

## ***Association of Juvenile Salmon and Estuarine Fish with Intertidal Seagrass and Oyster Aquaculture Habitats in a Northeast Pacific Estuary***

The Faculty of Oregon State University has made this article openly available.  
Please share how this access benefits you. Your story matters.

<b>Citation</b>	Dumbauld, B. R., Hosack, G. R., & Bosley, K. M. (2015). Association of Juvenile Salmon and Estuarine Fish with Intertidal Seagrass and Oyster Aquaculture Habitats in a Northeast Pacific Estuary. Transactions of the American Fisheries Society, 144(6), 1091-1110. doi:10.1080/00028487.2015.1054518
<b>DOI</b>	10.1080/00028487.2015.1054518
<b>Publisher</b>	Taylor & Francis
<b>Version</b>	Version of Record
<b>Terms of Use</b>	<a href="http://cdss.library.oregonstate.edu/sa-termsfuse">http://cdss.library.oregonstate.edu/sa-termsfuse</a>

ARTICLE

# Association of Juvenile Salmon and Estuarine Fish with Intertidal Seagrass and Oyster Aquaculture Habitats in a Northeast Pacific Estuary

**Brett R. Dumbauld\***

*U.S. Department of Agriculture, Agricultural Research Service, Hatfield Marine Science Center, 2030 Southeast Marine Science Drive, Newport, Oregon 97365, USA*

**Geoffrey R. Hosack<sup>1</sup>**

*Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, Oregon 97331, USA*

**Katelyn M. Bosley**

*Hatfield Marine Science Center, Department of Fisheries and Wildlife, Oregon State University, 2030 Southeast Marine Science Drive, Newport, Oregon 97365, USA*

---

## Abstract

Structured estuarine habitats, such as salt marshes, seagrass beds, and oyster reefs, are recognized as critical nurseries for juvenile fish and crustaceans. Estuarine habitat usage by fish, including juvenile Pacific salmon *Oncorhynchus* spp., was characterized by sampling with a modified tow net in Willapa Bay, Washington, where 20% of the intertidal area is utilized for shellfish aquaculture and thus is difficult to sample with conventional gear. Our goal was to compare fish use of relatively undisturbed habitats (open mudflat, seagrass, and channel habitats) with the use of nearby oyster culture habitat. Although many species showed significant temporal and spatial trends within the estuary, only Shiner Perch *Cymatogaster aggregata* exhibited a significant association with habitat. Juveniles of three salmonid species exhibited few associations with the low intertidal habitats over which they were captured or in the prey types they consumed there. Chinook Salmon *O. tshawytscha*, likely hatchery-released ocean-type fish, were the most common salmonid captured, and they utilized low intertidal areas throughout the summer as their mean size increased from 85 to 100 mm FL. Diets consumed by these larger juvenile Chinook Salmon were not associated with benthic habitat but instead consisted primarily of (1) insects from nearby marsh or terrestrial habitats and (2) planktonic prey, like decapod larvae and tunicate larvaceans. Juvenile Coho Salmon *O. kisutch* and Chum Salmon *O. keta* were captured earlier (April and May) and fed on a slightly different suite of prey taxa, which were also primarily pelagic rather than associated with the intertidal benthos. Our findings suggest that in this relatively shallow coastal estuary, the role of benthic habitat is not closely linked to its value as a source of food for large juvenile salmon out-migrants utilizing the low intertidal areas where aquaculture occurs.

---

Estuaries support a high diversity and density of fish and invertebrates (Beck et al. 2003; Gillanders et al. 2003; Able 2005). Within estuaries, structured habitats (e.g., marshes, seagrass, and other submerged aquatic vegetation [SAV]) provide

trophic resources and refuge from predators, thus allowing small fish and invertebrates to reach greater density and diversity relative to those in unstructured habitats (e.g., open mudflat; Deegan et al. 2000; Heck et al. 2003; but see Orth et al.

---

\*Corresponding author: brett.dumbauld@ars.usda.gov

<sup>1</sup>Present address: Commonwealth Scientific and Industrial Research Organisation, General Post Office Box 1538, Hobart, Tasmania 7001, Australia.

Received January 18, 2015; accepted May 19, 2015

1984; Minello et al. 2003; Mattila et al. 2008). Structure formed by other organisms, such as oysters, has also been documented to contain diverse and abundant nekton (Minello 1999; Lehnert and Allen 2002; Glancy et al. 2003; Coen and Grizzle 2007; Ferraro and Cole 2010; Stunz et al. 2010), and intertidal oyster aquaculture can provide similar structure and habitat for these organisms (Dealteris et al. 2004; Hosack et al. 2006; Coen et al. 2011; reviewed by Dumbauld et al. 2009).

Estuaries provide predation refugia and trophic resources for out-migrating juvenile Pacific salmon *Oncorhynchus* spp. during their stressful physiological transition from freshwater to marine habitats (Healey 1982; Levy and Northcote 1982; Simenstad et al. 1982; Thorpe 1994; Gregory and Levings 1998). Early survival and growth are important for out-migrating salmon smolts (Beamish and Mahnken 2001), and these factors are interrelated since growth and fish size at least partially determine the level of predation risk (Duffy and Beauchamp 2008; Daly et al. 2009). Higher mortality rates of Chinook Salmon *O. tshawytscha* have been recorded for marine waters compared with estuarine and transition zones (Macdonald et al. 1988; Woodson et al. 2013), and the size and habitat quality of estuaries along the U.S. Pacific coast have been positively correlated with the survival rates of hatchery Chinook Salmon (Magnusson and Hilborn 2003).

Because numerous stocks of salmon have declined to critically low levels (Nehlsen et al. 1991; Gustafson et al. 2007), estuarine habitats like seagrass have recently gained focus as essential habitat for juvenile salmonids. Seagrasses have also been declining worldwide (Orth et al. 2006; Waycott et al. 2009). Along the U.S. Atlantic and Pacific coasts, the focal native seagrass species is the common eelgrass *Zostera marina*. Use of nearshore habitats by juvenile salmon varies depending on the population (species and region), life history strategy, and ontogenetic stage (Healey 1985; Duffy et al. 2005; Fresh 2006), but eelgrass has been suggested to provide food resources and protection from predation for the early life history stages of salmon (Simenstad et al. 1982; Semmens 2008).

In many estuaries along the U.S. Pacific coast, aquaculture of Pacific oysters *Crassostrea gigas* (introduced from Japan in the 1920s) co-occurs with eelgrass at the same tidal elevation (from  $-0.5$  to  $1.0$  m mean lower low water [MLLW]). Concerns over aquaculture's impacts on seagrass as essential fish habitat—along with U.S. federal and state regulations that contain provisions for no net loss of SAV—have begun to generate management conflicts (Simenstad and Fresh 1995; Dumbauld et al. 2009). In Willapa Bay, Washington, oyster aquaculture has overlapped with eelgrass habitat for more than a century (Dumbauld et al. 2011), yet there is an emerging management conflict wherein eelgrass protection could affect the current practices used by the aquaculture industry. For example, the U.S. Army Corps of Engineers' recently re-issued (March 2012) Nationwide Permit 48 for shellfish culture requires "preconstruction notification" if dredge

harvesting, tilling, or harrowing is conducted in areas inhabited by SAV; it also requires an individual permit for proposed culture projects in a new area with more than  $0.2$  ha ( $0.5$  acres) of SAV. Both state and federal permit regulations necessitate the use of a buffer zone between new shellfish farming activity and any existing eelgrass. Recent studies have helped to quantify the temporal scale of shellfish aquaculture's direct influences (both positive and negative) on eelgrass (Rumrill and Poulton 2004; Tallis et al. 2009; Wisehart et al. 2007; Ruesink et al. 2012; Wagner et al. 2012); however, there is little scientific guidance regarding (1) the functional role and comparative value of oyster aquaculture and eelgrass habitats, particularly at the landscape scales that are relevant for estuarine fishes, including salmon stocks that are protected under the U.S. Endangered Species Act; and (2) how to uphold federal and state mandates to protect those stocks.

We evaluated the use of intertidal habitats by the estuarine fish community, including juvenile salmon, by (1) sampling with a modified tow net to compare the densities of estuarine fish and juvenile salmon in the low intertidal habitats where most aquaculture occurs, as an indicator of habitat associations; and (2) examining the frequency of prey taxa that were consumed by juvenile salmon in low intertidal habitats relative to the distribution of prey taxa that were sampled in concurrent neuston tows.

## METHODS

**Study area.**—Willapa Bay, Washington ( $46.72^{\circ}\text{N}$ ,  $124.01^{\circ}\text{W}$ ), contains extensive intertidal areas that extend over  $1$  km from shore and cover about half of the bay's surface area. The tidal range averages  $2.7$  m across the estuary (Banas et al. 2004). Eelgrass, on-bottom oyster culture (ground culture), and unvegetated tideflat are the three major low intertidal ( $-0.5$  to  $1.0$  m MLLW) habitats (Simenstad and Fresh 1995; Feldman et al. 2000; Dumbauld et al. 2011). About  $17\%$  of the total intertidal area ( $3,876$  of  $22,699$  ha) is used for commercial oyster culture, yielding a significant portion of the total oyster production in the United States; ground culture of oysters contributes over  $95\%$  of the total oyster production in Willapa Bay (Feldman et al. 2000). Both the native eelgrass *Z. marina* and the nonnative Japanese eelgrass *Z. japonica* are present, covering a roughly equivalent portion ( $21.7\%$  or  $4,934$  ha) of the estuary's intertidal area (Dumbauld and McCoy 2015). *Zostera japonica* has dramatically expanded its range over the last two decades and may have also facilitated the expansion of *Z. marina* in some areas (Bando 2006; B. R. Dumbauld, unpublished data).

**Fish collection.**—Since traditional seines and trawls are virtually impossible to tow over the shallow oyster culture grounds, we developed an experimental surface trawl to improve our ability to sample juvenile salmonids (Figure 1). The net was a two-boat trawl (tow net) that measured  $6.1$  m wide at the footline,  $9.1$  m long, and  $1.2$  m high, with  $1.27$ -cm

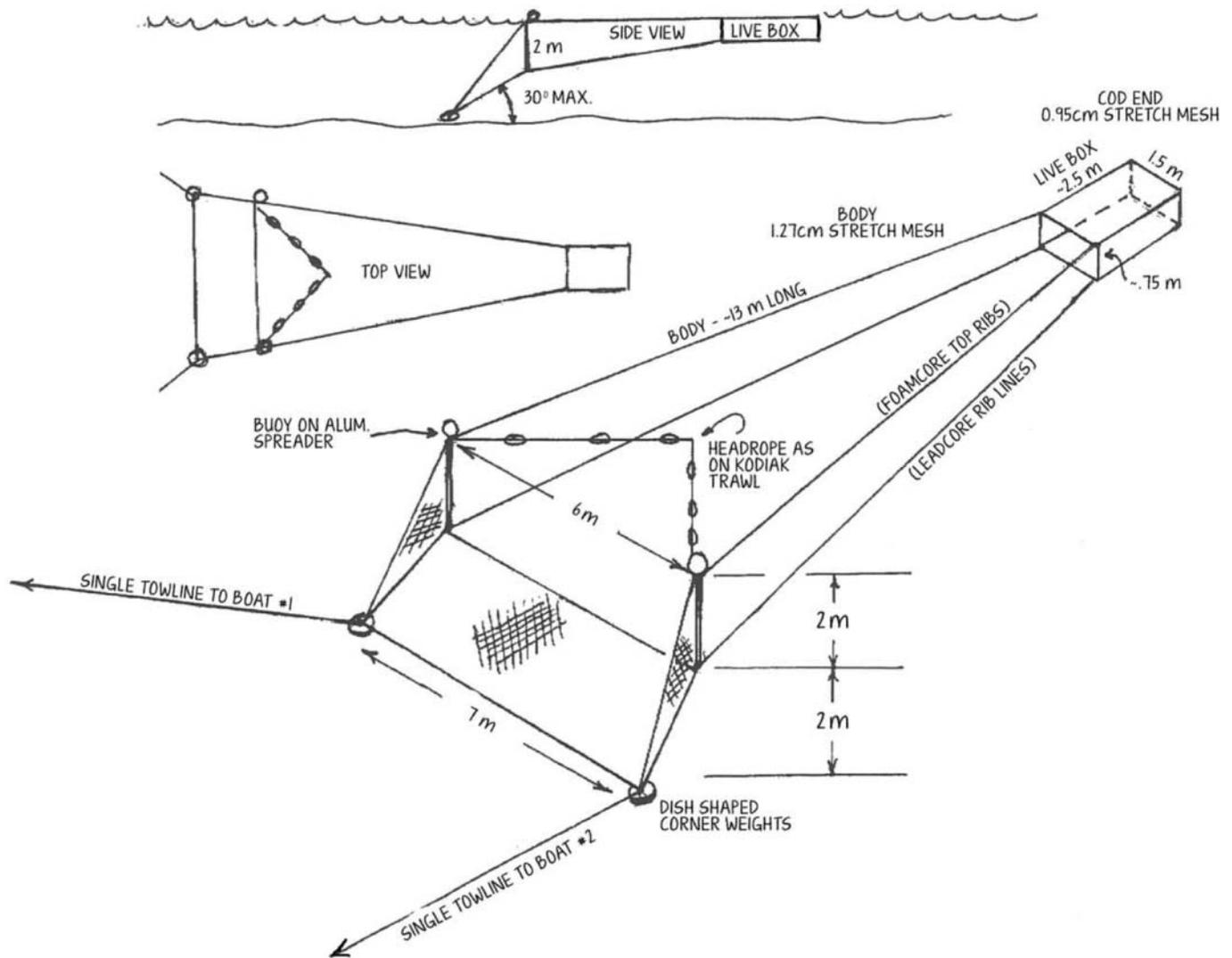


FIGURE 1. Experimental modified two-boat tow net used to capture juvenile salmon and other pelagic fishes over structured intertidal habitats (design and construction by Research Nets, Inc., Bothell, Washington). The low-profile tow net design allows deployment in the extremely shallow water that is typically found over a tidelflat in shallow estuaries at high tide. An apron extends a groundline downwards and forward of the net, effectively increasing the width of the net mouth, minimizing contact between the net body and substrate, and preventing fish from diving beneath the footline.

mesh in the body and 0.95-cm mesh in the cod end. The low-profile tow net design allowed for deployment in the shallow water typically found over broad estuarine tidelflats. Additionally, an apron extended a groundline downward and forward of the net, effectively increasing the width (7.9 m) and depth (variable, 1.2–2.3 m) of the net's mouth. The front apron, which was only anchored on each side by a dish-shaped corner weight, minimized contact between the net body and the substrate while preventing pelagic fishes (e.g., juvenile salmon) from diving beneath the footline.

During daytime spring high tides, we sampled three intertidal habitats (open mudflat, native eelgrass, and oyster ground culture) and the adjacent subtidal channel at five regions in the lower estuary: Stackpole, North Stackpole, Nemah, North Long

Island, and Nahcotta (Figure 2). We attempted to conduct a single tow over each habitat within each region, resulting in 20 tows (4 habitats  $\times$  5 regions) per month. Average water depth at the time of sampling was 1.8 m (range = 0.8–2.9 m) for the intertidal habitats and 8 m (range = 3–15 m) for the subtidal channel habitat. Average distance towed was 230 m (range = 50–670 m), as measured using a calibrated flowmeter (General Oceanics) held over the side of the boat. Sampling trips took place monthly in June–September 2002 to obtain seasonal data (targeting Chinook Salmon) and again in April–May 2003 (targeting Chum Salmon *O. keta* and Coho Salmon *O. kisutch*) and July 2003 (targeting Chinook Salmon). With the exception of salmon that were retained for stomach content analyses (see below), all of the captured fish and invertebrates were counted,

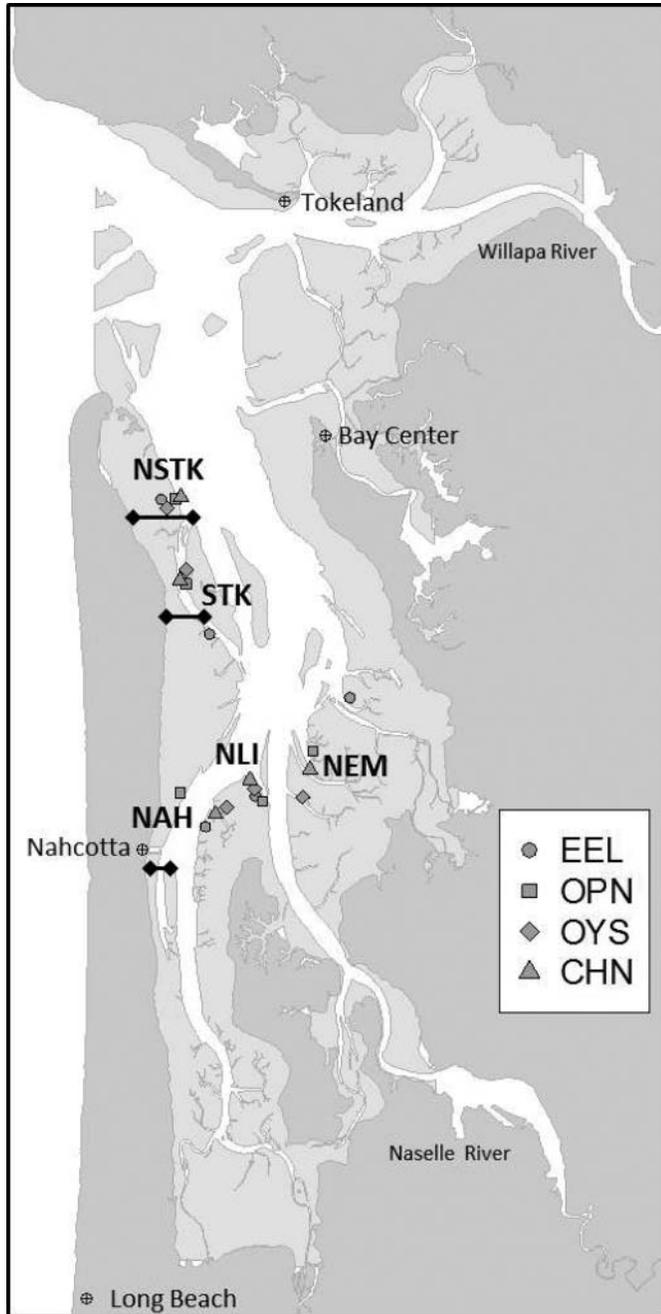


FIGURE 2. Map of Willapa Bay, Washington, showing the five regions (NAH = Nahcotta; NEM = Nemah; NLI = North Long Island; STK = Stackpole; NSTK = North Stackpole) and four habitats (EEL = eelgrass; CHN = channel; OPN = open, unstructured; OYS = oyster ground culture) where townet samples (2002 and 2003) and neuston samples (2003 only) were collected. Also shown are the locations of separate transects (lines) where neuston tows were made in 2003 to assess the relationships between the neuston community and distance to shore.

measured, and released. Length was determined as TL (mm) except for Shiner Perch *Cymatogaster aggregata* and salmonids, which were measured in FL (mm).

*Diet composition and neuston collection.*—We used gastric lavage to collect salmon diet samples in 2002. Each fish was measured, and the stomach contents were removed by using a modified garden pump sprayer with a custom nozzle and filtered seawater (Hartleb and Moring 1995). Stomach contents were washed into a fine-mesh sieve and fixed in a 10% solution of formaldehyde. In 2003, diet samples were from whole stomachs that were excised from fish injected with formaldehyde to prevent further digestion. Stomach contents were later identified to the lowest possible taxon under a dissecting scope. Number of individuals and biomass (wet weight and dry weight, g) were recorded for each taxon.

Concurrent with the fish survey tows in 2003, neuston tows were conducted to quantify prey types that were available in the water column, as benthic and epibenthic prey had already been quantified in the three intertidal habitats (Hosack et al. 2006; Ferraro and Cole 2010). Neuston samples were taken with a 0.5-m-diameter, 220- $\mu$ m net towed near the surface in the relatively shallow (<5-m) water column; these data were used to compare the observed stomach contents with prey availability in the water column at the point of capture. Neuston tow lengths were designed to be similar to the tow lengths used in fish sampling; the distance towed was recorded by using a calibrated flowmeter (General Oceanics) mounted in the net opening. Neuston samples were fixed in a 10% solution of buffered formaldehyde in the field, were transferred to a 70% solution of ethanol for storage, and were identified to the lowest possible taxon under a dissecting scope in the laboratory. Counts and biomass (wet weight and dry weight, g) were recorded for each taxonomic category. A second set of 12 neuston tows was made at three distances from the shoreline and at four locations along the Long Beach peninsula (Figure 2) to determine the origin of the various prey taxa.

*Analytical methods.*—Since underlying community gradients were unknown and potentially nonlinear, we used non-parametric multivariate techniques to investigate species-level differences in taxonomic composition of the fish catch, fish diet, and neuston samples collected in different habitats, regions, and months. All multivariate analyses for townet catch and neuston data were based on CPUE (number of individuals caught/[distance towed from flowmeter  $\times$  net mouth area], where the latter was calculated as the average area of the net mouth, including the apron for the tow net). Fish catch was averaged for those cases in which multiple tows were conducted within each habitat at a single location and time.

Separate species composition matrices were constructed for (1) CPUEs from townet sampling conducted in 2002 and 2003, (2) diet data (counts and biomass of prey taxa in individual salmon stomachs) collected in 2002 and 2003, and (3) CPUEs from neuston tows conducted in 2003 only. The prey taxa identified from salmon stomachs and the taxa identified in neuston tows were assigned to broader taxonomic categories reflecting the dominant types: barnacles (cyprids, nauplii, and exuviae); calanoid copepods; harpacticoid

copepods; cladocerans (*Evdadne* spp. and *Podon* spp.); caprellid amphipods; gammarid amphipods; other peracarids (cumaceans, isopods, mysids, etc.); decapod larvae (zoeae and megalopae/postlarvae of crabs and shrimps); insects (larvae and adults); spiders and mites; polychaetes, nematodes, and oligochaetes; mollusks; tunicates (larvaceans and larvae); and fish (larvae, juveniles, and adults; see Supplementary Table S.1 available in the online version of this article). These broader categories were based in part on previous estuarine studies (Brennan et al. 2004; Bollens et al. 2010; Duffy et al. 2010). Secondary matrices contained attribute information (e.g., month, region, and habitat) associated with individual net tows or salmon stomachs. Rarely occurring taxa (those present in <5% of the tows or stomachs) were excluded from the analyses to minimize variability and their influence on the community analyses. Data matrices were relativized by row totals and column maxima as necessary to standardize data as proportions and to reduce the CV.

Ordinations of species composition and diet matrices were conducted with nonmetric multidimensional scaling (NMDS) based on a Bray–Curtis coefficient of similarity within the *ecodist* and *BiodiversityR* packages in R (R Development Core Team 2012). The NMDS ordinations were displayed as plots, with samples (net catch or stomach contents) that were most similar in species composition being plotted close together and those that were dissimilar being plotted far apart. Visual examination and ordination solutions with stress values less than 0.20 were used to make selections, and overall differences in community composition were further examined by using nonparametric multiresponse permutation procedures (MRPPs) with Sorenson's distance measure (Mielke and Berry 2001). Analyses were conducted for three variables or groups, including habitat (eelgrass, open mudflat, oyster ground culture, and channel), region (Nahcotta, Nemah, North Long Island, Stackpole, and North Stackpole), and month (April–September, depending on the year). Indicator species analyses using the *labdsv* package in R (Roberts 2013) and 1,000 Monte Carlo randomizations were conducted to identify species that contributed most to between-group differences.

Selectivity for neustonic prey by salmonid juveniles sampled in 2003 was evaluated by using Ivlev's (1961) electivity index ( $E_i$ ),

$$E_i = (s_i - n_i) / (s_i + n_i),$$

where  $s_i$  = the proportion of the  $i$ th taxon in the stomach contents; and  $n_i$  = the proportion of the same  $i$ th taxon in the environment (neuston in this case). Electivity values were calculated for each juvenile salmon caught during 2003, and the individual values were then averaged for each species. Electivity values provide a simple measure of prey selection and vary from  $-1$  to  $1$ , with  $1$  indicating high selectivity (the prey type was never seen in the environment but was present in the stomach contents of all fish) and  $-1$  indicating low

selectivity (the prey item was never seen in the stomach contents of fish but was present in the environment). This simple index should be interpreted cautiously, as it involved pooling taxa across size ranges, sample sizes, and spatial and temporal scales. Most importantly, our analysis only considers the available planktonic prey taxa that were sampled with a neuston net, which has been shown to undersample some nekton groups and to oversample other zooplankters (Brodeur et al. 2011).

Finally, we examined differences in juvenile salmon and Shiner Perch density (as a count, with the sampled water volume scaled by mean and SD) and juvenile salmon size (FL and weight) by using generalized linear models and linear mixed-effects models (*lme4* package in R; Bates et al. 2012). Tow was added as a random factor to the mixed-effects models for size analyses because the fish from each tow could not be considered independent. Covariates used in these models included time (either scaled as the day of the year [for size] or as a fixed categorical factor [for density]) and habitat (evaluated as a fixed categorical factor). Models of the count data used a Poisson likelihood, and a Gaussian likelihood was used for the log transformed size data. Residuals and deviance values were compared to the fitted model values, and significance was determined using likelihood ratio tests of the full model containing the effect in question against the model without that effect; the  $P$ -values function was used for individual factor levels.

## RESULTS

### Fish Catch

Overall, 13 fish species and 2 decapod species were caught during 2002, but CPUE was highest for seven species of fish, all of which were included in the multivariate analyses (Table 1). With the exception of Shiner Perch and Threespine Sticklebacks, most species (including juvenile salmonids) exhibited their greatest abundances in June and July, with catch declining thereafter. Although few clear associations were observed in initial NMDS analyses and plots (Figure 3), subsequent MRPP analyses indicated no significant difference among groups defined by habitat (within group agreement  $A = 0.010$ ,  $P = 0.147$ ) or region ( $A = 0.004$ ,  $P = 0.341$ ); however, a strong difference by month was detected ( $A = 0.085$ ,  $P = 0.001$ ). Indicator species analyses revealed that Shiner Perch (indicator value [IV] = 0.490,  $P = 0.006$ ) were associated with eelgrass habitat and that Chinook Salmon were associated with the Stackpole region (IV = 0.689,  $P = 0.004$ ). The strongest relationships were temporal: Chinook Salmon, Northern Anchovy, and Surf Smelt were associated with June (IV = 0.426, 0.433, and 0.969, respectively;  $P < 0.01$ ), and these associations were visible when displayed as vectors on ordination plots (Figure 3). Shiner Perch were most abundant in July and August, and their density was

TABLE 1. Average CPUE (fish/100 m<sup>3</sup>; SE in parentheses) for the most abundant fishes collected in tow nets at all regions and habitats of Willapa Bay, 2002 and 2003 (*n* = number of tows).

Species <sup>a</sup>	2002				2003		
	Jun ( <i>n</i> = 14)	Jul ( <i>n</i> = 19)	Aug ( <i>n</i> = 20)	Sep ( <i>n</i> = 19)	Apr ( <i>n</i> = 20)	May ( <i>n</i> = 20)	Jul ( <i>n</i> = 20)
Chum Salmon <i>Oncorhynchus keta</i>	0.000	0.000	0.000	0.000	0.365 (0.146)	0.162 (0.056)	0.000
Coho Salmon <i>O. kisutch</i>	0.000	0.000	0.000	0.000	0.000	0.038 (0.010)	0.000
Chinook Salmon <i>O. tshawytscha</i>	0.389 (0.055)	0.230 (0.044)	0.268 (0.104)	0.071 (0.022)	0.000	0.000	0.438 (0.238)
Northern Anchovy <i>Engraulis mordax</i>	0.038 (0.014)	0.002 (0.002)	0.004 (0.003)	0.000	0.000	0.049 (0.019)	0.233 (0.180)
Pacific Herring <i>Clupea pallasii</i>	0.000	0.021 (0.015)	0.000	0.000	0.000	0.027 (0.014)	0.000
Surf Smelt <i>Hypomesus pretiosus</i>	5.680 (1.970)	0.151 (0.078)	0.007 (0.006)	0.002 (0.002)	0.000	12.99 (4.32)	0.018 (0.013)
Shiner Perch <i>Cymatogaster aggregata</i>	0.101 (0.073)	1.315 (0.910)	1.351 (0.762)	0.275 (0.227)	0.000	0.053 (0.041)	6.138 (5.722)
Pacific Sand Lance <i>Ammodytes hexapterus</i>	0.000	0.103 (0.089)	0.049 (0.033)	0.095 (0.053)	0.269 (0.206)	0.248 (0.131)	0.004 (0.004)
Threespine Stickleback <i>Gasterosteus aculeatus</i>	0.589 (0.073)	0.170 (0.910)	0.948 (0.762)	28.096 (11.407)	1.634 (0.796)	4.491 (2.021)	2.042 (1.040)

<sup>a</sup>Other species (fish and invertebrates) that were sampled but present in less than 5% of the tows were the Pacific Staghorn Sculpin *Leptocottus armatus*, Saddleback Gunnel *Pholis ornata*, Bay Pipefish *Syngnathus leptorhynchus*, Pile Perch *Damalichthys vacca*, Walleye Surfperch *Hyperprosopon argenteum*, Tubesnout *Aulorhynchus flavidus*, Kelp Greenling *Hexagrammos decagrammus*, Dungeness crab *Metacarcinus magister*, kelp crab *Pugettia producta*, and bay shrimp *Crangon nigricauda*.

clearly associated with structured eelgrass and oyster culture habitats (Figure 4; mixed-effects model, Table S.2;  $\chi^2 = 27.98$ ,  $df = 3$ ,  $P < 0.001$ ).

In 2002, Chinook Salmon were the most commonly collected juvenile salmonids. The density of juvenile Chinook Salmon declined from June through September (Figure 4), and there was no evidence for density differences associated with habitat (Table S.3;  $\chi^2 = 0.502$ ,  $df = 3$ ,  $P = 0.913$ ), as also seen in the NMDS analyses described above. Chinook Salmon FL did not vary with respect to habitat (Table S.4;  $\chi^2 = 3.03$ ,  $df = 3$ ,  $P = 0.387$ ) but exhibited a positive trend with significant differences over time, as fish appeared to grow over the summer ( $\chi^2 = 49.54$ ,  $df = 1$ ,  $P < 0.001$ ; mean  $\pm$  SE =  $0.04 \pm 0.005$  mm/d). Fork length varied with region ( $\chi^2 = 10.49$ ,  $df = 4$ ,  $P = 0.033$ ); individuals taken at North Long Island (mean  $\pm$  SE =  $88.7 \pm 0.78$  mm) were significantly larger than those collected from the Nahcotta region. Chinook Salmon weight exhibited a similar trend (Figure 4; Table S.5), with captured fish being significantly heavier over time; however, weight did not differ by habitat ( $\chi^2 = 3.807$ ,  $df = 3$ ,  $P = 0.283$ ) or by region ( $\chi^2 = 5.411$ ,  $df = 4$ ,  $P = 0.48$ ).

The suite of species caught during 2003 (14 fish species and 3 decapod species) was similar to that caught in 2002; CPUE was highest for nine fish species, which were used in the multivariate analyses (Table 1). Juvenile Chum Salmon and Coho Salmon were only caught during April and May, whereas juvenile Chinook Salmon were taken in July. Adult Surf Smelt and Pacific Sand Lances were most abundant in May samples, and larval Surf Smelt and Northern Anchovy were caught primarily during April and May, respectively. These patterns resulted in a significant association of species composition with month but not with habitat. The MRPP analyses indicated a significant difference in groups defined by month ( $A = 0.186$ ,  $P = 0.001$ ) and by region ( $A = 0.037$ ,  $P = 0.028$ ), but there was no significant difference in groups defined by habitat ( $A = 0.019$ ,  $P = 0.098$ ). Indicator species analyses showed only a few significant associations: Shiner Perch ( $IV = 0.289$ ,  $P = 0.015$ ) were associated with eelgrass habitat (see also Figure 4), and Threespine Sticklebacks were associated with channel habitat ( $IV = 0.391$ ,  $P = 0.013$ ) and with the Nahcotta region ( $IV = 0.346$ ,  $P = 0.007$ ).

Juvenile Coho Salmon sampled in May were the largest salmon out-migrants (mean  $\pm$  SE =  $132 \pm 22.4$  mm FL).

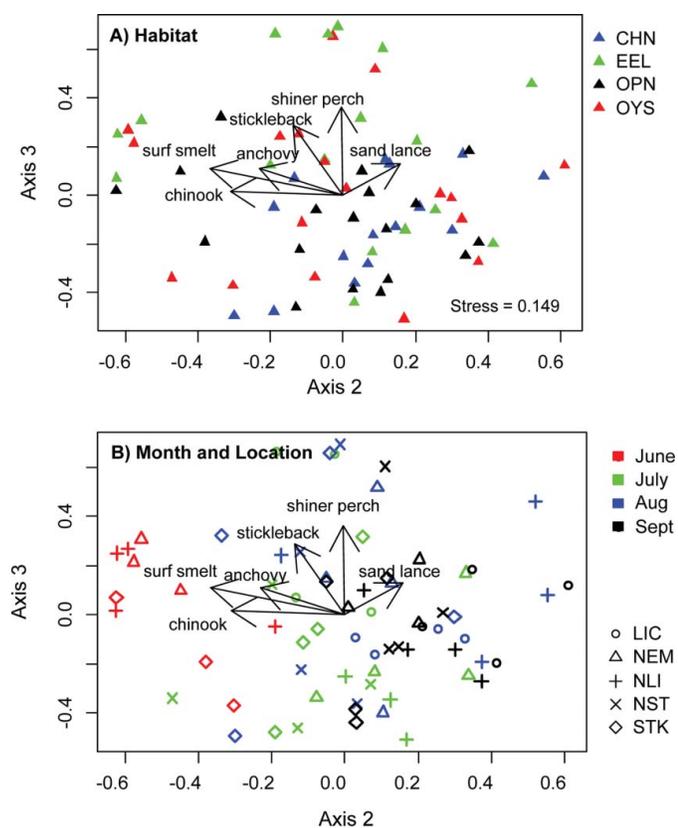


FIGURE 3. Nonmetric multidimensional scaling ordination of the townnet data collected during 2002 in (A) four habitats (symbols; CHN = channel; EEL = eelgrass; OPN = open, unstructured; OYS = oyster ground culture) and (B) five regions (NAH = Nahcotta; NEM = Nemah; NLI = North Long Island; NST = North Stackpole; STK = Stackpole) of Willapa Bay during four months (symbols). In each panel, vectors represent the individual fish species (see Table 1 for full names of species). Although there are few obvious associations, Shiner Perch appear to be associated with EEL and OYS habitat (panel A), axis 2 appears to be associated with month (panel B), and Surf Smelt are clearly associated with the month of June (panel B). [Figure available online in color.]

There was no evidence for a density difference associated with habitat (Table S.6), as confirmed in the NMDS analyses. We detected no differences in Coho Salmon size among habitats ( $\chi^2 = 2.237$ ,  $df = 3$ ,  $P = 0.525$ ) or among regions ( $\chi^2 = 2.806$ ,  $df = 4$ ,  $P = 0.423$ ; Table S.7), but only 17 individuals were caught. Juvenile Chum Salmon were the smallest salmonid out-migrants (mean  $\pm$  SE =  $61 \pm 9.2$  mm FL) and appeared to exhibit significant growth over time (Table S.8;  $\chi^2 = 47.93$ ,  $df = 1$ ,  $P < 0.001$ ; mean  $\pm$  SE =  $0.09 \pm 0.009$  mm/d). Although there was no apparent association with habitat in NMDS analyses, parametric analyses suggested that more Chum Salmon were caught over oyster culture habitat (Table S.9;  $\chi^2 = 65.92$ ,  $df = 3$ ,  $P < 0.001$ ). Significant differences in mean size of Chum Salmon were observed (1) in relation to habitat ( $\chi^2 = 8.465$ ,  $df = 3$ ,  $P = 0.0373$ ), with larger fish being sampled from channels; and (2) in relation to

region ( $\chi^2 = 15.920$ ,  $df = 4$ ,  $P = 0.003$ ), with larger fish being caught at North Stackpole ( $\bar{x} \pm SE = 65.75 \pm 1.04$  mm FL). The size of Chinook Salmon out-migrants sampled in July 2003 ( $\bar{x} \pm SE = 93 \pm 7.7$  mm FL) showed no association with habitat ( $\chi^2 = 0.641$ ,  $df = 3$ ,  $P = 0.887$ ) or region ( $\chi^2 = 5.937$ ,  $df = 4$ ,  $P = 0.204$ ; Table S.10), and significantly fewer Chinook Salmon were caught over eelgrass habitat relative to other habitats (Table S.11).

### Juvenile Salmon Diets

In total, 74 individual prey taxa were distinguished in the diets of juvenile Chinook Salmon ( $n = 149$ ) sampled during 2002. These taxa were categorized into 18 broad taxonomic groups for analyses (Table S.1), and the groups were further reduced to 14 diet categories after prey types that occurred in less than 5% of the stomachs were excluded. Although not obvious in overall NMDS analyses, seasonal trends in the diet were apparent (Figure 5, middle panel), and a significant temporal association was detected in subsequent MRPP analyses (month:  $A = 0.078$ ,  $P = 0.001$ ). Insects and barnacles were the most abundant groups found in the diets of juvenile Chinook Salmon, representing (on average) 56% and 24%, respectively, of prey numbers (Figure 5). Insect prey consisted mostly of dipterans and homopterans; although barnacle nauplii and barnacle cyprids were present, barnacle exuviae were most abundant. Tunicates (either larvae or *Oikopleura dioica* larvaceans) were also common, representing 4% of the prey items by number (Figure 5). Diet exhibited no association with habitat (Figure 5, left panel; MRPP analysis:  $A = 0.0017$ ,  $P = 0.298$ ) and only a weak association with region (Figure 5, right panel;  $A = 0.0107$ ,  $P = 0.031$ ). Indicator species analyses suggested a few significant associations based on prey number in the diet: barnacle exuviae were most often associated with fish collected from open habitat during June; tunicates were associated with fish sampled at Stackpole during September; and insects were most prevalent in stomach contents during September (Table 2). In addition, harpacticoids were associated with Chinook Salmon collected from the Nemah region.

When the diet was examined by weight, insects were slightly less important; broader categories of plant and other material (not counted) represented an average of 16% and 22%, respectively, of the weight consumed by juvenile Chinook Salmon. Decapod larvae (mostly brachyuran crab megalopae, some of which were further identified as Dungeness crabs) and barnacle exuviae were still important in the diet (means = 14% and 7%, respectively). Although not obvious from the initial NMDS analyses, clear seasonal trends in diet were apparent, resulting in significant temporal differences among groups defined by month ( $A = 0.052$ ,  $P = 0.001$ ) in the MRPP analysis. Differences were also observed among groups defined by region ( $A = 0.023$ ,  $P = 0.002$ ). Similar to the results for prey counts, significant differences in diet weight

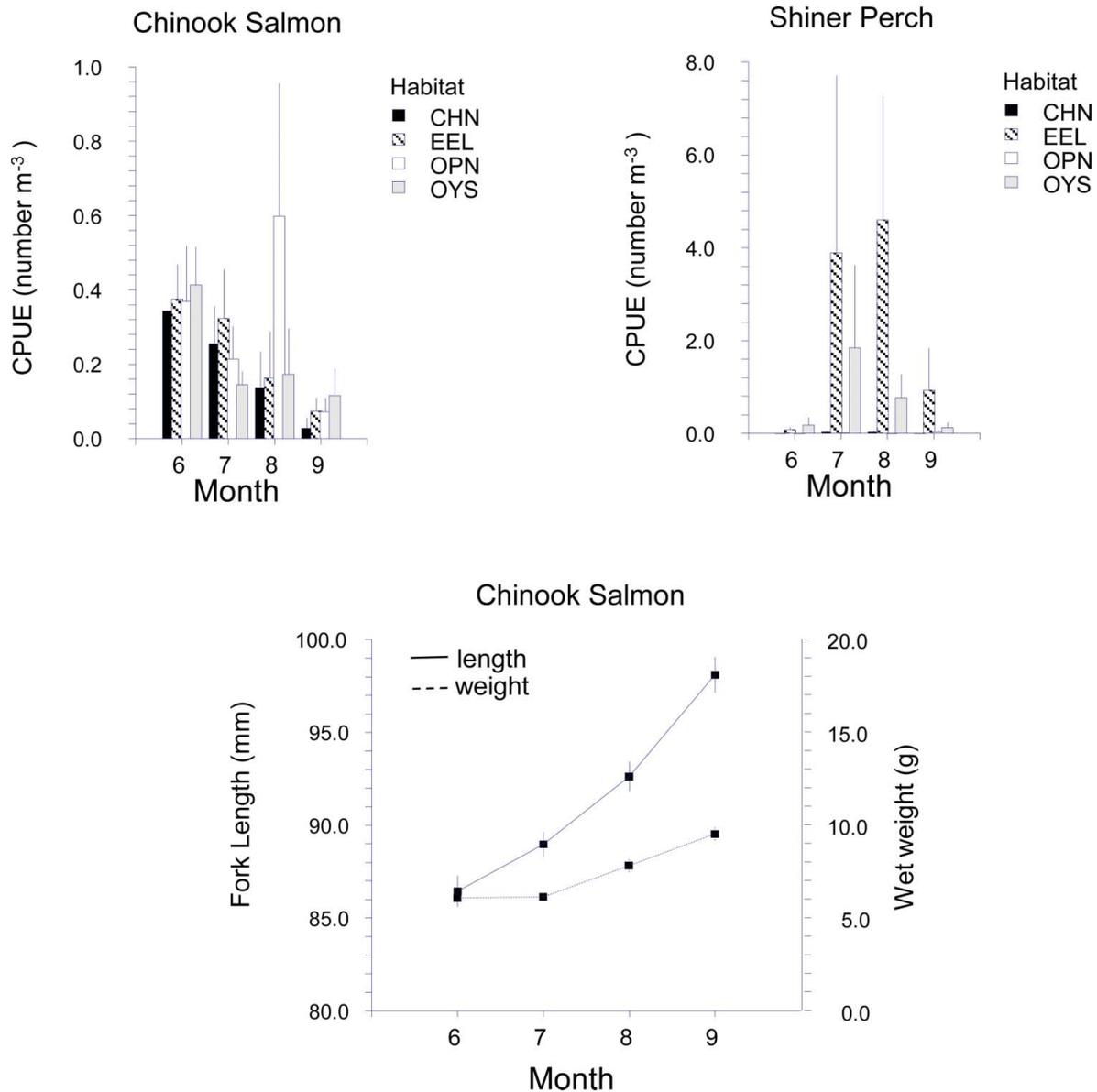


FIGURE 4. (A) Average (+SE) CPUE (fish/100 m<sup>3</sup>) of juvenile Chinook Salmon in four habitats (CHN = channel; EEL = eelgrass; OPN = open, unstructured; OYS = oyster ground culture); (B) average catch of Shiner Perch in the four habitats; and (C) average FL (mm) and weight (g) of juvenile Chinook Salmon in Willapa Bay from June to September 2002. [Figure available online in color.]

among habitats were not detected ( $A = 0.1$ ,  $P = 0.383$ ). Several significant results in indicator species analyses based on weight (Table 2) also mirrored the results for count data when the same prey species were still present in the Chinook Salmon diets: for example, decapod larvae were associated with fish collected from the North Long Island region and with fish sampled during June; tunicates were most important for fish collected from the Nemah region during September; and insects were most important for fish in the Stackpole region during September.

Forty-nine individual taxa were distinguished in the diets of juvenile salmon sampled during 2003 ( $n = 13$  Chinook

Salmon, 17 Chum Salmon, and 16 Coho Salmon). These taxa were again assigned to 18 broad taxonomic groups for analyses; the broad groups were further reduced to 12 diet categories after the exclusion of prey types that were consumed by less than 5% of the fish. The taxonomic composition of the diet was clearly different among the three salmonid species (Figure 6). Chinook Salmon consumed insects almost exclusively ( $\bar{x} = 87\%$ ; mostly dipterans, but also psocopterans, homopterans, and hymenopterans), whereas Chum Salmon preyed on insects ( $\bar{x} = 29\%$ ), tunicates ( $\bar{x} = 53\%$ ; mostly larvaceans), harpacticoids ( $\bar{x} = 9\%$ ; mostly *Harpacticus uniremis* and *H. septentrionalis*), and other

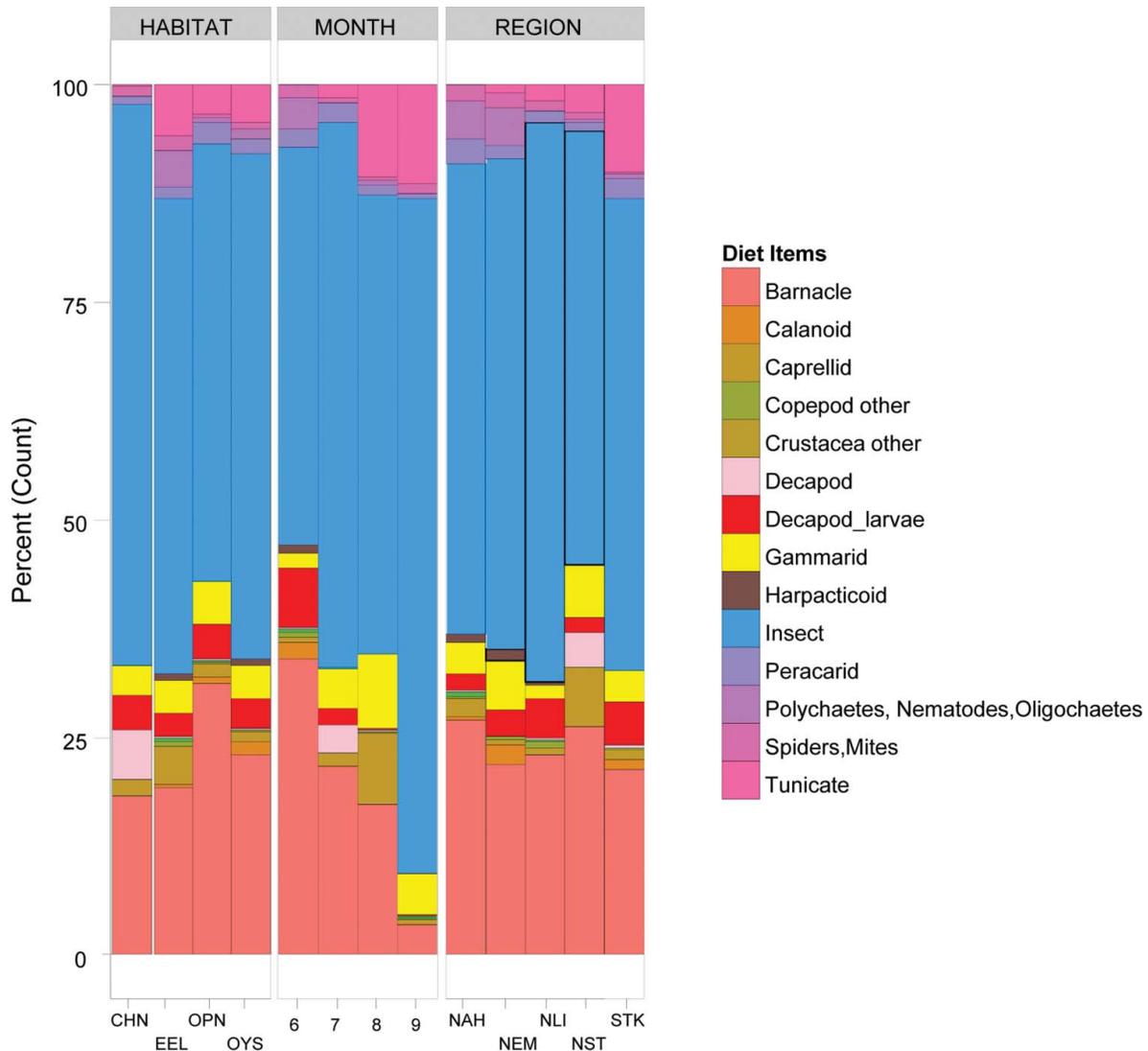


FIGURE 5. Mean proportion (by number) of several taxa in the diets of juvenile Chinook Salmon sampled from Willapa Bay during four months in 2002. Proportions are estimated for each habitat (left panel; CHN = channel; EEL = eelgrass; OPN = open, unstructured; OYS = oyster ground culture), month (middle panel), and region (right panel; NAH = Nahcotta; NEM = Nemah; NLI = North Long Island; NST = North Stackpole; STK = Stackpole). [Figure available online in color.]

peracarids ( $\bar{x} = 2\%$ ; cumaceans and tanaids). Decapod larvae (mostly Dungeness crab megalopae) and fish were the most abundant prey groups in Coho Salmon diets, representing an average of 50% and 18%, respectively, of the enumerated items. Coho Salmon also consumed insects ( $\bar{x} = 6\%$ ), gammarid amphipods ( $\bar{x} = 10\%$ ; mostly *Corophium* spp. and *Eohaustorius* spp.), and other peracarids ( $\bar{x} = 5\%$ ). These diet differences produced clear distinctions in prey associations among the salmon species, as evidenced by the NMDS analysis and subsequent MRPP analysis (Figure 7;  $A = 0.282$ ,  $P = 0.001$ ), but there was no apparent association with habitat ( $A = -0.008$ ,  $P = 0.613$ ). Sample sizes in the five regions were insufficient to permit an analysis of region as a factor. Results for month duplicated the trend for species, as Chum

Salmon were the only fish caught during two separate months. Results of indicator species analyses confirmed the patterns noted above but also showed the following significant associations based on prey counts: spiders and mites with Chinook Salmon; caprellid amphipods with Chinook Salmon; and calanoid copepods with Chum Salmon (Table 3). When 2003 data were analyzed based on weight, insects and other small food items became less important, and groupings such as plant matter and other unidentified taxa became more important. There was no significant difference among groups defined by habitat (MRPP analysis:  $A = 0.013$ ,  $P = 0.215$ ), and the results of indicator species analyses based on prey weight mirrored those for the count data (Table 3).

TABLE 2. Results of indicator species analyses (IV = indicator value) based on counts and weights of the most common taxa in the stomach contents of juvenile Chinook Salmon sampled from Willapa Bay in 2002 (see Table S.1 for a complete list of prey taxa and taxonomic groups). Only significant ( $P < 0.05$ ) results are given.

Factor	Class	Taxon	IV	<i>P</i>
<b>Counts</b>				
Habitat	Open, unstructured	Barnacle larvae/exuviae	0.284	0.034
	Channel	Decapod larvae	0.170	0.003
Region	Eelgrass	Polychaetes, nematodes, and oligochaetes	0.143	0.023
	Nemah	Harpacticoids	0.110	0.032
	Stackpole	Tunicates	0.190	0.010
	North Stackpole	Caprellids	0.322	0.0003
Month	Jun	Decapod larvae	0.124	0.032
		Barnacle larvae/exuviae	0.334	0.003
		Calanoids	0.136	0.015
	Aug	Decapod larvae	0.353	0.0002
		Polychaetes, nematodes, and oligochaetes	0.139	0.032
		Caprellids	0.394	0.0002
	Sep	Gammarids	0.372	0.0001
		Insects	0.307	0.002
		Tunicates	0.278	0.001
<b>Weights</b>				
Habitat	Open, unstructured	Barnacle larvae/exuviae	0.340	0.015
Region	Nemah	Insects and spiders	0.277	0.037
	North Long Island	Decapod larvae	0.184	0.022
	North Stackpole	Caprellids	0.334	0.0005
		Plants	0.307	0.013
Month	Nahcotta	Other	0.294	0.006
	Stackpole	Tunicates	0.230	0.0
	Jun	Decapod larvae	0.310	0.0006
		Caprellids	0.434	0.0001
	Aug	Plants	0.340	0.044
		Decapod larvae	0.134	0.021
		Insects and spiders	0.391	0.0006
Sep	Tunicates	0.263	0.008	

### Neuston

Overall, 54 individual taxa were distinguished in neuston tows conducted during 2003 ( $n = 63$ ); these taxa were grouped into 19 broad taxonomic groups for analyses and were further reduced to 18 diet categories when taxa that were present in less than 5% of the samples were removed. Samples of the neuston community in July differed from samples collected in April and May, resulting in detection of a significant temporal association by MRPP analysis (month:  $A = 0.157$ ,  $P = 0.001$ ). The most abundant groups in neuston samples (based on counts of individuals) were calanoid copepods ( $\bar{x} = 35\%$ , Figure 8); barnacles ( $\bar{x} = 16\%$ ; nauplii, cyprids, and exuviae); and the combined category consisting of polychaetes, nematodes, and oligochaetes ( $\bar{x} = 14\%$ ; mostly polychaete larvae but not identified any further). Other common items were decapod

larvae ( $\bar{x} = 6\%$ ; shrimp and crab larvae, including megalopae), harpacticoids ( $\bar{x} = 7\%$ ), cladocerans ( $\bar{x} = 7\%$ ; *Podon* spp. and *Evadne* spp.), and insects ( $\bar{x} = 4\%$ ; mostly dipterans). The neuston community was not associated with habitat (MRPP analysis:  $A = -0.012$ ,  $P = 0.906$ ) or region ( $A = 0.021$ ,  $P = 0.072$ , Figure 8). Indicator species analyses suggested that calanoids and caprellids were associated with July, whereas many of the other taxa were primarily associated with May (Table S.12). In examining data from 12 separate neuston samples taken along transects during July 2003, we found no significant association between the neuston community and distance to the shoreline (MRPP analysis:  $A = 0.014$ ,  $P = 0.322$ ), but indicator species analyses detected a significant relationship for gammarids (i.e., they were more common in samples collected closest to shore;  $IV = 0.841$ ,  $P = 0.020$ ).

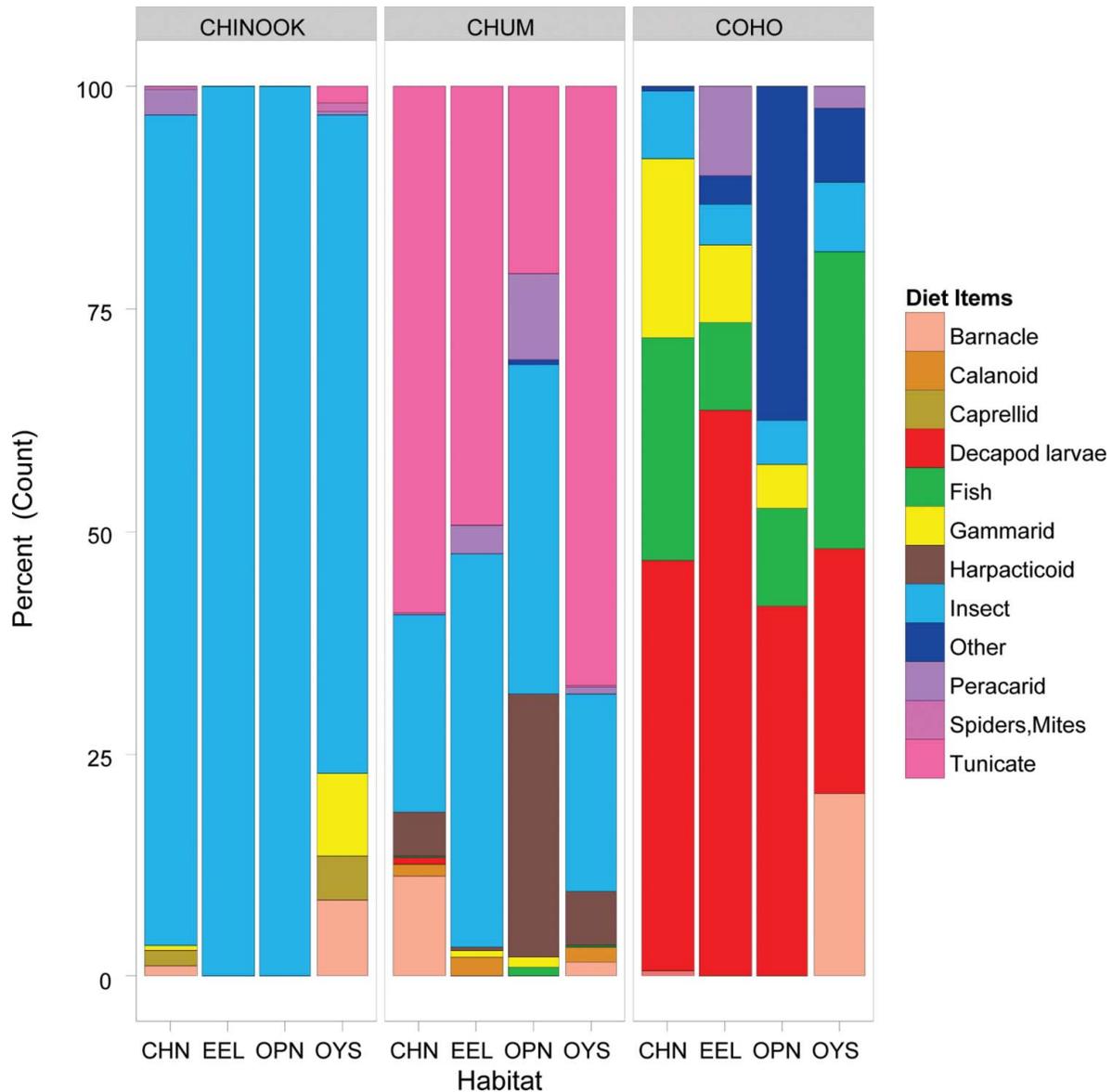


FIGURE 6. Mean proportion (by number) of several prey taxa in the diets of juvenile Chinook Salmon, Chum Salmon, and Coho Salmon sampled in four habitats of Willapa Bay (CHN = channel; EEL = eelgrass; OPN = open, unstructured; OYS = oyster ground culture) during 2003. [Figure available online in color.]

### Electivity Indices

Several taxa were present in the neuston samples but were not found in the stomach contents of any juvenile salmon collected during 2003; these taxa included cladocerans, other copepods (poecilostomatoids and cyclopoids), mollusk larvae, and the category consisting of polychaetes, nematodes, and oligochaetes. All three salmonid species demonstrated negative selection for calanoid copepods, barnacles, caprellids, spiders and mites, and other invertebrates ( $E < -0.25$ ). Chum Salmon exhibited positive selection for tunicates ( $E = 0.52$ ) and insects ( $E = 0.37$ ); other diet items were either consumed in proportion to

their abundance in the neuston ( $-0.25 < E < 0.25$ ; gammarids, other peracarids, harpacticoids, and fish) or were selected against ( $E = -0.81$ ; decapod larvae). Juvenile Chinook Salmon showed positive selection for insects ( $E = 0.93$ ) and gammarids ( $E = 0.34$ ); consumed other peracarids in proportion to their abundance in the neuston ( $E = 0.17$ ); and selected against decapod larvae, fish, and tunicates ( $E < -0.25$ ). Juvenile Coho Salmon weakly selected for fish ( $E = 0.24$ ); consumed decapod larvae in proportion to their abundance in the neuston ( $E = 0.07$ ); and exhibited negative selection for gammarids, insects, and other peracarids.

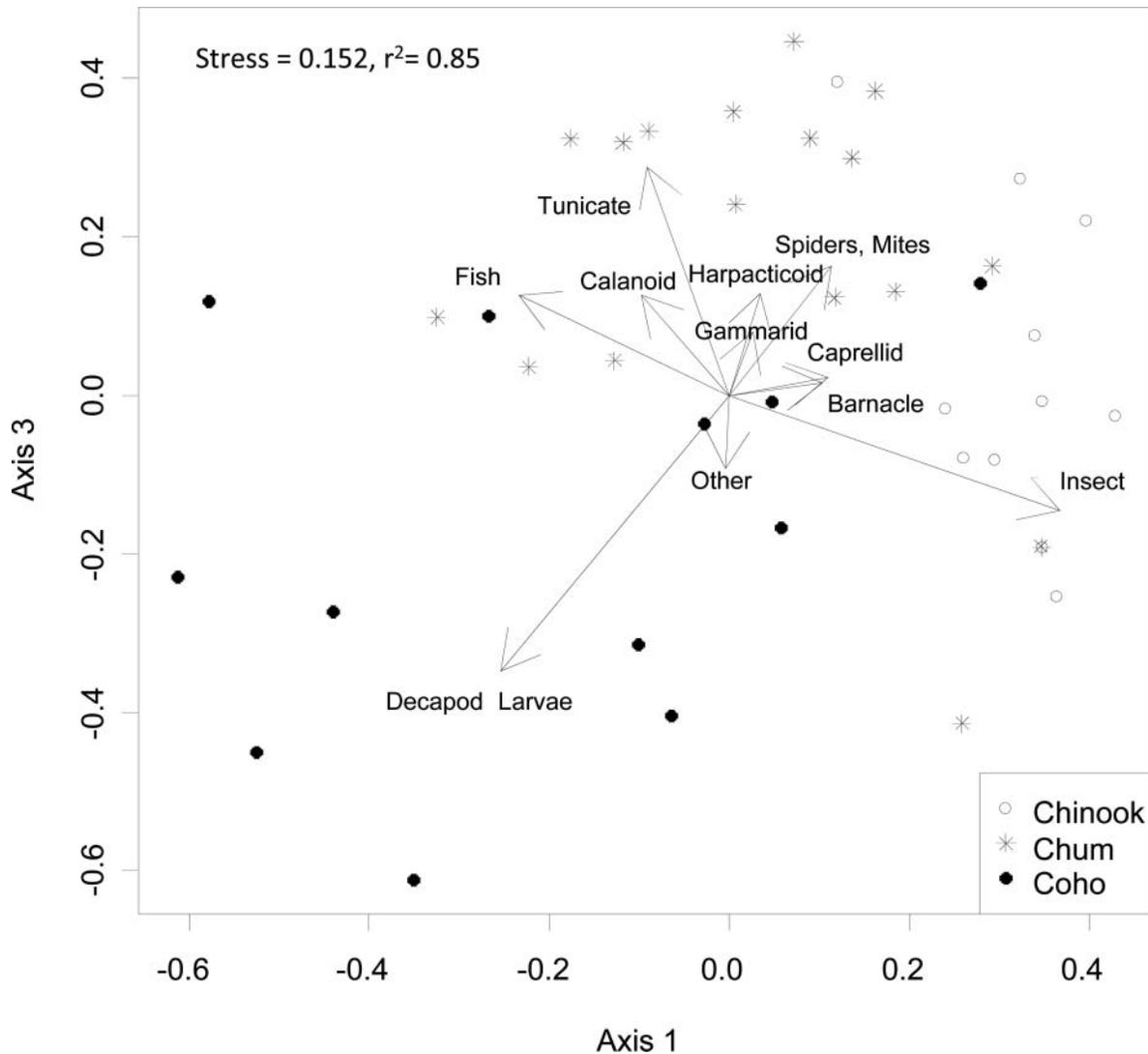


FIGURE 7. Nonmetric multidimensional scaling ordination of juvenile salmon diet data collected from Willapa Bay in 2003. Symbols distinguish salmon species; vectors represent the individual diet taxa. Overall diets display significant associations; individual prey taxon associations include decapod larvae with Coho Salmon, insects with Chinook Salmon, and tunicates with Chum Salmon.

## DISCUSSION

Using the two-boat tow net, we captured several species of juvenile salmon and pelagic forage fish that are known to be present in U.S. West Coast estuaries but that generally are inadequately sampled by traditional seines and bottom-oriented trawl or stationary gear over structured, three-dimensional substrate (e.g., oyster ground culture and seagrass habitats in this study). Although the tow net's low profile and apron allowed deployment over three-dimensional structure in shallow water, our catch was still restricted to fish that occupied at least a 1.5-m-deep water column, and some fish may have escaped in cases when towing speed varied due to the presence of dense eelgrass. Tows were conducted during daylight, but Willapa Bay is often turbid during spring tides, and the tow net may not fish as effectively in clear water.

There were few significant relationships between the fish community and habitat, but we identified several temporal and within-estuary spatial trends. The lack of significant differences among habitats is contrary to the generally accepted view that fish abundance and diversity are greater in structured and vegetated habitats than in unvegetated open habitats (Orth et al. 1984; Heck et al. 1989; Connolly 1994; Edgar and Shaw 1995). Other field studies have since reported a similar lack of correspondence between high fish diversity or abundance and the degree of habitat structure, with no increase in prey survival above a threshold in habitat complexity; some of these studies have examined the potential mechanisms involved (e.g., predator and prey identity and behavior; Rilov et al. 2007; Mattila et al. 2008; Humphries et al. 2011; Scheinin et al. 2012). We suggest that this relationship is likely specific

TABLE 3. Results of indicator species analyses (IV = indicator value) based on counts and weights of the most common taxa in the stomach contents of juvenile salmon sampled from Willapa Bay in 2003 (see Table S.1 for complete list of prey taxa and taxonomic groups). Only significant ( $P < 0.05$ ) results are given.

Factor	Class	Taxon	IV	P
<b>Counts</b>				
Habitat	Oyster	Barnacle	0.438	0.019
	ground culture	larvae/exuviae		
Species	Chum Salmon	Calanoids	0.529	0.0002
		Harpacticoids	0.529	0.0002
		Tunicates	0.754	0.0001
	Chinook Salmon	Caprellids	0.231	0.018
		Insects	0.716	0.0001
		Spiders and mites	0.306	0.021
	Coho Salmon	Decapod larvae	0.621	0.0001
		Fish	0.430	0.003
		Other	0.246	0.026
<b>Weights</b>				
Habitat	Eelgrass	Decapod larvae	0.287	0.043
Species	Chum Salmon	Calanoids	0.235	0.031
		Harpacticoids	0.353	0.004
		Tunicates	0.643	0.0001
		Other	0.509	0.005
	Chinook Salmon	Insects	0.672	0.0001
		Plants	0.740	0.0001
	Coho Salmon	Decapod larvae	0.624	0.0001
		Fish	0.345	0.006

to individual species (e.g., demersal foragers versus pelagic feeders) and even to individual life history stages, and the relationship may also depend on local conditions and the amount and form of structure present. Because our sampling method targeted the water column, we caught relatively few taxa that are directly associated with the benthos, such as English Sole *Parophrys vetulus*, Pacific Staghorn Sculpins, and Dungeness crabs, which have been sampled with other gear types (Deben et al. 1990; Holsman et al. 2006; Hosack et al. 2006).

Juvenile Chinook Salmon were the most abundant salmonid captured during our summer 2002 surveys. We found no significant association between benthic habitat and Chinook Salmon density; similar numbers of Chinook Salmon were caught over all three intertidal habitats and in nearby channels. However, our sampling was restricted to afternoon high slack tides, and smaller fish may have already moved to shallower water or may have been residing elsewhere in the estuary. Chinook Salmon are known to distribute broadly and to reside longer in estuaries than other species (Simenstad et al. 1982; Brennan et al. 2004; Duffy et al. 2005; Fresh 2006). They were present from June to September in our surveys, although their abundance declined over this period, presumably due to predation or movement out of the estuary. Larger Chinook

Salmon were also more abundant in collections from regions near the mouth of Willapa Bay, suggesting that they gradually moved in that direction before leaving the estuary. The only wild-type Chinook Salmon in the Willapa basin are from the North River–Smith Creek drainage, and this stock has been listed as depressed (Smith 1999; WDFW 2002). All other Chinook Salmon in the Willapa basin are of mixed origin—a composite of hatchery and naturally spawned fish. We could not distinguish between wild and hatchery Chinook Salmon because hatcheries were not fin-clipping or marking fish at the time of our survey; however, we suspect that most of the captured juveniles were of mixed origin and likely were hatchery-released fish based on their relatively large size, time of appearance (in early summer), and steady change in mean size from 85 mm FL during June to 98 mm FL during September (see Duffy et al. 2005 for similar data). Fall-run, ocean-type Chinook Salmon parr migrants (like those we caught) make extended and extensive use of estuarine tidal channels and marshes, but they are found in neritic habitats and are less tied to bottom habitat as they grow (Healey 1982; Levings et al. 1986; Murphy et al. 1988; Fresh 2006).

Juvenile Chum Salmon are known to utilize shallow intertidal areas as a migration corridor and nursery environment, and they have been extensively studied in Hood Canal and elsewhere in Puget Sound, Washington (Healey 1979; Simenstad et al. 1982; Fresh 2006; Young 2009). Chum Salmon have shorter estuarine residency periods than Chinook Salmon and are typically found earlier in the spring (Simenstad and Eggers 1981; Simenstad et al. 1982; Fresh 2006). We caught juvenile Chum Salmon in April and May 2003, but again we found no significant association with habitat in our NMDS analyses, although a univariate test suggested significantly more fish were found over oyster culture habitat. All Chum Salmon stocks in Willapa Bay are of native origin and wild production, and the stocks that have been studied are classified as healthy (WDFW 2002). Larger Chum Salmon were sampled in May ( $\bar{x} = 69.8$  mm FL) than in April ( $\bar{x} = 55.2$  mm FL), and significantly larger fish were taken at the North Stackpole site near the estuary mouth. These juvenile Chum Salmon were mostly larger than the juveniles observed by Young (2009), who linked the shoaling behavior of Chum Salmon to a strategy of remaining in very shallow water to avoid predation—but with the potential to forage in lower intertidal seagrass microhabitats at specific locations where beach slope and tide stage allowed.

For the few Coho Salmon we captured, no significant association was found between CPUE and habitat or region. Willapa Bay Coho Salmon stocks are of mixed origin; we suspect that our samples consisted primarily of hatchery fish. Recent data suggest that juvenile Coho Salmon of several year-classes (including small fry) utilize estuarine habitats (Miller and Sadro 2003; Neher et al. 2013; Jones et al. 2014), but we captured only larger Coho Salmon smolts ( $\bar{x} = 131.7$  mm FL) as they used Willapa Bay tideflat areas in April 2003.

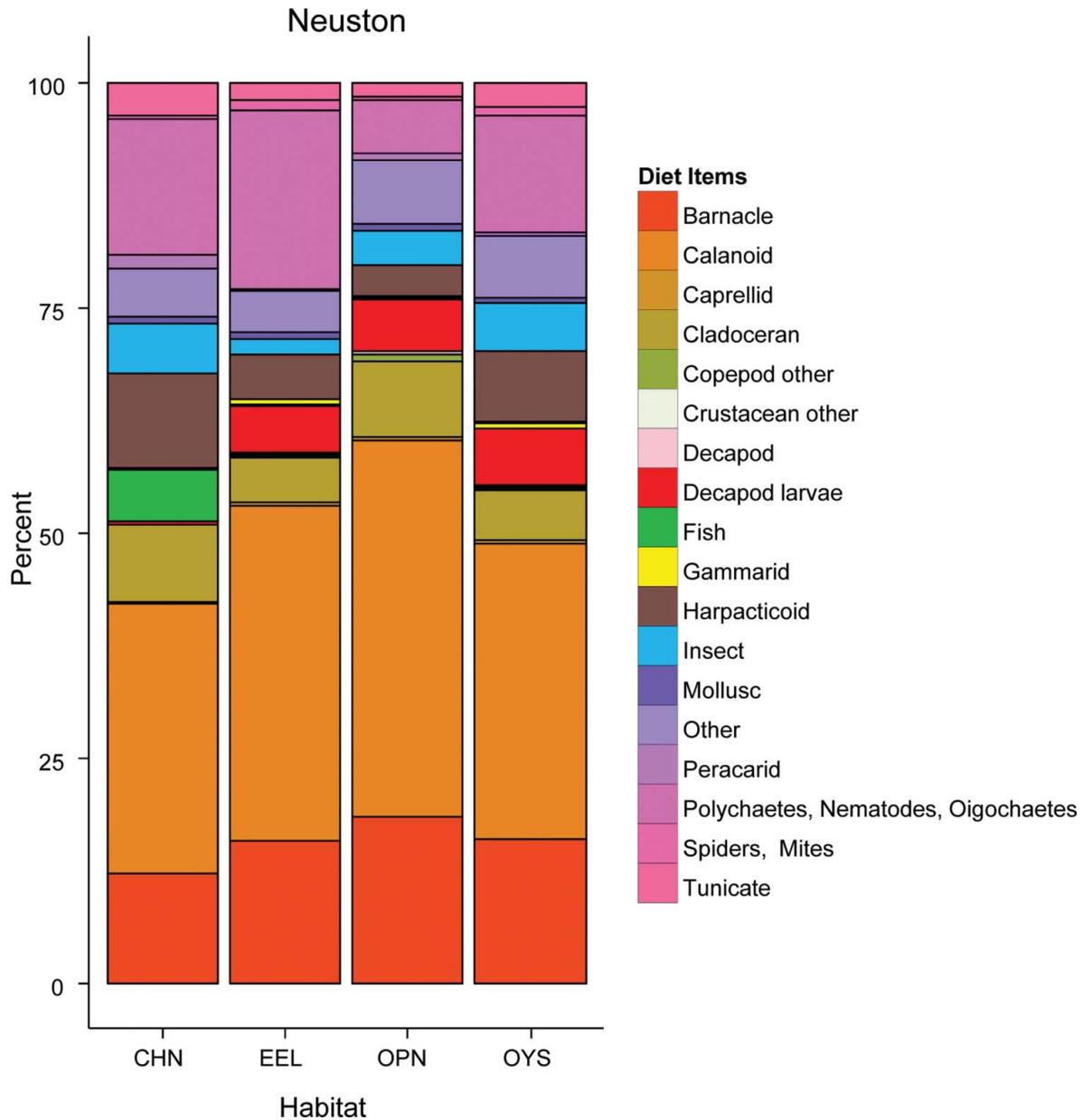


FIGURE 8. Mean proportion (by number) of several taxa in neuston tows conducted during 2003 over four habitats of Willapa Bay (CHN = channel; EEL = eelgrass; OPN = open, unstructured; OYS = oyster ground culture). [Figure available online in color.]

The tow net successfully captured several species of pelagic forage fish: Northern Anchovy, Surf Smelt, Pacific Herring, and Pacific Sand Lance. Temporal trends were apparent, with the majority of these forage fishes being most abundant in June, but no associations were observed between forage fish catch and habitat. This finding indicates that forage fishes were at least present over intertidal areas, but like salmon, they were not strongly associated with benthic habitat. We identified a significant association between Shiner Perch catch and the structured eelgrass and oyster ground culture habitats, with fewer fish being caught over open mudflat and channel

habitats. Association of Shiner Perch with eelgrass habitat has been noted by previous researchers using beach seines (Bayer 1985; Deben et al. 1990; Kelly et al. 2008). Shiner Perch are also known to feed on prey organisms associated with the benthos (Caine 1991; Williams 1994; Barry et al. 1996; Troiano et al. 2013), and thus they exhibit some site fidelity, utilizing these areas at high tide. Hosack et al. (2006) did not find a strong relationship between Shiner Perch and habitat, but those authors used fyke nets fished over a 24-h period, which potentially integrated the movement of Shiner Perch among habitats.

### Juvenile Salmon Diets and Electivity for Neuston Prey

The diets of juvenile salmon in Willapa Bay varied substantially among species, and the proportions of several individual taxa in Chinook Salmon and Chum Salmon diets varied over time and among regions within the bay. In general, diets were not associated with the intertidal habitat over which these salmon were caught. Some notable associations were evident, however, when diet composition was compared with the neuston community composition, suggesting that juvenile salmonids are opportunistic feeders that consume planktonic prey as well as other food items (e.g., insects) more broadly associated with location in the estuary. These prey types were generally more important than the benthic and epibenthic taxa associated with the intertidal habitats where oyster aquaculture takes place, but further studies utilizing enclosures should be used to more directly quantify local prey consumption. The salmon used in diet analyses were sampled during daylight afternoon tides; however, there is some evidence that juvenile salmon are selective diurnal feeders (Schabetsberger et al. 2003), so other prey types could also be important.

The feeding ecology of juvenile salmonids in marine waters along the U.S. West Coast has been widely studied, especially in fjords like Puget Sound and nearshore coastal waters (Healey 1982; Simenstad et al. 1982; Brodeur and Pearcy 1990; Schabetsberger et al. 2003; Brennan et al. 2004; Toft et al. 2007; Daly et al. 2009; Bollens et al. 2010; Duffy et al. 2010; Sturdevant et al. 2012), but less attention has been directed toward their feeding ecology in shallow coastal estuaries (Murphy et al. 1988; Gray et al. 2002). In the diets of Chinook Salmon sampled from Willapa Bay during 2002 and 2003, insects and spiders were by far the most common prey types, followed by barnacles (mostly exuviae), and tunicates (mostly larvaceans); decapod larvae, gammarid amphipods, and plant material were important in terms of biomass, although less important numerically. Insect taxa that are characteristic of vegetated marsh and other terrestrial shoreline habitats are important prey types for juvenile Chinook Salmon in Puget Sound, especially in tidal channels, the marshes themselves, or areas closer to shore (Brennan et al. 2004; Bollens et al. 2010; Duffy et al. 2010). Occasionally, insects have been identified as important prey for salmon captured relatively far from the open coastline, suggesting that the insects drift great distances, and they are actively selected by younger and smaller fish (Brodeur 1989). Insects were significantly more important as prey for Chinook Salmon captured during September and within the Nemah region, perhaps because more substantial marsh habitats are adjacent to this region. Barnacle exuviae and tunicate larvaceans have also been reported as common in Chinook Salmon diets (Brennan et al. 2004; Bollens et al. 2010), and decapod larvae (primarily Dungeness crab megalopae) were most important during June, coinciding with the typical period in which these highly mobile, visible prey enter the coastal estuaries (Roegner et al. 2003).

Temporal changes in the diet could also be linked to an ontogenetic shift, with larger items being consumed by larger fish (Keeley and Grant 2001; Daly et al. 2009). The juvenile Chinook Salmon in our samples had already reached the threshold (~60 mm) at which foraging shifts from benthic and wetland habitats to the water column. Therefore, over the months we sampled, shifts were only seen in prey taxa that made up small proportions of the diet, and they were seemingly linked more to the presence and abundance of various taxa in the environment (e.g., a switch from barnacles, copepods, and decapod larvae in June to caprellid amphipods, gammarid amphipods, and tunicates later in the summer). These seasonal trends were also apparent in the neuston sampled during 2003, with decapod larvae being most abundant in May. Electivity indices suggested that Chinook Salmon sampled in July positively selected for insects and gammarids, as these taxa were more common in the diets than in the neuston. Positive selection in this case merely implies that the juvenile Chinook Salmon found the prey items somewhere else, since we only evaluated the neuston. All three salmonid species showed negative selection for calanoid copepods, barnacles, caprellids, and spiders and mites. Calanoids have been shown to dominate estuarine zooplankton communities, including that in Willapa Bay (Graham and Bollens 2010), but they are less important in salmon diets (Bollens et al. 2010). Barnacles were consumed by Chinook Salmon but were much more abundant in the neuston; interestingly, the same was also true of caprellids and spiders, which typically are not considered neuston. Electivity values indicated that Chinook Salmon selected against decapod larvae, fish, and tunicates. Chinook Salmon have been reported to feed on these items, and decapod larvae were very abundant in the neuston during July 2003, but the Chinook Salmon we caught were relatively small ( $\bar{x} = 93$  mm FL) and perhaps had not yet made the transition to piscivory (Duffy et al. 2010).

Juvenile Chum Salmon sampled in Willapa Bay displayed a more taxonomically diverse diet than Chinook Salmon; smaller items like harpacticoid copepods, peracarids (cumaceans and tanaids), and even calanoid copepods were significantly more important for Chum Salmon, yet they still consumed mostly insects, tunicates, and barnacles. Fish also made up a significant gravimetric proportion of the diets consumed by Chum Salmon. Our results are consistent with those of Bollens et al. (2010), who reported a significant proportion of larvaceans in Chum Salmon diets sampled from Dabob Bay, Washington. Our findings are also consistent with analyses of stomach contents from Chum Salmon sampled in British Columbia and Alaska (Murphy et al. 1988; Romanuk and Levings 2010; Sturdevant et al. 2012). Based on values of *E*, Chum Salmon exhibited positive selection for insects and tunicates and negative selection for decapod larvae. Electivity indices were neutral for benthic and epibenthic prey taxa (harpacticoids, peracarids, and gammarids), suggesting that they

were consumed in proportion to their abundance in the neuston. Our NMDS analyses found no significant relationship between benthic habitat and the diets of Chum Salmon; however, Chum Salmon consumed more epibenthic-oriented prey types (including harpacticoids) than did Chinook Salmon and Coho Salmon, as has been consistently reported elsewhere, especially for smaller Chum Salmon inhabiting the very near-shore littoral environment (Simenstad et al. 1980, 1982; Simenstad and Eggers 1981). The Chum Salmon in our samples were between 50 and 60 mm FL, a transition point at which they reportedly begin feeding on more pelagic nekton and zooplankton (Simenstad et al. 1982).

The stomach contents of juvenile Coho Salmon were perhaps most distinct from those of juvenile Chinook Salmon in our study, with decapod larvae and fish together representing 68% (numerically) and 86% (gravimetrically) of the diet. Electivity indices suggested that Coho Salmon only weakly selected for fish and that they consumed decapod larvae in proportion to their abundance in the neuston; however, fishes that were caught in the neuston were perhaps less likely to be the same species found in the stomachs of Coho Salmon, which had clearly reached a size ( $\bar{x} = 132$  mm FL) where piscivory was important. Our results for juvenile Coho Salmon are similar to those reported from other estuaries, including nearby Grays Harbor, Washington, where the diets were similar across regions and habitats (Simenstad and Eggers 1981); in Puget Sound and Alaska (Brennan et al. 2004; Powers et al. 2006; Bollens et al. 2010); and in the nearshore coastal zone (Brodeur and Percy 1990; Schabetsberger et al. 2003; Daly et al. 2009). Coho Salmon diets were also clearly linked to the temporal presence of items in the environment during the relatively short period they spent in this region of Willapa Bay.

### **Aquaculture as a Disturbance to Estuarine Habitat for Juvenile Salmonids**

Our study was initiated primarily to distinguish whether intertidal oyster aquaculture in Willapa Bay influences the distribution and feeding ecology of juvenile salmonids. Bivalve aquaculture can be viewed as a disturbance that influences the system by (1) changing material processes, (2) altering substrate availability and physical structure, and (3) directly affecting resources via pulse disturbances, such as harvest activity (Simenstad and Fresh 1995; Dumbauld et al. 2009; Coen et al. 2011). Natural disturbances are key features in estuarine ecosystems along the Pacific coast of North America; Pacific salmon are resilient and have adapted to these changes over millennia by adopting multiple life history strategies (Greene et al. 2005; Schindler et al. 2008; Bottom et al. 2009; Healey 2009; Waples et al. 2009). The challenge is therefore to distinguish whether more recent anthropogenic disturbances, such as aquaculture, threaten this resilience.

Life history strategies of Pacific salmon range from species that move through estuaries relatively quickly as juveniles to

species that utilize estuaries more extensively for feeding or as refuge from predation during the period of growth and physiological transition from freshwater to seawater. These factors are interrelated, as fish size also partly determines predation risk (Duffy and Beauchamp 2008; Weitkamp et al. 2014). We noted significant temporal and spatial trends within Willapa Bay, but we found few significant differences in the density of juvenile salmon present over natural versus modified habitats or in the prey taxa they consumed—at least during daytime spring high slack tides, when the modified tow net could be deployed. Instead, we found that the prey base for these later ontogenetic stages of salmon consisted mostly of pelagic zooplankton or drift insects that (1) were produced elsewhere and consumed in the intertidal habitats or (2) were present more broadly and therefore were not influenced by aquaculture. Evidence such as the slightly higher prevalence of benthic and epibenthic prey taxa (including harpacticoids) in the stomach contents of much smaller juvenile Chum Salmon suggests that smaller salmonid juveniles utilizing upper intertidal areas or these same areas at different tidal stages might have a greater reliance on benthic prey. However, the majority of salmon that were sampled over the low intertidal habitats where oyster aquaculture is practiced had reached a size at which larger, more-neritic prey types were preferred.

Our data represent individual snapshots of juvenile salmon abundance; they do not provide evidence that juvenile salmon growth and survival are necessarily equal among these habitats over time. Two separate studies have suggested that juvenile salmon preferentially choose eelgrass habitat over aquaculture habitat as a refuge from predators. In a large field mesocosm study within Willapa Bay, Semmens (2008) observed that radio-tagged juvenile Chinook Salmon slowed down over and chose eelgrass habitat in preference to either open mudflat habitat or a small patch of oysters. This was potentially a response to avian predators, which greatly reduced the survival of fish over open mudflats. Behavioral studies in the laboratory also indicated that when Chinook Salmon smolts were exposed to a mock heron predator, they preferred the structure of eelgrass habitat over oyster culture or open mudflat habitat (Dumbauld et al. 2005). Avian predation is a significant source of juvenile salmon mortality in Pacific coast estuaries (Schreck et al. 2006; Clements et al. 2012), but additional work will be necessary to determine how habitat and tidal stage (especially for wading birds) and water clarity (Gregory and Levings 1998) further influence this source of mortality at the estuarine landscape scale.

As a disturbance, oyster aquaculture directly influences eelgrass via competition and displacement (Ruesink et al. 2012; Wagner et al. 2012) and via harvest activities (Wisehart et al. 2007; Dumbauld et al. 2009; Tallis et al. 2009). However, eelgrass is present in areas where aquaculture occurs, and all three habitats (eelgrass, oyster ground culture, and open mudflat) are interspersed over the intertidal landscape (Dumbauld and McCoy 2015). Seagrasses are declining in many estuaries

worldwide (Orth et al. 2006; Waycott et al. 2009) and at several locations along the U.S. West Coast, but this is not the case for Willapa Bay and several other estuaries where oyster aquaculture is currently practiced (Dumbauld et al. 2009, 2011; Dumbauld and McCoy 2015). Thus, we recommend that habitats be evaluated at the landscape scale in individual estuaries; locations of the protective cover provided by seagrass in relation to tidal channels, which are used as migration corridors between lower intertidal areas and marsh/wetland habitats, could also be evaluated at this scale.

At a greater temporal scale, oysters have been part of the estuarine ecosystem in Willapa Bay for as long as juvenile salmon have utilized the estuary, although the form and location of oyster habitat and harvest-related disturbances have changed with the introduction of Pacific oysters, which have replaced the native Olympia oyster *Ostrea lurida* (Coen et al. 2011; Dumbauld et al. 2011). Salmon stocks—and therefore salmon life history strategies—have also been influenced by humans, with hatchery Coho Salmon and Chinook Salmon stocks being emphasized in the Willapa watershed. Chum Salmon have also been supplemented but may more closely reflect the historical condition. Juvenile salmon are highly mobile and likely opportunistically feed and avoid predators over the entire estuarine landscape, so the availability of seagrass and oyster habitats at this larger landscape scale and at a longer temporal scale is important. At a regional scale, for example, long-term trends in Pacific salmon stocks have been linked to early marine growth and survival, and the size and habitat quality of estuaries along the U.S. Pacific coast have been positively correlated with the survival rates of hatchery Chinook Salmon (Koslow et al. 2002; Magnusson and Hilborn 2003; Duffy and Beauchamp 2011). Permanent (“press”) disturbances, such as the diking of marshes, the dredging and filling of shallower estuarine habitats, and even the hardening of shorelines, would be expected to have significant negative impacts on other stocks and life history variants characterized by smaller juveniles that utilize upper intertidal areas (Fresh 2006; Bottom et al. 2009). However, our research suggests that short-term (“pulse”) disturbances that alter the benthic substrate, such as oyster aquaculture, pose a less-significant threat to the use of lower intertidal areas by larger juvenile salmon out-migrants and to the resilience of Pacific salmon populations.

## ACKNOWLEDGMENTS

Funding for this study was provided by the U.S. Department of Agriculture (USDA) via the Western Regional Aquaculture Center (Grant 2001-38500-10495); the Washington Department of Fish and Wildlife; and the USDA Agricultural Research Service (Current Research Information System, Project Number 5358-63000-002-00D). Geoff Hosack received support from the Mamie Markham Research Scholarship (Oregon State University, Corvallis) and a Loosanoff fellowship

(School of Aquatic and Fishery Sciences, University of Washington, Seattle). We sincerely thank John Adler, Roxanne Barker, Hector Beltran, Aimee Christy, Jeff Cordell, Dallis Gilbert, Kirsten Holsman, Bruce Kauffman, Lee McCoy, Kim MacDonald, Mary O’Connor, Sean McDonald, Deanna Patterson, Brian Pickering, John Rodakowski, Jennifer Ruesink, Brice Semmens, Andy Suhrbier, and Carl Young for their assistance in the laboratory and field. Lee McCoy and Keith Bosley contributed advice and were instrumental in providing assistance in data sorting and analysis. The manuscript benefited greatly from comments by Jose Marin Jarrin, Elizabeth Daly, and several anonymous reviewers. We also express our gratitude to the Willapa Bay oyster growers for use of their tidelands and for in-kind support.

## REFERENCES

- Able, K. W. 2005. A re-examination of fish estuarine dependence: evidence for connectivity between estuarine and ocean habitats. *Estuarine Coastal and Shelf Science* 64:5–17.
- Banas, N. S., B. M. Hickey, P. MacCready, and J. A. Newton. 2004. Dynamics of Willapa Bay, Washington: a highly unsteady, partially mixed estuary. *Journal of Physical Oceanography* 34:2413–2427.
- Bando, K. J. 2006. The roles of competition and disturbance in a marine invasion. *Biological Invasions* 8:755–763.
- Barry, J. P., M. M. Yoklavich, G. M. Cailliet, D. A. Ambrose, and B. S. Antrim. 1996. Trophic ecology of the dominant fishes in Elkhorn Slough, California, 1974–1980. *Estuaries* 19:115–138.
- Bates, D. M., M. Maechler, and B. Bolker. 2012. lme4: linear mixed effect models using eigen and R package version 0.9999999-0. Available: [lme4.r-forge.r-project.org](http://lme4.r-forge.r-project.org). (June 2015).
- Bayer, R. D. 1985. Shiner Perch and Pacific Staghorn Sculpins in Yaquina estuary, Oregon. *Northwest Science* 59:230–240.
- Beamish, R. J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography* 49:423–437.
- Beck, M. W., K. L. Heck Jr., K. W. Able, D. L. Childers, D. B. Eggleston, B. M. Gillanders, B. S. Halpern, C. G. Hays, K. Hoshino, T. J. Minello, R. J. Orth, P. F. Sheridan, and M. P. Weinstein. 2003. The role of nearshore ecosystems as fish and shellfish nurseries. *Issues in Ecology* 1:1–12.
- Bollens, S. M., R. V. Hooff, M. Butler, J. R. Cordell, and B. W. Frost. 2010. Feeding ecology of juvenile Pacific salmon (*Oncorhynchus* spp.) in a northeast Pacific fjord: diet, availability of zooplankton, selectivity for prey, and potential competition for prey resources. *U.S. National Marine Fisheries Service Fishery Bulletin* 108:393–407.
- Bottom, D. L., K. Jones, C. A. Simenstad, and C. L. Smith. 2009. Reconnecting social and ecological resilience in salmon ecosystems. *Ecology and Society* [online serial] 14(1):5.
- Brennan, J. S., K. F. Higgins, J. R. Cordell, and V. A. Stamatidou. 2004. Juvenile salmon composition, timing, distribution, and diet in marine nearshore waters of central Puget Sound in 2001–2002. *King County Department of Natural Resources and Parks, Seattle*.
- Brodeur, R. D. 1989. Neustonic feeding by juvenile salmonids in coastal waters of the northeast Pacific. *Canadian Journal of Zoology* 67:1995–2007.
- Brodeur, R. D., E. A. Daly, C. E. Benkwitt, C. A. Morgan, and R. L. Emmett. 2011. Catching the prey: sampling juvenile fish and invertebrate prey fields of juvenile Coho and Chinook salmon during their early marine residence. *Fisheries Research* 108:65–73.
- Brodeur, R. D., and W. G. Pearcy. 1990. Trophic relations of juvenile Pacific salmon off the Oregon and Washington coast. *U.S. National Marine Fisheries Service Fishery Bulletin* 88:617–636.

- Caine, E. A. 1991. Caprellid amphipods: fast-food for the reproductively active. *Journal of Experimental Marine Biology and Ecology* 148:27–33.
- Clements, S., T. Stahl, and C. B. Schreck. 2012. A comparison of the behavior and survival of juvenile Coho Salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) in a small estuary system. *Aquaculture* 362:148–157.
- Coen, L., and R. E. Grizzle. 2007. The importance of habitat created by molluscan shellfish to managed species along the Atlantic coast of the United States. Atlantic States Marine Fisheries Commission, Habitat Management Series 8, Washington, D.C.
- Coen, L. D., B. R. Dumbauld, and M. L. Judge. 2011. Expanding shellfish aquaculture: a review of the ecological services provided by and impacts of native and cultured bivalves in shellfish dominated ecosystems. Pages 239–296 in S. E. Shumway, editor. *Shellfish aquaculture and the environment*. Wiley-Blackwell Scientific Publications, West Sussex, UK.
- Connolly, R. M. 1994. Removal of seagrass canopy: effects on small fish and their prey. *Journal of Experimental Marine Biology and Ecology* 184:99–110.
- Daly, E. A., R. D. Brodeur, and L. A. Weitkamp. 2009. Ontogenetic shifts in diets of juvenile and subadult Coho and Chinook salmon in coastal marine waters: important for marine survival? *Transactions of the American Fisheries Society* 138:1420–1438.
- Dealteris, J. T., B. D. Kilpatrick, and R. B. Rheault. 2004. A comparative evaluation of the habitat value of shellfish aquaculture gear, submerged aquatic vegetation and a non-vegetated seabed. *Journal of Shellfish Research* 23:867–874.
- Deben, W. A., W. D. Clothier, G. R. Ditsworth, and D. J. Baumgartner. 1990. Spatiotemporal fluctuations in the distribution and abundance of demersal fish and epibenthic crustaceans in Yaquina Bay, Oregon. *Estuaries* 13:469–478.
- Deegan, L. A., J. E. Hughes, and R. A. Rountree. 2000. Salt marsh ecosystem support of marine transient species. Pages 333–363 in M. P. Weinstein and D. A. Kreeger, editors. *Concepts and controversies in tidal marsh ecology*. Kluwer Academic Publishers, Boston.
- Duffy, E. J., and D. A. Beauchamp. 2008. Seasonal patterns of predation on juvenile Pacific salmon by anadromous Cutthroat Trout in Puget Sound. *Transactions of the American Fisheries Society* 137:165–181.
- Duffy, E. J., and D. A. Beauchamp. 2011. Rapid growth in the early marine period improves the marine survival of Chinook Salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 68:232–240.
- Duffy, E. J., D. A. Beauchamp, and R. M. Buckley. 2005. Early marine life history of juvenile Pacific salmon in two regions of Puget Sound. *Estuarine Coastal and Shelf Science* 64:94–107.
- Duffy, E. J., D. A. Beauchamp, R. M. Sweeting, R. J. Beamish, and J. S. Brennan. 2010. Ontogenetic diet shifts of juvenile Chinook Salmon in near-shore and offshore habitats of Puget Sound. *Transactions of the American Fisheries Society* 139:803–823.
- Dumbauld, B. R., and L. M. McCoy. 2015. Effect of oyster aquaculture on seagrass *Zostera marina* at the estuarine landscape scale in Willapa Bay, Washington (USA). *Aquaculture Environment Interactions* 7:29–47.
- Dumbauld, B. R., J. L. Ruesink, and S. Rumrill. 2005. The ecological role and potential impacts of molluscan shellfish culture in the estuarine environment. Report to the Western Regional Aquaculture Center, U.S. Department Agriculture, Agricultural Research Service, Newport, Oregon.
- Dumbauld, B. R., J. L. Ruesink, and S. S. Rumrill. 2009. The ecological role of bivalve shellfish aquaculture in the estuarine environment: a review with application to oyster and clam culture in West Coast (USA) estuaries. *Aquaculture* 290:196–223.
- Dumbauld, B. R., J. L. Ruesink, A. C. Trimble, and B. E. Kauffman. 2011. The Willapa Bay oyster reserves in Washington State: fishery collapse, creating a sustainable replacement, and the potential for habitat conservation and restoration. *Journal of Shellfish Research* 30:71–83.
- Edgar, G. J., and C. Shaw. 1995. The production and trophic ecology of shallow-water fish assemblages in southern Australia III: general relationships between sediments, seagrasses, invertebrates and fishes. *Journal of Experimental Marine Biology and Ecology* 194:107–131.
- Feldman, K. L., D. A. Armstrong, B. R. Dumbauld, T. H. DeWitt, and D. C. Doty. 2000. Oysters, crabs, and burrowing shrimp: review of an environmental conflict over aquatic resources and pesticide use in Washington State's (USA) coastal estuaries. *Estuaries* 23:141–176.
- Ferraro, S. P., and F. A. Cole. 2010. Ecological periodic tables for nekton usage of four U.S. Pacific Northwest estuarine habitats. *Canadian Journal of Fisheries and Aquatic Sciences* 67:1957–1967.
- Fresh, K. L. 2006. Juvenile salmon in Puget Sound. Puget Sound Nearshore Partnership, Technical Report 2006-6, Seattle.
- Gillanders, B. M., K. W. Able, J. A. Brown, D. B. Eggleston, and P. F. Sheridan. 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. *Marine Ecology Progress Series* 247:281–295.
- Glancy, T. P., T. K. Frazer, C. E. Cichra, and W. J. Lindberg. 2003. Comparative patterns of occupancy by decapod crustaceans in seagrass, oyster, and marsh-edge habitats in a northeast Gulf of Mexico estuary. *Estuaries* 26:1291–1301.
- Graham, E. S., and S. M. Bollens. 2010. Macrozooplankton community dynamics in relation to environmental variables in Willapa Bay, Washington, USA. *Estuaries and Coasts* 33:182–194.
- Gray, A., C. A. Simenstad, D. L. Bottom, and T. J. Cornwell. 2002. Contrasting functional performance of juvenile salmon habitat in recovering wetlands of the Salmon River estuary, Oregon, USA. *Restoration Ecology* 10:514–526.
- Greene, C. M., D. W. Jensen, G. R. Pess, and E. A. Steel. 2005. Effects of environmental conditions during stream, estuary, and ocean residency on Chinook Salmon return rates in the Skagit River, Washington. *Transactions of the American Fisheries Society* 134:1562–1581.
- Gregory, R. S., and C. D. Levings. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. *Transactions of the American Fisheries Society* 127:275–285.
- Gustafson, R. G., R. S. Waples, J. M. Myers, L. A. Weitkamp, G. J. Bryant, O. W. Johnson, and J. J. Hard. 2007. Pacific salmon extinctions: quantifying lost and remaining diversity. *Conservation Biology* 21:1009–1020.
- Hartleb, C. F., and J. R. Moring. 1995. An improved gastric lavage device for removing stomach contents from live fish. *Fisheries Research* 24:261–265.
- Healey, M. C. 1979. Detritus and juvenile salmon production in the Nanaimo estuary I: production and feeding rates of juvenile Chum Salmon (*Oncorhynchus keta*). *Journal of the Fisheries Research Board of Canada* 36:488–496.
- Healey, M. C. 1982. Juvenile Pacific salmon in estuaries: the life support system. Pages 315–341 in V. S. Kennedy, editor. *Estuarine comparisons*. Academic Press, New York.
- Healey, M. C. 1985. Juvenile Pacific salmon in estuaries: the life support system. Pages 415–428 in A. Yanez-Arancibia, editor. *Fish community ecology in estuaries and coastal lagoons: towards an ecosystem integration*. Universidad Nacional Autonoma De Mexico Press, Mexico City.
- Healey, M. C. 2009. Resilient salmon, resilient fisheries for British Columbia, Canada. *Ecology and Society* [online serial] 14(1):2.
- Heck, K. Jr., K. W. Able, M. P. Fahay, and C. T. Roman. 1989. Fishes and decapod crustaceans of Cape Cod eelgrass meadows: species composition, seasonal abundance patterns and comparison with unvegetated substrate. *Estuaries* 12:59–65.
- Heck, K. L., G. Hays, and R. J. Orth. 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series* 253:123–136.
- Holsman, K. K., P. S. McDonald, and D. A. Armstrong. 2006. Intertidal migration and habitat use by subadult Dungeness crab *Cancer magister* in a NE Pacific estuary. *Marine Ecology Progress Series* 308:183–195.
- Hosack, G. R., B. R. Dumbauld, J. L. Ruesink, and D. A. Armstrong. 2006. Habitat associations of estuarine species: comparisons of intertidal mudflat, seagrass (*Zostera marina*), and oyster (*Crassostrea gigas*) habitats. *Estuaries and Coasts* 29:1150–1160.

- Humphries, A. T., M. K. La Peyre, M. E. Kimball, and L. P. Rozas. 2011. Testing the effect of habitat structure and complexity on nekton assemblages using experimental oyster reefs. *Journal of Experimental Marine Biology and Ecology* 409:172–179.
- Ivlev, V. S. 1961. *Experimental ecology of the feeding of fishes*. Yale University Press, New Haven, Connecticut.
- Jones, K. K., T. J. Cornwell, D. L. Bottom, L. A. Campbell, and S. Stein. 2014. The contribution of estuary-resident life histories to the return of adult *Oncorhynchus kisutch*. *Journal of Fish Biology* 85:52–80.
- Keeley, E. R., and J. W. A. Grant. 2001. Prey size of salmonid fishes in streams, lakes, and oceans. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1122–1132.
- Kelly, J. R., H. Proctor, and J. P. Volpe. 2008. Intertidal community structure differs significantly between substrates dominated by native eelgrass (*Zostera marina* L.) and adjacent to the introduced oyster *Crassostrea gigas* (Thunberg) in British Columbia, Canada. *Hydrobiologia* 596:57–66.
- Koslow, A., A. J. Hobday, and G. W. Boehlert. 2002. Climate variability and marine survival of Coho Salmon (*Oncorhynchus kisutch*) in the Oregon production area. *Fisheries Oceanography* 11:65–77.
- Lehnert, R. L., and D. M. Allen. 2002. Nekton use of subtidal oyster shell habitat in a southeastern U.S. estuary. *Estuaries* 25:1015–1024.
- Levings, C. D., C. D. McAllister, and B. D. Chang. 1986. Differential use of the Campbell River estuary, British Columbia, by wild and hatchery-reared juvenile Chinook Salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 43:1386–1397.
- Levy, D. A., and T. G. Northcote. 1982. Juvenile salmon residency in a marsh area of the Fraser River estuary. *Canadian Journal of Fisheries and Aquatic Sciences* 44:1233–1246.
- Macdonald, J. S., C. D. Levings, C. D. McAllister, U. H. M. Fagerlund, and J. R. McBride. 1988. A field experiment to test the importance of estuaries for Chinook Salmon (*Oncorhynchus tshawytscha*) survival: short-term results. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1366–1377.
- Magnusson, A., and R. Hilborn. 2003. Estuarine influence on survival rates of Coho (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) released from hatcheries on the U.S. Pacific coast. *Estuaries* 26:1094–1103.
- Mattila, J., K. L. Heck Jr., E. Millstein, E. Miller, C. Gustafsson, S. Williams, and D. Byron. 2008. Increased habitat structure does not always provide increased refuge from predation. *Marine Ecology Progress Series* 361:15–20.
- Mielke, P. W., and K. J. Berry. 2001. *Permutation methods: a distance function approach*. Springer, New York.
- Miller, B. A., and S. Sadro. 2003. Residence time and seasonal movements of juvenile Coho Salmon in the ecotone and lower estuary of Winchester Creek, South Slough, Oregon. *Transactions of the American Fisheries Society* 132:546–559.
- Minello, T. J. 1999. Nekton densities in shallow estuarine habitats of Texas and Louisiana and the identification of essential fish habitat. Pages 43–75 in L. R. Benaka, editor. *Fish habitat: essential fish habitat and rehabilitation*. American Fisheries Society, Symposium 22, Bethesda, Maryland.
- Minello, T. J., K. W. Able, M. P. Weinstein, and C. G. Hays. 2003. Salt marshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis. *Marine Ecology Progress Series* 246:39–59.
- Murphy, M. L., J. F. Thedinga, and K. V. Koski. 1988. Size and diet of juvenile Pacific salmon during seaward migration through a small estuary in southeastern Alaska. *U.S. National Marine Fisheries Service Fishery Bulletin* 86:213–222.
- Neher, T. D. H., A. E. Rosenberger, C. E. Zimmerman, C. M. Walker, and S. J. Baird. 2013. Estuarine environments as rearing habitats for juvenile Coho Salmon in contrasting south-central Alaska watersheds. *Transactions of the American Fisheries Society* 142:1481–1494.
- Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16(2):4–21.
- Orth, R. J., T. J. B. Carruthers, W. C. Dennison, C. M. Duarte, J. W. Fourqurean, K. L. Heck, A. R. Hughes, G. A. Kendrick, W. J. Kenworthy, S. Olyarnik, F. T. Short, M. Waycott, and S. L. Williams. 2006. A global crisis for seagrass ecosystems. *Bioscience* 56:987–996.
- Orth, R. J., K. L. Heck Jr., and J. van Montfrans. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator–prey relationships. *Estuaries* 7:339–350.
- Powers, S. P., M. A. Bishop, and G. H. Reeves. 2006. Estuaries as essential fish habitat for salmonids: assessing residence time and habitat use of Coho and Sockeye salmon in Alaska estuaries. *North Pacific Fisheries Research Board*, Seattle.
- R Development Core Team. 2012. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
- Rilov, G., W. F. Figueira, S. J. Lyman, and L. B. Crowder. 2007. Complex habitats may not always benefit prey: linking visual field with reef fish behavior and distribution. *Marine Ecology Progress Series* 329:225–238.
- Roberts, D. W. 2013. *labdsv: ordination and multivariate analysis for ecology*. R package version 1.6.-1. Available: <http://ecology.msu.montana.edu/labdsv/R>. (June 2015).
- Roegner, G. C., D. A. Armstrong, B. M. Hickey, and A. L. Shanks. 2003. Ocean distribution of Dungeness crab megalopae and recruitment patterns to estuaries in southern Washington State. *Estuaries* 26:1058–1070.
- Romanuk, T. N., and C. D. Levings. 2010. Reciprocal subsidies and food web pathways leading to Chum Salmon fry in a temperate marine–terrestrial ecotone. *PLoS (Public Library of Science) One* [online serial] 5(4):e10073.
- Ruesink, J. L., J. P. Fitzpatrick, B. R. Dumbauld, S. D. Hacker, A. C. Trimble, E. L. Wagner, and L. M. Wischart. 2012. Life history and morphological shifts in intertidal seagrass following multiple disturbances. *Journal of Experimental Marine Biology and Ecology* 424–425:25–31.
- Rumrill, S. S., and V. K. Poulton. 2004. Ecological role and potential impacts of molluscan shellfish culture in the estuarine environment of Humboldt Bay, California. Report to the Western Regional Aquaculture Center, Oregon Department of State Lands, South Slough National Estuarine Research Reserve, Charleston, Oregon.
- Schabetsberger, R., C. A. Morgan, R. D. Brodeur, C. L. Potts, W. T. Peterson, and R. L. Emmett. 2003. Prey selectivity and diel feeding chronology of juvenile Chinook (*Oncorhynchus tshawytscha*) and Coho (*O. kisutch*) salmon in the Columbia River plume. *Fisheries Oceanography* 12:523–540.
- Scheinin, M., S. B. Scyphers, L. Kauppi, K. L. Heck, and J. Mattila. 2012. The relationship between vegetation density and its protective value depends on the densities and traits of prey and predators. *Oikos* 121:1093–1102.
- Schindler, D. E., M. D. Scheuerell, J. W. Moore, S. M. Jende, T. B. Francis, and W. J. Palen. 2008. Climate change, ecosystem impacts, and management for Pacific salmon. *Fisheries* 33:502–506.
- Schreck, C. B., T. P. Stahl, L. E. Davis, D. D. Roby, and B. J. Clemens. 2006. Mortality estimates of juvenile spring-summer Chinook Salmon in the lower Columbia River and estuary, 1992–1998: evidence for delayed mortality? *Transactions of the American Fisheries Society* 135:457–475.
- Semmens, B. X. 2008. Acoustically derived fine-scale behaviors of juvenile Chinook Salmon associated with intertidal benthic habitats in an estuary. *Canadian Journal of Fisheries and Aquatic Sciences* 65:2053–2062.
- Simenstad, C. A., and D. M. Eggers. 1981. Juvenile salmonid and baitfish distribution, abundance, and prey resources in selected areas of Grays Harbor, Washington. University of Washington, Fisheries Research Institute, Report FRI-UW-8116, Seattle.
- Simenstad, C. A., and K. L. Fresh. 1995. Influence of intertidal aquaculture on benthic communities in Pacific Northwest estuaries: scales of disturbance. *Estuaries* 18:43–70.
- Simenstad, C. A., K. L. Fresh, and E. A. Salo. 1982. The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon: an unappreciated function. Pages 343–364 in V. S. Kennedy, editor. *Estuarine comparisons*. Academic Press, New York.

- Simenstad, C. A., W. J. Kinney, S. S. Parker, E. O. Salo, J. R. Cordell, and H. Buechner. 1980. Prey community structure and trophic ecology of outmigrating juvenile Chum and Pink salmon in Hood Canal, Washington. University of Washington, Fisheries Research Institute, Report FRI-UW-8026, Seattle.
- Smith, C. J. 1999. Salmon and steelhead habitat limiting factors in the Willapa basin. Washington State Conservation Commission, Olympia.
- Stunz, G. W., T. J. Minello, and L. P. Rozas. 2010. Relative value of oyster reef as habitat for estuarine nekton in Galveston Bay, Texas. *Marine Ecology Progress Series* 406:147–159.
- Sturdevant, M. V., E. Fergusson, N. Hillgruber, C. Reese, J. Orsi, R. Forcht, A. Wetheimer, and B. Smoker. 2012. Lack of trophic competition among wild and hatchery juvenile Chum Salmon during early marine residence in Taku Inlet, Southeast Alaska. *Environmental Biology of Fishes* 94:101–116.
- Tallis, H. M., J. L. Ruesink, B. R. Dumbauld, S. D. Hacker, and L. M. Wiselhart. 2009. Oysters and aquaculture practices affect eelgrass density and productivity in a Pacific Northwest estuary. *Journal of Shellfish Research* 28:251–261.
- Thorpe, J. E. 1994. Salmonid fishes and the estuarine environment. *Estuaries* 17:76–93.
- Trojano, A. T., K. A. King, C. E. Grue, J. M. Grassley, and C. J. Ekblad. 2013. Brain acetylcholinesterase activity in Shiner Perch (*Cymatogaster aggregata*) and juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) after application of carbaryl to control burrowing shrimp within Willapa Bay, Washington. *Archives of Environmental Contamination and Toxicology* 65:779–789.
- Toft, J. D., J. R. Cordell, C. A. Simenstad, and L. A. Stamatou. 2007. Fish distribution, abundance, and behavior along city shoreline types in Puget Sound. *North American Journal of Fisheries Management* 27:465–480.
- Wagner, E. L., J. L. Ruesink, B. R. Dumbauld, S. D. Hacker, and L. M. Wiselhart. 2012. Density-dependent effects of an introduced oyster, *Crassostrea gigas*, on native intertidal eelgrass, *Zostera marina*. *Marine Ecology Progress Series* 468:149–160.
- Waples, R. S., T. Beechie, and G. R. Pess. 2009. Evolutionary history, habitat disturbance regimes, and anthropogenic changes: what do these mean for resilience of Pacific salmon populations? *Ecology and Society* [online serial] 14(1):3.
- Waycott, M., C. M. Duarte, T. J. B. Carruthers, R. J. Orth, W. C. Dennison, S. Olyarnik, A. Calladine, J. W. Fourqurean, K. L. Heck Jr., A. R. Hughes, G. A. Kendrick, J. W. Kenworthy, F. T. Short, and S. L. Williams. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the Academy of Natural Sciences of Philadelphia* 106:12377–12381.
- WDFW (Washington Department of Fish and Wildlife). 2002. Washington salmonid stock inventory (SaSi). WDFW, Olympia.
- Weitkamp, L. A., G. Goulette, J. Hawkes, M. O'Malley, and C. Lipsky. 2014. Juvenile salmon in estuaries: comparisons between North American Atlantic and Pacific salmon populations. *Reviews in Fish Biology and Fisheries* 24:713–736.
- Williams, G. D. 1994. Effects of habitat modification on distribution and diets of intertidal fishes in Grays Harbor estuary, Washington. Master's thesis. University of Washington, Seattle.
- Wiselhart, L. M., J. L. Ruesink, S. D. Hacker, and B. R. Dumbauld. 2007. Importance of eelgrass early life history stages in response to oyster aquaculture disturbance. *Marine Ecology Progress Series* 344:71–80.
- Woodson, L. E., B. K. Wells, P. K. Weber, R. B. MacFarlane, G. E. Whitman, and R. C. Johnson. 2013. Size, growth, and origin-dependent mortality of juvenile Chinook Salmon *Oncorhynchus tshawytscha* during early ocean residence. *Marine Ecology Progress Series* 487:163–175.
- Young, C. D. 2009. Shoaling behavior as a tool to understand microhabitat use by juvenile Chum Salmon, *Oncorhynchus keta*. Master's thesis. University of Washington, Seattle.