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RESEARCH ARTICLE

Enhanced invertebrate prey production following estuarine restoration supports foraging for multiple species of juvenile salmonids (*Oncorhynchus* spp.)

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Estuaries provide crucial foraging resources and nursery habitat for threatened populations of anadromous salmon. As such, there has been a global undertaking to restore habitat and tidal processes in modified estuaries. The foraging *capacity* of these ecosystems to support various species of out-migrating juvenile salmon can be quantified by monitoring benthic, terrestrial, and pelagic invertebrate prey communities. Here, we present notable trends in the availability of invertebrate prey at several sites within a restoring large river delta in Puget Sound, Washington, U.S.A. Three years after the system was returned to tidal influence, we observed substantial additions to amphipod, copepod, and cumacean abundances in newly accessible marsh channels (from 0 to roughly 5,000–75,000 individuals/m^2). In the restoration area, terrestrial invertebrate colonization was dependent upon vegetative cover, with dipteran and hymenopteran biomass increasing 3-fold between 1 and 3 years post-restoration. While the overall biodiversity within the restoration area was lower than in the reference marsh, estimated biomass was comparable to or greater than that found within the other study sites. This additional prey biomass likely provided foraging benefits for juvenile Chinook, chum, and coho salmon. Primary physical drivers differed for benthic, terrestrial, and pelagic invertebrates, and these invertebrate communities are expected to respond differentially depending on organic matter exchange and vegetative colonization. Restoring estuaries may take decades to meet certain success criteria, but our study demonstrates rapid enhancements in foraging resources understood to be used for estuary-dependent wildlife.

Key words: coastal wetlands, community recovery, emergent marsh, foraging capacity, prey biomass

Implications for Practice

- Benthic, terrestrial, and pelagic invertebrate prey biomass can meet or exceed levels found in comparable reference marshes within the early phases of delta restoration. Consequently, salmon may see immediate foraging benefits, even though morphometric functional benchmarks can take decades to attain.
- Benthic and pelagic invertebrates known to be salmonid prey (e.g. amphipods, copepods, insect larvae) are present after delta restoration, and colonization rates are likely driven by changes in physical factors such as sediment pH, organic matter content, and tidal mixing.
- Disturbance-tolerant terrestrial prey, such as dipterans, are the first to aggregate in restoration areas with greater inundation frequencies and less vegetation. Terrestrial prey (or surface drift) can be highly energy-dense, which may offset post-restoration deficits in abundance or biodiversity.

Introduction

Engineered structures, including dikes, levees, and shoreline armoring, adversely affect coastal estuaries by removing wetlands from tidal influence and making them inaccessible to aquatic species (OECD 1996; Toft et al. 2007; Morley et al. 2012). The conversion of estuarine habitat to coastal development is a global phenomenon. Lotze et al. (2006) estimate that up to 67% of coastal wetlands and 91% of resident species have been lost to human impacts. Because coastal estuaries provide crucial foraging resources and transitional nursery habitat during smoltification (Thorpe 1994; Beck et al. 2001), anadromous

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Pacific salmon (*Oncorhynchus* spp.) have been among the hardest-hit taxonomic groups along the North American Pacific coast (Simenstad & Cordell 2000). To address declining salmon populations, numerous restoration projects have been undertaken in the United States and Canada to remove or modify structural barriers in coastal ecosystems.

It is hypothesized that estuarine restoration benefits juvenile salmon by expanding the amount of available habitat and by increasing the availability of invertebrate prey at specific, critical times (Ellings 2011). Simenstad and Cordell (2000) set the foundation for this hypothesis by outlining a hierarchical restoration monitoring approach based on measurements of *opportunity* (habitat availability), *capacity* (production of prey resources), and *realized function* (measured benefit from *opportunity* and *capacity*, such as growth potential). The abundance and distribution of prey used by smolts in a restoring estuary, or its foraging *capacity*, play a crucial role in determining potential benefits to growth and survival. Prey biomass fluctuates spatiotemporally during the out-migration season due to environmental variation in water temperature, salinity, sediment, and vegetative cover (Bottom & Jones 1990; Williams & Williams 1998; Levin & Talley 2000). Relating invertebrate distribution and abundance to the environmental characteristics of newly restored habitats may identify factors contributing to limited productivity, and highlight adaptive management needs and options for improvements.

In addition to the overall availability of prey, their accessibility and energy content also contribute to the foraging *capacity* of a restoring system. While prey biomass is related to environmental factors, juvenile salmon prey selection depends on species, population source, size class, out-migration timing, and climate (Brodeur 1991; Keeley & Grant 2001; Sommer et al. 2001; Fig. 1). Chinook salmon (*Oncorhynchus tshawytscha*) can spend several weeks or months in the estuary (Simenstad et al. 1982; Thorpe 1994; Bottom et al. 2005), and typically feed on arthropods such as flies, spiders, and insects that fall into the water from surrounding terrestrial habitat. Smaller individuals will feed on epibenthic crustaceans (e.g. amphipods and harpacticoid copepods; Pearce et al. 1982; Gray et al. 2002). In contrast, chum and pink salmon (*Oncorhynchus keta* and *O. gorbuscha*) use the estuary intermittently. Because these species reach salt water at such a small size, they are more likely to feed on microbenthic crustaceans such as calanoid copepods, harpacticoid copepods, amphipods, and cumaceans (Kaczynski et al. 1973; Pearce et al. 1982). Coho can exhibit multiple life history strategies, with some subyearling and yearling individuals exhibiting extended use of estuarine habitat (Miller & Sadro 2003; Koski 2009; Jones et al. 2014). Spring migrant yearlings often forage in tidal estuaries, consuming fish larvae, larger amphipods, decapod larvae, and euphausiids (Thorpe 1994; Daly et al. 2009). Variable life history strategies among juvenile salmonids allow for resource niche partitioning and require spatial and temporal heterogeneity in invertebrate prey communities. Consequently, greater levels of invertebrate biodiversity within a restoration area, and throughout the estuarine habitat mosaic as a whole, should maximize foraging benefits for multiple salmonid species.

Coastal restoration has been shown to enhance invertebrate productivity, bolster prey biomass, and increase invertebrate biodiversity, but few studies have specifically examined the impact of large-scale, estuarine restoration on the foraging *capacity* of juvenile salmonids (Beck et al. 2001; Gray et al. 2002; Tanner et al. 2002; Table S1, Supporting Information). We set out to determine whether restoring tidal flow to coastal estuaries can promote prey productivity for juvenile salmonids and to relate this productivity to the functional attributes of the restoring system. We used the Nisqually River Delta—the location of the largest wetland restoration project in the Pacific Northwest, U.S.A.—to address this fundamental management question. We implemented a control-impact study design on 3 years of post-restoration monitoring data collected in accordance with Simenstad and Cordell's (2000) strategic monitoring framework. Our goal was to compare prey production in a previously nonfunctional restoration area to the abundance, biodiversity, and biomass of invertebrate prey observed in unaltered or older restoring habitat. We also quantified seasonal shifts in invertebrate community structure in relation to varying habitat characteristics at restored and reference sites.

Here we present data for benthic, terrestrial, and pelagic invertebrate communities, all of which contribute to juvenile salmon diet during their out-migration. Our expectation is that rapid, early-phase habitat changes in restored areas will lead to increases in invertebrate prey biomass (Ellings et al. 2016), and that a diversified mosaic of habitat types will increase prey productivity and diversity to support salmon species with varied life history strategies. While our results are limited to a single estuary, they have broader implications in demonstrating the functional value of restoring estuarine habitat and enhancements in foraging resources understood to be used for estuary-dependent wildlife.

Methods

Study Area

The Nisqually River Delta (47.08°N, 122.70°W) is one of the largest, salmon-bearing tidal estuaries in the Pacific Northwest, U.S.A. Since 1996, the Nisqually Indian Tribe and Billy Frank Jr. Nisqually National Wildlife Refuge have partnered to restore over 360 ha of delta habitat to tidal processes through multiple phased dike removal projects: a 3.6 ha Pilot restoration (1996 Restoration), a 12.5 ha Phase I (2002 Restoration), a 40 ha Phase II (2006 Restoration), and a 308 ha Phase III (2009 Restoration).

For nearly a century, these restoration sites were diked for agricultural use and were inaccessible to fish. Initial restoration actions in 1996–2006 included dike removal, filling in borrow ditches, and removal of tide gates to reestablish unrestricted tidal flow via Red Salmon Slough. The 2009 Restoration area was subsided, and prior to restoration the fallow agricultural field became a freshwater rain-fed wetland, which was increasingly degraded by invasive reed canary grass (*Phalaris arundinacea*). In 2009, restoration actions included the removal of exterior dikes and interior levees to reinstate flow regimes from Puget Sound and the Nisqually River. With the reintroduction of

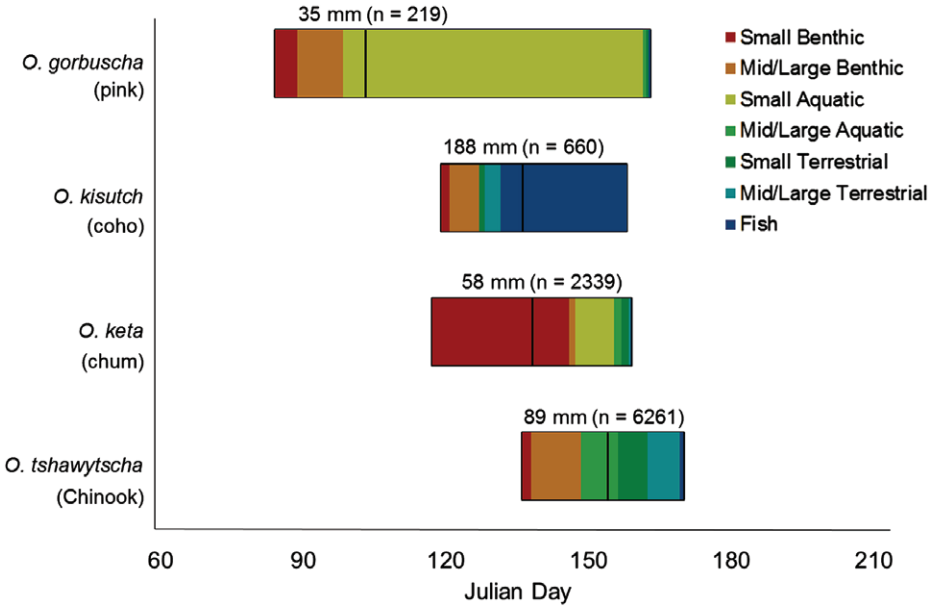

Figure 1. Box plot demonstrating how variation in outmigration timing, size, and diet allows for juvenile salmon niche partitioning in estuarine ecosystems. Boxes show median capture dates with upper and lower quartiles and were calculated based on 2003–2015 tribal beach seining surveys in the Nisqually River Delta. Median lengths (in mm) are shown above the boxes, while coarse dietary composition (as calculated from Pearce et al. 1982 and Simenstad et al. 1982) is color-coded. Small invertebrate prey represents taxonomic groups with a mean length < 1 mm. Sockeye salmon (*Oncorhynchus nerka*) are omitted, as only three individuals were captured at Nisqually between 2003 and 2015.

saltwater from Puget Sound, the freshwater vegetation and invasive reed canary grass died back and was gradually replaced by low tidal marsh plant species. These restoration actions collectively resulted in the removal of 8 km of dikes and reestablished over 44 ha of major tidal channels within a landscape mosaic of freshwater riverine, mesohaline, and salt marsh habitats (Ellings et al. 2016; Fig. 2).

Our study sites include two restored channels—2006 Restoration and 2009 Restoration (Madrone Unit)— each proximate to an undisturbed salt marsh channel (Red Salmon and Nisqually Reference, respectively). Restored sites vary widely in elevation, channel inundation rate, salinity, and vegetation. The 2006 Restoration is a higher-elevation site (approximately 2.75 m), with a moderately deep channel (52% inundation frequency) and substantial freshwater influence (5–10 PSU). Vegetation at 2006 Restoration consists of a variety of tall, overhanging species such as *Carex lyngbyei, Distichlis spicata,* and *Typha latifolia*. The 2009 Restoration is heavily subsided (approximately 1.85 m), with a deep channel (55% inundation frequency) and polyhaline salinity regime (15 PSU; Ellings et al. 2016). This site was largely unvegetated immediately after restoration, but as of publication hummocks of low salt marsh plant species such as *Spergularia* spp. have established in higher elevation areas.

Both reference channels lie in high salt marsh (approximately 2.5 m), but Red Salmon Reference is relatively shallow (47% inundation frequency) and is roughly 5 PSU more saline than the deeper Nisqually Reference channel (67% inundation frequency). The marsh plain at Red Salmon Reference is dominated by halophilic plant species, while Nisqually Reference is more brackish, containing a combination of fresh and salt marsh vegetation typical of the Pacific Northwest (Belleveau et al. 2015). Together, these study sites are representative of the full range of variation in restoring and unaltered habitats throughout the Nisqually River Delta. Sampling locations within sites were selected for accessibility and proximity to Tribal fyke traps (Fig. 2).

Data Collection

Benthic Invertebrates. From 2009 to 2012, we collected benthic invertebrates in August at five tidal sloughs within the 2009 Restoration area (Units 1–4 and Madrone Unit; Fig. 2), with additional seasonal sampling efforts conducted in 2012 at our four primary study sites to complement nearby terrestrial and pelagic invertebrate sampling. We collected six benthic cores by hand at each site during low tide using a stainless steel corer (10 cm in diameter, 10 cm deep). Coring locations were kept consistent each month using a handheld global positioning system (GPS). Within 1 week of collection, we sieved all samples with a U.S. no. 35 sieve (0.5 mm mesh). These samples were stored in a jar containing 95% ethanol and rose-bengal dye solution for later sorting and identification to lowest taxon.

We also collected sediment adjacent to each invertebrate sample to characterize soil physical properties, including percent soil organic matter (OM), pH, and percent silt, sand, and clay (A & L Western Agricultural Laboratories, Modesto, CA, U.S.A.). Water quality data including temperature (°C), salinity (PSU), and DO (mg/L) were acquired from each sampling location using a handheld YSI Model 85 multi-meter (Yellow Springs Instruments, Yellow Springs, OH, U.S.A.).

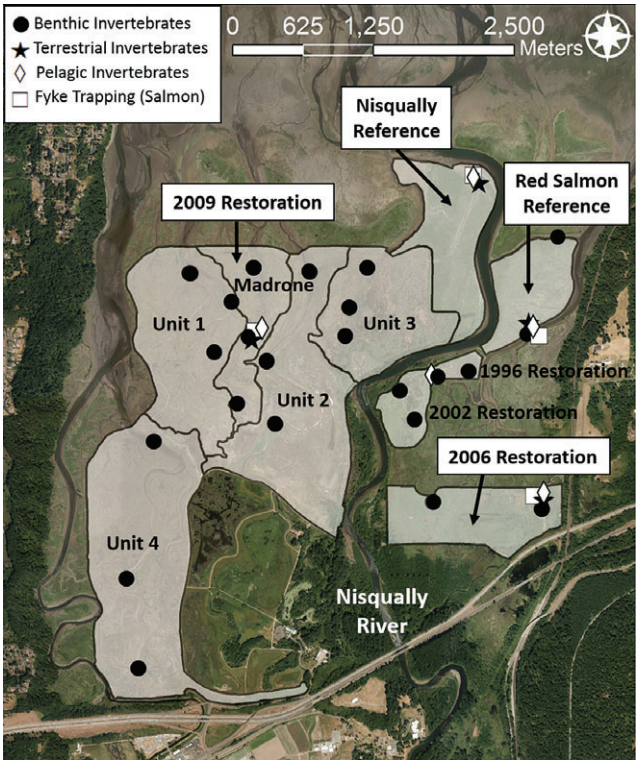

Figure 2. Map of all invertebrate sampling and fyke netting locations including benthic (circle), terrestrial (star), and pelagic (diamond) sampling sites. The four primary study sites are delineated with white labels and arrows. Aerial imagery was photographed and georeferenced by GeoTerra, Inc., Portland, OR, U.S.A.

Terrestrial Invertebrates. We sampled the distribution and abundance of terrestrial prey that fell into the water column using invertebrate fallout traps that were constructed with 55 × 38 cm Tupperware® bins. Styrofoam blocks allowed the traps to float along metal poles with the tide. We installed six fallout traps at each of our four primary study sites: Nisqually Reference, 2009 Restoration, Red Salmon Reference, and 2006 Restoration (Fig. 2). Traps were set once per month in April, May, June, and July of 2010–2012 for a total of 96 samples per year. During deployment, we left traps in the field for 46–50 hours (two tidal cycles), after which the bins were sieved through a 0.5-mm mesh and stored in 70% ethanol for preservation. Any tipped or overfilled traps were excluded from the analysis.

We measured vegetation adjacent to each fallout trap using a 0.25 × 0.25 m sampling quadrat after collecting each invertebrate fallout sample. These data included total percent vegetative cover, observed plant species, stem density, maximum height, and percent contribution to vegetative cover for each species.

Pelagic Invertebrates. We collected plankton samples via neuston tow to quantify prey organisms suspended within the water column at each of our four primary study sites (Fig. 2). Neuston sampling was conducted in April, May, June, and July of 2009–2012 in conjunction with fyke netting for juvenile salmon. A neuston net (0.4 × 0.2 m, 0.130 mm mesh) was pulled across the surface of the channel along a 120° arc measuring 3.85 m for an estimated total volume of 0.33 m^3. We conducted three separate neuston tows per-site on an outgoing tide. Invertebrates of terrestrial origin that fell into the water column were separated and labeled as surface drift. All samples were preserved in 90% ethanol for later identification. With each neuston tow, we collected accompanying water quality data including temperature (°C), salinity (PSU), and DO (mg/L; YSI Model 85 handheld meter).

Identification. We processed invertebrate samples at the U.S. Geological Survey, San Francisco Bay Estuary Field Station Invertebrate Ecology Laboratory using stereo dissection microscopes at a magnification range of 7 to 45×. Invertebrate specialists identified benthic, terrestrial, and pelagic invertebrates to lowest taxonomic level possible using dissection microscopes. Invertebrates were dried at 80°C for 24 hours in a drying oven and allowed to cool in a desiccator cabinet prior to obtaining dry weight biomass (0.01 mg semi microbalance; A&D HR-202i, Abington, Oxfordshire, UK).

Data Analysis

Environmental Variables. We ran an analysis of variance (ANOVA) for each of our environmental predictor variables (OM, % silt, % sand, % clay, water temperature, salinity, DO, and % vegetative cover) using year (2009–2012), site, and restoration status (restored or reference) as predictor variables. All statistical analyses were performed using R statistical software (R Core Development Team 2014). Percent sand, silt, and clay showed covariation (sand-silt: $r^2 = 0.960$, $p < 0.001$; sand-clay: $r^2 = 0.661$, $p < 0.001$), so only % sand was analyzed as an environmental variable. We used a QQ-plot, scale-location plot, and Shapiro–Wilk normality test to ensure that each environmental variable met model assumptions prior to all analyses.

Invertebrate Prey. We extrapolated invertebrate abundances per-core to unit area (m^2) or neuston tow volume (m^3). Core area, rather than volume, is an appropriate unit of measure for the standardization of benthic samples when invertebrates are not distributed evenly along a vertical gradient, and is commonly used in the literature (Simenstad & Thom 1996; Gray et al. 2002; Sundermann et al. 2011). We used these estimated densities to evaluate invertebrate prey community structure, biodiversity, key species abundance, and available prey biomass from 2009 to 2012. We performed our statistical analysis of invertebrate prey community structure at a broader taxonomic level, grouping species by phylum, order, or class to achieve common taxonomic groups that could be compared among sites (Table S2). We used a permutational multivariate analysis of variance (PERMANOVA) to relate taxonomic group densities to time since restoration, month, site, and restoration status. A backwards stepwise model selection process was performed to determine which of these variables explained the most variation

in community structure. Additionally, we conducted a redundancy analysis (RDA) on re-scaled sample data to visualize site-specific differences in community structure through time and to determine which environmental variables were primary drivers of taxonomic change (using an ANOVA on environmental terms). We used weighted sums of taxonomic scores to plot ordinations of sampling sites in space. Samples with missing environmental data were excluded from the analysis.

We performed an ANOVA on species diversity for each sample to relate biodiversity to year, month, site, and restoration status. We calculated Shannon's diversity index as:

$$H = -\sum_{i=1}^{S} p_i \ \ln p_i$$

where H is species diversity, S is the total number of species in the sample, and p_i is the proportion of S made up of the i_{th} species.

To examine the impact of restoration in the context of prey resources, we selected several key (i.e. relevant to juvenile salmon diet) invertebrate taxonomic groups for which the frequency of occurrence was sufficient to run a statistical analysis ($\beta = 0.8$; benthic: $n = 17$; terrestrial: $n = 12$; pelagic: $n = 12$; Table S2). For invertebrates captured via neuston tow, we analyzed planktonic and terrestrial groups separately. We ran a generalized linear model for each key species group using time since restoration, month, site, and each environmental factor as predictor variables. We used a backwards stepwise model selection process beginning from a full additive model to determine which of these predictor variables had the greatest effect on key species abundances. Of these taxa, we were able to obtain dry weight biomass (DWB) data for several aquatic and terrestrial prey species (Table 1). We used mean DWB measurements from a seasonal subsample of invertebrate prey to convert observed abundances to estimated biomass per m^2 (benthic, terrestrial invertebrates) or m^3 (pelagic invertebrates). We analyzed log transformed data using an ANOVA for each focal prey taxon and for overall, per-site biomass. Biomass was analyzed as a function of time, month, location, and site to determine the effects of the restoration on available foraging resources.

Results

Environmental Variables

Environmental characteristics differed among sites. The 2006 Restoration had the greatest water temperatures (means ± SD: 2009 Restoration = 19.86 ± 4.33°C, 2006 Restoration = 23.26 ± 4.17°C, Red Salmon Reference = 18.45 ± 3.02°C; $F_{[2,97]} = 6.901$, $p = 0.002$) and lowest salinities (2009 Restoration = 17.79 ± 7.69 PSU, 2006 Restoration = 12.98 ± 9.39 PSU, Red Salmon Reference = 16.62 ± 7.89 PSU; $F_{[2,97]} = 2.928$, $p = 0.058$). Change in sediment characteristics in the 2009 Restoration was characterized by an 82% decrease in organic matter between 2009 and 2012 ($F_{[1,43]} = 60.12$, $p < 0.001$), with overall composition (% sand) remaining unchanged. Water quality noticeably transformed from brackish to saltwater conditions (7.04 to 21.23 PSU; $F_{[1,65]} = 31.61$, $p < 0.001$). Percent vegetative cover decreased from 91.5% freshwater and invasive wetland plants to only 1% cover (i.e. mudflat) across all 2009 Restoration units ($F_{[1,73]} = 98.02$, $p < 0.001$), while percent cover at Red Salmon Reference and 2006 Restoration remained constant.

Table 1. Mean and standard deviation DWB estimates for target invertebrate prey species. Scale accuracy was 0.01 mg. Individual samples with weights below scale accuracy were not included in mean biomass calculations.

Taxonomic Group	n	*Mean DWB (mg)*	*SD DWB (mg)*
Acari	654	0.008	0.004
Americorophium sp.	478	0.149	0.077
Chironomidae	815	0.039	0.020
Chironomidae larvae	31	0.010	0.000
Dolichopodidae	825	0.808	0.273
Ephydridae	976	0.577	0.456
Gnorimosphaeroma insulare	5	4.520	—
Gnorimosphaeroma oregonensis	56	3.965	2.569
Harpacticoida	36,821	0.001	0.001
Hemigrapsus oregonensis	5	377.178	239.053
Monocorophium sp.	298	0.045	0.023
Mysida	110	3.162	1.028
Neomysis mercedis	578	3.532	1.285
Sciomyzidae	153	0.260	0.252
Sinelobus sp.	4	0.031	0.005
Tipulidae	151	0.503	0.296

Community Structure

We observed strong differences in benthic invertebrate community structure between restored sites, with greater densities of polychaete and oligochaete worms at 2006 Restoration ($F_{[7,110]} = 7.188$, $p < 0.001$). Benthic invertebrate communities changed through time at 2009 Restoration ($F_{[4,65]} = 2.232$, $p = 0.001$; Fig. 3). Temporal differences were most noticeable at lower elevations ($F_{[2,69]} = 2.881$, $p = 0.001$), with sharp increases in polychaete (0–2,519 individuals/m^2), arthropod (1,921–57,359 individuals/m^2), and nematode densities (0–8,549 individuals/m^2; Table S3). Seasonally, community structure did not shift between April and July, although certain species were more prevalent in some months than others ($F_{[3,15]} = 2.162$, $p < 0.042$). Polychaete, oligochaete, and nematode worm densities peaked in April, while arthropods such as copepods and dipteran larvae peaked mid-season in May and June. The RDA detected a significant influence of pH, OM, and % sand on benthic community structure, with insects and insect larvae associated with greater concentrations of OM, and harpacticoid copepods associated with sandier substrates ($F_{[1,44]} = 5.211$, $p < 0.001$; $F_{[1,44]} = 4.432$, $p = 0.002$; $F_{[1,44]} = 2.287$, $p = 0.044$; Fig. 4).

Terrestrial invertebrate community structure also exhibited temporal changes. Clear shifts occurred at restored and historically unaltered sites between 2010 and 2012, with the 2009 Restoration site exhibiting marked increases in dipteran and hymenopteran abundances (294–989 individuals/m^2;

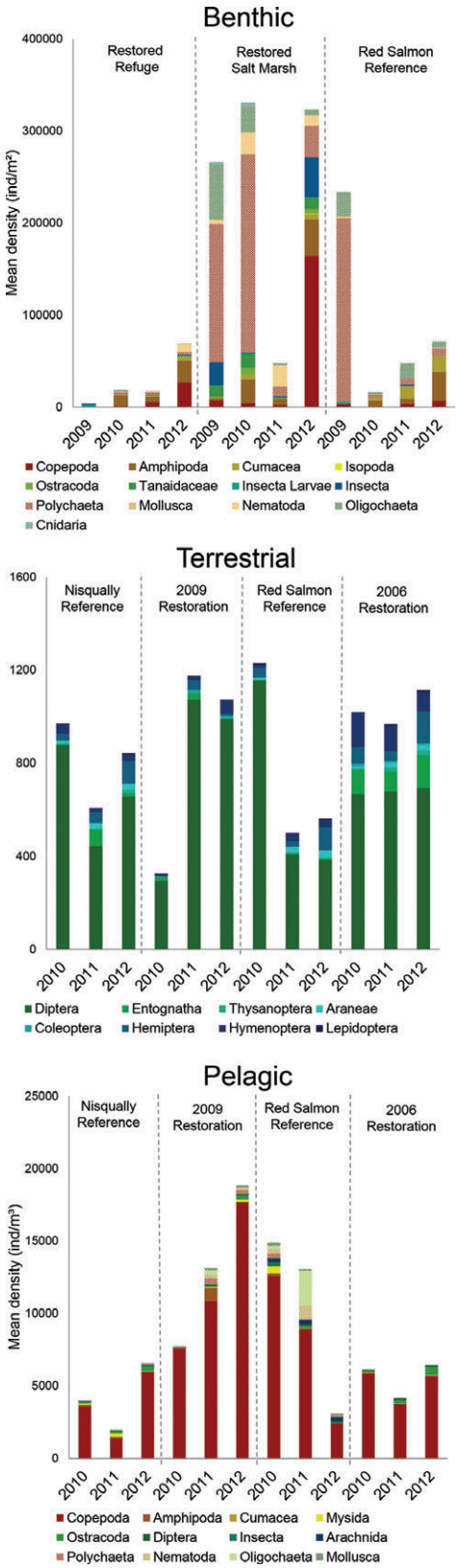

Figure 3. Yearly changes in benthic, terrestrial, and pelagic invertebrate community structure by major sampling site. Striped bars indicate taxa infrequently found in juvenile salmon diets.

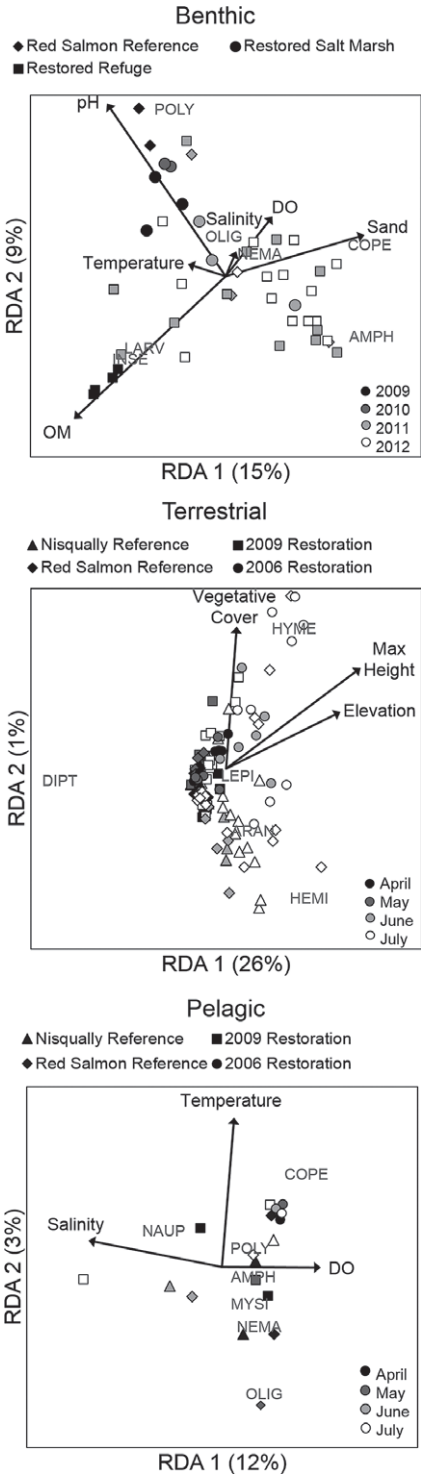

Figure 4. Scaled redundancy analysis (RDA) bi-plots for benthic, terrestrial, and pelagic invertebrate communities, with environmental loadings delineated as black arrows. Percentage of variation explained by RDA1 and RDA2 is denoted in *x*- and *y*-axis titles. Species scores for notable invertebrate taxa are labeled in each bi-plot with gray abbreviations (AMPH, Amphipoda; ARAN, Araneae; COPE, Copepoda; DIPT, Diptera; HEMI, Hemiptera; HYME, Hymenoptera; INSE, Insecta; LARV, Insecta larvae; LEPI, Lepidoptera; MYSI, Mysida; NAUP, assorted nauplii; NEMA, Nematoda; OLIG, Oligochaeta; POLY, Polychaeta).

12–61 individuals/m^2; Fig. 3; Table S4). Terrestrial invertebrate abundance varied between spring and summer months ($F_{[3,264]} = 2.958$, $p < 0.001$), and vegetative height and site elevation were primary driving factors at all sites ($F_{[1,136]} = 37.038$, $p < 0.001$; $F_{[1,136]} = 8.070$, $p = 0.002$). RDA output suggested that dipterans were more abundant at lower elevation sites with less vegetation, while hymenopterans and hemipterans were more common at sites with tall, overhanging plant cover (Fig. 4).

Pelagic invertebrates were influenced primarily by site, and neither planktonic invertebrates nor terrestrial drift varied seasonally or from year to year ($F_{[1,40]} = 2.944$, $p = 0.007$; $F_{[1,40]} = 2.234$, $p = 0.045$; Fig. 3). There were distinct differences in community structure among sites for planktonic invertebrates. For instance, all sites were dominated primarily by copepods, but the 2009 Restoration and Nisqually Reference sites had higher densities of nauplii in some years (Table S5). The 2009 Restoration also contained higher densities of amphipods than other sites. For terrestrial invertebrate drift, arachnids, dipterans, and Collembola were prevalent at all four sampling sites, but the Red Salmon Reference site had densities that were up to four times greater than any other site, and had the greatest prevalence of arachnid species (Fig. 3; Table S5). We did not have enough associated environmental data with neuston samples to run a robust RDA, but a bi-plot of the data suggested that copepods might be associated with higher water temperatures and DO (Fig. 4).

Biodiversity

Benthic species diversity increased through time by 62% at all sites across the Nisqually River Delta ($F_{[1,73]} = 14.080$, $p < 0.001$). When environmental variables were included as predictors, species diversity was found to correlate weakly with salinity ($df = 65$, $r^2 = 0.025$, $p = 0.015$). Throughout the 2009 Restoration area, species diversity was lower at Unit 1 and Madrone Unit compared to other locations (Unit 1 = 0.81 ± 0.56, Unit 2 = 1.11 ± 0.47, Unit 3 = 1.01 ± 0.52, Unit 4 = 1.02 ± 0.44, Madrone = 0.82 ± 0.50; $F_{[5,69]} = 4.285$, $p = 0.002$). Species diversity was greater overall at 2006 Restoration (1.13 ± 0.54) than at Red Salmon Reference (0.84 ± 0.54; $F_{[6,30]} = 3.641$, $p = 0.007$).

Terrestrial invertebrate biodiversity increased through time across all four sites (2010 = 1.10 ± 0.54, 2011 = 1.26 ± 0.57, 2012 = 1.39 ± 0.56; $F_{[1,274]} = 7.41$, $p = 0.006$). Diversity also peaked between spring and summer months with increases of roughly 77–300%, except in 2009 Restoration, where it peaked in May and then decreased up to 28% in June and July ($F_{[15,26]} = 12.09$, $p < 0.001$). Diversity was higher at 2006 Restoration (Nisqually Reference = 1.03 ± 0.63, 2009 Restoration = 1.11 ± 0.45, Red Salmon Reference = 1.33 ± 0.52, 2006 Restoration = 1.42 ± 0.46; $F_{[3,272]} = 7.28$, $p = 0.002$; Fig. 3). This was related to positive correlations between biodiversity and vegetative cover and plant height, as plant heights at 2006 Restoration were at least 16% greater than at any other site, including historic salt marshes ($df = 136$, $r^2 = 0.112$, $p < 0.001$; $df = 136$, $r^2 = 0.107$, $p < 0.001$).

Plankton species diversity was lower at the restored sites, especially at 2006 Restoration (2009 Restoration = 0.569 ± 0.253, Nisqually Reference = 0.760 ± 0.365, 2006 Restoration = 0.416 ± 0.145, Red Salmon Reference = 0.801 ± 0.357; $F_{[3,44]} = 4.401$, $p = 0.008$). Diversity for planktonic invertebrates did not change from year to year or seasonally. The species diversity of terrestrial drift also differed by site, and was lowest at 2009 Restoration (0.592 ± 0.410) and Red Salmon Reference (0.623 ± 0.192) compared with other sites (Nisqually Reference = 0.950 ± 0.271, 2006 Restoration = 1.039 ± 0.217; $F_{[3,41]} = 7.171$, $p = 0.001$). Diversity in terrestrial drift also did not appear to vary seasonally or year to year. Moreover, neither planktonic nor terrestrial invertebrate biodiversity was affected by any of the environmental predictors, including temperature, salinity, or DO.

Key Species Abundance and Biomass

Crustacean species (harpacticoid copepods, cumaceans, and corophiid amphipods) experienced delta-wide increases in abundance through time (Fig. 5; Table S3). Both *Americorophium* and *Monocorophium* amphipods increased in biomass between 2009 and 2012 across the entire Nisqually River Delta, with *Americorophium* biomass increasing from 0 to 334 mg/m^2 in 2009 Restoration, and *Monocorophium* biomass increasing from 0 to 258 mg/m^2 ($F_{[1,107]} = 7.706$, $p = 0.007$; $F_{[1,107]} = 33.676$, $p < 0.001$). Harpacticoid copepod biomass also increased from 0 to 27 mg/m^2 between 2009 and 2012 ($F_{[1,107]} = 11.118$, $p = 0.001$). Conversely, dipteran larvae exhibited a decline in population densities in 2010, followed by a rebound to initial abundances (Fig. 5; Table S3). Total benthic biomass, including crustaceans and dipteran larvae, increased through time at all sites, but was three times greater overall at 2006 Restoration and Red Salmon Slough compared to 2009 Restoration and Nisqually Reference ($F_{[1,109]} = 34.429$, $p < 0.001$; $F_{[1,109]} = 5.887$, $p = 0.017$; Fig. 6A). Mean biomass was greatest in the month of June, due to elevated *Americorophium* densities ($F_{[1,15]} = 8.866$, $p < 0.001$).

The 2009 Restoration had 5–67% lower abundances of all terrestrial invertebrate species. Nevertheless, total sample biomass was greater at the Nisqually Reference and 2009 Restoration sites than at the 2006 Restoration and Red Salmon Reference sites ($F_{[3,265]} = 8.109$, $p < 0.001$; Fig. 6B). Furthermore, increases in available terrestrial prey biomass between 2010 and 2012 were greatest at 2009 Restoration, even though year-to-year variation was high at all sites ($F_{[3,265]} = 6.549$, $p < 0.001$). Chironomids were least prevalent at 2009 Restoration overall, but experienced rapid increases in biomass through time (Nisqually Reference = 10.49 ± 11.02 mg/m^2, 2009 Restoration = 6.96 ± 7.04 mg/m^2, Red Salmon Reference = 7.17 ± 6.71 mg/m^2, 2006 Restoration = 17.72 ± 20.26 mg/m^2; $F_{[3,265]} = 3.686$, $p = 0.013$). Dolichopodidae also experienced considerable increases in biomass between 2010 and 2012 (Nisqually Reference = 263.05 ± 552.10 mg/m^2, 2009 Restoration = 273.01 ± 364.38 mg/m^2, Red Salmon

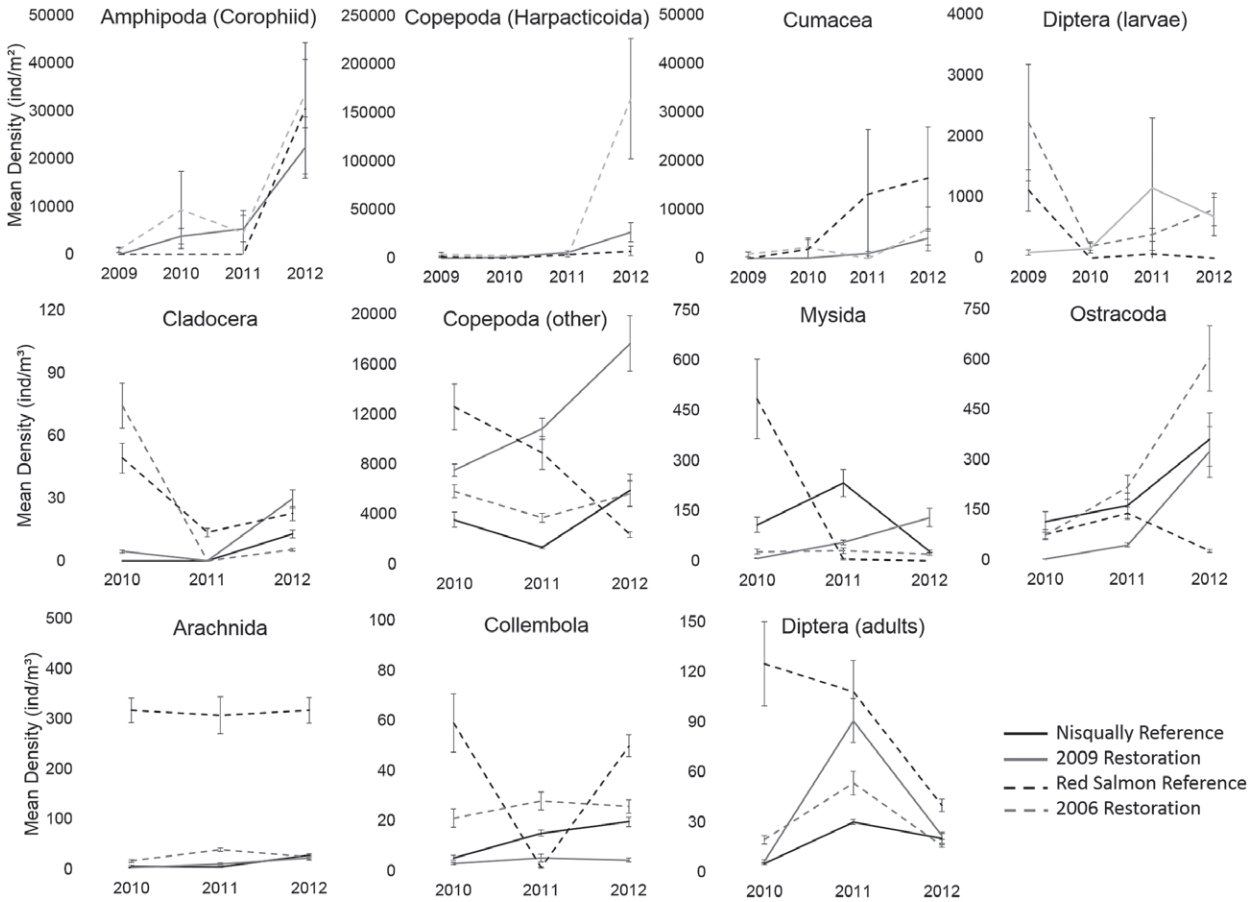

Figure 5. Post-restoration benthic (top), pelagic (middle), and terrestrial drift (bottom) prey densities through time for restored (gray) and historic (black) marsh sites. For benthic prey, the 2009 samples were collected from pre-restoration conditions. Error bars represent ±1 SE.

Reference = 255.10 ± 662.65 mg/m^2, 2006 Restoration = 63.46 ± 99.97 mg/m^2; $F_{[3,265]} = 13.984$, $p < 0.001$).

Key species abundances in pelagic samples were highly variable from year-to-year and month-to-month, especially for planktonic invertebrates. At 2009 Restoration, observed abundances of amphipods, copepods, cumaceans, mysids, ostracods, nauplii, and dipteran larvae were higher than or equivalent to abundances at the Nisqually Reference site (Fig. 5; Table S5). Conversely, at 2006 Restoration, abundances were generally lower than at the Red Salmon Reference site, especially for amphipods, copepods, cumaceans, mysids, nauplii, and dipteran larvae.

For drift invertebrates, year-to-year abundances remained relatively stable. Arachnids, Collembola, and dipteran adults were all up to 10 times more abundant at the Red Salmon Reference site (Fig. 5; Table S5). At 2009 Restoration, abundances of arachnids and Collembola were lower than at the other three sites, but abundances of dipteran adults increased through time (6.75–21.75 individuals/m^3) and were equivalent to, or greater than, other sites. Of the terrestrial drift species, only Dolichopodidae and Ephydridae flies were prevalent enough for biomass calculations. Both taxa were more prevalent in 2006 Restoration and Red Salmon Reference, but did not experience much year-to-year variation in biomass ($F_{[1,46]} = 4.378$, $p = 0.042$; $F_{[1,46]} = 4.530$, $p = 0.039$).

In terms of total pelagic prey biomass (including planktonic and terrestrial species), year-to-year differences were negligible, but among-site differences suggested that the Nisqually Reference site contained 2–8 times more pelagic invertebrate biomass than any other site (Fig. 6C). In terms of the proportion of biomass from crustacean (planktonic) as opposed to dipteran (terrestrial) sources, the 2009 Restoration and Nisqually Reference sites contained greater proportions of pelagic prey biomass regardless of restoration status (Nisqually Reference = 0.74 ± 0.41, 2009 Restoration = 0.67 ± 0.42, Red Salmon Reference = 0.27 ± 0.45, 2006 Restoration = 0.42 ± 0.46; $F_{[1,43]} = 7.984$, $p = 0.007$; Fig. 6D).

Discussion

Collective monitoring efforts in the Nisqually River Delta have shown that salmon habitat use and growth potential are affected by changes in biophysical and morphological characteristics in restored tidal channels (David et al. 2014; Ellings et al. 2016; Davis et al. 2017). Our findings expand upon these results by

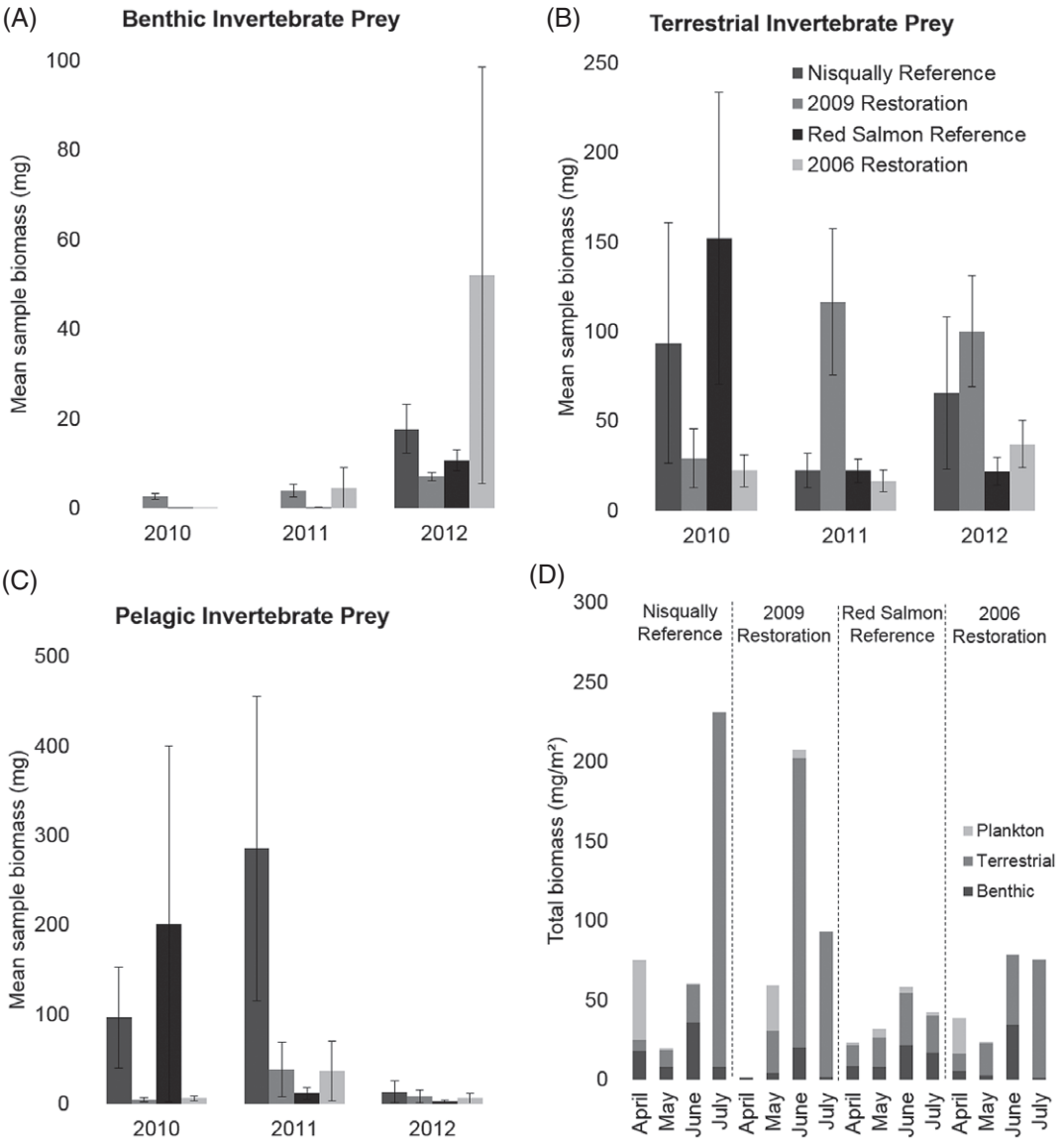

Figure 6. Post-restoration estimated biomass for all measured benthic (A), terrestrial (B), and pelagic (C) prey species. Mean per-sample biomass (mg) is plotted by year and location. Estimated monthly dry weight biomass (mg/m^2) from 2010 to 2012 is shown in the graph (D). Error bars represent $\pm$1 SE.

demonstrating the added value of restoration in enhancing foraging *capacity* for multiple salmon species. We found that invertebrate community structure changed noticeably, with substantial enhancements to benthic, terrestrial, and pelagic prey availability.

Benthic invertebrate communities experienced exponential gains in crustacean and insect biomass following the 2009 restoration. This increase in biomass mainly constituted common salmonid prey such as harpacticoid copepods, corophiid amphipods, and cumaceans, whose densities at restored sites increased from negligible abundances pre-restoration to an average of approximately 60,000 individuals/m^2 3 years post-restoration. Meanwhile, the abundances of these taxa at the older 2006 Restoration site remained elevated in all years. Benthic community structure was influenced by tidal inundation; therefore, lower elevation sites experienced the most notable increases in biodiversity and prey biomass after restoration. Both salinity and sediment substrate can affect benthic community structure in inundated habitat (Chapman & Brinkhurst 1981; Teske & Wooldridge 2003; Ferraro & Cole 2011). While salinity did not have a significant influence on benthic community structure in our RDA, we did observe an immediate shift from a dominance of insect larvae to crustaceans as organic matter from behind the historic dike was washed away. This suggests that large-scale restoration can improve invertebrate prey conditions for the entire river delta system via organic matter exchange (Howe & Simenstad 2011; Howe & Simenstad 2014).

Terrestrial invertebrate communities also changed through time at all sampling sites, especially within the newer restoration

area. At 2009 Restoration, biodiversity remained low throughout the year, and overall biomass was slightly less than at the Nisqually Reference site. Nevertheless, we did observe the greatest increases in abundance for mobile prey species such as coleopterans, dipterans, and hemipterans at this site as a result of their ability to colonize suitable habitat (Sobocinski et al. 2010). Furthermore, incidences of dipterans and hymenopterans that had fallen into the water column at 2009 Restoration were analogous to those at the Nisqually Reference site and 2006 Restoration in 2011 and 2012. Terrestrial invertebrate community composition was driven largely by the height of adjacent salt marsh vegetation, with species such as arachnids and hymenopterans being more abundant in the densely-vegetated emergent marshes at the 2006 Restoration and Red Salmon Reference sites. In the 2009 Restoration area, where vegetation was sparse, dipterans comprised most of the available terrestrial prey biomass, colonizing mudflats and floating *Ulva* algae within 1 year of the restoration. Mobile, disturbance-tolerant prey such as dipterans can provide short term benefits for salmon foraging in restoration areas (Gray et al. 2002; Cordell et al. 2011). As vegetation succession occurs and more invertebrate prey taxa colonize the restoration, one would expect to see sustained increases in overall terrestrial prey abundance and biodiversity (Cameron 1972; Desender & Maelfait 1999; Romanuk & Levings 2003).

Pelagic invertebrate abundances were the most spatiotemporally variable. Plankton were dominated by high densities of copepods and various nauplii known to be salmonid prey at all four sites, with abundances at 2009 Restoration demonstrating comparable community trends in 2010–2012. The prevalence of plankton at 2009 Restoration was no different than at either Nisqually Reference or 2006 Restoration despite notable differences in salinity. This, along with the rapid colonization of target prey, could be due to tidal mixing effects in the water column, which have been shown to have a strong impact on invertebrate dispersal (Palmer & Gusf 1985).

A lack of pre-restoration data meant we were unable to apply a before-after control-impact study design (BACI; Block et al. 2001) to monitor invertebrate communities at historic reference sites, but a space-for-time substitution did shed light on the rapid nature of invertebrate colonization patterns in disturbed habitat. If the tidal prism is restored, managers can expect to see immediate responses in pelagic zooplankton, which are easily distributed across sloughs via tidal forces. Similarly, benthic invertebrates such as burrowing amphipods and copepods may be quick to respond with increasing abundances following the broad-scale distribution of organic matter. Terrestrial invertebrates, some of which are dependent upon vegetative growth, may exhibit the slowest community responses to restoration actions. While disturbance-tolerant taxa such as dipterans can colonize early-phase restoration sites at high densities and are also energy-rich prey, restoration sites may lag in terrestrial biodiversity until vegetation has at least partially-colonized the marsh plain. The development of complex tidal channel networks with overhanging vegetation can lead to shaded waterways with more stable water temperatures (Beck et al. 2001; Bertness & Ewanchuk 2002; Whitcraft & Levin 2007), while also providing habitat and structure for terrestrial prey (Kneib 1984; Allan et al. 2003). Managers may choose to expedite certain processes by encouraging channel erosion or actively planting vegetation, although there are demonstrated risks to over-engineering a restoring ecosystem or encouraging homogeneity among habitats (Elliot et al. 2016).

Variation in local habitat types contributes to a diverse assemblage of benthic, terrestrial, and pelagic invertebrate species, which has positive implications for fish predators (Larkin et al. 2008). A wide range of invertebrate prey taxa and sizes promotes resource partitioning for the benefit of multiple species of juvenile salmon. In the Nisqually River Delta, the rapid colonization by harpacticoid copepods in the spring and summer provided potential prey for juvenile chum and early season Chinook salmon, which tend to prefer smaller crustacean species in the epibenthos (Feller & Kaczynski 1975; Pearce et al. 1982). Meanwhile, the establishment of larger benthic crustaceans, such as corophiid amphipods, provided potential prey for coho and natural- and hatchery-origin Chinook salmon. Chinook also selectively feed on dipteran species such as Chironomidae, Ephydridae, and Dolichopodidae during their seaward migration (Pearce et al. 1982; Shreffler et al. 1992). Davis et al. (2017) found that elevated dipteran biomass in the 2009 Restoration area contributed positively to juvenile Chinook salmon foraging in early phases of restoration. These consumptive patterns may have resulted in enhanced growth potential, since dipterans can have two to three times the energy density of some crustaceans (David et al. 2014). Finally, although we did not directly measure other fish or wildlife populations, salmon may not be the only guilds deriving foraging benefits from newly-available prey. Amphipods, copepods, polychaetes, and dipteran larvae are readily consumed by other fish and waterbirds (Hicklin & Smith 1984; Foy & Norcross 1999).

Estuaries are dynamic systems that exhibit extensive seasonal and annual variation in morphometry and productivity during restoration. The reestablishment of tidal inundation after the removal of engineered barriers creates a major disturbance, from which the system returns to a new equilibrium (Suding et al. 2004). Our post-restoration monitoring data from the Nisqually River Delta has demonstrated that even young restoration sites can greatly enhance foraging *capacity* through the addition of previously-inaccessible prey resources. Increasing *opportunity* potential (i.e. tidal regime, sedimentation patterns, vegetative establishment) and improving *capacity* may have additive benefits for out-migrating juvenile salmon, but progress remains contingent upon the trajectory and frequency of disturbance of the restoring system. Changes in inundation regimes, drought, and temperature extremes can present new challenges for restoration managers. Improving knowledge of invertebrate-habitat relationships across the entire estuarine gradient will bolster our understanding of the best restoration and enhancement actions to sustain salmon and wildlife populations into the future.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. A table summarizing currently available, peer-reviewed journal articles on post-restoration, coastal invertebrate communities.
Table S2. Invertebrate prey taxa found in restored and historic Nisqually marsh habitat (2009–2012).
Table S3. Statistical output for benthic invertebrate analyses by phylum and key prey taxonomic group.
Table S4. Statistical output for terrestrial invertebrate analyses by key prey taxa.
Table S5. Statistical output for aquatic invertebrate analyses (plankton and terrestrial) by key prey taxonomic groups.

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