Spatial and interannual variability of juvenile coho salmon growth in the Strait of Georgia (2012–2015)

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ABSTRACT: We conducted a 4 yr (2012–2015) study of regional growth of juvenile coho salmon *Oncorhynchus kisutch* in the Strait of Georgia (British Columbia, Canada). Size (fork length) and growth (insulin-like growth factor-1 [IGF-1] concentration) varied both regionally and interannually. Additionally, we found a positive relationship between IGF-1 concentration and fork length that varied between years, with slopes and *y*-intercepts higher in 2012 and 2014, respectively, as compared to 2013 and 2015. An ordinal increase of IGF-1 concentration from the south to north in 2012 and 2014 was coupled with an increase in the prevalence of both juvenile herring and juveniles of other fish species in the diet. Across all years, there was a positive relationship between regional mean IGF-1 concentration and regional mean percent of juvenile herring in the diet. Our study demonstrates relatively small-scale spatial heterogeneity in juvenile coho salmon growth that in part, was attributed to regional variation in diet. These findings also demonstrate the utility of short-term growth measures (such as IGF-1) for assessing relatively small-scale spatial and temporal differences in growth.

KEY WORDS: Juvenile salmon · *Oncorhynchus* · Growth · Strait of Georgia · Insulin-like growth factor-1 · IGF-1 · Diet · Coho salmon

1. INTRODUCTION

The Strait of Georgia in the northeastern Pacific is a semi-enclosed sea that is used as a nursery and feeding area by numerous species, including Pacific salmon (*Oncorhynchus* spp.), Pacific herring *Clupea pallasii*, and southern resident killer whales *Orcinus orca* (Beamish & MacFarlane 2014). Primary productivity varies regionally within the Strait of Georgia and is strongly influenced by the stability of the water column (Masson & Peña 2009). The offshore waters of the southern Strait of Georgia are highly stratified and productive due to the freshwater discharge from the Fraser River that forms a stable surface layer. In contrast, the Gulf Islands are only weakly stratified due to the strong tidal currents that mix the water column, resulting in high turbidity and low phytoplankton productivity (Johannessen et al. 2006, Masson & Peña 2009). Water stratification is intermediate in the offshore waters of the northern Strait of Georgia, as these waters are influenced by both the tidal mixing and freshwater input from northern inlets and passages and by the freshwater discharge from the Fraser River. Given this spatial

heterogeneity of productivity, it is possible to predict that feeding and growth of fishes, such as salmon and forage fish, may also vary regionally within the Strait of Georgia.

Early marine growth is positively correlated with survival of juvenile salmon (Healey 1982, Beamish et al. 2004, Duffy & Beauchamp 2011). The growth rate of juvenile salmon is directly (but not exclusively) related to both food consumption (quantity and quality) and temperature (Brett et al. 1969, 1982). Food quality (caloric density) can be directly assessed by examining prey items found in stomach contents and referring to laboratory analysis of energy density (Brodeur et al. 1992). Food quantity, or consumption, is difficult to directly assess for free-living fish, but is often approximated via stomach fullness (Brodeur et al. 1992). One could predict that higher growth rates result from greater food consumption and/or consumption of more calorie-dense food. One could also predict (given consistencies in diet) a thermal optimum for growth with lower growth above and below this optimum temperature (Brett et al. 1969). Relationships between short-term growth and diet in marine-rearing juvenile salmon have not been extensively examined.

Recent (within 5–7 d) growth rates of juvenile salmon can be assessed through measures of plasma insulin-like growth factor-1 (IGF-1) concentration (Beckman et al. 2004, Ferriss et al. 2014, Journey et al. 2018). IGF-1 is a hormone that is released from the liver and circulates in the blood, stimulating somatic growth (Duan 1998). Concentration of IGF-1 in the blood plasma varies with feeding and fasting (Shimizu et al. 2009), thus individual and annual differences in IGF-1 concentration may imply differences in feeding and/or caloric intake (diet quality or diet quantity). Moreover, IGF-1 concentrations are directly related to juvenile salmon growth rate (Beckman 2011).

The Department of Fisheries and Oceans Canada (DFO) performs annual juvenile salmon surveys in the Strait of Georgia and surrounding waters each summer (Beamish et al. 2010a, Sweeting et al. 2003). A near-continuous 20 yr time series of the abundance and distribution of juvenile coho salmon *Oncorhynchus kisutch* in the Strait of Georgia has been developed through these annual June/July and September trawl surveys, and several reports have documented decadal-scale changes in the survival and abundance of these fish (Beamish et al. 2000, 2008, 2010a, Sweeting et al. 2003). In addition to survival and abundance, results from these surveys also report on size, condition, and diet contents of juvenile salmon (Beamish et al. 2000, 2004).

We report herein on plasma IGF-1 concentrations of juvenile coho salmon captured during the June/July DFO Strait of Georgia surveys in 2012, 2013, 2014, and 2015. We had 2 primary objectives: (1) to assess if growth varied regionally or inter-annually within the Strait of Georgia and (2) to investigate potential relationships between growth and diet and/or water temperature to elucidate potential drivers of any variations in growth.

2. MATERIALS AND METHODS

2.1. Survey design

The DFO Strait of Georgia summer salmon survey is designed to assess overall abundance and distribution of juvenile salmonids in the entire Strait of Georgia, within the constraint of the number of ship days available within a given year. As such, tow locations (Fig. 1) and number of tows per region (Table 1) varied between years. The start and end latitude and longitude, net depth, and tow duration were recorded for each individual tow. Specifics of the complete survey design and methods are detailed in Sweeting et al. (2003) and Beamish et al. (2008).

2.2. Field sampling of juvenile salmon

Juvenile salmon were captured via trawl net aboard the CCGS 'W.E. Ricker' in late June and early July of 2012, 2013, 2014, and 2015. A modified mid-water rope trawl net was used, with the head-rope at the surface (0), 15, or 30 m depths, with an average net opening height between 12 and 18 m and net opening width between 28 and 42 m. Juvenile coho salmon assessed in this study were under 250 mm in fork length (assumed to be in their first year of ocean residence). Coho salmon were visually sorted from the overall catch, measured for fork length, and had blood samples collected at random, from 0 to 12 individuals per tow (sample size per tow dependent on overall salmon catch per tow). Blood samples were immediately centrifuged, the plasma removed with a pipet, and then stored frozen (−20°C). Plasma samples were transported frozen and stored at −80°C until processing at the Northwest Fisheries Science Center in Seattle, WA (USA). Following blood collection, stomachs from some individuals were visually assessed for fullness (% of total stomach volume occupied by prey items) and percent diet composi-
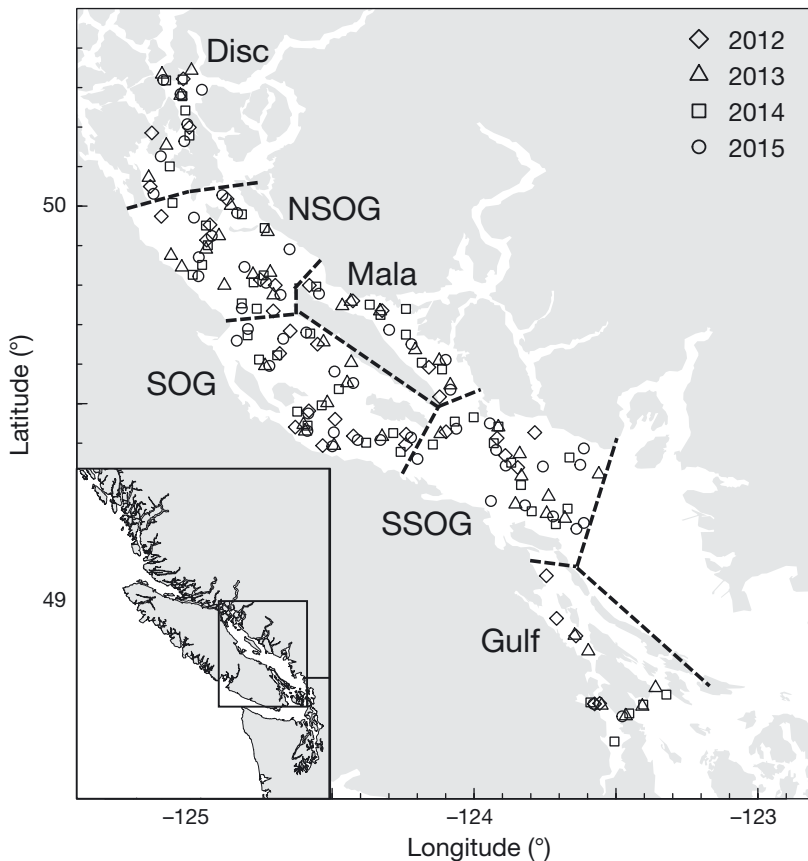
Fig. 1. Sampling area and regional boundaries within the Strait of Georgia (British Columbia, Canada). The regions are designated from north to south as: (1) Discovery Islands (Disc), (2) Northern Strait of Georgia (NSOG), (3) Mid Strait of Georgia (SOG), (4) Malaspina Strait (Mala), (5) Southern Strait of Georgia (SSOG), and (6) Gulf Islands (Gulf). The specific locations of non-zero catch of juvenile coho salmon per year are represented by diamonds (2012), triangles (2013), squares (2014), and circles (2015)

tion by taxon (genus or species, by estimated volume [cc]). Complete stomach analysis techniques are described by Sweeting & Beamish (2009).

2.3. Laboratory procedures

The IGF-1 concentration of plasma for individual fish was measured using the time-resolved fluorescence immunoassay developed by Small & Peterson (2005) as modified by Ferriss et al. (2014). Across individual assays (37 samples per assay), all samples within a year were standardized using inter-assay pools of coho salmon plasma at 3 known IGF-1 concentrations (low, medium, and high), corresponding to approximately 75, 50, and 25% binding in the immunoassay. Individual plasma 11-ketotestosterone concentrations were measured by immunosorbent assay (Cuisset et al. 1994) to identify precociously

maturing coho salmon males (age 2). The plasma concentration of IGF-1 for precocious males is not a reliable indicator of relative growth, thus these individuals were removed from further analysis (Beckman et al. 2004, Larsen et al. 2004).

2.4. Water column characteristics

Water column conductivity, temperature, and depth/pressure (CTD) were measured with a SBE 911plus CTD (Seabird Scientific) during the morning and the evening, before and after fishing trawl operations for the day. CTD cast locations were divided among 6 geographic regions (see Section 2.5). All CTD casts per region within a year were averaged to form a single regional mean per year, resulting in 4 temperature profiles per region across the 4 years of sampling. Regional water column properties (mixing) were indexed by assessing whether a thermocline was present. A thermocline was considered present in a region if at any 2 points in the regional average temperature profile the change in temperature was greater than 2°C with a depth change of less than 10 m (Defant 1961). Temperature at a depth of 5 m (always above the thermocline, if present) was regarded as the average temperature experienced by a fish, while temperature at a depth of 45 m (always below the thermocline, if present) was used as the minimum water temperature experienced by a fish per region.

2.5. Data analysis

All data were assessed within the context of spatial variation in the Strait of Georgia. The Strait of Georgia was divided into 8 regions (from north to south): Discovery Island, Desolation Sound, Northern Strait of Georgia, Mid Strait of Georgia, Malaspina Strait, Southern Strait of Georgia, Fraser River Plume, and Gulf Islands (Fig. 1) based on oceanographic and geographical boundaries. As sampling effort varied between years, tow location and effort were not consistent between years and within regions. Only geo-

Table 1. Physical water column properties and numbers of conductivity, temperature, and depth (CTD) casts, fishing tows, and salmon sampled per region within a year. The water temperatures at 5 and 45 m were averaged per region using all CTD casts within a year. Refer to Fig. 1 for regional abbreviations. IGF-1: insulin-like growth factor-1

Year	Region	Thermocline?	Temp at 5 m (°C)	Temp at 45 m (°C)	CTD casts (n)	Fishing tows (n)	Fish sampled for IGF-1 (n)
2012	Disc	Yes	15.3	9.2	4	3	16
	NSOG	Yes	16.1	9.0	7	4	26
	SOG	Yes	14.1	9.5	4	5	34
	Mala	Yes	15	8.7	2	4	17
	SSOG	Yes	14.6	8.8	5	7	24
	Gulf	No	10.9	9.3	8	5	22
2013	Disc	Yes	14.3	9.1	3	5	24
	NSOG	Yes	15.9	9.1	7	10	46
	SOG	Yes	15.6	9.8	4	9	41
	Mala	Yes	15.9	8.9	2	5	25
	SSOG	Yes	14.7	9.1	5	7	46
	Gulf	No	14.6	10.5	4	6	27
2014	Disc	Yes	17.2	9.3	3	5	26
	NSOG	Yes	16.8	9.3	7	10	61
	SOG	Yes	15.8	10.1	4	12	70
	Mala	Yes	18	9.3	2	7	43
	SSOG	Yes	16.2	9.1	4	10	65
	Gulf	No	12.1	9.8	4	3	21
2015	Disc	Yes	17.3	9.9	2	7	43
	NSOG	Yes	17.5	10.1	6	11	57
	SOG	Yes	17.7	10.3	6	14	95
	Mala	Yes	16.5	9.7	5	5	30
	SSOG	Yes	17.4	9.8	9	12	80
	Gulf	No	14.9	11.1	4	2	16

graphic regions where 10 or more juvenile coho salmon were captured in 3 or more different tows in all years were included in the analysis. Based on these criteria, samples collected in Desolation Sound and the Fraser River Plume were excluded from further analysis.

IGF-1 concentrations (ng ml^{-1}) and fork lengths (mm) were reported as regional means, calculated as the mean of individual IGF-1 concentrations (ng ml^{-1}) and individual fork lengths (mm) across all tows in that region for a given year. Given the attributes of the survey design and the pattern of catch, we do not have adequate power to assess if variation in IGF-1 concentration or fork length exists among tows within certain regions (low number of tows, low catch/tow); thus, we did not address variation between tows within a region. In order to assess annual differences, a yearly mean of regional means was calculated. The 6 regions differ in geographic size and fishing effort; thus, for the purpose of this study, regional abundance of juvenile coho salmon (catch per unit effort) was not assessed.

Differences among regions in IGF-1 concentration and fork length were assessed with 1-way ANOVAs with Tukey range tests (Tukey 1949) within a year.

Jarque-Bera tests (Jarque & Bera 1980) were used to assess normality of IGF-1 concentration and fork length within a region, and when necessary, IGF-1 concentrations within a year were log transformed prior to analysis. Linear models were then used to assess the relationship of regional IGF-1 concentration to regional fork length within each year (2012, 2013, 2014, and 2015). Additionally, linear models were used to assess the relationship of regional mean IGF-1 concentration to fork length, year, region, and temperature independently. Following this, year and region were used as covariates to explore the annual relationship of IGF-1 concentration to fork length among years. All statistical analyses were performed in RStudio (version 1.2.1335) using the 'stats' and 'htest' packages (R Core Team 2018, RStudio Team 2018).

Stomach content was analyzed separately from all other variables, as stomach content was not assessed for every individual fish sampled for IGF-1 and stomach content was not assessed in every region in every year. To assess the influence of prey quality on IGF-1 concentration, the presence of the most abundant taxa (all taxa that comprised more than 10% of overall diet contents in at least 2 of the 4 years) found in juvenile coho salmon stomachs was quantified.

Regional percentages of the 6 most abundant diet taxa were arcsine transformed and regressed with regional IGF-1 concentrations.

3. RESULTS

3.1. Water column temperature

Similar water temperature profiles were observed in 5 of the 6 regions (excluding the Gulf Islands) in all years (Fig. 2). Thermoclines were observed for all regions in all years, except for the Gulf Islands where no thermocline was apparent in any of the years (Table 1). In the Gulf Islands, the average water column temperature ranged from nearly 11°C (2012) to 15°C (2015) at 5 m to nearly 10°C at 45 m in all years (an absolute range of only 1–5°C between 5 and 45 m, depending on year). In the remaining regions, shallow thermoclines were found in all years, 5 m temperatures ranged from nearly 14°C (Discovery Islands, 2013) to 18°C (Malaspina, 2014) and 45 m temperatures ranged from 9 to 10°C in all years (an absolute range of 4–9°C temperature difference between 5 and 45 m, depending on year).

3.2. Regional variations in IGF-1 concentration and fork length

Mean juvenile coho salmon IGF-1 concentrations varied significantly among regions in the Strait of Georgia within a year for all 4 years of sampling (p < 0.05, Fig. 3). In 2012, mean IGF-1 concentrations in the Discovery Islands and Northern Strait of Georgia were significantly higher than in all other regions. In the Gulf Islands, Malaspina Strait, and Southern Strait of Georgia, IGF-1 concentrations were also significantly lower than in the Mid Strait of Georgia in 2012. This pattern of IGF-1 concentration variation repeated in 2014 when IGF-1 concentrations in the Discovery Islands and Northern Strait of Georgia were significantly higher than in all other regions, and Malaspina Strait, Southern Strait of Georgia, and Gulf Islands IGF-1 concentrations were significantly lower than those of all other regions. In 2013 and 2015, there was less overall variation among the regions, but Malaspina Strait samples had significantly lower mean IGF-1 concentrations when compared to all other regions in both years (p < 0.05, Fig. 3). These observed differences in regional mean IGF-1 concentration indicate that growth within the strait varies both among regions and years.

The highest overall annual mean of IGF-1 concentrations (mean of regional means) was found in 2012, followed by 2015, 2014, and lastly 2013 (Fig. 4, Table 2). However, the standard deviation from the mean of regional means was highest in 2014, followed by 2012, 2013, and 2015. These differences highlight that while variation in IGF-1 among regions within the strait exists in all years, the magnitude of variation (standard deviation) among regions also varies along with the maximum and minimum regional growth found in a year.

Juvenile coho salmon fork length varied significantly among regions in the Strait of Georgia both within and among regions for all 4 years of sampling (p < 0.05, Fig. 5). The largest annual variation in mean fork length among regions was seen in 2012 and 2014, when Malaspina Strait, Southern
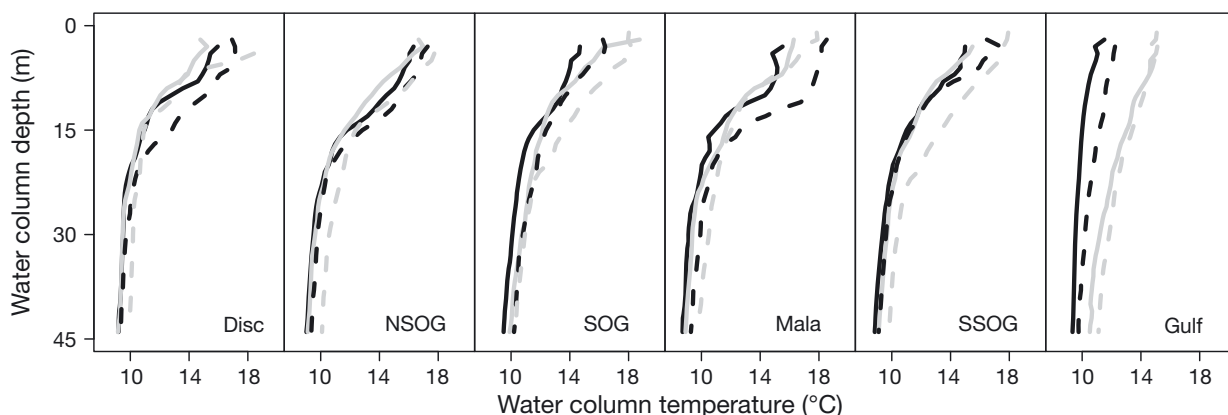

Fig. 2. Vertical water column temperature profile by region and year in the Strait of Georgia. Years are represented as solid black line (2012), solid gray line (2013), dotted black line (2014), and dotted gray line (2015). Significant thermoclines were found for all regions in all years (except the Gulf Islands). Corresponding data can be found in Table 1; refer to Fig. 1 for regional abbreviations
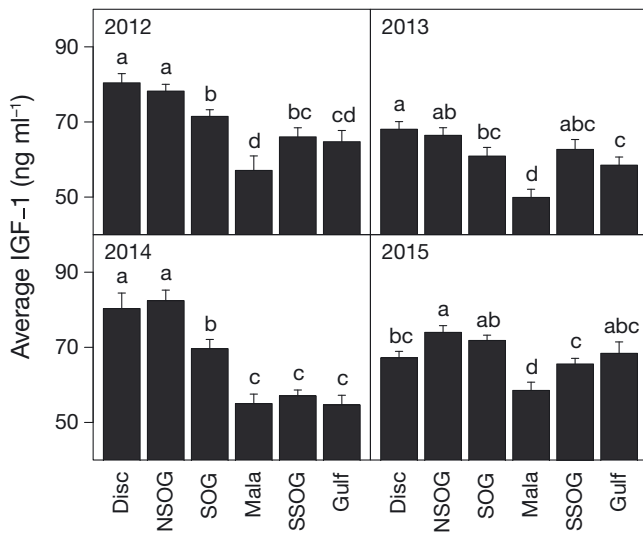
Fig. 3. Regional mean and SE of insulin-like growth factor-1 (IGF-1) concentration (ng ml^{-1}) of juvenile coho salmon captured in the Strait of Georgia per year. Significant differences within a year are indicated by different letters (p < 0.05, ANOVA). The number of tows and individual juvenile coho salmon sampled per region are given in Table 1; refer to Fig. 1 for regional abbreviations

Strait of Georgia, and Gulf Islands mean fork lengths were significantly lower than in the Discovery Islands and Northern Strait of Georgia. The highest overall annual mean (mean of means) and lowest range of means for fork length was seen in 2015 (Fig. 4, Table 2)

3.3. Linear regressions of IGF-1 concentration to fork length, year, region, and temperature

There were significant positive correlations between IGF-1 concentration and fork length ($R^2 = 0.81$, $F_{1,22} = 93.1$, p < 0.05) and between IGF-1 concentration and geographic region ($R^2 = 0.67$, $F_{5,18} = 7.4$, p < 0.05). We found no correlations between IGF-1 concentration and year ($R^2 = 0.13$, $F_{3,20} = 1.0$, p = 0.4) nor between IGF-1 concentration and water column temperature at 5 m ($R^2 = 0.05$, $F_{1,22} = 1.2$, p =

Table 2. Mean of regional means (±SE) of insulin-like growth factor-1 (IGF-1) concentration and coho salmon fork length

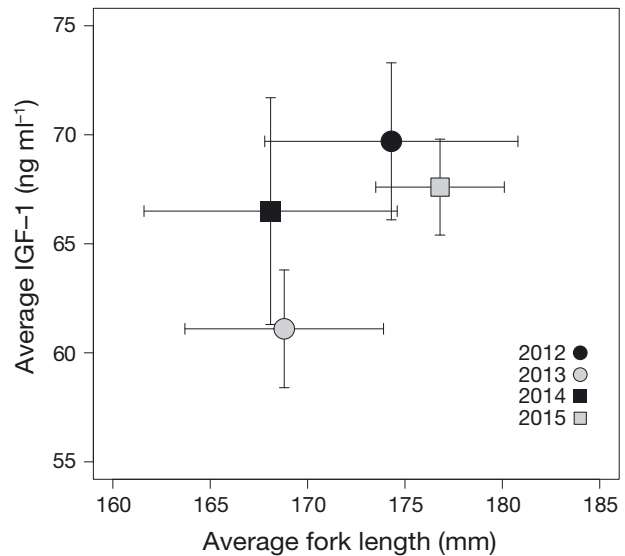| Year	IGF-1 concentration (ng ml^{-1})	Fork length (mm)
2012	69.7 ± 8.8	174 ± 16
2013	61.1 ± 6.5	169 ± 12
2014	66.5 ± 12.7	168 ± 16
2015	67.6 ± 5.4	177 ± 8

Fig. 4. Annual mean of regional means (±SE) of juvenile coho salmon insulin-like growth factor-1 (IGF-1) concentration (ng ml^{-1}) and fork length (mm). Corresponding data are provided in Table 2

0.28). The relationship between IGF-1 concentration and fork length was further explored utilizing year and region as covariates. The best-fit linear regression (strongest R^2) explaining variations among the IGF-1 concentration and fork length relationship was with year as a covariate (IGF-1 concentration ~ Fork length × Year; $R^2 = 0.93$, $F_{7,16} = 30.5$, p < 0.05, Fig. 6).

3.4. IGF-1 concentration and regional diet composition

Stomach content was analyzed separately from all other variables, as stomach content was not assessed for every individual fish sampled for IGF-1. The 6 most prevalent diet contents, as determined by the percent occurrence in stomachs among all years combined, were young-of-the-year (YOY) herring, other juvenile fish (combined: sandlance, pollock, rockfish, and unidentified fish remains), crab megalopae, crab zoeae, hyperiid amphipods, and euphasiids. These 6 diet contents comprised between 71% (Malaspina 2014) and 100% (Strait of Georgia 2012 and 2013 and Gulf Islands 2013) of the total stomach contents sampled in all years, excluding empty stomachs (Table 3). Notable observations were the low occurrences of YOY herring across all regions in 2013 and 2015 and the low occurrence of hyperiid amphipods in all regions in 2012.
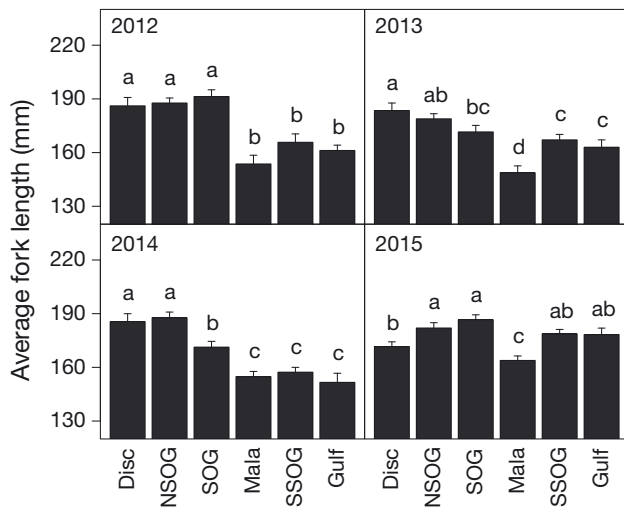
Fig. 5. Regional mean and SE of fork length (mm) of juvenile coho salmon captured in the Strait of Georgia per year. Significant differences within a year are indicated by different letters (p < 0.05, ANOVA). The number of tows and individual juvenile coho salmon sampled per region are given in Table 1; refer to Fig. 1 for regional abbreviations

lower to higher growth rates across the Strait both spatially and between years (Fig. 8). These differing growth rate measures suggest that variation in diet quantity and/or quality may exist and that diet may be a driver for differences in juvenile coho salmon growth found herein. In particular, spatial variation in growth was correlated with the presence of YOY herring in the diet of juvenile coho salmon. The lack of a direct relationship between regional mean growth of juvenile coho salmon and mean water column temperature suggests that variation in the quantity and quality of food resources drives much of the difference in growth that we measured during the early summer in the Strait of Georgia. Additionally, these findings demonstrate the utility of IGF-1 measures of growth for providing insight into the marine ecology of juvenile salmon. Other growth measures, such as scale or otolith increments, cannot provide the instantaneous, short-term signal afforded by IGF-1 measurements, which allow growth to be directly related to spatial location or stomach contents of juvenile salmon.
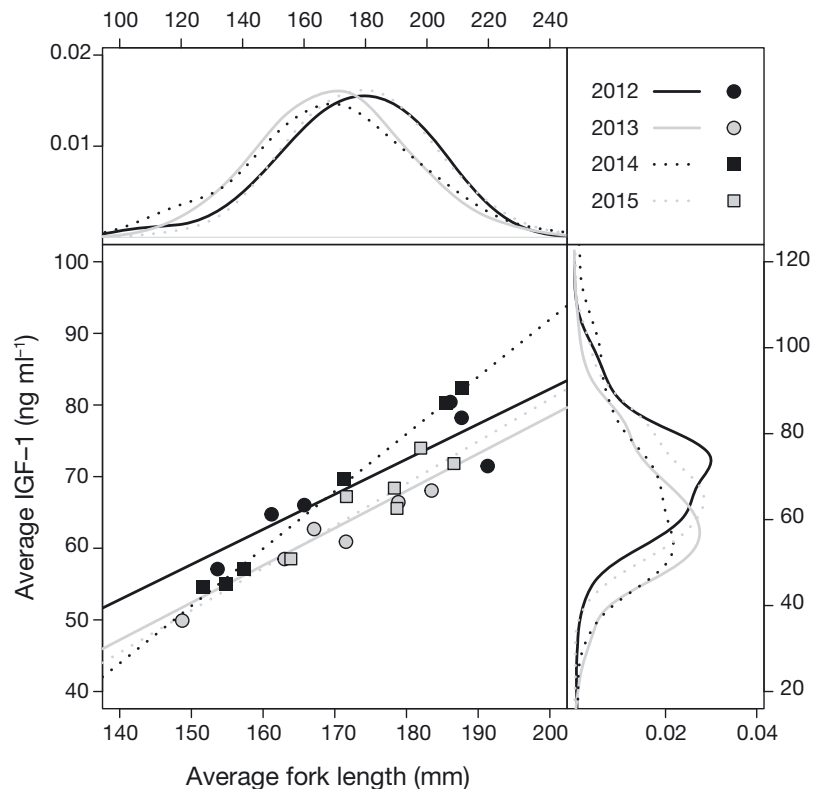
Positive and significant correlations were present between regional IGF-1 concentration and the occurrence of YOY herring ($R^2 = 0.48$, $F_{1,18} = 16.3$, $p < 0.05$) and other juvenile fish ($R^2 = 0.25$, $F_{1,18} = 6.13$, $p < 0.05$) in stomach contents (Fig. 7, Table 4). There were no other significant correlations between IGF-1 concentration and occurrence of specific diet taxa (crab megalopae, crab zoeae, hyperiid amphipods, euphausiids) (Table 4).

4. DISCUSSION

Our data suggest that both spatial and inter-annual variation in growth of juvenile coho salmon occurs in the Strait of Georgia. Low to intermediate growth was consistently found in the regions of the Gulf Islands and Malaspina Strait, while intermediate to high growth rates were found in the regions of the Northern Strait of Georgia and the Discovery Islands. However, inter-annual patterns among other geographic regions demonstrates a varying matrix of

Fig. 6. Relationship between mean regional insulin-like growth factor-1 (IGF-1) concentration (ng ml^{-1}) and mean regional fork length. Regression lines using Year as a covariate (IGF-1 ~ Fork length × Year; $R^2 = 0.93$, $F_{7,16} = 30.5$, $p < 0.05$) are shown. Frequency distributions are shown for individual IGF-1 concentrations (top) and fork length observed (right) within a sampling year. The corresponding statistical analysis can be found in the Appendix

Table 3. Mean regional diet composition (%) of juvenile coho salmon including total number of stomachs analyzed and number of empty stomachs. YOY: young-of-the-year; ND: no data were collected. Refer to Fig. 1 for regional abbreviations

Year	Region	Prevalence in diet by volume (%)						n	
		YOY herring	Crab megalopae	Crab zoeae	Hyperiid amphipods	Euphasiids	Other juvenile fish	Empty	Total
2012	Disc	56	12	6	0	1	24	0	16
	NSOG	25	42	9	0	4	8	2	16
	SOG	17	23	22	4	28	4	0	33
	Mala	14	27	6	6	25	7	1	7
	SSOG	7	30	37	3	1	15	1	24
	Gulf	ND	ND	ND	ND	ND	ND	ND	ND
2013	Disc	7	18	0	27	12	8	3	21
	NSOG	0	15	16	29	10	7	5	38
	SOG	0	26	12	52	10	0	0	5
	Mala	ND	ND	ND	ND	ND	ND	ND	ND
	SSOG	4	25	14	39	11	4	0	37
	Gulf	2	68	16	10	0	4	0	25
2014	Disc	37	17	1	10	1	16	4	26
	NSOG	15	34	7	31	3	4	0	25
	SOG	7	30	19	23	7	3	1	65
	Mala	3	29	7	21	2	10	4	35
	SSOG	0	49	23	13	3	1	2	65
	Gulf	ND	ND	ND	ND	ND	ND	ND	ND
2015	Disc	0	13	9	34	19	8	4	43
	NSOG	3	32	9	32	7	3	1	44
	SOG	2	36	14	23	13	4	1	75
	Mala	1	39	4	19	8	4	0	24
	SSOG	0	40	3	24	7	3	7	66
	Gulf	ND	ND	ND	ND	ND	ND	ND	ND

4.1. Regional differences

The growth of juvenile coho salmon in Malaspina Strait was consistently lower than in other regions. Similarly, the mean fork length of coho salmon in Malaspina Strait was also the lowest among regions in all years (significantly in 2013 and 2015). It is unclear why growth of juvenile coho salmon was reduced in Malaspina Strait; however, reduced prey resources for coho salmon is a simple and obvious inference. The water column was well stratified in Malaspina Strait, likely due to the influx of freshwater from Jervis Inlet and from the Fraser River, suggesting that the stability of the water column would have promoted primary productivity in this area. As noted previously, zooplankton sampling was too infrequent in this region to directly assess food abundance. We therefore cannot directly address our inference of reduced prey resources with data available from the concurrent survey.

It is interesting to note that Malaspina Strait is frequently used preferentially by migrating juvenile sockeye salmon *Oncorhynchus nerka* and steelhead *O. mykiss* (Peterman et al. 1994, Furey et al. 2015, Clark et al. 2016, Healy et al. 2017). Preferential use

of this region by juvenile salmon combined with the narrow width and smaller geographic area of Malaspina Strait compared to the Strait of Georgia may result in a higher density of juvenile salmon in this region. One could speculate that increased density of juvenile salmon could lead to lower prey availability, and thus, lower growth. A more directed study assessing prey density, salmon density, and salmon consumption as well as salmon growth would be needed to determine if lower growth rates in Malaspina Strait were due to lower prey density and subsequently, why prey density in Malaspina Strait might differ from other regions.

In contrast to Malaspina Strait, the Discovery Islands region had the highest regional mean IGF-1 concentration among 3 of the 4 years of sampling (2015 being the exception). The marine areas around the Discovery Islands were historically thought to be a poor rearing environment, due to extreme water column mixing and warm surface temperatures (Thomson 1981). In contrast, we found distinct thermoclines in all 4 years at our sampling locations, and water column temperatures were similar to the remainder of the Strait of Georgia, aside from the Gulf Islands region. In juvenile sockeye salmon, a
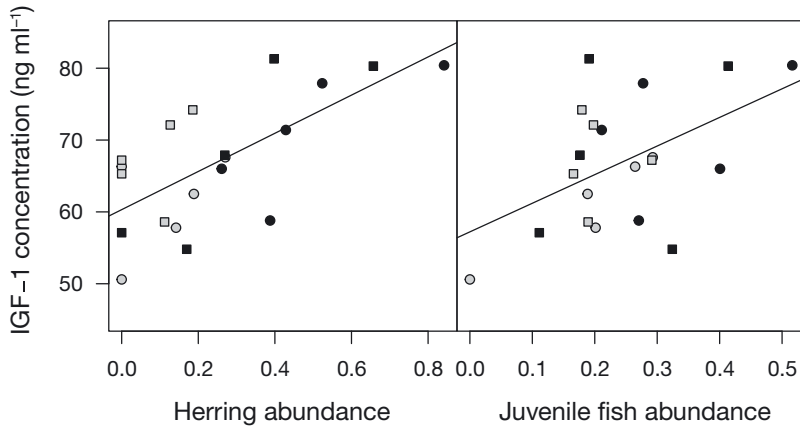
Fig. 7. Relationship between mean regional insulin-like growth factor-1 (IGF-1) concentration (ng ml^{-1}) and arcsine-transposed regional abundance (radians) of young-of-the-year herring (R^2 = 0.48, $F_{1,18}$ = 16.3, p < 0.05) and other juvenile fish (R^2 = 0.25, $F_{1,18}$ = 6.13, p < 0.05) in the diet contents. Abundance estimates for even years, 2012 and 2014, are in black circles and black squares, respectively, and for odd years, 2013 and 2015, in gray circles and gray squares, respectively

higher proportion of empty stomachs was seen in the Discovery Islands region when compared to the Strait of Georgia (Neville et al. 2016). This does not appear to be the case for juvenile coho salmon, though this could simply reflect local differences within the Discovery Islands region. Most of the samples of juvenile sockeye salmon analyzed by Neville et al. (2016) were obtained in lower Johnstone Strait, an area that is tidally mixed and found to be consistently poor for salmon growth (Journey et al. 2018). In addition, this region has been shown to have low zooplankton biomass (James et al. 2020). In contrast, for this study, juvenile coho salmon were obtained in the southern part of the Discovery Islands region, an area that may be subsidized by the highly productive waters of the Northern Strait of Georgia. As the surface flows around the Discovery Islands are northward toward Johnstone Strait and Queen Charlotte Strait (Thomson 1981), prey produced in the Northern Strait of Georgia may be transported northward and become available to juvenile salmon in the southern part of the Discovery Islands region.

The Gulf Islands region differs from the main basin Strait of Georgia as the water is often cold and well mixed. There was no significant thermocline present in any sample year, and the water at 5 m was consistently cooler than found in all other regions. In 2012, 2013, and 2014, IGF-1 concentrations of coho salmon in the Gulf Islands region were lower than for fish in other regions, except for Malaspina Strait and the Southern Strait of Georgia. The Gulf Islands region shares the properties of a cold, well mixed water column with Johnstone Strait, located at the northwest

entrance to the Strait of Georgia. Juvenile coho, chinook *O. tshawytscha*, pink *O. gorbuscha*, chum *O. keta*, and sockeye salmon in Johnstone Strait have previously been shown to have significantly lower IGF-1 concentration than those found in the Northern Strait of Georgia (Journey et al. 2018). These similar findings, of low IGF-1 concentrations in fish from disparate regions with well-mixed water columns, demonstrate a correlation between local oceanography and juvenile salmon growth. Well-mixed water columns may directly influence feeding and growth through low local productivity and prey resources, or directly influence prey consumption as the mixing may disperse juvenile salmon prey. Either situation would suggest poor feeding conditions.

4.2. Significance of regional differences

Many long-term studies of salmon productivity in the Strait of Georgia treat the area as a homogeneous unit and use annual trends in size, abundance, and adult returns to assess overall salmon response (Beamish et al. 2008). However, given the differences in regional productivity we found (Fig. 8), one might suggest that coho salmon productivity may be better assessed as the sum of differing regional productivities rather than a homogeneous average. However, 2 data gaps exist that limit the utility of applying a regional approach to salmon productivity based on this work: we do not report on potential regional variation in coho salmon population structure nor do we report on regional abundance of juvenile coho salmon.

Table 4. Results of regression analysis between regional mean insulin-like growth factor-1 (IGF-1) concentration and diet composition of juvenile coho salmon. YOY: young-of-the-year; *p < 0.05

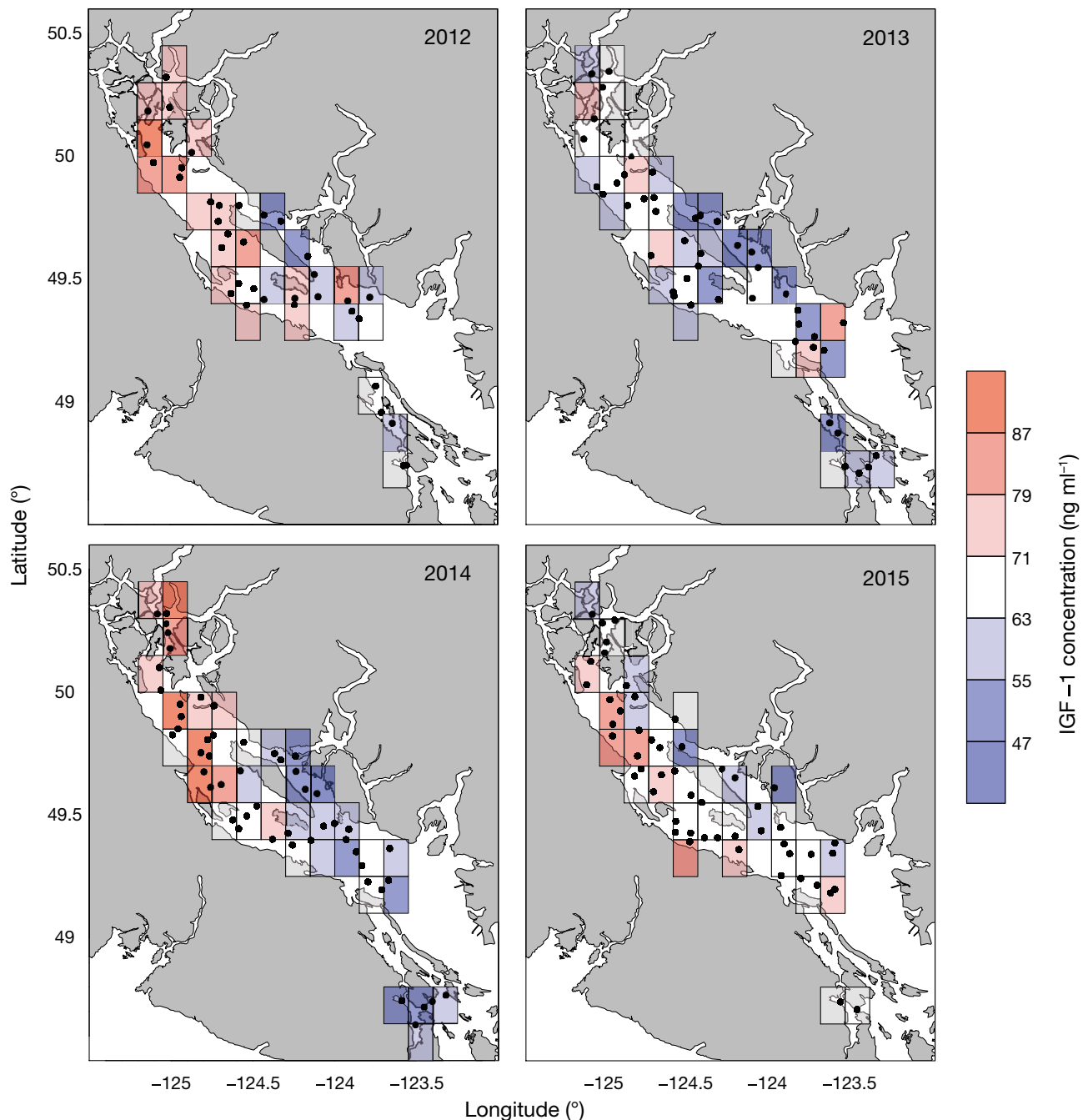| Diet item	R^2	F (df)	p
YOY herring	0.47	16.1 (1,18)	0.001*
Other juvenile fish	0.25	6.1 (1,18)	0.02*
Crab megalopae	0.10	2.1 (1,18)	0.17
Crab zoeae	0.04	0.7 (1,18)	0.39
Hyperiid amphipods	0.13	2.8 (1,18)	0.11
Euphasiids	0.02	0.3 (1,18)	0.59

Fig. 8. Strait of Georgia, with fish capture locations shown as points for sampling years 2012–2015. Latitudinal/longitudinal grid overlays are colored based on the mean insulin-like growth factor-1 (IGF-1) concentration of all individuals present in the grid in each year. Blue colors represent IGF-1 concentrations below the overall mean (white), and red colors represent IGF-1 concentrations above the mean

The juvenile coho salmon that we sampled in the Strait of Georgia undoubtedly originated from a variety of different populations, located on either the mainland or the East Coast of Vancouver Island (Beacham et al. 2016). Smolts from these different populations may have entered the Strait of Georgia at differing dates and at differing smolt sizes. Subse-

quently, individuals from these populations may have maintained a local residence within the Strait of Georgia or may have distributed themselves across the entire area. We have not assessed the genetic origin of the fish sampled herein and thus do not know whether fish in the regions we sampled represented well mixed groups of populations or whether there

were regional differences in population structure. We are not aware of any data suggesting that fish from differing populations may display aberrant plasma IGF-1 concentration or differing IGF-1 concentration versus growth relationships (Picha et al. 2008, Beckman 2011). Thus, we trust that our results are general for coho salmon found in the Strait of Georgia and are not the result of any specific population or mixture of fish. Nevertheless, different populations may reside in areas of differing productivity or respond to environmental stressors differently.

Due to varying size of regions and sampling effort within the regions, we are unable to make useful estimates of abundance in the various regions. If most of the fish from most of the populations are in a certain area (e.g. a region with high growth such as the Northern Strait of Georgia), growth variation in other regions would be relatively unimportant and could be essentially ignored with regard to assessing overall productivity. Our work might thus be considered as just one of several steps required to ascertain whether coho salmon productivity in the Strait of Georgia could be considered as a sum of a mosaic of regions and populations or as a homogeneous response across a group of populations within a specific region.

4.3. Growth and size

IGF-1 concentration generally increases with size in naturally rearing juvenile Pacific salmon (Ferriss et al. 2014, Chamberlin et al. 2017, Journey et al. 2018). The relationship between IGF-1 concentration and size in free-living juvenile salmon is likely complex, and open to speculation. However, faster-growing fish inevitably become larger than slower-growing fish; thus, in a steady-state condition, larger fish should have higher IGF-1 concentrations than smaller fish as they became larger by growing faster. Shimizu et al. (2009) found correlations between size and IGF-1 concentration in both 1 and 3 wk fasted fish, suggesting a correlation that is independent of growth rate. Yet, the actual relationship between size and IGF-1 concentration was weak, and the same study found no relationship between size and IGF-1 concentration in fed fish, suggesting that variations in feeding and growth between individuals overwhelmed any

variation in IGF-1 concentration related to individual size that was demonstrated in fasted fish. Moreover, in other laboratory experiments, small fish fed a high ration had higher IGF-1 concentrations than large fish fed low rations (Beckman et al. 2004), suggesting that any direct physiological effect of size on IGF-1 concentration is minimal.

Correlations between size and IGF-1 concentration could also be ecologically based, reflecting the foraging success of differently sized fish. Fish size is related to swimming speed; thus, prey capture efficiency could vary between smaller and larger fish (Bainbridge 1958). Fish size may also relate to gape limitations for prey, with smaller fish unable to capture and ingest relatively larger, energy-rich prey (Chamberlin et al. 2017). In this study, we observed a positive relationship between IGF-1 concentration and fork length in juvenile coho salmon, suggesting that larger fish had greater consumption levels (in either quality or quantity) and thus higher growth than smaller fish across all years. Interestingly, this relationship varied among years, perhaps indicating that size-related feeding conditions varied among years.

We may infer variations in size-related foraging based on characters of IGF-1 concentration versus fork length regression relationships (Fig. 9). Either the slope and/or intercept of IGF-1 versus length relationships may vary based on the size and abundance of prey items. The *y*-intercept of the fork length and IGF-1 concentration relationship was higher in 2012 compared to all other years. The change in *y*-intercept (IGF-1 concentration for a given fork length) in 2012 may indicate better size-independent foraging. Basically, this might be an indication of greater prey abundance that benefits all fish regardless of
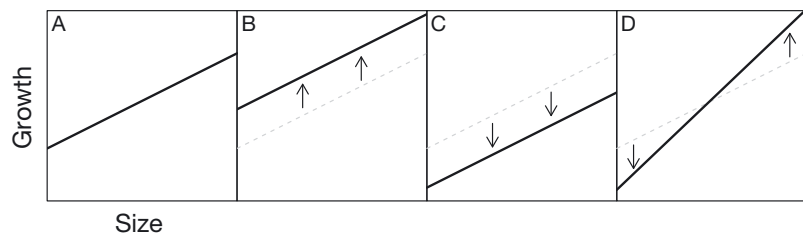
Fig. 9. Potential changes in relationships between growth (insulin-like growth factor-1 [IGF-1] concentration) and size (fork length). (A) A positive relationship between length and IGF-1 has been found in several studies including this one. (B) Increased or (C) decreased food resources (quantity or quality) may result in an increase or decrease, respectively, in the *y*-intercept (the solid line represents the change from baseline condition, shown as a dashed line). (D) Increases in size of food resources may result in varying size-dependent foraging, resulting in an increase in slope. Conversely, spatial variation in availability of food resources may also result in a varying slope as faster-growing fish also become larger

size all across the Strait of Georgia as compared to 2013–2015.

In contrast, the slope in 2014 was steeper than the slope found in other years. The differences in slope magnitude between 2012 and 2014 could reflect differences in the energy content of prey for coho salmon of differing sizes, differences in size-related foraging costs between years, or simply regional differences in prey consumption, growth, and thus size (Chamberlin et al. 2017). Foraging costs can decrease when larger prey of the same caloric density are available (Kerr 1971a,b, Sherwood et al. 2002a,b). An example of this may be that a larger high-calorie prey (such as YOY herring) may be consumed as fish get bigger and gape limitations are by-passed. Alternatively, the change in slope may be driven by regional differences in prey resources; with better feeding, higher growth and larger size found in some regions as compared to others. The data herein showed that YOY herring were prevalent in the stomachs in some regions in 2014 and not in others.

While some sampling of zooplankton does occur on these surveys, the sampling is not rigorous enough to generate region-specific prey abundances. In addition, the sampling gear used (bongo net) is not designed for sampling juvenile fishes such as YOY herring; thus, we do not have the ability to rigorously test the hypothesis of varying prey abundance described above with data collected during these surveys. Nonetheless, we suggest that variation in IGF-1 concentration and fork length relationships, such as we described above, may provide useful ecological inferences about juvenile coho salmon and their prey field. It is our intention to pursue opportunities to measure juvenile salmon IGF-1 concentration, document prey contents in stomachs, and quantitatively assess the prey field from which the fish were sampled to more rigorously determine how variation in IGF-1 concentration and fork length relationships relate to differing prey consumption by fish of varying size.

4.4. Growth and diet: prey quantity

Juvenile salmon growth is a function of prey quality (caloric density), prey quantity, and temperature (Brett et al. 1969). As described above, we do not present data documenting regional prey availability for juvenile coho salmon during our survey. However, some data suggest that productivity in the Strait of Georgia varies both annually and spatially. Gower & King (2018) reported that

the timing of the spring phytoplankton bloom occurred around the beginning of April in the Southern Strait of Georgia in 2012 and 2014, and approximately 3 wk earlier in 2013 and 2015. The timing of spring bloom tended to occur approximately 2 wk later in the Northern Strait of Georgia when compared to the Southern Strait of Georgia, except in 2015, when the bloom occurred 2 wk earlier in the North (Gower & King 2018). Thus, phytoplankton abundance varies both temporally and spatially. Of course, juvenile coho salmon do not directly feed on phytoplankton; instead, we found crab zoeae and megalopae, euphausiids, amphipods, and juvenile fishes in their stomachs during the survey in June and July. The distribution, nutritional quality, size, and abundance of these prey items could all be influenced by variation in the timing and intensity of the spring phytoplankton bloom and thus could be responsible for the growth variation we found. The stomach content analysis described here does not provide a good measure for assessing prey consumption; thus, we focus on discussion of prey quality (Section 4.5) with the acknowledgement that prey quantity likely varied between years.

4.5. Growth and diet: prey quality

The taxonomic composition and estimated caloric value of juvenile coho salmon stomach contents varied between years and regions. Of the prey items found, current literature suggests that hyperiid amphipods had the lowest caloric density at 2464 J g^{-1} (Davis et al. 1998). Crab zoeae and euphasiids have average caloric densities at 3362 and 4731 J g^{-1}, respectively (Higgs et al. 1995). Juvenile fish (unidentified, sculpin, and sandlance) and YOY herring have the highest caloric densities. Literature caloric values for juvenile fish were found to be between 4060 J g^{-1} (Anthony et al. 2000) and 6837 J g^{-1} (Higgs et al. 1995) and up to 9801 J g^{-1} (McBride et al. 1959) for YOY herring. Larval crab and juvenile herring become increasingly prevalent as food sources as fork length increases for Puget Sound chinook salmon (Duffy et al. 2010). Similarly, growth of juvenile chinook salmon off the Washington Coast was positively correlated to the proportion of forage fish such as the northern anchovy *Engraulis mordax* in the diet (Litz et al. 2019). Together, these data suggest that variation in diet quality could affect variation in juvenile coho salmon growth in the Strait of Georgia.

4.6. Growth and diet: YOY herring

The survival, and thus abundance, of YOY herring in the Strait of Georgia is associated with the timing of adult herring spawning and its relationship to the spring phytoplankton bloom (Schweigert et al. 2013). However, juvenile herring distribution within the Strait of Georgia, both annually and regionally, may be more dependent on spawn location and wind intensity during larval stages than on timing and location of spring phytoplankton bloom (Snauffer et al. 2014). YOY herring abundance in the Strait of Georgia has varied greatly between years from 1992–2016 (Boldt et al. 2019). For the years of our study (2012–2015), catch per unit effort of YOY herring in 2012 was approximately 4-fold higher than in 2013, 2014, and 2015 (Boldt et al. 2019). However, the lack of detailed information on the spatial distribution and size of YOY herring in the areas sampled in this study precludes us from directly assessing the effects of the abundance and size of YOY herring on the diet and growth of juvenile coho salmon in the Strait of Georgia (YOY herring catch during the Strait of Georgia juvenile salmon survey is merely anecdotal because trawls were conducted during the day at or near the surface when YOY herring are located deeper in the water column). Nonetheless, IGF-1 concentrations and herring abundance in the stomach were relatively high in 2012.

The higher prevalence of YOY herring in coho salmon stomachs in 2012 and 2014 could be the result of higher overall YOY herring abundance. The absence of YOY herring in coho salmon stomachs in 2013 and 2015 could have been the result of the presence of larger YOY herring that were beyond the gape limit of juvenile coho salmon in those years. Thus, the prevalence of YOY herring in 2012 and 2014 stomachs may indicate that YOY herring were not only abundant, but abundant in viable sizes for juvenile coho consumption.

Low abundance of YOY herring in the Strait of Georgia has been associated with poor juvenile salmon condition (a function of length and weight) and subsequent poor marine survival (Beamish & Sweeting 2012). Additionally, variability in growth of juvenile chinook salmon in Puget Sound was greater in years when herring were abundant, with the data suggesting that some larger juvenile chinook are able to exploit herring in their diet when present and thus grow faster (Chamberlin et al. 2017). The relationship between availability of YOY herring and recent growth reported here provides further data suggesting that YOY herring are a high-quality food item for juvenile salmon and that further examination of functional relationships between juvenile coho salmon and YOY herring may yield insights into the growth and survival of coho salmon.

4.7. Growth and temperature

Juvenile salmon growth may also be a function of water temperature (Brett et al. 1969, Brett et al. 1982, Plumb & Moffitt 2014). However, the effects of water temperature on juvenile salmon growth are relatively small over a wide range of temperatures near the optimal thermal window for growth, 11–18°C, at maximum feeding rates (Plumb & Moffitt 2014). In this study, there were no significant correlations between IGF-1 concentration and water temperature at 5 m for any of the 4 years, possibly because, at this depth, all water temperatures in the Strait of Georgia were within the physiological optimal thermal window for juvenile salmon growth. However, it should be noted that it is difficult to pinpoint the exact thermal regime experienced by juvenile coho salmon in the Strait of Georgia, as they are not limited to the top 5 m. Instead, they primarily reside within the top 45 m of the water column (Beamish et al. 2010a). Differences in the water temperature between 5 and 45 m varied among regions. Water is generally poorly stratified in the Gulf Islands due to strong tidal mixing. As a result, water temperature only differed by 1–5°C between 5 and 45 m in this region, depending on the year. Water temperature differences in the remaining regions ranged between 5 and 9°C from 5 to 45 m among all years. Nevertheless, these differences are expected to have few direct effects on the growth of juvenile coho salmon, as they were all within the thermal growth optima.

4.8. Competition with pink salmon?

Juvenile pink salmon are only abundant in marine waters of southern British Columbia during even years, as adults are only abundant in odd years (Beamish 2012). High abundances of juvenile pink salmon have been negatively correlated with the survival of coho salmon in the Strait of Georgia (Beamish et al. 2010b). An approximately 60% diet overlap exists between juvenile coho salmon and juvenile pink salmon in the Strait of Georgia (Beamish et al. 2010b). However, this large overlap in diet is largely due to larval crabs and amphipods, as juvenile pink salmon rarely consumed larval

fish (Beamish et al. 2010b). It is unlikely that the year-to-year differences in juvenile coho growth observed in our study were due to abundance of juvenile pink salmon: in years when juvenile pink salmon were abundant, juvenile coho salmon consumed relatively more high caloric density prey (juvenile fish) than low caloric density prey (hyperiid amphipods). In addition, mean IGF-1 concentrations were higher in years when juvenile pink salmon were present in the Strait of Georgia. Although certainly not conclusive, as there is no temporal overlap between studies, our results differ from those of Beamish et al. (2010b) and suggest that environmental factors other than simple pink salmon presence drive variation in growth and survival of juvenile coho salmon.

4.9. Summary

The small-scale geographical variations in growth that we observed, both regionally and interannually, indicate that the rearing environment experienced by juvenile coho salmon in the Strait of Georgia is heterogeneous. Specifically, growth in the Northern Strait of Georgia tends to be higher than in the Southern Strait of Georgia, and growth in regions around the Discovery Islands tends to be higher than in Malaspina Strait or among the Gulf Islands. These results suggest that mechanisms driving the abundance and distribution of juvenile fish and larger zooplankton will be related to variation in juvenile salmon growth. Studies to address these relationships will be difficult, as they require both sampling juvenile salmon and their prey field at relatively fine spatial and temporal scales. Different gear types are often needed to accomplish a sufficient characterization of both juvenile salmon and their prey. We trust that this report will stimulate discussion of and plans for such comprehensive sampling.

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Appendix. Additional analysis

Table A1. Linear models examining relationships of mean regional insulin-like growth factor-1 (IGF-1) concentration of juvenile coho salmon with length, year, region, and temperature. Shaded linear model (IGF-1~Length×Year) visualized in Fig. 6. Refer to Fig. 1 for regional abbreviations. *p < 0.05

Equation	Coefficients	Estimate	SE	t	p	R^2	F (df)	p
IGF-1~ Length	Intercept	−38.20	10.8	−3.53	0.002 *			
	Length	0.61	0.1	9.68	0.000 *	0.81	93.7 (1, 22)	0.000 *
IGF-1~ Year	Intercept	69.66	3.6	19.32	0.000 *			
	2013	−8.58	5.1	−1.68	0.108			
	2014	−3.14	5.1	−0.62	0.545			
	2015	−2.08	5.1	−0.41	0.688	0.13	1.0 (3, 20)	0.400
IGF-1~ Temp	Intercept	47.86	16.8	2.85	0.009 *			
	Temp	1.18	10.7	1.01	0.280	0.05	1.2 (1, 22)	0.284
IGF-1~ Length+Year	Intercept	−37.10	9.4	−3.94	0.000 *			
	Length	0.61	0.1	11.50	0.000 *			
	2013	−5.22	1.9	−2.77	0.012 *			
	2014	0.67	1.9	0.36	0.720			
	2015	−3.65	1.9	−1.96	0.065	0.89	38.6 (4, 19)	0.000 *
IGF-1~ Length*Year	Intercept	−15.77	13.7	−1.15	0.267			
	Length	0.49	0.1	6.26	0.000 *			
	2013	−9.83	21.9	−0.45	0.660			
	2014	−52.29	19.1	−2.74	0.015 *			
	2015	−21.40	30.8	−0.70	0.497			
	Length:2013	0.02	0.1	0.18	0.858			
	Length:2014	0.31	0.1	2.80	0.013 *			
	Length:2015	0.10	0.2	0.59	0.566	0.93	30.5 (7, 16)	0.000 *
IGF-1~ Length+Region	Intercept	−18.41	20.7	−0.89	0.386			
	Length	0.51	0.1	4.49	0.000 *			
	Gulf	−3.18	3.5	−0.91	0.374			
	Mala	−5.42	4.1	−1.32	0.205			
	NSOG	0.06	2.8	0.02	0.983			
	SOG	−4.77	2.8	−1.69	0.109			
	SSOG	−3.79	3.3	−1.16	0.261	0.85	16.1 (6, 17)	0.000 *
IGF-1~ Length*Region	Intercept	−70.18	61.3	−1.15	0.274			
	Length	0.79	0.3	2.35	0.036 *			
	Gulf	52.53	70.1	0.75	0.468			
	Mala	47.11	83.3	0.57	0.582			
	NSOG	−126.33	114.1	−1.11	0.290			
	SOG	76.48	73.3	1.04	0.317			
	SSOG	72.61	75.3	0.96	0.354			
	Length:Gulf	−0.31	0.4	−0.78	0.450			
	Length:Mala	−0.29	0.5	−0.58	0.570			
	Length:NSOG	0.68	0.6	1.10	0.294			
	Length:SOG	−0.45	0.4	−1.11	0.289			
	Length:SSOG	−0.43	0.4	−1.01	0.331	0.89	9.26 (11, 12)	0.000 *