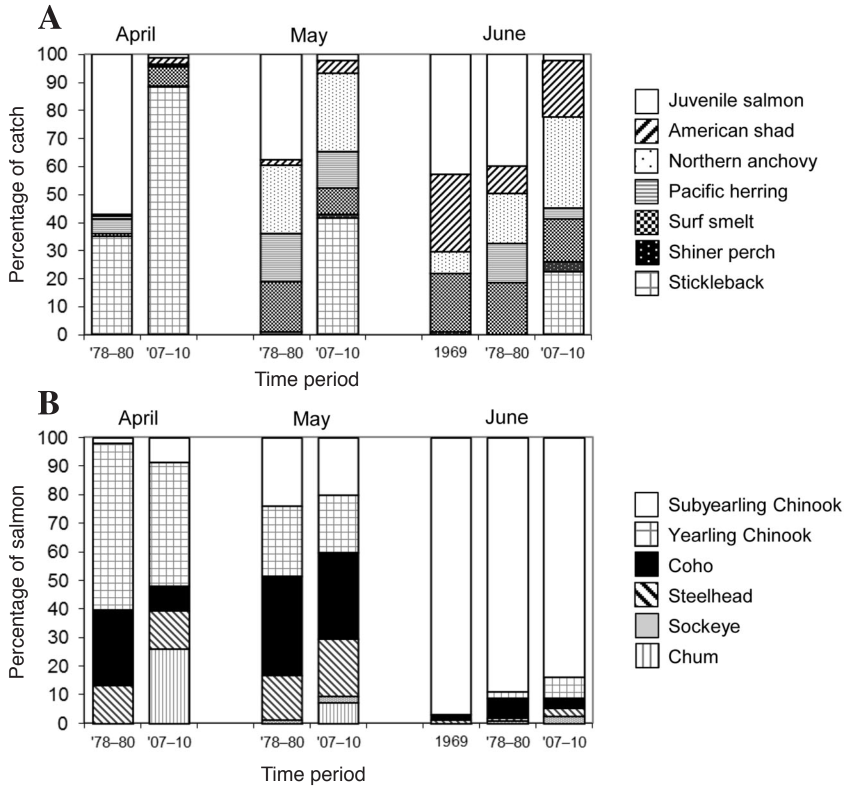

Figure 8

Comparison of purse seine catch data, summarized by month and time period from historical studies (1969, 1978–80) and our recent study (2007–10) of the fish assemblage in the lower Columbia River estuary. (**A**) Relative abundances of the dominant fish species—juvenile Pacific salmon (*Oncorhynchus* sp.; all species and age classes combined), American shad (*Alosa sapidissima*), northern anchovy (*Engraulis mordax*), Pacific herring (*Clupea pallasii*), surf smelt (*Hypomesus pretiosus*), shiner perch (*Cymatogaster aggregata*), and threespine stickleback (*Gasterosteus aculeatus*). (**B**) Species-and-age composition of juvenile salmon, which comprises subyearling and yearling Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), steelhead (*O. mykiss*), sockeye salmon (*O. nerka*), and chum salmon (*O. keta*). Data sources for other two studies: for the year 1969—Johnsen and Sims, 1973; for the years 1978–80—Dawley et al.[7] Johnsen and Sims (1973) did not differentiate between subyearling and yearling (age 1) Chinook salmon; therefore, all fish of this species were assigned to the subyearling Chinook category.

April, but our observation may reflect changes in hatchery practices.

Recoveries of fish tagged with CWTs and PIT tags indicate that individuals originated from all accessible portions of the Columbia River, including the lower, mid-, and upper Columbia and Snake and Willamette rivers (Table 5)—an observation that also was made in an earlier study (Dawley et al.[2]). However, tagging effort is not consistent throughout the Columbia River (RMIS database; FPC database); therefore, the relative number of fish originating from different parts of the Columbia River provided in Table 5 reflects both fish origins and tagging effort. In the extreme case, we recovered steelhead with CWTs from only the upper Columbia and Snake rivers because those basins are the only areas where steelhead tagged with CWTs are released.

Perhaps most surprising was our estimate that most of the juvenile salmon that we caught were of hatchery origin (91–99%; Table 4), percentages that are considerably higher than the hatchery percentages reported for adults (34–80%; NRC, 1996; ISAB[1]). The percentages of clipped subyearling (76.0%; Table 4) and yearling (86.9%) Chinook salmon we observed were also higher than the percentages reported for juvenile subyearling and yearling Chinook salmon collected in nearby shallow water with a beach seine in 2007–08 (53.2% and 73.7%, respectively; Roegner et al., in press). This finding suggests that relatively more unclipped (presumably wild) Chinook salmon were closer to shore.

This overwhelming hatchery origin is consistent with the low variation we observed in the timing of juvenile salmon presence and abundance in the estuary (Fig. 4) and fish size (Fig. 6), given that most hatchery fish are released at a target size and date, with little variation from year to year (FPC database). Accordingly, we would expect to see greater variation in both timing and size of salmon if more fish were of wild origin, because of the greater fine-scale life history diversity observed in other wild-dominated systems and historically within the Columbia River (Rich, 1920; Myers and Horton, 1982; Burke, 2004, Bottom et al., 2005; Campbell, 2010).

For our calculation of the percentage of hatchery fish, we assumed that the survival of all hatchery fish migrating from the hatchery to the estuary is equal. However, this assumption is unlikely to be true because fish that travel longer distances and pass through more mainstem dams have greater mortality (Williams et al., 2001). This differential mortality undoubtedly contributed to the inflated percentages of hatchery subyearling Chinook and coho salmon we estimated (>100% in multiple years because percentages of clipped fish in our catches exceeded percentages of clipped fish reported at hatcheries). For these 2 groups, survival rates were likely to differ by distance from the estuary, and the percentage of clipped fish varied as well. The percentage of clipped subyearling Chinook and coho salmon released in the upper Columbia and Snake rivers were much lower (43–46% for subyearling Chinook, 7–36% for coho) than the percentage of fish released lower in the basin (90% for subyearling Chinook, 76% for coho). Although these releases in the upper basin are a small fraction (<29%) of the total releases every year, higher expected mortality rates would inflate our estimates of hatchery influence, likely contributing to our extremely high estimates for both species. Consequently, the percentage of clipped fish we observed in the estuary for these 2 species (76–77%, Table 4) represent the minimum hatchery influence; the true level of hatchery influence cannot be estimated without methods of assigning origin for unclipped fish (e.g., using scales, otoliths, or other means). This bias should not influence estimates for yearling Chinook salmon or steelhead, however, because mark rates are more consistent across the Columbia basin (FPC database). Clearly, clipping all hatchery fish would greatly increase our ability to identify hatchery fish and result in better estimates of hatchery influence and detection of potential ecological interactions.

We also observed that clipped (hatchery) coho salmon and steelhead were larger than their unclipped (hatchery and wild) counterparts. In stream environments, such size discrepancies have been shown to have negative consequences for wild fish (Weber and Fausch, 2005), although whether this finding applies to estuarine environments has not been addressed (Naish et al., 2008). Two recent studies in which juvenile (age 1.0) Chinook and coho salmon were examined in marine environments revealed no evidence for competitive advantage (in the form of feeding intensity or prey selection) of larger hatchery individuals over their unclipped (and smaller) counterparts (Sweeting and Beamish, 2009; Daly et al., 2011).

We did not observe a size difference between clipped and unclipped subyearling and yearling Chinook salmon. However, actual size variation between clipped and unclipped Chinook salmon may have been confounded by our length-based age assignment; small, unclipped yearling Chinook salmon may have been incorrectly assigned to the subyearling age category while large, clipped subyearling Chinook salmon may have been assigned to the yearling category. In addition, the size of Chinook smolts released from different hatcheries can vary greatly (FPC database), adding to the confusion. Restriction of such size comparisons to specific salmon stocks (e.g., Daly et al., 2011) would help resolve this issue.

Historical comparisons of fish communities in the lower Columbia River estuary

The fish assemblage we observed in 2007–10 generally was similar to that documented 3 or more decades earlier (Haertel and Osterberg, 1967; McCabe et al., 1983; Bottom and Jones, 1990). For example, all the species that we consistently caught (Tables 2, 3) were listed as commonly occurring in lower estuary pelagic habitats by earlier researchers (e.g., McCabe et al., 1983; Dawley et al.[7]; Bottom and Jones, 1990). As in these earlier studies, we did not catch any marine fish that might be predatory on juvenile salmon (e.g., adult lingcod, Pacific hake [*Merluccius productus*], and Pacific chub mackerel [*Scomber japonicus*]), with the exception of adult salmon. Haertel and Osterberg (1967) report that Pacific tomcod were a common species in their survey of estuarine fish in the 1960s (both juveniles and older fish), and Dawley et al.[7] report occasionally catching eulachon (*Thaleichthys pacificus*) and redtail surfperch (*Amphistichus rhodoterus*), neither of which we have encountered. Although the absence of eulachon in our catches is likely due to their recent population decline (Gustafson et al., 2011), the reason for the absence of other fishes is unknown.

The difference in abundance of American shad (which were primarily juveniles) in the estuary in 1978–80 and in 2007–10 (in our study) is consistent with changes in counts of adults across Bonneville Dam (FPS database). Specifically, data from Dawley et al.[7] indicates that American shad contributed 1%, 2%, and 10% to the fish assemblage in April, May, and June, respectively, in 1978–80, when dam counts averaged 947,000 adults. The relative abundance of American shad we observed in our study was roughly twice as high (2%, 5%, and 20% in April, May, and June, respectively), consistent with twice as many adults crossing Bonneville Dam in 2007–10 (1.8 million; FPS database). By contrast, Johnsen and Sims (1973) report that in 1969, 27% of all fish caught were American shad, at a time when only 317,000 adults were counted crossing Bonneville Dam; the reason for this apparent discrepancy is unknown. Given the rapid expansion of American shad within the Columbia River (Hasselman et al., 2012a) and in marine waters along the west coast of North America (Pearcy and Fisher, 2011), there is increasing concern about the potential impacts of this exotic species on riverine, estuarine, and marine ecosystems (Pearcy and Fisher, 2011; Hasselman et al., 2012b).

As in our study, purse seines were used in 2 previous studies conducted in 1969 (Johnsen and Sims, 1973) and in 1978–80 (Dawley et al.[2, 7]) to sample the fish assemblage in open waters of the lower Columbia River estuary. However, these earlier studies used different-size nets (in length and depth but not mesh size) that were towed for 10 min before being closed. This methodological difference makes abundance comparisons among studies problematical, although we assume that species composition would be less affected (see discussion later in this section). These studies used the North Channel sampling location, eliminating possible site-specific differences. Comparison of the overall fish assemblage in the 3 time periods (1969, 1978–80, and 2007–10) indicates that the relative abundances of threespine stickleback and juvenile salmon are quite different between the earlier years and the most recent years (Fig. 8). Specifically, juvenile salmon in our study made up a small fraction (2%) of the overall catch, but historically they contributed between 43% and 57% of the total number of fish caught. In contrast, threespine stickleback were much more abundant in our study (averaging 88% of fish caught in April to 22% in June) than in earlier surveys (35% in April, <1% in either May or June) (Fig. 8A). Such changes in this estuarine fish community, if true, seem surprising at first glance but really are not unexpected given the substantial changes to fish assemblages documented farther upstream (Hughes et al., 2005; Maret and Mebane, 2005).

The relatively high proportion of juvenile salmon in estuarine catches in the late 1970s compared with that found in our study in 2007–10 could be a result of either lower juvenile salmon abundances, higher abundances of nonsalmon forage fish, or some combination of the two. Comparisons of hatchery production and total adult run size (hatchery and wild; size estimates for wild runs are not available basinwide) between the 2 time periods indicate that the latter—an increase in nonsalmon abundances—is largely responsible. For example, compared with the annual hatchery production levels (~140 million) in our survey years, hatchery production was similar (141 million) in 1969 and only moderately higher in 1978–80 (164–187 million) (Hilborn and Hare[8]). In addition, improvements to fish passage through mainstem dams have increased in-river survival (Williams et al., 2001), and, therefore, more juvenile salmon should currently survive downstream migration to the estuary than they did in earlier times. Similarly, a comparison of total (hatchery and wild) adult run sizes within the Columbia River between the 2 time periods indicates that total adult-run sizes were higher during our study than they were in the early 1980s. For example, annual counts of sockeye salmon and steelhead over Bonneville Dam in 1980–83 averaged 66,000 and 166,000 fish, respectively, but recent (2008–10) counts averaged 259,000 and 457,000 fish, respectively (FPC database). Similarly, estimated total in-river run size (which does not include catch in ocean fisheries that target fall [subyearling] Chinook and coho salmon) in 2008–10 for Chinook salmon (mean=843,000) and coho salmon (555,000) is higher now than in the early 1980s (556,000 Chinook and 294,000 coho salmon) (WDFW and ODFW[9]; PFMC, 2011). Assuming that predators, disease, and other sources of mortality are similar between the 2 time periods, these estimates of juvenile and adult abundances indicate that juvenile salmon should be as abundant—if not more so—in the Columbia River estuary during our study than they were 3 decades ago. This conclusion indicates that changes in the fish assemblage are most likely the result of increased abundance of nonsalmonids.

Methodological differences also may have contributed to these observed patterns because in the earlier studies the net was towed instead of being set in a circle as happens in round hauls. We examined whether this difference might influence catch composition by comparing the ratios of juvenile salmon or threespine stickleback to all fish caught in our round hauls (n=188) and tows (n=81) during cruises in which both were conducted. Although statistically significant differences were observed between tows and round hauls for the ratio of juvenile salmon to all fish (Bonferroni multiple comparison test, $P<0.05$), the differences were quite small (0.10 in round hauls, 0.12 in round hauls), and there were no statistically significant differences for the ratio of threespine stickleback to total catch between round hauls and tows (0.34 and 0.36, respectively). These results suggest that method of net deployment was unlikely to cause the observed differences. Although our abundance estimates are not directly comparable to the earlier data because of differences in techniques, our results certainly suggest that the abundance of nonsalmonids, especially of the threespine stickleback, has increased in recent years.

If these changes to the fish assemblage are indeed true, they likely reflect changes in environmental conditions in the Columbia River estuary. Over the last 150

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[8] Hilborn, R, and S. R. Hare. 1992. Hatchery and wild fish production of anadromous salmon in the Columbia River basin. Fisheries Research Institute, Univ. Washington, Seattle, WA, Tech. Rep. FRI-UW-9207. [Available from http://www.fish.washington.edu.]

[9] WDFW and ODFW (Washington Department of Fish and Wildlife and Oregon Department of Fish and Wildlife ODFW). 2002. Status report: Columbia River fish runs and fisheries, 1938–2000, 324 p. [Available from WDFW, 600 Capitol Way N., Olympia, WA 98501-1091.]

years, major changes to the estuary have included decreased magnitude of the spring freshet, decreased salinity intrusion, and changes in estuarine bathymetry, the latter of which has influenced circulation patterns and habitat availability (Sherwood et al., 1990; Bottom et al., 2005). However, how environmental conditions have changed in the last 30 years has received relatively little attention (Bottom et al., 2006). It is known that spring river flow has been greatly reduced due to increased storage capacity of the hydrosystem. For example, average river flow in May and June measured at The Dalles Dam in 1977–81 was similar to recent (2007–10) levels; however, spring river flow in the 1960s and early 1970s was considerably greater (Bottom et al., 2006). Unfortunately, long-term salinity data are not available to determine how these flow declines may have influenced salinity intrusion. Limited temperature data from these earlier years suggest spring river temperatures were within the range presently observed (USGS National Water Information System).

It has been suggested that fish distributions in the Columbia River estuary are determined in part by prey availability (Bottom and Jones, 1990; Simenstad et al., 1990). If there was a time lag between declines in flow rates and a response by the fish assemblage (as might be expected if their prey are responding to flow rates), it may explain potential changes in the fish assemblage over the last 3 decades. Increasing numbers of forage fish also may explain the increasing abundance of avian predators in the Columbia River estuary, where these predators were largely absent 3 decades ago (Roby et al., 2003; Lyons, 2010). At present, we do not know whether changes in the fish assemblage have been beneficial or detrimental to juvenile salmon in the Columbia River estuary. Depressed populations of forage fish in Maine river basins are thought to inhibit the recovery of Atlantic salmon through a variety of ecological processes (Saunders et al., 2006). Whether similar ecological interactions between forage fish and Pacific salmon are occurring in the Columbia River basin is unknown.

Conclusions

We studied juvenile salmon and their associated fish community in open waters of the lower Columbia River estuary during spring in 4 years, 2007–10. During this period, we observed predictable seasonal changes in the abundance of all species of juvenile salmon, with low abundances in mid-April, peak abundances in May, and near absence by late June, except for subyearling Chinook salmon, which reached peak abundances in late June or early July. All caught juvenile salmon originated from throughout the Columbia River basin, and the vast majority (>90%) were of hatchery origin. Hatchery (i.e., clipped) steelhead and coho salmon were larger than individuals of the same species of unknown origin (unmarked hatchery and wild) but hatchery Chinook salmon were not, likely because of size overlap between large hatchery subyearling Chinook salmon and small wild yearling Chinook salmon. Although there was some variability in the abundance, timing, and size of juvenile salmon between years, no single year was exceptional with respect to these factors, as might be expected for fish with strong environmental influence. We hypothesize that the limited interannual variability we observed would have been higher if the proportion of wild fish also had been higher.

In contrast to highly predictable seasonal abundance of juvenile salmon, the abundance and species composition of the larger estuarine fish assemblage were extremely variable at temporal scales ranging from hours to years. This high variability is likely in response to extremely dynamic physical environments in the Columbia River estuary. Comparisons of our results with similar studies conducted over the previous 3 decades suggest major changes in the estuarine fish assemblage as a result of recent higher contributions of forage fish and threespine stickleback. The consequences of this change—whether it is beneficial or detrimental—to juvenile salmon is currently poorly understood. Although our research program has greatly increased our understanding of estuarine ecology in open waters of the Columbia River estuary in general and of juvenile salmon in these habitats in particular, there is clearly much that we do not know and hope to find out.

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