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ARTICLE

Foraging and Growth Potential of Juvenile Chinook Salmon after Tidal Restoration of a Large River Delta

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Abstract

We evaluated whether restoring tidal flow to previously diked estuarine wetlands also restores foraging and growth opportunities for juvenile Chinook Salmon *Oncorhynchus tshawytscha*. Several studies have assessed the value of restored tidal wetlands for juvenile Pacific salmon *Oncorhynchus* spp., but few have used integrative measures of salmon performance, such as habitat-specific growth potential, to evaluate restoration. Our study took place in the Nisqually River delta, Washington, where recent dike removals restored tidal flow to 364 ha of marsh—the largest tidal marsh restoration project in the northwestern contiguous United States. We sampled fish assemblages, water temperatures, and juvenile Chinook Salmon diet composition and consumption rates in two restored and two reference tidal channels during a 3-year period after restoration; these data were used as inputs to a bioenergetics model to compare Chinook Salmon foraging performance and growth potential between the restored and reference channels. We found that foraging performance and growth potential of juvenile Chinook Salmon were similar between restored and reference tidal channels. However, Chinook Salmon densities were significantly lower in the restored channels than in the reference channels, and growth potential was more variable in the restored channels due to their more variable and warmer (2°C) water temperatures. These results indicate that some—but not all—ecosystem attributes that are important for juvenile Pacific salmon can recover rapidly after large-scale tidal marsh restoration.

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Estuarine wetlands provide diverse ecosystem services for humans (Barbier et al. 2011) and provide critical habitats for numerous fish and wildlife species during part or all of their life cycles (Deegan et al. 2000; Beck et al. 2001). Along the Pacific Rim, estuaries are important for the growth and survival of juvenile Pacific salmon *Oncorhynchus* spp. (Healey 1980; Simenstad et al. 1982; Magnusson and Hilborn 2003). Estuaries offer a gradient of salinities for the physiological transition from freshwater to salt water (Iwata and Komatsu 1984), turbid waters that limit predation (Gregory and Levings 1998; De Robertis et al. 2003), and abundant invertebrate communities that support productive foraging and rapid growth for juvenile Pacific salmon prior to ocean entry (Reimers 1973; Healey 1980; Simenstad et al. 1982). These estuarine functions are particularly important for ocean-type life history forms of Chinook Salmon *O. tshawytscha*, which often feed and grow in estuaries for extended periods before completing their migration to the ocean (Healey 1982; Levy and Northcote 1982). However, human development in many estuaries has resulted in substantial habitat loss, particularly of tidal wetlands (Boulé et al. 1983; Emmett et al. 2000). For example, 68% of Oregon's tidal wetlands have been diked or filled (Good 2000), and Washington's Puget Sound river deltas have lost 99% of their oligohaline transition wetlands, 90% of freshwater tidal wetlands, 46% of estuarine mixing wetlands, and 24% of euryhaline unvegetated tidal wetlands (Simenstad et al. 2011). The loss of estuarine wetlands has contributed to the decline of Chinook Salmon populations (Magnusson and Hilborn 2003), resulting in increased efforts to restore juvenile Pacific salmon habitat in estuaries. These restoration projects are often dike removals or breaches, which return natural tidal inundation regimes to historic estuarine ecosystems with the expectation that restoring natural physical processes will also restore the ecological functions that support juvenile Pacific salmon (Simenstad and Cordell 2000; Gray et al. 2002).

Several studies have assessed the equivalence of natural and restored tidal wetlands in terms of attributes that are important for juvenile Pacific salmon, yet few studies have used integrative measures of salmon physiological performance (e.g., habitat-specific growth potential) to evaluate restoration. Previous studies have documented the presence of juvenile salmon in restored wetlands (Shreffler et al. 1990; Levings and Nishimura 1997), have compared the diets of salmon in restored and reference (natural) habitats (Gray et al. 2002; Roegner et al. 2010), and have used enclosure experiments to compare growth rates (Miller and Simenstad 1997). Recently, bioenergetics models have been used to simulate habitat-specific consumer growth rate potential by using measurements of the environmental drivers of consumer growth from restored and reference habitats as model inputs (Gray 2005; Cordell et al. 2011). Bioenergetics models are mass-balance equations wherein the energy stored as growth by an individual equals the energy consumed minus the energy used in metabolism and lost as waste (Hanson et al. 1997; Chipps and Wahl 2008). The growth rate potential of a consumer is the growth rate that is expected based on data describing the primary variables that regulate growth (Brandt et al. 1992; Tyler and Brandt 2001). Analyses of habitat-specific growth potential provide a way to integrate multiple environmental variables that influence the physiological status of consumers into the common currency of growth (Brandt et al. 1992; Madon et al. 2001; Gray 2005).

A fundamental question underlying many studies of habitat restoration is whether restored and reference habitats differentially benefit (e.g., promote survival or fitness of) the focal species. However, it is difficult to estimate how habitats used during one life stage influence overall survival and fitness for Pacific salmon and similar species that integrate across multiple ecosystems during their lifetime. Alternatively, habitat-specific growth rate potential can be used to approximate habitat influence on survival in juvenile Pacific salmon because survival is often strongly size selective (Beamish et al. 2004; Moss et al. 2005; Woodson et al. 2013) and the survival rates of Pacific salmon are positively correlated with juvenile size and juvenile growth rate in estuarine and coastal marine environments (Cross et al. 2008; Duffy and Beauchamp 2011; Tomaro et al. 2012). Thus, growth rate potential is a useful measure of different habitats' relative value to juvenile Pacific salmon and likely to other species for which survival is positively correlated with growth and size. Here, we build upon studies that used a bioenergetics growth potential approach to assess restoration (Gray 2005; Cordell et al. 2011) by incorporating empirically derived rates of consumption by juvenile Pacific salmon in both restored and reference tidal marsh channels into growth rate potential simulations using the Fish Bioenergetics model (Kitchell et al. 1977; Hanson et al. 1997). Fish growth is largely controlled by consumption rate, prey energy content, consumer energy content, consumer size, and temperature. Of these variables, growth is most sensitive to consumption (Kitchell et al. 1977), but previous attempts to quantify consumption rates of juvenile Pacific salmon as part of restoration assessments have been unsuccessful (Gray 2005; Cordell et al. 2011).

Our goal was to evaluate the degree to which removing dikes and restoring tidal flow to habitats also restore the ecological attributes of natural estuarine wetlands that support the foraging and growth of juvenile Chinook Salmon. The study took place within the Nisqually River delta, Washington, where a series of large-scale dike removals had recently occurred. Specifically, we compared the density, foraging performance (instantaneous ration [I] and diet energy density [ED_{diet}]), diet composition, and simulated growth potential of juvenile Chinook Salmon in two restored and two reference tidal marsh channels during a 3-year period after restoration. We hypothesized that (1) measures of juvenile Chinook Salmon density, foraging performance, and growth potential

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would initially be lower in restored habitats than in reference habitats but would rapidly approach equivalence as time since restoration increased; and (2) diet similarity between juvenile Chinook Salmon foraging in reference habitats and those foraging in restored habitats would increase as time since restoration increased. Additionally, because initial observations indicated temperature differences between reference and restored tidal channels, we also explicitly evaluated the influence of water temperature on the growth potential of juvenile Chinook Salmon.

STUDY AREA

The Nisqually River delta is a drowned-river-valley estuary located at the southern end of Puget Sound (Figure 1). The delta is managed by the Nisqually National Wildlife Refuge (NWR) and the Nisqually Indian Tribe. The Nisqually River originates from glaciers on Mt. Rainier and flows approximately 125 km before entering Puget Sound (47.08°N, 122.70°W; Figure 1). Historically, the Nisqually River delta supported 1,500 ha of intertidal estuarine wetlands. More than 600 ha of wetlands (primarily tidal marsh) were diked, separated from tidal flow, and converted to pasture land in the early 1900s (Tanner 1999). Reconnection of these lost wetlands was identified by the Nisqually Indian Tribe (NCRT 2001) and the Nisqually NWR (USFWS 2005) as a priority for recovering the Nisqually River fall Chinook Salmon population (fall-spawning adults; juveniles primarily enter marine waters as subyearlings). This population is the predominant Chinook Salmon life history type in the Nisqually River and is one of 27 Chinook Salmon stocks that comprise the threatened Puget Sound evolutionarily significant unit (Ellings and Hodgson 2007). Four sections of dike were removed to restore tidal marsh in 1996, 2002, 2006, and 2009 (Figure 1). In total, these dike removals restored tidal flow to 364 ha for the first time in a century, representing the largest tidal marsh restoration project in the northwestern contiguous United States. The Nisqually River delta also has large tracts of wetlands that are relatively unaltered, including one of the largest intact floodplain forests in the region (Collins and Montgomery 2002). Thus, the restoration of the Nisqually River delta provides a useful contrast with salmon-focused estuary restorations that are smaller (Gray et al. 2002) or that occur within highly urbanized settings (Shreffler et al. 1990, 1992; Simenstad and Thom 1996; Cordell et al. 2011).

We sampled marsh areas that were reconnected in 2006 (hereafter, "2006 Restored") and 2009 (hereafter, "2009 Restored"; Figure 1). We also sampled two reference marsh areas that were relatively undisturbed. One reference area was adjacent to the mouth of the Nisqually River (hereafter, "Nisqually Reference"). The second reference area was between the Nisqually River and Red Salmon Slough (hereafter, "RSS Reference"; Figure 1). Both areas are typical of Pacific Northwest estuarine marshes (Simenstad et al. 2000) and of the extant marsh within the Nisqually River delta and are thus appropriate reference habitats. Prior to dike removal, the 2006 Restored area was dominated by pasture grasses, while the 2009 Restored area consisted of terrestrial and freshwater habitats dominated by invasive plants. After each dike removal, terrestrial and freshwater plants were killed by salt water. Both restored habitats had subsided due to the loss of sediment input, oxidation of soil organic matter, and compaction by grazing animals (Frenkel and Morlan 1991; Portnoy and Giblin 1997). By 2012, the 2006 Restored plant community primarily consisted of the native salt-marsh plants *Jaumea carnosa*, *Distichlis spicata*, *Sarcocornia perennis*, and *Carex lyngbyei*, with patches of bare mud present; the 2009 Restored area was dominated by bare mud at lower elevations, with patches of *Sarcocornia perennis* and *Spergularia* spp. at higher elevations. The plant community at Nisqually Reference primarily was composed of the native salt-marsh species *C. lyngbyei*, *D. spicata*, *Agrostis gigantea*, and *Triglochin maritima*, while RSS Reference supported *T. maritima*, *D. spicata*, and *J. carnosa*.

METHODS

Fish sampling.—We sampled a single tidal channel network within each restored and reference marsh area to assess fish assemblage composition and juvenile Chinook Salmon densities and diets. These tidal marsh channels are flooded and accessible to fish from mid to high tides. During low tides, the channels become dewatered or nearly so, with base flow water depths no greater than 0.25 m. Each channel network has a single defined inlet within the tide range (neap tides) we sampled. Additional details on the four tidal channels are provided in Supplementary Table S.1 (in the online version of this article). We used a fyke net (3.2-mm mesh; Levy and Northcote 1982; Gray et al. 2002) at each channel to capture fish once per month from April to July in 2010, 2011, and 2012. A net was set across a channel at high tide, and the wings of the net were tied off to posts on each side of the channel. The wings blocked the channel (although imperfectly; see below) so that fish attempting to exit the channel during the ebb tide would enter the fyke net. Once the water level was low enough for us to access the fyke net, we removed fish from the cod end of the net until the channel became dewatered or until 4 h after high tide, when we removed the net from the channel. We enumerated the total catch of each species. Up to 10 juvenile Chinook Salmon of hatchery origin (identified by adipose fin clip or with a coded wire tag reader) and up to 10 juveniles of natural origin were kept for diet analysis. However, we pooled hatchery- and natural-origin fish for all analyses due to small sample sizes in some months. Fish that were kept for diet analysis were euthanized using tricaine methanesulfonate and were placed on ice. After we returned from the field, we weighed the euthanized fish to the nearest 0.1 g and stored them in ethanol.

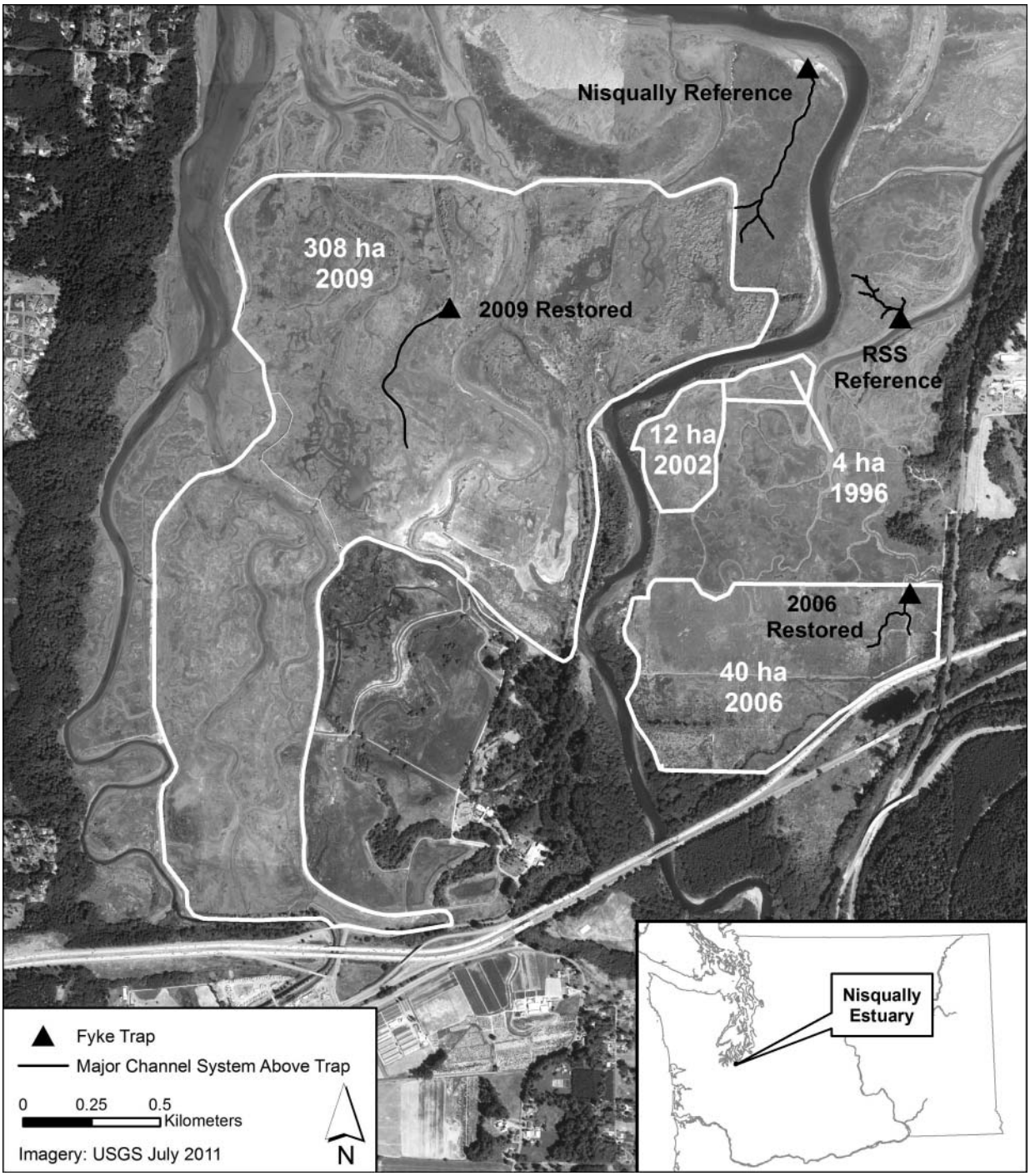

FIGURE 1. The Nisqually River delta, Washington, with dike removals and fyke-net sampling locations identified. The white lines indicate where dikes were removed; the white lettering denotes the amount of area reconnected by each dike removal and the year of dike removal (RSS = Red Salmon Slough; USGS = U.S. Geological Survey).

Juvenile Chinook Salmon density was calculated for each sampling event by using the raw catches, the tidal channel network surface area above each fyke net, and trap efficiency estimates. While all four tidal channels were dewatered or nearly dewatered during the ebb tide, there were places upstream of the nets where it was possible for fish to hold during low tide. Additionally, we observed that the net wings were not completely efficient at blocking the movement of fish in the tidal channels, and the nets appeared to vary in efficiency among the four channels. Thus, we needed to quantify the

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efficiency of our sampling efforts at each tidal channel before estimating Chinook Salmon densities. To quantify net efficiency, a one-time mark–recapture study was conducted at each net site separately from our standard monthly sampling. We used a beach seine to capture Chinook Salmon outside of the channel being evaluated and then marked each fish with a fin clip. After setting the fyke net according to our standard procedures, we released the marked fish at least 50 m upstream of the net. Net efficiency was assessed as the proportion of recaptures made during the trapping effort. We then calculated density for each sampling event by dividing the raw catch by the net efficiency and in turn dividing that number by the channel surface area. To evaluate whether juvenile density differed among the four channels, we used a repeated-measures ANOVA on rank-transformed densities.

Temperature.—To quantify temperature in each of the four tidal marsh channels, we installed Solinst LTC loggers (Solinst, Georgetown, Ontario), which measured water level, temperature, and conductivity at 15-min intervals. Each logger was installed at a fixed location approximately 15 cm from the sediment surface. Depending on the tide level, the loggers measured conditions at the surface, middle, or bottom of the water column. We calculated daily mean temperatures for each channel from the 15-min-interval readings after excluding the readings obtained when loggers were exposed to the air during low tides.

Chinook Salmon diet composition, foraging performance, and consumption rates.—We acquired diet composition and foraging performance metrics by processing the juvenile Chinook Salmon retained for diet analysis. The stomach of each fish was removed, and the total contents were weighed (blotted wet mass, nearest 0.0001 g). Prey organisms were then sorted to the lowest feasible taxonomic resolution by using a dissecting microscope. Finally, each unique prey taxon was enumerated and weighed separately.

To determine whether the diet composition for Chinook Salmon foraging in the restored tidal channels had become more similar to the diet composition for those foraging in the reference tidal channels through time since dike removal, we calculated the multivariate similarity of diets for fish sampled in restored and reference channels and regressed our metric of similarity against time since restoration. Many taxa were infrequently consumed, so any taxon that was found in fewer than 5% of the stomachs was excluded from analysis. Masses of prey taxa consumed by each fish were converted to proportions of the total stomach content mass and then were used to calculate a pairwise resemblance matrix using the Bray–Curtis association coefficient (Bray and Curtis 1957). We then performed permutational multivariate ANOVA (PERMANOVA; Anderson 2001) using the resemblance matrix for all pairwise combinations of restored and reference tidal channels within each month. A PERMANOVA test was only performed when at least four individuals' diets had been sampled from both channels. We fitted a linear regression (weighted by the combined sample size of diets from each comparison) to the PERMANOVA pseudo-F-ratios as a function of the age (i.e., number of years since restoration) of the restored area used in the comparison to determine whether diet similarity between Chinook Salmon in restored channels and those in reference channels increased through time. As with univariate ANOVA F-ratios, PERMANOVA pseudo-F-ratios represent the ratio of between-group to within-group variation; thus, for this analysis, pseudo-F-ratios are a measure of diet composition similarity between channels relative to within-channel variation in diet composition.

As a measure of stomach fullness, we calculated I for each Chinook Salmon:

$$I = 100 \times \frac{\text{stomach content mass}}{\text{fish mass} - \text{stomach content mass}}. \quad (1)$$

We also calculated ED_{diet} for each Chinook Salmon,

$$\text{ED}_{diet} = \frac{\sum M_i \times \sum E_i}{\sum M_i}, \quad (2)$$

where E is energy density (kJ/g wet mass) and M is prey mass summed over i prey taxa. Energy densities of prey taxa were acquired from the literature (Table S.2).

We used linear models to assess the influence of channel identity, month, year, and juvenile Chinook Salmon density on the I ($\log_e[x + 0.1]$ transformed) and ED_{diet} of juvenile Chinook Salmon. For both I and ED_{diet}, we evaluated eight models that were unique combinations of the explanatory variables. We used an information-theoretic model selection approach (Anderson et al. 2000) to determine which variables best explained the variation in I and ED_{diet}. We evaluated the relative support for each model by using Akaike's information criterion adjusted for small samples size (AIC_c) and AIC_c weights.

To quantify the daily ration (D; g food·g fish^{-1}·d^{-1}) for juvenile Chinook Salmon, we used Eggers' (1977) model with a correction factor:

$$D = 24 \times R \times \bar{I} - (\bar{I}_0 - \bar{I}_t), \quad (3)$$

where 24 is the number of hours in a day, R is the gastric evacuation rate, $\bar{I}$ is the mean instantaneous ration of fish sampled regularly throughout a 24-h period, and $\bar{I}_0$ and $\bar{I}_t$ are the mean instantaneous rations of fish sampled at the beginning and end of the 24-h period.

We estimated the R of juvenile Chinook Salmon for each sampling event; this was done using a model we developed by compiling results from *Oncorhynchus* spp. studies that reported water temperature and fish mass for experiments or observational studies where R was measured. Attempts to explain variation in R-values of fishes have considered temperature, prey type, prey size, meal size, and consumer size as explanatory

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variables (Bromley 1994). We focused on temperature and consumer mass because these were the most commonly reported variables in the literature. We excluded studies in which the fish were force fed or starved for long periods of time before the start of experimental trials. We also did not use data from fish heavier than 50 g, as our focus was juvenile Pacific salmon that would normally be found in nearshore estuarine and marine environments. The compiled rates were fitted to the temperature and mass data by using a linear model of the form:

$$\log_e R = \log_e \alpha + (\beta_1 \times \text{temperature}) + (\beta_2 \times \text{mass}) \quad (4)$$

following He and Wurtsbaugh (1993). We used the back-transformed (exp), bias-corrected form of the fitted model to predict R for juvenile Chinook Salmon from each sampling event on the basis of mean fish mass and daily mean water temperature.

To quantify daily $\bar{I}$, we conducted a diel feeding study (Doble and Eggers 1978) on May 29–30, 2012. We sampled five Chinook Salmon for diet analysis in both restored and reference tidal marsh habitats every 3 h over a 24-h period except at night, when we only sampled Chinook Salmon within the reference habitats. The diel feeding study provided a single estimate of Chinook Salmon $\bar{I}$ within restored and reference habitats. We then assumed that the I of a fish sampled at a certain point during the day was related to $\bar{I}$ across the whole day, and we used the diel study results to calculate an adjusted $\bar{I}$ for each monthly sampling event. For the diel feeding study, we used fyke nets to capture Chinook Salmon during the daytime ebb tide—the same time and tide interval as our monthly fyke-net sampling. Using this comparable sampling interval, we calculated an adjusted $\bar{I}$ for each fyke-net sampling event:

$$\bar{I} = (\bar{I}_f / \bar{I}_{df}) \times \bar{I}_d, \quad (5)$$

where $\bar{I}_f$ is the mean instantaneous ration of Chinook Salmon from a monthly fyke-net sampling event, $\bar{I}_{df}$ is the mean instantaneous ration of Chinook Salmon sampled from the comparable time frame during the diel feeding study (daytime ebb tide), and $\bar{I}_d$ is the mean instantaneous ration from the entire diel feeding study. Values of $\bar{I}_{df}$ and $\bar{I}_d$ were calculated separately for restored and reference habitats. Because we only sampled Chinook Salmon in reference habitats during the hours of darkness, we used the I-values of reference fish to calculate the $\bar{I}_d$ of fish in restored marshes. We also calculated $\bar{I}_0$ and $\bar{I}_t$ from the diel feeding study; these numbers are applied as correction factors for use when I differs between samples collected at the beginning and end of the sampling period (Eggers 1979; Hayward 1991). Finally, we substituted the results of equation (5) and the predicted sampling-event-specific R into equation (3) to derive D for each fyke-net sampling event.

Chinook Salmon energy density.—We collected eight natural-origin and eight hatchery-origin fish for analysis in June 2012 to quantify the ED of juvenile Chinook Salmon ($ED_{Chinook}$) from the Nisqually River delta. The fish were frozen and their stomach contents were removed; we then weighed, dried, reweighed, and ground each fish to a fine powder. We combusted pellets of each powdered fish in a Parr 1425 semi-micro bomb calorimeter to quantify $ED_{Chinook}$ (kJ/g wet mass).

Bioenergetics growth potential simulations.—We used the Fish Bioenergetics model (Hanson et al. 1997) to evaluate the effects of site-specific biotic and abiotic conditions on the growth rate potential of juvenile Chinook Salmon in restored and reference tidal channels. The model runs on a daily time step and can be solved to simulate either consumption or growth. We used data for consumption, ED_{diet}, consumer ED (i.e., $ED_{Chinook}$), consumer mass, and water temperature as model inputs to solve for growth. The temperature logger in the Nisqually Reference channel failed from April to June in both 2010 and 2012; we therefore substituted RSS Reference temperatures for the Nisqually Reference Chinook Salmon growth simulations during these periods, as temperatures in the two channels were highly correlated ($R^2 = 0.92$, $P < 0.001$). Consumption rates were input into the model as proportions of maximum theoretical consumption given fish mass and water temperature (Hanson et al. 1997). We converted each daily ration D to a proportion of maximum consumption by using the consumption equation within the model. We used physiological parameters for Chinook Salmon from Stewart and Ibarra (1991), and we calculated waste losses as a function of consumer mass, temperature, and ration size.

We used the model to simulate specific growth rate potential (g growth·g fish^{-1}·d^{-1}) for each sampling event in which we captured at least four juvenile Chinook Salmon for diet analysis. For each sampling event, we ran the model using the following inputs: mean consumption rate, mean ED_{diet}, and mean mass of the juvenile Chinook Salmon captured for diet analysis; the overall mean $ED_{Chinook}$ for Nisqually River juveniles; and each daily mean temperature recorded in the channel during the month of sampling. Thus, each growth potential simulation comprised 30–31 individual growth rates, one for each daily mean temperature within a month. Simulating growth for the range of temperatures measured at a site allowed us to assess how temperature affects the range of growth potential within a tidal channel. Each model simulation was for a single time step (1 d).

RESULTS

Fish Presence, Abundance, and Density

Fish assemblages varied seasonally and among the four tidal channels but were generally consistent among years (Table S.3). Juvenile Chinook Salmon were the most abundant and frequently occurring salmonid in the delta. We found Chinook Salmon in the reference channels on 87.5% of the sampling events and in restored channels on 75% of the events.

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Chinook Salmon densities were significantly higher in the reference channels than in the restored channels ($F = 8.4$; df = 3, 33; $P < 0.001$), especially during the peak out-migration months of May and June. However, density differences between the restored and reference channels decreased through time (mean difference = 0.218 fish/m^2 in 2010; 0.144 fish/m^2 in 2011; and 0.026 fish/m^2 in 2012; Figure 2). Other salmonids were either seasonally abundant (juvenile Chum Salmon *O. keta* and juvenile Pink Salmon *O. gorbuscha*) or sporadically present (juvenile Coho Salmon *O. kisutch* and Cutthroat Trout *O. clarkii*) across the four channels (Table S.3). Sculpins (primarily Pacific Staghorn Sculpin *Leptocottus armatus*) were ubiquitous and abundant, and Shiner Perch *Cymatogaster aggregata* were abundant during June and July; together, these two taxa accounted for 85% of the total catch from all sampling events (Table S.3).

Water Temperature

Daily mean water temperatures were significantly warmer in the restored tidal channels than in the reference channels (paired *t*-test: $t = 35.9$, df = 365, $P < 0.001$) during the primary Chinook Salmon out-migration season (April–July) across all 3 years, with the caveat that this comparison included only a single reference channel in 2 of the 3 years. Temperatures in the restored channels were 2.0 ± 1.1°C (mean ± SD) warmer than those in the reference channels, and temperature differences were particularly apparent in June and July (Figure 3). Additionally, the range of temperatures within individual months was often greater in the restored channels. The mean within-month SD and range of temperatures were 0.8°C and 3.0°C, respectively, for the reference channels but were 1.4°C and 5.4°C, respectively, for the restored channels.

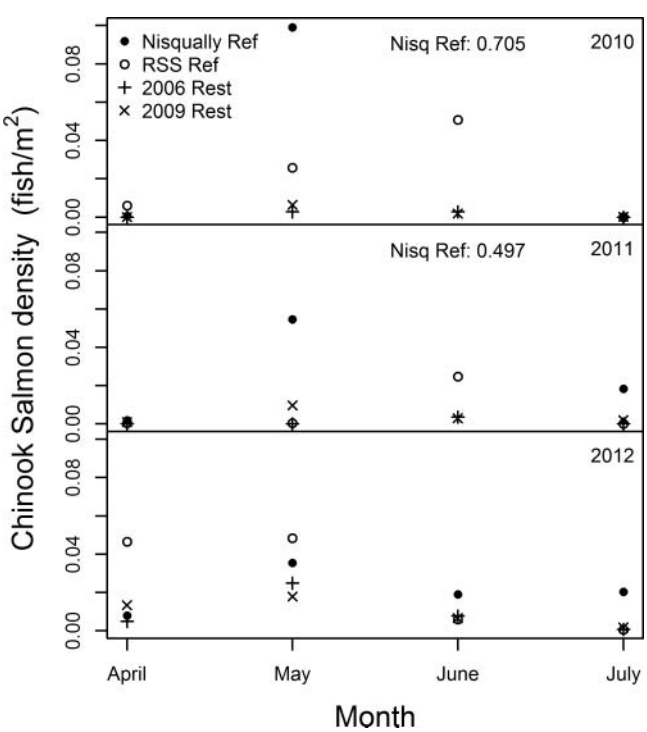

FIGURE 2. Juvenile Chinook Salmon densities for each fyke-net sampling event in 2010, 2011, and 2012 (2006 Rest and 2009 Rest = tidal channels restored in 2006 and 2009; Nisqually Ref = Nisqually Reference channel; RSS Ref = Red Salmon Slough Reference channel). Densities in the Nisqually Reference channel were substantially higher for June 2010 and 2011 than for all other sampling events and thus are given but not plotted.

Chinook Salmon Diet Composition and Foraging Performance

Juvenile Chinook Salmon consumed a diverse array of prey ranging from epibenthic crustaceans (Mysida and Amphipoda [primarily Gammaroidea and Corophiidae]) to emergent dipteran flies (Dolichopodidae, Chironomidae, Ceratopogonidae, and Ephydridae) and terrestrial insects (Hemiptera; Figure 4). Chinook Salmon diet composition varied among channels, months, and years; however, dissimilarity in diet composition between restored and reference channels declined with increasing years since restoration ($F = 4.3$, df = 1, 25, $P = 0.048$, $R^2 = 0.15$; Figure 5).

The linear model of Chinook Salmon *I* with the most support included the explanatory variables of Chinook Salmon density and channel identity (Tables 1, S.4). However, this model explained little of the variation in the data ($R^2 = 0.06$). Even the full model, which had weak support, explained little variation ($R^2 = 0.07$; Figure S.1; Table 1), indicating that the variables we considered did not strongly influence Chinook Salmon *I*.

The linear model of Chinook Salmon ED_{diet} with the most support was the full model with Chinook Salmon density, channel, month, and year as explanatory variables (Tables 2, S.5). There was a negative relationship between ED_{diet} and Chinook Salmon density, and ED_{diet} was higher for Chinook Salmon foraging in the restored channels and during June and July (Figure S.2; Table S.5). The best ED_{diet} model explained more of the variation in its dependent variable ($R^2 = 0.31$) than the best *I* model.

Gastric Evacuation Model

We identified 10 studies of salmonid gastric evacuation rates *R* (60 estimates of *R* in total; Table S.6) that met our screening criteria. Four of the studies were of Chinook Salmon, two were of Sockeye Salmon *O. nerka*, two were of Rainbow Trout *O. mykiss*, and two were of Coho Salmon. Water temperatures in these studies ranged from 2°C to 23°C (mean = 10.7°C), fish mass ranged from 0.9 to 43.3 g (mean = 14.2 g), and *R* ranged from 0.006 to 0.446 per hour (mean = 0.155 per hour). A linear model of $\log_e R$ as a function of water temperature and fish mass was significant and explained over half of the variation in the data ($F = 36.6$, df = 2, 57, $P < 0.001$; $R^2 = 0.56$). To predict

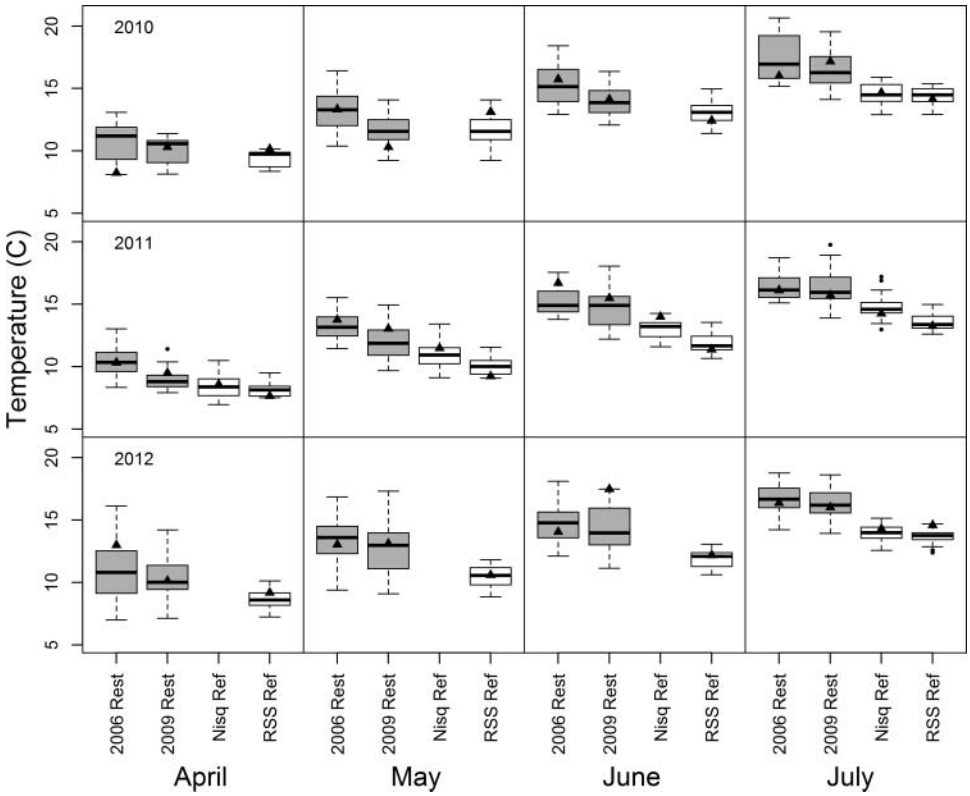

FIGURE 3. Daily mean temperatures (°C) for the four tidal channels sampled during April–July 2010, 2011, and 2012 (gray-shaded boxes = restored [Rest] channels [restored in 2006 and 2009]; open boxes = reference [Ref] channels: Nisqually [Nisq Ref] and Red Salmon Slough [RSS Ref]). Line within box = median; ends of box = interquartile range; whisker = 1.5 × interquartile range; circles = data beyond 1.5 × interquartile range; and black triangles indicate the temperatures on the days of fyke-net sampling. The temperature logger in the Nisqually Reference channel failed during April–June in 2010 and 2012.

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Chinook Salmon R for each sampling event, we used the back-transformed, bias-corrected model

$$R = 0.0612 \times \exp[(0.1139 \times \text{temperature}) - (0.0422 \times \text{mass}) + 0.1790]. \quad (6)$$

Diel Feeding Study

During the diel feeding study (May 29–30, 2012), daily $\overline{I}_d$ of juvenile Chinook Salmon was 1.01% in reference habitats and 1.53% in restored habitats (Figure S.3). Chinook Salmon I varied throughout the day, declining after dark but then increasing again early in the morning (0330 hours). Interestingly, the I in reference habitats was lowest on the first morning of the study but peaked at the same time (0930 hours) the next morning.

Chinook Salmon Energy Density

The $ED_{Chinook}$ of natural-origin juveniles sampled in June 2012 was 4,171 ± 186.3 J/g (mean ± SD), while the $ED_{Chinook}$ of hatchery-origin juveniles was 3,999 ± 101.6 J/g. We used the mean $ED_{Chinook}$ of the combined natural- and hatchery-origin fish (4,085 J/g) as the consumer ED for all growth simulations.

Bioenergetics Growth Simulations

Given our estimated consumption rates and other inputs, the simulated growth potential of juvenile Chinook Salmon appeared to be marginally higher in the reference tidal channels (range = 0.006–0.053 $g \cdot g^{-1} \cdot d^{-1}$) than in the restored channels (range = 0.006–0.046 $g \cdot g^{-1} \cdot d^{-1}$) during 2010; however, there was no clear difference in growth potential between restored and reference channels during 2011 or 2012 (Figure 6). Simulated growth potential varied seasonally and among the four channels within individual months but was not consistently higher in either the reference channels or the restored channels. Negative growth potential was only simulated for one event in 2012, primarily the result of a low consumption rate (A. T. David, unpublished data). Although growth potential was not consistently higher in one habitat, the range of growth potential within individual months was often greater in restored channels than in reference channels, particularly during June and July (Figure 6), due to the greater range of temperatures in the restored channels. The mean

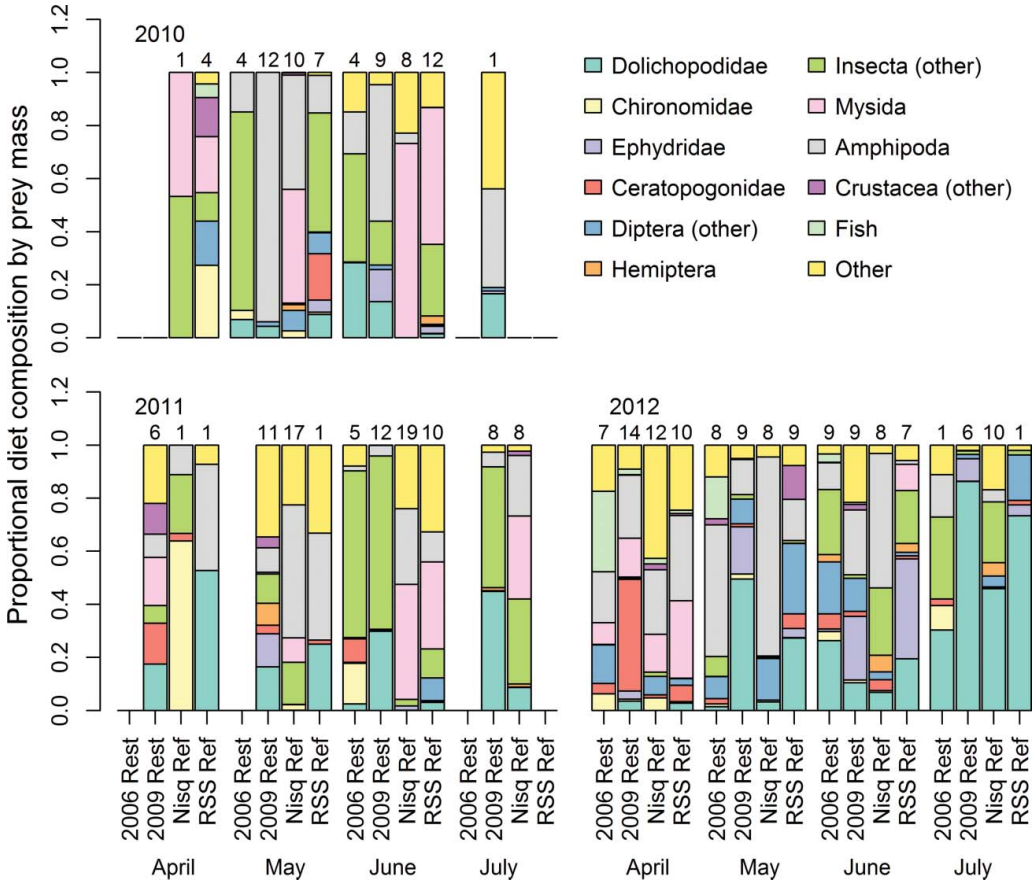

FIGURE 4. Mean proportional diet composition (by prey mass) for juvenile Chinook Salmon at each fyke-net sampling event in restored (Rest) channels (restored in 2006 and 2009) and reference (Ref) channels (Nisqually [Nisq Ref] and Red Salmon Slough [RSS Ref]). The numbers above the bars are sample sizes (number of fish analyzed for diet composition).

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within-month SD and range of growth potential were 0.0013 and 0.0046 $g \cdot g^{-1} \cdot d^{-1}$, respectively, for the reference channels but were 0.0030 and 0.0121 $g \cdot g^{-1} \cdot d^{-1}$, respectively, for the restored channels.

DISCUSSION

Separate but related lines of evidence indicated that restoration of tidal flow to the Nisqually River delta is rapidly restoring many of the ecological attributes of natural tidal marsh ecosystems that are important for juvenile Chinook Salmon. The foraging performance and growth rate potential of Chinook Salmon juveniles were similar in the restored and reference channels, and densities and diet composition displayed trajectories of increasing similarity between the restored and reference channels. However, not all attributes achieved reference conditions. Water temperatures in the restored channels were warmer and more variable than those in the reference channels, potentially constraining growth opportunities for juvenile Chinook Salmon in the restored tidal channels when temperatures peak during summer. Additionally, although the magnitude of differences in Chinook Salmon density declined through time, mean densities were still greater in reference channels than in restored channels during 2012.

We caught juvenile Chinook Salmon, other Pacific salmon species, and native non-salmonid fishes in both of the restored channels, including during the first salmon out-migration season after the 2009 dike removal. For channels restored in 2002 and 2006, juvenile Pacific salmon also accessed the channels during the first salmon out-migration season after tidal flow restoration (Ellings and Hodgson 2007; Nisqually Indian Tribe, unpublished data). We observed a negative relationship between the time since restoration and the degree of dissimilarity in Chinook Salmon diets between restored and reference channels, suggesting that the invertebrate prey communities of the restored marsh areas became more similar to the invertebrate prey communities of natural tidal marsh ecosystems over time. Chinook Salmon densities were significantly higher in the reference tidal channels than in restored channels, but by 2012 the density differences had decreased. However, it is worth noting

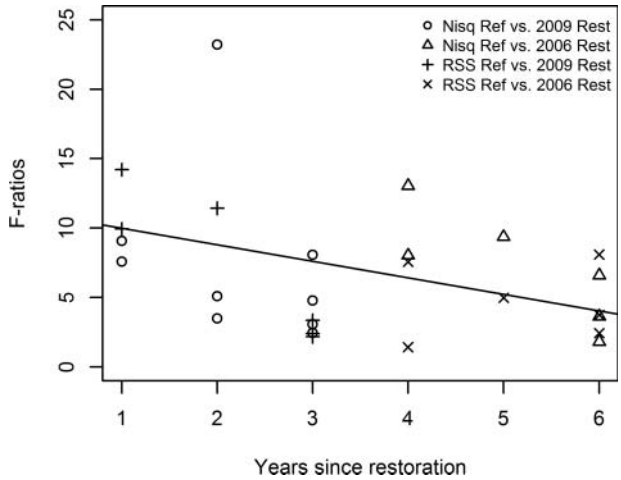

FIGURE 5. PERMANOVA pseudo *F*-ratios from within-month pairwise comparisons of diet composition for Chinook Salmon in restored (Rest) channels (restored in 2006 and 2009) and reference (Ref) channels (Nisqually [Nisq Ref] and Red Salmon Slough [RSS Ref]) as a function of years since restoration. As with univariate ANOVA *F*-ratios, PERMANOVA pseudo-*F*-ratios represent the ratio of between-group to within-group variation; thus, for this analysis, pseudo-*F*-ratios serve as a measure of diet composition similarity between channels relative to within-channel variation.

that the smaller differences were more a result of reduced densities in reference channels than increased densities in restored channels. Lower densities may indicate that the restored marsh areas do not yet have the same capacity to support juvenile Chinook Salmon as the reference marsh areas. Alternatively, the differences in density may be explained in part by differences in landscape position. Both of the reference channels are closer to the Nisqually River than the restored channels and may contain higher densities than channels in the restored marshes simply due to the existence of more direct access (Simenstad and Cordell 2000). In contrast to differences in fish density, our two measures of foraging performance, I and ED_{diet}, varied little among the channels; when differences were apparent, they indicated that Chinook Salmon foraging performance was better in the restored channels than in the reference channels.

Our findings corroborate other research showing that juvenile Pacific salmon rapidly access newly available estuarine habitat and forage on locally produced prey (Shreffler et al. 1990, 1992; Levings and Nishimura 1997; Miller and Simenstad 1997; Gray et al. 2002; Roegner et al. 2010). More broadly, fish generally respond rapidly to restoration actions or the removal of anthropogenic stressors in coastal ecosystems (Able et al. 2008; Borja et al. 2010; Raposa and Talley 2012). However, few studies have used integrative metrics of habitat quality to compare the value of restored and reference estuary ecosystems for juvenile Pacific salmon or other fishes (although see Miller and Simenstad 1997 and Teo and Able 2003).

Measures of realized function, such as habitat-specific growth potential of focal species, are more difficult to obtain than abundances or diet composition, but they provide a more robust evaluation of restoration performance (Simenstad and Cordell 2000). Building upon the comparative growth potential simulations of Gray (2005) and Cordell et al. (2011), we quantified the consumption rates of juvenile Chinook Salmon by using a combined approach that included instantaneous measures of stomach fullness, a diel feeding study, and a gastric evacuation rate model. One assumption of our method is that instantaneous and daily mean measures of stomach fullness are correlated—that is, if a fish consumes more at a given point during the day, then it consumes more during the whole day. However, the lack of a clear diel pattern in I coupled with large differences in I for the single time period we sampled on consecutive days suggests that this assumption may not be completely valid. Our small sample size for each sampling period ($n = 5$ fish/habitat) may have been insufficient to permit accurate characterization of juvenile Chinook Salmon feeding rates, as fish foraging success is often strongly right skewed (Armstrong and Schindler 2011). Although our method of estimating consumption is an improvement over simple instantaneous measures of stomach fullness, uncertainty was likely greater for consumption rates than for other inputs to the growth simulations.

Given the estimated consumption rates and other empirical inputs, the bioenergetics simulations indicated that the growth

TABLE 1. Summary of Akaike's information criterion (AIC_c; corrected for small sample size) ranking of linear models for the instantaneous ration (I) of juvenile Chinook Salmon; K = number of parameters.

Model	K	ΔAIC_c	AIC_c weight	R^2
$\log_e(I + 0.1) \sim$ Density + Channel	6	0.0	0.759	0.06
$\log_e(I + 0.1) \sim$ Channel	5	2.7	0.200	0.05
$\log_e(I + 0.1) \sim$ Density + Channel + Month + Year	11	6.4	0.030	0.07
$\log_e(I + 0.1) \sim$ Channel + Month + Year	10	9.1	0.008	0.06
$\log_e(I + 0.1) \sim$ Year	4	12.3	0.002	0.01
$\log_e(I + 0.1) \sim$ Density + Year	5	14.3	<0.001	0.01
$\log_e(I + 0.1) \sim$ Month	5	15.1	<0.001	0.01
$\log_e(I + 0.1) \sim$ Density + Month	6	16.8	<0.001	0.01

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TABLE 2. Summary of Akaike's information criterion (AIC_c; corrected for small sample size) ranking of linear models for juvenile Chinook Salmon diet energy density (ED_{diet}); K = number of parameters.

Model	K	ΔAIC_c	AIC_c weight	R^2
$ED_{diet} \sim$ Density + Channel + Month + Year	11	0.0	0.987	0.31
$ED_{diet} \sim$ Density + Month	6	8.9	0.012	0.26
$ED_{diet} \sim$ Channel + Month + year	10	12.6	0.002	0.27
$ED_{diet} \sim$ Month	5	53.6	<0.001	0.13
$ED_{diet} \sim$ Density + Channel	6	59.8	<0.001	0.12
$ED_{diet} \sim$ Density + Year	5	62.7	<0.001	0.10
$ED_{diet} \sim$ Channel	5	67.2	<0.001	0.08
$ED_{diet} \sim$ Year	4	83.8	<0.001	0.02

opportunities provided to juvenile Chinook Salmon by the restored tidal marsh channels were similar to the growth opportunities provided by the reference channels, particularly after 2010. Simulated growth rate potential was highly variable among months and among channels within individual months, but there was no consistent difference in growth potential between reference and restored channels. The similarity in mean foraging performance and growth rate potential between habitats suggests that the restored marsh areas have nearly the same capacity to support juvenile Chinook Salmon foraging and growth as the reference marsh areas within the Nisqually River delta. However, if we assume that fish distribute themselves throughout the delta in a way that maximizes their consumption and growth rates, the lower densities of Chinook Salmon in the restored tidal channels indicate that these areas do not yet have the same capacity to support juvenile

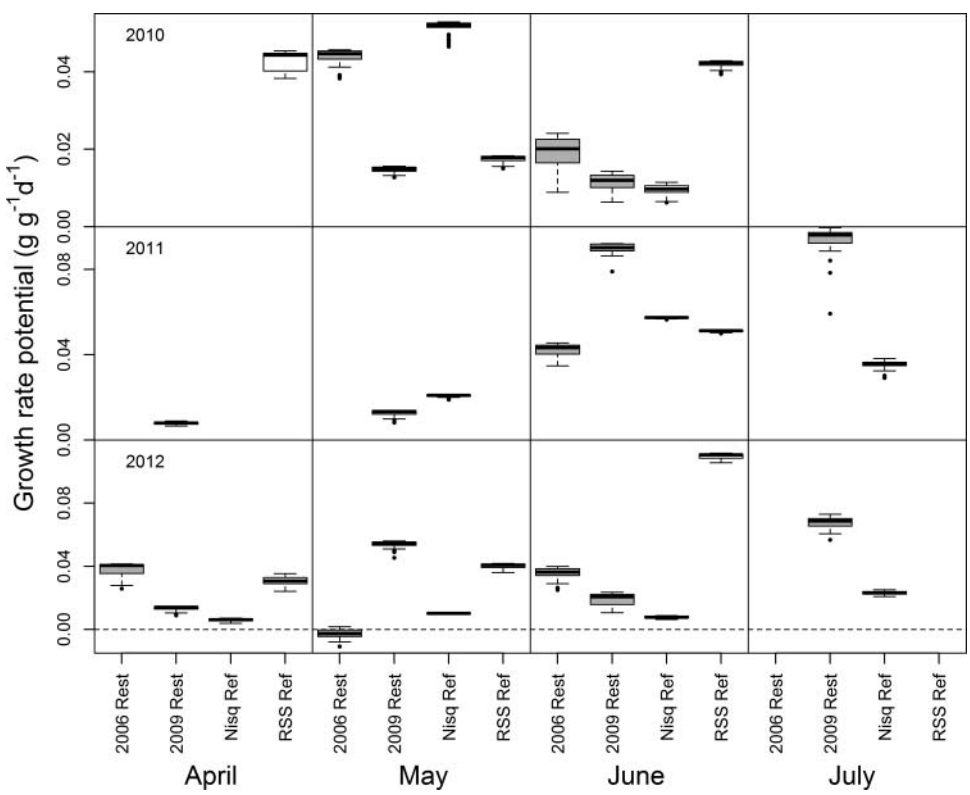

FIGURE 6. Simulated growth rate potential (g growth·g $fish^{-1}$·d^{-1}) of juvenile Chinook Salmon for sampling events in which at least four fish were captured for diet analysis (gray-shaded boxes = restored [Rest] channels [restored in 2006 and 2009]; open boxes = reference [Ref] channels: Nisqually [Nisq Ref] and Red Salmon Slough [RSS Ref]). Growth rate potential was simulated by using the Fish Bioenergetics model parameterized for Chinook Salmon and by using empirically derived inputs from each sampling event. Each box-and-whisker plot is composed of growth potential simulations for each of the daily mean temperatures observed in the given tidal channel during the month of sampling (i.e., 30–31 separate growth rates). Line within box = median; ends of box = interquartile range; whiskers = 1.5 × interquartile range; and circles = data beyond 1.5 × interquartile range.

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Chinook Salmon production as do the reference marsh areas. Unfortunately, as noted above, the small number of sampling locations in our study makes it difficult to determine whether the lower Chinook Salmon densities in the restored channels were solely the result of their restoration status.

Although simulated growth potential was not consistently higher in either restored or reference tidal channels, the more variable and warmer water temperatures in the restored channels, particularly during June and July, resulted in a greater range of growth potential in the restored marshes within individual months. Similarly, Gray (2005) found that mean growth potential of Chinook Salmon was comparable among three restored marshes and one reference marsh in the Salmon River estuary of Oregon but that growth potential was more variable in the restored marshes. Gray (2005) did not identify a cause of the greater variability, although water temperatures in two of the restored marshes were generally warmer than those in the reference marsh.

We attribute the greater temperature range and warmer temperatures in the restored tidal channels to greater sensitivity of the water in those channels to air temperature and solar irradiance; we suspect that this is a consequence of physical differences between the restored and reference marsh areas. Currently, width : depth ratios in the restored tidal channels are greater than those in the reference channels (mean ratios in 2011 = 7.5 for 2006 Restored, 38.2 for 2009 Restored, 1.7 for Nisqually Reference, and 4.5 for RSS Reference; I. Woo and J. Y. Takekawa, unpublished data), resulting in increased water surface area relative to water volume in the tidal channels exposed to solar irradiance and the atmosphere. Additionally, reference marsh areas comprised plant communities with nearly 100% cover, while less than 10% of the 2009 Restored area was vegetated by 2012. Due to subsidence, the reconnected wetlands are lower in elevation than much of the natural marsh within the delta. The most subsided restoration area, 2009 Restored, is approximately 0.8 m lower in mean elevation than RSS Reference (Woo and Takekawa, unpublished data). At high tide, a shallow layer of water often covers much of the mud surface of the 2009 Restored area. During warm, sunny days, this water appears to heat rapidly before draining into tidal channels on the ebb tide. In contrast, significant sheet flow on the reference marsh areas only occurs during spring high tides, and even then the water is shaded by extensive vegetation. Subsidence and lack of vegetation are probably less responsible for the warm temperatures in the 2006 Restored marsh area, as the vegetation coverage and marsh elevation for that area are closer to those of the reference marsh areas than to those of the 2009 Restored area (Woo and Takekawa, unpublished data).

Elevated water temperatures during summer in the restored tidal channels may suppress Chinook Salmon growth potential to levels below that of the reference channels or may prevent them from accessing the restored channels. How warm these channels can become before Chinook Salmon growth is depressed or before Chinook Salmon access is precluded depends partly on food availability. Juvenile Pacific salmon can tolerate the higher water temperatures often found in shallow-water wetlands if they are able to increase prey consumption to keep pace with the higher metabolic costs of inhabiting areas with warmer temperatures (Jeffres et al. 2008; Beauchamp 2009). However, increasing consumption will ameliorate the effects of warmer temperatures only to a point, as metabolic costs continue to rise with temperature, while maximum consumption rates plateau (Beauchamp 2009).

To our knowledge, no other study has identified this important difference in temperature regimes between natural and recently restored tidal wetlands (but see Gray 2005). We suggest that future tidal marsh restoration projects involve close monitoring of water temperatures, particularly when temperature-sensitive species are an impetus for restoration. It is unclear how long it will take for temperature regimes in the restored channels to take on the characteristics of the temperature regimes in reference channels. Unlike other metrics we sampled, there was no indication that the temperature regimes in restored channels were on a trajectory toward the reference temperature regimes during our study. Convergence of the temperature regimes likely depends on sediment accretion, changes in channel morphology, and marsh plant growth. Morphology of a restored tidal marsh and channel can take up to several decades to converge on reference conditions (Williams and Orr 2002). Sediment accretion rates on the Nisqually River delta and changes in the morphology of the restoration areas are actively being monitored. Two dams in the upper Nisqually River watershed trap sediment and dampen peak flows, potentially reducing the amount of sediment that is available to the delta. Given the uncertain and potentially substantial length of time necessary for the restored marsh areas to take on the full physical characteristics of natural tidal marshes, our findings raise concerns over whether the restored tidal channels will provide growth opportunities equivalent to those in natural tidal channels over the duration of the spring–summer out-migration season for juvenile Pacific salmon.

Although we are confident in our results and interpretation, we acknowledge that the sample size was limited ($n = 2$ restored marsh areas and 2 reference marsh areas), our sampling schedule was of relatively low frequency (once per month), and one of the two temperature loggers in the reference channels failed for the majority of the sampling season in 2 out of 3 years. Despite these shortcomings, our results are still valid and useful given the relatively paucity of information on the questions we addressed, the rarity of both large-scale estuary restoration projects and high-quality reference habitats, and the 3-year duration of the study. Furthermore, our results generally align with the results of similar studies, indicating that our results are not an artifact of low sample size (both in spatial replication and sampling frequency).

Landscape attributes, such as the large size of the restoration areas and connectivity with natural wetlands, may

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promote the recovery of the restored habitats, while landscape alterations such as dams may constrain the restored habitats from fully manifesting the functions of natural tidal marsh ecosystems, at least in the near future (Simenstad et al. 2006). The recovery of an ecosystem is likely to depend on the spatial extent of restoration and the landscape setting in which the restoration takes place (Simenstad et al. 2006; Palmer 2009; Moreno-Mateos et al. 2012). For example, tidal channel length and surface area scale with marsh island area as power functions with exponents greater than 1.0, suggesting that removal of dikes around one large marsh island would yield greater increases in total channel length and surface area than the removal of dikes around multiple smaller marsh islands of equivalent total area (Hood 2007). In addition to differences that are a function of scale alone, restoration project size is probably most important for projects within modified landscapes. Anthropogenic disturbances or forcing may have a greater impact on small sites. For example, recruitment of native vegetation was suppressed in small (0.01–1.01-ha) tidal wetland restoration sites within the highly urbanized Duwamish River estuary (Washington) due to the foraging of resident Canada Geese *Branta canadensis*, which have few alternative feeding habitats (Simenstad et al. 2005). As part of a comparison between juvenile Pacific salmon habitats in the same Duwamish River restoration sites and urbanized, degraded habitats, Cordell et al. (2011) found that growth potential for juvenile Pacific salmon in the restored habitats was no better than that in urbanized habitats. Cordell et al. (2011) speculated that because the restoration projects were small in size, the production of invertebrate prey in restored habitat patches was insufficient to permit detection of a response. Furthermore, studies of restoration projects within urbanized settings have found that ecological attributes of restored systems follow convoluted trajectories or may never attain reference levels during the time span of monitoring (Simenstad and Thom 1996; Zedler and Callaway 1999; Stranko et al. 2012).

In contrast, with their relatively large size, ecological connectivity, and semi-natural setting, the Nisqually River delta restorations may not be constrained to an ecological state distinct from that of natural tidal marshes. The bioenergetics simulations identified potential temperature-driven constraints on the growth value of recently restored tidal channels to juvenile Chinook Salmon, and lower Chinook Salmon densities suggested that the restored channels did not yet have the same capacity as natural tidal channels to support Chinook Salmon production. However, our results indicated that even in the early stages of recovery (1–6 years after dike removal), the restored marsh areas provide the core suite of ecological functions that are critical for out-migrating, ocean-type Pacific salmon. Additionally, while we focused on the relative value of restored and reference channels, the removal of dikes increased the amount of intertidal estuarine wetland by 42% within the Nisqually River delta and likely increased the delta's overall capacity to support the broader community of estuarine fishes, birds, and invertebrates.

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