# Size-selective mortality and environmental factors affecting early marine growth during early marine life stages of sub-yearling Chinook salmon in Puget Sound, Washington

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# Abstract

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Body size, mediated through biotic and abiotic factors affecting growth, is fundamental in determining survival as larger animals are usually less vulnerable to predation, starvation, and extreme environmental conditions (Peterson & Wroblewski 1984; Sogard 1997). Size-selective mortality is a prevalent force regulating marine survival for many anadromous salmonid species, including ESA-listed Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, WA. The "critical size – critical period" hypothesis suggests that marine survival of anadromous Pacific Salmon (*Oncorhynchus spp.*) is controlled by two size-selective survival bottlenecks – one during the first marine summer and another during the first marine winter (Beamish and Mahnken 2001). Previous research has indicated a strong positive relationship between the size of juvenile ESA-listed Chinook salmon (*O. tshawytscha*) in Puget Sound and their survival to adulthood, indicating that early marine growth drives survival (Duffy 2009). Before investigating the drivers of early marine growth, however, it is imperative to understand whether size-selective mortality occurs prior to July in Puget Sound. If so, we may be able to augment marine survival by directing conservation and restoration efforts toward the habitats or regions of Puget Sound where size-selective mortality occurs. Additionally, we must account for any size-selective mortality in estimating early marine growth, as observed weight in July would reflect an artificially inflated "apparent" growth if smaller individuals were experiencing disproportionately high mortality. In this study, we repeatedly sampled nine stocks of both wild and hatchery-origin sub-yearling Chinook salmon during their outmigration into and rearing in Puget Sound. We used scale morphometrics to determine if size-selective mortality is affecting sub-yearling Chinook salmon during their first marine summer rearing in Puget Sound, and if so, where and when that size-selective mortality occurs. We found no evidence of size-selective mortality occurring between habitats or between sampling periods within habitats, suggesting that weight of juvenile Chinook as measured in July is representative of early marine growth and that size-selective mortality occurs later in the summer or outside Puget Sound during the first marine winter. We then focused on understanding differences in growth rates across time, among habitats, and among stocks of juvenile Chinook salmon, and used bioenergetic models to determine the relative influence of prey quality, prey availability, and temperature on early marine growth rates We found that sub-yearling Chinook were larger and grew faster in offshore than in nearshore habitats, and that this difference in growth rate was likely due to differences in prey availability and may have been exacerbated by higher nearshore temperatures. The results of this study can be used to direct restoration and conservation efforts aimed at supporting early marine growth of juvenile Chinook in Puget Sound, and can augment our understanding of distribution patterns and feeding behaviors of Pacific salmon during critical growth periods.

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# Introduction

Body size, mediated by environmental factors affecting growth, is fundamental in determining survival as larger animals are usually less vulnerable to predation, starvation, and extreme environmental conditions (Peterson & Wroblewski 1984; Sogard 1997). The relationship between size and survival in ecosystems where the intensity of size-related mortality varies over time and space has been codified in the "critical size-critical period" hypothesis (Beamish and Mahnken 2001). This hypothesis, which was formed to describe variable patterns of growth and survival in populations of anadromous fish, postulates that individuals must reach a certain size (absolute or relative to other individuals) in order to survive a critical period during which mortality is high and size-selective.

Size-selective mortality is prevalent during marine life stages of Pacific salmon (*Oncorhynchus spp.*; coho: Beamish et al. 2004, Holtby et al. 1990; pink: Cross et al. 2008; chinook: Duffy and Beauchamp 2011; chum: Healey 1982; sockeye: Henderson and Cass 1991; steelhead: Ward et al. 1989, Thompson and Beauchamp 2014). Though the timing, location, and agents of the majority of marine mortality are unclear, the "critical size-critical period" hypothesis suggests that Pacific salmon populations experience two size-related survival bottlenecks – one due to predation during their first marine summer and the other due to starvation during their first marine winter – that largely regulate marine survival.

Marine survival of Chinook salmon is highly correlated with size during their first marine growth season throughout their range, both within (Claiborne et al. 2011, Woodson et al. 2013) and among years (Duffy and Beauchamp 2011, Tomaro et al. 2012). This suggests that early marine growth conditions play a critical role in determining survival to adulthood. However, the period in which growth matters most to survival is unknown, as is the relative importance of environmental factors regulating growth within that period.

Chinook salmon in the Salish Sea (the Straight of Georgia, Canada and Puget Sound, Washington) have exhibited particularly low and declining marine survival rates since 1980 (Ruggerone and Goetz 2004, Sharma et al. 2012), such that Puget Sound Chinook salmon are now listed as threatened under the Endangered Species Act. Smolt-to-adult survival rates for hatchery-reared sub-yearling Chinook salmon within Puget Sound have averaged less than 1% over the past three decades (Kilduff et al. 2014), while stocks from adjacent regions (i.e. west coast of Vancouver Island and coast of Washington) have not shown similar declines (Kilduff et al. 2015). This pattern suggests factors affecting marine survival may be occurring within Puget Sound and has motivated recent research efforts to isolate potential mechanisms.

Puget Sound is a deep glacial fjord comprised of four basins with different oceanographic and ecological characteristics (Moore et al. 2008). This study focused on sub-yearling Chinook salmon from the Nooksack, Skagit, Snohomish, and Nisqually rivers (**Figure 1**), which drain into the North, Whidbey, and South basins of Puget Sound. Each of these rivers supports both wild and hatchery-produced Chinook salmon. Sub-yearling "ocean-type" juveniles predominate throughout Puget Sound (Healey 1991), though in some snow-dominated watersheds up to half of the juvenile Chinook salmon may exhibit a stream-type life history strategy (Beechie et al. 2006). Sub-yearling Chinook salmon generally enter marine waters between May and July and rear in Puget Sound for most of the summer (Duffy et al. 2005). During their outmigration they move through and feed in tidally influenced estuarine deltas, shallow nearshore marine habitats, and into the epi-pelagic offshore habitat within Puget Sound (Duffy et al. 2005). Both within and across river systems, growing conditions and predation risk may differ among habitats and across time such that each combination of habitat and sample period represents a separate “life stage” for juvenile Chinook.

Previous research identified a strong positive relationship between marine survival and the weight of sub-yearling Chinook salmon sampled in July in offshore habitats within Puget Sound (Duffy and Beauchamp 2011). However, it is unclear whether size-selective mortality had occurred prior to that life stage. If so, growth between marine entry and some earlier life stage might be most critical in determining survival. If significant size-selective mortality had not occurred prior to the offshore July life stage, the growth period between marine entry and the offshore July life stage would be most critical for survival.

Once the critical growth period is identified, bioenergetics models can be used to determine the environmental factors affecting early marine growth and the scale at which those factors vary. From a bioenergetics perspective, prey quality, prey availability and water temperature are the major environmental factors affecting growth (Beauchamp 2009). Growth rate at a given temperature increases with an increase in the energetic quality of prey and with the amount of prey consumed. The range of temperatures at which positive growth is possible depends on the size of the salmon, the composition of its diet, and its feeding rate (Beauchamp 2009). The spatial and temporal variation in these ecological factors affecting growth could differ considerably among populations, habitats or basins within Puget Sound. Thus, the key processes limiting growth during critical periods might differ among stocks of Chinook salmon and could operate on different habitats or at different times. Identifying the critical growth periods for Chinook salmon in Puget Sound, as well as the factors affecting growth and the temporal and spatial scales on which they act during those critical growth periods, can help guide restoration and conservation efforts that will most effectively support early marine growth and survival. Because growth rates at different life stages can also affect migration strategies and distribution patterns of Pacific Salmon species, understanding the drivers of differences in growth rates among habitats and life stages can also lead to a more thorough understanding of movement, distribution, and survival patterns of Pacific salmon

## Research Objectives

Chapter 1: The objective of chapter 1 was to identify patterns of size-selective mortality both within and between habitats during the first marine growth season for sub-yearling Chinook salmon in Puget Sound. To address this objective we compared average growth histories created from scale morphometrics from nine stocks of wild and hatchery-origin sub-yearling Chinook salmon. For each stock, average growth histories were compared across fish sampled in different habitats and in different sample periods within habitats.

Chapter 2: The objectives of chapter 2 were (1) to identify differences in weight and growth rate across time, among habitats, and among stocks; and (2) to determine the relative influence of prey quality, prey availability, and water temperature on growth of sub-yearling Chinook salmon during early marine life stages in Puget Sound. To address these objectives we used bioenergetics models parameterized with metabolic rates for juvenile Chinook salmon and informed with observed weight, temperature, and diet data to estimate consumption and feeding rate over time. We used scale growth trajectories to ensure that average observed weights accurately reflected actual growth. We then determined whether growth rates changed over time, among habitats, or among stocks, and then analyzed variation in average prey quality, average feeding rate, and average water temperature over the same dimensions to determine which environmental factors had the greatest influence on growth.

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# Chapter 1 – Size-selective mortality of hatchery and wild sub-yearling Chinook salmon (*Oncorhynchus tshawytscha*) during early marine life stages in Puget Sound

## Abstract

Body size can be critical to an animal's fitness. Larger individuals may have higher survival rates as they are often less susceptible to predation, starvation, and extreme environmental conditions (Peterson and Wroblewski 1984, Sogard 1997). In marine ecosystems, survival to adulthood can be largely influenced by size-selective mortality during juvenile life stages (Sogard 1997). The "critical size – critical period" hypothesis suggests that marine survival of anadromous Pacific Salmon (*Oncorhynchus spp.*) is controlled by two size-selective survival bottlenecks – one during the first marine summer and another during the first marine winter (Beamish and Mahnken 2001). Previous research has indicated a strong positive relationship between the size of juvenile ESA-listed Chinook salmon (*O. tshawytscha*) in Puget Sound and their survival to adulthood, indicating that early marine growth drives survival (Duffy 2009). Before investigating the drivers of early marine growth, however, it is imperative to understand whether size-selective mortality occurs prior to July in Puget Sound. If so, we may be able to augment marine survival by directing conservation and restoration efforts toward the habitats or regions of Puget Sound where size-selective mortality occurs. Additionally, we must account for any size-selective mortality in estimating early marine growth, as observed weight in July would reflect an artificially inflated "apparent" growth if smaller individuals were experiencing disproportionately high mortality. We repeatedly sampled nine stocks of sub-yearling Chinook during their outmigration into and rearing in Puget Sound. We used scale morphometrics to determine if size-selective mortality is affecting sub-yearling Chinook salmon

during their first marine summer rearing in Puget Sound, and if so, where and when that size-selective mortality occurs. We found no evidence of size-selective mortality occurring between habitats or between sampling periods within habitats, suggesting that weight of juvenile Chinook as measured in July is representative of early marine growth and that size-selective mortality occurs later in the summer or outside Puget Sound during the first marine winter.

## Introduction

Body size, mediated through biotic and abiotic factors affecting growth, is fundamental in determining an animal's survival. Because larger animals are usually less vulnerable to predation, starvation, and extreme environmental conditions (Peterson and Wroblewski 1984, Sogard 1997), ecological conditions that affect growth and size are key to an animal's survival and fitness. The relationship between size and survival in ecosystems where the intensity of size-related mortality varies over time and space has been codified in the "critical size-critical period" hypothesis (Beamish and Mahnken 2001). This hypothesis, which was formed to describe variable patterns of growth and survival in populations of anadromous fish, postulates that individuals must reach a certain size (absolute or relative to other individuals) in order to survive a critical period during which mortality is high and size-selective.

Size-selective mortality during juvenile life stages can regulate survival of many marine fishes (Sogard 1997), including Pacific salmon (*Oncorhynchus spp.*; coho: Holtby et al. 1990, Beamish et al. 2004; pink: Cross et al. 2008; chinook: Duffy and Beauchamp 2011; chum: Healey 1982; sockeye: Henderson and Cass 1991; steelhead: Ward et al. 1989, Thompson and Beauchamp 2014). The "critical size-critical period" hypothesis (Beamish and Mahnken 2001) suggests that Pacific salmon populations experience two size-related survival bottlenecks – one due to predation during their first marine summer and the other due to starvation during their first marine winter – that largely regulate marine survival.

Throughout their range, marine survival of Chinook salmon (*O. tshawytscha*) is highly correlated with size achieved during their first marine growth season, both within (Claiborne et al. 2011, Woodson et al. 2013) and among years (Duffy and Beauchamp 2011, Tomaro et al. 2012). This is consistent with the "critical size-critical period" hypothesis (Beamish and Mahnken 2001) and suggests that marine mortality is size-selective and that the survival of juvenile Chinook could be determined by the size they achieve during their first marine growth season.

Marine survival rates of Chinook salmon in Puget Sound have declined drastically since 1980 (Ruggerone and Goetz 2004, Sharma et al. 2012). Smolt-to-adult survival rates for hatchery-reared sub-yearling Chinook within Puget Sound have averaged less than 1% over the past three decades (Kilduff et al. 2014), while stocks from adjacent regions (i.e. west coast of Vancouver Island and coast of Washington) have not shown similar declines (Kilduff et al. 2015). This pattern suggests factors affecting marine survival may be occurring within Puget Sound and has motivated recent research efforts to isolate potential mechanisms.

Previous research revealed a strong positive correlation between marine survival of Puget Sound hatchery release groups and their body mass in July, after most sub-yearling hatchery-origin Chinook salmon have increased their body mass by a factor of 2-4 while feeding for approximately one month in offshore epi-pelagic habitats within Puget Sound (Duffy and Beauchamp 2011, Beauchamp and Duffy 2011). That work suggested that growth achieved prior to July was critical to survival. However, prior to investigating factors influencing this critical early marine growth period we must understand whether the positive relationship between size and survival was influenced by size-selective processes during or before this offshore feeding period. If so, the body mass in July would represent “apparent” growth achieved, which would be artificially inflated if a greater proportion of smaller fish had been culled from the population. In order to understand the actual growth achieved by juvenile Chinook salmon during their first marine summer it is imperative to understand the scale and intensity of stage-specific growth and size-selective mortality occurring prior to mid-summer in Puget Sound.

If size-selective mortality occurs within Puget Sound during the first marine growth season, examining when and where it occurs will suggest processes that drive marine survival. It may also guide future monitoring that could be used to forecast marine survival, and steer restoration or conservation efforts within Puget Sound toward particular habitats that may augment early marine growth and survival of Chinook salmon. Size-selective mortality is a convenient indicator of factors affecting marine survival as it integrates effects of biological status (size, growth rate) and processes (starvation, predation) with behavior (foraging, predator avoidance) into one metric rather than conforming to a classical “top-down” or “bottom-up” approach in describing mortality. Evaluating size-selective mortality allows us to investigate mortality through characteristics of survivors rather than mechanisms of death, which are difficult to observe or detect in marine environments.

The objective of this study was to examine where, when, and the extent to which sub-yearling Chinook salmon may experience size-selective mortality during their outmigration from freshwater to rearing habitats in Puget Sound. We evaluated size-selective mortality across habitats and life stages (habitat/sampling period combinations) by comparing the growth history of juveniles sampled in one life stage with the growth history of individuals sampled in subsequent life stages (assumed to be “survivors” of the previous life stage). Average growth histories of migrating juveniles in each habitat were determined using scale analysis, a standard technique for analyzing age and back-calculating size-at-age of salmonids (Ricker 1992). Specifically, we were interested in understanding (1) whether size-selective mortality occurs in transitions between habitats or life stages (i.e. within habitats between sampling periods), (2) the scale of geographic and temporal variability in size-selective mortality across four focal watersheds and associated marine areas, and (3) whether hatchery and wild populations exhibit similar patterns of size-selective mortality.

## Methods

### *Study System and Sample Collection*

Puget Sound is a deep glacial fjord comprised of four basins with different oceanographic and ecological characteristics (Moore et al. 2008). This study focused on sub-yearling Chinook salmon from the Nooksack, Skagit, Snohomish, and Nisqually rivers (**Figure 1**), which drain into the North, Whidbey, and South basins of Puget Sound. Each of these rivers supports both wild and hatchery-produced Chinook salmon. Sub-yearling "ocean-type" juveniles predominate throughout Puget Sound (Healey 1991), though in some snow-dominated watersheds up to half of the juveniles may exhibit a stream-type life history strategy (Beechie et al. 2006). Sub-yearling Chinook generally enter marine waters between May and July and rear in Puget Sound for most of the summer (Duffy et al. 2005). During their outmigration they move through and feed in tidally influenced estuarine deltas, shallow nearshore marine habitats, and into the epi-pelagic offshore habitat within Puget Sound (Duffy et al. 2005). Both within and across river systems, growing conditions and predation risk may differ among habitats and across time such that each combination of habitat and sample period represents a separate "life stage" for juvenile Chinook.

Because wild and hatchery Chinook salmon display different migration and distribution patterns in Puget Sound (Rice et al. 2011), this study sampled both wild and hatchery juveniles and examined their growth histories separately. Hatchery-origin Chinook salmon can be identified by a clipped adipose fin, a coded wire tag (CWT) implanted in their nasal cavity, or both. CWTs, which can be detected with specialized metal detectors, are encoded with information about the hatchery of origin, broodstock, release age, release date, and release site of the individual. Some hatcheries also apply unique thermal marks to the otoliths of Chinook they release by manipulating the water temperature in which the juveniles are reared. Like CWTs, these thermal marks can be used to determine the origin of the fish.

We collected both natural origin and hatchery-reared sub-yearling Chinook in freshwater, estuarine tidal delta (hereafter "estuary"), nearshore marine ("nearshore"), and offshore epi-pelagic ("offshore") habitats within Puget Sound associated with the Nooksack, Skagit, Snohomish, and Nisqually rivers (**Figure 1**). Hatchery-origin individuals were identified by an adipose fin clip and/or the presence of a CWT. We sampled downstream-migrating smolts in freshwater habitats using smolt traps, in estuarine and nearshore habitats using beach seines (following Duffy et al. 2005), and in offshore habitats using a purse seine (*F.V. Franciscan I*, approximate net dimensions: 402 m long, fished effectively to 22 m; bunt constructed of 1cm knotless mesh to 18 m, 1.3 cm knotless mesh to 73 m, 2 cm knotless mesh to 146 m, 9cm knotted mesh to 402 m). We also collected sub-yearling Chinook from hatcheries in the Nisqually, Snohomish, and Skagit watersheds in the week prior to release for baseline size and growth history data (**Table 1**). Sampling occurred approximately every two weeks from early May through early August for offshore habitats, late January through late July for freshwater habitats, and late January through early October for estuarine and nearshore habitats (with some variation among watersheds). All samples were collected in 2014. These sampling periods were determined mainly by historical presence of juvenile sub-yearling Chinook in each habitat at different times of year (Duffy et al. 2005, Rice et al. 2011).

During each sampling event we recorded total counts, mark types, fork lengths, and weights of hatchery and wild Chinook salmon. Up to 30 hatchery-origin Chinook in each sampling event were lethally sampled for CWT and otolith extraction and reading; up to 30 unmarked Chinook were sampled live and released whenever possible. From each individual we sampled scales, diet (via gastric lavage in the field or dissection in the lab), and caudal fin tissue used for genetic stock identification of unmarked (natural-origin) Chinook. Scales were taken from the "preferred area" on the side of the fish, from the second to the seventh rows of scales above the lateral line and on a diagonal from the posterior insertion of the dorsal fin to the front of the anal fin (Mosher 1968, Shearer 1992). Scales were stored in a piece of folded wax paper in a coin envelope. Diet samples lavaged in the field were frozen in a small zip-lock plastic bag in water from the sample site; whole stomachs dissected in the lab were frozen in a small zip-lock plastic bag. Fin clips were stored in 95% ethanol. Otoliths were removed in the lab and stored dry.

### *Stock Definition and Identification*

To test whether mortality was size-selective, we tracked defined groups ("stocks") of wild and hatchery juveniles exhibiting similar outmigration patterns from each watershed and looked for changes in the frequency distribution and average size-at-age of each stock as evidence of size-selective mortality. In order to minimize variation in genetic predisposition to growth and exposure to different growth environments prior to sampling, all data analyses were performed on separate identifiable stocks of fish originating from the same hatchery-release group or wild population. A hatchery-origin stock was defined as a group of fish from the same broodstock released from the same hatchery at the same time, as determined by CWTs or thermal otolith thermal marks. Wild fish were assigned to specific populations using a 192 SNP (single nucleotide polymorphism) panel for Puget Sound Chinook salmon (Fournier et al. 1984, Millar 1987, Warheit et al. 2013). Population information was used to aggregate fish into natural-origin stocks for our analyses. Genetic stock identification was limited to the Skagit and Nooksack watersheds for this study.

### *Approach and Assumptions*

We used scale morphometrics to identify size-selective mortality within each stock. Because scales grow in proportion to the fish's length and circuli are laid down at a relatively constant rate throughout the growing season (Fisher and Pearcy 1990, Ricker 1992), the scale radius at a given circulus is proportional to the length of the fish at a given age, and the increase in scale radius between circuli is approximately proportional to growth rate. We tested the assumption that scale radius is proportional to fish length by fitting a regression of scale radius and fish length using scales from all sub-yearling Chinook under 300 mm fork length that were sampled during this study, and referred back to this regression to ensure that it was consistent across scale samples from each cohort. To test the assumption that circulus count was a reasonable proxy for age (i.e. time), we fit a regression of time (day of year) and circulus count separately for each stock to determine whether the relationship was linear. Although circulus deposition rate can also be affected by growth rate (Bilton 1971, Fisher and Pearcy 1990, Beakes et al. 2014), which might vary across habitats throughout the summer or across time within habitats, the covariance of time and habitat precluded meaningful statistical analyses to test the effect of habitat (i.e. growth rate) on circulus count.

Our methods for identifying size selective mortality (see below) also assume that (1) juvenile Chinook occupied each habitat sequentially rather than moving back and forth between habitats, and (2) fish did not leave the offshore regions associated with their natal watershed (i.e., within an approximately 25 km radius of the estuarine delta) at different rates based on their marine entry size or date. To verify these assumptions, we analyzed otoliths from a subset of sub-yearling Chinook from a single wild stock caught in the Skagit nearshore (n = 15) and offshore (n = 18) between early June and early July (nearshore) and between early July and early August (offshore). Otolith microchemistry was analyzed to reconstruct size of each juvenile Chinook upon first encountering salt water. Juvenile sagittal otoliths were prepared for chemical analysis by thin sectioning in the sagittal plane. Otolith material was first removed from the distal and proximal surfaces until primordia were exposed or nearly exposed, similar to methods used in Volk et al. (Volk et al. 2010) and Campbell et al (Campbell et al. 2015). All otolith chemistry was conducted at the Keck Collaboratory for Plasma Mass Spectrometry at Oregon State University using a sThermo X series II inductively coupled plasma mass spectrometer paired with a Photon Machines G2 193-nm excimer laser (LA-ICPMS). Ablated material was transported from the laser to the mass spectrometer using helium as the carrier gas. The LA-ICPMS operating conditions were as follows: 13 L/min cooling gas, 0.95 L/min auxiliary gas, 0.75 L/min Helium. The laser beam diameter was set at 30 microns, scanned at 5 microns/second at a pulse rate of 8 Hz. Laser transects were drawn from the otolith core to the otolith edge in the dorsal/posterior quadrant (~ 25° from the midline). Inflection points for calcium (Ca) and strontium (Sr) and deflection (Ca) were recorded. Transformation to otolith distances was completed based from a laser scan speed of 5um/sec as used in Claiborne and Campbell (Claiborne and Campbell 2016). To reconstruct residency in marine water we completed daily increment analysis from the otolith edge to the point of Sr:Ca inflection (Pannella 1971, Volk et al. 2010).

To test our assumptions of sequential migration and unbiased migration out of the offshore habitat, we examined relationships between capture date and size and date of marine entry for nearshore and offshore samples. If juvenile Chinook were moving through habitats sequentially and then remaining offshore until emigration from Puget Sound, we expected to find a positive relationship between sample date and marine entry date in the nearshore but not the offshore, and to find less variation in marine entry date in the nearshore than in the offshore. If fish were migrating out of our study system or out of a given habitat at different rates based on marine entry size or date, we expected there would be positive relationships between capture date and marine entry date and marine entry size for all fish combined and separately for nearshore and offshore samples. A wild stock was used for this analysis because marine entry size and timing are more variable for wild populations than for hatchery release groups, so results would be conservative for hatchery stocks.

### *Identifying Size-selective Mortality*

To evaluate size-selective mortality we used only sub-yearling Chinook of known origin that were caught and sampled in habitats associated with their natal watershed to exclude those that may have experienced different growth environments. We only looked for evidence of size-selective mortality in stocks from our focal watersheds from which at least 10 fish had been collected in at least two life stages (habitat/sample period combinations). We analyzed scales from all fish in each stock that fit these criteria.

To prepare scales for measurement we created impressions of up to 10 scales from each fish by mounting them on gummed cards and pressing them into acetate strips (Cross et al. 2008). For each fish we selected the scale to be imaged and measured based on quality of the scale (avoiding damaged or regenerated scales) and clarity of the impression. The acetate impressions were imaged with a digital camera attached to a Leica MZ6 microscope fitted with 20x oculars and a 2.0x objective (camera model: Lumenera Infinity1-3c; camera lens attachment: Diagnostic Instruments 1.0x HR100-CMT; total magnification ranged from 64x to 160x depending on the size of the scale). Scale measurements were taken from scale images with ImagePro or ImageJ software. For each scale we recorded total circulus count, total scale radius, and scale radius at each circulus. Scale radii at each circulus were used to create individual growth histories. Individual growth histories were then averaged to assess mean size-at-age for each stock as sampled in different life stages. Prior to averaging individual growth histories in each of these analyses we plotted all individual growth histories of fish from each life stage on a single set of axes to visually ensure that they exhibited a central tendency.

To determine whether size-selective mortality was associated with specific habitats or life stages, we evaluated average growth histories at two different scales for each stock. To look for larger scale, habitat-specific size-selective mortality we averaged growth histories of fish caught in each habitat across all sampling periods. To evaluate finer scale, life stage-specific size-selective mortality within and across habitats, we averaged growth histories for fish caught in the same life stage (habitat and sample period). Any average scale radius measurements that came from fewer than three measurements at that circulus were excluded to avoid spurious patterns due to low sample size.

For both habitat- and life stage-specific analyses, we looked for changes in average size-at-age between subsequent habitats or life stages within each stock by plotting average growth histories for sequential life stages. If size-selective mortality occurred, subsequent life stages should show *higher* size-at-age at circuli formed during previous life stages, as average size-at-age would increase as smaller fish dropped out of the stock (**Figure 2a**). The opposite trend, in which later life stages show *lower* size-at-age, could indicate size-selective migration, since average size-at-age would decrease as smaller or slower growing fish migrated into the habitat and larger or faster growing fish migrated out of the habitat (**Figure 2b**). No change in stage-specific growth histories among life stages or habitats would suggest that size-selective mortality did not occur within that stock (**Figure 2c**).

## Results

We identified seven hatchery and two wild stocks of sub-yearling Chinook that were sampled sufficiently in two or more sampling events throughout the summer. There were two hatchery-origin stocks from each of the Nooksack (Kendall Creek and Skookum Creek hatcheries), Skagit (spring and summer releases from Marblemount hatchery), and Snohomish (Bernie Kai-Kai Gobin Tulalip and Wallace hatcheries) watersheds and one stock from the Nisqually watershed (Nisqually Clear Creek hatchery; **Table 1**). The wild stocks originated from the Nooksack Fall and the Upper Skagit Summer populations. For hatchery stocks, peak outmigration times across all habitats ranged from early May to late July (**Figure 3**). Peak catches in the estuary and nearshore habitats preceded peak offshore catches in all but the Snohomish Wallace stock, in which peak catches in the estuary and nearshore coincided with those in the offshore. The wild stocks exhibited more protracted outmigrations than the hatchery stocks.

*Approach & Assumptions*

Our samples confirmed that scale radius was proportional to fork length (FL = 173.764 * SR + 21.808; $r^2 = 0.85$; N = 2591) and that circulus count explained the majority of variation in age (i.e. time) for all except the Snohomish Tulalip stock (**Table 2**). The deviation of the Snohomish Tulalip stock from this pattern could be the result of large variation in hatch timing within the hatchery, which would create a wider range of circulus counts (i.e. ages) among fish from that stock sampled on a given day. Excluding the Snohomish Tulalip stock, circulus deposition rates ranged from 4.6 to 8.3 days with hatchery stocks exhibiting significantly shorter deposition rates than wild stocks (hatchery: 5.9 ± 0.76 days, wild: 7.9 ± 0.57 days, t =-3.33, df = 6, $p = 0.02$).

Otolith microchemistry patterns for the wild Skagit Upper Summer stock revealed a positive correlation between capture date and marine entry date for fish sampled in the nearshore ($F = 6.992$; df = 1,13; $p = 0.02$), but not in the offshore ($F = 0.628$; df = 1,16; $p = 0.4$; **Figure 4a**), indicating that fish used the nearshore as a transitional habitat but tended to remain offshore after leaving nearshore habitats. The variance in marine entry date for fish sampled in the nearshore was lower than that in the offshore ($F = 0.283$, df = 13,17; $p = 0.03$), which also suggested that fish moved through the nearshore and then linger offshore. One sample was deemed an outlier and excluded from this analysis based on a marine entry date that was outside the lower quartile minus 1.5 times the interquartile range. Finally, capture date was positively correlated with marine entry size for fish sampled in the nearshore ($F = 4.664$; df = 1,13; $p = 0.05$), but not in the offshore ($F = 0.082$; df = 1,16; $p = 0.8$; **Figure 4b)**. These results also supported our assumptions that juvenile Chinook used the nearshore as a transitional habitat and that there was no effect of marine entry size or date on juvenile Chinook migration out of the offshore area associated with their natal watershed.

### *Identifying Size-selective Mortality*

We found little evidence of size selective mortality among juvenile life stages from marine entry through early August in Puget Sound. In the habitat-specific analysis, the Upper Skagit Summer and Nooksack Skookum Creek stocks showed some apparent divergence between average growth histories for the nearshore and offshore habitats. The divergence was not significant for the Skagit Upper Summer stock (t = -1.918, df = 8, $p = 0.09$) but was significant for the Nooksack Skookum Creek Stock (t = -3.2074, df = 11, $p = 0.008$; **Figure 5**). However, the regression of scale radius and fork length from nearshore scale samples from the Nooksack Skookum Creek stock did not align with the benchmark regression of scale radius and fork length, suggesting that nearshore scales had been taken above the "preferred area". This would result in an underestimation of scale radius at each circulus, which would artificially exaggerate the divergence in size-at-age between nearshore and offshore samples. The other seven stocks showed no divergence between average growth histories at the habitat scale throughout the sampling period.

The life stage-specific analysis also showed little evidence for size-selective mortality. Again, a few stocks (Nisqually Clear Creek, Nooksack Kendall Creek, and Nooksack Skookum Creek) showed some divergence in average growth histories between life stages, but in all cases overlapping standard deviations suggest that divergence is not likely due to size-selective mortality (**Figure 6**).

## Discussion

We found little evidence for size-selective mortality affecting sub-yearling Chinook salmon from marine entry through early August in Puget Sound. This was evident in both large-scale (habitat) and fine-scale (life stage) analyses. Though both analyses showed some apparent divergence between average growth histories for different life stages, these divergences were either not statistically significant or, in the case of the Nooksack Skookum Creek stock, were likely due to questionable scale radius data. We expected that wild stocks, which would vary more in size and date of outmigration (Rice et al. 2011), might show stronger size-selective mortality than the more homogenous hatchery stocks, as variation is a prerequisite to selection. However, we found no difference in patterns of size-selective mortality between hatchery and wild stocks.

Previous research showed a strong relationship between the size of juvenile Chinook salmon in July and smolt-to-adult returns, indicating that size-selective mortality may drive overall marine survival (Duffy and Beauchamp 2011). Our results suggest that significant size-selective mortality does not occur in Puget Sound prior to mid-summer. This means that weight as measured in July is a reasonable estimate of early marine growth, as earlier size-selective mortality has not artificially inflated the average size by culling smaller individuals. Taken together, these results suggest that early marine growth achieved through at least July is critical to marine survival and could provide a useful predictor of adult returns. This is consistent with studies on Chinook and other species of Pacific salmon and steelhead, both within Puget Sound and throughout the west coast, that have shown similar positive relationships between marine survival and early marine growth (Healey 1982, Henderson and Cass 1991, Beamish et al. 2004, Cross et al. 2008, Duffy and Beauchamp 2011, Tomaro et al. 2012, Thompson and Beauchamp

2014). Therefore understanding drivers of growth throughout the first marine summer can help channel resources into restoration or conservation activities that will have the greatest impact on overall marine survival.

Our methods made three key assumptions that we tested using fish collected for this study. The first was that scale radius at a specific circulus would be proportional to size at a given age for each stock. Our results confirmed that scale radius was proportional to size, and that juvenile Chinook formed circuli at a relatively constant rate within each stock, confirming our assumption that a circulus or range of circuli corresponds to a particular age or life stage within a stock. We also assumed that changes in back-calculated size-at-age within a stock would be due to size-selective mortality or size-selective migration among sampling habitats rather than migration of faster or slower growing fish out of Puget Sound. Otolith analyses suggested that migration out of the study system was not related to marine entry size or date, and that fish transitioned from the nearshore to the offshore rather than frequently moving between the two habitats. Previous studies and sampling efforts also indicate that this study accounted for the common habitat usage patterns expressed by sub-yearling Chinook in Puget Sound. Migration patterns of both hatchery and wild sub-yearling Chinook show sequential pulses of Chinook transitioning from estuarine and nearshore marine habitats to epi-pelagic offshore habitats within Puget Sound through early and mid-summer (Duffy et al. 2005, Rice et al. 2011). Additionally, mid-water trawl survey data suggest that juvenile Chinook occupy the epi-pelagic offshore habitat within Puget Sound throughout the temporal scope of this study (Kemp 2014).

This study cannot rule out the possibility that juvenile Chinook experience size-selective mortality at the basin or Puget Sound scale. For example, fish in the Skagit Summer stock, which were smallest at hatchery release, may have experienced higher mortality than stocks with a larger size at release. We cannot make any conclusions about size-selective mortality between stocks, as a scale-based analysis of size-selective mortality at the basin- or Puget Sound-scale is precluded by variation in hatch timing, outmigration timing, and circulus deposition rates across watersheds and between wild and hatchery stocks and because different scale regions are associated with different life stages for each stock. Inference of size-selective mortality across stocks would require that stocks were sampled as a group in the same time and place, and that a given life stage could be associated with a single circulus benchmark across those stocks. However, comparing our juvenile scale samples to scales from surviving adults from each stock will give more conclusive evidence of size-selective mortality during the first marine growth season. Those patterns would also emerge from a comparison of adult and juvenile scales from the same stock.

We conclude that the strong size-selective mortality experienced by Puget Sound Chinook salmon occurs after July and operates on life stages either within or outside Puget Sound. However, the size achieved by July strongly influences survival to adulthood (Duffy and Beauchamp 2011). Therefore, understanding the factors that most influence growth during this critical period will be essential for guiding restoration and recovery efforts. This study is the first step toward a deeper understanding of the mechanisms driving early marine growth and the connection between growth and survival. Other studies have suggested that size affects survival of Chinook salmon only in years with low overall survival, indicating that size-independent factors can be equally or more important in some years (Holtby et al. 1990, Quinn et al. 2005, Claiborne et al. 2011, Woodson et al. 2013). The next step in this research should be to understand the interannual variation in early marine growth and size-selective mortality and compare that with interannual trends in marine survival. To understand the variability of our results across larger spatial and temporal scales, future work should also compare the results presented here to size-selective mortality trends in other large bays and inland waterways (i.e. San Francisco Bay and Southeast Alaska), investigate how large-scale oceanic conditions affect processes within these inland seas, and compare trends in early marine growth across a greater temporal scale. This research could elucidate the conditions under which size-selective mortality and early marine growth regulate marine survival, and which other factors affect marine survival when size-selective mortality does not.

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## Tables

**Table 1.** Hatchery rearing and release information for hatchery-origin stocks included in the analyses. Integrated hatcheries use wild fish in their broodstock; segregated hatcheries use only hatchery-origin fish.

| Stock | Release Date(s) | Total Fish Per Pound | Mean Length (mm) | CV Length (%) | Broodstock Run Time | Hatchery Type |
|---|---|---|---|---|---|---|
| Nisqually Clear Creek | 4/22-30/14 | 55 | 87.7* | 9.0* | Fall | Segregated |
| Snohomish Tulalip | 5/21-29/14 | 90 | 68.4* | 12.6* | Summer | First generation segregated** |
| Snohomish Wallace | 6/1-7/14 | 75 | 80.2 | 7.7 | Summer | Integrated |
| Skagit Spring | 6/12/14 | 80 | 114 | 3.9 | Spring | Segregated |
| Skagit Summer | 6/25/14 | 100 | 73 | 8.4 | Summer | Integrated |
| Nooksack Kendall Creek | 4/15/14-5/16/14 | 92.6 | 77.8 | 4.6 | Spring | Segregated |
| Nooksack Skookum Creek | 6/2-5/14 | 80 | Not available | Not available | Spring | Integrated*** |

*calculated from samples received from hatchery, not reported by hatchery
**segregated broodstock are offspring of integrated broodstock
***captive broodstock from wild Nooksack Spring population, kept at USGS Manchester facility

**Table 2.** Output of linear regressions of time and circulus count for each cohort. “H” and “W” denote hatchery and wild stocks, respectively

| Stock | Circulus Deposition Rate | Intercept | $r^2$ |
|---|---|---|---|
| Nisqually Clear Creek (H) | 6.7 | 44.462 | 0.528 |
| Snohomish Tulalip (H) | 2.7 | 129.037 | 0.275 |
| Snohomish Wallace (H) | 5.9 | 108.797 | 0.565 |
| Skagit Spring (H) | 5.6 | 111.875 | 0.714 |
| Skagit Summer (H) | 6.6 | 122.557 | 0.891 |
| Skagit Upper Summer (W) | 7.5 | 81.272 | 0.536 |
| Nooksack Kendall Creek (H) | 4.6 | 89.445 | 0.579 |
| Nooksack Skookum Creek (H) | 6.0 | 109.731 | 0.885 |
| Nooksack Fall (W) | 8.3 | 81.322 | 0.808 |

## Figures

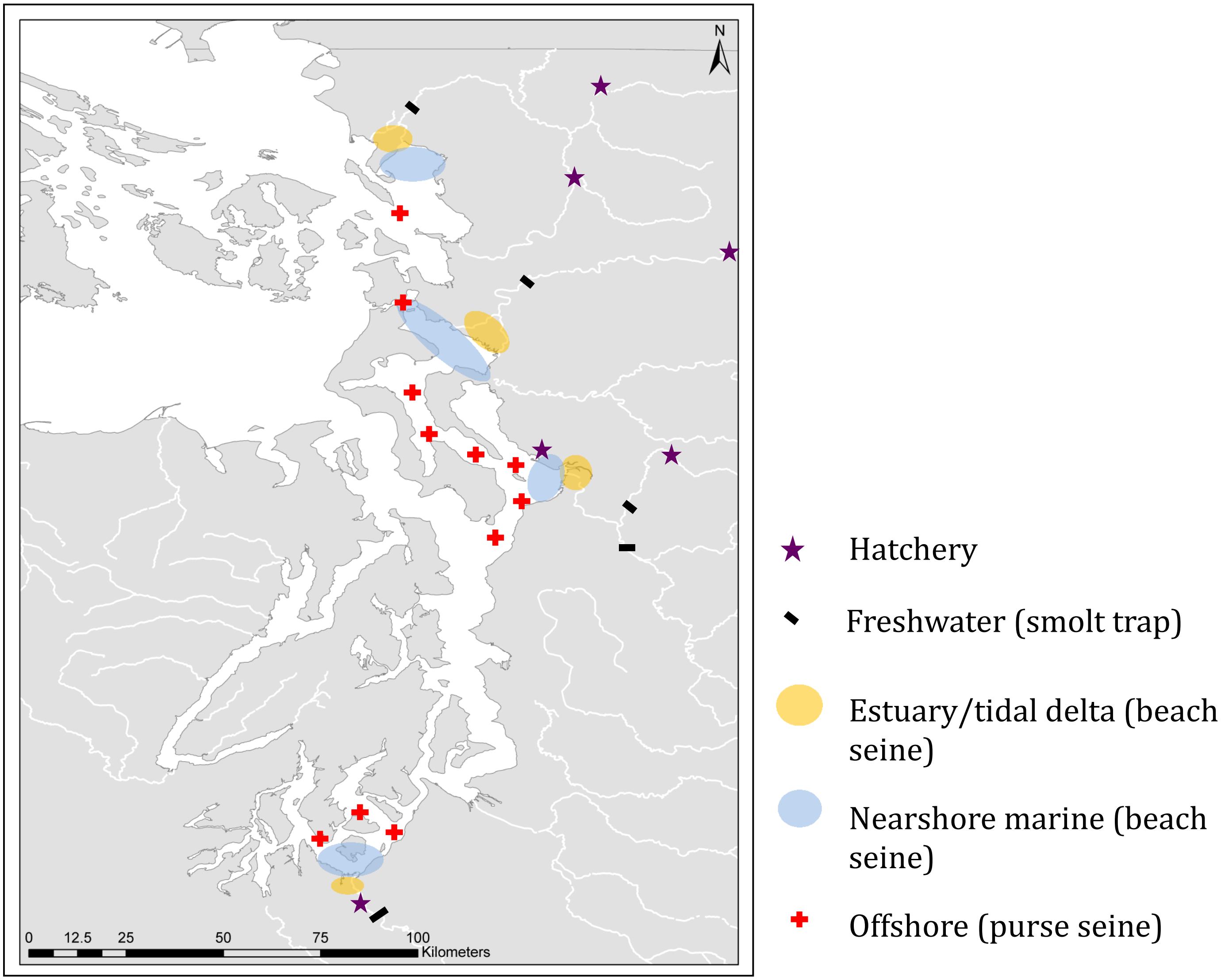

**Figure 1.** Sampling map showing approximate locations of juvenile Chinook sampling efforts in each habitat and watershed.

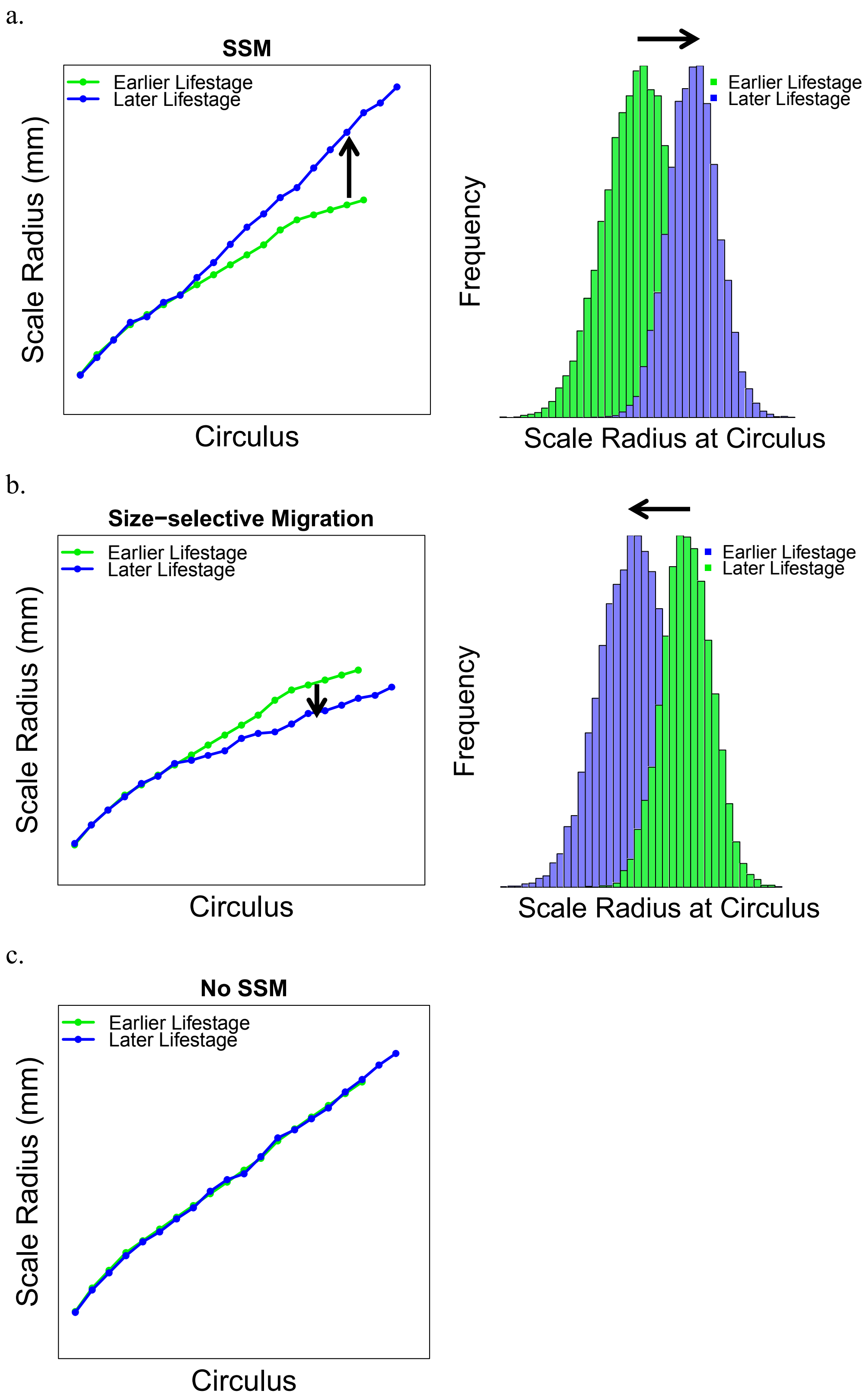

**Figure 2.** Theoretical comparisons of average growth histories indicating (a) size-selective mortality, (b) size-selective migration, or (c) neither

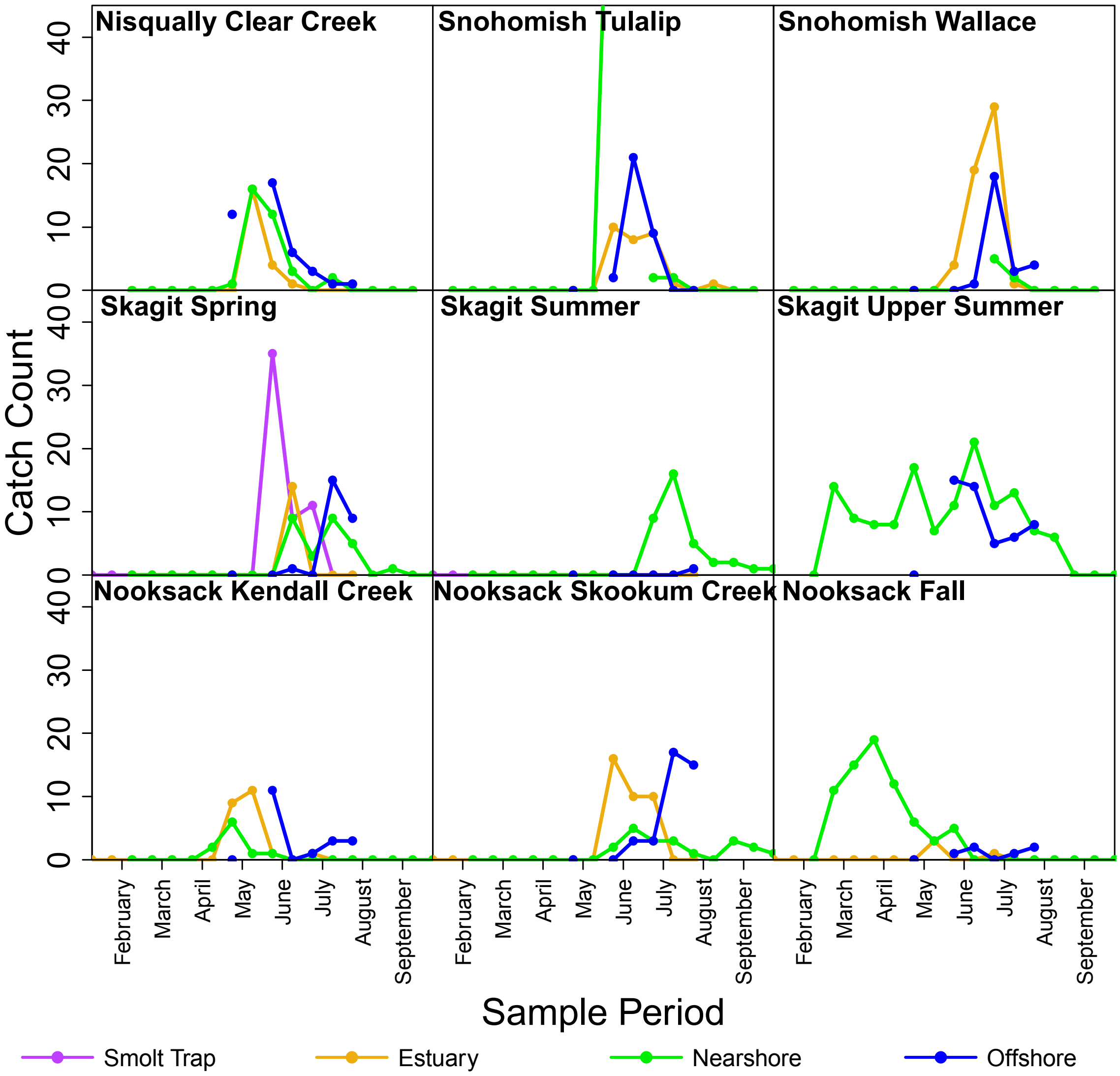

**Figure 3.** Catch of each stock by life stage (habitat/sample period combination). Points are only plotted for periods in which sampling occurred in each habitat.

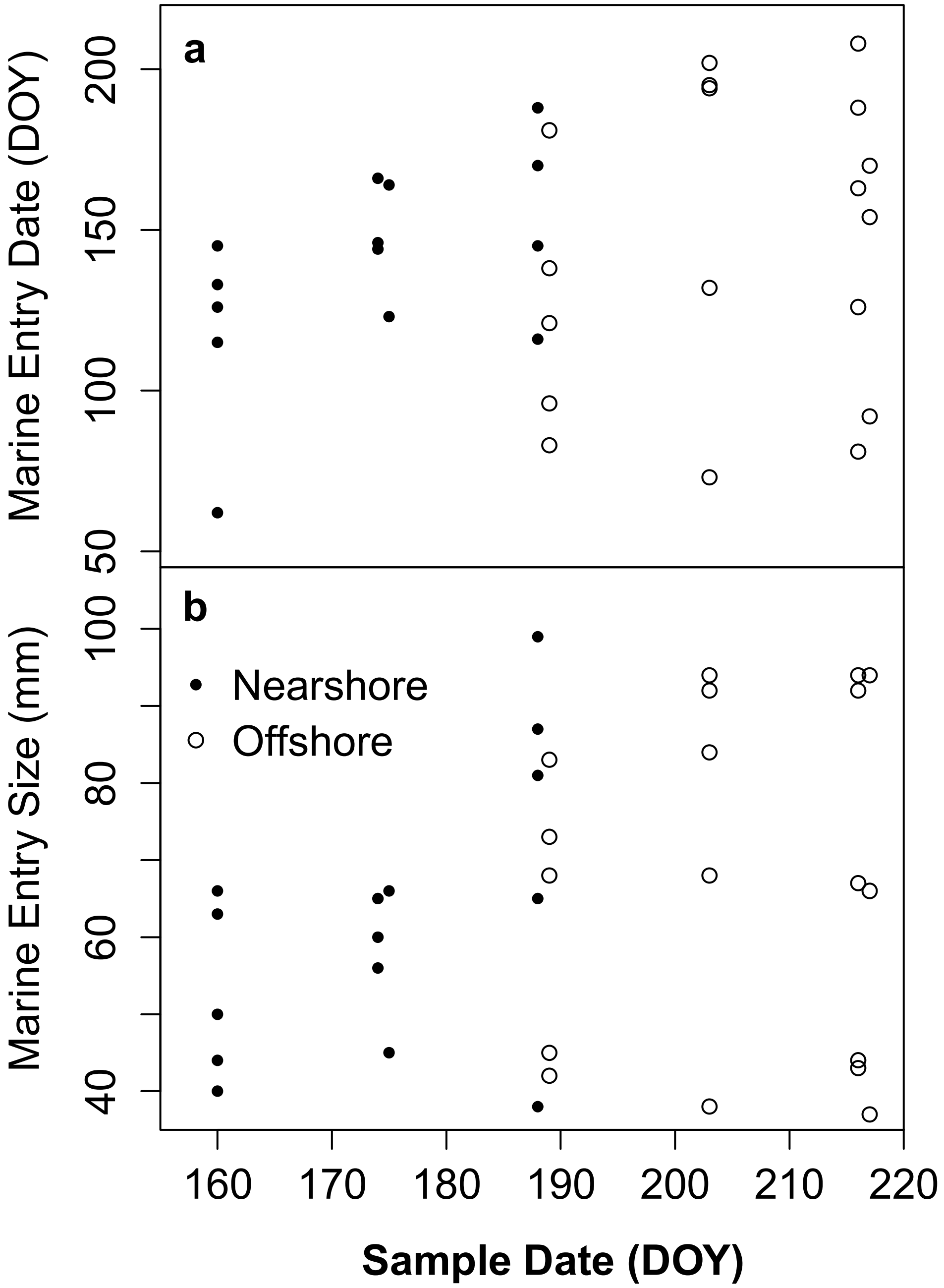

**Figure 4.** Relationships between sample date and (a) marine entry date and (b) marine entry size.

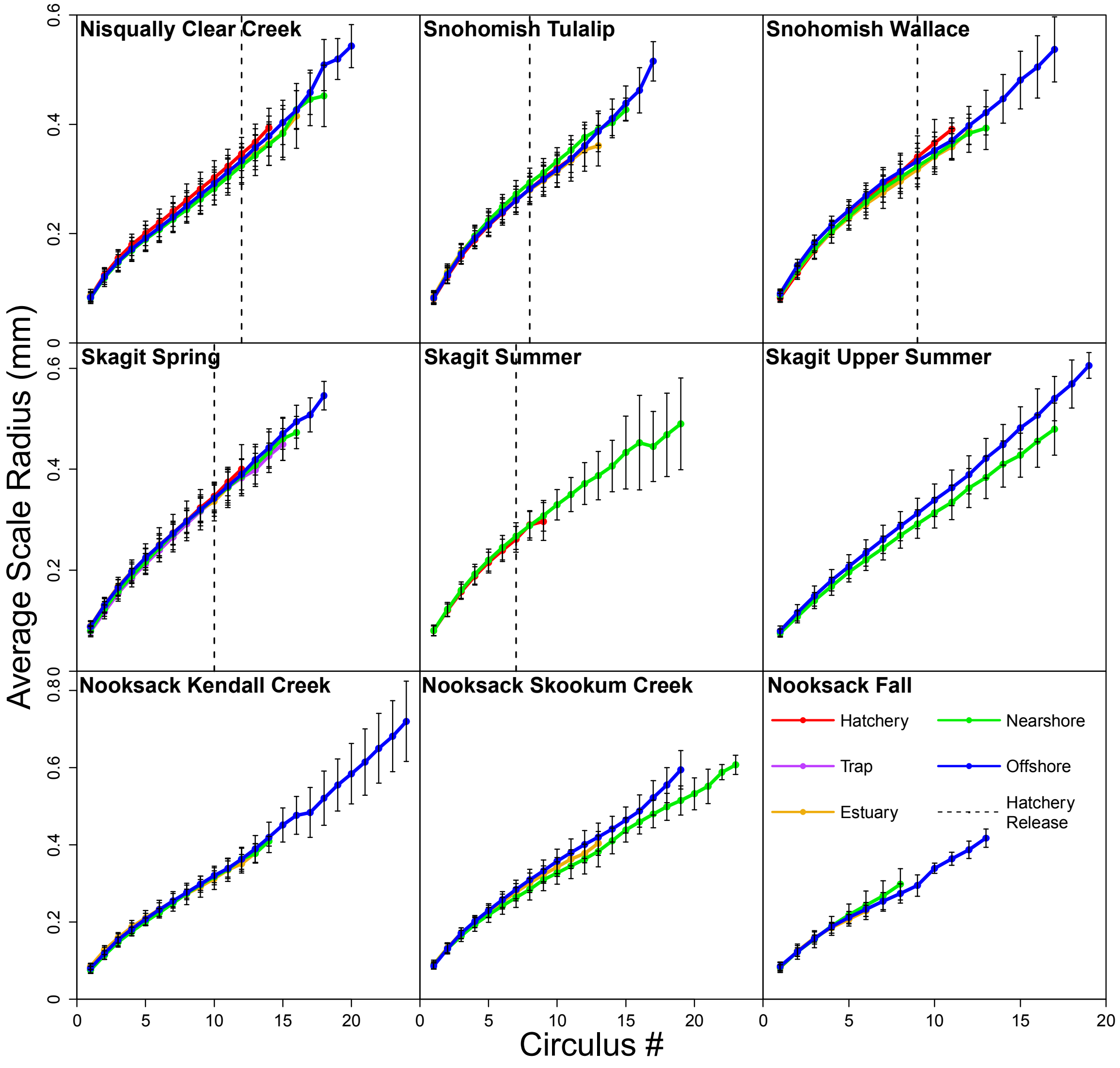

**Figure 5.** Habitat-specific growth histories (average size-at-age ± SD) for 9 stocks Vertical dashed lines indicate modal circulus count at hatchery release.

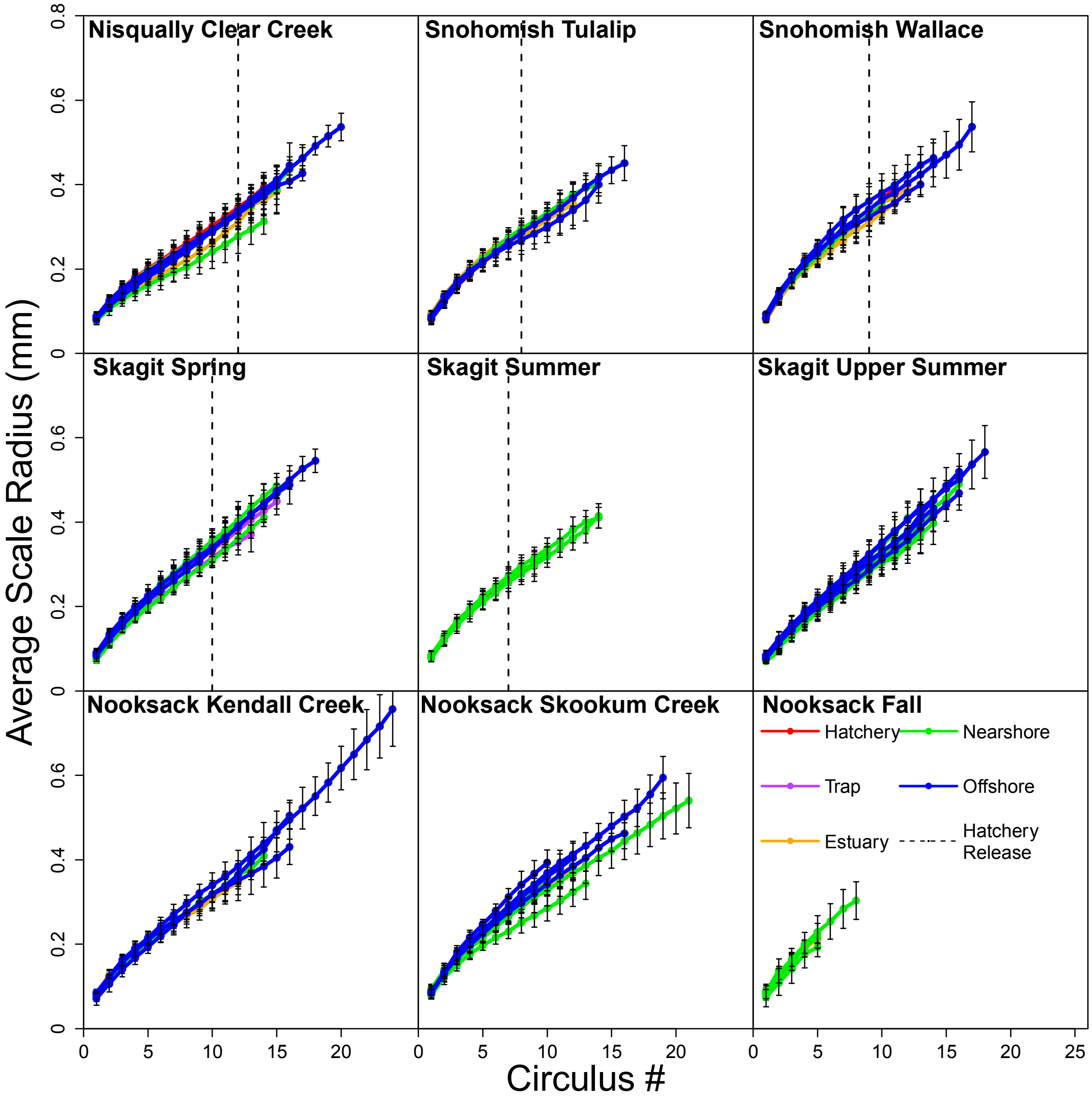

**Figure 6.** Life stage-specific growth histories (average size-at-age ± SD) for 9 stocks. Vertical dashed lines indicate modal circulus count at hatchery release.

# Chapter 2 – Ecological factors affecting stage-specific growth of hatchery and wild Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound

## Abstract

Size-selective mortality is a prevalent force regulating marine survival for many anadromous salmonid species, including ESA-listed Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, WA. However, there is no strong evidence that size-selective mortality occurs for juvenile Chinook salmon between marine entry and a previously identified critical growth period associated with offshore feeding through July of the first marine growth season. Therefore, growth achieved through mid-summer could influence size-related survival bottlenecks at later life stages. This study provides a mechanistic understanding of factors affecting growth of sub-yearling Chinook salmon across different habitats and regions in Puget Sound. The objectives were to compare the weights and growth rates of juvenile Chinook salmon from different populations across habitats and time during their first marine growth season in Puget Sound and to determine whether prey quality, prey availability, or water temperature influenced growth rate differences. To address these objectives we repeatedly sampled seven hatchery-origin and two wild stocks of sub-yearling Chinook salmon every two weeks in estuary, nearshore, and offshore marine habitats associated with four major rivers flowing into Puget Sound, WA. During each sampling event we recorded juvenile weights, took scale and diet samples, and measured water temperature. We used bioenergetics models to examine the relative roles of prey quality, prey availability, and temperature in regulating stage-specific growth rates of juvenile Chinook salmon across stocks, habitats, and time. Juvenile Chinook salmon were larger and grew faster in offshore habitats than juveniles sampled concurrently in nearshore habitats. Diet analysis and bioenergetics modeling suggested that differences in feeding rate and water temperature interacted to confer higher growth rates in offshore habitats. Feeding rates were generally low across Puget Sound, suggesting that prey availability limited overall early marine growth. Growth was relatively insensitive to temperature fluctuations in offshore habitats, whereas warmer temperatures in more than half of the observed nearshore growth periods reduced growth considerably under the feeding rates estimated by model simulations.

## Introduction

An animal's ability to survive and reproduce is often related to its body size, which is directly affected by ecological conditions that affect growth. These conditions include abiotic factors like temperature, which affects metabolism, and biotic factors such as prey quality and abundance. In marine ecosystems, these ecological factors vary with large-scale climatic and oceanographic indices and on smaller spatial and temporal scales based on patchy food availability and thermal conditions. Temperature, food quality, and food availability interact on both large and small scales to regulate growth, size, and survival.

The ecological factors that regulate marine survival of Pacific salmon are poorly understood. Climatic indices like the Pacific Decadal Oscillation and North Pacific Gyre Oscillation correlate with marine survival (Mantua et al. 1997, Kilduff et al. 2015) but mechanisms underlying these correlations have not been adequately described. In the California Current, changes in zooplankton communities associated with ocean temperature and currents have been suggested as an indirect link between climate indices and marine survival of salmon based on correlations (Keister et al. 2011), but the underlying mechanisms have yet to be examined through an integrated food web study combining climate and water temperature data with information on zooplankton availability and their energetic contribution to salmon growth.

Size-selective mortality is prevalent during marine life stages of Pacific salmon (coho: Beamish et al. 2004, Holtby et al. 1990; pink: Cross et al. 2008; chinook: Duffy and Beauchamp 2011; chum: Healey 1982; sockeye: Henderson and Cass 1991; steelhead: Ward et al. 1989, Thompson and Beauchamp 2014), though the timing, location, and agents of the majority of marine mortality are unclear. Marine survival of Chinook salmon is highly correlated with size during their first marine growth season throughout their range both within (Claiborne et al. 2011, Woodson et al. 2013) and among years (Duffy and Beauchamp 2011, Tomaro et al. 2012), suggesting that early marine growth conditions play a critical role in determining survival.

For ESA-listed Chinook salmon in Puget Sound, WA, marine survival seems to hinge on growth during early marine life stages. There is little evidence that size-selective mortality occurs between marine entry and a previously identified critical growth period associated with offshore feeding through July of the first marine growth season (Chapter 1; Duffy and Beauchamp 2011). This suggests that size-selective mortality bottlenecks occur at later life stages, either within or outside Puget Sound. The strong correlation between marine survival and weight in July for hatchery-origin Puget Sound Chinook salmon (Duffy and Beauchamp 2011), the lack of correlation between marine survival and size at hatchery release or outmigration for multiple species of Pacific salmon (Holtby et al. 1990, Quinn et al. 2005, Duffy and Beauchamp 2011, Tomaro et al. 2012), and the lack of evidence of size-selective mortality within Puget Sound through mid-summer (Chapter 1) all suggest that marine survival of Puget Sound Chinook salmon depends largely on marine growth achieved through at least mid-summer of their first year.

From a bioenergetic perspective, prey quality, prey availability and water temperature all affect growth of juvenile Chinook salmon (Beauchamp 2009). Growth rate at a given temperature increases with an increase in the energetic quality of prey and with the amount of prey consumed. The range of temperatures at which positive growth is possible depends on the size of the salmon, the composition of its diet, and its feeding rate (Beauchamp 2009). The spatial and temporal variation in these ecological factors affecting growth could differ considerably among populations, habitats or basins within Puget Sound. Thus, the key processes limiting growth or survival might differ among stocks of Chinook salmon and could operate on different habitats or at different times.

The goal of this study was to provide a mechanistic understanding of factors affecting growth of hatchery-origin and wild sub-yearling Chinook salmon during their first summer rearing in the marine waters of Puget Sound. We hypothesized (1) that growth rates of juvenile Chinook salmon would differ across time, among habitats, or among regions of Puget Sound, and (2) that prey quality, prey availability, and water temperature would differ across time, among habitats, or among regions of Puget Sound.

## Methods

We combined empirically measured water temperatures, stage-specific weights of sub-yearling Chinook salmon, and diet data from sub-yearling Chinook salmon in bioenergetic model simulations to determine the relative importance of prey quality, prey availability, and temperature in contributing to the body mass that sub-yearling Chinook salmon achieve during their first summer in Puget Sound, WA. We calculated average growth rates between life stages (combinations of habitat and time) using average weights after analyzing scale-based growth trajectories to ensure that fish caught in each life stage exhibited similar growth histories.

### *Study System*

Puget Sound is a deep glacial fjord comprised of four basins with different oceanographic and ecological characteristics (Moore et al. 2008a). This study focused on sub-yearling Chinook salmon from the Nooksack, Skagit, Snohomish, and Nisqually rivers (**Figure 1**), which drain into the North, Whidbey, and South basins of Puget Sound. Each of these rivers supports both wild and hatchery-produced Chinook salmon. Sub-yearling "ocean-type" juveniles predominate throughout Puget Sound (Healey 1991), though in some snow-dominated watersheds up to half of the juveniles may exhibit a stream-type life history strategy (Beechie et al. 2006). Sub-yearling Chinook generally enter marine waters between May and July and rear in Puget Sound for most of the summer (Duffy et al. 2005). During their outmigration they move through and feed in tidally influenced estuarine deltas, shallow nearshore marine habitats, and into the epi-pelagic offshore habitat within Puget Sound (Duffy et al. 2005). Both within and across river systems, growing conditions and predation risk may differ among habitats and across time such that each combination of habitat and sample period represents a separate "life stage" for juvenile Chinook.

Because wild and hatchery Chinook salmon display different migration and distribution patterns in Puget Sound (Rice et al. 2011), this study sampled both wild and hatchery juveniles and examined their growth histories separately. Hatchery-origin Chinook salmon are identifiable as they are marked with a clipped adipose fin, a coded wire tag (CWT) implanted in their nasal cavity, or both. CWTs, which can be detected with specialized metal detectors, are encoded with information about the hatchery of origin, broodstock, release age, release date, and release site of the individual. Some hatcheries also apply unique thermal marks to the otoliths of Chinook they release by manipulating the water temperature in which the juveniles are reared. Like CWTs, these thermal marks can be used to determine the origin of the fish.

### *Sample Collection and Processing*

We collected both natural-origin and hatchery-reared sub-yearling Chinook in freshwater, estuarine tidal delta (hereafter "estuary"), nearshore marine ("nearshore"), and offshore epi-pelagic ("offshore") habitats within Puget Sound associated with the Nooksack, Skagit, Snohomish, and Nisqually rivers (**Figure 1**). Sub-yearlings were identified in the field based on size and timing, and age was verified later in the lab using CWTs, thermal otolith marks, or scale morphometrics. Hatchery-origin individuals were identified by an adipose fin clip or the presence of a CWT. To obtain stage-specific weights, diet data, and water temperatures we sampled downstream-migrating smolts in freshwater habitats using smolt traps, in estuarine and nearshore habitats using beach seines (following Duffy et al. 2005), and in offshore habitats using a purse seine (*F.V. Franciscan I*, approximate net dimensions: 402 m long, fished effectively to 22 m; bunt constructed of 1 cm knotless mesh to 18 m, 1.3 cm knotless mesh to 73 m, 2 cm knotless mesh to 146 m, 9 cm knotted mesh to 402 m). Sampling occurred approximately every two weeks from late January through late July for freshwater habitats, late January through early October for estuarine and nearshore habitats (with some variation among watersheds), and from early May through early August for offshore habitats. All samples were collected in 2014. These sampling periods were determined mainly by the historical presence of sub-yearling Chinook in each habitat at different times of year (Duffy et al. 2005, Rice et al. 2011).

During each sampling event we recorded total counts, mark types, fork lengths, and weights of hatchery and wild Chinook salmon. Up to 30 hatchery-origin Chinook in each sampling event were lethally sampled for CWT and otolith extraction and reading; up to 30 unmarked Chinook were sampled live and released whenever possible. From each individual we sampled scales, diet (via gastric lavage in the field or dissection in the lab), and caudal fin tissue used for genetic stock identification of unmarked (natural-origin) Chinook. Scales were taken from the "preferred area" on the side of the fish, from the second to the seventh rows of scales above the lateral line and on a diagonal from the posterior insertion of the dorsal fin to the front of the anal fin (Mosher 1968, Shearer 1992). Scales were stored in folded wax paper in a coin envelope. Diet samples taken in the field were frozen in a small zip-lock plastic bag in water from the sample site; stomach samples taken in the lab were frozen in a small zip-lock plastic bag. Fin clips were stored in 95% ethanol. Otoliths were removed in the lab and stored dry in labeled vials.

Temperature data were recorded concurrently with fish and zooplankton sampling when possible, and data gaps were supplemented by available measurements within reasonable temporal and spatial proximity (**Table 1**). Offshore temperatures were recorded immediately prior to fish sampling using a CTD (SBE 19plus V2 SeaCAT) and were averaged over the top 15 m of the water column. Estuary and nearshore temperatures were averaged from the surface to the bottom at each sample site.

Diet contents from at least 10 non-empty samples (where possible) from sub-yearling Chinook in each life stage (unique habitat and sample period combination) and watershed bin were separated into 21 prey groups based on taxonomic order and energy density (**Table 2**). A blotted wet weight (to the nearest 0.0001 g) was recorded for each prey group. Total diet weight was calculated by adding wet weights of all prey categories (excluding indigestible and unidentified digested material). We then calculated the proportion of each individual diet comprised of each prey group by dividing each prey group's blotted wet weight by the total diet weight. An energy density for each diet was calculated by summing the products of each prey group's energy density and its diet proportion (**Table 2, Table A1**). Prey proportions were averaged over all non-empty diets within each life stage in each watershed.

### *Stock Identification*

We repeatedly sampled nine defined stocks of wild and hatchery juveniles exhibiting the modal outmigration patterns from each watershed. A hatchery-origin stock was defined as a group of fish from the same broodstock released from the same hatchery at the same time, as determined by CWTs or thermal otolith marks. Wild fish were assigned to specific populations using a 192 SNP (single nucleotide polymorphism) panel for Puget Sound Chinook salmon (Fournier et al. 1984, Millar 1987, Warheit et al. 2013). Genetic stock identification for wild stocks was limited to the Skagit and Nooksack watersheds for our study. The stocks followed in this study included two hatchery-origin stocks from each of the Nooksack (Kendall Creek and Skookum Creek hatcheries), Skagit (spring and summer releases from Marblemount hatchery), and Snohomish (Bernie Kai-Kai Gobin Tulalip and Wallace hatcheries) watersheds, one hatchery-origin stock from the Nisqually watershed (Nisqually Clear Creek hatchery), and two wild stocks originating from the Nooksack Fall and the Upper Skagit Summer populations. The stage-specific weight calculations and bioenergetics simulations were performed on separate stocks of fish originating from the same hatchery-release group or wild population that were caught and sampled in their natal watershed.

### *Scale Analysis*

For each stock, we used scale morphometrics to ensure that fish sampled within each life stage exhibited similar growth histories, as the scale radius at a given circulus is proportional to the length of the fish at a given age (Fisher and Pearcy 1990, Ricker 1992; Chapter 1). To prepare scales for measurement we created impressions of up to 10 scales from each fish by mounting them on gummed cards and pressing them into acetate strips (Cross et al. 2008). For each fish we selected the scale to be imaged and measured based on quality of the scale (avoiding damaged or regenerated scales) and clarity of the impression. The acetate impressions were imaged with a digital camera attached to a Leica MZ6 microscope fitted with 20x oculars and a 2.0x objective (camera model: Lumenera Infinity1-3c; camera lens attachment: Diagnostic Instruments 1.0x HR100-CMT; total magnification ranged from 64x to 160x depending on the size of the scale). Scale measurements were taken from scale images with ImagePro or ImageJ software. For each scale we recorded total circulus count, total scale radius, and scale radius at each circulus. Scale radii at each circulus, which are proportional to size-at-age, were used to create growth histories for individual fish. Similar individual growth histories were averaged to compare mean size-at-age for each stock at different life stages. Prior to averaging individual growth histories in each of these analyses we plotted all individual growth histories of fish from each stock and life stage on a single set of axes to visually ensure that they exhibited a strong central tendency.

### *Bioenergetics modeling*

In constructing bioenergetics model simulations, we focused on sub-yearling Chinook from stocks originating in our four focal watersheds (the Nisqually, Snohomish, Skagit, and Nooksack rivers) from which at least 10 fish had been collected in at least two life stages (habitat/sample period combinations). Within these stocks, we calculated average stage-specific weights using only fish that were caught and sampled in their natal watershed and adjacent marine waters (within an approximately 25 km radius of the estuarine delta) to exclude those that may have experienced vastly different growth environments. We only calculated average weights and growth rates for life stages (habitat/sample period combinations) from which scale samples from at least three individuals from the same stock were taken so that we could use scale morphometrics to ensure that fish in each life stage had similar growth histories. For the wild stocks, since most fry migrants had not formed scales before entering the estuary and nearshore habitats, we did not differentiate between fry and parr migrants and likely excluded early life stages in which only fry migrants were sampled due to a lack of scale samples.

Mean weights were calculated for all offshore life stages that met the above criteria. For estuary and nearshore habitats, mean weights were calculated for life stages that met the above criteria and in which sample size was greater than 25% of the maximum catch in that habitat for that stock (see Chapter 1 Figure 3). We used this subset of samples to focus our analysis on the growth scenarios that represented the modal migration patterns through the estuary and nearshore, whereas all offshore life stages were included for each stock given that the offshore was the final habitat occupied before emigration from Puget Sound. When wet weights were not measured in the field, they were calculated from thawed weights measured in the lab (Wet Weight = 0.9196 * Thawed Weight - 0.0622; $r^2 = 0.99$, N = 388) or wet fork lengths (Wet Weight = 0.000007 * Wet Fork Length$^{3.1071}$; $r^2 = 0.98$, N = 1457). Regressions of thawed and wet weight and wet weight and wet fork length were calculated using all sub-yearling Chinook salmon sampled in 2014.

Bioenergetics model simulations were used to diagnose which factors affected growth during different periods in different habitats for each stock. We used a version of the Wisconsin fish bioenergetics model (Hanson et al. 1997) coded into R for running our simulations. The bioenergetics model is an energy-balance equation that calculates daily weight gain of the juvenile Chinook, daily consumption (in grams) of each prey category, and an overall feeding rate over a specified simulation period. The average stage-specific weights calculated above were used as initial and final weight inputs in bioenergetics model simulations. Daily feeding and growth rates were fit to the initial and final body mass inputs, thermal experience, diet composition, and energy densities of juvenile Chinook and their diet through the duration of each simulation. The feeding rate was reported as a percent of the theoretical maximum consumption rate (%Cmax) for Chinook salmon of a given mass and thermal experience. The feeding rate can be used as a proxy for prey availability within a specific habitat for that specific size of consumer (Beauchamp 2009). Bioenergetic models were parameterized for juvenile Chinook salmon (Stewart and Ibarra 1991, modified by Plumb and Moffitt 2015 for the upper temperature dependent consumption equation) and used empirically measured inputs for life stage-specific weight, water temperature (**Table 1**), and temporal changes in diet composition (**Table 2**). We used diet data from any sub-yearling Chinook (hatchery or wild) that were sampled in the life stage (habitat/sample period combination) of interest. Energy density of juvenile Chinook salmon (4085 J/g; David et al. 2014) and their prey came from literature values and were held constant across all simulations (**Appendix Table A1**). The model changes temperature and diet inputs daily using linear interpolation between the measured values associated with the initial and final life stages.

For each stock, transitions between each life stage were treated as separate bioenergetics simulations such that factors affecting growth could be attributed to the appropriate habitats and temporal scales. Life stages in which fish from each stock were sampled were organized into "growth scenarios," or sets of consecutive life stages that reflected the major movement and growth scenarios observed among habitats over time (Chapter 1). These growth scenarios were constructed under the assumptions that fish did not lose weight and always moved in the direction of salt water when changing habitats. We calculated growth rates for juvenile Chinook between nearshore life stages, between nearshore and offshore life stages, and between offshore life stages for each stock. We also included estuarine life stages for the Nisqually Clear Creek stock. Growth rates were calculated by dividing the difference between average weight in the initial and final life stages by the number of days between life stages. Based on the similarities in scale-based individual growth histories within life stages, and in average growth histories between life stages, we felt confident that these average growth rates would accurately reflect growth rates of juvenile Chinook salmon in those growth scenarios. We used a Kruskal Wallis H test to determine whether growth rates varied across time, among stocks, or among habitat transition types (nearshore-nearshore, nearshore-offshore, offshore-offshore).

We then used the bioenergetics model to calculate feeding rates for juvenile Chinook in each growth scenario. Bioenergetics simulations were run to simulate feeding rates associated with transitions between two nearshore life stages, two offshore life stages, and between nearshore and offshore life stages for each stock. For the Nisqually Clear Creek stock, we also ran bioenergetics simulations to simulate feeding rate during transitions between estuary, nearshore, and offshore life stages. Meaningful simulations could not be run for the Snohomish

Wallace Hatchery stock because useable sample sizes only occurred during one sample period and were simultaneous in both nearshore and offshore habitats.

At this point we had stock-specific average growth rates and feeding rates calculated for transitions between life stages, as well as stock-specific observed weight and watershed-specific diet quality and temperature data associated with individual life stages. To determine the relative importance of prey quality (observed diet composition from each life stage multiplied by the energy density of each prey item), prey availability (calculated feeding rate between two life stages), and water temperature in determining growth, we looked for similarities between the dimensions over which each of these factors varied (time, stock/watershed, and habitat/habitat transition) and the dimensions over which growth rate varied. We used permutational multivariate analysis of variance (PERMANOVA, PRIMER_7 software) to identify whether juvenile Chinook weight, energy density of the diet, feeding rate, and thermal experience differed among stocks/watersheds or habitats/habitat transitions. A multivariate approach was used in order to simultaneously evaluate the relative variation in each ecological factor and to account for the covariation between time and the weight of juvenile Chinook salmon. PERMANOVA is based on distance or dissimilarity measures and, through permutation techniques, approximates a "pseudo" *F* statistic to evaluate differences among groups. PERMANOVA does not require data to meet the many assumptions of traditional MANOVA techniques and is rather robust to unbalanced designs. Data were square-root transformed and Euclidean distances were calculated for each test. The advantage of using PERMANOVA on single response variables based on Euclidean distances is that it yields Fishers traditional univariate *F*-statistic.

## Results

### *Stage-specific weights and growth rates*

Catch counts and average weights showed that all stocks used habitats sequentially and grew through time (**Figure 2**, see Chapter 1 Figure 3). Hatchery stocks were released between late April and late June at an average of 3-6 g. Average stage-specific nearshore weights ranged from less than 1 g in early March and early April (Nooksack Fall and Skagit Upper Summer stocks) to 12 g in late August (Skagit Upper Summer). Offshore weights ranged from 5 g in early May (Nisqually Clear Creek) to nearly 25 g in July and August (Nisqually Clear Creek and Nooksack Skookum Creek). The Nooksack Kendall Creek stock had a much higher maximum average weight of nearly 69 g in the offshore in August. Offshore weights were only available for seven of the nine stocks due to low offshore sample sizes in the Skagit Summer and Nooksack Fall stocks. Average stage-specific weights in the offshore in July (the life stage at which size is highly correlated with survival; Duffy and Beauchamp 2011) ranged from 11 g (Nooksack Skookum Creek) to 23 g (Nisqually Clear Creek) and averaged 14 g across all stocks that were sampled in the offshore in July. During the same period, average stage-specific weights in the nearshore ranged from 4 g (Skagit Summer) to nearly 8 g (Nooksack Skookum Creek and Skagit Spring) and averaged 6 g across all stocks sampled in the nearshore in July (**Figure 2**).

Across Puget Sound, fish collected offshore were larger on average (12.9 ± 10.6 g) than those collected nearshore (4.7 ± 3.0 g) during the same sampling periods ($F = 12.6$, df = 1, $p = 0.004$). Weight did not differ among stocks during the same sampling period ($F = 0.84$, df = 6, $p = 0.50$), suggesting that hatchery and natural origin stocks did not differ appreciably in weight at any given time. Absolute weight gain over the course of this study was highest in offshore habitats (**Figure 2**).

Growth rate did not differ significantly across time (Kruskal-Wallis chi-squared = 36.7, df = 27, $p = 0.10$) or among stocks (Kruskal-Wallis chi-squared = 7.8, df = 7, $p = 0.35$), but did differ among habitat transitions (Kruskal-Wallis chi-squared = 12.1, df = 4, $p = 0.017$). Growth rates (mean ± 2SD) were lowest for nearshore growth simulations (0.11 ± 0.11 g/d), higher for offshore growth simulations (0.32 ± 0.31 g/d), and highest for nearshore-offshore growth simulations (0.42 ± 0.28 g/d; **Figure 3A**). Only the nearshore and nearshore-offshore growth rates differed significantly (post-hoc Kruskal multiple comparisons test, $p = 0.05$). Mean growth rate was higher for nearshore-offshore than nearshore growth simulations (Welch's t = -3.815, df = 15, $p = 0.002$). These results did not change when we repeated these tests using proportional growth rates (g/g*d). Because the actual transition from nearshore to offshore feeding occurs over a much shorter period than that encompassed by the nearshore-offshore growth simulations, it is unlikely that the high average growth rate for nearshore-offshore growth scenarios is due to the transition itself, and more likely that it reflects the higher offshore growth rates given the difference in average growth rates between nearshore and offshore growth simulations.

*Factors affecting growth*

Juvenile Chinook exhibited an ontogenetic shift from feeding predominantly on terrestrial insects (7-75% by mass hymenoptera (12670 J/g), diptera (4339 J/g), and other orders) in estuary and nearshore habitats to crab larvae (25-95% by mass zoea (3395 J/g) and megalops (4225 J/g)) as they moved into offshore habitats (**Figures 3B, A1; Table 2**). The Nooksack stocks differed from all others in that shrimp (4730 J/g) and sand lance (5060 J/g; Kendall Creek stock only) also contributed substantially to offshore energy consumption. Nearshore diets from the Nisqually watershed were an interesting exception in that they contained fewer insects (1-18%) and more larval crab (24-51%), whereas nearshore diets from other watersheds contained just 0-

20% crab larvae. The composite energy density of diets averaged 4449 ± 1796 J/g across Puget Sound and did not vary among watersheds (*F* = 2.04, df = 7, *p* = 0.094) or habitats (*F* = 0.12, df = 1, *p* = 0.73; **Figure 4**).

Feeding rates were lowest in nearshore growth simulations (34.1 %Cmax), higher in offshore growth simulations (41.1 %Cmax), and highest in growth simulations that bracketed nearshore-offshore transitions (59.6 %Cmax), though differences in feeding rate among habitat types were not significant (*F* = 2.112, df = 2, *p* = 0.14; **Figures 3B, 5**). Feeding rates did not differ significantly among watersheds (*F* = 0.326, df = 7, *p* = 0.94), and averaged 45.0 ± 20.8% Cmax across Puget Sound. Feeding rates ranged from 18 %Cmax (Nooksack Skookum Creek, scenario 4, nearshore late June to nearshore early July) to 108 %Cmax (Skagit Upper Summer, scenario 10, nearshore early June – offshore late June; **Table 1**). This feeding rate above 100% likely resulted from an overestimation of growth or underestimation of prey energy density for the life stages involved in that simulation.

Average daily mean water temperature was warmer nearshore (13.7 ± 2.5˚C) than offshore (10.2 ± 0.9˚C) across Puget Sound (*F* = 10.980, df = 1, *p* = 0.002; **Figure 6**) but temperature did not differ significantly among watersheds (*F* = 1.690, df = 3, *p* = 0.187). Thermal experience ranged from 7.9˚C (Skagit Upper Summer, nearshore early March) to 18.5˚C (Nooksack Skookum Creek, nearshore early July; **Table 1**).

Prey quality likely did not drive differences in growth rate between habitats, as the average energy densities of diets did not differ significantly between nearshore and offshore habitats, even though nearshore diets consisted of higher quality prey than offshore diets (hymenoptera and diptera vs. crab megalops). Growth rates were slightly more sensitive to thermal constraints in nearshore habitats where fish had lower feeding rates than in offshore habitats (**Figure 6**). For the smaller Chinook rearing in nearshore habitats, 69% of the temperatures recorded in nearshore life stages were above the optimal growth temperature range (10-12˚C) for fish of the average nearshore weight (4.7 g) feeding at the average nearshore feeding rate (34 %Cmax) on the overall average prey energy density (4450 J/g) in our simulations (**Figure 6**). Furthermore, the lower and upper ends of the range of nearshore temperatures resulted in growth rates that were 79% and 24%, respectively, of the growth rate at the optimum temperature. In contrast, all offshore temperatures were between 9 and 13˚C, within 1˚C of the 10-12˚C optimum temperature range at the average offshore size (12.9 g). This temperature range resulted in a range of growth rates that were 90% to 93% of the growth rate at the optimum temperature for the average offshore feeding rate (41 %Cmax) and overall average prey energy density (4450 J/g).

While differences in temperature may have intensified the differences in growth rate between habitats, the lower feeding rates we observed in nearshore compared to offshore habitats and the low average feeding rate throughout Puget Sound suggest that growth was most limited by prey availability. Though nearshore and offshore feeding rates were not significantly different, increasing the nearshore feeding rate by just 20% from 34 %Cmax (the average nearshore feeding rate in this study) to 41 %Cmax (the average offshore feeding rate) without changing the energetic quality of the diet would have resulted in a roughly 40% increase in growth rate at the optimal growth temperature (from 0.019 g/g*d to 0.027 g/g*d). Across Puget Sound, shifting the feeding rate from 45% Cmax (the average feeding rate throughout Puget Sound in this study) to 65% Cmax (one standard deviation above the average) without changing the energetic quality of the diet would result in a nearly 2-fold increase in growth rate across a range of temperatures (from 0.031 to 0.054 g/g*d in the nearshore and from 0.022 to 0.039 g/g*d in the offshore). This allometric scaling of growth rate with feeding rate shows that growth rates observed in this study could be increased dramatically with only a slight increase in feeding rate.

## Discussion

Juvenile Chinook weights, growth rates and total weight gain during the first marine growth season were higher in offshore habitats throughout Puget Sound and did not differ significantly among cohorts or over time. This suggests that ecological factors are more favorable for growth in offshore habitats than in nearshore habitats throughout Puget Sound. Previous studies have also shown that juvenile Chinook salmon in Puget Sound are larger offshore than nearshore (Beamer et al. 2007, Duffy et al. 2010), but this study is the first to mechanistically link habitat-specific weight gain with ecological factors affecting growth of juvenile Chinook salmon during a critical growth period. This study's findings, combined with the strong positive correlation between survival and the weight of juvenile Chinook when sampled offshore in July (Duffy and Beauchamp 2011), suggest that offshore growth and feeding ecology is especially critical to marine survival.

Lower feeding rates in the nearshore, exacerbated by less optimal temperatures, were likely responsible for lower growth rates in nearshore compared to offshore habitats. The range of temperatures that confer positive growth potential for juvenile Chinook salmon depends on the size of the fish, the rate at which it is feeding, and the energetic quality of its diet (Beauchamp 2009). Higher feeding rates and higher prey energy densities increase the growth rate attainable at a given temperature, expand the range of temperatures over which positive growth rates are possible, and allow higher growth rates toward the upper limit of a fish's thermal tolerance. The higher nearshore temperatures observed in this study would have resulted in decreased growth potential in nearshore habitats compared to offshore habitats given equal energy densities and feeding rates, and resulted in even lower growth rates when combined with the lower nearshore feeding rates.

Feeding rates reported here were similar to those reported for juvenile Chinook in the Salmon River estuary in Oregon (31-60 %Cmax; Bieber 2005, Gray 2005), though other studies of juvenile Chinook in Puget Sound reported higher feeding rates (55-90 %Cmax; Beauchamp and Duffy 2011). This difference may be due to differences in bioenergetics parameters used between studies. The default bioenergetics model software increases the energy density of juvenile Chinook as they grow (Energy Density = 5764 + 0.9862*Wt(g)), which would necessitate an increase in feeding rate to attain the same amount of growth, whereas we held Chinook energy density constant throughout our study. A similar effect would result from using the default initial energy density for Chinook salmon in the bioenergetics software, which is 25% higher than the energy density we used for our models (Hanson et al. 1997). We based our Chinook energy density on measured values from juvenile Chinook salmon sampled in Puget Sound (David et al. 2014), and kept Chinook energy density constant throughout the summer in our bioenergetics simulations based on studies of Chinook and coho salmon in the northeast Pacific that show that energy density increases as a function of time rather than size (Trudel et al. 2005).

The bioenergetics framework used in this study can be used to understand how differences in food availability and temperature can affect the feeding behavior and distribution of juvenile Chinook salmon. For example, certain combinations of high temperatures and low prey availability would make some habitats useless for foraging juvenile salmon because they offer no growth opportunity. This would exacerbate density-dependent processes, which might result in lower growth rates for entire cohorts of juvenile salmon or different distribution patterns. Lower prey availability and higher temperatures in the nearshore may also push juvenile Chinook out of the nearshore habitat in search of better growth conditions. Similarly, higher prey availability and cooler temperatures in offshore habitats may pull juvenile Chinook into offshore habitats. The warmer nearshore temperatures and higher offshore growth rates observed in this study suggest that juvenile Chinook salmon may maximize their overall early marine growth by moving offshore earlier.

The results of this study can also guide restoration and conservation efforts aimed at supporting juvenile Chinook salmon growth in Puget Sound. Because growth rate was most heavily influenced by feeding rate and temperature, human actions that bolster prey availability or reduce the maximum temperature in nearshore habitats may be most effective in supporting higher early marine growth of juvenile Chinook salmon. Climate change could reduce early marine growth in Puget Sound if feeding rates remain at levels observed in this study, as the optimal temperature range for growth becomes both narrower and colder at lower feeding rates (Beauchamp 2009). Though the nearshore temperatures we observed were similar to those previously observed in nearshore and estuarine areas throughout Puget Sound (Rice et al. 2011), the highest temperatures in this study were about a degree above the highest average temperatures in 2011. Increased sea surface temperature has been correlated with reduced survival of Chinook salmon from Washington and Oregon (Sharma et al. 2012), and sea surface temperatures in Puget Sound are most directly influenced by air temperatures (Moore et al. 2008b), which are expected to rise by 14.8˚C by 2080 (Elsner et al. 2009). If water temperatures warm with air temperatures as predicted, juvenile Chinook salmon may experience diminished growth conditions in Puget Sound unless prey quality or prey availability increase.

This study took a mechanistic approach to investigating factors affecting early marine growth of juvenile Chinook salmon at a variety of temporal and spatial scales during a critical growth period. Though we did not track growth rates of individual fish, scale measurements verified that fish within each stock had similar growth histories within and among life stages, suggesting that average growth rates could be calculated using changes in average stage-specific weights. This approach prevented potential artificial inflation of growth estimates based on observed weights that could result from size-selective processes.

Our results, combined with previous research indicating a positive relationship between survival and the weight of juvenile Chinook salmon offshore in July, suggest that offshore feeding and growth may be the most important stage during the first marine summer in determining overall marine survival. This adds to a growing body of literature that suggests that Pacific salmon survival rates depend on critical growth periods that occur during early marine life stages, and food availability has emerged as a key factor regulating growth during those critical periods for multiple Pacific salmon species and systems (Duffy 2003, Beauchamp et al. 2007). Recognizing the mechanisms through which ecological factors affect growth will lead to a more thorough understanding of movement, distribution, and survival patterns of Pacific salmon.

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## Tables

**Table 1.** Bioenergetics model inputs and outputs for each stock and growth cohort. Each simulation starts in the life stage directly above the simulation name and ends in the life stage in the same row as the simulation name.

**Nisqually Clear Creek**

| **SCEN1** | Habitat | Sampling Period | Mean Day of Year | Simulation Day | N (fish sampled) | Weight (g) | Growth Increment | Avg Prey Energy Density (J/g) | Temp (˚C) | P-value (feeding rate) | Total Consumption (g) | Growth Efficiency (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Hatchery | Late April 4/22-30/14 | 118 | 1 | 138 | 6.10 | | | | | | |
| Sim1 | Offshore | Early May 5/11/14 | 131 | 13 | 12 | 5.30 | -0.80 | 4097 | 9.2 | | | |
| Sim2 | Offshore | Early June 6/7-8/14 | 158 | 40 | 17 | 10.62 | 5.32 | 3899 | 10.9 | 0.4455 | 13.9 | 38.20 |
| Sim3 | Offshore | Late June 6/18-19/14 | 169 | 51 | 6 | 12.44 | 1.82 | 3924 | 11.0 | 0.3498 | 6.6 | 27.54 |
| Sim4 | Offshore | Early July 7/9-10/14 | 191 | 73 | 3 | 23.06 | 10.62 | 3927 | 9.0 | 0.5748 | 26.2 | 40.53 |
| **SCEN2** | | | | | | | | | | | | |
| | Hatchery | Late April 4/22-30/14 | 118 | 1 | 138 | 6.10 | | | | | | |
| Sim5 | Estuary | Late May 5/19-22/14 | 140 | 22 | 16 | 6.29 | 0.19 | 4867 | 11.8 | | | |
| Sim6 | Offshore | Early June 6/7-8/14 | 158 | 40 | 17 | 10.62 | 4.33 | 3899 | 10.9 | 0.4293 | 10.4 | 41.67 |

Table 1 (continued)

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sim3 | Offshore | Late June 6/18-19/14 | 169 | 51 | 6 | 12.44 | 1.82 | 3924 | 11.0 | 0.3498 | 6.6 | 27.54 |
| Sim4 | Offshore | Early July 7/9-10/14 | 191 | 73 | 3 | 23.06 | 10.62 | 3927 | 9.0 | 0.5748 | 26.2 | 40.53 |
| **SCEN3** | | | | | | | | | | | | |
| | Hatchery | Late April 4/22-30/14 | 118 | 1 | 138 | 6.10 | | | | | | |
| Sim7 | Nearshore | Late May 5/19-22/14 | 140 | 22 | 16 | 6.16 | 0.06 | 4238 | 11.5 | | | |
| Sim8 | Offshore | Early June 6/7-8/14 | 158 | 40 | 17 | 10.62 | 4.46 | 3899 | 10.9 | 0.4744 | 11.2 | 39.71 |
| Sim3 | Offshore | Late June 6/18-19/14 | 169 | 51 | 6 | 12.44 | 1.82 | 3924 | 11.0 | 0.3498 | 6.6 | 27.54 |
| Sim4 | Offshore | Early July 7/9-10/14 | 191 | 73 | 3 | 23.06 | 10.62 | 3927 | 9.0 | 0.5748 | 26.2 | 40.53 |
| **SCEN4** | | | | | | | | | | | | |
| | Hatchery | Late April 4/22-30/14 | 118 | 1 | 138 | 6.10 | | | | | | |
| Sim7 | Nearshore | Late May 5/19-22/14 | 140 | 22 | 16 | 6.16 | 0.06 | 4238 | 11.5 | | | |
| Sim9 | Nearshore | Early June 5/30/14-6/9/14 | 153 | 35 | 12 | 9.76 | 3.60 | 3526 | 11.8 | 0.5384 | 9.3 | 38.73 |
| Sim10 | Offshore | Late June 6/18-19/14 | 169 | 51 | 6 | 12.44 | 2.68 | 3924 | 11.0 | 0.3798 | 10.0 | 26.68 |

Table 1 (continued)

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sim4 | Offshore | Early July 7/9-10/14 | 191 | 73 | 3 | 23.06 | 10.62 | 3927 | 9.0 | 0.5748 | 26.2 | 40.53 |
| **SCEN5** | | | | | | | | | | | | |
| | Hatchery | Late April 4/22-30/14 | 118 | 1 | 138 | 6.10 | | | | | | |
| Sim5 | Estuary | Late May 5/19-22/14 | 140 | 22 | 16 | 6.29 | 0.19 | 4867 | 11.8 | | | |
| Sim11 | Nearshore | Early June 5/30/14-6/9/14 | 153 | 35 | 12 | 9.76 | 3.47 | 3526 | 11.8 | 0.4829 | 8.5 | 40.80 |
| Sim10 | Offshore | Late June 6/18-19/14 | 169 | 51 | 6 | 12.44 | 2.68 | 3924 | 11.0 | 0.3798 | 10.0 | 26.68 |
| Sim4 | Offshore | Early July 7/9-10/14 | 191 | 73 | 3 | 23.06 | 10.62 | 3927 | 9.0 | 0.5748 | 26.2 | 40.53 |
| **Snohomish Tulalip** | | | | | | | | | | | | |
| **SCEN1** | Habitat | Sampling Period | Mean Day of Year | Simulation Day | N (fish sampled) | Weight (g) | Growth Increment | Avg Prey Energy Density (J/g) | Temp (˚C) | P-value (feeding rate) | Total Consumption (g) | Growth Efficiency (%) |
| | Hatchery | Late May 5/28/14 | 148 | 1 | 60 | 3.87 | | | | | | |
| Sim1 | Nearshore | Early June 6/3/14 | 154 | 6 | 93 | 5.61 | 1.74 | 2736 | 15.2 | | | |
| Sim2 | Offshore | Late June 6/17-18/14 | 168 | 20 | 21 | 7.62 | 2.01 | 4201 | 12.9 | 0.4712 | 7.9 | 25.49 |

Table 1 (continued)

**Skagit Spring**

| **SCEN1** | Habitat | Sampling Period | Mean Day of Year | Simulation Day | N (fish sampled) | Weight (g) | Growth Increment | Avg Prey Energy Density (J/g) | Temp (˚C) | P-value (feeding rate) | Total Consumption (g) | Growth Efficiency (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Hatchery | Early June 6/12/14 | 163 | 1 | 60 | 5.29 | | | | | | |
| Sim1 | Nearshore | Late June 6/23-25/14 | 175 | 12 | 9 | 5.57 | 0.28 | 4677 | 14.4 | | | |
| Sim2 | Nearshore | Late July 7/21-23/14 | 203 | 40 | 9 | 7.84 | 2.27 | 4655 | 14.4 | 0.2862 | 9.7 | 23.52 |
| Sim3 | Offshore | Early August 8/4-5/14 | 216 | 53 | 9 | 15.22 | 7.38 | 6022 | 10.4 | 0.5480 | 12.0 | 61.50 |
| **SCEN2** | | | | | | | | | | | | |
| | Hatchery | Early June 6/12/14 | 163 | 1 | 60 | 5.29 | | | | | | |
| Sim1 | Nearshore | Late June 6/23-25/14 | 175 | 12 | 9 | 5.57 | 0.28 | 4677 | 14.4 | | | |
| Sim4 | Offshore | Late July 7/22/14 | 203 | 40 | 15 | 12.57 | 7.00 | 4126 | 9.7 | 0.4421 | 16.9 | 41.32 |
| Sim5 | Offshore | Early August 8/4-5/14 | 216 | 53 | 9 | 15.22 | 2.65 | 6022 | 10.4 | 0.2838 | 6.7 | 39.50 |

Table 1 (continued)

**Skagit Summer**

| **SCEN1** | Habitat | Sampling Period | Mean Day of Year | Simulation Day | N (fish sampled) | Weight (g) | Growth Increment | Avg Prey Energy Density (J/g) | Temp (˚C) | P-value (feeding rate) | Total Consumption (g) | Growth Efficiency (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | Hatchery | Late June 6/18/14 | 169 | 1 | 94 | 3.15 |  |  |  |  |  |  |
| Sim1 | Nearshore | Early July 7/7/14 | 188 | 19 | 9 | 4.10 | 0.95 | 4972 | 14.5 |  |  |  |
| Sim2 | Nearshore | Late July 7/21-23/14 | 204 | 35 | 16 | 4.93 | 0.83 | 4655 | 14.4 | 0.2539 | 3.8 | 21.90 |
| Sim3 | Nearshore | Early August 8/4-5/14 | 216 | 47 | 5 | 8.33 | 3.40 | 6872 | 15.3 | 0.4142 | 6.0 | 56.66 |

**Skagit Upper Summer**

| **SCEN1** | Habitat | Sampling Period | Mean Day of Year | Simulation Day | N (fish sampled) | Weight (g) | Growth Increment | Avg Prey Energy Density (J/g) | Temp (˚C) | P-value (feeding rate) | Total Consumption (g) | Growth Efficiency (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | Nearshore | Early March 3/11-12/14 | 71 | 1 | 14 | 0.63 |  | 3856 | 7.9 |  |  |  |
| Sim1 | Nearshore | Early April 4/7-11/14 | 98 | 28 | 8 | 0.96 | 0.32 | 4007 | 10.2 | 0.2335 | 1.3 | 25.36 |
| Sim2 | Nearshore | Late April 4/21-25/14 | 113 | 43 | 8 | 1.77 | 0.81 | 3590 | 9.6 | 0.4247 | 2.1 | 38.88 |

Table 1 (continued)

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sim3 | Nearshore | Early May 5/8-9/14 | 128 | 58 | 17 | 3.71 | 1.94 | 4051 | 11.7 | 0.5474 | 4.6 | 42.47 |
| Sim4 | Offshore | Early June 6/3/14 | 154 | 84 | 15 | 8.60 | 4.90 | 3726 | 10.7 | 0.4853 | 12.8 | 38.19 |
| Sim5 | Offshore | Late June 6/17/14 | 168 | 98 | 14 | 8.77 | 0.17 | 3588 | 9.9 | 0.2153 | 4.0 | 4.18 |
| Sim6 | Offshore | Early July 7/8/14 | 189 | 119 | 5 | 13.80 | 5.03 | 5081 | 9.4 | 0.4047 | 12.3 | 40.76 |
| Sim7 | Offshore | Late July 7/22/14 | 203 | 133 | 6 | 14.67 | 0.87 | 4126 | 9.7 | 0.2114 | 5.4 | 16.19 |
| Sim8 | Offshore | Early August 8/4-5/14 | 216 | 146 | 8 | 18.25 | 3.58 | 6022 | 10.4 | 0.3135 | 8.4 | 42.83 |
| **SCEN2** | | | | | | | | | | | | |
| | Nearshore | Late May 5/20-27/14 | 143 | 73 | 7 | 2.54 | | 3945 | 12.5 | | | |
| Sim9 | Nearshore | Early June 6/9/14 | 160 | 90 | 11 | 3.81 | 1.27 | 4821 | 15.1 | 0.3332 | 4.0 | 32.00 |
| Sim10 | Offshore | Late June 6/17/14 | 168 | 98 | 14 | 8.77 | 4.96 | 3588 | 9.9 | 1.0801 | 9.8 | 50.80 |
| Sim6 | Offshore | Early July 7/8/14 | 189 | 119 | 5 | 13.80 | 5.03 | 5081 | 9.4 | 0.4047 | 12.3 | 40.76 |
| Sim7 | Offshore | Late July 7/22/14 | 203 | 133 | 6 | 14.67 | 0.87 | 4126 | 9.7 | 0.2114 | 5.4 | 16.19 |
| Sim8 | Offshore | Early August 8/4-5/14 | 216 | 146 | 8 | 18.25 | 3.58 | 6022 | 10.4 | 0.3135 | 8.4 | 42.83 |

Table 1 (continued)

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **SCEN3** | | | | | | | | | | | | |
| | Nearshore | Late May 5/20-27/14 | 143 | 73 | 7 | 2.54 | | 3945 | 12.5 | | | |
| Sim9 | Nearshore | Early June 6/9/14 | 160 | 90 | 11 | 3.81 | 1.27 | 4821 | 15.1 | 0.3332 | 4.0 | 32.00 |
| Sim11 | Nearshore | Late June 6/23-30/14 | 175 | 105 | 21 | 3.90 | 0.09 | 4677 | 14.3 | 0.1941 | 2.4 | 3.69 |
| Sim12 | Offshore | Early July 7/8/14 | 189 | 119 | 5 | 13.80 | 9.90 | 5081 | 9.4 | 0.8973 | 16.0 | 61.82 |
| Sim7 | Offshore | Late July 7/22/14 | 203 | 133 | 6 | 14.67 | 0.87 | 4126 | 9.7 | 0.2114 | 5.4 | 16.19 |
| Sim8 | Offshore | Early August 8/4-5/14 | 216 | 146 | 8 | 18.25 | 3.58 | 6022 | 10.4 | 0.3135 | 8.4 | 42.83 |
| **SCEN4** | | | | | | | | | | | | |
| | Nearshore | Late May 5/20-27/14 | 143 | 73 | 7 | 2.54 | | 3945 | 12.5 | | | |
| Sim9 | Nearshore | Early June 6/9/14 | 160 | 90 | 11 | 3.81 | 1.27 | 4821 | 15.1 | 0.3332 | 4.0 | 32.00 |
| Sim11 | Nearshore | Late June 6/23-30/14 | 175 | 105 | 21 | 3.90 | 0.09 | 4677 | 14.3 | 0.1941 | 2.4 | 3.69 |
| Sim13 | Nearshore | Early July 7/7-9/14 | 188 | 118 | 11 | 7.50 | 3.60 | 4972 | 15.1 | 0.5243 | 7.4 | 48.82 |
| Sim14 | Offshore | Late July 7/22/14 | 203 | 133 | 6 | 14.67 | 7.17 | 4126 | 9.7 | 0.5899 | 14.6 | 49.05 |
| Sim8 | Offshore | Early August 8/4-5/14 | 216 | 146 | 8 | 18.25 | 3.58 | 6022 | 10.4 | 0.3135 | 8.4 | 42.83 |

Table 1 (continued)

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **SCEN5** | | | | | | | | | | | | |
| | Nearshore | Late July 7/21-23/14 | 203 | 133 | 13 | 5.05 | | 4655 | 14.4 | | | |
| Sim15 | Nearshore | Late August 8/18-19/14 | 231 | 160 | 6 | 12.31 | 7.26 | 7707 | 14.6 | 0.3458 | 12.5 | 58.24 |
| **Nooksack Kendall Creek** | | | | | | | | | | | | |
| **SCEN1** | Habitat | Sampling Period | Mean Day of Year | Simulation Day | N (fish sampled) | Weight (g) | Growth Increment | Avg Prey Energy Density (J/g) | Temp (˚C) | P-value (feeding rate) | Total Consumption (g) | Growth Efficiency (%) |
| | Nearshore | Early May 5/7-9/14 | 129 | 1 | 6 | 5.09 | | 4142 | 14.2 | | | |
| Sim1 | Offshore | Early June 6/2/14 | 153 | 24 | 11 | 13.14 | 8.05 | 4203 | 9.9 | 0.5810 | 18.1 | 44.51 |
| Sim2 | Offshore | Early August 8/4/14 | 216 | 87 | 3 | 68.67 | 55.53 | 3944 | 10.4 | 0.6163 | 134.0 | 41.44 |
| **Nooksack Skookum Creek** | | | | | | | | | | | | |
| **SCEN1** | Habitat | Sampling Period | Mean Day of Year | Simulation Day | N (fish sampled) | Weight (g) | Growth Increment | Avg Prey Energy Density (J/g) | Temp (˚C) | P-value (feeding rate) | Total Consumption (g) | Growth Efficiency (%) |
| | Nearshore | Late June 6/20-23/14 | 172 | 1 | 5 | 6.49 | | 4582 | 16.6 | | | |
| Sim1 | Offshore | Early July 7/7/14 | 188 | 16 | 3 | 10.67 | 4.18 | 6214 | 9.4 | 0.3936 | 8.0 | 52.14 |

Table 1 (continued)

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sim2 | Offshore | Late July 7/21/14 | 202 | 30 | 17 | 12.06 | 1.39 | 3951 | 9.8 | 0.2235 | 4.8 | 28.66 |
| Sim3 | Offshore | Early August 8/4/14 | 216 | 44 | 15 | 24.53 | 12.47 | 3944 | 10.4 | 0.8839 | 26.8 | 46.55 |
| **SCEN2** | | | | | | | | | | | | |
| | Nearshore | Late June 6/20-23/14 | 172 | 1 | 5 | 6.49 | | 4582 | 16.6 | | | |
| Sim4 | Nearshore | Early July 7/8/14 | 189 | 17 | 3 | 6.52 | 0.03 | 8890 | 18.5 | 0.1811 | 3.5 | 0.85 |
| Sim5 | Offshore | Late July 7/21/14 | 202 | 30 | 17 | 12.06 | 5.54 | 3951 | 9.8 | 0.4257 | 8.6 | 64.43 |
| Sim3 | Offshore | Early August 8/4/14 | 216 | 44 | 15 | 24.53 | 12.47 | 3944 | 10.4 | 0.8839 | 26.8 | 46.55 |
| **SCEN3** | | | | | | | | | | | | |
| | Nearshore | Late June 6/20-23/14 | 172 | 1 | 5 | 6.49 | | 4582 | 16.6 | | | |
| Sim4 | Nearshore | Early July 7/8/14 | 189 | 17 | 3 | 6.52 | 0.03 | 8890 | 18.5 | 0.1811 | 3.5 | 0.85 |
| Sim6 | Nearshore | Late July 7/18-21/14 | 201 | 29 | 3 | 7.86 | 1.34 | 5164 | 17.0 | 0.2527 | 4.2 | 32.10 |
| Sim7 | Offshore | Early August 8/4/14 | 216 | 44 | 15 | 24.53 | 16.67 | 3944 | 10.4 | 0.9799 | 31.6 | 52.69 |

Table 1 (continued)

| **Nooksack Fall** | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **SCEN1** | Habitat | Sampling Period | Mean Day of Year | Simulation Day | N (fish sampled) | Weight (g) | Growth Increment | Avg Prey Energy Density (J/g) | Temp (˚C) | P-value (feeding rate) | Total Consumption (g) | Growth Efficiency (%) |
| | Nearshore | Early April 4/7-8/14 | 98 | 15 | 19 | 0.48 | | 4317 | 11.2 | | | |
| Sim1 | Nearshore | Late April 4/21-25/14 | 113 | 30 | 12 | 1.23 | 0.75 | 3596 | 11.3 | 0.3474 | 1.2 | 61.79 |
| **SCEN2** | | | | | | | | | | | | |
| | Nearshore | Early May 5/6/14 | 126 | 43 | 6 | 1.10 | | 4413 | 12.6 | | | |
| Sim2 | Nearshore | Early June 6/6/14 | 157 | 74 | 5 | 2.35 | 1.25 | 4418 | 17.1 | 0.2454 | 2.6 | 47.17 |

*Temperature data were recorded concurrently with fish sampling, with these exceptions:

1. Snohomish nearshore early June: used average of temperature measurements on 6/3/14 from site "sb1" near “priest point” site where fish were sampled
2. Snohomish offshore late June: used average of daily temperature measurements from Mukilteo mooring MUK01SR off of Boeing Pier at 3.3m and 13.3 m depth MLLW
3. Skagit smolt trap early June: used average of daily temperature measurements from USGS gauge “12181000 Marblemount”
4. Skagit offshore late June: used average of temperature measurements in top 6m of water column from WA Dept. of Ecology Marine Water Quality Monitoring Buoy SKG003 on 6/23/14
5. Nooksack offshore late June: used average of water temperature measurements in top 9.5m of water column from WA Dept. of Ecology Marine Water Quality Monitoring Buoy BLL009 on 6/23/14.

**Table 2.** Average prey proportions and energy densities for each stock and bioenergetics scenario. The twelve most common prey items are listed individually and the rest are included in the “other” category. See Table 1A for more information on each of the 21 prey groups.

| **Nisqually Clear Creek** | **Prey Energy Density (J/g):** | | 12670 | 10930 | 7211 | 5060 | 4730 | 4339 | 4225 | 3548 | 3395 | 3379 | 2994 | 1980 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Habitat | Sim Day | N Diets | Hymenoptera | Hemiptera | Insect (other) | Sand Lance | Shrimp (Post-larval/Adult) | Diptera (adult) | Crab Megalops | Other Fish | Crab Zoea | Crustacean (other)/Rare Invert | Amphipod | Worm | Other |
| Hatchery | 1 | | | | | | | | | | | | | | |
| Estuary | 22 | 28 | 0.000 | 0.000 | 0.371 | 0.000 | 0.000 | 0.151 | 0.002 | 0.000 | 0.097 | 0.012 | 0.138 | 0.107 | 0.121 |
| Nearshore | 22 | 21 | 0.091 | 0.000 | 0.001 | 0.000 | 0.000 | 0.086 | 0.035 | 0.042 | 0.198 | 0.213 | 0.103 | 0.108 | 0.124 |
| Nearshore | 35 | 16 | 0.003 | 0.000 | 0.000 | 0.000 | 0.000 | 0.006 | 0.189 | 0.063 | 0.321 | 0.130 | 0.031 | 0.064 | 0.194 |
| Offshore | 13 | 24 | 0.000 | 0.000 | 0.013 | 0.295 | 0.020 | 0.000 | 0.031 | 0.149 | 0.141 | 0.197 | 0.064 | 0.000 | 0.091 |
| Offshore | 40 | 13 | 0.000 | 0.000 | 0.000 | 0.000 | 0.006 | 0.001 | 0.625 | 0.008 | 0.106 | 0.226 | 0.005 | 0.000 | 0.023 |
| Offshore | 51 | 18 | 0.001 | 0.022 | 0.000 | 0.000 | 0.001 | 0.003 | 0.536 | 0.006 | 0.132 | 0.155 | 0.006 | 0.001 | 0.137 |
| Offshore | 73 | 18 | 0.006 | 0.000 | 0.001 | 0.000 | 0.006 | 0.000 | 0.635 | 0.000 | 0.135 | 0.080 | 0.007 | 0.000 | 0.131 |
| **Snohomish Tulalip** | | | | | | | | | | | | | | | |
| Habitat | Sim Day | N Diets | Hymenoptera | Hemiptera | Insect (other) | Sand Lance | Shrimp (Post-larval/Adult) | Diptera (adult) | Crab Megalops | Other Fish | Crab Zoea | Crustacean (other)/Rare Invert | Amphipod | Worm | Other |
| Nearshore | 6 | 12 | 0.000 | 0.000 | 0.005 | 0.000 | 0.000 | 0.069 | 0.001 | 0.000 | 0.000 | 0.375 | 0.000 | 0.528 | 0.022 |
| Offshore | 20 | 10 | 0.001 | 0.017 | 0.006 | 0.000 | 0.000 | 0.010 | 0.760 | 0.000 | 0.191 | 0.008 | 0.003 | 0.000 | 0.003 |
| **Skagit Spring** | | | | | | | | | | | | | | | |
| Habitat | Sim Day | N Diets | Hymenoptera | Hemiptera | Insect (other) | Sand Lance | Shrimp (Post-larval/Adult) | Diptera (adult) | Crab Megalops | Other Fish | Crab Zoea | Crustacean (other)/Rare Invert | Amphipod | Worm | Other |
| Nearshore | 12 | 19 | 0.025 | 0.072 | 0.009 | 0.000 | 0.000 | 0.531 | 0.019 | 0.000 | 0.000 | 0.057 | 0.145 | 0.000 | 0.141 |
| Nearshore | 40 | 20 | 0.009 | 0.048 | 0.098 | 0.000 | 0.000 | 0.412 | 0.044 | 0.090 | 0.079 | 0.094 | 0.032 | 0.000 | 0.094 |

Table 2 (continued)

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Offshore | 40 | 11 | 0.011 | 0.012 | 0.001 | 0.000 | 0.000 | 0.051 | 0.646 | 0.000 | 0.132 | 0.010 | 0.113 | 0.000 | 0.023 |
| Offshore | 53 | 18 | 0.183 | 0.031 | 0.072 | 0.036 | 0.000 | 0.098 | 0.309 | 0.057 | 0.007 | 0.039 | 0.048 | 0.001 | 0.119 |

**Skagit Summer**

| Habitat | Sim Day | N Diets | Hymenoptera | Hemiptera | Insect (other) | Sand Lance | Shrimp (Post-larval/ Adult) | Diptera (adult) | Crab Megalops | Other Fish | Crab Zoea | Crustacean (other)/ Rare Invert | Amphipod | Worm | Other |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Hatchery | 1 | | | | | | | | | | | | | | |
| Nearshore | 19 | 10 | 0.083 | 0.014 | 0.095 | 0.000 | 0.000 | 0.254 | 0.105 | 0.185 | 0.101 | 0.079 | 0.072 | 0.000 | 0.011 |
| Nearshore | 35 | 20 | 0.009 | 0.048 | 0.098 | 0.000 | 0.000 | 0.412 | 0.044 | 0.090 | 0.079 | 0.094 | 0.032 | 0.000 | 0.094 |
| Nearshore | 47 | 11 | 0.290 | 0.030 | 0.049 | 0.000 | 0.089 | 0.288 | 0.021 | 0.000 | 0.001 | 0.036 | 0.040 | 0.000 | 0.156 |

**Skagit Upper Summer**

| Habitat | Sim Day | N Diets | Hymenoptera | Hemiptera | Insect (other) | Sand Lance | Shrimp (Post-larval/ Adult) | Diptera (adult) | Crab Megalops | Other Fish | Crab Zoea | Crustacean (other)/ Rare Invert | Amphipod | Worm | Other |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nearshore | 1 | 9 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.371 | 0.000 | 0.000 | 0.000 | 0.115 | 0.128 | 0.000 | 0.386 |
| Nearshore | 28 | 10 | 0.000 | 0.009 | 0.000 | 0.000 | 0.000 | 0.619 | 0.000 | 0.000 | 0.007 | 0.061 | 0.240 | 0.000 | 0.064 |
| Nearshore | 43 | 9 | 0.000 | 0.004 | 0.000 | 0.000 | 0.000 | 0.214 | 0.000 | 0.074 | 0.000 | 0.311 | 0.308 | 0.000 | 0.089 |
| Nearshore | 58 | 10 | 0.001 | 0.009 | 0.090 | 0.000 | 0.000 | 0.354 | 0.000 | 0.055 | 0.000 | 0.109 | 0.274 | 0.000 | 0.108 |
| Nearshore | 73 | 10 | 0.000 | 0.026 | 0.010 | 0.000 | 0.040 | 0.307 | 0.000 | 0.100 | 0.004 | 0.097 | 0.270 | 0.000 | 0.146 |
| Nearshore | 90 | 10 | 0.002 | 0.070 | 0.109 | 0.000 | 0.000 | 0.446 | 0.056 | 0.004 | 0.049 | 0.130 | 0.004 | 0.000 | 0.129 |
| Nearshore | 105 | 19 | 0.025 | 0.072 | 0.009 | 0.000 | 0.000 | 0.531 | 0.019 | 0.000 | 0.000 | 0.057 | 0.145 | 0.000 | 0.141 |
| Nearshore | 118 | 10 | 0.083 | 0.014 | 0.095 | 0.000 | 0.000 | 0.254 | 0.105 | 0.185 | 0.101 | 0.079 | 0.072 | 0.000 | 0.011 |
| Nearshore | 133 | 20 | 0.009 | 0.048 | 0.098 | 0.000 | 0.000 | 0.412 | 0.044 | 0.090 | 0.079 | 0.094 | 0.032 | 0.000 | 0.094 |
| Nearshore | 160 | 21 | 0.361 | 0.017 | 0.168 | 0.000 | 0.047 | 0.208 | 0.011 | 0.014 | 0.001 | 0.027 | 0.022 | 0.041 | 0.083 |
| Offshore | 84 | 28 | 0.008 | 0.013 | 0.006 | 0.000 | 0.000 | 0.043 | 0.056 | 0.058 | 0.662 | 0.071 | 0.009 | 0.016 | 0.058 |
| Offshore | 98 | 9 | 0.000 | 0.009 | 0.005 | 0.105 | 0.111 | 0.008 | 0.048 | 0.010 | 0.305 | 0.065 | 0.138 | 0.176 | 0.019 |
| Offshore | 119 | 10 | 0.051 | 0.037 | 0.141 | 0.000 | 0.000 | 0.039 | 0.439 | 0.000 | 0.230 | 0.006 | 0.049 | 0.000 | 0.010 |

Table 2 (continued)

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Offshore | 133 | 11 | 0.011 | 0.012 | 0.001 | 0.000 | 0.000 | 0.051 | 0.646 | 0.000 | 0.132 | 0.010 | 0.113 | 0.000 | 0.023 |
| Offshore | 146 | 18 | 0.183 | 0.031 | 0.072 | 0.036 | 0.000 | 0.098 | 0.309 | 0.057 | 0.007 | 0.039 | 0.048 | 0.001 | 0.119 |

**Nooksack Kendall Creek**

| Habitat | Sim Day | N Diets | Hymenoptera | Hemiptera | Insect (other) | Sand Lance | Shrimp (Post-larval/ Adult) | Diptera (adult) | Crab Megalops | Other Fish | Crab Zoea | Crustacean (other)/ Rare Invert | Amphipod | Worm | Other |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nearshore | 1 | 16 | 0.064 | 0.000 | 0.052 | 0.063 | 0.000 | 0.005 | 0.000 | 0.000 | 0.021 | 0.412 | 0.107 | 0.132 | 0.146 |
| Offshore | 24 | 12 | 0.055 | 0.000 | 0.000 | 0.148 | 0.010 | 0.039 | 0.058 | 0.248 | 0.128 | 0.024 | 0.000 | 0.062 | 0.228 |
| Offshore | 87 | 12 | 0.000 | 0.018 | 0.003 | 0.083 | 0.211 | 0.005 | 0.132 | 0.058 | 0.178 | 0.098 | 0.086 | 0.002 | 0.127 |

**Nooksack Skookum Creek**

| Habitat | Sim Day | N Diets | Hymenoptera | Hemiptera | Insect (other) | Sand Lance | Shrimp (Post-larval/ Adult) | Diptera (adult) | Crab Megalops | Other Fish | Crab Zoea | Crustacean (other)/ Rare Invert | Amphipod | Worm | Other |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nearshore | 1 | 10 | 0.017 | 0.021 | 0.069 | 0.000 | 0.000 | 0.614 | 0.023 | 0.032 | 0.000 | 0.179 | 0.032 | 0.002 | 0.009 |
| Nearshore | 17 | 6 | 0.521 | 0.032 | 0.019 | 0.000 | 0.000 | 0.382 | 0.000 | 0.000 | 0.000 | 0.001 | 0.037 | 0.000 | 0.008 |
| Nearshore | 29 | 10 | 0.119 | 0.001 | 0.004 | 0.000 | 0.082 | 0.465 | 0.005 | 0.000 | 0.000 | 0.225 | 0.006 | 0.000 | 0.093 |
| Offshore | 16 | 10 | 0.192 | 0.030 | 0.210 | 0.000 | 0.000 | 0.065 | 0.158 | 0.100 | 0.059 | 0.021 | 0.023 | 0.114 | 0.029 |
| Offshore | 30 | 12 | 0.000 | 0.001 | 0.001 | 0.000 | 0.000 | 0.003 | 0.684 | 0.083 | 0.106 | 0.083 | 0.005 | 0.027 | 0.006 |
| Offshore | 44 | 12 | 0.000 | 0.018 | 0.003 | 0.083 | 0.211 | 0.005 | 0.132 | 0.058 | 0.178 | 0.098 | 0.086 | 0.002 | 0.127 |

Table 2 (continued)

**Nooksack Fall**

| Habitat | Sim Day | N Diets | Hymenoptera | Hemiptera | Insect (other) | Sand Lance | Shrimp (Post-larval/Adult) | Diptera (adult) | Crab Megalops | Other Fish | Crab Zoea | Crustacean (other)/ Rare Invert | Amphipod | Worm | Other |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nearshore | 15 | 22 | 0.000 | 0.063 | 0.127 | 0.000 | 0.000 | 0.054 | 0.001 | 0.000 | 0.060 | 0.176 | 0.230 | 0.117 | 0.173 |
| Nearshore | 30 | 21 | 0.009 | 0.000 | 0.028 | 0.000 | 0.000 | 0.182 | 0.000 | 0.000 | 0.000 | 0.073 | 0.372 | 0.056 | 0.280 |
| Nearshore | 43 | 11 | 0.091 | 0.000 | 0.063 | 0.000 | 0.000 | 0.003 | 0.000 | 0.000 | 0.030 | 0.508 | 0.156 | 0.026 | 0.123 |
| Nearshore | 74 | 22 | 0.000 | 0.019 | 0.014 | 0.000 | 0.000 | 0.393 | 0.463 | 0.000 | 0.000 | 0.027 | 0.026 | 0.000 | 0.057 |

## Figures

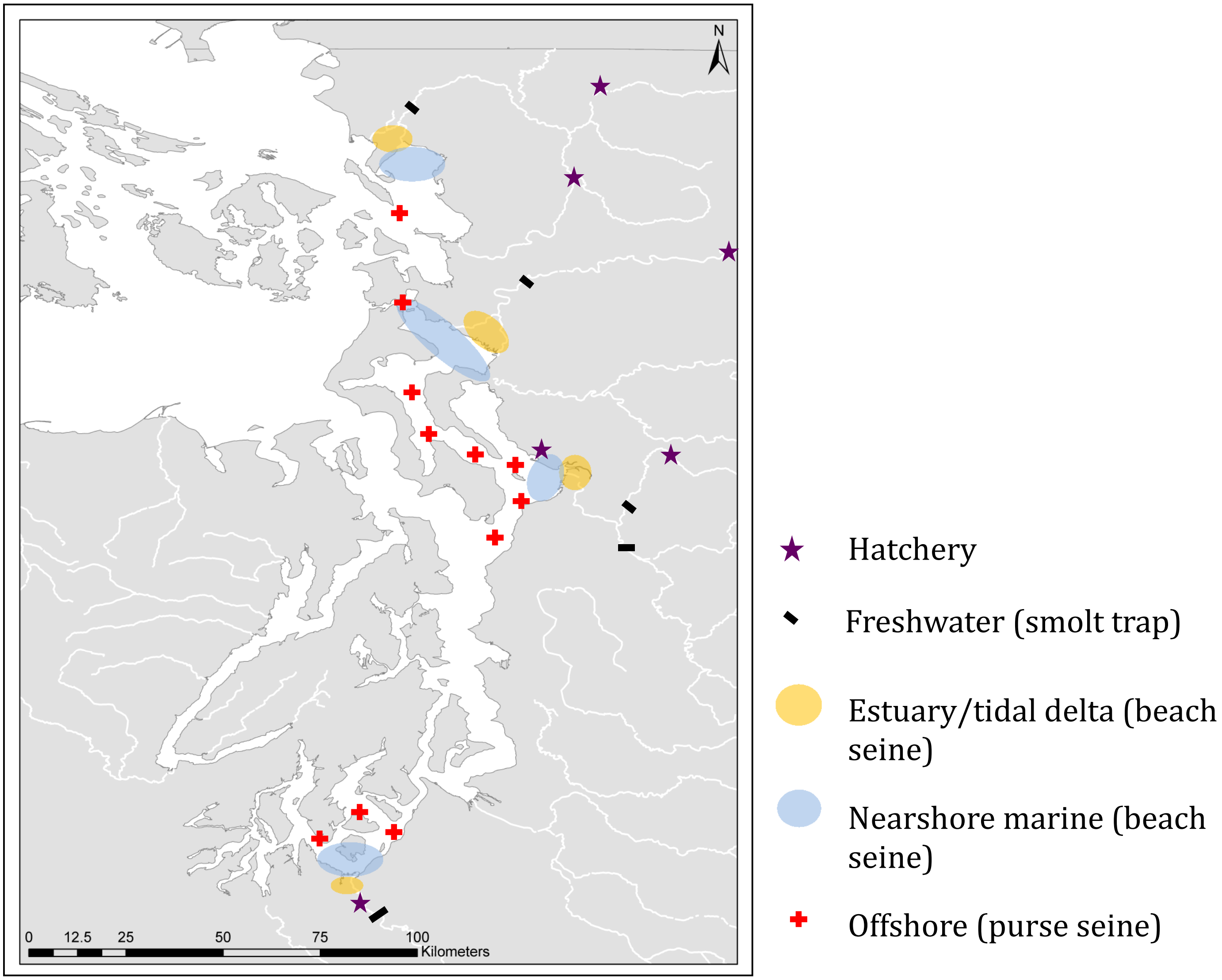


**Figure 1.** Sampling map showing approximate locations of juvenile Chinook sampling efforts in each habitat and watershed.

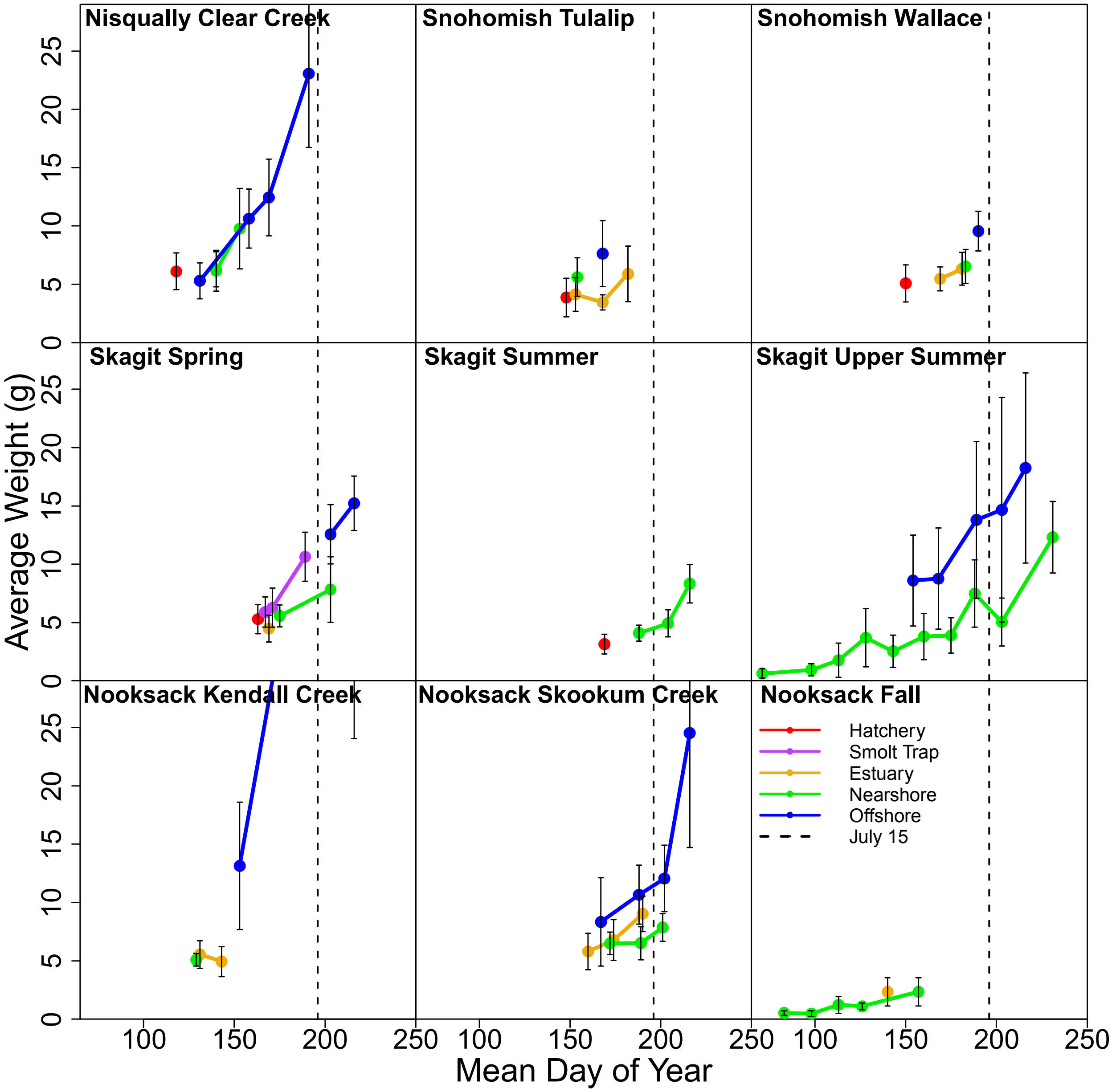


**Figure 2.** Stage-specific weights for juvenile Chinook in each stock. Error bars indicate standard deviation.

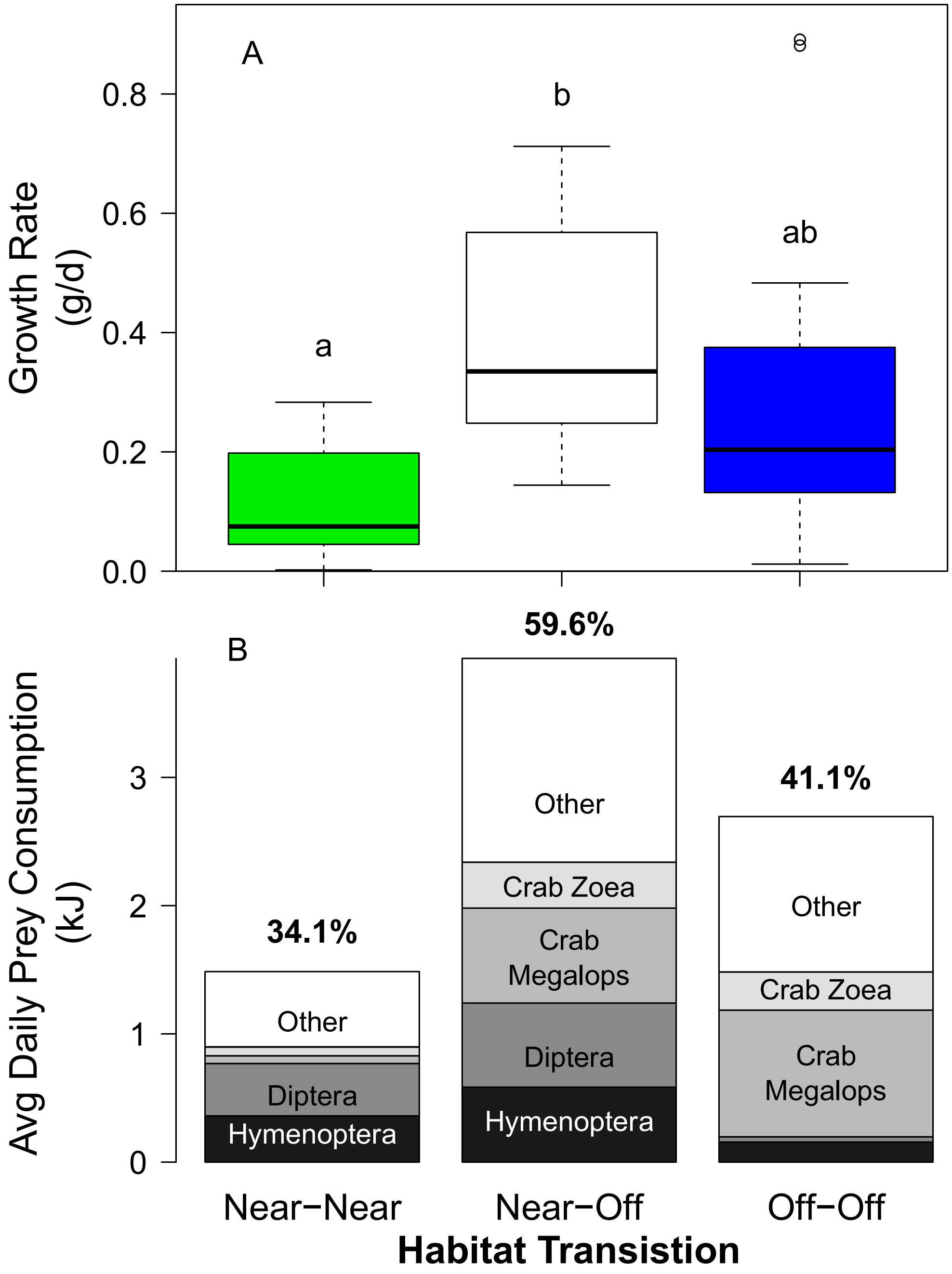


**Figure 3.** (A) Average habitat-specific growth rates (g/d) and (B) average habitat-specific daily prey consumption (kJ) and feeding rates (%Cmax) for juvenile Chinook in each stock. Average growth rates were calculated as differences between average stage-specific weights. Average daily prey consumption is an output of the bioenergetics model. Percentages above consumption bars indicate average feeding rate. See Appendix Figure A1 for stock-specific prey consumption.

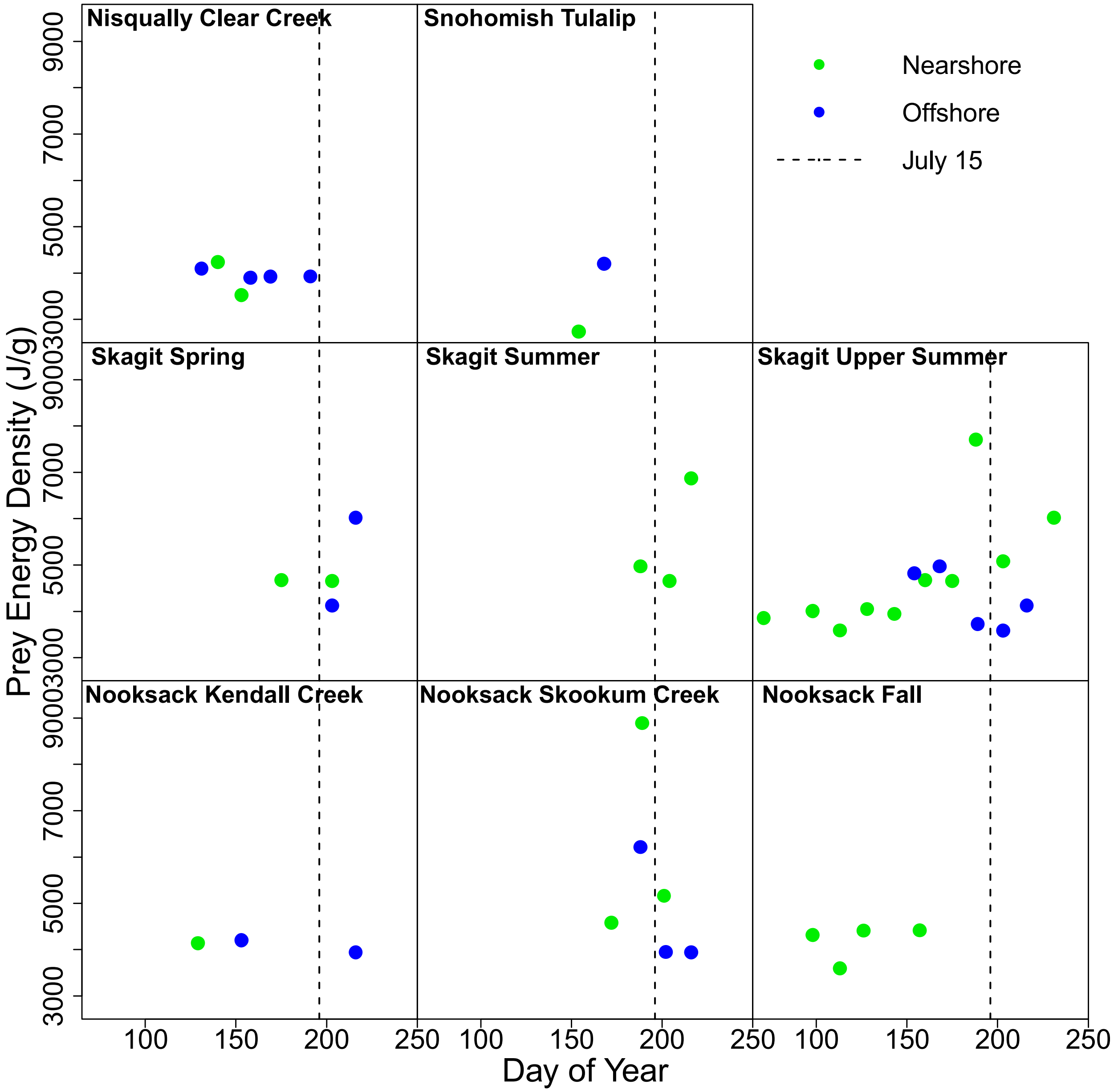


**Figure 4.** Stage-specific average prey energy density for all stocks.

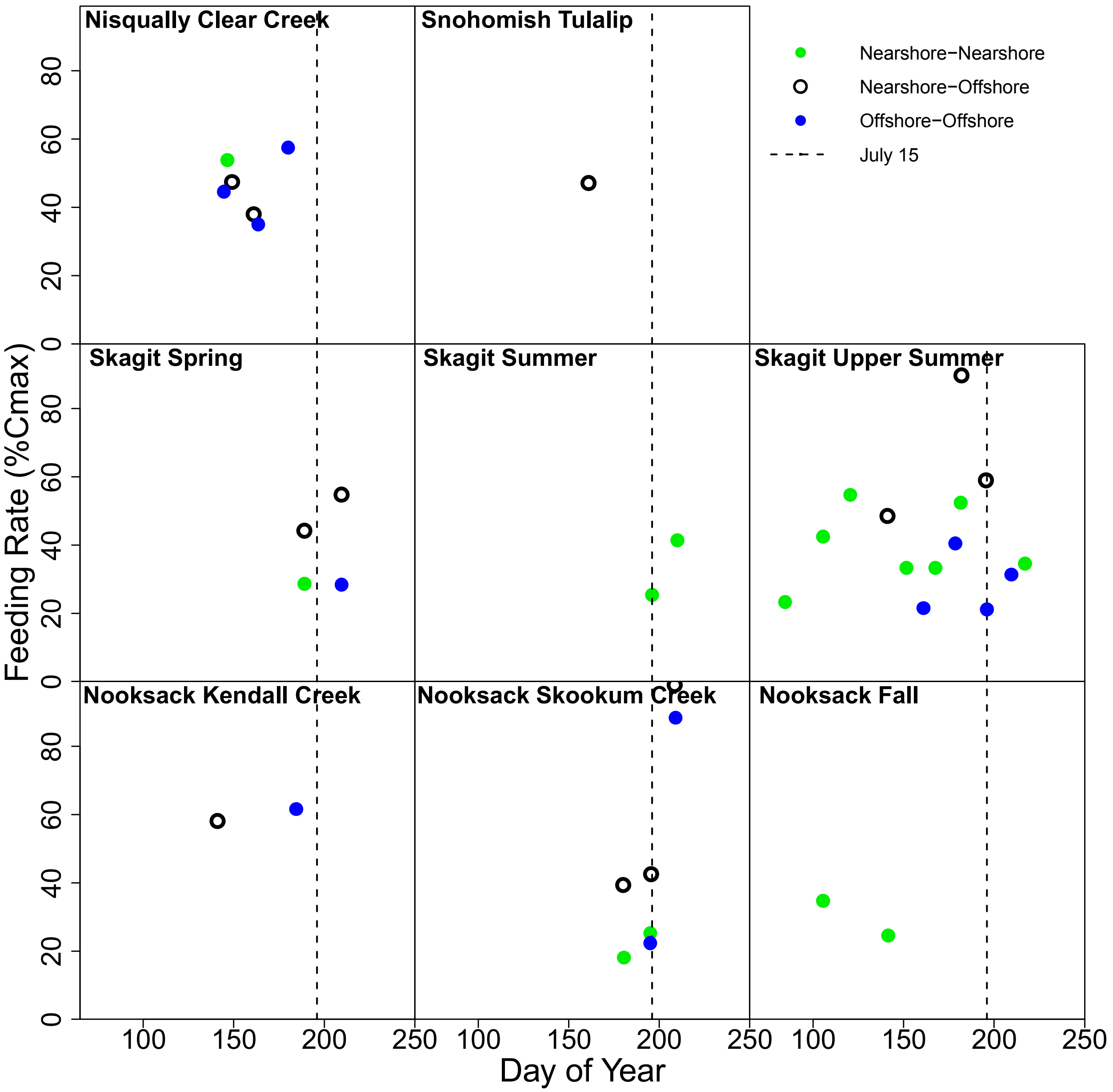


**Figure 5.** Stage-specific feeding rates for all growth stocks.

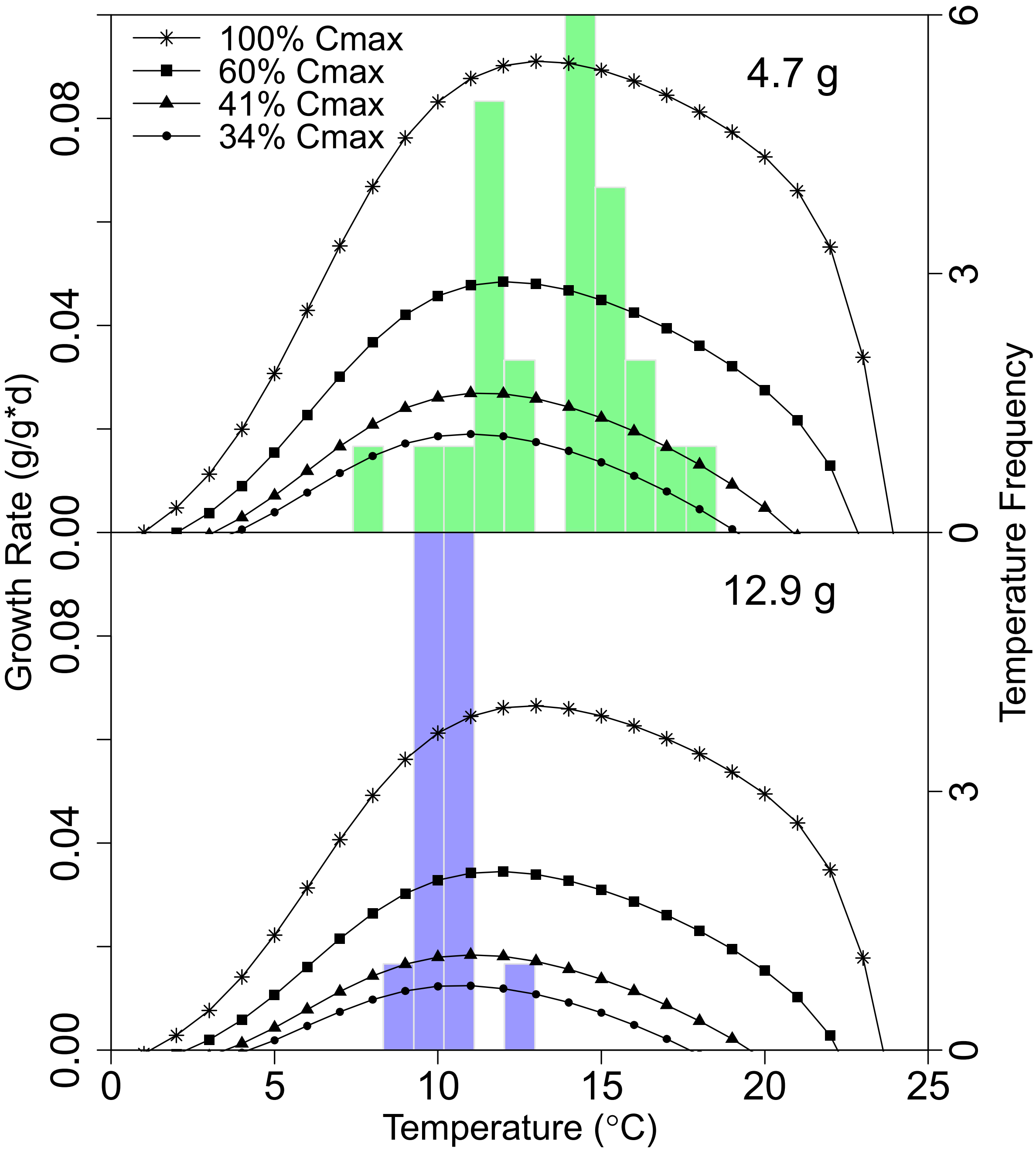


**Figure 6.** Temperature-growth curves for Chinook of the average nearshore (top panel) and offshore (bottom panel) weight at average habitat-specific feeding rates overlaid with a frequency histogram of water temperatures observed throughout the study in nearshore (green) and offshore (blue) habitats.

# Appendix

**Table A1.** Prey energy densities and literature sources. Energy densities for bioenergetics prey categories are averages of energy densities of the taxon categories included in each category.

| Bioenergetics Prey Category | Bioenergetics Category Energy Density (J/g) | Taxon Categories | Taxon Category Energy Density (J/g) | Source + Notes |
|---|---|---|---|---|
| Diptera (adult) | 4339 | Digested Insect Parts | 4339 | David 2014 Masters Thesis |
| | | Diptera Adult | 4339 | David 2014 Masters Thesis |
| Insect (other) | 7211 | Lepidoptera Adult | 8500 | Gray 2005 (Lepidoptera adult and larvae) |
| | | Rare Insects | 7183 | David 2014 Masters Thesis |
| | | Unid Adult Insects | 7412 | Bieber 2005 (Other Insecta) |
| | | unID Insect Eggs (Describe in notes) | 6000 | David 2014 (Eggs) |
| | | Psocoptera adult | 6430 | Norberg 1978 |
| | | Trichoptera Adult | 7760 | Gray 2005 (Trichoptera Adult) |
| | | Coleoptera Adult | 7970 | Gray 2005 (Coleoptera Adult) |
| | | Psocoptera Nymph | 6430 | Norberg 1978 |
| Insect Pupa | 3140 | Diptera Pupa | 3140 | Gray 2005 (Diptera pupa appendix F) |
| | | UnID Insect Pupa | 3140 | David 2014 Masters Thesis |
| Insect Larvae | 4375 | Diptera Larvae | 2580 | Gray 2005 (Diptera Larvae) |
| | | Unid Insect Larvae | 2580 | David 2014 Masters Thesis |
| | | Lepidoptera Larva | 8500 | Gray 2005 (Lepidoptera adult and larvae) |
| | | Coleoptera Larvae | 2405 | Gray 2005 (Coleoptera Larvae) |
| | | Tricoptera Larvae | 5810 | Gray 2005 (Trichoptera Larvae) |
| Hemiptera | 10930 | Hemiptera adult | 10930 | Gray 2005 (Hemiptera adult and immature) |
| | | Hemiptera Larva/Nymph | 10930 | Gray 2005 (Hemiptera adult and immature) |
| Hymenoptera | 12670 | Hymenoptera | 12670 | Gray 2005 (Hymenoptera) |
| Aquatic Nymph/Adult | 4059 | Ephemeroptera Nymph | 3664 | Pizzul et al. 2009 |
| | | Ephemeroptera adult | 3664 | Pizzul et al. 2009 |
| | | Plecoptera Nymph | 4125 | Pizzul et al. 2009 |
| | | Plecoptera adult | 4125 | Pizzul et al. 2009 |
| | | Unid Aquatic Nymph | 3895 | Madi Gamble's Estimate |
| | | Odonata adult and nymph | 4879 | David 2014 (Odonata adult and nymph) |
| Collembola/Arachnid | 5471 | Collembola | 5621 | Gray 2005 (Collembola) |
| | | Arachnida | 5320 | Gray 2005 (Arachnids) |

Table A1 (continued)

| | | | | |
|---|---|---|---|---|
| Crustacean (other)/Rare Invert | 3379 | Digested Crustacean | 3370 | Bieber 2005 (Other crustacean) |
| | | Barnacle slough | 2160 | Lucas et al 1979 from David 2014 |
| | | Calanoida | 4620 | Higgs et al. 1995 |
| | | Harpacticoidas | 4620 | Higgs et al. 1995 |
| | | UnID Copepod | 4620 | Higgs et al. 1995 |
| | | Cladocera | 1370 | Higgs et al. 1995 |
| | | Cumaceans | 3370 | Bieber 2005 (Other crustacean) |
| | | Unid Crustacean | 3370 | Bieber 2005 (Other crustacean) |
| | | Barnacle Cyprid | 2160 | Lucas et al 1979 from David 2014 |
| | | Ostracods | 3370 | Bieber 2005 (Other crustacean) |
| | | Rare Invertebrates (list taxon in notes) | 3093 | David 2014 Masters Thesis |
| | | Unid invert | 3370 | David 2014 Masters Thesis |
| | | Cyclopoida | 4620 | Higgs et al. 1995 |
| | | Tanaidacea | 3370 | Bieber 2005 (Other crustacean) |
| | | Siphonostomatoida | 4620 | Higgs et al. 1995 |
| | | Larvacea | 3180 | Davis et al. 1998 |
| | | Juvenile Barnacle (between cyprid and adult) | 2160 | Lucas et al 1979 from David 2014 |
| Amphipod | 2994 | Amphipod but NOT Caprellid, Corophium, or Hyperiid ("OTHER") | 2970 | David 2014 (Amphipods) |
| | | Corophiidae | 3065 | David 2014 (Corophiidae) |
| | | unID Amphipod | 2970 | David 2014 (Amphipods) |
| | | Caprellida | 2970 | David 2014 (Caprellidea) |
| Crab Megalops | 4225 | Decapod megalops | 4225 | Jose Marin Jarrin thesis 2012 |
| | | Crab (post-larval) | 4225 | Jose Marin Jarrin thesis 2012 |
| | | Paguroidea Megalops | 4225 | Jose Marin Jarrin thesis 2012 |
| | | Paguroidea Adult (Hermit Crabs) | 4225 | Jose Marin Jarrin thesis 2012 |
| Crab Zoea | 3395 | Decapod zoea | 3395 | Nishiyama 1972 |
| | | "Shrimp" Zoea (all shrimp zoea including krill and mysid) | 3395 | Nishiyama 1972 |
| Euphausid | 4729 | Euphausia | 4729 | Higgs et al. 1995 |
| Mysid | 3550 | Mysid | 3550 | Gray 2005 (Mysida) |
| Shrimp (Postlarval/Adult) | 4730 | UnID Shrimp (not sure if mysid/krill, etc.) | 4730 | David 2014 Masters Thesis |
| | | Other Shrimp (shrimp that is NOT krill or mysid) | 4730 | Davis 1993 |
| Hyperiid | 2464 | Hyperiids | 2464 | Davis et al. 1998 (Hyperiid amphipods) |

Table A1 (continued)

| | | | | |
|---|---|---|---|---|
| Worm | 1980 | Polychaetes | 1980 | Gray 2005 (Oligo-, Polycheates) |
| | | Unid Worm | 1980 | David 2014 Masters Thesis |
| | | Chaetognatha | 1980 | David 2014 Masters Thesis |
| Isopod | 2960 | Isopods | 2960 | David 2014 (Isopoda) |
| Other Fish | 3548 | UnID Fish | 3500 | David 2014 Masters Thesis |
| | | Other Fish | 3500 | David 2014 Masters Thesis |
| | | Digested Fish | 3500 | David 2014 Masters Thesis |
| | | Herring | 3690 | Anthony et al 2000 (Pacific herring <100mm) |
| Salmonid | 3410 | unid salmonid | 3410 | Anthony et al 2000 (Pink salmon <100mm) |
| | | pink | 3410 | Anthony et al 2000 (Pink salmon <100mm) |
| | | chum | 3410 | Anthony et al 2000 (Pink salmon <100mm) |
| Sand Lance | 5060 | sand lance | 5060 | Anthony et al 2000 (Pacific sand lance <100mm) |

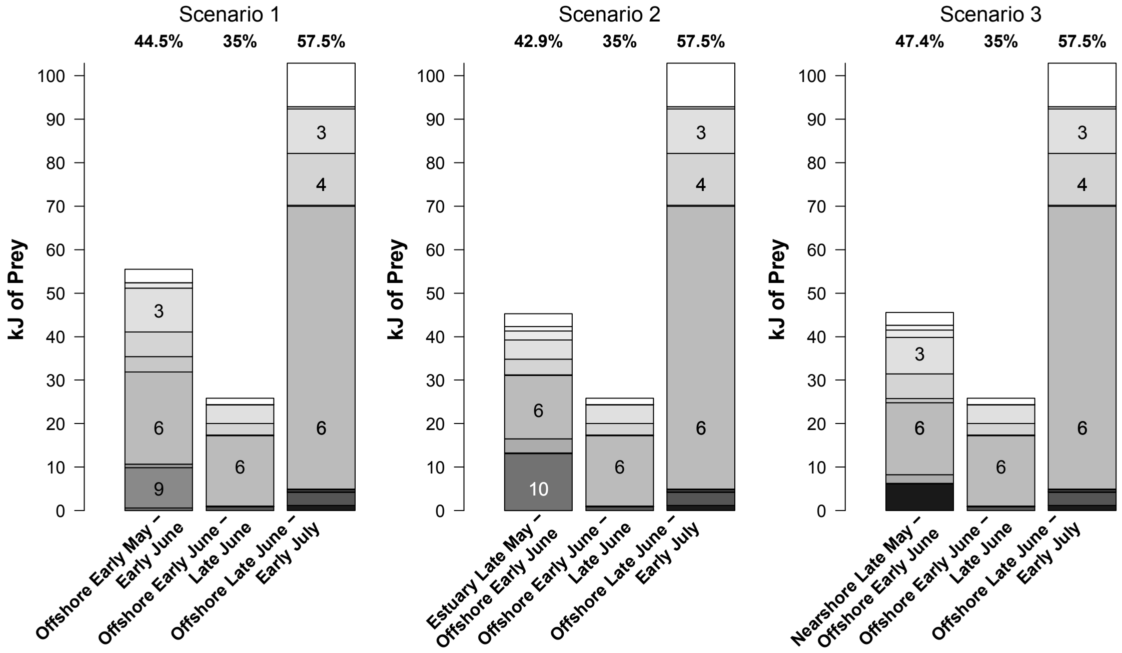
**Figure A1.** Joules of prey consumed for each growth scenario for each stock (a-h). Values above the bars indicate feeding rates (%Cmax) for each simulation as a percentage of the theoretical maximum consumption rate for the given diet and thermal experience.

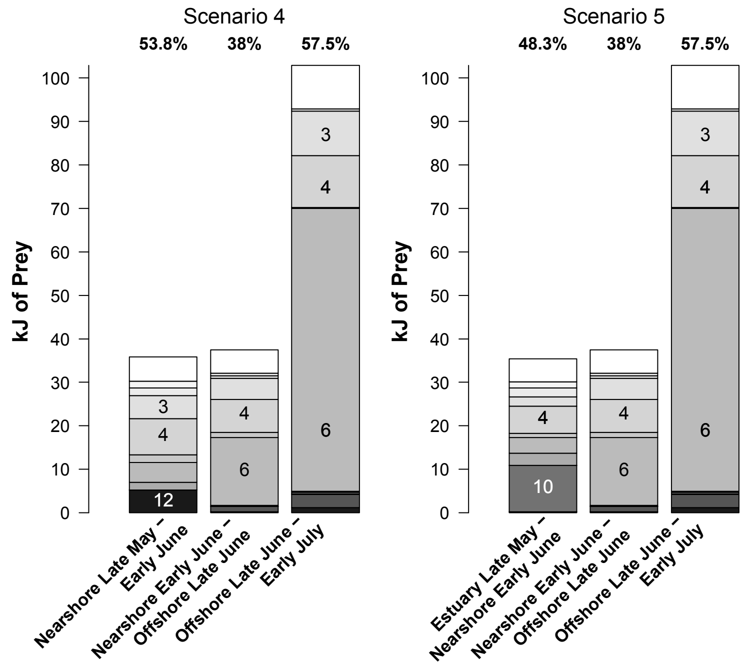
Legend:

High Energy Density Low

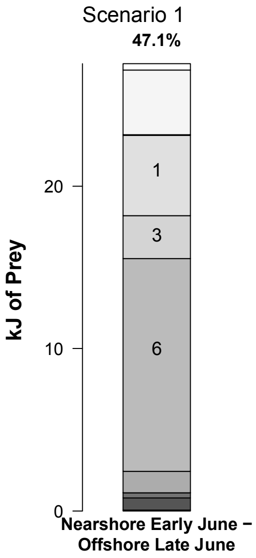
- □ Other
- □ 1. Worm
- □ 2. Amphipod
- □ 3. Crustacean (other)/Rare Invert
- □ 4. Decapod Zoea
- □ 5. Other Fish
- ▨ 6. Decapod Megalops
- ▨ 7. Diptera (adult)
- ▨ 8. Shrimp (Postlarval/Adult)
- ▨ 9. Sandlance
- ■ 10. Insect (other)
- ■ 11. Hemiptera
- ■ 12. Hymenoptera

a. Nisqually Clear Creek

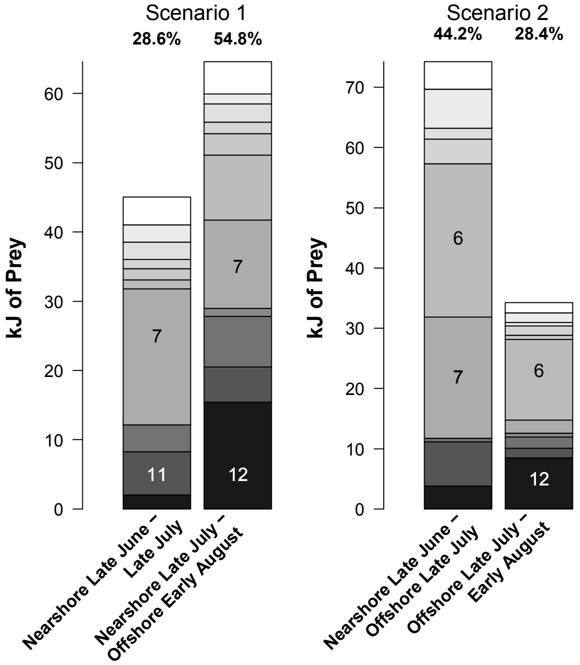




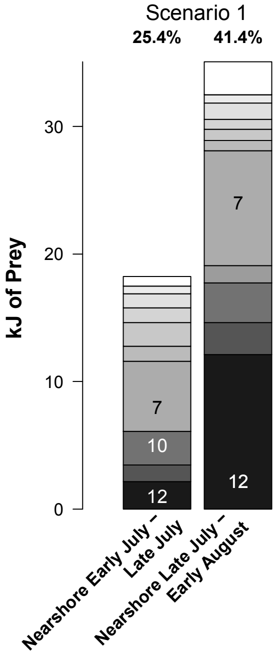
b. Snohomish Tulalip



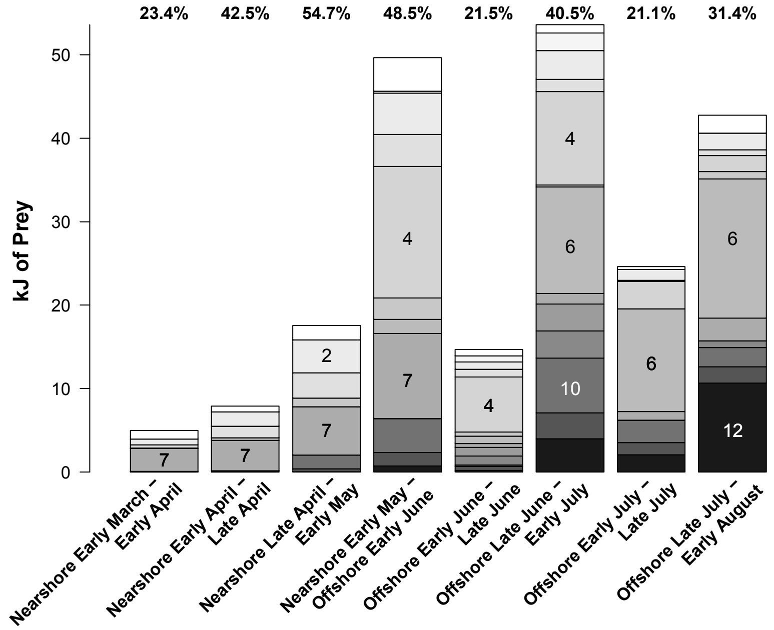
c. Skagit Spring

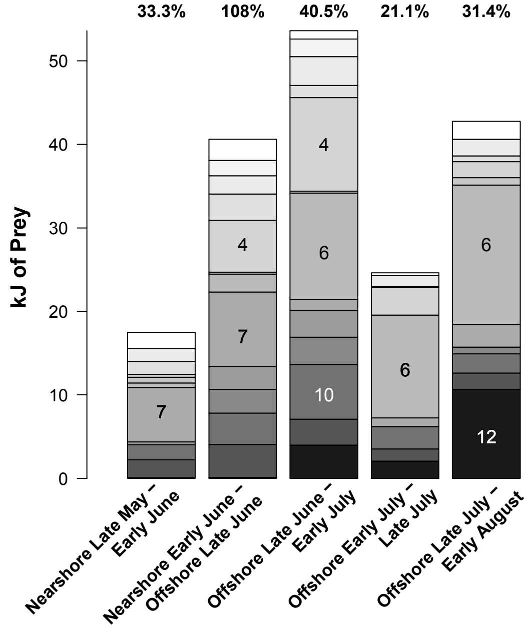


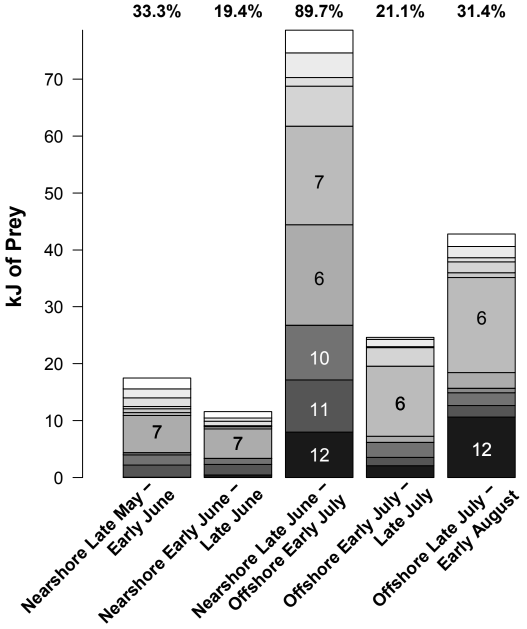
d. Skagit Summer

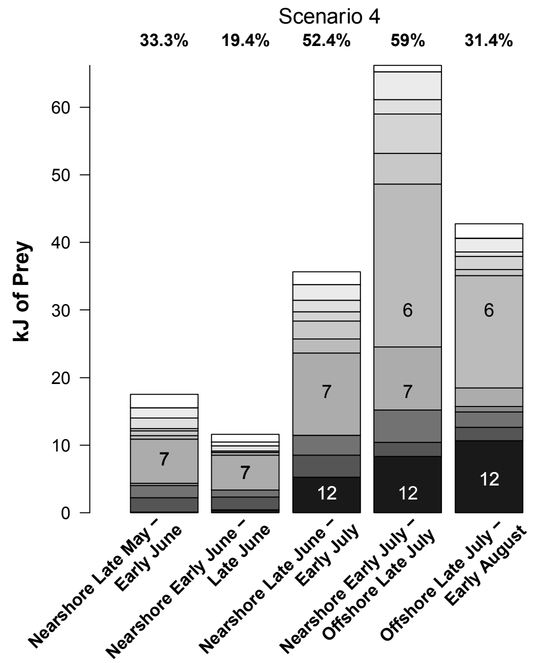


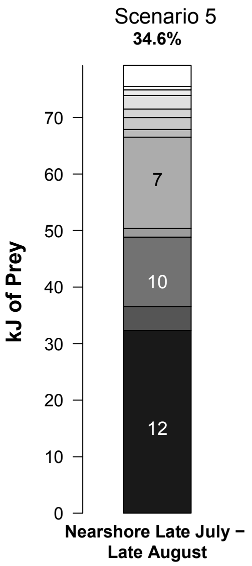
## e. Skagit Upper Summer


Scenario 1

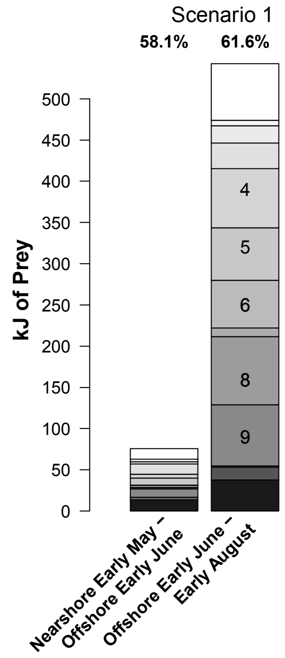

Scenario 2


Scenario 3

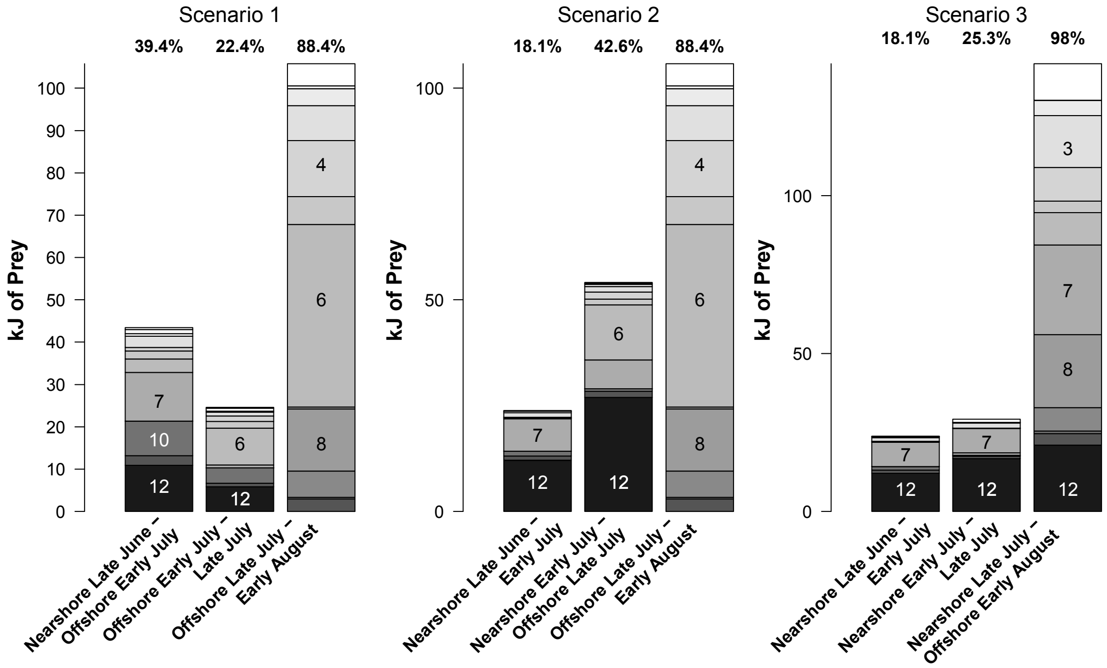




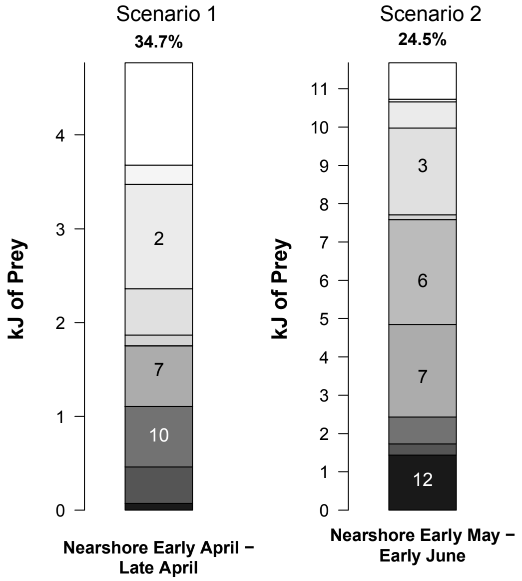
## f. Nooksack Kendall Creek



## g. Nooksack Skookum Creek



## h. Nooksack Fall



## Conclusions

- Sub-yearling Chinook from the Nooksack, Skagit, Snohomish, and Nisqually Rivers moved sequentially through estuarine, nearshore, and offshore habitats during their first marine growth season in Puget Sound. Wild stocks had a more protracted outmigration than hatchery-origin stocks.
- Scale radius was proportional to fish length, and circulus deposition rates were relatively constant throughout the growing season within each stock of sub-yearling Chinook in this study. Circulus deposition rates ranged from 4.6 to 8.3 days and were shorter for hatchery stocks than for wild stocks.
- Otolith microchemistry and microstructure analysis of a subset of samples from the wild Skagit Upper Summer stock revealed that sub-yearling Chinook used the nearshore as a transitional habitat but tended to remain offshore after leaving nearshore habitats.
- There was little evidence that size-selective mortality occured within or between habitats in Puget Sound through early August. Size-selective mortality may have occurred later in the first marine growth season or outside of Puget Sound.
- Sub-yearling Chinook were larger and had higher growth rates in offshore habitats compared to nearshore habitats. Weights and growth rates did not differ between stocks during the same sampling period, and growth rates did not differ across time. Absolute weight gain (growth rate x time) was highest in offshore habitats across Puget Sound.
- There was no difference in average prey quality across time, among habitats, or among stocks.

- Juvenile Chinook salmon exhibited an ontogenetic shift from feeding predominantly on terrestrial insects (hymenoptera and diptera) in estuary and nearshore habitats to crab larvae (zoea and megalops) as they moved into offshore habitats.
- Average feeding rates were higher in offshore than nearshore growth simulations but did not differ among stocks or across time.
- Average water temperatures were significantly higher and had a wider range in nearshore habitats compared to offshore habitats but did not differ among stocks or across time.
- Higher prey availability and lower temperatures likely interacted to confer higher growth rates in offshore habitats compared to nearshore habitats for sub-yearling Chinook in this study.
- Future restoration and conservation efforts aimed at augmenting prey availability and reducing the maximum temperature in nearshore habitats may be most effective in supporting higher early marine growth rates of juvenile Chinook salmon in Puget Sound.