



Running the trophic gauntlet: Empirical support for reduced foraging success in juvenile salmon in tidally mixed coastal waters

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Abstract

The productivity of Fraser River sockeye salmon has declined in recent years, with 2019 being the lowest return on record. The cause of the decline is still not fully understood; however, bottom-up drivers and trophic interactions during the early marine migration are considered to be important contributing factors. McKinnell et al. (Fisheries Oceanography, 23, 2014 and 322) developed a “trophic gauntlet hypothesis,” proposing that low biological productivity leads to an energy deficit from poor foraging opportunities in migrating salmon. When combined with poor foraging conditions in typically productive waters elsewhere on the migration, low marine survival may result. Our study examined prey availability and stomach fullness of juvenile sockeye salmon along the 120 km stretch of the coastal migration through the Discovery Islands and Johnstone Strait to determine whether this section of the migration is indeed food limited. We observed low stomach fullness throughout tidally mixed waters, providing empirical support for the trophic gauntlet hypothesis. Zooplankton abundance was high in these regions so it appeared that unfavourably small prey size may have been the cause of low foraging success. We also observed foraging hotspots at both ends of the gauntlet, indicating that such areas may be key feeding grounds for migratory salmon.

KEYWORDS

feeding, juvenile, migration, mixing, salmon, trophic dynamics, zooplankton

1 | INTRODUCTION

The survival of Fraser River sockeye salmon (*Oncorhynchus nerka*) has become increasingly variable in the last ten years, with the highest (2010) and lowest (2019) returns in recorded history observed (Pacific Salmon Commission, 2019). In 2009, the number of recruits per spawner fell below the replacement level for the first time. Given the immense ecological, social and economic importance of this species, this precipitated a judicial inquiry into the cause of declines (Cohen, 2012a, b, c). One of the key findings was that the

primary causes of long-term declines were likely occurring during the early marine migration, and further research into drivers was recommended.

Juvenile sockeye salmon emerge from the Fraser River into the marine environment in the spring. Over 90% of juveniles migrate north through the productive waters of the Strait of Georgia (SoG), entering the inside passage between Vancouver Island and mainland British Columbia (BC), to continue up the coast to the Gulf of Alaska (Clark et al., 2016; Welch et al., 2011). Survival in the inside passage, particularly in the Discovery Islands (DI) and Johnstone Strait (JS), is

lower than freshwater survival (Clark et al., 2016). Waters from the SoG flush through the narrow channels and steep-sided inlets of the DI resulting in some of the strongest tidal rapids in the world (Lin & Fissel, 2014) and highly mixed waters in the northern and western passages. JS lies to the northwest and consists of one main channel that is fully vertically mixed, generating light-limited, high nutrient, low chlorophyll conditions and is connected in the north to the stratified and more productive waters of Queen Charlotte Strait (QCSt) and Queen Charlotte Sound (QCS) (Thomson, 1981).

In 2014, McKinnell, Curchitser, Groot, Kaeriyama and Trudel suggested that this tidally mixed region of the BC coast may play an instrumental role in the early marine survival of northward migrating sockeye salmon. They proposed a “trophic gauntlet hypothesis” (TGH), which postulates that juvenile salmon experience an energy deficit during their migration through JS and that the survivors through this region would be those with sufficient energy reserves. Furthermore, recovery from this challenge would depend on their ability to find adequate food upon exiting the gauntlet. In the winter of 2006–2007, unusually high snowpack accumulation led to high freshwater discharge to the coastal ocean in spring 2007 and the development of a deep, stable and low-density surface layer. Paired with anomalous wind patterns, this stable low-density surface layer was retained in QCSt/QCS and would have resulted in reduced phytoplankton production in this area. McKinnell, Curchitser, Groot, Kaeriyama, and Trudel (2014) hypothesized that the cumulative effects of poor foraging conditions in JS with little opportunity to recover in QCSt/QCS caused the low returns in 2009.

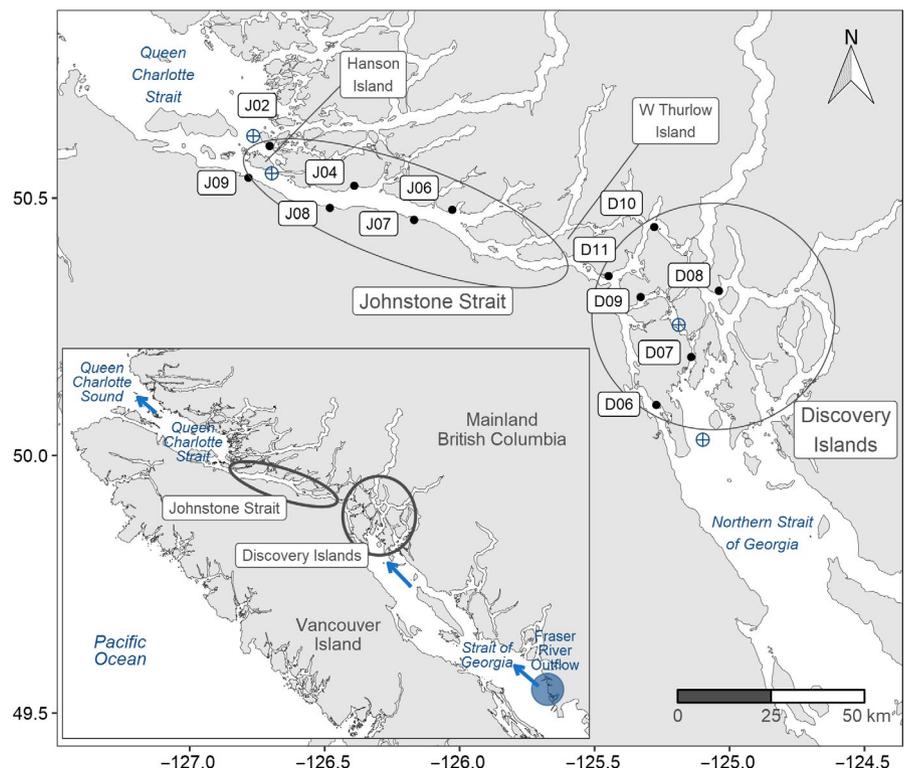
Since the TGH was developed, only one study has set out to test it empirically. Journey, Trudel, Young, and Beckman (2018) measured the differences in insulin-like growth factor-1 (IGF1) in five salmon

species along their coastal migration route in BC. Growth was lower in both JS and QCSt than in the northern SoG (NSoG), lending support to the TGH. However, that study did not resolve which factors were responsible for reduced growth. The foundation for the TGH is an assumed sparse prey field in JS. Here, we specifically examined prey availability and stomach fullness of sockeye salmon along the inside passage through the DI and JS. We hypothesized that prey abundance and biomass and sockeye stomach fullness would be lower in these regions of intense mixing than in the seasonally productive waters of the SoG and QCSt.

2 | METHODS

We collected juvenile sockeye salmon from twelve sites across the DI and JS region, positioned to capture the major migratory routes (Figure 1). JS was defined as the region between Hanson Island in the west and West Thurlow Island in the east, and the DI as the archipelago between West Thurlow Island and the NSoG. West Thurlow Island is the approximate location of a permanent density front that limits water exchange between the two regions (Thomson, 1981). Hakai Institute's Juvenile Salmon Program sampled each site once between June 1 and June 9, 2015 (Table 1). We selected this period to correspond with the peak sockeye outmigration through the study area (Johnson, Gan, Janusson, & Hunt, 2018). Salmon were collected using a hand-operated purse seine deployed from a small open boat. A detailed description of the sampling methodology can be found in Hunt et al. (2018). From each seine, 10 sockeye were sampled. In the laboratory, we extracted and weighed the stomach contents and calculated a gut fullness index (GFI) by dividing the weight of

FIGURE 1 Map of twelve juvenile salmon seining sites (labelled black dots) distributed across each migratory route through the Discovery Islands and Johnstone Strait and four zooplankton sampling sites (blue crosshairs) distributed across the northern Strait of Georgia, Discovery Islands, Johnstone Strait and Queen Charlotte Strait. Inset map of juvenile Fraser River sockeye salmon migratory route north from the Fraser River along the BC coast [Colour figure can be viewed at wileyonlinelibrary.com]



Region	Site	Latitude	Longitude	Date	Temp (°C)	Sal (psu)
DI	D06	50.098	-125.271	June 4	12.3	28.2
	D07	50.191	-125.142	June 5	18.2	25.4
	D08	50.319	-125.040	June 4	16.8	19.3
	D09	50.308	-125.329	June 5	11.8	28.4
	D10	50.444	-125.279	June 5	10.7	28.4
	D11	50.349	-125.448	June 1	11.0	29.0
JS	J06	50.478	-126.028	June 7	9.9	28.6
	J07	50.457	-126.169	June 6	10.0	28.7
	J04	50.527	-126.387	June 8	10.0	28.8
	J08	50.480	-126.413	June 7	10.8	28.5
	J09	50.539	-126.782	June 7	11.7	28.7
	J02	50.603	-126.702	June 9	9.5	29.1

TABLE 1 Environmental parameters measured at fish collection sites in the Discovery Islands (DI) and Johnstone Strait (JS) in June 2015. Temperature and salinity are averages of the surface and 1 m measurements collected with a YSI

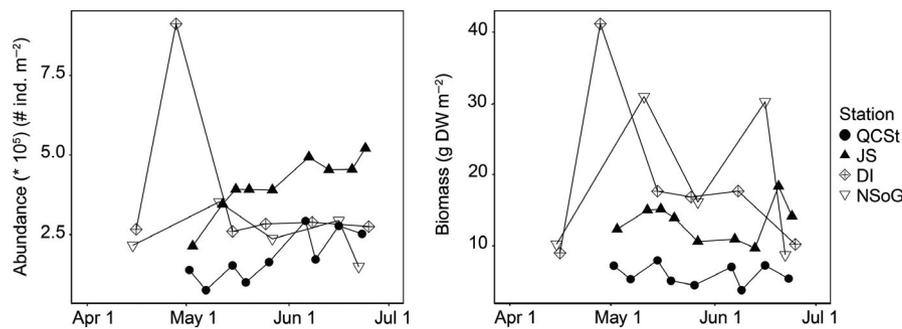


FIGURE 2 Abundance and biomass (dry weight - DW) per square metre calculated from vertical zooplankton tows conducted in the Northern Strait of Georgia (NSoG), Discovery Islands (DI), Johnstone Strait (JS) and Queen Charlotte Strait (QCSt) in 2015. Points represent data from a single net tow at each station

the stomach contents by the weight of the fish and converting to a percentage. A YSI sensor measured temperature and salinity at 0 and 1 m depth at the locations of fish capture.

Hakai Institute's Oceanography Program sampled zooplankton weekly to biweekly from late April to late June 2015. They conducted vertical tows from 5 m above the bottom, or a maximum depth of 300 m, using a 0.5 m diameter bongo net with a mesh size of 250 μm (Figure 1). A detailed description of the methods can be found in Mahara, Pakhomov, Jackson, & Hunt, 2019. Zooplankton were enumerated and weighed to the nearest mg. Data are presented as ind. m^{-2} and $\text{mg dry weight (DW) m}^{-2}$. We compared values between regions using the Kruskal-Wallis test, followed by pairwise Mann-Whitney U tests with a Bonferroni correction factor.

3 | RESULTS AND DISCUSSION

Water properties in each region were distinct from one another, with greater spatial variability in the DI (Table 1). The stations D07 and D08 in the southeast had the highest temperature and lowest salinity, indicative of stratification. The remaining sites had low temperature and high salinity indicative of deep tidal mixing. These observations are consistent with previous oceanographic observations in the region (Thomson, 1981).

Zooplankton abundance and biomass were significantly different between regions (Kruskal-Wallis, $p < .05$). Counter to our hypothesis,

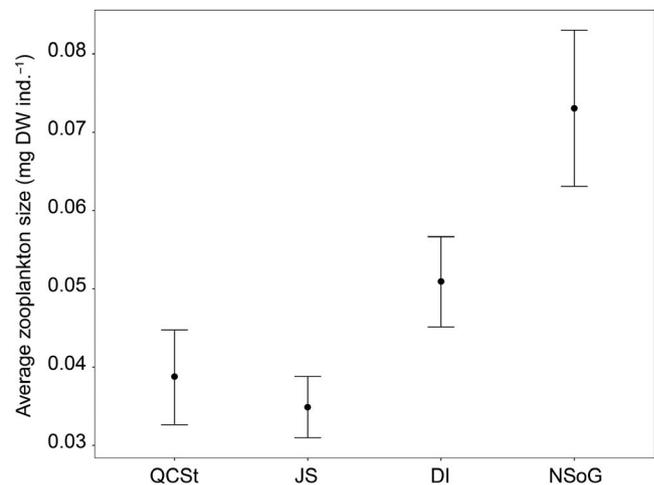


FIGURE 3 Zooplankton size (mg DW ind.^{-1}) averaged for each region over the 2015 sampling period (April-July). Bars represent ± 1 standard error. See Figure 1 for zooplankton station positions

total abundance was significantly higher in JS and lower in QCSt than in all other regions (Mann-Whitney U test, Bonferroni corrected $\alpha < 0.05$) (Figure 2). Total biomass, however, was highest in the NSoG and DI and while both JS and QCSt had lower biomass, only QCSt was significantly lower (Mann-Whitney U test, Bonferroni corrected $\alpha < 0.05$). The discrepancy between abundance and biomass in JS suggests that this region had a high abundance of small zooplankton.

Indeed, there were large regional differences in the size of potential zooplankton prey. The average zooplankton size was largest in the NSoG and smallest in JS and QCSt (Figure 3). Previous studies show that juvenile salmon prefer prey > 1.4 mm in size (Craddock, Blahm, & Parente, 1976; English, 1983), while data for this region demonstrate a preference of juvenile sockeye salmon for prey > 2 mm (James, 2019). The size distribution of potential zooplankton prey was therefore more favourable for juvenile sockeye salmon in the NSoG and less favourable in JS and QCSt.

The GFIs were low throughout the DI and JS, with the notable exception of the southern and northernmost sites where GFIs were significantly higher (Figure 4). Excluding these two sites (due to their proximity to the more productive stratified waters beyond the study area), the median GFI was 0.20% for the DI and 0.48% for JS. These values are indicative of poor foraging conditions throughout the well mixed regions and were lower than previous values measured elsewhere in coastal BC. In the NSoG, juvenile sockeye salmon collected during the summers of 2009 and 2010 had a median GFI of 1.78% (Price, Glickman, & Reynolds, 2013), while those collected along the north coast of BC in the summers of 2000–2002 had a median GFI of 1.18% (Brodeur et al., 2007) (Figure 4). In addition, surveys from earlier years reported average GFIs ranging from 0.73% to 1.15% in the SoG in the summers of 1975 and 1976 for chinook (*O. tshawytscha*), coho (*O. kisutch*) and chum (*O. keta*) (Healey, 1980). Thus, the GFIs that we measured in the well mixed DI and JS regions were on the extreme low end of values previously reported for juvenile salmon in the northeast Pacific and support poor foraging success as the driver of low juvenile salmon growth in this region (Journey et al., 2018).

We suggest that the size and distribution of zooplankton in these mixed waters may be driving the differences in foraging success between regions. It is known that juvenile salmon are size-selective foragers (Bollens, vanden Hooff, Butler, Cordell, & Frost, 2010; Brodeur, 1989). However, the average prey size decreased as the

juveniles migrated north from the NSoG. Tidal mixing may generate a sparsely distributed prey field of smaller organisms, which would require greater time and energy spent foraging, and lead to lower growth (LeBrasseur, 1969). Reduced foraging success may lead to longer foraging times and reduced swimming performance, particularly after periods of starvation, both of which may increase vulnerability to predation (Illing, Moyano, Berg, Hufnagl, & Peck, 2018; Litz, Miller, Copeman, & Hurst, 2017). Indeed, Clarke et al. (2016) used telemetry to demonstrate reduced survival for juvenile salmon migrating through the DI and JS region.

Juvenile sockeye have a median travel time of 11 days through the DI and JS (Chandler, King, & Boldt, 2017). This is sufficient time for significant weight loss and reductions in growth rates and overall size, even after returning to healthy foraging conditions (Bar, 2014; Nikki, Pirhonen, Jobling, & Karjalainen, 2004). Our data therefore provide empirical support for the TGH, whereby juvenile sockeye salmon may not be consuming enough prey to meet their basic metabolic needs and thus experience an energy deficit during their passage through JS (McKinnell et al., 2014). Furthermore, our study measured the full geographic extent of the trophic gauntlet, demonstrating reduced foraging success from the first tidal rapids at the southern end of the DI to the sill at the western end of JS where it connects with QCSt, a distance of approximately 120 km.

Our study recorded exceptionally high foraging success at the southern and northernmost sites. These sites are situated where the stratified waters of the NSoG and QCSt meet the well mixed waters of the DI and JS, respectively. Throughout the world's coastal oceans, convergence of thermally stratified and mixed waters creates "fronts," where productivity is notably higher than in the surrounding waters (Boyd, 1973; Perry, Dilke, & Parsons, 1983; Simpson & Hunter, 1974). Plankton accumulate along these fronts (Franks, 1992; Genin, Jaffe, Reef, Richter, & Franks, 2005), and the ability to locate and use prey aggregations can be essential for higher trophic

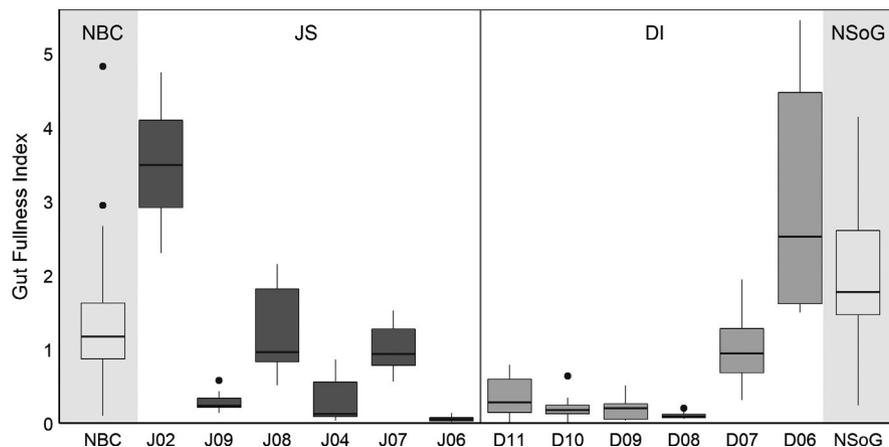


FIGURE 4 Median and interquartile values of gut fullness indices (GFIs) across four regions from south to north: northern Strait of Georgia (NSoG), Discovery Islands (DI), Johnstone Strait (JS) and northern British Columbia (NBC). Data from our research in June 2015 are shown with filled box plots (DI and JS) while those from other studies are shown in the grey bands on either side of the plot. Data for the NSoG are adapted from Price et al. (2013) and show GFIs for juvenile sockeye collected in late May 2009 and early June 2010 ($n = 23$). Data for NBC are adapted from Brodeur et al. (2007) and show GFIs for juvenile sockeye collected from May to July, 2000–2002 ($n = 65$). Box plot whiskers represent the farthest non-outlier values from the median. Outliers are plotted as dots

levels (Anraku, 1975; Mohammadian, Hansson, & De Stasio, 1997). Our data clearly showed enhanced foraging success of migrating juvenile salmon in such regions relative to those captured in other regions (Figure 4). It is plausible that these foraging hotspots enable them to prepare for and recover from passage through the trophic gauntlet.

In conclusion, despite no decrease in prey density in mixed waters, the availability of suitably sized prey likely presented poor foraging conditions for juvenile salmon in both the DI and JS. The high biomass of small zooplankton in tidally mixed regions, despite low primary production, likely reflected a combination of accumulation through the interaction of local circulation and diel vertical migration and high predation on larger zooplankton by zooplanktivorous fish and invertebrates (N. Mahara, E. A. Pakhomov, H. Dosser, & B. P. V. Hunt, unpublished data). The low stomach fullness measured across these regions provides empirical support for the TGH and is consistent with, and likely the cause of, low growth performance measured throughout this area. The impacts of lower foraging success and growth throughout this region are expected to be of concern in years when conditions in the SoG and QCSt are poor for juvenile salmon survival. Furthermore, foraging hotspots at the interface between mixed and stratified waters may provide important preparation and recovery points for passage through poor foraging environments.

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CONFLICT OF INTEREST

The authors certify that they have no conflicts of interest relating to the subject matter of this manuscript.

AUTHOR CONTRIBUTIONS

BPV Hunt and EA Pakhomov contributed to the development of the research programme concept and design. SE James, EA Pakhomov and BPV Hunt contributed to the project development and to writing the initial draft. BPV Hunt managed the Juvenile Salmon Program. SE James contributed to the collection of juvenile salmon data and performed all laboratory and data analyses related to salmon diets. N Mahara contributed to the collection of zooplankton data and related laboratory and data analyses. All authors participated in the writing and revision of the final manuscript and have provided approval for publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Juvenile Sockeye Diets Hakai 2015–2016 repository in the Hakai Metadata Catalogue at <https://doi.org/10.21966/3s9g-w013>.

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