

# Variable prey consumption leads to distinct regional differences in Chinook salmon growth during the early marine critical period

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**ABSTRACT:** Growth during the early marine critical period is positively associated with survival and recruitment for Pacific salmon *Oncorhynchus* spp., so it is important to understand how certain foraging strategies may bolster growth in estuarine and marine environments. To elucidate how spatiotemporal and demographic differences in diet contribute to growth rate variability, we analyzed stomach contents in tandem with morphometric and hormonal indices of growth for sub-yearling Chinook salmon *O. tshawytscha* captured in Puget Sound, Washington, USA. Regional dietary patterns indicated that fish caught in northern Puget Sound ate insects in the estuarine and nearshore habitats, followed by decapod larvae, euphausiids, or forage fish in the offshore zone. In southern Puget Sound, fish ate insects in the estuary but were more likely to eat mysids and other crustaceans in the nearshore zone. In the marine habitats adjacent to the San Juan Islands, subyearlings ate forage fish, and their stomachs were as much as 1.4 to 3 times fuller than salmon captured in other regions. Scale-derived growth rates and insulin-like growth factor-1 levels showed distinct growth advantages for San Juan Islands fish which were strongly associated with the early adoption of piscivory. However, consumption of larger crustaceans such as mysids and euphausiids was also associated with greater relative growth regardless of where individuals were captured. These findings highlight how spatiotemporal differences in prey quantity, prey profitability, and individual foraging strategies result in variable growth rates among salmon populations. Specifically, they emphasize the role of piscivory in promoting early marine growth for out-migrating Chinook salmon.

**KEY WORDS:** Somatic growth · Stomach content analysis · Scale morphometry · Insulin-like growth factor-1 · *Oncorhynchus tshawytscha* · Puget Sound

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## 1. INTRODUCTION

Growth and body condition are crucial determinants of survival and recruitment for a variety of fish species (Sogard 1997). For anadromous Pacific salmon *Oncorhynchus* spp., this relationship is exempli-

fied by the critical size and period hypothesis, which postulates that salmon experience 2 distinct episodes of potential mortality in their first year of life (Beaugh & Mahnken 2001). The first and arguably most important of these episodes occurs during the early marine critical period when juvenile salmon are sus-

ceptible to predation, especially if they are smaller than the average size of other concurrently available prey (Parker 1971, Duffy & Beauchamp 2008). The second occurs during their first marine winter when salmon are more likely to survive seasonal energy deficits and increased metabolic demands if they reach a specific size (Beamish et al. 2004). In the Pacific Northwest, USA, the abundance and population diversity of Pacific salmon have declined substantially, indicating that they may be failing to reach these critical benchmarks for growth and survival (Ruckelshaus et al. 2002, Kilduff et al. 2015).

Lower abundances of Pacific Northwest salmon have been attributed to numerous factors including loss of freshwater and estuarine rearing habitats, overfishing, competition between wild and hatchery stocks, and loss of genetic diversity (Nehlsen et al. 1991, Bottom et al. 2005, Naish et al. 2007, McClure et al. 2008). Anthropogenic modifications to riverine, estuarine, and marine environments have resulted in shifts in the accessibility, abundance, and composition of prey resources, leading to concerns about potential density-dependent effects and lower productivity in juvenile salmon (Wipfli & Baxter 2010, David et al. 2016, Hall et al. 2018). Additionally, climate change is expected to affect the distribution and extent of coastal habitats, the energetic needs of juvenile salmon, and the availability of forage fish and other prey species, potentially compounding the negative effects of anthropogenic habitat loss on prey abundance and, consequently, salmon growth and survival (Beauchamp 2009, Wainwright & Weitkamp 2013, Greene et al. 2015).

Body size and the availability and energy density (ED) of prey (i.e. their profitability) play major roles in mediating juvenile salmon growth (Rosenfeld et al. 2005, Beauchamp 2009, Rosenfeld & Raeburn 2009). Larger body size is generally associated with improved access to abundant or high-quality prey (Edmundson & Mazumder 2001, Sommer et al. 2001, Schindler et al. 2005, Tomaro et al. 2012). For instance, in marine environments salmon tend to grow faster when forage fish are consumed, because they are large and thus have a higher ratio of energy content to handling time and metabolic costs (Litz et al. 2018). In riverine and estuarine environments, insect drift bolsters growth by providing terrestrial subsidies of high-quality, energy-rich prey (Sommer et al. 2001, Romanuk & Levings 2005, Rosenfeld & Raeburn 2009, Davis et al. 2019). Juvenile salmon often face tradeoffs in prey quantity and quality as they move across coastal habitats such that energy-rich drift invertebrates are consumed more frequently in

riverine and estuarine environments, while energy-poor crustaceans are encountered at high densities in the marine environment (Healey 1980, Davis et al. 2019, Woo et al. 2019). These tradeoffs, along with regional and seasonal shifts in prey communities, are likely to result in distinct, spatiotemporal differences in early marine growth (Duffy et al. 2010). Faster growing juvenile salmon increase their chances of survival by avoiding predation, resisting starvation during times of prey scarcity, and increasing their tolerance to environmental stress (Shuter & Post 1990, Sogard 1997). Consequently, a detailed analysis of juvenile salmon diets in Pacific Northwest estuaries and their adjacent marine habitats would shed light on how different foraging strategies lead to regional differences in early marine growth and survival.

Fish growth can be evaluated using bioenergetics models (Kitchell et al. 1977, Beauchamp et al. 1989, Beauchamp 2009) or via direct measurements of size, calcified structures, and hormone levels (Duguid et al. 2018). Mean fork length (FL) and weight have been used to monitor growth through time *in situ* (Beauchamp et al. 2004), but this method is susceptible to size-selective processes that can bias apparent growth and is thus more useful for studying populations in controlled laboratory conditions (e.g. Wipfli et al. 2003, Ebersole et al. 2006, Jeffres et al. 2008). Morphometric indices of growth use calcified structures such as otoliths and scales, where the spacing between circuli is considered an index of relative growth within a cohort (Fukuwaka & Kaeriyama 1997, Courtney et al. 2000). These microstructural elements are useful because they record the size of a fish at regular intervals throughout its entire life; however, circulus formation intervals vary by size and can be intrinsically influenced by growth rate (Duguid et al. 2018). Alternatively, hormone levels provide a snapshot of growth at time of capture. Insulin-like growth factor-1 (IGF-1) is a plasma hormone known to stimulate and support cellular growth in individual animals (Mommensen 1998). Several factors may affect the production of IGF-1 including photoperiod, temperature, and nutrition (e.g. food quality and quantity; Picha et al. 2008, Beckman 2011). More recently, researchers have used IGF-1 levels to compare growth rates in fish, including salmonids, across a variety of environmental conditions (Beckman et al. 2004, Larsen et al. 2010, Stefansson et al. 2012) and as a function of individual size (Beaudreau et al. 2011).

Juvenile salmon diet and growth have been studied as independent measurements of population health (Duffy et al. 2010, Duffy & Beauchamp 2011, Gamble et al. 2018). Bioenergetics models shed some

light on the relationship between the two, but more can be accomplished by integrating modeling with contemporary empirical data (Duffy & Beauchamp 2011, Connelly et al. 2018). We integrated stomach content analyses with morphometric and hormonal indices of growth to elucidate how regional, seasonal, and demographic differences in diet contributed to the early marine growth of Endangered Species Act-listed (NMFS 1999) Puget Sound Chinook salmon *O. tshawytscha*. Puget Sound's salmon populations have demonstrated lower marine survival rates when compared to adjacent regions in the Pacific Northwest despite experiencing similar environmental stressors upon reaching the ocean, indicating that their decline is driven by conditions during the early marine critical period (Ruggerone & Goetz 2004, Sharma et al. 2013, Zimmerman et al. 2015, Ruff et al. 2017). Furthermore, historical variability in diets among different regions within Puget Sound provides an excellent opportunity to relate dietary differences to growth (Duffy et al. 2010).

We analyzed 2 yr of data from the estuarine and marine habitats of 4 major Puget Sound watersheds and the marine areas adjacent to the San Juan Islands, which represent an important early marine rearing habitat for juveniles originating from the Nooksack, Skagit, and potentially other rivers. Our primary objectives for this study were to (1) analyze spatiotemporal and demographic differences in juvenile Chinook salmon stomach contents, (2) evaluate the influence of spatiotemporal and demographic factors on juvenile Chinook salmon growth, and (3) relate dietary patterns to size-specific consumption and growth. We predicted that observed growth would be greatest in habitats where juvenile Chinook salmon consumed energy-rich prey such as terrestrial and aquatic insects or forage fish or in habitats where they ate large quantities of prey (regardless of its energy content). Our study represents a complementary approach to traditional diet analyses and bioenergetics modeling in that it directly links juvenile salmon consumption with physiological condition, thereby yielding insights that could contribute to regional management strategies.

## 2. MATERIALS AND METHODS

### 2.1. Study area

Puget Sound, Washington, USA, is a partially mixed fjord estuary fed by ocean exchange through the Strait of Juan de Fuca and seasonal freshwater

inputs from more than 10 000 rivers and streams. It consists of several sub-basins, including Admiralty Inlet, Hood Canal, Whidbey Basin, Central Basin, and Southern Basin (Burns 1985). Puget Sound is 140 m deep on average, with a maximum depth of 286 m in the Central Basin. Tides are mixed semi-diurnal with magnitudes ranging from 2.6 to 4.4 m along a latitudinal gradient (from north to south; Mofjeld & Larsen 1984). A series of sills and benches, along with variable inputs from large rivers, results in significant stratification of water masses and broadly variable hydrological residence times (0.7–73 d; Ebbesmeyer et al. 1988, Babson et al. 2006). Mean surface temperature and dissolved oxygen concentration vary seasonally, but differences do not vary consistently among sub-basins (Moore et al. 2008, Roberts et al. 2014).

Our study focused on the estuarine, nearshore (shoreline; <10 m depth), and offshore (epipelagic; 30–280 m bottom depth) habitats within and adjacent to four coastal watersheds in Puget Sound, as well as the nearshore and offshore habitats adjacent to the San Juan Islands (Fig. 1). In northern Puget Sound, the Nooksack River feeds into Bellingham Bay and the Strait of Georgia, whereas the Skagit River flows into Whidbey Basin. The San Juan Islands are positioned where the Strait of Juan de Fuca connects to the Strait of Georgia from the Pacific Ocean. In central Puget Sound, the Snohomish River flows directly into the Whidbey Basin just north of the Central Basin, which is separated from the Southern Basin by a shallow sill at the Tacoma Narrows. The Nisqually River is the largest river in southern Puget Sound, flowing directly into the Southern Basin. Estuarine and marine habitats vary biologically and physically among the 4 watersheds with respect to habitat availability, geomorphology, hydrology, and Chinook salmon abundance (Table 1). Historically, each watershed (hereafter, region) has supported millions of Chinook salmon and other salmon species, but over the past century these populations have declined to varying degrees, becoming increasingly reliant on hatchery supplementations (Ford 2011, Rice et al. 2011, Greene et al. 2015).

### 2.2. Data collection

We sampled the estuarine, nearshore, and offshore habitats of Puget Sound in 2014 and 2015 (Fig. 1). We used beach seines or lampara nets to catch fish in the estuary and nearshore every 2 wk from February through October (methods outlined in Duffy et al.

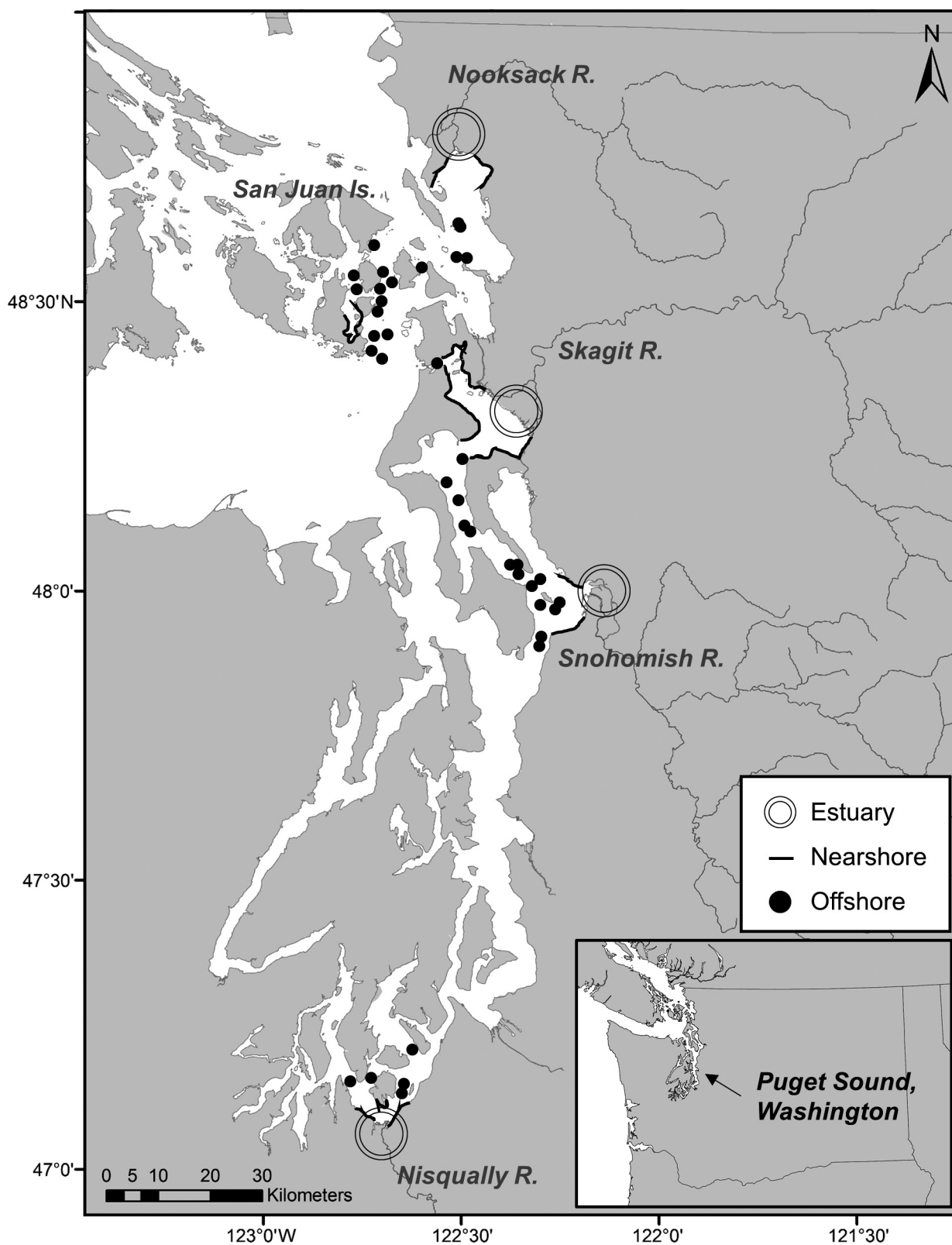


Fig. 1. Puget Sound, Washington, USA, with estuary, nearshore, and offshore sampling locations from each study region

Table 1. Environmental, hydrological, and demographic descriptions of the Nisqually, Snohomish, Skagit, and Nooksack watersheds. Additional information can be found in Connelly et al. (2018)

	Nisqually	Snohomish	Skagit	Nooksack
<b>Environmental characteristic</b>				
Habitat loss (%)	71.2	89.3	74.1	76.6
Wetland channel area (ha)	248.8	136.6	294.0	44.0
Tidal range (m)	4.12	3.38	3.37	2.59
Mean annual river discharge (cfs)	2100	10 000	18 000	3200
<b>Average water temperature range (March–August)</b>				
Nearshore: 2014 (°C)	8–15	7–18	8–15	8–20
Nearshore: 2015 (°C)	9–N/A <sup>a</sup>	10–N/A <sup>a</sup>	10–16	9–21
<b>Average water temperature range (May–August)</b>				
Offshore: 2014 (°C)	10–14	10–12	10–12	9–14
Offshore: 2015 (°C)	11–15	11–15	11–12	10–13
<b>Juvenile Chinook populations</b>				
Years analyzed	2010–2015	2001–2015	1994–2015	2005–2015
Total out-migrants (1000s)	34.7–245.7	33.6–1024.3	1000.2–7712.3	33.1–325.3
Hatchery releases (1000s)	3350–4260	1820–4300	150–890	610–1940
<sup>a</sup> No temperature data available for July or August				

2005, Rubin et al. 2018). We also used fyke traps to sample some estuarine tidal sloughs that dewatered during spring tides. Offshore areas were sampled using a purse seine (402 m long fished effectively to 22 m, 1 cm mesh to 18 m in the bunt, 1.3 cm mesh to 73 m, 2 cm mesh to 146 m, 9 cm mesh to 402 m; FV ‘Franciscan I’), where seining was carried out every 2 wk from May through early August.

We identified and enumerated all fish captured. Juvenile salmon were measured to the nearest 1 mm (FL), weighed to the nearest 0.1 g (wet weight), and checked for adipose fin clips or coded wire tags (CWT). We retained a subset of each catch for sampling, including 10 marked and 10 unmarked juvenile Chinook salmon per set. When possible, unmarked fish were sedated with buffered tricaine methanesulfonate (MS-222) and processed live, including gastric lavage for stomach contents, scales for aging, and fin clips for genetic sampling. Marked fish were euthanized in MS-222 and stored on ice in the field prior to dissection. Sample processing for lethally sampled fish consisted of removing whole stomachs for diet analysis, otoliths and scales for aging, blood for IGF-1, and fin tissue samples for genetic sampling. We assigned rearing origin (hatchery or wild) based on the presence or absence of CWT, adipose fin clips, or thermal otolith markings, and assigned a natal watershed (stock) for marked fish using CWT codes. For northern Puget Sound fish, we also used a genetic panel of 192 single nucleotide polymorphisms for Puget Sound salmon to assign

rearing origin and stock information to unmarked fish and fish that did not have a CWT (Warheit et al. 2013, Connelly et al. 2018, Gamble et al. 2018). We were able to determine whether 74 % of our samples were of wild or hatchery origin using hatchery markings and genetic analyses. Nevertheless, unless discussing a subset of fish for which stock has been identified, we refer to all unmarked fish as unmarked rather than wild hereafter, to account for a small subset of unclassified individuals (<9 %; Rice et al. 2011) that may have been unmarked hatchery fish.

In 2014 and 2015, we obtained data from more than 10 000 juvenile salmon, but for our analyses we focused on subyearling Chinook salmon captured at the height of the out-migration and marine growing season (March–August). Age was based on the size or number of scale annuli, which is indicative of the number of growing periods a fish experienced through its life (Groot & Margolis 1991). Fish >200 mm FL were omitted even if they had not laid down their first scale annulus, to avoid the potential confounding effects of gonadal growth when our analyses were focused on morphometric and hormonal indices of somatic growth (Beckman 2011). Although we sampled throughout most of Puget Sound, we limited our diet and growth analyses to subyearlings captured in the estuarine, nearshore, and offshore habitats of our 5 study regions. Overall, about 3400 fish were included in our analyses (Table S1 in the Supplement at [www.int-res.com/articles/suppl/m640p147\\_supp.pdf](http://www.int-res.com/articles/suppl/m640p147_supp.pdf)).



### 2.3. Chinook salmon stomach contents

We collected Chinook salmon stomach contents using gastric lavage (from live fish) or whole specimens (from lethal samples); samples were frozen in the field shortly after collection. Gastric lavage, whereby water is used to flush consumed prey items from the stomach, has been shown to extract up to 96 % of stomach contents in a variety of fish species (Kamler & Pope 2001, Waters et al. 2004). We removed whole stomachs in the laboratory using a scalpel or scissors, being careful to check the mouth and esophagus for contents before cutting as high on the esophagus as possible. Intestinal contents were excluded from our processed diet samples. Prey items from each sample were identified under a Leica MZ6 dissecting microscope (Leica Camera AG), weighed to the nearest 0.1 mg, and assigned to a prey taxonomic group for analysis (Table S2). Broader prey taxonomic groups were assigned by class or order and included taxa with similar ED values whenever possible. We recorded weights as blot-dried wet weight biomass (WWB). If an item was too light to register on the scale, we logged it as 0.01 mg. For the analysis of dietary composition, we removed fish with empty stomachs and omitted measurements of indigestible and unidentifiable material to avoid classifying them as single taxa. We assumed digested material was representative of the prey taxa observed in the identifiable portion of the diet sample, although soft-bodied taxa such as annelids and insect larvae may have been underrepresented due to their faster digestion rates (Arai et al. 2003, Preston et al. 2017). Because diets are a snapshot of what fish were eating in the hours prior to capture, we included any subyearling that fit the aforementioned size criteria for analysis, regardless of whether stock or rearing origin had been validated.

### 2.4. Body size and consumption metrics

In addition to diet, we used measurements of stomach fullness and dietary ED to quantify the consumption patterns of subyearling Chinook salmon. Because consumption and absolute daily growth vary with size (i.e. allometrically), we also assessed how FL changed through time across regions and habitat types. We calculated stomach fullness for the aforementioned subset of fish (but also including those with empty stomachs) as:

$$\text{Fullness \%} = 100 \times \frac{\text{Stomach content weight (g)}}{\text{Total fish weight (g)} - \text{Stomach content weight (g)}} \quad (1)$$

We calculated dietary ED as:

$$\text{ED}_{\text{tot}} = \sum p_i \text{ED}_i \quad (2)$$

where  $p_i$  is the proportional gravimetric contribution of prey taxon  $i$  to the total WWB (mg) of all stomach contents, and  $\text{ED}_i$  is the ED ( $\text{J g}^{-1}$ ) of taxon  $i$  (Table S2).

### 2.5. Morphometric and hormonal indices of growth

#### 2.5.1. Scale-derived growth rate

Scales are a common morphometric method for aging and estimating growth in bony fishes because their circuli are added at a relatively constant rate through time (Casselman 1990, Fukuwaka & Kaeriyama 1997). We collected scales from subyearling Chinook salmon using the methods outlined in Gamble et al. (2018). We back-calculated FL at each scale circulus for each fish using the Fraser-Lee method (Pierce et al. 1996, Martinson et al. 2000). This approach relies on the linear relationship between fish size and scale radius (Fig. S1) and assumes that a broader width between circuli is indicative of faster growth over a specific period. The Fraser-Lee equation is:

$$L_i = \frac{S_i}{S_c} \times (L_c - c) + c \quad (3)$$

where  $L_i$  is length at circulus  $i$ ,  $L_c$  is length at time of capture,  $S_i$  is scale width at circulus  $i$ ,  $S_c$  is scale width at time of capture, and  $c$  is an estimate of fish length at time of first scale formation (35 mm based on a regression of FL with scale radius for fish <100 mm).

Because most growth models present growth rates in terms of body weight ( $\text{g d}^{-1}$ ) rather than length, we converted estimated lengths to weights using a log-log regression curve of weight against FL ( $r^2 = 0.98$ ; Fig. S1). We then calculated growth rates using the equation:

$$G = \frac{\ln\left(\frac{W_t}{W_0}\right)}{t} \quad (4)$$

where  $G$  is growth rate,  $W_t$  is the estimated weight for the most recent circulus,  $W_0$  is the estimated

weight for the penultimate circulus, and  $t$  is the estimated number of days it takes to lay down 1 circulus. Although deposition time can vary depending on multiple intrinsic and extrinsic factors, subyearling Chinook salmon in Puget Sound take approximately 6 d to deposit a single circulus during the spring–summer growing season (Gamble et al. 2018), so we used this as our  $t$ -value.

Recent growth was estimated by averaging back-calculated growth rates for the 3 most recent circulus intervals. This allowed us to avoid uncertainty related to variation in timing of circulus formation by opting to use growth rates that were averaged over roughly 18 d. Because this increased the probability that fish had reared in a location other than where they were captured, and because early life ontogenetic factors may have driven growth patterns, we analyzed only those fish from identifiable stocks that could be tracked through time and that had originated from within the watershed of capture. The exception was the San Juan Islands, which are near the Nooksack and Skagit watersheds and are important rearing habitat for juvenile Chinook salmon originating from these and other watersheds. Thus, we included consumption and growth metrics for wild and hatchery subyearlings from the nearby Skagit and Nooksack watersheds that were sampled around the San Juan Islands. We analyzed fish from 9 identified stocks: Nisqually Clear Creek Hatchery, Snohomish Tulalip Hatchery, Snohomish Wallace Hatchery, Upper Skagit Summer Wild, Skagit Spring Hatchery, Skagit Summer Hatchery, Nooksack Fall Wild, Nooksack Kendall Creek Hatchery, and Nooksack Skookum Creek Hatchery (Gamble et al. 2018).

### 2.5.2. IGF-1

We assessed the concentration of IGF-1 in subyearling Chinook salmon captured in northern Puget Sound (Skagit, Nooksack, San Juan Islands) as a complementary approach to morphometric scale measurements. Because of the limitations of comparing IGF-1 concentrations across seasons (Beaudreau et al. 2011, Beckman 2011), we limited our analysis to fish sampled during the summer months (June–August). We analyzed only those fish for which stock had been identified and was equivalent to the watershed of capture with the exception of the San Juan Islands fish. Samples from each region were representative of the observed length distributions of the entire catch; however, blood samples were not taken from any fish <50 mm FL. Each fish was measured

and weighed, and a blood sample was taken immediately after the fish was euthanized. Blood was drawn using heparinized Nielsen tubes placed into 5 ml microtubes and stored on wet ice for no more than 2 h before being spun in a centrifuge for 5 min at 5000 rpm. Plasma was then separated from the red blood cells and immediately frozen. Samples were transferred to a  $-80^{\circ}\text{C}$  freezer within 12 h and stored until laboratory processing occurred. We measured IGF-1 in plasma using a fluorescence-based immunoassay following the methods of Ferriss et al. (2014). All samples were processed and analyzed in duplicate to assess coefficient of variation (CV). We excluded any samples with a CV exceeding 10% ( $n = 63$ ) from the study.

## 2.6. Statistical analysis

We used multivariate analyses to assess the proportional gravimetric contribution (in WWB) of each prey taxonomic group to the diets of individual subyearling Chinook salmon. Data were arcsine square root transformed prior to analysis to reduce the effect of highly abundant prey taxa. We used a PERMANOVA on a Bray-Curtis similarity matrix of the transformed data to identify significant dietary differences. Specifically, we evaluated the effects of year of capture (2014, 2015), month of capture (March, April, May, June, July, August), region of capture (Nisqually, Snohomish, Skagit, Nooksack, San Juan Islands), habitat (estuary, nearshore, offshore), size class (<50, 51–75, 76–100, 101–125, 126–150, 151–175, 176–200 mm), and rearing origin (unmarked, hatchery) on dietary composition. We used a backward stepwise model selection process to identify significant predictor variables, starting from a full model that included year of capture, an interaction effect between habitat and month of capture (or size class) nested within year, and an interaction effect between region of capture and origin nested within habitat. Residual  $R^2$  was used as the model trimming criterion with the goal of minimizing the amount of unexplained variance. We iteratively removed 1 predictor variable at a time, selecting variables with the lowest  $R^2$  or highest  $p$ -value and stopping when all remaining variables and interaction effects were significant or when residual  $R^2$  increased by more than 0.01 if a term was removed. We used the betadisper function to check for multivariate homogeneity of group dispersions and similarity percentages (SIMPER) to evaluate the contribution of each prey taxon to among-group dissimilarity. All multivariate analy-

ses were conducted using the *vegan* package in R 3.4.1 (R Core Team 2018).

We used a combination of univariate and multivariate techniques to analyze spatiotemporal and demographic differences in consumption and growth indices. We checked the distributions of the response variables (FL, stomach fullness, ED, scale-derived growth rate, and IGF-1 concentration) prior to analysis and ensured that model residuals met model assumptions for normality and homogeneity of variance (Zuur et al. 2010). We used generalized linear models (GLMs) with a log-link Gaussian function for FL, a Tweedie (zero-augmented gamma) distribution for stomach fullness, and an identity-link Gaussian function for ED to evaluate spatiotemporal and demographic trends for size and consumption. For scale-derived growth and IGF-1 concentration, we used a GLM with a log-link Gaussian function and normal Gaussian distribution, respectively, to assess the relationship between growth and the predictor variables. The GLM structure was practical for our analysis because it allowed for an uneven sampling design and constrained model output to positive (and thus biologically relevant) values.

We employed a model parameterization and hypothesis testing procedure on a set of candidate models including temporal (year, month), spatial (region, habitat), and demographic (size class, origin) predictor variables (Tables S3 & S4). We nested regional and origin-level effects within habitat and month to ensure that we were comparing trends for fish that were captured in the same habitat type at a similar point in time. For FL, we used day of year in lieu of month and did not include the size class variable in our candidate models. Our hypotheses were that consumption and/or growth were (1) affected exclusively by out-migration timing (year, month); (2) affected by a combination of temporal and spatial factors (habitat, region); (3) related to temporal and demographic factors (size, origin); and (4) determined by some combination of temporal, spatial, and demographic effects.

We compared model fits among candidate models using Akaike's information criterion (AIC), where a AIC value  $>2$  between the best-fit model and the next most parsimonious model was considered robust evidence for model support (Burnham & Anderson 2002). A Tukey's HSD post hoc test was used to conduct among-group comparisons for significant categorical predictor variables. We conducted all GLM analyses and model selection procedures using R statistical software, where the *agricolae* package was used to employ Tukey's post hoc tests on the best-fit models.

In addition to univariate analyses, we used a canonical correspondence analysis (CCA; Ter Braak 1986) to relate Chinook salmon dietary assemblages to size-specific consumption and growth patterns. CCA is an ordination procedure that is typically used to relate assemblages of species to their physical environment. In this case, we related the diets of multiple size classes of Chinook salmon to scale-derived growth rate, IGF-1 concentration, stomach fullness, dietary ED, and FL (to account for the potential effect of size). Because of different sample sizes, we analyzed scale-derived growth and IGF-1 separately but included stomach fullness, ED, and FL in both analyses to account for potential associations among variables. Prey data were expressed as the arcsine square root transformed gravimetric contribution to stomach content WWB. All predictor variables were treated as continuous, with scale-derived growth, stomach fullness (empty stomachs omitted due to lack of associated diet data), and FL log transformed. A backward stepwise selection procedure was implemented for 2 broader size classes of fish (51–100 and 101–150 mm FL; Ter Braak & Verdonschot 1995, Guisan et al. 1999), where each variable was tested for significance using a permutation test with 1000 model permutations and a cutoff of  $p < 0.05$ . For each iteration, the predictor variable with the highest non-significant  $p$ -value was removed until all remaining variables were significant. Output from each CCA was presented as a biplot of axes 1 and 2, with continuous response variables represented by vector arrows and prey taxa labeled in 2-dimensional space.

### 3. RESULTS

#### 3.1. Chinook salmon stomach contents

Diet composition varied by month and habitat type, with significant regional and origin-level effects occurring in each habitat (Fig. 2, Table 2). These 4 variables accounted for roughly 33 % of dietary variation among individuals, with most of this variation




Fig. 2. Bar plots of monthly, habitat-specific, and regional differences in the proportional gravimetric composition of sub-yearling Chinook salmon diets in Puget Sound. Prey taxa are grouped by dipterans (DIPT), adult insects (hemipterans, hymenopterans, palaeopterans, arachnids, collembolans, and other insects [INSE]), insect pupae and larvae (INSL), amphipods (AMPH), mysids (MYSI), decapod larvae (DECA), euphausiids and shrimp (EUSH), other crustaceans (CRUS), annelids (ANNE), and fish (FISH). The number above each bar indicates sample size for 2014 and 2015 combined.



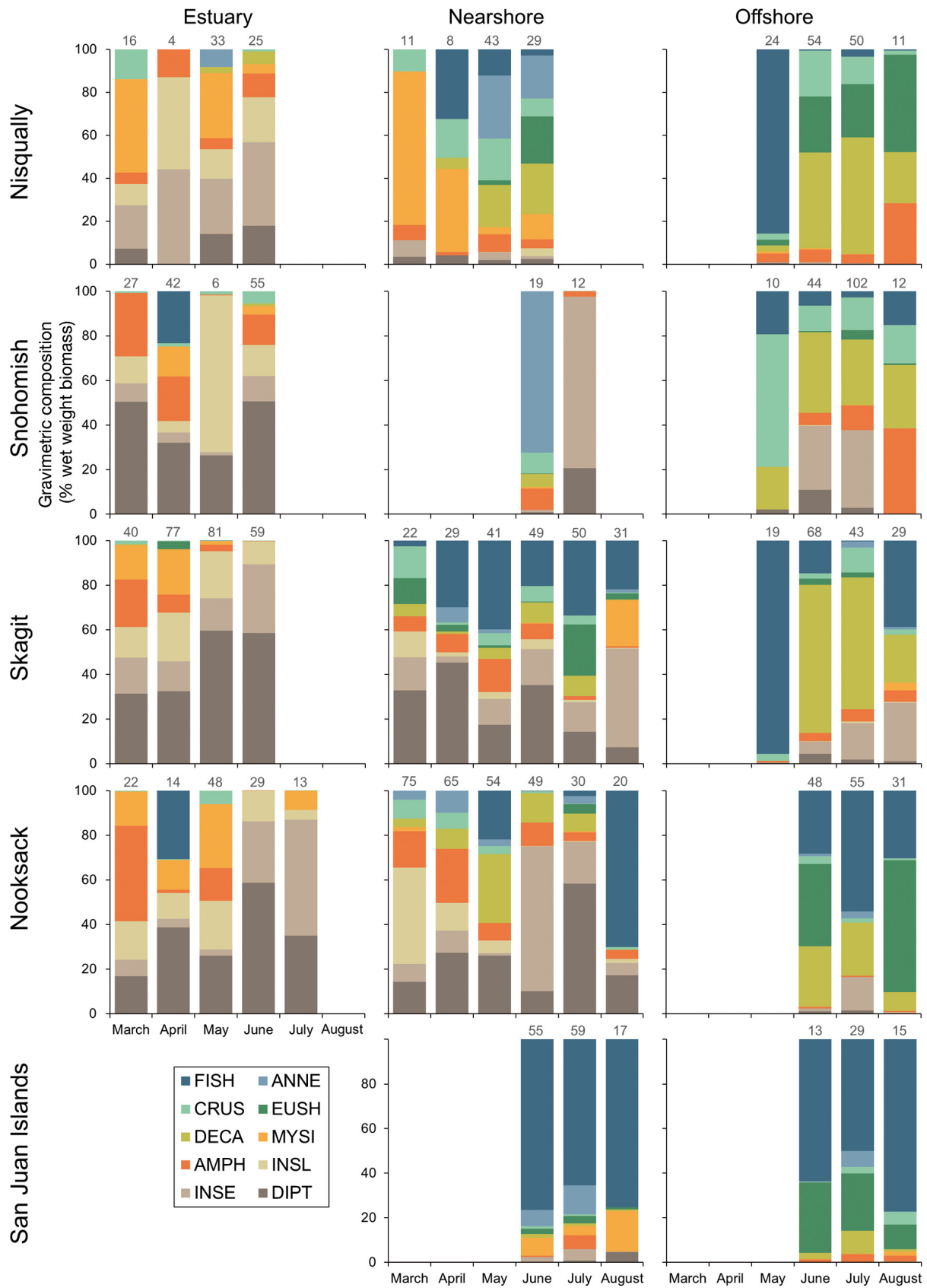


Table 2. PERMANOVA evaluating spatiotemporal differences in the proportional gravimetric composition (% wet weight biomass) of sub-yearling Chinook salmon diets. Slash (/) indicates a nested effect

Variable	df	Mean SS	F	R <sup>2</sup>	p
Month	5	9.38	39.20	0.07	<0.01
Habitat	2	35.76	149.40	0.10	<0.01
Month × Habitat	7	1.87	7.80	0.02	<0.01
(Month × Habitat)/Region	41	2.00	8.34	0.12	<0.01
(Month × Habitat)/Origin	12	0.35	1.47	0.01	0.02
(Month × Habitat)/ (Region × Origin)	25	0.38	1.57	0.01	<0.01
Residuals	1923	0.24		0.67	
Total	2015				

(24%) explained by spatial (regional and habitat-level) effects. Month explained a greater amount of variance than size class, so we used the monthly variable to explain both temporal and ontogenetic dietary trends. Tests for homogeneity of group dispersions found that within-group variation in dietary composition was significantly less ( $p < 0.01$ ) for the Skagit than for any other region and was less in the estuary than in the nearshore and offshore zones ( $p < 0.01$ ). Consequently, statistical output from the PERMANOVA concerning regional and habitat-specific dietary differences may have been affected by within-group variability or location effects.

In estuarine habitat, the diets of fish captured in the Snohomish, Skagit, and Nooksack watersheds were highly similar (Table 3). Dipteran prey exerted the most influence on regional dietary differences (SIMPER) such that adult dipterans represented 20 to 60% of dietary WWB in the Snohomish, Skagit, and Nooksack watersheds but less than 20% in the Nisqually watershed, where other adult insects such as hemipterans and palaeopterans contributed up to 40% of WWB (Fig. 2). Insect larvae, amphipods, and mysids were also highly prevalent in the diets of subyearling Chinook salmon captured in estuarine habitat, regardless of region.

In nearshore habitat, the diets of subyearlings captured in the Skagit and Nooksack watersheds were highly similar, consisting of adult dipterans and insects, insect larvae (earlier in the season), amphipods, decapod larvae, and forage fish

(Fig. 2, Table 3). The frequent consumption of insect prey in the nearshore areas of these watersheds set them apart from subyearlings captured at Nisqually, where insects comprised less than 10% of dietary WWB. Instead, subyearlings from Nisqually ate mostly mysids, decapod larvae, and other crustaceans. The diets of subyearlings captured adjacent to the San Juan Islands also differed from those in the Skagit and Nooksack watersheds because they were composed almost entirely of forage fish. The dietary composition of subyearling Chinook

salmon captured in the Snohomish was least similar to other regions; however, only a small sample of 31 fish from June and July were analyzed, making it difficult to elucidate nearshore trends for this watershed. These few Snohomish nearshore diets were composed of mostly annelids and adult insects.

In offshore habitat, diets from subyearlings captured in the Nooksack and San Juan Islands regions were most similar, consisting of fish and euphausiids with some contributions from decapod larvae (Fig. 2, Table 3). As in the nearshore zone, the high proportion of forage fish prey distinguished the San Juan Islands from the Nisqually, Snohomish, and Skagit regions, where the consumption of decapod larvae was far more common. At Nisqually, forage fish con-

Table 3. Bray-Curtis similarity indices (BCI) for regional comparisons of sub-yearling Chinook salmon diet within each habitat type. BCI values range from 0 to 1, with a value of 0 indicating no similarity and a value of 1 indicating complete overlap in the gravimetric composition (% wet weight biomass) of salmon diets

	Nisqually	Snohomish	Skagit	Nooksack
<b>Estuary</b>				
Snohomish	0.69			
Skagit	0.73	0.76		
Nooksack	0.80	0.85	0.83	
<b>Nearshore</b>				
Snohomish	0.53			
Skagit	0.67	0.63		
Nooksack	0.60	0.65	0.81	
San Juan Islands	0.62	0.43	0.67	0.53
<b>Offshore</b>				
Snohomish	0.71			
Skagit	0.68	0.76		
Nooksack	0.65	0.58	0.72	
San Juan Islands	0.63	0.46	0.63	0.75

tributed up to 90 % of dietary WWB in May but were barely observed in June, July, or August. During the summer months, subyearlings captured in the Nisqually offshore ate a mix of decapod larvae, euphausiids, amphipods, and other crustaceans. A similar pattern emerged in the Skagit watershed, where forage fish were highly abundant in diets in May, but subyearlings switched to decapod larvae and adult insects during the summer. Adult insects, while less common than in the estuarine and near-shore diets, were still observed in the offshore areas of the Snohomish, Skagit, and Nooksack watersheds.

### 3.2. Body size and consumption metrics

The best-fit model for FL included significant interaction effects between day of year and region and day of year and rearing origin nested within habitat type and year (Table 4, Table S3). In estuarine habitat, fish from the Nisqually and Nooksack watersheds were 14 to 23 mm larger on average than fish from the Snohomish and Skagit watersheds (Tukey's HSD;  $p < 0.01$ ), especially later in the year (Fig. 3). In near-

shore habitat, subyearlings captured at Nisqually were larger than those captured in the Skagit and Nooksack watersheds from March through May, while fish captured near the San Juan Islands were as much as 40 mm longer than fish from any other region in July and August. This trend was similar in the offshore, where the largest fish were captured at Nisqually in June, and near the San Juan Islands in July and August. Habitat-specific size differences between unmarked and hatchery fish were especially prevalent early in the out-migration season in the estuary and nearshore habitats. Hatchery fish were 43 % larger than unmarked fish on average in April (mean  $\pm$  SD: hatchery =  $76.33 \pm 3.06$  mm, unmarked =  $53.24 \pm 19.21$  mm) but were only 4 % larger than unmarked fish by August (hatchery =  $129.94 \pm 23.75$  mm, unmarked =  $124.61 \pm 26.09$  mm).

The best-fit model for stomach fullness indicated that consumption varied regionally among fish captured in the same habitat type in the same month and year (Table 4, Table S3). Specifically, fish captured in the nearshore and offshore areas of the San Juan Islands during the summer months consumed as much as 1.4 to 3 times more prey biomass relative to their body size than fish from any other region (Fig. 4). Overall, subyearlings captured in the nearshore had stomachs that were ~40 % fuller (mean  $\pm$  SD:  $1.27 \pm 1.44$  %) than fish captured in the estuary ( $0.90 \pm 0.92$  %) or offshore zones ( $0.93 \pm 1.12$  %; Tukey's HSD;  $p < 0.01$ ). This trend was consistent between years but was likely driven in part by the higher abundance of San Juan Islands subyearlings sampled in the nearshore, especially during July and August when broader seasonal differences indicated that stomachs were fullest ( $1.15 \pm 1.24$  and  $1.27 \pm 1.42$  %, respectively).

An interaction effect between region and rearing origin drove differences in dietary ED for fish captured in the same habitat type in the same month and year (Table 4, Table S3). In estuarine and nearshore habitats, the diets of fish captured in the Skagit and Nooksack watersheds contained up to  $2000 \text{ J g}^{-1}$  more ED than the diets of fish caught in the Nisqually and Snohomish watersheds, especially during the summer

Table 4. Best-fit model output for generalized linear models of fork length (FL), stomach fullness, and dietary energy density (ED). We used a cutoff of  $p < 0.05$  to indicate which spatial, temporal, and demographic predictor variables and interaction effects were significant. Slash (/) indicates a nested effect

Variable	df	F	p
<b>FL</b>	2003		
Year	1	1195.32	<0.01
Year/Habitat	4	1269.43	<0.01
Year/Habitat/Region	19	117.93	<0.01
Year/Habitat/Day	6	492.87	<0.01
Year/Habitat/Origin	5	25.69	<0.01
Year/Habitat/(Region $\times$ Day)	19	7.94	<0.01
Year/Habitat/(Origin $\times$ Day)	5	4.15	<0.01
Year/Habitat/(Region $\times$ Origin)	14	1.39	0.21
Year/Habitat/(Region $\times$ Origin $\times$ Day)	13	1.69	0.13
<b>Stomach fullness</b>	2003		
Year	1	7.14	<0.01
Year/Habitat	4	11.32	<0.01
Year/Month	10	5.27	<0.01
Year/(Habitat $\times$ Month)	13	2.74	<0.01
Year/(Habitat $\times$ Month)/Region	63	3.85	<0.01
<b>Dietary ED</b>	2003		
Year	1	0.27	0.61
Year/Habitat	4	8.47	<0.01
Year/Month	10	31.45	<0.01
Year/(Habitat $\times$ Month)	13	2.91	<0.01
Year/(Habitat $\times$ Month)/Region	63	8.94	<0.01
Year/(Habitat $\times$ Month)/Origin	18	1.02	0.43
Year/(Habitat $\times$ Month)/(Region $\times$ Origin)	36	2.70	<0.01

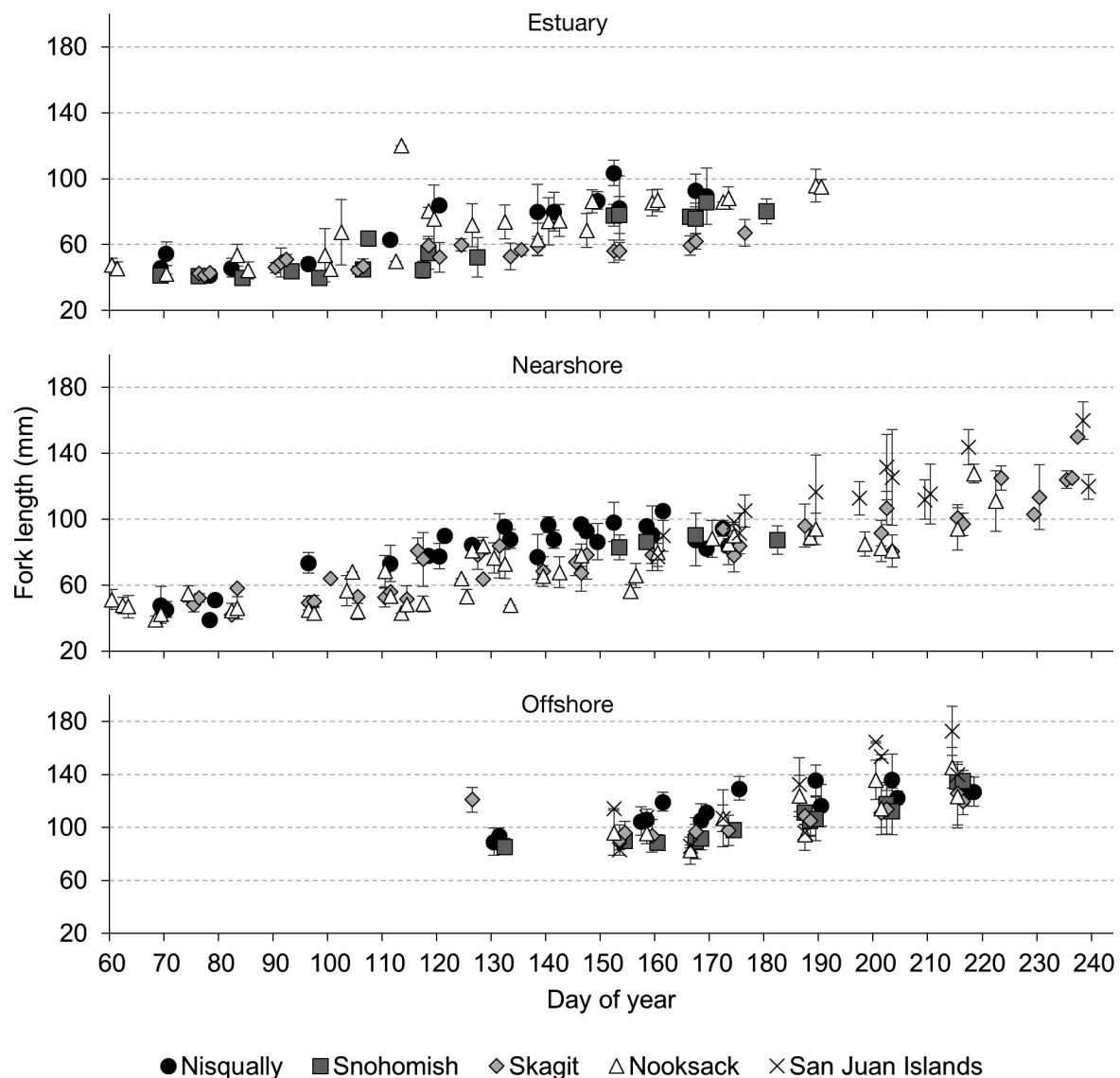


Fig. 3. Daily mean  $\pm$  SD fork length (mm) of Puget Sound subyearling Chinook salmon captured in different regions, with panels separating fish from different habitat types. Plots include composite data from 2014 and 2015 unmarked and hatchery fish

(Fig. 4). This trend was partially driven by hatchery fish in the Skagit and Nooksack watersheds. In estuarine habitat, Nooksack hatchery fish had diets that were about  $1000 \text{ J g}^{-1}$  more energy dense on average than unmarked fish, while in the nearshore, hatchery fish from the Skagit and Nooksack watersheds had diets that were about 800 to  $1300 \text{ J g}^{-1}$  more energy dense. In offshore habitat, fish captured in the Snohomish watershed had the highest ED diets in June and July, while fish caught in the Skagit watershed had the highest ED diets in August. Unmarked fish diets were 300 to  $800 \text{ J g}^{-1}$  more energy dense on average than hatchery fish diets in the offshore, regardless of region. Dietary

ED was greatest in July and August for both sampling years, but the increase through time was significantly higher in 2014 (31% increase) than in 2015 (13% increase; Tukey's HSD;  $p < 0.01$ ). Late season increases in dietary ED were also more pronounced in estuarine and nearshore habitats than in the offshore zone.

### 3.3. Scale-derived growth rate

The best-fit model for scale-derived growth rate included temporal (year), spatial (habitat, region), and demographic (size class, origin) predictor vari-

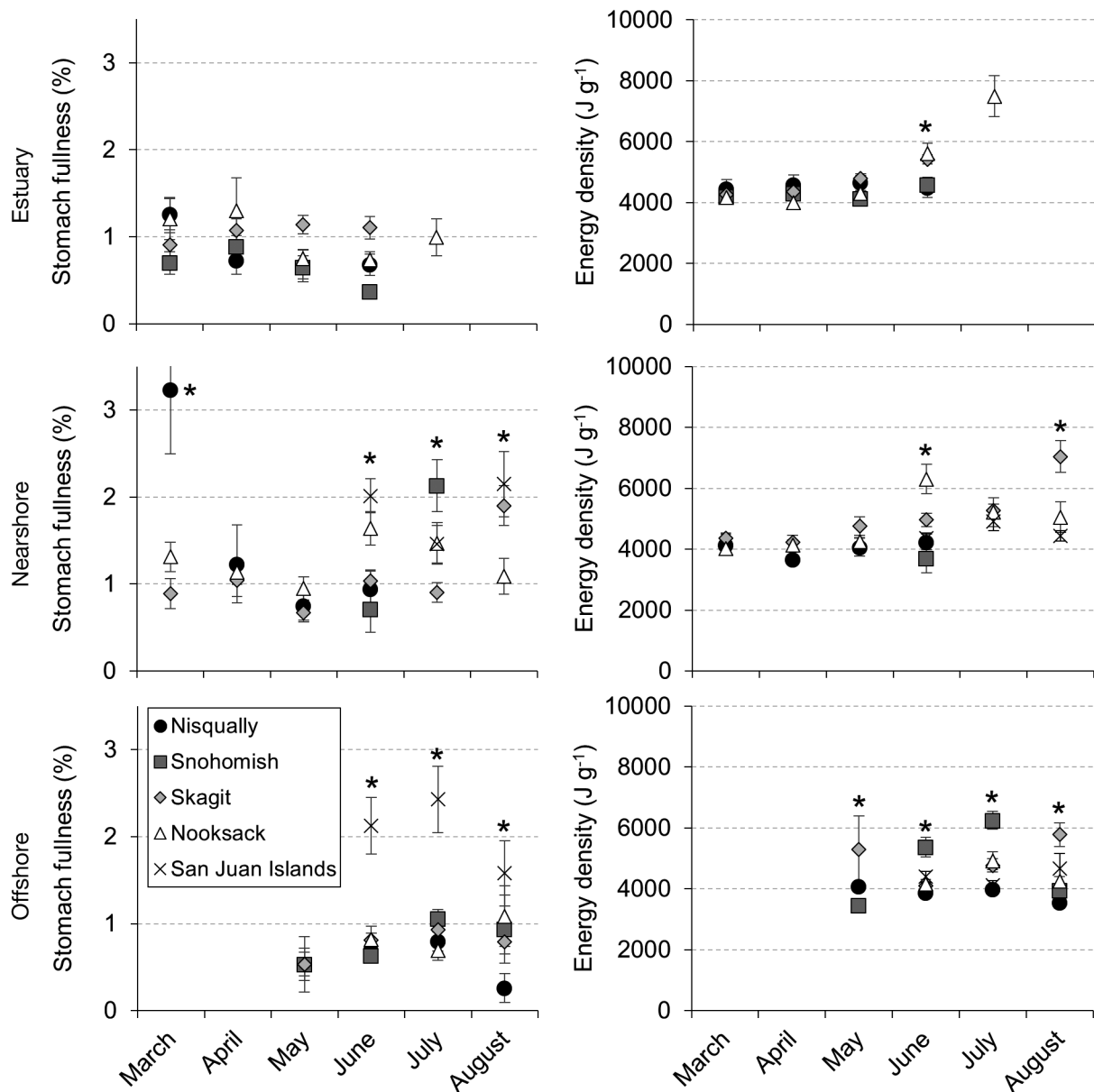


Fig. 4. Stomach fullness (left) and dietary energy density (right) for subyearling Chinook salmon captured in different habitat types throughout the out-migration season. \*Significantly different (Tukey's HSD;  $p < 0.01$ ) regional differences in fish from the same month and habitat type. Points and error bars represent monthly mean  $\pm$  SE values for each of the 5 study regions

ables (Table S4), but rearing origin did not significantly influence growth rate variability for similarly sized fish that were captured in the same habitat type (Table 5). Regional effects were prevalent for some size classes of fish. Most notably, fish captured in the nearshore areas of the San Juan Islands had 0.105 to 0.150 g d<sup>-1</sup> greater growth rates than fish in any other region for the 101 to 125 mm size class and 0.061 to 0.324 g d<sup>-1</sup> greater growth rates for the 126 to 150 mm size class

(Tukey's HSD;  $p < 0.01$ ; Fig. 5). Regional differences in estuarine habitat were not discernible, regardless of size class. Scale-derived growth rates were almost twice as great in 2015 as in 2014 (mean  $\pm$  SD: 2014 =  $0.169 \pm 0.131$  g d<sup>-1</sup>, 2015 =  $0.312 \pm 0.260$  g d<sup>-1</sup>); however, this was likely driven by the positive allometric relationship between size and daily growth, and may have been skewed by a greater relative abundance of larger (100–200 mm FL) subyearling Chinook salmon in 2015.



Table 5. Best-fit model output for generalized linear models of scale-derived growth rate and insulin-like growth factor-1 (IGF-1) concentration. We used a cutoff of  $p < 0.05$  to indicate which spatial, temporal, and demographic predictor variables and interaction effects were significant. Slash (/) indicates a nested effect

Variable	df	F	p
<b>Scale-derived growth rate</b>	1502		
Year	1	1128.50	<0.01
Year/Size	5	1567.32	<0.01
Year/Habitat	2	0.60	0.55
Year/(Habitat $\times$ Size)	5	2.83	<0.01
Year/(Habitat $\times$ Size)/Region	43	3.33	<0.01
Year/(Habitat $\times$ Size)/Origin	10	1.29	0.23
Year/(Habitat $\times$ Size)/(Region $\times$ Origin)	10	0.98	0.46
<b>IGF-1 concentration</b>	1153		
Year	1	50.31	<0.01
Year/Size	10	60.69	<0.01
Year/Habitat	2	16.91	<0.01
Year/(Habitat $\times$ Size)	8	5.87	<0.01
Year/(Habitat $\times$ Size)/Region	31	3.16	<0.01
Year/(Habitat $\times$ Size)/Origin	20	1.82	0.02
Year/(Habitat $\times$ Size)/(Region $\times$ Origin)	17	2.47	<0.01

### 3.4. IGF-1

Regional and origin-level effects significantly predicted IGF-1 concentration for fish of similar size classes captured in the same habitat and year (Table 5, Table S4). Subyearlings in the San Juan Islands exhibited higher IGF-1 concentrations than fish caught in the Skagit or Nooksack watersheds, where differences were significant for fish 51 to 125 mm FL in the nearshore habitat and for fish 126 to 150 and 176 to 200 mm FL in the offshore habitat (Tukey's HSD;  $p < 0.01$ ; Fig. 5). Origin-level effects were less obvious, even when regional differences were accounted for. Generally, unmarked fish 76 to 150 mm FL had IGF-1 concentrations that were about  $4 \text{ ng ml}^{-1}$  greater than similarly sized hatchery fish in the nearshore, while differences between unmarked and hatchery fish in the offshore were indistinct. Similar to scale-derived growth rates, hormone levels were positively associated with size class in both years. IGF-1 values were  $5 \text{ ng ml}^{-1}$  lower in 2014 than in 2015, which may have been driven by a higher proportion of larger subyearling Chinook salmon (100–200 mm FL) in 2015.

### 3.5. CCA

Scale-derived growth rate, IGF-1, dietary ED, and stomach fullness were all significantly associated with specific dietary assemblages for Chinook salmon

that were 51 to 100 and 101 to 150 mm FL (Fig. 6, Table 6). A roughly  $90^\circ$  angle between the stomach fullness and dietary ED eigenvectors for all analyses indicated little apparent relationship between these 2 consumption parameters. Conversely, both scale-derived growth and IGF-1 were clearly associated with stomach fullness but not dietary ED. Growth metrics were also strongly correlated with body size for fish 51 to 100 mm FL but not for fish 101 to 150 mm FL. Sub-yearling Chinook salmon with a greater proportion of forage fish and large-bodied crustaceans (mysids, euphausiids, and shrimp) in their diets showed faster scale-derived growth rates, greater IGF-1 concentrations, and fuller stomachs than fish that had consumed dipterans, insect larvae, amphipods, decapod larvae, and other crustaceans. Biplots of CCA output demonstrated that these diets were most characteristic of subyearlings captured in the nearshore and offshore habitats of the San Juan Islands, which is consistent with our prior analyses of diet and growth.

## 4. DISCUSSION

Dietary patterns in subyearling Puget Sound Chinook salmon *Oncorhynchus tshawytscha* were closely related to morphometric and hormonal indices of growth. Typical ontogenetic dietary shifts were characterized by the consumption of adult insects in the estuary with a transition to crab larvae, euphausiids, or forage fish in the nearshore and offshore habitats. Consumption patterns were also strongly influenced by region such that subyearlings captured in northern Puget Sound—especially in the marine areas surrounding the San Juan Islands—were more likely to have eaten forage fish than those caught in central or southern Puget Sound. This has broader implications for Chinook salmon growth and survival, because the consumption of forage fish and large crustaceans (mysids and euphausiids) was associated with fuller stomachs, faster scale-derived growth rates, and higher IGF-1 concentrations (Fig. 7). Indeed, our analyses indicate that regional differences in the composition, quantity, and profitability of prey likely played a role in determining seasonal size distributions and growth rate variability.

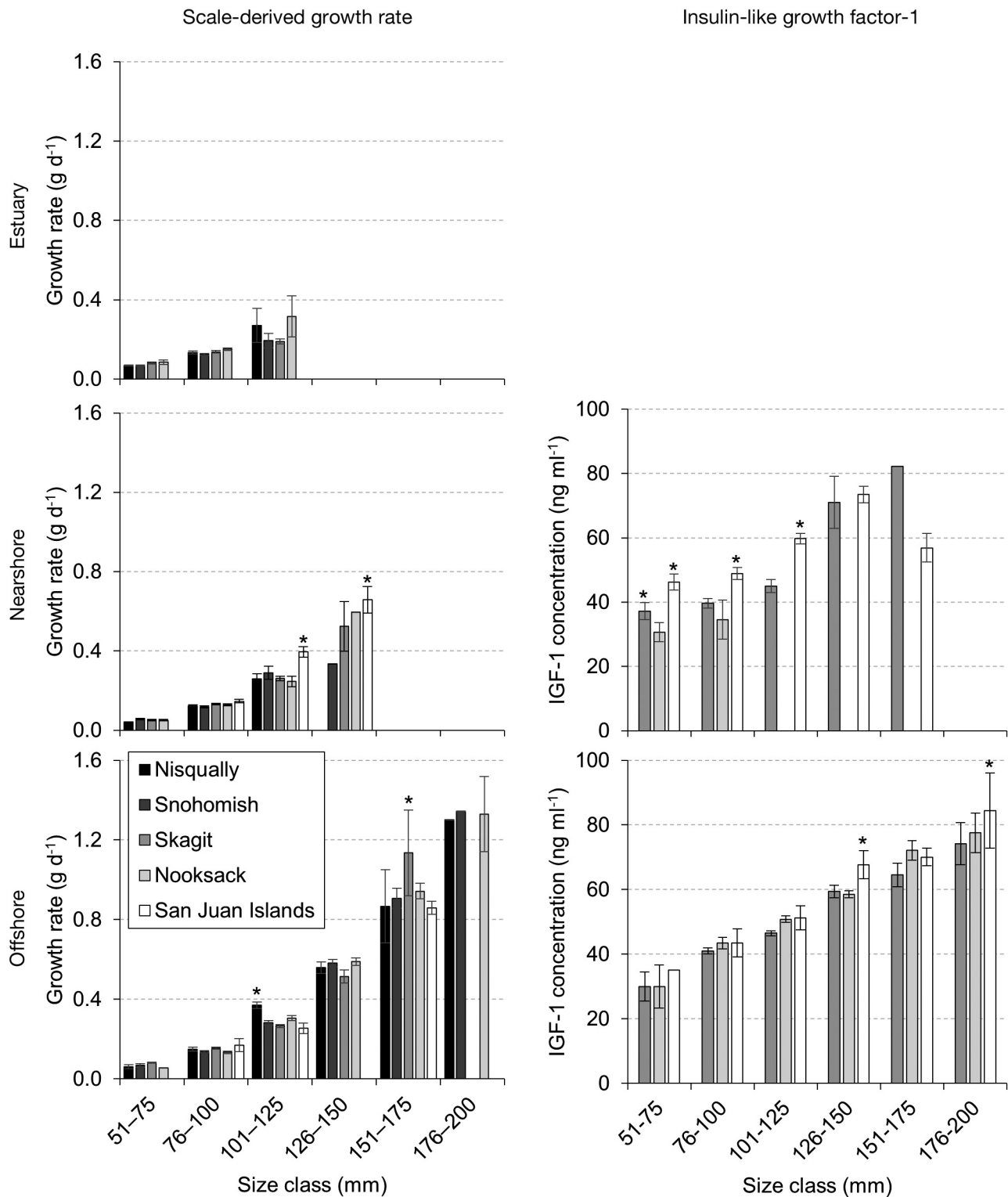


Fig. 5. Mean scale-derived growth rates (left) and insulin-like growth factor-1 values (right) for subyearling Chinook salmon captured in different habitat types in different regions of Puget Sound. Analyses were separated by size class to account for the allometric relationship between both growth metrics and fork length. \*Regions with significantly greater growth rates than other similarly sized fish from the same habitat type. Error bars represent  $\pm 1$  SE

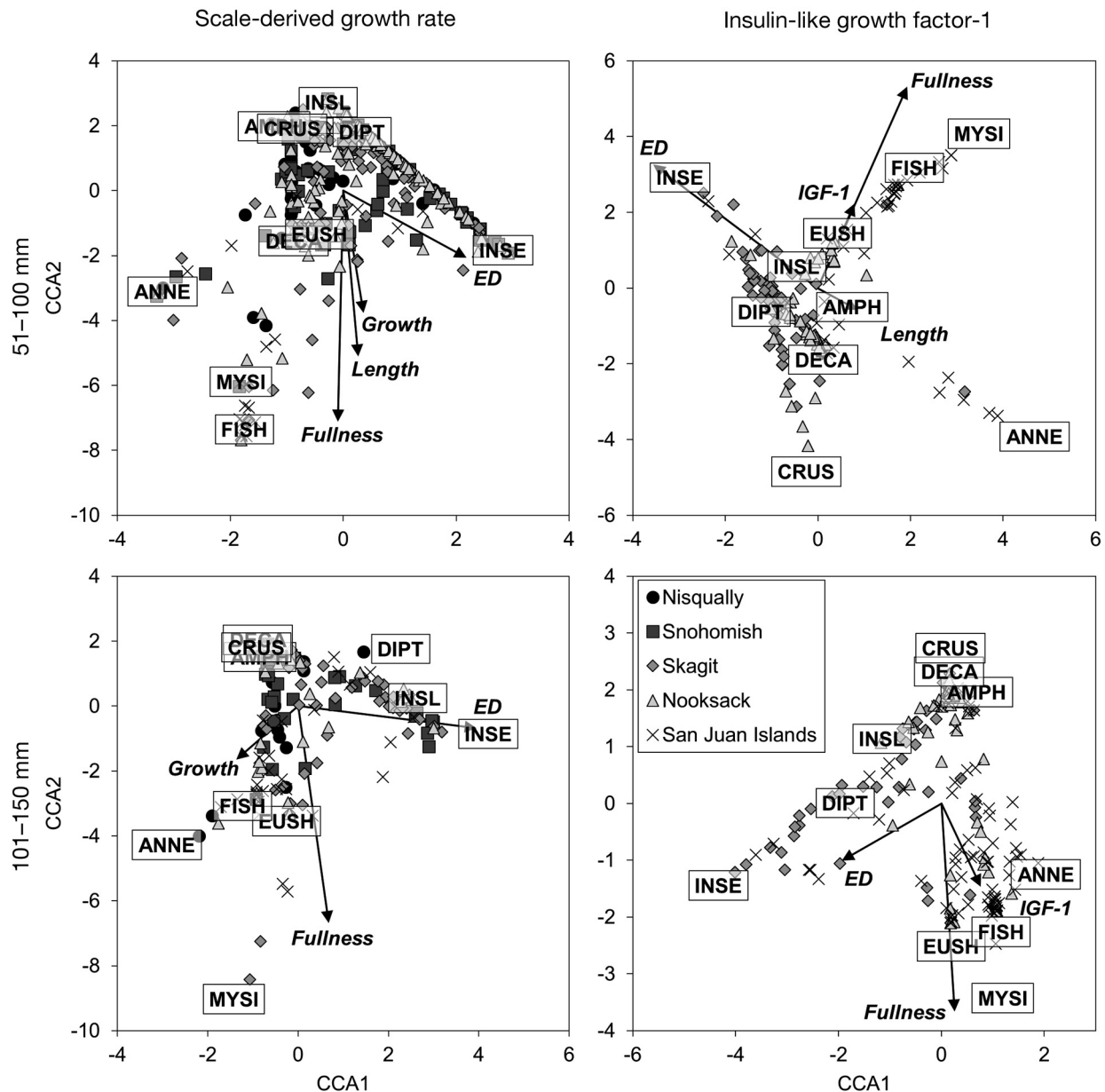


Fig. 6. Canonical correspondence analysis (CCA) bi-plots showing ordination output for subyearling Chinook salmon of 2 different size classes (51–75 and 75–100 mm fork length [FL] fish and 101–125 and 126–150 mm FL fish were grouped for analysis). Scale-derived growth (left) and insulin-like growth factor-1 (right) were analyzed separately due to different sample sizes. Species labels show prey taxa with highly significant ( $p < 0.01$ ) loadings on axes 1 and 2, including dipterans (DIPT), adult insects (hemipterans, hymenopterans, palaeopterans, arachnids, collembolans, and other insects [INSE]), insect pupae and larvae (INSL), amphipods (AMPH), mysids (MYSI), decapod larvae (DECA), euphausiids and shrimp (EUSH), other crustaceans (CRUS), annelids (ANNE), and fish (FISH). Vectors show consumption and growth variables that were significantly ( $p < 0.05$ ) associated with specific dietary assemblages. ED: energy density

Chinook salmon stomach contents differed spatially, temporally, and demographically, but regional and habitat-level differences accounted for almost a quarter of the dietary variation. Within-group variation in dietary composition was significantly less for the Skagit than for any other region, which may have

led to estimated error rates in the PERMANOVA that were overly liberal or conservative (Anderson & Walsh 2013); however, lower variation may also be indicative of less beta-diversity in stomach contents due to prey availability, habitat use, or dietary selectivity (Anderson et al. 2006). In the Skagit and Nook-

Table 6. Canonical correspondence analysis (CCA) output examining the relationship between dietary composition and scale-derived growth rate, insulin-like growth factor-1 (IGF-1), stomach fullness, dietary energy density (ED), and fork length (FL). CCA analyses were run separately for scale-derived growth rate and IGF-1 and for fish 51 to 100 and 101 to 150 mm FL. Var: percentage of variance explained by each model; N/A: variable non-significant and not included in the full model

Variable	— 51–100 mm FL —			— 101–150 mm FL —		
	Var (%)	F	p	Var (%)	F	p
Full model (scales)	13	14.33	<0.01	16	13.61	<0.01
Scale-derived growth rate (log)		3.70	<0.01		2.99	<0.01
Stomach fullness (log)		10.36	<0.01		10.65	<0.01
ED		36.92	<0.01		27.20	<0.01
FL (log)		6.34	<0.01		N/A	N/A
Full model (IGF-1)	16	7.24	<0.01	17	13.90	<0.01
IGF-1		3.58	<0.01		3.79	<0.01
Stomach fullness (log)		8.19	<0.01		14.39	<0.01
ED		13.49	<0.01		23.51	<0.01
FL (log)		3.71	<0.01		N/A	N/A

sack watersheds, typical habitat shifts were characterized by the consumption of dipterans and insects in the estuarine and nearshore habitats, followed by decapod larvae, euphausiids, or forage fish in the offshore zone. Consumption differences among habitats were similar in the Snohomish watershed with the exception that subyearlings rarely exhibited piscivory. At Nisqually, the consumption of insect prey was less common than in the other 3 coastal watersheds and occurred exclusively in the estuarine habitat. Once fish moved to the nearshore and offshore zones, they ate decapod larvae, mysids, and other crustaceans, with only a few isolated instances of piscivory in May. These trends are consistent with the diet

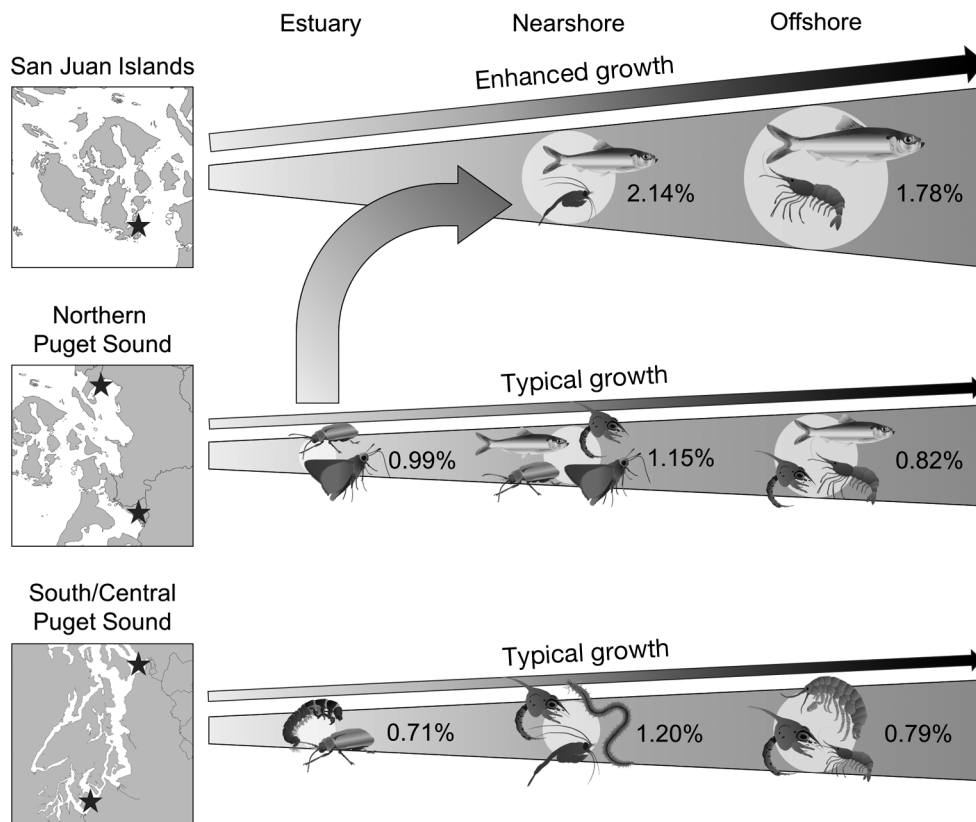


Fig. 7. Postulated relationship between the dietary composition of subyearling Puget Sound Chinook salmon, stomach fullness (presented as a percentage of body size), and growth. Study regions are indicated by stars and include the San Juan Islands, the Skagit and Nooksack watersheds in northern Puget Sound, the Nisqually watershed in southern Puget Sound, and the Snohomish watershed in central Puget Sound. The width of the bar represents stomach fullness and overall energy acquisition. Fish captured in the marine habitats adjacent to the San Juan Islands were comprised of wild and hatchery stocks from the Nooksack and Skagit watersheds. Clip art was downloaded from IAN Image Library (<http://ian.umces.edu/imagelibrary>)

shifts observed by Duffy et al. (2010), who found a predominance of insect prey in the stomachs of Chinook salmon captured in the nearshore zones of northern and central Puget Sound and a predominance of crustaceans in southern Puget Sound. Conversely, forage fish were observed in roughly half of the diets of fish captured in the nearshore and offshore habitats of the San Juan Islands and generally comprised more than 75 % of average stomach content WWB.

Dietary composition was directly related to the stomach fullness, dietary ED, and growth indices of subyearling Chinook salmon throughout Puget Sound. Scale-derived growth rate and IGF-1 concentration both increased with FL, which varied regionally and by habitat type. Nisqually subyearlings were larger than individuals captured in any other region from March through May, regardless of habitat, while subyearlings captured in the nearshore and offshore zones of the San Juan Islands were largest in July and August. Early season trends were in part driven by relative proportions of sampled hatchery fish (range 0–75 %), which were almost 25 mm larger than unmarked fish in April. In southern Puget Sound, hatchery stocks can comprise up to 98 % of juvenile Chinook salmon rearing in nearshore habitats, while hatchery stocks represent less than half of the northern Puget Sound population (Duffy et al. 2005, Rice et al. 2011). Furthermore, hatchery fish are often released at a larger size than their wild counterparts (Weber & Fausch 2003, Tatara & Berejikian 2012, Davis et al. 2018). By July, size differences between hatchery and unmarked salmon were marginal, which may have been due to discrepancies in growth or larger hatchery fish leaving Puget Sound earlier than smaller hatchery fish. As such, it was more likely that the larger size of San Juan Islands subyearlings was the result of optimal rearing conditions and prey availability as opposed to hatchery influence. Sampled San Juan Islands fish were composed of hatchery and wild Skagit and Nooksack stocks that had migrated from their natal watershed. Although there is evidence that salmon migratory distributions are influenced by body size (i.e. larger fish tend to migrate farther; Freshwater et al. 2016), our supposition that the growth of fish captured adjacent to the San Juan Islands was driven primarily by their dietary patterns was supported by the morphometric and hormonal indices of growth, regardless of size class.

Scale-derived growth rates for San Juan Islands Chinook salmon (of Skagit and Nooksack stocks) were as much as 0.061 to 0.324 g d<sup>-1</sup> higher than any

other region for 101 to 150 mm FL fish captured in nearshore habitat. IGF-1 concentrations also exhibited substantial differences between fish caught near the San Juan Islands and fish caught in the Skagit and Nooksack watersheds. Hormone levels were 3 to 15 ng ml<sup>-1</sup> higher on average for subyearlings captured in the marine habitats of the San Juan Islands, especially for smaller (51–125 mm) individuals from the nearshore zone. This corroborates our findings that San Juan Islands fish were larger and consumed up to 3 times as much prey biomass as fish captured in the Nisqually, Snohomish, Skagit, and Nooksack watersheds. When analyzed in tandem with stomach contents, we found that both growth indices were associated with fuller stomachs and with the consumption of forage fish and large-bodied crustaceans—diets typically observed in the nearshore and offshore habitats of the San Juan Islands and the offshore areas of the Nooksack watershed. Dietary ED was strongly associated with the consumption of adult insects and dipterans due to their high energy content but was not related to either metric of growth.

Our findings directly support our fourth hypothesis—that consumption and growth are affected by a combination of temporal, spatial, and demographic effects. They corroborate previous studies that observed spatiotemporal and demographic patterns in scale-derived growth rates (Gamble et al. 2018) and IGF-1 concentrations for various species of Pacific salmon throughout the Salish Sea (Chamberlin et al. 2017, Journey et al. 2018). We attributed regional trends to variable prey consumption, but several biotic and abiotic factors such as temperature, ration, and initial size can influence apparent differences in circulus deposition and IGF-1 concentrations and thus recent growth rates (Shimizu et al. 2009, Beakes et al. 2014, Duguid et al. 2018). Gamble (2016) and Connelly et al. (2018) applied a bioenergetics approach to describe differences in growth among Chinook salmon captured in the nearshore and offshore habitats of Puget Sound and found the colder temperatures experienced in offshore habitats had a significant effect on observed scale growth. Size-related differences in consumption rates and metabolic requirements may have also influenced our interpretation of the growth indices (Beauchamp 2009, Perry et al. 2015, Duguid et al. 2018, Davis et al. 2019). Fish size is known to have a positive allometric relationship with IGF-1 concentrations, such that larger fish, which generally have higher absolute maximum consumption and metabolic rates, tend to exhibit higher IGF-1 levels (Beckman et al. 2001).



However, Shimizu et al. (2009) found that although the positive relationship was consistent among fed and fasted fish, the intercept was significantly higher for fed fish, indicating consumption also contributed to observed differences in IGF-1 concentration. We accounted for the potential confounding effect of allometry by conducting the CCA separately for 2 size classes of fish: 51 to 100 and 101 to 150 mm FL. The relationship between piscivory and growth was highly apparent for fish in both size classes, supporting our assertion that dietary composition was associated with the fuller stomachs, larger body size, and faster growth rates of subyearling salmon captured near the San Juan Islands.

In Puget Sound, the optimal foraging strategy for promoting juvenile Chinook salmon growth appears to be to consume large quantities of insects in the estuary and nearshore during the spring and then take advantage of forage fish and large crustaceans in the nearshore and offshore when available in the summer (where waters are generally cooler; Gamble 2016). Fish may also default to crab larvae when encounter rates of more energetically desirable prey are insufficient to satisfy metabolic and growth demands. The scale-derived growth rates of Nisqually fish were no worse than those of the subyearlings caught in the Snohomish, Skagit, or Nooksack watersheds for any size class despite a greater prevalence of mysids and other crustaceans in their diets. This implies that the consumption of mysids, euphausiids, and other large crustaceans is a viable option for promoting early marine growth in estuaries where terrestrial subsidies (insects) and forage fish are scarce.

Piscivory appears to be the most beneficial foraging strategy for Puget Sound Chinook salmon, provided they have reached a large enough size to avoid gape limitations (Brodeur 1991, Daly et al. 2009, Litz et al. 2017). The predominant fish species found in gut contents of juvenile Chinook salmon were Pacific herring *Clupea pallasii* and Pacific sand lance *Ammodytes hexapterus*. The occurrence of Pacific herring in diets was generally more widespread and accounted for a greater proportion of individual diets compared to sand lance, though proportions of the 2 species in diets from the San Juan Islands were equivalent in some months. While these species appear to be important for supporting juvenile salmon growth, little is known about the abundance and distribution of the ages or size classes that support piscivory. In general, forage fish of edible size (such as the late spawning Cherry Point herring population) are observed less frequently in southern Puget Sound than in northern Puget Sound, which may

explain the regional patterns in piscivory that we observed in the current study (Gustafson et al. 2006, Landis & Bryant 2010, Greene et al. 2015, Siple & Francis 2016). Although northern anchovy *Engraulis mordax* have increased in prevalence in southern Puget Sound in recent years (Duguid et al. 2019), they were not present in diets during our study, and it remains to be seen whether anchovy are present at appropriate sizes during the out-migration season for juvenile salmon consumption. Future research efforts would fill additional information gaps to support the maintenance of forage fish, which clearly play a role in supporting the early marine growth of Puget Sound Chinook salmon.

Our findings support modeling efforts and empirical evidence from throughout the Pacific Northwest, demonstrating the importance of abundant and diverse prey resources for the growth and survival of juvenile salmon (Brodeur et al. 1992, Marin Jarrin 2012, Gamble 2016, Litz et al. 2018, Davis et al. 2019). Subyearling Chinook salmon exhibited a variety of foraging strategies that varied by habitat type and region, demonstrating considerable plasticity that was likely influenced by the relative availability of specific prey taxa. These results have important management implications for the preservation and enhancement of coastal habitats and their associated prey. By encouraging terrestrial subsidies through the maintenance of estuarine tidal marsh habitats, exploring linkages between specific management actions and aquatic prey productivity, and encouraging the conservation of forage fish stocks, managers may improve rearing conditions for juvenile Chinook salmon and other Pacific salmon species, thereby encouraging their early marine growth and survival.

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