Assessing early marine growth in juvenile Chinook salmon: factors affecting variability in individual growth in Northern Puget Sound

Joshua Chamberlin[1], Madilyn Gamble[2], Kristin Connelly[2], Jennifer Gardner[2], Russel Barsh[3], Mike O'Connell[6], Julie Keister[4], Dave Beauchamp[5], Michael Schmidt[6], Brian Beckman[1], Kenneth Warheit[7]

[1] NOAA, Northwest Fisheries Science Center

[2] University of Washington, School of Aquatic and Fishery Science

[3] Kwiaht

[4] University of Washington, School of Oceanography

[5] U.S Geological Survey, Western Fisheries Research Center

[6] Long Live the Kings

[7] Washington Department of Fish and Wildlife

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1. Executive Summary

Results

- Prompted by observed declines in marine survival of ESA listed Chinook salmon populations from the Salish Sea, we initiated a study to evaluate critical growth periods during early marine residence and assess potential factors or mechanisms that may affect growth during the period via assessment of prey availability/consumption, temperature variability, and potential competitive interactions.
- We sampled juvenile sub-yearling Chinook salmon from freshwater, estuary, nearshore and offshore marine habitats throughout Puget Sound including the San Juan Islands throughout the entire migration period. Sampling occurred weekly in freshwater habitats and bi-weekly in the estuary, nearshore, and offshore areas. All individual Chinook salmon were measured (fork length), checked for external marks and CWTs, and subsequently sampled for some combination of scales, diet contents, otoliths, and blood (IGF-1). Concurrent sampling of zooplankton assemblages were conducted during overlapping periods of Chinook salmon migration and use for comparisons with diet composition and to assess prey availability.
- Puget Sound populations of Chinook salmon were of primary interest for our study and local recovery actions. We used genetic stock identification (GSI) techniques and specifically the single nucleotide polymorphism (SNP) 192 baseline (Warheit et al.2014) to assign individual natural origin fish captured throughout this study to specific populations or aggregations. The majority of the samples were assigned to populations originating in Puget Sound and specifically the Skagit and Nooksack watersheds.
- We also identified a significant contribution of Canadian fish late in 2014 and throughout the summer in 2015. Presence of Canadian fish in 2014 was mostly limited to August whereas Canadian fish, predominantly Big Qualicum fish, were present through the summer and contributed up to 40% of the observed Chinook in some regions.
- Using GSI and coded-wire tag recoveries we identified 9 unique cohorts/populations (7 hatchery, 2 natural origin) used for subsequent analysis of scale growth trajectories and bioenergetics analyses. Cohort-specific analysis of scale growth trajectories from juvenile Chinook salmon revealed no evidence of size selective mortality occurring during the initial summer in marine waters. While our results do not preclude the possibility of SSM occurring at a later time period, it suggests, given previous research relating growth to survival, that growth in all habitats throughout the time period is important for subsequent survival.
- Analysis of zooplankton assemblage and diet composition revealed both seasonal and region variability largely driven by seasonal patterns of decapods and ctenophores in the zooplankton assemblage and the marked increase in fish prey found in stomach contents of fish captured in the San Juan Islands and to some degree Bellingham Bay. In addition, there was relatively little overlap between the zooplankton assemblage and

the diet composition for fish from all regions. In general, fish captured in the offshore had a higher overlap with the local zooplankton assemblage than those captured in the nearshore and showed some coherence between sample types for the presence/abundance of decapods.

- Fish prey was disproportionally important for the San Juan Islands and the size distribution of prey fish revealed a significant component of the local forage fish population were available as prey for the majority of juvenile Chinook salmon inhabiting the islands. Pacific herring and Pacific sand lance were the primary species found in the gut contents of fish from the region and also represented the two most abundant species (CPUE) encountered in the nearshore habitats of the San Juan Islands during the study period.
- Comparisons of Pacific herring and Pacific sand lance lengths from stomach contents with size frequency distributions from nearshore beach seine sets in the San Juan Islands showed a significant proportion of each species were available as prey to juvenile Chinook salmon inhabiting the region. Furthermore, relative proportions of each species found in the diets of juvenile Chinook salmon reflected changes in CPUE observed in nearshore beach seine catches.
- Absolute growth rates as assessed via concentrations of IGF-1 in individual fish and through bioenergetics simulations were elevated in the nearshore habitats of the San Juan Islands relative to other habitats and regions. Diet composition likely played a large role in driving the observed difference in absolute growth rates. A constrained analysis of principal coordinates indicated an increase in fish prey was associated with higher concertation of IGF-1 in fish captured in the San Juan Islands.
- Standardized growth rates (i.e. grams of growth per gram of fish) were similar between the natal nearshore habitats and the nearshore habitats in the San Juan Islands yet both were higher than the natal offshore habitat for cohort(s) where such comparisons were possible. Similarity among the nearshore habitats in each region were likely due to the presence of high quality prey (terrestrial insects and fish, respectively) and the optimal surface temperatures experienced during residence in each respective habitat.

Conclusions

- Past work (Beamer and Fresh 2012) and our efforts support the notion that primary alignment should be with the Whidbey Basin, in particular Skagit, and with Nooksack efforts. We recommend considering the San Juans in the context of priorities to target for improving the productivity of these populations in particular. However, other Puget Sound fish were present, so this doesn’t discount the value of the San Juan Islands to the overall ESU.
- The San Juan Islands appear to be uniquely beneficial as juvenile Chinook salmon rearing given the observed temperature patterns and the presence of fish in the majority of diets. Specifically, the contribution of both Pacific herring and Pacific sand lance is unique to the region compared to other rearing areas in northern Puget Sound and the benefit of increased contributions are reflected in individual growth rates.

- The presence and unique size structure of the forage fish population in the islands appears to provide this growth benefit. While forage fish have long been included in efforts related to salmon recovery in the San Juan Islands, our results provide empirical evidence as to the growth benefits conveyed through predation on “local” forage fish, specifically Pacific herring and Pacific sand lance, and the degree to which salmon that inhabit the San Juan Islands rely on forage fish as prey.
- We recommend further efforts geared toward understanding the population dynamics driving the Pacific herring and Pacific sand lance populations that uniquely support juvenile salmon in the San Juan Islands including abundance/distribution, current and potential spawning habitat assessments, population structure/diversity, and feeding ecology.
- We also recommend considering/recognizing the increased presence and abundance of Northern anchovy and their potential implication upon local food webs.
- Lastly, we suggest decreasing the priority of efforts supporting surf smelt with regard to juvenile Chinook salmon productivity and recovery in the region. While surf smelt were present in the catch (Figures 6.3.1), few showed up in the Chinook diets. This is likely a function of both availability and potentially, preference. Surf smelt were typically smallest when Chinook were not present (May and September) and were far less abundant than Pacific herring or sand lance.
- Current efforts are underway to support evaluation of Pacific herring population diversity and structure as found in the gut contents of juvenile Chinook salmon in the San Juan Islands. Analyses will be completed by the summer of 2019. Similarly, efforts to understand the ecology and movement of sub-adult resident Chinook in the San Juan Islands and greater Puget Sound are underway. Project will focus on growth and movement patterns as well as diet and population composition in Marine Area 7.

2. Introduction

During the 1980s, marine survival (smolt-to-adult returns: SARs) for several ESA-listed Puget Sound and Strait of Georgia Chinook salmon stocks declined. Recent analysis of survival trends for Salish Sea stocks has shown great variability, but little coherence with stocks from other regions such as the Washington Coast, which seem to be greatly affected by North Pacific Gyre Oscillation. The strong geographic coheherence in survival trends suggest that factors operating within the Salish Sea have strong influence on the overall marine survival of Chinook that originate here (Ruff et al. 2017).

Size-selective mortality has been widely reported during the juvenile stages of many species in marine environments (Sogard 1997) and can be the predominant force affecting marine survival and adult abundance. Size-selective mortality is known to affect juvenile anadromous salmon during their early marine phase. Evidence of strong size-selective mortality for hatchery Chinook salmon in Puget Sound (Duffy and Beauchamp 2011) and coho salmon in the Strait of Georgia (Beamish et al. 2004) has linked higher adult returns to larger sizes achieved during early months of marine life, highlighting the importance of understanding the relationship between early marine growth periods and overall marine survival. However, it is likely that the relationship varies by population and/or specific habitat type or geographic area (Beamish et al. 2004, Duffy and Beauchamp 2011, Tomaro et al. 2012).

While evidence of size-selective mortality exists for anadromous salmon in the Salish Sea, there is considerable uncertainty around the factors that affect the relationship between early marine growth and survival and how they vary in space and time. Resource availability can directly and indirectly affect growth and ultimately survival via reduced consumption and/or increased competition.

Up until now, little information existed regarding the performance (growth/survival) of individual fish from natural-origin Puget Sound Chinook populations as they inhabit different habitats and geographic regions during their early marine phase. Previous research has shown that ESA-listed Chinook salmon inhabit the San Juan Islands during the typical outmigration period (Beamer and Fresh 2010). Individuals from Nooksack River and Whidbey Basin populations in particular have been consistently encountered in the nearshore marine areas of the archipelago from April-September; a period when individuals from these populations are also present in waters closer to their natal systems (Beamer et al. 2005, Rice et al. 2012).

This report describes the results of a two-year study to evaluate the role and drivers of juvenile (sub-yearling) Chinook salmon growth and the potential influence of, size-selective mortality for ESA-listed Puget Sound Chinook populations that inhabit the San Juan Islands. The report is framed around the primary objectives of the project:

a) identify the periods of critical growth during early marine residence and determine where that growth is occurring;

b) identify the Chinook prey and the dietary value of prey items;

c) establish the mechanistic relationships between growth and potential limiting factors including temperature, food supply, and competition[1];

d) within this sampling framework, opportunistically initiate a better understanding of the resident (sub-adult) Chinook life history common to the San Juan marine environment (relative abundance, origin, dietary needs and growth variation between resident and ocean migrants);[2] and

e) use this information to inform recovery planning in the San Juan Islands.

Our work was performed during the juvenile marine residence period in the nearshore and offshore areas of the San Juan Islands where ESA-listed, Whidbey Basin and Nooksack Chinook populations are present. We collaborated with in-river, estuarine, nearshore, and some offshore sampling efforts in the Whidbey Basin and Bellingham Bay to capture as much of the range of juvenile marine residence for the targeted populations as possible. Emerging genetic techniques were used to better discriminate the Chinook stocks than could be done previously. This work supports the prioritization of recovery efforts, to better account for the ecological conditions that support the growth, productivity, and survival of Chinook salmon that utilize the San Juans. This project complimented similar work that occurred in Central/South Puget Sound as part of a collective effort to investigate the Salish Sea-wide decline in marine survival of Chinook, coho and steelhead, called the Salish Sea Marine Survival Project.

While this project focused on Chinook salmon, we methodically collected and archived samples of all non ESA listed anadromous salmonid and forage fish species encountered. These archives, stored at the US Geological Survey Western Fisheries Research Center, provide additional opportunity to explore growth and survival patterns among species and evaluate effects of competition and/or predation.

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[1] Assessment of competition is ongoing. Delays were caused by staff transitions. Updated information will be provided if competition is deemed a critical factor.

[2] Unfortunately, no resident type Chinook were caught in during our sampling events. However, a resident directed study begins in late 2017 that will address many facets of this objective.

3. Study Area(s) and Sampling Design

We sequentially sampled outmigrating juvenile sub-yearling Chinook salmon through four separate habitat types, or life stages, (freshwater, estuary, nearshore, and offshore) associated with four major watersheds throughout Puget Sound (Figure 3.1, Table 3.1) as described below. Sections 5.2 and 7.2 incorporated data from all regions/watersheds while the remaining sections focused on northern Puget Sound (Skagit, Nooksack, and San Juan Islands) (Figure 3.2). Freshwater, estuary, and the majority of nearshore sites were sampled as part of ongoing monitoring programs conducted by state or federal agencies as well as local tribal entities. Offshore sites were selected based on a minimum depth requirement and described in the General Sampling Methods section. Nearshore sites within the San Juan Islands were selected based on Beamer and Fresh (2012) to represent sites and habitat types known to be used by Chinook salmon and by northern Puget Sound populations in particular (Figure 3.3).

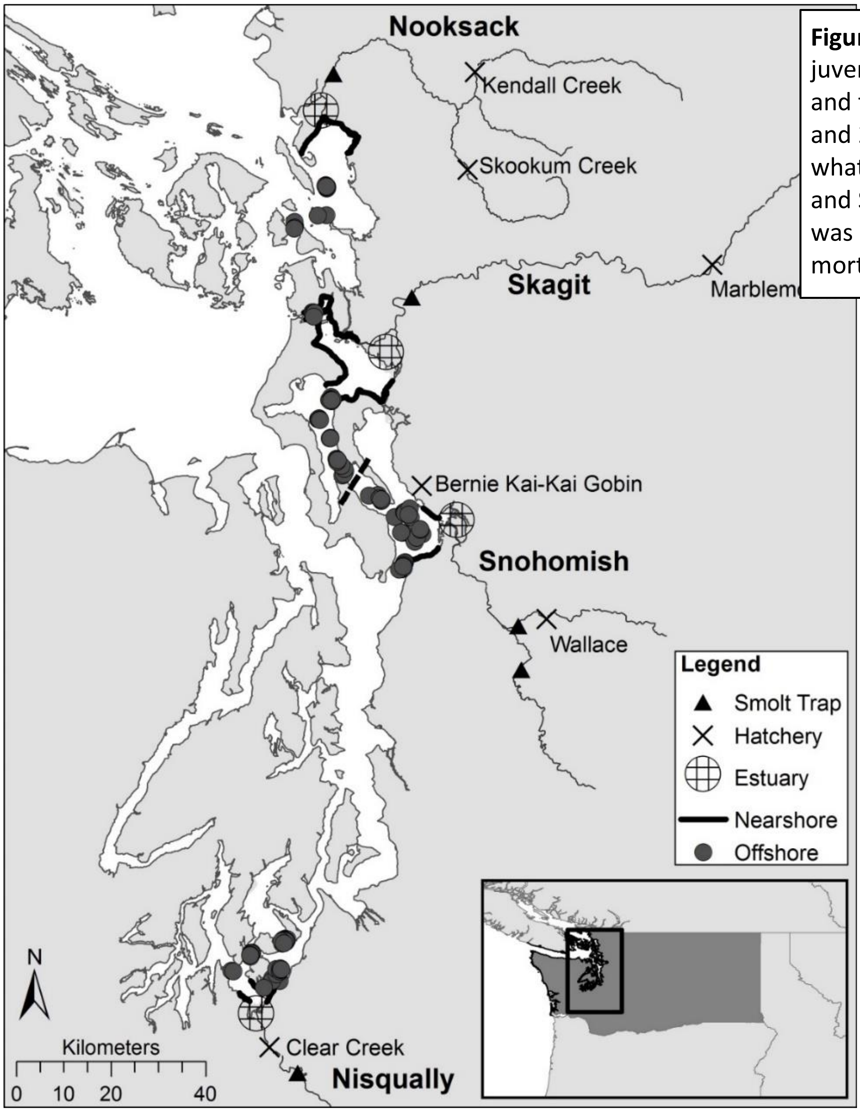


Figure 3.1 Map showing approximate locations of juvenile Chinook salmon sampling efforts in each habitat and focal watershed in Puget Sound, WA during 2014 and 2015. The black dashed line differentiates between what was considered the offshore region of the Skagit and Snohomish watersheds. The extent of this sampling was used for population-specific analysis of size selective mortality and bioenergetics simulations.

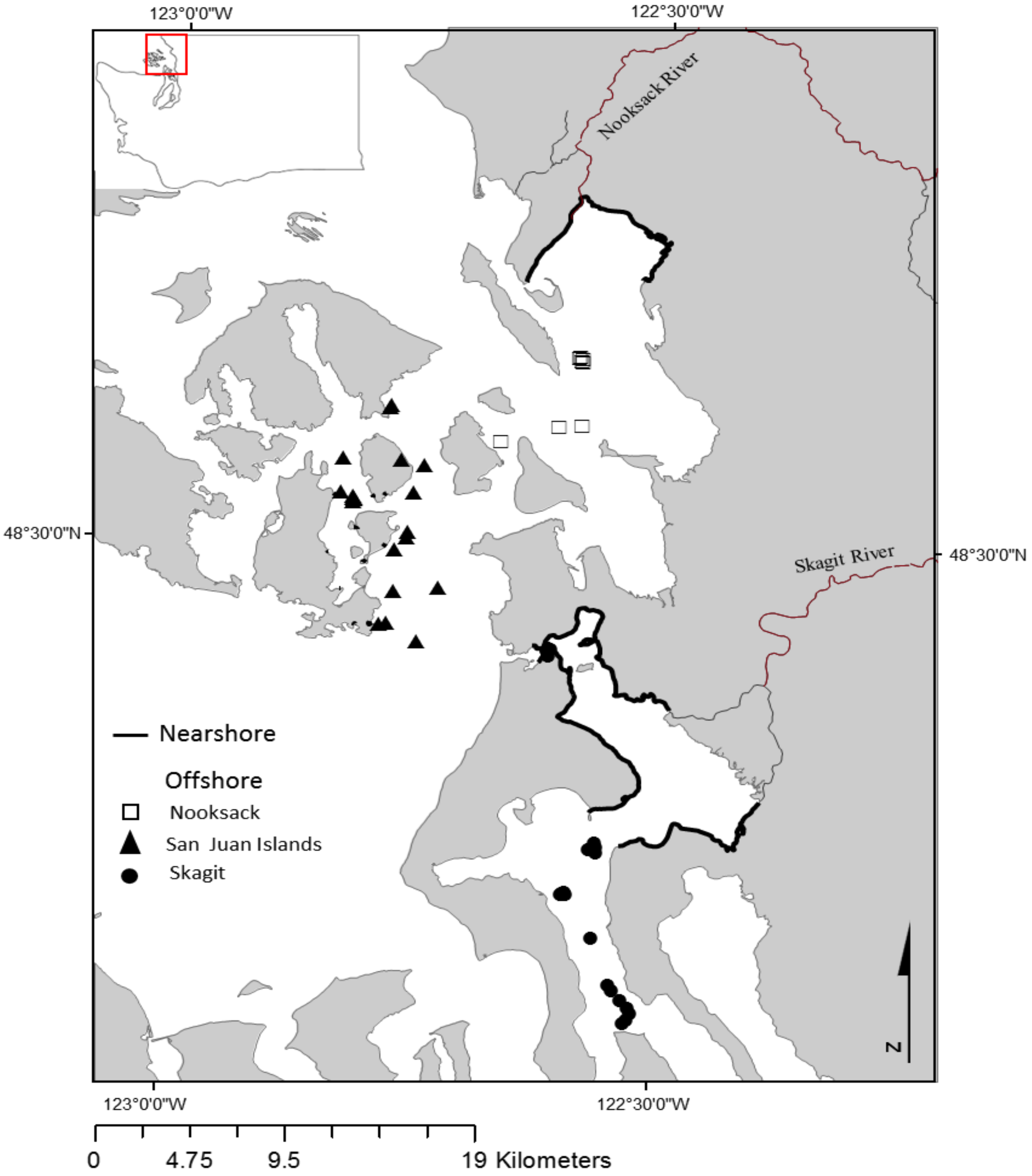


Figure 3.2. Northern Puget Sound fish sampling locations. Northern Puget Sound includes Nooksack and Skagit River watersheds as well as the San Juan Islands.

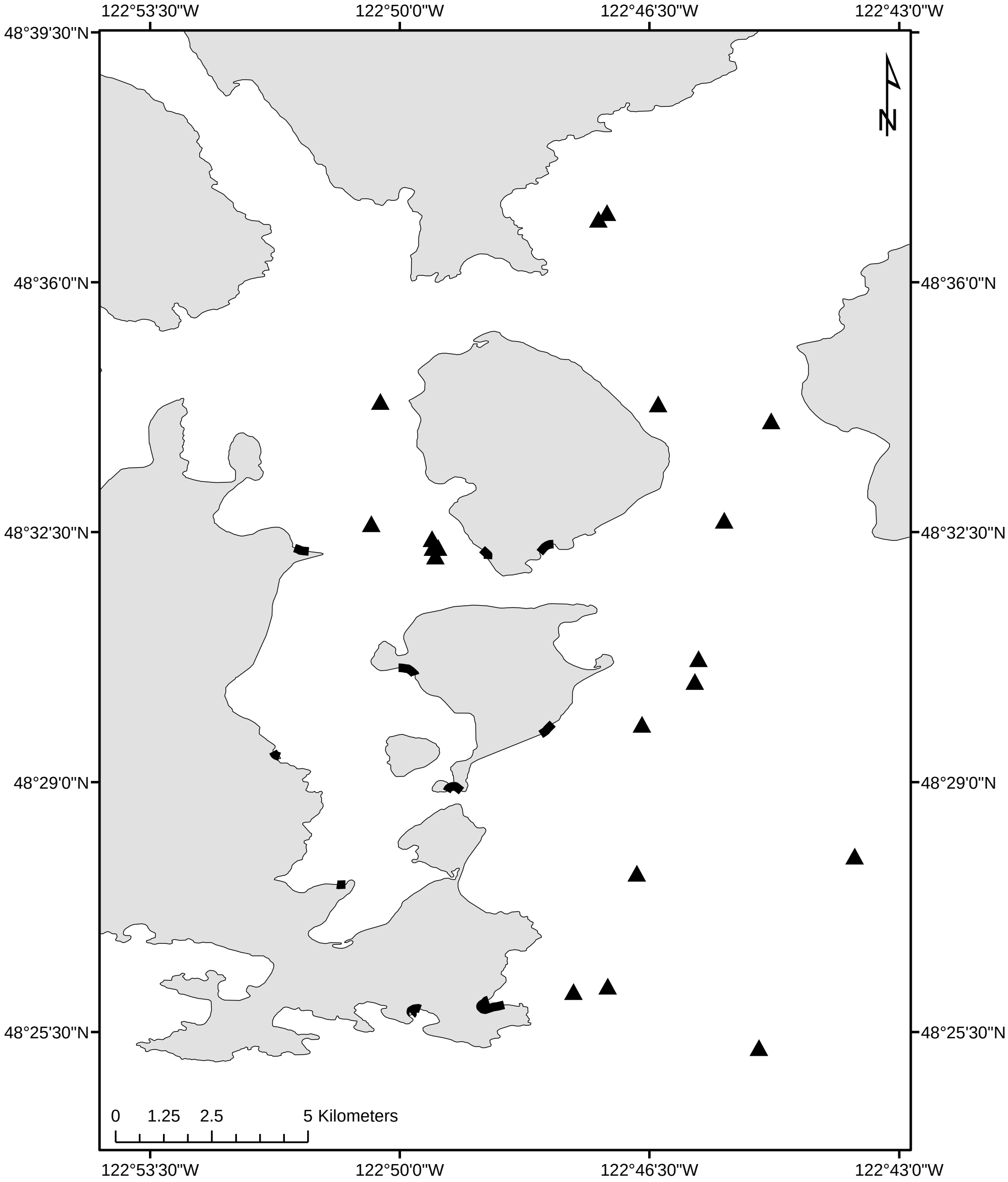


Figure 3.3. Locations of offshore (triangles) and nearshore (black lines) fish sampling stations for 2014-2015.

Table 3.1. Sampling frequency and distribution among habitat types and watersheds.

	Freshwater			Estuary			Nearshore			Offshore		
Watershed	# sites	freq	season	# sites	freq	season	# sites	freq	season	# sites	freq	season
San Juan Islands							9	bi-weekly	May-Sep	2-5	6 tot	May-Aug
Nooksack	1	weekly		10	bi-weekly	Mar-Oct	13	bi-weekly	Mar-Oct	2-3	6 tot	May-Aug
Skagit	1	weekly	Feb-Aug	8	bi-weekly	Mar-Oct	22	bi-weekly	Mar-Oct	5-6	6 tot	May-Aug
Snohomish	2	weekly	Feb-Jun	36	bi-weekly	Feb-Oct	10	bi-weekly	Feb-Oct	4-6	6 tot	May-Aug
Nisqually	1	weekly		~10	bi-weekly	Feb-Sep	~25	bi-weekly	Feb-Sep	3-4	6 tot	May-Aug

4. General sample collection methods

4.1 Fish Sampling

Smolt traps and hatcheries: Freshwater samples were collected via smolt traps or directly from hatcheries prior to release. Smolt traps operated by WDFW and tribal agencies were sampled weekly through out the migration period within all watersheds of interest. A subset of samples were collected directly from all hatcheries as identified in our cohort selection (Section 5.2) to provide baseline for analysis of scale growth for hatchery reared fish specifically.

Estuary & Nearshore: Fish collections in the estuary and nearshore habitats throughout all regions were conducted using beach seines of various sizes or fyke traps, depending on the particular habitat being sampled. Nearshore sites in the Skagit region were sampled with a large beach seine (36.6 m x 3.7m, 3mm mesh size) by fixing one end of the net on the beach while the other end is set by boat across the current at an approximate distance of 65% of the net’s length. After a given amount of time, the boat end is brought to the shoreline edge and pulled in by hand. Open water round-haul sets were also made in Skagit Bay by bringing one end of the small beach seine net around to meet the other end. Large net sampling protocols were also used for sampling subtidal fringe habitats in Bellingham Bay. Nearshore sites in the San Juan Islands were sampled using the large seine but under the Puget Sound protocol. Beach seines used under the Puget Sound protocol are set perpendicular to the beach at a distance of approximately 30m. Both ends of the net are then pulled toward the shore simultaneously until all fish are funneled to the center of the net. In addition to large seine sampling methods, shallow intertidal habitats in Bellingham aby were sampled using a small beach seine (24.4m x 1.8m, 3mm mesh size) and a drag and haul method, where both ends of the net are pulled down the beach for a given distance and then pursed up, yielding a catch.

Offshore: Offshore sampling was conducted using a purse seine (FV 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). The net was set and held open for 10-20 minutes before being closed and pursed to secure the catch. Fish were funneled into the bunt end of the net and held alongside the vessel before being transferred to onboard tanks with flow through seawater from the site or counted and directly released. All salmonids were brought on board and placed into holding tanks.

During each sampling event we recorded total counts, mark types, fork lengths, and weights of hatchery- and natural-origin Chinook. Up to 30 hatchery-origin Chinook in each sampling event were lethally sampled for blood collection for IGF-1, and CWT and otolith extraction and reading; up to 30 unmarked Chinook were lethally sampled in northern watershed for blood collection for IGF-1 and in southern watersheds were sampled live and released whenever possible. From each individual we collected scales and caudal fin tissue (used for genetic stock identification of unmarked 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 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. Fin clips were stored in 100% ethanol. Otoliths were removed in the lab and stored dry. Diets were collected via gastric lavage in the field or dissection in the lab. Diet samples taken in the field were frozen in a small zip-lock bag in water from the sample site; stomach samples taken in the lab were frozen in a small zip-lock bag.

4.2 Zooplankton sampling

Zooplankton sampling occurred approximately every two weeks from March through October in the offshore environment and concurrently with fish sampling when those sampling periods overlapped (May-August) in 2014-2015. Plankton were collected by conducting daytime field collections using vertical tows and bongo tows. Vertical tows were conducted with a 60-cm ring net with 200-µm mesh that was lifted vertically from ~5 m off the seafloor through the whole water column. Bongo tows were conducted with 60-cm paired ring (bongo) nets with 335-µm mesh, towed obliquely through the upper 30 or 60 m in a double-oblique (down and up) tow. Flow meters were attached to the nets to quantify the water volume sampled (m^3). A depth sensor (ReefNet Sensus Ultra) was attached to the bongo net frame to accurately record tow depths and determine if target depths were achieved. The nets were gently rinsed with seawater and the contents were preserved using $NaHCO_3$-buffered formalin diluted in seawater to achieve a final concentration of 5% formalin.

5. Identify the periods of critical growth during early marine residence and determine where that growth is occurring

5.1 Genetic stock identification

5.1.1 Methods

Genetic stock identification (GSI) analyses use genotypic data to assign a set of samples of unknown origin to baseline samples of known origin. For this project, we used a baseline dataset genotyped with the LOA-CTC set of single nucleotide polymorphisms (SNPs) (Warheit et al., 2013), and the conditional maximum likelihood method of Fournier et al. (1984) and Millar (1987) (see also Anderson et al. 2008), with Rannala and Mountain (1997) likelihoods, to calculate posterior probabilities and assign individuals of unknown origin. The procedure uses an expectation-maximization (EM) algorithm and Bayes' Theorem with initial flat priors using the following equation:

$$P(assignement|source) \propto Likelihood(assignment, source) x\, P(source)$$

After each EM iteration source probabilities were updated using the mean source population assignment vector. For each individual of unknown origin the population with the highest posterior probability, after the EM algorithm converges, is the assigned population.

There are three primary sources of error for GSI analysis: (1) power of baseline data to differentiate source populations, (2) population assignments based on lower posterior probabilities, and (3) source population not present in the baseline. These sources of error are discussed in several sections below.

A baseline dataset was used, comprised of SNP genotypes from 4779 individuals from 34 populations within the Salish Sea. Four of the populations were from British Columbia, and 30 populations from Puget Sound, Hood Canal, and the Strait of Juan de Fuca. These baseline data represented the potential source populations for the juvenile Chinook samples (Table 5.1.1). However, the UpperCascadeSp population from the Skagit River was represented by only eight samples, with no assignment support and was therefore removed from the baseline for this project. Source populations can be pooled into aggregates of populations, and since the posterior probabilities are additive within an individual, the total posterior probability from a pool of source populations is equal to or greater than that from any single source population from within that pool (Table 5.1.1). That is, when pooling source populations into aggregates posterior probabilities increase, providing more confidence in the assignment, but at the cost of specificity (i.e., your assignments usually are now from a broader geographic area [e.g., upper Skagit versus Skagit River Basin]).

A sample of unknown origin is assigned to a population with the highest posterior probability; however, the posterior probability can be low, (e.g., less than 0.50), providing little confidence in the assignment. There are no standard procedures for determining a probability threshold for accepting an assignment as the correct assignment. We considered a posterior probability as significant if it was greater than 0.70. The choice of 0.70 was somewhat arbitrary, but if the highest probability for an individual was 0.70, the second highest probability could be no more than 0.30, which is less than half that of the highest probability.

The third source of assignment error mentioned above occurs when the source population for an individual of unknown origin is not present in the baseline dataset. To evaluate the likelihood that a population was indeed present in the baseline we calculated probabilities of inclusion (ProbInc) for each of the juvenile Chinook. ProbInc uses likelihood scores and a Monte Carlo procedure to evaluate separately the probability that an individual of unknown origin is from each source population. As with the posterior probabilities discussed above, the threshold for ProbInc is arbitrary. We selected a cutoff of 0.05, with ProbInc < 0.05 indicating that the individual of unknown origin can be excluded from that source population. I considered an individual to be excluded from all potential source populations in the baseline data if its maximum ProbInc across all populations was less than 0.05. Of the 1420 juvenile Chinook samples with usable genotypes, 151 (10.6%) had ProbInc < 0.05, and 90 (6.3%) had ProbInc = 0.00.

5.1.2 Results

A total of n = 1420 samples were analyzed for genetic stock identification in 2014-15 (Table 5.1.2). Individuals were assigned to 29 and 36 separate populations or aggregates in 2014 and 2015, respectively. Assignments represented individuals from British Columbia, Puget Sound, and the Strait of Juan de Fuca. Upper Skagit Summer fish accounted for 30% (n = 422) of all assignments from all regions/habitats across both years.

Samples from the Skagit region were largely represented by fish originating from the Skagit River (Figures 5.1.1, 5.1.2). In both years between 58% and 75% of samples from the Skagit nearshore and offshore habitats were assigned to populations originating within the Skagit River. Nearshore samples were assigned to 15 populations/aggregations in 2014 and 11 populations/aggregations in 2015. Assignments represented populations from the Lower/Mid Strait of Georgia to central Puget Sound. The population/aggregation with the highest percentage outside the Skagit River was the Whidbey basin aggregation (12.5-15.3%) which is made up of populations from the Skagit, Stillaguamish, and/or Snohomish Rivers.

Assignments for Skagit offshore samples were more evenly distributed among populations/aggregations than those from the nearshore, yet still weighted toward populations originating from the Skagit River or Whidbey basin (Figure 5.1.1, 5.1.2). Individuals were assigned to more populations/aggregations in the offshore compared to the nearshore within a given year. Samples collected in 2015 represented more populations/aggregations outside of the Skagit/Whidbey basin than samples collected from 2014 (25.5% and 10%, respectively). The distribution of populations/aggregations were similar to the nearshore though indicated a higher percentage of the samples represented populations from BC and central/south Puget Sound.

Across both years in total, individual assignments for juvenile Chinook captured in the nearshore and offshore habitats within the Nooksack region again overwhelmingly represented local populations/aggregations (Figure 5.1.3, 5.1.4). Nearshore samples were assigned to 14 populations/aggregations in each year. The majority of nearshore samples in both years assigned to the Nooksack Fall (Samish) (45.2%) and NF/MF Nooksack Spring (13.3%).

Table 5.1.1. Baseline populations and aggregations used to assign individual samples to population of origin.

Source Population	BasePopulation	Aggregation Level				
		1	2	3	4	5
BigQualicumHat	BigQualicumHat	BigQualicum	BigQualicum	LStraitGeorgia	StraitGeorgia	BritishColumbia
UFraser	UFraser	FraserR_Early	FraserR	FraserR	StraitGeorgia	BritishColumbia
SouthThompson	SouthThompson	SouthThompson_Early	FraserR	FraserR	StraitGeorgia	BritishColumbia
HarrisonR	HarrisonR	FraserR_Late	FraserR	FraserR	StraitGeorgia	BritishColumbia
Nooksack_KendallCkH	NFMFNooksackSp	NFMFNooksackSp	NooksackSp	Nooksack	NorthPugetSound	PugetSound
NFMFNooksackSp	NFMFNooksackSp	NFMFNooksackSp	NooksackSp	Nooksack	NorthPugetSound	PugetSound
SFNooksackSp	SFNooksackSp	SFNooksackSp	NooksackSp	Nooksack	NorthPugetSound	PugetSound
SamishFa	SamishFa	NooksackFall(Samish)	NooksackFall(Samish)	NooksackFall(Samish)	Fall_Aggregate	PugetSound
Skagit_MarblemountSpH	Skagit_MarblemountSpH	Skagit_MarblemountSpH	Skagit	WhidbeyBasin	NorthPugetSound	PugetSound
Skagit_MarblemountSuH	UpperSkagitSu	SkagitSu	Skagit	WhidbeyBasin	NorthPugetSound	PugetSound
UpperSkagitSu	UpperSkagitSu	SkagitSu	Skagit	WhidbeyBasin	NorthPugetSound	PugetSound
UpperCascadeSp	Removed	Removed	Removed	Removed	Removed	Removed
SuiattleSp	SuiattleSp	SkagitSp	Skagit	WhidbeyBasin	NorthPugetSound	PugetSound
UpperSauk	UpperSauk	SkagitSp	Skagit	WhidbeyBasin	NorthPugetSound	PugetSound
LSkagitFa	LSkagitFa	SkagitFa	Skagit	WhidbeyBasin	NorthPugetSound	PugetSound
NFStillaguamishSu	NFStillaguamishSu	StillaguamishSu	Stillaguamish	WhidbeyBasin	NorthPugetSound	PugetSound
SFStillaguamishFa	SFStillaguamishFa	StillaguamishFa	Stillaguamish	WhidbeyBasin	NorthPugetSound	PugetSound
SkykomishSu	SkykomishSu	SnohomishSu	Snohomish	WhidbeyBasin	NorthPugetSound	PugetSound
SnoqualmieFa	SnoqualmieFa	SnohomishFa	Snohomish	WhidbeyBasin	NorthPugetSound	PugetSound
Issaquah	Issaquah	Issaquah	LakeWashington	Duwamish_LakeWA	Fall_Aggregate	PugetSound
Bear	Bear	Bear	LakeWashington	Duwamish_LakeWA	Fall_Aggregate	PugetSound
Cedar	Cedar	Cedar	LakeWashington	Duwamish_LakeWA	Fall_Aggregate	PugetSound
Green_SoosCkH	GreenFa	GreenRFall	GreenR	Duwamish_LakeWA	Fall_Aggregate	PugetSound
Green	GreenFa	GreenRFall	GreenR	Duwamish_LakeWA	Fall_Aggregate	PugetSound
WhiteSp	WhiteSp	WhiteSp	WhiteSp	WhiteSp	WhiteSp	PugetSound
Puyallup	Puyallup	Puyallup	Puyallup_White	Puyallup_White	Fall_Aggregate	PugetSound
Nisqually_ClearCkH	NisquallyFa	NisquallyFa	Nisqually	SouthPugetSound	Fall_Aggregate	PugetSound
NisquallyFa	NisquallyFa	NisquallyFa	Nisqually	SouthPugetSound	Fall_Aggregate	PugetSound
Skokomish_GAdamsH	SkokomishFa	Skokomish	HoodCanal	HoodCanal	Fall_Aggregate	PugetSound
SFSkokomishFa	SkokomishFa	Skokomish	HoodCanal	HoodCanal	Fall_Aggregate	PugetSound
NFSkokomishFa	SkokomishFa	Skokomish	HoodCanal	HoodCanal	Fall_Aggregate	PugetSound
HammaHammaFa	HammaHammaFa	HammaHamma	HoodCanal	HoodCanal	Fall_Aggregate	PugetSound
Dungeness	Dungeness	Dungeness	Dungeness	SJD	SJD	PugetSound
Elwha	Elwha	Elwha	Elwha	SJD	SJD	PugetSound

Table 5.1.2. Juvenile Chinook samples for GSI analysis by habitat, region, and year.

	2014		2015	
	Nearshore	Offshore	Nearshore	Offshore
SJI	91	16	67	8
Nooksack	148	65	115	85
Skagit	234	143	118	110

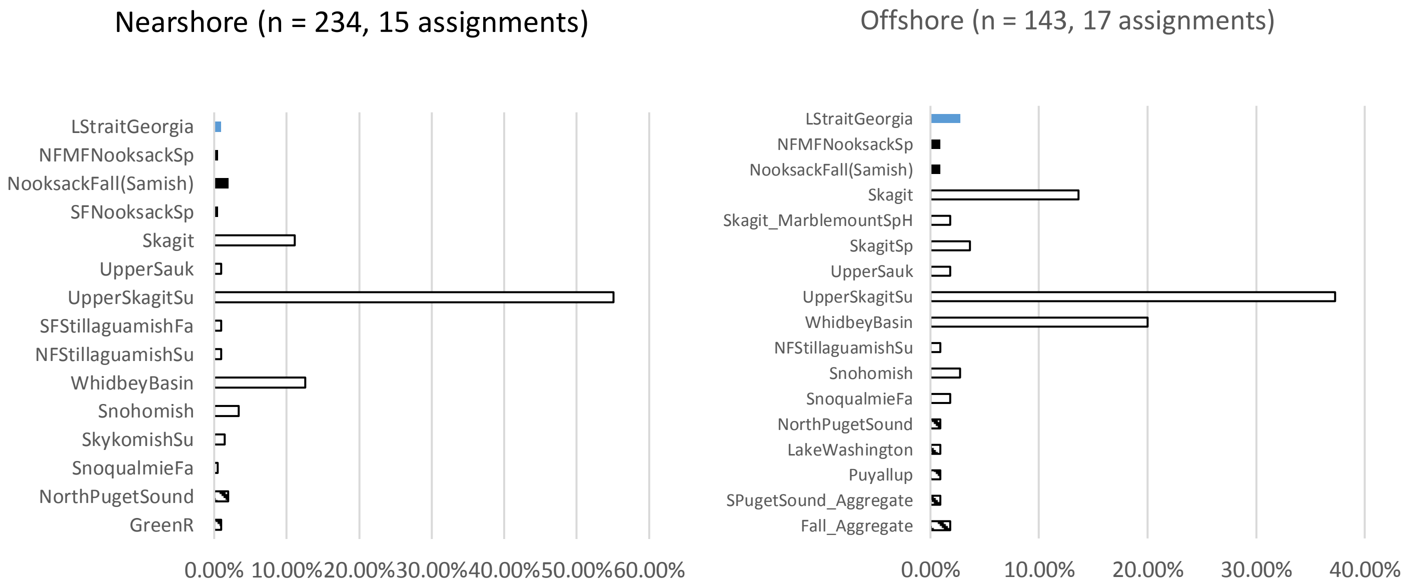
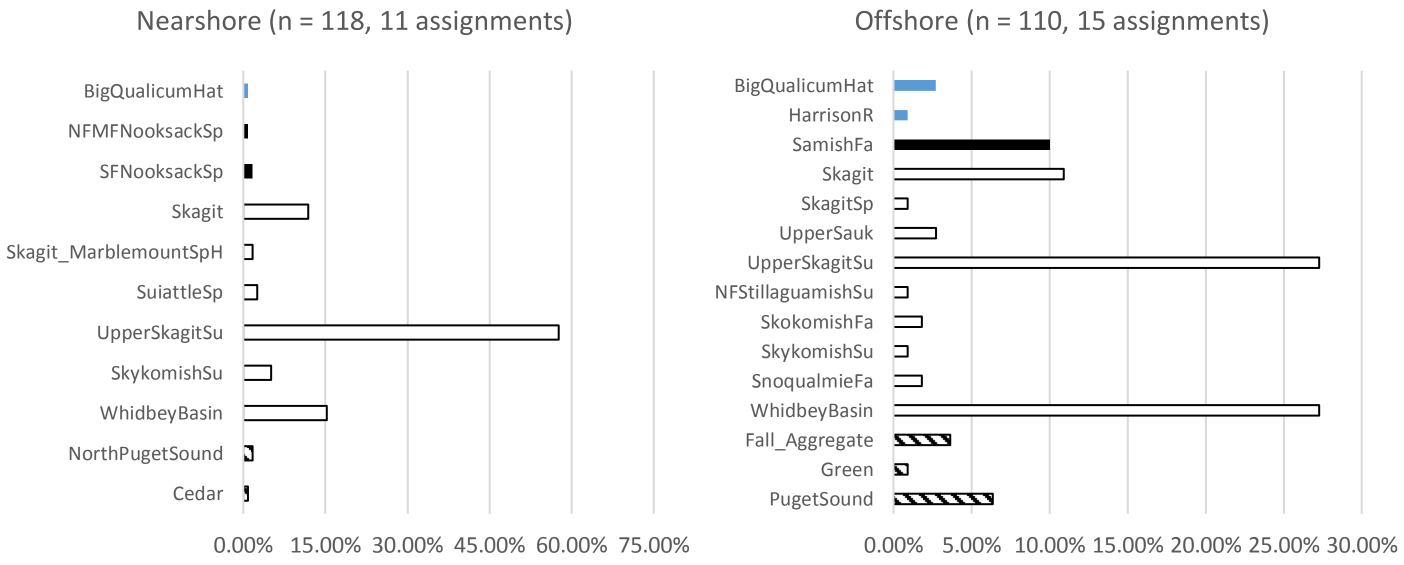
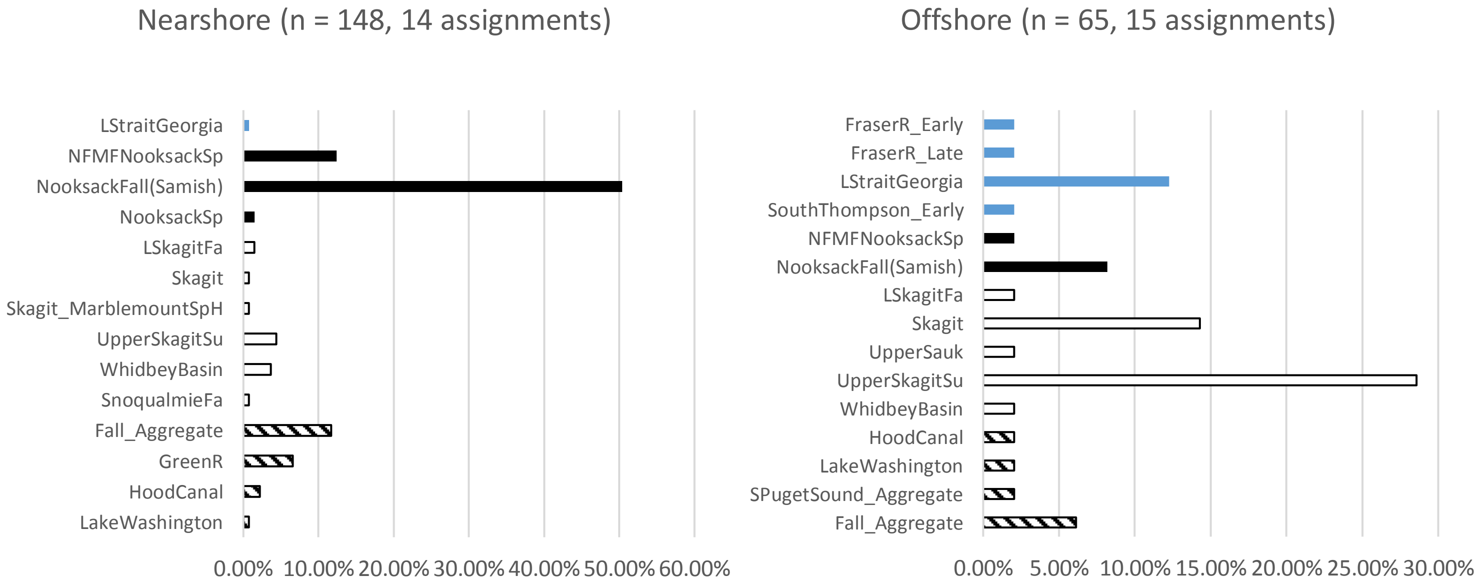


Figure 5.1.1. Percentage of samples assigned to specific populations or aggregations captured in nearshore and offshore habitats of the Skagit region in 2014. Populations grouped by general geographic regions; BC (blue filled), Nooksack/Bellingham Bay (black filled), Skagit/Whidbey basin (unfilled), Puget Sound/Hood Canal (pattern fill).


Nearshore (n = 118, 11 assignments)

Offshore (n = 110, 15 assignments)

Figure 5.1.2. Percentage of samples assigned to specific populations or aggregations captured in nearshore and offshore habitats of the Skagit region in 2015. Populations grouped by general geographic regions; BC (blue filled), Nooksack/Bellingham Bay (black filled), Skagit/Whidbey basin (unfilled), Puget Sound/Hood Canal (pattern fill).


Nearshore (n = 148, 14 assignments)

Offshore (n = 65, 15 assignments)

Figure 5.1.3. Percentage of samples assigned to specific populations or aggregations captured in nearshore and offshore habitats of the Nooksack region in 2014. Populations grouped by general geographic regions; BC (blue filled), Nooksack/Bellingham Bay (black filled), Skagit/Whidbey basin (unfilled), Puget Sound/Hood Canal (pattern fill).

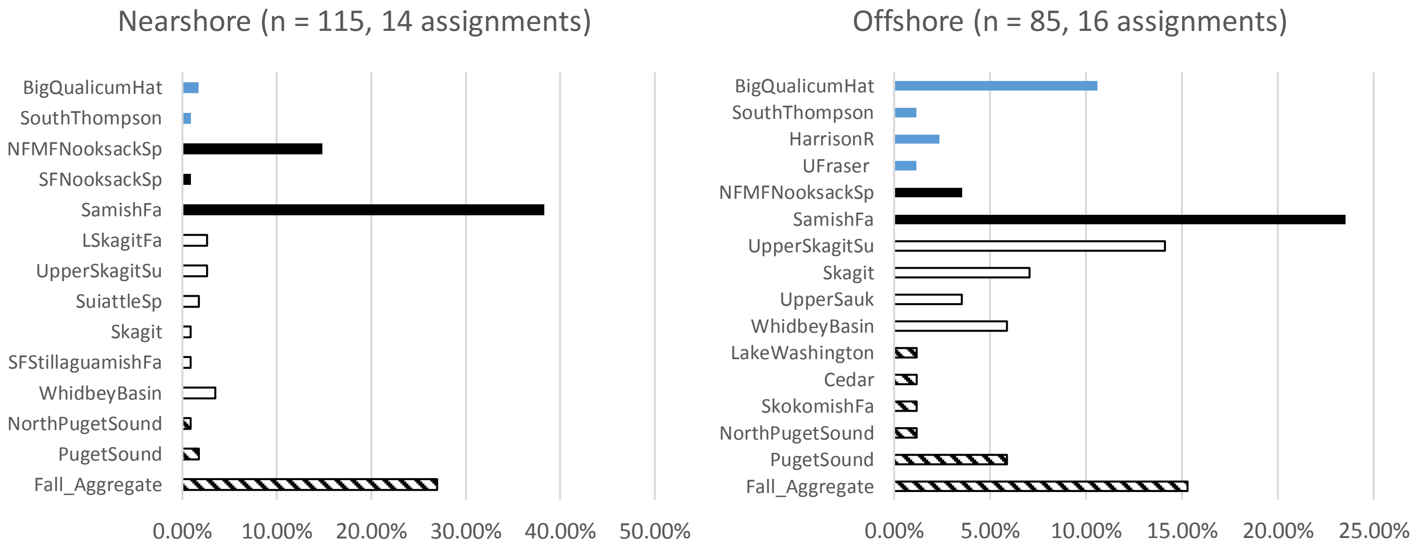


Figure 5.1.4. Percentage of samples assigned to specific populations or aggregations captured in nearshore and offshore habitats of the Nooksack region in 2015. Populations grouped by general geographic regions; BC (blue filled), Nooksack/Bellingham Bay (black filled), Skagit/Whidbey basin (unfilled), Puget Sound/Hood Canal (pattern fill).

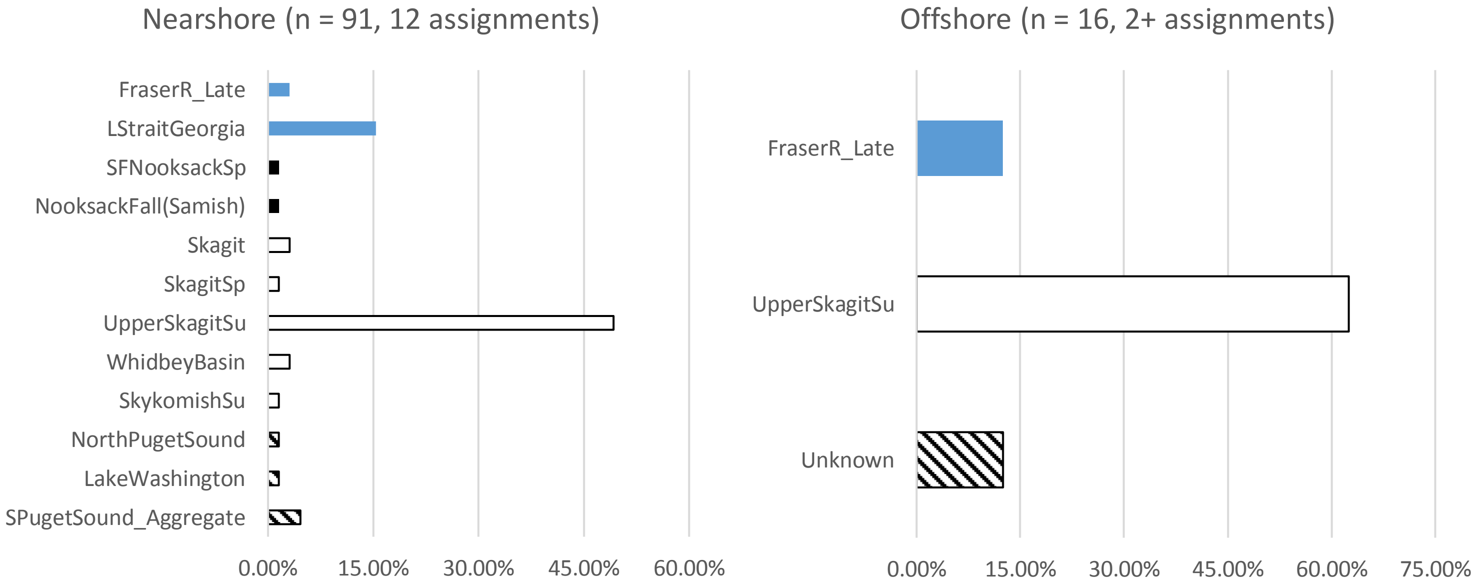


Figure 5.1.5. Percentage of samples assigned to specific populations or aggregations captured in nearshore and offshore habitats of the San Juan Islands region in 2014. Populations grouped by general geographic regions; BC (blue filled), Nooksack/Bellingham Bay (black filled), Skagit/Whidbey basin (unfilled), Puget Sound/Hood Canal (pattern fill).

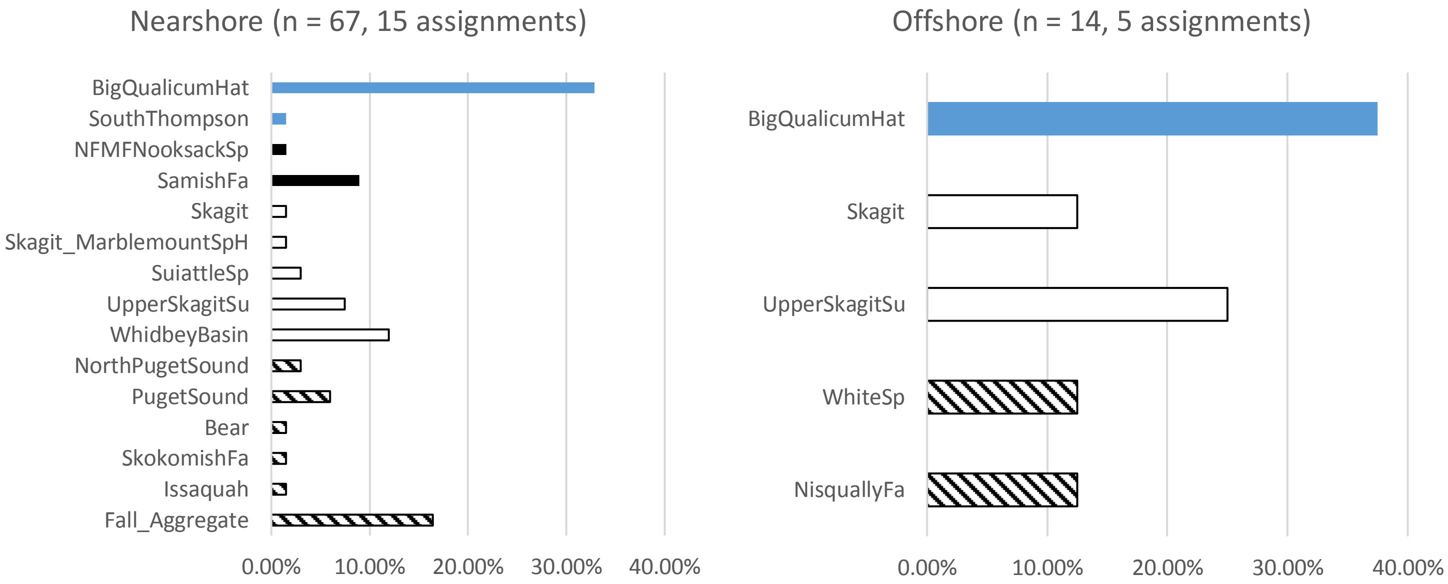


Figure 5.1.6. Percentage of samples from unmarked individuals assigned to specific populations or aggregations captured in nearshore and offshore habitats of the San Juan Islands region in 2015. Populations grouped by general geographic regions; BC (blue filled), Nooksack/Bellingham Bay (black filled), Skagit/Whidbey basin (unfilled), Puget Sound/Hood Canal (pattern fill).

Individuals were assigned to populations/aggregations from the Lower Strait of Georgia to central Puget Sound. The population/aggregation that had the highest contribution outside of the Nooksack River was the Fall Aggregate (12-27%) which largely represents, or includes, populations from central Puget Sound and Hood Canal as well as Nooksack Fall (Samish).

Assignments for Nooksack offshore samples were more evenly represented among populations/aggregations within and outside the local area (Figure 5.1.3, 5.1.4). The total number of assignments in each year was slightly higher for the offshore with 15 assignments in 2014 and 16 in 2015. Offshore sample assignments indicated a considerable increase in fish from both BC and the Skagit region compared to the nearshore habitat. Nearly a third of all offshore samples from 2014 (29.7%) assigned to the Upper Skagit Summer population. In addition, 11% of all offshore samples from 2015 assigned to the Big Qualicum, a hatchery population on the east side of Vancouver Island.

Population assignments for samples taken from the nearshore and offshore habitats in the San Juan Islands were variable from year to year and dominated by Upper Skagit Summer in 2014 and Big Qualicum in 2015 (Figure 5.1.5, 5.1.6). In general, the distribution of samples among populations/aggregations was similar for nearshore and offshore within a given year although the offshore habitat was represented by fewer samples and far fewer assignments. Approximately 50% of the samples collected from the nearshore in 2014 were assigned to the Upper Skagit Summer population. Interestingly only 3% of the samples were assigned to Nooksack populations while roughly one fifth (~19%) of nearshore samples were assigned to Lower Strait of Georgia/Fraser River populations. The remainder of the samples assigned to other Skagit or Whidbey basin populations/aggregations or central/south Puget Sound aggregations.

Nearshore samples in 2015 were more evenly distributed among the population assignments with the exception of the Big Qualicum group which represented a third (33%) of all samples.

Of the remaining 14 population/aggregation assignments, 7 were represented by a single fish. The Fall Aggregate group comprised 16.5%, while Upper Skagit Summer, Nooksack Fall (Samish), and Whidbey basin aggregate combined to account for the remaining ~45% of samples.

Within each year, nearshore assignments by month were relatively consistent though some patterns were evident (Figures 5.1.7, 5.1.8). Upper Skagit Summer were present in all months in the nearshore habitats in both years while Lower Strait of Georgia and Big Qualicum fish were present in all months in 2014 and 2015, respectively. Fish assigned to populations from the Nooksack were present only in July during 2014 and in relatively low proportions. The same populations were present in higher proportions in June and July in 2015. Central and south Puget Sound/Hood Canal populations/aggregations were present in all months in both years with the exception of August 2014 though the relative proportions of fish from these groups appeared to be higher in 2015.

The spatial distribution of samples from the San Juan Islands nearshore was difficult to assess given the lack of sample distribution among sites in both years (Appenidx). However, where comparisons were possible between sites (White Cliff and Runstad in 2014) the assignment distributions were similar suggesting population distribution within the SE San Juan Islands is consistent from site to site (Figure 5.1.9).

Assignments for samples from the offshore habitat in the San Juan Islands were much more limited due to significantly lower samples sizes in both years (Table 5.1.2). However, the percentages assigned to specific populations/aggregations showed the same pattern observed for samples from the nearshore (Figures 5.1.7, 5.1.8). Again, Upper Skagit Summer fish were present in both years as well as a large influx of Big Qualicum fish in 2015. A small percentage of fish (12.5%, n=2) were assigned to Unknown in 2014. These represent either populations not included in the beeline or may not be Chinook salmon.

Temporal distribution of sample assignments for fish captured in the offshore of the San Juan Islands was difficult to assess in 2014 given the majority of samples (87.5%, n= 14) were collected in June alone. However, the distribution was relatively even in 2015 and showed a strong presence of Big Qualicum fish early followed by the presence of fish from the Skagit River system. In each of June and August there were fish present form Central/South Puget Sound populations. Spatial distribution for sample assignments for offshore fish in the San Juan Islands was not possible due to extremely low sample sizes at each site.

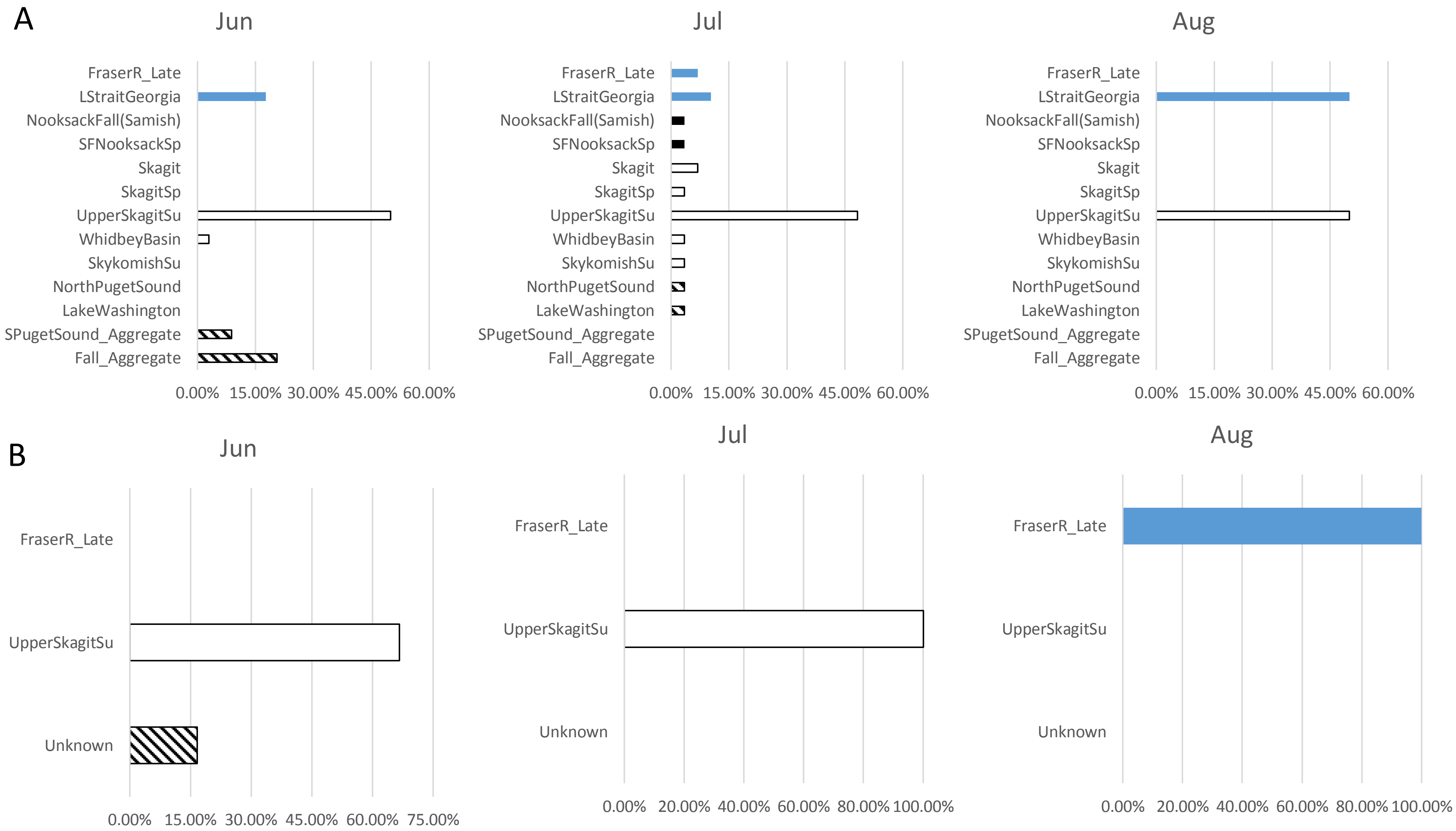


Figure 5.1.7. Sample assignments by month for 2014 San Juan Islands nearshore (A) and offshore (B) habitats. Populations grouped by general geographic regions; BC (blue filled), Nooksack/Bellingham Bay (black filled), Skagit/Whidbey basin (unfilled), Puget Sound/Hood Canal (pattern fill).

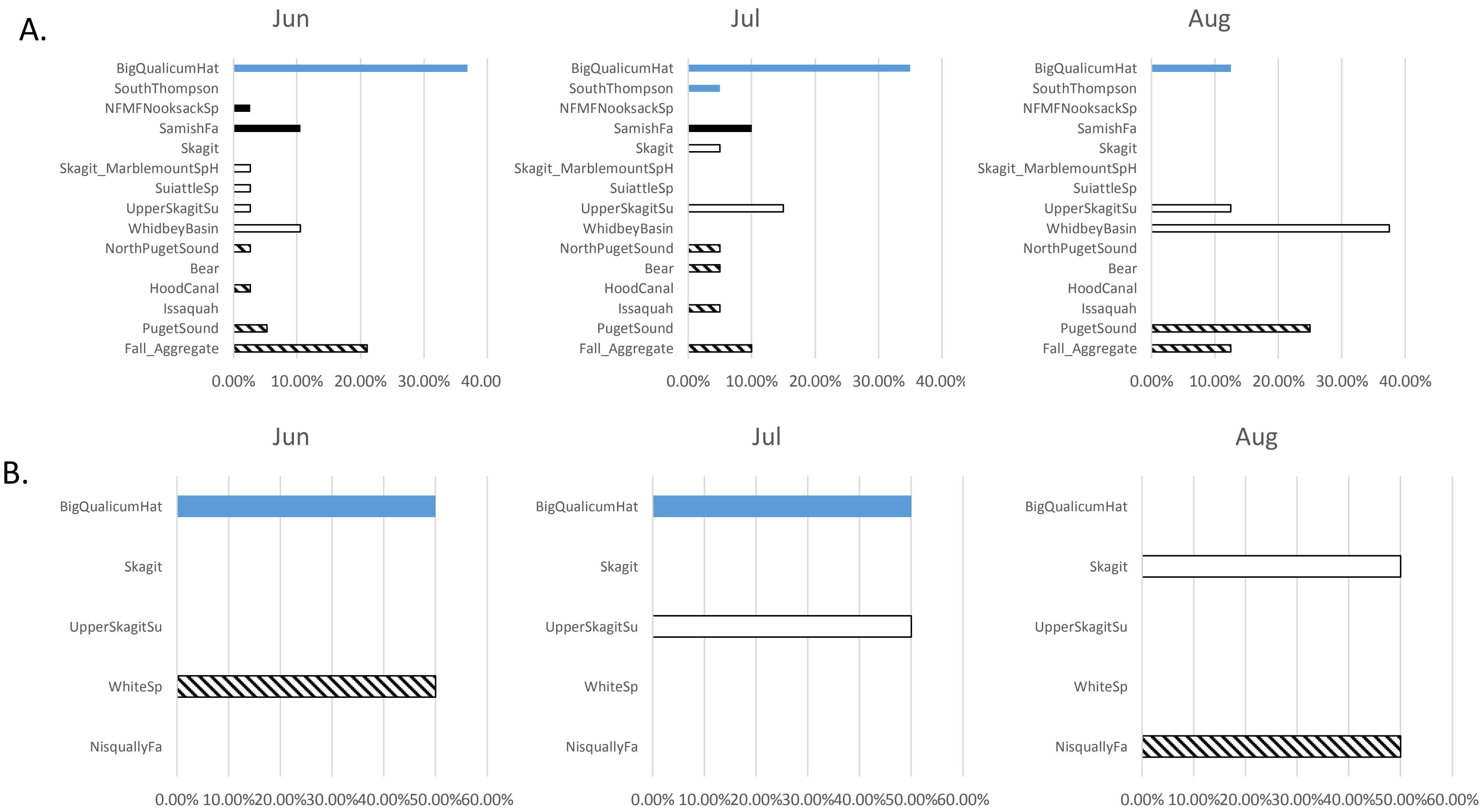


Figure 5.1.8. Sample assignments by month for 2015 San Juan Islands nearshore (A) and offshore (B) habitats. Populations grouped by general geographic regions; BC (blue filled), Nooksack/Bellingham Bay (black filled), Skagit/Whidbey basin (unfilled), Puget Sound/Hood Canal (pattern fill).

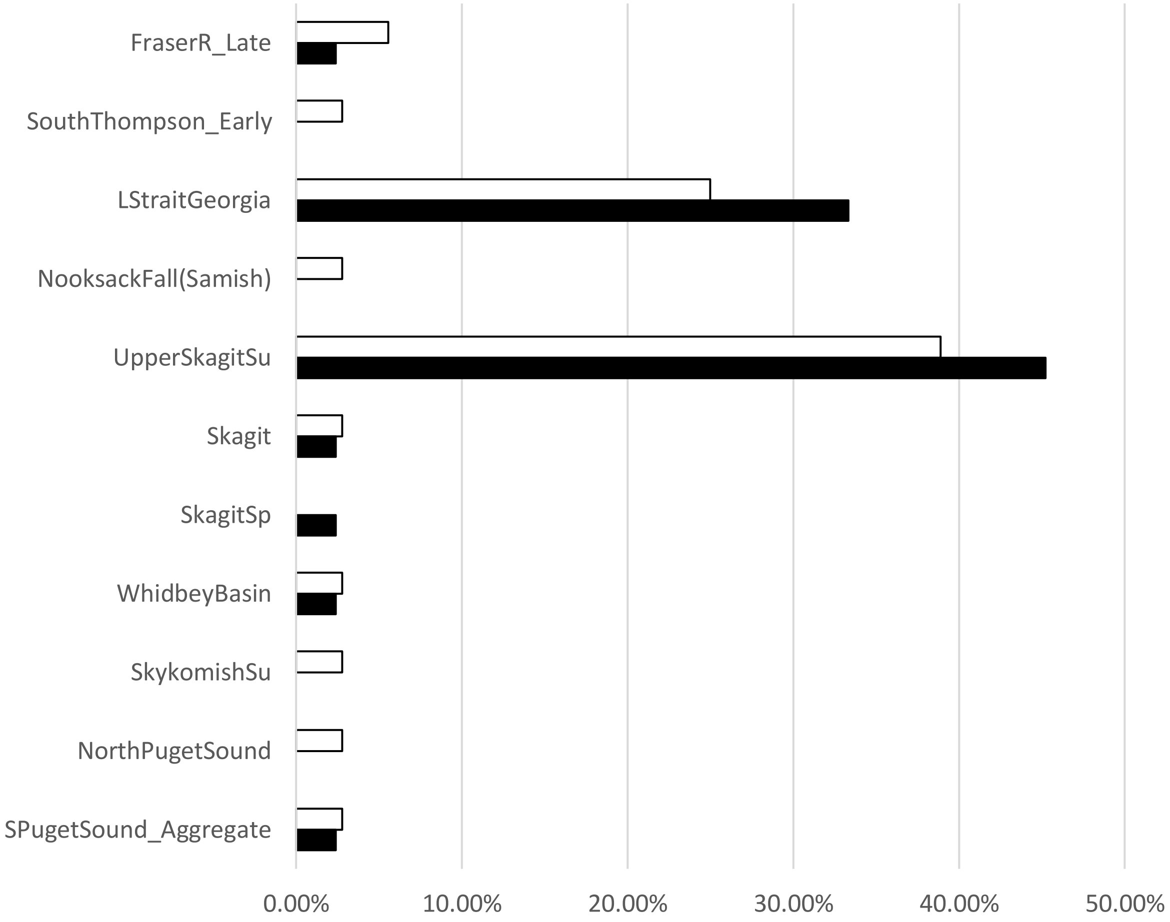


Figure 5.1.9. Population/aggregation assignment percentages for nearshore juvenile Chinook samples from Runstad (unfilled) and White Cliff (filled) sites in 2014.

5.1.3 Conclusions

- The distribution of populations was different among regions and between years. In general, the nearshore habitats had more consistent population distribution within each region but among years. The majority of the nearshore samples collected in each of the Skagit and Nooksack regions primarily represented local population groups.
- Offshore samples generally represented more populations than were found in the nearshore in the Skagit and Nooksack but not in the San Juan Islands.
- The main difference between years was the large increases in Canadian populations (i.e. Big Qualicum) present in 2015, primarily in the Nooksack and San Juan Islands.
- Populations from the Skagit River, and primarily Upper Skagit summer fish, were the most predominant across all regions, habitats and between years.

- Upper Skagit summer fish were the most predominant population found at sites, nearshore and offshore, sampled within the San Juan Islands during 2014. The proportion of fish representing Upper Skagit summer population decreased in the nearshore during 2015 coupled with a sizable increase in Big Qualicum (BC) fish in both nearshore and offshore sites during the same year.
- The distribution of populations differed by month and year within the nearshore habitat of the San Juan Islands. In 2014, the proportion of Canadian populations generally increased through time, Nooksack populations were primarily present during July and the Skagit populations remained relatively consistent and predominant throughout all months. In 2015, Canadian populations were present earlier and in higher proportions as were populations from the Nooksack River.
- Although difficult to assess the fine scale spatial distribution of populations in the San Juan Islands nearshore due to sample sizes, where possible we observed similar distribution between the sites with the highest number of samples suggesting potentially consistent distribution among sites in the southeast San Juan Islands.

5.2 Identifying periods of critical growth through size-selective mortality

In order to understand the range of growth opportunities juvenile Chinook salmon encounter during their first marine summer, it is imperative to understand the scale and intensity of stage-specific growth and size-selective mortality occurring before mid-summer in multiple habitats throughout Puget Sound. By sampling frequently and across habitats, it may be possible to identify when and where growth opportunities and size-selective mortality occur within Puget Sound. 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. Understanding how size-selective mortality operates in Puget Sound can potentially guide future monitoring, be used to forecast marine survival, and steer restoration or conservation efforts to particular habitats that augment early marine growth, and thus survival, of Chinook salmon.

The objectives of this segment were (1) to document the distribution of sub-yearling Chinook Salmon smolts from particular stocks across habitats and time throughout Puget Sound; (2) to determine whether scale morphometrics could be used to compare back-calculated fork length at age within or between stocks on a two-week temporal scale; (3) to examine the extent to which sub-yearling Chinook Salmon experience size-selective mortality during their outmigration and early marine rearing in Puget Sound; and (4) to compare these trends between years. We captured sub-yearling smolts in four river systems draining into Puget Sound using smolt traps, beach seines, and a purse seine in 2014 and 2015. To determine how scale morphometrics could be used to assess size-selective mortality, we tested the relationships between scale radius and fork length at capture and between circulus count and time. Size-selective mortality was evaluated across habitats and "life stages" (defined as habitat and sampling period combinations) by comparing the average growth history (back-calculated fork lengths) of juveniles sampled in one life stage with that of individuals sampled in subsequent life stages, which were assumed to be survivors of the previous life stage.

5.2.1 Methods

Sample collection: Samples were collected as described in the introduction to this report. For this section, we also collected sub-yearling Chinook salmon from hatcheries in each of the four watersheds in the week before release to record pre-release fork-length frequency distributions, mean fork length and weight, and growth histories (Table 5.2.1).

Stock identification and distribution: 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-origin or natural-origin stock. A hatchery-origin stock was defined as a group of fish originating from the same broodstock released from the same hatchery at the same time, as determined by CWTs or thermal otolith marks. Natural-origin fish were selected based on assignments described in previous section.

We focused this study on stocks of sub-yearling Chinook salmon that were caught and sampled in habitats associated with their natal watershed to exclude those that may have experienced different growth environments. We only included stocks from our four focal watersheds from which at least 10 fish had been collected in each of two or more life stages. For each stock that fit these criteria we plotted total catch count by date and habitat to examine stock-specific distribution within and between years.

Scale morphometrics: We used scale morphometrics to test for 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 whether scale radius was proportional to fish length by fitting a geometric mean regression of fish fork length to scale radius (Ricker 1992) using scales from all fish from our sampled stocks, separately for each year, and referred back to this regression to ensure that it was consistent across scale samples from each stock. In this and all subsequent analyses, we excluded scale samples from fish within our stocks when (a) the scale radius : fork length regression indicated that the scale radius was much too small to be from the preferred area for a fish of that length, or (b) the scale had at least 5 more circuli than the fish with the next highest circulus count within a life stage.

To test whether circulus count was a reasonable proxy for age (i.e. time) on a two-week temporal scale during the first marine growing season, we fit a linear regression of time (day of year) to circulus count separately for each stock to account for differences in age among stocks.

Table 5.2.2. Hatchery rearing and release information for hatchery-origin Chinook Salmon stocks sampled in Puget Sound in 2014 and 2015. CV is coefficient of variation. Weight, length, and length CV were calculated from hatchery samples received in the lab unless otherwise noted. Comparisons of lengths and weights measured from hatchery samples in the lab to those reported by RMIS indicate that in most cases our samples are smaller than average. Integrated hatcheries manage hatchery and natural fish as a single population, generally using both hatchery- and natural-origin fish as broodstock; segregated hatcheries use only hatchery-origin fish as broodstock.

Stock name	Hatchery name	Release date(s)	Mean weight (g)	Mean length (mm)	Length CV (%)	Brood-stock run time	Hatchery type
			2014				
Nooksack Kendall[d] Creek	Kendall Creek	4/15/2014-5/16/2014	5.03 [a]	78 [a]	Not Available	Spring	Integrated
Nooksack Skookum Creek[d]	Skookum Creek	6/2/2014-6/5/2014	5.67 [a]	Not Available	Not Available	Spring	Captive brood[c]
Skagit Spring	Marblemount	6/12/14	6.75	82.69	8.38	Spring	Segregated
Skagit Summer	Marblemount	6/25/14	4.08	70.39	7.28	Summer	Integrated[b]
Snohomish Tulalip	Bernie Kai-Kai Gobin	5/21/2014-5/29/2014	3.87	68.42	12.59	Summer	Integrated
Snohomish Wallace	Wallace	6/1/2014-6/7/2014	5.08	74.16	10.55	Summer	Integrated
Nisqually Clear Creek	Clear Creek	5/1/2014-6/1/2014	7.7	87.18	9.60	Fall	Segregated
			2015				
Nooksack Kendall Creek	Kendall Creek	4/15/2015-5/13/2015	5.96 [a]	77.74	8.02	Spring	Integrated
Nooksack Skookum Creek[d]	Skookum Creek	5/20/2015-6/4/2015	5.89[a]	Not Available	Not Available	Spring	Captive brood[c]
Skagit Spring	Marblemount	6/1/15	6.26	82.67	4.25	Spring	Segregated
Skagit Summer	Marblemount	6/11/15	3.99	77.04	7.73	Summer	Integrated[b]
Snohomish Tulalip	Bernie Kai-Kai Gobin	5/1/2015-5/12/2015	5.74	78.75	7.06	Summer	Integrated
Snohomish Wallace	Wallace	6/1/2015-7/6/2015	5.51	79.3	6.85	Summer	Integrated
Nisqually Clear Creek	Clear Creek	5/4/2015-6/20/2015	9.19	93.37	9.99	Fall	Segregated

[a] value reported by RMIS, not calculated from samples received from hatchery.

[b] same population as Upper Skagit Summer natural-origin stock, but spawned, reared, and released from hatchery.

[c] captive broodstock from fish captured as juveniles in the SF Nooksack River and genetically identified as the SF Nooksack spring Chinook population. Captive fish held at both Kendall Hatchery and NOAA Fisheries facility in Manchester, WA. All fish spawned at Kendall, and reared and released from Skookum.

[d] samples were not available from these hatcheries.

Growth analysis & identifying size-selective mortality: To test whether mortality was size-selective, we looked for changes in the frequency distribution and average size at age of each stock. To evaluate size-selective mortality we used only sub-yearling Chinook Salmon 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 looked for evidence of size-selective mortality in stocks from our focal watersheds from which at least 10 fish had been collected in each of two or more life stages. We analyzed scales from all fish in each stock that fit these criteria. We then compared fish caught within their natal watershed to those caught in the offshore or nearshore of the San Juan Islands, to better understand how that region may function as an alternative rearing habitat for Puget Sound Chinook.

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 largest scale that was not damaged or regenerated to be imaged and measured. The acetate impressions were imaged using Image-Pro 9.0 software with a digital camera (Lumenera Infinity1-3c camera with Diagnostic Instruments 1.0x HR100-CMT lens attachment) attached to a Leica MZ6 microscope fitted with 20x oculars and a 2.0x objective for a total magnification range of 64x to 160x. Scale measurements were recorded from scale images with Image-Pro or ImageJ software. For each scale we recorded total circulus count, total scale radius along the anterior-posterior axis, and scale radius at each circulus. For each fish, scale radii at each circulus were used to back-calculate fork length using the Fraser Lee method (Ricker 1992). Back-calculated fork lengths were then used to create individual growth histories. Individual growth histories of fish from each habitat and life stage were plotted on a single set of axes to visually ensure that the distribution of growth histories was approximately normal. Individual growth histories were then averaged to assess mean size at age for each stock as sampled in different habitats and life stages.

We evaluated average growth histories (back-calculated fork length at each circulus) at two different temporal/spatial scales for each stock. To examine larger scale, habitat-specific size-selective mortality, growth histories for fish from each stock caught within each habitat were averaged across all sampling periods in which three or more usable scale samples were available. To evaluate finer scale, life stage-specific size-selective mortality within and across habitats, we averaged growth histories for fish caught within the same life stage for all life stages with three or more usable scale samples. We excluded scale radius at circulus averages that came from fewer than three measurements. This finer-scale life stage analysis was only included for 2015 samples as scale sampling in 2014 wasn't consistent enough to detect fine scale differences in back-calculated fork length-at-circulus.

For both habitat- and life stage-specific analyses, we looked for changes in average size at age (average back-calculated fork length at circulus) between subsequent habitats or life stages within each stock by plotting average growth histories for sequential life stages. If size-selective mortality occurred between two life stages, the later life stage should show *larger* average size at age (i.e., scale radius at circulus) at circuli formed during previous life stages, because average size at age would increase as smaller fish dropped out of the stock (Figure 5.2.1 A, C).

No change in stage-specific growth histories among life stages or habitats would suggest that size-selective mortality did not occur between those life stages or habitats (Figure 5.2.1 B).

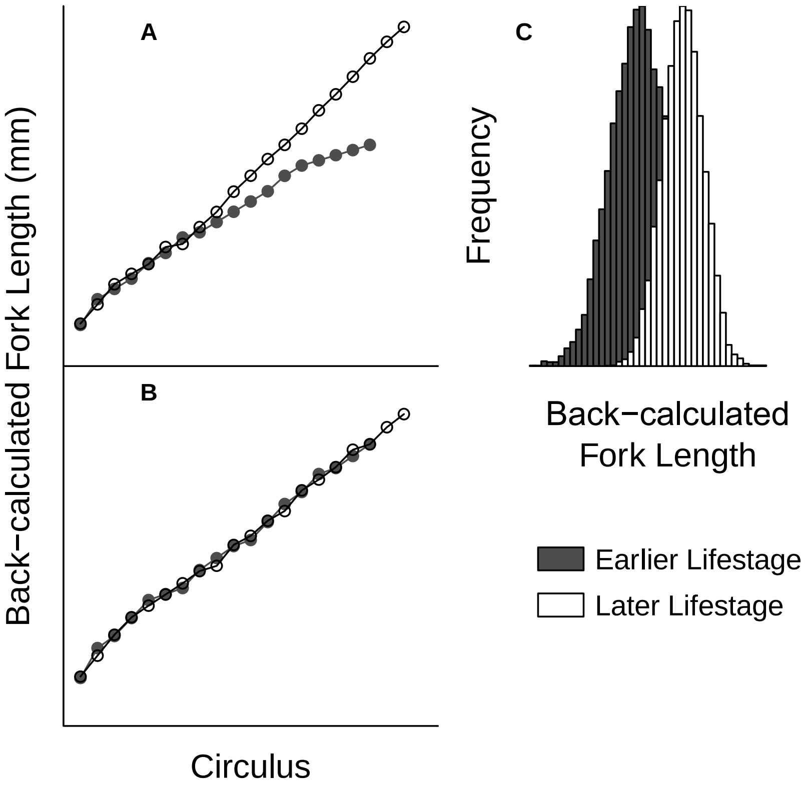


Figure 5.2.1. Theoretical comparisons of average growth histories indicating **(A)** size-selective mortality or **(B)** no size-selective mortality. Histograms **(C)** show the change in the distribution of size-at-age if size-selective mortality occurs.

5.2.2 Results

Stock identification & distribution

From the 10,700 sub-yearling Chinook salmon caught and sampled across all habitats and both years (7,020 individuals in 2014 and 3,680 in 2015), we identified seven hatchery-origin and two natural-origin stocks of sub-yearling Chinook salmon from which at least 10 fish had been collected in each of two or more life stages within their natal watershed throughout the summer. Catches from these nine stocks totaled 1323 fish in 2014 and 1233 fish in 2015 (Figure 5.2.2, Table 5.2.2). Of these, there were 1099 individuals in 2014 and 960 individuals in 2015 with usable scale samples (Table 5.2.2). There were two hatchery-origin stocks from each of the Nooksack (Kendall Creek and Skookum Creek hatcheries), Skagit (“spring” and “summer” populations 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 5.2.1). These hatchery-origin stocks represent both segregated and integrated programs (Table 5.2.1). Comparisons of lengths and weights measured from hatchery samples in the lab to those reported by the Regional Mark Information System (RMIS; http://www.rmpc.org/) indicate that in most cases our hatchery samples are smaller than average, as our samples were collected slightly prior to release. The natural-origin stocks originated from the Nooksack Fall and the Upper Skagit Summer populations. The Upper Skagit Summer stock is the source population for the Marblemount Summer stock, allowing investigation of hatchery effects while controlling for population.

Table 5.2.1. Number of scales used in habitat-specific average growth histories by stock. Blank cells indicate zeros. Sample sizes include only scales from life stages in which 3 or more useable scale samples were taken. "SJI Nearshore" indicates stock fish caught outside of their natal watershed in the San Juan Islands nearshore.

Stock	Hatchery	Smolt Trap	Estuary	Near-shore	Off-shore	SJI Nearshore	Total
			2014				
Nooksack Kendall Creek			20	6	21		47
Nooksack Skookum Creek			36	14	35	4	89
Nooksack Fall (N)				38			38
Skagit Spring	59	55	14	17	18		163
Skagit Summer	61			26			87
Upper Skagit Summer (N)				97	45	35	177
Snohomish Tulalip	60		22	58	28		168
Snohomish Wallace	61		51	5	23		140
Nisqually Clear Creek	93		20	31	38		182
Total							**1091**
			2015				
Nooksack Kendall Creek	33		3	6	55		97
Nooksack Skookum Creek			10		80		90
Nooksack Fall (N)				15	19		34
Skagit Spring	29	21	10	42	66		168
Skagit Summer	30		6	39	7		82
Upper Skagit Summer (N)				59	40		99
Snohomish Tulalip	30		27	3	69		129
Snohomish Wallace	30		7	8	90		135
Nisqually Clear Creek	30		7	26	37		100
Total							**934**

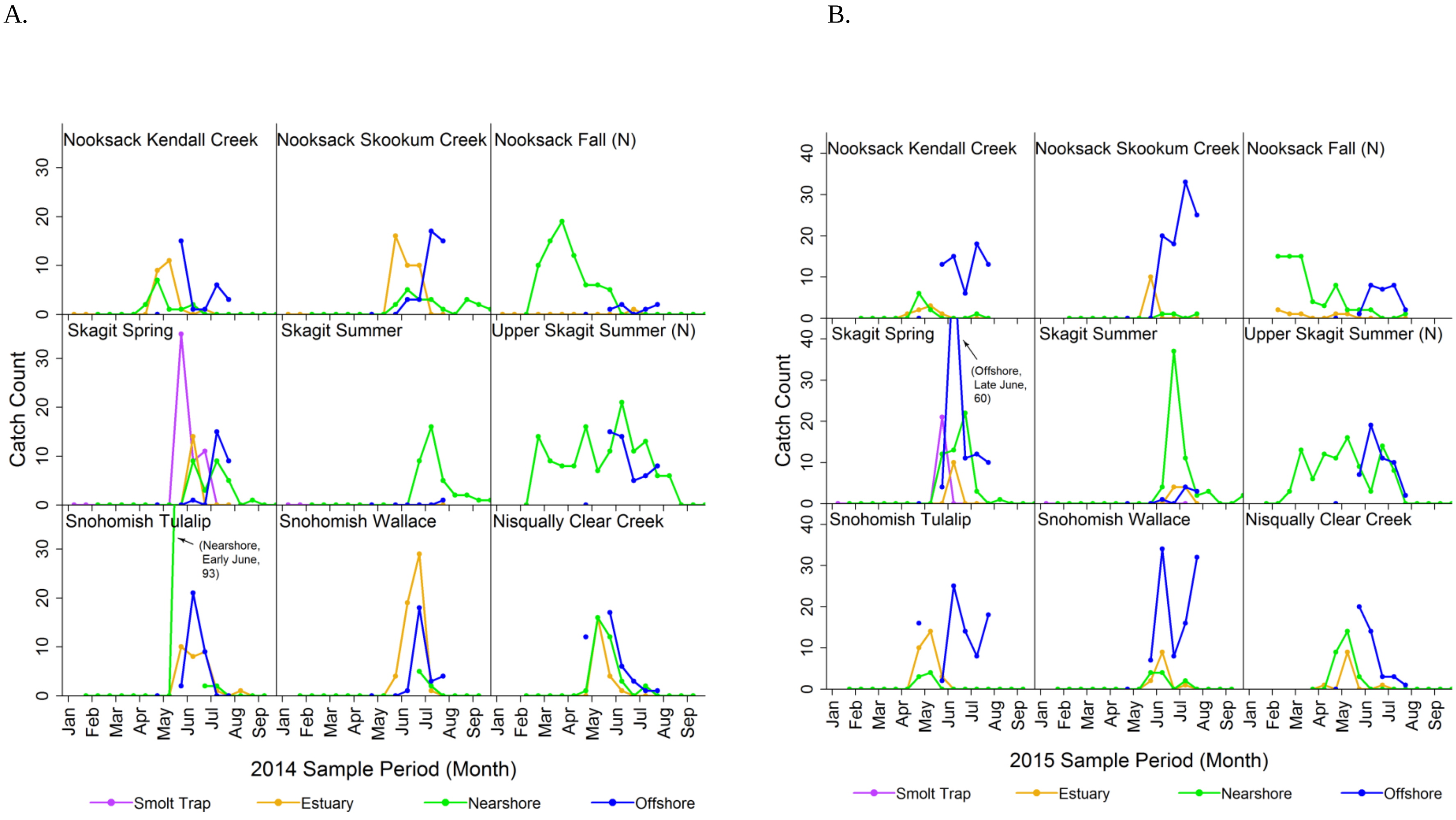


Figure 5.2.2. Catch of each stock by life stage (habitat and sample period combination) in 2014 **(A)** and 2015 **(B)**. Points are only plotted for periods in which sampling occurred in each habitat. Natural-origin stocks are indicated by "(N)" following the stock name. Detailed catch numbers for each life stage are available in Appendix Table A1.

For hatchery stocks in both years, peak catch counts within specific habitats ranged from early May to late July, and generally followed the expected sequence of smolt trap, estuary, nearshore, and offshore (**Figure 5.2.2**). Peak catches in the estuary and nearshore habitats preceded peak offshore catches for all but the Snohomish Wallace stock, in which peak catches in the estuary and nearshore coincided with those offshore in both years. These trends suggested that fish moved sequentially from estuary and nearshore habitats to offshore habitats, though potentially at different rates depending on stock. Nearshore catches of fish from the natural-origin stocks where higher over a longer period in both years, suggesting a more protracted outmigration and use of the nearshore compared to hatchery stocks. In 2015, peak catches in the offshore habitats associated with the Snohomish, Skagit, and Nooksack watersheds were earlier than in 2014, which suggests that the majority of fish moved through the estuary and nearshore faster in 2015 than in 2014. However, hatchery releases in these stocks were also slightly later in 2015 than in 2014 (Table 1), so this result should be interpreted conservatively.

Scale morphometrics

Scale radius (SR) was linearly related to fork length (FL) for both years, verifying that scale radius could be used as a proxy for fish length:

2014: $FL = 184.771 * SR + 17.220$ ($N = 1099$, $r^2 = 0.784$)

2015: $FL = 173.481 * SR + 13.722$ ($N = 960$, $r^2 = 0.942$)

Circulus count explained the majority (53-93%) of variation in sample date for all stocks in both years except the Snohomish Tulalip stock in 2014 (**Figure 5.2.3; Table 5.2.3**), showing that circulus count could be used as a proxy for fish age within most stocks. The Tulalip stock in 2014 also deviated from the others in that estuary samples tended to have fewer circuli than nearshore samples at the same date. Excluding the 2014 Snohomish Tulalip stock, circulus deposition rates ranged from 4.4 to 8.3 days in 2014 and 4.6 to 8.0 in 2015. Circulus deposition rates were not statistically different between years for hatchery-origin ($t = 1.19$, df = 11, $P = 0.26$) or natural-origin stocks ($t = 0.84$, df = 2, $P = 0.49$). Across years, hatchery-origin stocks exhibited significantly faster deposition rates than natural-origin stocks (mean ± SD deposition rate for hatchery-origin: 5.61 ± 0.65 days per circulus, natural-origin: 7.71 ± 0.58 days per circulus; $t = 5.79$, df = 15, $P < 0.001$). The scale sampling protocol was refined and more consistent in 2015 compared to 2014, resulting in less scale sampling error, a stronger FL:SR regression and stronger regressions for circulus deposition rate (**Table 5.2.3**). This improvement in scale sampling allowed for comparison of growth histories at the finer life stage level for 2015.

Table 5.2.3. Circulus deposition rates and r^2 values from linear regressions of time and circulus count by year.

Stock	Circulus Deposition Rate (days per circulus)	R^2
2014		
Nooksack Kendall Creek	4.45	0.55
Nooksack Skookum Creek	5.97	0.89
Nooksack Fall (N)	8.31	0.81
Skagit Spring	5.57	0.72
Skagit Summer	6.57	0.89
Skagit Upper Summer (N)	7.62	0.55
Snohomish Tulalip	2.76	0.28
Snohomish Wallace	5.87	0.57
Nisqually Clear Creek	6.57	0.53
2015		
Nooksack Kendall Creek	6.12	0.90
Nooksack Skookum Creek	4.55	0.85
Nooksack Fall (N)	6.95	0.93
Skagit Spring	5.57	0.83
Skagit Summer	5.49	0.82
Skagit Upper Summer (N)	7.95	0.70
Snohomish Tulalip	5.63	0.91
Snohomish Wallace	5.14	0.89
Nisqually Clear Creek	5.38	0.82

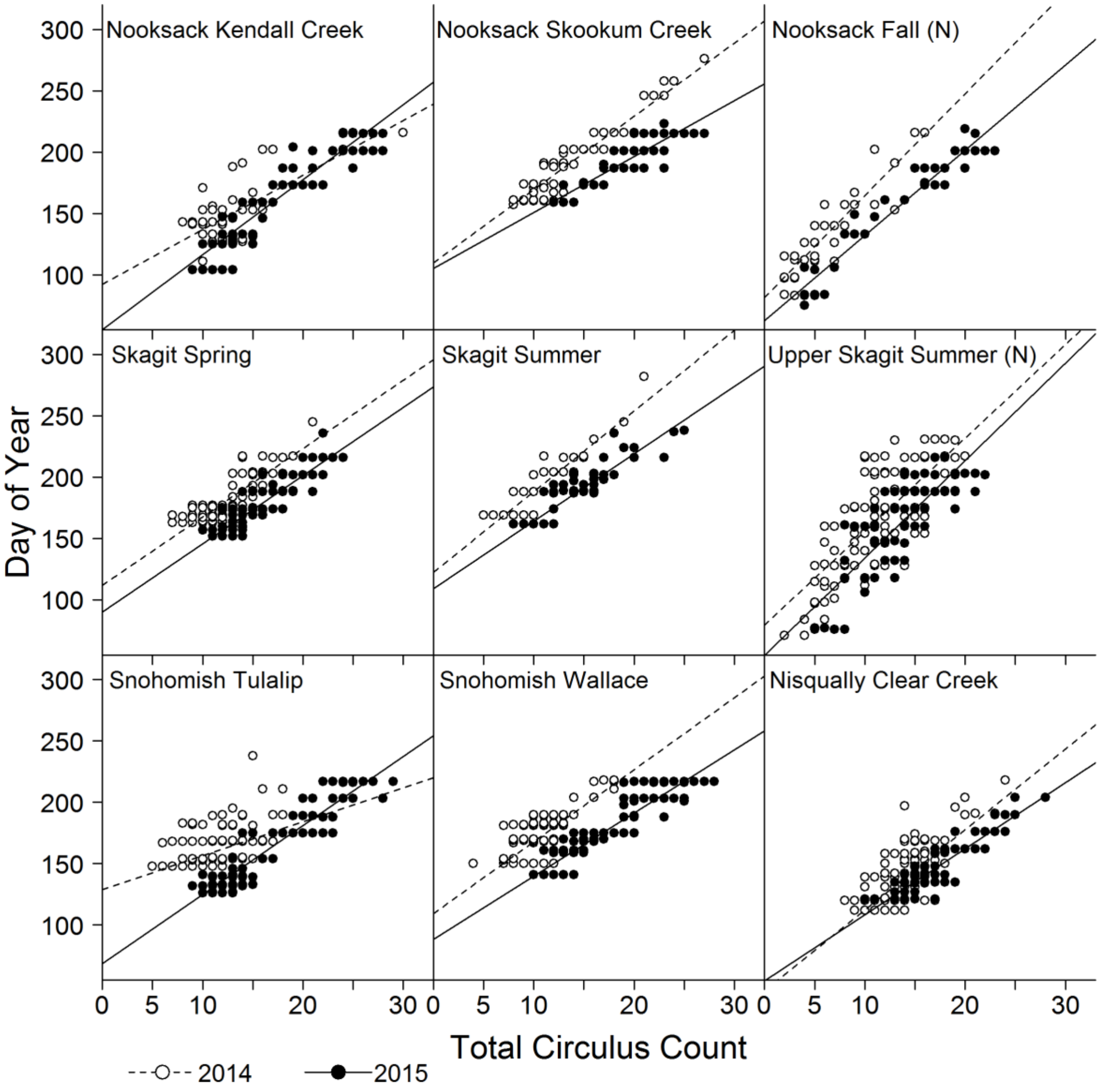


Figure 5.2.3. Linear regressions of sample date and total circulus count for 9 stocks of Chinook Salmon show that circulus count can be a proxy for time throughout the duration of this study. Natural-origin stocks are indicated by "(N)" following the stock name.

Growth analysis & 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 both years (**Figure 5.2.4**). In the 2014 habitat-specific analysis, the Nooksack Kendall Creek and Upper Skagit Summer stocks showed some apparent divergence between average growth histories for the nearshore and offshore habitats (**Figure 5.2.4A**). The divergence at the last common circulus was not significant for the Upper Skagit Summer stock (circulus 17, t = -1.804, df = 7, P = 0.114), but was significant for the Nooksack Kendall Creek stock (circulus 14, Welch's t = -5.429, df= 17.72, P < 0.001). However, the mean residuals of the geometric mean regression of scale radius and fork length for the nearshore and offshore Nooksack Kendall Creek samples are quite different from one another, indicating that the nearshore scale samples for this stock were larger than expected for their length and offshore scale samples were smaller than expected. This would result in an underestimation of back-calculated fork length at each circulus for nearshore scales and an overestimation of back-calculated fork length at each circulus for offshore scales, which would artificially exaggerate the divergence in size at age between nearshore and offshore samples. Indeed, the difference in back-calculated fork length between nearshore and offshore samples in this stock is 15.85 mm at the last shared circulus, and the difference between the mean residuals for nearshore and offshore samples is 11.19 mm. In other words, small differences in scale sampling explain 71% of the divergence between nearshore and offshore average growth histories for the Nooksack Kendall Creek stock. Other stocks did not exhibit such a pronounced difference in mean residuals between habitats.

Though sampling error may explain a significant portion of the apparent divergence in 2014 (supported by examination of residuals and the relatively weaker relationship between scale radius and fork length in that year $r^2 = 0.78$), it is also important to note that for all stocks which show divergence, the divergence between trajectories begins at very early circulus counts (approximately circulus 2-6 depending on stock). For all hatchery stocks with hatchery samples, divergence is occurring before hatchery release. Early divergence of trajectories indicates a degree of size-selective habitat use within stocks, with the fish that had smaller average size-at-age more frequently captured in nearshore habitats than in offshore habitats. This scale finding was supported by observed fish weights, with offshore weights heavier than nearshore weights during the same sampling period for multiple stocks.

In 2015, there was no apparent divergence between habitat trajectories within stocks. The life stage-specific analysis in 2015 also showed little evidence for size-selective mortality, as growth histories for different life stages overlapped both within and among habitats for each stock (**Figure 5.2.5**).

We only encountered fish from our stocks in the San Juan Islands in adequate sample size to create scale growth trajectories (at least 3 fish captured in a life stage) for two stocks captured in the nearshore in 2014: the Nooksack Skookum Creek and Upper Skagit Summer (N) stocks. Sample sizes of our stocks captured in the San Juan Islands were inadequate for the nearshore in 2015 and in both offshore sampling years. Scale growth trajectories of fish from the Nooksack Skookum Creek and the Upper Skagit Summer (N) stocks caught in the San Juan Islands nearshore in 2014 closely resemble their natal watershed offshore trajectory (**Figure 5.2.6**). The San Juan Islands nearshore trajectory for Nooksack Skookum Creek begins to diverge from the offshore line at later circulus numbers, however the divergence is not significant.

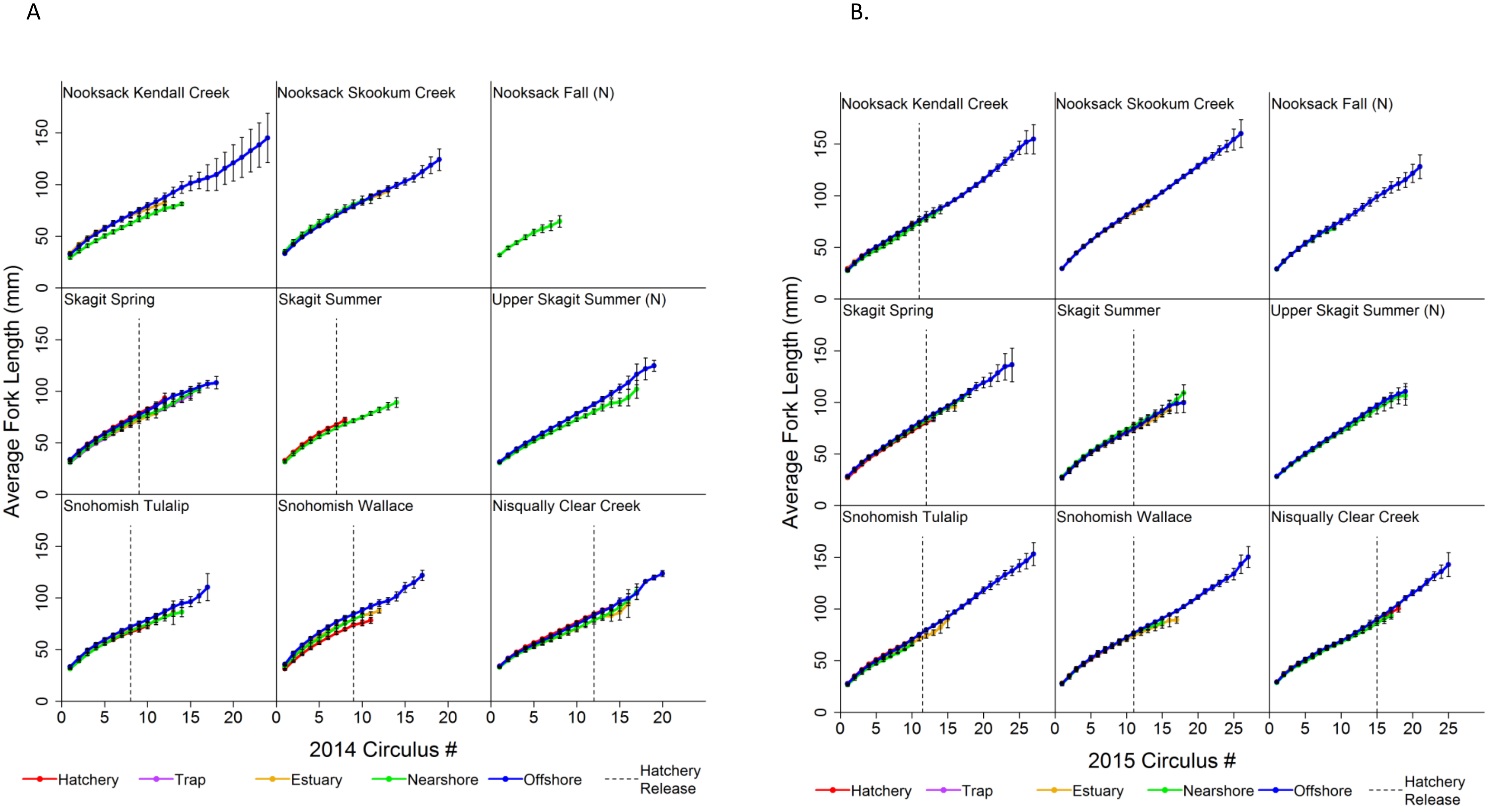


Figure 5.2.4. Habitat-specific growth histories (average back-calculated fork length at circulus ± 1.96 SE) for 9 stocks of Chinook Salmon in 2014 **(A)** and 2015 **(B)** show little evidence of size-selective mortality among habitats. Each curve represents size at age averaged across all juveniles sampled in a particular habitat, regardless of sample period (sample sizes for each stock and habitat are available in Table 2). Vertical dashed lines indicate median circulus count at hatchery release where pre-release hatchery samples were available. Natural-origin stocks are indicated by “(N)” following the stock name. Note that a given circulus number does not indicate a common date among stocks.

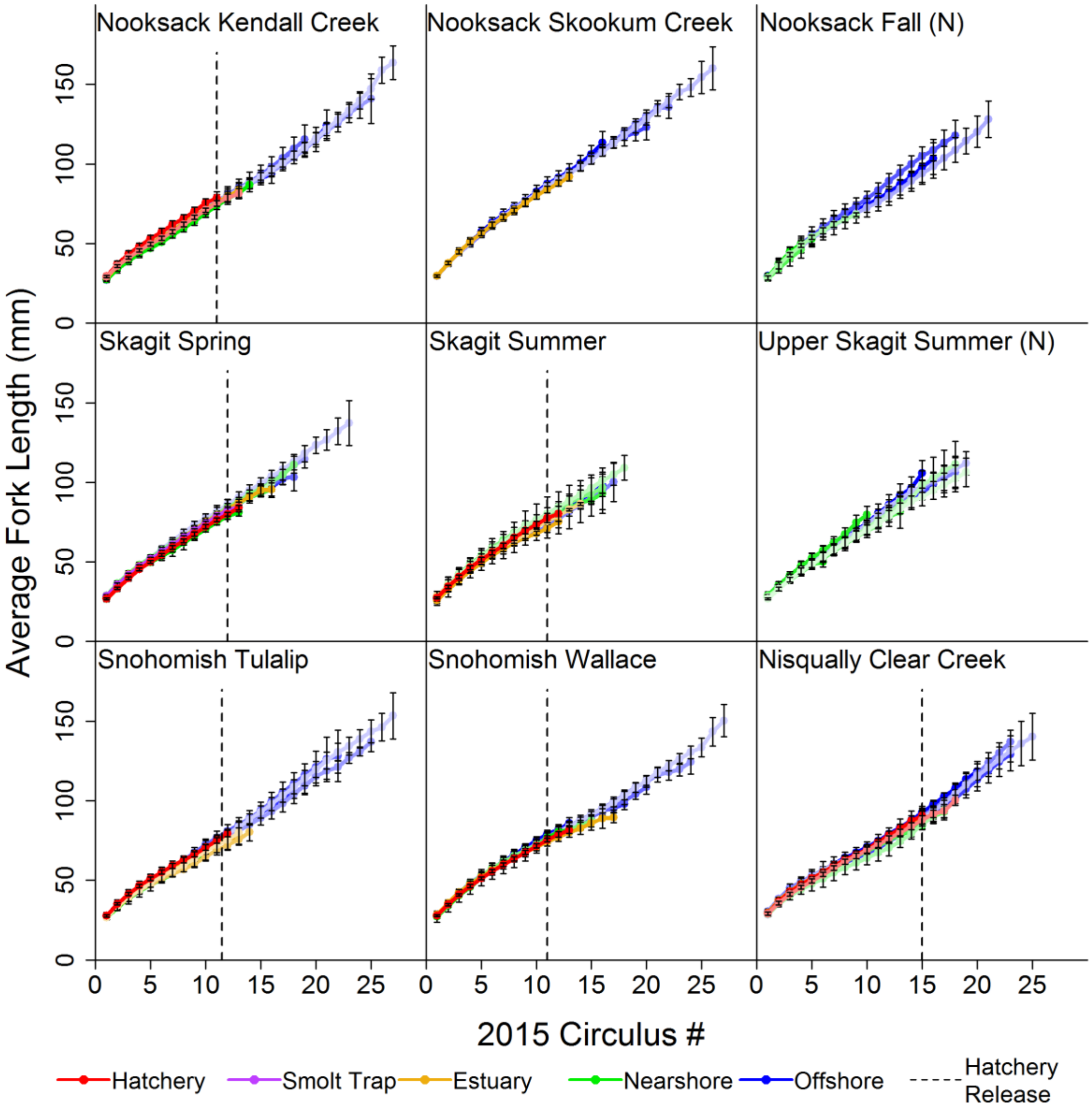


Figure 5.2.5. Life stage-specific growth histories (average back-calculated fork length at circulus ± 1.96 SE) for 9 stocks of Chinook Salmon in 2015 show little evidence of size-selective mortality among life stages. Shading of trajectories within habitats indicates sampling period, with earlier sampling periods represented by dark-shaded lines and later periods represented by light-shaded lines. Each curve represents size at age averaged across all juveniles sampled in a particular habitat and sample period. Each average back-calculated fork length represents an average of at least three scale samples (sample sizes for each stock and sampling period are available in Appendix Table A1). Vertical dashed lines indicate median circulus count at hatchery release where pre-release hatchery samples were available. Natural-origin stocks are indicated by “(N)” following the stock name. Note that a given circulus number does not indicate a common date among stocks.

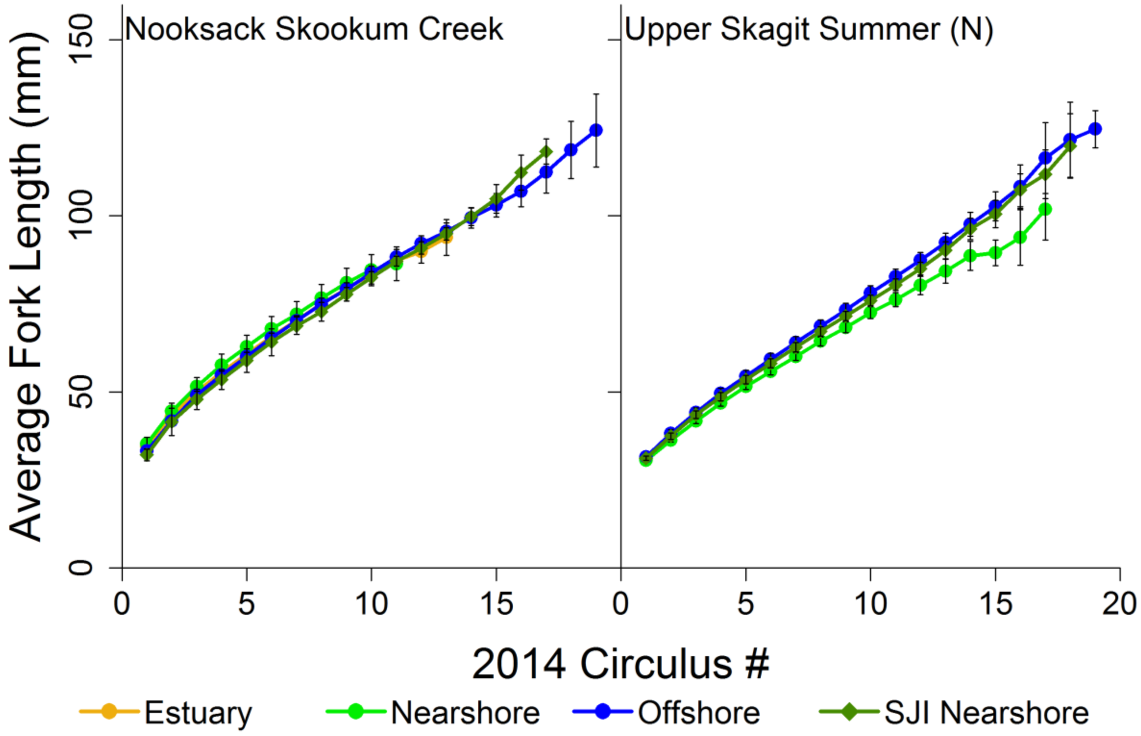


Figure 5.2.6. Habitat-specific growth histories (average back-calculated fork length at circulus ± 1.96 SE) for fish caught in the San Juan Islands nearshore in 2014 compared to fish caught in habitats associated with their natal watershed. San Juan Island (SJI) nearshore trajectories closely track the natal watershed offshore trajectory. Each curve represents size at age averaged across all juveniles sampled in a particular habitat, regardless of sample period (sample sizes for each stock and habitat are available in Table 2). Natural-origin stocks are indicated by "(N)" following the stock name. Note that a given circulus number does not indicate a common date among stocks.

5.2.3 Conclusions

- Peak catches in each habitat type were generally sequential throughout the migration period, especially for hatchery populations. Natural-origin populations were much more prevalent in nearshore habitats during the early months and had a more protracted outmigration period.

- Scale radius was strongly, and positively, correlated with fork length while circulus count explained the majority of the variation in sample date suggesting circulus count was a good proxy for age within most stocks/populations.

- We observed very little, if any, evidence of size-selective mortality occurring from marine entry to the end of the summer in any of the stocks/populations we analyzed. The is some divergence in growth trajectories between the nearshore and offshore growth curves for the Nooksack Kendall Creek (hatchery) and the Upper Skagit Summer stocks in 2014. However, only the Nooksack Kendall Creek was significantly different and cold be the result of sampling error due to the size of scales used in each of the separate habitat types.

- We observed some evidence for size-selective habitat use whereby within a stock when divergence occurs at an early circuli, it suggests smaller fish may more frequently inhabit nearshore habitats rather than move to offshore areas.

- Fish from the Nooksack Kendall Creek and Upper Skagit Summer populations were found in high enough number sin the San Juan Islands to compare growth trajectories for fish from each population inhabiting their natal nearshore/offshore habitats and the San Juan Islands concurrently. For each population, growth trajectories of fish found in the San Juan Islands closely matched trajectories for fish from their natal offshore regions and although there was some apparent divergence for the Nooksack Kendall Creek population it was not significant. However, trajectories of these fish were generally different from the trajectories observed in the natal nearshore habitats for both populations.

- Although no single critical period of growth could be identified from our analyses and given the observed relationship between growth and survival suggests all growth during the outmigration period is essential and variability among habitat types or regions is likely of importance.

5.3 Discussion

Genetic stock identification of juvenile Chinook salmon captured in nearshore and offshore habitats within northern Puget Sound including the San Juan Islands revealed two primary patterns: 1) local populations dominate estuary habitats and remain a prominent proportion of fish in natal nearshore and offshore habitats, 2) population distribution becomes more mixed as you move from estuary to offshore and from early summer to late summer. Populations structure in the San Juan Islands nearshore habitats was generally similar to what was observed in the offshore habitats within the Nooksack and Skagit regions. While these patterns held consistent for each region, the specific distribution of populations within each habitat and region were different.

The overall number of populations represented in the offshore habitats of each region was greater than the number of populations represented in the nearshore habitats. Such a pattern makes sense given sequential habitat use and increasing distribution through time as has been verified in previous research in Puget Sound (Rice et al. 2011). Nearshore habitats within the Skagit and Nooksack were dominated by their respective natal populations with the greatest contribution from the Upper Skagit Summers and Nooksack Fall (naturalized Samish hatchery fish), respectively. In total, more than 90% of the fish in the Skagit nearshore represented populations form within Whidbey Basin. Populations from British Columbia were also present in the nearshore and offshore habitats within each region although more prevalent in offshore catches. Furthermore, we observed an increase in the proportion of Big Qualicum hatchery fish in particular during 2015. The increased presence, most notably in the San Juan Islands, could have been influenced by an earlier release date of nearly twice the number of unmarked fish compared to 2014 (~1.6 million v. 2.9 million fish; RMIS).

Fish from throughout Puget Sound, the Strait of Juan de Fuca, and British Columbia were found to use the nearshore and offshore habitats within the San Juan Islands. For this study we focused primarily on the southeast portion of the San Juan archipelago to increase the probability that we would encounter fish from Puget Sound, specifically the Nooksack and Skagit. Beamer et al. (2012) found a higher proportion of Puget Sound fish, including the populations of interest, in this particular area compared to other areas within the islands which tended to be dominated by fish from British Columbia. Throughout this study we found primarily Puget Sound fish in this particular region although the distributions were significantly different between 2014 and 2015. Upper Skagit summer fish represented nearly half of all wild Chinook captured in the nearshore habitats in the San Juan islands in 2014. While they were also present in 2015 they accounted for only 8%. Nooksack population represented roughly 9% of the wild Chinook in the nearshore habitats in both years which is somewhat significant given the low population size in the Nooksack. Seasonal pattern of population distribution within the islands was relatively stable indicating consistent use for a group of populations, primarily northern Puget Sound Chinook. However, we did observe fish from British Columbia populations. In general, Canadian fish represented a low proportion than those from Puget Sound fish with the exception during the month of August or the Big Qualicum situation mentioned above.

In an effort to identify critical growth periods for sub-yearling Chinook salmon we analyzed growth histories among fish captured in each sequential habitat used by juveniles during outmigration. We evaluated population or cohort specific growth trajectories of juvenile Chinook salmon to account for any difference in size and/or growth rates within each population group. Groups were selected based on CWT recoveries and GSI as described in section 4.1. Our analysis of growth trajectories revealed no evidence for size selective mortality during the first summer in marine waters. We did detect some apparent size-selective habitat use, with relatively smaller size-at-age fish occupying nearshore habitats to a greater degree. This finding is not surprising given the benefits nearshore habitat may provide for small juvenile salmon (i.e. feeding and growth opportunities, serving as a predation refuge, physiological transition zone and migration corridor (Fresh 2006)).

Given that we did not detect size-selective mortality for sub-yearling Chinook salmon through mid-summer, we could not identify particular habitats or life stages that might be most crucial for conservation. 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 before mid-summer. Taken together, these results suggest that early marine growth through mid-summer – regardless of the habitat in which it is achieved – may be critical to marine survival and could provide a useful predictor of adult returns.

Comparisons of growth trajectories between fish from a given cohort captured in their natal watershed and the San Juan Islands revealed very little to no difference. Although sample sizes were small, growth histories from the two groups of fish were very similar and tracked the trajectories of fish captured in their natal offshore habitat extremely well. Such a result makes sense given fish must transit through their natal offshore habitats to get to the San Juan Islands. However, given the similarities, we can likely assume no size selective process, mortality or habitat use, was operating between fish inhabiting their natal offshore habitat and those that were inhabiting the San Juan Islands nearshore. This result is important for interpreting or comparing growth rates, and the factors that affect growth within the San Juan Islands, among the regions as discussed in the following sections. Given the San Juan Islands are solely used as rearing habitat for listed populations of Chinook salmon, understanding any potential limitations to, or the lack thereof, access would be crucial for recovery planning.

This study cannot rule out the possibility that juvenile Chinook salmon experience size-selective mortality at the basin- or Puget Sound-scale prior to July. 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. However, the lack of relationship between size at release and marine survival (Duffy and Beauchamp 2011) suggests that if size-selective mortality is operating among stocks rather than within stocks it is likely due to differences in growth after hatchery release rather than size at release. We did not make any conclusions about size-selective mortality among 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 natural-origin and hatchery stocks. This means that scale regions associated with specific life stages vary among stocks, and thus scale radius at a specific circulus averaged among stocks does not represent size at age. Inference of size-selective mortality across stocks would require analyses to control for variation in the relationship between circulus count and time for different stocks, as both circulus deposition rate and intercept differed among stocks.

6. Identify the Chinook prey and the dietary value of prey items

6.1 Spatial and temporal comparisons of zooplankton assemblage in northern Puget Sound

6.1.1 Methods

Preserved samples were delivered to the University of Washington for processing and analysis in Dr. Keister's laboratory. In the laboratory, the entire sample was briefly examined and the rare, larger organisms were removed for measurement and identification. Then, the sample was split with a Folsom plankton splitter, and the organisms that were rare and large in that split were removed for analysis. Finally, the split was diluted to a known volume and two small aliquots were taken. All organisms in these subsamples were enumerated, identified, staged (for certain taxa), and measured. Crab larvae were measured for carapace length (mm) following the methods of Hirota and Fukuda (1985). Abundances (#/m3) were calculated from counts and volume of water filtered. Biomass was calculated by converting abundances to carbon weight using values and length-weight regressions found in the literature (Table A1).

Zooplankton assemblages were analyzed using several multivariate methods or procedures**.** Species abundance/density and composition were compared among regions and life stage both seasonally (months) and between sampling years (2014-15) using permutational multivariate analysis of variance (PERMANOVA). PERMANOVA is a robust analytical tool based on similarity (dissimilarity) matrices that uses permutations of the original data to develop the test statistic rather than relying upon a traditional *F* distribution making it immune to the normal assumptions associated with traditional multivariate analysis of variance techniques. We used an $\alpha = 0.05$ to test for significant differences among our factors and/or covariates. Where PERMANOVA results suggested significant differences we used the PERMDISP routine to further assess whether differences were indeed due to spatial or temporal variation in assemblages or composition, or were instead a function of different, or heterogeneous, multivariate dispersions. Although significant differences in multivariate dispersions does not preclude any location or time effect on species assemblage, it may suggest some of the difference is attributable to species diversity rather than abundance/relative proportions. Zooplankton density matrices were square root transformed and standardized to sample total (relative abundance) prior to analysis to reduce skew in the data and aid interpretation of the results. Transformed zooplankton densities were used to create a resemblance matrix based on Bray-Curtis similarities. Similarities of 100 occur when two samples are exactly the same whereas similarities of 0 occur when two samples share no species in common. Analyses to test for Year effects did not include Nooksack samples due to samples within that region only being collected in 2015. Test for month and region effects included all data. Station depth was included in our analysis of variance tests due to hypothesized differences in assemblages as a function of bottom depths at each station. Station depth was included as a continuous variable and test were run using Type I sequential sum of squares where the effect of station depth was accounted for prior to the inclusion of the main factors of interest. Finally, we analyzed zooplankton assemblages with the San Juan Islands separately to evaluate the local variability as a function of Year, Month and Site.

To visualize results of PERMANOVA or differences among samples we used two common ordination techniques; non-metric multi-dimensional scaling (NMDS) plots and principal coordinates analysis (PCO). NMDS ordinations are typically used to plot data (similarities) in 2 dimensional, unit-less space where points closer to one another are more similar than those further apart. PCO is different than NMDS in that it is a projection of points onto axes that maximize total variation in the units of chosen similarity measure and thus variation along each axis can be quantified. PCO plots were used to visualize the magnitude of specific effects and to explore potential interactions.

6.1.2 Results

Zooplankton assemblage

A total of 99 oblique plankton tows were completed among the four regions from May-Aug 2014-15 (Table 6.1.1). Twenty-one species groups were identified in zooplankton samples with an additional category for indigestible items (Table in Appendices). All groups were represented in at least one sample in every region with the exception of Nudibrachia, which only occurred in one sample in the Nooksack region in 2015. Nudibranchia were excluded from the dataset prior to statistical analysis. The most abundant group (52 – 74% of total biomass) in all regions was “other” crustaceans which was largely representative of several species of copepods.

Table 6.1.1. Zooplankton sampling effort by Year, Month and Region

	2014				2015			
Region	May	Jun	Jul	Aug	May	Jun	Jul	Aug
Nooksack					4	5	6	6
SJI North	4	4	3	1	2	4	4	4
SJI South	4	3	2	3	4	4	4	4
Skagit	2	2	4	2	4	3	3	4

Station depth did not significantly (p = 0.464) effect species assemblages and was removed for analysis of the remaining factors of interest. Zooplankton assemblages also differed between years, months, and among regions. There was a significant seasonal (p = 0.007), or monthly, effect and a marginally significant effect by region (p = 0.052; Table 6.1.2) on zooplankton species assemblages. However, the significant interactions between the month effect and both region and year suggest the differences in species assemblage among months were not consistent within regions or between years (Table 6.1.2).

Table 6.1.2. PERMANOVA table of results for tests of main effects: Year, Month, and Region. Station depth was removed as a covariate (p = 0.464) and subsequent models were fit using Type III SS to test main effects and first order interactions.

Factors	Abbrev.	Type	Levels
Year	Ye	Random	2
Region	Re	Random	3
Month	Mo	Fixed	4

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Ye	1	2050.7	2050.7	6.3809	0.188	30
Re	2	3849.4	1924.7	5.0405	*0.054*	119
Mo	3	4322.1	1440.7	1.6647	***0.007***	998
YexRe	1	323.54	323.54	1.5593	0.157	999
YexMo	3	2047.2	682.4	3.2888	***0.001***	999
RexMo	6	2518.1	419.68	2.0227	***0.001***	998
Res	76	15769	207.49			
Total	92	32998				

The Region x Month interaction largely preserved regional differences while revealing overlap in assemblages among regions in certain months (Figure 6.1.1). Plankton assemblages were most different among regions in the month of July. PCO1 explained 40% of the variation in the region x Month plankton assemblage. Variability along PCO1 was primarily driven by the Echinodermata and Bryozoa and to a lesser degree ctenophores and decapod zoea. San Juan Islands and Nooksack assemblages were similar due to higher relative biomass of Echinodermata and bryozoan compared to Skagit (Figure 6.1.2). Skagit and Nooksack regions had higher presence of decapod zoea and megalopae compared to the San Juan Islands. Assemblages in the Skagit and San Juan Islands were the least similar with the exception of assemblage in Skagit during August when the proportion of decapods and Echinodermata were the lowest and highest, respectively, within the region.

However, some of the differences can be attributed to greater variability in zooplankton assemblages among the regions (PERMDISP, F = 3.296, p = 0.003). Assemblages were much more dispersed in the San Juan Islands in June and July and in the Skagit during May and August (Table 6.1.3). Variability in zooplankton assemblages in the Nooksack were relatively consistent from month to month and generally less dispersed than any other region.

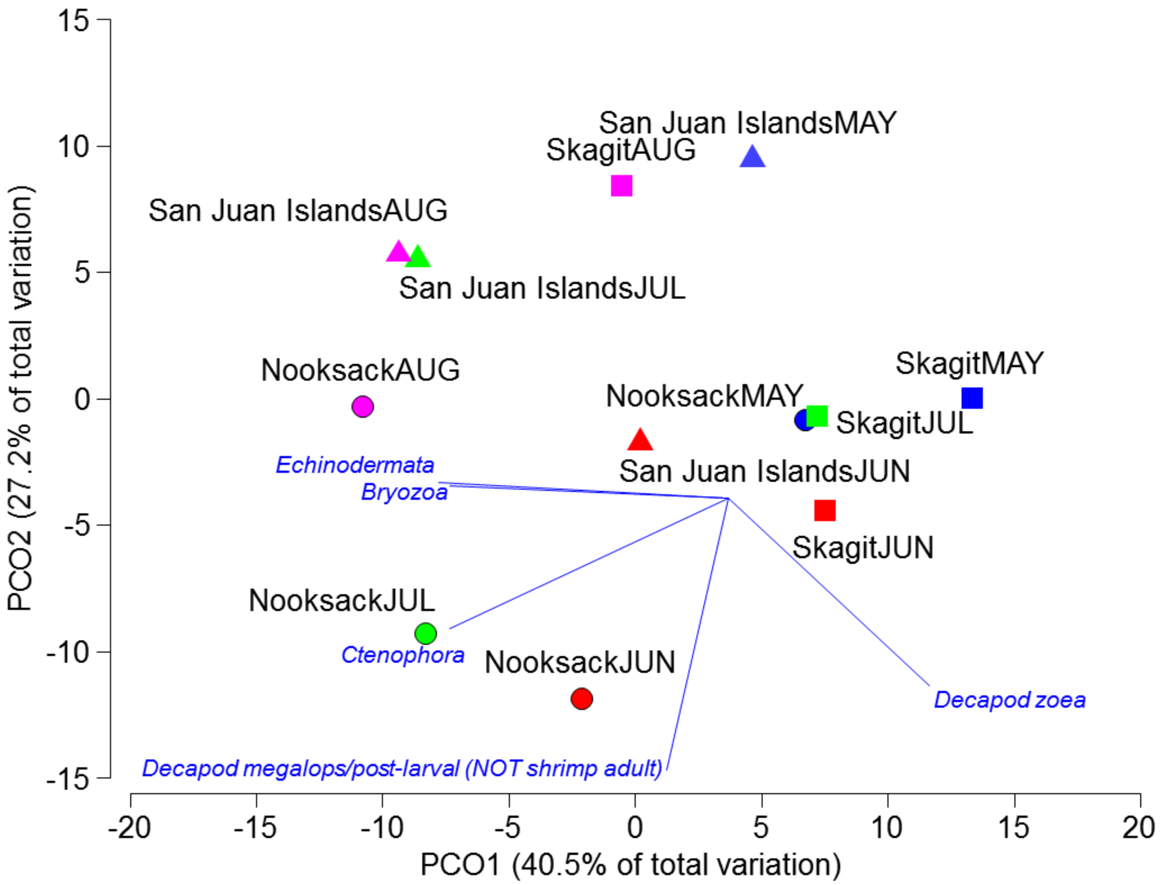


Figure 6.1.1. Principal coordinates plot on centroids for Region x Month zooplankton assemblage. Nooksack (filled circles, San Juan Islands (filled triangles), and Skagit (filled squares) regions by May (blue), June (red), July (green) and August (pink). Centroids represent the mean assemblage composition within each cell. Vectors represent zooplankton groups with Pearson correlation > 0.80 along the PCO axis.

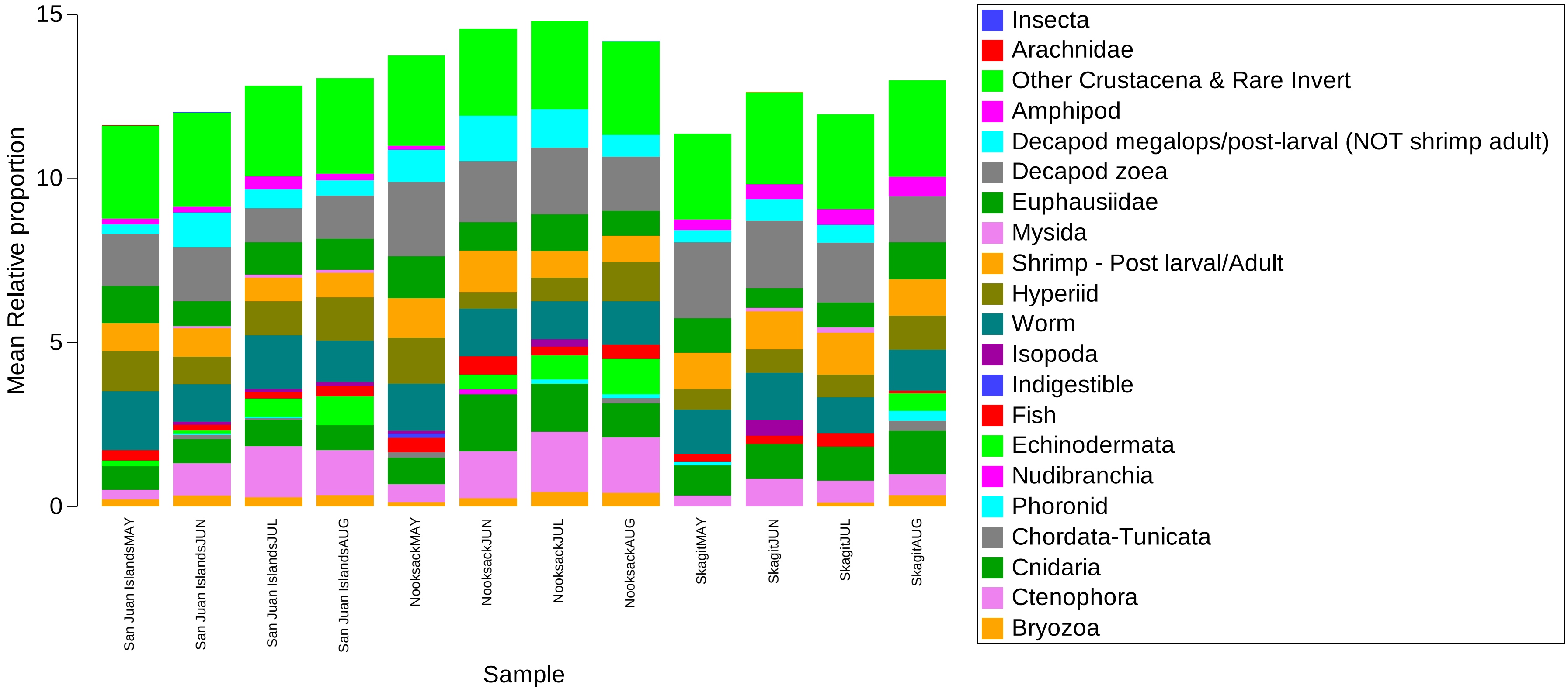


Figure 6.1.2. Average relative proportions ($x^{1/4}$) for zooplankton assemblages among region x month groups.

Table 6.1.3. Mean distances (Bray-Curtis) with standard error for within cell zooplankton assemblage for Region x Month interaction.

Group	n	$\bar{d}$	SE
San Juan IslandsMAY	14	13.64	1.443
San Juan IslandsJUN	14	17.215	1.9194
San Juan IslandsJUL	13	16.922	0.84911
San Juan IslandsAUG	12	12.592	0.57989
NooksackMAY	4	7.949	1.3845
NooksackJUN	4	11.358	1.573
NooksackJUL	6	9.8286	0.59839
NooksackAUG	6	9.4071	1.2
SkagitMAY	6	17.063	1.835
SkagitJUN	5	13.38	2.0206
SkagitJUL	6	14.616	2.2402
SkagitAUG	3	16.602	3.3827

Year x Month interactions were mostly due to the differences among years (Figure 6.1.3). The trajectory, or direction, of shifts in zooplankton assemblages from month to month were generally the same within a year but the years were clearly different. PCO1 explained ~45% of the variation among assemblages for year x month groups and generally explained differences by month. The variability along PCO1 was largely a function of decapod zoea and ctenophores. In general, decoapod zoea biomass decreased from May through August whereas ctenophore biomass increased (Figure 6.1.4). PCO2 explained ~27% of the total variability and was correlated with hyperiid amphipods, euphausiids, worms and to a lesser degree, Echinodermata biomass (Figure 6.1.3). Difference along PCO2 largely reflected variability among years with a higher presence of each of the correlated categories present in 2015 (Figure 6.1.4).

Again, multivariate dispersions of zooplankton assemblages were not homogenous among the year x month cells (PERMDISP, F = 3.581, p = 0.007). Although dispersions were heterogeneous, the range of mean distance to centroids for each group was not exceptionally large (Table 6.1.4). Assemblage dispersion was higher in May and June of 2014 and in July and August in 2015.

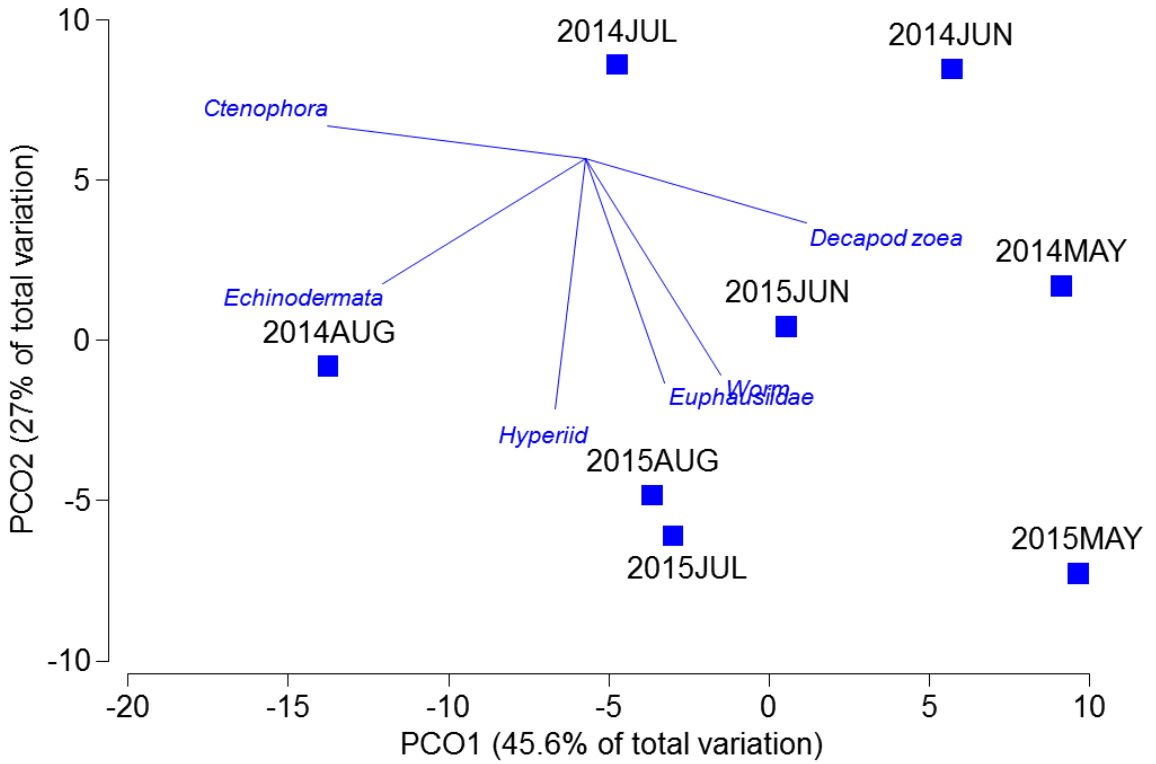


Figure 6.1.3. Principal coordinates plot on centroids for Year x Month zooplankton assemblage. Centroids represent the mean assemblage composition within each cell. Vectors represent zooplankton groups with Pearson correlation > 0.80 along the PCO axis.

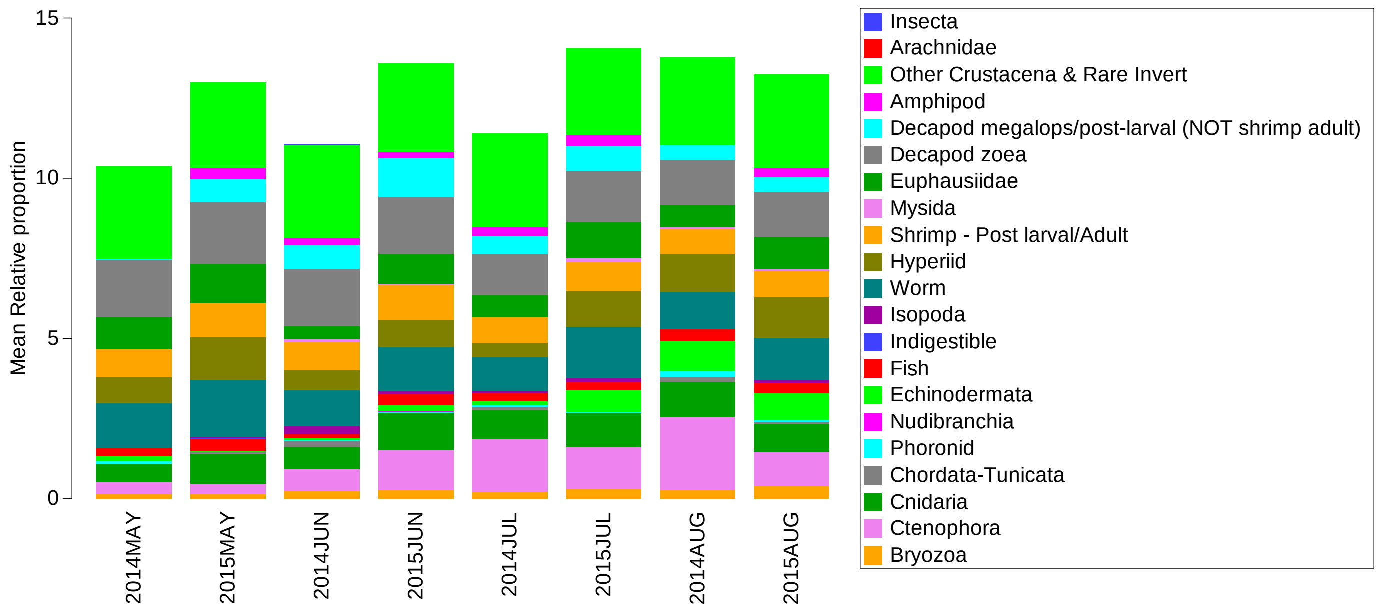


Figure 6.1.4. Average relative proportions (density) for zooplankton assemblages among region x month groups.

Table 6.1.4. Mean distances (Bray-Curtis) with standard error for within cell zooplankton assemblage for Year x Month interaction.

Group	n	$\bar{d}$	SE
2014 May	10	14.909	1.7753
2015 May	14	13.215	1.0662
2014 Jun	9	19.884	1.1512
2015 Jun	14	14.855	1.0822
2014 Jul	9	14.761	1.6855
2015 Jul	16	17.125	1.261
2014 Aug	5	9.8357	1.7335
2015 Aug	16	13.521	1.026

San Juan Island zooplankton assemblages

Zooplankton assemblages within the San Juan Islands followed similar patterns to those observed for all regions. Assemblages differed by month and between years, and there was a significant interaction between month and year suggesting seasonal differences were not uniform from 2014 to 2015 (Table 6.1.5). We also observed differences in zooplankton assemblage among sites that were consistent among months and between years.

Table. 6.1.5. PERMANOVA table of results for zooplankton assemblages in the San Juan Islands in 2014-15.

Factor	Abbrev.	Type	Levels
Site	Si	Fixed	5
Month	Mo	Fixed	4
Year	Ye	Fixed	2

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Si	4	1521.1	380.27	1.8479	0.013	998
Mo	3	3614.9	1205	5.8554	0.001	999
Ye	1	1147.6	1147.6	5.5768	0.001	998
SixMo	12	2162	180.17	0.87552	0.716	998
SixYe**	2	284.28	142.14	0.69072	0.775	997
MoxYe	3	1624.9	541.63	2.632	0.001	997
Res	27	5556.2	205.78			
Total	52	17870				

Differences in zooplankton assemblages in early 2014 (May and June) were characterized by higher relative biomass of post larval shrimp before shifting to a higher presence of ctenophores in July and August (Figure 6.1.5, 6.1.6). Increased presence of ctenophores in 2014 was paired with an uptick in relative biomass of cnidarians (Figure 6.1.6). Assemblages in 2015 overall had lower presence of ctenophores and cnidarians, while relative biomass of hyperiid amphipods and polychaetes (worms) were elevated compared to 2014. Differences in zooplankton assemblages among months within 2015 were generally less pronounced than observed for 2014 samples.

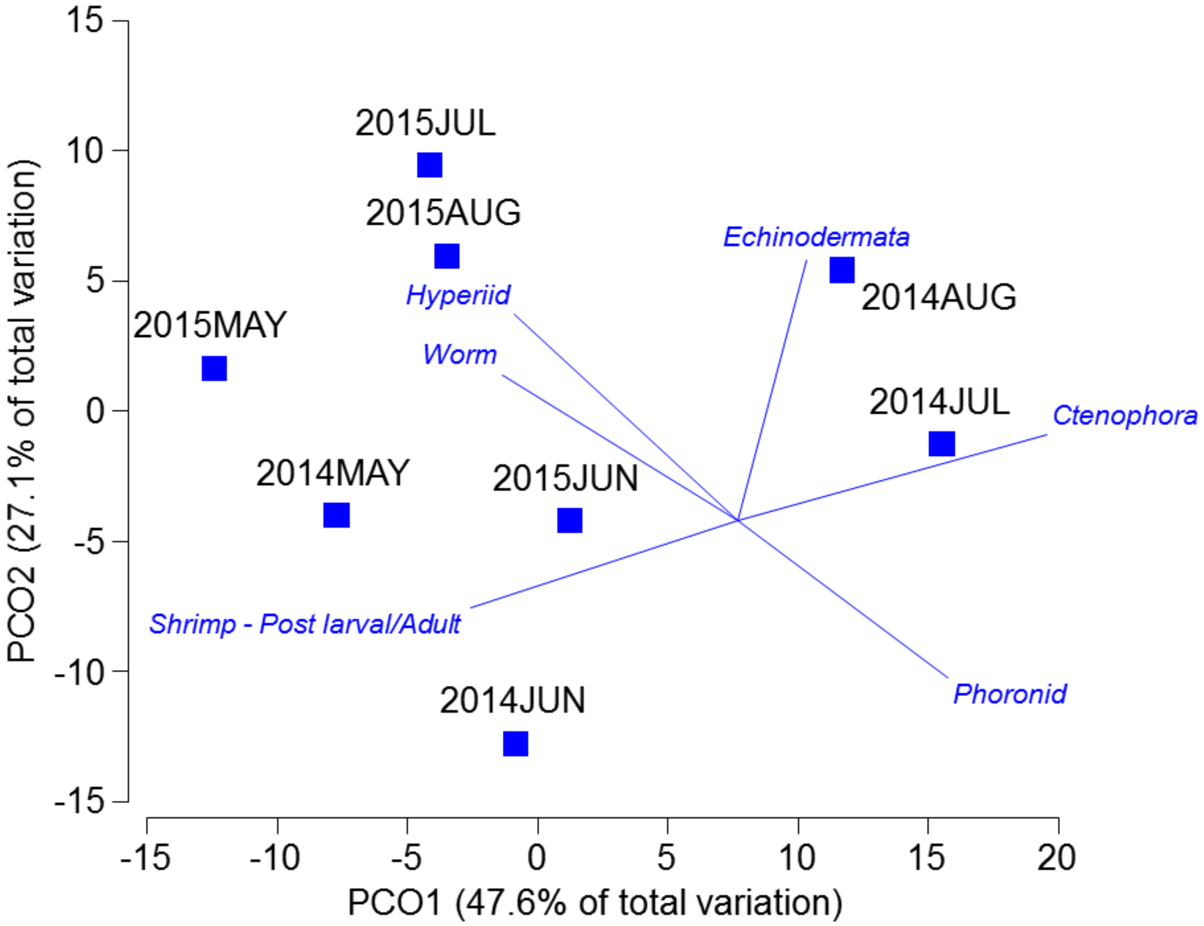


Figure 6.1.5. Principal coordinates (PCO) plot on Year x Month centroids of zooplankton assemblages in the San Juan Islands. Only categories with ρ > 0.8 are displayed.

Zooplankton assmeblages also varied by site when combined over the two year sampling period (Table 6.1.5). The shallow sation in Cowlitz Bay was most distinct given its higher relative biomass of ctenophoes and tunicates; the majority of these categroies captured in 2014 (Figure 6.1.7). In contrast, the other stations had higher relative biomass of shrimp comapred to the shallow Cowlitz site. Of those sites Watmogugh (shallow and deep) and Cowlitz (both deep) sites were disitnguished by high relative biomass of amphipods (not hyperiid), decapods, mysids, polychaetes, and hyperiids, echinoderms, and eupahuasiids, respectively (Figure 6.1.8). Cowltiz deep sites also had higher relative proportions of “other” crustaceans (i.e. copepods). Differences among sites of different depths was not signficant (PERMANOVA; p = 0.708).

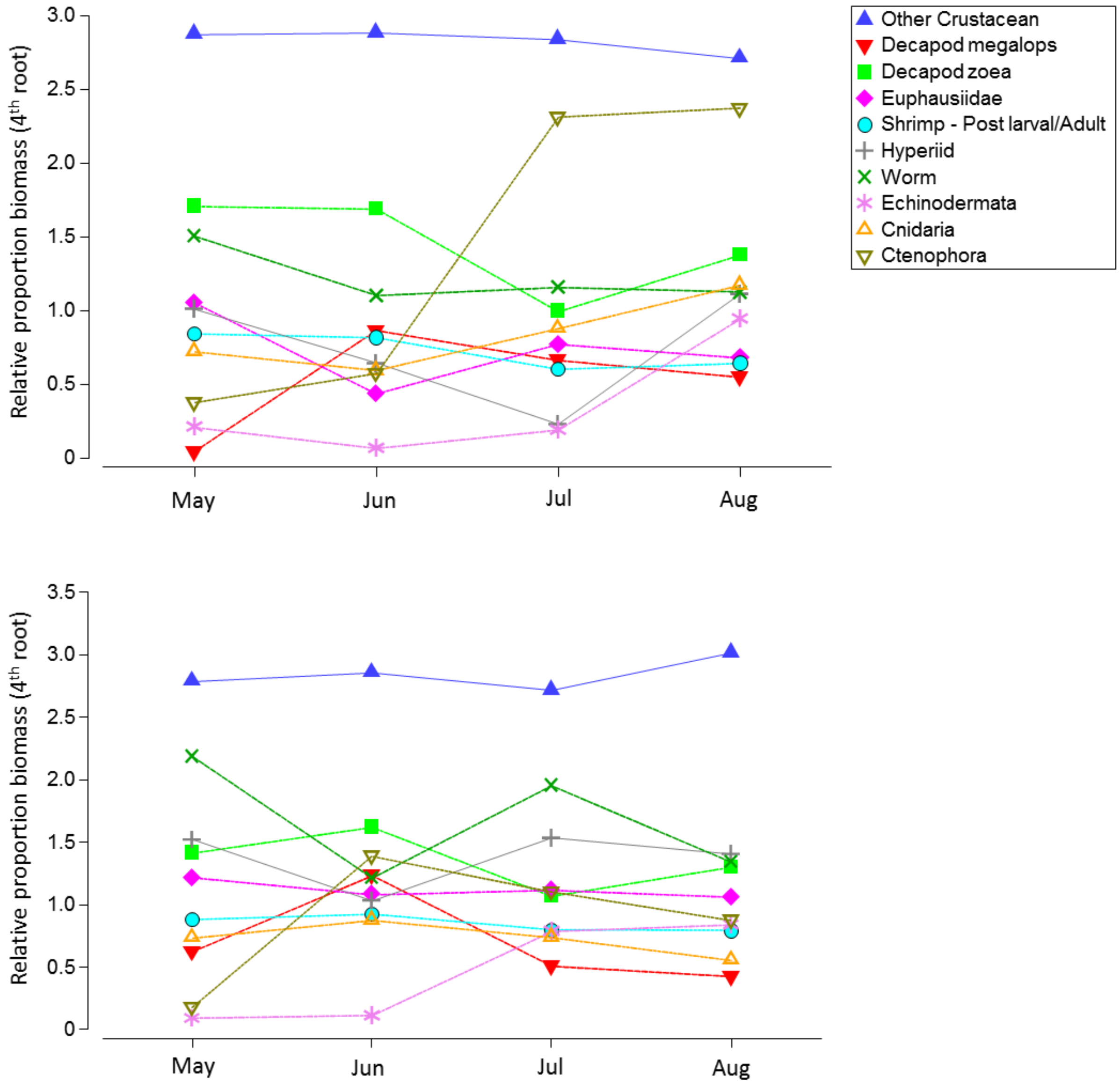


Figure 6.1.6. Mean relative proportions (biomass) by month for 2014 (top panel) and 2015 (bottom panel) zooplankton assemblages. Only categories that account for > 5% of total biomass are displayed.

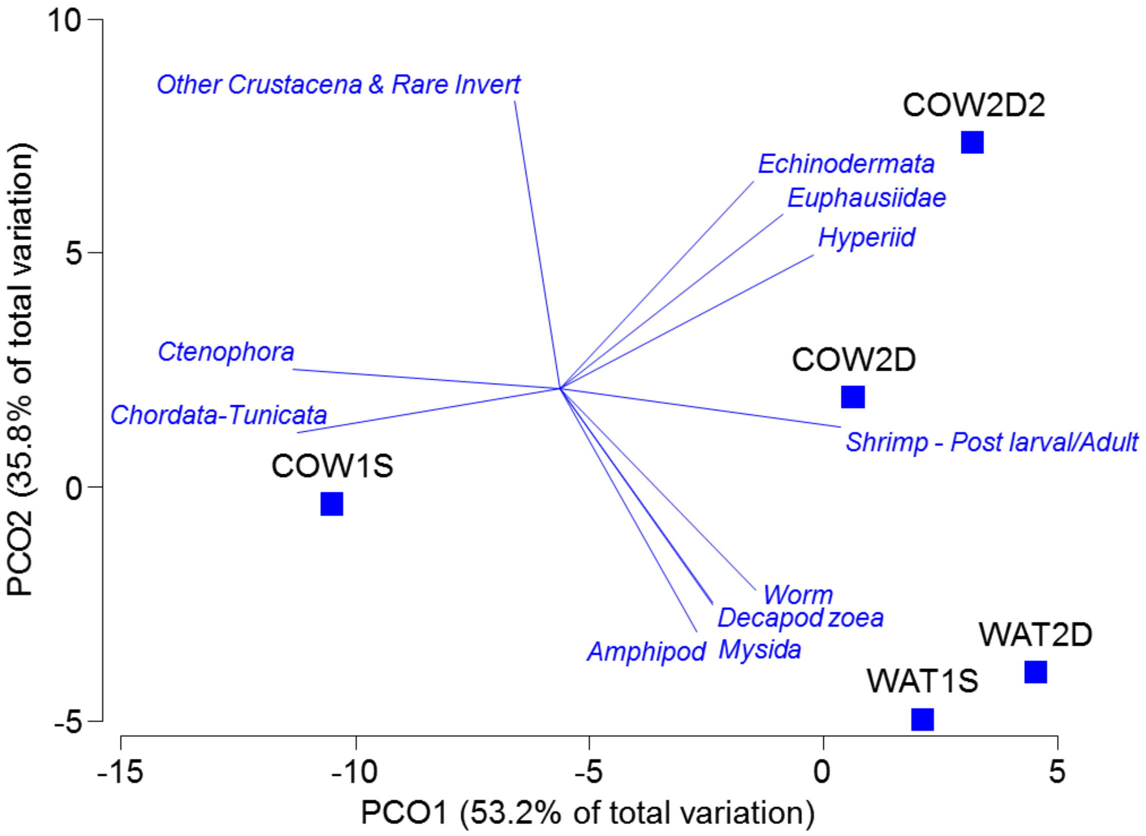


Figure 6.1.7. Principal coordinates (PCO) plot on Year x Month centroids of zooplankton assemblages in the San Juan Islands. Only categories with ρ > 0.8 are displayed.

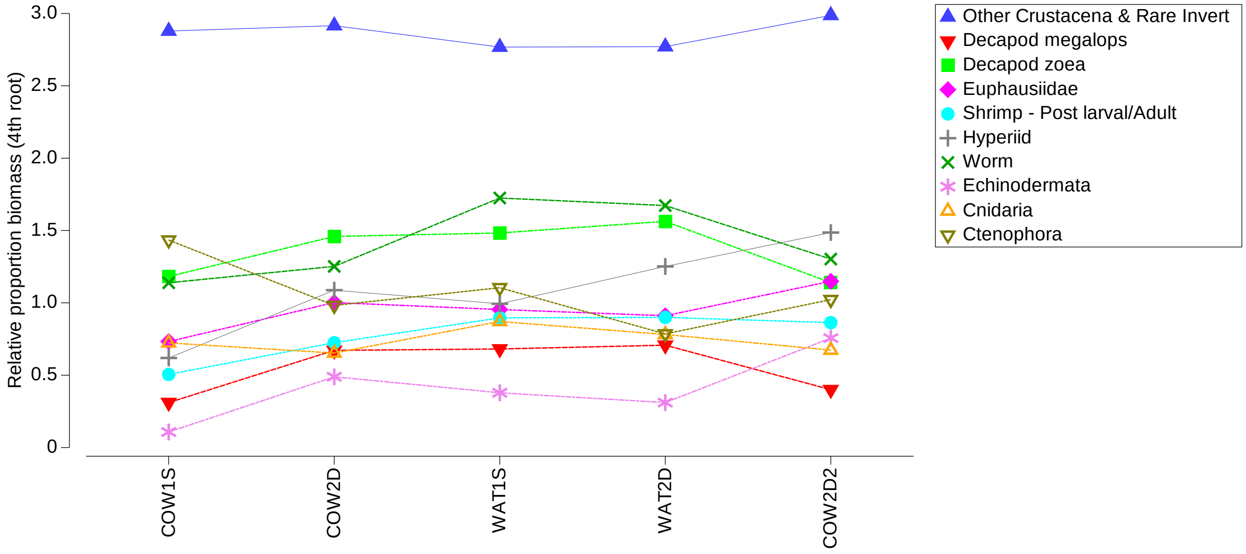


Figure 6.1.8. Mean relative proportions (biomass) by site for 2014 (top panel) and 2015 (bottom panel) zooplankton assemblages acorss all months. Only categories that account for > 5% of total biomass are displayed.

6.1.3 Conclusions

- We observed strong monthly effect of zooplankton species assemblages though the direction or magnitude of the effect was not consistent within regions or between years. Results suggest prey availability may change throughout the summer and varies within and among regions and years.
- Regional assemblages showed clear differences with periods of overlap, or similarity, occurring during mismatched months between each region (i.e. San Juan Islands May and Skagit August).
- Echinoderms, bryozoans, ctenophores and decapods (zoea and megalopae) appeared to drive the variation in zooplankton assemblage between regions and among months. Decapods generally decreased from May to August while ctenophores increased during the same period when years were combined.
- Assemblages were least variable among months in the Nooksack region and most variable within the Skagit region.
- Yearly differences were strongly associated with increased in euphausiids, hyperiids and polychaetes in 2015 when all regions were combined.
- Assemblages from the San Juan Islands showed similar seasonal and annual patterns as the entire dataset. Monthly differences were more pronounced in 2014 and largely reflected an increased presence of ctenophores in the late summer. 2015 assemblages were less variable and appeared to have higher proportions of hyperiids and polychaetes and lower presence of ctenophores and cnidarians compared to 2014.
- Zooplankton assemblages differed considerably among sites though depth did not drive the apparent differences.

6.2 Spatial and temporal comparisons of diet composition (JuneJulAug in PRIMER file)

6.2.1 Methods

Diet composition for Chinook salmon was analyzed using several multivariate methods or procedures**.** Prey biomass from stomach contents were compared among regions and lifestage both seasonally (months) and between sampling years (2014-15) using permutational multivariate analysis of variance (PERMANOVA). PERMANOVA is a robust analytical tool based on similarity (dissimilarity) matrices that uses permutations of the original data to develop the test statistic rather than relying upon a traditional *F* distribution making it immune to the normal assumptions associated with traditional multivariate analysis of variance techniques. Where PERMANOVA results suggested significant differences we used the PERMDISP routine to further assess whether differences were indeed due to spatial or temporal variation in assemblages or composition, or were instead a function of different, or heterogeneous, multivariate dispersions. Although significant differences in multivariate dispersions does not preclude any location or time effect on species assemblage, it may suggest some of the difference is attributable to species diversity rather than abundance/relative proportions. We removed any all zero samples or diet categories as well as all indigestible quantities prior to our analyses. Diet composition biomass matrices were standardized to sample total (relative abundance) and transformed appropriately prior to analysis to reduce skew in the data and aid interpretation of the results. Transformed relative proportions were used to create a resemblance matrix based on Bray-Curtis similarities. Similarities of 100 occur when two samples are exactly the same whereas similarities of 0 occur when two samples share no species in common. We tested for differences among regions, habitats, months, years, and at the site level and included all first order interactions. In addition to the analysis over all regions, we performed a detailed evaluation using the suite of analyses for samples collected only with the San Juan Islands.

To visualize results of PERMANOVA or differences among samples we used two common ordination techniques; non-metric multi-dimensional scaling (NMDS) plots and principal coordinates analysis (PCO). NMDS ordinations are typically used to plot data (similarities) in 2 dimensional, unit-less space where points closer to one another are more similar than those further apart. PCO is different than NMDS in that it is a projection of points onto axes that maximize total variation in the units of chosen similarity measure and thus variation along each axis can be quantified. PCO plots were used to visualize the magnitude of specific effects due to potential interactions using data centroids or group means.

6.2.2 Results

A total of 836 diets were processed from the nearshore and offshore habitats of each region from May-Aug in 2014-15 (Table 6.2.1). The majority of samples were collected in June and July in all regions; no samples were collected from the San Juan Islands during May. More offshore samples were collected in each year in the Skagit and Nooksack regions while the opposite was true for the San Juan Islands.

PERMANOVA results suggests diet composition varied significantly among life stages (or habitat types) and regions but the degree or magnitude of the regional differences was not uniform among months (Table 6.2.2). Similarly, while we observed monthly differences in diet composition among the regions, these differences were not uniform across years.

Table 6.2.1. Sample counts and distribution among regions, months, lifestage, and year.

		2014				2015			
		May	Jun	Jul	Aug	May	Jun	Jul	Aug
Nooksack	Nearshore	36	31	16	11	22	18	11	9
	Offshore	1	27	27	20		25	23	16
San Juan Islands	Nearshore		46	47	7		10	21	10
	Offshore		16	8	1		11	23	14
Skagit	Nearshore	22	31	33	21	20	21	21	10
	Offshore	30	52	24	19		20	22	10

Table 6.2.2. Table of results for PERMANOVA analysis of relative proportions in diet composition.

Factors	Abbrev.	Type	Levels
Sample Watershed	Sa	Random	3
Lifestage	Li	Fixed	2
Month	Mo	Fixed	3
Year	Ye	Random	2
Site	Si	Random	68

Source	df	SS	MS	Pseudo-F	P(perm)	perms
Sa	2	47058	23529	3.586	0.026	999
Li	1	52780	52780	3.551	0.025	999
Mo	2	14525	7262	0.503	0.954	999
Ye	1	14519	14519	2.293	0.097	998
SaxLi	2	18028	9014	2.530	0.062	998
SaxMo	4	38559	9640	3.589	0.002	998
SaxYe	2	13765	6883	2.057	0.115	999
LixMo	2	8873	4436	1.880	0.114	999
LixYe	1	7852	7852	2.015	0.115	999
MoxYe	2	21807	10903	3.135	0.019	999
Si(YexLixSa)	74	252240	3409	1.745	0.001	999
Res	576	1125200	1954			
Total	693	2183400				

Differences in diet composition between life stages was strongly driven by terrestrial insects and decapods, both zoea and megalopae. Nearshore diet composition was dominated by terrestrial insects while offshore diets had a far greater contribution of decapods (Figure 6.2.1). Fish were also present in relatively high proportions in both life stages. Nearshore diets appeared to have a higher proportion of fish than offshore diets. However, this pattern was strongly influenced by the regional differences as described below. Offshore diets were also more variable than nearshore diets (PERMDISP, F = 18.61, p = 0.001) with mean distances to their respective centroids of 54.96 and 50.98, respectively.

Offshore diets appeared to be much more variable than the associated nearshore diets within each region (Figure 6.2.1). Offshore diets in the Skagit region were dominated by decapod zoea and megalopae and had a high presence of terrestrial insects, especially in 2015. Offshore Nooksack diets were highly variable but had a relatively strong presence of decapod megalopae, and to some degree decapod zoea, in 2015. Offshore diets from the San Juan Islands again had a higher overall presence of fish in most months as well as a significant contribution of euphausid prey.

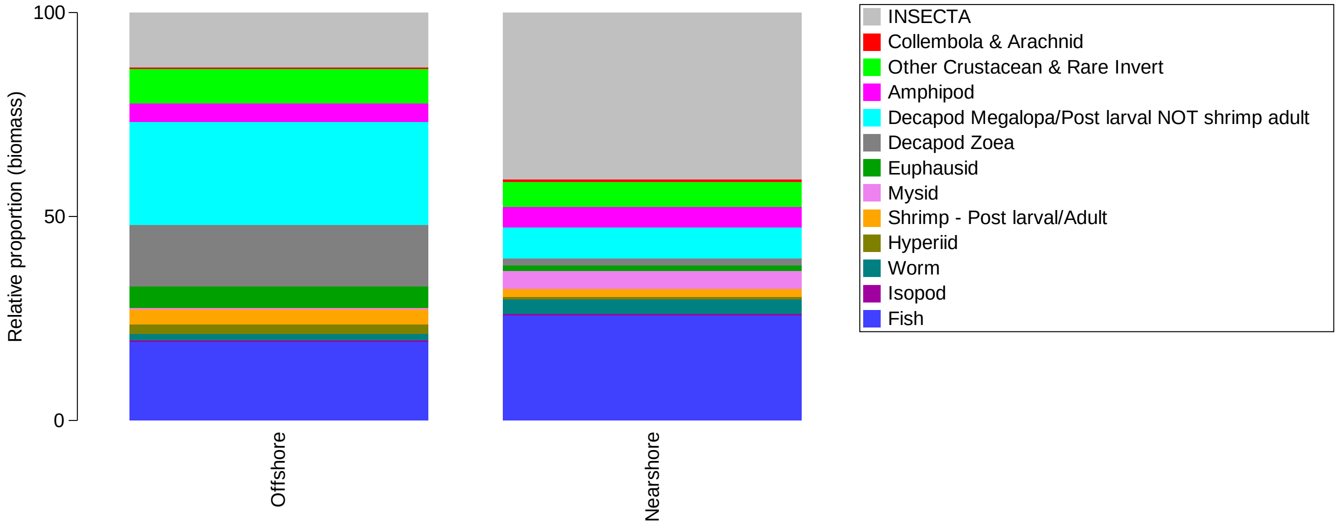


Figure 6.2.1. Mean relative proportions (biomass) found in stomach contents between offshore and nearshore Chinook salmon diets across all regions, months and between years.

Regional differences in diet composition were also present in our data (Table 6.2.1). Diet composition in the Skagit and Nooksack regions were more similar to one another than to the diets from the San Juan Islands. In general, the differences were captured by the high presence of fish in diets from fish captured in the San Juan Islands (Figure 6.2.2). In contrast, diets from the Skagit and Nooksack region had generally lower presence of fish in diets and a high contribution of both terrestrial insects and decapods. Both Pacific sand lance and Pacific herring contributed considerably to diets form the San Juan Islands with very little contribution from terrestrial insects.

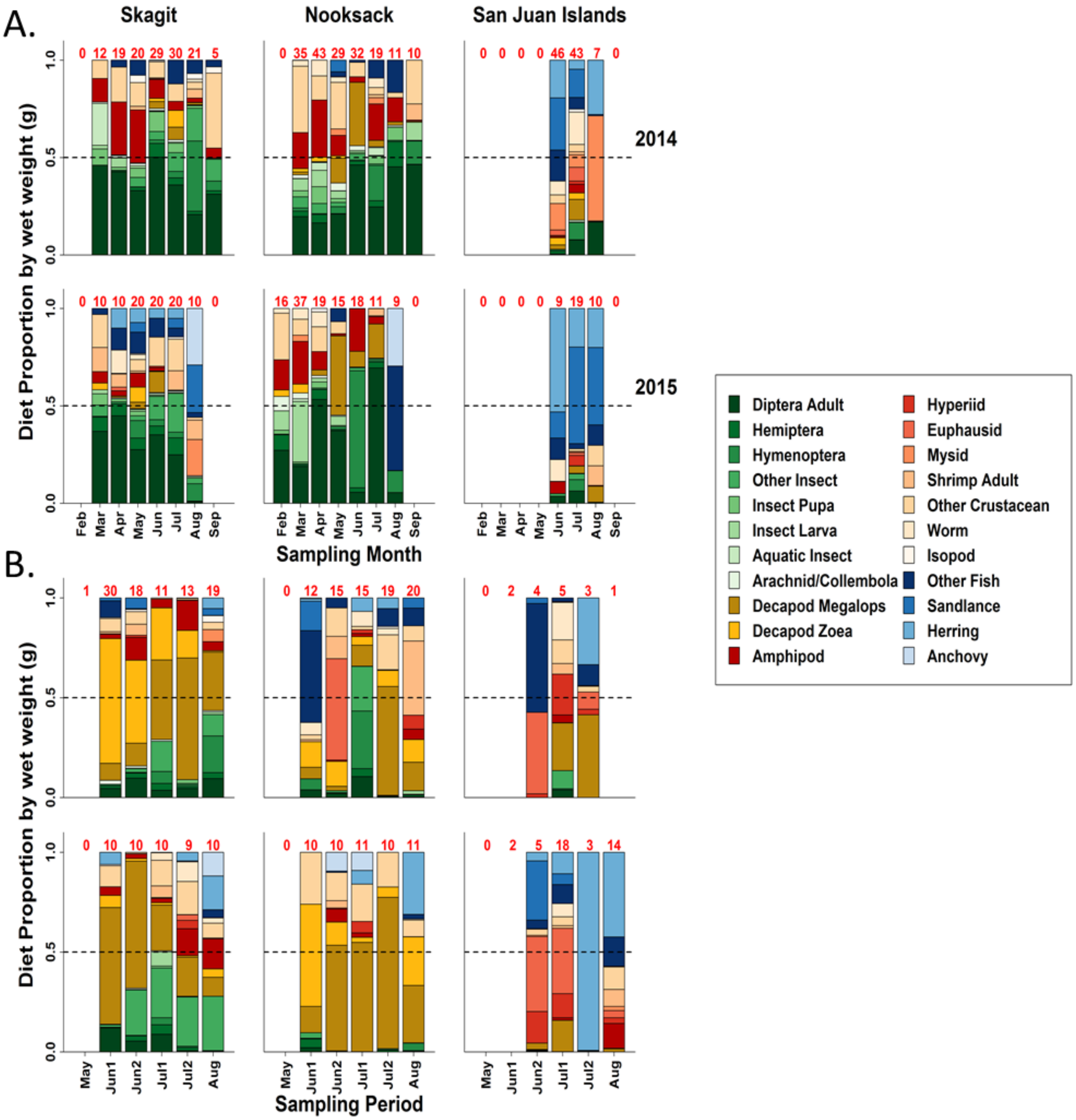


Figure 6.2.2. Juvenile Chinook salmon diet composition from nearshore (A) and offshore habitats by year and sampling period.

Significant differences in diet composition were also observed among months within each region (Table 6.2.1). The majority (84%) of variation in the region x month diet composition groups was explained along the primary PCO axis (Figure 6.2.3). Variation along PCO axis 1 was again explained by the presence of fish in one direction and insects and decapods in the other direction. In most months, the diets in the Nooksack and Skagit regions were categorized by the high presence of insects and decapod megalopae/zoea. Skagit diets appeared to show a strong contribution of insects in all months with a decreasing presence of decapods from June through July (Figure 6.2.4). Again, diets in the San Juan Islands had a higher contribution of fish than other region in most months. However, San Juan Islands diets in July and Nooksack diets in Aug were more similar than other region x month groups due to the decrease in contribution of fish to San Juan Islands diets and the increase in contribution of fish to the Nooksack diets. The decrease in the contribution of fish to the San Juan Islands diet was paired with an increase in decapod megalopae (Figure 6.2.4).

Our observed differences in relative proportions in diet composition among months within each region cannot be separated from potential differences in dispersion or variability in diversity (PERMDISP, F = 8.590, p = 0.001). Diet composition was somewhat less variable in June than the others months although we could not detect any systematic pattern or changes among cells (Table 6.2.3).

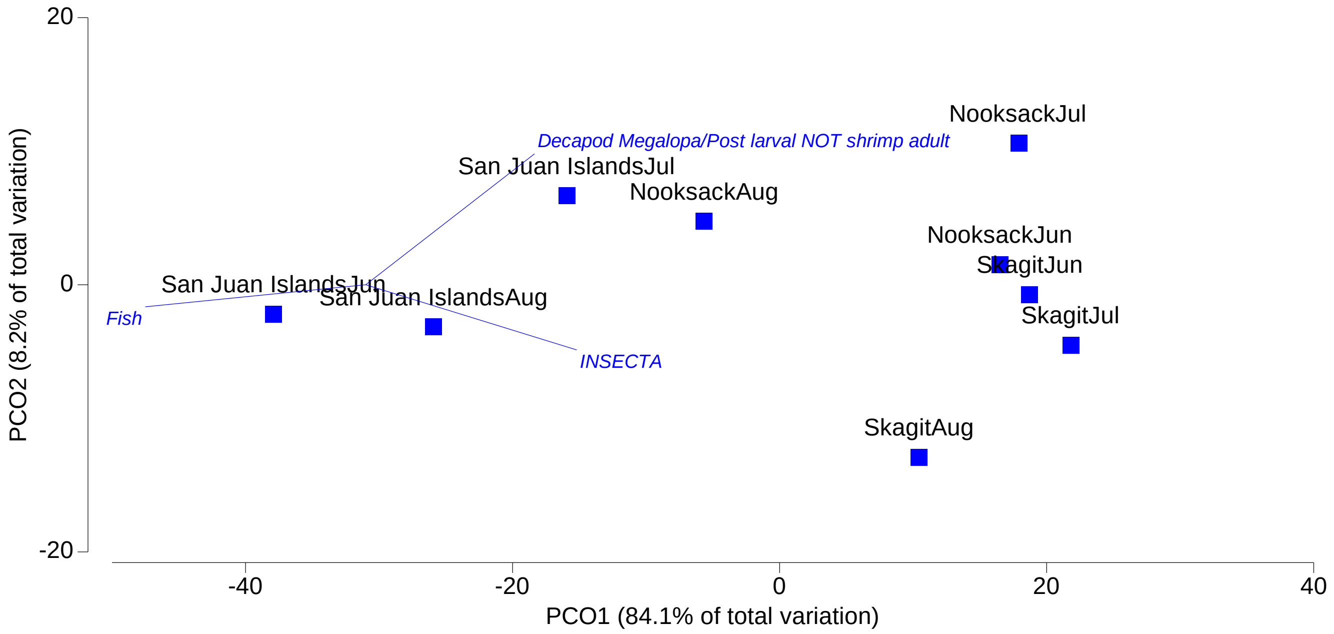


Figure 6.2.3. Principal coordinates plot on centroids for Region x Month diet composition (relative proportions). Centroids represent the mean diet composition within each cell. Vectors represent diet categories with Pearson correlation > 0.90 along the PCO axis.

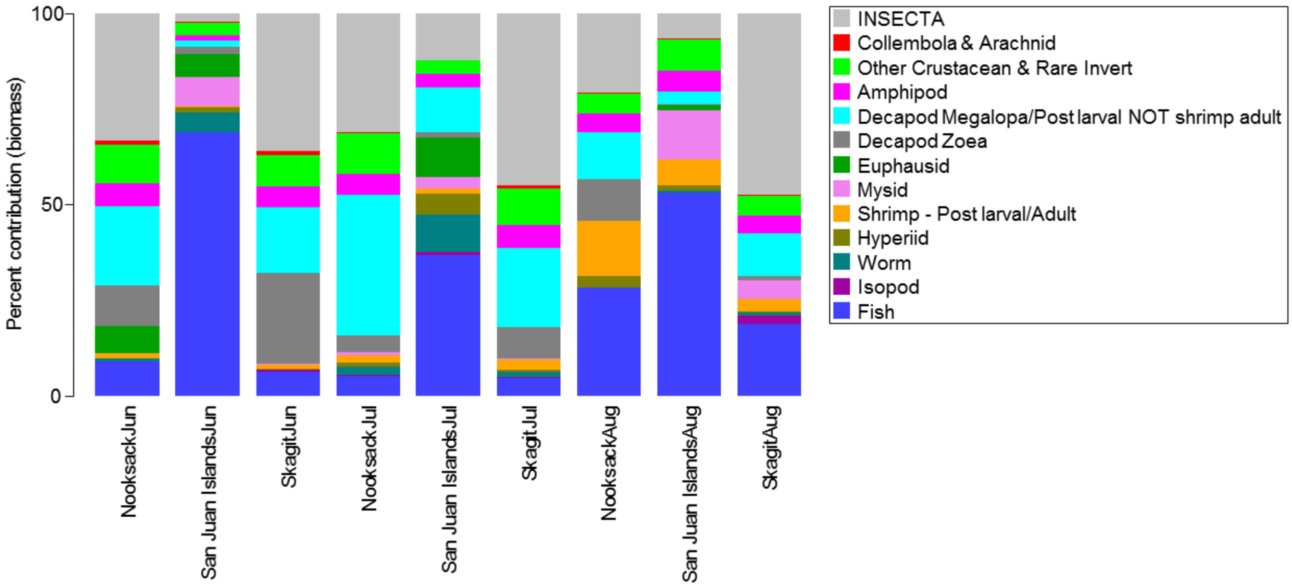


Figure 6.2.4. Mean percent contribution by biomass of diet categories for region x month groups.

Table 6.2.3. Mean distances (Bray-Curtis) from group centroid with standard error for within cell diet composition for Region x Month interaction. Higher values for mean distance represent greater dispersion within each group.

Group	n	$\bar{d}$	SE
Nooksack Jun	93	50.636	1.5104
San Juan Islands June	82	38.493	2.4885
Skagit June	117	49.645	1.2108
Nooksack July	73	49.316	1.6442
San Juan Islands July	93	54.775	0.99799
Skagit July	93	44.888	1.512
Nooksack August	51	55.614	1.5216
San Juan Islands August	32	49.49	2.8767
Skagit August	60	45.39	2.0298

We also observed a significant interaction among month and year suggesting temporal patterns in diet composition varied between years (Table 6.2.1). Approximately 77% of the variation in diet composition among the month x year groups was explained along PCO1 (Figure 6.2.4). Both fish and insects were highly correlated with PCO1. Diets collected in 2015 had a higher relative proportion of fish, decapod megalopae, and other crustaceans (i.e. copepods) than samples collected in 2014 (Figure 6.2.5). Specifically, differences between 2014 and 2015 were attributed to the increased contribution of fish in July 2015 and the significantly high contribution in August 2015. On average, diet composition in August 2015 was nearly 50% fish (Table). However, within group similarities were rather low reflecting the significantly spatial differences described above.

Finally, differences in diet composition also occurred at the site level. However, there is a strong likelihood that these differences reflect differences in multivariate dispersion or variation among sites (PERMDIP, p = 0.001). While difference in dispersion may not preclude any true differences in diet composition among sites within each region, we were not able to differentiate between the two possible sources.

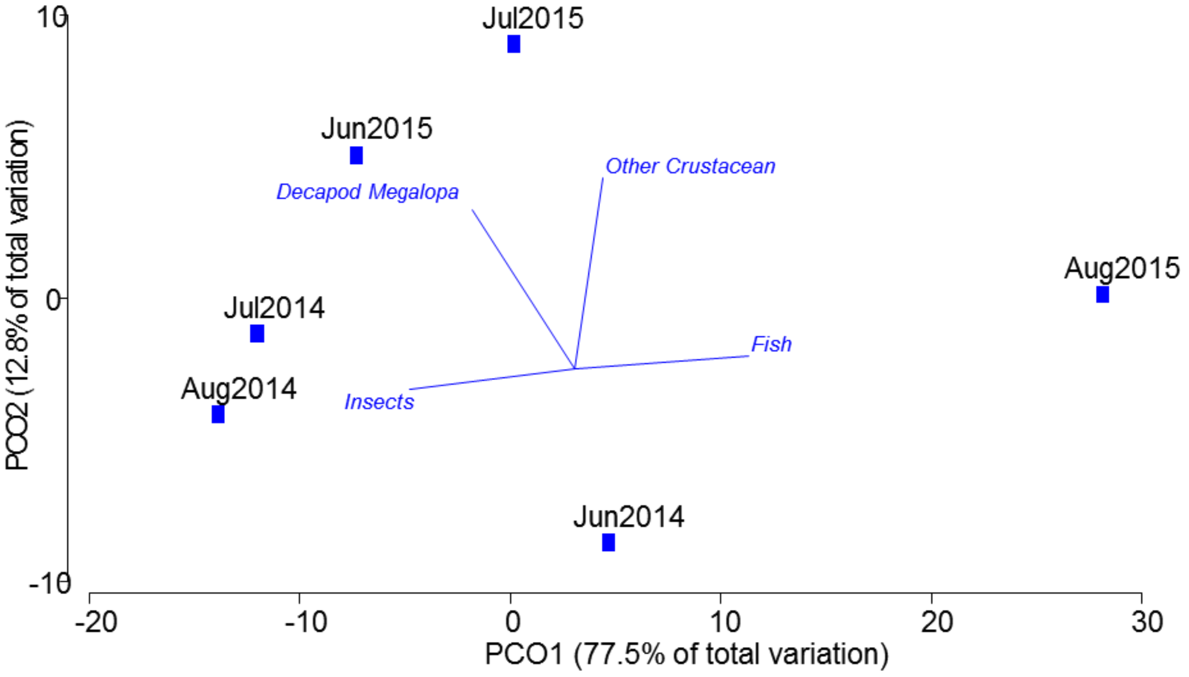


Figure 6.2.4. Principal coordinates plot on centroids for Year x Month diet composition (relative proportions). Centroids represent the mean diet composition within each cell. Vectors represent diet categories with Pearson correlation > 0.90 along the PCO axis.

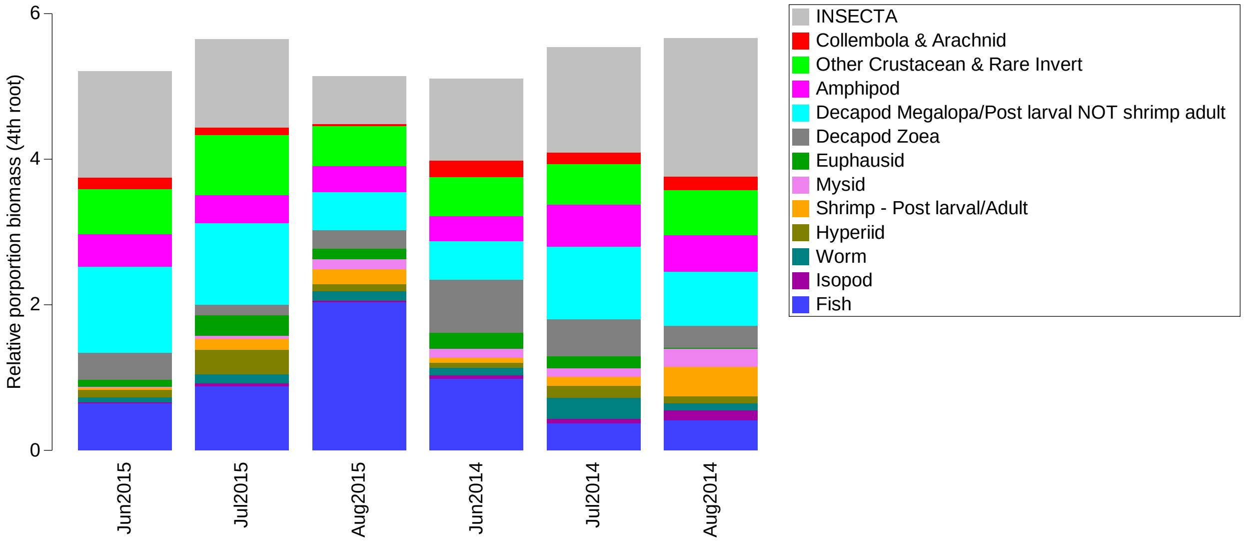


Figure 6.2.4. Mean percent contribution by biomass of diet categories for year x month groups.

Table 6.2.3. Mean distances (Bray-Curtis) from group centroid with standard error for within cell diet composition for Year x Month interaction. Higher values for mean distance represent greater dispersion within each group.

Group	n	$\bar{d}$	SE
2014 Jun	193	56.608	0.61
2014 Jul	145	53.373	1.006
2014 Aug	79	48.821	1.83
2015 Jun	99	51.143	1.295
2015 Jul	114	53.326	0.945
2015 Aug	64	46.4	2.32

San Juan Islands Diet Composition

Diet composition in the San Juan Islands was not significantly different between months, years, or life stages at $\alpha = 0.05$ (Table 6.2.4). However, there was a marginally significant difference among month x year groups ($p = 0.066$). Diets collected in 2014 had a higher contribution from insects, mysids and polychaetes (worms) whereas diets in 2015 had higher contribution from, primarily, fish prey (Figure 6.2.5). PCO plots of year x month groups showed variability in diet composition variability was strongly driven by fish, decapods, insects and mysids (Figure 6.2.6). Diets in all months during 2015 and in June of 2014 had higher contribution from fish prey than either July or August of 2014 (Figure 6.2.7). Diet composition during July 2014 had an increased contribution from decapod megalopae while diets from fish captured in August of 2014 had unusually high contribution from mysids and, to a lesser degree, insects.

Diet composition was more variable in 2014 than 2015 (Table 6.2.5). Bray Curtis similarities for 2014 ranged between 42 and 56 for June through August. In contrast, similarities in 2015 were much higher and had a narrower range (Table 6.2.5). The most consistent month for diet composition between years was June (Table). In both years, diets from June had high proportion of fish relative to other categories. July diets typically had the highest contribution of decapod megalopae in either year but the magnitude was considerably different between 2014 and 2015.

Table 6.2.4. PERMANOVA table of results for diet composition in the San Juan Islands Jun-Aug 2014-15.

Factors	Abbrev.	Type	Levels
Year	Ye	Random	2
Month	Mo	Fixed	3
Lifestage	Li	Fixed	2

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Ye	1	4358.4	4358.4	2.236	0.088	999
Mo	2	7036.7	3518.3	0.921	0.519	345
Li	1	2716.3	2716.3	1.536	0.312	6
YexMo	2	7640.4	3820.2	1.960	0.066	998
YexLi	1	1751.9	1751.9	0.899	0.456	999
MoxLi	2	5486.2	2743.1	1.408	0.216	997
Res	29	56520	1949			
Total	38	86682				

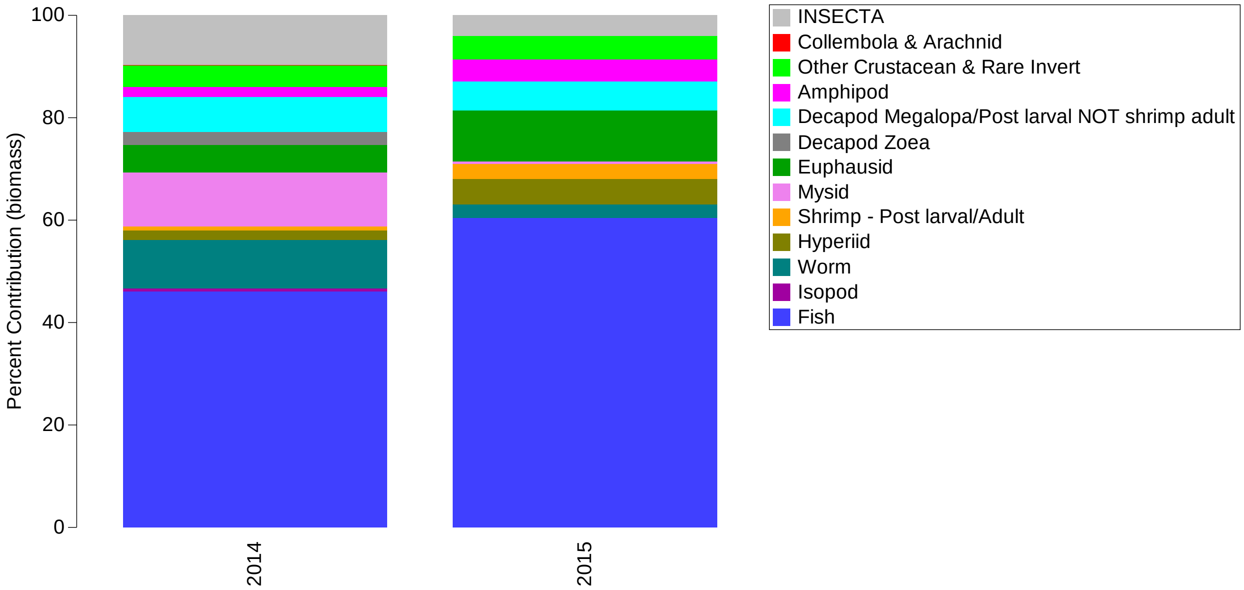


Figure 6.2.5. Mean percent contribution of diet categories by year for juvenile Chinook salmon captured in the San Juan Islands.

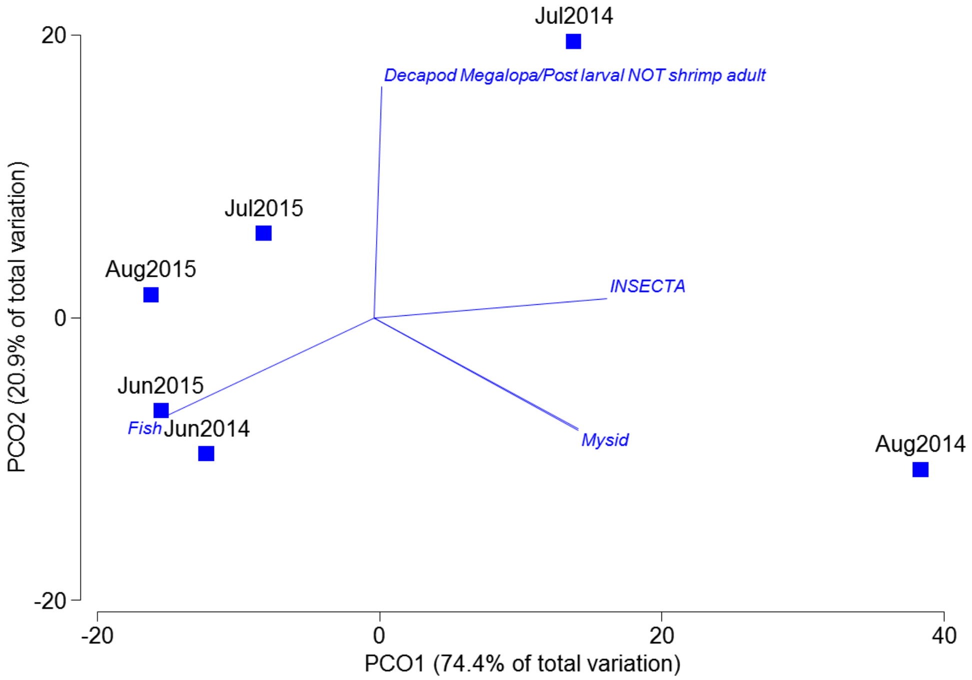


Figure 6.2.6. Principal coordinates plot on centroids for Year x Month diet composition (relative proportions) from juvenile Chinook salmon captured in the San Juan Islands. Centroids represent the mean diet composition within each cell. Vectors represent diet categories with Pearson correlation > 0.90 along the PCO axis.

Table 6.2.5. Bray Curtis similarities for diet composition from juvenile Chinook salmon captured in the San Juan Islands. Values can range from 0 (no similarity) to 100 (identical).

	June 2015	July 2015	Aug 2015	June 2014	July 2014	Aug 2014
June 2015						
July 2015	79.457					
Aug 2015	78.090	73.468				
June 2014	86.820	72.207	76.170			
July 2014	56.798	67.707	63.058	56.864		
Aug 2014	38.929	37.704	30.269	42.875	47.128	

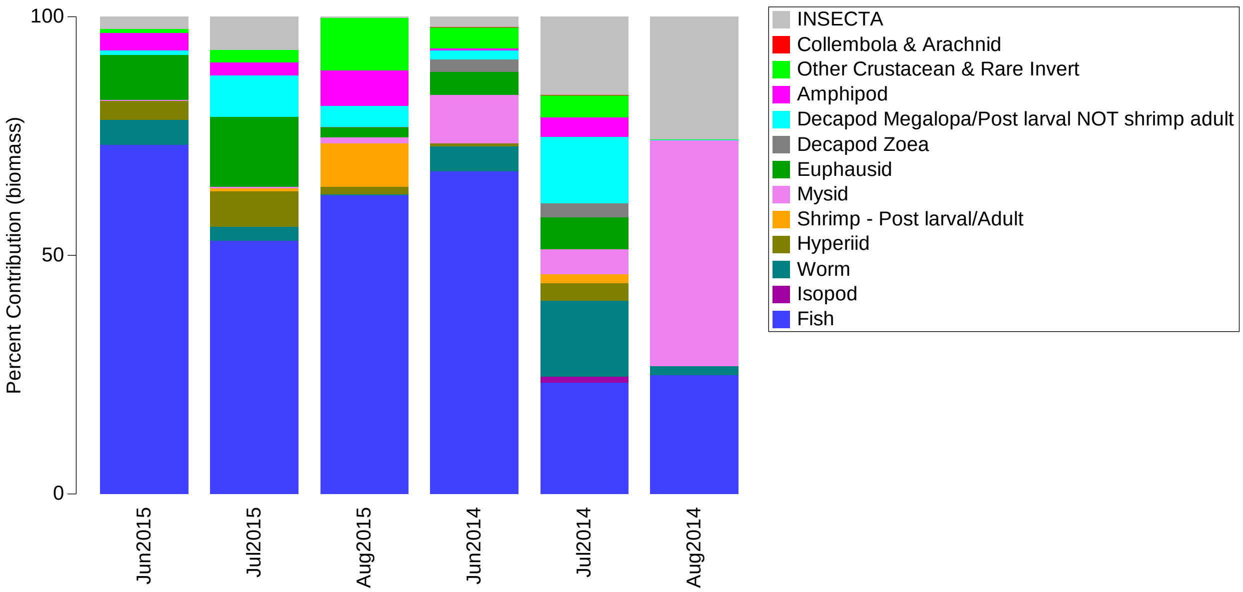


Figure 6.2.7. Mean percent contribution of diet categories for year x month groups for juvenile Chinook salmon captured in the San Juan Islands.

Differences among year x month and lifestage by month groups can be partially explained by differences in dispersion (PERMDISP, F = 6.648, p = 0.004; F = 13.157, p = 0.001, respectively). Diet composition was highly variable in some month x year groups (Table 6.2.6). Average distance to centroids was generally higher in 2014 compared to 2015 although standard errors were consistently high across years.

Table 6.2.6. Mean distances (Bray-Curtis) to centroid (average) with standard error for within cell diet composition for Year x Month interaction. Higher values represent greater dispersion within each group.

Group	n	$\bar{d}$	SE
2015 Jun	20	36.473	5.285
2015 Jul	42	47.620	2.472
2015 Aug	24	42.249	3.549
2014 Jun	62	39.085	2.812
2014 Jul	51	56.197	1.035
2014 Aug	8	43.427	6.916

6.2.3 Conclusions

- Diet composition varied significantly between nearshore and offshore samples as well as among the different regions in North Puget Sound. Differences between life stages were strongly driven by the presence of terrestrial insects in nearshore diets and the higher prevalence of decapod megalops and zoea in offshore diet samples.

- Regional differences were also observed and were due to the higher proportions of fish and lower contribution of insects in diets from the San Juan Islands compared to Nooksack and Skagit diet samples.

- Region x month differences in diet composition were again strongly influenced by the presence of fish in diets but also revealed shifting regional patterns in diet composition through the months. However, region x month differences may also be due to differences in dispersion (variability) among groups.

- Month x year patterns largely reflected increased proportion of decapods and fish in diets collected during 2015. Most notably were the increased proportions of fish during July and August of 2015 with an apparent decrease in the proportion of fish during June when compared to samples from 2014.

- Diets collected from fish captured in the San Juan Islands were relatively consistent between months, years and life stages. In general, the proportion of fish in the diets increased in 2015 relative to 2014 while the contribution of mysids appeared to be higher in 2014. August 2014 diets were least similar to other month x year diet groups with higher proportions of insects and low proportions fish.

6.3 Fish prey distribution, abundance, composition, and size.

Diet composition in the San Juan Islands was unique compared to other regions evaluated in northern Puget Sound due to the high contribution of fish prey. Fish were found in more than half of all diets from the San Juan Islands and accounted for, on average, half the weight of contents within individual diets from both nearshore and offshore life stages (Table 6.3.1). The primary species represented in juvenile Chinook salmon diets in the San Juan Islands were Pacific herring and Pacific sand lance (Figure 6.2.2, section above). We explored how the distribution, abundance, and size composition of these species, as observed in the nearshore habitats of the San Juan Islands (see Methods in section 4), related to presence in Chinook diets in 2014 and 2015. We also evaluated the sizes at which predation was occurring for both Chinook salmon and the prey species. Where possible, we used measurements of fish found in the stomach contents of juvenile Chinook salmon to estimate a mean length for known prey of each species for comparisons to the size frequencies observed in the general population.

Table 6.3.1. Proportion of individuals juvenile Chinook salmon diets that contained fish prey and the mean contribution of fish prey by weight from each region across all months and years.

	Prop. Diets	Mean Contribution
San Juan Islands	61%	50%
Nooksack	15%	11%
Skagit	14%	10%

Pacific sand lance and Pacific herring were the most abundant species sampled in the nearshore habitats of the San Juan Islands (Figure 6.3.1). Although catches were highly variable, catch per unit effort of the primary species were orders of magnitude greater than any other species encountered in nearshore habitats. Catch per unit effort of Pacific herring and Pacific sand lance was considerably higher in 2015 compared to 2014 (Figure 6.3.2). However, abundance appeared to peak for both species in August of both years. CPUE for herring was typically higher than CPUE of sand lance in the early summer but the patterned reversed in the late summer.

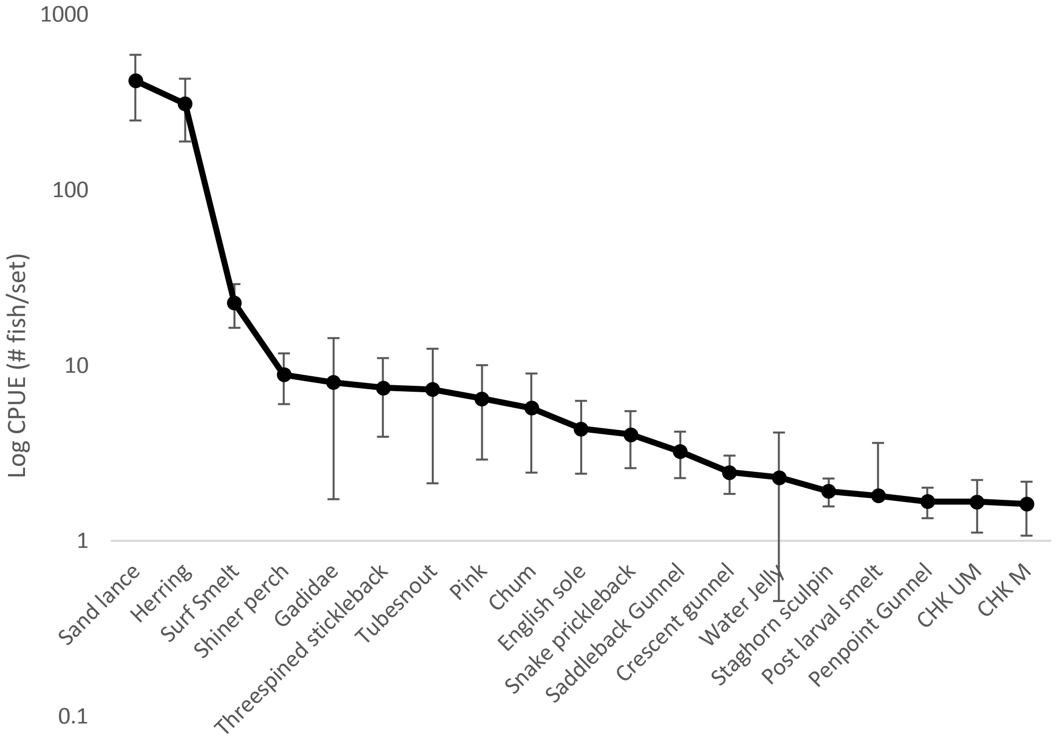


Figure 6.3.1. Log catch per unit effort (# fish / set) for each species sampled in the nearshore habitats of the San Juan islands from May- Sept 2014-15.

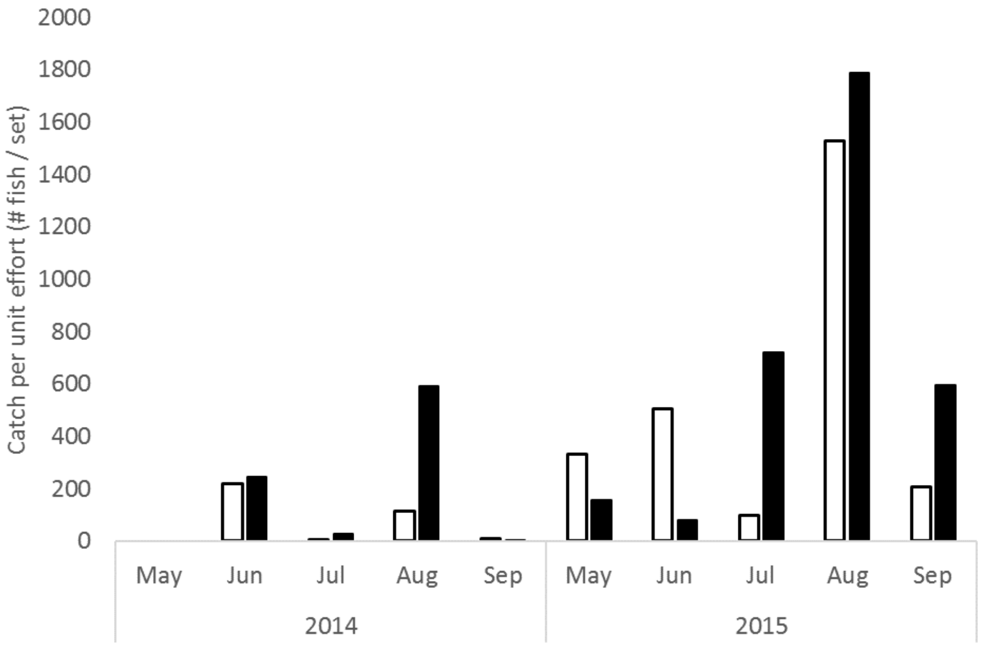


Figure 6.3.2. Catch per unit effort (# fish / set) for each Pacific Herring (unfilled) and Pacific sand lance (filled) by month and year sampled in the nearshore habitats of the San Juan Islands.

The proportion of Pacific herring and Pacific sand lance in diets of juvenile Chinook salmon were reasonably correlated with CPUE of both species from June – August (Figure 6.3.3). Temporal patterns of herring CPUE were nearly identical to the proportion represented in the diets of juvenile Chinook salmon. Both CPUE and diet proportion for herring were high in June, dipped in July and then rebounded again in August. Patterns between sand lance CPUE and diet proportion were also very similar. Both CPUE and diet proportion scaled together during June and July showing an increase in both datasets. However, while sand lance CPUE increased considerably in August, the proportion of sand lance in the diet decreased.

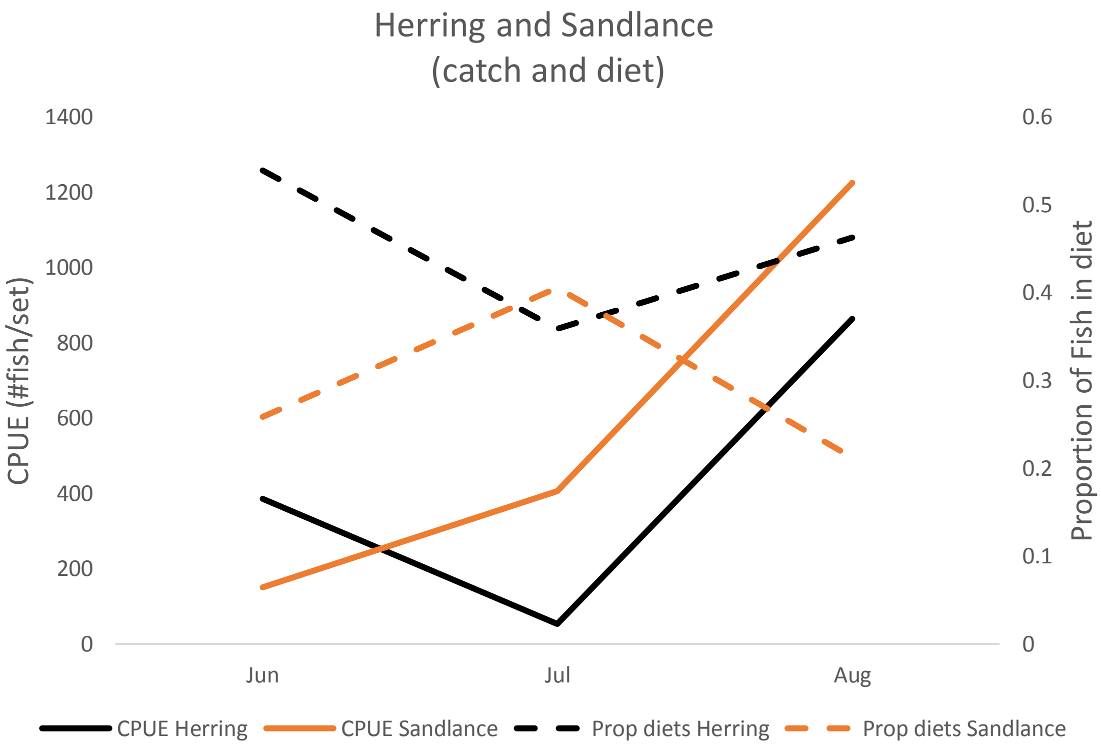


Figure 6.3.3. Monthly catch per unit effort for Pacific herring and sand lance and associated mean proportion (biomass) of each respective species in individual juvenile Chinook salmon diets from 2014-2015.

Distribution of Pacific Herring and Pacific sand lance across the sites sampled was not uniform (Figure 6.3.4). Pacific herring were present at more sites than Pacific sand lance but where sand lance were present they were found in higher abundance. The proportion of herring and sand lance found in juvenile Chinook diets at each site followed patterns of distribution to some degree but presence of either species at a given site did not guarantee presence in individual diets (Figure 6.3.4). However, where CPUE was highest, the proportion of each species in the diets was generally elevated although exceptions were observed. Both James Island and N.

Spencer had high CPUE for herring and sand lance but no diets were available to compare diet contributions for either species.

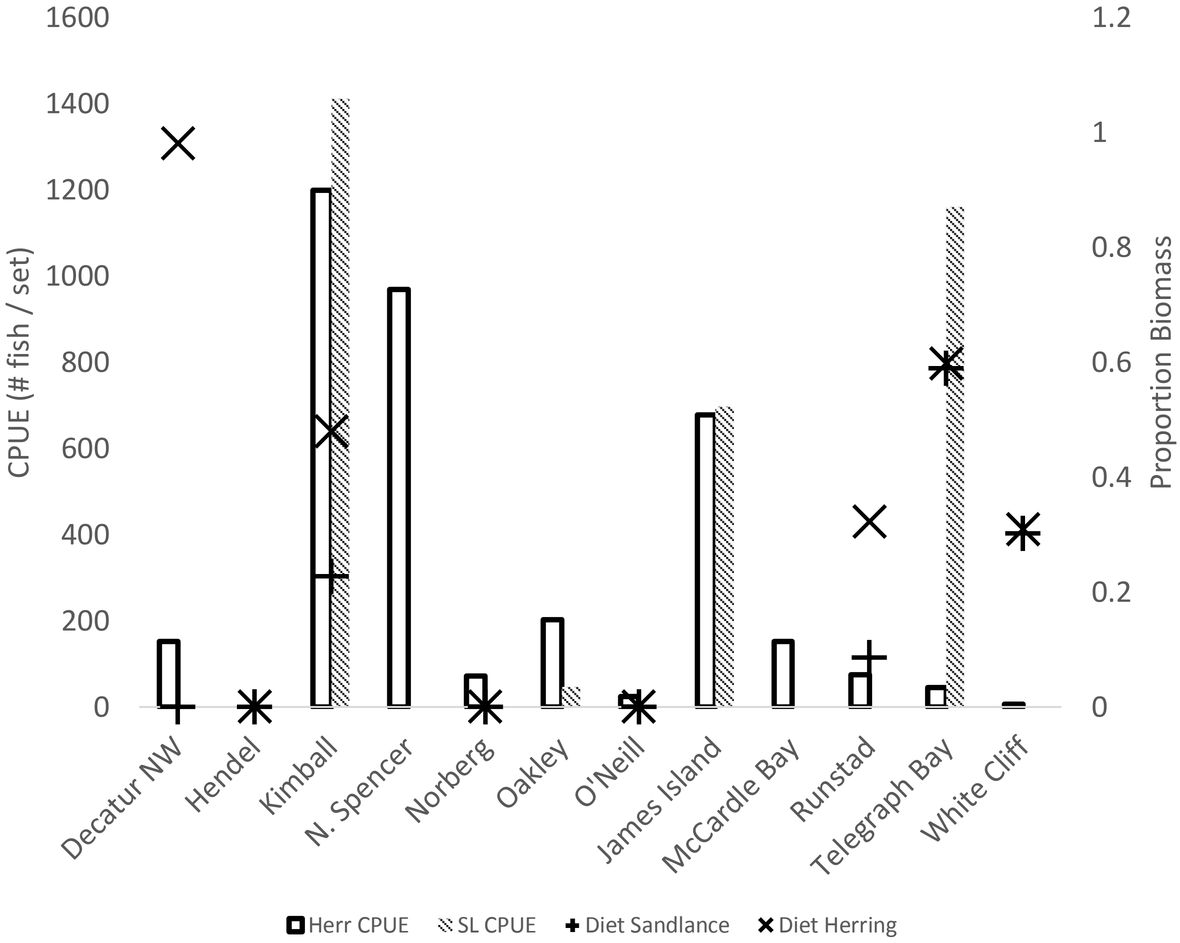


Figure 6.3.4. Catch per unit effort by site for Pacific herring (unfilled) and sand lance (shaded) and associated mean proportion (biomass) of each respective species in individual juvenile Chinook salmon diets from 2014-2015.

We used fork lengths of Chinook salmon and both prey species to determine a empirical predator:prey size ratio for all samples where fish were found in individuals guts. Samples used to directly estimate fork lengths of Pacific herring and Pacific sand lance found in the stomach contents of juvenile Chinook salmon captured in the San Juan Islands were limited (n= 15 and 47, respectively). Sample sizes were increased (n = 77 and 66, respectively) using regression equations for spinal length to fork length for both species (Figure 6.3.5).

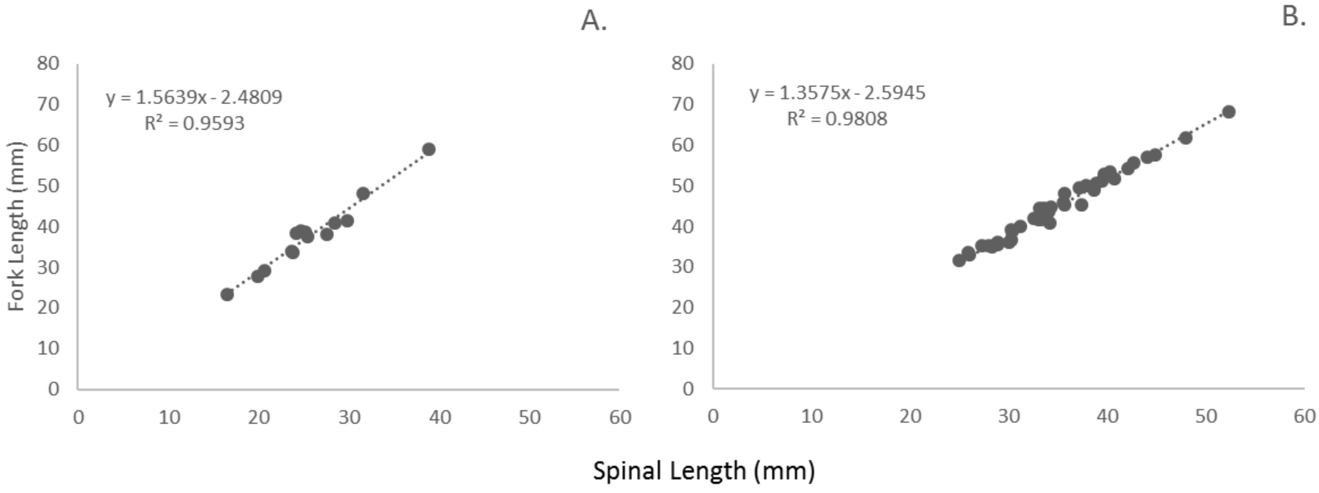


Figure 6.3.5. Fork length to spinal length regression estimates for Pacific Herring (A) and Pacific sand lance (B) as found in individual diets of juvenile Chinook salmon.

Mean prey:predator size ratios were generally consistent from year to year and ranged between 0.31 and 0.56 (Table 6.3.2). Mean sand lance ratios were typically higher than ratios observed for herring and ratios for both species tended to increase through time. Maximum ratios consistently higher for sand lance in 2014 and generally higher in 2015 with the exception of 2015.

Table 6.3.2. Mean (maximum) observed prey length to predator length ratios for Pacific herring and Pacific sand lance found in individual Chinook salmon diets.

	2014		2015	
	Herring	sand lance	Herring	sand lance
June	0.31 (0.49)	0.33 (0.58)	0.37 (0.51)	0.34 (0.41)
July	0.41 (0.41)	0.56 (0.57)	0.37 (0.44)	0.43 (0.61)
August	0.40 (0.40)		0.39 (0.46)	0.44 (0.51)

Fork lengths of both Pacific herring and Pacific sand lance generally increased through time (Figure 6.3.6). Herring were usually smaller than sand lance in any given month although the difference was minimal in August and September. Larger sand lance were present in May before a smaller size class became present in June and appeared to reside for the remainder of the summer. Juvenile Chinook salmon also increased in size from May through August (Figure 6.3.7). The median size of Chinook in most months was between 1 and 2x greater than the median size of either Pacific herring or Pacific sand lance with the exception of the large sand lance present in May.

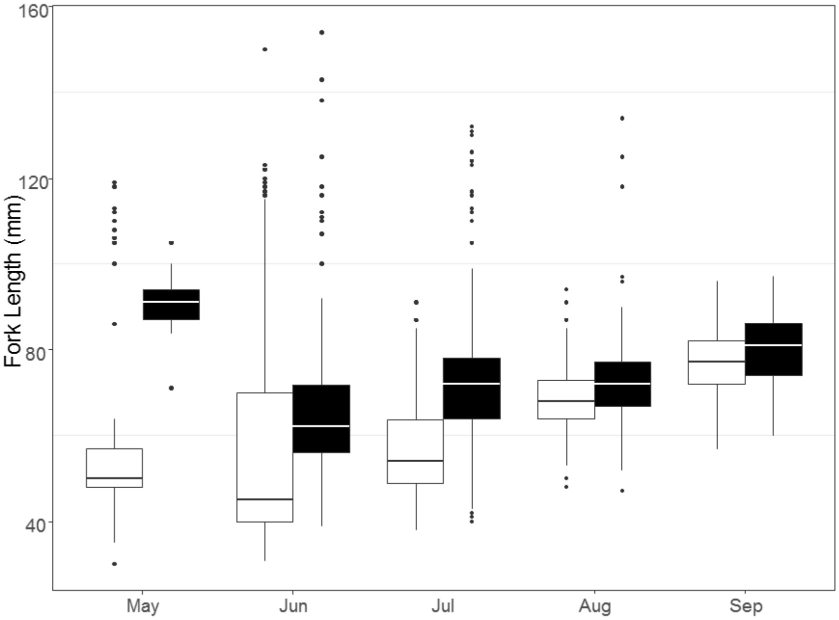


Figure 6.3.6. Boxplots of fork lengths by month for Pacific herring (unfilled) and Sand lance (filled) captured in the San Juan Islands. Horizontal lines are medians, boxes represent the first and third quartiles, and vertical lines the upper and lower 95%. Dots indicate outliers in the data

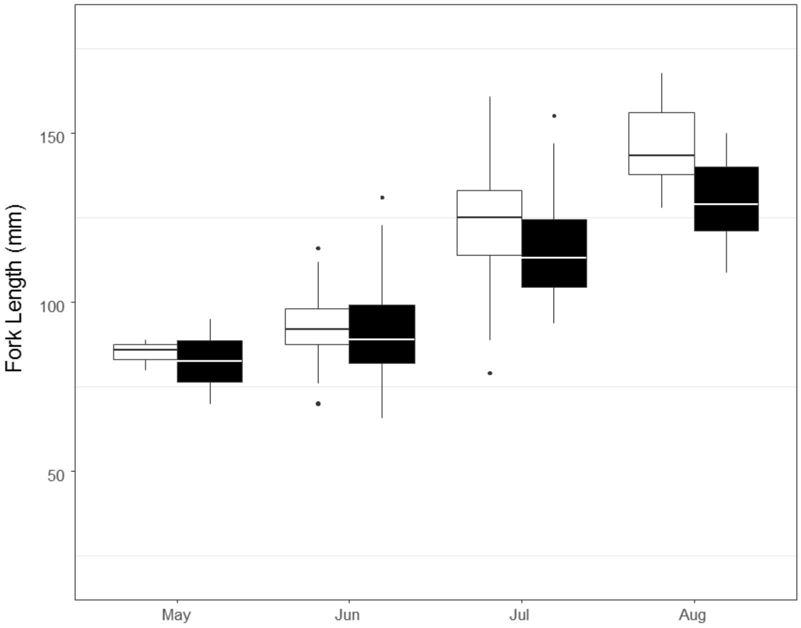


Figure 6.3.7. Boxplots of fork lengths by month for marked (unfilled) and unmarked (filled) juvenile Chinook salmon captured in the San Juan Islands. Horizontal lines are medians, boxes represent the first and third quartiles, and vertical lines the upper and lower 95%. Dots indicate outliers in the data.

Using the estimated prey:predator size ratios and the known size distributions through time of Chinook salmon and both prey species, we can estimate the proportion of the herring and sand lance population that is available for predation. Sizeable proportions of each prey fish population were available for consumption to Chinook salmon of average and above average size in all months (Figure 6.3.8). In June, a significant proportion of the herring population could potentially be preyed upon by juvenile Chinook salmon however, the proportion decreased steadily through time. In contrast, very little of the sand lance population was small enough for potential predation by juvenile Chinook in June though the proportion increased considerably in July and into August. These patterns follow the patterns in diet proportion and prey fish abundance we observed as described above (Figure 6.3.8)

In most months the difference between available proportions for the upper 50% and the upper 25% of the Chinook population was quite large with the exception of sand lance in June (Figure 6.3.8). On average there was an additional 17% of the herring and/or sand lance population available for predation for Chinook salmon that represented the largest 25% in any given month. The maximum size at which sand lance could be preyed upon (79mm) was larger than that for Pacific herring (65mm) likely due to difference in body form and morphometric constraints (gape width) in juvenile Chinook salmon.

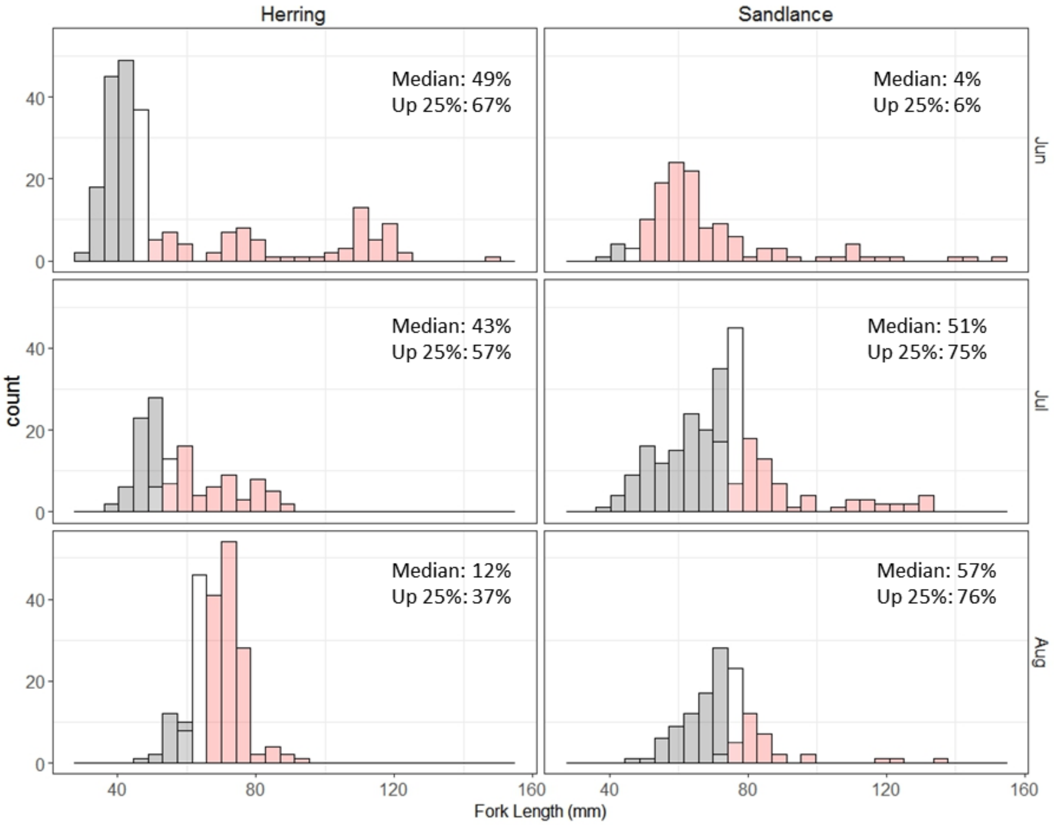


Figure 6.3.8. Length frequency histograms by month for Pacific herring and Pacific sand lance representing potential availability as prey for juvenile Chinook salmon in the upper 50% (shaded) and upper 25% (unfilled) of the population for fork length. Red bars represent the reminder of the respective populations not available to the size classes described above.

6.3.1 Conclusions

- The proportion of diet samples that contained fish were significantly higher in the San Juan Islands than either the Nooksack or Skagit regions and the mean relative proportion of fish in diets samples was considerably higher in the San Juan Islands (~50%).
- Catch per unit effort (CPUE) of Pacific herring and Pacific sand lance in nearshore beach seine samples in the San Juan Islands during 2014-15 were orders of magnitude higher than any other species encountered. CPUE of both species was generally higher in 2015 compared to 2014 and fluctuated by month with higher proportions of Pacific herring early in the summer followed by peak CPUE of Pacific sand lance later in the summer.
- Monthly changes in mean proportion of each species found in juvenile salmon diets was closely correlated with changes in monthly CPUE of each species.
- In general, the proportion of each species in individual diets from particular sites were higher when CPUE of each species at a particular site was elevated.
- The relationship between predator size and prey size for each species was consistent from year to year and the ratio generally increased through time from June – August. Ratios were typically higher for Pacific sand lance compared to Pacific herring.
- Based on length frequencies for both species as well as juvenile Chinook salmon and the relationship between predator size and prey size, there were considerable proportions of the local herring and sand lance populations available as prey to the average or above average Chinook salmon in habituating the area.

6.4 Zooplankton and Diet comparison: how well does prey availability represent diet composition?

6.4.1 Methods

Zooplankton assemblage and diet composition biomass data were combined to assess the level of overlap between prey availability and prey found in stomach contents of juvenile Chinook salmon. Zooplankton assemblage data contained several categories or species groups that are not commonly found in the diets of juvenile salmonids. Therefore, we reduced the set of variables to include only those believed to represent a prey field index (PFI) which included all the categories used for diet composition analyses. To reduce the effect of site variability in diet composition when comparing with zooplankton assemblages, diets were averaged across all sites within a given region for each month x year combination. We performed separate analyses for offshore diets and nearshore diets given differences we observed in diet composition among the habitat types. Prior to analysis we standardized the data to relative proportions for each sample or sample group (diets) and 4th root transformed proportions to reduce skew in the data.

We used a suite of multivariate techniques to visualize and test for differences between zooplankton assemblage and diet composition data within regions and months and between years. NMDS plots were used primarily to visualize potential differences in composition between zooplankton and diet samples due to the factors tested. PERMANOVA procedures were used to statistically test differences due to sample type as well as any interaction between sample type and year, month, or region. We were not explicitly interested in testing the single factors of year, month, or region for this analysis as it had been done in the previous section with the separate zooplankton assemblage and diet composition datasets. PCO plots were created to visualize difference due to interactions while SIMPER (percent similarity) procedures were run to quantify differences (mean dissimilarities) and to assign variability to particular diet/zooplankton categories.

6.4.2 Results

We evaluated a total of N = 141 samples (nearshore diets = 22, offshore diets = 20, zooplankton = 99) across 13 diet/zooplankton categories (Table A1) were analyzed. Initial inspection of NMDS plots showed separation among diet and zooplankton samples although distances appeared greater between zooplankton samples and nearshore diet samples compared to offshore diet samples (Figure 6.4.1). Diets also appeared to be much more variable, or dispersed compared to zooplankton samples which were all tightly grouped.

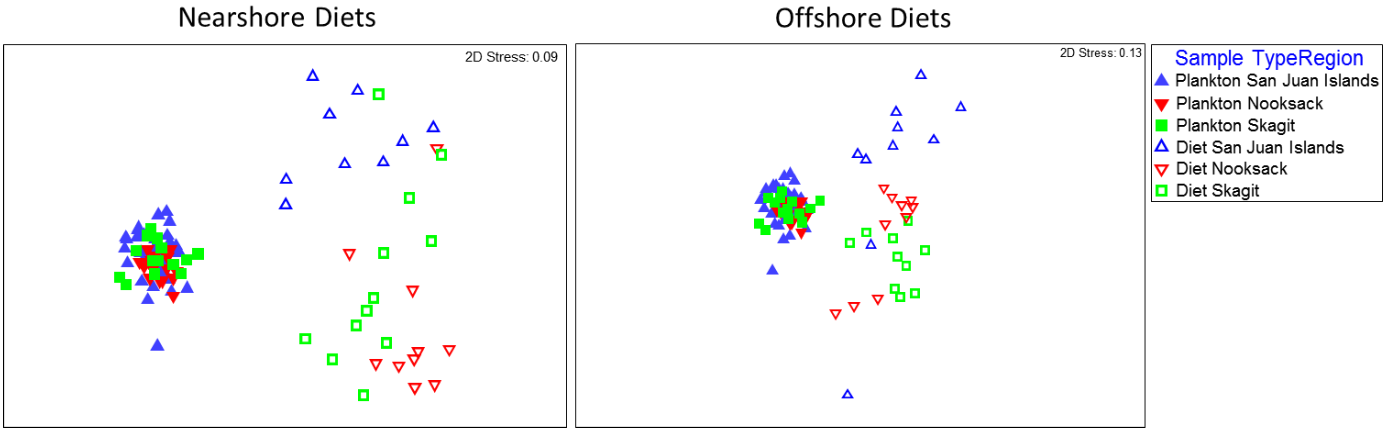


Figure 6.4.1. NMDS plots of zooplankton assemblage and juvenile Chinook salmon diet composition by sample type (zooplankton/diet) and regions. Separate panels represent comparisons between zooplankton and both nearshore and offshore diet composition.

PERMANOVA results for comparisons between zooplankton samples and both nearshore and offshore diets revealed some similar patterns (Table 6.4.1). Sample type (zooplankton vs. diet) was clearly significant in both tests and alone explained a considerable proportion of the total variation in each dataset (32% for nearshore diets, 27% for offshore diets). All interactions between sample type and the other factors of interest were significant with the exception of the Sample type x Month interaction in the analysis of nearshore diets and zooplankton assemblages (Table 6.4.1).

Mean dissimilarity among Sample Types was 71.91 for nearshore diets and 57.68 for offshore diets (Table 6.4.2). Differences were primarily driven by copepods, fish, insects and, to a lesser degree, decapod megalops, decapod zoea, and worms (Table 6.4.2). In general, zooplankton assemblages had far higher proportions of copepods than was represented in diet composition while the opposite was true for both fish prey and insects. Comparisons between zooplankton assemblages and nearshore diets revealed additional differences in the proportions of decapod zoea. Decapod zoea were present in considerably higher proportion than found in nearshore diet samples. For offshore diet comparisons, additional differences were driven by discrepancies in the proportions of decapod megalops. Offshore diets had higher proportions of decapod megalops than were present in the zooplankton assemblages.

Table 6.4.1. PERMANOVA results table for analysis of overlap between zooplankton assemblages and nearshore and offshore diet composition. Where number of unique permutations <25, p values were obtained using Monte Carlo simulations.

Factors	Abbrev.	Type	Levels
Sample Type	Sa	Fixed	2
Year	Ye	Random	2
Region	Re	Fixed	3
Month	Mo	Fixed	3

Nearshore	Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
	Sa	1	71093	71093	23.869	0.007	6
	Ye	1	2541.1	2541.1	7.0081	0.001	998
	Re	2	10888	5443.9	15.014	0.001	997
	Mo	2	3384.3	1692.1	4.6667	0.001	998
	SaxYe	1	3127.6	3127.6	8.6256	0.001	998
	SaxRe	2	9277.2	4638.6	12.793	0.001	997
	SaxMo	2	1442.1	721.06	1.9886	0.065	999
	Res	88	31909	362.6			
	Total	99	1.38E+05				

Offshore	Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
	Sa	1	34312	34312	26.686	0.004	6
	Ye	1	482.37	482.37	1.1906	0.332	999
	Re	2	12469	6234.7	15.388	0.001	999
	Mo	2	2434.9	1217.5	3.0049	0.003	999
	SaxYe	1	1371.7	1371.7	3.3856	0.007	999
	SaxRe	2	6218.2	3109.1	7.6739	0.001	998
	SaxMo	2	1822.8	911.41	2.2495	0.031	999
	Res	87	35248	405.15			
	Total	98	96558				

Table 6.4.2. SIMPER (similarity percentages) results for comparisons between zooplankton assemblages and nearshore and offshore diet composition. Means are 4th root transformed relative proportions. Percent contribution reflects the effect of particular categories on the overall dissimilarity between sample types.

Nearshore	Average dissimilarity = 71.91	Plankton	Diet		
	Category	Mean	Mean	Contrib%	Cum.%
	Insecta	0.01	2.07	15.37	15.37
	Other Crustacean & Rare Invert	2.83	0.9	14.72	30.09
	Fish	0.28	1.56	11.16	41.26
	Decapod zoea	1.56	0.32	9.86	51.11
	Worm	1.32	0.35	9.09	60.2
	Hyperiid	0.95	0.18	6.62	66.82
	Shrimp - Post larval/Adult	0.9	0.41	6.13	72.95
	Amphipod	0.25	0.93	6.11	79.06
	Decapod megalops	0.74	1.06	6.07	85.13
	Euphausiidae	0.87	0.2	5.78	90.91

Offshore	Average dissimilarity = 57.68	Plankton	Diet		
	Category	Mean	Mean	Contrib%	Cum.%
	Other Crustacean & Rare Invert	2.83	1.1	15.7	15.7
	Fish	0.28	1.81	14.85	30.56
	Insecta	0.01	1.23	10.42	40.98
	Decapod megalops	0.74	1.67	10.25	51.23
	Worm	1.32	0.63	8.51	59.74
	Decapod zoea	1.56	1.07	8.11	67.85
	Euphausiidae	0.87	0.48	7.56	75.42
	Shrimp - Post larval/Adult	0.9	0.52	6.92	82.34
	Amphipod	0.25	0.84	6.45	88.79
	Hyperiid	0.95	0.56	5.98	94.77

Interactions between Sample Type and year, month, and region were largely driven by the extreme differences between the relative proportions of items in zooplankton assemblages and diet samples (Figure 6.4.2). The first PCO axis (PCO1) explained between 68.6 – 96.4% of the total variation and was strongly correlated with sample type (Figure 6.4.2). The remaining variation was due to the regional, monthly and annual differences in diet composition as explained in section 5.2. Diet composition was typically more variable among the regions, months and across years than were the zooplankton assemblages.

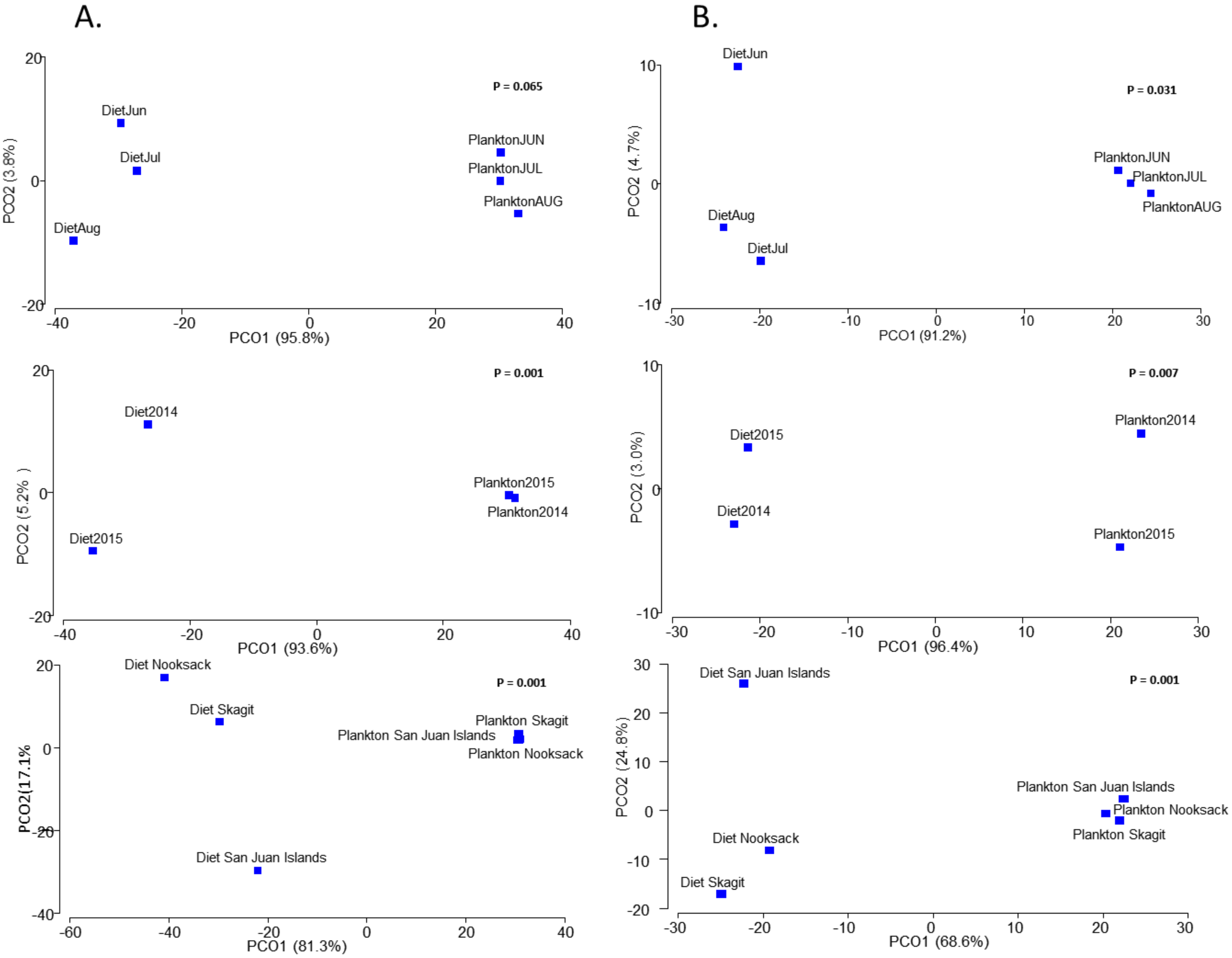


Figure 6.4.2. Principal coordinates plots on centroids for Sample Type x Month, Sample Type x Year, and Sample Type x Region interactions including nearshore (Column A) and offshore (Column B) diets.

6.4.3 Conclusions

- The relative proportions of items found in zooplankton assemblages and diet composition were significantly different. Prey availability, as represented by the assemblage samples, does not accurately reflect the relative proportions of the items found in stomach contents of juvenile Chinook salmon, which may suggest prey selectivity is occurring to some degree.

- High relative proportions of “other” crustaceans (i.e. copepods) were not reflected in diet samples while the high proportions of insects, fish prey, and to some degree decapods in diet samples were not reflected in the zooplankton assemblages. Some of these discrepancies may be explained by sampling gear/methods. Methods used to sample zooplankton assemblages do not accurately sample surface waters where insects are commonly found and may not be efficient at sampling post larval/juvenile fish.

6.5 Discussion

The results from scale growth trajectory analysis revealed no evidence for size selective mortality occurring during the first summer of marine residence for juvenile Chinook salmon and thus must assume growth throughout this period is critical for improved survival. Therefore, understanding factors that affect growth, how they change regionally and/or seasonally, is important for evaluating growth conditions for outmigrating juvenile salmon. We evaluated zooplankton assemblage, as a proxy for prey availability, and diet composition in juvenile Chinook salmon and assessed the degree of overlap between the two components to determine if juvenile chinook diets reflected species composition of the zooplankton assemblage. Such information could be useful for development of a prey field index for Puget Sound Chinook salmon.

Both zooplankton assemblage and diet composition varied among regions and through time although there was very little overlap between the zooplankton assemblage data and the species composition in stomach contents of juvenile Chinook salmon. Offshore diets were more closely related to assemblage data although still reflected considerable difference in relative contribution of species groups. The lack of overlap between plankton assemblage and diet composition is somewhat common and suggests some degrees of prey selectivity which has been observed along the coast of the north Pacific (Schabetsberger et al. 2003) as well as within local Puget Sound watersheds (Beamer et al. 2017). While zooplankton assemblages undoubtedly constrain prey availability, they do not necessarily predict diet composition. Instead, juvenile Chinook salmon appear to elect certain prey independent of its relative biomass/abundance within the zooplankton assemblage.

The most consistently abundant species group found in zooplankton assemblages within all regions and across all months and in both years were copepods. While copepods regularly contributed more than half of the biomass within the zooplankton assemblage they rarely, on average, contributed more than 10% to diets within each month and region though contributions were slightly higher in 2015 than 2014. In contrast, the most predominant species groups found in diets of juvenile chinook salmon (terrestrial insects and fish) were hardly ever accounted for in zooplankton assemblages. These differences were much more pronounced when comparing nearshore diets to zooplankton assemblage as nearshore diets in all regions were represented by a high contribution of insects and/or fish prey. However, some of the discrepancies between the two datasets can likely be explained by zooplankton sampling methods which do not directly or efficiently sample terrestrial insects or fish. Terrestrial insects are found at the water surface which is not sampled by the current zooplankton protocol and fish, at least at a certain size, may be able to avoid the bongo nets completely. However, it is important to note that juveniles Chinook in northern Puget Sound are relying heavily on prey not directly related (insects), or only indirectly related (larval/juvenile fish), to zooplankton abundance.

We did observe some species groups within the zooplankton assemblage that may provide insight in to how/why certain species groups vary within juvenile salmon diets. The seasonal differences in zooplankton assemblages within each region was largely a function of decreasing decapod abundance and increasing ctenophore abundance from May through August with a late increase in echinoderm and bryozoan biomass. While ctenophores, echinoderms and bryozoans were rarely represented in diets of juvenile salmonids, decapods, zoea and megalopae life stages, represented a considerable component of the diet and the contribution varied seasonally and among regions. Decapod zoea were the most evenly represented group within both the assemblage data and diet composition. Decapod megalops were similar to some degree though most often had higher contribution to juvenile diets than was represented in the assemblage data. Skagit and Nooksack diets had considerably higher presence of decapods when compared to the San Juan Islands, both within the zooplankton assemblage and juvenile salmon stomach contents and the proportion within each sample type generally decreased simultaneously. Decapods in the zooplankton assemblage and diet contents from the San Juan Islands, although much less pronounced than the other regions, did peak together in June indicating some coherence between the patterns in the data sets.

Annual variation in zooplankton assemblage and diet composition was less coherent than the seasonal trends among regions. Euphausiids and hyperiids were more abundant in the zooplankton assemblage during 2015. The difference was reflected to some degree in the diets from fish captured in the San Juan Islands but not in the Nooksack or Skagit. Inter-annual differences in diet composition largely reflected an increase in fish prey, which is known to not be represented in zooplankton samples. While the mechanism or reason for an increase in fish prey is unknown, there is a correlation to increased presence of Northern Anchovy in the area during 2015. Interestingly, we also observed an increase in decapod megalops in the diets from Nooksack and Skagit during 2015 that was not paired with an observed increase in decapod megalops in the zooplankton assemblage

Within the San Juan Islands, the patterns in zooplankton assemblage and diet composition followed the general pattern with one major exception; the contribution of fish to Chinook diets. While fish contributed to some degree, to the diets in all regions, fish were found in more than half the diets evaluated from fish captured in the San Juan Islands and accounted for a large proportion of the relative biomass of each diet. The most prevalent species found in the diets, Pacific herring and Pacific sand lance, were also the most abundant species captured in beach seine catches in the SE SJI. Interestingly, the proportion of each species found in the gut contents of juvenile Chinook salmon followed patterns of CPUE for both species indicating local changes in abundance can alter or effect the overall contribution to juvenile salmonid diets. In addition to the high abundances of these prey species, the size distribution of the local herring and sand lance populations are structured such that a considerable proportion are available as prey. In some months more than half of the herring and sand lance inhabiting the nearshore areas of the San Juan Island are small enough to be prey for the average size Chinook observed within each month. The co-occurrence of these small herring and sand lance provide both a high biomass of high-energy prey unique to nearshore habitats in northern Puget Sound.

7. Evaluating individual growth & establishing the mechanistic relationships between growth & potential limiting factors including temperature, food supply, & competition

7.1 Evaluating individual growth rates in Chinook salmon

7.1.1 Methods

Individual growth rates were assessed by evaluating concentration of insulin like growth factor-1 (IGF-1) in individual Chinook salmon captured throughout Puget Sound. Insulin-like growth factor-1 (IGF-1) is a plasma hormone known to stimulate and support cellular growth in individual animals (Mommsen 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 fishes, and in particular salmonids, across a variety of conditions (e.g. temporal/seasonal, physical etc. (Beckman et al. 2004, Larsen et al. 2010, Stefansson et al. 2012) and as a function of individual size (Beaudreau et al. 2011).

Due to the limitations of comparing IGF-1 concentrations across seasons (Beaudreau et al. 2011, Beckman 2011) we limited our analyses to fish sampled during the summer months (June-August). Similarly, we reduced the sample set to individuals < 200 mm fork length given the potential for sexual maturation (gonadal growth) to bias our interpretation of IGF-1 conetrations (Beckman 2011). A total of 12 individuals (0.9%) were removed from the entire dataset prior to analysis. A subset of both marked (hatchery origin) and unmarked (presumed natural origin) Chinook salmon from each site were euthanized for growth analysis. Fish were selected at random and assumed to represent the observed length distributions of the entire catch. However, blood samples were not taken from any fish < 50 mm fork length due to the small volume of bllod available from smaller fish. 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 and placed into 5ml micro tubes and stored on wet ice for no more than 2 hrs before being spun in a centrifuge for 5 minutes at 5000 rpm. Plasma was then separated from the red blood cells and immediately frozen. Samples were transferred to the -80C freezer within 12 hours and stored until lab processing occurred.

In brief, IGF-1 was measured 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). Samples (n =63) that had a CV that exceed 10% were excluded from the study.

We used a combination of univariate and multivariate techniques to evaluate differences in individual growth rates of Chinook salmon. Our analyses focused on describing differences in individual growth rates as a function of individual size, location and habitat (nearshore v offshore) of capture, temporal pattern (Year and month), and the influence of diet composition or prey type/resources. We used traditional univariate regression techniques to partition variation in individual growth rates among the factors of interest. Multivariate techniques were used to incorporate and compare multiple data sets including individual growth/size information and diet composition for individual fish.

7.1.2 Results

A total of N = 1224 juvenile Chinook salmon were sampled for IGF-1 concentration in 2014 and 2015 (Table 7.1.1). Samples were collected in all three regions of interest and represented both nearshore and offshore life stages. No nearshore samples were taken from the Nooksack in 2015, from the Skagit in August 2015, nor after June in 2014 due to absence or very low presence in the beach seine catches. Mean IGF-1 concentrations across the entire sample set were higher in 2015 compared to 2014 ($t = -4.509$, $p < 0.001$) as were mean fork lengths of individual Chinook salmon ($t = -9.908$, $p < 0.001$). However, differences between years were only significant within the Skagit ($t = -2.729$, $p = 0.006$) and Nooksack ($t = -6.656$, $p < 0.001$) and not within the San Juan Islands ($t = -1.430$, $p = 0.155$).

Table 7.1.1. Sample sizes to assess IGF-1 concentration in juvenile Chinook salmon among regions and months and between life stages and years.

		2014			2015		
		Jun	Jul	Aug	Jun	Jul	Aug
Nooksack	Nearshore	28					
	Offshore	55	37	45	67	106	52
SJI	Nearshore	52	59	7	8	17	7
	Offshore	16	6	1	10	21	14
Skagit	Nearshore	34	39	11	21	35	
	Offshore	94	97	48	105	99	45

Although differences in mean IGF-1 concentrations differed within the Skagit and Nooksack between years, the general patterns, or relative concentrations, among all regions and across habitats in both years were remarkably consistent (Figure 7.1.1). IGF-1 concentrations appeared to be consistently higher in the San Juan Islands than in the other regions. The largest observe differences appeared to exist between the nearshore habitats among the regions. IGF-1 concentrations in the San Juan Islands nearshore were more similar to, and typically higher than, concentrations observed in the offshore habitats of either the Skagit or the Nooksack. The largest difference within a region occurred between nearshore and offshore concentration observed in the Nooksack although comparisons were only made for 2014.

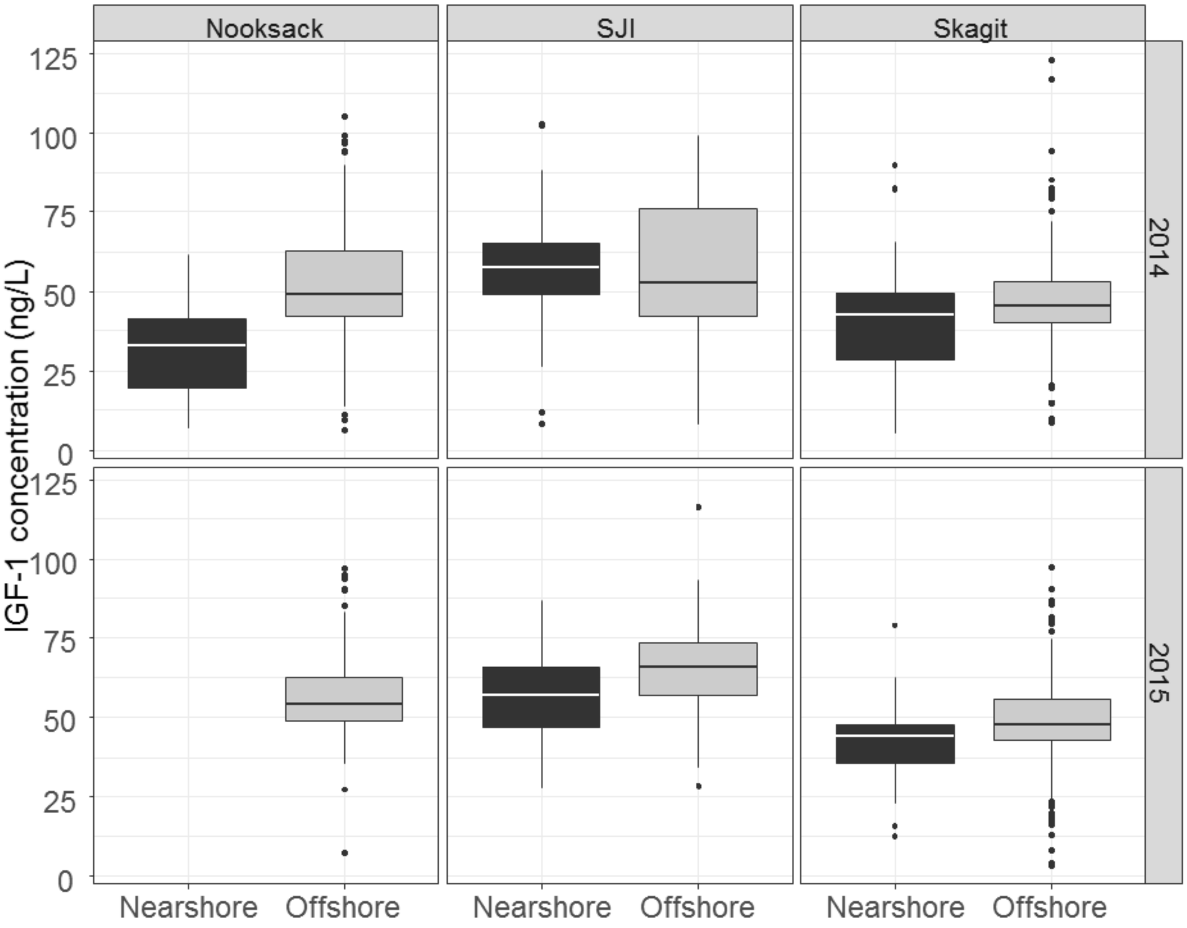


Figure 7.1.1. Boxplots of IGF-1 concentrations by region and lifestage in 2014-2015. Horizontal lines are medians, boxes represent the first and third quartiles, and vertical lines the upper and lower 95%. Dots indicate outliers in the data.

IGF-1 concentration was strongly and positively related to individual fork length of juvenile Chinook salmon (Figure 7.1.2). Linear model results indicated fork length accounted for the majority of the total explained variation ($R^2 = 0.44$) in IGF-1 concentrations (Figure 7.1.3). The majority of the remaining variance was explained by regional differences while less than 10% of the total variance was explained by lifestage, month, and year combined. The slopes of the relationship between fork length and IGF-1 concentrations among regions was not uniform but the differences were not significant (Table 7.1.2). In contrast, the intercepts were significantly different consistent with the test for means as described above. The slope of the relationship between IGF-1 concentration and fork length for fish captured in the San Juan Islands and

Skagit regions were very similar although the intercept in the San Juan Islands was considerably higher.

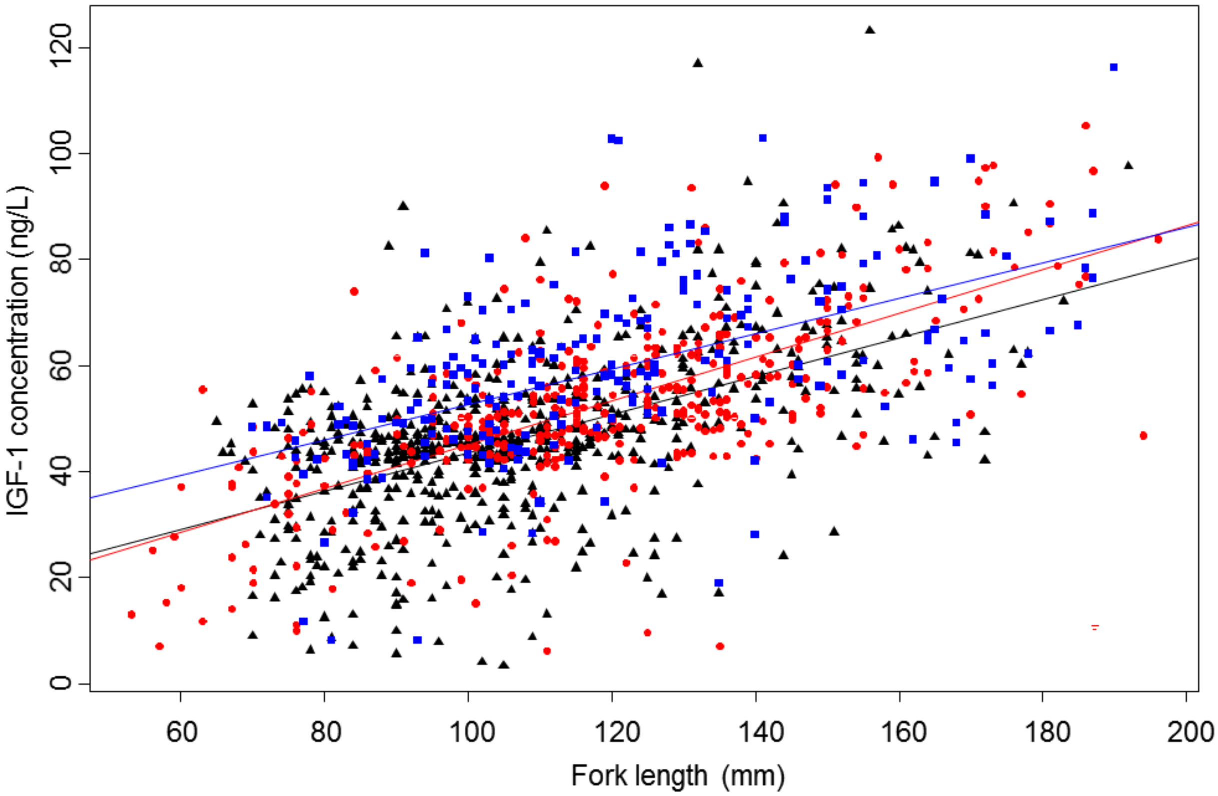


Figure 7.1.2. Scatterplot of IGF-1 concentration by fork length for fish captured in the San Juan Islands (blue squares), Nooksack (red dots), and Skagit (black triangles).

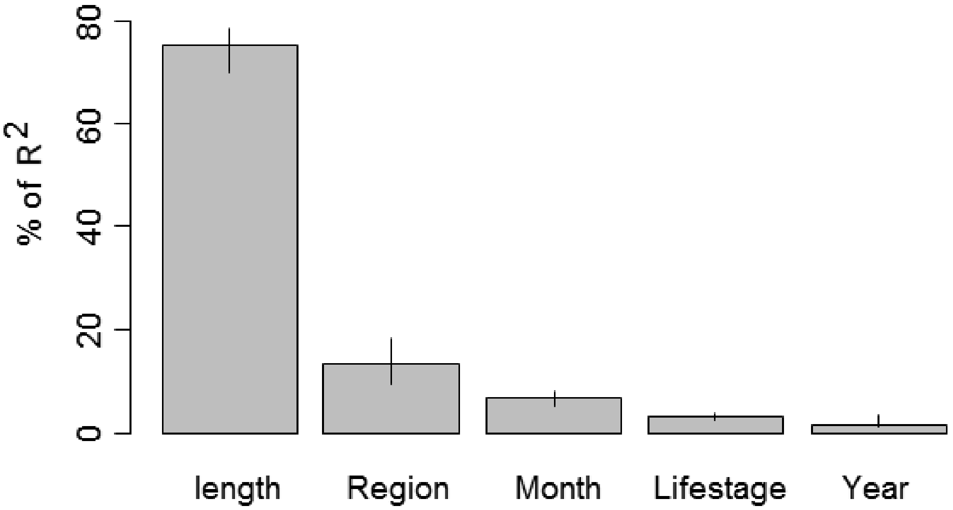


Figure 7.1.3. Bar plot of relative importance (% R^2) for each term in the linear regression model. Percentages are means for each term fit in different order with 95% bootstrapped confidence intervals.

Table 7.1.2. Intercept and slope values for regression models evaluating IGF-1 concentration as a function of fork length within each region. Letters in parentheses denote statistically significant (α = 0.05) groups using post-hoc Tukey HSD test.

	Intercept	Slope
Nooksack	4.14 (a)	0.41 (a)
SJI	19.56 (b)	0.33 (a)
Skagit	7.56 (c)	0.36 (a)

Juvenile Chinook salmon appeared to be larger during the sampling period in 2015 compared to 2014 across all regions and life stages (Table 7.1.3). Length frequencies of Chinook within each lifestage was relatively consistent between the Nooksack and Skagit regions though length distributions from the Nooksack offshore habitats in 2015 included a greater number of larger fish (Figure 7.1.4). Chinook in the San Juan Islands captured in both the nearshore and offshore habitats appeared to be more similar to the distributions found in the offshore habitats of the other regions. Larger fish were much more abundant in the nearshore habitats of the San Juan Islands when compared to the size distributions sampled from the nearshore areas of either the Nooksack or the Skagit regions. Similarly, the smallest Chinook salmon captured in the San Juan Islands nearshore were most similar to the mean fish size, or mode of the length distribution, from the nearshore of the Skagit and Nooksack.

Table 7.1.3. Mean fork lengths (SD) of juvenile Chinook salmon by region, year and lifestage.

	2014		2015	
	Nearshore	Offshore	Nearshore	Offshore
Nooksack	71.8 *(13.2)*	117.1 *(30.7)*	n/a	126.1 *(19.8)*
San Juan Islands	108.5 *(18.2)*	136.8 *(28.8)*	120.0 *(27.4)*	145.9 *(29.5)*
Skagit	86.1 *(16.0)*	108.1 *(19.2)*	91.7 *(12.5)*	117.9 *(23.6)*

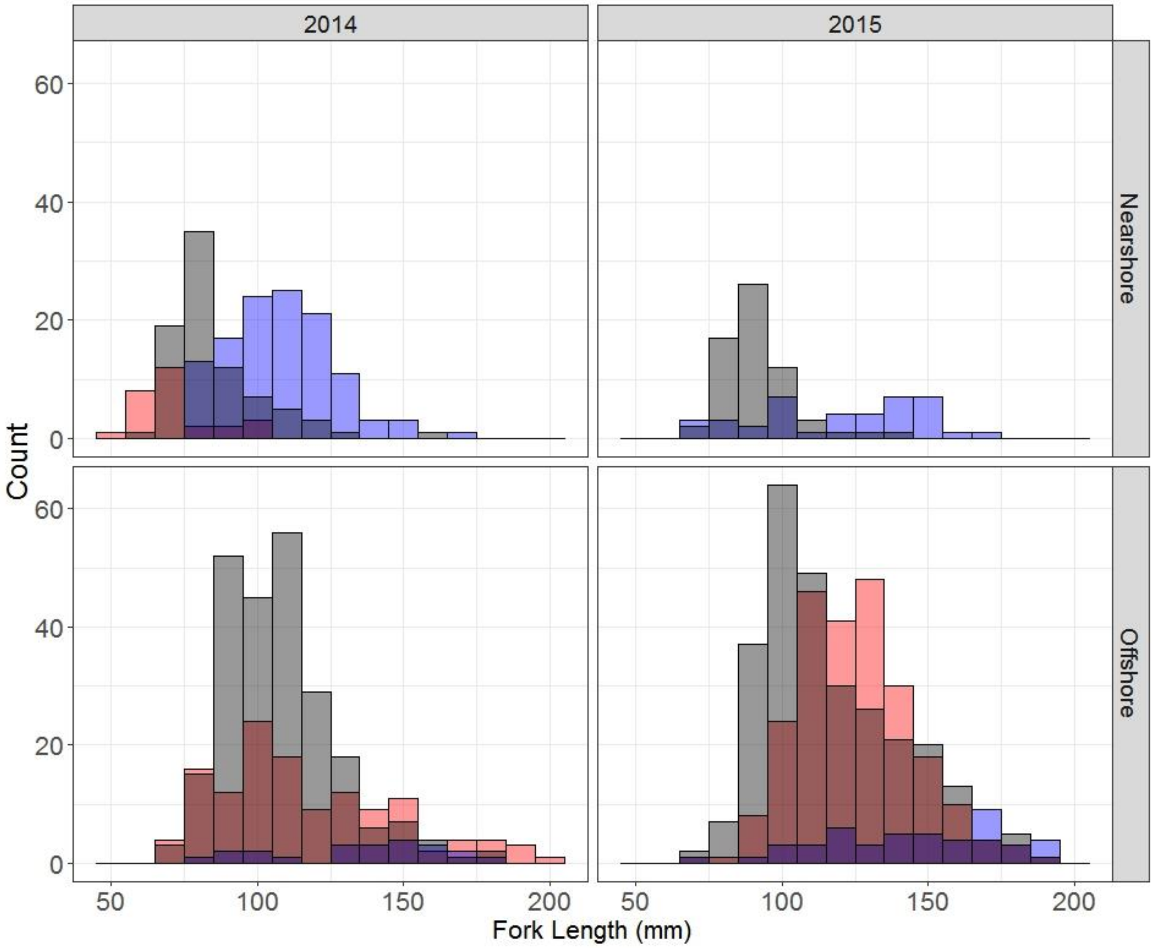


Figure 7.1.4. Length frequency distributions of Chinook salmon sampled for IGF-1 from the nearshore and offshore habitats of the Nooksack (red), San Juan Islands (blue), and Skagit (gray) regions between Jun and Aug 2014-15.

Although some size differences existed between the regions, IGF-1 concentrations for fish of within specified size classes were often higher in the San Juan Islands within a given month compared to either the Nooksack or Skagit regions, especially in the nearshore habitats (Figure 7.1.5). Difference in IGF-1 concentrations were most notable in the smaller size classes within the nearshore. The greatest differences occurred in August when concentration found in fish captured in the San Juan Islands were nearly double those found in fish captured in the Skagit nearshore. IGF-1 concentrations within size classes for fish captured in the offshore habitats were more similar across regions though values were elevated in June, and to some degree August, for the larger fish in the Nooksack and San Juan Islands compared to the Skagit region.

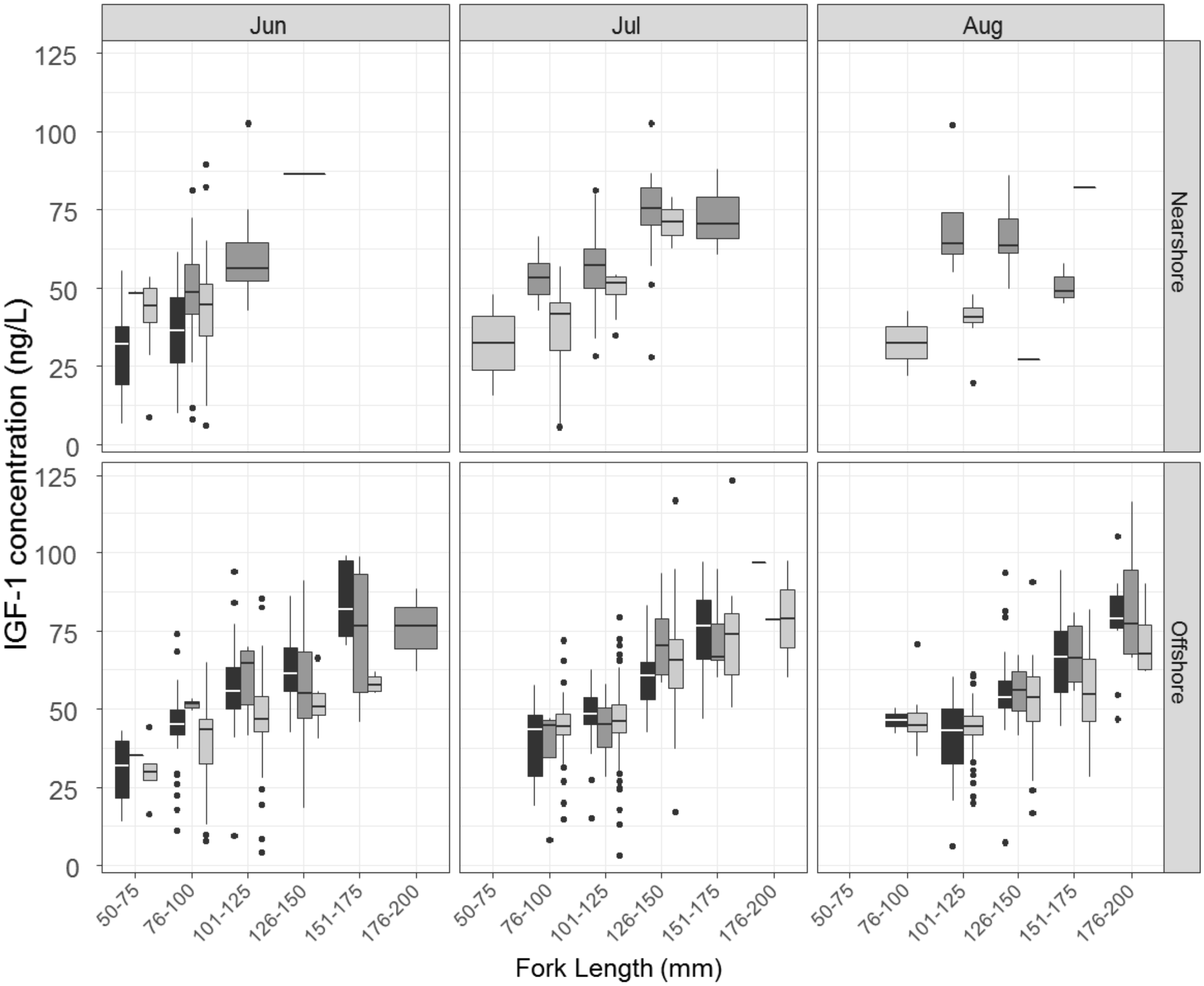


Figure 7.1.5. Boxplots of IGF-1 concentration by fork length within nearshore and offshore habtiats in Nooksack (black), San Juan Islands (dark grey), and Skagit (light grey) regions. Fork lengths were binned into 25mm size bins for comparison. Horizontal lines are medians, boxes represent the first and third quartiles, and vertical lines the upper and lower 95%. Dots indicate outliers in the data.

While variability in fish size may play a role in describing difference in IGF-1 concentrations among regions, observed differences still exist for fish of similar size and the relationship between size and IGF-1 concentration remains variable among the regions. Diet composition was observed to be significantly different among the regions (see section 6.2). Evaluating observed diet differences as a function of fork length and IGF-1 concentrations reveals interesting patterns. Differences in diet composition can be condensed and described by the relative proportion of insects, decapod megalopae, decapod zoea, “other” crustaceans (i.e. copepods, barnacle larvae, etc.) and fish in each particular diet (ρ = 0.960, Figure 7.1.6, Table 7.1.4). Mean group similarity (Bray Curtis), a measure of variability among samples within a group (0-100; 100 = identical diets), and the mean relative proportions of representative diet items was relatively high in all groups with the exception of group B. Diets within groups C and D were represented by relative proportion of insects and fish, respectively, greater than 50%.

Table 7.1.4. Diet group descriptions and within group metrics.

Diet Group	Mean w/in group Sim	Species	Mean Rel Prop	% Contrib
A	50.48	Decapod Megalopa	44.31	77.6
B	22.18	Decapod Zoea	2.94	61.05
		Other Crustacean	0.37	19.57
C	53.1	Insects	50.82	83.26
D	66.9	Fish	76.77	95.25

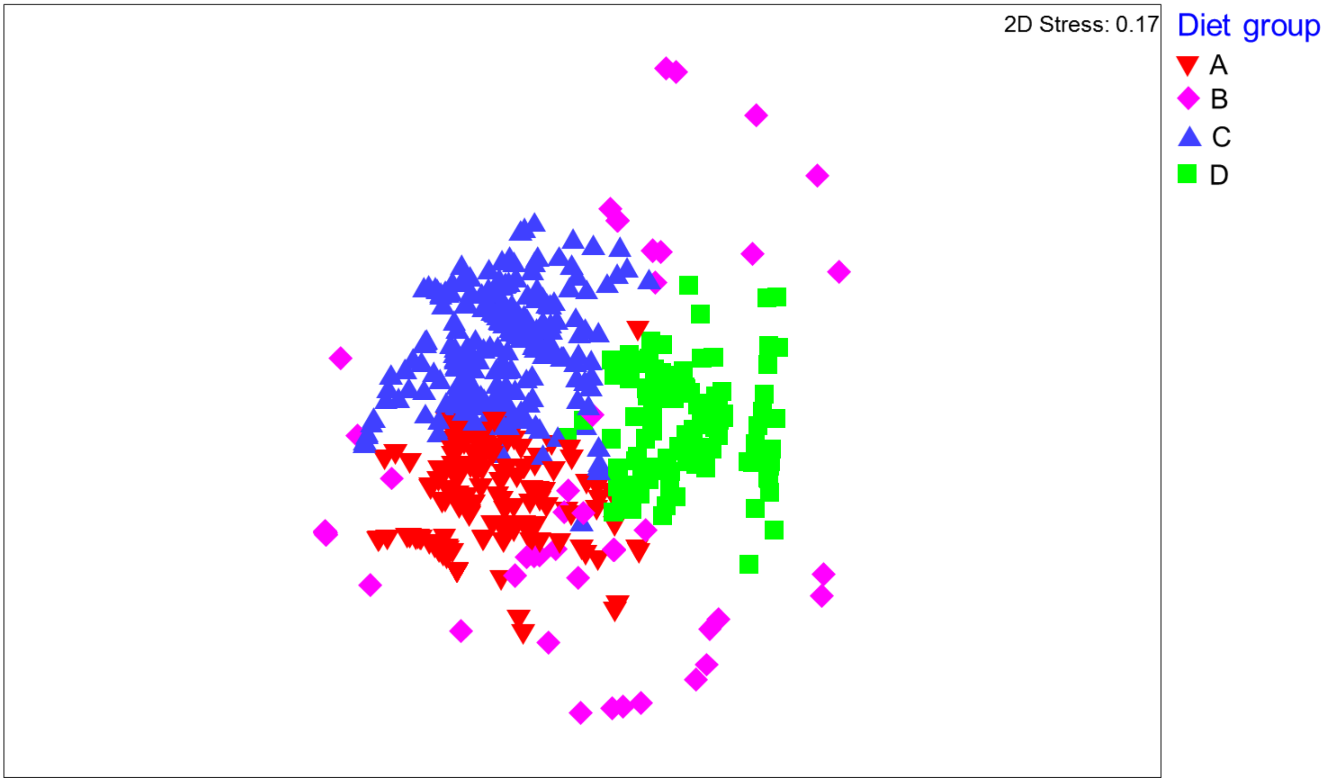


Figure 7.1.6. NMDS plot of individual diets from Nooksack, San Juan Islands, and Skagit regions represented by diet groups. Groups were identified by selecting the smallest number of diet items with the highest rank correlation (Spearman) to the entire dataset.

Constrained ordination of diet composition data as a function of fork length and IGF-1 concentrations suggests when fish are large enough to incorporate fish into their diets or when prey fish are small enough for consumption, IGF-1 concentrations are elevated (Figure 7.1.7). Along the axis representing fork length there is a clear progression from mostly insects (group C) in the diets of smaller fish thru decapod zoea and other crustaceans (group B) and onto decapod megalopae (group A) and fish (group D). Variability in IGF-1 concentrations is evident for groups A-C whereas the majority of diets classified into group D are separated from the rest of the samples and at the upper extent of the IGF-1 concentration axis for these data.

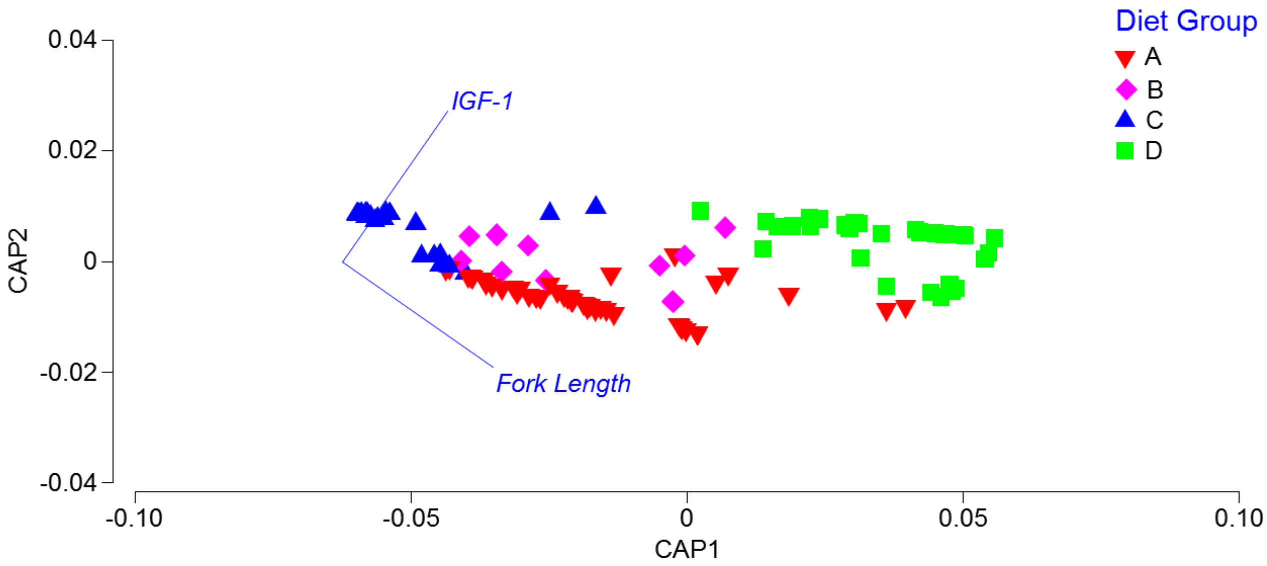


Figure 7.1.7. Constrained analysis of principal coordinates (CAP) for Chinook salmon diet composition as a function of individual fork length (mm) and IGF-1 concentration. Canonical correlation of axis 1 and 2 were δ= 0.52 and δ= 0.09, respectively.

7.1.3 Conclusions

- Median IGF-1 values differed by habitat and region but patterns were relatively consistent among years. The biggest difference occurred in the nearshore habitats where samples from the San Juan Islands were significantly higher than those from the Nooksack or Skagit. Offshore samples showed similar patterns but the differences were not as pronounced.

- There is a clear positive relationship between IGF-1 concentration and fork length across all samples and fork length accounts for the majority of the variation in IGF-1 concentrations suing simple linear models. However, the mean IGF-1 concentration (intercept) and the magnitude of the relationship between fork length and iGF-1 concentration (slope) differ among region.

- Size distributions among habitats were different in the San Juan Islands compared to the Nooksack and Skagit regions. Fish in the San Juan Islands nearshore habitats were typically larger than those in the nearshore of the Skagit or Nooksack and were more similar to the distribution found in the offshore habitats for those regions.

- IGF-1 concentrations for fish of a given size class were typically elevated in the San Juan Islands nearshore compared to the other regions. IGF-1 concentrations in offshore samples were typically more consistent among regions within a given size class though samples from the Nooksack and San Juan Islands were slightly elevated during the early sampling period.

- Incorporating diet composition data, fork lengths, and IGF-1 concentrations reveals how regional differences in diet composition and individual size are related to IGF-1 concentrations. Where fish are incorporated into the diet (San Juan Islands), IGF-1 concentrations are higher. Therefore, where fish are big enough to eat other fish and/or prey fish are small enough to be eaten, increased growth rates were observed.

7.2 Bioenergetics: growth rate, feeding rate and the effect of temperature

We used a bioenergetics framework to determine which factors affect fish growth during the early marine period for juvenile Chinook salmon. Growth conditions of habitats occupied by fish during the first marine summer critical growth period were examined to diagnose where growth opportunities exist in Puget Sound, and conversely, were growth limitations may occur. Our specific objectives to addressed were, (1) Examine differences in sub-yearling Chinook size using mass, growth rate and specific growth rate as metrics, (2) Determine water temperatures, diet composition and prey energy to be used as inputs to bioenergetics models, (3) Use bioenergetics models to fit prey consumption and feeding rate to observed ecological data, (4) Compare differences in growth metrics to explanatory ecological data, including feeding rate (a proxy for prey availability), temperature and prey energy density information. We hypothesized that growth rates of juvenile Chinook salmon would differ across time, among habitats, and among regions of Puget Sound, and that prey quality, prey availability, and water temperature would differ across similar scales. Competition was not assessed through this analysis but is being incorporated in the near future.

7.2.1 Methods

We combined empirically measured water temperatures, stage-specific weights of sub-yearling Chinook salmon, and diet data from sub-yearling Chinook salmon in bioenergetics 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. Simulations were run for individual stocks identified following the methods in **Section 4.2.** Scale growth trajectories from **Section 4.2** were used to verify that fish within stocks exhibited similar enough growth histories. Scale-based growth histories also verified that observed weights were representative of actual growth by confirming that no size-selective processes had occurred prior to weight sampling.

Temperature data collection

Temperature data were recorded concurrently with fish and zooplankton sampling when possible, and data gaps were estimated by iterating between temperatures from the preceding and following life stage (**Appendix A2**). 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 taken as the average of surface and bottom temperatures at each sample site when both values were available. There was a high level of agreement between surface and bottom temperatures and in cases when only one value was available, it was used.

Bioenergetics modeling

In constructing bioenergetics model simulations, we focused on sub-yearling Chinook from the same nine stocks we identified in **Section 4.2**. These stocks originate in our four focal watersheds (the Nisqually, Snohomish, Skagit, and Nooksack rivers). Within these stocks, we only considered 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. When possible for comparison, we also considered fish from these same stocks caught in the San Juan Islands. We only included life stages (habitat/sample period combinations) from which at least three individuals of a stock were sampled. Based on the findings from **Section 4.2**, we determined that fish from a single stock exhibited similar growth trajectories within habitats. Therefore, all fish of one stock in one habitat could be used to calculate growth for bioenergetics modeling. For the natural-origin stocks, it was known that both fry and parr migrants had been sampled, but they could not be distinguished based on scale growth trajectories, thus it was assumed that all fish from these stocks were experiencing the same growth.

Geometric mean weights were calculated for all offshore and nearshore life stages that met the above criteria (**Appendix A2)**, however, there was some irregularity in the progression of mean weights throughout the season for some stocks, likely due to small sample sizes. Therefore, we fit smoothed growth trajectories by regressing log-transformed weight by date. We then simulated growth between points on the regression of growth rather than between the geometric mean weights of fish captured at each sampling event (Table 6.2.1). When wet weights were not measured in the field, they were calculated from thawed weights measured in the lab (using size specific regressions; **Table 6.2.2**) or wet fork length (**Table 6.2.2**). When wet fork lengths were not available, they were calculated from thawed fork lengths measured in the lab (Wet Weight=10^(3.205*log10(Wet FL)-5.350)).

Bioenergetics model simulations were used to estimate feeding rate (a proxy for prey availability) 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 weights calculated from the regressions of weight over time were used as initial and final weight inputs in bioenergetics model simulations (**Table 6.2.1)**. 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). Bioenergetics 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 water temperature (**Appendix A2**), and temporal changes in diet composition (**Appendix A3**). 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 A3**). 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 within a habitat were treated as separate bioenergetics simulations such that factors affecting growth could be attributed to the appropriate habitats and temporal scales. Growth scenarios were constructed by linking life stages within one habitat consecutively in time. We calculated growth for juvenile Chinook between nearshore life stages and between offshore life stages for each stock. We were not able to model simulations for other habitats (estuary or freshwater) due to a lack of temperature data. Growth rates were calculated for each simulation by dividing the difference between input weights in the initial and final life stages by the number of days between life stages.

Table 6.2.1. Regressions of log transformed weight:time used to calculate weight inputs to the bioenergetics model

Stock	Habitat	Equation	N	R^2
2014				
Nooksack Fall (N)	Nearshore	Weight (g)=10^(0.0089*Day-0.8954)	73	0.64
Nooksack Kendall Creek	Offshore	Weight (g)=10^(0.0072*Day-0.0408)	24	0.38
Nooksack Skookum Creek	Nearshore	Weight (g)=10^(0.0050*Day+0.0162)	14	0.68
Nooksack Skookum Creek	Offshore	Weight (g)=10^(0.0112*Day-1.1088)	38	0.43
Nisqually Clear Creek	Nearshore	Weight (g)=10^(0.0063*Day-0.0814)	31	0.15
Nisqually Clear Creek	Offshore	Weight (g)=10^(0.0100*Day-0.5067)	38	0.71
Skagit Spring	Nearshore	Weight (g)=10^(0.0061*Day-0.2204)	26	0.47
Skagit Spring	Offshore	Weight (g)=10^(0.0053*Day+0.0295)	24	0.18
Skagit Summer	Nearshore	Weight (g)=10^(0.0088*Day-0.9571)	30	0.4
Skagit Summer	Nearshore	Weight (g)=10^(0.0076*Day-0.6455)	130	0.74
Upper Skagit Summer (N)	Offshore	Weight (g)=10^(0.0053*Day+0.0510)	48	0.29
Snohomish Tulalip	Offshore	Weight (g)=10^(0.0141*Day-1.4885)	30	0.48
Snohomish Wallace	Offshore	Weight (g)=10^(0.0078*Day-0.4247)	25	0.49
Upper Skagit Summer (N) in San Juan Island	Nearshore	Weight (g)=10^(0.0079*Day-0.4371)	35	0.48
2015				
Nooksack Fall (N)	Nearshore	Weight (g)=10^(0.0084*Day-0.6720)	60	0.52
Nooksack Fall (N)	Offshore	Weight (g)=10^(0.0083*Day-0.2973)	23	0.25
Nooksack Kendall Creek	Offshore	Weight (g)=10^(0.0116*Day-0.8080)	65	0.68
Nooksack Skookum Creek	Offshore	Weight (g)=10^(0.0111*Day-0.7515)	96	0.68
Nisqually Clear Creek	Nearshore	Weight (g)=10^(0.0076*Day-0.1614)	26	0.49
Nisqually Clear Creek	Offshore	Weight (g)=10^(0.0098*Day-0.2984)	40	0.65
Skagit Spring	Nearshore	Weight (g)=10^(0.0088*Day-0.5512)	50	0.62
Skagit Spring	Offshore	Weight (g)=10^(0.0103*Day-0.7668)	97	0.8
Skagit Summer	Nearshore	Weight (g)=10^(0.0116*Day-1.2670)	55	0.74
Skagit Summer	Offshore	Weight (g)=10^(0.0174*Day-2.4422)	7	0.87
Upper Skagit Summer (N)	Nearshore	Weight (g)=10^(0.0069*Day-0.2936)	95	0.63
Upper Skagit Summer (N)	Offshore	Weight (g)=10^(0.0056*Day+0.0287)	47	0.19
Snohomish Tulalip	Offshore	Weight (g)=10^(0.0100*Day-0.5271)	81	0.8
Snohomish Wallace	Offshore	Weight (g)=10^(0.0120*Day-1.0718)	97	0.82

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 or two offshore life stages, for each stock. We did not simulate feeding rates between nearshore and offshore habitats for any stock due to an inability to determine which fish were moving between habitats. Forcing simulations between these two habitats could give artificially inflated growth and feeding rates as there was evidence of size-selective habitat use with the fish that had smaller average size-at-age more frequently captured in nearshore habitats than in offshore habitats (**Section 4.2**).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. To determine the dimensions over which growth rate varied we used model comparisons of linear regressions of log10 transformed weights over time considering the factors of habitat and stock as well as interactions. We then examined visually if prey quality, prey availability (feeding rate), or temperature varied on similar scales. We were precluded from doing more in depth statistical tests due to the unbalanced nature of the design and the covariance of all factors with time. Each year was handled separately in this analysis, with between year comparisons only being done visually.

Table 6.2.2. Year and treatment specific thawed regressions for thawed to wet fork length and weight

Measurement	Treatment/ Size Class	Year	Equation	N	R^2	Thawed Measurements Used
Fork Length	None	2014	1.019*FL+2.208	1150	0.988	31-189 mm
Fork Length	None	2015	1.024*FL+2.208	576	0.988	27-242 mm
Fork Length	Ethanol Soaked	Both	1.062*FL-1.641	333	0.985	36-151 mm
Fork Length	IGF Taken	2014	1.044*FL	309	0.999	54-244 mm
Fork Length	IGF Taken	2015	1.056*FL	362	0.999	63-201
Fork Length	Standard Length	Both	0.931*FL+12.065	159	0.928	27-87 mm
Weight	Thaw 0-6.5g	Both	1.167*Weight	201	0.996	0-6 g
Weight	Thaw >=6.5g	Both	1.067*Weight+0.580	636	0.997	0-182 g

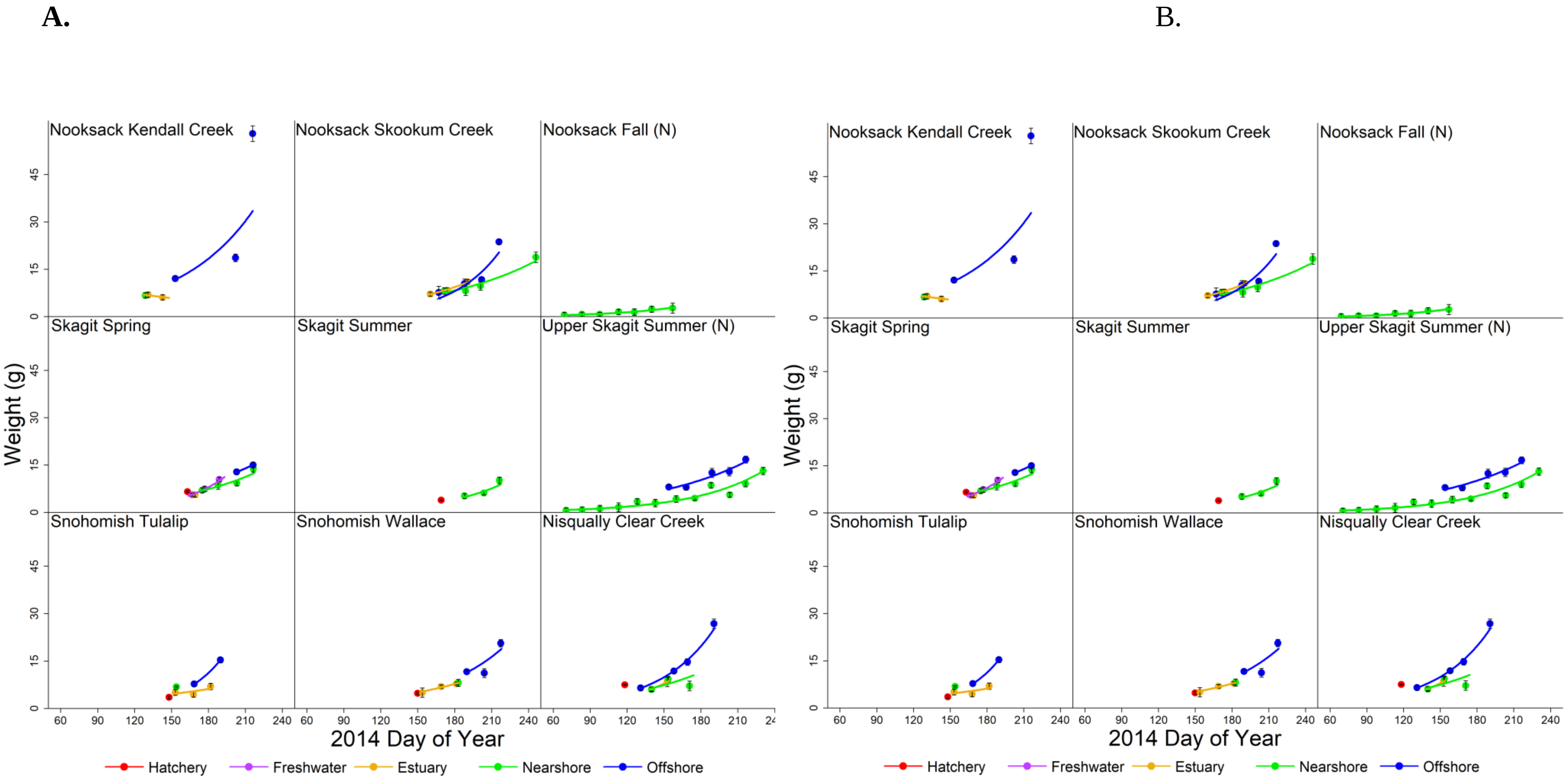


Figure 6.2.1 Geometric mean weights for each life stage (habitat and time period combination) for **(A)** 2014 and **(B)** 2015. Error bars are two geometric standard errors. If error bars aren't seen they are smaller than the point. Line on the graph are from linear regressions of log10 transformed weight. These regressions were used for weight inputs into the bioenergetics model simulations. Day 182 corresponds to July 1.

7.2.2 Results

Stage-specific weights and growth rates

Catch counts and average weights showed that all stocks grew in weight through time again suggesting each population used habitats sequentially (**Figure 6.2.1**, **Figure 4.2.1**). Year specific linear regressions of weight and sampling day of year revealed that weight changed over time but also differed by stock and habitat. Across Puget Sound and throughout our sample period, fish collected offshore in 2014 were larger than those collected in the nearshore. A similar trend was seen in 2015 though offshore and nearshore weights appeared more similar at concurrent periods than they had in 2014 (**Figure 6.2.1)**. Absolute weight gain (g) over the course of this study was highest in offshore habitats and appeared to be elevated for the Nooksack Kendal Creek, Snohomish Wallace, and Nisqually Clear Creek stocks (**Figure 6.2.1**). Weights of fish from the Nooksack Skookum Creek and Upper Skagit Summer (N) stocks caught in the San Juan Islands (SJI) nearshore during 2014, exhibit weight gains most comparable to that of their natal watershed offshore habitat (**Figure 6.2.2**). Differences in absolute weight gain among stocks and habitats suggests that each stock and habitat combination have different absolute growth rates (g/d) and should be examined individually to assess ecological factors affecting growth metrics.

Absolute growth rate (g/d) increased with time and was highest in the offshore, where fish were larger and thus able to put on more grams of growth each day (**Figure 6.2.3**). In both years, growth rates (g/d) were more variable in the offshore than the nearshore. Offshore growth rates (g/d) for most stocks were higher than nearshore with some exceptions (most notable, Upper Skagit Summer **Figure 6.2.3**). In both years, Nisqually and Nooksack hatchery stocks appear to have higher absolute growth rates (g/d) in the offshore than the Skagit and Snohomish stocks.. There is slight evidence that the Upper Skagit Summer stock caught in the SJI nearshore had higher absolute growth rates (g/d) compared to natal watershed habitats. Furthermore, their growth rate (g/d) was higher than any other nearshore simulation (**Figure 6.2.3**).

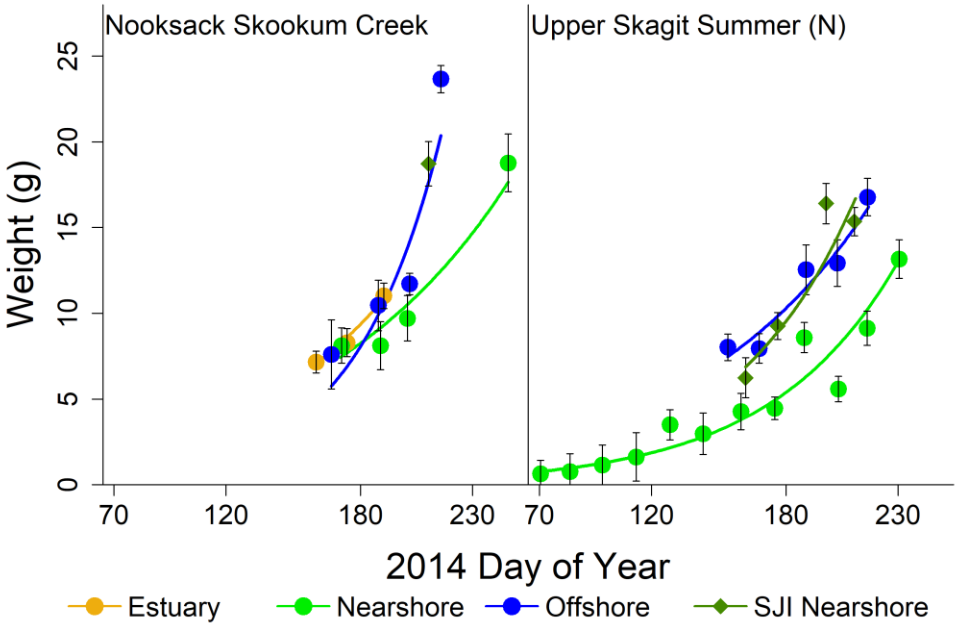


Figure 6.2.2. Geometric mean weight over time for all stocks that had enough fish caught in the San Juan Islands (SJI) to be considered. Error bars are two geometric standard errors. Day 182 corresponds to July 1.

When scaled by body size, specific growth rate (g/g*d) did not vary over time but did vary with stock and habitat (**Figure 6.2.4).** There do not appear to be trends in specific growth rate by natal watershed within habitats (**Figure 6.2.4**). In 2014, the Nooksack Skookum Creek nearshore and Upper Skagit Summer offshore fish exhibited the lowest specific growth rates, while in 2015 Upper Skagit Summer had the lowest specific growth rates in both the nearshore and offshore simulations (**Figure 6.2.4**). Interestingly, Upper Skagit Summer fish caught in the alternative SJI nearshore habitat in 2014 had specific growth rates closely tracking that of the natal watershed nearshore habitat, despite having weights (**Figure 6.2.2**) and scale-based growth trajectories (see **Section 4.2**, **Figure 4.2.6**) most similar to the offshore habitat.

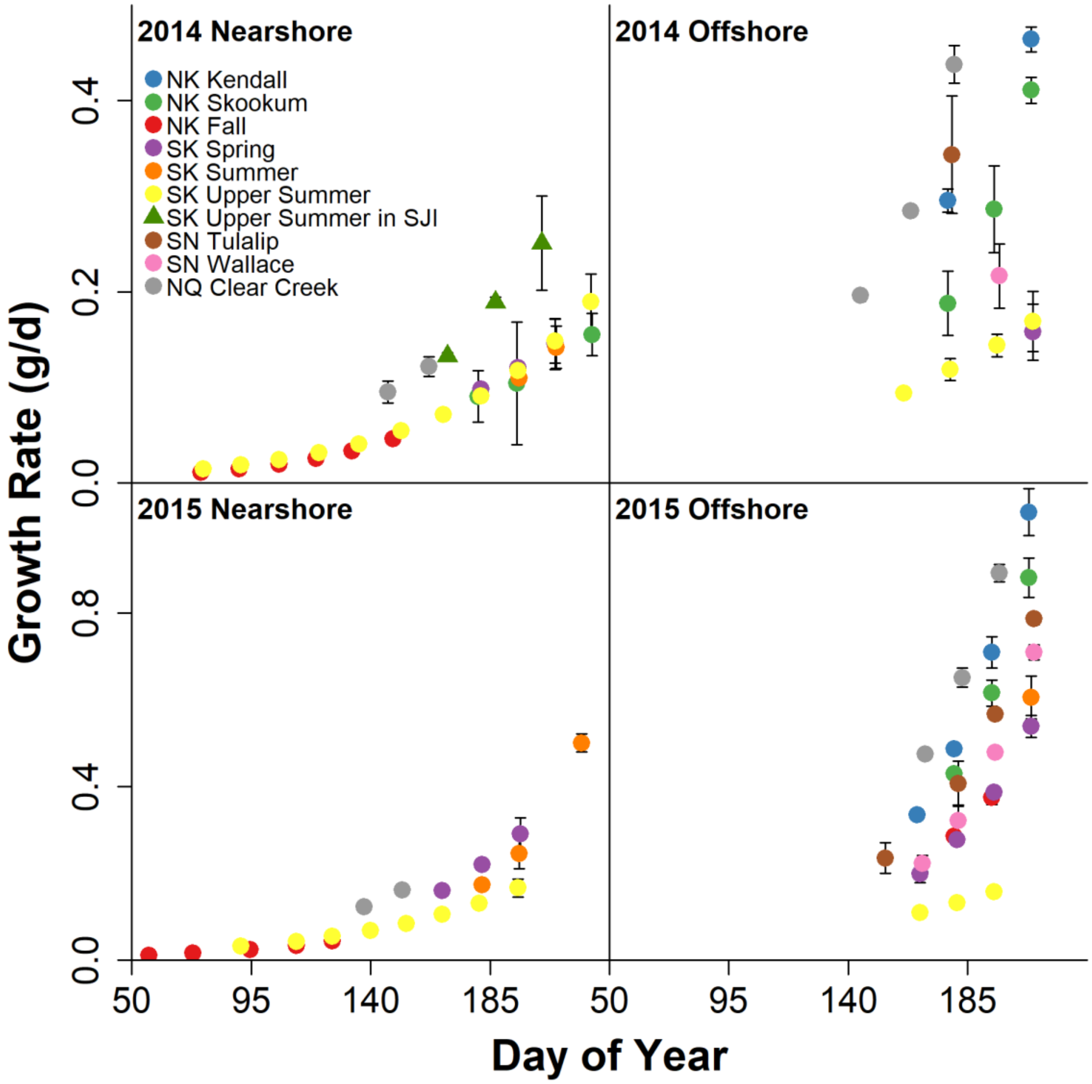


Figure 6.2.3. Growth rate over time for nearshore and offshore habitats in 2014 and 2015. Error bars are two standard errors. Error bars that aren't visible are smaller than points. Day 182 corresponds to July 1. Note that y-axis scales differ between years.

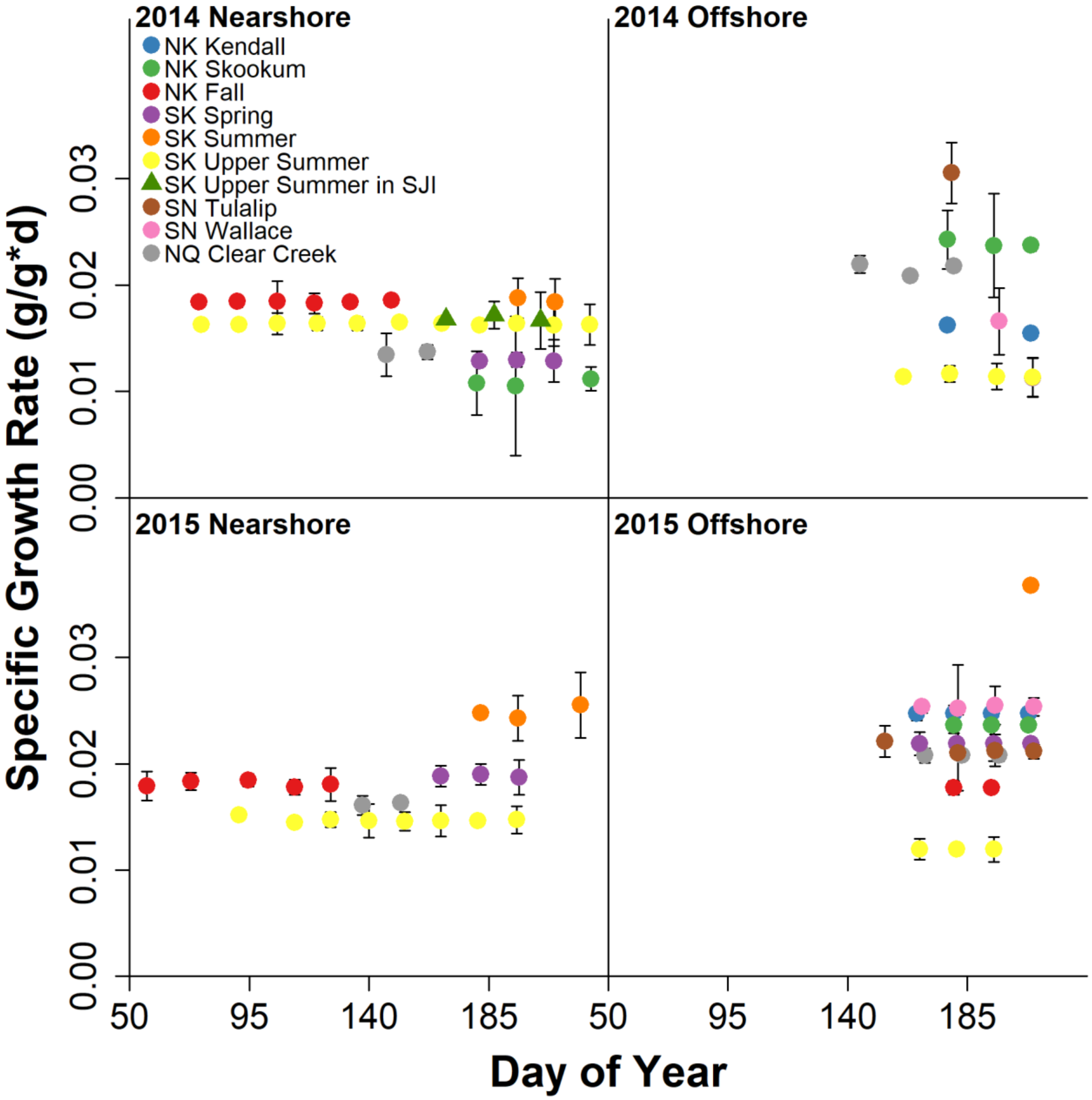


Figure 6.2.4. Specific growth rate over time for nearshore and offshore habitats in 2014 and 2015. Error bars are two standard errors. Error bars that aren't visible are smaller than points. Day 182 corresponds to July 1.

Factors affecting growth

The combination of temperature, feeding rate, and prey energy impacts the scope for growth of juvenile Chinook (**Figure 6.2.5**). The interaction of feeding rate and temperature is very important, as at low feeding rates the optimal temperature range over which growth can occur becomes much smaller. In addition, increased feeding rate can greatly increase specific growth rate (g/g*day) at optimal temperatures. Feeding rate was generally higher in offshore than nearshore for both years and higher in 2015 than 2014 (**Figure 6.2.6**). In 2014, feeding rate varied from 0.23-0.44 in the nearshore to 0.27-0.58 in the offshore, and in 2015, it varied 0.24-0.50 in the nearshore and from 0.28-0.78 in the offshore. Feeding rate appeared to increase over time in 2015 but did not show a consistent trend in 2014. Looking at individual stocks and habitats, feeding rate appears to vary on the same scale as growth rate for certain stocks (Nisqually Clear Creek) but not for others (Nooksack Fall). Averaging across all stocks and habitats Cmax(%) was 35% in 2014 and 45% in 2015.

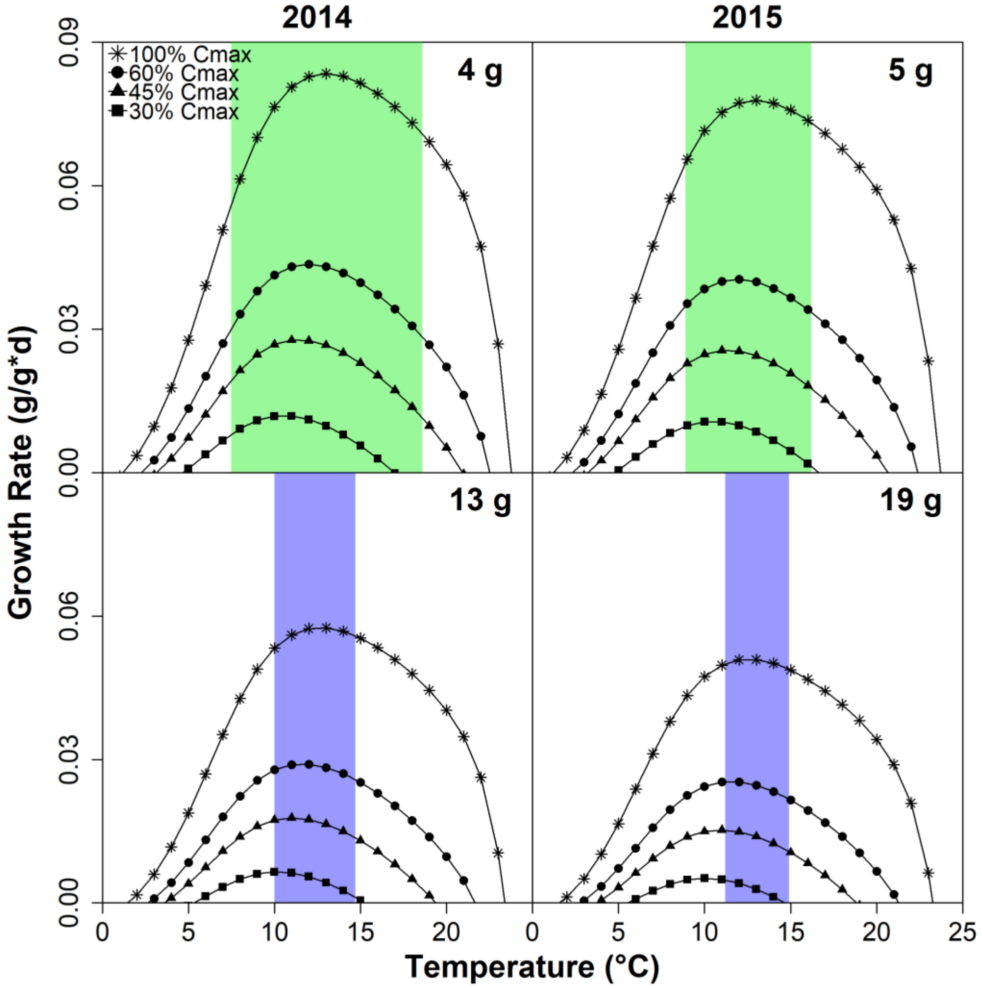


Figure 6.2.5. Temperature dependent growth curves for different feeding rates and fish sizes. Consumer energy density and prey energy density were held constant (4085 J/g, 4000 J/g). Green bars represent nearshore temperatures that fish experienced and blue bars represent offshore temperatures that fish experienced. Size in each habitat and year was estimated from a Puget Sound wide average of the data. Average Cmax(%) was 35% in 2014 and 45% in 2015.

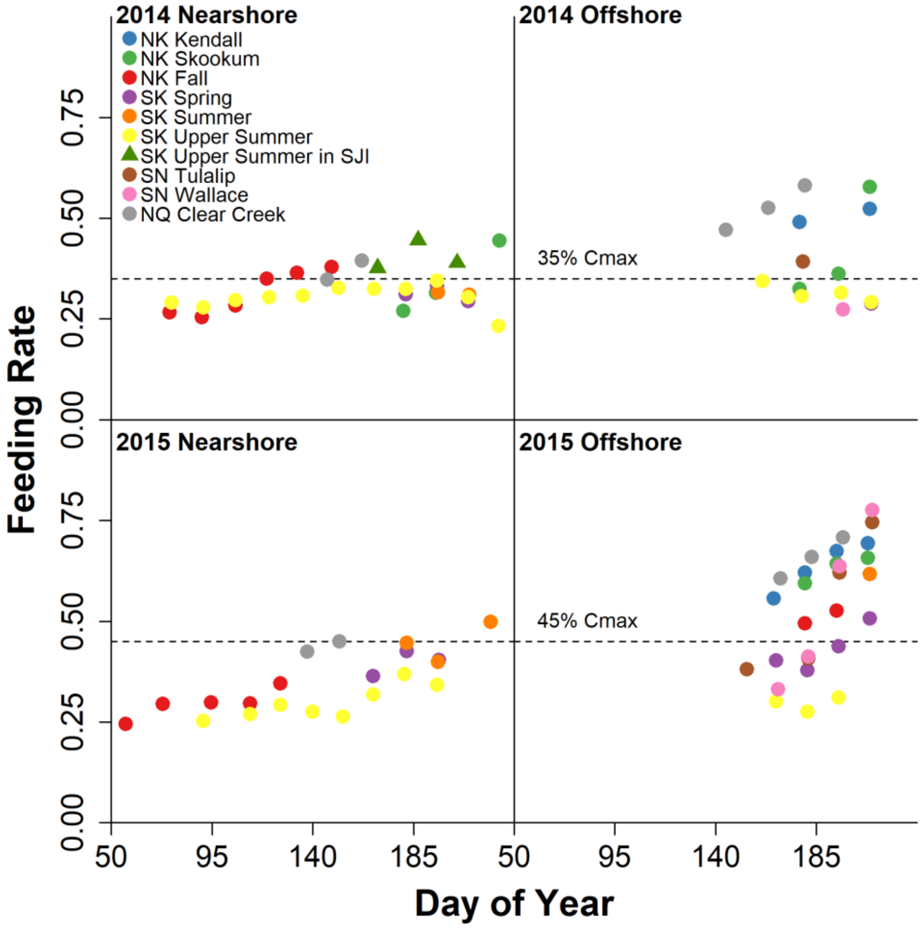


Figure 6.2.6. Feeding rate (Cmax) over time for nearshore and offshore habitats in 2014 and 2015. Day 182 corresponds to July 1.

Prey quality, measured by average diet energy density, did not show any trends with watershed, stock or times and showed only very slight trends with habitat (**Figure 6.2.7**). Average prey energy densities were highly variable, particularly in the nearshore in 2014, suggesting fish capitalize on patchy resources such as insect hatches. Nearshore energy densities were slightly higher than offshore in both years when looked at across all watersheds. Median energy density for the nearshore in 2014 was 4583 J/g and in 2015 was 4656 J/g, while offshore in 2014 was 4119 J/g and offshore in 2015 was 4118 J/g. Daily consumption of prey groups when converted to energy consumed in kilojoules shows how each prey group contributes fish growth (**Appendix A4**).

The contribution of specific prey groups to juvenile Chinook daily energy consumption varied by watershed, habitat and to a lesser degree, simulation period (**Appendix A4**). Juvenile Chinook in the nearshore of the Nooksack and Skagit watersheds relied heavily on insects (Nooksack 2014: 60%, 2015: 67%; Skagit 2014: 75%, 2015: 68%), aquatic invertebrates (Nooksack 2014: 39%, 2015: 33%; Skagit 2014: 21%, 2015: 18%) and fish prey (Nooksack 2014: 2%, 2015: 0%; Skagit 2014: 5%, 2015: 13%) in order to satisfy their daily energy needs. Marine invertebrates, insects, and larval fish (37%, 40%, and 23%) had the greatest proportional contribution to daily energy for fish in the San Juan Islands nearshore. Nisqually nearshore simulations showed a much greater reliance than the other watersheds on crustacean and marine invertebrate energy sources (2014: 28% larval crab, 39% other crustacean/invert, 30% insects; 2015: 35% larval crab, 48% other crustacean/invert, 17% insect). Offshore energy budgets in both years had high proportions of crustacean prey, notably crab megalops, however, different watersheds had greater reliance on larval crab than others. Nisqually offshore energy was almost exclusively crustacean derived (2014: 90%; 2015: 98%) of which roughly half was crab megalops (2014: 54%, 2015: 40%). Snohomish stocks had high energy contributions of both insects (2014: 62%, 2015: 34%) and larval crab (2014: 35%, 2015: 20%) and they consumed some fish, while Nooksack and Skagit stocks obtained their daily energy from larval crab (Nooksack 2014: 35%, 2015: 67%; Skagit 2014: 47%, 30%), insects (Nooksack 2014: 25%, 2015: 5%; Skagit 2014: 38%, 2015: 51%) and smaller proportions of larval fish.

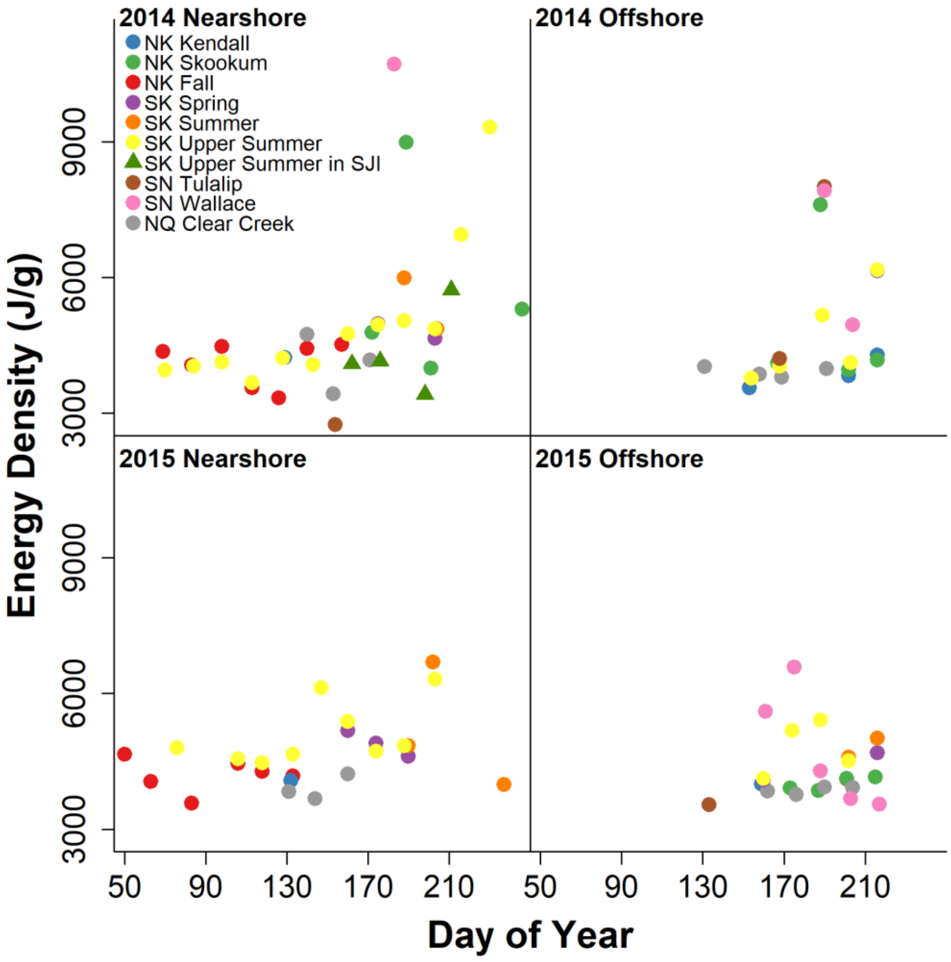


Figure 6.2.7. Average diet energy density for each life stage used in bioenergetics modeling. Day 182 corresponds to July 1.

Temperatures experienced by outmigrating fish were cooler in the offshore than nearshore in both years (**Figures 6.2.8, 6.2.9**). The range of temperatures in the offshore was close to optimal for fish in both years, even though offshore temperatures were on average higher in

2015 than in 2014 (**Figure 6.2.5, 6.2.8 6.2.9**). We encountered fish over a broader range of temperatures in the nearshore in 2014 than in 2015. Temperatures in the nearshore associated with sampling periods in which we caught fish did not significantly differ between years, however, fish avoid habitats during extreme temperatures and therefore this comparison may not capture the true variation in temperatures seen in these watersheds and habitats.

Due to the fact that growth rates were found to differ between each stock and habitat within each year, and that we were unable to conduct further statistical tests due to an unbalanced design, we were not able to determine if any one factor of prey availability, prey quality, or temperature was most important for conferring higher growth to fish. Most likely, a combination of factors are subtly interacting with stock, habitat and time to confer variable growth. In the absence of more robust models, conclusions must be drawn from a theoretical bioenergetics-based understanding of the relationship between temperature, prey quality and prey availability.

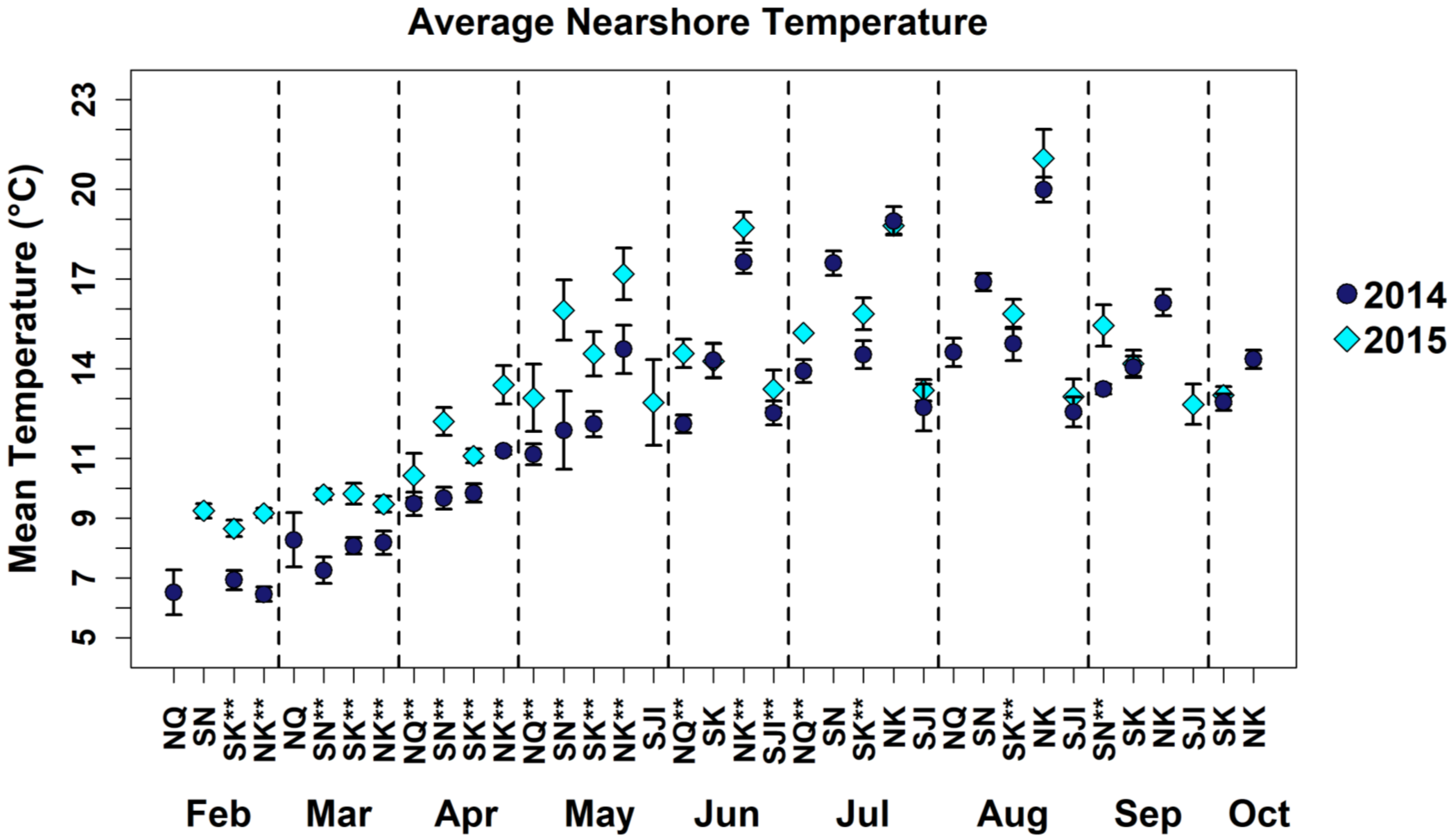


Figure 6.2.8. Comparison of nearshore temperatures in 2014 and 2015. Points represent monthly average temperatures. 2015 significantly warmer (**), 2015 significantly cooler (°°) ($p<0.05$). Watershed key: NQ=Nisqually, NK=Nooksack, SJI= San Juan Islands, SK=Skagit, SN=Snohomish. Temperature data was not available for all watersheds in all months and years. Unpublished data.

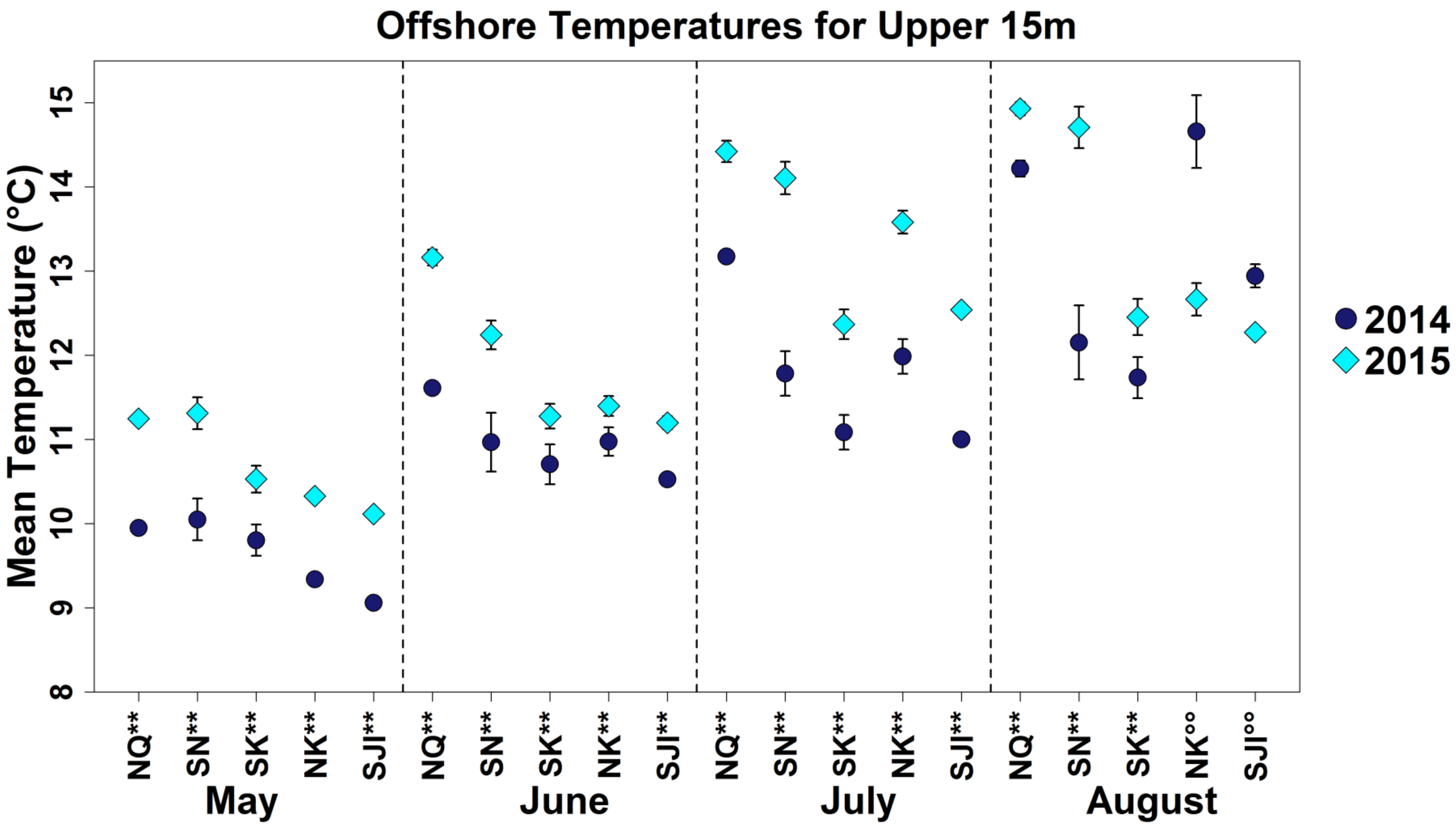


Figure 6.2.9. Comparison of offshore temperatures in 2014 and 2015 as measured using CTD casts. Points represent average temperatures over the upper 15m and are averages of all casts conducted in a month. 2015 significantly warmer (**), 2015 significantly cooler (°°) ($p<0.05$). Watershed key: NQ=Nisqually, NK=Nooksack, SJI= San Juan Islands, SK=Skagit, SN=Snohomish. Unpublished data.

7.2.3 Conclusions

- Stock specific geometric mean weights increased through time suggesting sequential use of each habitat similar to results from scale growth trajectories in Section 4.1. However, weights did differ by stock and habitat through tie indicating potential differences in absolute growth among stocks and/or habitats.

- In general, fish collected in the offshore habitats were larger than those collected in the nearshore habitats. The pattern was consistent between years though the discrepancy between the two habitats was less pronounced during 2015.

- Absolute weight gain and absolute growth were typically highest, yet more variable, in the offshore habitats in both years and for all stocks. The exception was the Upper Skagit Summer stock which had higher absolute growth rates in the nearshore habitat.

- Growth rates differed considerably by stock within habitat type and across years.

- Growth rates for stocks that were captured in the San Juan Islands were typically higher than the observed growth rates from the natal nearshore habitats and more closely matched those observed for the natal offshore habitats.

- We observed no apparent trends in specific growth rate (growth rate scaled to body size) although there were considerable differences among and within stocks and habitat types.

- Estimated feeding rates (%Cmax) were generally higher in the offshore habitats than the nearshore habitats and were higher in 2015 compared to 2014.

- Diet energy densities were highly variable and showed no consistent pattern or trend within or among stocks, habitats, or years. Diet composition also varied by stock, habitat and to some degree, year, as reported in section 5.2.

- Temperatures were also highly variable among the regions and habitats. Overall, 2014 was cooler than 2015 and offshore temperatures were generally cooler than nearshore temperature. Nearshore habitats also experienced a wider range of temperatures than observed for the offshore habitats. Temperatures were not generally consistent among regions within each habitat type.

7.3 Discussion

We used IGF-1 concentrations and bioenergetics simulations to evaluate and compare growth rates among regions and habitat types to assess factors that affect growth during initial residence in marine water in northern Puget Sound. In general, both methods found similar results although the mechanisms by which the variability was occurring were slightly different yet not mutually exclusive. Observed IGF-1 concentrations and simulated growth rates both varied among the regions and habitats types suggesting growing conditions are not consistent and particular areas and/or habitat types are more beneficial to overall fish growth than others at particular times.

Absolute growth rates were typically higher in the offshore habitats compared to nearshore habitats. The exception were the IGF-1 concentrations and simulated growth rates observed in fish captured in the San Juan Islands nearshore which were similar to those from fish captured in the offshore habitats elsewhere. While these observed differences in growth rate may be significant it is important to consider the potential bias comparing absolute growth rates given differences in individuals size of fish among the regions/habitats. We found a significant relationship between IGF-1 concentrations and fork length within all regions indicating individual size was positively related individual growth rates. Such a relationship is common when growth is not standardized to individual size and generally reflects differences in metabolic demands as well as maximum feeding rates or potential growth rates, both as a proportion of body size (review by Beckman 2011). Indeed, this relationship has been observed in several studies involving salmonids and IGF-1 including within Salish Sea (Chamberlin et al. 2017). Size distributions within the habitats among the regions were different; fish were larger in the offshore habitats compared to the nearshore except in the San Juan Islands where fish in the nearshore were more similar in size to fish captured in the offshore of other areas. However, when IGF-1 concentrations were compared among fish within specific size ranges, concentrations were still higher in fish captured in the San Juan Islands nearshore indicating size alone did not account for the observed differences.

Comparisons of specific growth rates (standardized by size) via the bioenergetics simulations also suggests the general differences among the habitat types and regions were not solely due to differences in individual size but also reveal some interesting differences not observed in the comparisons of absolute growth rates. The increased growth rates in the offshore habitats were still evident though the variability was somewhat muted or decreased. In addition, where possible within the stock-specific analysis framework used for these simulations, the Upper Skagit Summer fish captured in the SJI nearshore had higher specific growth rates than those captured in the Skagit offshore habitats corroborating the results of the IGF-1 analysis. Further population specific simulation would be needed to evaluate this result across other populations and to remove any potential population specific bias in the results. Interestingly, once standardized by individual size, growth rates within the nearshore habitats in all regions were more similar than suggested by comparison of IGF-1 concentration and ay again, indicate local conditions rather than size may explain the observed differences.

In addition to size, we evaluated the effect of prey composition and temperature on observed and simulated growth rates. Our analysis of diet composition revealed similar patterns of variability among habitats and regions. We combined individual size data and diet composition and found that, while larger fish had elevated IGF-1 concentrations in general, where those fish were able to incorporate prey fish into their diets, concentrations were further increased indicating higher growth rates. Similar evaluations were performed using the bioenergetics simulations via comparison of diet energy density and feeding rates. Average diet energy density was highly variable did not show any clear or consistent pattern among the regions or habitats types. This may reflect the high level of variability in diets as confirmed in section 5.2 and suggest fish may capitalize on patchy resources. Feeding rate was slightly higher in the offshore habitats although the pattern was strongly driven by simulations for 2015. However, feeding rate for Upper Skagit Summer fish in the SJI was slightly higher than the feeding rate for those fish in the Skagit nearshore or offshore which may reflect the difference between fish prey and zooplankton prey as a function of total diet biomass. Finally, the inconsistencies between the two methods when evaluating the effect of prey or diet composition may be due to the averaging used for bioenergetics simulations. Each simulation uses an average observed diet for fish captured within the simulation time period which could mute any differences experienced by an individual fish given differences in diet composition. Our IGF-1/diet analysis was performed at the individual level and retained all the information pertinent to each individual fish.

Temperature may also help explain the observed and/or simulated differences in growth rates among the regions and habitat types. Temperature can significantly affect the metabolic processes that influence growth especially where prey is limited and/or feeding rates reduced. Temperatures were on average cooler and varied less in the offshore habitats compared to the nearshore habitats in both years. Yet offshore temperatures also remained in the range near the peak of the estimated growth curves given the observed feeding rates. Again, the thermal regime observed in the San Juan Islands nearshore was more similar to the offshore regime in other regions which would help to explain the observed growth similarities. However, there were clearly periods of peak, or optimal, thermal conditions observed in the nearshore habitats in all regions which suggest timing is also important for determining growth conditions within each area.

In conclusion, our results indicate that growth varies among habitats and regions and that diet composition/prey availability and temperature regimes play a role in determining the growth benefit to individual fish inhabiting the various areas. Our work also suggest that each habitat and region can, and does, offer considerable growth opportunities to individuals fish yet timing may play an important role in determining the overall magnitude of the potential benefits. However, it is important to also recognize the unique rearing conditions observed in the San Juan Islands and their influence on individual growth. The significant presence/abundance of small young of the year forage fish that contribute to salmon prey are reflected in local growth rates providing an additional benefit to fish that rear in the nearshore habitats during outmigration in Puget Sound.

8. Informing recovery planning in the San Juan Islands

The goal of our work was to evaluate growth during the early marine period for outmigrating juvenile Chinook in northern Puget Sound. Specifically, we focused on identifying which populations are using the San Juan Islands, and on identifying critical growth periods and the relative differences between food availability, consumption, and growth among natal nearshore and offshore habitats for the Skagit and Nooksack watersheds as well as a common rearing area, the San Juan Islands.

Alignment with other recovery planning efforts

Assessing the Chinook population structure in the San Juan Islands can help determine how best to align with other recovery plans. The focal area, Southeast San Juan Islands, was selected based upon previous studies that suggest that part of the San Juans is where wild Puget Sound Chinook are most frequent (Beamer and Fresh 2012). The past work and our efforts support the notion that primary alignment should be with the Whidbey Basin, in particular Skagit, and with Nooksack efforts. We recommend considering the San Juans in the context of priorities to target for improving the productivity of these populations in particular. However, other Puget Sound fish were present, so this doesn't discount the value of the San Juan Islands to the overall ESU. More based upon past work than this, we also recommend spatially prioritizing actions that most likely contribute the primary habitats that Puget Sound natural-origin Chinook utilize vs. all Chinook, which includes a great amount of Canadian-origin fish.

San Juans are uniquely beneficial

No size-selective mortality was found to occur among the nearshore and offshore habitats assessed in Puget Sound, which would have been a clear indicator of specific habitats (and associated ecological conditions) to focus on for recovery purposes. However, the absence of size-selective mortality among habitats in Puget Sound through July doesn't refute the past notion that growth in Puget Sound through July is critical to the overall marine survival of out migrating Chinook (Duffy and Beauchamp 2011). Further, absolute growth rates for stocks that were captured in the San Juan Islands were typically higher than the observed growth rates from the natal nearshore habitats and more closely matched those observed for the natal offshore habitats.

Two specific elements likely contribute to this growth advantage.

First, the thermal regime observed in the San Juan Islands nearshore was generally cooler and more similar to the offshore regime in other regions. Given that the San Juans are an offshore island, this is logical. This study was not designed to determine whether there are action that can be done to maintain or improve water temperatures. However, the San Juan Islands recovery planning can already consider this an asset, providing nearshore habitat more tolerant of climate change.

Second, fish were found in more than half of all diets from the San Juan Islands and accounted for, on average, half the weight of contents within individual diets from both nearshore and offshore life stages. Specifically, the contribution of both Pacific herring and Pacific sand lance is unique to the region compared to other rearing areas in northern Puget Sound and the benefit of increased contributions are reflected in individual growth rates. Furthermore, the reduced abundance, or biomass, of other essential prey items as observed in other regions and habitats (e.g. decapod larvae, euphausiids, terrestrial insects), suggests the forage fish prey resource is not only beneficial but may be essential for maintaining growth in the region.

The presence and unique size structure of the forage fish population in the islands appears to provide this growth benefit. While forage fish have long been included in efforts related to salmon recovery in the San Juan Islands, our results provide empirical evidence as to the growth benefits conveyed through predation on “local” forage fish, specifically Pacific herring and Pacific sand lance, and the degree to which salmon that inhabit the San Juan Islands rely on forage fish as prey[3]. While surf smelt were present in the catch (Figures 6.3.1), few showed up in the Chinook diets. This is likely a function of both availability and potentially, preference. Surf smelt were typically smallest when Chinook were not present (May and September) and were far less abundant than Pacific herring or sand lance. Given this, we recommend that recovery efforts focused on juvenile Chinook productivity increase the priority of efforts supporting Pacific herring and Pacific sand lance productivity, and decrease the priority of efforts supporting surf smelt. For example, we recommend downgrading or eliminating bullet three of page 8 of PIAT II (2017)[4] “Rearing Chinook, spawning surf smelt and rearing surf smelt” as a variable to include in the Fish Use Geographic Prioritization. An ongoing assessment of resident sub-adult Chinook occupying the San Juan Islands will further contribute to determining the overall value of prioritizing these forage fish for Chinook recovery.

Recommendations for Pacific herring and Pacific sand lance actions

We also propose further efforts geared toward understanding the population dynamics driving the Pacific herring and Pacific sand lance populations that uniquely support juvenile salmon in the San Juan Islands:

<u>Abundance and Distribution of Pacific sand lance</u>: Basic knowledge of abundance and distribution of both species is critical for management and/or protection in the region. While this is generally known for Pacific herring (Pentilla 2007, Siple and Francis 2015), very little is known about current or historical abundance and distribution of Pacific sand lance. Recent efforts focused on Pacific sand lance in the Salish Sea have shown very broad distribution and within the San Juan Islands have focused primarily on San Juan Channel (Blaine 2006, Sisson and Baker 2017). Expanding effort or focus beyond San Juan Channel and incorporating several

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[3] These findings are consistent with coincident work by Russel Barsh (see Appendices)

[4] PIAT II. Strategic Salmon Recovery Planning in the San Juan Islands: Nearshore Marine Habitat Restoration and Protection Prioritization. July 2017. Friends of the San Juans.

recent datasets would help to update our knowledge of local distribution of the species and provide, at least, a foundation for evaluating current abundances.

Identify Spawning Habitat of Pacific sand lance*:* Identifying current and potential spawning habitat for Pacific sand lance in the San Juan Islands may further guide protection or recovery strategies. While this information largely exists for Pacific herring in the region and has been in initiated for Pacific sand lance (FSJ 2004), more complete assessment, inventory, and monitoring would be recommended. Recently funded work to further develop spatial models used to predict spawning habitat could be used in conjunction with field sampling to positively identify and subsequently track Pacific sand lance spawning in the region.

Population Structure/Diversity: Understanding the population structure and/or genetic diversity of the Pacific herring and sand lance populations that support juvenile Chinook rearing in the region would help focus management actions that directly benefit salmon recovery in the region. Analysis of prey size suggests the majority of forage fish prey are consumed as young-of-year fish indicating local or near-local sources of herring and sand lance support rearing in the region. The Cherry Point herring stock is a likely source given its adjacent location to the SJI and late spawn timing. Ongoing research as part of the Salish Sea Marine Survival Project is using genetic stock identification of herring found in the gut contents sampled during this project to specifically answer this question. However, while we recommend a similar approach for Pacific sand lance, there is no baseline genetic stock information available, locally or broadly, for the species. Initializing efforts to understand the population structure/genetic diversity of Pacific sand lance in the region and how potential diversity is allocated spatially or effects phenology would be extremely valuable for focusing protection and recovery efforts on highest priority sand lance stocks that support Chinook productivity while providing foundational biological information which is currently missing.

Feeding ecology of Pacific herring and Pacific sand lance: Although our results indicated a lack of overlap between diet contents of Chinook salmon and the local zooplankton assemblage, a similar approach would be useful for evaluating the feeding ecology of both forage fish species. Copepods were the most abundant species found in the local zooplankton assemblage though rarely found in the diets of juvenile Chinook salmon Both Pacific herring and sand lance are known to feed more commonly on copepods than Chinook salmon (Tribble 2000, Osgood et al. 2016). Given the momentum behind the established zooplankton monitoring program in the region, we recommend development of a program that evaluates and/or monitors overlap between zooplankton assemblages and forage fish diets. Baseline information on feeding ecology would also provide opportunity to evaluate growth and the factors effecting growth for local forage fish populations.

It should be noted that increasing presence of Northern anchovy in Puget Sound should be tracked. The presence of Northern anchovy over time appears to be correlated with warm water periods (Duguid et al. in review). If climate change does increase their presence, Northern anchovy could become a fundamental player in the Puget Sound food chain.

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Appendix A1.

Appendix Table XX. Categories used in analysis of zooplankton and diet composition analyses. Where specifc categories represent multiple species, life stages, or groups of organisms a list is provided.

New Category	Old Category
Insecta	Digested Insect Parts Diptera Adult Diptera Adult - Nematocera Diptera Adult - Brachycera Lepidoptera Adult Rare Insects (list taxon in notes) Unid Adult Insects unID Insect Eggs (Describe in notes) Psocoptera adult Trichoptera Adult Coleoptera Adult Psocoptera Nymph Diptera Pupa UnID Insect Pupa Diptera Larvae Unid Insect Larvae Lepidoptera Larva Coleoptera Larvae Tricoptera Larvae Hemiptera adult Hemiptera Larva/Nymph Hymenoptera Ephemeroptera Nymph Ephemeroptera adult Plecoptera Nymph Plecoptera adult Unid Aquatic Nymph Odonata adult and nymph
Collembola & Arachnid	Collembola Arachnida
Other Crustacean & Rare Invert	Digested Crustacean Unid Crustacean Unid invert

	Juvenile Barnacle (between cyprid and adult)
	Barnacle slough
	Barnacle Cyprid
	Cumaceans
	Calanoida
	Harpacticoidas
	UnID Copepod
	Cyclopoida
	Siphonostomatoida
	Cladocera
	Ostracods
	Tanaidacea
	Larvacea
	Rare Invertebrates (list taxon in notes)
	Rare Invertebrates (list taxon in notes)
	Rare Invertebrates (list taxon in notes)
	Rare Invertebrates (list taxon in notes)
	Rare Invertebrates (list taxon in notes)
Amphipod	Amphipod ("OTHER")
	Corophiidae
	unID Amphipod
	Caprellida
Decapod megalops/post-larval (NOT shrimp adult)	Crab megalops (Brachyura, Anomura)
	post-larval Crab (Brachyura, Anomura)
	Paguroidea Megalops
	Paguroidea Adult (Hermit Crabs)
Decapod zoea	Crab zoea (Brachyura, Amonura)
	"Shrimp" Zoea (all shrimp zoea including krill and mysid)
Euphausid	Euphausia
Mysid	Mysid
Shrimp - Post larval/Adult	UnID Shrimp (not sure if mysid/krill, etc.)
	Other Shrimp (shrimp that is NOT krill or mysid)
Hyperiid	Hyperiids
Worm	Polychaetes
	Unid Worm
	Chaetognatha
Isopod	Isopods
Indigestible	Plant Material
	Other Mat
	Nematoda

Digested Material	DigestedMat
Fish	UnID Fish unid salmonid pink chum sand lance Other Fish Digested Fish Herring Anchovy
Cnidaria	Cnidaria-Anthozoa
	Cnidaria-Hydrozoa
	Cnidaria-Hydrozoa-Anthomedusae
	Cnidaria-Hydrozoa-Leptomedusae
	Cnidaria-Hydrozoa-Linmomedusae
	Cnidaria-Hydrozoa-Trachymedusae
	Cnidaria-Scyphozoa
	Cnidaria-Siphonophorae
	Cnidaria-Siphonophorae-Calycophoran
	Cnidaria-Siphonophorae-Physonect
Dinoflagellata	Dinoflagellata
Echinodermata	Echinodermata
Ctenophora	Ctenophora
Bryozoa	Bryozoa
Chordata-Tunicata	Chordata-Tunicata
Nudibranchia	Nudibranchia
Phoronid	Phoronid

Appendix A2. Bioenergetics model inputs and outputs for each stock and growth stock. 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.

						2014							
						Nooksack Fall (N)							
	Habitat	**Sampling Period**	**Mean Day of Year**	**Simulation Day**	**N**	**Mean Weight[a] (g)**	**Input Weight[b] (g)**	**Growth Rate (g/d)**	**Avg Prey Energy Density (J/g)**	**Temp[c] (°C)**	**P-value (feeding rate)**	**Total Consumption (g)**	**Growth Efficiency (%)**
	Nearshore	Early March 3/10/2014	69	1	10	0.52	0.50		4358	7.5			
Sim1	Nearshore	Late March 3/24-3/25/2014	83	15	15	0.74	0.66	0.011	4055	9.1	0.2659	0.6	28.10
Sim2	Nearshore	Early April 4/7-4/8/2014	98	30	19	0.70	0.89	0.014	4467	11.2	0.2544	0.9	26.72
Sim3	Nearshore	Late April 4/21-4/25/2014	113	45	12	1.50	1.20	0.019	3557	11.3	0.2838	1.3	24.45
Sim4	Nearshore	Early May 5/6/2014	126	58	6	1.44	1.56	0.025	3329	12.3	0.3501	1.7	20.79
Sim5	Nearshore	Late May 5/20/2014	140	72	6	2.35	2.06	0.033	4430	16.9	0.3640	2.4	20.47
Sim6	Nearshore	Early June 6/6/2014	157	89	5	2.69	2.89	0.046	4515	17.0	0.3784	3.9	21.26
						Nooksack Kendall Creek							
	Offshore	Early June 6/2/2014	153	1	15	12.06	11.69		3562	11.0			
Sim1	Offshore	Late July 7/21/2014	202	50	6	18.59	26.47	0.296	3821	12.4	0.4907	55.9	26.63
Sim2	Offshore	Early August 8/4/2014	216	64	3	57.92	33.43	0.464	4280	14.7	0.5231	26.6	26.16

	Habitat	Sampling Period	Mean Day of Year	Simulation Day	N	Mean Weight[a] (g)	Input Weight[b] (g)	Growth Rate (g/d)	Avg Prey Energy Density (J/g)	Temp[c] (°C)	P-value (feeding rate)	Total Consumption (g)	Growth Efficiency (%)
						Nooksack Skookum Creek							
	Nearshore	Late June 6/20-6/23/2014	172	1	5	8.12	7.52		4780	16.8			
Sim1	Nearshore	Early July 7/8/2014	189	18	3	8.12	9.15	0.090	8988	18.5	0.2699	6.6	24.07
Sim2	Nearshore	Late July 7/18-7/21/2014	201	30	3	9.71	10.50	0.104	3988	18.6	0.3150	6.6	21.15
Sim3	Nearshore	Early September 9/3/2014	246	75	3	18.77	17.63	0.155	5295	17.0	0.4439	39.4	17.38
	Offshore	Late June 6/16/2014	167	1	3	7.61	5.76		4105	11.3*			
Sim1	Offshore	Early July 7/7/2014	188	22	3	10.46	9.89	0.188	7597	11.8	0.3248	8.3	48.16
Sim2	Offshore	Late July 7/21/2014	202	36	17	11.71	14.19	0.286	3964	12.4	0.3621	9.4	47.10
Sim3	Offshore	Early August 8/4/2014	216	50	15	23.65	20.35	0.411	4165	14.7	0.5775	19.6	31.49
						Nisqually Clear Creek							
	Nearshore	Late May 5/19-5/22/2014	140	1	16	5.94	6.38		4738	11.7			
Sim1	Nearshore	Early June 5/30-6/9/2014	153	14	12	9.27	7.71	0.095	3423	11.8	0.3474	5.6	24.00
Sim2	Nearshore	Late June 6/17-6/23/2014	171	32	3	7.09	10.02	0.122	4170	12.0	0.3942	10.1	22.81
	Offshore	Early May 5/11/2014	131	1	12	6.44	6.36		4031	10.0			
Sim1	Offshore	Early June 6/7-6/8/2014	158	28	17	11.82	11.85	0.196	3853	11.6	0.4715	17.2	32.37

	Habitat	Sampling Period	Mean Day of Year	Simulation Day	N	Mean Weight[a] (g)	Input Weight[b] (g)	Growth Rate (g/d)	Avg Prey Energy Density (J/g)	Temp[c] (°C)	P-value (feeding rate)	Total Consumption (g)	Growth Efficiency (%)
Sim2	Offshore	Late June 6/18-6/19/2014	169	39	6	14.70	15.27	0.285	3795	12.1*	0.5256	11.6	29.60
Sim3	Offshore	Early July 7/9-7/10/2014	191	61	3	26.79	25.34	0.438	3984	13.0	0.5817	33.2	30.38
						Skagit Spring							
	Nearshore	Late June 6/23-6/25/2014	175	1	9	7.02	6.92		4967	14.5			
Sim1	Nearshore	Early July 7/7/2014	188	14	3	8.72	8.29	0.098	5038	14.3	0.3115	5.6	24.71
Sim2	Nearshore	Late July 7/21-7/23/2014	203	29	9	9.32	10.22	0.121	4652	14.4	0.3322	7.8	24.70
Sim3	Nearshore	Early August 8/4-8/5/2014	216	42	5	13.80	12.26	0.145	6945	15.3	0.2943	6.9	28.98
	Offshore	Late July 7/22/2014	203	1	15	12.83	12.82		4119	11.3			
Sim1	Offshore	Early August 8/4-8/5/2014	216	14	9	15.05	15.03	0.158	6147	11.7	0.2878	7.4	29.57
						Skagit Summer							
	Nearshore	Early July 7/7/2014	188	1	9	5.22	4.88		5981	14.3			
Sim1	Nearshore	Late July 7/21-7/23/2014	204	17	16	6.14	6.74	0.109	4858	14.4	0.3156	5.7	33.19
Sim2	Nearshore	Early August 8/4-8/5/2014	216	29	5	10.18	8.58	0.142	6945	15.3	0.3104	5.1	35.56
	Nearshore	Early March 3/11-3/12/2014	70	1	14	0.66	0.78		3950	7.9			
Sim1	Nearshore	Late March 3/24-3/25/2014	84	15	9	0.78	0.99	0.014	4036	8.2	0.2910	0.8	26.25

	Habitat	Sampling Period	Mean Day of Year	Simulation Day	N	Mean Weight[a] (g)	Input Weight[b] (g)	Growth Rate (g/d)	Avg Prey Energy Density (J/g)	Temp[c] (°C)	P-value (feeding rate)	Total Consumption (g)	Growth Efficiency (%)
Upper Skagit Summer (N)													
Sim2	Nearshore	Early April 4/7-4/11/2014	98	29	8	1.16	1.27	0.019	4121	10.1	0.2779	1.1	26.01
Sim3	Nearshore	Late April 4/21-4/25/2014	113	44	8	1.63	1.66	0.024	3667	9.6	0.2960	1.6	24.68
Sim4	Nearshore	Early May 5/8-5/9/2014	128	59	16	3.50	2.16	0.031	4216	11.6	0.3038	2.0	24.64
Sim5	Nearshore	Late May 5/20-5/27/2014	143	74	7	2.98	2.81	0.041	4071	12.6	0.3078	2.7	24.54
Sim6	Nearshore	Early June 6/9/2014	160	91	11	4.27	3.79	0.054	4751	15.2	0.3271	4.1	24.20
Sim7	Nearshore	Late June 6/23-6/30/2014	175	106	21	4.47	4.93	0.072	4956	14.3	0.3246	4.4	25.85
Sim8	Nearshore	Early July 7/7-7/9/2014	188	119	11	8.58	6.20	0.091	5038	15.0	0.3244	4.6	27.44
Sim9	Nearshore	Late July 7/21-7/23/2014	203	134	13	5.59	8.08	0.117	4858	14.4	0.3449	6.7	27.87
Sim10	Nearshore	Early August 8/4-8/5/2014	216	147	6	9.14	10.15	0.148	6945	15.3	0.3044	6.1	33.41
Sim11	Nearshore	Late August 8/18-8/19/2014	230	161	6	13.16	12.99	0.189	9319	14.6	0.2320	6.0	47.05
	Offshore	Early June 6/3/2014	154	1	15	8.03	7.47		3767	10.7			
Sim1	Offshore	Late June 6/17/2014	168	15	14	7.95	8.87	0.094	4032	10.8*	0.3438	6.3	22.38
Sim2	Offshore	Early July 7/8/2014	189	36	5	12.54	11.48	0.119	5164	11.0	0.3058	9.6	27.10

	Habitat	Sampling Period	Mean Day of Year	Simulation Day	N	Mean Weight[a] (g)	Input Weight[b] (g)	Growth Rate (g/d)	Avg Prey Energy Density (J/g)	Temp[c] (°C)	P-value (feeding rate)	Total Consumption (g)	Growth Efficiency (%)
Sim3	Offshore	Late July 7/22/2014	203	50	6	12.93	13.64	0.144	4119	11.3	0.3143	8.0	27.09
Sim4	Offshore	Early August 8/4-8/5/2014	216	63	8	16.78	16.01	0.169	6165	11.7	0.2914	7.8	29.85
						Snohomish Tulalip							
	Offshore	Late June 6/17-6/18/2014	168	1	21	7.71	7.58		4204	10.9*			
Sim1	Offshore	Early July 7/8-7/9/2014	190	23	9	15.28	15.48	0.344	8001	10.7	0.3921	13.1	57.80
						Snohomish Wallace							
	Offshore	Early July 7/8-7/9/2014	190	1	18	11.59	11.38		7911	10.7			
Sim1	Offshore	Late July 7/23/2014	204	15	3	11.19	14.63	0.217	4953	13.0	0.2737	7.4	45.00
						Upper Skagit Summer in San Juan Islands							
	Nearshore	Early July 7/17/2014	198	1	4	16.40	13.22			11.5			
Sim1	Nearshore	Late July 7/29-7/30/2014	211	14	11	15.35	16.73	0.251		12.5	0.3893	10.6	32.46
						2015							
						Nooksack Fall (N)							
	Nearshore	Late February 2/19-2/20/2015	50	1	15	0.45	0.56		4659	9.2			
Sim1	Nearshore	Early March 3/2-3/5/2015	63	14	15	0.96	0.72	0.012	4056	8.9	0.2449	0.6	27.94
Sim2	Nearshore	Late March 3/16-3/25/2015	83	34	15	1.12	1.07	0.016	3575	10.2	0.2950	1.4	24.91
Sim3	Nearshore	Early April 4/14-4/16/2015	106	57	4	1.30	1.67	0.025	4460	12.8	0.2985	2.4	24.68

	Habitat	Sampling Period	Mean Day of Year	Simulation Day	N	Mean Weight[a] (g)	Input Weight[b] (g)	Growth Rate (g/d)	Avg Prey Energy Density (J/g)	Temp[c] (°C)	P-value (feeding rate)	Total Consumption (g)	Growth Efficiency (%)
Sim4	Nearshore	Late April 4/28/2015	118	69	3	1.28	2.11	0.034	4276	13.0	0.2961	1.7	25.19
Sim5	Nearshore	Early May 5/13-5/14/2015	133	84	8	3.25	2.83	0.045	4174	15.8	0.3463	3.1	23.04
	Offshore	Late June 6/22/2015	173	1	8	13.35	13.94		3906	11.4			
Sim1	Offshore	Early July 7/6/2015	187	15	7	20.10	18.23	0.286	3853	13.5	0.4942	15.7	27.49
Sim2	Offshore	Late July 7/20/2015	201	29	8	22.85	23.85	0.375	4105	13.6	0.5266	20.7	27.05
Nooksack Kendall Creek													
	Offshore	Early June 6/8/2015	159	1	13	9.31	11.04		4000	11.4			
Sim1	Offshore	Late June 6/22/2015	173	15	15	19.39	16.06	0.335	3906	11.4	0.5568	15.0	33.61
Sim2	Offshore	Early July 7/6/2015	187	29	6	22.69	23.37	0.488	3853	13.5	0.6213	22.7	32.31
Sim3	Offshore	Late July 7/20/2015	201	43	18	35.48	34.02	0.709	4118	13.6	0.6740	33.0	32.18
Sim4	Offshore	Early August 8/3/2015	215	57	13	45.19	49.50	1.033	4155	12.7	0.6933	44.2	34.97
Nooksack Skookum Creek													
	Offshore	Late June 6/22/2015	173	1	20	14.63	14.94		3906	11.4			
Sim1	Offshore	Early July 7/6/2015	187	15	18	21.41	21.40	0.430	3853	13.5	0.5940	20.5	31.61
Sim2	Offshore	Late July 7/20/2015	201	29	33	31.79	30.63	0.616	4118	13.6	0.6421	29.3	31.44

	Habitat	Sampling Period	Mean Day of Year	Simulation Day	N	Mean Weight[a] (g)	Input Weight[b] (g)	Growth Rate (g/d)	Avg Prey Energy Density (J/g)	Temp[c] (°C)	P-value (feeding rate)	Total Consumption (g)	Growth Efficiency (%)
Sim3	Offshore	Early August 8/3/2015	215	43	25	42.44	43.86	0.882	4155	12.7	0.6569	38.6	34.21
Nisqually Clear Creek													
	Nearshore	Early May 5/7-5/14/2015	131	1	9	6.72	6.79		3827	11.2			
Sim1	Nearshore	Late May 5/21-5/28/2015	144	14	14	8.56	8.52	0.124	3671	13.6	0.4250	7.3	23.74
Sim2	Nearshore	Early June 6/8-6/11/2015	160	30	3	11.24	11.27	0.162	4219	14.4	0.4497	11.7	23.47
	Offshore	Early June 6/11/2015	162	1	20	19.33	19.25		3840	12.7			
Sim1	Offshore	Late June 6/25/2015	176	15	14	25.84	26.38	0.475	3764	13.6	0.6067	25.2	28.39
Sim2	Offshore	Early July 7/9/2015	190	29	3	40.47	36.15	0.651	3927	14.3	0.6592	34.8	28.11
Sim3	Offshore	Late July 7/23/2015	204	43	3	47.47	49.54	0.892	3916	14.9	0.7083	47.4	28.31
Skagit Spring													
	Nearshore	Early June 6/8-6/9/2015	160	1	12	7.03	7.31		5182	13.7			
Sim1	Nearshore	Late June 6/22-6/24/2015	174	15	13	9.85	9.72	0.161	4904	15.0	0.3645	7.6	32.02
Sim2	Nearshore	Early July 7/7-7/13/2015	190	31	22	13.97	13.46	0.220	4616	15.5	0.4255	12.6	29.81
Sim3	Nearshore	Late July 7/21-7/22/2015	203	44	3	13.30	17.54	0.291	6321	16.2	0.4044	12.1	33.41
	Offshore	Early June 6/9/2015	160	1	4	7.70	7.59		4088	11.4			

	Habitat	Sampling Period	Mean Day of Year	Simulation Day	N	Mean Weight[a] (g)	Input Weight[b] (g)	Growth Rate (g/d)	Avg Prey Energy Density (J/g)	Temp[c] (°C)	P-value (feeding rate)	Total Consumption (g)	Growth Efficiency (%)
Sim1	Offshore	Late June 6/23/2015	174	15	60	10.70	10.58	0.199	5181	11.2	0.4031	8.0	37.00
Sim2	Offshore	Early July 7/7/2015	188	29	11	13.96	14.74	0.278	5420	12.1	0.3786	9.8	42.51
Sim3	Offshore	Late July 7/21/2015	202	43	12	18.77	20.54	0.387	4507	12.6	0.4383	14.9	39.32
Sim4	Offshore	Early August 8/4/2015	216	57	10	31.45	28.63	0.539	4694	12.5	0.5071	21.8	37.05
Skagit Summer													
	Nearshore	Late June 6/23/2015	174	1	4	5.38	5.56		4720	16.0			
Sim1	Nearshore	Early July 7/13/2015	190	17	37	8.62	8.51	0.174	4850	15.5	0.4462	9.1	32.28
Sim2	Nearshore	Late July 7/21-7/22/2015	202	29	11	11.51	11.71	0.246	6690	16.2	0.3989	8.1	39.19
Sim3	Nearshore	Late August 8/24-8/26/2015	237	64	3	30.18	29.75	0.501	3992	15.3	0.4981	48.4	39.41
	Offshore	Late July 7/21/2015	202	1	4	12.04	12.04		4590	12.6			
Sim1	Offshore	Early August 8/4/2015	216	15	3	21.13	21.13	0.606	5016	12.5	0.6176	19.6	46.21
Upper Skagit Summer (N)													
	Nearshore	Late March 3/17-3/18/2015	76	1	13	1.46	1.69		4800	10.1			
Sim1	Nearshore	Early April 4/14-4/16/2015	106	31	6	2.16	2.72	0.033	4558	11.1	0.2520	3.6	28.54
Sim2	Nearshore	Late April 4/27-4/28/2015	118	43	12	5.04	3.29	0.044	4469	11.3	0.2700	2.1	26.91

	Habitat	Sampling Period	Mean Day of Year	Simulation Day	N	Mean Weight[a] (g)	Input Weight[b] (g)	Growth Rate (g/d)	Avg Prey Energy Density (J/g)	Temp[c] (°C)	P-value (feeding rate)	Total Consumption (g)	Growth Efficiency (%)
Sim3	Nearshore	Early May 5/12-5/15/2015	133	58	11	5.76	4.17	0.055	4653	14.6	0.2930	3.5	25.46
Sim4	Nearshore	Late May 5/26-5/28/2015	147	72	16	5.88	5.20	0.069	6123	14.4	0.2751	3.7	27.90
Sim5	Nearshore	Early June 6/8-6/10/2015	160	85	9	4.95	6.39	0.085	5379	13.5	0.2637	3.9	30.90
Sim6	Nearshore	Late June 6/22-6/23/2015	174	99	3	5.44	7.98	0.106	4720	15.2	0.3181	5.9	27.23
Sim7	Nearshore	Early July 7/7-7/8/2015	188	113	14	8.93	9.95	0.132	4850	15.6	0.3692	8.0	24.64
Sim8	Nearshore	Late July 7/21-7/22/2015	203	128	8	11.87	12.62	0.167	6321	16.2	0.3425	9.3	28.31
	Offshore	Early June 6/9/2015	160	1	7	8.56	8.38		4122	11.4			
Sim1	Offshore	Late June 6/23/2015	174	15	19	9.54	10.04	0.110	5181	11.2	0.3010	6.1	26.99
Sim2	Offshore	Early July 7/7/2015	188	29	11	13.79	12.02	0.132	5420	12.1	0.2755	6.5	30.51
Sim3	Offshore	Late July 7/21/2015	202	43	10	13.45	14.40	0.158	4507	12.6	0.3102	8.6	27.83
Snohomish Tulalip													
	Offshore	Early May 5/13/2015	133	1	16	6.49	6.26		3540	11.3			
Sim1	Offshore	Late June 6/24/2015	175	43	25	15.09	16.40	0.236	6583	12.7	0.3809	24.0	39.88
Sim2	Offshore	Early July 7/7-7/8/2015	188	56	14	24.04	22.10	0.407	4289	14.1	0.4078	14.3	40.83
Sim3	Offshore	Late July 7/22/2015	203	71	8	34.06	31.17	0.567	3672	14.1	0.6206	31.4	29.16

	Habitat	Sampling Period	Mean Day of Year	Simulation Day	N	Mean Weight[a] (g)	Input Weight[b] (g)	Growth Rate (g/d)	Avg Prey Energy Density (J/g)	Temp[c] (°C)	P-value (feeding rate)	Total Consumption (g)	Growth Efficiency (%)
Sim4	Offshore	Early August 8/4-8/5/2015	217	85	18	42.29	42.96	0.786	3553	14.7	0.7459	44.8	26.37
						Snohomish Wallace							
	Offshore	Early June 6/10/2015	161	1	7	6.92	7.13		5605	11.8			
Sim1	Offshore	Late June 6/24/2015	175	15	34	10.40	10.48	0.223	6583	12.7	0.3318	6.7	49.95
Sim2	Offshore	Early July 7/7-7/8/2015	188	28	8	15.20	14.98	0.322	4289	14.1	0.4124	10.7	43.28
Sim3	Offshore	Late July 7/22/2015	203	43	16	24.86	22.64	0.479	3672	14.1	0.6360	24.9	31.05
Sim4	Offshore	Early August 8/4-8/5/2015	217	57	32	32.04	33.28	0.710	3553	14.7	0.7764	37.9	28.16

[a] Mean weight is geometric mean weight for all stock fish in a life stage

[b] Input weight is weight used for bioenergetics simulations, calculated from linear regression of log10 transformed weight over time. Linear regressions were calculated individually for each habitat, stock and year

[c] Temperatures were calculated from data collected concurrently with fish except when it was unavailble. In those cases temperature for the lifestage was calculated by iterating temperature between the preceding and following life stages. Ititerated temperatures are labeled with a *

Appendix A3. Average prey proportions and energy densities for each stock and bioenergetics scenario

Prey Energy Density (J/g):			4594	7211	3140	4375	10930	12670	4059	5471	3379	2994	4225	3395	4729	3550	4730	2464	1980	2960	3548	3410	5060	3690	3440
Habitat	Sim Day	N Diets	Diptera Adult	Other Insect	Insect Pupa	Insect Larva	Hemiptera	Hymenoptera	Aquatic Insect	Collembola Arachnid	Other Crustacean	Amphipod	Decapod Megalops	Decapod Zoea	Euphausid	Mysid	Shrimp	Hyperiid	Worm	Isopod	Other Fish	Salmonid	~~Sandlance~~sand lance	Herring	Anchovy
2014																									
Nooksack Fall (N)																									
Nearshore	1	15	0.323	0.133	0.004	0.080	0.000	0.003	0.000	0.044	0.254	0.091	0.000	0.000	0.000	0.000	0.000	0.000	0.067	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	15	20	0.102	0.002	0.051	0.048	0.050	0.024	0.002	0.000	0.446	0.255	0.014	0.001	0.000	0.000	0.000	0.001	0.004	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	30	24	0.213	0.069	0.015	0.100	0.078	0.000	0.036	0.005	0.179	0.203	0.001	0.042	0.000	0.000	0.000	0.000	0.058	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	45	19	0.167	0.031	0.156	0.065	0.000	0.009	0.043	0.002	0.051	0.366	0.000	0.000	0.000	0.000	0.000	0.000	0.109	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	58	7	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.799	0.148	0.000	0.048	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	72	16	0.383	0.009	0.092	0.001	0.004	0.001	0.001	0.133	0.022	0.065	0.231	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.012	0.000	0.044	0.000	0.000
Nearshore	89	21	0.364	0.015	0.011	0.016	0.020	0.000	0.000	0.034	0.028	0.028	0.485	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Nooksack Kendall Creek																									
Offshore	1	8	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.034	0.000	0.086	0.150	0.000	0.000	0.015	0.000	0.000	0.000	0.341	0.342	0.008	0.018	0.005
Offshore	50	14	0.008	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.238	0.003	0.545	0.094	0.000	0.000	0.000	0.000	0.023	0.012	0.000	0.071	0.000	0.000	0.000
Offshore	64	4	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.250	0.000	0.000	0.000	0.000	0.736	0.000	0.000	0.000	0.014	0.000	0.000	0.000	0.000
Nooksack Skookum Creek																									
Nearshore	1	8	0.519	0.086	0.000	0.000	0.027	0.022	0.000	0.010	0.224	0.041	0.029	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.040	0.000	0.000	0.000	0.000
Nearshore	18	6	0.382	0.019	0.003	0.004	0.032	0.521	0.000	0.002	0.001	0.037	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	30	11	0.156	0.003	0.067	0.003	0.031	0.031	0.000	0.006	0.062	0.259	0.056	0.000	0.000	0.056	0.027	0.000	0.085	0.000	0.068	0.090	0.000	0.000	0.000
Nearshore	75	9	0.418	0.000	0.000	0.101	0.000	0.127	0.000	0.000	0.249	0.007	0.006	0.000	0.000	0.000	0.091	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Offshore	1	10	0.008	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.216	0.010	0.019	0.183	0.477	0.000	0.000	0.000	0.000	0.000	0.000	0.073	0.000	0.000	0.000
Offshore	22	14	0.112	0.240	0.000	0.000	0.043	0.310	0.000	0.000	0.017	0.016	0.113	0.047	0.000	0.000	0.000	0.020	0.082	0.000	0.000	0.000	0.000	0.000	0.000
Offshore	36	13	0.009	0.001	0.000	0.005	0.001	0.000	0.000	0.000	0.256	0.005	0.669	0.042	0.000	0.000	0.000	0.000	0.000	0.013	0.000	0.000	0.000	0.000	0.000
Offshore	50	16	0.004	0.002	0.001	0.023	0.013	0.000	0.000	0.000	0.033	0.002	0.178	0.143	0.000	0.000	0.343	0.087	0.000	0.000	0.051	0.057	0.063	0.000	0.000

Prey Energy Density (J/g):			4594	7211	3140	4375	10930	12670	4059	5471	3379	2994	4225	3395	4729	3550	4730	2464	1980	2960	3548	3410	5060	3690	3440
Habitat	Sim Day	N Diets	Diptera Adult	Other Insect	Insect Pupa	Insect Larva	Hemiptera	Hymenoptera	Aquatic Insect	Collembola Arachnid	Other Crustacean	Amphipod	Decapod Megalops	Decapod Zoea	Euphausid	Mysid	Shrimp	Hyperiid	Worm	Isopod	Other Fish	Salmonid	~~Sandlance~~sand lance	Herring	Anchovy
Nisqually Clear Creek																									
Nearshore	1	13	0.059	0.001	0.008	0.046	0.000	0.144	0.000	0.050	0.279	0.165	0.004	0.139	0.000	0.000	0.000	0.007	0.098	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	14	12	0.010	0.000	0.042	0.002	0.001	0.000	0.000	0.000	0.169	0.052	0.211	0.240	0.000	0.041	0.000	0.012	0.083	0.053	0.083	0.000	0.000	0.000	0.000
Nearshore	32	9	0.038	0.113	0.063	0.019	0.005	0.008	0.000	0.000	0.229	0.183	0.120	0.000	0.066	0.112	0.042	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000
Offshore	1	21	0.013	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.182	0.082	0.036	0.185	0.048	0.002	0.023	0.004	0.000	0.000	0.120	0.001	0.300	0.000	0.000
Offshore	28	14	0.001	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.255	0.004	0.575	0.115	0.000	0.000	0.005	0.033	0.000	0.000	0.008	0.001	0.000	0.000	0.000
Offshore	39	17	0.001	0.000	0.000	0.000	0.008	0.000	0.000	0.000	0.164	0.007	0.532	0.140	0.009	0.008	0.001	0.123	0.001	0.000	0.006	0.000	0.000	0.000	0.000
Offshore	61	13	0.001	0.001	0.000	0.000	0.000	0.009	0.000	0.000	0.068	0.000	0.695	0.077	0.021	0.000	0.006	0.118	0.000	0.000	0.000	0.003	0.000	0.000	0.000
Skagit Spring																									
Nearshore	1	17	0.572	0.010	0.084	0.004	0.080	0.028	0.004	0.012	0.061	0.118	0.014	0.000	0.008	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	14	10	0.254	0.095	0.001	0.002	0.014	0.083	0.000	0.008	0.079	0.072	0.106	0.101	0.000	0.000	0.000	0.000	0.000	0.000	0.185	0.000	0.000	0.000	0.000
Nearshore	29	13	0.294	0.108	0.102	0.012	0.039	0.013	0.000	0.017	0.145	0.037	0.067	0.027	0.000	0.001	0.000	0.000	0.000	0.000	0.138	0.000	0.000	0.000	0.000
Nearshore	42	11	0.288	0.049	0.022	0.007	0.030	0.290	0.000	0.001	0.036	0.040	0.021	0.001	0.000	0.000	0.089	0.000	0.000	0.055	0.000	0.071	0.000	0.000	0.000
Offshore	1	9	0.065	0.010	0.026	0.000	0.015	0.014	0.000	0.000	0.012	0.217	0.562	0.075	0.000	0.000	0.001	0.002	0.000	0.003	0.000	0.000	0.000	0.000	0.000
Offshore	14	16	0.112	0.121	0.000	0.014	0.035	0.173	0.000	0.010	0.030	0.051	0.235	0.007	0.000	0.071	0.000	0.001	0.000	0.036	0.001	0.000	0.040	0.063	0.000
Skagit Summer																									
Nearshore	1	5	0.305	0.187	0.000	0.004	0.011	0.154	0.000	0.013	0.011	0.145	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.170	0.000	0.000	0.000	0.000
Nearshore	17	18	0.457	0.099	0.079	0.008	0.053	0.010	0.000	0.016	0.105	0.036	0.048	0.088	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	29	11	0.288	0.049	0.022	0.007	0.030	0.290	0.000	0.001	0.036	0.040	0.021	0.001	0.000	0.000	0.089	0.000	0.000	0.055	0.000	0.071	0.000	0.000	0.000
Upper Skagit Summer (N)																									
Nearshore	1	9	0.371	0.000	0.110	0.025	0.000	0.000	0.252	0.000	0.115	0.128	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	15	Iterated	0.475	0.000	0.060	0.040	0.005	0.000	0.126	0.002	0.091	0.196	0.000	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	29	9	0.579	0.000	0.011	0.056	0.010	0.000	0.000	0.004	0.068	0.264	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	44	7	0.255	0.000	0.029	0.059	0.006	0.000	0.006	0.007	0.148	0.395	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.095	0.000	0.000	0.000	0.000
Nearshore	59	8	0.319	0.112	0.029	0.030	0.011	0.001	0.000	0.000	0.137	0.292	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.069	0.000	0.000	0.000	0.000
Nearshore	74	9	0.341	0.011	0.013	0.002	0.029	0.001	0.000	0.025	0.121	0.217	0.000	0.004	0.000	0.000	0.044	0.000	0.000	0.082	0.111	0.000	0.000	0.000	0.000
Nearshore	91	8	0.523	0.137	0.139	0.001	0.018	0.003	0.000	0.014	0.025	0.005	0.070	0.061	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000

Prey Energy Density (J/g):			4594	7211	3140	4375	10930	12670	4059	5471	3379	2994	4225	3395	4729	3550	4730	2464	1980	2960	3548	3410	5060	3690	3440
Habitat	Sim Day	N Diets	Diptera Adult	Other Insect	Insect Pupa	Insect Larva	Hemiptera	Hymenoptera	Aquatic Insect	Collembola Arachnid	Other Crustacean	Amphipod	Decapod Megalops	Decapod Zoea	Euphausid	Mysid	Shrimp	Hyperiid	Worm	Isopod	Other Fish	Salmonid	~~Sandlance~~sand lance	Herring	Anchovy
Nearshore	106	14	0.541	0.009	0.119	0.005	0.092	0.021	0.005	0.015	0.071	0.100	0.011	0.000	0.009	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	119	10	0.254	0.095	0.001	0.002	0.014	0.083	0.000	0.008	0.079	0.072	0.106	0.101	0.000	0.000	0.000	0.000	0.000	0.000	0.185	0.000	0.000	0.000	0.000
Nearshore	134	18	0.457	0.099	0.079	0.008	0.053	0.010	0.000	0.016	0.105	0.036	0.048	0.088	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	147	11	0.288	0.049	0.022	0.007	0.030	0.290	0.000	0.001	0.036	0.040	0.021	0.001	0.000	0.000	0.089	0.000	0.000	0.055	0.000	0.071	0.000	0.000	0.000
Nearshore	161	9	0.133	0.333	0.002	0.001	0.002	0.488	0.000	0.000	0.000	0.003	0.001	0.000	0.000	0.000	0.000	0.000	0.036	0.000	0.000	0.000	0.000	0.000	0.000
Offshore	1	27	0.050	0.001	0.000	0.000	0.014	0.008	0.000	0.021	0.074	0.024	0.090	0.627	0.001	0.000	0.011	0.001	0.000	0.007	0.071	0.000	0.000	0.000	0.000
Offshore	15	18	0.097	0.019	0.000	0.002	0.025	0.004	0.000	0.011	0.063	0.114	0.113	0.417	0.000	0.000	0.056	0.011	0.000	0.010	0.005	0.000	0.053	0.000	0.000
Offshore	36	11	0.036	0.151	0.000	0.000	0.034	0.060	0.000	0.009	0.005	0.044	0.399	0.261	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Offshore	50	9	0.065	0.010	0.026	0.000	0.015	0.014	0.000	0.000	0.012	0.217	0.562	0.075	0.000	0.000	0.001	0.002	0.000	0.003	0.000	0.000	0.000	0.000	0.000
Offshore	63	19	0.095	0.107	0.000	0.012	0.030	0.184	0.000	0.008	0.037	0.045	0.293	0.006	0.000	0.060	0.000	0.001	0.000	0.033	0.002	0.000	0.034	0.053	0.000
Snohomish Tulalip																									
Offshore	1	10	0.010	0.006	0.000	0.000	0.017	0.001	0.000	0.003	0.008	0.003	0.760	0.191	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Offshore	23	49	0.059	0.110	0.000	0.000	0.007	0.426	0.000	0.016	0.013	0.007	0.146	0.164	0.001	0.002	0.000	0.048	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Snohomish Wallace																									
Offshore	1	48	0.060	0.112	0.000	0.000	0.007	0.415	0.000	0.017	0.013	0.007	0.149	0.168	0.001	0.002	0.000	0.049	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Offshore	15	24	0.120	0.038	0.005	0.010	0.038	0.050	0.000	0.002	0.045	0.028	0.610	0.028	0.008	0.008	0.006	0.000	0.000	0.000	0.006	0.000	0.000	0.000	0.000
Upper Skagit Summer (N) in San Juan Islands																									
Nearshore	1	20	0.005	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.031	0.027	0.200	0.071	0.056	0.046	0.025	0.011	0.313	0.000	0.067	0.000	0.100	0.048	0.000
Nearshore	14	21	0.154	0.005	0.000	0.000	0.001	0.181	0.020	0.000	0.049	0.064	0.026	0.002	0.080	0.086	0.008	0.024	0.006	0.032	0.019	0.042	0.202	0.000	0.000
2015																									
Nooksack Fall (N)																									
Nearshore	1	14	0.307	0.003	0.023	0.112	0.092	0.000	0.000	0.085	0.204	0.109	0.000	0.038	0.000	0.000	0.000	0.000	0.027	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	14	19	0.233	0.000	0.006	0.322	0.007	0.000	0.007	0.029	0.167	0.130	0.000	0.035	0.000	0.063	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	34	13	0.187	0.000	0.023	0.151	0.011	0.000	0.012	0.049	0.013	0.400	0.000	0.000	0.000	0.000	0.000	0.000	0.154	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	57	8	0.533	0.000	0.013	0.000	0.068	0.000	0.000	0.003	0.171	0.183	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.029	0.000	0.000	0.000	0.000	0.000
Nearshore	69	7	0.526	0.008	0.031	0.002	0.047	0.003	0.000	0.022	0.079	0.030	0.078	0.000	0.000	0.000	0.000	0.000	0.175	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	84	13	0.308	0.000	0.006	0.055	0.007	0.000	0.000	0.004	0.100	0.108	0.411	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Prey Energy Density (J/g):			4594	7211	3140	4375	10930	12670	4059	5471	3379	2994	4225	3395	4729	3550	4730	2464	1980	2960	3548	3410	5060	3690	3440
Habitat	Sim Day	N Diets	Diptera Adult	Other Insect	Insect Pupa	Insect Larva	Hemiptera	Hymenoptera	Aquatic Insect	Collembola Arachnid	Other Crustacean	Amphipod	Decapod Megalops	Decapod Zoea	Euphausid	Mysid	Shrimp	Hyperiid	Worm	Isopod	Other Fish	Salmonid	~~Sandlance~~sand lance	Herring	Anchovy
Offshore	1	11	0.049	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.174	0.060	0.481	0.105	0.000	0.000	0.034	0.005	0.000	0.000	0.006	0.000	0.000	0.085	0.000
Offshore	15	10	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.106	0.024	0.603	0.028	0.000	0.000	0.000	0.063	0.000	0.000	0.000	0.000	0.000	0.076	0.100
Offshore	29	8	0.000	0.007	0.000	0.000	0.011	0.003	0.000	0.000	0.217	0.000	0.698	0.064	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Nooksack Kendall Creek																									
Offshore	1	10	0.020	0.027	0.000	0.000	0.045	0.004	0.000	0.000	0.260	0.000	0.131	0.512	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Offshore	15	11	0.049	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.174	0.060	0.481	0.105	0.000	0.000	0.034	0.005	0.000	0.000	0.006	0.000	0.000	0.085	0.000
Offshore	29	10	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.106	0.024	0.603	0.028	0.000	0.000	0.000	0.063	0.000	0.000	0.000	0.000	0.000	0.076	0.100
Offshore	43	9	0.000	0.006	0.000	0.000	0.009	0.003	0.000	0.000	0.193	0.000	0.732	0.057	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Offshore	57	10	0.006	0.001	0.000	0.001	0.001	0.042	0.000	0.000	0.091	0.000	0.314	0.170	0.000	0.000	0.000	0.001	0.006	0.000	0.025	0.000	0.000	0.342	0.000
Nooksack Skookum Creek																									
Offshore	1	11	0.049	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.174	0.060	0.481	0.105	0.000	0.000	0.034	0.005	0.000	0.000	0.006	0.000	0.000	0.085	0.000
Offshore	15	10	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.106	0.024	0.603	0.028	0.000	0.000	0.000	0.063	0.000	0.000	0.000	0.000	0.000	0.076	0.100
Offshore	29	9	0.000	0.006	0.000	0.000	0.009	0.003	0.000	0.000	0.193	0.000	0.732	0.057	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Offshore	43	10	0.006	0.001	0.000	0.001	0.001	0.042	0.000	0.000	0.091	0.000	0.314	0.170	0.000	0.000	0.000	0.001	0.006	0.000	0.025	0.000	0.000	0.342	0.000
Nisqually Clear Creek																									
Nearshore	1	10	0.003	0.002	0.000	0.000	0.008	0.017	0.000	0.000	0.639	0.010	0.257	0.063	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	14	7	0.005	0.001	0.007	0.000	0.001	0.001	0.000	0.005	0.369	0.039	0.279	0.151	0.052	0.000	0.002	0.001	0.000	0.089	0.000	0.000	0.000	0.000	0.000
Nearshore	30	6	0.255	0.000	0.000	0.000	0.022	0.000	0.000	0.016	0.082	0.000	0.094	0.087	0.088	0.293	0.058	0.000	0.003	0.000	0.000	0.000	0.000	0.000	0.000
Offshore	1	10	0.005	0.000	0.000	0.000	0.007	0.000	0.000	0.000	0.450	0.004	0.320	0.035	0.124	0.000	0.007	0.047	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Offshore	15	10	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.231	0.105	0.258	0.124	0.031	0.000	0.173	0.077	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Offshore	29	10	0.000	0.001	0.000	0.000	0.000	0.003	0.000	0.000	0.258	0.002	0.377	0.112	0.070	0.000	0.119	0.058	0.001	0.000	0.000	0.000	0.000	0.000	0.000
Offshore	43	10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.135	0.000	0.644	0.015	0.000	0.000	0.003	0.135	0.000	0.000	0.001	0.000	0.066	0.000	0.000
Skagit Spring																									
Nearshore	1	10	0.369	0.050	0.001	0.004	0.080	0.051	0.000	0.003	0.278	0.028	0.115	0.005	0.000	0.000	0.000	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	15	9	0.261	0.212	0.008	0.000	0.012	0.013	0.020	0.006	0.023	0.008	0.111	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.216	0.000	0.000	0.110	0.000
Nearshore	31	9	0.355	0.042	0.000	0.004	0.053	0.000	0.000	0.013	0.283	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.025	0.000	0.000	0.111	0.111	0.000
Nearshore	44	9	0.110	0.356	0.000	0.003	0.070	0.065	0.001	0.000	0.074	0.002	0.001	0.000	0.000	0.000	0.220	0.000	0.000	0.000	0.100	0.000	0.000	0.000	0.000

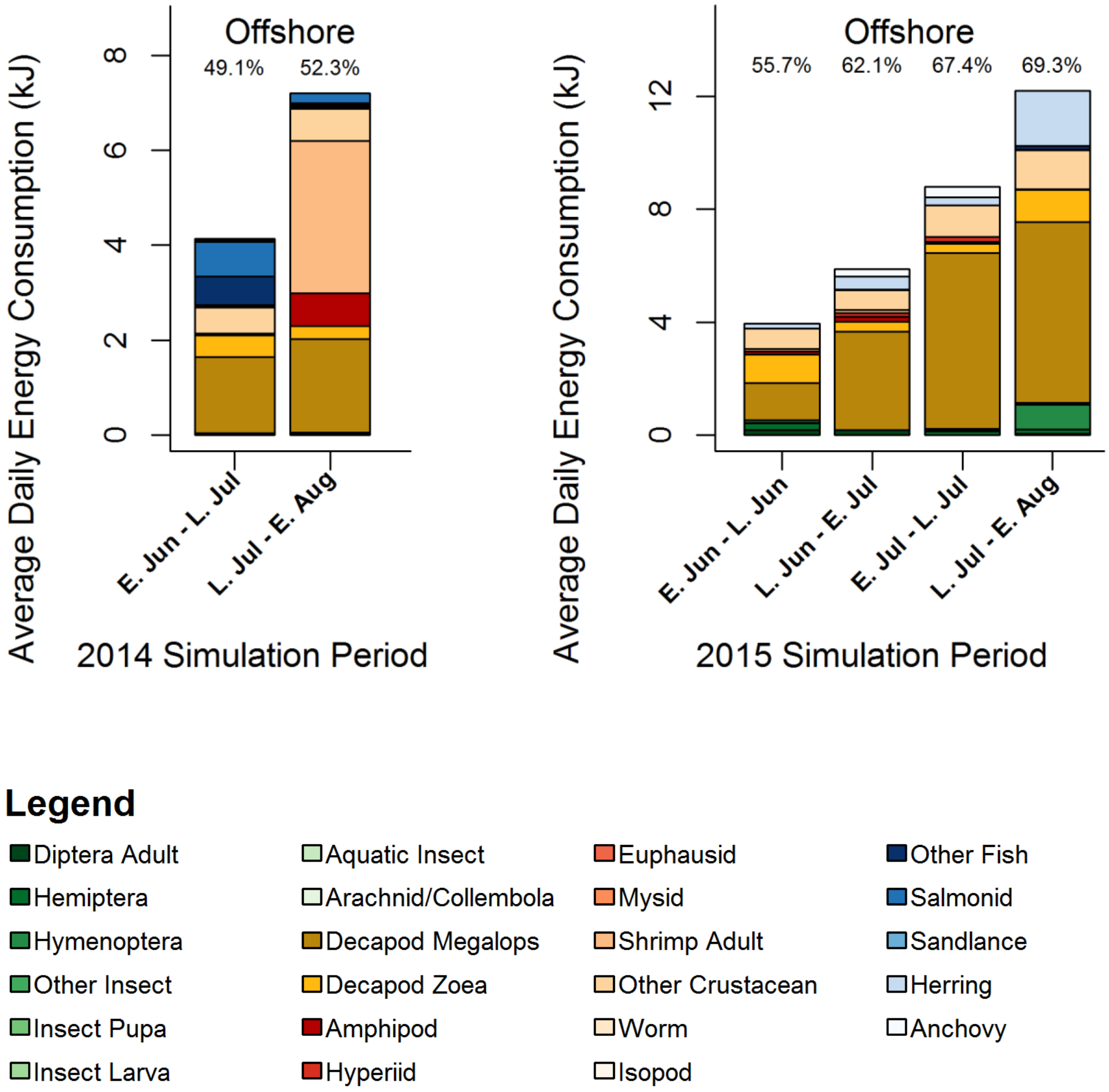
Prey Energy Density (J/g):			4594	7211	3140	4375	10930	12670	4059	5471	3379	2994	4225	3395	4729	3550	4730	2464	1980	2960	3548	3410	5060	3690	3440
Habitat	Sim Day	N Diets	Diptera Adult	Other Insect	Insect Pupa	Insect Larva	Hemiptera	Hymenoptera	Aquatic Insect	Collembola Arachnid	Other Crustacean	Amphipod	Decapod Megalops	Decapod Zoea	Euphausid	Mysid	Shrimp	Hyperiid	Worm	Isopod	Other Fish	Salmonid	~~Sandlance~~sand lance	Herring	Anchovy
Offshore	1	9	0.133	0.013	0.000	0.001	0.003	0.001	0.000	0.001	0.117	0.048	0.540	0.068	0.000	0.000	0.000	0.000	0.000	0.006	0.000	0.000	0.000	0.068	0.000
Offshore	15	9	0.060	0.254	0.000	0.002	0.030	0.002	0.000	0.008	0.007	0.026	0.596	0.015	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Offshore	29	10	0.089	0.249	0.010	0.071	0.047	0.036	0.000	0.005	0.128	0.022	0.229	0.013	0.000	0.000	0.059	0.004	0.037	0.000	0.002	0.000	0.000	0.000	0.000
Offshore	43	9	0.006	0.247	0.000	0.000	0.016	0.006	0.000	0.003	0.166	0.135	0.197	0.008	0.027	0.000	0.001	0.042	0.099	0.000	0.005	0.000	0.000	0.043	0.000
Offshore	57	8	0.006	0.339	0.001	0.000	0.002	0.000	0.000	0.000	0.093	0.188	0.119	0.053	0.000	0.000	0.000	0.006	0.032	0.001	0.006	0.000	0.000	0.007	0.148
Skagit Summer																									
Nearshore	1	9	0.313	0.194	0.008	0.000	0.001	0.004	0.020	0.000	0.023	0.000	0.111	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.216	0.000	0.000	0.110	0.000
Nearshore	17	8	0.471	0.054	0.000	0.005	0.088	0.000	0.000	0.018	0.326	0.007	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.028	0.000	0.000	0.000	0.000	0.000
Nearshore	29	9	0.135	0.394	0.000	0.003	0.115	0.065	0.001	0.000	0.074	0.002	0.001	0.000	0.000	0.000	0.110	0.000	0.000	0.000	0.100	0.000	0.000	0.000	0.000
Nearshore	64	5	0.000	0.000	0.000	0.013	0.000	0.000	0.000	0.010	0.030	0.000	0.000	0.000	0.000	0.200	0.200	0.000	0.000	0.000	0.006	0.000	0.148	0.000	0.394
Offshore	1	8	0.007	0.261	0.000	0.000	0.018	0.007	0.000	0.003	0.096	0.150	0.221	0.009	0.031	0.000	0.001	0.038	0.111	0.000	0.000	0.000	0.000	0.048	0.000
Offshore	15	6	0.008	0.453	0.001	0.000	0.002	0.000	0.000	0.000	0.008	0.251	0.025	0.004	0.000	0.000	0.000	0.007	0.043	0.001	0.000	0.000	0.000	0.009	0.187
Upper Skagit Summer (N)																									
Nearshore	1	10	0.370	0.058	0.057	0.022	0.073	0.004	0.000	0.000	0.169	0.059	0.000	0.034	0.000	0.000	0.124	0.000	0.000	0.000	0.031	0.000	0.000	0.000	0.000
Nearshore	31	Iterated	0.427	0.016	0.018	0.006	0.075	0.007	0.000	0.005	0.048	0.020	0.007	0.009	0.017	0.000	0.033	0.000	0.109	0.000	0.112	0.000	0.000	0.091	0.000
Nearshore	43	8	0.448	0.001	0.004	0.000	0.076	0.007	0.000	0.007	0.003	0.005	0.009	0.000	0.023	0.000	0.000	0.001	0.149	0.000	0.142	0.000	0.000	0.125	0.000
Nearshore	58	7	0.310	0.052	0.051	0.000	0.073	0.003	0.000	0.004	0.030	0.000	0.000	0.077	0.000	0.000	0.025	0.000	0.000	0.000	0.174	0.000	0.000	0.202	0.000
Nearshore	72	8	0.324	0.016	0.011	0.023	0.022	0.220	0.001	0.004	0.101	0.063	0.060	0.027	0.000	0.000	0.004	0.000	0.000	0.000	0.124	0.000	0.000	0.001	0.000
Nearshore	85	9	0.409	0.056	0.002	0.004	0.089	0.057	0.000	0.003	0.257	0.010	0.103	0.006	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Nearshore	99	9	0.313	0.194	0.008	0.000	0.001	0.004	0.020	0.000	0.023	0.000	0.111	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.216	0.000	0.000	0.110	0.000
Nearshore	113	8	0.471	0.054	0.000	0.005	0.088	0.000	0.000	0.018	0.326	0.007	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.028	0.000	0.000	0.000	0.000	0.000
Nearshore	128	9	0.110	0.356	0.000	0.003	0.070	0.065	0.001	0.000	0.074	0.002	0.001	0.000	0.000	0.000	0.220	0.000	0.000	0.000	0.100	0.000	0.000	0.000	0.000
Offshore	1	8	0.150	0.015	0.000	0.002	0.003	0.002	0.000	0.001	0.088	0.050	0.538	0.076	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.076	0.000
Offshore	15	9	0.060	0.254	0.000	0.002	0.030	0.002	0.000	0.008	0.007	0.026	0.596	0.015	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Offshore	29	10	0.089	0.249	0.010	0.071	0.047	0.036	0.000	0.005	0.128	0.022	0.229	0.013	0.000	0.000	0.059	0.004	0.037	0.000	0.002	0.000	0.000	0.000	0.000
Offshore	43	9	0.006	0.247	0.000	0.000	0.016	0.006	0.000	0.003	0.166	0.135	0.197	0.008	0.027	0.000	0.001	0.042	0.099	0.000	0.005	0.000	0.000	0.043	0.000
Snohomish Tulalip																									

Prey Energy Density (J/g):			4594	7211	3140	4375	10930	12670	4059	5471	3379	2994	4225	3395	4729	3550	4730	2464	1980	2960	3548	3410	5060	3690	3440
Habitat	Sim Day	N Diets	Diptera Adult	Other Insect	Insect Pupa	Insect Larva	Hemiptera	Hymenoptera	Aquatic Insect	Collembola Arachnid	Other Crustacean	Amphipod	Decapod Megalops	Decapod Zoea	Euphausid	Mysid	Shrimp	Hyperiid	Worm	Isopod	Other Fish	Salmonid	~~Sandlance~~sand lance	Herring	Anchovy
Offshore	1	10	0.113	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.491	0.000	0.002	0.293	0.000	0.000	0.000	0.000	0.000	0.000	0.100	0.000	0.000	0.000	0.000
Offshore	43	10	0.112	0.027	0.000	0.000	0.063	0.253	0.000	0.001	0.238	0.051	0.146	0.001	0.018	0.000	0.009	0.018	0.000	0.000	0.063	0.000	0.000	0.000	0.000
Offshore	56	10	0.067	0.026	0.000	0.002	0.029	0.011	0.000	0.050	0.313	0.035	0.203	0.000	0.006	0.001	0.092	0.006	0.001	0.000	0.042	0.000	0.000	0.000	0.115
Offshore	71	10	0.001	0.006	0.000	0.000	0.019	0.000	0.000	0.000	0.364	0.024	0.217	0.024	0.008	0.000	0.100	0.218	0.000	0.001	0.004	0.000	0.000	0.000	0.014
Offshore	85	10	0.000	0.001	0.000	0.000	0.001	0.000	0.000	0.000	0.347	0.015	0.192	0.010	0.028	0.000	0.058	0.132	0.000	0.001	0.003	0.000	0.000	0.000	0.212
Snohomish Wallace																									
Offshore	1	10	0.277	0.164	0.000	0.013	0.091	0.029	0.000	0.006	0.013	0.054	0.353	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Offshore	15	10	0.112	0.027	0.000	0.000	0.063	0.253	0.000	0.001	0.238	0.051	0.146	0.001	0.018	0.000	0.009	0.018	0.000	0.000	0.063	0.000	0.000	0.000	0.000
Offshore	28	10	0.067	0.026	0.000	0.002	0.029	0.011	0.000	0.050	0.313	0.035	0.203	0.000	0.006	0.001	0.092	0.006	0.001	0.000	0.042	0.000	0.000	0.000	0.115
Offshore	43	10	0.001	0.006	0.000	0.000	0.019	0.000	0.000	0.000	0.364	0.024	0.217	0.024	0.008	0.000	0.100	0.218	0.000	0.001	0.004	0.000	0.000	0.000	0.014
Offshore	57	10	0.000	0.001	0.000	0.000	0.001	0.000	0.000	0.000	0.347	0.015	0.192	0.010	0.028	0.000	0.058	0.132	0.000	0.001	0.003	0.000	0.000	0.000	0.212

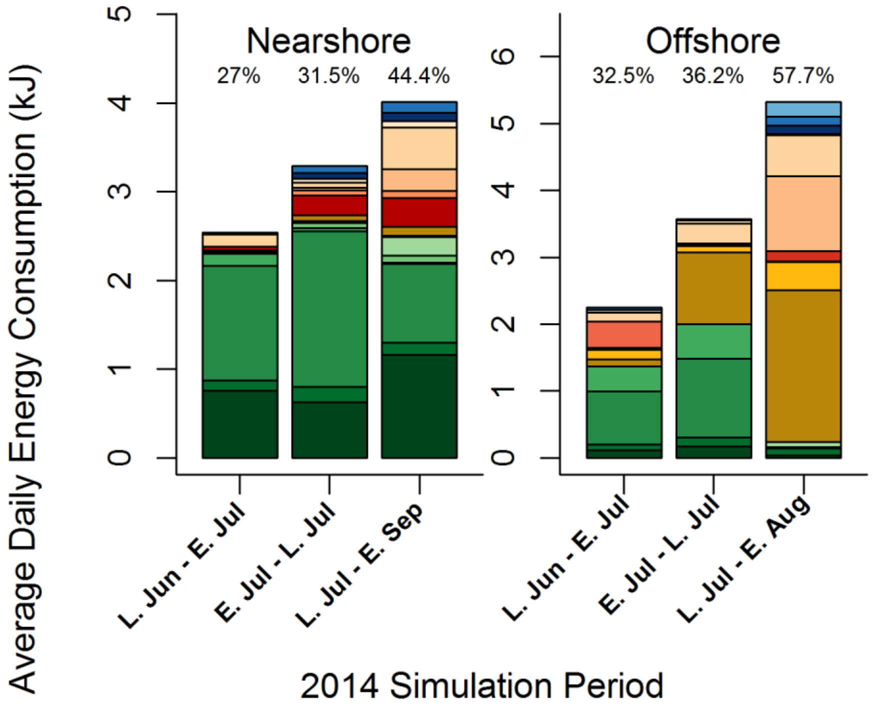
Appendix A4. Average daily kilojoules (kJ) of prey consumed for each growth scenario for each stock (A-I), habitat and year.

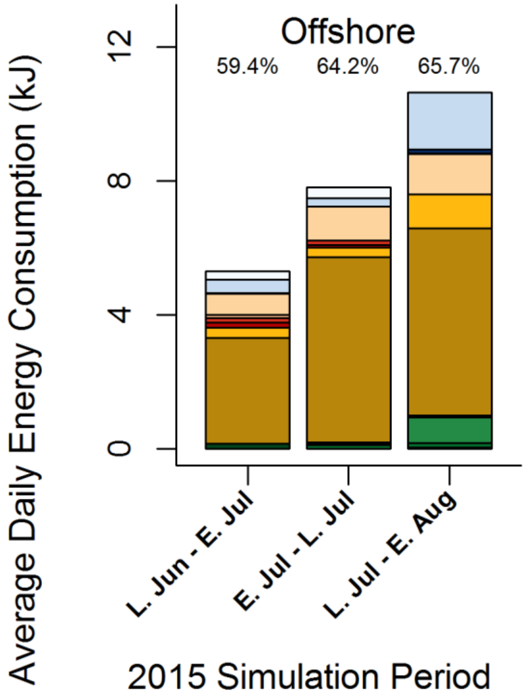
Values above the bars indicate feeding rates (%Cmax) for each simulation as a percentage of the theoretical maximum consumption rate for the given diet and thermal experience. Bar size represents total energy needs and has not been scaled by fish weight (larger fish require more energy). "SJI Nearshore" in Figure F shows the average daily energy consumption for fish from that stock in the San Juan Islands alternative rearing habitat.

A. Nooksack Kendall Creek

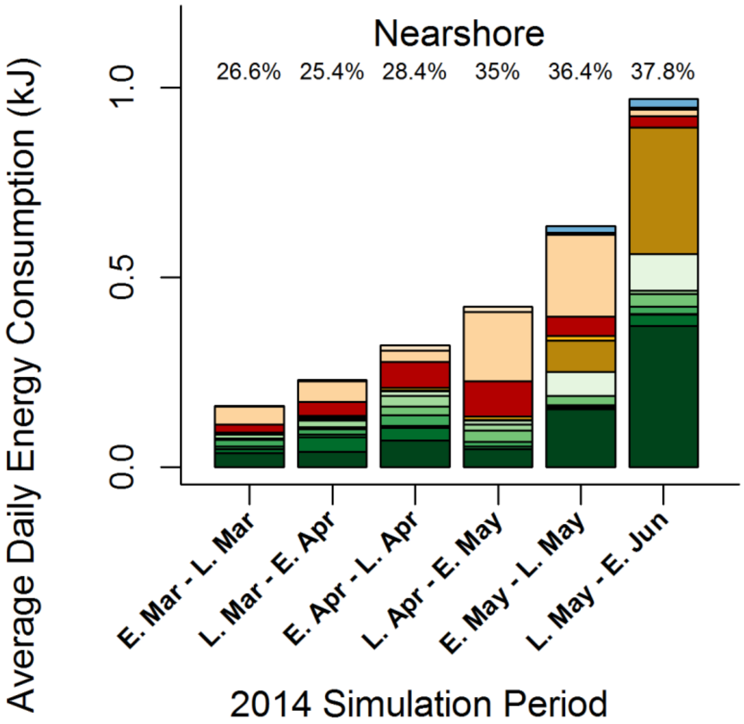


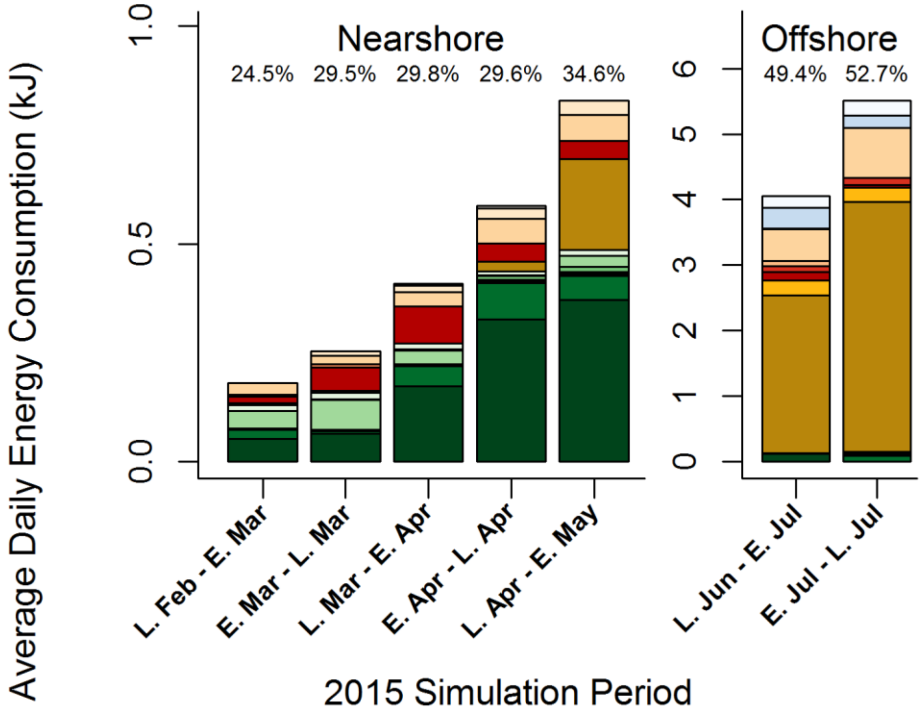
B. Nooksack Skookum Creek



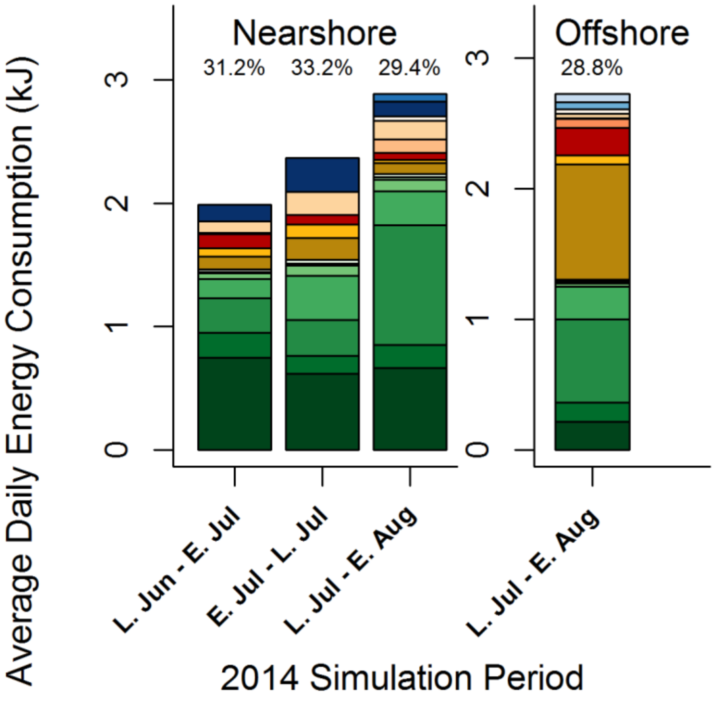


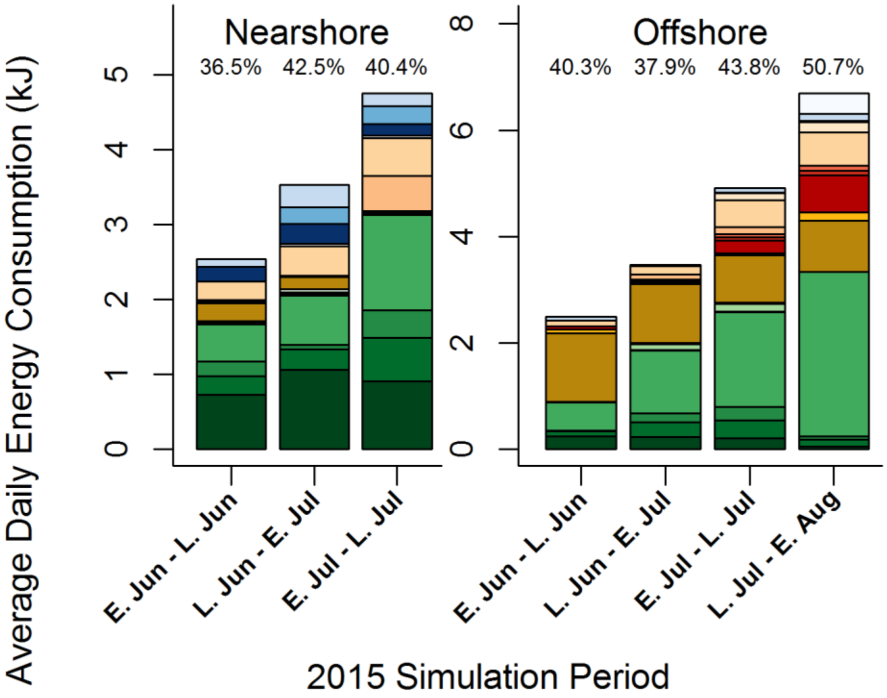
C. Nooksack Fall (N)



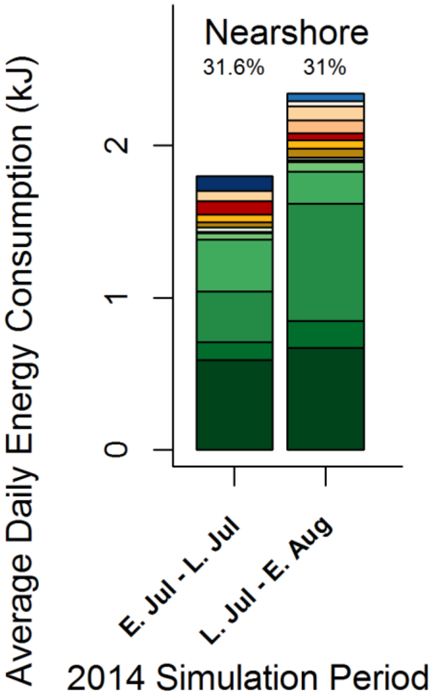


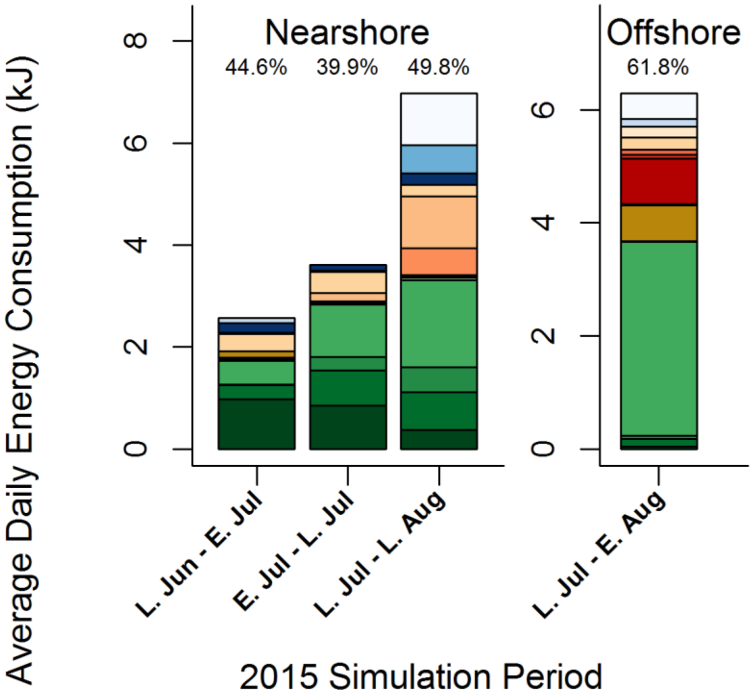
D. Skagit Spring



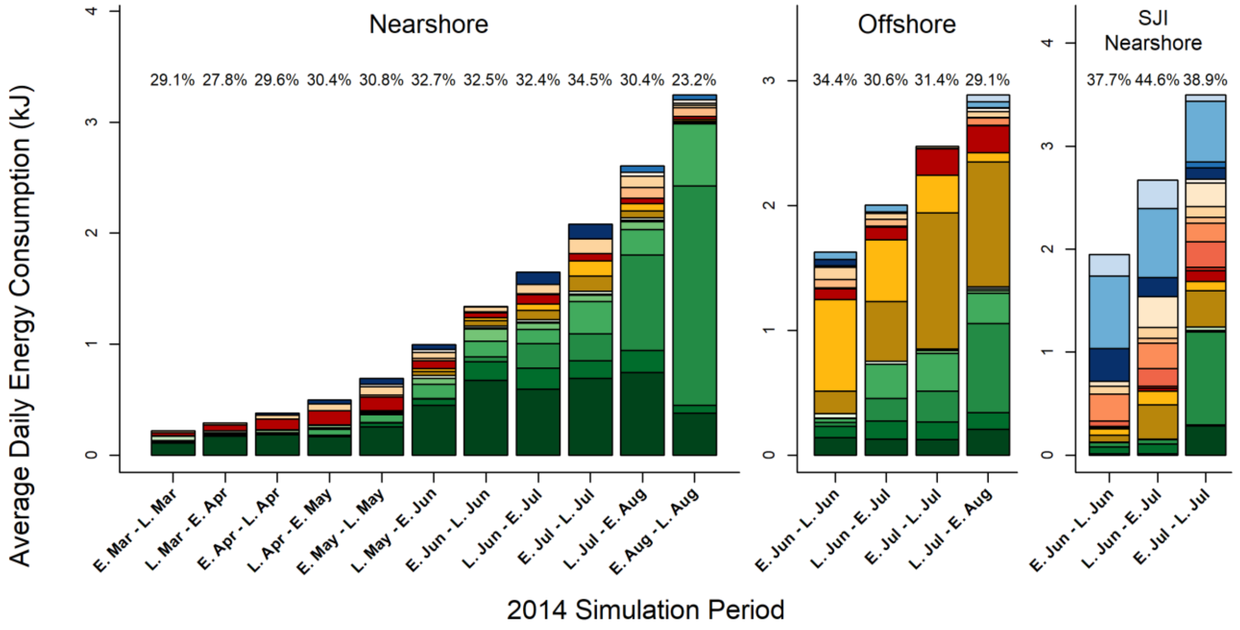


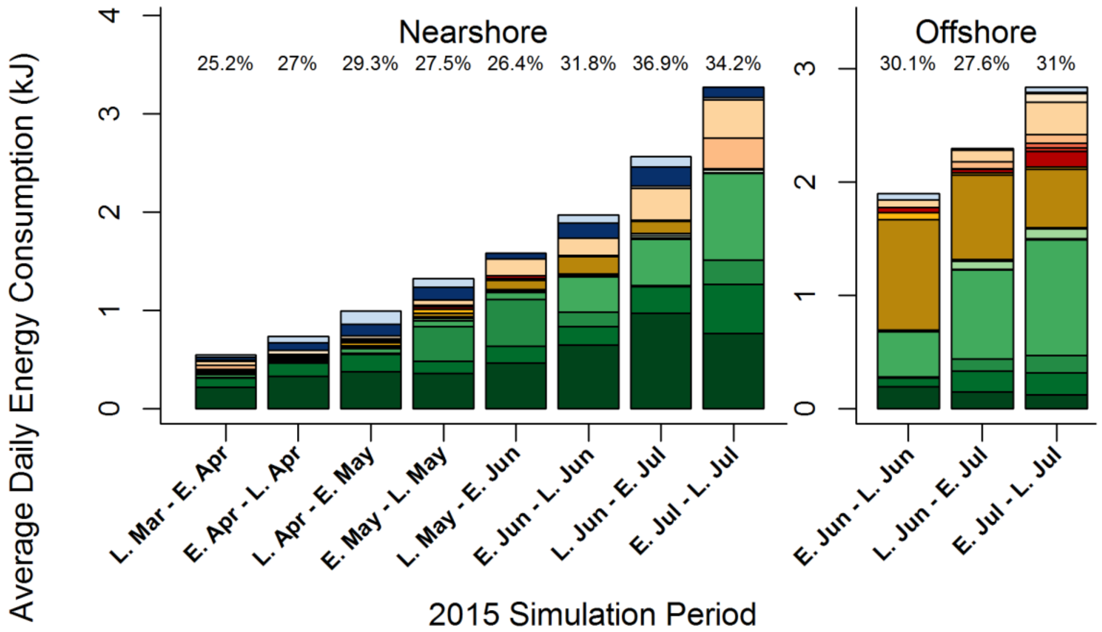
E. Skagit Summer



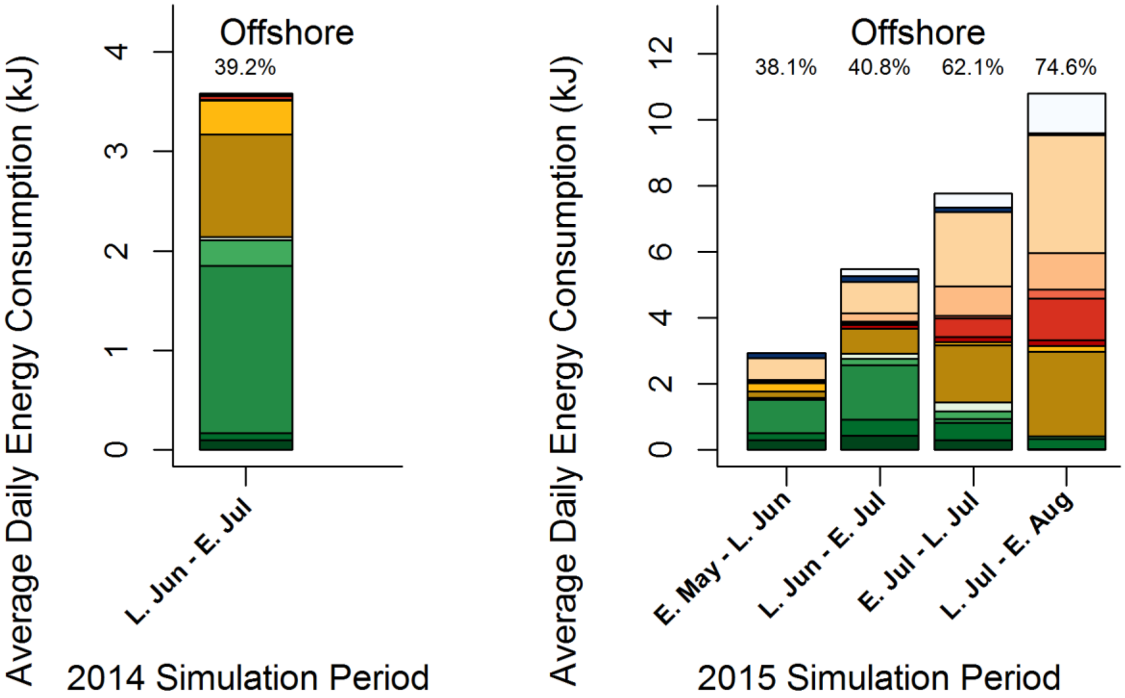


F. Upper Skagit Summer (N)

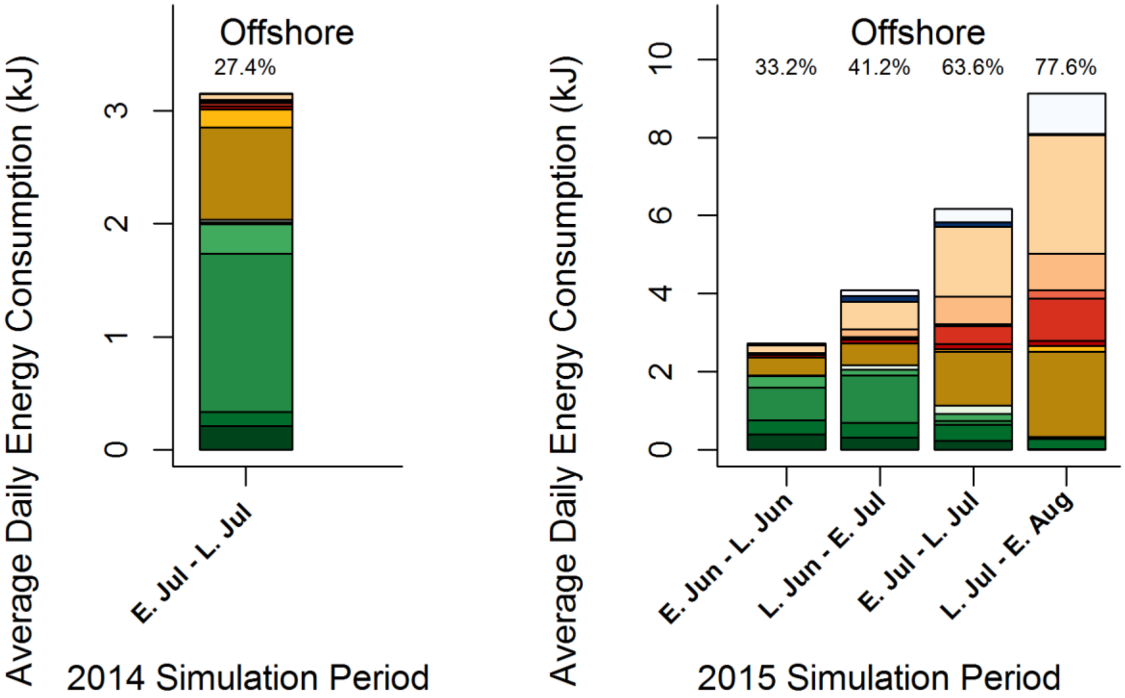




G. Snohomish Tulalip



H. Snohomish Wallace



I. Nisqually Clear Creek