Dynamic coastal pelagic habitat drives rapid changes in growth and condition of juvenile sockeye salmon (*Oncorhynchus nerka*) during early marine migration

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Abstract

Migrating marine taxa encounter diverse habitats that differ environmentally and in foraging conditions over a range of spatial scales. We examined body (RNA/DNA, length-weight residuals) and nutritional condition (fatty acid composition) of juvenile sockeye salmon (*Oncorhynchus nerka*) in British Columbia, as they migrated through coastal waters that varied oceanographically over tens of kilometers. Fish were sampled in the stratified, productive northern Strait of Georgia (NSoG); the highly mixed, unproductive Johnstone Strait (JS); and the transitional zone of Queen Charlotte Strait (QCS). Body and nutritional condition responded rapidly to changes in prey availability and were lowest in JS with low prey availability, supporting the Tropic Gauntlet Hypothesis, additionally we saw signs of compensatory growth in QCS. Juvenile salmon leaving the SoG in 2016 had significantly lower condition than in 2015, despite higher zooplankton biomass in 2016. We propose that this was due to the higher abundance of low food quality southern zooplankton species in 2016. This study highlights the importance of including food quality as a parameter to understand changes in fish condition and survival between years. Furthermore, small scale variation in oceanographic dynamics impact foraging conditions and need to be considered when assessing early marine survival of juvenile salmon.

Keywords: fatty acids, RNA/DNA, zooplankton biomass, environmental variation, compensatory growth, zooplankton species composition

Introduction

Diverse marine taxa from fish and squid to whales undertake long-distance marine migrations. These migrations can reduce the risk of predation and diseases, provide access to spawning grounds, and increase foraging opportunities. Anadromous fish undertake long-distance marine migrations, often travelling as juveniles from the mouths of their natal watersheds to the open ocean to forage and returning to freshwater as adults to reproduce. During their coastal outmigration, anadromous fish encounter interconnected and diverse ecosystems that differ in their physics, nutrient status and productivity levels, yielding highly contrasting foraging conditions and opportunity for growth (Holt, 2008; Polis et al., 2004). The effects of spatial variation in prey availability among migration routes are important for predicting the survival of fish stocks but are commonly understudied.

Pacific salmon (*Oncorhynchus* spp.) are a group of anadromous species that experience extreme spatial variations in ecosystem attributes during their early marine life, during which they typically migrate from estuaries to the coastal ocean and then to the open ocean. The first months after Pacific salmon enter the ocean have been identified as a particularly important life phase, with mortalities up to 80-90% estimated for tagged salmon (Welch et al., 2011). Growth and mortality during this phase may contribute significantly to the interannual variability and long-term population trends of salmon stocks (Friedland et al., 2000; Mueter et al., 2005). Although there are likely numerous factors that influence juvenile salmon survival during their early marine phase, correlative evidence suggests that feeding conditions play an important role (Beamish et al., 2012; Duffy and Beauchamp, 2011). Through impacts on growth, feeding conditions have the potential to affect vulnerability to predation (Gliwicz, 2003), ability to survive stressful ocean conditions (Lasker, 1978), and the body condition required to survive their first ocean winter (Beamish and Mahnken, 2001).

Recent research from North America's west coast has drawn attention to the potential influence of small-scale coastal marine conditions on juvenile salmon survival (Ferriss et al., 2014; Hunt et al., 2018; Journey et al., 2018; McKinnell et al., 2014). Outmigrating juvenile Fraser River sockeye (*Oncorhynchus nerka)* first enter the ocean into the stratified, comparatively warm, and highly productive Strait of Georgia basin (SoG, Fig. 1). Many of the juveniles migrate northwards through the SoG into the tidally mixed Discovery Islands (DI) and Johnstone Strait (JS) before reaching the productive Queen Charlotte Strait (QCS) (McKinnell et al., 2014). In the Trophic Gauntlet Hypothesis (TGH), McKinnell et al. (2014) proposed that strong tidal mixing in JS causes light limited primary production, leading to sparse prey fields for migrating juvenile sockeye salmon. Subsequent research has demonstrated that tidally mixed waters in JS are indeed characterized by poor foraging conditions, with a prevalence of small zooplankton (< 2 mm; Mahara et al. (2021)), corresponding with low foraging success for migrating juvenile sockeye salmon (James et al., 2020). Low insulin-like growth factor 1 (IGF-1) levels in JS compared to higher levels in the northern Strait of Georgia (NSoG), Queen Charlotte Strait and Queen Charlotte Sound supports an impact of these foraging conditions on juvenile salmon growth (Ferriss et al., 2014; Journey et al., 2018). Poor foraging conditions can be expected to reduce growth and increased mortality (Duffy and Beauchamp, 2011), especially when foraging opportunities before or after JS are also poor (James et al., 2020).

Relating growth proxies to environmental conditions needs to consider the integration time of the proxy used. IGF-1 is a biochemical proxy of growth that has been shown to integrate feeding conditions experienced over 4-14 days (Beckman et al., 2004), relatively long when assessing the response of fast migrating organisms over short distances (Duguid et al., 2018; Gabillard et al., 2006; Pierce et al., 2005). The need for precise handling when sampling in the field, and the difficulty in sampling from individuals smaller than 120mm also make the IGF-1 method difficult

to routinely apply in juvenile salmon research (Duguid et al., 2018; Ferriss et al., 2014). Another growth proxy commonly used in fish ecology and fishery research is RNA/DNA ratio (Clemmesen and Doan, 1996). The underlying principle of using the ratio of RNA to DNA is that the concentration of DNA per cell is constant, whereas the RNA concentration per cell varies with its anabolic activity. The RNA/DNA ratio integrates feeding history over a period of 1-5 days (Buckley et al., 1999; Clemmesen and Doan, 1996; Wright and Martin, 1985), which makes it useful for assessing fish response to rapid spatial changes in coastal migration habitat. RNA/DNA can be effectively sampled irrespective of individual size and can be sampled from individuals frozen in the field without any degradation.

Another variable that needs to be considered when assessing fish growth response is the available prey. Prey quantity is often considered one of the main drivers of growth, survival, and abundance of marine organisms (Bilton and Robins, 2011), however, prey quality also plays a critical role (Litz et al., 2017). Fatty acids (FA), and essential fatty acids (EFA) in particular, are useful indicators of both food quality and the nutritional condition of a fish (Tocher, 2003). EFAs are not synthesised *de novo* by vertebrates in sufficient quantities to meet their physiological demands (Xu et al., 2018). Rather, EFAs are primarily synthesised by phytoplankton and subsequently reach consumers through trophic transfer (Dalsgaard et al., 2003). Marine carnivorous fish, such as sockeye salmon, have only a limited ability to convert EFAs into important long-chained PUFAs such as docosahexaenoic acid (DHA; 22:6n-3), eicosapentaenoic acid (EPA; 20:5n-3), and therefore must be obtained from their diets (NRC, 2011). Studies have shown that DHA and EPA concentrations measured in fish tissue are similar to levels in the prey consumed (Jin et al., 2017). Total amounts of DHA and EPA are known to affect the development, growth, and survival of juvenile marine fish (Mourente et al., 1991) and are of major importance during periods of rapid growth (Jin et al., 2017) (Table 1). Low levels of DHA and EPA can lead to reduced growth, maldevelopment, reduced reproduction, and ultimately decreased survival

(Copeman and Parrish, 2002) (Table 1). Stored FAs, especially DHA and EPA, are also important when fish experience times of food limitation and starvation, for energy mobilization, hyperphagia, and for compensatory growth.

Experimental studies have shown that food quality changes, especially micronutrient limitation, and associated fatty acid changes lead to reduced RNA/DNA as lipid and protein metabolism is compromised when supply is limited (Boersma et al., 2008). The fatty acid composition integrates the feeding history over a period of approximately one week in juvenile Chinook salmon (Garzke et al. in rev), and using RNA/DNA and fatty acids in combination therefore provides a useful approach to identify changes in nutritional and physiological condition in organisms (Clemmesen, 1994; John et al., 2001; Malzahn et al., 2007; Paulsen et al., 2014; Xu et al., 2009)

In this study, we examine the response of juvenile sockeye salmon nutritional condition when migrating through complex oceanographic habitats in coastal British Columbia, Canada, including a region previously demonstrated to provide food poor conditions. We show that juvenile sockeye salmon nutritional condition responds rapidly to changes in foraging conditions. Furthermore, we show that the response and subsequent recovery are dependent on fish nutritional condition before entering food poor areas. Zooplankton biomass changes alone are not sufficient to explain changes in fish condition between years, and we suggest that the trophic gauntlet hypothesis needs to be extended by including prey quality, here measured with respect to fatty acids, in addition to quantity.

Materials and Methods

Ethics Statement

This study did not involve endangered or protected species and was carried out under the guidelines of the Canadian Council on Animal Care. Juvenile salmon were collected under DFO license number 'XR 42 2015' and 'XR 92 2016' with approval from UBC's Animal Care Committee (Protocol A19-0025). The study was carried out in compliance with the ARRIVE guidelines 2.0 (www.arriveguidelines.org).

Study location

Juvenile sockeye salmon were sampled at 6 locations between the NSoG and QCS (Fig. 1) in 2015 (6 May - 7 July) and 2016 (14 May - 6 July), in three regions along their outmigration route (Table S1). From south to north: the Discovery Islands (DI), JS, and southern QCS (Fig. 1). Based on oceanographic sampling (Dosser et al., 2021), the DIs have water properties of the northern SoG and JS has water properties of QCS. The JS sites were all located within JS proper, where water depth was > 300 m. The QCS site was located in water <150 m deep to the north of the JS sill. Assuming RNA/DNA turnover rates of 1-5 days, the RNA/DNA ratios of fish collected in the DI were expected to predominantly reflect their migration experience through the northern SoG. Given this and the NSoG water properties, we henceforth refer to the DI as NSoG. Based on RNA/DNA replacement rates, JS fish would reflect conditions in the DI-JS, and QCS fish would reflect the transition from JS to QCS. According to tagging data, the travel rates of juvenile sockeye between these regions are < 2 days for NSoG to DI, ca. 7 days from DI to JS, and ca. 4 days from JS to QCS (Furey et al., 2015; Johnston, 2020; Rechisky et al., 2018; Welch et al., 2011).

Juvenile Salmon Sampling

Fish were collected from a 6 m motorized vessel at distances of 5 - 60 m from shore, using a purse seine designed for manual deployment and retrieval (bunt: 27 x 9 m with 13 mm mesh; tow 46 x 9 m with 76 mm mesh) (Hunt et al., 2018). Captured fish were initially held alongside the

vessel in a submerged portion of the seine's bunt, allowing fish to swim without contacting the net and minimizing stress. Individual fish were transferred from the net by capturing them using a seawater-filled plastic jug with the end cut off. The fish were euthanized with MS-222 solution (250 mg L^{-1}) in a 532 mL plastic bag with a unique identifier and frozen using liquid nitrogen vapour in a dry-shipper (MVE Doble-47). Individuals were stored at -80°C until further dissection in the lab. A total of 1,233 juvenile sockeye were collected across all stations and years (weight: min. 2.8 g – 32.8 g (mean: 12.66g, median: 11.5g); length: min. 63mm – 145mm (mean: 106.43mm, median: 106mm)), and a maximum of 20 individuals at each seine event. Juvenile salmon were collected under Fisheries and Oceans Canada (DFO) license number 'XR 42 2015' and 'XR 92 2016' with approval from UBC's Animal Care Committee (Protocol A19-0025). Juvenile salmon sampling and handling were in accordance with the DFO and UBC Animal Care Committee guidelines.

Laboratory analysis

Five sockeye salmon were randomly selected from the total caught and were retained from each purse seine for a given site and day for further analysis of RNA/DNA and fatty acids (n=187). Before dissection fish were measured and weighed (mean weight = 9.07 g; range 1.27 – 38.85 g). White muscle tissue was collected from close to the dorsal fin for RNA/DNA analysis, and 400-600 mg of muscle tissue from close proximity to the dorsal fin for fatty acid analysis. Tissue samples were then returned to a -80 ^{o}C freezer until further analysis. In total, 187 juvenile salmon were processed across all regions and both years for fatty acids composition and RNA/DNA ratio (2015: n=87: NSoG (n=16), JS (n=34), QCS (n=37); 2016: n=100: NSoG (n=22), JS (n=37), QCS (n=41)).

RNA/DNA analysis

RNA/DNA was measured in crude muscle tissue homogenates using the non-specific, nucleic acid intercalating fluorescence dye RiboGreen (Gorokhova and Kyle, 2002). Nucleic acid quantification from white-muscle tissues followed a modified protocol by Caldarone et al (2006) and Clemmesen et al. (1993). For RNA and DNA extraction, 1% N-lauroylsarcosine (VWR, Cat. No. VWRV0719-500G) was added to the samples, followed by homogenization with glass beads (VWR Cat. No. 12621-154), shaken for 30 min in a Retsch cell mill. Samples were centrifuged for 10 min at 14,000 x *g* and the supernatant diluted to match the RiboGreen saturation range (1:20, 1:30, 1:50, 1:100 and 1:200). Triplicate aliquots from the diluted sample were added to a black, flat-bottom 96-well microtiter plate. Standard solutions of rRNA (*Eschericia coli* 16S and 23S rRNA, Quant-iT RiboGreen RNA assay Kit Thermo Fisher Scientific Cat. No. R11490) and DNA (calf thymus, VWR, Supp. No. MB-102-01100) were diluted to final concentrations between 0 µg/mL and 3 µg/mL. 1x RiboGreen was added to each well and incubated for 5 min. Fluorescence was measured on a VarioSkan Flash Microplate Reader (ThermoFisher Scientific; excitation = 500 nm, emission= 525 nm), with the signal representing the fluorescence of RNA and DNA combined. Ribonuclease A (bovine pancreas, Alpha Aesar, Cat. No. CAAAJ62232-EX3) was added to each well and incubated at 37°C for 30 min. Fluorescence of the digested samples were measured to determine the DNA only. The RNA concentration was calculated by subtracting the DNA fluorescence and DNA+RNA fluorescence. The RNA/DNA was calculated for each well, and samples where the coefficient of variation (CV) for either RNA or DNA concentration in triplicate wells exceeded 15% were excluded from further analysis following.

Fatty acid analysis

Fatty acid analyses were performed following a slightly modified version of the protocol described in Puttick et al. (2009) using a one-step fatty acid methyl ester (FAME) method. Wet weights of all muscle samples were measured, freeze-dried, and dry weight measured for calculations of moisture content. FAMEs were obtained by reaction in a solution of 2.0 mL of 3 N HCl in CH_3OH

(Sigma-Aldrich cat. #90964-500ML). Nonadecanoic acid (C19:0) was used as an internal standard (Abdulkadir and Tsuchiya, 2008). FAMEs were analysed with a gas chromatograph (Scion 436-GC, Scion Instruments Canada, Edmonton, Alberta, Canada) using a flame ionization detector (FID). FAMEs were separated on a 50 m column (Agilent J&W CP-Sil 88 for FAME, Santa Clara, California, USA) using hydrogen as the carrier gas. Peaks were identified against an external standard (GLC 455 and GLC 37 Nu-chek Prep, Inc., Elysian, Minnesota, USA.

Oceanographic sampling

CTD profiles were collected every one to two weeks to characterise the regional oceanographic conditions. CTD stations were in close proximity (0-2 km) to the salmon sampling stations (Fig. S1). An RBR maestro or a SeaBird 19plus V2 CTD was used (Halverson et al., 2017). For the purpose of this study, we present temperature (^{o}C) and salinity (psu) data integrated over the upper 10 m of the water column, where salmon were captured.

Zooplankton sampling

Zooplankton were collected approximately every fortnight in the NSoG, and every 4-7 days in JS and QCS (Fig. 1). A Bongo net (250 µm mesh size, mouth diameter 0.5 m) was deployed vertically from near-bottom or a maximum of 300 m depth to the surface. Filtered water volume during each tow was measured using a General Oceanics mechanical flowmeter. Collected zooplankton were preserved in 5% buffered formaldehyde-seawater solution. Zooplankton were identified to the lowest taxonomic level possible, counted, and taxon specific biomass was estimated by multiplying the mean dry weight (DW) of each species and stage by their abundance (Mahara et al., 2018). Zooplankton abundance and biomass data were integrated over the water column and presented as ind. m^{-2} and mg dry weight (DW) m^{-2}. Since the zooplankton samples were integrated over 0-300 m depth, they overestimate the available zooplankton biomass and abundance for juvenile salmon, given that they likely forage in the top 30 m. Therefore, for the

purpose of this study we only included zooplankton species that had been demonstrated to be consumed by the juvenile sockeye salmon in 2015 and 2016 (see species list Table S2, based on James (2019)).

Statistical analyses

Juvenile sockeye salmon length-weight residuals were calculated for all collected fish that were used for RNA/DNA and fatty acid analyses from both 2015 and 2016 (n=187 out of n=1,233) based on ln(weight) to ln(fork length) residuals from ordinary least squares linear regression (Reist, 2011). Positive length-weight residuals indicate that the salmon was heavier than expected for their fork length. Multivariate tests were performed using the R package vegan (Oksanen et al., 2017). Two-way ANOVA for unbalanced data (type II Sum of Squares) was used to individually test differences between years and regions for the response variables: temperature and salinity from CTD measurements, zooplankton biomass, length-weight residuals, RNA/DNA, total FA (TFA), saturated FA (SFA), monounsaturated FA (MUFA), polyunsaturated FA (PUFA), EPA, and DHA. If the interaction term was non-significant, the model was reduced by removing the interaction term and analyzed the main effects. Prior to this analysis, normal distribution was tested using a Shapiro-Wilk test and transformed data when necessary to achieve normal distribution (log for temperature and zooplankton biomass, and RNA/DNA). Year and sampling region were set as fixed explanatory factors. Tukey HSD tests were used for each significant ANOVA to distinguish region-to-region and year-to-year differences. Differences were deemed significant where $p < 0.05$.

Results

Overall, we found that RNA/DNA and length-weight residuals, supported an energetic deficit among migrating juvenile sockeye salmon in JS consistent with the TGH. We also found that that

in 2015 fish were in better nutritional condition when entering JS compared to 2016 despite higher zooplankton biomass in 2016. Additionally, fish sampled in 2015 at QCS showed a two-fold increase in RNA/DNA from JS whereas in 2016 the RNA/DNA only marginally increased from 5.06 to 5.41. The fatty acid profiles showed that NSoG fish had significantly higher initial FA concentrations in 2015 than 2016, although the entry FA concentrations were different in between both years, all FAs groups significantly decreased in JS in both years.

Juvenile salmon condition

Fish length-weight residuals differed significantly between years ($p < 0.001$, Table 2) but not between regions ($p=0.8$, Table 2). Overall, juvenile salmon were significantly heavier than expected based on their length in 2015, whereas in 2016 juveniles were lighter than expected (Fig. 2A). Juvenile salmon had significantly higher length-weight residuals in NSoG in 2015 compared to 2016 (Tukey HSD, $p <0.01$) and also showed significantly higher length-weight residuals in JS in 2015 than 2016 (Tukey HSD, $p<0.05$), although no difference was detected between both years in QCS (Tukey HSD, $p=0.14$, Fig. 2A).

Juvenile salmon RNA/DNA differed significantly by both region and year ($p <0.001$) and the interaction of year and region ($p = 0.02$, Table 2). Across both years, mean RNA/DNA was the lowest in JS (5.82 ± 0.41), the highest in QCS (9.01 ± 1.01), and intermediate in the NSoG (5.97 ± 0.38; Fig. 2B). However, RNA/DNA was significantly higher (Tukey HSD, $p > 0.001$) in 2015 (7.90 ± 0.61) than 2016 (4.96 ± 0.24). In the NSoG, juvenile salmon had a significantly lower (Tukey HSD, $p = 0.003$) RNA/DNA in 2016 (4.39 ± 0.28) than 2015 (8.15 ± 0.39) and exited QCS with significantly lower (Tukey HSD, $p = 0.001$) RNA/DNA in 2016 (5.41 ± 0.76) than 2015 (12.59 ± 1.27). In 2015, RNA/DNA decreased from the NSoG to JS (Tukey HSD, $p = 0.07$), and increased significantly from JS levels to QCS levels (Tukey HSD, $p < 0.001$). But in 2016, fish arrived in

NSoG with low RNA/DNA, and decreased further in JS and only increased slightly in QCS (Tukey HSD, $p = 0.98$). The increase in RNA/DNA from JS to QCS was ~ 83.98% in 2015 and ~6.47% in 2016. There was no significant correlation between fish RNA/DNA ratio and fish size ($R = 0.07$, $p = 0.34$, $df = 163$, Table S3). Genetic stock identification showed that 98% of the 2015 and 100% of 2016 were Fraser River salmon (Table S4).

Zooplankton

The biomass of zooplankton species that were known to be consumed by juvenile sockeye salmon in the study region was significantly higher ($F = 7.99$, $p < 0.01$; Table 2; Fig. 3A) in QCS (66.12 ± 10.08 mg dry weight (DW) m^{-2}, Tukey HSD: $p < 0.001$) than in JS (39.72 ± 4.02 mg DW m^{-2}) and the NSoG (37.84 ± 5.53 mg DW m^{-2}) (Table 2, Fig. 3A). Zooplankton biomass was significantly lower ($F = 11.14$, $p < 0.01$) in 2015 (37.50 ± 3.92 mg DW m^{-2}) than 2016 (57.93 ± 7.12 mg DW m^{-2}). Contrary to biomass, the abundance of zooplankton prey species for juvenile sockeye salmon (Table S2) was the highest in JS (346,755 ± 27,264 ind m^{-2}) and the lowest in the QCS (201,159 ± 16,478 ind m^{-2}), and NSoG (217,241 ind ± 39,960 ind m^{-2}, Table 2, Fig. 3B). Zooplankton abundance was significantly higher in 2016 ($F = 12.62$, $p <0.001$, 307,546 ± 26,822 ind m^{-2}) than 2015 (232,377 ± 26,822 ind m^{-2}; Table 2). Average individual zooplankton size calculated as total prey species biomass divided by total prey species abundance (Fig. S2) was significantly different between regions ($F = 8.148$, $p < 0.001$), with the smallest average zooplankton size in NSoG (2.52µg DW ind^{-1} ± 6.10) and largest size in QCS (5.74 µg DW ind^{-1} ± 11.13). There was no difference in average zooplankton size between NSoG and JS. The composition of available zooplankton prey species for juvenile sockeye salmon also differed considerably between the sampled regions. The NSoG and QCS had more large crustacean species (Amphipoda, Decapoda) than JS (dominated by Copepoda, Cirripedia; Fig. S3).

Nutritional status

Total FA and the FA groups SFA, MUFA, PUFA, DHA+EPA had a significant interaction term of year and region and showed comparable distribution patterns (Fig. 4A-E; Table 2). In 2015, juvenile salmon had the highest FA levels in the NSoG (Fig. 4 A-E) and showed a significant decrease in FA concentrations in JS and then slightly increased in QCS. In 2016, FA levels in NSoG fish were significantly lower than in 2015 ($p < 0.05$), increased slightly but not significantly in JS fish to levels similar to 2015 in JS, and remained constant in QCS fish (Fig. 4 A-E).

Discussion

Juvenile salmon encounter diverse ocean conditions during their early marine life. Research on juvenile Fraser River sockeye salmon has measured significant regional and temporal differences in growth (IGF-1) during their migration along the British Columbia Coast (Ferriss et al., 2014; Journey et al., 2018). However, the potential link between juvenile salmon growth and fish nutritional condition or oceanographic conditions was not explored. In this study, we explicitly linked the body condition of juvenile salmon (RNA/DNA) to their nutritional condition (fatty acids) and prey availability (zooplankton biomass). RNA/DNA and fatty acid data showed that body condition and nutritional condition of juvenile sockeye salmon changed rapidly over a ~ 120 km section of their migration route. These variations appeared to be partially due to differences in zooplankton availability, which was consistently low in Johnstone Strait (JS) supporting the Trophic Gauntlet Hypothesis (TGH) of McKinnell et al. (2014), but also to differences in prey quality. Importantly, the response of juvenile salmon to periods of starvation was affected by their condition upon entering poor foraging areas, as was their subsequent recovery when leaving food poor areas. Below we discuss the role of coastal oceanographic variation in determining fish condition, the cumulative effect of fish encountering a mosaic of habitats during migration, and

the importance of taking into account spatial variability in migration habitat when considering salmon response to climate change.

In our study system, the majority of outmigrating juvenile sockeye salmon travel northwards from the Fraser River through the Strait of Georgia (SoG) before entering a section of tidally mixed channels in the Discovery Islands (DI) and JS (Furey et al., 2015). In the SoG, surface waters are relatively warm, with low salinity and stratified, which is correlated with high phytoplankton biomass, high zooplankton biomass and high mean zooplankton size (James et al., 2020; Mahara et al., 2021). Ocean conditions become cooler and saltier as the fish move north into the DI, JS, and Queen Charlotte Strait (QCS). This change in ocean conditions is driven by the deep tidal mixing that brings cold and salty deep water to the surface (McKinnell et al., 2014). Phytoplankton biomass is low through the tidally mixed northern Discovery Islands and Johnstone Strait, leading to both low zooplankton biomass and smaller zooplankton size. This pattern is, however, reversed in QCS.

Across both years of this study, juvenile sockeye salmon RNA/DNA ratios supported the TGH, with high fish condition in the NSoG and QCS, and low condition in JS. The link between RNA/DNA and feeding success is supported by an extensive juvenile sockeye salmon stomach fullness analysis from the same region, which found high stomach fullness in the NSoG (Gut Fullness Index (GFI) = 1-2 %), low fullness in DI (GFI = 0.2 %), low fullness in JS (GFI = 0.48 %), and full stomachs in QCS (GFI = 3.5%) (James et al., 2020). Length-weight residuals showed a weaker response over the migration route, reflecting their longer integration times and highlighting the importance of more sensitive growth proxies, with faster turnover, to understand the response of fish to small scale regional changes in conditions. Notably, RNA/DNA ratios and length-weight residuals were significantly lower in 2016 than 2015, despite higher zooplankton biomass and abundance in that year, indicating that another factor was contributing to juvenile salmon

nutritional and body condition. The low RNA/DNA ratios in NSoG fish in 2016 were also reflected in low length-weight residuals, suggesting that feeding conditions may have been poor through most of the SoG in that year.

Corresponding with the observed changes in growth proxies, there were significant differences in juvenile sockeye salmon fatty acid profiles both spatially and between years. Stored lipids and fatty acids in fish tissues are important to mobilize energy from muscle, liver and viscera by FA β-oxidation processes during starvation phases (Halver and Hardy, 1989). During starvation, saturated FA (SFA) are the first FAs to be mobilized for ATP production, followed by monounsaturated FA (MUFA) and then polyunsaturated FA (PUFA) (Wen et al., 2006). In 2015, we detected a decrease of TFA, SFA, MUFA, and PUFA along the migration corridor, with lowest concentrations in JS, indicating that fish had oxidized FAs stored in white muscle tissue for ATP production. In 2016, juvenile salmon sampled in the NSoG had lower concentrations of TFA, SFA, MUFA, and PUFA than 2015, indicating that the nutritional condition of salmon was already very low when they reached the NSoG, with less FAs stored in white muscle tissue as an energy reserve for starvation periods. Two potential scenarios may have resulted in FA differences of NSoG salmon in 2015 and 2016: (1) food quantity was low in the Strait of Georgia and FA reserves for mobilizing energy had already been depleted, or (2) the food quality of the available food in SoG was lower in 2016. Zooplankton surveys showed that biomass was in fact significantly higher in 2016 than 2015 in the NSoG (Perry et al., 2021), suggesting that lower food quality (DHA + EPA) in 2016 was the driver of both lower fish FA content and RNA/DNA ratios in that year. As outlined in the introduction, low DHA and EPA availability in prey have important implications for fish condition, including reduced growth rates, visual maldevelopment with negative effects on hunting efficiency, an increase in FAs that are considered as pro-inflammatory (Table 1), and reduced capacity for compensatory growth (Ballantyne et al., 2003; Bou et al., 2017).

Compensatory growth is a phase of accelerated growth that follows a period of limited growth once non-limiting conditions are encountered (Ali et al., 2003). When fish re-enter non-limited food conditions, food intake increases, cell mitosis is accelerated, and food utilization is enhanced. Compensatory growth in fish can either result in partial, total or excess body mass recovery, and return to their normal growth rate values (Ali et al., 2003). RNA/DNA ratios in QCS from 2015 showed compensatory growth in juvenile salmon after passing through JS, where RNA/DNA were low and FA concentrations were lower due to needed energy mobilization. The RNA/DNA ratio almost doubled from JS to QCS in 2015. However, in 2016 when juvenile salmon already had low condition and depleted energy reserves in the NSoG, no compensatory growth was observed in in RNA/DNA ratios. Studies with Atlantic salmon have shown that compensatory growth success depends on the quality of food available (Johansen et al., 2001). Johansen et al. (2001) showed in an experimental study that Atlantic salmon were not able to fully compensate for growth loss on a lipid poor diet but were with a lipid rich diet. Turchini et al (2007) proposed the term 'lipo-compensatory growth' after showing that Murray cod were able to compensate starvation and refuel fatty acid storage when fed with high fatty acid diets.

As DHA and EPA are important biomolecules for growth and are only taken up through the diet, high prey quality or high availability of DHA and EPA while re-feeding is necessary to support needs during enhanced growth and mitosis. El-Sabaawi et al. (2009a) showed substantial variability in FA content among zooplankton species in the SoG. Large calanoid copepods, such as *Neocalanus plumchrus* and *Calanus marshallae*, and amphipods have higher DHA+EPA concentrations than other species. Our data showed that the JS zooplankton community was dominated by small copepod species, which tend to have low FA content (Hiltunen et al., 2021). Both the NSoG and QCS had a high abundance of larger copepods, euphausiids, and amphipods, with the latter two groups both having relatively large size (> 10 mm) and high DHA and EPA content (Hiltunen et al., 2021), i.e., prey was more nutritious in the NSoG and QCS than JS. This

observation supports prey quality as an important factor in the overall better nutritional health of fish in the NSoG and QCS. Furthermore, Galbraith et al (2017) showed that a higher proportion of southern copepod species (*Acartia sp.*, *Clausocalanus sp.*, *Calocalanus sp.*, *Ctenocalanus sp.*, *Mesocalanus sp.*, *Paracalanus sp.*) and chaetognath species (*Mesosagitta minima*, *Serratosagitta bierii*, *Parasagitta euneritica*) occurred in the NSoG in 2016, but more local zooplankton species such as *Neocalanus plumchrus* and *Euphausia pacifica* in 2015. This shift in species composition between 2015 and 2016 may account for the lower FA content of juvenile salmon in the NSoG in 2016.

The better body and nutritional condition of juvenile salmon leaving the NSoG in 2015 appeared to compensate for low food availability in JS. This supports the importance of good foraging conditions, with high quality food, for enduring periods of poor foraging conditions. Protracted periods of starvation may lead to not only slower recovery from starvation periods but may also have long-term impacts on the physiology of the fish (Nikki et al., 2004). Our data showed that fish with higher RNA/DNA ratio in 2015 had a higher recovery success in QCS than 2016. Starvation periods longer than 3-4 weeks can decrease digestive enzyme activity, inhibiting the ability of fish to sufficiently digest food when available again, resulting in overall lower body size and higher mortality (Abolfathi et al., 2012). This is highly relevant to juvenile salmon migrating through the BC coastal ocean. The migration of juvenile sockeye salmon through the DI and JS takes approximately 14 days, while time spent in the SoG is estimated to be between 30 and 50 days (Preikshot et al., 2012). Thus, as suggested by McKinnell et al (2014), anomalously poor foraging conditions in the SoG and/or QCS, coupled with typically poor foraging conditions in the DI and JS, may have an additive effect that impacts early marine survival of juvenile salmon. This study empirically links foraging conditions to the nutritional health of juvenile salmon and, further, provides evidence that low nutritional health can reduce recovery when entering good foraging areas.

FAs that are important to food quality are produced at the base of the food web by phytoplankton and transferred through trophic interactions to higher trophic levels. But also, FA composition varies between zooplankton species resulting in changes of FA availability with zooplankton species changes for predators such as juvenile salmon. Future environmental change leading to more abundant southern copepod species can directly affect juvenile salmon body and nutritional condition during their migration even though zooplankton biomass might not be affected. Therefore, it is important to consider food quality effects on salmon condition especially for making predictions or modelling approaches.

Conclusions

This study demonstrates that regional differences in prey quantity and quality have important implications for the growth and health of juvenile sockeye salmon during their early marine migration. Poor growth through Johnstone Strait supports the Trophic Gauntlet Hypothesis of McKinnell et al (2014), and reduction in health due to poor foraging conditions. Despite similar food quantity in the NSoG in 2015 and 2016, juvenile sockeye salmon emerging from SoG in 2016 had low fatty acid concentrations, potentially due to a higher abundance of low-quality southern zooplankton prey. The lower nutritional health of fish in 2016 had a negative effect on their recovery from starvation after passing though the DI-JS corridor where food availability is consistently low. We propose that the outmigration corridor for juvenile salmon should be defined as a series of interconnected gauntlets which may be differently affected by inter-annual variation driven by large-scale climate events. The recovery of juvenile salmon from regions with naturally poor foraging conditions may depend on the availability of prey in adjacent areas and be

negatively affected by extreme climate events and climate change that reduce the quality and quality of prey in historically productive areas.

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Author contributions

JG - Laboratory and Statistical analysis, Visualization, Writing and Editing; **BPVH** – Project Conceptualization, Methodology, Writing and Editing; **SG** – Project Conceptualization, Methodology, Field program, Investigation, Editing; **IF, BTJ** - Project Conceptualization, Methodology, Field program, Investigation, Editing **MK** - Project Conceptualization, Methodology, Field program, Investigation, Editing; **NM** - Field program, Zooplankton Data, Editing; **EAP** - Project Conceptualization, Methodology, Editing; **LR** - Project Conceptualization, Methodology, Field program, Investigation, Editing**.**

Additional Information

Supplementary information accompanies this paper

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Figure 1 Map of sampling locations (black points) for juvenile salmon. Encircled points indicate the sampling regions, blue point indicates Fraser River outflow, and blue arrows indicate the primary Fraser sockeye salmon migration route. Inset map shows the location of the study area on the British Columbia coast. Figure created with R package 'PBSmapping' (Schnute et al., 2021)[68].

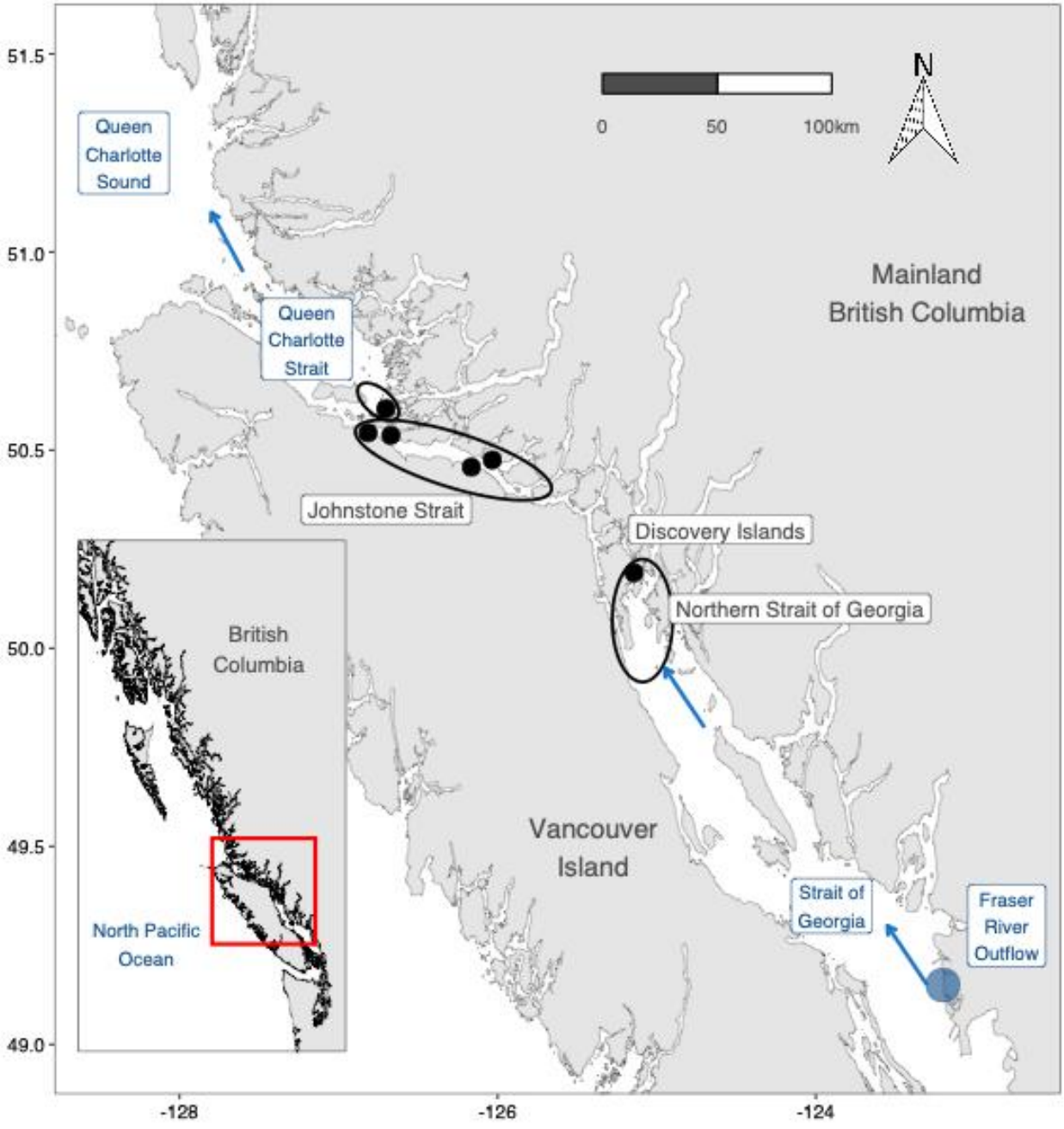


Figure 2 Annual and regional mean of A) length-weight residuals of fish sampled for RNA/DNA (black; n=162) and all fish sampled during the study (grey, n=1,233), B) RNA / DNA ratio. NSoG = northern Strait of Georgia; JS = Johnstone Strait; QCS = Queen Charlotte Strait. Error bars denote ± SE

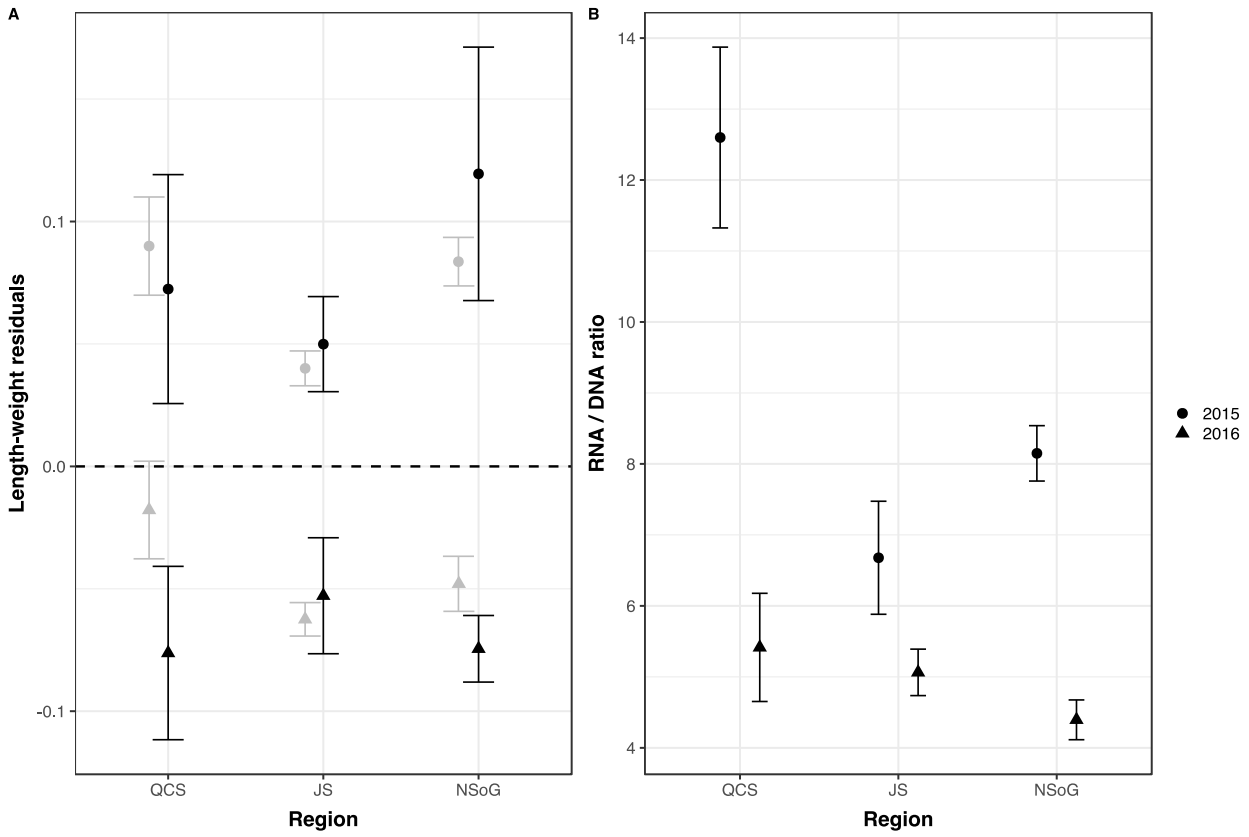


Figure 3 Annual and regional A) biomass and B) abundance of zooplankton > 1 mm in length. (error bars denote ± SE). NSoG = northern Strait of Georgia; JS = Johnstone Strait; QCS = Queen Charlotte Strait; 2015 is indicated by circles and 2016 by triangles.

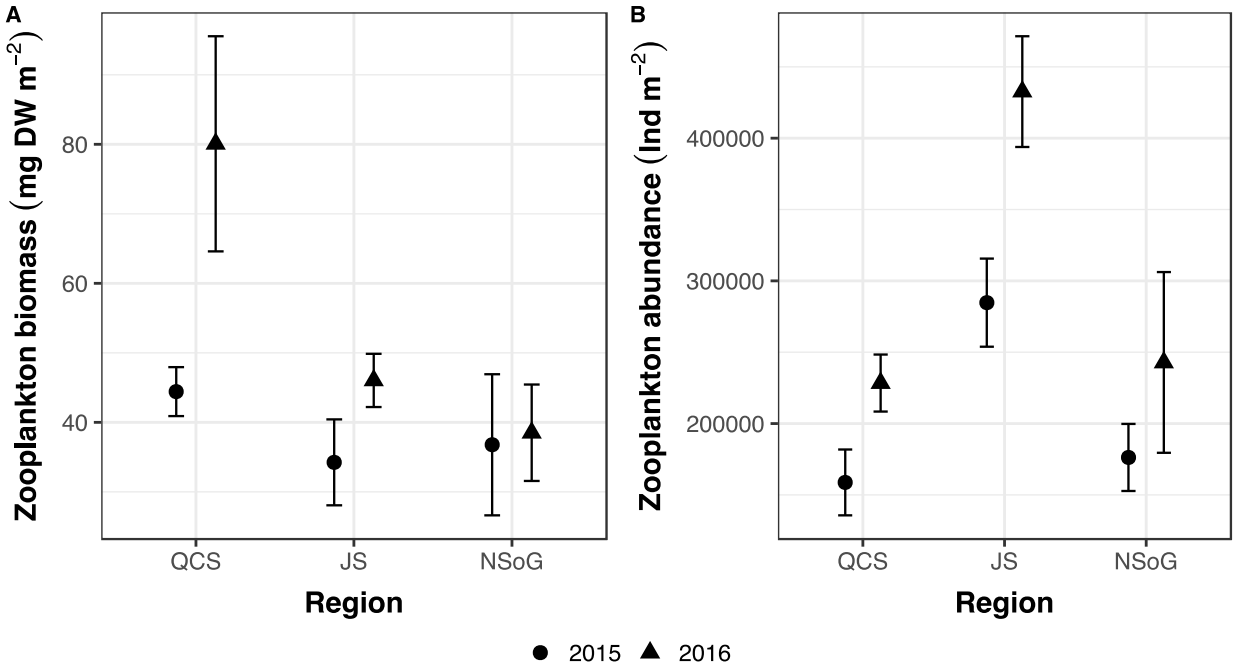
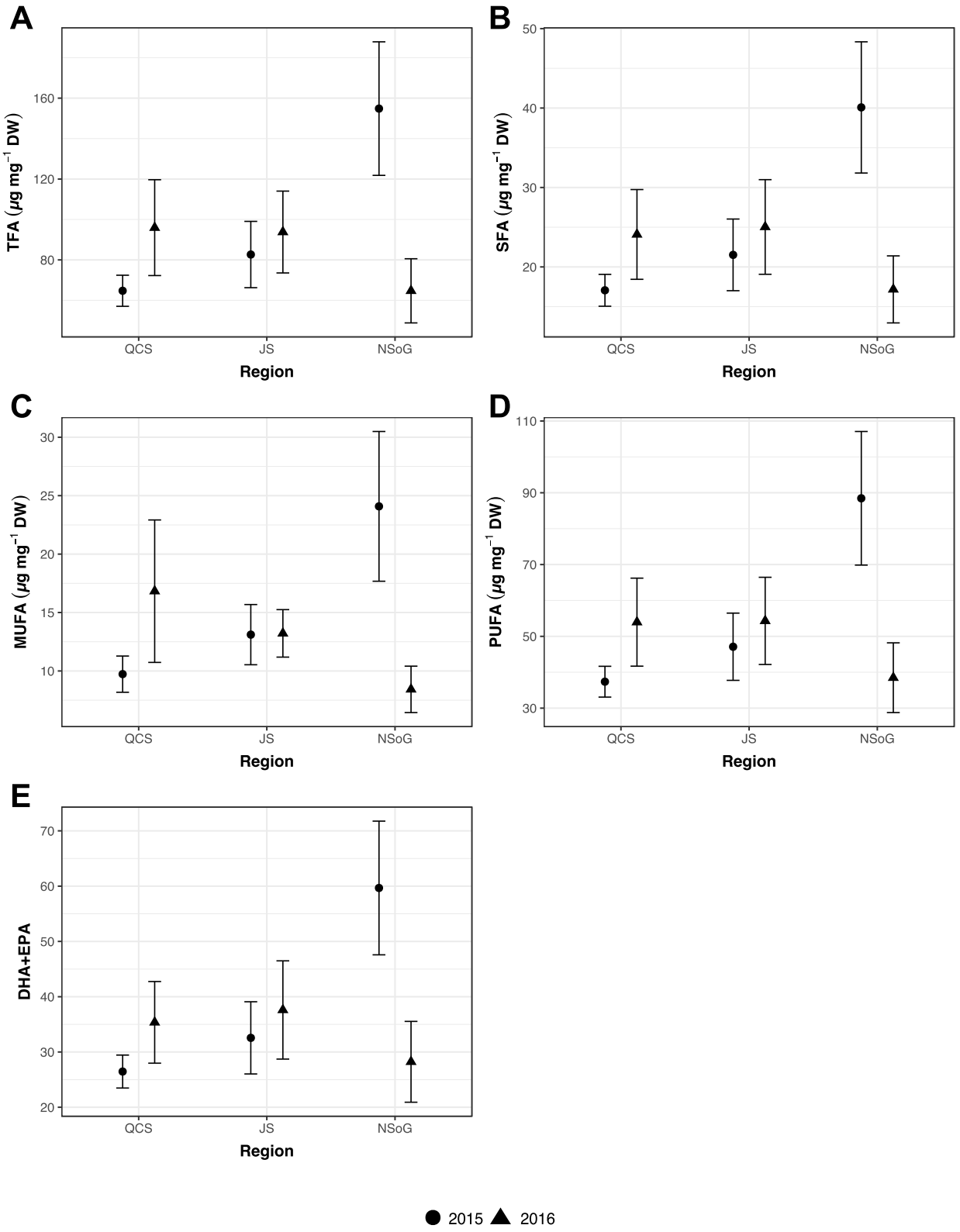


Figure 4 Annual and regional mean fatty acid concentrations (µg FA per mg dry weight of white muscle tissue) A) total fatty acids (TFA), B) saturated fatty acids (SFA), C) monounsaturated fatty acids (MUFA), D) polyunsaturated fatty acids (PUFA), and E) DHA + EPA (docosahexaenoic acid + eicosapentaenoic acid). Error bars denote ± SE. NSoG = northern Strait of Georgia; JS = Johnstone Strait; QCS = Queen Charlotte Strait.


A
TFA (μg mg⁻¹ DW)
160
120
80
QCS
JS
NSoG
Region
B
SFA (μg mg⁻¹ DW)
50
40
30
20
QCS
JS
NSoG
Region
C
MUFA (μg mg⁻¹ DW)
30
25
20
15
10
QCS
JS
NSoG
Region
D
PUFA (μg mg⁻¹ DW)
110
90
70
50
30
QCS
JS
NSoG
Region
E
DHA+EPA
70
60
50
40
30
20
QCS
JS
NSoG
Region
2015
2016

769