



Migration timing affects the foraging ecology of Fraser River sockeye salmon stocks in coastal waters of British Columbia, Canada

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ABSTRACT: Coastal migrations of juvenile Pacific salmon *Oncorhynchus* spp. have evolved to take advantage of optimal ocean foraging conditions and maximize early marine growth and survival. The growth and survival of salmon during the early marine period is affected by both the diversity of encountered coastal habitats, with varying productivity and plankton phenology, and stock-specific migration timings that determine the match–mismatch with their prey. In 2015 and 2016, we investigated temporal and spatial patterns in environmental conditions and zooplankton prey as well as diets and stock composition of juvenile Fraser River sockeye *O. nerka* during their outmigration through the tidally mixed Discovery Islands and Johnstone Strait in British Columbia (Canada). Three groups of sockeye diet profiles reflected variations in environmental conditions and prey communities. First, in the Discovery Islands, earlier migrating stocks primarily encountered and foraged on small, energy-poor zooplankton prey (barnacles and cladocerans). Second, later migrating stocks foraged mainly on larger, more energy-rich copepod and larvacean prey. And third, in the highly mixed waters of Johnstone Strait, large energy-rich calanoid copepods dominated diets irrespective of migration timing and year. Foraging success was typically low throughout the areas sampled and across the migration period, which may amplify the importance of prey nutritional quality. Our findings highlight the importance of accounting for spatial and temporal differences in foraging environments for migrating species such as juvenile salmon. Furthermore, we demonstrate that the timing of stock migration affects the foraging conditions experienced.

KEY WORDS: Pacific salmon · Migration · Diet · Phenology · Zooplankton · Stock composition

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1. INTRODUCTION

Juvenile Pacific salmon *Oncorhynchus* spp. experience high mortality in the early marine phase (Bax 1983, Percy 1992), with survival strongly related to body size (Friedland et al. 2000, Moss et al. 2005). Early marine growth is fuelled by the quantity and quality of prey consumed (Farley et al. 2007). Therefore, early marine foraging conditions can have com-

pounding effects that propagate through the species' life cycle to affect overall survival and productivity (Healey 2011). The coastal habitats through which juvenile salmon navigate are highly variable over small spatial scales in physical, chemical, and biological properties, impacting the quantity and quality of the prey field they encounter (Thomson 1981, Brodeur et al. 2007). Coastal habitats also vary over time, with seasonal fluctuations in environmental

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conditions driving the phenology of salmon prey communities from the bottom up (Mahara et al. 2019). Therefore, the timing of the juvenile salmon migration directly determines the encountered environmental conditions and prey fields. Migration timing and routes vary considerably among stocks from the same system, potentially driving stock-specific success or failure (Scheuerell et al. 2009, Wilson et al. 2021). Spatial, temporal, and stock-specific variability of early marine foraging ecology have typically been studied in isolation. However, their interaction needs to be considered when assessing the cumulative effects of foraging ecology on early marine survival.

Every spring, sockeye salmon *O. nerka* from the Fraser River embark on a northwards migration to the Gulf of Alaska through highly dynamic coastal waters (Tucker et al. 2009). The majority of Fraser River sockeye spend 20–50 d transiting the stratified and productive Strait of Georgia before taking the northern route through the tidally mixed Discovery Islands and Johnstone Strait (Welch et al. 2011, Preikshot et al. 2012, Stevenson et al. 2019), hereafter referred to as the tidally mixed zone (TMZ). Migration through this region peaks in late May or early June (Johnson et al. 2019). The transition between the Discovery Islands and Johnstone Strait is marked by a frontal zone, with stark differences in oceanographic properties on either side (Dosser et al. 2021). Salmon pass from estuarine-like, warmer, and less saline waters to oceanic, cooler, and more saline waters. Stomach fullness and growth are lower across this section of the migration than elsewhere along the coast and it is hypothesized that this may be related to poor foraging conditions (Journey et al. 2018, James et al. 2020). The migration continues northward into the productive and more stratified waters of Queen Charlotte Sound, the turbulent waters of Hecate Strait, and along the north coast of British Columbia (BC). Thus, during the first months at sea, juvenile sockeye salmon experience highly contrasting ocean conditions.

Juvenile salmon not only experience spatial variability along their early marine migration but also temporal variations in ocean conditions. Salmon that undertake migrations that overlap with seasonal peaks in prey abundance have higher survival rates (Chittenden et al. 2010, Satterthwaite et al. 2014). Zooplankton are the primary prey of juvenile sockeye, and their phenology is synchronized with ocean temperatures and spring bloom timing (Mackas et al. 2012). Governed by environmental conditions, zooplankton phenology can be as diverse as the coastal

landscape itself. Therefore, migration timing is a key determinant of the match between salmon and their prey across each section of their coastal migration. Temperate marine ecosystems are characterized by a spring increase in primary production that leads to an increase in zooplankton biomass and a shift in zooplankton community composition from smaller larval stages and herbivores to larger adult stages and omnivores and carnivores (Harrison et al. 1983, Tommasi et al. 2013, Mahara et al. 2019). Thus, both the abundance of zooplankton and their nutritional quality change over the course of the salmon's early marine migration period (Carr-Harris et al. 2018).

There are 63 genetically and geographically distinct stocks of sockeye salmon in the Fraser River watershed, each with its own migration pattern (Beacham et al. 2004). Both migration timing and duration are highly variable among populations of the same species (Wilson et al. 2023). Migration characteristics are influenced by the life history of the stock (e.g. freshwater residence time), the distance between rearing waters and points of ocean entry, and body size (Burgner 1991, McGlaufflin et al. 2011, Freshwater et al. 2019). Younger ages (i.e. age-0 sockeye smolts) initiate their marine migration later than older juveniles (i.e. age-2 sockeye smolts). In addition, larger juveniles tend to migrate to the sea more rapidly than smaller juveniles (Freshwater et al. 2019). However, environmental processes can also generate interannual variation in migration dynamics (Kovach et al. 2013). As a result, there is considerable diversity in the marine migration initiation and duration across Fraser River sockeye stocks, leading to unique trends in marine growth and survival.

The objective of this study was to explore the changes in foraging conditions encountered by juvenile Fraser River sockeye salmon stocks over their outmigration through a tidally mixed section of their coastal migration known to pose a trophic challenge. We expected that prey fields and salmon diets would differ on either side of an oceanographic front and would change over the course of the migration. Specifically, we expected to see more high-quality prey items later in the migratory period, corresponding to the phenology of the zooplankton community pursuant to the spring bloom. In addition, we anticipated that the stock of origin would influence migration timing and, therefore, foraging success. We examined juvenile sockeye salmon collected from the TMZ over 2 yr and used genetic stock identification to determine stock-specific juvenile run timing, which we then related to oceanographic conditions and the phenology of their prey. This study provides

new insights into the foraging ecology of juvenile salmon in mixed coastal waters and the relevance of migration timing in determining the early marine survival of a culturally, commercially, and ecologically valuable species.

2. MATERIALS AND METHODS

2.1. Fish collection

Juvenile sockeye salmon were collected throughout the TMZ in 2015 and 2016 as part of the Hakai Institute Juvenile Salmon Program (Hunt et al. 2018), a long-term program that monitors the early life history of juvenile salmon in coastal BC (Fig. 1). Since 2015, the program has sampled the Fraser River juvenile salmon outmigration through the Discovery Islands and Johnstone Strait each year between May and July. Salmon are caught using a modified purse seine (bunt: 27 × 9 m with 13 mm mesh; tow: 46 × 9 m with 76 mm mesh) deployed by hand from 6–8 m twin-outboard motorized vessels that fish to a depth of 9 m. Schools of migrating salmon are located and captured at the surface by searching for signs of sur-

face activity between dawn and early afternoon. After the seine has been set, the net is hauled in and the bunt brought alongside the boat so that a sample of the school can be taken (up to 30 sockeye and 10 individuals of other salmon species). The school size and species composition are estimated before being released. The fish brought on board are euthanized with a lethal dose of tricaine methanesulfonate (MS-222), measured for weight and length, and a fin clip is taken from one of the caudal lobes for genetic stock identification. Fish are then transferred to a cryogenic dry-shipper and flash-frozen at -196°C for transport to the laboratory (UBC Animal Care Committee Protocol A19-0025, Fisheries and Oceans Canada license number XR 63 2019). Fin clips are stored on Whatman paper and sent to the Molecular Genetics Lab at the Pacific Biological Station in Nanaimo for genetic stock identification.

Juvenile sockeye salmon migration timing was determined for the Discovery Islands and Johnstone Strait using data from all stations sampled (approximately weekly) in these 2 regions in 2015 and 2016 (Johnson et al. 2022; Fig. 1). Depth at the sites ranged from ~10–25 m. Of the total captures, a subset of 2547 fish were analyzed for genetic stock identifica-

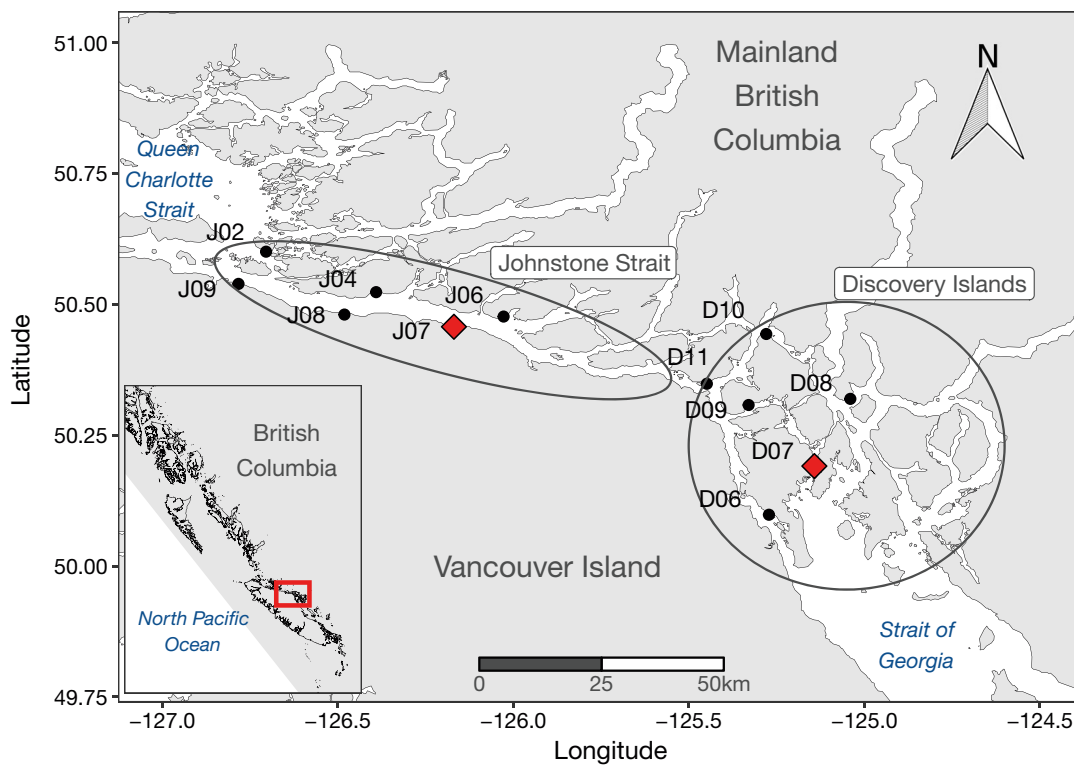


Fig. 1. Salmon sampling locations in the tidally mixed zone between the Strait of Georgia and Queen Charlotte Strait. Diet analyses were conducted with samples from D07 in the Discovery Islands and J07 in Johnstone Strait (red diamonds), exclusively. Sites were sampled weekly throughout the salmon migration in 2015 and 2016

tion (see Table 1). To characterize salmon diets, we narrowed our focus to 2 sampling locations from within the TMZ: one in the seasonally stratifying southern extent of the Discovery Islands (D07), and one in the permanently mixed waters of the eastern reach of Johnstone Strait (J07; Fig. 1). We randomly selected and processed up to 10 sockeye from each site collection from mid-May to late June in 2015 and 2016 ($n = 200$; see Table 2).

In the lab, salmon stomachs were removed and stored in 95% ethyl alcohol prior to conducting taxonomic analyses. Ethanol preservation can make samples brittle and difficult to manipulate (Steedman 1976). Furthermore, the constant evaporation of the preservative makes obtaining a sample weight nearly impossible. Therefore, prior to analysis, stomachs were removed from the preservative and soaked in water for 30 min for rehydration (Mills et al. 1982). Samples were then blotted dry and weighed to the nearest 0.1 mg. Ethanol preservation can also cause samples to lose weight (Wetzel et al. 2005), so an ethanol conversion factor was applied to stomach content weights to make them comparable to other fresh weights (see Supplement S1 at www.int-res.com/articles/suppl/m719p093_supp.pdf).

Stomachs were cut open from the start of the esophagus to the pyloric sphincter and the contents were removed, weighed, and identified to the lowest taxonomic resolution possible. 'Empty' stomachs were those visually assessed as containing no traces of food. Prey items were grouped into one of 5 size categories: <1, 1–2, 2–5, 5–10, and >10 mm. Each taxonomic group in each stomach was counted and weighed to determine relative abundance and relative biomass.

2.2. Environmental and zooplankton data collection

Water temperature and salinity at 0 and 1 m depth were measured with a Yellow Springs Instruments (YSI) Pro30, and water clarity (in m beneath the surface) was measured with a Secchi disk from the location of fish capture.

To characterize temporal trends in zooplankton abundance, biomass, and size for the migratory period through this region, we looked at all available surface zooplankton samples collected by the Hakai Institute's Juvenile Salmon and Oceanography programs from May to early July in 2015 and 2016. Zooplankton samples were collected using a 50 cm diameter, 250 μm mesh ring net towed horizontally through the top meter of the water column at $\sim 1 \text{ m s}^{-1}$ for up to 2–3 min or until there was notable coloration

in the net. The net was equipped with a General Oceanics flowmeter to estimate the volume of water filtered. Samples were preserved using a buffered solution of 4% formaldehyde in seawater.

In the lab, zooplankton were size-fractionated using a 250, 1000, 2000 μm sieve stack. Each size fraction was rinsed with fresh water, blotted dry, and weighed to the nearest 0.1 mg (wet weight). Zooplankton were counted, measured for length, and identified to the lowest taxonomic level. Total zooplankton counts were extrapolated from subsamples and normalized by converting to abundance per cubic meter of water sampled.

2.3. Data analysis

The peak migration period in each year was established by using the capture dates for the first and third quartiles of cumulative sockeye catch. The first and last dates of sockeye capture were used to establish the entire migration period, which was broken down into the early (first quartile), peak (first to third quartile), and late (fourth quartile) migration timing groups.

Genetic stock identification was performed by the Molecular Genetics Laboratory (Pacific Biological Station, Fisheries and Oceans Canada), whereby a suite of 14 microsatellite loci were compared to a baseline genotypic library of known stocks (Beacham et al. 2004). The 'Coastwide210613' baseline was used, which contains 243 sockeye genotypes spanning from Oregon to Alaska, 63 of which are stocks from the Fraser River. The probability of the stock of origin was determined for each fish using a Bayesian model called 'CBayes'), which compares mixtures of stocks. For improved confidence in stock assignments, we only looked at samples with a >70% probability of assignment to a given stock. Individual stocks were then combined into 'stock management groups', hereafter referred to as 'stock groups' based on management units used by the Pacific Salmon Commission for in-season sockeye management. Stock groups were based on geographic proximity, shared life history strategies, and the confidence to accurately distinguish different conservation units (as defined by Holtby & Ciruna 2007) from each other (S. Latham pers. comm.). This study focused on stock groups rather than individual stocks.

A gut fullness index (GFI) was used as a measure of foraging success, expressed as the proportion of the individual's body weight made up of the stomach contents:

$$\text{GFI} = M_{\text{sc}}(M)^{-1} 100 \quad (1)$$

where M_{sc} is the mass of the stomach contents (g) and M is the mass of the fish (g). This formula standardizes for differences in fish size (Chipps & Garvey 2007).

For visualization of zooplankton and diet composition, the taxonomic categories were reduced to the following 8 major groupings: amphipods, barnacles (naupliar and cyprid stages), calanoid copepods, cladocerans, decapods (zoea and megalopa), euphausiids, larvaceans, and 'other'. The latter category consisted mainly of gastropods, bivalves, polychaetes, insects, and fish and zooplankton eggs. Unidentifiable digested matter was excluded from taxonomic analyses along with empty stomachs ($n = 8$). Detailed taxonomic information was retained for multivariate analyses. Rare taxa (those occurring in a single sample) were subsequently re-assigned to a higher taxonomic level (e.g. order) to reduce the effect of an outlying family or genus.

Non-parametric multivariate techniques were used to analyze the diet composition. Relative biomass was arcsine-square-root transformed to spread the distribution of values and reduce the influence of abundant or rare species (Zar 1999). A cluster analysis was then performed using the average-linkage method between Bray-Curtis rank dissimilarities to identify diet types using a dendrogram (Ferreira & Hitchcock 2009). The optimal number of diet clusters was determined using the 'NbClust' package in R (R Development Core Team 2022) and visual inspection of the dendrogram.

An analysis of similarity (ANOSIM), the non-parametric multivariate analogue to ANOVA, was conducted to test for significant differences in taxonomic composition within and between diet clusters, migration timing groups, sites, years, and stock groups (Clarke 1993). This method compares within- and between-group ranked differences, producing a global R-value which approaches '0' when within-group differences are greater than between-group differences, and approaches '1' when the opposite is true. When significant differences were detected between groups (e.g. $p < 0.05$), a similarity percentages test (SIMPER) was conducted to determine which taxa best explained the differences between groups.

Non-metric multidimensional scaling (NMDS) ordination was used to pro-

ject the rank dissimilarities between samples into a 2-dimensional ordinate space. The NMDS ordination shows similar diets closer together and dissimilar diets farther apart. A version of Clarke & Ainsworth's (1993) BIO-ENV model was run to determine which environmental parameters (time of day, day of the year, average sea surface temperature, average sea surface salinity, Secchi depth, zooplankton abundance, zooplankton biomass, fish fork length, total catch) had the maximum correlation with the diet rank dissimilarities. The best-fitting model outputs were overlaid on the ordination as vectors, with the direction of the arrow indicating an increase in the value of that parameter.

All statistical analyses were conducted in R statistical software v.4.1.0 (R Development Core Team 2022), with multivariate analyses performed using the 'vegan' package in R (Oksanen et al. 2022).

3. RESULTS

3.1. Sockeye

Stock identification with an assignment probability of $>70\%$ was possible for 1683 (882 in 2015, 801 in 2016) of the 2547 samples analyzed. Of these, 96.1 and 97.6% were of Fraser River origin in 2015 and 2016, respectively (Table 1). The 2015 migration was dominated by sockeye from the Chilko stock group

Table 1. Number and percentage of juvenile sockeye salmon for genetically identified stock groups that had a probability of assignment of $>70\%$. Fish were retained by the Hakai Institute Juvenile Salmon Program from all sites throughout the Discovery Islands and Johnstone Strait in 2015 and 2016

System	Stock group	2015		2016		
		n	%	n	%	
Fraser	Chilko	333	37.8	147	18.4	
	Quesnel	154	17.5	121	15.1	
	Late_Shuswap_Portage	86	9.8	395	49.3	
	Early_Thompson	60	6.8	84	10.5	
	Late_Stuart_Stellako	60	6.8	17	2.1	
	Pitt	42	4.8	0	–	
	Birkenhead_Big_Silver	32	3.6	3	0.4	
	Nadina_Gates_Bowron_Nahatlatch	31	3.5	14	1.7	
	Early_Stuart	27	3.1	0	–	
	Weaver_Cultus	12	1.4	0	–	
	Raft_North_Thompson	10	1.1	0	–	
	Chilliwack	1	0.1	1	0.1	
	Other	Nimpkish	15	1.7	14	1.7
		Woss Lake	12	1.4	4	0.5
Phillips		4	0.5	0	–	
Sakinaw		2	0.2	1	0.1	
Baker Lake		1	0.1	0	–	

(37.8%), while the 2016 migration was dominated by the Late-Shuswap-Portage stock group (49.3%; Table 1, see Table S2.1 in Supplement S2 for full stock composition).

Migration timing of juvenile sockeye salmon through the TMZ was consistent between years (Fig. 2). The first sockeye were collected in the Discovery Islands on 12 and 13 May, with catches continuing until 14 July and 6 July in 2015 and 2016, respectively. The peak migration through the Discovery Islands ran from 21 May to 2 June in 2015 and from 18 May to 1 June in 2016 (Table 2, Fig. 2). The first sockeye were captured in Johnstone Strait 1 wk later, on 20 May in both years, with catches continuing until 10 and 6 July, respectively. The peak migration through Johnstone Strait ran from 27 May to 6 June in 2015 and from 28 May to 10 June in 2016 (Table 2, Fig. 2).

Some Fraser River stock groups showed temporal segregation in migration through the TMZ, al-

though most showed considerable overlap (Fig. 2). Captures of the most abundant stock groups (i.e. Chilko, Quesnel) were largely responsible for defining the 'peak' migratory period. Although they were captured over longer periods (12 May–7 July), their median date of capture was 28 May in 2015 and 4 June in 2016. By contrast, the median date of capture of some stocks fell within the 'early' migratory period (15–20 May), such as the Raft-North Thompson, Weaver-Cultus, Late Stuart-Stellako, and Nadina-Gates-Bowron-Nahatlatch stock groups in the Discovery Islands in 2015 (Fig. 2). The remaining stock groups had median capture dates after the peak migration. While the overall timing of migration was similar in 2016, the median capture date of several individual stocks was earlier in 2016 than in 2015 (see Supplement S2, Figs. S2.1 & S2.2, Table S2.2 for detailed stock group migration timing).

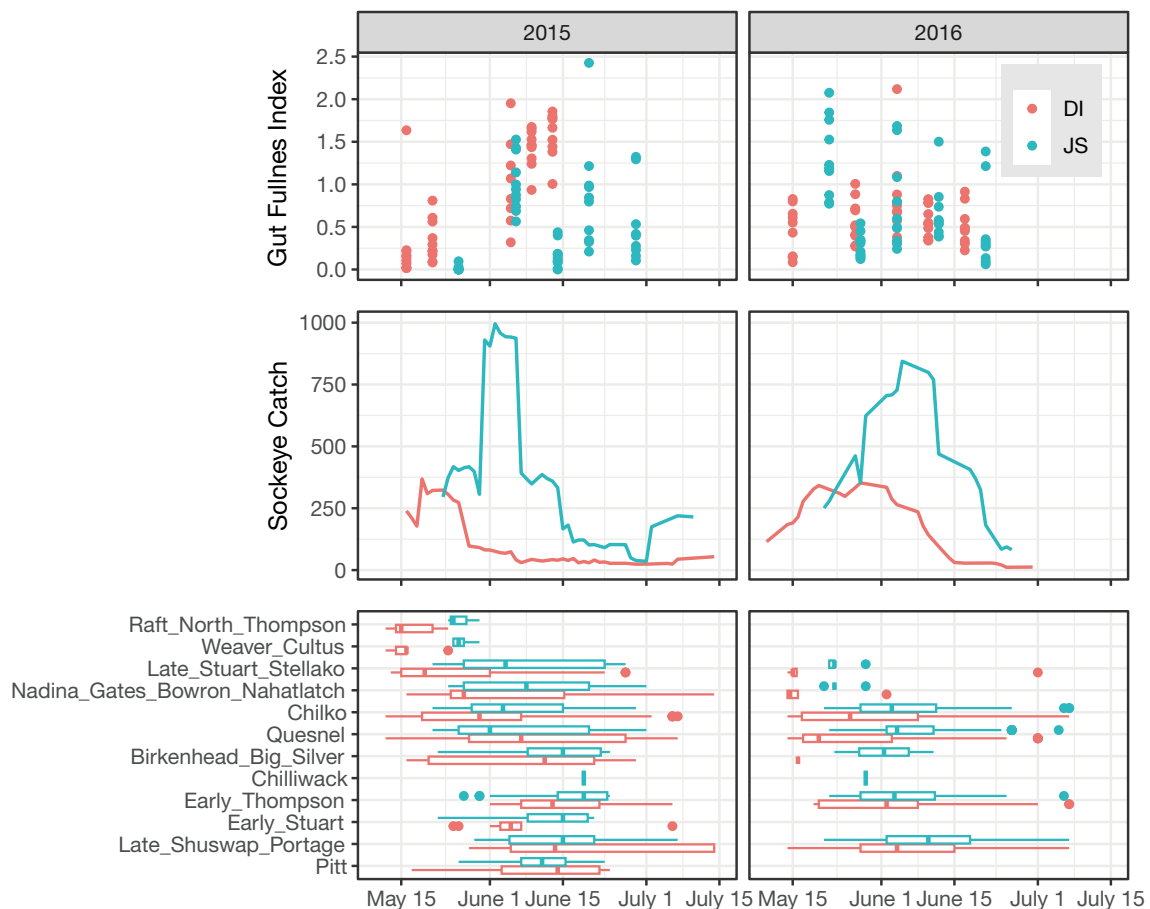


Fig. 2. Foraging success and migration timing of Fraser River sockeye salmon captured in the Discovery Islands (DI) and Johnstone Strait (JS) in 2015 and 2016. Top: gut fullness indices of a subset of sockeye sampled for diets. Middle: 7 d rolling average of juvenile sockeye catch in the DI and JS in each year from all sites sampled by the Hakai Institute Juvenile Salmon Program. Bottom: median dates of capture and interquartile range of genetic stock management groups (probability of assignment > 70%) for sockeye sub-sampled for genetic stock identification; horizontal lines: 95% percentiles; dots: outliers

Table 2. Dates, sample sizes, median fork lengths (FL; mm), median fish weights (FW; g), and median gut fullness indices (GFI) for juvenile sockeye salmon sampled for diet composition analysis from early, peak, and late migration timing groups in 2015 and 2016 for the Discovery Islands (site D07) and Johnstone Strait (site J07)

Year	Timing	Dates	n	FL (range)	FW (range)	GFI (range)
Discovery Islands						
2015	Early	16 May	10	102 (94–128)	10.9 (9.0–22.5)	0.13 (0.02–1.64)
	Peak	21 May	10	100 (96–104)	9.8 (7.8–11.2)	0.26 (0.08–0.81)
	Late	5–13 Jun	29	106 (90–119)	14.4 (9.1–19.3)	1.46 (0.32–1.95)
2016	Early	14 May	10	114 (88–128)	12.9 (5.6–17.0)	0.55 (0.09–0.83)
	Peak	26 May	10	92 (79–98)	6.4 (5.8–8.1)	0.51 (0.27–1.01)
	Late	3–16 Jun	30	94 (84–110)	8.3 (6.6–11.3)	0.56 (0.22–2.12)
Johnstone Strait						
2015	Early	26 May	9	109 (99–130)	16.8 (10.5–25.2)	0.00 (0.00–0.10)
	Peak	6 Jun	11	115 (101–132)	14.6 (11.4–19.8)	0.94 (0.56–1.53)
	Late	14–29 Jun	31	116 (103–128)	18.6 (11.6–24.1)	0.33 (0.00–2.43)
2016	Early	21–27 May	20	92 (85–118)	7.7 (5.9–14.3)	0.66 (0.12–2.08)
	Peak	3–11 Jun	20	102 (90–125)	10.3 (7.2–14.4)	0.55 (0.24–1.68)
	Late	20 Jun	10	114 (103–128)	13.9 (10.6–16.9)	0.29 (0.06–1.39)

Juvenile sockeye increased in size over the migratory period through the TMZ in both years (Table 2). A factorial ANOVA found that fork lengths were significantly different between years ($F_{1,3209} = 519.99$, $p < 0.001$), sample sites ($F_{1,3209} = 177.23$, $p < 0.001$), and migratory periods ($F_{2,3209} = 371.8$, $p < 0.001$), with significant interactions between variables. Specifically, fork lengths were shorter in 2016 than in 2015 ($p < 0.001$), shorter in the Discovery Islands than in Johnstone Strait ($p < 0.001$), and larger during the late migration than during the early or peak migrations ($p < 0.001$).

3.2. Environmental conditions

Environmental conditions in the Discovery Islands were more variable over the course of the sockeye migratory period than in Johnstone Strait (Fig. 3). Weekly mean sea surface temperatures in the Discovery Islands ranged from 11.2–14.1 and 10.5–14.2°C in 2015 and 2016, respectively, while those in Johnstone Strait ranged from 9.3–11.2 and 10–10.5°C in 2015 and 2016, respectively. Weekly mean sea surface salinities in the Discovery Islands ranged from 26.5–30.0 and 25.1–28.3 psu in 2015 and 2016, respectively, while those in Johnstone Strait ranged from 28.5–29.4 and 29.5–31.7 psu in 2015 and 2016, respectively. Water clarity in the Discovery Islands was lowest in early May (~6–8 m). In 2015, the Discovery Islands water clarity increased through the season to a maximum of ~13 m in July, compared to 2016, wherein it peaked in June at ~11 m and

decreased through July to ~7 m. In Johnstone Strait, water clarity was more consistent over the season and was greater in 2015 (12 ± 2 m) than 2016 (10 ± 2 m). Conditions during the peak migratory period were similar between years, although salinities were higher at both sites in 2016 compared to 2015.

From mid- to late June in 2015, environmental conditions in the Discovery Islands more closely resembled those of Johnstone Strait (Fig. 3), but this transition was not seen in 2016. Overall, conditions in the Discovery Islands were warmer and fresher than in Johnstone Strait in both years.

3.3. Prey field

A Kruskal-Wallis test revealed no significant difference in zooplankton biomass between migration periods ($H_2 = 2.11$, $p = 0.349$), but significantly higher biomass in 2016 than in 2015 ($H_1 = 4.80$, $p = 0.029$; Fig. 3). In the Discovery Islands, zooplankton biomass in the 2016 early migratory period (1660 mg m^{-3}) was almost 4 times that of the 2015 early migratory period (448 mg m^{-3}). There was no significant difference in biomass between the 2 sites ($H_1 = 2.21$, $p = 0.137$).

Overall, >95% of the zooplankton community in the surface waters of the TMZ were <2 mm throughout the migratory period (Fig. 3). Larger zooplankton (>2 mm) became more abundant during the late migratory period in both years; however, the only significant shift in size was observed during the peak migratory period in Johnstone Strait ($H_2 = 8.51$, $p =$

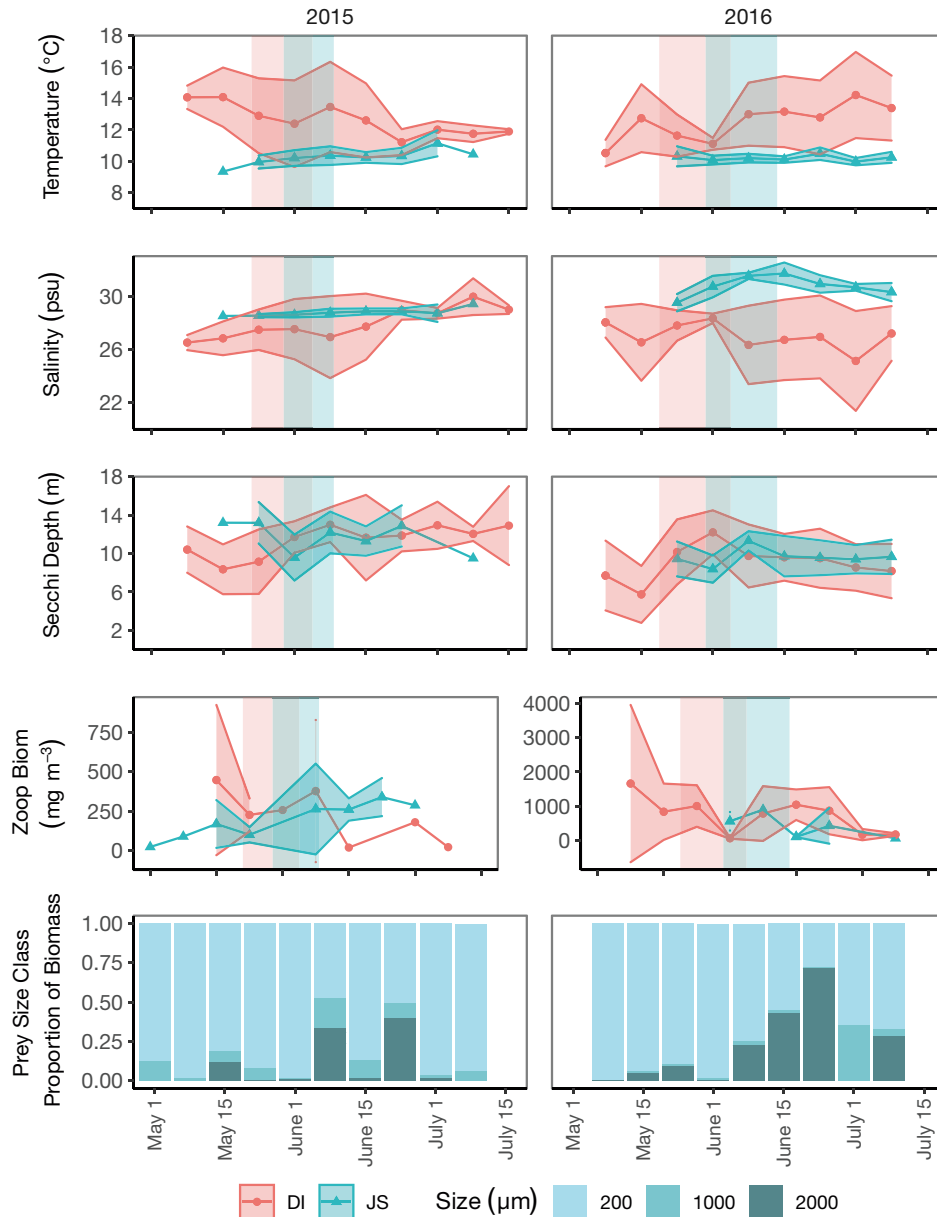


Fig. 3. Mean sea surface temperature, salinity, Secchi depth, zooplankton biomass (Zoop Biom), and proportion of prey by size class from measurements at all stations in the Discovery Islands (DI) and Johnstone Strait (JS) in 2015 and 2016. Prey size classes are summarized for both locations combined each year. Shaded areas around the mean: \pm SD; red shaded vertical bars: DI peak migration period; blue shaded vertical bars: JS peak migration period

0.014), when the mean size of the organisms (biomass / abundance) was significantly larger (0.48 ± 0.69 mg) than during the early migration (0.08 ± 0.04 mg; Dunn test, $p = 0.014$).

Taxonomic composition of the surface zooplankton varied over time and between sites (Fig. 4). In the Discovery Islands, barnacles, cladocerans, and copepods were the most abundant taxa throughout the juvenile sockeye migratory period. During the early migration of 2015, the surface community in the Discovery Islands was composed of an average (\pm SD) of

$52 \pm 8\%$ barnacles (i.e. nauplii), with a more equal mix of barnacles, cladocerans, and copepods during the peak migration transitioning to a community of $41 \pm 21\%$ copepods on average during the late migration. In 2016, the surface zooplankton community in the Discovery Islands was composed of predominantly cladocerans and copepods during the early and peak migration (cladocerans: 38 ± 17 and $39 \pm 21\%$, respectively; copepods: 22 ± 14 and $29 \pm 23\%$, respectively), with copepods once again having the highest relative abundance during the late

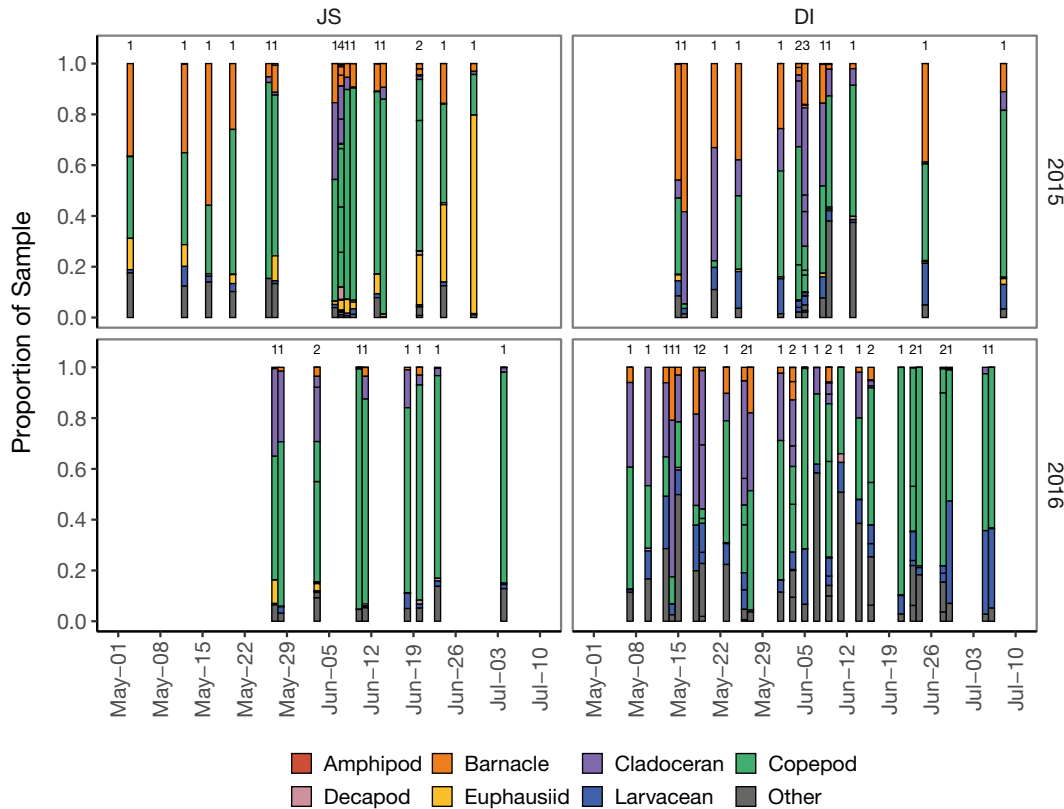


Fig. 4. Relative abundance of zooplankton taxa sampled from the surface waters throughout Johnstone Strait (JS) and the Discovery Islands (DI) and during the juvenile sockeye salmon migration in 2015 and 2016. Number of tows per sample date are shown above each bar

migration ($56 \pm 19\%$). In Johnstone Strait, copepods dominated throughout the sockeye migration, making up 49 ± 20 , 51 ± 16 , and $63 \pm 28\%$ of the surface zooplankton community in the early, peak, and late migrations of 2015, respectively, and 48 , 72 ± 16 , and $80 \pm 5\%$ of the community during the early, peak, and late migrations of 2016, respectively.

3.4. Diets

A 3-way factorial ANOVA revealed no significant effects of year, location, or time period on GFI, but a significant 3-way interaction ($F_{2,177} = 6.99$, $p = 0.001$, partial eta-squared = 0.08). Post hoc analyses using Tukey's HSD showed that the effect of migration timing on GFIs was moderated by both the location and the year, with higher GFIs late in the 2015 migratory period through the Discovery Islands ($p < 0.001$; Fig. 2). The lowest GFIs (0.02 and 0.09 in 2015 and 2016, respectively) were measured in the early migration period through the Discovery Islands in both years. Overall, the median GFI for the entire migration through the TMZ was 0.52 in 2015 and 0.53 in 2016. Mean GFIs were similar across stock

groups, with only 3 significant differences between individual stocks: south Chilko had significantly higher GFIs than both Birkenhead ($p = 0.033$) and Pitt River sockeye ($p = 0.046$), and Seymour sockeye had higher GFIs than Lower Shuswap sockeye ($p = 0.043$).

Sockeye diet composition was clustered strongly by site, a spatial association that persisted throughout the migratory period and between years (Fig. 5). Two distinct diet clusters were identified with 89% dissimilarity: Cluster A, composed of mostly Johnstone Strait diets and some of the late 2015 Discovery Island diets, and Cluster B, composed of the remaining Discovery Island diets. A number of sub-clusters were also identified with $\geq 75\%$ dissimilarity (ANOSIM: $R = 0.83$, $p = 0.001$). Cluster A comprised one large subcluster with 112 samples (A1), and one small subcluster with 6 samples (A2). Cluster B comprised 3 subclusters (B1, B2, and B3). Three other clusters were identified with high levels of dissimilarity in diets, each with only one or 2 samples (total $n = 5$); these were treated as outliers and excluded from subsequent analyses. Diets in Cluster A1 were characterized by a greater biomass of calanoid copepods, namely *Metridia* and *Calanus* spp., with most food

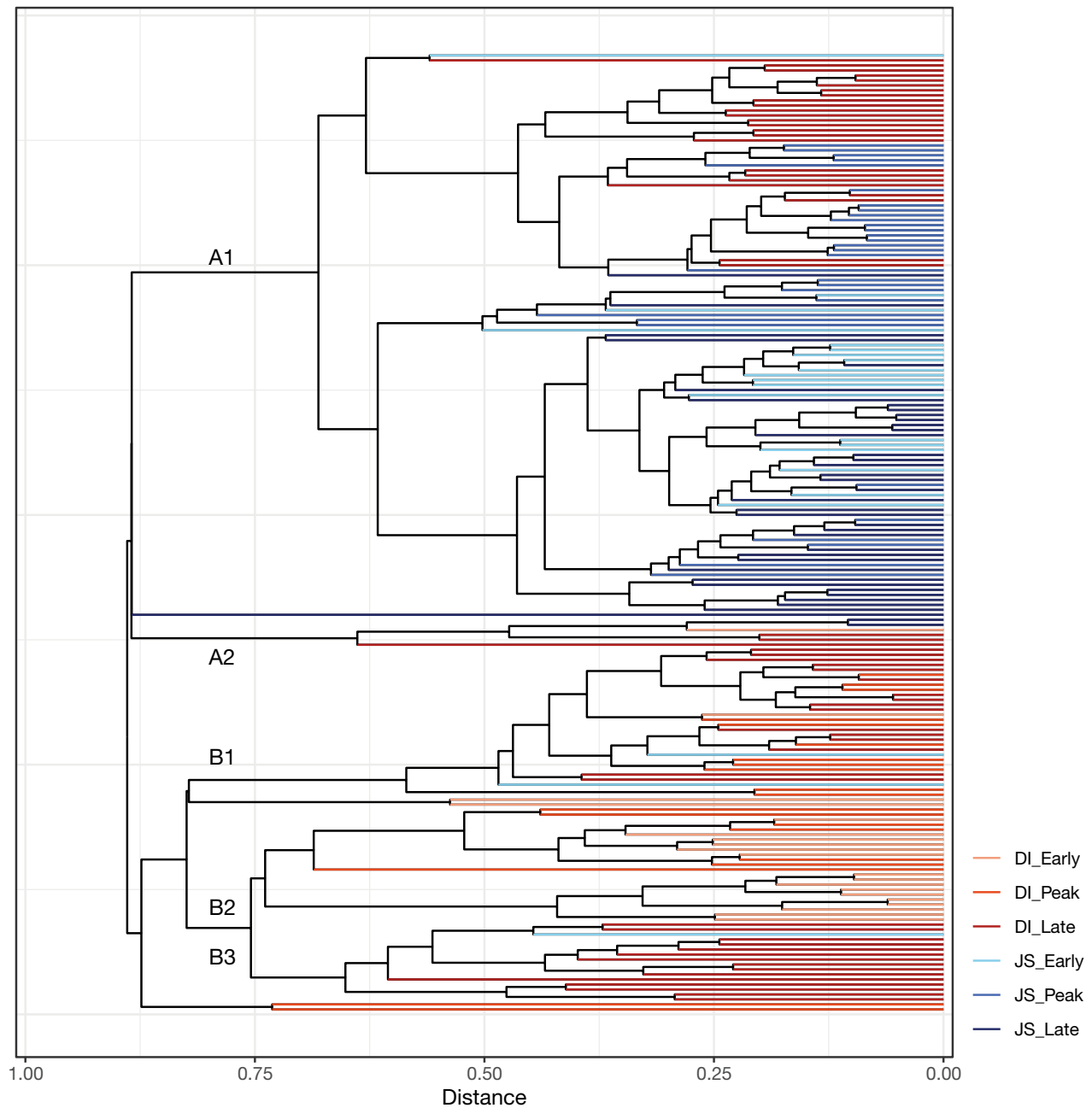


Fig. 5. Dendrogram of a cluster analysis comparing the diet composition of juvenile sockeye salmon using Bray-Curtis rank dissimilarities of transformed relative biomass of diet items. Dendrogram branches are coloured by site (DI: Discovery Islands, site D07; JS: Johnstone Strait, site J07) and migration timing (early, peak, late), with unique diet clusters identified as A1, A2, B1, B2, and B3. Outliers (<3 samples cluster⁻¹) are not labelled

items in the 2–5 mm size category, while the 6 individuals in Cluster A2 fed almost exclusively on amphipods and euphausiids, prey items that were often larger than 10 mm (Fig. 6, Table S2.3). By contrast, diets in Cluster B1 were characterized by a greater biomass of larvaceans 2–5 mm in length and included mostly peak- and late-migrating sockeye in the Discovery Islands (Fig. 6, Table S2.3). Diets in

Clusters B2 and B3 had a greater biomass of small prey items, including barnacles and cladocerans with early and late-migrating sockeye, respectively (Fig. 6, Table S2.3).

There was a significant difference in sockeye diets between sites ($R = 0.40$, $p = 0.001$), but not between years ($R = 0.07$, $p = 0.001$). Within samples from each site, we also detected differences in sockeye diets

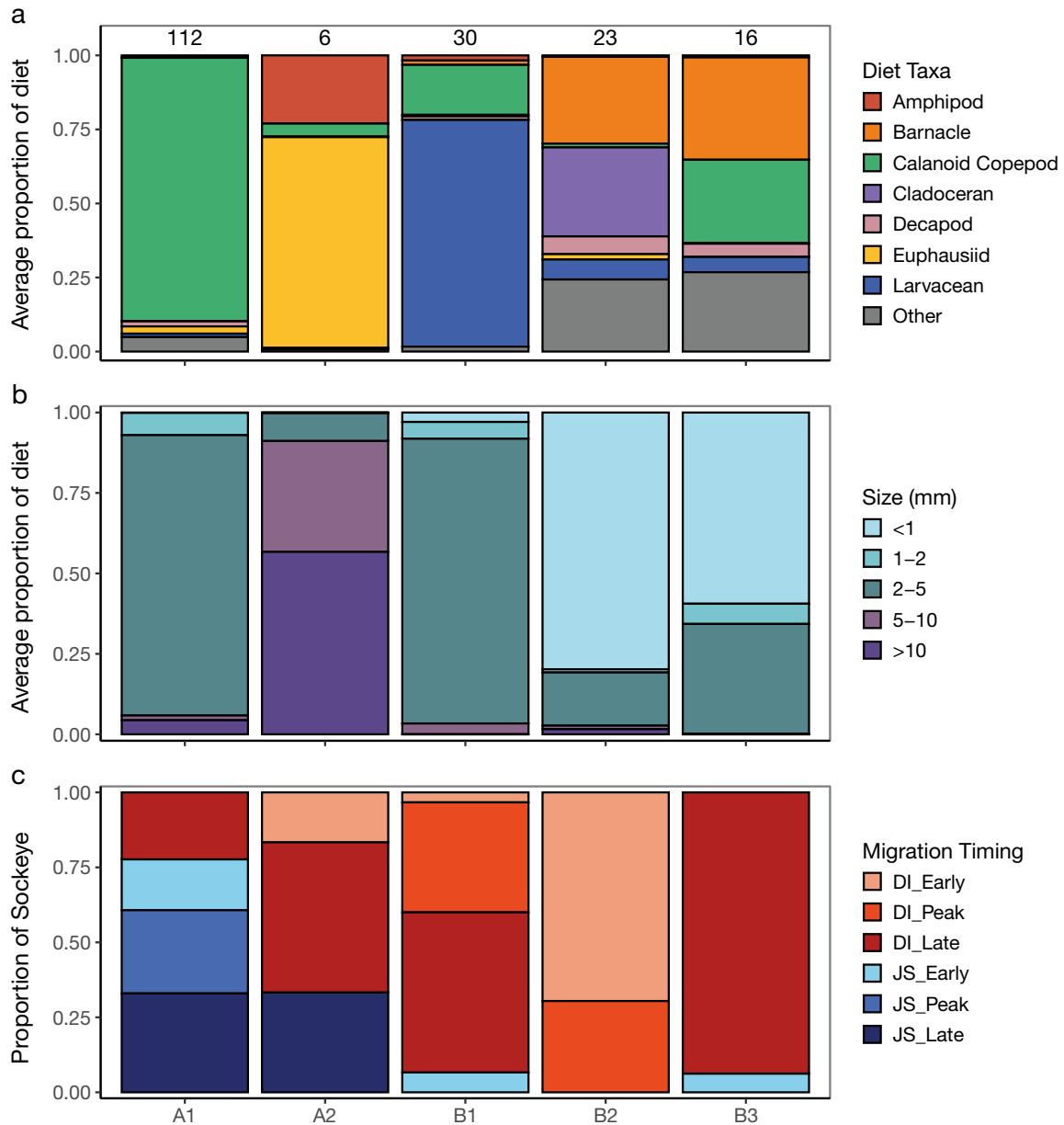


Fig. 6. Average proportion (by weight) of each (a) prey taxa and (b) prey size in the diets of juvenile sockeye salmon, as well as (c) migration timing group in each cluster (A1, A2, B1, B2, and B3) identified through Bray-Curtis rank dissimilarities. Samples were collected from a single site in both the Discovery Islands (DI; site D07) and Johnstone Strait (JS; site J07) throughout the migratory period in May–June of 2015 and 2016. The number of stomach samples in each cluster is noted above each bar in (a)

between early, peak, and late migration timing groups (DI: $R = 0.32$, $p = 0.001$; JS: $R = 0.40$, $p = 0.001$), although there was a wide range in dissimilarities between diets within each group. In addition, there was no significant difference between diet composition within stocks or between stocks ($R = 0.04$, $p = 0.167$).

The separation of clusters was most strongly influenced by differences in sea surface temperature and water clarity, with Clusters A1 and A2 containing diets from cooler, clearer waters than those in Clusters B1, B2, and B3 (Fig. 7).

4. DISCUSSION

The phenology of environmental conditions in the ocean determines the timing of primary production as well as the recruitment success and production of zooplankton, thereby influencing the quantity and temporal distribution of the prey field experienced by zooplanktivorous fish. This can be particularly important for fish species that time their reproduction to match the peak of zooplankton production. This is also true for migratory species such as salmon that,

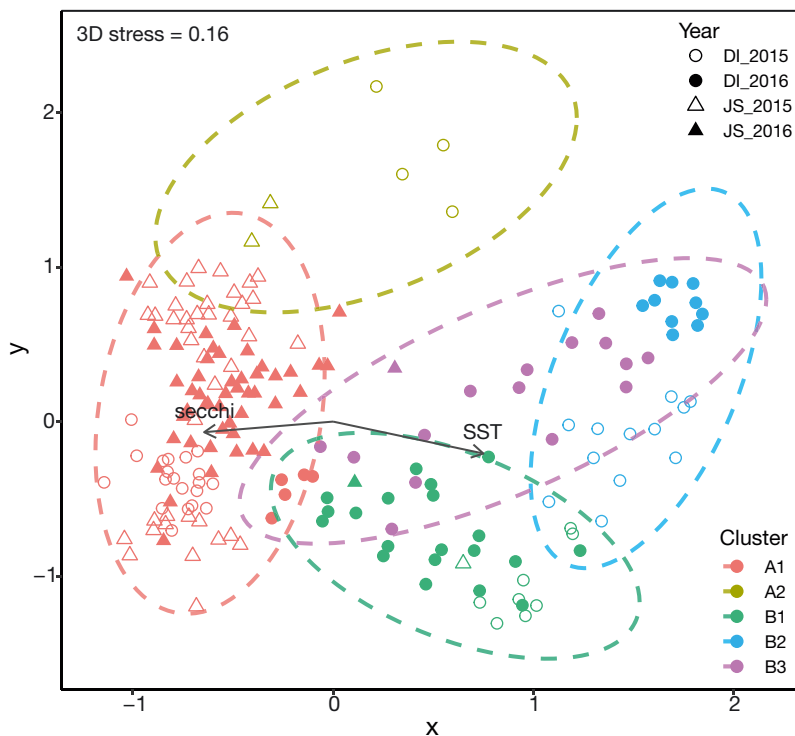


Fig. 7. Ordination of Bray-Curtis rank dissimilarities calculated for arcsine-square-root transformed relative biomass of diet items consumed by juvenile sockeye collected from the Discovery Islands (DI; site D07, circles) and Johnstone Strait (JS; site J07, triangles) from mid-May to late June of 2015 (empty symbols) and 2016 (filled symbols). Ellipses: 95% CIs around cluster means. The best environmental predictors of the rank dissimilarities are overlain as vectors based on bioenv modelling. SST: sea surface temperature ($^{\circ}\text{C}$); secchi: water clarity (m)

through evolution, align their seaward migration with optimal prey conditions. Plankton phenology may indeed vary interannually due to shifts in climatic conditions (e.g. Allen & Wolfe 2013) and spatially due to regional differences in oceanographic conditions (e.g. Marchese et al. 2022). In this study, seasonal changes in the foraging experience of juvenile Fraser River sockeye salmon were examined during their outmigration in 2015 and 2016, in 2 tidally mixed locations on the BC coast: the Discovery Islands and Johnstone Strait. By incorporating genetic stock information, we were able to characterize patterns in migration timing and early marine conditions at the stock management level. Differences in environmental conditions, namely temperature and visibility, as well as prey community composition were reflected by distinct diet profiles. Stocks arriving earlier in the Discovery Islands encountered a prey field replete with small, energy-poor prey, though with higher zooplankton abundance in 2016, while later stocks foraged on larger, higher-energy copepod and larvacean prey. Calanoid copepods

dominated diets in the highly mixed waters of Johnstone Strait irrespective of migration timing and year. Although low foraging success was common in the TMZ throughout the migration period, the copepod-dominated diet delivered the highest per unit of mass energy content compared to other diets (Table S2.4). Our findings highlight the fine-scale foraging dynamics of juvenile sockeye across the entirety of their migration through a coastal TMZ.

The surface zooplankton community that was encountered by outmigrating salmon differed seasonally, interannually, and spatially. The significantly higher biomass in 2016 was likely related to the later spring bloom in the northern Strait of Georgia in 2016 compared to 2015 (Mahara et al. 2019). The 2016 sockeye migration overlapped with an earlier stage of the seasonal zooplankton cycle when zooplankton were more abundant. The higher biomass was attributed to an abundance of small, naupliar zooplankton stages, cladocerans, and meroplankton (barnacles). Per unit mass, the barnacle/cladoceran-dominated diet provided up to 28 and ~20% less energy than copepod

and euphausiid/amphipod- or larvacean/copepod-dominated diets, respectively (Table S2.4). Therefore, both the increase in prey size and the shift in taxonomic composition suggest that the energetic quality of the prey field increased over the migratory period.

Although the stomachs of the early migrating sockeye contained large numbers of prey, the prey items were small and of low nutritional quality, and we did not observe a corresponding increase in the GFI. Therefore, the 'match' between early migrants and their prey in 2016 did not appear to be advantageous. Better foraging opportunities (i.e. the highest GFIs) were observed when large copepods and euphausiids made up the bulk of the diet (i.e. late 2015 migration) rather than when small (<1 mm) prey were consumed. Therefore, sockeye migrating during the peak or late migration likely encountered more favourable foraging conditions as smaller meroplankton settled out of the surface waters and were replaced by larger taxa. Although we lacked early season zooplankton collections from Johnstone Strait in 2016, we did not observe the same temporal succession in community

composition over the course of the migratory period in this area. Relatively constant conditions in Johnstone Strait appeared to be maintained by strong tidal mixing rather than varying with regional annual cycles in environmental conditions, which is consistent with the literature for this area (McKinnell et al. 2014, Dosser et al. 2021).

We observed low GFIs throughout the migratory period, which supports the similar spatial pattern previously reported in the TMZ (James et al. 2020). Comparatively, GFIs of 1.8–1.9 have been reported off the south coast of BC (Brodeur et al. 2007) and in the northern Strait of Georgia and Discovery Islands (Price et al. 2013). However, the median GFIs in the Discovery Islands and Johnstone Strait across the migratory period were 0.52 and 0.53, respectively, indicating consistently poor foraging conditions for juvenile sockeye salmon during their migration.

The 2 most apparent patterns in the juvenile sockeye diets were the strong spatial separation between the Discovery Islands and Johnstone Strait and the distinction of early migration diets from those in the other timing groups. In Johnstone Strait, waters are sourced from the north, through Queen Charlotte Sound and Queen Charlotte Strait, and host more of a boreal zooplankton community (i.e. *Pseudocalanus*, *Calanus*, and *Acartia* spp.) (Mackas & Galbraith 2002). Inflow and outflow speeds are more than 10 times faster than those observed in the southern Discovery Islands (Khangaonkar et al. 2017), with a net outflow in the upper water column and a net inflow in the lower water column (Thomson 1976). Large calanoid copepods (e.g. *Metridia* and *Calanus* spp.) that undergo diel vertical migration may have higher retention rates than zooplankton that are restricted to surface waters where outflow dominates (e.g. larvaceans and cladocerans) (Tommasi et al. 2014), making them more common in the diet. Water clarity was consistently high in Johnstone Strait; however, it transitioned from low to high over the migratory period in the Discovery Islands. Poor visibility for a visual forager like sockeye may have driven them to opportunistically consume large aggregations of smaller, less nutritious prey rather than being able to search for and target larger prey.

Wilson et al. (2023) recently demonstrated that Pacific salmon migration timing and breadth are highly variable within species across watersheds, and here we showed that both of these migration characteristics can also be highly variable among stocks within a watershed, with implications for stock-specific foraging experience. The dominant stock groups in our study had protracted migrations

through the area (i.e. Chilko, Late Shuswap-Portage, and Quesnel) that encompassed several diet profiles. For instance, earlier Chilko River migrants encountered more of the smaller prey with a high proportion of barnacles and cladocerans (diet type B2), while the later Chilko River migrants encountered more larvaceans (diet type B1). Protracted migrations likely facilitate a bet-hedging strategy, whereby exposure to a broader range of environmental conditions reduces the risk of the entire population being caught in a period of unfavourable conditions for survival. However, there were also stock groups with relatively truncated migrations through the area, such as the Raft-North-Thompson and Weaver-Cultus stock groups. Although there was no significant difference in diet profiles among the stock groups in our study, the groups with truncated migrations were more likely to have experienced a trophic mismatch with their prey. The Raft-North-Thompson, Weaver-Cultus, and Late-Stuart-Stellako groups were predominantly captured during the early migratory period, when small, energy-poor prey were prolific, and visibility in the surface waters of the Discovery Islands was poor: conditions that yielded low foraging success during this section of their migration. In contrast, the Late-Shuswap-Portage, Early-Stuart, and Pitt stock groups were predominantly captured after the peak in zooplankton abundance, when larger prey were more prevalent and visibility was better: conditions that were more favourable for higher foraging success and, ultimately, survival.

The contrast in prey sizes between diet profiles may reflect size-selective foraging behaviour. Small (<1 mm) zooplankton dominated the surface zooplankton community throughout most of the migratory period in both the Discovery Islands and Johnstone Strait, although the relative proportions of larger prey (>2 mm) increased in mid to late June. Capturing a true representation of the zooplankton prey field available to salmon is challenging, and most methods and gear types have proven to be inadequate (Brodeur et al. 2011). Knowing these challenges, we sought to provide a general characterization of the prey field in the TMZ during the sockeye outmigration rather than explicitly pairing prey samples to sockeye samples in space and time. Salmon are known to occur in the upper water column and feed near the surface (Brodeur 1989); therefore, our near-surface collections of juvenile sockeye and their prey were not an inaccurate representation of foraging dynamics. Studies conducting vertical zooplankton tows to 20 m depth have also reported a higher abundance of larger zooplankton in salmon diets

than in the net tows (Chittenden et al. 2010, Price et al. 2013). Therefore, size selectivity appears to be influenced by prey availability and visibility and persists through the TMZ.

Our results illustrate not only the importance of migration timing in the early marine foraging ecology of juvenile salmon but also the need to account for spatial heterogeneity and stock-specific variability. When the juvenile salmon outmigration is out of sync with the phenology of their prey, foraging success, and ultimately growth and survival, can be low. However, the quality of prey may be more important than the quantity when considering trophic matches or mismatches. Over the 5 wk sampling period of this study, we observed dramatic changes in salmon diets, in part due to rapid changes in the zooplankton community in the southern TMZ but also due to stark contrasts in oceanographic properties across habitat types. Thus, factors other than prey phenology can also be important for foraging success. Variations in migration timing within and between stocks can result in significantly different foraging opportunities, resulting in varying growth and survival trajectories. Another factor not assessed by our study was density-dependent effects on foraging success, and we recommend this as a line of research in the future.

The challenges faced during the early marine period are cumulative; unfavourable conditions experienced in one habitat, including carryover effects from freshwater, may make it more difficult for sockeye to successfully navigate subsequent challenging environments. Therefore, year classes that face sub-optimal environmental conditions elsewhere along their freshwater and early marine migration may experience lower survival rates as a result of the additional challenges encountered in TMZs. Salmon migration timings are shifting at different and unpredictable rates independent of spring bloom timing, increasing the likelihood of trophic mismatches (Wilson et al. 2023). Warming waters can also increase the metabolic rates and energetic needs of migratory salmon (Trudel & Welch 2002), exacerbating the negative effects of trophic mismatch. Therefore, TMZs are expected to play an important role in moderating early marine survival in the future. More broadly, accounting for spatial and temporal heterogeneity in the marine environment encountered by migrating salmon as it relates to the specific migration timing of individual stocks can improve our understanding of stock-specific differences in marine growth and survival. Given the ongoing monitoring of the juvenile sockeye migration through these waters by the Hakai Institute, future studies could link juvenile and

adult return time series to better understand the cumulative drivers of marine growth and survival for this highly valued species.

Data availability. The data sets used in this study are publicly available and can be accessed at <https://doi.org/10.21966/tmch-5606>.

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