Intra and inter-annual patterns of juvenile Pacific salmon (*Oncorhynchus)* growth in the Strait of Georgia, British Columbia

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Abstract

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Aquatic and Fishery Science

Early marine growth in juvenile salmon is positively correlated with overall survival to reproductive age. This study consists of two parts, in the first, regional patterns of juvenile coho (*Oncorhynchus kisutch*), Chinook (*O. tshawytscha*), chum (*O. keta*), pink (*O. gorbusha*), and sockeye (*O. nerka*) salmon early marine growth were analyzed over a three-year period (2012-2014) to provide insight into possible mechanisms regulating regional and inter-annual variation in survival. Insulin-like growth factor-1 (IGF1), a hormone used to assess instantaneous growth in fishes, was measured in late June and early July in the Strait of Georgia, Johnstone Strait, and Queen Charlotte Strait throughout the inside passage of British Columbia. All species showed significantly lower IGF1 concentration in both Johnstone and Queen Charlotte Strait when compared to the Northern Strait of Georgia ($p<0.05$). The second part of the study focused on coho and chum salmon in the Strait of Georgia. Coho salmon in 2012 and 2014 showed a strong similar pattern of IGF1 concentration and diet composition, with significantly lower IGF1 concentration in the south when compared to the north in each year ($p<0.05$). Coho salmon in 2013 showed less variation in IGF1 concentration and diet composition from north to south within the main basin of the Strait of Georgia. Overall, there was less regional variation in IGF1 concentration for chum salmon than coho salmon. However, chum salmon in Malaspina Strait had significantly higher IGF1 concentration in 2013 and 2014 when compared to the remainder of regions in the Strait of Georgia ($p<0.05$). There is a significant correlation between IGF1 concentration in coho salmon and the percent of herring in their diet among years ($p<0.05$).

There were no correlations between sea-surface temperate, thermocline presence, or water column stability among years of high growth and years of low growth in the Strait of Georgia. These results show that there is significant regional variation in IGF1 concentration for juvenile salmon in the Strait of Georgia and surrounding waters.

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CHAPTER 1

Testing the Trophic Gauntlet Hypothesis: juvenile salmon growth in Johnstone and Queen Charlotte Straits

1.1 INTRODUCTION

Johnstone Strait and Discovery Passage comprise the narrowest, coldest, and often deepest sections of the primary inside passage of costal British Columbia. The physical properties of Johnstone Strait lead to extreme and daily tidal water column mixing, preventing stratification and the development of a thermocline such as in the Strait of Georgia (Thomson, 1981). The Trophic Gauntlet Hypothesis (McKinnell et al., 2014) suggests that Johnstone Strait exists in a state of "perpetual biological winter" due to the inhibition of phytoplankton production by the tidal mixing and as such provides a poor growth environment for juvenile sockeye salmon due to a lack of prey. Thus, each year, the migratory corridor of Johnstone Strait presents a trophic challenge for juvenile salmon as they migrate out of the Strait of Georgia to the Pacific Ocean. When the consistently poor conditions of Johnstone Strait are coupled with poor conditions in Queen Charlotte Strait and/or Queen Charlotte Sound, migrating individuals may not quickly recover their growth pattern after exiting Johnstone Strait. High juvenile salmon mortality and low adult returns in the subsequent years may result (McKinnell et al., 2014). This may have been the case in 2007 resulting in the infamous 2009 sockeye salmon crash (DFO, 2012). Growth throughout early marine migration months is related to juvenile salmon survival to adulthood (Parker, 1962; Healey, 1982; Cross et al., 2009; Beamish et al., 2010(a); Duffy and Beauchamp, 2011). Thus, prolonged marine residence in regions of poor growth potential may greatly impact juvenile mortality and adult returns.

Juvenile coho (*Oncorhynchus kisutch*), Chinook (*O. tshawytscha*), chum (*O. keta*), pink (*O. gorbusha*), and sockeye (*O. nerka*) salmon from the Fraser River, the southwest British

Columbia Coast and the East Coast of Vancouver Island all commence early marine rearing in the Strait of Georgia, spending weeks to months in the region. Total juvenile salmon abundance in the Strait of Georgia during the summer varies greatly among years, but estimates often exceed 60 million (Beamish et al., 2005). Subsequent entry into the Pacific Ocean from the Strait of Georgia by juvenile salmon is possible via two primary routes, southward through the Strait of Juan de Fuca or northwestward through Johnstone and Queen Charlotte Straits. A preference to migrate northward through Johnstone Strait instead of through the Strait of Juan de Fuca exists for some species and likely may be stock specific (Groot and Cooke, 1987; Melnychuk et al., 2010). The exact proportions of migrants between the two routes may vary greatly from year to year (Healy, 1980). In addition to orientation, speed and timing of outmigration also varies among species and stocks. Most research on residence time in the Strait of Georgia and Johnstone Strait has been done for Fraser River sockeye salmon. Juvenile sockeye salmon have been estimated to spend (on average) anywhere between 24 and 54 days in the Strait of Georgia (Welch et al., 2009; Preikshot et al. 2012). Sockeye salmon are likely one of the fastest moving species during marine/coastal migration, whereas coho, Chinook, chum, and pink salmon most often spend longer in the Strait of Georgia (Melynchuk, et al. 2010).

Low growth of juvenile salmon in Queen Charlotte Strait has been previously observed (Ferriss et al., 2014). Measuring the concentration of plasma IGF1 assessed growth in this study. IGF1 is a hormone released from the liver that causes cells to divide and varies with feeding and fasting (Shimizu et al., 2009). IGF1 concentrations are indicative of instantaneous growth in juvenile salmon and may be a useful ecological tool (Beckman at al, 2004; Beckman, 2011; Ferriss et al., 2014). This study tested a component of the Trophic Gauntlet Hypothesis, decreased growth in Johnstone Strait, by utilizing IGF1 concentration as an indicator of region-

specific growth in juvenile salmon. This analysis also serves to highlight the use of IGF1 concentration as an environmental indicator of ecosystem health by demonstrating relevant discrete ecological measures of juvenile salmon growth.

1.2 METHODS

1.2.1 Study location

Sampling of juvenile salmon for this study was divided among four regions (from south to north): the Northern Strait of Georgia, Johnstone Strait, Queen Charlotte Strait, and Queen Charlotte Sound (Figure 1.1). These four regions represent distinct geographic areas before (Northern Strait of Georgia), during (Johnstone Strait), immediately following (Queen Charlotte Strait), and after a complete exit (Queen Charlotte Sound) of the defined trophic gauntlet. Regional boundaries were kept consistent across all years, but exact tow locations and sample sizes per region were not. Traveling northwest from the start of the Northern Strait of Georgia, the approximate linear displacement distance of the regions are as follows: Northern Strait of Georgia, 48 km; Discovery Passage, 61 km (area between Northern Strait of Georgia and Johnstone Strait, no data collection); Johnstone Strait, 66 km; Queen Charlotte Strait, 90 km; and Queen Charlotte Sound, 90 km.

1.2.2 Field sampling

Juvenile salmon were captured via fishing trawls aboard the C.C.G.S. W.E. Ricker and F/V Viking Storm in late June and early July of 2012, 2013, and 2014. Specifics of survey design and complete methods are detailed in Beamish et al. (2008). In this study, juvenile salmon were visually identified by species, weighed, measured for fork length, and blood samples were collected via heparinized syringe. Blood samples were immediately centrifuged, the plasma removed from the red blood cells, and stored frozen (-20 °C). Plasma samples were transported

frozen and stored at -80 °C until processing at the Northwest Fisheries Science Center (NWFSC) in Seattle, WA. Juvenile coho, Chinook, chum, pink (2012 and 2014), and sockeye (2012 and 2013 only) salmon were collected. Water column conductivity, temperature, and depth/pressure (CTD) were measured on both vessels with SBE 911plus CTD (Seabird Scientific). Due to the nature of trawl survey sampling and the geographic size of each region, sample sizes per region were not equal, nor were exact sample locations consistent across years. Additionally, some regions for some species do not have comparable sample numbers for any given year. Only regions with a sample size greater than 3 individuals were included in analyses.

Individual salmon were divided into 6 species classes per year: coho, chum, pink, and sockeye salmon of fork lengths less than 250 mm (fish of this size were in their first year of ocean residence for all species); and to correct for differences in age class, Chinook salmon were divided into two categories based solely on length, individuals smaller than 150 mm in fork length were termed Chinook-1 (in their first year of ocean residence having entered marine waters without spending a winter in freshwater) and those larger than or equal to 150 mm in fork length were termed Chinook-2 (in their first year of ocean residence having spent one winter in freshwater). Fifteen total species sets (one species class per year) were used in statistical testing: coho 2012, 2013, and 2014; Chinook-1 2013 and 2014; Chinook-2 2012, 2013, and 2014; chum 2012, 2013, and 2014; pink 2012 and 2014; and sockeye 2012 and 2013.

1.2.3 Laboratory techniques

Concentration of plasma IGF1 for individual fish was measured each summer (2012, 2013, and 2014) following their collection using the time-resolved fluorescence immunoassay developed by Small and Peterson (2005) as modified by Ferriss et al. (2014). Uniformity and speed in processing samples was enhanced using an automated pipetting workstation (Perkin-

Elmer). Across individual assays, all samples were standardized using inter-assay pools of coho salmon plasma at three known IGF1 concentrations (low, medium, and high), corresponding to approximately 75, 50, and 25 % binding in the immunoassay. Data standardization and complete laboratory techniques are detailed in Ferriss et al. (2014). Additionally, plasma 11-ketotestosterone (11-KT) concentration was measured only in coho salmon by immunosorbent assay (Cuisst at al, 1994) to exclude maturing coho salmon males, as their concentration of IGF1 is not exclusively indicative of relative growth (Beckman et al., 2004; Larsen et al., 2004). Maturing males were not collected within the given size slots for other salmon species.

1.2.4 Statistical analysis

In order to discern differences among regions and years within each species, analysis of variance tests (ANOVAs) were used to compare mean regional IGF1 concentration and mean regional fork length. The following linear models were used to assess the relationship between IGF1 concentration (ng/mL), fork length (mm), and region within each species class per year:

IGF1 concentration (ng/mL) ~ fork length (mm) [Model 1]

IGF1 concentration (ng/mL) ~ fork length (mm) + Region [Model 2]

For length-standardized comparisons within a year, the above-mentioned linear models (Model 2) were then used to generate a calculated IGF1 concentration for each region based on a common (annual average) fork length per species. The common average fork lengths were: 190, 130, 180, 130, 120, and 120 mm for coho, Chinook-1, Chinook-2, chum, pink, and sockeye salmon, respectively. All statistical analyses were performed among regions per species group per year using the ‘stats’ package in RStudio (R Core Team, 2014).

1.2.5 Oceanographic Analysis

CTD cast locations were divided into the same four geographic regions as the trawl locations. All CTD casts per region were combined and used to generate mean temperature by depth in 5-meter increments starting at a depth of approximately 2 m. The depth in meters was calculated from the pressure in dbars with the following equation from Saunders (1981) [1]:

$$z = (1 - c_1)p - c_2 p^2 \quad (1.1)$$

where: z is depth in m, p is pressure in dbar, $c_1 = (5.92 + 5.25\sin^2 \Phi) \times 10^{-3}$, Φ is latitude, and $c_2 = 2.21 \times 10^{-6}$ m db^{-2}.

Presence or absence of a regional water column thermocline was estimated using depth-to-depth (pressure-to-pressure) absolute temperature differences where the thermocline is the depth range midpoint from the line with the maximum slope where both $dz \geq 10$ m and $dT \geq 2$℃ using the following equation (Defant, 1961; Reilly and Fiedler, 1994) [2]:

$$\frac{-dT}{dz} = \frac{T_b - T_a}{z_b - z_a} \quad (1.2)$$

Mean surface temperature and presence/absence of a thermocline were used to assess differences in physical oceanography among years and regions.

1.3 RESULTS

1.3.1 Regional differences in IGF1 concentration

Juvenile salmon from Johnstone Strait had lower mean IGF1 concentration when compared to salmon from the Northern Strait of Georgia in all tests. Of the 13 total IGF1 concentration comparisons, twelve were significantly lower in Johnstone Strait when compared to the Northern Strait of Georgia ($p<0.02$, Figure 1.2, Table 1.1). A non-significant difference for Chinook-2 was found in 2012.

Salmon from Queen Charlotte Strait had lower mean IGF1 concentration when compared to salmon from the Northern Strait of Georgia in all comparisons. Of the 11 total IGF1 concentration comparisons, nine were significantly lower in Queen Charlotte Strait when compared to the Northern Strait of Georgia ($p<0.04$, Figure 1.2). Both non-significant IGF1 concentration differences were found in chum salmon (2012 and 2013).

Salmon from Queen Charlotte Sound followed a general trend of higher mean IGF1 concentration when compared to salmon from either Johnstone or Queen Charlotte Straits, however Queen Charlotte Sound was not sampled for IGF1 concentration in 2014. As such, there are fewer comparisons available, six total, between Queen Charlotte Sound and both Johnstone Strait and Queen Charlotte Strait. In all six comparisons, mean IGF1 concentrations in salmon from Johnstone Strait were significantly lower than in salmon from Queen Charlotte Sound ($p<0.05$, Figure 1.2). Additionally, in all six tests, mean IGF1 concentrations in salmon from Queen Charlotte Strait were lower than in salmon from Queen Charlotte Sound, five of the six comparisons were significant ($p<0.05$, Figure 1.2).

1.3.2 Regional differences in mean fork length

Mean fork lengths of coho, chum, and sockeye salmon were generally lowest in the Northern Strait of Georgia across all three years (Figure 1.3, Table 1.2). Little to no variation in fork length was observed among regions for Chinook-1, Chinook-2, and pink salmon. For Chinook salmon, mean fork length did not vary among the four regions for either Chinook-1 or Chinook-2 in either 2013 and 2014. For the remaining 11 annual significant species-specific comparisons, 9 showed the lowest mean fork length in the Northern Strait of Georgia (the exception being pink salmon 2012 and 2014). For species sampled in Queen Charlotte Sound, mean fork length was significantly higher than the other regions in four of the six available

comparisons: chum salmon 2012 and 2013, pink salmon 2012, and sockeye salmon 2012, but not sockeye salmon in 2013 or coho salmon in 2012.

1.3.3 Region specific relationships between IGF1 concentration and fork length

Annually, there was a positive relationship between IGF1 concentration and fork length in each species class. Of these 15 linear regressions, 10 significant positive relationships between IGF1 concentration and fork length were found (Table 1.3 Model 1; $p<0.02$). Slopes for two of the non-significant relationships were slightly positive (coho, 2013; Chinook-2, 2014) and three slopes were approximately zero (coho, 2012; Chinook-2, 2012; and sockeye, 2013). No significant negative relationships were found.

To address the IGF1 concentration and fork length relationship by region and observe differences in IGF1 concentration independent of length, ANCOVAs (Model 2) were used to compare IGF1 concentrations across possible fork lengths within a year, with region as a covariate (Table 1.3 Model 2; $p<0.01$). Significant regression coefficients of determination were found for all fifteen ANCOVAs. R-squared values ranged from 0.69 (chum 2012, $p<0.05$) to 0.19 (sockeye 2013, $p<0.05$).

Length standardized IGF1 concentrations in the Northern Strait of Georgia were significantly greater than found in either Johnstone or Queen Charlotte Strait for all species in all years (Figure 1.4, $p<0.05$). These results suggest that measured differences in IGF1 concentration between regions are independent of differences in regional fork length and thus reflect differences in growth between the regions. Length standardized IGF1 concentrations in Queen Charlotte Sound were greater than those found in the Northern Strait of Georgia for pink, chum, and sockeye salmon in 2012 and chum salmon in 2013.

1.3.4 Physical Oceanography by region

A thermocline was identified in all years of sampling in both the Northern Strait of Georgia and Queen Charlotte Sound (Figure 1.5, Table 1.4). No thermocline was present in any sampling year in Johnstone or Queen Charlotte Straits. The thermocline in the Northern Strait of Georgia was the strongest measured across regions in each of the three years with a temperature difference (°C) between the depths 10 and 20 meters of 3.7, 3.5, and 3.6, respectively. A thermocline was present in Queen Charlotte Sound between the depths 10 and 20 meters, but weaker, with temperature differences of 2.1 and 2.4 respectively (Figure 1.5). Water temperature in Johnstone Strait was highly uniform, with temperature differences ranging from 1.4, 0.8, and 0.7 °C from the depths of 2 to 100 meters across 2012, 2013, and 2014. Queen Charlotte Strait had slightly more variation in temperature with depth, but was still considered well mixed, temperature differences ranging between 3.2, 3.2, and 2.4 °C from the depths of 2 to 100 meters across 2012, 2013, and 2014.

1.4 DISCUSSION

These results are overwhelmingly consistent with the predicted outcome of decreased growth in Johnstone Strait compared to the Northern Strait of Georgia, developed from an application of the Trophic Gauntlet Hypothesis (McKinnell et al., 2014). In all instances, across all juvenile salmon species, and across the three-year sampling period, average IGF1 concentration (our proxy for instantaneous growth rate) was lower in Johnstone and Queen Charlotte Straits when compared to both the Northern Strait of Georgia and Queen Charlotte Sound. If the Northern Strait of Georgia is considered the origin of juveniles migrating outward, there is a substantial decrease in growth rate evident in both Johnstone and Queen Charlotte Straits as compared to the Northern Strait of Georgia. After leaving the well-mixed waters of

Johnstone and Queen Charlotte Straits and entering Queen Charlotte Sound, growth increases to levels equal to or (more often) greater than found in the Northern Strait of Georgia.

The pattern of decreased mean IGF1 concentration in Johnstone and Queen Charlotte Straits is independent of fish size, directly suggesting reduced food resources in Johnstone and Queen Charlotte Straits. This is based on several assumptions. The first being that juvenile salmon spend enough time in each region that IGF1 concentration of individual salmon collected in that region reflect the food resources there and that growth in a region is dependent upon food resources in that region. The second being that all juvenile salmon sampled originated in the Northern Strait of Georgia. The third being that the individuals sampled in each region reflect growth conditions across each geographic region.

The duration individuals have resided in their region of capture prior to sampling is unknown and may influence IGF1 concentration and our interpretation of the IGF1 signal. Although neither the exact ocean entry date nor the path and speed of a salmon's outmigration prior to capture is known, the likely maximum travel time between regions can be estimated. Assuming an optimal travel speed of 1 body length/s (Brett, 1983) the fastest displacement distance of individuals of 90, 150, or 250 mm long would be 7.8, 12.9, and 21.6 km per day, respectively. Given the approximate distance between the start of the Northern Strait of Georgia and the start of Queen Charlotte Sound (265 km), an individual of 150 mm on a straight track could travel this route in 20 days. This is a rudimentary minimum estimate of duration within a region as it does not incorporate increase in body length over time and assumes 24-hour constant travel along the most direct path between regions. However, under these assumptions, the approximate travel time across each region for an individual of 150 mm would be 3.7 days (Northern Strait of Georgia), 4.7 days (gap between the Northern Strait of Georgia and Johnstone

Strait), 5.1 days (Johnstone Strait), and 7 days (Queen Charlotte Strait). The time between food consumption and measurable increases in IGF1 concentration in laboratory-reared individuals varies, depending on feeding regime (Beckman, 2011) but may be at minimum 3 days (Pierce et al., 2005). Travel time between the end of the Northern Strait of Georgia and the end of Johnstone Strait can be estimated ~9.8 days, indicating that measured IGF1 concentration in Johnstone Strait is indicative of the conditions encountered in Johnstone Strait.

Two primary factors influencing growth, and thus IGF1 concentration, are quantity/quality of food consumption and water temperature (Brett at al, 1969; Beauchamp 2009). Neither stomach contents/compositions nor food abundance in the water column were directly measured in this study. However, basic environmental conditions known to influence common prey for juvenile salmon may give some insight on food abundance in the different regions. Stratification of the water column has an effect on the spatial distribution of plankton and other pelagic organisms (Rutherford et al., 1999). The absence of a thermocline could indicate an area of lower productivity leading to lower food abundance. In all three years sampled, both Johnstone and Queen Charlotte Straits lacked a distinct thermocline and were thus well mixed, whereas the Northern Strait of Georgia had a defined thermocline at approximately 15 meters. Thus, water column characteristics in the Northern Strait of Georgia would predict higher plankton productivity than water column characteristics in Johnstone and Queen Charlotte Straits. This is consistent with previous measurements of Johnstone Strait productivity compared to surrounding regions (McKinnell et al., 2014).

In a laboratory setting, optimal growth is a result of both temperature and food availability, but these relationships takes unique form in the complete absence of food/starvation (Brett et al., 1969). Growth is dependent on both temperature and food availability, however; the

amount of food needed for maximum growth increases with increasing temperature. Conversely, the effects of the absence of food (fasting) decrease with decreasing temperature. Thus, the colder temperatures in Johnstone and Queen Charlotte Straits may reduce the negative effects of decreased food supply in comparison to the situation when water is completely mixed and warm. Thus significant mortality might be associated with the challenge of the trophic gauntlet of Johnstone Strait only in years when food availability is also limited in the relatively warmer surface waters of Queen Charlotte Strait and Queen Charlotte Sound.

Johnstone and Queen Charlotte Straits present a consistent and likely unique challenge to out-migrating individual salmon compared to those traveling southwestward through the Strait of Juan de Fuca. The common phenomenon of decreased growth in Johnstone Strait in all species in all years suggests that there may be constant inter- and intra-species competition resulting from low food availability. The oceanography and complete mixing of Johnstone and Queen Charlotte Straits are not unique to the coastal Pacific, but the length and mandatory use as a migration corridor for northwestward bound migrants from the Strait of Georgia is unique. The differing environmental conditions and geographic location of the Strait of Georgia and Johnstone Strait offer a unique situation to further study the effects of temperature, prey availability, and oceanography on juvenile salmon growth and physiology.

There were some annual patterns that may indicate differences in species-specific responses to the decreased biological productivity encountered in Johnstone Strait. Coho salmon generally differ from other sampled species in having similar IGF1 concentrations in Queen Charlotte Sound and Northern Strait of Georgia in 2012 (the only sample year with Queen Charlotte Sound representation). A possible explanation for this observation is that the mean fork length in Queen Charlotte Sound was not significantly different from Northern Strait of Georgia

(as you would expect given their distance apart in the outmigration). Chum salmon differ slightly from the other species in that they showed a significant decrease in IGF1 concentration between Northern Strait of Georgia and Johnstone Strait all three years, but only showed a significant decrease in IGF1 concentration between Northern Strait of Georgia and Queen Charlotte Strait in 2014. Additionally, the significant increase of IGF1 concentration between Johnstone Strait and Queen Charlotte Sound is two-fold in both 2012 and 2013, the largest increase of any other species. This may indicate that as a whole, juvenile chum salmon are indeed victims of the conditions in Johnstone Strait, but may recover more rapidly than the other four species. Inclusion of life-history knowledge (and a large discrepancy of IGF1 concentration between the two life history patterns) led to the separation of Chinook salmon into Chinook-1 and Chinook-2. The separation of the classes by size likely diminishes observed differences in mean fork length between regions. Had there been larger sample sizes, an inclusion of stock-specific analyses could introduce more information on the magnitude of decrease between the Northern Strait of Georgia and Johnstone and Queen Charlotte Straits. Juvenile sockeye salmon are thought to exit the Strait of Georgia and enter open waters at a faster rate than other species (Melynchuk, et al. 2010). Given that the species known to travel the quickest through the sample regions consistently follows the growth pattern, IGF1 concentration of individuals collected in each region can be more readily assumed to represent growth conditions in the region in which they are captured. While there was little difference in mean fork length between regions within a year for pink salmon, both years strictly followed the pattern of decreased IGF1 concentration in Johnstone and Queen Charlotte Straits when compared to the Northern Strait of Georgia and Queen Charlotte Sound (2012 only).

The use of juvenile salmon IGF1 concentration in this analysis sets aside some environmental variation between years, as well as species-specific differences in life history and diet preference, to show a persistent pattern of marine growth in Johnstone Strait. Thus, in terms of expanding the overall implications of our findings on marine survival in a given year, IGF1 concentration analysis must be coupled with core environmental and biological differences between conditions encountered by juvenile salmon in the Strait of Georgia and Johnstone and Queen Charlotte Straits.

The presence of this reduced growth pattern across species provides an example of the strong and pervasive influence regional ocean conditions have upon the growth and survival of out-migrating juvenile salmon separate from prior freshwater or early marine growth experiences. Regardless of annual mean IGF1 concentration or annual fork length, the pattern observed is consistent, indicating that while the magnitude of the growth reduction may vary, the underlying environmental conditions persist among years. Growth was consistently lower in Johnstone and Queen Charlotte Straits when compared to the Northern Strait of Georgia. These results discretely measured and directly support the component of the Trophic Gauntlet Hypothesis (McKinnell et al., 2014) suggesting poor growth conditions in Johnstone Strait. The complete ramifications of these findings, and their impact on marine survival of juvenile salmon, is likely dependent on the quality of the marine environment encountered in Queen Charlotte Sound and beyond in any given year.

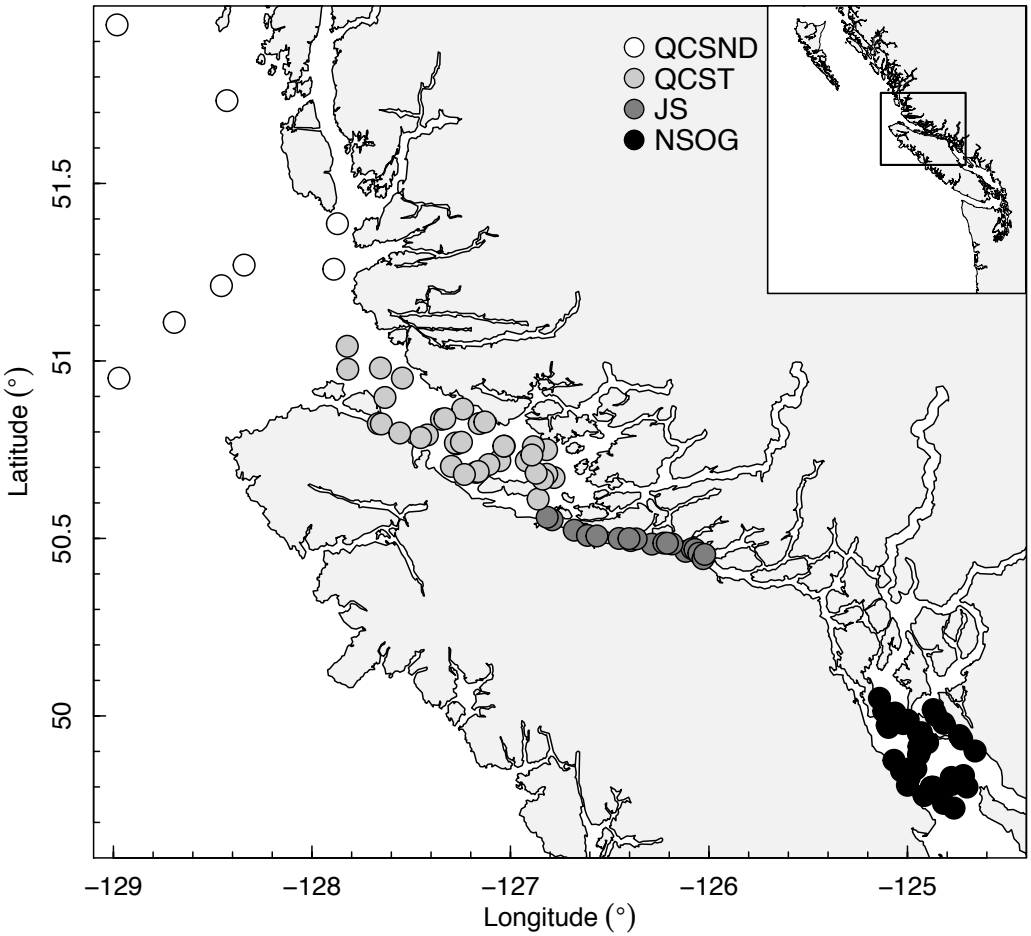


Figure 1.1 Map of study area in British Columbia, Canada. The tow location from all three sample years (2012, 2013, 2014) are shown and color coordinated by region: Queen Charlotte Sound (QCSND), Queen Charlotte Strait (QCST), Johnstone Strait (JS), and the Northern Strait of Georgia (NSOG) in white, light gray, dark gray, and black; respectively. Sampling conducted in late June and early July on W.E. Ricker.

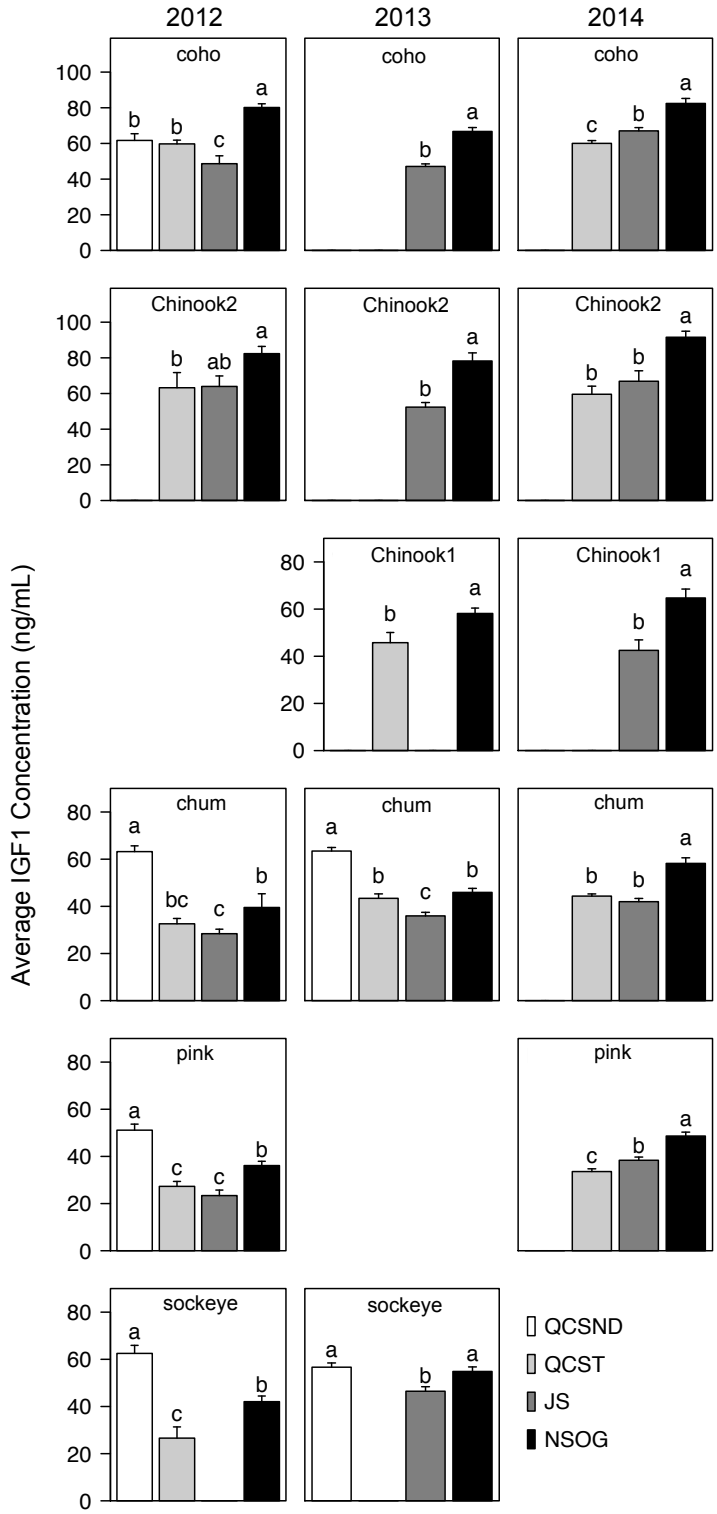


Figure 1.2. Average IGF1 (± standard error) concentration (ng/mL) per region per species per year. Statistically significant differences between regions are represented above a given column in a given year, with differences represented by different letters (ANOVA; $p<0.05$). The Northern Strait of Georgia (NSOG) in black, Johnstone Strait (JS) in dark gray, Queen Charlotte Strait (QCST) in light gray, and Queen Charlotte Sound (QCSND) in white.

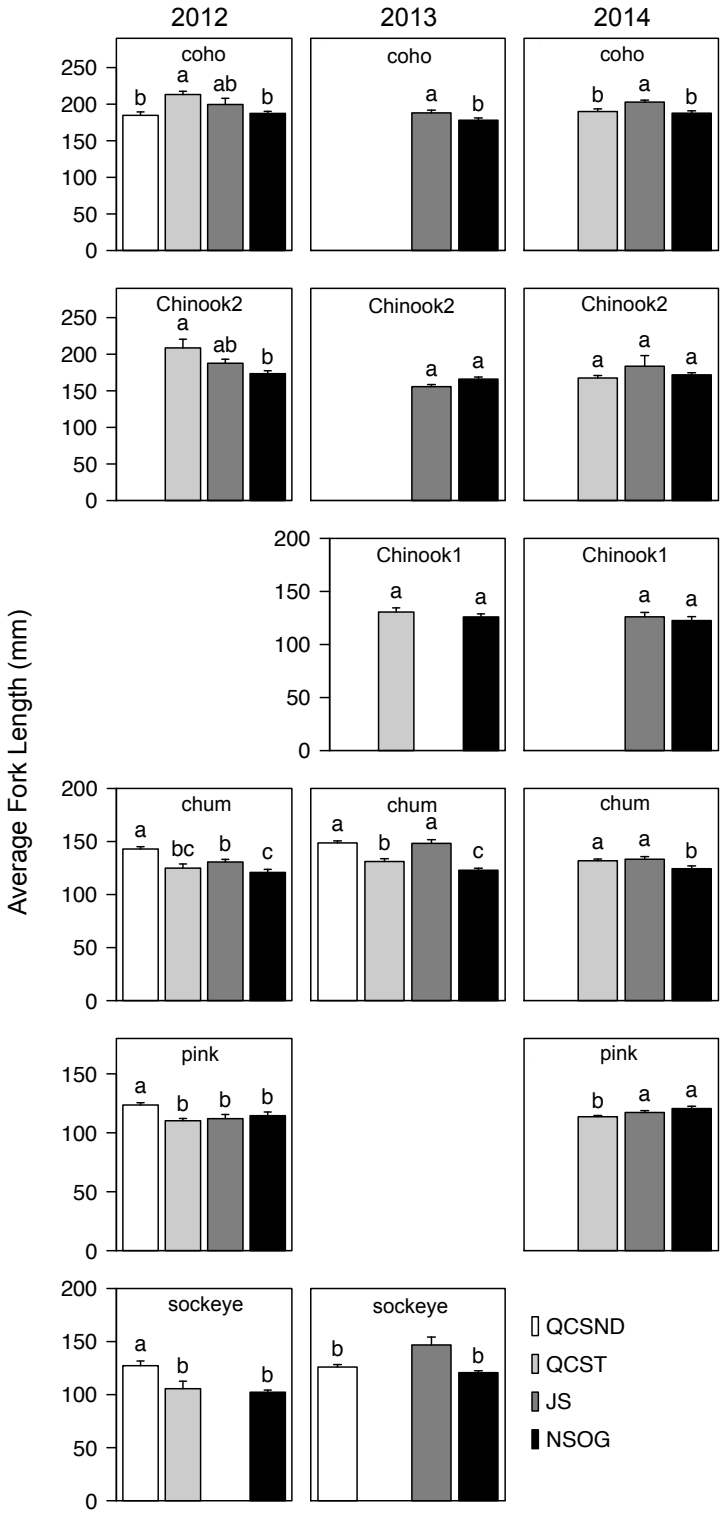


Figure 1.3. Average fork length (± standard error) (mm) per region per species per year. Statistically significant differences between regions are represented above a given column in a given year with differences represented by different letters (ANOVA; $p<0.05$). The Northern Strait of Georgia (NSOG) in black, Johnstone Strait (JS) in dark gray, Queen Charlotte Strait (QCST) in light gray, and Queen Charlotte Sound (QCSND) in white.

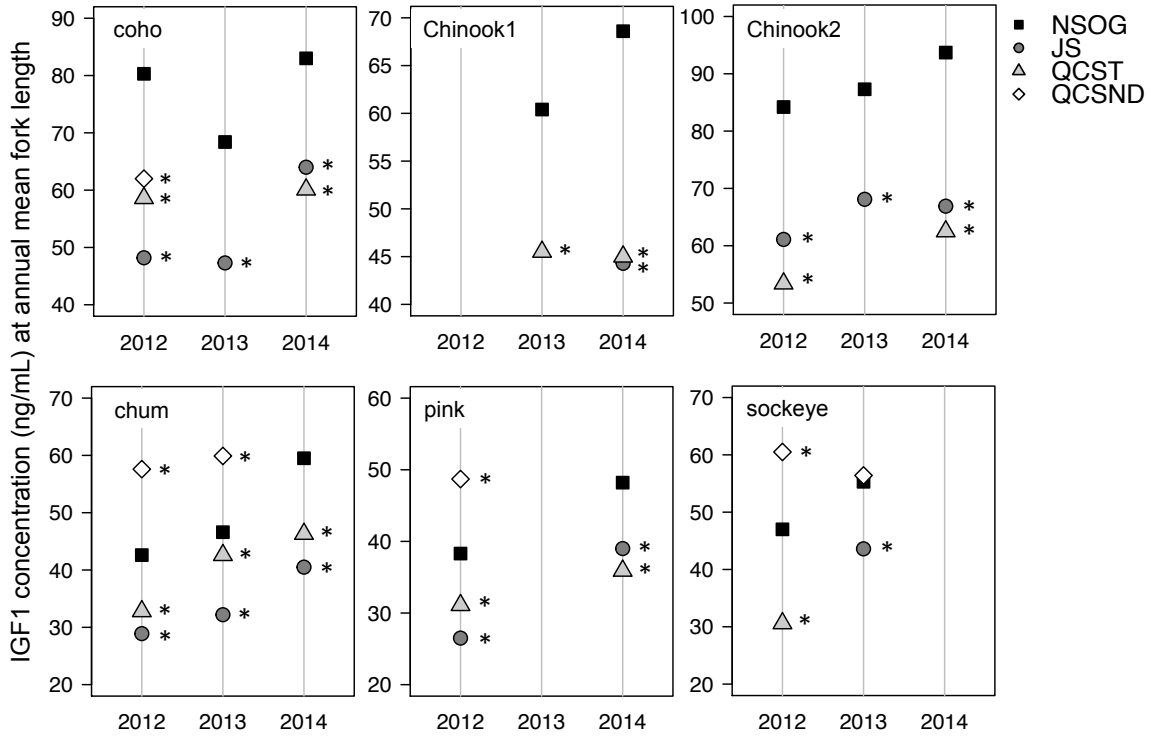


Figure 1.4. Length standardized IGF1 concentrations (ng/mL) per region determined through linear model (Model 2, Table 1.3) at species specific annual mean. Northern Strait of Georgia (NSOG) in black, Johnstone Strait (JS) in dark gray, Queen Charlotte Strait (QCST) in light gray, and Queen Charlotte Sound (QCSND) in white. Significant differences in y-intercept and calculated IGF1 concentration when compared to the Northern Strait of Georgia shown with asterisk ($p<0.05$).

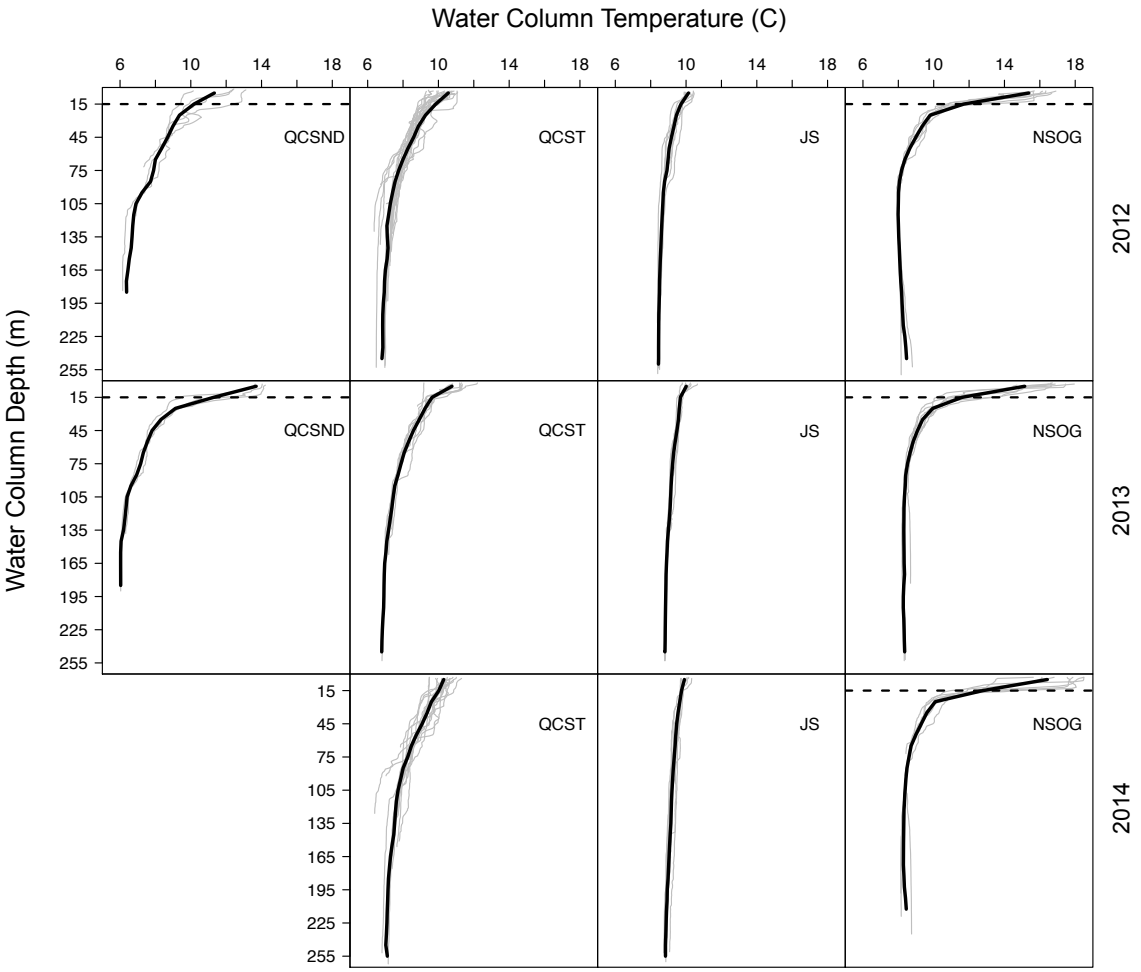


Figure 1.5. Temperature profiles for Queen Charlotte Sound (QCSND), Queen Charlotte Strait (QCST), Johnstone Strait (JS), and the Northern Strait of Georgia (NSOG) in 2012, 2013, and 2014. Gray lines indicate individual profiles while black line indicates mean profile in 5-meter increments. Thermoclines are represented by dashed line when appropriate. Average location and exact number of casts shown in Table 1.4.

Table 1.1 Average IGF1 concentration (ng/mL) including standard error and sample size per region. ND indicates inadequate sample size collected for that region in that year (n<3).

Average IGF1 Concentration (ng/mL) + SE (n)					
Species & Year		NSOG	JS	QCST	QCSND
coho	2012	80.15 + 2.08 (25)	48.65 + 4.41 (7)	59.75 + 2.09 (14)	61.69 + 3.76 (15)
	2013	66.72 + 2.19 (42)	47.11 + 1.42 (38)	ND	ND
	2014	82.42 + 2.81 (61)	67.04 + 1.83 (48)	60.04 + 1.57 (77)	ND
Chinook1	2012	ND	ND	ND	ND
	2013	58.15 + 2.28 (29)	ND	45.77 + 4.31 (5)	ND
	2014	64.72 + 3.78 (22)	42.5 + 4.45 (13)	ND	ND
Chinook2	2012	82.35 + 4.06 (14)	63.96 + 5.89 (3)	63.23 + 8.5 (5)	ND
	2013	78.24 + 4.54 (13)	52.36 + 2.58 (3)	ND	ND
	2014	91.55 + 3.38 (30)	66.88 + 5.86 (5)	59.58 + 4.53 (12)	ND
chum	2012	42.67 + 5.94 (8)	28.4 + 1.91 (20)	32.6 + 2.26 (37)	63.2 + 2.45 (10)
	2013	45.91 + 1.71 (52)	35.95 + 1.51 (43)	43.4 + 1.88 (32)	63.45 + 1.51 (31)
	2014	58.21 + 2.31 (38)	41.98 + 1.37 (58)	44.34 + 0.92 (102)	ND
pink	2012	36.12 + 1.81 (27)	23.39 + 2.34 (10)	27.3 + 2.09 (43)	51.13 + 2.56 (14)
	2013	ND	ND	ND	ND
	2014	48.64 + 1.66 (38)	38.36 + 1.36 (60)	33.58 + 1.16 (119)	ND
sockeye	2012	42.05 + 2.39 (41)	ND	26.59 + 4.75 (5)	62.51 + 3.41 (11)
	2013	54.86 + 1.92 (26)	46.47 + 1.91 (10)	ND	56.66 + 1.8 (19)
	2014	ND	ND	ND	ND

Table 1.2. Average fork length (mm) including standard error and sample size per region. Six region averages with IGF1 concentration measurements have individuals without reported lengths, noted with asterisk. ND indicates inadequate sample size collected for that region in that year (n<3).

Average Fork Length (mm) + SE (n)					
Species & Year		NSOG	JS	QCST	QCSND
coho	2012	187.40 + 2.80 (25)	199.57 + 8.43 (7)	213.21 + 4.39 (14)	184.73 + 4.66 (15)
	2013	178.10 + 3.05 (42)	188.10 + 3.72 (37)*	ND	ND
	2014	187.72 + 3.17 (61)	202.83 + 2.69 (48)	189.96 + 3.61 (77)	ND
Chinook1	2012	ND	ND	ND	ND
	2013	126.0 + 2.85 (29)	ND	130.60 + 3.92 (5)	ND
	2014	122.59 + 3.65 (22)	126.08 + 4.14 (13)	ND	ND
Chinook2	2012	173.43 + 3.98 (14)	187.67 + 5.49 (3)	208.60 + 11.87 (5)	ND
	2013	166.0 + 2.82 (13)	155.67 + 2.85 (3)	ND	ND
	2014	171.8 + 2.88 (30)	183.60 + 14.51 (5)	167.50 + 3.39 (12)	ND
chum	2012	120.86 +2.86 (7)	130.67 + 2.45 (15)*	124.91 + 3.89 (32)	142.90 + 2.19 (10)
	2013	122.92 + 1.87 (52)	148.24 + 3.46 (33)*	131.13 + 2.67 (31)*	148.65 + 1.91 (31)
	2014	124.34 + 2.67 (38)	133.28 + 2.47 (58)	131.82 + 1.64 (102)	ND
pink	2012	114.52 + 3.12 (27)	112.00 + 3.52 (10)	110.23 + 1.90 (43)	126.57 + 1.92 (14)
	2013	ND	ND	ND	ND
	2014	120.55 + 1.97 (38)	117.23 + 1.58 (60)	113.61 + 1.06 (111)*	ND
sockeye	2012	102.27 + 2.00 (41)	ND	105.60 + 7.04 (5)	127.27 + 4.40 (11)
	2013	120.73 + 1.77 (26)	146.80 + 7.44 (10)	ND	126.00 + 2.34 (19)
	2014	ND	ND	ND	ND

Table 1.3. Statistical model output of two linear models of IGF1 concentration (ng/mL), fork length (mm), and region per species per year. Model 1 is a linear regression of IGF1 concentration and fork length. Model 2 is a linear regression of IGF1 concentration and fork length with Region as a covariate. ND indicates inadequate sample size collected for that region in that year (n<3).

Species & Year		Model 1		Model 2	
		R^2	p-value	R^2	p-value
coho	2012	0.03	0.17	0.52	1.50E-08
	2013	0.00	0.48	0.46	8.90E-11
	2014	0.08	6.30E-05	0.36	2.20E-16
Chinook1	2012	ND	ND	ND	ND
	2013	0.34	3.00E-04	0.52	1.10E-05
	2014	0.16	0.02	0.51	3.30E-05
Chinook2	2012	0.00	0.71	0.38	0.03
	2013	0.29	0.03	0.45	0.02
	2014	0.02	0.34	0.44	1.30E-05
chum	2012	0.34	4.20E-07	0.67	1.50E-13
	2013	0.05	0.01	0.47	2.20E-16
	2014	0.12	8.60E-07	0.42	2.20E-16
pink	2012	0.30	1.40E-08	0.49	2.00E-12
	2013	ND	ND	ND	ND
	2014	0.15	5.90E-09	0.27	3.60E-14
sockeye	2012	0.21	3.00E-04	0.37	1.50E-05
	2013	0.01	0.60	0.19	0.01
	2014	ND	ND	ND	ND

Table 1.4. Average locations of CTD casts per region shown by mean latitude, mean longitude, and cast number per year. Presence or absence of thermocline indicated as calculated from Equation 2 in Methods. ND indicates no casts collected.

CTD Casts					
Region & Year		Mean Latitude	Mean Longitude	# of casts	Thermocline presence
NSOG	2012	49.85	-124.81	6	Yes
	2013	49.91	-124.88	7	Yes
	2014	49.94	-124.93	7	Yes
JS	2012	50.49	-126.37	6	No
	2013	50.51	-126.40	5	No
	2014	50.49	-126.32	7	No
QCST	2012	50.81	-127.28	20	No
	2013	50.75	-127.17	8	No
	2014	50.82	-127.33	16	No
QCSND	2012	51.22	-128.40	5	Yes
	2013	51.12	-128.67	4	Yes
	2014	ND	ND	ND	ND

CHAPTER 2

Intra- and inter-annual patterns of early marine growth in juvenile coho and chum salmon in the Strait of Georgia

2.1 INTRODUCTION

The Strait of Georgia is a highly productive freshwater fed marine fjord in coastal British Columbia. It is bound on the west by Vancouver Island and on the east by mainland British Columbia (Figure 2.1). In the north, the Strait of Georgia connects to the Pacific Ocean via Johnstone and Queen Charlotte Straits and in the southwest connects via the Strait of Juan de Fuca. Salmon runs in rivers that discharge into the Strait of Georgia are of great commercial and recreational value to British Columbia. The Strait of Georgia serves as an important early marine residence and adult return pathway for Pacific salmon species (Thompson, 1981). Juvenile salmon of five main species from both mainland British Columbia Rivers such as the Fraser and Squamish Rivers and from Vancouver Island Rivers such as the Cowichan and Nanaimo Rivers begin their marine residence by entering the Strait of Georgia. Juvenile Chinook (*Oncorhynchus tshawytscha*), chum (*O. keta*), coho (*O. kisutch*), pink (*O. gorbuscha*), and sockeye (*O. nerka*) are present in numbers often exceeding 50 million in the summer months (Beamish et al., 2005).

Marine residence of juvenile salmon in the Strait of Georgia ranges from weeks to months, with most juvenile salmon leaving by autumn. Both juvenile pink and chum salmon enter the Strait of Georgia from March to May. Distinct populations of coho, Chinook, and sockeye salmon have different ocean entry dates, however most juvenile coho and some populations of Chinook salmon enter the Strait of Georgia almost exclusively in May (Beamish et al., 2010a; Beamish et al., 2010c).

Recent trends in abundance and productivity vary among the salmon species utilizing the Strait of Georgia. In the past fifty years, there have been substantial declines in the early marine

survival of coho (Beamish et al., 2010a), Chinook (Beamish et al., 2012b), and sockeye (Peterman et al., 2010) salmon in the Strait of Georgia. Despite all time high releases of coho salmon smolts from hatcheries, adult coho salmon returns are at an all time low (Beamish et al., 2010a). Returns of highly monitored Chinook salmon stocks have experienced decreased marine survival over the last two decades (Beamish et al., 2012b). Additionally, the lowest Fraser River adult sockeye salmon return on record was observed in 2009 despite large numbers of juveniles entering the Strait of Georgia in 2007 (Thompson et al., 2012 and Beamish et al., 2012a). Although this 2009 event was transitory, as adult returns the subsequent year were similar to adult returns prior to 2009. In contrast, adult returns of chum salmon (1980s-1990s) appear to be stable (Henderson and Graham, 1998) and chum salmon smolt abundance in the Strait of Georgia has likely increased over the last few decades (Beamish et al., 1998). Juvenile pink abundance and survival in the Strait of Georgia is at an all time high (Beamish et al., 2012a). Pink salmon have a strict two year life cycle, resulting in distinct even and odd year stocks. For the marine waters of southern British Columbia, juvenile pink salmon are abundant only in even years (2012, 2014, etc.) (Beamish et al., 2012a). High abundance of pink salmon have been shown to negatively impact the survival of Chinook (Ruggerone and Goetz, 2004), coho (Beamish et al., 2010b), chum (Beacham and Starr, 1982), and sockeye salmon (Ruggerone and Neilson, 2005).

Variation in both abundance and early marine growth of juvenile salmon may be due to variations in food resources. Early marine growth is positively correlated with survival to reproductive age in juvenile salmon (Parker, 1962; Healey 1982; Duffy and Beauchamp, 2011) and the growth rate of juvenile salmon is directly related to both food consumption and metabolic rate, which are influenced by temperature (Brett et al., 1969). The Strait of Georgia

has undergone changes in both juvenile salmon abundance and productivity. Additionally, there has been a shift in zooplankton communities (Li et al., 2013) that play an important role in juvenile salmon diet in the Strait of Georgia. Zooplankton community shifts are often explained by oceanographic events such as strong positive Pacific Decadal Oscillation (PDO) phases or the occurrence of El Ninos (Mackas et al., 2007). But on a smaller scale, zooplankton communities and productivity can also be explained by current water column conditions and stability (Reygondeau and Beaugrand, 2010). Additionally, shifts in juvenile salmon diet can be linked to changes in ocean condition (Brouder et al., 2007; Sweeting and Beamish, 2009).

The growth rate of juvenile salmon can be assessed and measured through plasma insulin-like growth factor-1 (IGF1) concentration (Beckman et al., 2004; Ferriss et al., 2014). IGF1 is a hormone released from the liver that circulates in the blood and stimulates tissue growth (Duan, 1998). Concentration of IGF1 in the blood plasma varies with feeding and fasting (Shimizu et al., 2009). Discrete measurements of IGF1 concentration and inferred growth may aid in explaining where and under what conditions juvenile salmon species survival varies within the Strait of Georgia.

The Strait of Georgia is a unique location to study early marine juvenile salmon growth as it is home to a variety of oceanographically distinct regions. These regions include; deep, stratified, and narrow channels as found in the Discovery Islands and Desolation Sound, shallow well-mixed waters surrounding islands as found in the Gulf Islands, and wide, stratified open basins as found in the Southern and Northern Strait of Georgia. These regions provide a natural laboratory in which to compare growth via IGF1 concentration, quality of diet composition, and temperature profiles among regions and years between species. In this study, juvenile coho and chum salmon were used to assess both inter and intra annual patterns in IGF1 concentration.

2.2 METHODS

2.2.1 Study location

The Strait of Georgia was divided into eight regions for this study (from south to north): the Gulf Islands (Gulf), Fraser River Plume (Plume), Southern Strait of Georgia (SSOG), Malaspina Strait (Mala), Mid Strait of Georgia (SOG), Northern Strait of Georgia (NSOG), Desolation Sound (Des), and Discovery Islands (Disc) (Figure 2.1). These regions represent distinct oceanographic and geological delineations in the Strait of Georgia. Regional boundaries were kept consistent across all years, but exact tow locations (Figure 2.2) and sample sizes per region were not.

2.2.2. IGF1 concentration and fork length

2.2.2a Field sampling

Juvenile salmon were captured via trawl net aboard the C.C.G.S. W.E. Ricker in late June and early July of 2012, 2013, and 2014. All fishing was conducted with a modified mid-water rope trawl with the head-rope at the surface (zero meters) or 15 meters deep with an average net opening height between 12 and 18 meters and net opening width between 28 and 42 meters. Specifics of survey design and complete methods are detailed in Sweeting et al. (2003) and Beamish et al. (2008). But as it pertains to this study, juvenile salmon were visually identified by species, weighed, measured for fork length, and blood samples were collected via heparinized syringe from juvenile coho and chum salmon. Blood samples were immediately centrifuged, the plasma removed from the red blood cells, and stored frozen (-20 °C). Plasma samples were transported frozen and stored at -80 °C until processing at the Northwest Fisheries Science Center (NWFSC) in Seattle, WA. Only fish smaller than 250 mm in fork length were used in this study, ensuring that all fish were in their first year of ocean residence. Sample size varied

between tow, region, species, and year. Often total trawl sample size greatly exceeded IGF1 sampled trawl size. Minimum number of blood plasma samples collected per trawl was three individuals per species. Only regions with a sample size greater than 7 individuals were included in analyses.

2.2.2b Laboratory techniques

Concentration of plasma IGF1 for individual fish was measured each summer (2012, 2013, and 2014) following their collection using the time-resolved fluorescence immunoassay developed by Small and Peterson (2005) as modified by Ferriss et al. (2014). Uniformity and speed in processing samples was enhanced using an automated pipetting workstation (Perkin-Elmer). Across individual assays, all samples were standardized using inter-assay pools of coho salmon plasma at three known IGF1 concentrations (low, medium, and high), corresponding to approximately 75, 50, and 25 % binding in the immunoassay. Data standardization and complete laboratory techniques are detailed in Ferriss et al. (2014). Additionally, plasma 11-ketotestosterone (11-KT) concentration was measured only in coho salmon by immunosorbent assay (Cuisst at al, 1994) to exclude maturing coho salmon males, as their concentration of IGF1 is not exclusively indicative of relative tissue growth (Beckman et al., 2004; Larsen et al., 2004). Maturing males were not collected within the given size slots for chum salmon.

2.2.2c Statistical analysis

In order to discern differences among regions and years within coho and chum salmon metrics, analysis of variance tests (ANOVAs) were used to compare regional IGF1 concentration and regional fork length. Linear models were then used to assess the relationship of IGF1 concentration to fork length within each species class per year. Additionally, linear models and analysis of covariance tests (ANCOVAs) were used to assess the relationship of regional mean

IGF1 and fork length, utilizing year and region location (North v South) as covariates. North classified regions were: the Discovery Islands, Desolation Sound, Northern Strait of Georgia, and Mid Strait of Georgia, whereas South classified regions were: Malaspina Strait, Southern Strait of Georgia, Fraser River Plume, and Gulf Islands. Multiple linear models were explored using the parameters: IGF1 concentration, fork length, year, and region. Models were evaluated on their significance by Akaike information criterion (AIC) value (Anderson, 2008) and biological applicability. Annual and regional comparisons between coho and chum salmon were made using the regional mean of individual residuals from the linear regression of IGF1 concentration and fork length. All statistical analyses were preformed between regions per species per year using the 'stats' package in RStudio (R Core Team, 2014).

2.2.3 Diet composition

2.2.3a Field sampling

The same Department of Fisheries and Oceans Canada (DFO) scientist visually analyzed stomach fullness, digestion, and diet composition to the species level for each fish individually following blood plasma sampling in all three years. Fullness was described as both percent of stomach full (%) and volume (cubic centimeters). Digestion was described as percent decomposition of stomach contents. Only regions where diet data were collected for all three years in both coho and chum salmon were included in analysis. These four regions were: the Discovery Islands, Northern Strait of Georgia, Mid Strait of Georgia, and Southern Strait of Georgia.

2.2.3b Diet classification for statistical analysis

For the purpose of comparing diet composition to IGF1 concentration, individual fish were classified as having predominately one diet composition. Only stomachs that were at least

30% full were used in comparative IGF1 concentration and diet composition analyses. Stomachs fullness reported as 10 or 20 % were classified as empty because the overall volume collected and identified was low. Empty stomachs were included in the overall regional diet composition for IGF1 sampled fish, however given that their IGF1 concentration is not indicative of the growth related to their diet composition (or lack there of) they were not included in IGF1 concentration comparisons between diet compositions. Diet was categorized for coho and chum salmon as follows: crab megalops and/or crab zoea (larval crab), hyperiid amphipods, whole young of the year herring and/or herring remains, larval fish, euphasiids, gammarid amphipods, larval shrimp, calanoid copepods, decomposed matter, ctenophores, other, or empty. The other category is comprised of two subclasses: (1) stomachs with unique diet components that were not seen in large numbers such as insects or polychaetes and (2) stomachs in which one diet component did not comprise more than 50% of the stomach composition (often an equal mix of crab megalops, crab zoea, hyperiid amphipods, and euphasiids). Due to their prevalence in combination with one another, crab zoea and crab megalops were visually identified separately, but categorized together for diet composition and IGF1 concentration comparison as larval crab. Decomposed matter was only found in chum salmon. Decomposed matter was defined as stomach contents too digested for proper identification to a family or species level.

Annual overlap of diet composition across all three years for the four selected regions was estimated using Schoener's (1970) index of diet overlap within each species. Additionally, diet composition overlap (for IGF1 sampled individuals) per region was measured within each year. ANOVAs were used to assess differences in IGF1 concentration per diet composition within each year and species. Regional IGF1 concentration per region was regressed with percent

diet composition of young of the year herring per region across all three years in juvenile coho salmon.

2.2.4 Oceanography

Water column conductivity, temperature, and depth/pressure (CTD) were measured with a SBE 911plus CTD (Seabird Scientific). CTD cast locations were divided into the same eight geographic regions as the trawl locations (Figure 2.2). All CTD casts per region were combined and used to generate mean temperature by depth starting at a depth of either 2 or 3 meters. The depth in meters was calculated from the pressure in dbars with the following equation from Saunders (1981) [1]:

$$z = (1 - c_1)p - c_2 p^2 \quad (2.1)$$

where: z is depth in m, p is pressure in dbar, $c_1 = (5.92 + 5.25\sin^2 \Phi) \times 10^{-3}$, Φ is latitude, and $c_2 = 2.21 \times 10^{-6}$ m db^{-2}.

Presence or absence of a regional water column thermocline was estimated using depth-to-depth (pressure-to-pressure) absolute temperature differences where the thermocline is the depth range midpoint from the line with the maximum slope where both $dz \geq 10$m and $dT \geq 2$℃ using the following equation (Defant, 1961; Reilly and Fiedler, 1994) [2]:

$$\frac{-dT}{dz} = \frac{T_b - T_a}{z_b - z_a} \quad (2.2)$$

Water column stability was measured by calculating water column density with the 'oce' package in RStudio (Kelly and Richards, 2015). Static water column stability (E) was calculated using average density at the top (3 meters depth) and average density at 15 meters (given the shallow thermocline present in the Strait of Georgia) using the following equation [3]:

$$E = \left(\frac{\partial \rho}{\partial z}\right) \quad (2.3)$$

where: ρ is density in kg/m^3 and z is depth in meters. Static stability greater than zero, equal to zero, and less than zero indicate a stable, neutral, and unstable water column respectively.

Differences in sea surface temperature (measured at 3 meters), thermocline presence, and static water stability were used to quantify water column characteristics for comparisons to salmon growth. Additionally, variations in sea surface temperature among years were compared to variations in IGF1 concentration among years.

2.3 RESULTS

2.3.1 IGF1 concentration

There were significant differences in mean IGF1 concentration among regions for coho salmon across all three years ($p<0.05$, Figure 2.3 panels A-C). In 2012, mean IGF1 concentrations in the Discovery Islands and Northern Strait of Georgia were significantly higher than all other regions, Desolation Sound and Mid Strait of Georgia IGF1 concentrations were intermediate, and Southern Strait of Georgia, Gulf Islands, and Malaspina Strait IGF1 concentrations were the lowest. This pattern of IGF1 concentration variations repeated in 2014 when mean coho salmon IGF1 concentrations in the Discovery Islands, Desolation Sound, and Northern Strait of Georgia were significantly higher than all other regions, Mid Strait of Georgia IGF1 concentration was intermediate, and Malaspina Strait, Southern Strait of Georgia, Fraser Plume, and Gulf Islands IGF1 concentrations were significantly lower than all other regions. In 2013 there was less variation between the regions within the year, but Malaspina Strait had significantly lower mean IGF1 concentration when compared to all other regions save Desolation Sound.

There were significant differences in mean IGF1 concentration between regions in chum salmon across all three years ($p<0.05$, Figure 2.3 panels D-F). In 2013 and 2014 mean IGF1

concentration for chum salmon in Malaspina Strait was significantly higher than the Mid Strait of Georgia.

2.3.2 Fork length

There were significant differences in mean fork length of coho salmon between regions across all three years ($p<0.05$, Figure 2.4 panels A-C). The strongest variation in mean fork length between regions was seen in 2014 when the Malaspina Strait, Southern Strait of Georgia, Fraser River Plume, and Gulf Islands mean fork lengths were significantly lower than all other regions.

There were significant differences in mean fork length between regions in chum salmon across all three years ($p<0.05$, Figure 2.4 panels D-F). The most pronounced difference was seen in 2014 when the fish sampled from the Gulf Islands had significantly lower mean fork length than all other regions.

2.3.3 IGF1 concentration and fork length

A significant positive correlation was present between individual IGF1 concentration and individual fork length when all three years of coho salmon data were examined together ($p<0.05$, Figure 2.5 panel A). The generation of regional means of the individual residuals from this common linear regression across all years allows comparison between years and regions within the species. The most positive regional mean residuals were seen in the Discovery Islands, Desolation Sound, and the Northern Strait of Georgia in 2012 and 2014 (Figure 2.5 panels B and D). Malaspina Strait had negative mean residuals in all three years and all regions had negative residuals in 2013, save the Fraser River Plume (Figure 2.5 panel C).

There was also a significant positive correlation between the regional mean IGF1 concentration and regional mean fork length across all three years for coho ($p<0.05$, Figure 2.6

panel A). A linear model including regional mean IGF1 concentration, regional mean fork length, year, and an interaction term between fork length and year was used to compare the relationship between mean IGF1 concentration and mean fork length between years ($p<0.05$, Figure 2.6 panel B). The correlation between IGF1 concentration and fork length is similar between 2012 and 2013, however there was a greater y-intercept, in 2012. The relationship (slope) between IGF1 concentration and fork length was similar in 2012 and 2013. The spatial variation in size of juvenile coho salmon in 2014 was strongly divided between small sized fish in the south (the Gulf Islands, Southern Strait of Georgia, Fraser River Plume, and Malaspina Strait) compared to larger sized fish in the north (the Discovery Islands, Desolation Sound, and Northern Strait of Georgia). This spatial variation in size directly influences the significantly more positive linear relationship between IGF1 and length present in 2014 when compared to 2012 and 2013. (Full model exploration is shown in Table 2.1).

A significant, but less explanatory positive correlation was present between individual IGF1 concentration and individual fork length of chum salmon across all three years ($p<0.05$, Figure 2.7 panel A). The regional mean of individual residuals for chum salmon from this common linear regression of IGF1 and fork length across all years were almost always positive in 2014, the exception being residuals from the Gulf Islands. In 2013, the only positive mean residuals were seen in Malaspina Strait. There was also a significant positive correlation between regional mean IGF1 concentration and regional mean fork length across all three years for chum salmon ($p<0.05$, Figure 2.6 panel C). A linear model including regional mean IGF1 concentration, regional mean fork length, year, and an interaction term between fork length and year was used to compare the relationship between mean IGF1 concentration and mean fork length for chum salmon between years ($p<0.05$, Figure 2.6 panel D). The correlation between

chum salmon IGF1 concentration and fork length is similar between 2012 and 2014, however the magnitude (y-intercept) of the relationship was greater in 2014, indicating higher IGF1 concentrations were present in 2014. (Full model exploration is shown in Table 2.2.)

An overall comparison of regional and inter-annual variation in growth between coho and chum salmon was generated by plotting the regional mean of individual residuals per year from the IGF1 concentration and fork length regressions (Figure 2.8). Mean positive residuals (IGF1 concentration and fork length) were seen for both coho and chum salmon in Desolation Sound in 2012, in no regions in 2013, and in Desolation Sound, Discovery Islands, and Northern and Mid Strait of Georgia in 2014. Positive coho salmon residuals and negative chum salmon residuals were seen in Discovery Islands, Northern and Southern Strait of Georgia, and Fraser River Plume in 2012. Negative coho salmon residuals and positive salmon chum residuals were seen in Malaspina Strait in 2013, and the Southern Strait of Georgia, Fraser River Plume, and Malaspina Strait in 2014. Negative residuals were seen in both salmon species in the Mid Strait of Georgia and Malaspina Strait in 2012, and all regions, save Malaspina Strait and Fraser River Plume, in 2013, and the Gulf Islands in 2014.

2.3.4. Diet composition

Inter-annual differences in the diets of coho salmon were found, with diets in 2013 significantly different than diets of salmon sampled in 2012 and 2014 (Schoener's Index >0.6, Figure 2.9 panel A). Approximately 50% of coho salmon diet was classified as crab megalops and crab zoea (larval crab) in 2012 and 2014, but in 2013, only 20% of individuals had the same crab classification. In contrast, almost 50% of coho salmon diet was classified as hyperiid in 2013, far higher than seen in 2012 (2%) and 2014 (10%). Additionally, the largest percentage of

herring and larval fish in coho salmon diet were seen in 2012 (~40%), with the lowest percentage in in 2013 (~10%), while the value for 2014 (~20%) was intermediate.

There were significant regional differences in coho salmon diet composition between the Discovery Islands and Northern, Mid, and Southern Strait of Georgia in 2012 and 2014 (Schoener's Index <0.6, Figure 2.9 B). Additionally, in 2012 and 2014, diet composition of coho salmon from the Southern Strait of Georgia consisted largely of larval crab (75%) and this was distinctly different from coho salmon found in the Northern Strait of Georgia and Discovery Islands where diets were largely comprised of herring and larval fish (~85% in 2012 and ~50% in 2014).

Inter-annual differences in the diets of chum salmon were also found with diets in 2012 significantly different than diets of salmon sampled in 2013 and 2014 (Schoener's Index >0.6, Figure 2.10 panel A). In 2012, larval crab, gammarid, and larval fish comprised approximately 50% of the overall diet, whereas in 2013 and 2014, larval fish were completely absent from the diet, and only 5% of the diet was classified as larval crab and gammarids. In contrast, approximately 60% of the chum salmon diet in 2013 and 2014 were composed of ctenophores and hyperiid, however these categories only comprised 5% of the chum salmon diet in 2012.

There were significant regional differences in chum salmon diet composition between the Discovery Islands and Northern, Mid, and Southern Strait of Georgia in 2013 and 2014 (Schoener's Index <0.6, Figure 2.10 panel B). Unlike in coho salmon, there was no apparent shift in diet composition between regions in the south and regions in the north in chum salmon.

2.3.5 IGF1 concentration and diet composition

Coho salmon IGF1 concentration was highest in individuals with herring diets as compared larval crab diets and all other prey ($p<0.05$, Figure 2.11 panels B-D). Additionally,

there was a significant positive correlation between the percent of herring in the diet per region and regional mean IGF1 concentration ($p<0.05$, Figure 2.11 panel A).

2.3.6. IGF1 concentration and oceanography

Similar surface water temperatures existed in each region in 2012, 2013, and 2014 (Figure 2.12 panels A-C). The only exception was the Gulf Islands, which had much higher temperatures in 2013 (15.1 °C) relative to those in 2012 (12.2 °C) and 2014 (11.1 °C). There was no correlation between regional mean water temperature at 3 meters and IGF1 concentration in coho or chum salmon.

Thermoclines were identified in the Discovery Islands, Desolation Sound, Northern, Mid, and Southern Strait of Georgia, and Malaspina Strait in all three years. No thermocline was identified in the Gulf Islands in all three years. A thermocline was identified in the Fraser River Plume in 2014, but not in 2012 or 2013.

All observed water column stability calculations were positive and above zero, indicating there were no unstable water columns (Figure 2.12 panels D-F). Water column stability was measured between the depths of 3 and 15 meters to determine the stability of the mixed layer within the thermocline. The most stable mixed layers were seen in the Fraser River Plume in 2012 and 2014 and the least stable was seen in the Gulf Islands in all three years (Table 2.3). There was no correlation between regional water column stability and IGF1 concentration in coho or chum salmon.

2.4 DISCUSSION

Overall, these results show that there is regional and inter-annual variation in marine growth of juvenile coho and chum salmon within the Strait of Georgia. There are multiple factors that influence the observed small scale variation of growth within the this area, but potentially

the most important are resulting body size and diet composition. Given that juvenile coho and chum salmon do not always display the same pattern of variations in growth among years, these factors may have species specific degrees of importance.

There was one observed pattern consistent between coho and chum salmon – growth in 2013 appeared to be lower than in 2012 or 2014. The comparison between regional means of individual residuals from the regression of IGF1 concentration and fork length for both coho and chum salmon shows universal negative residuals in 2013 (exception Malaspina Strait in chum salmon). For coho salmon in 2012 and 2014, IGF1 concentration patterns were similar between years and indicated better growth when compared to 2013. Additionally, the significant annual diet composition overlap and a northward transition in diets seen across regions in 2012 and 2014 were not present in 2013. Mean coho salmon IGF1 concentration across all regions was lowest in 2013, in particular in the northern regions of the Discovery Islands, Desolation Sound, and the Northern Strait of Georgia, when compared to 2012 and 2014. Additionally in 2013, there was a complete absence of young of the year herring and herring remains, and a marked increase in the proportion of hyperiid amphipods found in the diet of these juvenile coho salmon when compared to 2012 and 2014. In chum salmon, IGF1 concentration was on average higher (and possibly with more regional variation) in 2014 than in 2012 and 2013, but diet patterns were more similar in 2013 and 2014 when compared to 2012. The variations between annual IGF1 concentration patterns were not as well explained by differences in diet composition in juvenile chum salmon as they were in juvenile coho salmon.

The differing correlations between IGF1 concentration and fork length between years in both coho and chum salmon may be interpreted biologically in different ways. 1) A change in magnitude (y-intercept) between years without a change in relationship (slope) was seen between

2012 and 2013 in coho salmon and in 2012 and 2014 in chum salmon. This indicates consistently higher (larger y-intercept: coho salmon (2012) and chum salmon (2014)) IGF1 concentration proportional to increases in fork length. Biologically, this can be interpreted as higher overall growth in 2012 for coho salmon and in 2014 for chum salmon. The higher observed growth in one year compared to another could also be interpreted as a result of individuals encountering better quality prey, higher quantity prey, or residence in optimal temperature consistently across regions in one year compared to another regardless of fork length. 2) An increase in the steepness of the relationship (slope) between IGF1 concentration and fork length, and subsequent change in y-intercept, as seen in coho in 2014, indicates that there is a stronger relationship between IGF1 and fork length compared to other years. This could be interpreted as environmental growth conditions where there are growth benefits to be had for achieving a larger fork length such as higher quality prey once a particular gape limit is met or increased foraging success at a larger size. An abrupt chance in diet would force the steep increase in growth given a small increase in length. 3) In contrast, a decrease in the steepness of the relationship (slope) between IGF1 concentration and fork length, and subsequent change in y-intercept, as seen in chum in 2013, indicates that there is a weaker relationship between IGF1 concentration and fork length than in other years. This change may be interpreted as a weak or independent relationship between IGF1 concentration, fork length, and diet, where there appears to be no growth benefit to achieving a larger fork length. Regional or inter-annual differences in the relationships between IGF1 concentration and fork length may provide key clues into variation in prey resources for juvenile salmon. Further work may help us understand how to interpret these changes with regard to prey abundance, prey size, prey quality, and juvenile salmon size and thus better understand the ecology of growth and survival for juvenile salmon.

Evidence of competition between either coho or chum and pink salmon would be observed as annual differences in IGF1 depending on the presence or absence of juvenile pink salmon. There is no evidence in this study for competition between juvenile pink salmon and either coho or chum salmon in June and July in the Strait of Georgia. Juvenile pink salmon were present in the Strait of Georgia in 2012 and 2014. However, coho and chum salmon both displayed relatively low growth in 2013, a year when juvenile pink salmon were almost completely absent. These findings are contrary to previous studies with supporting evidence-indicating competition between juvenile pink and coho salmon (Beamish et al., 2010b) and between juvenile pink and chum salmon (Beacham and Starr, 1982; Beamish et al., 2010b) as measured by stomach fullness and adult return rates. A shift in prey availability or prey abundance may explain the low growth of coho salmon, but that does not explain the low growth for chum salmon whose diet composition were similar diet in 2013 to 2014 (their best growth year in this study). Without the inclusion of another year of data when juvenile pink salmon are absent, the potential impact of juvenile pink salmon on coho or chum salmon growth cannot be further addressed.

The Gulf Islands, Fraser River Plume, and Malaspina Strait are oceanographically different from the main basin Strait of Georgia. In turn, growth patterns of juvenile chum and coho salmon may differ in these areas. The Gulf Islands, cut off almost completely from the Fraser River Plume and remainder of the Strait of Georgia by the cluster of Gabriola, Valdes, Galiano, Saturna, and Saltspring Islands, are often cold and well mixed and show little variation in temperature or salinity from 3 to 40 meters. Low mean IGF1 concentration and mean negative residuals in chum salmon from the Gulf Islands were found in all three years. Low IGF1 concentration (all years) and mean negative residuals (2013 and 2014 only) were also found in

coho salmon. Given that the water is well mixed and not stratified, the primary productivity in the Gulf Islands may be lower in all years and thus provide scant food resources for juvenile salmon.

There is little evidence in this study of competition between coho and chum salmon. Only in one year of sampling (2012) did juvenile coho salmon appear to thrive whereas juvenile chum salmon appeared to not. Overall, there was little overlap in stomach content between chum and coho salmon examined for this study, supporting the inference that prey fields may differ. However, it is noted that one region in particular, Malaspina Strait, had strongly differing patterns of IGF1 concentration across the species. Malaspina Strait is oceanographically similar to the main basin Strait of Georgia in oceanography, consisting of a warm top layer, stratification of temperature and salinity, and stability. However it becomes progressively narrower than the Mid Strait of Georgia, its counterpart to the west of Texada Island. For all years of coho salmon data, IGF1 concentration was significantly lower in Malaspina Strait when compared to the Strait of Georgia, whereas in 2013 and 2014 chum salmon IGF1 concentration was significantly higher in Malaspina Strait when compared to the Mid Strait of Georgia. Currently there are no obvious oceanographic differences available to explain this species specific difference.

Neither measurements of water column temperature nor stability provided much power to explain differences in mean IGF1 concentration or correlation between IGF1 concentration and fork length among years in either chum or coho salmon. Laboratory based studies on the physiological bioenergetics of juvenile salmon have utilized variable temperatures to assess differences in growth, metabolic activity/demand, and overall performance at different temperatures (Brett et al., 1969; Beauchamp et al., 2007). Temperature can absolutely control growth rate. However, it is very difficult to infer the thermal experience of juvenile salmon in

the Strait of Georgia. These difficulties are induced by 1) the Strait of Georgia has a thermally stratified water column, with a relatively shallow thermocline and 2) The fish captured in this study were caught with a rope trawl net with an opening of between 12 and 18 meters. Fish caught in the rope trawl might be above the thermocline, below the thermocline or migrating across the thermocline at some regular (or irregular) interval. The nature of trawl sampling does not allow for directed specific fishing at narrow depth windows. Thus the exact depth and temperature of the water juvenile salmon inhabited prior to their capture cannot be established. Diel migrations have been described in juvenile salmon in marine environments (Parker et al., 1969; Neilson and Perry, 1990). Thus, juvenile salmon in the Strait of Georgia may be experiencing fluctuations between temperatures of 8 and 18 °C within a given day. The warmest mean water temperature observed in the Strait of Georgia in these years was in Desolation Sound in 2014 at 19.3 °C at 3 meters, however mean water temperature at 40 meters was 9.4 °C. Overall, perhaps it's not surprising that there were no correlations between IGF1 and temperature as the assessment of temperature was quite simplistic as compared to the potentially thermal complexity experienced by juvenile salmon in the Strait of Georgia.

Differences and changes in mean temperature and oceanography have been correlated to phytoplankton abundance and production in many studies (Mackas et al., 2007; Reygondeau and Beaugrand, 2011) and shifts in zooplankton abundance and species occurrence have been found within the Strait of Georgia (Li et al., 2013; Irvine and Crawford, 2013). Variation in phytoplankton abundance and bloom occurrence should induce variation in the abundance of zooplankton, a primary foundation of the prey field for juvenile salmon. Thus, if zooplankton production was limiting early marine growth in juvenile coho and chum salmon in the Strait of Georgia, oceanographic variation among years should have a strong relationship to growth. Our

analyses did not provide any evidence for a relationship between oceanography and salmon growth. However, we did observe both regional and inter-annual variations in growth between both chum and coho salmon. The stomach diet analysis revealed little evidence for copepods, the primary focus of most zooplankton studies, within the diet of either chum or coho salmon in the Strait of Georgia. Instead, the diets of these animals consisted of larger and older prey items like amphipods, crab larvae, euphausiids, and larval and juvenile fish. Thus traditional oceanographic studies of phytoplankton and copepods may not provide direct evidence for changing food supplies of juvenile salmon as there is an additional trophic step between traditional oceanographic studies and these observed salmon diets. Focused studies on crab larvae, amphipods, and larval and juvenile fish will be required to understand varying food supplies for juvenile salmon in the Strait of Georgia.

There are significant correlations between IGF1 concentration and regional variation in the presence of herring in the diet for juvenile coho salmon. The overall percent of young of the year herring in the diet as well as the northward shift from diets high in larval crab to diets high in herring appear to be important clues for the basis for varying growth in coho salmon. An analysis of herring productivity in the Strait of Georgia in 2012, 2013, and 2014 would aid in identifying its influence on coho salmon growth. If 2013 was a less productive year for both young of the year herring and larval crab, their decreased occurrence in coho salmon diets may have resulted in lower IGF1 concentration. This indicates that herring, rather than zooplankton abundance, may be important for juvenile coho salmon growth in more northern regions of the Strait of Georgia.

The stomach content results in this study are used to aid in understanding and explaining variations in IGF1 concentration between regions and years, however, they do not represent a

complete diet analysis of juvenile salmon in the entire Strait of Georgia. It is important to realize that there are lags between the consumption of individual food items and the circulating concentration of IGF1. The measured IGF1 concentration and stomach contents for an individual fish may not represent a temporally accurate comparison. Diet contents represent food consumption over hours, whereas IGF1 concentration represents growth over 7-10 days (Pierce et al., 2005). The distinct spatial patterns in IGF1 concentration for coho salmon suggest that juvenile coho salmon are resident in regions within the Strait of Georgia for at least one week, the period needed for dietary changes to become evident in changes in IGF1 concentration. This further validates the use of IGF1 concentration in small-scale regional comparisons within the Strait of Georgia, allowing region specific IGF1 concentration and region specific diet composition to be correlated. By averaging IGF1 concentration and diet composition across regions we expect to generate a representative relationship for the region as a whole. Thus, we can compare IGF1 concentration to diet contents by region and by year regardless of the temporal lag between feeding and IGF1 concentration relating to specific individuals. Thus, by using IGF1 concentration we may identify regions of relatively low or high productivity.

The use of IGF1 concentration as an environmental indicator of juvenile salmon growth in the Strait of Georgia offers a unique opportunity as each IGF1 concentration measure in an individual species represents a replicate measure of growth across species. A large majority of published research on juvenile Pacific salmon research focuses on one or two species separately (Trudel and Hertz, 2013). Additionally, the Strait of Georgia is often studied as one complete unit, averaging measures such as size, diet, and abundance across the entire area. Given the differences in growth observed here in both coho and chum salmon across regions within the Strait of Georgia, this may not be appropriate. Multiple measures of growth across species at a

small scale may help identify if there are overall high levels of marine mortality as a result of residence in the Strait of Georgia. In addition, localized or regional variability in growth and survival is difficult to quantify in a migratory species, and general abundance (in the Strait of Georgia as a whole) is not as informative to localized or regional variations in growth or survival. Further use of IGF1 concentration assessments across species to identify universally high growth year verses a universally low growth year will allow environmental comparisons such as zooplankton bloom and herring productivity to be more directly linked to juvenile Pacific salmon growth between years.

The differences observed in this analysis of IGF1 concentration across a three year sampling period introduces a means of assessing the productivity and quality of ocean residence in the Strait of Georgia for juvenile Pacific salmon. In the Strait of Georgia, growth in both juvenile coho and chum salmon does vary between proximally close regions within a year. In addition, juvenile coho and chum salmon growth varies between years both annually and regionally. In coho salmon this variation in growth is associated with similar variation in diet composition both annually and regionally, this represents the first in situ comparison of growth and diet in juvenile salmon and highlights the importance of diet for driving differences in growth. It also highlights the ability of IGF1 concentration to illuminate the feeding and growth ecology of juvenile salmon. IGF1 concentration comparisons revealed that there was one year in which universal low growth persisted in both species, though environmental factors influencing this low growth were less apparent. The IGF1 concentration analyses provide evidence that rearing was sub-optimal in 2013 and suggests additional measures are needed to ascertain why. The Strait of Georgia is biologically diverse and complex. The quantification of juvenile salmon growth and survival in this area requires a combination of spatial and geographic scales to

understand the mechanisms impacting the patterns of juvenile salmon growth. IGF1 concentration measurements provide a useful tool for providing growth measures at temporal and geographic scales that will help understand the ecological mechanisms regulating juvenile salmon survival in this area.

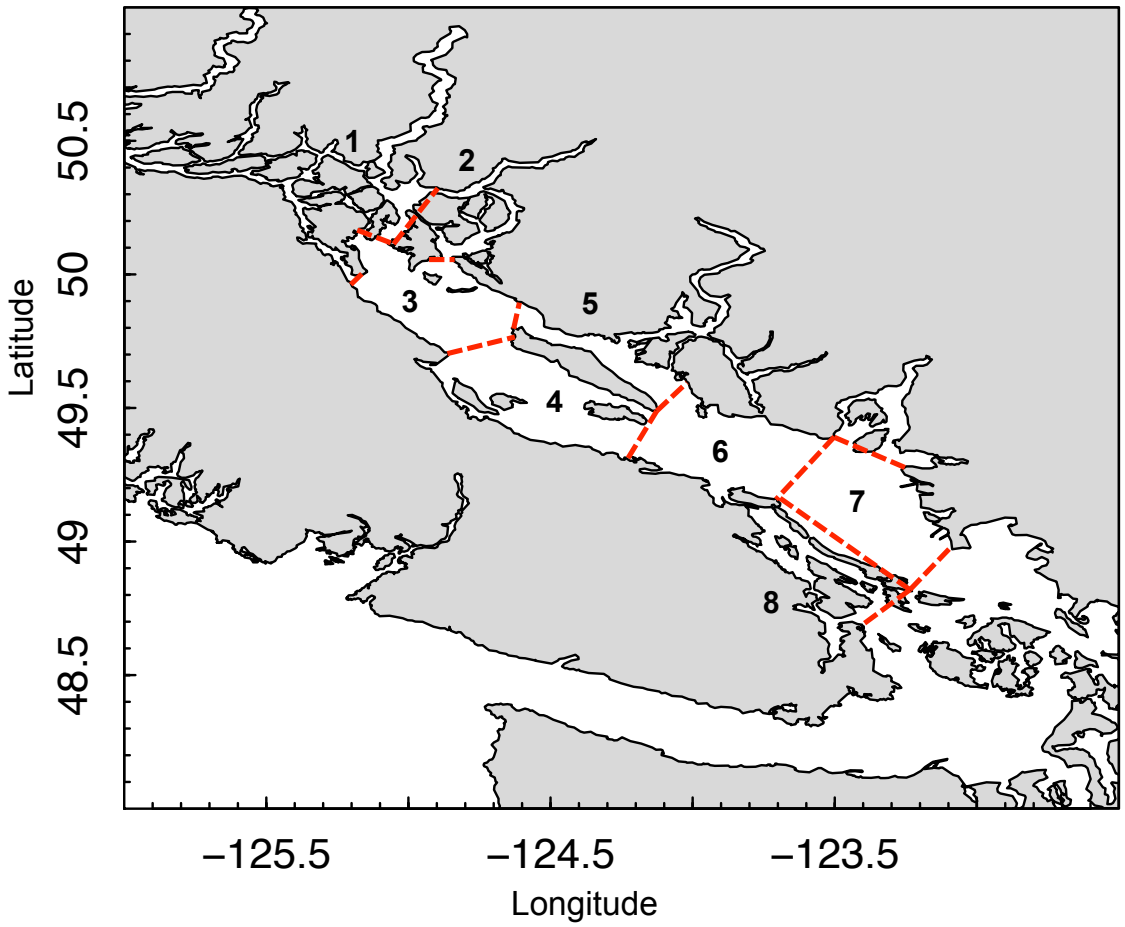


Figure 2.1. Map of the Strait of Georgia and regional delineations used in IGF1 analysis. From north to south (1 to 8): Discovery Islands (Disc), Desolation Sound (Des), Northern Strait of Georgia (NSOG), Mid Strait of Georgia (SOG), Malaspina Strait (Mala), Southern Strait of Georgia (SSOG), Fraser River Plume (Plume), and the Gulf Islands (Gulf).

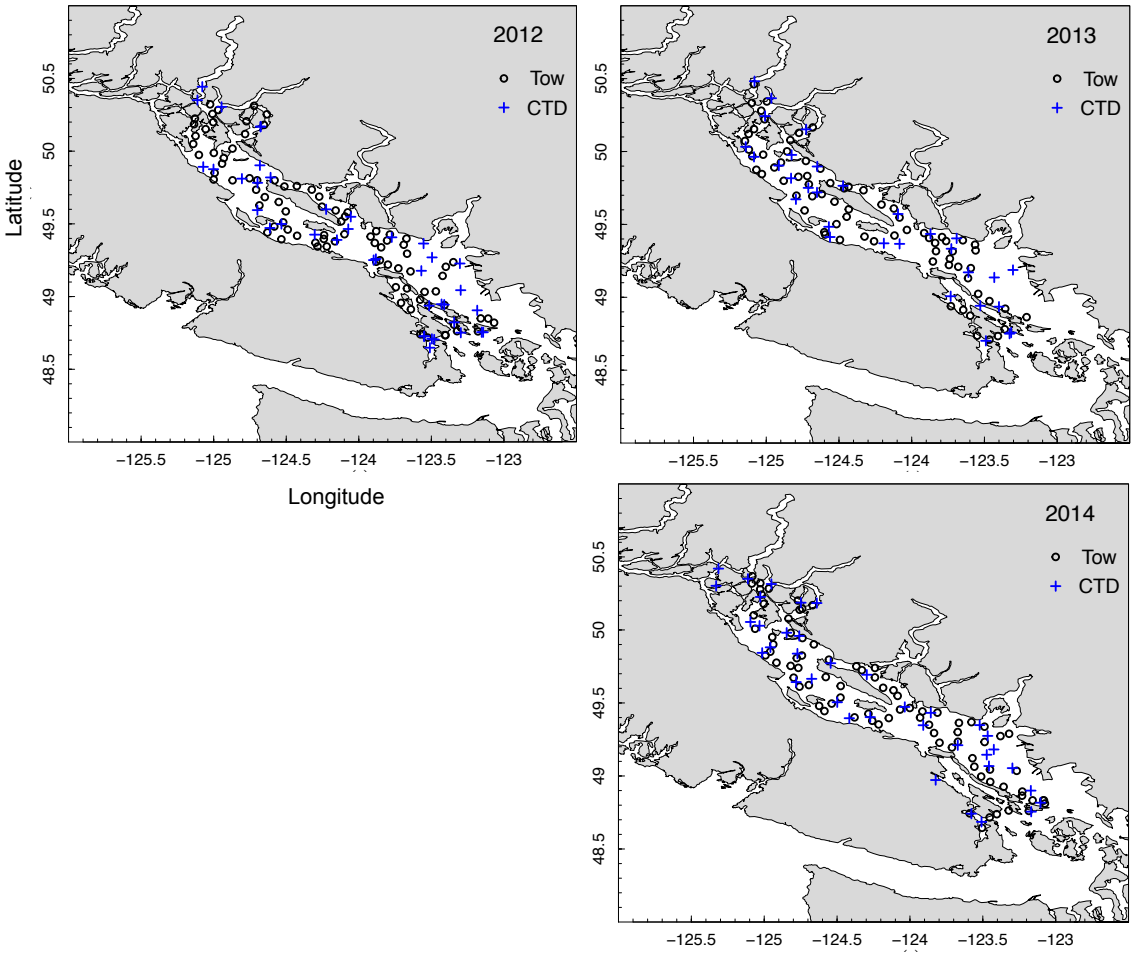


Figure 2.2. Map of fishing trawl (with IGF1 sampled fish collected) and CTD cast locations in 2012, 2013, and 2014. Non zero IGF1 sampled trawl locations are indicated with open black circles. CTD cast locations are indicated with blue plus sign.

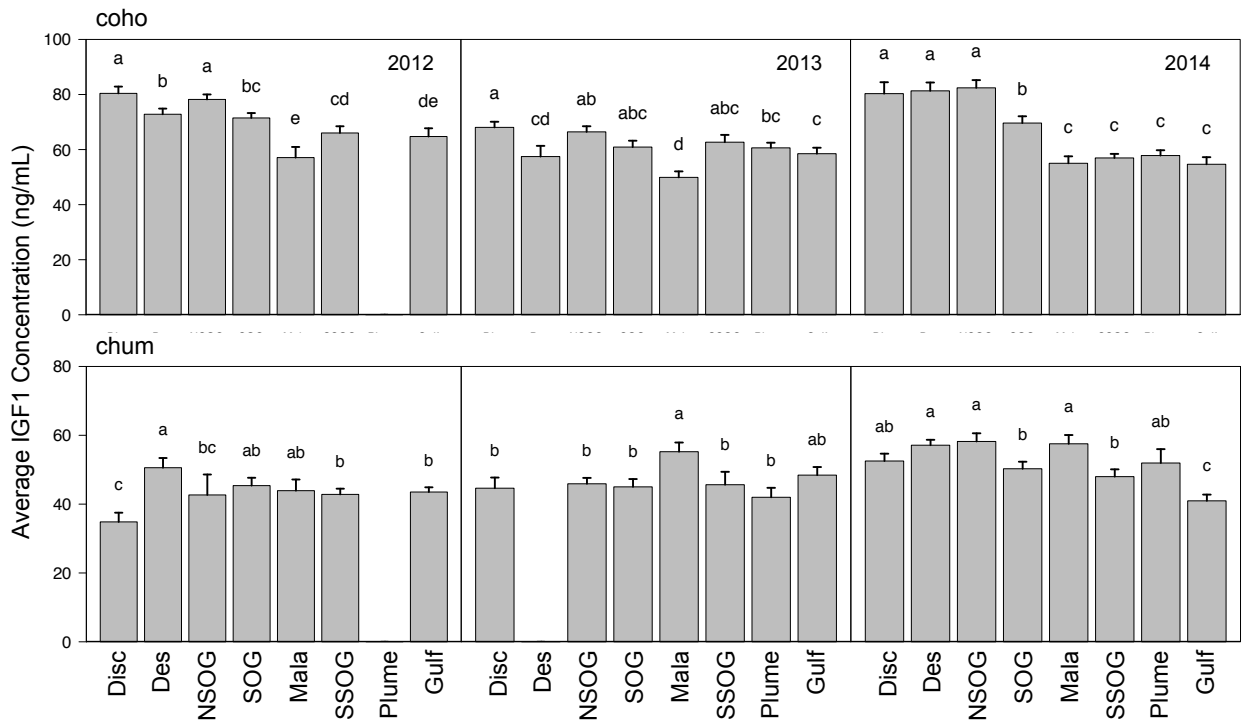


Figure 2.3. Mean IGF1 concentration (ng/mL) (±SE) per region for coho (top row) and chum salmon (bottom row) in 2012, 2013, and 2014. Significant differences within a year and species are indicated alphabetically (ANOVA, $p<0.05$). Absent bars indicate regions where less than the minimal sample size was collected from that region in that year ($n<7$).

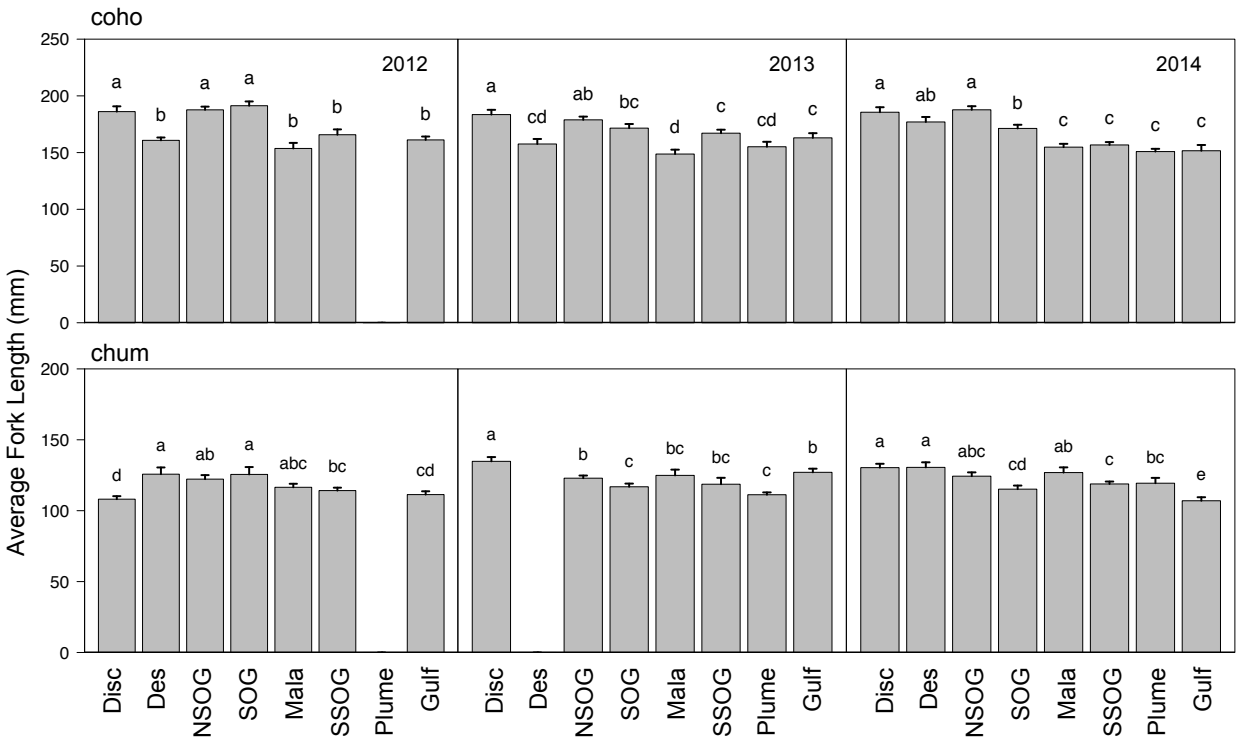


Figure 2.4. Mean fork length (mm) (±SE) per region for coho (top row) and chum salmon (bottom row) in 2012, 2013, and 2014. Significant differences within a year and species are indicated alphabetically (ANOVA, $p<0.05$). Absent bars indicate regions where less than the minimal sample size was collected from that region in that year ($n<7$).

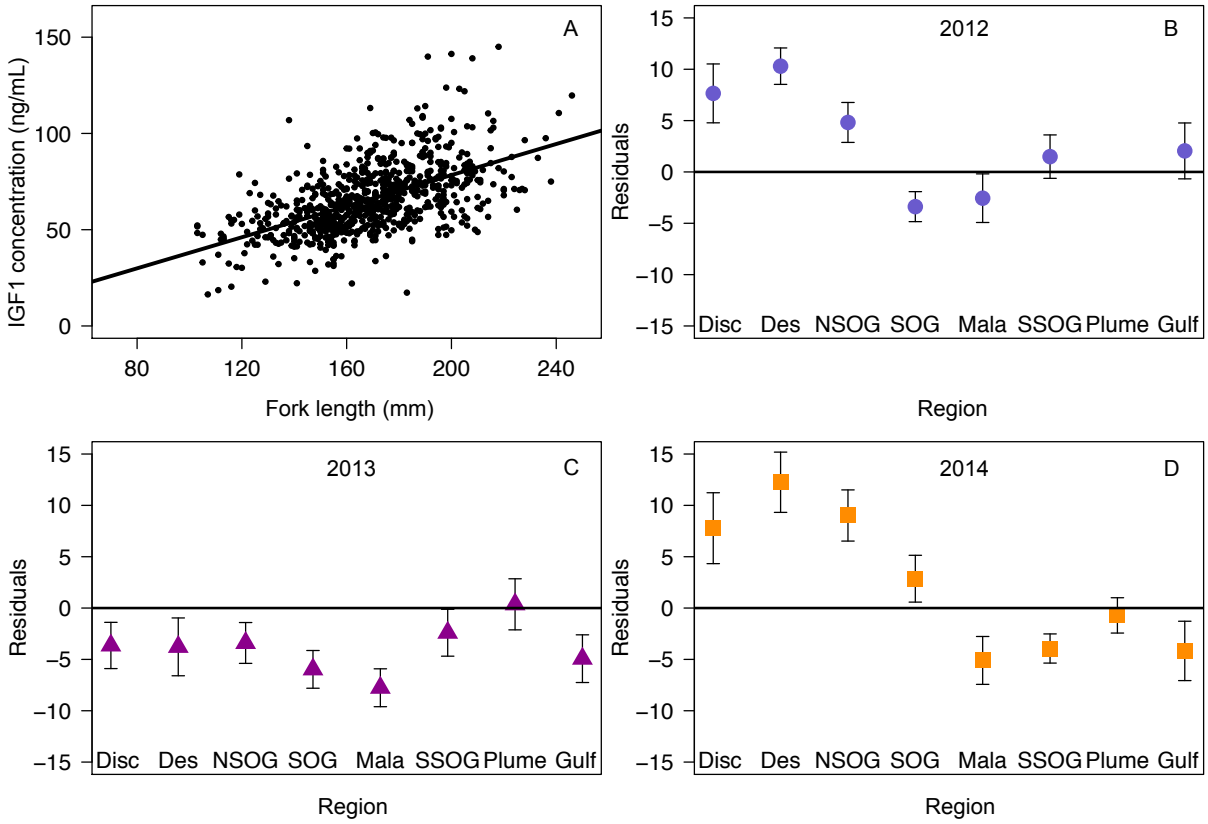


Figure 2.5. Correlation between individual juvenile coho salmon fork length (mm) and individual IGF1 concentration (ng/mL) for all individuals combined in 2012, 2013, and 2014 (A) (R-squared = 0.32, $p<0.05$). The mean residuals of that correlation per region per year 2012, 2013, and 2014 are shown in panel B, C, and D, respectively.

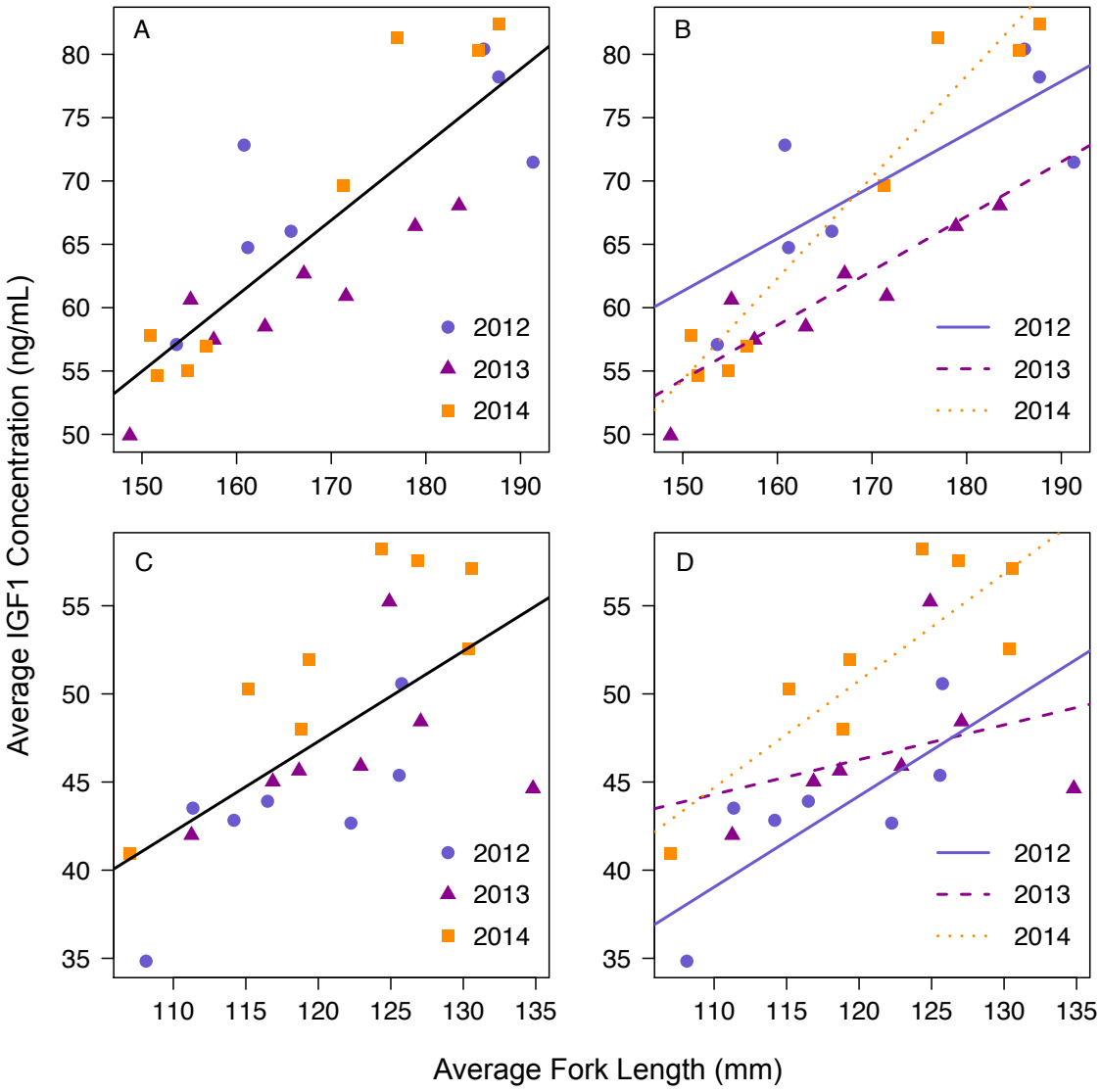


Figure 2.6. Correlation of mean fork length (mm) per region per year and mean IGF1 concentration (ng/mL) per region per year for coho (A) and chum (C) salmon with a common slope and common y-intercept for all three years (R-squared = 0.71 and 0.38, respectively, $p<0.05$). Correlations of mean fork length (mm) per region and mean IGF1 concentration (ng/mL) per region with year (2012, 2013, or 2014) and the interaction of year and fork length (mm) as covariates for coho (B) and chum (D) salmon (R-squared = 0.84 and 0.64, respectively, $p<0.05$).

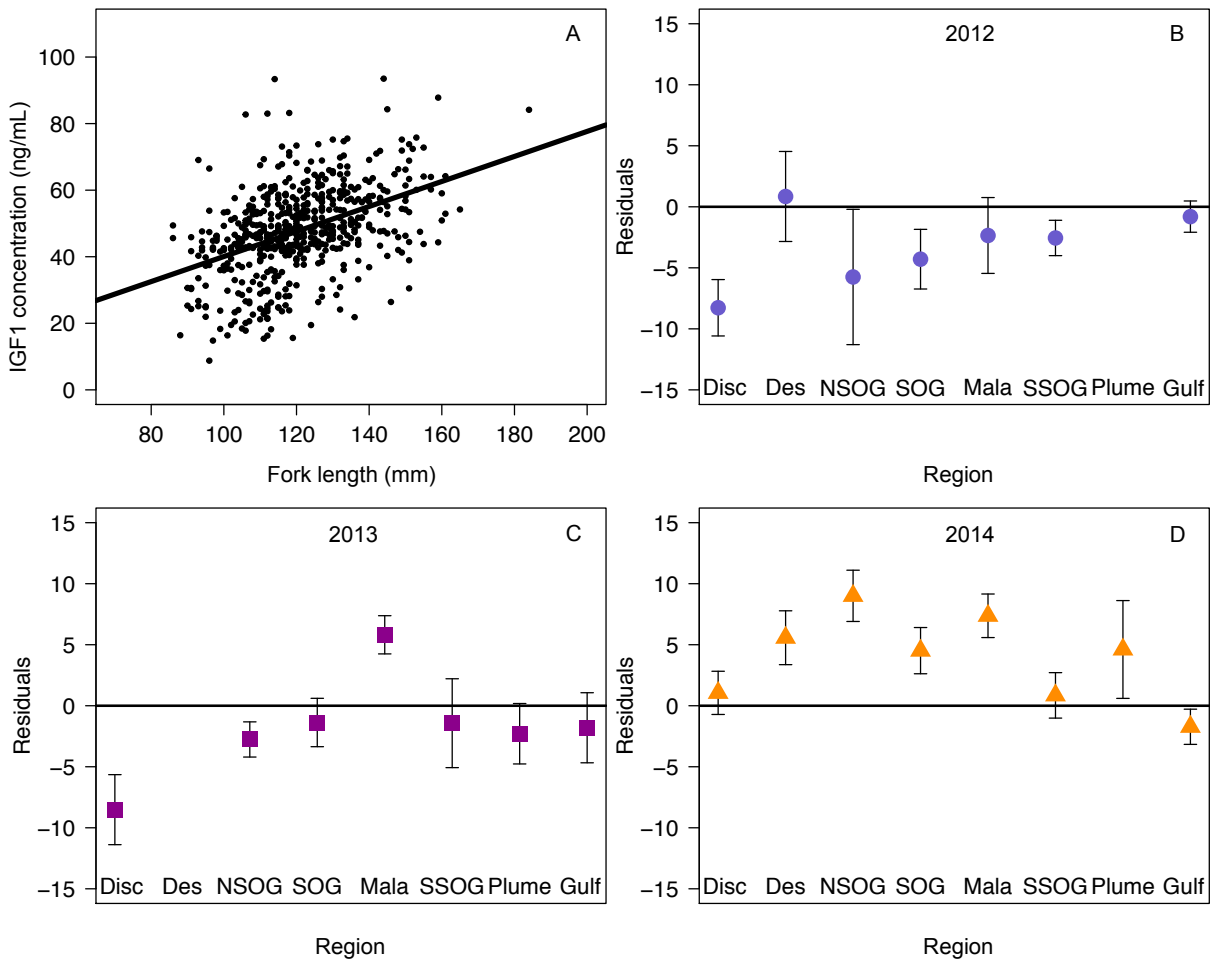


Figure 2.7. Correlation between individual juvenile chum salmon fork length (mm) and individual IGF1 concentration (ng/mL) for all individuals combined in 2012, 2013, and 2014 (A) (R-squared = 0.19, $p<0.05$). The mean residuals of that correlation per region per year 2012, 2013, and 2014 are shown in panel B, C, and D, respectively.

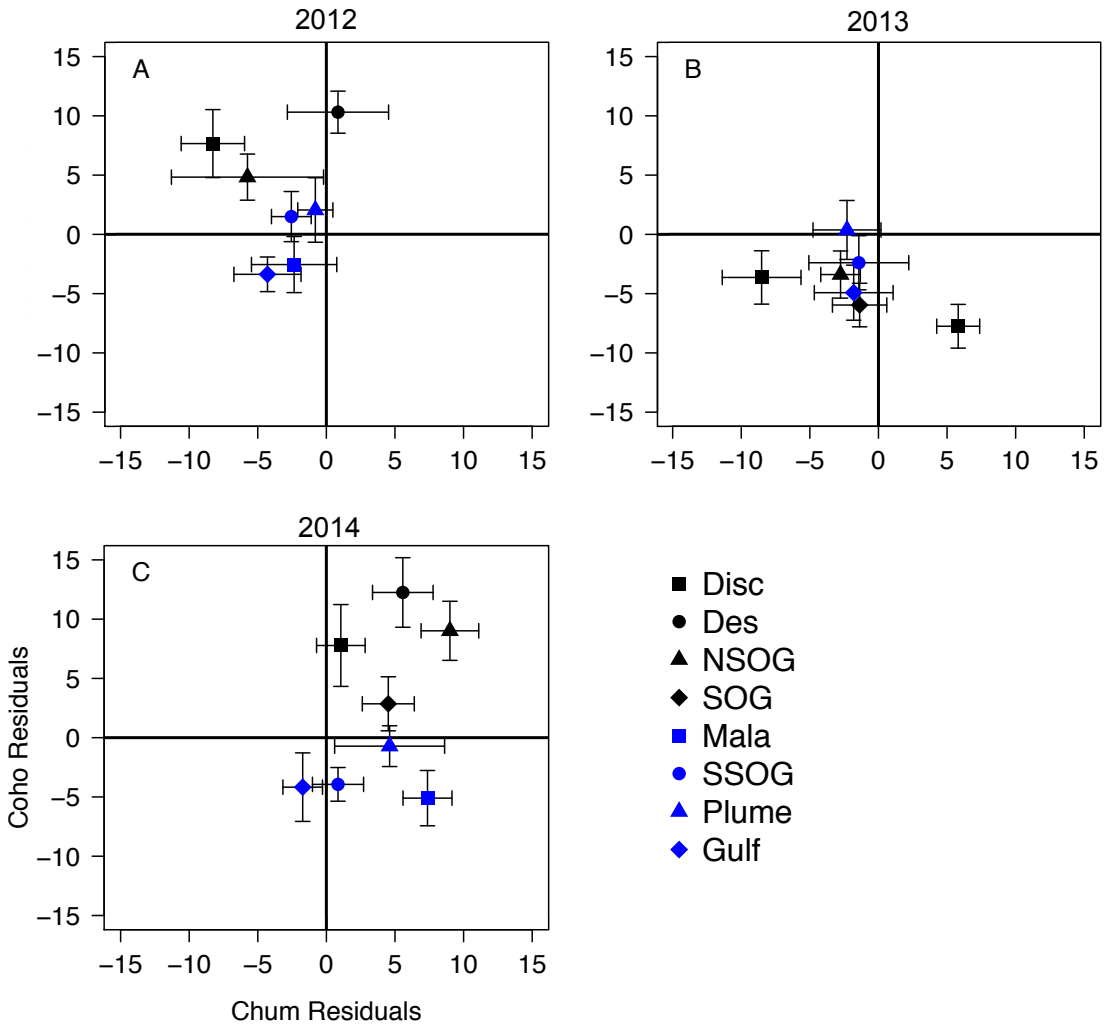


Figure 2.8. Mean coho residuals (±SE) per region per year from Figure 2.5 panels B, C, and D and mean chum residuals (±SE) per region per year from Figure 2.7 panels B, C, and D.

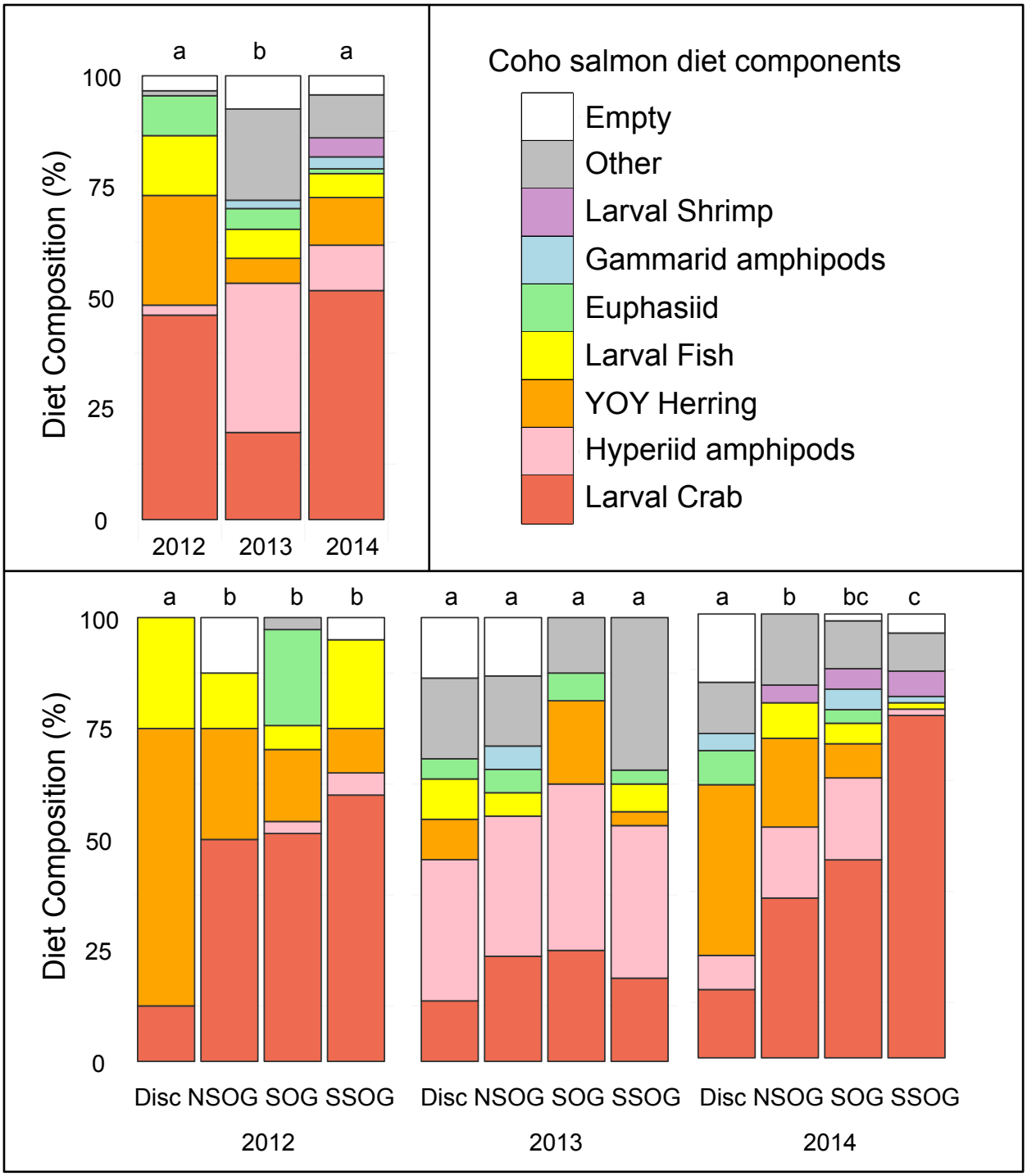


Figure 2.9. A) Stomach contents of coho salmon sampled for IGF1 concentration in the in 2012, 2013, and 2014. Significant diet overlap was seen between 2012 and 2014 (Schoener's Index > 0.60). B) Dietary composition of coho salmon sampled for IGF1 concentration in the Discovery Islands, Northern, Mid, and Southern Strait of Georgia in 2012, 2013, and 2014 per region. Significant overlap was seen among all regions in 2013 (Schoener's Index >0.60). Significant overlaps among regions within a year are indicated alphabetically (Schoener's Index > 0.60).

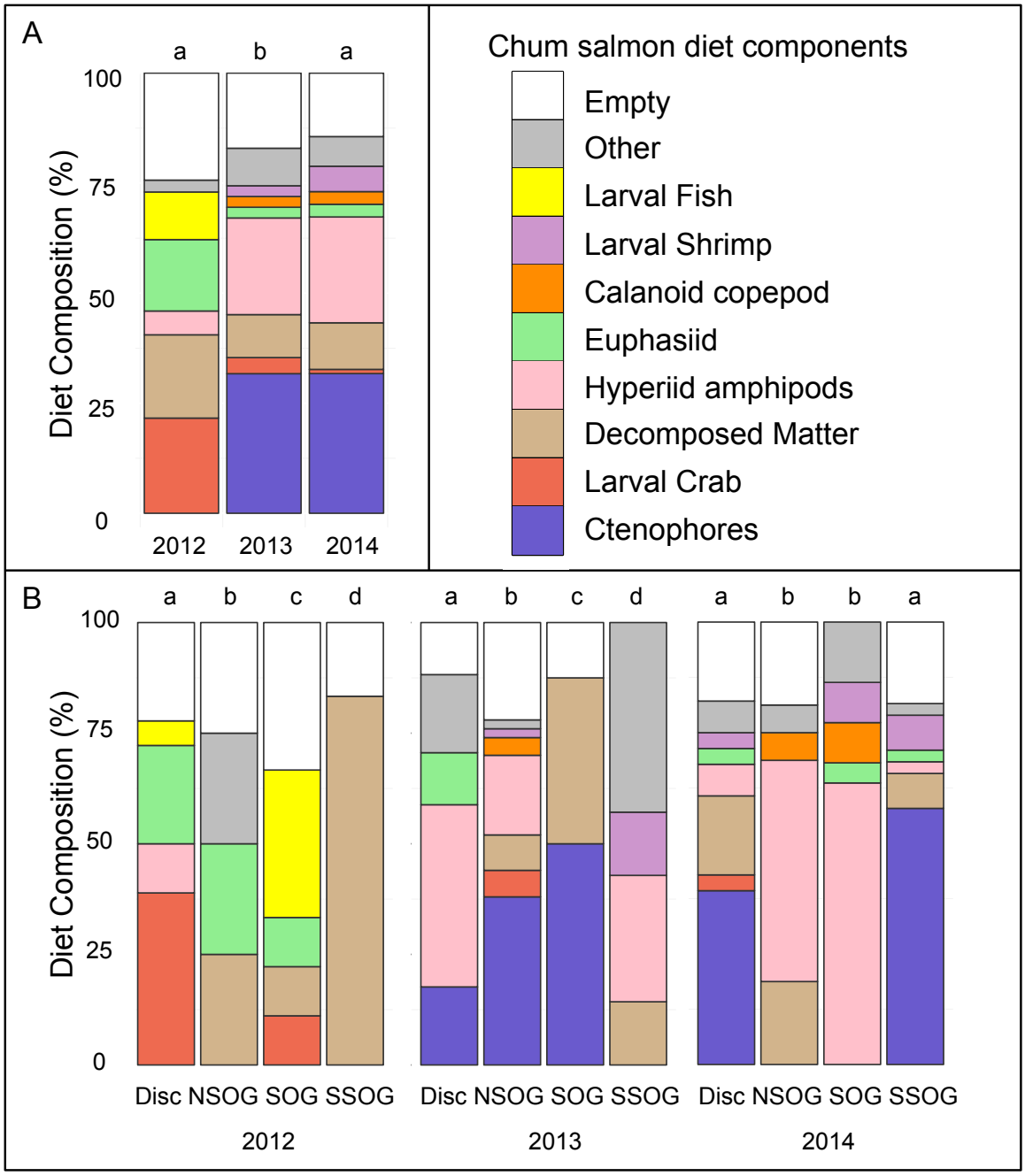


Figure 2.10 A) Dietary composition of chum salmon sampled for IGF1 concentration in 2012, 2013, and 2014. Significant overlap was seen between 2013 and 2014 (Schoener's Index > 0.60). B) Dietary composition of chum salmon sampled for IGF1 concentration in the Discovery Islands, Northern, Mid, and Southern Strait of Georgia in 2012, 2013, and 2014 per region. Significant overlaps between regions within a year are indicated alphabetically (Schoener's Index > 0.60).

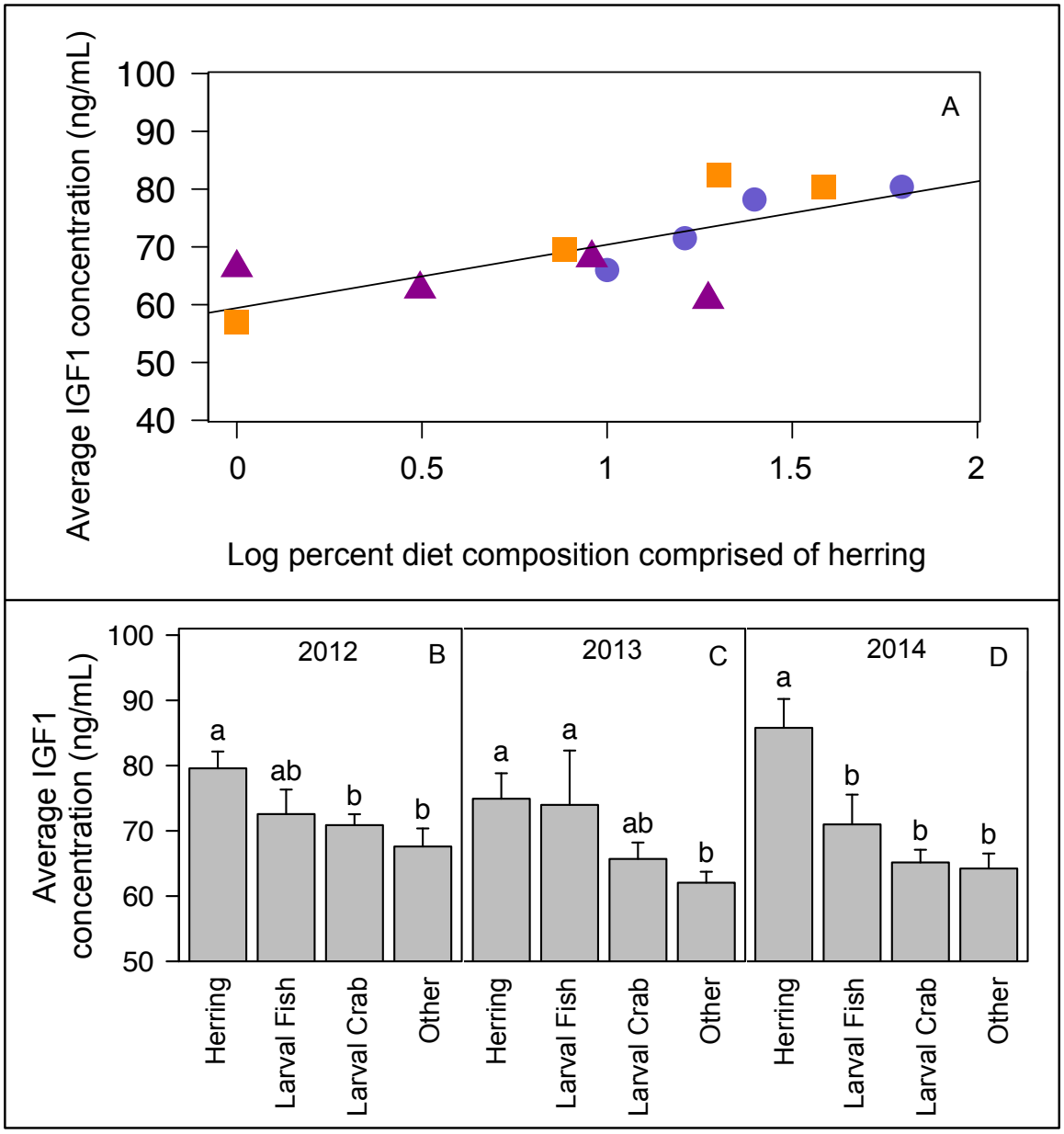


Figure 2.11 A) Log correlation of overall regional percent of dietary preferences equal to herring and regional mean IGF1 concentration for juvenile coho salmon across 2012, 2013, and 2014. (R-squared = 0.48, $p<0.05$. B,C,D) Mean IGF1 concentration (ng/mL) per dietary component of Herring, Larval Fish, Crab Larvae (Crab Zoea and Crab Megalops), and all other components per year in coho salmon ($p<0.05$). Significant differences are indicated alphabetically.

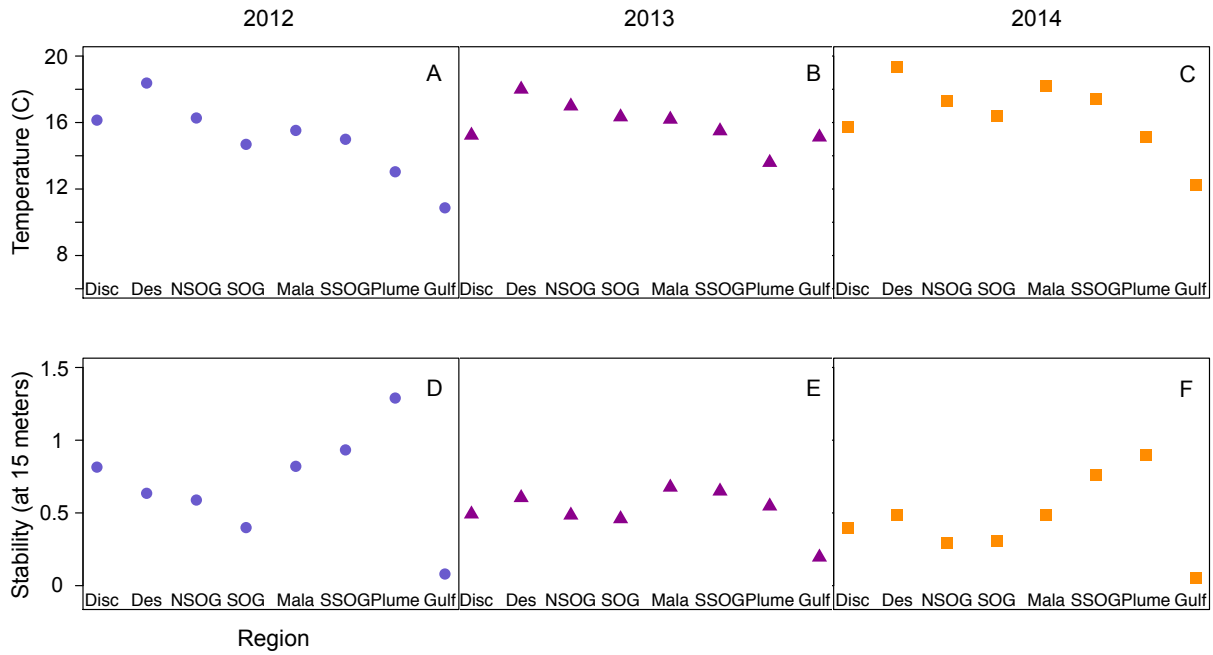


Figure 2.12. Regional mean water column temperature at 3 meters per year (A, B, C). Mean Water column stability per region, as calculated from water column density difference between 3 meters and 15 meters per year (D, E, F). All water columns are stable as all values are > 0.

Table 2.1. Statistical output results of different linear models in coho salmon across all years using the parameters regional mean IGF1 concentration, fork length, Year, and Location (Region: North v South). AIC calculations identify best fit from 3 models: Model IGF ~ Length, IGF1 ~ Length + Year, and IGF1 ~ Length + Year + Length:Year.

Model	Coefficents	Estimate	p	R^2	p	AIC	deltaAIC
IGF ~ Length	Intercept	-34.5	0.02				
	Length	0.6	2.60E-07	0.71	2.60E-07	83.4	0
IGF ~ Region	Intercept	72.5	2.00E-16				
	South	-13.9	8.10E-05	0.51	8.10E-05	95.7	12.3
IGF ~ Length + Year	Intercept	-33.9	0.01				
	Length	0.57	1.90E-07				
	2012	5.74	0.03				
	2014	5.97	0.02	0.78	4.90E-07	83.6	0.2
IGF ~ Length + Region	Intercepth	-17.1	0.46				
	Length	0.5	7.80E-04				
	South	-3.3	0.35	0.7	1.60E-06	86.5	3.1
IGF ~ Length + Year + Length:Year	Intercept	-10.2	0.63				
	Length	0.43	0.003				
	2012	9.39	0.74				
	2014	-55.5	0.05				
	Length:2012	-0.02	0.92				
	Length:2014	0.37	0.031	0.84	3.70E-07	84.1	0.7
IGF ~ Length + Year + Region	Intercept	-10.6	0.6				
	Length	0.44	8.80E-04				
	2012	6.3	0.02				
	2014	6.1	0.01				
	South	-4.4	0.16	0.79	1.00E-06	86	2.6
Full Model	-	-	-	0.87	4.60E-05	123.5	40.1

Table 2.2. Statistical output results of different linear models in chum salmon across all years using the parameters regional mean IGF1 concentration, fork length, Year, and Location (Region: North v South). AIC calculations identify best fit from 2 models: Model IGF ~ Length and IGF1 ~ Length + Year.

Model	Coefficents	Estimate	p	R^2	p	AIC	deltaAIC
IGF ~ Length	Intercept	-14.23	0.4				
	Length	0.51	1.00E-03	0.38	1.00E-03	75.8	4.6
IGF ~ Year	Intercept	46.7	6.40E-16				
	2012	-3.3	0.23				
	2014	5.4	0.05	0.31	0.01	81.1	9.9
IGF ~ Length + Year	Intercept	-8.9	0.52				
	Length	0.45	6.80E-04				
	2012	-1.2	0.57				
	2014	5.7	0.008	0.63	1.00E-04	71.2	0
IGF ~ Length + Region	Intercept	-23.3	0.21				
	Length	0.58	9.00E-04				
	South	2.5	0.26	0.39	4.00E-03	78.4	7.2
IGF ~ Length + Year + Length:Year	Intercept	22.6	0.35				
	Length	0.2	0.32				
	2012	-40.46	0.26				
	2014	-44.72	0.17				
	Length:2012	0.3	0.28				
	Length:2014	0.4	0.13	0.64	4.40E-04	78.6	7.4
IGF ~ Length + Year + Region	Intercept	-17.98	0.25				
	Length	0.52	5.00E-04				
	2012	-0.57	0.79				
	2014	5.94	0.006				
	South	2.16	0.23	0.64	2.00E-04	74.4	3.2
Full Model	-	-	-	0.75	3.00E-03	120.4	49.2

Table 2.3. Oceanography data. Thermocline presence, water column temperature, water column temperate range, stability, and mean Latitude and Longitude of CTD cast locations for each region within each year.

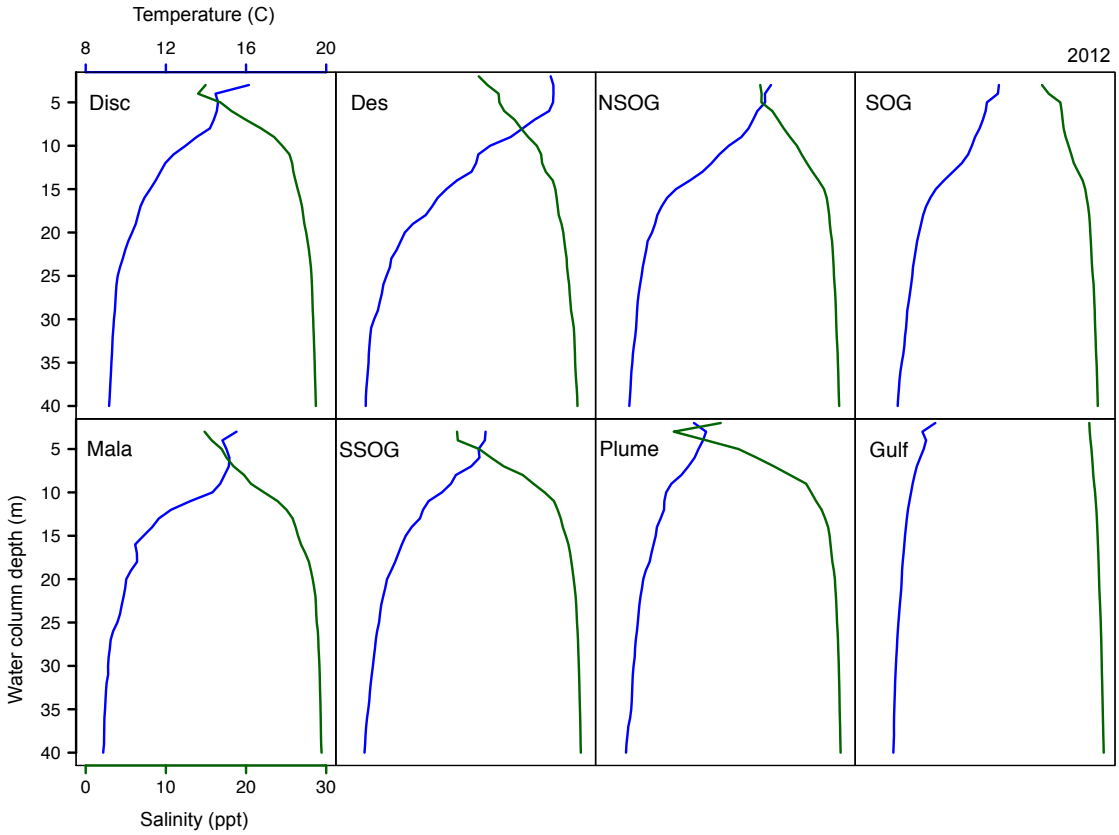
Year	Region	Thermocline Presence	Temperature at 3 meters	Temperature at 40 meters	Temperature Range	Median Temperature	Stability @ 15 m	Mean Latitude	Mean Longitude
2012	Disc	Yes	16.1	9.2	7.0	10.0	0.63	50.50	-124.99
	Des	Yes	18.4	9.0	9.4	10.7	0.81	50.17	-124.68
	NSOG	Yes	16.3	9.2	7.1	10.1	0.08	49.85	-124.81
	SOG	Yes	14.7	9.6	5.1	10.6	0.82	49.50	-124.54
	Mala	Yes	15.5	8.9	6.7	9.9	0.59	49.57	-124.14
	SSOG	Yes	15.0	8.9	6.0	9.9	1.29	49.36	-123.96
	Plume	No	13.0	9.0	4.0	9.8	0.40	49.11	-123.41
	Gulf	No	11.1	9.4	1.6	9.8	0.93	48.75	-123.40
2013	Disc	Yes	15.2	9.3	5.9	10.0	0.60	50.36	-125.02
	Des	Yes	18.0	9.1	8.9	9.0	0.49	50.15	-124.73
	NSOG	Yes	17.0	9.3	7.7	10.3	0.20	49.91	-124.88
	SOG	Yes	16.3	10.1	6.2	11.4	0.68	49.57	-124.64
	Mala	Yes	16.2	9.0	7.2	10.3	0.48	49.67	-124.28
	SSOG	Yes	15.5	9.2	6.3	10.3	0.55	49.38	-123.91
	Plume	No	13.6	9.5	4.1	10.2	0.46	49.11	-123.44
	Gulf	No	15.1	10.6	4.6	12.0	0.65	48.83	-123.48
2014	Disc	Yes	15.7	9.9	5.8	10.5	0.49	50.32	-125.14
	Des	Yes	19.3	9.4	10.0	11.0	0.40	50.19	-124.69
	NSOG	Yes	17.3	9.4	7.8	10.4	0.05	49.94	-124.93
	SOG	Yes	16.4	10.3	6.1	11.7	0.48	49.55	-124.59
	Mala	Yes	18.2	9.4	8.8	10.6	0.29	49.73	-124.42
	SSOG	Yes	17.4	9.3	8.2	10.2	0.90	49.41	-124.02
	Plume	No	15.1	9.5	5.7	10.2	0.31	49.11	-123.40
	Gulf	No	12.2	9.8	2.4	10.7	0.76	48.79	-123.52

Supplemental Table 2.1. Mean IGF1 concentration (±SE) per region with sample size as presented in Figure 2.3 for coho and chum salmon in 2012, 2013, and 2014.

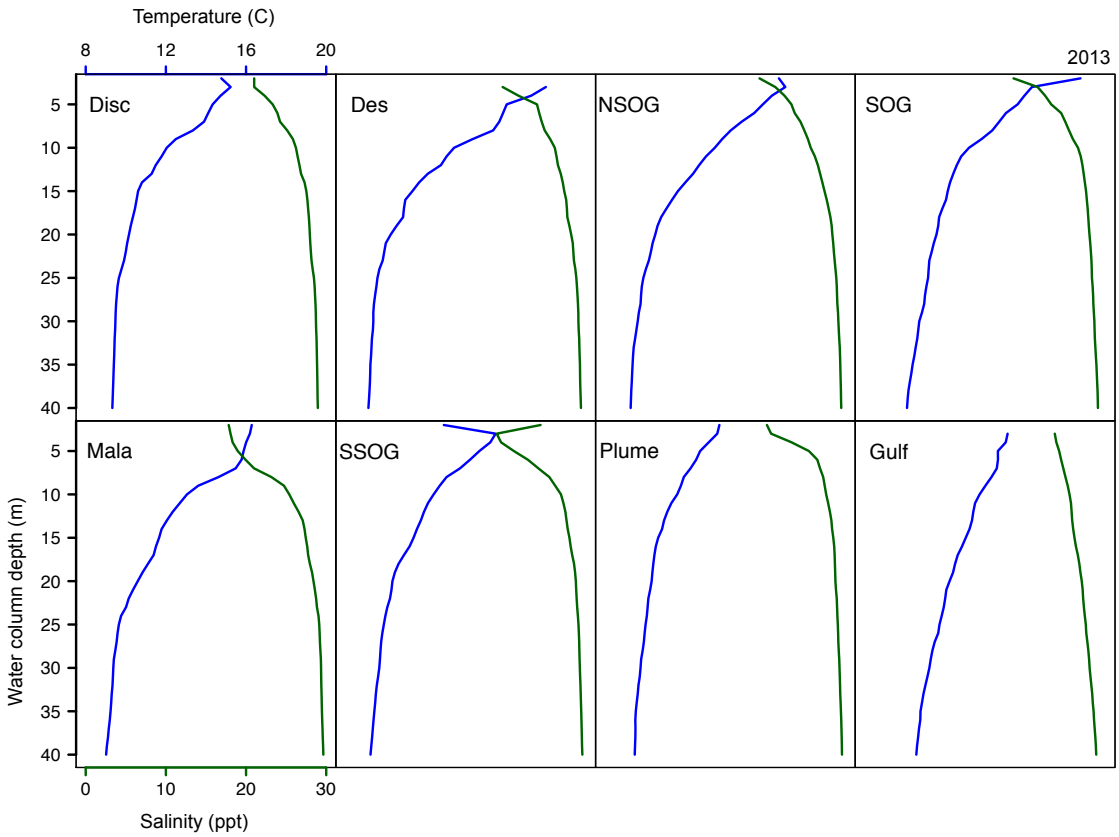
Average IGF1 Concentration (ng/mL) + SE (n)						
Region	coho			chum		
	2012	2013	2014	2012	2013	2014
Disc	80.41 + 2.46 (16)	68.06 + 2.04 (24)	80.32 + 4.14 (26)	34.84 + 2.67 (24)	44.63 + 3.09 (27)	52.53 + 2.13 (33)
Des	72.83 + 2.05 (19)	57.46 + 3.89 (12)	81.33 + 3.03 (22)	50.58 + 2.82 (12)	ND	57.12 + 1.57 (20)
NSOG	78.21 + 1.81 (26)	66.43 +2.04 (46)	82.42 + 2.81 (61)	42.67 + 5.94 (8)	45.91 + 1.71 (52)	58.21 + 2.37 (38)
SOG	71.48 + 1.78 (34)	60.91 + 2.31 (41)	69.63 + 2.46 (70)	45.38 + 2.28 (12)	45.02 + 2.27 (29)	50.28 + 2.04 (38)
Mala	57.09 + 3.86 (17)	49.9 +2.18 (25)	55.02 + 2.53 (43)	43.91 + 3.25 (18)	55.23 + 2.67 (20)	57.53 + 2.55 (16)
SSOG	66.03 + 2.43 (24)	62.68 + 2.65 (46)	56.96 + 1.47 (70)	42.83 + 1.66 (33)	45.64 + 3.75 (9)	47.99 + 2.12 (46)
Plume	ND	60.62 + 1.87 (7)	57.83 + 1.93 (50)	ND	41.99 + 2.75 (8)	51.95 + 4.03 (13)
Gulf	64.74 + 2.99 (22)	58.5 + 2.17 (27)	54.66 + 2.58 (21)	43.52 + 1.37 (31)	48.43 +2.35 (31)	40.96 + 1.81 (32)

Supplemental Table 2.2. Mean fork length (±SE) per region and sample size as presented in Figure 2.3 for coho and chum salmon in 2012, 2013, and 2014.

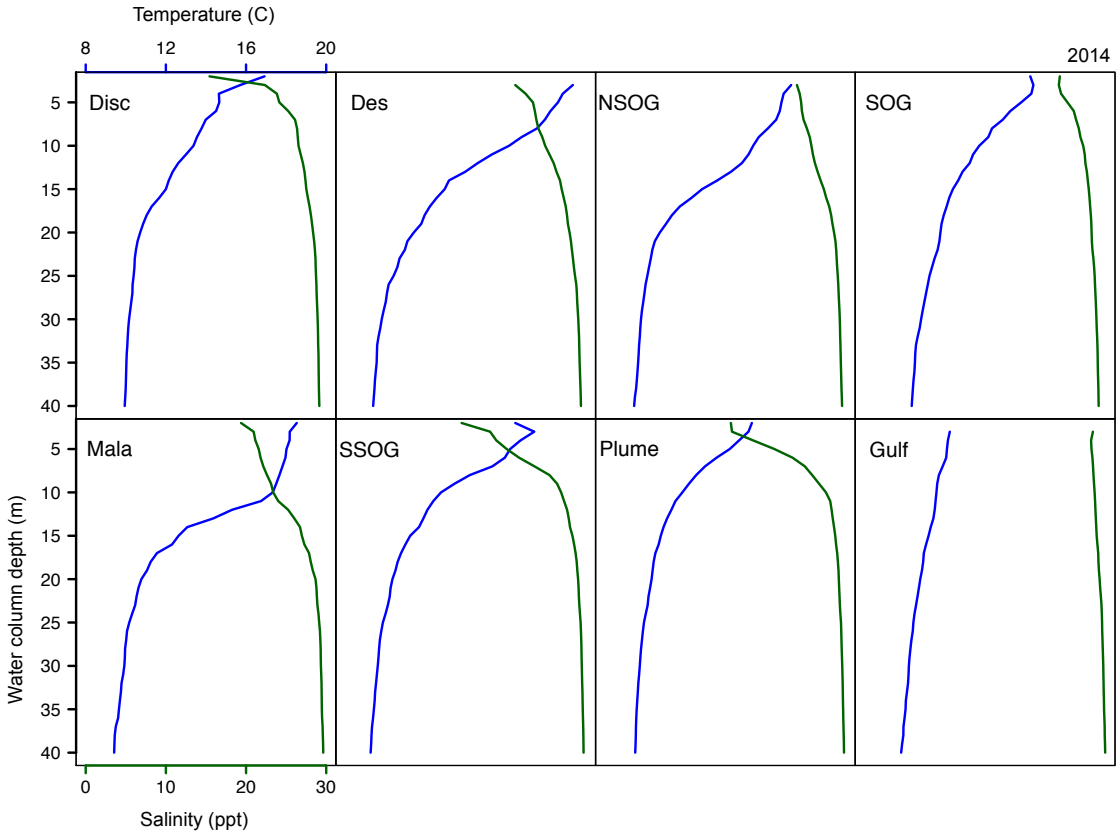
Average Fork Length (mm) + SE (n)						
Region	coho			chum		
	2012	2013	2014	2012	2013	2014
Disc	186.1 + 4.7 (16)	183.5 + 4.2 (24)	185.6 + 4.4 (26)	108.1 + 2.1 (24)	134.8 + 3.0 (27)	130.4 + 2.7 (33)
Des	160.8 + 2.5 (19)	157.6 + 4.4 (12)	177.0 + 4.4 (22)	125.7 + 4.7 (12)	ND	130.6 + 3.6 (20)
NSOG	187.7 +2.8 (26)	178.9 + 2.8 (46)	187.7 + 3.2 (61)	122.3 + 2.8 (8)	122.9 + 1.9 (52)	124.3 + 2.7 (38)
SOG	191.3 + 3.8 (34)	171.6 + 3.6 (41)	171.3 + 3.2 (70)	125.6 + 5.2 (12)	116.9 + 2.3 (29)	115.2 + 2.5 (38)
Mala	153.7 + 4.9 (17)	148.7 + 3.9 (25)	154.8 + 2.9 (43)	116.5 + 2.5 (18)	124.9 + 4.1 (20)	126.9 + 3.7 (16)
SSOG	165.8 + 4.7 (24)	167.1 + 3.1 (46)	156.74 + 2.5 (70)	114.2 + 2.1 (33)	118.7 + 4.5 (9)	118.9 + 1.7 (46)
Plume	ND	155.1 + 4.4 (7)	150.9 + 2.4 (50)	ND	111.3 + 1.6 (8)	119.4 + 3.8 (13)
Gulf	161.2 + 3.0 (22)	163.0 + 4.1 (27)	151.6 + 5.1 (21)	111.4 + 2.3 (31)	127.1 + 2.6 (31)	107 + 2.5 (32)



Supplemental Figure 2.1. Regional CTD cast profiles of water column temperature (°C) in blue and water column salinity (ppt) in green in 2012.



Supplemental Figure 2.2. Regional CTD cast profiles of water column temperature (°C) in blue and water column salinity (ppt) in green in 2013.



Supplemental Figure 2.3. Regional CTD cast profiles of water column temperature (°C) in blue and water column salinity (ppt) in green in 2014.

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