The effects of wetland loss and restoration on the foraging performance and growth potential of Juvenile Chinook salmon in Pacific Northwest estuaries

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Abstract

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During the transition of juveniles from fresh water to estuarine and coastal environments, the survival of Pacific salmon (*Oncorhynchus spp.*) can be strongly size-selective and cohort abundance is partly determined. Because the quantity and quality of food consumed influence juvenile salmon growth, high rates of prey and energy acquisition during estuarine residence are important for survival. Human activities may have affected the foraging performance of juvenile salmon in estuaries by reducing the area of wetlands and by altering the abundance of conspecifics. To improve our understanding of the effects of wetland loss and conspecific density on juvenile salmon foraging performance and diet composition in estuaries, I assembled Chinook salmon (*O. tshawytscha*) diet and density data from nine U.S. Pacific Northwest estuaries across a gradient of wetland loss. We evaluated the influence of wetland loss and conspecific density on juvenile Chinook salmon instantaneous ration and energy ration, two measures of foraging performance, and whether the effect of density varied among estuaries with different levels of wetland loss. We also assessed the influence of wetland loss and three other covariates on salmon diet composition. There was no evidence of a direct effect of wetland loss on juvenile salmon foraging performance, but wetland loss mediated the effect of conspecific density on salmon foraging performance and altered salmon diet composition. These results suggest that habitat loss can interact with conspecific density to constrain the foraging performance of juvenile fishes, and ultimately their growth, during a life-history stage when survival is positively correlated with growth and size. I also evaluated whether restoring tidal flow to previously diked estuarine wetlands also restores foraging and growth opportunities for juvenile Chinook salmon. Several studies have assessed the value of restored tidal wetlands for juvenile salmon, but few have used integrative measures of salmon physiological performance, such as habitat-specific growth potential, to evaluate restoration. Our study took place in the Nisqually River delta, where recent dike removals restored tidal flow to 364 ha of marsh, the largest tidal marsh restoration in the Pacific Northwest. To compare Chinook salmon foraging performance and growth potential in two restored and two reference marshes over three years post-restoration, we sampled fish assemblages, water temperatures, and juvenile Chinook salmon diet composition and consumption rates, and used these data as inputs to a bioenergetics model. We found that juvenile Chinook salmon foraging performance and growth potential were similar between the restored and reference marshes. However, densities of Chinook salmon were significantly lower in the restored marshes and growth potential was more variable in the restored marshes due to their more variable and warmer (2° C) water temperatures compared to the reference marshes. These results indicate that some but not all ecosystem attributes that are important to juvenile salmon rapidly recover following large-scale tidal marsh restoration.

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Acknowledgements

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Introduction

The juvenile stage of many fishes is an important life history period when variation in foraging performance can affect survival and regulate population dynamics (Anderson 1988; Beaugrand et al. 2003; Kennedy et al. 2008). Failure of juvenile fishes to acquire sufficient prey may result in death due to starvation (Kennedy et al. 2008), lengthen the period of vulnerability to size-dependent predation due to suppressed growth (Anderson 1988; Sogard 1997), force individuals to adopt riskier behaviors to capture prey thereby increasing their vulnerability to predation (Biro et al. 2003), or expend more energy to capture prey (Giacomini et al. 2013). Human modifications to the environment could potentially affect the foraging performance of juvenile fishes by altering the overall abundance of prey, the types of prey, or the intensity of competition for prey (e.g., Toft et al. 2007; Francis and Schindler 2009; Naiman et al. 2012). Impacts to the foraging performance of juvenile fishes could in turn reduce individual growth rates and may be partly responsible for the declines of many fish populations. However, our understanding of human impacts on the foraging performance of juvenile fishes is limited for many imperiled species, constraining our ability to prioritize recovery actions. Additionally, it is unclear whether we can reverse human impacts through ecosystem restoration aimed at promoting foraging and growth opportunities for juvenile fishes. In this thesis, I first evaluate whether and to what degree human alterations of estuaries have affected the foraging performance of juvenile Pacific salmon (*Oncorhynchus* spp.) by synthesizing data from nine estuaries along the west coast of North America. I then evaluate the efficacy of a large-scale tidal wetland restoration project to ameliorate human alterations and to restore foraging and growth opportunities for juvenile Pacific salmon rearing in estuaries.

The transition of juveniles from fresh water to estuarine and coastal marine environments is a critical period in the life cycle of Pacific salmon, during which a substantial proportion of a cohort's total smolt-to-adult mortality can occur (Pearcy 1992; Beamish and Mahnken 2001; Wells et al. 2012). During this transition, survival can be strongly size selective (Healey 1982a; Beamish et al. 2004; Moss et al. 2005; Woodson et al. 2013) and the survival rates of salmon are positively correlated with both size and growth rate in estuarine and coastal environments (Cross et al. 2008; Duffy and Beauchamp 2011; Tomaro et al. 2012), although identifying the specific period (i.e., estuarine vs. coastal ocean) when growth and size are most important has been difficult. These patterns are likely a result of size-selective vulnerability to predation (Parker 1971) and starvation (Beamish et al. 2004; Biro et al. 2004), both favoring larger individuals. Thus, the survival of individual salmon and the abundance of whole cohorts may depend in part on rapid growth during estuarine and early marine residence (Beamish and Mahnken 2001), although evidence that survival is unrelated to size and growth also exists (Fisher and Pearcy 1988; Miller et al. 2013). Because the amount and energy content of prey consumed affect juvenile salmon growth (Willette et al. 2001; Quinn 2005; Beauchamp 2009), high rates of prey (and energy) acquisition in the estuarine environment can be critical for survival (Levings 1994). Despite the importance of foraging to the survival of juvenile Pacific salmon, we lack a thorough understanding of the natural and human-induced factors that regulate foraging performance and diet composition in estuaries.

Agriculture, aquaculture, and residential and industrial development have resulted in substantial loss and modification of wetlands in many Pacific Rim estuaries (Emmett et al. 2000; Good 2000; Simenstad et al. 2011). Ocean-type (those that migrate to the ocean as sub-yearlings) juvenile Chinook salmon (*O. tshawytscha*) are generally considered to be more sensitive to changes in estuarine conditions than other Pacific salmon due to their prolonged estuarine residence and feeding (Healey 1982b; Levy and Northcote 1982; Simenstad et al. 1982). In accordance with this view, survival rates of hatchery Chinook salmon are positively correlated with the percentage of estuarine habitat in natural condition (Magnusson and Hilborn 2003). The mechanisms behind the relationship between estuarine habitat and Chinook salmon survival are not well understood. One explanation is that loss and modification of wetlands reduces invertebrate prey availability (Bottom et al. 2005). However, other explanations have also been suggested, such as loss of habitats that provide refuge from predation (Magnusson and Hilborn 2003) and the chemical contamination of estuaries (Meador 2014).

Humans have also altered the abundance of juvenile salmon in estuaries (Simenstad et al. 1982; Rice et al. 2011), potentially changing the frequency and intensity of density-dependent foraging performance for juvenile salmon. In the U.S. Pacific Northwest (PNW), many salmon populations are substantially depressed relative to historic levels (Nehlsen et al. 1991, NRC 1996), which should reduce the intensity of competition. However, habitat loss and degradation may reduce the carrying capacity of ecosystems, making density-dependent processes important at lower abundances than for more pristine ecosystems (Achord et al. 2003). Also, hatcheries release large numbers of juvenile salmon into many watersheds, often in pulses over a shorter period than outmigration of naturally spawned populations (Simenstad et al. 1982; Rice et al. 2011). Because hatchery abundance is typically not regulated by natural constraints, there may be mismatches between the abundance of releases and ecosystem carrying capacity (Zaporozhets and Zaporozhets 2005; Kostow 2009). Extensive evidence for density-dependent juvenile salmon growth due to trophic competition exists for freshwater ecosystems (Milner et al. 2003; Grant and Imre 2005; Schindler et al. 2005). While the potential for density-dependence in estuarine and coastal marine ecosystems has clear theoretical support (Walters and Juanes 1993), empirical evidence for density-dependent foraging performance, growth, and survival is mixed, with studies demonstrating negative effects of density (Reimers 1973; Healey 1979; Neilson et al. 1985; Ruggerone and Goetz 2004; Rice et al. 2011), no effects (Levings et al. 1986; Healey 1991; Brodeur 1992; Daly et al. 2012), or mixed effects (Healey 1980; Sturdevant et al. 2011). Furthermore, there is little information on whether estuarine habitat loss magnifies the intensity of intraspecific competition for migrating juvenile salmon (Rice et al. 2011).

Given the substantial human alterations to many Pacific Rim estuaries, another critical uncertainty is whether it is possible to reverse these alterations and restore the estuarine wetlands important to migrating Pacific salmon (Simenstad and Cordell 2000; Simenstad et al. 2000). One of the main methods of restoring estuarine wetlands is to breach or remove dikes that exclude tidal flow from lands that were historically tidally influenced (Neckles et al. 2002; Roman and Burdick 2012). While it is relatively straightforward to restore tidal exchange, the dominant physical process that structures estuarine wetlands, there remains considerable uncertainty as to whether associated communities and ecosystem processes also recover, and how long recovery takes (Moreno-Mateos et al. 2012). More information is needed on the conditions under which restoring tidal flow will ultimately restore the food webs, temperature regimes, and other ecological attributes that promote productive foraging and rapid growth for juvenile salmon within estuarine wetlands. Information is especially needed on how restoration size and landscape setting influence restoration performance (Palmer et al. 2005; Simenstad et al. 2006; Moreno-Mateos et al. 2012). While these factors have been suggested to have potentially strong influences on ecosystem recovery, empirical studies have only recently started to address these topics (e.g., Moreno-Mateos et al. 2012).

To improve our understanding of the effects of wetland loss and conspecific density on juvenile salmon foraging performance and diet composition in estuaries, I assembled data on relative density and diet of juvenile Chinook salmon from nine PNW estuaries across a range of proportional wetland loss. While the estuarine foraging habits of juvenile salmon have been extensively examined (e.g., Healey 1980, 1982b; Simenstad et al. 1982; Macdonald et al. 1987), few studies have conducted quantitative comparisons of diet composition or foraging performance among multiple estuaries. Indeed, comparisons among estuaries with different degrees of wetland loss and degradation may be a useful scale of analysis for the diet composition and foraging performance of mobile consumers such as juvenile salmon and may help to address questions that would otherwise be unanswerable with data from multiple sites within a single estuary.

To evaluate the efficacy of dike removal to restore the ecosystem processes and functions of estuarine wetlands that are important to juvenile salmon, I compared the foraging performance and growth potential of juvenile Chinook salmon in natural, reference tidal marshes and recently restored (one to six years post-removal) tidal marshes within the Nisqually River delta, location of the largest tidal marsh restoration project to date in the PNW. Several studies have assessed the equivalence of natural and restored tidal wetlands in terms of the attributes important to juvenile salmon; yet, few studies have used integrative measures of salmon physiological performance, such as habitat-specific growth potential, to evaluate restoration. Analyses of growth rate potential, the expected growth rate of a consumer given data on the primary variables that regulate growth (Brandt et al. 1992; Tyler and Brandt 2001), provide a way to integrate multiple environmental variables which influence the physiological status of consumers into the common currency of growth (Brandt et al. 1992; Madon et al. 2001; Gray 2005). Because of the importance of growth and size during estuarine and early marine residence to juvenile salmon survival and the integrative nature of growth as a consumer's response to its environment, simulated growth potential is an excellent metric for evaluating the equivalence of restored and reference tidal wetlands in terms of their value for juvenile salmon. In this thesis, I build upon studies that used a growth-potential approach to assess restoration (Gray 2005; Cordell et al. 2011) by incorporating empirically-derived juvenile salmon consumption rates in both restored and reference tidal wetlands 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 juvenile salmon consumption rates as part of restoration assessments have been unsuccessful (Gray 2005; Cordell et al. 2011).

In the first part of this thesis, I evaluate the effects of estuarine wetland loss and conspecific density on two measures of juvenile Chinook salmon foraging performance – instantaneous ration and energy ration – and evaluate whether the effect of density varies among estuaries with different degrees of wetland loss. I also evaluate the association among four covariates (wetland loss, salinity, day of year, and fish size) and the diet composition of juvenile Chinook salmon to identify the factors that most strongly influence estuarine diet composition, along with the similarities and differences in diet composition among estuaries.

In the second part of my thesis I evaluate the degree with which restoring tidal flow to large tracts of historical tidal wetlands also restores the ecological attributes of natural estuarine wetlands that support the foraging and growth of juvenile Chinook salmon. Specifically, I compare the density, foraging performance, diet composition, and simulated growth potential of juvenile Chinook salmon in two restored and two reference marshes over three consecutive years. The restored marshes ranged from one to six years post-removal during the study. I hypothesize that (1) measures of juvenile Chinook salmon density, foraging performance, and growth potential will initially be lower in restored habitats than reference habitats, but will rapidly approach equivalence as time since restoration increases and (2) diet similarity among juvenile Chinook salmon foraging in reference and restored habitats would increase as time since restoration increases.

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Chapter 1: Wetland loss, juvenile salmon foraging performance, and conspecific density dependence in Pacific Northwest estuaries

Abstract

During the transition of juveniles from fresh water to estuarine and coastal environments, the survival of Pacific salmon (*Oncorhynchus spp.*) can be strongly size-selective and cohort abundance is partly determined. Because the quantity and quality of food consumed influence juvenile salmon growth, high rates of prey and energy acquisition during estuarine residence are important for survival. Human activities may have affected the foraging performance of juvenile salmon in estuaries by reducing the area of wetlands and by altering the abundance of conspecifics. To improve our understanding of the effects of wetland loss and conspecific density on juvenile salmon foraging performance and diet composition in estuaries, we assembled Chinook salmon (*O. tshawytscha*) diet and density data from nine U.S. Pacific Northwest estuaries across a gradient of wetland loss. We evaluated the influence of wetland loss and conspecific density on juvenile Chinook salmon instantaneous ration and energy ration, two measures of foraging performance, and whether the effect of density varied among estuaries with different levels of wetland loss. We also assessed the influence of wetland loss and three other covariates on salmon diet composition. There was no evidence of a direct effect of wetland loss on juvenile salmon foraging performance, but wetland loss mediated the effect of conspecific density on salmon foraging performance and altered salmon diet composition. These results suggest that habitat loss can interact with conspecific density to constrain the foraging performance of juvenile fishes, and ultimately their growth, during a life-history stage when survival is positively correlated with growth and size.

Introduction

The juvenile stage of many fishes is an important life history period when variation in foraging performance can affect survival and regulate population dynamics (Anderson 1988; Beaugrand et al. 2003; Kennedy et al. 2008). Failure of juvenile fishes to acquire sufficient prey may result in death due to starvation (Kennedy et al. 2008), lengthen the period of vulnerability to size-dependent predation due to suppressed growth (Anderson 1988; Sogard 1997), force individuals to adopt riskier behaviors to capture prey thereby increasing their vulnerability to predation (Biro et al. 2003), or expend more energy to capture prey (Giacomini et al. 2013). Human modifications to the environment could potentially affect the foraging performance of juvenile fishes by altering the overall abundance of prey, the types of prey, or the intensity of competition for prey (e.g., Toft et al. 2007; Francis and Schindler 2009; Naiman et al. 2012;), with population-level consequences. However, our understanding of human impacts on the foraging performance of juvenile fishes is limited for many imperiled species, constraining our ability to design or prioritize recovery actions. Here we evaluate how human alterations of estuaries have affected the foraging performance of juvenile Pacific salmon (*Oncorhynchus spp.*) by synthesizing data from nine estuaries along the west coast of North America.

The transition of juveniles from fresh water to estuarine and coastal marine environments is a critical period in the life cycle of Pacific salmon, during which a substantial proportion of a cohort's total smolt-to-adult mortality can occur (Pearcy 1992; Beamish and Mahnken 2001; Wells et al. 2012). During this transition, survival can be strongly size selective (Healey 1982a; Beamish et al. 2004; Moss et al. 2005; Woodson et al. 2013) and the survival rates of salmon are positively correlated with both size and growth rate in estuarine and coastal environments (Cross et al. 2008; Duffy and Beauchamp 2011; Tomaro et al. 2012). These patterns are likely a result of size-selective vulnerability to predation (Parker 1971) and starvation (Beamish et al. 2004; Biro et al. 2004), both favoring larger individuals. Thus, the survival of individual salmon and the abundance of whole cohorts depend in part on rapid growth during estuarine and early marine residence (Beamish and Mahnken 2001), although evidence that survival is unrelated to size and growth also exists (Fisher and Pearcy 1988; Miller et al. 2013). Because the amount and energy content of prey consumed affect juvenile salmon growth (Willette et al. 2001; Quinn 2005; Beauchamp 2009), high rates of prey (and energy) acquisition in the estuarine environment can be critical for survival (Levings 1994). Despite the importance of foraging to the survival of juvenile Pacific salmon, we lack a thorough understanding of the natural and human-induced factors that regulate foraging performance and diet composition in estuaries.

Agriculture, aquaculture, and residential and industrial development have resulted in substantial loss and modification of tidal wetlands in many Pacific Rim estuaries (Emmett et al. 2000; Good 2000; Simenstad et al. 2011). Ocean-type (those that migrate to the ocean as sub-yearlings) juvenile Chinook salmon (*O. tshawytscha*) are generally considered to be more sensitive to changes in estuarine conditions than other Pacific salmon due to their prolonged estuarine residence and feeding (Healey 1982b; Levy and Northcote 1982; Simenstad et al. 1982). In accordance with this view, survival rates of hatchery Chinook salmon are positively correlated with the percentage of estuarine habitat in natural condition (Magnusson and Hilborn 2003). The mechanisms behind the relationship between the quantity of natural estuarine habitat and Chinook salmon survival are not well understood. One explanation is that loss and modification of wetlands reduces invertebrate prey availability (Bottom et al. 2005b). However, other explanations have also been suggested, such as loss of habitats that provide refuge from predation (Magnusson and Hilborn 2003) and chemical contamination (Meador 2014).

Humans have also altered the abundance of juvenile salmon in estuaries (Simenstad et al. 1982; Rice et al. 2011), potentially changing the frequency and intensity of density-dependent foraging performance for juvenile salmon. In the U.S. Pacific Northwest (PNW), many salmon populations are substantially depressed relative to historic levels (Nehlsen et al. 1991; NRC 1996), which should reduce the intensity of competition. However, habitat loss and degradation may reduce the carrying capacity of ecosystems, making density-dependent processes important at lower abundances than for more pristine ecosystems (Achord et al. 2003). Also, hatcheries release large numbers of juvenile salmon into many watersheds, often in pulses over a shorter period than outmigration of naturally spawned populations (Simenstad et al. 1982; Rice et al. 2011). Because hatcheries are typically not regulated by natural constraints, there may be mismatches between the abundance of releases and ecosystem carrying capacity (Zaporozhets and Zaporozhets 2005; Kostow 2009). Extensive evidence for density-dependent juvenile salmon growth due to trophic competition exists for freshwater ecosystems (Milner et al. 2003; Grant and Imre 2005; Schindler et al. 2005). While the potential for density-dependence in estuarine and coastal marine ecosystems has clear theoretical support (Walters and Juanes 1993), empirical evidence for density-dependent foraging performance, growth, and survival is mixed, with studies demonstrating negative effects of density (Reimers 1973; Healey 1979; Neilson et al. 1985; Ruggerone and Goetz 2004; Rice et al. 2011), no effects (Levings et al. 1986; Healey 1991; Brodeur 1992; Daly et al. 2012), or mixed effects (Healey 1980; Sturdevant et al. 2011). Furthermore, there is little information on whether estuarine habitat loss magnifies the intensity of intraspecific competition for migrating juvenile salmon (Rice et al. 2011).

To improve our understanding of the effects of tidal wetland loss and conspecific density on juvenile salmon foraging performance and diet composition in estuaries, we assembled data on relative density and diet of juvenile Chinook salmon from nine PNW estuaries across a range of proportional wetland loss. While the estuarine foraging habits of juvenile salmon have been extensively examined (e.g., Healey 1980, 1982b; Simenstad et al. 1982; Macdonald et al. 1987), few studies have quantitatively compared diet composition or foraging performance among multiple estuaries. Indeed, comparisons among estuaries with different degrees of wetland loss and degradation may be a useful scale of analysis for the diet composition and foraging performance of mobile consumers such as juvenile salmon and may help to address questions that would otherwise be unanswerable with data from only a single estuary. In this paper, we evaluated the effects of estuarine wetland loss and conspecific density on juvenile Chinook salmon instantaneous ration and energy ration, two measures of foraging performance, and evaluated whether the effect of density varies among estuaries with different degrees of wetland loss. We also evaluated the association among four covariates (wetland loss, salinity, day of year, and fish size) and the diet composition of juvenile Chinook salmon to understand how these factors influence estuarine diet composition, and to identify similarities and differences in diet composition among estuaries. We expected that both wetland loss and conspecific density will negatively affect juvenile salmon foraging performance, and that density will have a stronger, negative effect in estuaries that have suffered the most extensive wetland losses.

Methods

Data sources

We assembled data from six studies of juvenile Chinook salmon in nine PNW estuaries collected between 1998 and 2012. Salmon were sampled from the Duwamish and Nisqually river estuaries in Washington, the Columbia River estuary, and the Alsea, Coquille, Nestucca, Salmon, Siuslaw, and Yaquina river estuaries in Oregon (Figure 1.1). Each study had unique goals and objectives, but all used standard estuarine juvenile salmon sampling methods and are thus comparable for the purposes of the present analyses. We describe the general protocols used in these studies and refer readers to Table 1.1 and references therein for specifics about each study and estuary. Some of these data have been previously published, some exist in reports and student theses, and some are otherwise unpublished.

All salmon were collected between February and October, with most between April and July, the season of peak juvenile Chinook salmon migration in PNW estuaries (Healey 1982b; Simenstad et al. 1982). The frequency of sampling varied among studies, but was typically weekly, biweekly, or monthly. Sampling methods used to capture juvenile salmon included boat-set beach and river seines, fyke trap nets, and enclosure nets. For all sampling methods, each catch was first enumerated by species. Subsamples of typically ten or fewer of both natural and hatchery-origin (identified by adipose fin clip or coded wire tag) sub-yearling (ocean-type) juvenile Chinook salmon were retained from catches. Except in the Duwamish River estuary, all subsampled salmon were sacrificed in the field using an overdose of tricaine methanosulfate (MS-222). Measurements of subsampled fish included mass (to the nearest 0.1 g) and fork length (to the nearest 1 mm). Salmon were stored in either 10% formalin or 95% ethanol for later stomach contents analysis. In the Duwamish River estuary, gastric lavage was used to obtain the stomach contents of approximately 60% of the subsampled juvenile Chinook salmon without sacrificing these fish. Prior to being lavaged, salmon were anaesthetized in a bath of MS-222, and measured for mass and length. Stomach contents were then removed using a modified garden pump sprayer with a custom nozzle and filtered seawater. Contents were washed into a 106-μm sieve and stored in 10% formalin. Salmon were immediately placed in a bucket of seawater for recovery and then released. Mass was not recorded for approximately 40% of juvenile salmon sampled for diet analysis in the Duwamish and 5% in the Nisqually estuaries. We estimated the masses of these fish using length-mass regressions.

Water column salinity (psu) was typically recorded at each sampling event using a portable water chemistry meter except for Duwamish River estuary sampling in 2003 and all Columbia River estuary sampling. We assumed that salinity was zero for all sampling in the Columbia River as the sampling sites were above the upstream edge of salinity intrusion during spring and early summer when salinity intrusion is attenuated by high river flows. We calculated monthly mean salinities for all sites sampled in the Duwamish in 2005 and applied those values to all Duwamish sampling events.

Diet processing

All diets were processed according to a standard protocol by the Wetland Ecosystem Team at the University of Washington's School of Aquatic and Fishery Sciences. For salmon retained whole, the stomach was first removed and the contents removed from the stomach. Contents from each stomach and lavage sample were weighed (blotted wet mass to the nearest 0.0001 g) and prey organisms from each sample were sorted to the lowest feasible taxonomic resolution using a dissecting microscope. Each unique prey taxon was then enumerated and weighed separately. As a measure of consumption or foraging rate, we calculated the instantaneous ration (R) of each juvenile Chinook salmon as the mass of stomach contents as a percentage of fish body mass without the contents. As a measure of energy consumption, we calculated the energy ration (E) of each Chinook salmon as the sum of individual prey taxon masses multiplied by the energy density (kJ g^{-1} wet mass) of each prey taxon, divided by fish mass without the stomach contents. Thus, energy ration equals kJ consumed per gram of fish. Energy densities of prey taxa were acquired from the literature (Table A.1.1).

Estuary wetland loss

We used data on proportional estuary wetland loss due to human development from Simenstad et al. (2011) for the Washington estuaries, from Marcoe and Pilson (2012) for the Columbia River estuary, from Bottom et al. (2005a) for the Salmon River estuary, and from Good (2000) for the other Oregon estuaries. Because large dike-removal wetland restoration projects were implemented in the Nisqually and Salmon river estuaries after the estimates of wetland loss were calculated, but prior to sampling, we adjusted downward the proportional wetland losses in these estuaries by the area of tidal wetlands restored.

Density estimates

We estimated densities of juvenile Chinook salmon for sampling events in the Nisqually, Duwamish, and Oregon estuaries. We used the weekly mean catch-per-set (CPUE) of river and beach seine sets, respectively, in the Duwamish and Nisqually river estuaries as a relative measure of density. We calculated true densities for sampling events in the Oregon estuaries, where fyke trap nets were used to sample dendritic tidal channel networks. The bank-full surface area of each channel network was estimated using aerial photographs and a geographic information system. The channel network surface areas were then used with fish catches and trap-specific efficiency estimates from mark-recapture studies to calculate juvenile Chinook salmon densities (fish m^{-2}) for each fyke net sampling event. Fyke trap nets were also used to sample tidal channel networks in the Columbia River estuary, but because some data necessary to calculate density were lacking, we were unable to estimate densities in the Columbia. Finally, we did not estimate densities for enclosure net sampling in the Duwamish River estuary.

Statistical analysis

We used linear regression to test the hypothesis that estuarine wetland loss negatively affects juvenile Chinook salmon instantaneous ration (*R*) and energy ration (*E*). We first transformed *R* [$\log_e(x + 0.1)$] and *E* [$\log_e(x + 0.01)$] to normalize these data. We then regressed the mean transformed *R* and *E* of each estuary against the proportion of wetlands lost in that estuary. For the Duwamish River estuary, only *R* and *E* values calculated from whole-stomach samples were used in this analysis because the *R* and *E* values of lavage samples were significantly smaller on average than whole-stomach samples (*R*: t = -9.6, df = 749, $P < 0.0001$; *E*: t = -7.8, df = 749, $P < 0.0001$), potentially due to incomplete removal of stomach contents by gastric lavage or some unaccounted variable.

Because we used both relative (CPUE) and true (fish m^{-2}) measures of conspecific density, we were unable to directly evaluate evidence for an effect of conspecific density and an interaction effect between conspecific density and wetland loss on *R* and *E* within a single model. Instead, we evaluated the effect of conspecific density on *R* and *E* separately for the Nisqually (CPUE), Duwamish (CPUE), and Salmon (fish m^{-2}) river estuaries and for the remaining Oregon estuaries (fish m^{-2}) together. We combined data from the Oregon estuaries other than the Salmon River because there were relatively few sampling events within each of these estuaries. We used linear regression to assess the relationship between transformed *R* and *E* and conspecific density for these four estuaries/sets of estuaries. Thus, we indirectly evaluated evidence for an interaction between estuarine wetland loss and conspecific density on juvenile Chinook salmon *R* and *E* by comparing the statistical relationships between *R* and *E* and conspecific density among estuaries encompassing a wide range of proportional wetland loss: Salmon (13%), Nisqually (41%), other Oregon (59-94%), and Duwamish (99%). We only used salmon captured via seine for the regressions based on the Duwamish River estuary data, but we used both whole-stomach and gastric lavage samples so we included an additional intercept term within each model to account for the fact that R and E of salmon sampled via gastric lavage were smaller on average than for whole-stomach samples.

We first explored the juvenile Chinook salmon stomach composition data using descriptive metrics. We calculated the frequency of consumption of each prey taxon across all non-empty stomachs. For taxa consumed by at least 5% of all Chinook salmon (20 taxa), we also calculated the mean proportional stomach contents contribution by mass across all non-empty stomachs and for only stomachs containing each prey taxon. To visually compare diet composition among the estuaries, we grouped stomach samples according to season (Early: Feb-April; Middle: May-June; Late: July-October) and salinity regime (Freshwater tidal – oligohaline [0-5 psu], mesohaline [5-18 psu], polyhaline [18-30 psu]), for a total of nine season by salinity groupings. For each grouping, we plotted the mean proportional stomach contents composition by mass in each estuary for a reduced set of prey taxa.

We used canonical correspondence analysis (CCA) (ter Braak 1986) to relate variation in juvenile salmon estuarine stomach contents composition to four covariates. CCA is a constrained ordination technique that first summarizes variation in the response variables among the observations into a series of synthetic, orthogonal axes using iterative reciprocal averaging among the observation and response variable scores. CCA then performs a multiple regression among the covariates and the observation scores to determine the correspondence between the explanatory covariates and both the observations and response variables (ter Braak 1986; Palmer 1993; Økland 1996). Statistical significance of the covariates is assessed using permutation tests and the results of the ordination are plotted to visualize the correspondence among observations, response variables, and predictor covariates. Our unit of observation was an individual sampling event (sampling location x date). The response variables were the mean proportional stomach contents contribution by mass of 16 prey taxa; those taxa consumed by at least 5% of all salmon, excluding coarse resolution groupings (e.g., “Amphipoda, other”; see results). Our explanatory covariates were day of the year, salinity, mean salmon fork length, and proportional wetland loss within an estuary. All covariates were standardized to a mean of zero and unit variance. We used the R software for statistical computing for all analyses (R Core Team 2013). The CCA was implemented using the *Vegan* package (Oksanen et al. 2012).

Results

Effects of wetland loss and conspecific density on instantaneous ration and energy ration

There was no relationship between mean juvenile Chinook salmon instantaneous ration, *R*, and estuarine wetland loss ($F_{1,7} = 0.7$, $p = 0.42$, $R^2 = 0.10$; Figure 1.2a). In the two estuaries with the greatest proportion of intact wetlands, the Salmon and the Nisqually, there was no relationship between *R* and conspecific density (Salmon River estuary: $F_{1,533} = 0.3$, $p = 0.56$, $R^2 < 0.01$; Figure 1.2b. Nisqually River estuary: $F_{1,501} = 2.2$, $p = 0.14$, $R^2 < 0.01$; Figure 1.2c). In contrast, there were significant, negative relationships between *R* and conspecific density for estuaries with the greatest proportional wetland losses, the remaining Oregon estuaries and the Duwamish (Oregon estuaries: $F_{1,337} = 22.7$, $p < 0.0001$, $R^2 = 0.06$; Figure 1.2d. Duwamish River estuary: $F_{2,748} = 57.6$, $p < 0.0001$, $R^2 = 0.13$; Figure 1.2e).

The effects of wetland loss and conspecific density on juvenile Chinook salmon energy ration, *E*, followed similar patterns. There was no relationship between mean juvenile Chinook salmon *E* and wetland loss ($F_{1,7} = 0.5$, $p = 0.51$, $R^2 = 0.07$; Figure 1.3a). Neither were there relationships between *E* and conspecific density for the Salmon and Nisqually river estuaries (Salmon River estuary: $F_{1,533} = 2.3$, $p = 0.13$, $R^2 < 0.01$; Figure 1.3b. Nisqually River estuary:

$F_{1,501} = 1.3$, $p = 0.25$, $R^2 < 0.01$; Figure 1.3c). However, there were significant, negative relationships between E and conspecific density for estuaries with the greatest proportional wetland losses, the remaining Oregon estuaries and the Duwamish (Oregon estuaries: $F_{1,336} = 11.5$, $p = 0.0008$, $R^2 = 0.03$; Figure 1.3d. Duwamish River estuary: $F_{2,748} = 41.5$, $p < 0.0001$, $R^2 = 0.10$; Figure 1.3e).

Diet composition

Juvenile Chinook salmon consumed a diverse array of prey taxa across the nine PNW estuaries. Dipterans (flies) and amphipods were the most frequently consumed taxa, accounting for five of the six most frequently consumed prey categories (Figure 1.4). Other frequently consumed taxa included insects such as hemipterans (plant hoppers), hymenopterans (wasps, bees, and ants), and coleopterans (beetles), and crustaceans such as cumaceans, mysids, and copepods. Broadly, the stomach contents of juvenile Chinook salmon were dominated by insects and crustaceans, while annelid worms, and other arthropods such as collembolans (springtails) and arachnids (spiders, mites), were less commonly consumed. Interestingly, three taxa that were consumed relatively infrequently — annelids, mysids, and trichopterans (caddisflies) — contributed large proportions of the total stomach contents mass when consumed (Figure 1.4).

Permutation tests of the canonical correspondence analysis indicated that our constraining covariates explained a significant amount of the total variation in the diet composition of juvenile Chinook salmon among 396 observations ($F_{4,391} = 11.7$, $P = 0.002$, N. perm = 500), although the proportion accounted for was relatively small (11%). Separate permutation tests of each constraining covariate indicated that all covariates accounted for a significant amount of the variation in diet composition (Table 1.2). While some observations from the Nisqually and Duwamish river estuaries clearly separated themselves in the CCA tri-plot, there was otherwise little consistent separation among observations from different estuaries, suggesting considerable consistency in juvenile Chinook salmon diet composition among the estuaries (Figure 1.5). Consumption of ephemeropterans (mayflies) and trichopterans was associated with estuaries with the smallest wetland losses, while consumption of collembolans and hymenopterans was associated with greater wetland losses. Salmon fork length, date of capture, and water column salinity were all moderately correlated, making it difficult to completely partition the influence of these covariates on salmon diet composition (Figure 1.5). Consumption of ephemeropterans, trichopterans, and annelids was associated with lower salinities, and consumption of psocopterans with higher salinities. Mysids were consumed by larger salmon. When grouped by season and salinity, the proportional diet composition of juvenile Chinook salmon displayed similar patterns as in the CCA tri-plot. There was a moderate degree of similarity in diet composition among estuaries within each grouping, although there were instances of marked differences, such as Nisqually River estuary salmon feeding extensively on mysids (Figure 1.6). Generally, the contribution of crustaceans to the diet composition increased with increasing salinity, while the contribution of dipterans decreased. Ephemeropterans, plecopterans (stoneflies), and trichopterans (EPT in Figure 1.6) also appeared to be consumed more extensively in estuaries with the smallest wetland losses.

Discussion

Summary of findings

We found no evidence of a direct, negative effect of wetland loss on two measures of juvenile Chinook salmon foraging performance (instantaneous ration, *R*, a measure of prey consumption; energy ration, *E*, a measure of energy consumption). However, there was evidence that wetland loss mediates the intensity of density-dependent foraging performance, whereby there was no effect of conspecific density on *R* or *E* in the two estuaries with less than 50% wetland loss, but there was a significant, negative effect of density on *R* and *E* in the estuaries with greater than 50% wetland loss. In terms of diet composition, salmon consumed a diverse array of prey, but their diets were composed largely of insects (especially dipteran flies) and epibenthic crustaceans associated with intertidal wetlands. Wetland loss, salinity, fish size, and date of sampling all were associated with variation in juvenile salmon estuarine diet composition.

Estuarine wetland loss and salmon foraging performance

The lack of evidence for a direct, negative effect of wetland loss on salmon foraging performance was somewhat surprising, given the large difference in the magnitude of wetland loss and other human impacts among the estuaries at the ends of the spectrum. It is possible that consequences of wetland loss may manifest themselves in other ways than impacts to foraging. Because there are strong benefits to juvenile salmon for growing rapidly during estuarine and early marine residence (Beamish et al. 2004; Duffy and Beauchamp 2011), salmon in highly modified estuaries may take greater risks, and thus incur higher predation mortality, to consume similar amounts of prey as salmon in more natural estuaries. For example, juvenile trout in a series of experimental lakes grew at similar rates despite differences in prey abundance, but trout in the lakes with lower prey abundance were more active and foraged in riskier habitats, and thus experienced higher predation mortality from larger trout than did juvenile trout in the lakes with higher food abundance (Biro et al. 2003). Juvenile salmon may also respond to wetland loss by altering the timing and duration of estuarine residence, possibly by spending less time in estuaries and migrating earlier to the ocean (Greene and Beechie 2004; Greene et al. 2005).

Alternatively, interannual variation in prey availability, non-random sampling, and unaccounted variables resulting from our use of multiple data sources could obscure the effects of wetland loss. For example, we compared data from different estuaries that were collected in different years. Temporal climatic-oceanographic fluctuations can drive substantial variation in salmon marine prey availability (e.g., Wells et al. 2012; Daly et al. 2013), but the magnitude of natural interranual variation in secondary productivity within estuaries has been examined little. Furthermore, sampling locations were generally not randomly chosen within estuaries and only in two estuaries (Duwamish and Nisqually) did sampling encompass the spatial extent of the estuary and temporal extent of the juvenile migration. Sampling was either spatially or temporally limited in the other estuaries. While all the Oregon estuaries except the Salmon River estuary had lost greater than 50% of their wetlands, sampling within these systems was primarily focused on the remaining patches of relatively natural wetlands, often concentrated in the upper, oligohaline reaches. Thus, the salmon in our analysis were not uniformly representative of the foraging performance and diet composition of the larger population of salmon migrating through these estuarine systems. Similarly, sampling was not entirely consistent among estuaries with respect to other factors which influence consumption rates. Juvenile salmon consumption rates vary with the time of day (Doble and Eggers 1978) and tide level (Levings et al. 1991). While all sampling occurred during daylight hours, sampling was not fully standardized among estuaries with respect to tide level or time of day. We suggest that future studies seeking to address similar questions should sample multiple estuaries synoptically, use consistent methodologies and gear types, and distribute sampling locations across the breadth of the estuarine gradient.

Conspecific density and salmon foraging performance

While there was no evidence of a direct effect of wetland loss on juvenile salmon foraging performance, wetland loss did appear to mediate the effect of conspecific density on salmon foraging performance. The lower foraging performance at higher conspecific densities in estuaries with extensive wetland loss suggests reductions in per capita prey availability. This reduction in availability could be due to lower abundances of potential prey, fewer low-risk foraging habitats, or both. By contrast, in the estuaries with extensive intact wetlands, prey abundance and low-risk foraging habitats were sufficient such that increases in salmon density had little effect on per capita prey availability, at least relative to other processes. Efforts aimed at conservation and recovery of Pacific salmon populations sometimes assume that because many populations are reduced relative to historic levels, density-dependent processes are unimportant relative to density-independent factors regulating foraging, growth, and survival (Achord et al. 2003; Greene and Beechie 2004). Yet, our results suggest that wetland loss can interact with conspecific density to constrain the foraging performance of juvenile salmon, and thus potentially their growth and survival, during a life-history stage when mortality significantly influences adult cohort size. This finding complements research indicating that by reducing ecosystem carrying capacity, habitat loss and degradation can make density-dependent processes important even for populations which would typically be considered small or low-density (Achord et al. 2003; Walters et al. 2013).

Our findings align with concerns that releases of hatchery-produced salmon may interact synergistically with habitat loss to negatively impact wild salmon populations (Hoekstra et al. 2007; Rice et al. 2011). Watersheds experiencing major habitat loss often have large hatchery operations to compensate for the lost production of wild populations, but our results suggest that wild juvenile Chinook salmon will be most vulnerable to trophic competition with ocean-type hatchery Chinook salmon in highly modified estuaries. On a more optimistic note, the two estuaries where no effect of density was evident, the Salmon and Nisqually river estuaries, have both undergone extensive dike removals to restore tidal wetlands. While we have no data prior to the dike removals with which to compare, our results suggest that wetland restoration may alleviate trophic competition among juvenile salmon in estuaries, corroborating the findings of other research in these systems (Bottom et al. 2005b, C.S. Ellings, unpublished data).

Implications of our findings are not that foraging performance is completely density-independent in the Salmon and Nisqually river estuaries, or other, more pristine estuaries, but that the effect of density is less in these estuaries than in estuaries that have lost extensive wetlands. While the role of density dependence in population regulation has long been debated, it is now generally accepted that most populations are under at least some density-dependent control (Turchin 1999; Brook and Bradshaw 2006; Sutherland et al. 2013). Furthermore, our analyses used observational data, from which effects of density can be difficult to detect due to positive covariance between density and habitat quality (Shima and Osenberg 2003). Our estimated effects of density are likely conservative because peak salmon abundance in estuaries often coincides with high levels of production or biomass of their primary invertebrate prey (Pearcy 1992). These processes may also be partly responsible for the low amount of variation explained by density even in the estuaries where density had an effect.

We also should interpret these results cautiously due to the nature of the data we used in this analysis. Interannual variation in prey availability within an estuary could mask the effects of conspecific density on foraging performance. While there were sufficient data to compare the relationship between foraging performance and density among years within the Salmon and Nisqually river estuaries (i.e., analysis of covariance), there were not for the other Oregon estuaries or the Duwamish. Conversely, it is possible that the negative effect of density evident in the Oregon estuaries is simply a result of other differences among the estuaries from which we pooled data. Additionally, we used two different measures of conspecific density in different estuaries. These two density measures may correspond differently to the intra-specific interactions that individual consumers actually experience, biasing our results. Yet, our results were “balanced” such that both density measures had no effect and a negative effect on foraging performance within an estuary/estuary group, suggesting the results were not an artifact of the measure of density used. Finally, juvenile Chinook salmon not only share prey with each other, but also with other fishes (e.g., McCabe et al. 1983). Inter-specific resource sharing, as well as intra-specific resource sharing, likely influences the foraging performance of juvenile Chinook salmon. A full evaluation of the drivers of Chinook salmon foraging performance should include data on other fishes and their overlaps in diet with Chinook salmon. However, we think focusing on intra-specific interactions is justified because quantifying the degree of diet overlap and intensity of trophic interaction among species is often exceptionally difficult, and because from a management perspective the intensity of intra-specific interactions is more likely to be altered through human intervention than the intensity of inter-specific interactions (e.g., recovery of Chinook salmon populations or changes to hatchery practices).

Salmon diet composition

Our analysis of 2,658 stomach samples found that although juvenile Chinook salmon consumed a diverse array of prey across nine PNW estuaries, only a few taxa, particularly dipteran flies and amphipods, were ubiquitously consumed. Other studies have also shown that while the proportions of specific taxa in the diets of Juvenile Chinook salmon vary among estuaries, Chinook salmon feed extensively on relatively few taxa during estuarine residence. Almost all the prey taxa we identified from stomachs in this study are also consumed by juvenile Chinook salmon in other PNW estuaries (Healey 1982b; Simenstad et al. 1982; Higgs et al. 1995). Many of these taxa are associated with benthic and epibenthic environments of emergent marshes and other tidal wetland habitats (Healey 1982b; Simenstad et al. 1982; Simenstad et al. 2000), or derive much of their energy from primary production in tidal wetlands (Maier and Simenstad 2009), highlighting the vulnerability of juvenile salmon prey to loss or degradation of estuarine wetlands. Diking and development of wetlands could impact many of these invertebrate taxa by blocking access to habitats used on a regular basis (e.g., benthos and marsh plain), or by disrupting the transfer of energy from primary production in intertidal wetlands to invertebrate consumers in other parts of estuaries.

Similar to previous research (Healey 1982b; Macdonald et al. 1987), the diets of juvenile Chinook salmon varied seasonally, along the salinity gradient, and according to fish size. Importantly, wetland loss was also associated with the types of prey that salmon consumed. Ephemeropterans, trichopterans, and plecopterans were consumed more extensively in estuaries with the smallest proportional wetland losses. In freshwater ecosystems these taxa are sensitive to human land use modification (e.g. Harding et al. 1998), and our results suggest they are also sensitive to wetland loss and other human modifications to estuaries, at least in the low-salinity upper reaches of estuaries. Hymenopterans and collembolans were consumed more extensively in estuaries with greater wetland losses, which may indicate reduced availability of wetland associated prey and greater reliance on terrestrial prey that fall onto the water surface. It was unclear why consumption of more typical estuarine wetland prey, such as amphipods, appeared minimally impacted by wetland loss.

In addition to patterns of diet composition related to the covariates we considered, there were also some notable differences among the estuaries. In particular, Nisqually River estuary salmon fed extensively on mysids at times, but mysids were rarely consumed elsewhere. Mysids are distributed throughout North American Pacific coast estuaries (Carlton 2007), and are consumed by Chinook salmon in other estuaries (Higgs et al. 1995; Cordell et al. 2007), so it is unclear why only Nisqually salmon consumed them extensively, although it is likely related to the large size of some of the salmon sampled in the Nisqually River estuary. Mysids, annelids, and trichopterans were all consumed relatively infrequently, but comprised large proportions of salmon stomach prey mass when consumed. Furthermore, consumption of these taxa was responsible for many of the highest instantaneous rations of all the salmon we analyzed (A.T. David, unpublished data). The transition from feeding primarily on invertebrates to fishes has been highlighted as an important dietary shift that promotes rapid growth and accumulation of energy reserves for juvenile salmon during early marine residence (Daly et al. 2009; Duffy et al. 2010). Consumption of these large (mysids, annelids) and energy rich (trichopterans) invertebrates may also promote rapid growth in the estuary before salmon transition to piscivory in local epipelagic habitats or the coastal environment.

Conclusions

We have shown evidence that estuarine wetland loss can magnify the effect of conspecific density on juvenile Chinook salmon foraging performance, and depending on the position in the estuary can alter the consumption of some invertebrate taxa. Our results should be interpreted cautiously because of the limitations outlined above and by the low proportion of variance explained by our models; yet, by assembling data from multiple estuaries we were able to uncover trends and potential relationships that otherwise would have been difficult to identify. Because of the survival value of productive foraging and rapid growth for juvenile salmon in the estuarine environment, increases in the intensity of density-dependent foraging performance likely contribute to the relationship between the fraction of an estuary in natural condition and Chinook salmon survival documented by Magnusson and Hilborn (2003). However, it is surely not the only factor involved. For example, chemical contamination of estuaries, a result of development that often follows wetland loss, also reduces Chinook salmon survival (Meador 2014). Our study expands understanding of how juvenile salmon use estuaries and emphasizes the importance of restoring estuarine wetlands to the recovery of Pacific salmon populations. Given our documented interactive effect of tidal wetland loss and fish density, it will likely be difficult to recover many salmon populations, particularly ocean-type Chinook salmon populations, without first restoring large areas of estuarine wetlands and other habitats (e.g., riverine floodplains) that in their natural state provide productive foraging and growth opportunities for juvenile salmon before the salmon complete their migration to the ocean.

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Tables and Figures

Table 1.1. Details on estuaries from which we assembled data.

Estuary	Relevant references	Number of fish sampled	Years sampled	Percent of wetlands lost
Alsea	(Bieber 2005)	74	2004	59.1
Columbia	(Lott 2004)	285	2002-2003	68.4
Coquille	(Bieber 2005)	43	2003	94.3
Duwamish	(Cordell et al. 2011; Ruggerone et al. 2006)	988	2003; 2005	98.9
Nestucca	(Bieber 2005)	50	2003	91.3
Nisqually	Unpublished	503	2010-2012	41.3
Salmon	(Bieber 2005; Bottom et al. 2005b; Gray 2005; Gray et al. 2002)	570	1998-2002; 2004	13.1
Siuslaw	(Bieber 2005)	158	2003-2004	62.7
Yaquina	(Bieber 2005)	32	2003	70.6

Table 1.2. Results of permutation tests (N. perm = 500) evaluating the significance of each constraining covariate in a canonical correspondence analysis of juvenile Chinook salmon proportional diet composition. Results are from a type II sums of squares variance partitioning.

Term	df	*F*	*P*
% wetland loss	1	13.7	0.002
Day of year	1	10.1	0.002
Salinity	1	9.9	0.002
Fork length	1	12.5	0.002
Residuals	391		

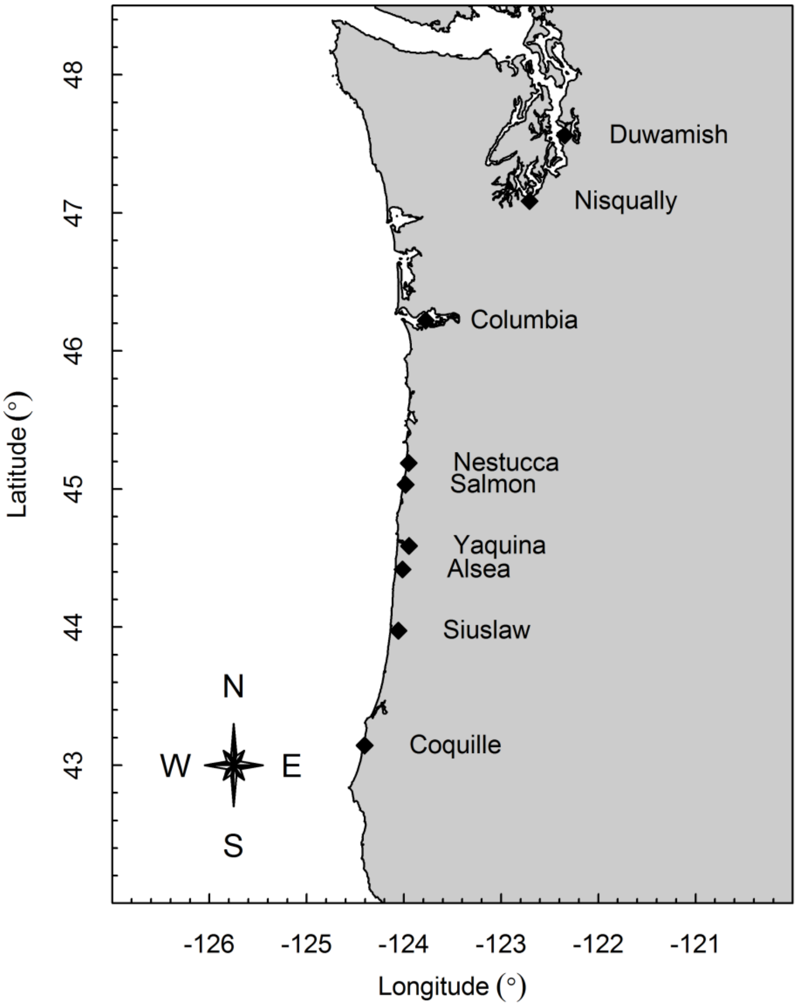

Figure 1.1. The U.S. Pacific Northwest with the estuaries included in our analysis.

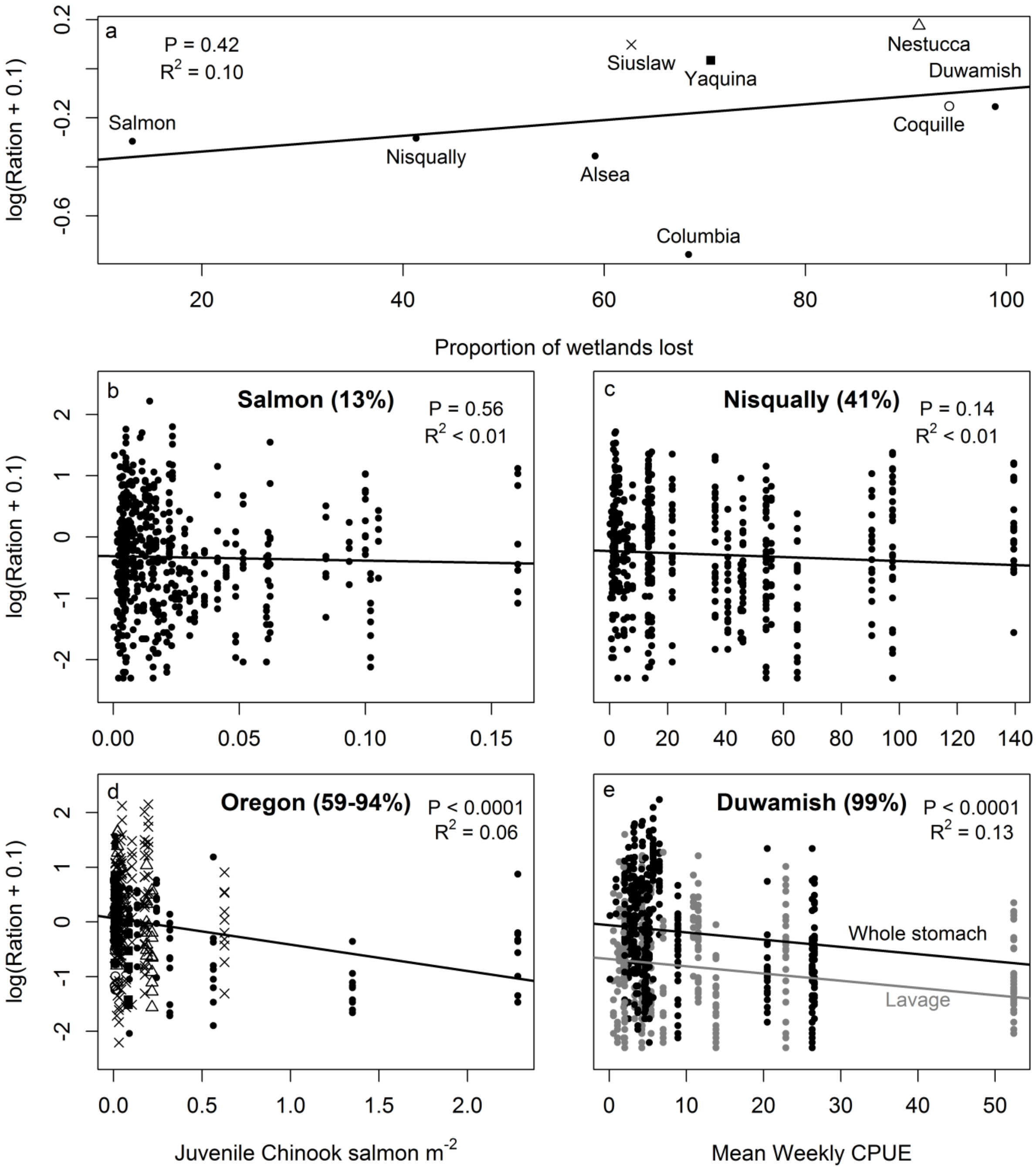

Figure 1.2. (a) The relationship between mean juvenile Chinook salmon instantaneous ration, *R*, and proportional wetland loss for nine Pacific Northwest estuaries. (b-e) The relationship between juvenile Chinook salmon *R* and conspecific density for four estuaries/sets of estuaries across a range of proportional wetland loss. The symbols representing each data point in (d)

correspond to the symbols representing the Alsea, Coquille, Nestucca, Siuslaw, and Yaquina river estuaries in (a).

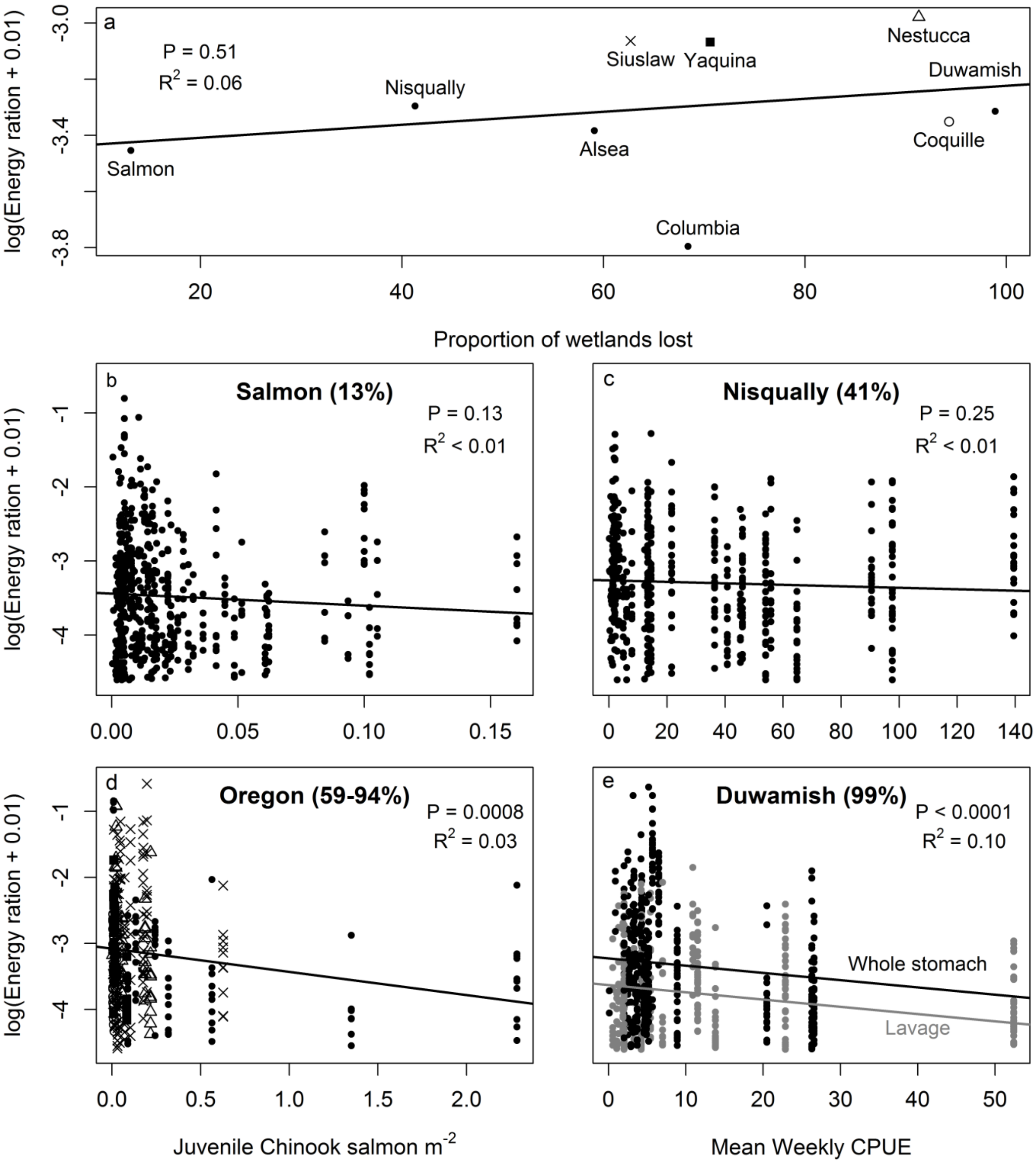

Figure 1.3. (a) The relationship between mean juvenile Chinook salmon diet energy ration, *E*, and proportional wetland loss for nine Pacific Northwest estuaries. (b-e) The relationship between juvenile Chinook salmon *E* and conspecific density for four estuaries/sets of estuaries

across a range of proportional wetland loss. The symbols representing each data point in (d) correspond to the symbols representing the Alsea, Coquille, Nestucca, Siuslaw, and Yaquina river estuaries in (a).

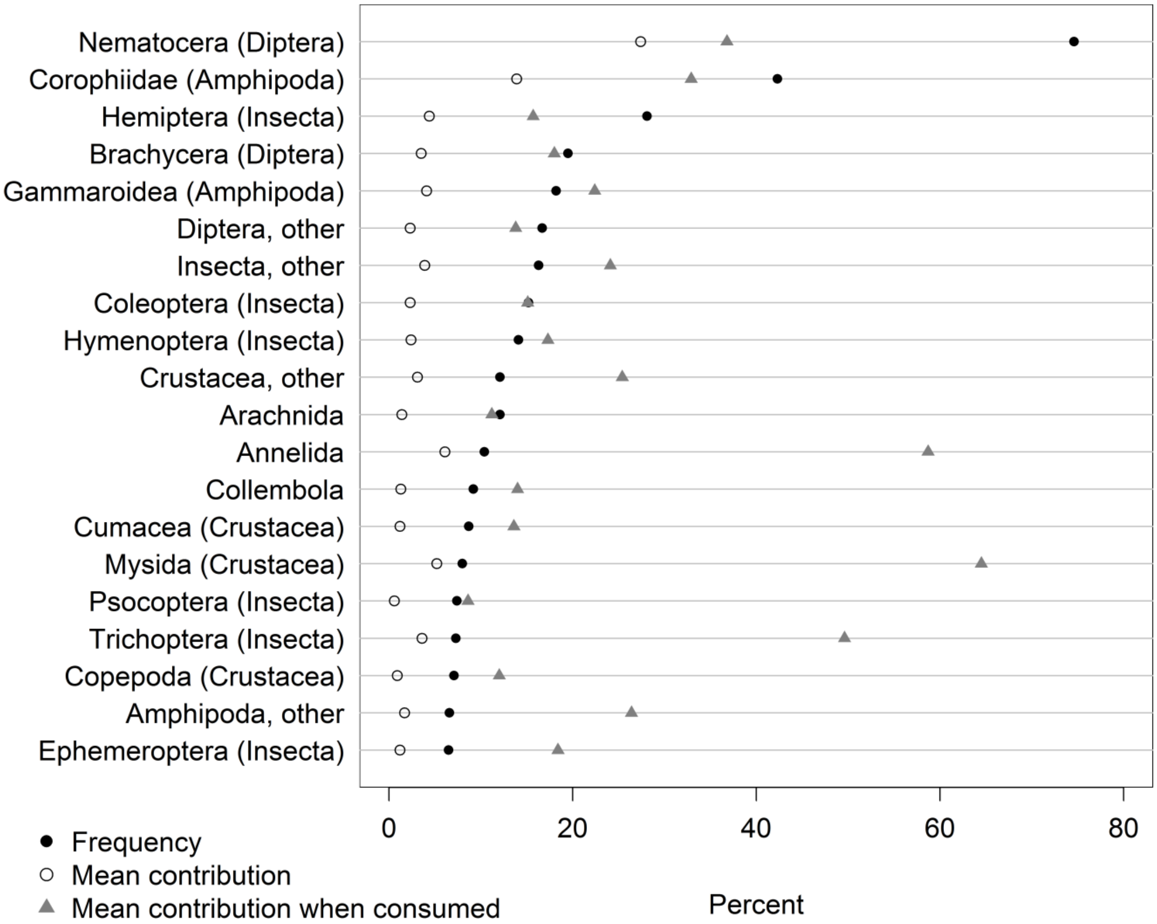

Figure 1.4. Frequency of consumption, mean proportional stomach contents contribution by mass, and mean proportional contribution when consumed for the 20 most frequently consumed prey taxa from 2,658 juvenile Chinook salmon in nine Pacific Northwest estuaries.

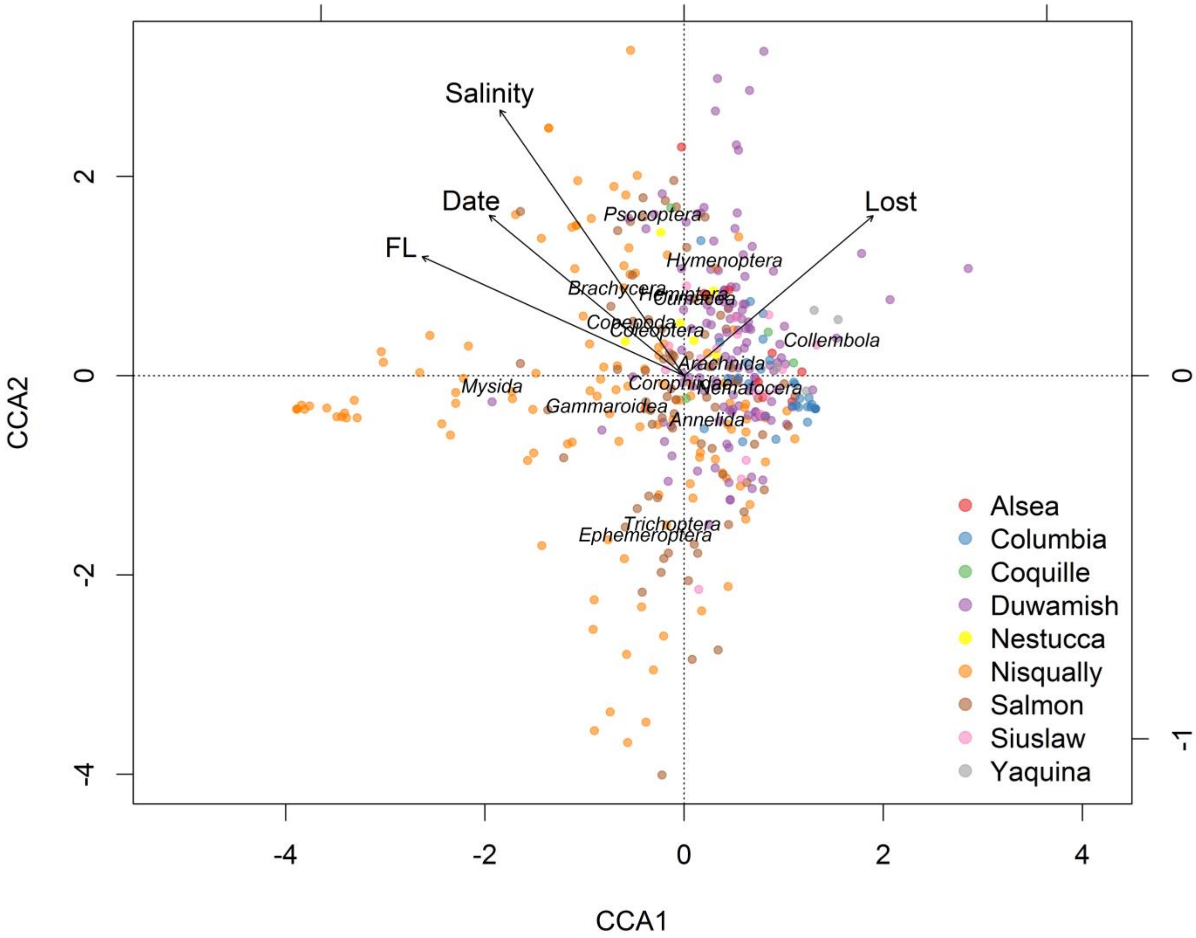

Figure 1.5. Canonical correspondence analysis tri-plot displaying the relationships among the mean proportional stomach contents composition of juvenile Chinook salmon from 396 sampling events in nine Pacific Northwest estuaries (observations; colored points), 16 prey taxa consumed by those salmon (response variables; italicized text), and explanatory covariates (arrows and text). Salinity = water column salinity; Date = date of capture; FL = mean salmon fork length; Lost = proportional wetland loss within an estuary. The observations are plotted in weighted-average (WA) score space. Observations and response variables are scaled symmetrically, which results in inter-observation and inter-response variable relationships both displayed reasonable well, but neither represented completely faithfully.

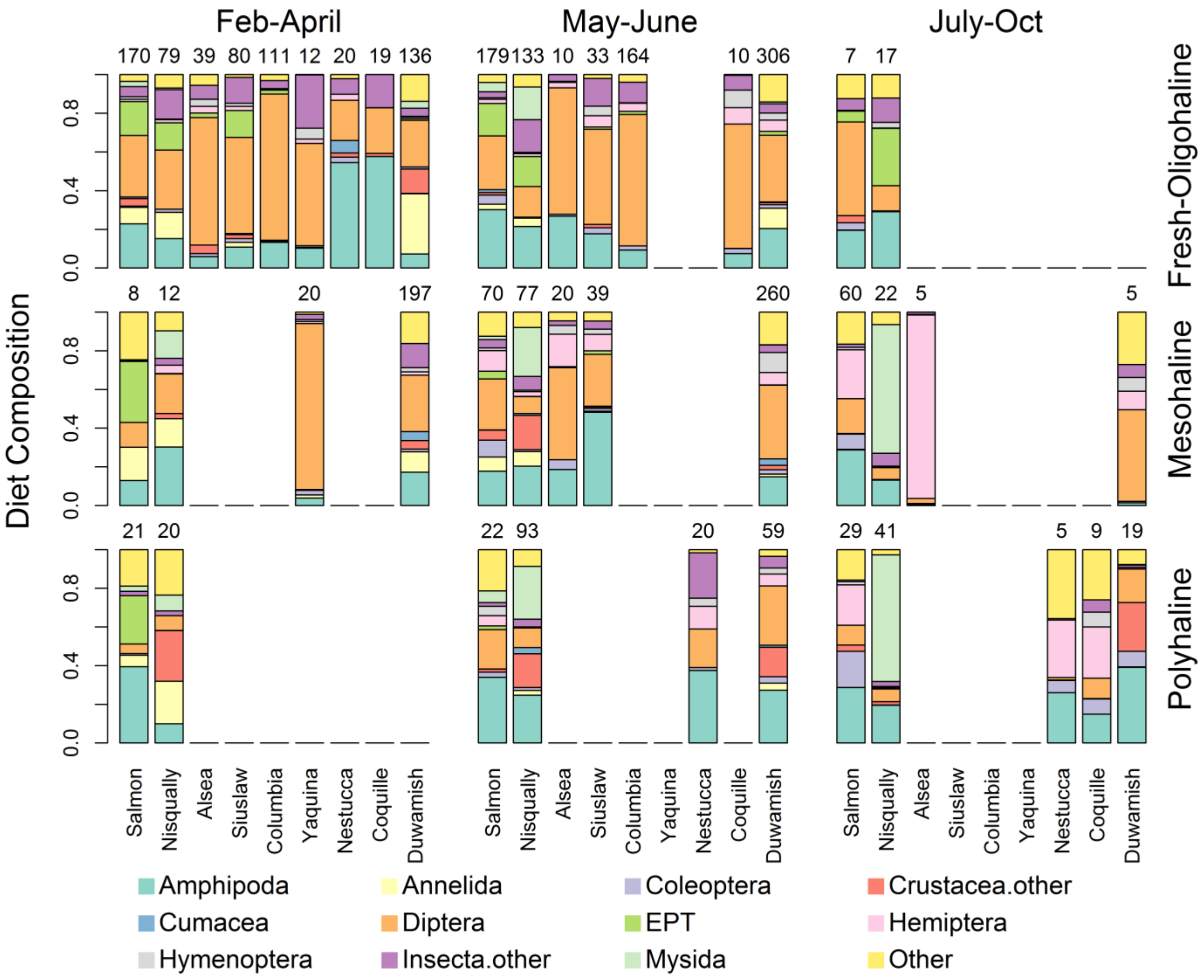

Figure 1.6. Mean proportional diet composition by prey mass of juvenile Chinook salmon for each of nine Pacific Northwest estuaries. Data are grouped by season and salinity. The number above each bar is the number of diet samples from that estuary within each salinity by season grouping. The estuaries are ordered from least to greatest proportional wetland loss. EPT is a combination of Ephemeroptera, Plecoptera, and Trichoptera.

Chapter 2: Foraging and growth potential of juvenile Chinook salmon following tidal restoration of a large river delta

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 salmon, but few have used integrative measures of salmon physiological performance, such as habitat-specific growth potential, to evaluate restoration. Our study took place in the Nisqually River delta, where recent dike removals restored tidal flow to 364 ha of marsh, the largest tidal marsh restoration in the U.S. Pacific Northwest. To compare Chinook salmon foraging performance and growth potential in two restored and two reference marshes over three years post-restoration, we sampled fish assemblages, water temperatures, and juvenile Chinook salmon diet composition and consumption rates, and used these data as inputs to a bioenergetics model. We found that juvenile Chinook salmon foraging performance and growth potential were similar between the restored and reference marshes. However, densities of Chinook salmon were generally lower in the restored marshes and growth potential was more variable in the restored marshes due to their more variable and warmer (2° C) water temperatures compared to the reference marshes. These results indicate that some but not all ecosystem attributes that are important to juvenile salmon rapidly recover following large-scale tidal marsh restoration.

Introduction

Estuarine wetlands provide diverse ecosystem services for humans (Barbier et al. 2010) and critical habitats for numerous fish and wildlife species during part or all of their life cycle (Deegan et al. 2000; Beck et al. 2001). Along the Pacific Rim, estuaries are important to the growth and survival of juvenile Pacific salmon (*Oncorhynchus* spp.) (Healey 1980; Simenstad et al. 1982; Magnusson and Hilborn 2003). Estuaries provide a gradient of salinities for the physiological transition from fresh water 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 resulting in productive foraging and rapid growth (Reimers 1973; Healey 1980; Simenstad et al. 1982). These estuarine functions are particularly important for ocean-type life history forms, including Chinook salmon *O. tshawytscha*, because they 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 of many estuaries has resulted in substantial habitat loss, particularly of tidal wetlands (Boule´ 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%, 90%, 46%, and 24% of their oligohaline transition, freshwater, estuarine mixing, and euryhaline unvegetated tidal wetlands, respectively (Simenstad et al. 2011). The loss of estuarine wetlands has contributed to the decline of Pacific salmon populations (Magnusson and Hilborn 2003), resulting in increased efforts to restore juvenile salmon habitat in estuaries. These restoration projects are often dike removals or breaches, returning natural tidal inundation regimes to historic estuary ecosystems with the expectation that restoring natural physical processes will also restore the ecological functions that support juvenile salmon (Simenstad and Cordell 2000; Gray et al. 2002).

Several studies have assessed the equivalence of natural and restored tidal wetlands in terms of the attributes important to juvenile salmon; yet, few studies have used integrative measures of salmon physiological performance, such as 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), compared the diets of salmon in restored and reference (natural) habitats (Gray et al. 2002; Roegner et al. 2010), and used enclosure experiments to compare growth rates (Miller and Simenstad 1997). Recently, a bioenergetics growth potential approach has been used to model 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). Analyses of growth rate potential, the expected growth rate of a consumer given data on the primary variables which regulate growth (Brandt et al. 1992; Tyler and Brandt 2001), provide a way to integrate multiple environmental variables which 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 ecosystem restoration is whether restored and reference habitats differentially benefit (e.g., promote survival or fitness) focal species; yet, estimating how habitats used in one life stage influence overall survival and fitness is difficult for species such as salmon that integrate across multiple ecosystems during their lifetime. But, because juvenile salmon survival is often strongly size selective (Beamish et al. 2004; Moss et al. 2005; Woodson et al. 2013) and the survival rates of salmon are positively correlated with both juvenile size and growth rate in estuarine and coastal marine environments (Cross et al. 2008; Duffy and Beauchamp 2011; Tomaro et al. 2012), habitat-specific growth rate potential can be used to approximate habitat influence on survival. Thus, growth rate potential is a useful measure of the relative value of different habitats or ecosystems to juvenile 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 juvenile salmon consumption rates in both restored and reference tidal marshes 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 juvenile salmon consumption rates as part of restoration assessments have been unsuccessful (Gray 2005; Cordell et al. 2011).

Our study took place within the Nisqually River delta, a drowned-river valley estuary located at the southern end of Puget Sound (Figure 2.1). The delta is managed by the Nisqually National Wildlife Refuge 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 2.1). Historically, the Nisqually River delta supported 1,500 ha of intertidal estuarine wetlands. More than 600 ha of wetlands, primarily emergent tidal marsh, were diked, separated from tidal flow, and converted to pasture land in the early 1900s (Tanner 1999). Reconnection of these lost estuarine wetlands was identified by the Tribe (NCRT 2001) and the Refuge (USFWS 2005) as a priority for recovering the Nisqually fall Chinook salmon population (fall spawning adults; juveniles primarily enter marine waters as sub-yearlings), the predominant Chinook salmon life history type in the Nisqually River and one of 27 stocks that comprise the threatened Puget Sound Chinook salmon evolutionarily significant unit (Ellings and Hodgson 2007). Four sections of dike were removed to restore tidal marsh in 1996, 2002, 2006, and 2009

(Figure 2.1). In total, these dike removals returned tidal flow to 364 ha for the first time in a century, the largest aggregate tidal marsh restoration in the Pacific Northwest of the Continental U.S. The Nisqually River delta also has relatively large tracts of tidal wetlands that are relatively unaltered, and upstream of tidal influence the Nisqually River flows through 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 within highly urbanized settings (Shreffler et al. 1990, 1992; Simenstad and Thom 1996; Cordell et al. 2011; Simenstad et al. 2005).

Our goal was to evaluate the degree with which restoring tidal flow within the Nisqually River delta also restores the ecological attributes of natural estuarine wetlands that support the foraging and growth of juvenile Chinook salmon. Specifically, we compared the density, foraging performance (instantaneous ration, diet energy density), diet composition, and simulated growth potential of juvenile Chinook salmon in two restored and two reference marshes over three years post-restoration. We hypothesized that (1) measures of juvenile Chinook salmon density, foraging performance, and growth potential would initially be lower in restored habitats than reference habitats, but would rapidly approach equivalence as time since restoration increased and (2) diet similarity among juvenile Chinook salmon foraging in reference and restored habitats would increase as time since restoration increased. Additionally, because initial observations indicated temperature differences between reference and restored tidal wetlands, we also explicitly evaluated the influence of water temperature on juvenile Chinook salmon growth potential.

Methods

Study sites

We sampled relict tidal channel systems in the marshes reconnected in 2006 and 2009, hereafter referred to as 2006 Restored and 2009 Restored (Figure 2.1). We also sampled channel systems in two reference marshes that are relatively undisturbed. One reference marsh was adjacent to the mouth of the Nisqually River, hereafter referred to as Nisqually Reference. The second reference marsh was between the Nisqually River and Red salmon Slough, hereafter referred to as RSS Reference (Figure 2.1). These two marshes are typical of Pacific Northwest estuarine marshes (Simenstad et al. 2000) and of the extant marshes within the Nisqually River delta and are thus appropriate reference ecosystems. Prior to dike removal, 2006 Restored was dominated by pasture grasses, while 2009 Restored consisted of terrestrial and freshwater habitats dominated by invasive plants. Following each dike removal, terrestrial and freshwater plants were killed by saltwater. Both restored marshes had subsided relative to the surrounding salt marshes 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, 2006 Restored plant community consisted of native salt marsh plants *Jaumea carnosa*, *Distichlis spicata*, *Sarcocornia perennis,* and *Carex lyngbyei,* with patches of bare mud present, while 2009 Restored was dominated by bare mud at lower elevations with patches of *S. perennis* and *Spergularia* spp. at higher elevations. The plant community at Nisqually Reference primarily was composed of native salt marsh species *C. lyngbyei*, *D. spicata*, *Agrostis gigantean*, and *Triglochin maritima*, while RSS Reference supported *T. maritima*, *D. spicata*, and *J. carnosa*.

Fish sampling

We sampled each restored and reference marsh tidal channel to assess fish assemblage composition and juvenile Chinook salmon densities and diets. At each channel, we used a fyke trap net (3.2 mm mesh) (Levy and Northcote 1982; Gray et al. 2002) to capture fish during a neap tide series once per month from April - July 2010, 2011, and 2012. Nets were set at high tide, trapping fish exiting the channel during the ebb tide. We periodically removed fish from the cod end of the net until the channel 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 each of juvenile hatchery (identified by adipose fin clip or by using a coded wire tag reader) and natural-origin Chinook salmon 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 kept for diet analysis were euthanized using tricaine methanosulfate and placed on ice. After returning from the field, euthanized fish were weighed to the nearest 0.1 g and then stored in ethanol.

We calculated juvenile Chinook salmon densities for each sampling event using the catches, trap efficiency estimates, and the tidal channel area above each fyke net. To quantify trap efficiency, we conducted a mark-recapture study at each trap site. We used a beach seine to capture Chinook salmon outside of the channel being evaluated and then marked the fish with a fin clip. After setting the fyke net, we released the marked fish at least 50 m upstream of the net. Trap efficiency was assessed as the proportion of recaptures during the trapping effort.

We calculated densities for each sampling event by dividing the raw catch by the trap efficiency and dividing that number by the channel area. To evaluate whether densities differed among the four channels, we used repeated-measures ANOVA with rank-transformed densities.

Temperature

To quantify temperature in each of the four tidal channels, we installed Solinst LTC (Solinst, Georgetown, Ontario, Canada) loggers that measured water level, temperature, and conductivity at 15 min intervals. Each logger was installed at a fixed location ~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 readings when the loggers were exposed to the air during low tides.

Chinook salmon diet composition, foraging performance, and consumption rates

We acquired diet composition and other foraging metrics by processing each juvenile Chinook salmon. Each stomach was removed and the total contents were weighed (blotted wet mass to the nearest 0.0001 g). Prey organisms were then sorted to the lowest feasible taxonomic resolution using a dissecting microscope. Finally, each unique prey taxon was enumerated and weighed separately.

To determine whether the diet composition of Chinook salmon foraging in the restored marshes had become more similar to the diet composition of Chinook salmon foraging in the reference marshes through time since dike removal, we calculated the multivariate similarity of restored and reference Chinook salmon diets across the three years of the study and regressed our metric of similarity against time. As many taxa were infrequently consumed, we excluded from multivariate analysis any taxon that was found in less than 5% of stomachs. Prey taxa masses for each fish were converted to proportions of their total stomach contents mass and then were used to calculate a pairwise resemblance matrix of the fish using the Bray-Curtis association coefficient (Bray and Curtis 1957). We performed permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) using the resemblance matrix for all pair-wise combinations of restored and reference tidal channels within each month. A PERMANOVA test was only performed when at least four individual Chinook salmon diets had been sampled from both channels. We fit a linear regression (weighted by the combined sample size of diets from each comparison) to the PERMANOVA pseudo F-ratios as a function of sampling year to determine if diet similarity among Chinook salmon in restored and reference marshes increased through time. As with univariate ANOVA *F*-ratios, PERMANOVA pseudo *F*-ratios represent the ratio of between to within group variation and thus for this analysis are a measure of diet composition similarity between marshes relative to within marsh variation in diet composition.

As a measure of stomach fullness, we calculated the instantaneous ration, I, for each Chinook salmon as the stomach contents mass as a percent of the total body mass without the contents. We also calculated the diet energy density, ED, for each Chinook salmon as the sum of individual prey taxon masses multiplied by the energy density (kJ/g wet mass) of each prey taxon, divided by sum of prey taxon masses. Energy densities of prey taxa were acquired from the literature (Table A.2.1).

We used linear models to assess the influence of marsh identity, month, year, and juvenile Chinook salmon density on the instantaneous ration [$\log_e(x + 0.1)$ transformed] and diet energy density of juvenile Chinook salmon. For both instantaneous ration and diet energy density 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 instantaneous ration and diet energy density. We evaluated the relative support for each model using Akaike's Information Criterion adjusted for small samples size (AIC_C) and AIC_C weights.

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

$$D = 24 \times R \times \bar{I} - (\bar{I}_0 - \bar{I}_t), \tag{1}$$

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 R of juvenile Chinook salmon for each sampling event using a model we developed and derived $\bar{I}$ using the Chinook salmon stomachs from each sampling event in conjunction with a diel feeding study. We also calculated $\bar{I}_0$ and $\bar{I}_\mathrm{t}$ from the diel feeding study; these numbers are used as a correction factor for when the instantaneous rations of fish at the beginning and end of the sampling period differ (Eggers 1979; Hayward 1991).

We developed the gastric evacuation model by compiling results from studies of *Oncorhynchus* spp. 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 variables (Bromley 1994). Of these variables, temperature has the strongest influence on R, which rises exponentially with temperature (Elliott and Persson 1978). Consumer size is generally negatively correlated with R, although the relationship is less definitive than for temperature (Bromley 1994). Other variables, such as prey size, have also successfully explained variation in R (He and Wurtsbaugh 1993); however, we focused on temperature and consumer mass because these were the most commonly reported variables in the literature. We excluded studies which force-fed fish or starved fish for long periods of time before beginning experimental trials. We also did not use data from fish heavier than 50 g as our focus was juvenile salmon that would normally be found in nearshore estuarine and marine environments. The compiled rates were fit to the temperature and mass data using a linear model of the form:

$$\log_e(R) = \log_e(\alpha) + \beta_1 \times \text{temperature} + \beta_2 \times \text{mass}, \tag{2}$$

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 Chinook salmon mass and daily mean water temperature.

To quantify daily mean instantaneous ration, $\bar{I}$, we conducted a diel feeding study (Doble and Eggers 1978) on May 29-30, 2012. We sampled 5 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 reference habitats. The diel feeding study provided a single estimate of Chinook salmon $\bar{I}$ within the Nisqually River Delta. We then assumed that I of a fish sampled at a certain point during the day is related to $\bar{I}$ across the whole day and used the diel study results to calculate an adjusted $\bar{I}$ for each of our monthly Sampling events. During the diel feeding study, we used fyke traps to capture Chinook salmon during the daytime ebb tide, the same time and tide interval as our monthly fyke trap sampling. Using this comparable sampling interval, we calculated $\bar{I}$ for each fyke sampling event as:

$$\bar{I} = (\bar{I}_f / \bar{I}_{df}) \times \bar{I}_d, \tag{3}$$

where $\bar{I}_f$ is the mean instantaneous ration of Chinook salmon from a monthly fyke trap sampling event, $\bar{I}_{df}$ is the mean instantaneous ration of Chinook salmon sampled from the comparable time frame during the diel feeding study, and $\bar{I}_d$ is the mean instantaneous ration from the whole diel feeding study. For the hours of darkness when we only sampled Chinook salmon in reference habitats, we used the reference fish I values in the calculation of $\bar{I}_d$ for fish in the restored habitats. We substituted the results of equation (3) and the predicted sampling event-specific gastric evacuation rates into equation (1) to derive D for each fyke trap sampling event.

Chinook salmon energy density

We collected 8 natural-origin and 8 hatchery-origin fish for analysis in June 2012 to quantify the energy density of juvenile Chinook salmon from the Nisqually River delta. The fish were frozen, and after removing their stomach contents, we 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 their energy density (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 potential of juvenile Chinook salmon in restored and reference tidal marshes. Bioenergetics models are mass balance equations where 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; Madon et al. 2001; Chipps and Wahl 2008). Fish Bioenergetics uses species-specific parameters derived from laboratory experiments for each of the physiological processes (Hansen et al. 1997). The model runs on a daily time step and can be solved to simulate either consumption or growth. We used data for consumption, diet energy density, consumer energy density, consumer mass, and water temperature as model inputs to solve for growth. The temperature logger in the Nisqually Reference channel failed from April-June 2010 and 2012; we substituted RSS Reference temperatures for the Nisqually Reference Chinook salmon growth simulations during these periods. 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 using the consumption equation within the model. We used the physiological parameters for Chinook salmon from Stewart and Ibarra (1991) and 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 we ran the model using the following inputs: the mean consumption rate, mean diet energy density, and mean mass of the juvenile Chinook salmon captured for diet analysis, along with the overall mean Nisqually juvenile Chinook salmon energy density, and each daily mean temperature recorded in that channel during the month sampling took place. 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 channel system. Each model simulation was for a single time step (one day).

Results

Fish presence, abundance, and density

Fish assemblages varied seasonally and among the four marshes, but were generally consistent among years (Table A.2.2). 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. Chinook salmon densities were significantly higher in the reference channels ($F = 8.4$, df = 3, 33, $P < 0.001$), especially during the peak outmigration months of May and June. However, differences in densities between the restored and reference channels decreased through time (2010 mean difference = 0.218 fish/m^2; 2011 = 0.144 fish/m^2; 2012 = 0.026 fish/m^2) (Figure 2.2). 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. clarki*) across the four channels (Table A.2.2). Sculpins (primarily staghorn sculpin

Leptocottus armatus) were ubiquitous and abundant, and shiner perch *Cymatogaster aggregata* were abundant during June and July, together accounting for 85% of the total catch from all sampling events (Table A.2.2).

Water temperature

Daily mean water temperatures were significantly higher in the restored tidal channels than the reference channels (paired *t*-test; $t = 35.9$, df = 365, $P < 0.001$) during the primary juvenile Chinook salmon outmigration season (April-July) across all three years. Temperatures in the restored channels were 2.0 ± 1.1° C (mean ± SD) warmer than in the reference channels and temperature differences were particularly apparent in June and July (Figure 2.3). Additionally, the range of temperatures within individual months was often greater in the restored channels. The mean within-month standard deviation and range of temperatures for the reference channels were 0.8° C and 3.0° C, but were 1.4° C and 5.4° C for the restored channels.

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, Ephydridae), and terrestrial insects (Hemiptera) (Figure 2.4). Chinook salmon diet composition varied among marshes, months, and years; however, dissimilarity in Chinook salmon diet composition between restored and reference marshes declined with increasing years since restoration ($F = 6.5$, df = 1 , 25, $P = 0.017$, $R^2 = 0.21$) (Figure 2.5). Pairwise PERMANOVA comparisons between the 2006 Restored and the reference marshes had pseudo *F*-ratios that were smaller on average (5.9) than the pairwise comparisons between the 2009 Restored and the reference marshes (7.4) as we predicted because the 2006 Restored had more time to converge toward reference conditions.

The linear model of Chinook salmon instantaneous ration, *I*, with the most support included the explanatory variables Chinook salmon density and marsh identity (Table 2.1, A.2.3). 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 ($R^2 = 0.07$; Table 2.1; Figure A.2.1), indicating that the variables we considered did not strongly influence Chinook salmon *I*.

The linear model of Chinook salmon diet energy density, *ED*, with the most support was the full model with Chinook salmon density, marsh, month, and year as explanatory variables (Table 2.2, A.2.4). There was a negative relationship between *ED* and Chinook salmon density, and *ED* was higher for Chinook salmon foraging in the restored marshes and during June and July (Figure A.2.2; Table A.2.4). The best diet *ED* 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 (60 evacuation rate estimates in total; Table A.2.5) that met our screening criteria. Four of the studies were of Chinook salmon, two of Sockeye salmon *O. nerka*, two of Rainbow Trout *O. mykiss*, and two of Coho salmon. Water temperatures in these studies ranged from 2 to 23^{o} C (mean = 10.7^{o} C), fish mass ranged from 0.9 to 43.3 g (mean = 14.2 g), and gastric evacuation rates ranged from 0.006 to 0.446/h (mean = 0.155/h). A linear model of $\log_e(R)$ as a function of water temperature and fish mass was significant and explained over half the variation in the data ($F = 36.6$, df = 2, 57, $P < 0.001$, $R^2 = 0.56$). We used the back-transformed (exp), bias corrected model:

$$R = 0.0612 \times \exp(0.1139 \times \text{temperature} - 0.0422 \times \text{mass} + 0.1790), \qquad (4)$$

to predict Chinook salmon *R* for each sampling event.

Diel feeding study

During the May 29-30, 2012 diel feeding study, juvenile Chinook salmon daily mean instantaneous ration, $\bar{I}_d$, was 1.01% in reference habitats and 1.53% in restored habitats (Figure A.2.3). Chinook salmon $\bar{I}$ varied throughout the day, declining after dark but then increasing again early in the morning (0330 hours). Interestingly, Chinook salmon $\bar{I}$ in the reference habitats was lowest the first morning of the study but peaked at the same time (0930 hours) the subsequent morning.

Chinook salmon energy density

The energy density of natural-origin Chinook salmon sampled in June 2012 was 4171 ± 186.3 J/g (mean ± SD) while the energy density of hatchery-origin Chinook salmon was 3999 ± 101.6 J/g. We used the mean energy density of the combined natural- and hatchery-origin fish (4085 J/g) as the consumer energy density for all growth simulations.

Bioenergetics growth simulations

Given our estimated consumption rates and other inputs, simulated growth potential of juvenile Chinook salmon appeared marginally higher in the reference tidal marshes (range: 0.006 – 0.053 g g^{-1} d^{-1}) than the restored marshes (range: 0.006 – 0.046 g g^{-1} d^{-1}) in 2010; however, there was no clear difference in growth potential between restored and reference marshes in either 2011 or 2012 (Figure 2.6). Simulated growth potential varied seasonally and among the four marshes within individual months but was not consistently higher in either the reference or restored marshes. Negative growth potential was only simulated for one event in 2012. A low consumption rate was the primary cause of negative growth (A.T. David, unpublished data). While growth potential was not consistently higher in one habitat, the range of growth potential within individual months was often greater in the restored marshes, particularly in June and July (Figure 2.6), due to the greater range of temperatures in the restored marshes. The mean within-month standard deviation and range of growth potential for the reference channels were 0.0013 and 0.0046 g g^{-1} d^{-1} but were 0.0030 and 0.0121 g g^{-1} d^{-1} for the restored channels.

Discussion

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

We caught juvenile Chinook salmon, other Pacific salmon species, and native, non-salmonid fishes in both restored marshes, including during the first salmon outmigration season after the 2009 dike removal. Juvenile salmon also accessed the 2006 and 2002 restored marshes during the first salmon outmigration season after tidal flow was restored (Ellings and Hodgson 2007; Nisqually Indian Tribe, unpublished data). We also observed a negative relationship between time since restoration and the degree of dissimilarity between restored and reference marsh Chinook salmon diets, suggesting that the invertebrate prey communities of the restored marshes increased in similarity with natural tidal marsh ecosystems. Chinook salmon densities were significantly higher in the reference marshes, but by 2012 differences in densities had decreased. Yet, it is worth noting that the smaller differences were more a result of reduced densities in the reference marshes than increased densities in the restored marshes. Lower densities may indicate that the restored marshes do not yet have the same capacity to support juvenile salmon as the reference marshes. Alternatively, the differences in densities may be explained in part by differences in landscape position. Both 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 more direct access (Simenstad and Cordell 2000). In contrast to differences in fish density, our measures of foraging performance, instantaneous ration and diet energy density, varied little among the marshes, and when differences were apparent, they indicated that Chinook salmon foraging performance was better in the restored marshes.

Our findings corroborate other research showing that juvenile 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, fishes 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 salmon or other fishes (although see Miller and Simenstad 1997; Teo and Able 2003).

While more difficult to obtain than abundances or diet composition, measures of realized function, such as habitat-specific growth potential of focal species, provide a more robust evaluation of restoration performance (Simenstad and Cordell 2000). We built upon the comparative growth potential simulations of Gray (2005) and Cordell et al. (2011) by quantifying juvenile Chinook salmon consumption rates using a combination of instantaneous measures of stomach fullness, a diel feeding study, and a gastric evacuation rate model. An 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 point during the day then it consumes more during the whole day. However, the lack of a clear diel pattern in instantaneous ration coupled with large differences in instantaneous rations for the single time period we sampled on consecutive days suggests this assumption may not be completely valid. Our small sample size for each sampling period (n = 5 per habitat) may have been insufficient to accurately characterize the feeding rates of juvenile Chinook salmon as foraging success in fishes is often strongly right skewed (Armstrong and Schindler 2011). While our method of consumption estimation is an improvement over simple instantaneous measures of stomach fullness, uncertainty was likely greatest for consumption rates relative to other inputs to the growth simulations.

Given our estimated consumption rates and other empirical inputs, the bioenergetics simulations indicated that the restored marshes provided opportunities for juvenile Chinook salmon growth that were similar to growth opportunities in the reference marshes, particularly after 2010. Simulated growth rate potential was highly variable among months and among marshes within individual months, but there was no consistent difference in growth potential between reference and restored marshes. Together, similarity in mean foraging performance and growth rate potential between the habitats suggest that the restored marshes have nearly the same capacity to support juvenile salmon foraging and growth as reference marshes within the Nisqually River delta. Yet, if we assume that salmon distribute themselves throughout the delta in a way that maximizes their consumption and growth rates, the lower densities of salmon in the restored tidal channels would suggest that the restored marshes do not yet have the same capacity to support juvenile salmon production as do the reference marshes. Unfortunately, as noted above, our small number of sampling locations makes it difficult to determine if the lower salmon densities in the restored marshes are solely a result of their restoration status.

Although simulated growth potential was not consistently higher in either restored or reference marshes, more variable and warmer water temperatures in the restored tidal 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 Chinook salmon growth potential was comparable among three restored 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 in the reference marsh.

We attribute the greater range of temperatures and warmer temperatures in the restored tidal channels to greater sensitivity of the water in those channels to air temperature and solar irradiance, which we suspect is a consequence of physical differences between the restored and reference marshes. Currently, restored tidal channel width-depth ratios are greater than the reference channels (mean 2011 W-D ratios: Nisqually Reference = 1.7; RSS Reference = 4.5; 2006 Restored = 7.5; 2009 Restored = 38.2; 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 marshes were comprised of plant communities with nearly 100% cover while <10% of the 2009 Restored marsh was vegetated by 2012, although patches of higher elevation along the old dike footprint were ~95% vegetated. Due to subsidence, the reconnected wetlands are lower in elevation than some natural marshes within the delta. The most subsided restored marsh, 2009 Restored, is approximately 0.8 m lower in mean elevation than RSS Reference (I. Woo and J.Y. Takekawa, unpublished data). At high tide, a shallow layer of water often covers much of the mud surface of 2009 Restored. 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 marshes only occurs during the highest spring 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 as its vegetation coverage and marsh elevation are closer to the reference marshes than the 2009 Restored marsh (I. Woo and J.Y. Takekawa, unpublished data).

Elevated water temperatures during summer in the restored marshes may suppress Chinook salmon growth potential to levels below that of the reference marshes or prevent them from accessing the restored marsh channels. How warm these channels can become before Chinook salmon growth is depressed or access precluded depends partly on food availability. Juvenile salmon can tolerate the higher water temperatures often found in shallow-water wetlands if they are able to increase their consumption rates to keep pace with the higher metabolic costs of warmer temperatures (Jeffres et al. 2008; Beauchamp 2009). However, increasing consumption will ameliorate 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, although see Gray (2005). We suggest that future tidal marsh restoration projects closely monitor water temperatures, particularly when temperature-sensitive species are an impetus for restoration. It is unclear how long it will take for the temperature regimes in the restored marshes to take on the characteristics of reference marshes. Unlike other metrics we sampled, there was no indication that the temperature regimes in the restored marshes were on a trajectory towards the reference regimes during our study. Convergence of the temperature regimes will likely be a function of sediment accretion, changes in channel morphology, and marsh plant growth. Restored tidal marsh and channel morphology 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 restored marshes are actively being monitored. Two dams in the upper Nisqually watershed trap sediment and dampen peak flows, potentially reducing the amount of sediment available to the delta. Given the uncertain and potentially substantial length of time necessary for the restored marshes to take on the full physical characteristics of natural tidal marshes, our findings raise concerns over the duration and consistency of the spring and the summer outmigration season that the restored marshes will provide growth opportunities for juvenile salmon that are equivalent to growth opportunities in natural tidal marshes.

Landscape attributes such as the large size of the restored marshes and connectivity with natural wetlands may 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 (Parker 1997; 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 one, suggesting that removing dikes around one large marsh island would increase total channel length and surface area more than removing dikes around multiple smaller marsh islands of equivalent total area (Hood 2007). In addition to differences that are a function of scale alone, the size of a restoration project is likely most important for projects within modified landscapes. Anthropogenic disturbances or forcing may have 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 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 of juvenile salmon habitats in the same Duwamish restoration sites with urbanized, degraded habitats, Cordell et al. (2011) found that growth potential for juvenile salmon in the restored habitats was no better than urbanized habitats. Those authors speculated that because the restoration projects were small in size, the restored habitat patches produced insufficient invertebrate prey for them to detect 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 its relatively large size, ecological connectivity, and semi-natural setting, the Nisqually River delta restoration may not be constrained to an ecological state distinct from that of natural tidal marsh. While the bioenergetics simulations identified potential temperature-driven constraints on the growth value of recently restored marshes to juvenile salmon, and lower salmon densities suggested that the restored marshes do not yet have the same capacity to support salmon production as do natural marsh ecosystems, our results indicated that even in the early stages of recovery (1-6 years post dike-removal), the restored marshes are providing the core suite of ecological functions critical to outmigrating, ocean-type salmon. Additionally, while we focused on the relative value of restored and reference marshes, removing dikes increased the amount of intertidal estuarine wetlands by 42% within the delta, and likely increased the delta’s overall capacity to support the broader community of estuarine fishes, birds, and invertebrates.

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Tables and Figures

Table 2.1. Summary of small-sample size Akaike Information Criterion (AIC_C) ranking of juvenile Chinook salmon instantaneous ration linear models.

Models	K	$\Delta\text{AIC}_\text{C}$	AIC_C weight	R^2
$\log_e(I + 0.1)$ ~ Density + Marsh	6	0.0	0.759	0.06
$\log_e(I + 0.1)$ ~ Marsh	5	2.7	0.2	0.05
$\log_e(I + 0.1)$ ~ Density + Marsh + Month + Year	11	6.4	0.03	0.07
$\log_e(I + 0.1)$ ~ Marsh + Month + Year	10	9.1	0.008	0.06
$\log_e(I + 0.1)$ ~ Year	4	12.3	0.002	0.01
$\log_e(I + 0.1)$ ~ Density + Year	5	14.3	<0.001	0.01
$\log_e(I + 0.1)$ ~ Month	5	15.1	<0.001	0.01
$\log_e(I + 0.1)$ ~ Density + Month	6	16.8	<0.001	0.01

Table 2.2. Summary of small-sample size Akaike Information Criterion (AIC_C) ranking of juvenile Chinook salmon diet energy density linear models.

Models	K	$\Delta\text{AIC}_\text{C}$	AIC_C weight	R^2
ED ~ Density + Marsh + Month + Year	11	0.0	0.987	0.31
ED ~ Density + Month	6	8.9	0.012	0.26
ED ~ Marsh + Month + year	10	12.6	0.002	0.27
ED ~ Month	5	53.6	<0.001	0.13
ED ~ Density + Marsh	6	59.8	<0.001	0.12
ED ~ Density + Year	5	62.7	<0.001	0.1
ED ~ Marsh	5	67.2	<0.001	0.08
ED ~ Year	4	83.8	<0.001	0.02

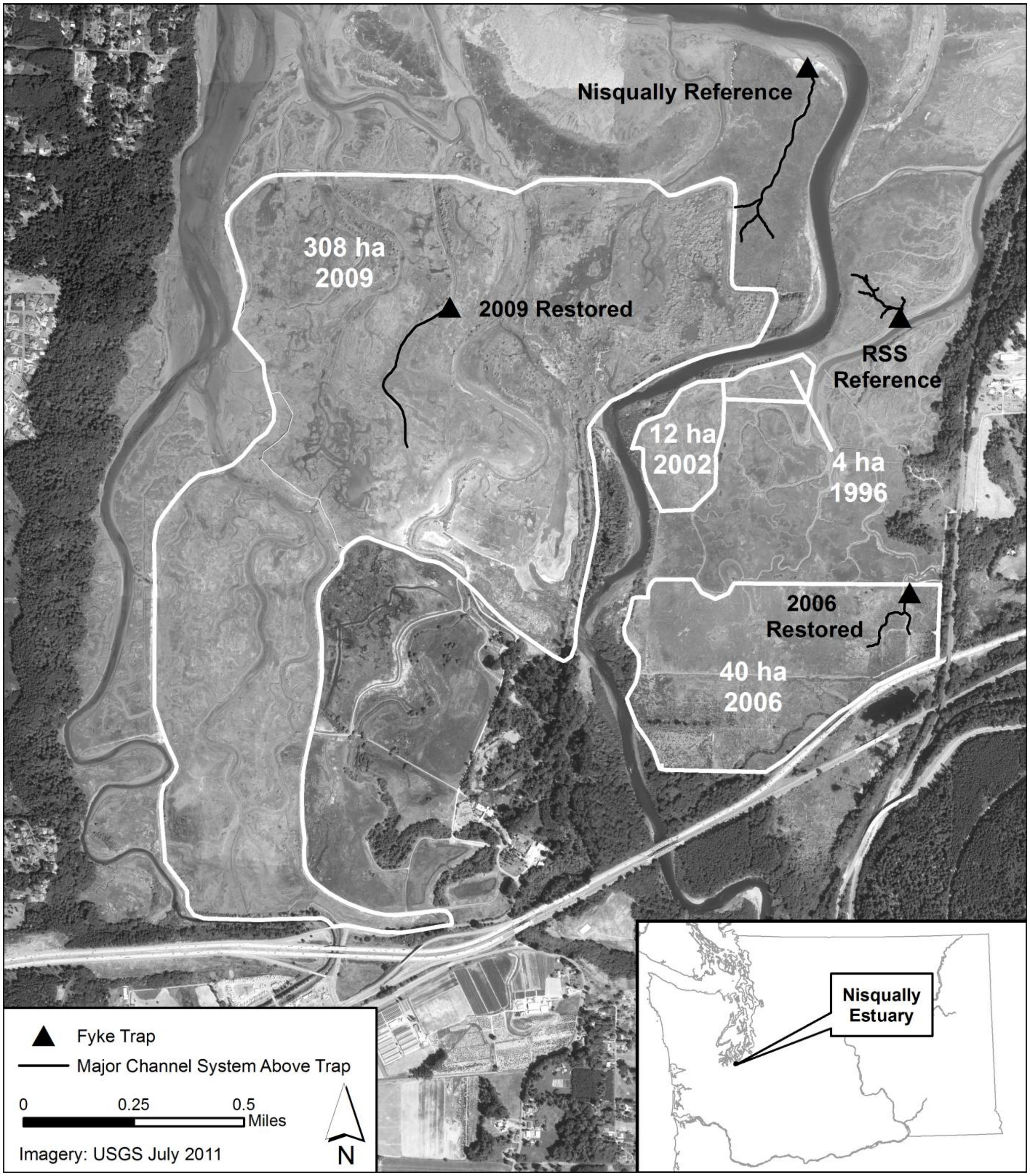

Figure 2.1. The Nisqually River delta with dike removals and fyke trap sampling locations identified. The white lines indicate where dikes were removed and the white lettering denotes the amount of area reconnected by each dike removal and the year each dike was removed.

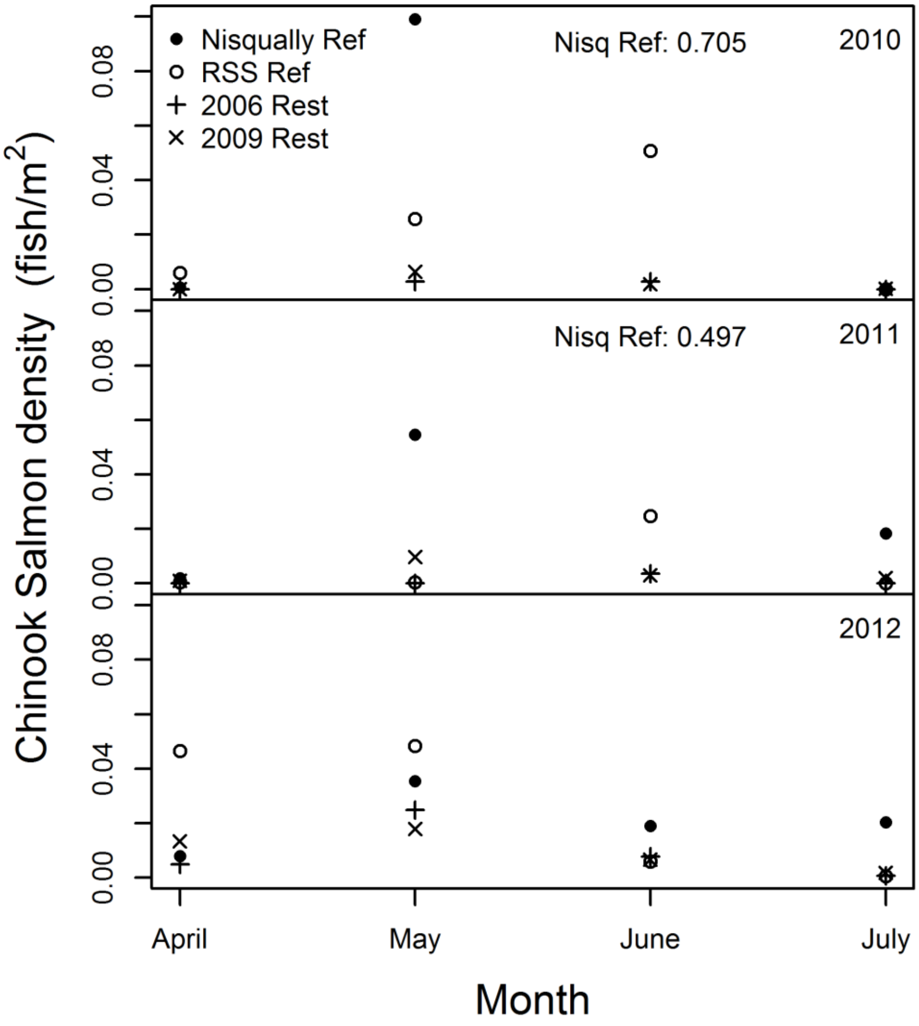

Figure 2.2. Juvenile Chinook salmon densities for each fyke trap sampling event in 2010, 2011, and 2012. Densities in the Nisqually Reference channel were substantially higher in June 2010 and 2011 than all other sampling events and thus are given but not plotted.

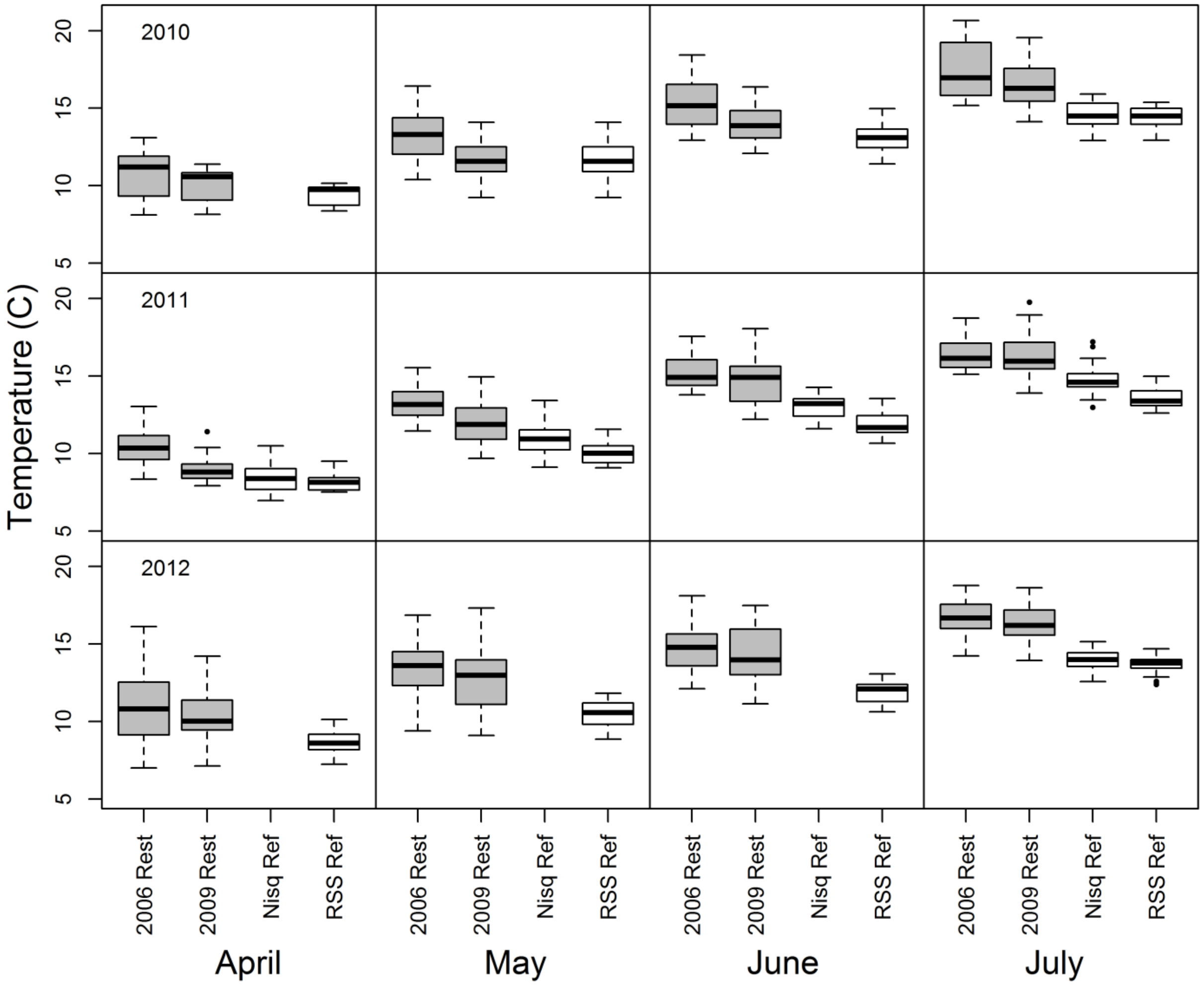

Figure 2.3. Daily mean temperatures for the four marsh channels sampled during April – July 2010, 2011, and 2012. The restored marsh channels are colored gray while the reference marsh channels are colored white. The temperature logger in the Nisqually Reference channel failed from April-June 2010 and 2012.

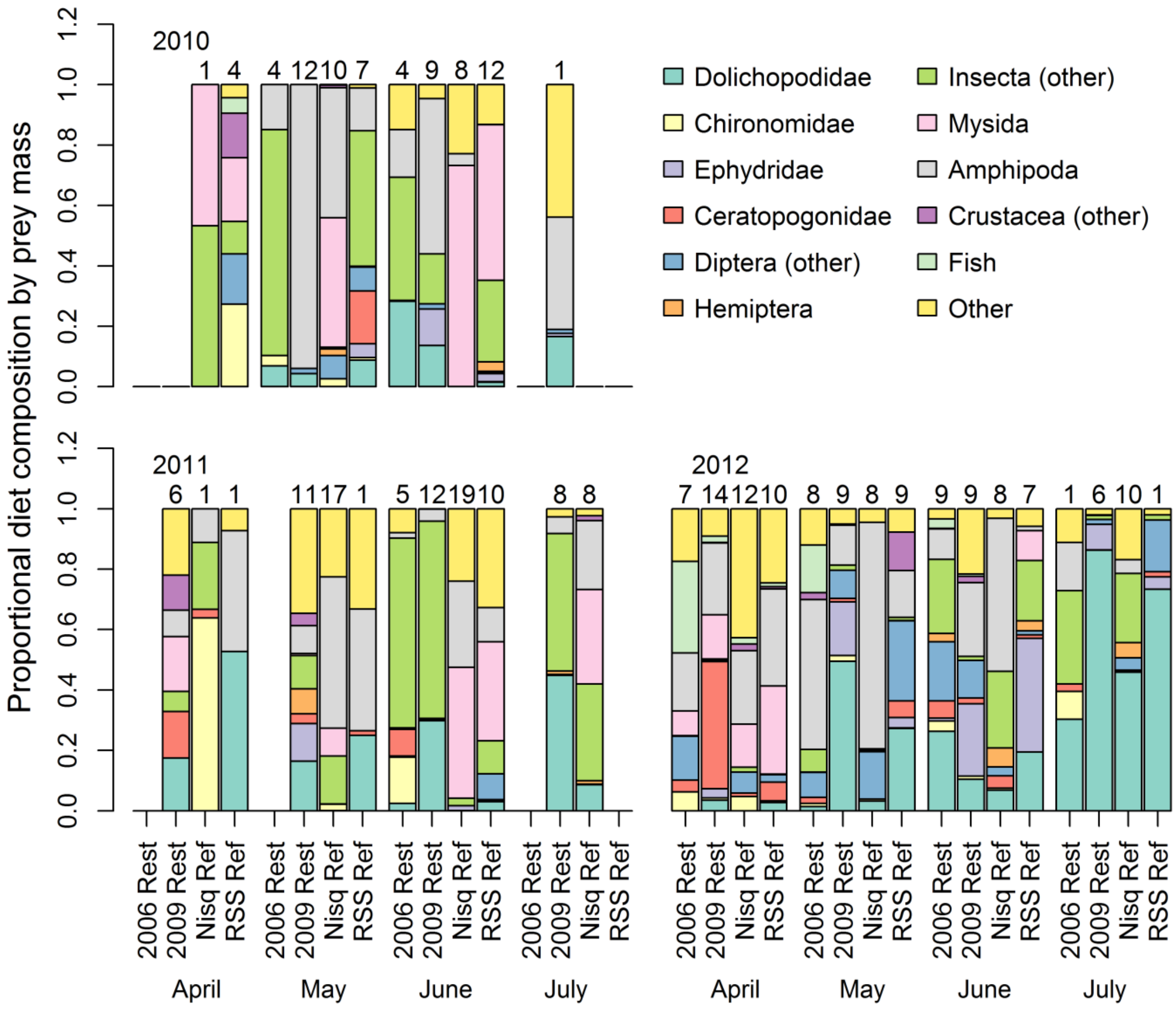

Figure 2.4. Mean proportional diet composition by prey mass of juvenile Chinook salmon for each fyke trap sampling event. The numbers above the bars are sample sizes.

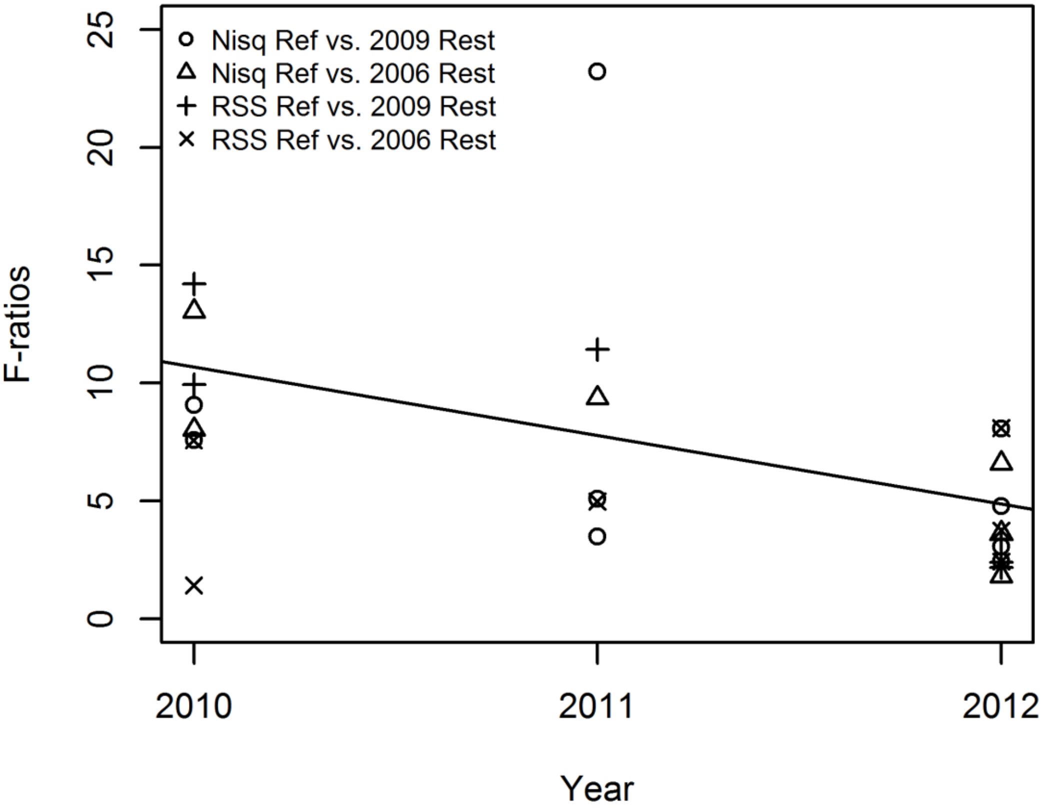

Figure 2.5. PERMANOVA pseudo *F*-ratios from within-month pairwise comparisons of reference and restored marsh Chinook salmon diet composition for each of the three years of the study. The line is the best fit line from a linear regression of *F*-ratios vs. year, weighted by the combined sample size of diets used in each comparison. As with univariate ANOVA *F*-ratios, PERMANOVA pseudo *F*-ratios represent the ratio of between to within group variation and thus for this analysis are a measure of diet composition similarity between marshes relative to within marsh variation in diet composition.

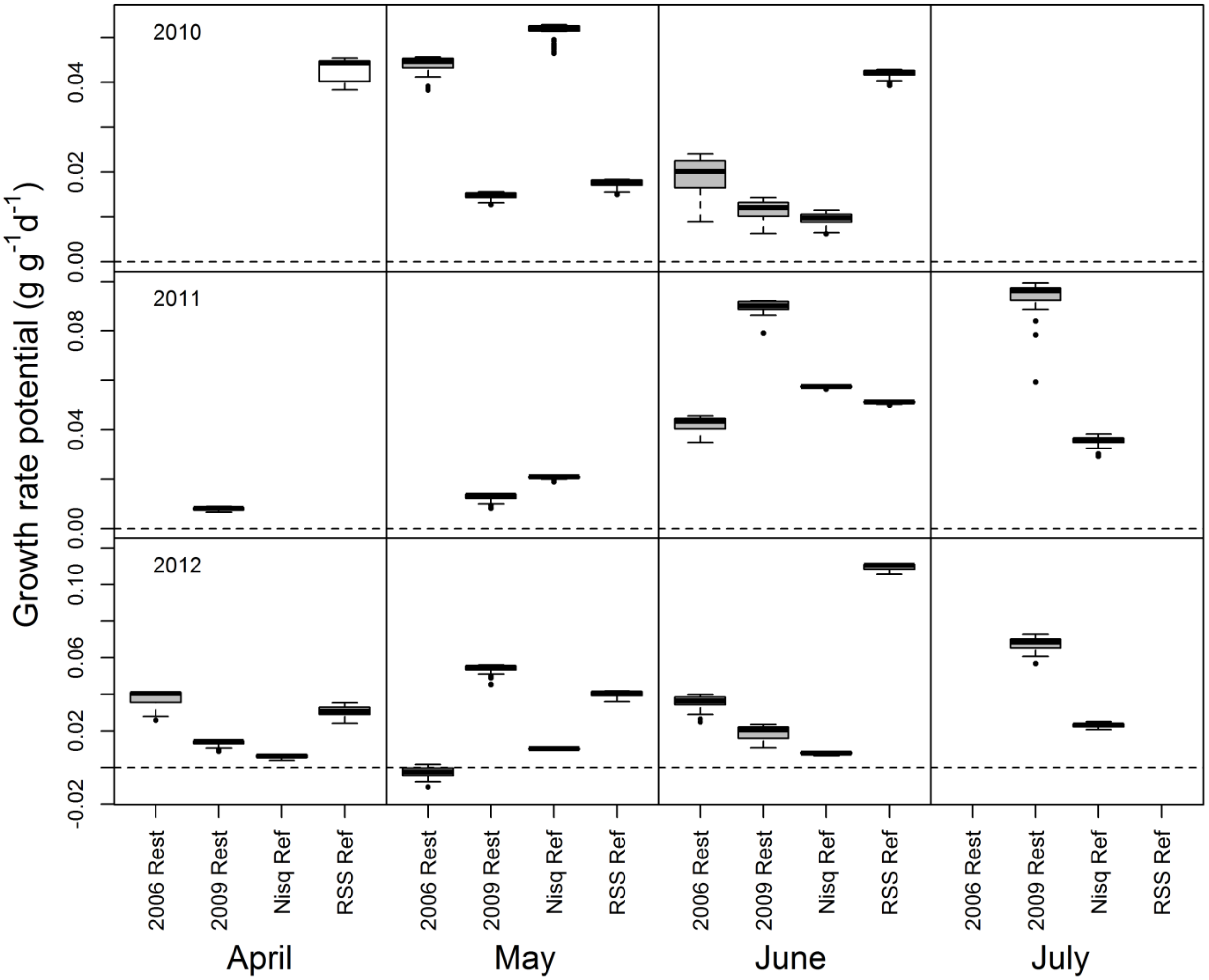

Figure 2.6. Simulated growth rate potential of juvenile Chinook salmon for each sampling event when at least four salmon were captured for diet analysis. Growth potential was simulated using the Fish Bioenergetics model parameterized for Chinook salmon and using empirically derived inputs from each sampling event. Each box and whisker is composed of growth potential simulations for each of the daily mean temperatures observed in that marsh channel during the month when the sampling event took place (i.e., 30-31 separate growth rates). The restored marsh channels are colored gray while the reference marsh channels are colored white.

Conclusions

In my first chapter, I found evidence that human-induced wetland loss in Pacific Northwest estuaries can negatively affect the foraging performance of juvenile salmon and also alter their diet composition, although in sometimes subtle ways. In the second part of my thesis, I found evidence that removing dikes and restoring tidal flow to wetlands that were historically tidally influenced can rapidly restore foraging and growth opportunities for juvenile salmon rearing in estuaries. However, some attributes of tidal wetlands appear to take long periods of time to recover, suggesting that restored tidal marshes may take decades to achieve equivalence with natural, undiked tidal marshes. Yet, even if full recovery takes many years, our results and the results of similar studies all suggest that restored tidal wetlands provide many of the functions of natural tidal wetlands that are important for juvenile salmon and other estuarine species, even in the first few years after restoration.

While the results of this thesis improve our understanding of how juvenile Pacific salmon interact with estuarine wetlands, and how humans can impact those interactions, both negatively and positively, our understanding of these topics would still benefit from more information. The strength of the analysis of the effects of estuarine wetland loss on juvenile salmon foraging was to scale up from the typical level of analysis – that of a single estuary – to comparisons among multiple estuaries that varied in the factor of interest (wetland loss). In contrast, the study of estuary restoration focused on a single estuary. While we learned much from this study, restoration ecology needs to scale up and evaluate multiple separate restoration projects as part of a single study, treating individual restoration projects as the appropriate unit of replication. Studies of multiple restoration projects of different ages, sizes, and landscape settings will help us to identify the factors that constrain and promote ecosystem recovery after restoration.

Another basic question where considerably uncertainty remains is the spatial and temporal scales at which juvenile salmon interact with the estuarine environment, particularly in terms of foraging behavior. We sample the stomach contents of juvenile salmon to make inferences about how salmon are interacting with their environment and how human modifications to the environment impact salmon. But, when we sample a fish we often have little understanding of its prior experience and whether the prey in its stomach was consumed in its current location, or in a distant habitat. The assumption that the stomach contents of a juvenile salmon tells us something useful about how that fish was interacting with its environment and sharing resources with other consumers depends upon the spatial and temporal scales at which juvenile salmon forage and the methodology used to capture the fish. Yet, we have a limited understanding of the foraging behavior of juvenile salmon in estuaries, such as the specific microhabitats used by salmon to forage, the distances salmon travel while actively foraging, and residence times in different estuarine habitats. Focused studies on these topics would greatly improve our understanding of how juvenile Pacific salmon interact with the estuarine environment.

Appendices

Table A.1.1. Energy densities compiled from the literature for prey items found in the stomachs of juvenile Chinook salmon from nine Pacific Northwest estuaries. These values were used to calculate the energy ration of each juvenile Chinook salmon we processed.

Prey type	Taxonomic grouping for analysis	Energy density (kJ g^{-1} wm)	Source	Source taxa and notes
Acalypterate muscoid	Brachycera	9.293	Brodmann and Reyer 1999	Muscidae
Acari	Arachnida	5.320	Gray 2005	Araneae
Agromyzidae	Brachycera	8.920	Gray 2005	Other Diptera
Allorchestes sp	Amphipoda, other	2.970	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Americhelidium sp	Amphipoda, other	2.970	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Americorophium salmonis	Corophiidae	3.065	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Americorophium sp	Corophiidae	3.065	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Americorophium spinicorne	Corophiidae	3.065	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Amphipoda	Amphipoda, other	2.970	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Ampithoe sp	Amphipoda, other	2.970	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Ampithoidae	Amphipoda, other	2.970	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Ampulicinae	Hymenoptera	12.670	Gray 2005	Hymenoptera
Anisogammarus sp	Gammaroidea	2.875	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Annelida	Annelida	1.980	Gray 2005	Annelida
Anthomyiidae	Brachycera	13.057	Brodmann and Reyer 1999	Anthomyiidae
Aphididae	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Aphididae adult	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Aphididae immature	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Aphididae nymph	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Aphidoidea	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Aphidoidea nymph	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Apoidea	Hymenoptera	12.670	Gray 2005	Hymenoptera
Araneae	Arachnida	5.320	Gray 2005	Araneae
Araneae egg case	Arachnida	5.320	Gray 2005	Araneae
Arthropoda	Arthropoda	7.412	Bieber 2005	Other Insecta
Auchenorrhyncha	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Baetidae adult	Ephemeroptera	3.664	Pizzul et al. 2009	Ephemeroptera
Baetidae nymph	Ephemeroptera	3.664	Pizzul et al. 2009	Ephemeroptera
Bibionidae adult	Nematocera	8.805	Brodmann and Reyer 1999	Bibionidae
Bivalvia	Bivalvia	3.574	Ciancio et al. 2007	Mean of 3 values
Bivalvia siphon	Bivalvia	3.574	Ciancio et al. 2007	Mean of 3 values
Bombyllidae adult	Brachycera	8.920	Gray 2005	Other Diptera
Bosmina	Cladocera	1.370	Higgs et al. 1995	Cladocera. Mean of 189 values
Bostrichidae adult	Coleoptera	7.970	Gray 2005	Coleoptera adult

Brachycera	Brachycera	8.920	Gray 2005	Other Diptera
Brachycera adult	Brachycera	8.920	Gray 2005	Other Diptera
Brachycera larva	Brachycera	2.580	Gray 2005	Diptera larva
Brachycera pupa	Brachycera	8.920	Gray 2005	Other Diptera
Brachyura megalopa	Decapoda	3.360	Higgs et al. 1995	Crab zoea
Brachyura zoea	Decapoda	3.360	Higgs et al. 1995	Crab zoea
Brachyura zoea-megalopa	Decapoda	3.360	Higgs et al. 1995	Crab zoea
Braconidae	Hymenoptera	12.670	Gray 2005	Hymenoptera
Calanoida	Copepoda	4.620	Higgs et al. 1995	Copepoda. Mean of 8 values
Calanus sp	Copepoda	4.620	Higgs et al. 1995	Copepoda. Mean of 8 values
Callianassa zoea	Decapoda	3.360	Higgs et al. 1995	Crab zoea
Calliopius sp	Amphipoda, other	2.970	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Canacidae	Brachycera	8.920	Gray 2005	Other Diptera
Cancer sp megalopa	Decapoda	3.360	Higgs et al. 1995	Crab zoea
Cantharidae	Coleoptera	7.940	Gray 2005	Cantharidae adult
Caprellidea	Amphipoda, other	2.970	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Carabidae adult	Coleoptera	10.085	Chen et al. 2004	Carabidae
Carabidae larva	Coleoptera	2.405	Gray 2005	Coleoptera larva
Caridea	Decapoda	3.360	Higgs et al. 1995	Crab zoea
Caridea zoea	Decapoda	3.360	Higgs et al. 1995	Crab zoea
Cecidomyiidae	Nematocera	3.830	Gray 2005	Chironomidae adult
Cecidomyiidae adult	Nematocera	3.830	Gray 2005	Chironomidae adult
Cecidomyiidae pupa	Nematocera	3.830	Gray 2005	Chironomidae adult
Ceratopogonidae	Nematocera	3.830	Gray 2005	Chironomidae adult
Ceratopogonidae adult	Nematocera	3.830	Gray 2005	Chironomidae adult
Ceratopogonidae emergent	Nematocera	3.830	Gray 2005	Chironomidae adult
Ceratopogonidae larva	Nematocera	2.580	Gray 2005	Diptera larva
Ceratopogonidae pupa	Nematocera	3.830	Gray 2005	Chironomidae adult
Cercopidae	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Cercopidae adult	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Chalcidoidea	Hymenoptera	12.670	Gray 2005	Hymenoptera
Chaoboridae larva	Nematocera	2.580	Gray 2005	Diptera larva
Cheiragonidae	Decapoda	3.360	Higgs et al. 1995	Crab zoea
Chilopoda	Chilopoda	7.412	Bieber 2005	Other Insecta
Chironomidae	Chironomidae	3.830	Gray 2005	Chironomidae adult
Chironomidae adult	Chironomidae	3.830	Gray 2005	Chironomidae adult
Chironomidae adult parts	Chironomidae	3.830	Gray 2005	Chironomidae adult
Chironomidae emergent	Chironomidae	3.830	Gray 2005	Chironomidae adult
Chironomidae larva	Chironomidae	2.580	Gray 2005	Diptera larva
Chironomidae pupa	Chironomidae	3.830	Gray 2005	Chironomidae adult
Chloroperidae	Plecoptera	4.125	Pizzul et al. 2009	Plecoptera
Chloropidae	Brachycera	8.920	Gray 2005	Other Diptera
Chloropidae adult	Brachycera	8.920	Gray 2005	Other Diptera

Chrysididae	Hymenoptera	12.670	Gray 2005	Hymenoptera
Chrysomelidae adult	Coleoptera	7.970	Gray 2005	Coleoptera adult
Chrysopidae	Neuroptera	7.412	Bieber 2005	Other Insecta
Cicadellidae	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Cicadellidae adult	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Cicadellidae nymph	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Cirripedia adult	Cirripedia	2.160	Lucas et al. 1979	Cirripedia cypris
Cirripedia cerri	Cirripedia	2.160	Lucas et al. 1979	Cirripedia cypris
Cirripedia cypris	Cirripedia	2.160	Lucas et al. 1979	Cirripedia cypris
Cirripedia exuvia	Cirripedia	2.160	Lucas et al. 1979	Cirripedia cypris
Cirripedia nauplii	Cirripedia	3.280	Lucas et al. 1979	Cirripedia nauplii
Cladocera	Cladocera	1.370	Higgs et al. 1995	Cladocera. Mean of 189 values
Coleoptera	Coleoptera	7.970	Gray 2005	Coleoptera adult
Coleoptera adult	Coleoptera	7.970	Gray 2005	Coleoptera adult
Coleoptera larva	Coleoptera	2.405	Gray 2005	Coleoptera larva
Coleoptera pupa	Coleoptera	7.970	Gray 2005	Coleoptera adult
Collembola	Collembola	5.621	Gray 2005	Collembola
Coniopterygidae	Neuroptera	7.412	Bieber 2005	Other Insecta
Copepoda	Copepoda	4.620	Higgs et al. 1995	Copepoda. Mean of 8 values
Corixidae	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Corixidae adult	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Corophiidae	Corophiidae	3.065	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Corycaeus anglicus	Copepoda	4.620	Higgs et al. 1995	Copepoda. Mean of 8 values
Crangon zoea	Decapoda	3.360	Higgs et al. 1995	Crab zoea
Crustacea	Crustacea, other	3.370	Bieber 2005	Other Crustacea
Crustacea nauplii	Crustacea, other	3.370	Bieber 2005	Other Crustacea
Crustacea parts	Crustacea, other	3.370	Bieber 2005	Other Crustacea
Culicidae adult	Nematocera	3.830	Gray 2005	Chironomidae adult
Cumacea	Cumacea	3.370	Bieber 2005	Other Crustacea
Cumella vulgaris	Cumacea	3.370	Bieber 2005	Other Crustacea
Curculionoidea	Coleoptera	6.982	Chen et al. 2004	Curculionoidea
Cyclopoida	Copepoda	4.620	Higgs et al. 1995	Copepoda. Mean of 8 values
Dactylopusia sp	Copepoda	4.620	Higgs et al. 1995	Copepoda. Mean of 8 values
Daphnia sp	Cladocera	1.370	Higgs et al. 1995	Cladocera. Mean of 189 values
Decapoda megalopa	Decapoda	3.360	Higgs et al. 1995	Crab zoea
Decapoda zoea	Decapoda	3.360	Higgs et al. 1995	Crab zoea
Decapoda zoea-megalopa	Decapoda	3.360	Higgs et al. 1995	Crab zoea
Delphacidae	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Delphacidae adult	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Delphacidae nymph	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Dermaptera nymph	Dermaptera	7.412	Bieber 2005	Other Insecta
Diapriidae	Hymenoptera	12.670	Gray 2005	Hymenoptera
Diastylopsis tenuis	Cumacea	3.370	Bieber 2005	Other Crustacea

Diplopoda	Diplopoda	7.412	Bieber 2005	Other Insecta
Diptera	Diptera, other	8.920	Gray 2005	Other Diptera
Diptera adult	Diptera, other	8.920	Gray 2005	Other Diptera
Diptera adult parts	Diptera, other	8.920	Gray 2005	Other Diptera
Diptera emergent	Diptera, other	8.920	Gray 2005	Other Diptera
Diptera larva	Diptera, other	2.580	Gray 2005	Diptera larva
Diptera pupa	Diptera, other	8.920	Gray 2005	Other Diptera
Dirt	Undigestable material	0.000	NA	
Dolichopodidae	Brachycera	6.200	Gray 2005	Dolichopodidae adult
Dolichopodidae adult	Brachycera	6.200	Gray 2005	Dolichopodidae adult
Dolichopodidae larva	Brachycera	2.580	Gray 2005	Diptera larva
Dolichopodidae pupa	Brachycera	6.200	Gray 2005	Dolichopodidae adult
Drosophilidae adult	Brachycera	8.920	Gray 2005	Other Diptera
Dynamenella sp	Isopoda	2.960	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Egg	Eggs	6.000	Author's estimate	
Elateridae adult	Coleoptera	6.469	Chen et al. 2004	Elateridae
Empididae	Brachycera	8.984	Brodmann and Reyer 1999	Empididae
Empididae adult	Brachycera	8.984	Brodmann and Reyer 1999	Empididae
Empididae larva	Brachycera	2.580	Gray 2005	Diptera larva
Empididae pupa	Brachycera	8.984	Brodmann and Reyer 1999	Empididae
Encyrtidae	Hymenoptera	12.670	Gray 2005	Hymenoptera
Eogammarus confervicolus	Gammaroidea	2.875	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Eogammarus sp	Gammaroidea	2.875	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Ephemeroptera adult	Ephemeroptera	3.664	Pizzul et al. 2009	Ephemeroptera
Ephemeroptera nymph	Ephemeroptera	3.664	Pizzul et al. 2009	Ephemeroptera
Ephydridae	Brachycera	8.920	Gray 2005	Other Diptera
Ephydridae adult	Brachycera	8.920	Gray 2005	Other Diptera
Ephydridae larva	Brachycera	2.580	Gray 2005	Diptera larva
Ephydridae pupa	Brachycera	8.920	Gray 2005	Other Diptera
Ephydridae pupa parts	Brachycera	8.920	Gray 2005	Other Diptera
Epilabidocera longipedata	Copepoda	4.620	Higgs et al. 1995	Copepoda. Mean of 8 values
Euphausiacea	Euphausiacea	4.729	Higgs et al. 1995	Mean of 24 values
Exosphaeroma sp	Isopoda	2.960	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Fish	Fish	6.830	Higgs et al. 1995	Mean of 20 values
fish eggs	Fish	6.830	Higgs et al. 1995	Mean of 20 values
Fish larva	Fish	6.830	Higgs et al. 1995	Mean of 20 values
Flatworms	Flatworms	3.000	Author's estimate	
Foraminifera	Foraminifera	2.000	Author's estimate	
Formicidae	Hymenoptera	5.689	Brodmann and Reyer 1999	Formicidae
Gammaridea	Amphipoda, other	2.970	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Gammaroidea	Gammaroidea	2.875	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Gastropoda	Gastropoda	2.611	Davis et al. 1998	Limacina spp.
Gnorimosphaeroma sp	Isopoda	2.960	Cordell et al. 2011; Gray 2005	Mean of values from both studies

Harpacticoida (Huntemania)	Copepoda	4.620	Higgs et al. 1995	Copepoda. Mean of 8 values
Harpacticoida	Copepoda	4.620	Higgs et al. 1995	Copepoda. Mean of 8 values
Harpacticus sp	Copepoda	4.620	Higgs et al. 1995	Copepoda. Mean of 8 values
Hemerobioidea	Neuroptera	7.412	Bieber 2005	Other Insecta
Hemiptera	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Hemiptera adult	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Hemiptera immature	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Hemiptera nymph	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Hemiptera parts	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Heptageniidae	Ephemeroptera	3.664	Pizzul et al. 2009	Ephemeroptera
Heteroceridae adult	Coleoptera	7.970	Gray 2005	Coleoptera adult
Heteroptera	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Heteroptera adult	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Huntemannia jadensis	Copepoda	4.620	Higgs et al. 1995	Copepoda. Mean of 8 values
Hyale sp	Amphipoda, other	2.970	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Hydroptillidae larva	Trichoptera	5.810	Gray 2005	Trichoptera (larval, emergent)
Hymenoptera	Hymenoptera	12.670	Gray 2005	Hymenoptera
Hymenoptera adult	Hymenoptera	12.670	Gray 2005	Hymenoptera
Hymenoptera larva	Hymenoptera	12.670	Gray 2005	Hymenoptera
Hymenoptera pupa	Hymenoptera	12.670	Gray 2005	Hymenoptera
Hyperia sp	Amphipoda, other	2.464	Davis et al. 1998	Hyperiid amphipods
Hyperiidae	Amphipoda, other	2.464	Davis et al. 1998	Hyperiid amphipods
Hypogastruridae larva	Collembola	5.621	Gray 2005	Collembola
Ichneumonidae	Hymenoptera	12.670	Gray 2005	Hymenoptera
Ichneumonoidea	Hymenoptera	12.670	Gray 2005	Hymenoptera
Inorganic matter	Undigestable material	0.000	NA	
Insecta	Insecta, other	7.412	Bieber 2005	Other Insecta
Insecta adult	Insecta, other	7.412	Bieber 2005	Other Insecta
Insecta larva	Insecta, other	7.412	Bieber 2005	Other Insecta
Insecta nymph	Insecta, other	7.412	Bieber 2005	Other Insecta
Insecta pupa	Insecta, other	7.412	Bieber 2005	Other Insecta
Isopoda	Isopoda	2.960	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Isotomidae	Collembola	5.621	Gray 2005	Collembola
Jassa sp	Amphipoda, other	2.970	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Lepidoptera	Lepidoptera	8.500	Gray 2005	Lepidoptera (Adult and larval)
Lepidoptera adult	Lepidoptera	8.500	Gray 2005	Lepidoptera (Adult and larval)
Lepidoptera larva	Lepidoptera	8.500	Gray 2005	Lepidoptera (Adult and larval)
Leptochelia dubia	Tanaidacea	3.370	Bieber 2005	Other Crustacea
Leptophlebiidae nymph	Ephemeroptera	3.664	Pizzul et al. 2009	Ephemeroptera
Limnoria sp	Isopoda	2.960	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Limnoria tripuntata	Isopoda	2.960	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Lonchopteridae	Brachycera	8.920	Gray 2005	Other Diptera
Lygaeidae	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)

Manyunkia sp	Annelida	1.980	Gray 2005	Annelida
Megaspilidae	Hymenoptera	12.670	Gray 2005	Hymenoptera
Microlepidoptera	Lepidoptera	8.500	Gray 2005	Lepidoptera (Adult and larval)
Micropezidae adult	Brachycera	8.920	Gray 2005	Other Diptera
Miridae	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Misc/unidentifiable	Misc/unidentifiable	5.000	Author's estimate	
Monocorophium insidiosum	Corophiidae	3.065	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Monocorophium sp	Corophiidae	3.065	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Monstrilloida	Copepoda	4.620	Higgs et al. 1995	Copepoda. Mean of 8 values
Mordellidae	Coleoptera	7.970	Gray 2005	Coleoptera adult
Muscidae	Brachycera	9.293	Brodmann and Reyer 1999	Muscidae
Muscidae adult	Brachycera	9.293	Brodmann and Reyer 1999	Muscidae
Muscidae larva	Brachycera	2.580	Gray 2005	Diptera larva
Muscidae pupa	Brachycera	9.293	Brodmann and Reyer 1999	Muscidae
Muscoidea	Brachycera	9.293	Brodmann and Reyer 1999	Muscidae
Mycetophilidae	Nematocera	3.830	Gray 2005	Chironomidae adult
Mysida	Mysida	3.550	Gray 2005	Mysida
Neanthes limnicola	Annelida	1.980	Gray 2005	Annelida
Nematocera	Nematocera	3.830	Gray 2005	Chironomidae adult
Nematocera adult	Nematocera	3.830	Gray 2005	Chironomidae adult
Nematocera pupa	Nematocera	3.830	Gray 2005	Chironomidae adult
Nematoda	Nematoda	3.000	Author's estimate	
Neomysis mercedis	Mysida	3.550	Gray 2005	Mysida
Neomysis sp	Mysida	3.550	Gray 2005	Mysida
Nereidae	Annelida	1.980	Gray 2005	Annelida
Nippoleucon hinumensis	Cumacea	3.370	Bieber 2005	Other Crustacea
Notoptera nymph	Notoptera	7.412	Bieber 2005	Other Insecta
Odonata adult	Odonata	4.879	Higgs et al. 1995	Mean of 37 values
Oligochaeta	Annelida	1.980	Gray 2005	Annelida
Oligochinus lighti	Amphipoda, other	2.970	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Oniscoidea	Isopoda	2.960	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Onychiuridae	Collembola	5.621	Gray 2005	Collembola
Orchesella	Collembola	5.621	Gray 2005	Collembola
Orthoptera adult	Orthoptera	7.412	Bieber 2005	Other Insecta
Orthoptera nymph	Orthoptera	7.412	Bieber 2005	Other Insecta
Osteichthyes	Fish	6.830	Higgs et al. 1995	Mean of 20 values
Ostracoda	Ostrocoda	3.370	Bieber 2005	Other Crustacea
Paguridae zoea	Decapoda	3.360	Higgs et al. 1995	Crab zoea
Phlaeothripidae	Thysanoptera	7.412	Bieber 2005	Other Insecta
Phoridae adult	Brachycera	8.920	Gray 2005	Other Diptera
Photis sp	Amphipoda, other	2.970	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Phoxocephalidae	Amphipoda, other	2.970	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Pinnotheridae zoea	Decapoda	3.360	Higgs et al. 1995	Crab zoea

Pipunculidae	Brachycera	8.920	Gray 2005	Other Diptera
Plant material	Plant material	3.850	Gray 2005	Plant material
Platynereis bicanaliculata	Annelida	1.980	Gray 2005	Annelida
Plecoptera adult	Plecoptera	4.125	Pizzul et al. 2009	Plecoptera
Plecoptera nymph	Plecoptera	4.125	Pizzul et al. 2009	Plecoptera
Podon	Cladocera	1.370	Higgs et al. 1995	Cladocera. Mean of 189 values
Polychaeta	Annelida	1.980	Gray 2005	Annelida
Porcellanidae zoea	Decapoda	3.360	Higgs et al. 1995	Crab zoea
Proctotrupoidea	Hymenoptera	12.670	Gray 2005	Hymenoptera
Pselaphidae adult	Coleoptera	7.970	Gray 2005	Coleoptera adult
Pseudoscorpiones	Arachnida	5.320	Gray 2005	Araneae
Psocoptera	Psocoptera	7.412	Bieber 2005	Other Insecta
Psocoptera adult	Psocoptera	7.412	Bieber 2005	Other Insecta
Psocoptera nymph	Psocoptera	7.412	Bieber 2005	Other Insecta
Psychodidae	Nematocera	3.830	Gray 2005	Chironomidae adult
Psychodidae adult	Nematocera	3.830	Gray 2005	Chironomidae adult
Psychodidae larva	Nematocera	2.580	Gray 2005	Diptera larva
Psychodidae pupa	Nematocera	3.830	Gray 2005	Chironomidae adult
Psyllidae	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Psyllidae adult	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Ptychopteridae adult	Nematocera	7.947	Brodmann and Reyer 1999	Tipulidae
Ramellogammarus sp	Gammaroidea	2.875	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Rhagionidae adult	Brachycera	11.104	Brodmann and Reyer 1999	Rhagionidae
Rock	Undigestable material	0.000	NA	
Saduria entomon	Isopoda	2.960	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Saldidae	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Saldidae adult	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Saldidae nymph	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Sand	Undigestable material	0.000	NA	
Sandlance juvenile	Fish	6.830	Higgs et al. 1995	Mean of 20 values
Scatopsidae adult	Nematocera	3.830	Gray 2005	Chironomidae adult
Scelionidae	Hymenoptera	12.670	Gray 2005	Hymenoptera
Sciaridae	Nematocera	3.830	Gray 2005	Chironomidae adult
Sciaridae adult	Nematocera	3.830	Gray 2005	Chironomidae adult
Sciomyzidae	Brachycera	8.920	Gray 2005	Other Diptera
Sculpin	Fish	6.830	Higgs et al. 1995	Mean of 20 values
Sepsidae adult	Brachycera	8.920	Gray 2005	Other Diptera
Sialidae	Insecta, other	7.412	Bieber 2005	Other Insecta
Simuliidae larva	Nematocera	2.580	Gray 2005	Diptera larva
Simuliidae pupa	Nematocera	3.830	Gray 2005	Chironomidae adult
Sinelobus stanfordi	Tanaidacea	3.370	Bieber 2005	Other Crustacea
Sminthuridae	Collembola	5.621	Gray 2005	Collembola
Sphaeroceridae adult	Brachycera	8.920	Gray 2005	Other Diptera

Sphaeromatidae	Isopoda	2.960	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Staphylinidae	Coleoptera	7.970	Gray 2005	Coleoptera adult
Staphylinidae adult	Coleoptera	7.970	Gray 2005	Coleoptera adult
Staphylinidae larva	Coleoptera	2.405	Gray 2005	Coleoptera larva
Symphyta larva	Hymenoptera	12.670	Gray 2005	Hymenoptera
Syrphidae adult	Brachycera	8.568	Brodmann and Reyer 1999	Syrphidae
Talitridae	Amphipoda, other	3.040	Gray 2005	Talitridae
Tanaidacea	Tanaidacea	3.370	Bieber 2005	Other Crustacea
Tanyderidae larva	Nematocera	2.580	Gray 2005	Diptera larva
Thalestris sp	Copepoda	4.620	Higgs et al. 1995	Copepoda. Mean of 8 values
Thysanoptera	Thysanoptera	7.412	Bieber 2005	Other Insecta
Thysanoptera larva	Thysanoptera	7.412	Bieber 2005	Other Insecta
Tipulidae	Nematocera	7.947	Brodmann and Reyer 1999	Tipulidae
Tipulidae adult	Nematocera	7.947	Brodmann and Reyer 1999	Tipulidae
Tipulidae larva	Nematocera	2.580	Gray 2005	Diptera larva
Tipulidae pupa	Nematocera	7.947	Brodmann and Reyer 1999	Tipulidae
Trichoptera	Trichoptera	7.760	Gray 2005	Trichoptera adult
Trichoptera adult	Trichoptera	7.760	Gray 2005	Trichoptera adult
Trichoptera emergent	Trichoptera	5.810	Gray 2005	Trichoptera (larval, emergent)
Trichoptera larva	Trichoptera	5.810	Gray 2005	Trichoptera (larval, emergent)
Trichoptera pupa	Trichoptera	5.810	Gray 2005	Trichoptera (larval, emergent)
Turbellaria	Flatworms	3.000	Author's estimate	

Table A.2.1. Energy densities compiled from the literature for prey items found in the stomachs of Nisqually River delta juvenile Chinook salmon. These values were used to calculate the diet energy density of each juvenile Chinook salmon we processed.

Prey type	Taxonomic grouping for analysis	Energy density ($kJ\ g^{-1}$ wm)	Source	Source taxa and notes
Acari	Arachnida	5.320	Gray 2005	Araneae
Araneae	Arachnida	5.320	Gray 2005	Araneae
Pseudoscorpion	Arachnida	5.320	Gray 2005	Araneae
Hypogastruridae	Collembola	5.621	Gray 2005	Collembola
Onychiuridae	Collembola	5.621	Gray 2005	Collembola
Americorophium salmonis	Corophiidae	3.065	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Americorophium sp	Corophiidae	3.065	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Americorophium spinicorne	Corophiidae	3.065	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Amphipoda	Amphipoda, other	2.970	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Ampithoe sp	Amphipoda, other	2.970	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Ampithoe valida	Amphipoda, other	2.970	Cordell et al. 2011; Gray 2005	Mean of values from both studies

Anisogammarus pugettensis	Amphipoda, other	2.875	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Brachyura megalopa	Decapoda larva	3.360	Higgs et al. 1995	Crab zoea
Brachyura zoea	Decapoda larva	3.360	Higgs et al. 1995	Crab zoea
Calanoida	Calanoida	4.620	Higgs et al. 1995	Mean of 8 values
Caridea megalopa	Decapoda larva	3.360	Higgs et al. 1995	Crab zoea
Caridea zoea	Decapoda larva	3.360	Higgs et al. 1995	Crab zoea
Cirripedia cipris	Cirripedia larva	2.160	Lucas et al. 1979	Cirripedia cipris
Cirripedia nauplii	Cirripedia larva	3.280	Lucas et al. 1979	Cirripedia nauplii
Corophiidae	Corophiidae	3.065	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Crangon sp	Decapoda larva	3.360	Higgs et al. 1995	Crab zoea
Cumacea	Cumacea	3.370	Bieber 2005	Other Crustacea
Cumella vulgaris	Cumacea	3.370	Bieber 2005	Other Crustacea
Decapoda megalopa	Decapoda larva	3.360	Higgs et al. 1995	Crab zoea
Decapoda zoea	Decapoda larva	3.360	Higgs et al. 1995	Crab zoea
Eogammarus confervicolus	Eogammarus confervicolus	2.875	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Epilabidocera longipedata	Calanoida	4.620	Higgs et al. 1995	Mean of 8 values
Gnorimosphaeroma oregonense	Isopoda	2.960	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Grandidierella japonica	Amphipoda, other	2.970	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Harpacticoida	Harpacticoida	4.620	Higgs et al. 1995	Mean of 8 values
Harpacticus uniremis group	Harpacticoida	4.620	Higgs et al. 1995	Mean of 8 values
Hyperiidae	Amphipoda, other	2.464	Davis et al. 1998	Hyperiid amphipods
Leptochelia dubia	Tanaidacea	3.370	Bieber 2005	Other Crustacea
Limnoria lignorum	Isopoda	2.960	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Monocorophium acherusicum	Corophiidae	3.065	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Monocorophium insidiosum	Corophiidae	3.065	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Monocorophium sp	Corophiidae	3.065	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Mysida	Mysida	3.550	Gray 2005	Mysida
Neomysis mercedis	Mysida	3.550	Gray 2005	Mysida
Nippoleucon hinumensis	Cumacea	3.370	Bieber 2005	Other Crustacea
Paguridae megalopa	Decapoda larva	3.360	Higgs et al. 1995	Crab zoea
Pinnotheridae megalopa	Decapoda larva	3.360	Higgs et al. 1995	Crab zoea
Pinnotheridae zoea	Decapoda larva	3.360	Higgs et al. 1995	Crab zoea
Porcellanidae zoea	Decapoda larva	3.360	Higgs et al. 1995	Crab zoea
Sinelobus stanfordi	Tanaidacea	3.370	Bieber 2005	Other Crustacea
Sphaeromatidae	Isopoda	2.960	Cordell et al. 2011; Gray 2005	Mean of values from both studies
Talitridae	Amphipoda, other	3.040	Gray 2005	Talitridae
Tanaidacea	Tanaidacea	3.370	Bieber 2005	Other Crustacea
Unidentifiable crustacea	Crustacea, other	3.370	Bieber 2005	Other Crustacea
Aphididae	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Auchenorrhyncha	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Baetidae nymph	Ephemeroptera	3.664	Pizzul et al. 2009	Ephemeroptera
Brachycera	Diptera, other	8.920	Gray 2005	Other Diptera
Brachycera adult	Diptera, other	8.920	Gray 2005	Other Diptera

Brachycera pupa	Diptera, other	8.920	Gray 2005	Other Diptera
Cantharidae	Coleoptera	7.940	Gray 2005	Cantharidae adult
Carabidae	Coleoptera	10.085	Chen et al. 2004	Carabidae
Ceratopogonidae	Ceratopogonidae	3.830	Gray 2005	Chironomidae adult
Ceratopogonidae adult	Ceratopogonidae	3.830	Gray 2005	Chironomidae adult
Ceratopogonidae larva	Ceratopogonidae	2.580	Gray 2005	Diptera larva
Ceratopogonidae pupa	Ceratopogonidae	3.830	Gray 2005	Chironomidae adult
Cercopidae	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Chalcidoidea	Hymenoptera	12.670	Gray 2005	Hymenoptera
Chironomidae	Chironomidae	3.830	Gray 2005	Chironomidae adult
Chironomidae adult	Chironomidae	3.830	Gray 2005	Chironomidae adult
Chironomidae larva	Chironomidae	2.580	Gray 2005	Diptera larva
Chironomidae pupa	Chironomidae	3.830	Gray 2005	Chironomidae adult
Chloropidae adult	Diptera, other	8.920	Gray 2005	Other Diptera
Cicadellidae	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Coleoptera	Coleoptera	7.970	Gray 2005	Coleoptera adult
Coleoptera larva	Coleoptera	2.405	Gray 2005	Coleoptera larva
Delphacidae	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Diptera larva	Diptera, other	2.580	Gray 2005	Diptera larva
Diptera pupa	Diptera, other	8.920	Gray 2005	Other Diptera
Dolichopodidae	Dolichopodidae	6.200	Gray 2005	Dolichopodidae adult
Dolichopodidae adult	Dolichopodidae	6.200	Gray 2005	Dolichopodidae adult
Dolichopodidae larva	Dolichopodidae	2.580	Gray 2005	Diptera larva
Dolichopodidae pupa	Dolichopodidae	2.580	Gray 2005	Diptera larva
Empididae adult	Diptera, other	8.984	Brodmann and Reyer 1999	Empididae
Ephemerellidae nymph	Ephemeroptera	3.664	Pizzul et al. 2009	Ephemeroptera
Ephemeroptera nymph	Ephemeroptera	3.664	Pizzul et al. 2009	Ephemeroptera
Ephydridae	Ephydridae	8.920	Gray 2005	Other Diptera
Ephydridae adult	Ephydridae	8.920	Gray 2005	Other Diptera
Ephydridae larva	Ephydridae	2.580	Gray 2005	Diptera larva
Ephydridae pupa	Ephydridae	8.920	Gray 2005	Other Diptera
Figitidae	Hymenoptera	12.670	Gray 2005	Hymenoptera
Formicidae	Hymenoptera	5.689	Brodmann and Reyer 1999	Formicidae
Hemiptera	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Hemiptera parts	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Heteroptera	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Hymenoptera	Hymenoptera	12.670	Gray 2005	Hymenoptera
Ichneumonoidea	Hymenoptera	12.670	Gray 2005	Hymenoptera
Immature Sternorrhyncha	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Insecta larva	Insecta, other	7.412	Bieber 2005	Other Insecta
Lepidoptera	Lepidoptera	8.500	Gray 2005	Lepidoptera (Adult and larval)
Lepidoptera larva	Lepidoptera	8.500	Gray 2005	Lepidoptera (Adult and larval)
Limnephilidae	Trichoptera	7.760	Gray 2005	Trichoptera adult

Miridae	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Muscidae adult	Diptera, other	9.293	Brodmann and Reyer 1999	Muscidae
Muscidae larva	Diptera, other	2.580	Gray 2005	Diptera larva
Mymaridae	Hymenoptera	12.670	Gray 2005	Hymenoptera
Nematocera	Diptera, other	3.830	Gray 2005	Chironomidae adult
Nematocera adult	Diptera, other	3.830	Gray 2005	Chironomidae adult
Nematocera pupa	Diptera, other	3.830	Gray 2005	Chironomidae adult
Phoridae adult	Diptera, other	8.920	Gray 2005	Other Diptera
Proctotrupoidea	Hymenoptera	12.670	Gray 2005	Hymenoptera
Psocoptera	Psocoptera	7.412	Bieber 2005	Other Insecta
Psychodidae adult	Diptera, other	3.830	Gray 2005	Chironomidae adult
Psyllidae	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Saldidae	Hemiptera	10.930	Gray 2005	Hemiptera (adult and immature)
Scatopsidae	Diptera, other	3.830	Gray 2005	Chironomidae adult
Sciaridae	Diptera, other	3.830	Gray 2005	Chironomidae adult
Sciaridae adult	Diptera, other	3.830	Gray 2005	Chironomidae adult
Staphylinidae	Coleoptera	7.970	Gray 2005	Coleoptera adult
Staphylinidae larva	Coleoptera	7.970	Gray 2005	Coleoptera adult
Tipulidae	Diptera, other	7.947	Brodmann and Reyer 1999	Tipulidae
Tipulidae adult	Diptera, other	7.947	Brodmann and Reyer 1999	Tipulidae
Tipulidae larva	Diptera, other	2.580	Gray 2005	Diptera larva
Unidentifiable insecta	Insecta, other	7.412	Bieber 2005	Other Insecta
Unknown Diptera	Diptera, other	8.920	Gray 2005	Other Diptera
Unknown Diptera adult	Diptera, other	8.920	Gray 2005	Other Diptera
Fish	Fish	6.830	Higgs et al. 1995	Mean of 20 values
Macoma siphons	Bivalvia	3.574	Ciancio et al. 2007	Mean of three values
Nematoda	Nematoda	3.000	Author's estimate	
Nereidae	Polychaeta	1.980	Gray 2005	Annelida
Polychaeta	Polychaeta	1.980	Gray 2005	Annelida
Plant material	Plant material	3.850	Gray 2005	Plant material

Table A.2.2. Fish catches for each fyke trap sampling event in the Nisqually River delta in 2010, 2011, and 2012. Large catches were subsampled and the final expanded count calculated from the subsample.

Year	Month	Sampling Location	Threespine Stickleback *Gasterosteus aculeatus*	Wild Chinook Salmon *O. tshawytscha*	Hatchery Chinook Salmon *O. tshawytscha*	Chum Salmon *O. keta*	Wild Coho Salmon *O. kisutch*	Hatchery Coho salmon *O. kisutch*	Cutthroat Trout *O. clarki*	Pacific Herring *Clupea harengus pallasi*
2010	April	Nisqually Reference	0	1	0	81	0	0	1	0
2010	April	RSS Reference	3	12	0	108	0	0	0	0
2010	April	2009 Restored	3	0	0	12	0	9	1	0
2010	April	2006 Restored	2	0	0	0	1	0	0	0
2010	May	Nisqually Reference	0	9.6	141.2	383.4	5.8	4.4	0	0
2010	May	RSS Reference	0	4.3	47.2	46.2	0	0	0	0
2010	May	2009 Restored	6	2	36	0	5	6	0	1
2010	May	2006 Restored	6	0	4	0	0	0	0	0
2010	June	Nisqually Reference	5.6	73	1000.6	0	9.2	0	0	0
2010	June	RSS Reference	0	11.3	90.3	6.7	5.7	0	0	0
2010	June	2009 Restored	4	0	11	0	1	0	0	11
2010	June	2006 Restored	2	2	2	0	0	0	0	0
2010	July	Nisqually Reference	2	0	0	0	2	0	0	0
2010	July	RSS Reference	0	0	0	0	0	0	0	0
2010	July	2009 Restored	66	1	0	0	0	0	0	0
2010	July	2006 Restored	3	0	0	0	0	0	0	0
2011	April	Nisqually Reference	1	3	0	115	1	3	0	0
2011	April	RSS Reference	4	1	0	45	0	1	0	0
2011	April	2009 Restored	3	6	0	1	1	1	1	0
2011	April	2006 Restored	6	0	0	3	2	0	0	0
2011	May	Nisqually Reference	3	8	75	10	16	3	0	0
2011	May	RSS Reference	1	1	0	1053	0	0	0	0
2011	May	2009 Restored	23	1	56	0	0	0	0	0
2011	May	2006 Restored	5	0	0	6	0	1	0	0
2011	June	Nisqually Reference	5	12	745	18	0	0	0	0

2011	June	RSS Reference	0	0	49.5	22	2.75	0	0	0
2011	June	2009 Restored	18	2	16	1	0	0	0	0
2011	June	2006 Restored	123	1	4	67	0	0	0	0
2011	July	Nisqually Reference	1	8	20	1	3	0	2	0
2011	July	RSS Reference	3.3	0	0	0	0	0	0	0
2011	July	2009 Restored	11	4	8	0	0	0	0	3
2011	July	2006 Restored	28	0	0	0	0	0	1	0
2012	April	Nisqually Reference	2	6	6	127	1	0	0	0
2012	April	RSS Reference	7	11	82	11	0	0	0	0
2012	April	2009 Restored	2	9	70	5	3	1	1	0
2012	April	2006 Restored	12	7	0	30	1	0	1	0
2012	May	Nisqually Reference	4	3	51	11	0	0	13	0
2012	May	RSS Reference	29	3	94	56	0	1	0	0
2012	May	2009 Restored	22	8	97	4	0	0	0	0
2012	May	2006 Restored	69	0	35	8	1	10	0	0
2012	June	Nisqually Reference	0	3	26	2	0	1	8	0
2012	June	RSS Reference	10	3	9	0	0	0	0	0
2012	June	2009 Restored	38	4	35	0	0	0	0	0
2012	June	2006 Restored	286	5	6	1	0	0	0	0
2012	July	Nisqually Reference	14	11	20	1	5	0	1	0
2012	July	RSS Reference	19	0	1	0	0	0	0	0
2012	July	2009 Restored	92	1	10	0	0	0	0	0
2012	July	2006 Restored	103	1	0	0	0	0	1	0

Table A.2.2. Continued.

Year	Month	Sampling Location	Pink Salmon *O. gorbuscha*	Sculpin (primarily Staghorn Sculpin *Leptocuttus armatus*)	Starry Flounder *Platichthys stellatus*	Saddleback Gunnel *Pholis ornata*	Steelhead Trout *O. mykiss*	Sand Lance *Ammodytes hexapterus*	Surf Smelt *Hypomesus pretiosus*	Shiner Perch *Cymatogaster aggregata*	Unknown	Unknown lamprey
2010	April	Nisqually Reference	259	2	2	0	0	1	0	0	0	0
2010	April	RSS Reference	12	429	0	0	0	0	0	3	0	0
2010	April	2009 Restored	27	6	0	0	0	0	0	0	0	0
2010	April	2006 Restored	1	5	0	0	0	0	0	0	0	0
2010	May	Nisqually Reference	0	279.2	0	0	0	0	0	0	0	0
2010	May	RSS Reference	0	3226.1	0	0	0	0	0	373.7	0	0
2010	May	2009 Restored	0	53	0	0	0	0	0	0	0	0
2010	May	2006 Restored	0	40	0	0	0	0	0	573	0	0
2010	June	Nisqually Reference	0	35.2	0	0	0	0	1	4.6	0	0
2010	June	RSS Reference	0	1999.3	11.3	0	0	0	0	517.7	0	0
2010	June	2009 Restored	0	93	0	0	0	0	0	233	0	0
2010	June	2006 Restored	0	30	0	0	0	0	0	255	0	0
2010	July	Nisqually Reference	0	1171	0	0	0	0	1	32	0	0
2010	July	RSS Reference	0	247.5	5.5	0	0	0	0	940.5	0	0
2010	July	2009 Restored	0	483	3	0	0	0	0	192	0	0
2010	July	2006 Restored	0	15	0	0	0	0	0	144	0	0
2011	April	Nisqually Reference	0	105	0	0	0	0	0	0	0	0
2011	April	RSS Reference	0	73	0	0	0	0	0	0	0	0
2011	April	2009 Restored	0	8	0	1	0	0	2	0	0	0
2011	April	2006 Restored	0	139	0	0	0	0	0	0	0	0
2011	May	Nisqually Reference	0	281	0	0	0	0	0	1	0	0
2011	May	RSS Reference	0	1242	0	0	0	0	0	0	0	0
2011	May	2009 Restored	0	191	0	2	0	0	0	0	0	0
2011	May	2006 Restored	0	93	0	0	0	0	0	0	0	0
2011	June	Nisqually Reference	0	257	0	0	0	0	0	0	0	0
2011	June	RSS Reference	0	4215.75	0	0	0	0	0	1050.5	0	0
2011	June	2009 Restored	0	694	1	10	0	0	3	207	0	0

2011	June	2006 Restored	0	243	1	0	0	0	0	1	0	0
2011	July	Nisqually Reference	0	619	0	0	0	0	0	229	0	0
2011	July	RSS Reference	0	3157.3	13.3	0	0	0	0	2859.3	0	0
2011	July	2009 Restored	0	25	2	0	0	302	264	1360	0	0
2011	July	2006 Restored	0	9	0	0	0	0	0	393	0	0
2012	April	Nisqually Reference	16	25	1	1	3	0	1	3	0	0
2012	April	RSS Reference	1	711	0	0	0	0	0	0	0	0
2012	April	2009 Restored	59	57	0	0	0	0	79	5	0	0
2012	April	2006 Restored	0	54	0	0	0	0	1	56	0	0
2012	May	Nisqually Reference	0	137	0	2	0	0	0	0	0	0
2012	May	RSS Reference	0	1603	3	0	0	0	1	61	0	0
2012	May	2009 Restored	0	245	0	6	0	0	0	113	6	0
2012	May	2006 Restored	0	44	0	0	0	0	0	1205	0	0
2012	June	Nisqually Reference	0	146	0	0	0	0	0	1	0	0
2012	June	RSS Reference	0	921	3	0	0	0	0	890	0	0
2012	June	2009 Restored	0	587	0	5	0	0	0	1952	0	0
2012	June	2006 Restored	0	223	0	0	0	0	0	276	0	0
2012	July	Nisqually Reference	0	403	2	0	0	0	0	122	0	0
2012	July	RSS Reference	0	1158	16	0	0	0	0	1163	0	0
2012	July	2009 Restored	0	561	0	1	0	0	1	2740	0	0
2012	July	2006 Restored	0	68	0	0	0	0	0	64	0	1

Table A.2.3. Model summary for the AICc top-ranked Chinook salmon instantaneous ration linear model.

Coefficients	Estimate	SE	*T*	*P*
Intercept	-0.771	0.106	-7.244	<0.001
Density	0.783	0.361	2.171	0.031
2006 Restored	0.143	0.175	0.818	0.414
2009 Restored	0.526	0.137	3.848	<0.001
RSS Reference	0.464	0.148	3.130	0.002

Table A.2.4. Model summary for the AICc top-ranked Chinook salmon diet energy density linear model.

Coefficients	Estimate	SE	*T*	*P*
Intercept	2.971	0.365	8.144	<0.001
Density	-2.876	0.752	-3.822	<0.001
2006 Restored	1.020	0.327	3.119	0.002
2009 Restored	0.758	0.252	3.007	0.003
RSS Reference	0.654	0.285	2.291	0.023
July	2.307	0.345	6.687	<0.001
June	1.900	0.278	6.849	<0.001
May	1.024	0.274	3.734	<0.001
2011	0.533	0.246	2.163	0.031
2012	0.681	0.244	2.790	0.006

Table A.2.5. Data compiled from studies of salmonid gastric evacuation rates for development of a predictive model of evacuation rate as a function of water temperature and fish mass.

Study	Species	Mean fish wet mass (g)	Mean evacuation rate	Temperature (°C)
Principe et al. 2007[a]	Chinook Salmon	0.973	0.2144	10
Principe et al. 2007	Chinook Salmon	1.022	0.2663	13
Principe et al. 2007	Chinook Salmon	1.483	0.276	16
Principe et al. 2007	Chinook Salmon	2.62	0.3518	19
Dobble and Eggers 1978[b]	Sockeye Salmon	1.1	0.405	13.25
Dobble and Eggers 1978	Sockeye Salmon	1.5	0.466	13.25

Dobble and Eggers 1978	Sockeye Salmon	2.6	0.329	13.25
Dobble and Eggers 1978	Sockeye Salmon	3.4	0.179	13.25
Dobble and Eggers 1978	Sockeye Salmon	3.2	0.267	9.25
Dobble and Eggers 1978	Sockeye Salmon	4.1	0.159	9.25
Dobble and Eggers 1978	Sockeye Salmon	6.0	0.191	9.25
Dobble and Eggers 1978	Sockeye Salmon	8.5	0.232	9.25
Dobble and Eggers 1978	Sockeye Salmon	10.1	0.182	9.25
Dobble and Eggers 1978	Sockeye Salmon	4.9	0.162	11
Dobble and Eggers 1978	Sockeye Salmon	6.0	0.14	11
Dobble and Eggers 1978	Sockeye Salmon	8.5	0.199	11
Dobble and Eggers 1978	Sockeye Salmon	11.5	0.179	11
Dobble and Eggers 1978	Sockeye Salmon	15.2	0.118	11
Dobble and Eggers 1978	Sockeye Salmon	17.5	0.085	11
Dobble and Eggers 1978	Sockeye Salmon	7.1	0.093	8.25
Dobble and Eggers 1978	Sockeye Salmon	8.5	0.034	8.25
Dobble and Eggers 1978	Sockeye Salmon	11.5	0.041	8.25
Dobble and Eggers 1978	Sockeye Salmon	15.2	0.034	8.25
Dobble and Eggers 1978	Sockeye Salmon	19.6	0.017	8.25
Dobble and Eggers 1978	Sockeye Salmon	22.3	0.108	8.25
Dobble and Eggers 1978	Sockeye Salmon	7.1	0.109	5.75
Dobble and Eggers 1978	Sockeye Salmon	8.5	0.033	5.75
Dobble and Eggers 1978	Sockeye Salmon	11.5	0.042	5.75
Dobble and Eggers 1978	Sockeye Salmon	15.2	0.056	5.75
Dobble and Eggers 1978	Sockeye Salmon	19.6	0.02	5.75
Dobble and Eggers 1978	Sockeye Salmon	22.3	0.082	5.75
Benkwitt et al. 2009[c]	Chinook Salmon	5.9	0.0407	9.3
Benkwitt et al. 2009	Chinook Salmon	6.5	0.0589	10.7
Benkwitt et al. 2009	Chinook Salmon	6.0	0.0807	13.9
Brodeur and Pearcy 1987	Coho Salmon	34.4	0.081	11.4
Kawaguchi et al. 2007	Rainbow Trout	33.8	0.042	9
Kawaguchi et al. 2007	Rainbow Trout	34.5	0.051	12
Kawaguchi et al. 2007	Rainbow Trout	43.3	0.006	2
Brett and Higgs 1970	Sockeye Salmon	36.2	0.0252	5.5
Brett and Higgs 1970	Sockeye Salmon	30.1	0.0525	9.9
Brett and Higgs 1970	Sockeye Salmon	30.7	0.0885	14.9
Brett and Higgs 1970	Sockeye Salmon	34.6	0.1132	20.1
Brett and Higgs 1970	Sockeye Salmon	30.0	0.1114	23
Windell et al. 1976	Rainbow Trout	22.0	0.079	5
Windell et al. 1976	Rainbow Trout	35.0	0.12	10
Windell et al. 1976	Rainbow Trout	27.0	0.184	15
Windell et al. 1976	Rainbow Trout	30.0	0.281	20
Kolok and Rondorf 1987	Chinook Salmon	16.4	0.152	14
Kolok and Rondorf 1987	Chinook Salmon	23.1	0.142	10

Kolok and Rondorf 1987	Chinook Salmon	23.1	0.092	15
Rugerone 1989	Coho Salmon	10.0	0.168	5
Rugerone 1989	Coho Salmon	10.0	0.196	7
Rugerone 1989	Coho Salmon	10.0	0.288	10
Rugerone 1989	Coho Salmon	10.0	0.329	13
Simenstad unpublished[d]	Chinook Salmon	0.9	0.240	11
Simenstad unpublished	Chinook Salmon	2.3	0.158	11
Simenstad unpublished	Chinook Salmon	9.3	0.262	15.7
Simenstad unpublished	Chinook Salmon	14.1	0.222	15.7
Simenstad unpublished	Chinook Salmon	4.1	0.297	9.6
Simenstad unpublished	Chinook Salmon	1.6	0.248	8.4

[a] Masses and evacuation rates were obtained directly from the lead author.

[b] Masses estimated from a length - mass equation in Ruggerone and Rogers (1992).

[c] Masses are medians.

[d] Data from unpublished research in the Columbia River estuary by C.A. Simenstad.

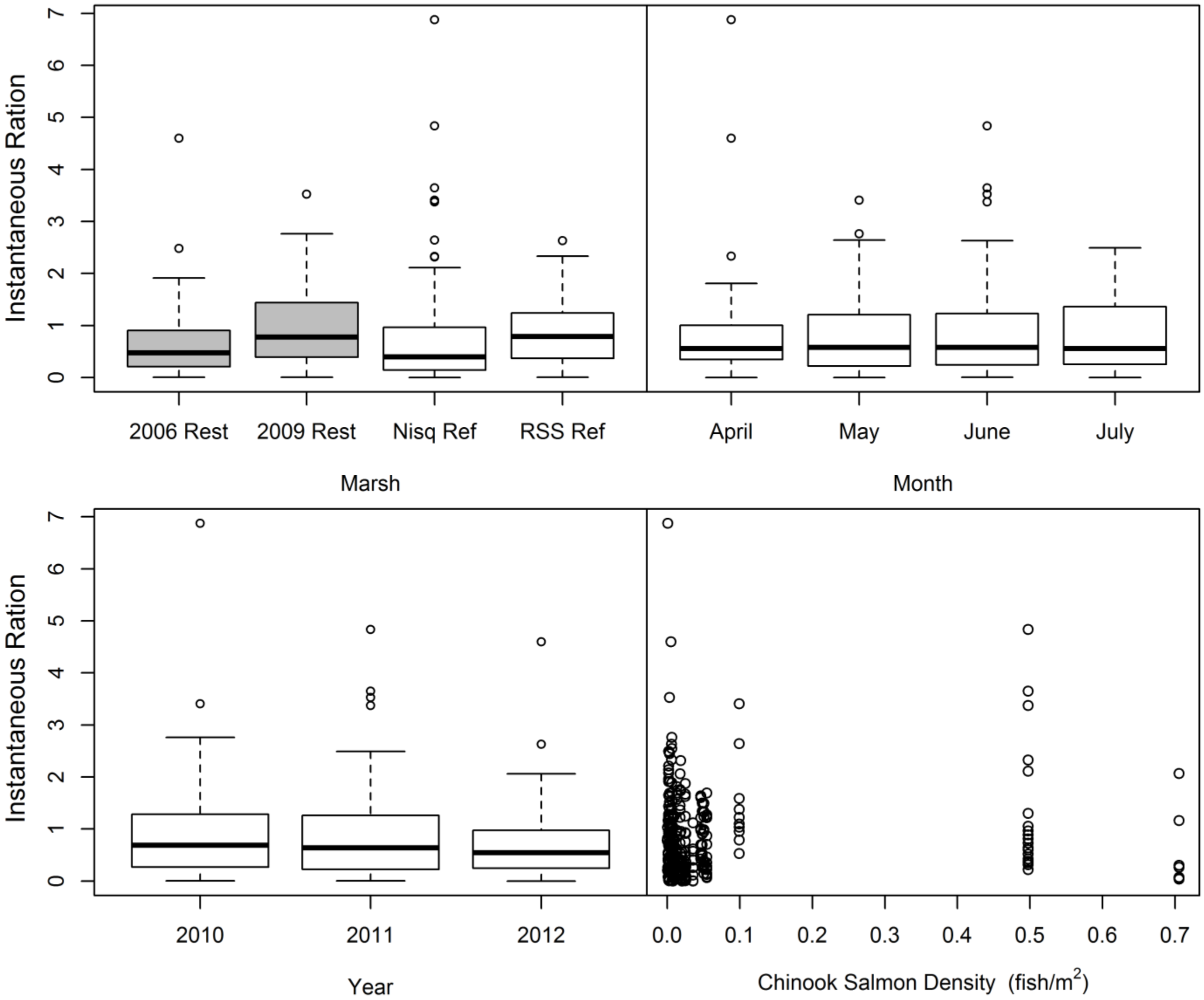

Figure A.2.1. Variation in juvenile Chinook salmon instantaneous ration among marshes, months, years, and Chinook Salmon densities. In the top left panel, the restored marsh channels are colored gray while the reference marsh channels are colored white.

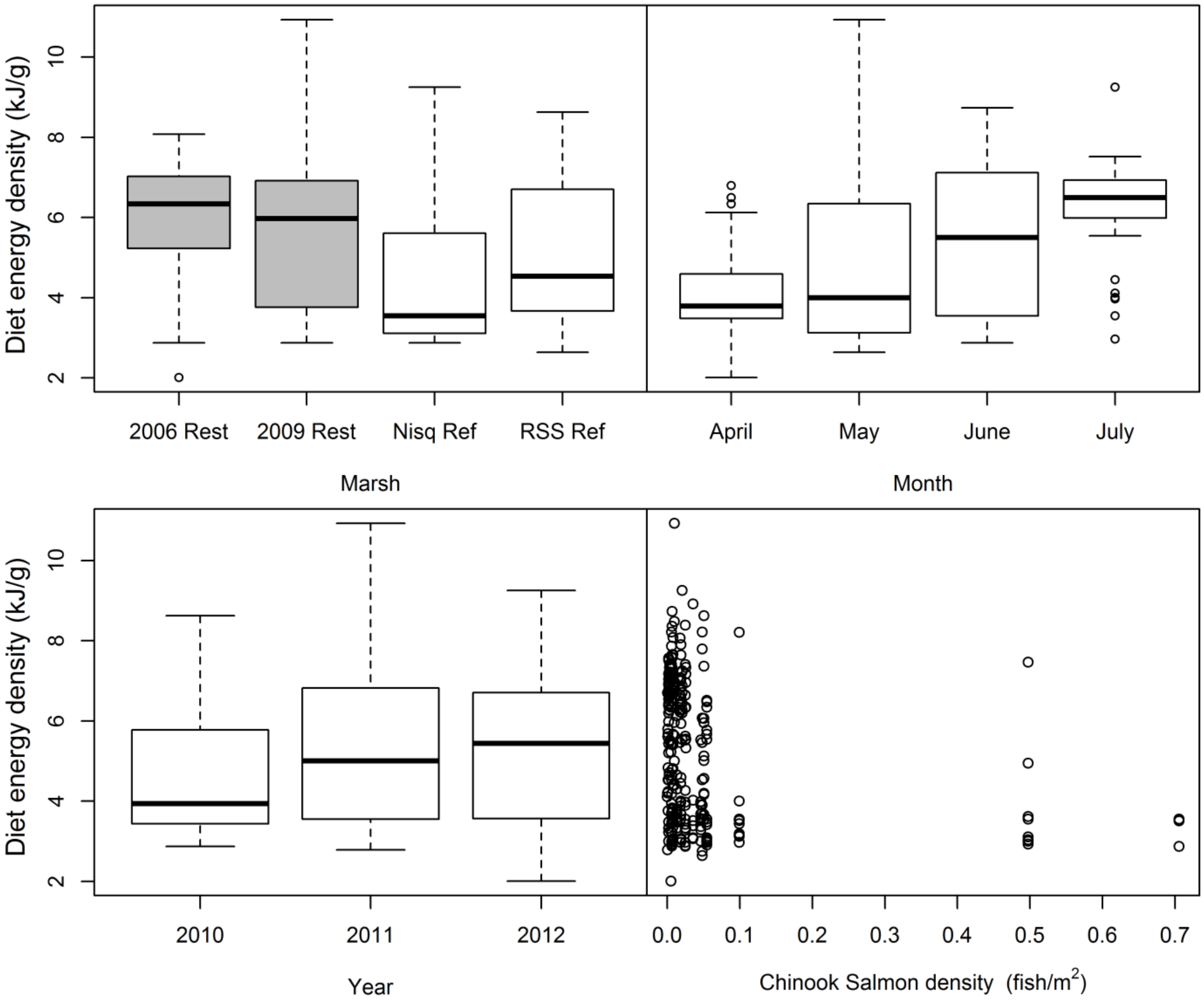

Figure A.2.2. Variation in juvenile Chinook salmon diet energy density among marshes, months, years, and Chinook Salmon densities. In the top left panel, the restored marsh channels are colored gray while the reference marsh channels are colored white.

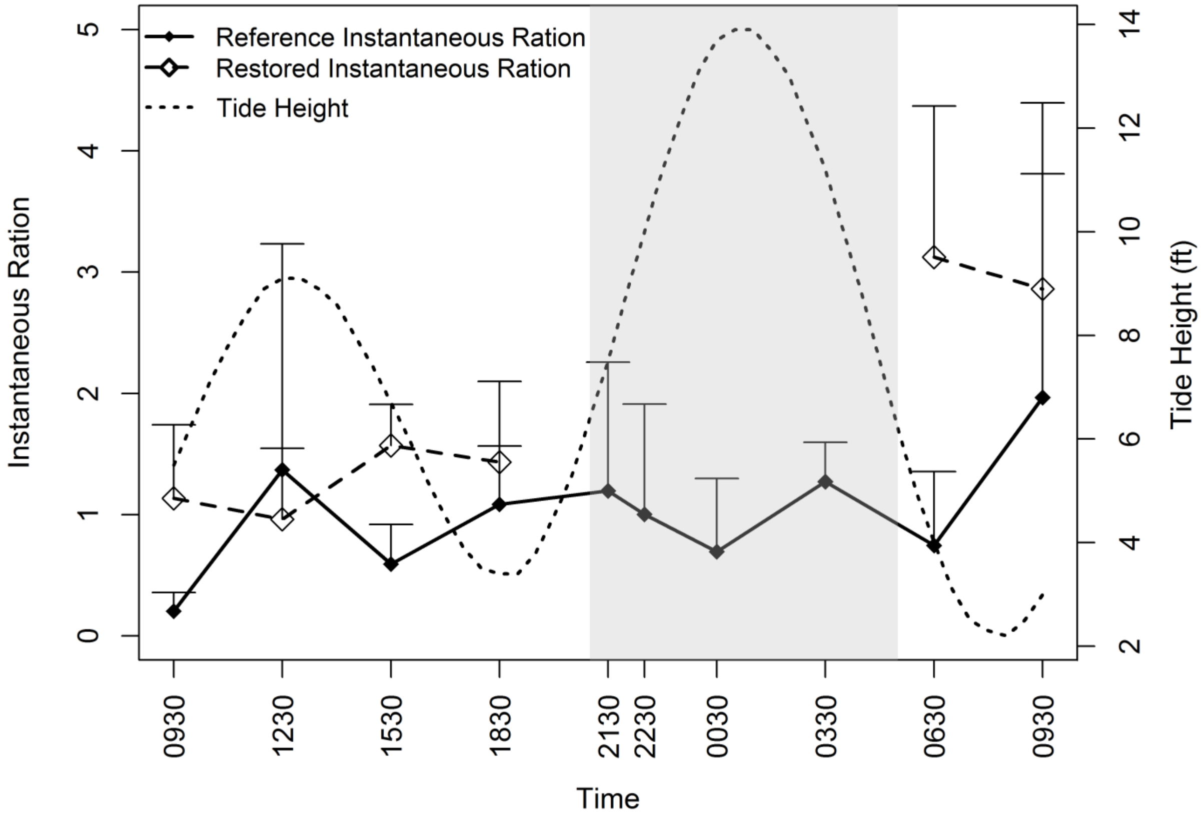

Figure A.2.3. Diel variation in instantaneous ration for juvenile Chinook salmon sampled simultaneously in both reference and restored habitats within the Nisqually River delta over a 24 h period from 29-30 May, 2012. The hours of darkness are indicated in gray. Error bars represent + 1 SD.

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