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RESEARCH ARTICLE

# Gauging resource exploitation by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in restoring estuarine habitat

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**In the context of delta restoration and its impact on salmonid rearing, success is best evaluated based on whether out-migrating juvenile salmon can access and benefit from suitable estuarine habitat. Here, we integrated 3 years of post-restoration monitoring data including habitat availability, invertebrate prey biomass, and juvenile Chinook salmon (*Oncorhynchus tshawytscha*) physiological condition to determine whether individuals profited from the addition of 364 ha of delta habitat in South Puget Sound, Washington, United States. Productivity in the restored mudflat was comparable to reference sites 3 years after dike removal, surpassing a mean total of 6 million kJ energy from invertebrate prey. This resulted from the development of a complex network of tidal channels and a resurgence in dipteran biomass that was unique to the restoration area. Consequently, a notable shift in invertebrate consumption occurred between 2010 and 2011, whereby individuals switched from eating primarily amphipods to dipteran flies; however, dietary similarity to the surrounding habitat did not change from year to year, suggesting that this shift was a result of a change in the surrounding prey communities. Growth rates did not differ between restored and reference sites, but catch weight was positively correlated with prey biomass, where greater prey productivity appeared to offset potential density-dependent effects. These results demonstrate how the *realized function* of restoring estuarine habitat is functionally dependent. High prey productivity in areas with greater connectivity may support healthy juvenile salmon that are more likely to reach the critical size class for offshore survival.**

**Key words: energy availability, habitat connectivity, invertebrate prey, realized function, tidal estuary, wetland construction**

### Implications for Practice

- The rapid formation of tidal channel networks and the recolonization of disturbance-tolerant invertebrate prey species after delta restoration allow juvenile Chinook salmon to access and benefit from newly restored habitat.
- Among-site variation in invertebrate prey can result in notable dietary differences, but these differences alone are not indicative of juvenile salmon physiological condition or growth rates.
- Significant relationships between physiology and rearing origin, salmon densities, and prey energy availability suggest that restoration practitioners can improve the *realized function* of a restoring estuary by increasing its accessibility and connectivity to highly productive habitat.

## Introduction

Coastal estuaries are ecologically and economically valuable ecosystems, but they are also among the world's most threatened habitats (Bassett et al. 2013; Sheaves et al. 2015). Estuaries are important to some anadromous salmon species, with juveniles spending significant portions of their development in emergent tidal marshes as they complete their seaward migration (Reimers 1973; Levings et al. 1986; Groot & Margolis 1991). Chinook salmon (*Oncorhynchus tshawytscha*) in particular are believed to be the most estuarine-dependent species of Pacific salmon, with residence times as long as 6 months in some larger, intact systems (Simenstad et al. 1982; Magnusson & Hilborn 2003). Estuarine residency is positively associated with successful Chinook growth and development,

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[Correction added on 08 January 2018, after first online publication: Author names of the reference Woo et al. 2018 were changed accordingly.]

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since this habitat provides a rich array of invertebrate prey and an intricate network of tidal channels for juveniles to use as refugia (Healey 1982). Consequently, coastal wetland deterioration has contributed to ensuing declines in Chinook and other Pacific salmon populations (Simenstad et al. 1982; Simenstad 1997).

Over the last few decades, salmon declines have prompted large-scale restoration projects along the Pacific Coast of North America. Post-restoration monitoring and adaptive management are improving with experience, and restoration practitioners benefit from novel approaches to assess juvenile salmon response to habitat change (Diefenderfer et al. 2016). Simenstad and Cordell (2000) laid the foundation for a monitoring framework by which restoration success criteria are evaluated based on long-term measures of *opportunity*, *capacity*, and *realized function*, where *opportunity* is related to habitat availability, *capacity* is related to individuals' ability to forage in newly available habitats, and *realized function* refers to direct physiological responses (i.e. foraging and growth) that result from improvements in habitat and prey availability. Measures of habitat use and prey consumption are well-studied in multiple restored estuarine systems (Gray et al. 2002; Bottom et al. 2005; Roegner et al. 2010), but a limited number of post-restoration monitoring studies have been extensive enough to link such metrics to the physiological responses of juvenile salmon (Miller & Simenstad 1997). A detailed analysis of these linkages would represent a comprehensive assessment of the three-tiered monitoring framework, with an emphasis on the *realized function* of restoring estuaries.

Our goal for this study was to determine whether habitat and prey availability in a restoring large river delta could be linked to the physiological characteristics of juvenile Chinook salmon, including catch weight, body condition, and growth rate. To accomplish this goal, we used a control-impact study design to compare metrics between restored and reference sites in the Nisqually River Delta. Nisqually's post-restoration monitoring framework has guided the ongoing collection of physical and biological data (Ellings 2011) including intensively monitored fish populations, and assessments of habitat availability (Ellings et al. 2016), invertebrate prey availability (Woo et al. 2018), and growth potential (David et al. 2014). Woo et al. (2018) observed substantial increases in benthic, terrestrial, and pelagic invertebrate biomass within 3 years of dike removal; however, different invertebrate species can have different energy densities, and may vary in size or ease of capture (Brey et al. 1988; Gray 2005). Furthermore, this energy is of little utility if juvenile salmon cannot access and forage in prey-rich sites, or if thermal conditions present metabolic limitations. As such, data on the morphometry of the delta and its ability to support crucial prey guilds are necessary to elucidate the relationship between the productivity of restoring estuarine habitat and the physiological benefits derived from available prey resources. Such information, as presented herein, can be used to guide decisions concerning future restoration efforts, habitat improvement projects, and hatchery release strategies for ESA-listed Chinook salmon.

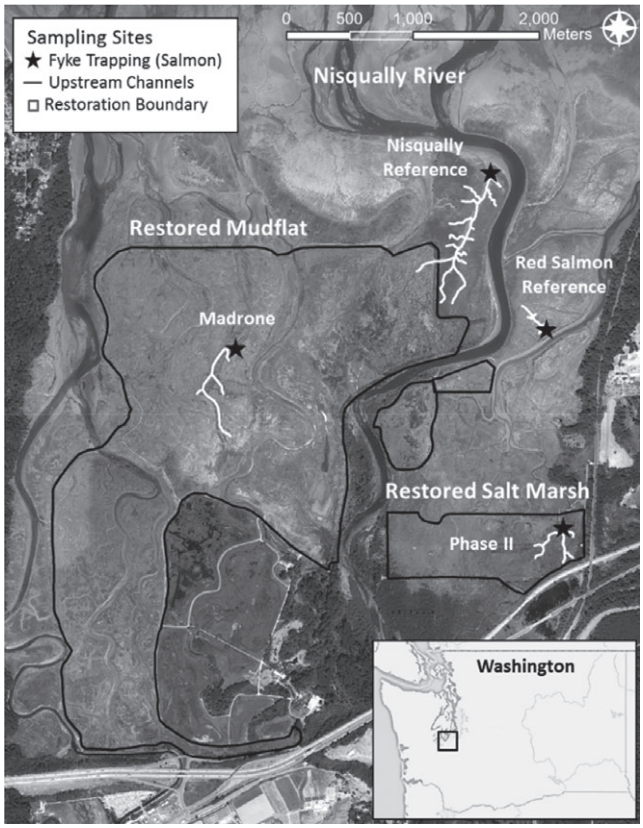


Figure 1. Map of all fyke netting locations (stars) on the Nisqually River Delta (Washington, United States), including the 2009 restored mudflat and 2006 restored salt marsh (outlined in black).

## Methods

### Study Area

The Nisqually Delta forms the terminus of the Nisqually River (47.08°N, 122.70°W; Fig. 1), flowing directly into the southern end of Puget Sound, Washington, United States. Historically, the delta was comprised of a diverse array of habitat types, including more than 1,500 ha of estuarine wetlands. In the early 1900s, more than 600 ha of estuarine habitat were leveed for agricultural use, resulting in its removal from tidal influence, loss of sediment input, and eventual subsidence. This habitat conversion was a barrier to fish access, and directly impacted the native salmon that used the Nisqually River. The threatened Nisqually fall Chinook stock were especially hard-hit, and were locally extirpated in the 1960s and subsequently reintroduced through hatchery efforts. Currently, annual runs of 20,000–450,000 natural-origin Chinook salmon and up to 4 million hatchery-origin Chinook salmon out-migrate concurrently through the Nisqually Delta each year.

The Nisqually Delta has been managed by Billy Frank Jr. Nisqually National Wildlife Refuge in conjunction with the Nisqually Indian Tribe (hereafter Tribe) since 1974. The Tribe began restoration efforts in the mid-1990s. Three phased restorations were conducted in higher-elevation (2–3 m NAVD88) salt marsh habitat on the east side of the Nisqually

River in 1996, 2002, and 2006. Subsequently, the Refuge opened up roughly 308 ha of subsided (1.5–2 m NAVD88) estuarine habitat to tidal processes on the west side of the river in 2009 (USFWS 2005). Within 1 year of dike removal, almost all the freshwater wetland vegetation was washed to sea, leaving behind an extensive intertidal mudflat. Successional regrowth saw the gradual return of low marsh species such as perennial pickleweed (*Salicornia pacifica)* and sandspurry (*Spergularia* spp.) in higher elevation areas, but as of 2012, more than three-fourths of the restoring marsh remained bare.

To evaluate the *realized function* of the restoring Nisqually Delta, we studied two restored channels—Phase II (2006 Restored) and Madrone Slough (2009 Restored)—each proximate to an undisturbed salt marsh channel (Red Salmon and Nisqually Reference, respectively, Fig. 1). Phase II and Nisqually Reference run through emergent estuary marsh habitat typical of the Pacific Northwest and contain a combination of halophilic (*Triglochin maritima*, *Potentilla anserina pacifica*, *Distichlis spicata*) and freshwater (*Typha* sp., *Juncus* sp.) vegetation types as a result of frequent freshwater influence. Dense, overhanging swaths of *Carex lyngbyei* dominate the channel edge at both of these sites. Madrone and Red Salmon Sloughs are further out on the delta, and are primarily influenced by seawater. The northern end of Red Salmon Slough includes vegetation common to high-elevation salt marshes of the Pacific Northwest such as *Deschampsia cespitosa*, *Hordeum* sp., and *P. anserina pacifica* (Belleveau et al. 2015). As of 2012, Madrone Slough was comprised of mudflat habitat, with sparse regrowth of low marsh vegetation. The tidal channels at Madrone were also still developing through erosive processes at this time (Ellings et al. 2016).

### Data Collection and Analysis

**Habitat Accessibility.** We examined post-restoration habitat accessibility across the entire restoring delta and at target study sites using 2011 aerial imagery (Bergman Photographic Services Inc., Portland, OR, U.S.A.), hand-digitized channel morphology (Ellings et al. 2016), and LiDAR imagery flown at low tide in winter 2011 (Watershed Sciences Inc., Portland, OR, U.S.A.). We used continuous data from four Solinst LTC data loggers (Solinst, Georgetown, Ontario, Canada)—one at the entrance of each target study site—to derive accompanying information on water temperature (°C) and water level. Data loggers were installed in the center of each slough, and suspended 15 cm above the channel bottom. We used a real-time kinematic global positioning system (RTK GPS) to relate water level (inundation depth) to a vertical datum of NAVD88.

To quantify channel morphometry, we calculated summary statistics for all tidal channels using ArcGIS 10.2 software (ESRI Inc., Redlands, CA, U.S.A.). We used the digitized tidal channel polygon layer and the 2011 LiDAR DEM to calculate total channel area (ha) and channel volume ($m^3$) within restoration boundaries and within the four target study sites (Fig. 1). We measured the wetted length of channel between each fyke trapping event and the Nisqually mainstem (m) to determine travel distance and tortuosity (Ellings et al. 2016). To estimate the inundation frequency of each study site, we calculated the percentage of time a data logger was submerged, although total channel depth was spatially variable. Optimal depth for juvenile Chinook salmon is roughly ≥0.4 m (Hering et al. 2010), so we calculated accessibility as the percentage of time water depth was above the baseline elevation plus 0.4 m.

**Energetic Input.** We used 2010–2012 invertebrate prey densities as analyzed by Woo et al. (2018) to quantify the total energetic input of the restored salt marsh and mudflat habitat. The mean energy density (kJ/g; ED) of several representative prey taxa was derived from literature values (Table S1, Supporting Information). We selected representative taxa based on their frequency of occurrence in juvenile Chinook diets; in most cases, these taxa comprised 90–100% of gut content biomass. Prey density (individuals/$m^2$) was multiplied by prey ED and mean mass per individual taxon (g) to calculate per $m^2$ ED. To estimate the amount of benthic energy added to the restoring delta, we multiplied the total channel area by the average per $m^2$ ED of target benthic prey items in each year. The same procedure was performed using pelagic invertebrate ED and total channel volume. To estimate terrestrial energy input, we measured a 5 m buffer around each digitized tidal channel edge in ArcGIS. We multiplied the total buffer area of the restored sites and target study sites by the calculated ED of terrestrial invertebrate prey. These calculations represented a generalized estimate of added energy, as they did not account for spatial heterogeneity in invertebrate prey biomass related to diel movement, tidal variation, water quality, or vegetative community structure.

**Invertebrate Prey Consumption.** We used juvenile Chinook salmon diet samples to determine whether food resources available in tidal channels were being effectively utilized. Fish were captured with fyke traps set across the mouth of each tidal channel during a falling high tide on a neap tide series. Traps were set at least once per month from April through July, 2010–2012. All four study channels were accessible to juvenile salmon at mid- or high tide, and became almost entirely dewatered at low tide, resulting in moderate to high trap efficiencies (David et al. 2014). The Nisqually Reference site was an exception, as it was adjacent to the Nisqually mainstem and had a high base flow. As such, pooling within the central channel made it difficult to achieve 100% trap efficiency.

We processed all captured fish according to standard sampling procedures (Gray 2005; Ellings & Hodgson 2007). Up to 10 natural-origin and 10 hatchery-origin Chinook salmon were retained for diet and otolith analysis during each sampling event. Hatchery marking programs in Puget Sound are not 100% effective, but we were able to use otolith microstructure data from 2010 and 2011 samples to verify that these unmarked fish were natural-origin. In 2012, an accidental release of unmarked hatchery Chinook hindered our ability to distinguish between natural- and hatchery-origin individuals. We excluded 2012 fish without corresponding otolith data from any analyses in which differences between natural- and hatchery-origin body condition were compared.

Between 2010 and 2012, we sampled a total of 289 juvenile Chinook salmon from study sites on the Nisqually Delta, including 169 marked (hatchery-origin) and 120 unmarked (assumed natural-origin) fish. Of the sampled individuals, 97 were captured from the Nisqually Reference Slough, 92 from Madrone Slough, 62 from the Red Salmon Reference Slough, and 38 from the Phase II Slough. For each retained juvenile Chinook, we collected various measures of body condition, including length (mm), weight (g), and total stomach content wet mass (mg). Stomachs were blotted, and contents were weighed and preserved in ethanol for diet analysis. We sorted all stomach contents to the lowest possible taxonomic resolution using a dissecting microscope, and enumerated and weighed each prey taxon separately for further analysis.

We examined yearly, seasonal, and among-site differences in prey preference using a permutational multivariate analysis of variance (PERMANOVA) with specific taxon abundances as the response variable, and year, month, origin (natural or hatchery), and site as predictor variables. We grouped invertebrate prey to broader taxonomic levels (i.e. phylum or class) to improve statistical robustness and ease of visualization (Table S2). We used a Bray–Curtis association coefficient (Bray & Curtis 1957) to calculate proportion similarity indices (PSI) between prey abundances in fish diet and prey availability in the surrounding habitat. We calculated PSI using the equation:

$$PSI_{ij} = \frac{2C_{ij}}{S_i + S_j}$$

where $S_i$ is the sum of prey abundances in fish diet $i$, $S_j$ is the sum for the site at which that fish was captured, and $C_{ij}$ represents the sum of lower abundances for only those prey taxa that were common between each diet-site pair. Thus, a PSI value of 0 represents complete dissimilarity in prey communities, and a PSI value of 1 represents complete overlap. We calculated the PSI between each individual Chinook salmon and the benthic, terrestrial, and pelagic prey communities within its respective catch site. Comparisons between dietary and site-specific prey composition were only conducted between corresponding yearly and monthly time periods to ensure spatiotemporal overlap. To evaluate among-site differences in PSI values, we used a log-transformed linear model including year, month, origin, and site as predictor variables. We conducted individual analyses on benthic, terrestrial, aquatic, and combined PSI values at each site to examine prey preference.

**Juvenile Chinook Resource Use and Body Condition.** We collected several measures of juvenile Chinook body condition and resource use for each retained individual. Length (mm) and weight (g) were measured upon capture; however, we also conducted our analyses using Fulton's condition factor ($K$) as it is a commonly used coefficient for evaluating overall body condition (Jin et al. 2015). Fulton's condition factor is calculated as:

$$K = 100 \times \frac{W}{L^3}$$

We used instantaneous ration (the wet weight of the gut contents divided by the total wet weight of the individual minus the weight of its gut contents) as an estimate of relative fullness at time of capture. The total energetic content (J) of each gut sample was derived according to procedures outlined by David et al. (2014), with between-site comparisons of instantaneous ration and energetic content also outlined in the Supporting Information.

To evaluate growth and residence time, otoliths from 93 juvenile Chinook trapped in 2010–2011 were extracted, processed, and analyzed at the U.S. GS Western Fisheries Research Center. Time of delta entry was determined by the presence of a distinct check on the otolith microstructure associated with change of habitat from fresh to salt water (Lind-Null et al. 2008). We derived delta growth rate by subtracting the back-calculated fork length at delta entry using the biological intercept method (Campana 1990) and dividing by its total delta residence time before sacrifice. Similarly, we calculated recent growth rates by back-calculating each individual's size within 1 week prior to capture and dividing by 7 days. We made the implicit assumption that recent growth was more likely a result of energy input from tidal channels, as longer-term (> 1 week) delta growth could have included time periods when individuals were still moving in and out of transitional and estuarine habitat. To account for variation in growth based on size, we derived allometric growth by standardizing each individual's estimated growth rate by its length at the time it was captured.

**Statistical Analysis.** To identify environmental factors that influenced juvenile salmon growth and residency, we evaluated body condition and resource use for individual fish using a generalized linear model with a gamma distribution for non-negative values. We analyzed weight, Fulton's condition, delta residence time, and recent allometric growth as response variables, and origin (hatchery vs. natural), and site as predictor variables. Additionally, we analyzed a suite of predictor variables related to the *opportunity* and *capacity* of the restoring delta, including site-specific habitat availability (≥0.4 m depth), distance from the Nisqually River mainstem, tortuosity at mean high water (MHW), mean monthly water temperature, available invertebrate prey biomass, PSI, juvenile Chinook density, and total juvenile salmon density. We used a forward–backward stepwise model selection process to determine which of these metrics had the greatest effect on body condition and growth.

## Results

### Habitat Accessibility

The 2009 restoration added access to 43 ha of tidal sloughs, with over 66 ha of adjacent terrestrial habitat (5 m channel buffer; Table S3). Channel volume varied at each study site based on tidal inundation, with most channels achieving sufficient depths for accessibility (≥0.4 m) above mean tidal level (MTL; Ellings et al. 2016). The percentage of time each study site was inundated, the percentage of time was accessible to juvenile Chinook salmon, and its distance from the Nisqually mainstem

**Table 1.** Habitat availability and accessibility metrics for each of the four target study sites, including two restored marsh sites (Madrone, Phase II) and two reference marsh sites (Nisqually Reference, Red Salmon Reference). We calculated all metrics using digitized imagery and a 2011 DEM in ArcMap 10.2 software (ESRI, Redlands, CA, U.S.A.). MTL, MHW, and MHHW are abbreviations for mean tidal level, mean high water, and mean high high water, respectively. Percent time inundated represents the amount of time each site was breached by the tide, whereas percent time available represents the percent of time mid-channel depth met or exceeded 0.4 m.

| | *Metric* | *Nisqually Reference* | *Madrone* | *Red Salmon Reference* | *Phase II* |
|---|---|---|---|---|---|
| Habitat availability | Major channel area (ha) | 4.14 | 2.05 | 4.73 | 0.53 |
| | Minor channel area (ha) | 0.60 | 0.50 | 0.53 | 0.29 |
| | Total channel area (ha) | 4.74 | 2.55 | 5.27 | 0.82 |
| | Channel buffer channel (ha) | 9.07 | 8.04 | 11.69 | 3.72 |
| | Channel volume MTL ($m^3$) | 23,518 | 9,929 | 14,124 | 1,581 |
| | Channel volume MHW ($m^3$) | 49,686 | 21,864 | 39,622 | 4,258 |
| | Channel volume MHHW ($m^3$) | 60,858 | 26,966 | 51,439 | 5,518 |
| Habitat accessibility | Distance from mainstem at MTL (m) | 94 | 2,561 | 1,310 | 2,887 |
| | Distance from mainstem at MHW (m) | 94 | 1,929 | 1,310 | 2,887 |
| | Path tortuosity at MTL | 0.65 | 0.31 | 0.50 | 0.21 |
| | Path tortuosity at MHW | 0.66 | 0.82 | 0.61 | 0.21 |
| | Percent time inundated (%) | 69 | 59 | 62 | 63 |
| | Percent time available (%) | 59 | 47 | 50 | 48 |

are outlined in Table 1. All four sites, including recently restored Madrone Slough, were accessible to juvenile Chinook salmon for roughly the same amount of time, but restored sites had less habitat availability than reference sites in terms of channel area, adjacent terrestrial habitat, and channel volume. The Nisqually Reference site was closest to the river mainstem and had the greatest channel volume at all tides. Conversely, restored Phase II was 326–2,793 m farther from the river mainstem than any other site, and had the least amount of channel area by more than 80%.

### Energetic Input

Available energy input from invertebrate prey in the restored salt marsh and mudflat habitat increased through time, with maximum annual energetic estimates reaching 6 million kJ during the 2012 out-migration season. This included roughly 650,000 kJ worth of terrestrial and aquatic prey biomass contribution from Madrone Slough (Fig. 2). Greater prey biomass at Madrone resulted in an overall energy availability that was comparable to both reference sites, despite 50% less channel area (Woo et al. 2018; Fig. 2). In contrast, invertebrate prey energy availability was up to 95% lower at Phase II, topping out at 150,000 kJ in 2012. This trend was largely driven by aforementioned limitations in channel area.

### Invertebrate Prey Consumption

Invertebrate prey consumption varied by site, taking into account both yearly and seasonal variation ($F_{[3,279]} = 3.319$, $p < 0.001$). Juvenile Chinook salmon at both reference sites consumed primarily mysids, with amphipods, dipterans, terrestrial insects, and arachnids also contributing to gut content biomass. At Phase II, where guts were least full, Chinook consumed amphipods and dipterans almost exclusively, while at Madrone, diets shifted from a crustacean-based diet in 2010 to an almost entirely dipteran-based diet in 2011 and 2012

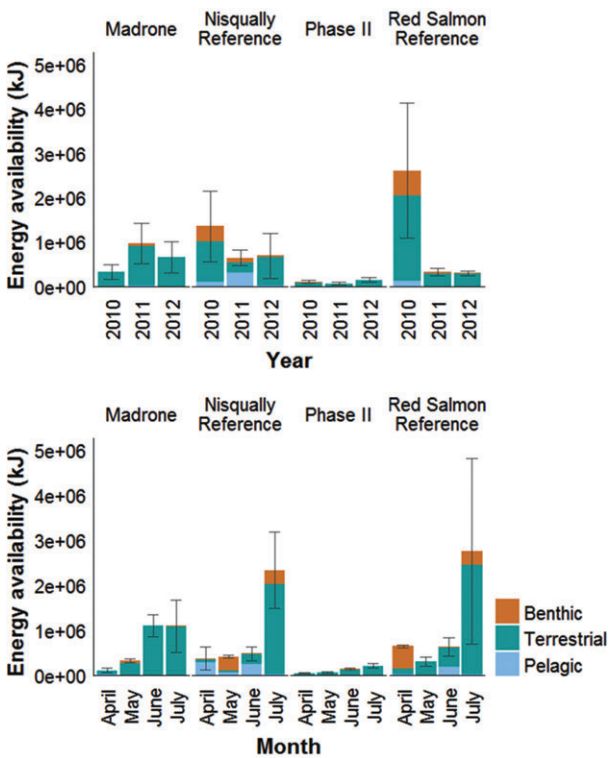


Figure 2. Mean yearly energy availability (top) and monthly energy availability (bottom) at all four study sites, including benthic, terrestrial, and pelagic invertebrate prey. Error bars represent ±1 SE for total energy availability.

(Fig. 3). Hatchery- and natural-origin juvenile Chinook did not appear to differ in prey preference ($F_{[1,168]} = 1.649$, $p = 0.097$), even when yearly and seasonal differences were accounted for.

PSI values calculated for all observed invertebrate taxa grouped together (benthic, terrestrial, and pelagic) did not differ between hatchery- and natural-origin fish, but did differ

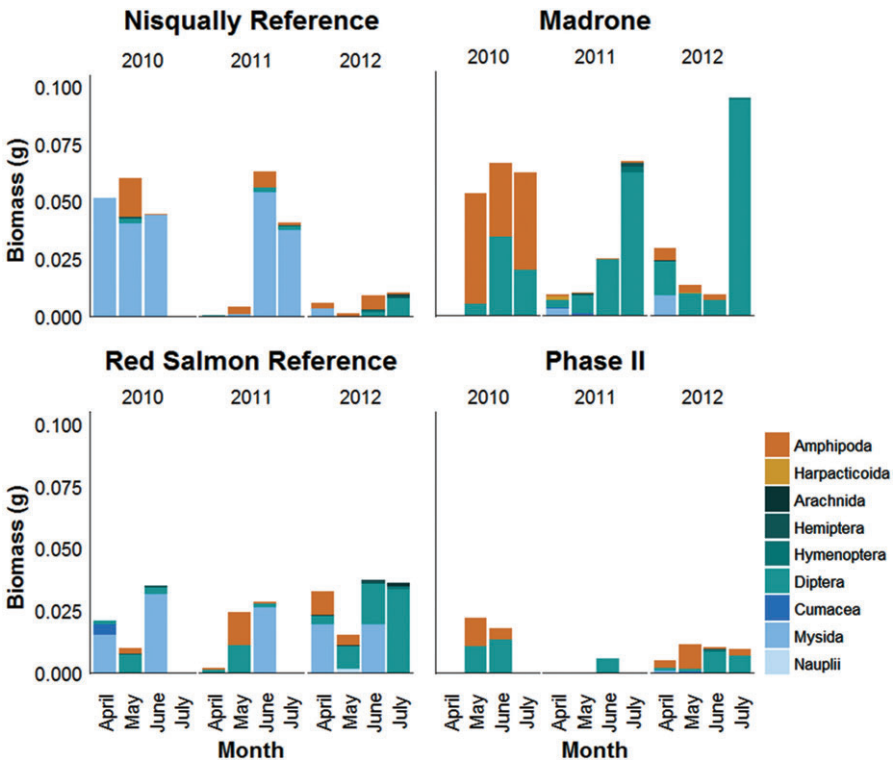


Figure 3. Mean monthly gut content biomass and proportion contribution by various invertebrate taxa. Trends show a contrast in invertebrate prey consumption between reference (left) and restored (right) sites. Taxa are grouped by benthic (orange), terrestrial (teal), and pelagic (light blue) prey samples.

among sites ($F_{[1,162]} = 1.265$, $p = 0.262$; $F_{[3,273]} = 3.859$, $p = 0.009$). Overall, PSI values were greatest for fish captured at the Nisqually Reference site (Nisqually Reference = 0.178 ± 0.148, Madrone = 0.071 ± 0.131, Red Salmon Reference = 0.074 ± 0.092, Phase II = 0.083 ± 0.098; Table 2). When analyses were conducted separately for each group, we found that the terrestrial invertebrate taxa observed in juvenile Chinook salmon diets were most consistent with those observed in the surrounding environment (Fig. 4). Benthic PSI values were stable through time at the Red Salmon Reference and Phase II sites, but decreased between 2010 and 2012 at Madrone ($F_{[2,182]} = 21.604$, $p < 0.001$; Fig. 4). Conversely, terrestrial invertebrate PSI values increased at Madrone between 2010 and 2012 ($F_{[3,255]} = 3.098$, $p < 0.027$). Pelagic invertebrate PSI was comparatively low at all sites except for the Nisqually Reference site in 2010, and did not change through time ($F_{[1,269]} = 0.099$, $p = 0.753$).

### Juvenile Chinook Resource Use and Body Condition

Juvenile Chinook weight differed significantly among sites and between hatchery- and natural-origin fish. Individuals captured at Madrone exhibited up to 18% greater body mass than fish captured at the Phase II or Red Salmon Reference sites to the east of the Nisqually River, and had similar mass to fish captured at the Nisqually Reference site ($F_{[3,161]} = 4.175$, $p = 0.007$; Fig. S1). Hatchery-origin individuals were also 18% larger than natural-origin individuals in 2010 and 2011 ($F_{[1,161]} = 9.931$, $p = 0.002$; Fig. S2). Conversely, body condition, as calculated using Fulton's condition factor, did not differ among sites ($F_{[3,165]} = 1.432$, $p = 0.235$) or by origin ($F_{[1,165]} = 0.500$, $p = 0.720$; Fig. S2). Of the individuals we captured in the tidal marsh sites, hatchery-origin Chinook had spent 43% less time in the delta than natural-origin Chinook (Hatchery = 9.35 ± 0.65 days, Natural = 16.79 ± 1.17 days; $F_{[1,87]} = 5.860$, $p < 0.001$; see Lind-Null & Larsen 2010), but delta residence time did not differ among sites (Table S4).

Some of the physiological metrics were correlated with habitat accessibility and prey availability within each study site. Juvenile Chinook salmon catch weight was positively associated with available invertebrate prey biomass ($F_{[1,283]} = 8.594$, $p = 0.004$) and negatively correlated with in-channel Chinook density ($F_{[1,283]} = 6.552$, $p = 0.011$), with these variables explaining up to 45% of size variance when yearly and seasonal differences were accounted for. There was also a significant interactive relationship between available prey biomass and salmon densities (Table S5), where interspecific competition was negatively correlated with catch weight at sites with low prey biomass, and positively correlated at sites with high prey biomass ($F_{[1,282]} = 10.252$, $p = 0.002$; Fig. 5). Fulton's condition factor was influenced by aquatic prey biomass ($F_{[1,284]} = 4.423$, $p = 0.036$), but this variable only explained 16% of variation in body condition. Because invertebrate prey biomass also varied seasonally and by site (Woo et al. 2018), site-specific differences had an indirect effect on Chinook size ($F_{[1,284]} = 152.362$, $p < 0.001$; $F_{[1,284]} = 11.387$, $p < 0.001$).

**Table 2.** Mean and SD PSI for fish captured at each of four study sites in the Nisqually Delta. We calculated PSI using a Bray–Curtis association coefficient, comparing invertebrate prey composition in juvenile Chinook diet samples to invertebrate prey observed at each fish's respective catch site during the monthly sampling period. A PSI value of 0 indicates no similarity, whereas a PSI value of 1 signifies complete overlap.

| *Month* | *Catch Site* | n | *Mean PSI* | *SD PSI* |
|---|---|---|---|---|
| April | Madrone | 20 | 0.09 | 0.22 |
| | Nisqually Reference | 11 | 0.06 | 0.04 |
| | Phase II | 7 | 0.07 | 0.03 |
| | Red Salmon Reference | 15 | 0.12 | 0.05 |
| May | Madrone | 27 | 0.11 | 0.16 |
| | Nisqually Reference | 28 | 0.12 | 0.12 |
| | Phase II | 12 | 0.08 | 0.07 |
| | Red Salmon Reference | 17 | 0.07 | 0.06 |
| June | Madrone | 29 | 0.07 | 0.07 |
| | Nisqually Reference | 34 | 0.16 | 0.14 |
| | Phase II | 18 | 0.11 | 0.08 |
| | Red Salmon Reference | 29 | 0.06 | 0.05 |
| July | Madrone | 15 | 0.04 | 0.02 |
| | Nisqually Reference | 16 | 0.25 | 0.15 |
| | Phase II | 1 | 0.19 | |
| | Red Salmon Reference | 1 | 0.12 | |

Residence time was strongly associated with Chinook salmon densities such that delta residence times were shorter when within-channel densities were higher ($F_{[1,87]} = 6.679, p = 0.011$; Fig. 6). These higher-density channels were also more connected to the Nisqually mainstem (Table 1). For recent allometric growth, none of the examined environmental variables had as strong an effect as rearing origin, which was singularly the most significant driving factor ($F_{[1,91]} = 10.220, p = 0.002$; Table S4). Recent growth rates were 14% greater on average for natural-origin Chinook than for hatchery-origin Chinook (Fig. S2).

## Discussion

The *realized function* of a restoring estuary is representative of the physiological benefits that juvenile salmon and other fish species may derive from resultant increases in prey and space. In the Nisqually River Delta, the addition of 44 ha of functional tidal channels between 1996 and 2009 increased the total foraging area of the estuary to more than 200 ha (Ellings et al. 2016). At the restored Madrone site, this translated to an estimated 320,000 kJ of previously inaccessible prey biomass, increasing to 650,000 kJ in 2012. Seasonal energy estimates at Madrone were comparable to both reference sites 3 years post-restoration, despite 50% less foraging area. This is because prey biomass densities were almost double those observed at the other three study sites (Woo et al. 2018). In contrast, prey energy availability was up to 95% lower at restored Phase II where invertebrates were largely inaccessible from a limited channel network. Our calculations assumed a uniform distribution of prey throughout the study area, and did not take into account complex relationships between invertebrate densities and biophysical variables. Nevertheless, these results highlight how measurements of space *and* prey (i.e. *opportunity* and *capacity*) are necessary for estimating productivity and energy availability.

Among-site variation in energy availability and prey composition resulted in distinct dietary differences. In general, juvenile Chinook consumed more pelagic and benthic crustaceans such as mysids and amphipods at reference sites, and more terrestrial invertebrates such as dipterans and hemipterans at restored sites. David et al. (2014) found that salmon diets in the 2009 and 2006 restored habitat became more similar through time to salmon diets in the reference habitat. A comparison of invertebrate prey communities in Chinook gut contents to those found in surrounding habitat (PSI) supported this finding, and showed that the shift in dietary similarity between 2010 and 2012 was a direct result of juvenile salmon switching their targeted prey from benthic to terrestrial invertebrates in the restoring marsh. This may be because terrestrial invertebrate biomass more than tripled at the recently restored Madrone site between 2010 and 2011/2012, while benthic and pelagic invertebrate biomass remained steady (Woo et al. 2018). Despite notable shifts in available and consumed prey communities, PSI values were consistent from year to year at all four sites. As such, juvenile Chinook diet was likely driven by the availability and accessibility of prey, rather than by prey selectivity (Rondorf et al. 1990; Gregory & Northcote 1993; Schabetsberger et al. 2003).

In addition to analyzing dietary differences, we related several measures of habitat quality and prey availability to juvenile Chinook body condition and growth in order to identify environmental factors that could be driving physiological responses. Although dietary preferences clearly varied between restored and reference sites, site-specific differences in physiology were limited to catch weight. Juvenile Chinook were up to 18% larger at Madrone than at other study sites, particularly Phase II, where gut fullness was lowest; however, these differences were not reflected in overall body condition. David et al. (2014) constructed a bioenergetically based growth potential model that predicted lower growth rates for juvenile Chinook using Madrone Slough in 2010, but not 2011 or 2012.

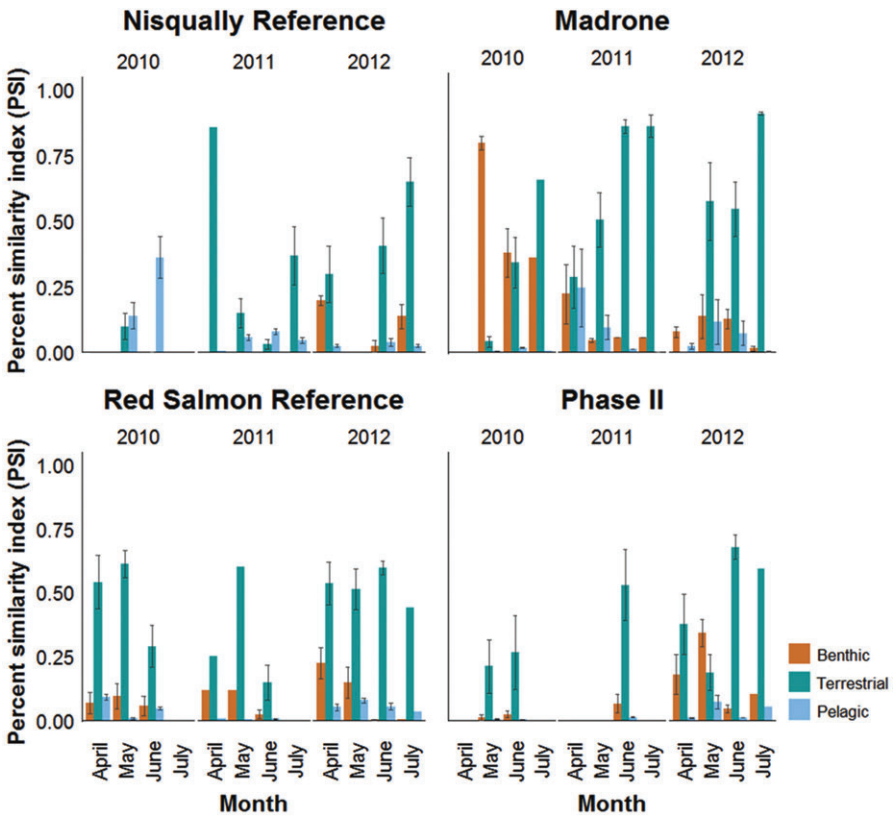


Figure 4. Mean yearly and monthly proportion similarity index (PSI) values separated out for terrestrial, benthic, and pelagic invertebrates. PSI was calculated using a Bray–Curtis association coefficient comparing species abundances in fish diet and the surrounding habitat. A PSI value of 0 signifies complete dissimilarity in prey communities, and a PSI value of 1 signifies complete overlap. Error bars represent ±1 SE.

Our otolith-derived allometric growth rates did not detect evidence of reduced growth for individuals captured at Madrone in 2010. Movement in and out of other, prey rich sites may have allowed individuals to compensate for reduced foraging capacity in the first year after restoration when prey densities were still scarce (Woo et al. 2018), but without telemetry, we have no way to assess site fidelity. Other factors related to growth potential, such as thermal experience, may have also driven trends in size. Ellings et al. (2016) found similar water temperatures at most sites throughout the Nisqually Delta, although summer temperatures in the 2009 restoration area were up to 2°C warmer than at reference sites.

Barring yearly and seasonal variation, trends in catch weight were also driven by rearing origin, interspecific densities, and available prey biomass. Most notably, negative density-dependent effects on catch weight were offset in more productive sites, suggesting that competition for prey, not space, drives variation in growth potential (Keeley 2001; Grant & Imre 2005; Martinussen et al. 2010). In the Nisqually Delta, Chinook densities are driven by hatchery release, with hatchery juvenile production being as much as 20 times greater than natural production (Rice et al. 2011). Higher salmon densities and shorter residence times at sites with greater connectivity to the river mainstem (such as Nisqually Reference and Red Salmon Reference) suggested that these sites were more frequently used by newly arriving juveniles that had not yet distributed throughout the delta. Thus, the negative consequences of density dependence are most likely to occur adjacent to the Nisqually mainstem during the period of volitional hatchery release. We observed a negative relationship between salmon densities and catch weight, but the high-density pulse during hatchery release could also have an effect on movement, with more dominant individuals driving weaker fish to seek refuge in suboptimal habitat (Mason & Chapman 1965; Reimers 1968; Taylor 1990). More extensive data from mark-recapture or telemetry studies would be needed to parse out whether potential behavioral effects were ameliorated by restoration efforts.

Although it was not a parameter directly related to restoration practices, rearing origin had a significant effect on three of the four physiological response variables. Despite being smaller in size, our study found that the natural-origin juvenile Chinook salmon captured in restored and reference channels consistently outgrew their hatchery-origin counterparts. Hatchery salmon may experience a greater frequency of developmental obstacles, including smaller brain sizes, greater susceptibility to disease, and deficits in foraging behaviors (Maule et al. 1996; Brown & Day 2002; Kihslinger et al. 2006; Daly et al. 2012), but studies suggest that smolt-to-adult returns are more likely driven by spring growth rates than initial body condition (Beckman et al. 1999). Furthermore, studies have observed a positive

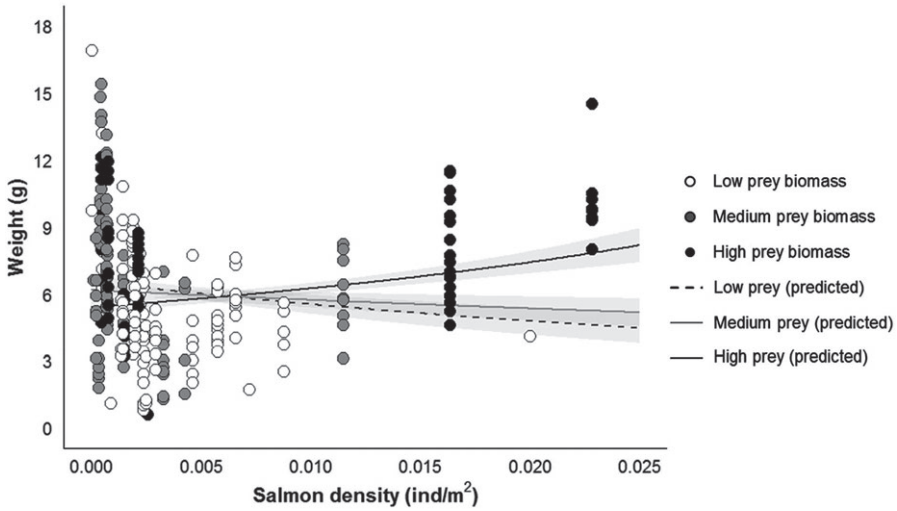


Figure 5. Scatterplot showing an interactive relationship between invertebrate prey biomass and interspecific competition (total salmon densities) affecting catch weight. The full generalized linear model accounted for strong yearly and seasonal variation. Invertebrate prey biomass estimates are sorted and grouped into equal tertiles representing low (0–50 g/m$^2$), medium (51–200 g/m$^2$), and high (201–1,000 g/m$^2$) biomass measurements. Raw data are displayed as colored points, whereas lines represent modeled relationships for low, medium, and high biomass sites with 95% confidence intervals displayed in gray.

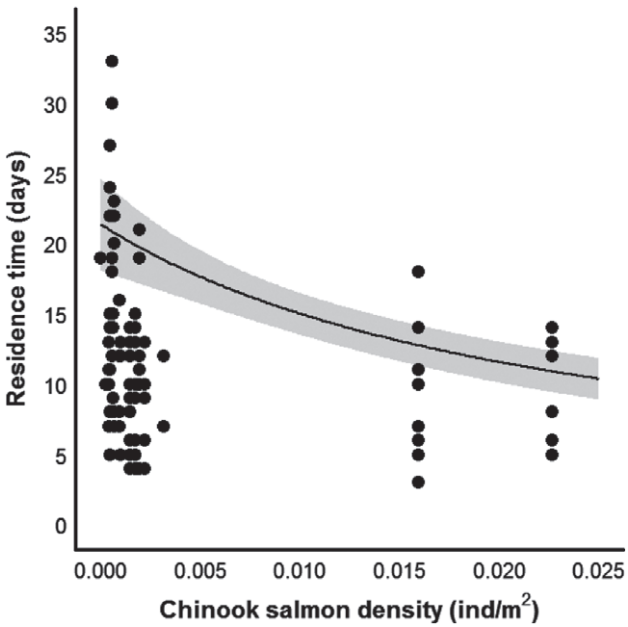


Figure 6. Scatter plot showing the raw data and modeled relationship between within-channel Chinook salmon densities and juvenile Chinook residence time. The gray panel represents upper and lower 95% confidence intervals.

correlation between hatchery juvenile Chinook body mass when they first enter the offshore habitat in July, and their subsequent marine survival (Duffy & Beauchamp 2011). Residence in a prey-rich environment such as the Nisqually Delta could offset long-term negative effects from hatchery rearing by increasing bioenergetic growth potential; however, given current rearing strategies, few hatchery-origin individuals are observed using the delta after the month of July. Otolith-derived residency data found that hatchery-origin Chinook occupied the delta for an average of 9 days, as compared to 17 for natural-origin Chinook. An additional analysis of pre- and post-restoration otolith data throughout the entire delta habitat matrix would further parse out the relationship between residence time, connectivity, and density dependence, and would inform crucial management decisions regarding the quantity and timing of hatchery release.

The results of this study corroborate previous evidence that estuarine restoration benefits juvenile salmon by promoting growth and residency. Such effects have been observed in multiple systems throughout the Pacific Northwest, United States. For instance, in the Salmon River Estuary, a broader spectrum of life history strategies was detected after the removal of several dike systems (Bottom et al. 2005). Juvenile Chinook stayed in the estuary for up to a month, and used restoring and historic habitats similarly despite clear differences in channel morphometry and invertebrate prey communities (Gray et al. 2002; Volk et al. 2010). In the Chehalis River, otolith microstructure analysis did not find differences in the growth or residence times of Chinook and coho salmon in a created slough, even though apparent foraging restrictions were detected (Miller & Simenstad 1997). Similarly, in the Duwamish River Estuary, Cordell et al. (2011) observed higher densities of juvenile Chinook salmon using a restored site, and found that modeled growth potentials were the same between restored and reference sites even though diets differed. These trends reveal that the presence of specific physical features, plant biota, or invertebrate taxa in a target restoration area is less important than its functional contribution to the greater delta habitat mosaic (Simenstad & Cordell 2000; Simenstad et al. 2002).

The *realized function* of restoring estuarine habitat is driven by the intersection of availability and connectedness of suitable habitat (i.e. its *opportunity* potential), and local densities of accessible prey and competitors (i.e. foraging *capacity*). Our

study demonstrates that it is these factors combined that determine effective resource use by out-migrating juvenile salmon in historic and restoring tidal marsh. A rich population of invertebrates in a specific habitat will be of little consequence to individuals if there is not a connected tidal network in which they may forage. Conversely, higher degrees of connectivity in smaller area channels may lead to density-dependent effects, although these effects could be offset if prey resources in adjacent habitat are rich enough. These patterns have been observed at larger scales throughout Puget Sound, where wetland loss has constrained foraging performance, potentially through density-dependent mechanisms (Simenstad et al. 2002; David et al. 2016). Managers who are currently enacting monitoring efforts in restoring ecosystems could benefit from considering these trade-offs in their adaptive management framework, while also accounting for balances in habitat suitability for other wildlife such as shorebirds and waterfowl. With this information, managers can maximize the benefit of restoring estuarine habitat by optimizing overlap between accessibility and productivity. Adaptive adjustments to spatial extent, depth, and connectivity in prey-rich habitat (regardless of its biotic composition) can encourage successful foraging and growth. Furthermore, by specifically increasing the functionality of tidal channel networks in areas with high productivity, managers can avoid making unnecessary anthropogenic changes to vulnerable restoring habitat, while maximizing the utility of habitat where out-migrating juvenile salmon are expected to benefit most.

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## Supporting Information

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

**Table S1**. Representative invertebrate prey taxa for which biomass and energy density (ED) were calculated.
**Table S2**. Invertebrate prey taxa observed in juvenile Chinook diet samples.
**Table S3**. Total channel area opened to salmon foraging after the 2009 removal of Brown Farm Dike (Restored Mudflat) and 1996–2006 removal of several levees to the east of the Nisqually River (Restored Salt Marsh).
**Table S4**. Output from a forward–backward stepwise model selection process evaluating parameter relationships to catch weight (g), Fulton's condition factor ($K$), delta residence time (days), and recent allometic growth rate (mm $mm^{-1}$ $day^{-1}$).
**Table S5**. Post-restoration (2010–2012) estimated seasonal dry-weight biomass (DWB; $mg/m^2$) for all measured benthic, terrestrial, and pelagic taxa.
**Figure S1**. Mean monthly catch weight and Fulton's condition factor for juvenile Chinook salmon caught at target study sites on the Nisqually River Delta in 2010–2012.
**Figure S2**. Boxplots showing differences in physiological condition between hatchery and natural origin juvenile Chinook salmon captured at four study sites in the Nisqually River Delta (2010–2011).

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