Variation in juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) diets across the channel and habitats of the lower Fraser River, British Columbia, Canada

Colin D. Levings, Derek J.H. Nishimura, Edward Gregr, Timber R. Whitehouse, Herb Herunter, and Colin R. Bates

Fisheries and Oceans Canada
Science Branch - Pacific Region
Ecosystem Science Division
Pacific Science Enterprise Centre
4160 Marine Drive, West Vancouver, B.C., V7V 1N6

2023

Canadian Technical Report of Fisheries and Aquatic Sciences 3548

Fisheries and Oceans Canada Pêches et Océans Canada

Canada

Canadian Technical Report of Fisheries and Aquatic Sciences

Technical reports contain scientific and technical information that contributes to existing knowledge but which is not normally appropriate for primary literature. Technical reports are directed primarily toward a worldwide audience and have an international distribution. No restriction is placed on subject matter and the series reflects the broad interests and policies of Fisheries and Oceans Canada, namely, fisheries and aquatic sciences.

Technical reports may be cited as full publications. The correct citation appears above the abstract of each report. Each report is abstracted in the data base *Aquatic Sciences and Fisheries Abstracts*.

Technical reports are produced regionally but are numbered nationally. Requests for individual reports will be filled by the issuing establishment listed on the front cover and title page.

Numbers 1-456 in this series were issued as Technical Reports of the Fisheries Research Board of Canada. Numbers 457-714 were issued as Department of the Environment, Fisheries and Marine Service, Research and Development Directorate Technical Reports. Numbers 715-924 were issued as Department of Fisheries and Environment, Fisheries and Marine Service Technical Reports. The current series name was changed with report number 925.

Rapport technique canadien des sciences halieutiques et aquatiques

Les rapports techniques contiennent des renseignements scientifiques et techniques qui constituent une contribution aux connaissances actuelles, mais qui ne sont pas normalement appropriés pour la publication dans un journal scientifique. Les rapports techniques sont destinés essentiellement à un public international et ils sont distribués à cet échelon. II n'y a aucune restriction quant au sujet; de fait, la série reflète la vaste gamme des intérêts et des politiques de Pêches et Océans Canada, c'est-à-dire les sciences halieutiques et aquatiques.

Les rapports techniques peuvent être cités comme des publications à part entière. Le titre exact figure au-dessus du résumé de chaque rapport. Les rapports techniques sont résumés dans la base de données *Résumés des sciences aquatiques et halieutiques.*

Les rapports techniques sont produits à l'échelon régional, mais numérotés à l'échelon national. Les demandes de rapports seront satisfaites par l'établissement auteur dont le nom figure sur la couverture et la page du titre.

Les numéros 1 à 456 de cette série ont été publiés à titre de Rapports techniques de l'Office des recherches sur les pêcheries du Canada. Les numéros 457 à 714 sont parus à titre de Rapports techniques de la Direction générale de la recherche et du développement, Service des pêches et de la mer, ministère de l'Environnement. Les numéros 715 à 924 ont été publiés à titre de Rapports techniques du Service des pêches et de la mer, ministère des Pêches et de l'Environnement. Le nom actuel de la série a été établi lors de la parution du numéro 925.

Canadian Technical Report of
Fisheries and Aquatic Sciences 3548

2023

VARIATION IN JUVENILE CHINOOK SALMON (ONCORHYNCHUS TSHAWYTSCHA) DIETS ACROSS THE CHANNEL AND HABITATS OF THE LOWER FRASER RIVER, BRITISH COLUMBIA, CANADA

By

Colin D. Levings[1], Derek J.H. Nishimura[2], Edward Gregr[3], Timber R. Whitehouse[1], Herb Herunter[1], and Colin R. Bates[4]

[1]Fisheries and Oceans Canada
Science Branch – Pacific Region
Ecosystem Science Division
Pacific Science Enterprise Centre
4160 Marine Drive, West Vancouver, B.C., V7V 1N6

[2]Fisheries and Oceans Canada
Fisheries Protection Program
Suite 200 401 Burrard Street, Vancouver B.C., V6C 3S4

[3]Scitech Environmental Consultants,
2136 Napier St., Vancouver, B.C., V5L 2N9

[4]Quest University
3200 University Blvd.
Squamish, B.C., V8B 0N8

© His Majesty the King in Right of Canada, as represented by the Minister of the
Department of Fisheries and Oceans, 2023

Cat. No. Fs97-6/3548E-PDF ISBN 978-0-660-48916-2 ISSN 1488-5379

Correct citation for this publication:

Levings, C.D., Nishimura, D.J.H, Gregr, E., Whitehouse, T.R., Herunter, H., and Bates, C.R. 2023. Variation in juvenile Chinook salmon (*Oncorhynchus tshawytscha*) diets across the channel and habitats of the lower Fraser River, British Columbia, Canada. Can. Tech. Rep. Fish. Aquat. Sci. 3548: viii + 22 p.

Table of Contents

TABLE LEGEND..v

FIGURE LEGEND.. vi

ABSTRACT.. vii

RESUME viii

1.0 INTRODUCTION..1

2.0 STUDY SITE 2

3.0 METHODS……….…………………………………………………………………..……..5

- 3.1 SAMPLING TECHNIQUES 5
- 3.2 STOMACH CONTENT ANALYSIS 6
- 3.3 DATA SETS..6
- 3.4 HABITAT SOURCES MAPPING...7
- 3.5 STATISTICAL METHODS 7

4.0 RESULTS……………………………………………………………………..…..……….7

- 4.1 DOMINANT PREY DATA SET...7
- 4.2 TRANSECT AND SEASONAL TRENDS IN HABITAT-SOURCED PREY........................8
  - 4.2.1 Fry 8
  - 4.2.2 Smolts..9
  - 4.2.3 Use of Bayesian Inference for Beta Regression and Zero-or-One Inflated Beta (Zoib) Regression for Further Analysis..9
  - 4.2.4 Habitat Source Analysis 10
- 4.3 DATA TABLES 11
- 4.4 FIGURES...13

5.0 DISCUSSION……………………………………………………………………..…..………16

- 5.1 COMPARISONS WITH PREVIOUS STUDIES 16

5.2 PRODUCTION HABITAT SOURCE IN RELATION TO FOOD HABITS AND PREY DISPERSAL MECHANISMS 16

6.0 ACKNOWLEDGEMENTS 19

7.0 LITERATURE CITED 19

TABLE LEGEND

TABLE 1: Dominant prey data set showing percent that each taxon accounted for in all stomachs examined in Chinook salmon fry, smolts (mixture of hatchery and wild fish) and hatchery-reared smolts. Fourth column shows code used for taxa analysed in habitat source data set. When code is used in consecutive rows, data were aggregated. Fifth column shows the area of habitat sources: MSMS: intertidal mud/ intertidal sand/ marsh/ shallow water; T-S: trees and shrubs; CH: channel; CHIA: chironomid adults; CHIR: chironomid pupae and larvae; EPHE: Ephemeroptera; PLEC: plecopterans; TRIC: trichopterans; and ARBO: arboreal insects. 11

TABLE 2: Mean percentage of counts of seven prey groups in stomach contents of individual juvenile Chinook salmon, arrayed by transect and month. Table 2a,b: fry; Table 2c,d: smolts. See Figure 2 for prey abbreviations. CHIA: chironomid adults; CHIR: chironomid pupae and larvae; EPHE: Ephemeroptera; PLEC: plecopterans; TRIC: trichopterans; and ARBO: arboreal insects. 12

FIGURE LEGENDS

FIGURE 1: 1986 air photo (BCC534/80) of the study area on Queens Reach showing location of the sampling transects for surface trawls. Insets show lower Fraser River and the Fraser River watershed. Barges on Transect E were not present during the trawling in 1988........................ 4

FIGURE 2a: Violin plots for percent composition of taxa in Chinook salmon fry stomach contents by transect. Wider sections of the violin plot represent a higher probability of observations taking a given value, the thinner sections correspond to a lower probability. Each dot represents the percent composition of prey in an individual fish and each half of the plot shows the frequency distribution. CHIA-chironomid adults; CHIR: chironomid pupae and larvae; EPHE: Ephemeroptera; PLEC: plecopterans; CLAD: cladocerans; and ARBO: arboreal insects..........13

FIGURE 2b: Violin plot for percent composition of taxa in Chinook salmon fry stomach contents by month. CHIA: chironomid adults; CHIR: chironomid pupae and larvae, EPHE: Ephemeroptera; PLEC: plecopterans; CLAD: cladocerans; and ARBO: arboreal insects 13

FIGURE 2c: Violin plot for percent composition of taxa in Chinook salmon smolt stomach contents by transect. CHIA: chironomid adults; CHIR: chironomid pupae and larvae; EPHE – Ephemeroptera; PLEC: -plecopterans; TRIC: trichopterans; and ARBO: arboreal insects 14

FIGURE 2d: Violin plot for percent composition of taxa in Chinook salmon smolt stomach contents by month by transect. CHIA: chironomid adults; CHIR: chironomid pupae and larvae; EPHE: Ephemeroptera; PLEC: plecopterans: TRIC: trichopterans; and ARBO: arboreal insects..........14

FIGURE 3: Results of Zero-inflated Beta Regression to test for differences in abundance of chironomid larvae and pupae between seasons (summarized over all transects). Apr = April; Aug = August; Jul = July; Jun = June. 15

ABSTRACT

Levings, C.D., Nishimura, D.J.H, Gregr, E., Whitehouse, T.R., Herunter, H., and Bates, C.R. 2023. Variation in juvenile Chinook salmon (*Oncorhynchus tshawytscha*) diets across the channel and habitats of the lower Fraser River, British Columbia, Canada. Can. Tech. Rep. Fish. Aquat. Sci. 3548: viii + 22 p.

Results of stomach content analyses from Chinook salmon (*Oncorhynchus tshawytscha*) fry and smolts are presented from a surface trawl survey at Queens Reach, lower Fraser River, British Columbia, Canada. The trawl was towed on five one-km long transects parallel to the shore, and approximately 100 m apart, from January to August 1988. Sampling frequency was one to three trips per week. Chironomid larvae dominated fry stomach contents (42%) and also were important in smolt diets (17%). Cladocerans were only found in fry and more arboreal insects were consumed by smolts. Ephemeroptera, Plecopterans, Trichoptera, and a variety of arboreal insects were also found. Using a habitat source data set, taxa prey abundance in stomach contents was uniformly distributed across the transects. Prey produced on the most extensive shallow water habitat (mudflats, sandflats, marshes, shallow water) dominated fry diet and arboreal insects from shrubs and trees were also important for smolts. Channel rearing-migration habitat was subsidized by food produced on the shoreline habitat. Distal habitat food sources such as upstream gravel bars and possibly upstream tidal lakes were also important. Results suggest that a broad-scale, multi-reach approach is required to manage and conserve lower Fraser River juvenile Chinook salmon habitats.

RESUMÉ

Levings, C.D., Nishimura, D.J.H, Gregr, E., Whitehouse, T.R., Herunter, H., and Bates, C.R. 2023. Variation in juvenile Chinook salmon (*Oncorhynchus tshawytscha*) diets across the channel and habitats of the lower Fraser River, British Columbia, Canada. Can. Tech. Rep. Fish. Aquat. Sci. 3548: viii + 22 p.

Les résultats des analyses du contenu stomacal d'alevins et de smolts du saumon chinook (*Oncorhynchus tshawytscha*) qui sont présentés ont été obtenus à partir d'un relevé au chalut de surface effectué à Queens Reach, dans le cours inférieur du fleuve Fraser, en Colombie-Britannique, au Canada. Le chalut a été remorqué dans cinq transects d'une longueur d'un kilomètre, parallèles à la rive et espacés d'environ 100 mètres, de janvier à août 1988. L'échantillonnage était effectué d'une à trois fois par semaine. Les larves de chironomidés composaient principalement le contenu stomacal des alevins (42 %) et occupaient également une place importante dans l'alimentation des smolts (17 %). Des cladocères se trouvaient également dans l'estomac d'alevins, et un plus grand nombre d'insectes arboricoles ont été observés dans l'estomac de smolts. Des éphéméroptères, des plécoptères, des trichoptères et divers insectes arboricoles ont également été détectés. À l'aide d'un ensemble de données de base sur l'habitat, l'abondance des proies dans le contenu stomacal, par taxon, a été uniformément distribuée entre les transects. Les proies se trouvant dans l'habitat d'eau peu profonde le plus vaste (les vasières, les laisses de sable, les marais et les eaux peu profondes) dominaient le régime alimentaire des alevins, et les insectes provenant d'arbustes et d'arbres occupaient une place importante dans l'alimentation des smolts. Les aliments produits dans l'habitat riverain s'ajoutaient à ceux de l'habitat de croissance et de migration du chenal. Les sources d'aliments de l'habitat distal, comme les barres de gravier en amont et possiblement les lacs côtiers en amont, étaient également importantes. Les résultats semblent indiquer qu'il faut adopter une approche à grande échelle et à portée multiple pour gérer et conserver l'habitat des juvéniles du saumon chinook dans le cours inférieur du fleuve Fraser.

1.0 INTRODUCTION

The objective of a detailed cross-channel surface trawl survey conducted in 1988 Queens Reach on the lower Fraser River, British Columbia, Canada was to determine the environmental basis of the production of foods eaten by the young Chinook salmon (*Oncorhynchus tshawytscha*). Chinook salmon are one of the six species of migratory salmonids in the Fraser River system and are important for cultural reasons and ecosystem functioning. They spawn in numerous tributaries as well as the main stem river, ranging up to 1200 kilometre (km) from the mouth. Their juvenile stages migrate to the sea as fry (fish less than one year old) or smolts (fish usually one year old), exhibiting a variety of life history strategies within those time frames (Bourett et al. 2016). These strategies involve downstream movement at various seasons, patterns that involve a rearing migration enabling feeding and growth in the lower Fraser River (Levings, 2004). The feeding habits of juvenile Chinook salmon while on the seaward migration in rivers and streams to the estuary and ocean are an important aspect of the species' fry and smolt life history stages. Energy requirements may be substantial for these stages to support osmoregulation changes during smoltification, predator avoidance and challenges while swimming in strong currents (Levings, 2016).

We were particularly interested in spatial and temporal differences in young Chinook salmon feeding habits relative to assumed availability of prey and local/distant habitat sources and seasonal changes. The lower Fraser River is located in a highly urbanized and industrial region (Metro Vancouver, 2022 population 2.6 M), and, together with climate change, aquatic habitats are under constant threat from further development (Kehoe et al, 2020). Information on habitat sources contributing to the diet of juvenile Chinook salmon are therefore important for fish habitat and ecosystem management. We looked at these questions using a subset of prey data likely being produced on the proximate shoreline habitat on the Reach (nearshore trees and shrubs, marsh, mudflats, sandflats, and channel habitats) as well as distal gravel and cobble habitats upstream. Data on these topics are sparse for the highly industrialized lower Fraser River.

Our data for cross-channel differences in juvenile chinook salmon feeding are therefore unique for the Fraser River system and likely for the species. There have been several detailed accounts of juvenile chinook salmon feeding habits in the estuary proper (e.g., Levings et al, 1991; Macdonald, 1984). However there are only two other available detailed reports on juvenile chinook salmon diets in the tidal freshwater reaches of the Fraser River, above the influence of salt water. In 1973 Northcote et al (1979) sampled with beach seines on the south shore of the river, on Parsons Channel, about five km upstream from Queens Reach. The stomach content data from this site were summarized in figures together with data from two other downstream locations in the region they called "lower mainstem". In their data set, chironomid larvae and pupae were the most common and abundant taxa in fry and smolt stomachs. Chinook salmon fry in a tidal creek draining into the river about five km upstream of Queens Reach mainly ate dipteran larvae, pupae and adults, amphipods and springtails (Levings et al, 1995). There are also a few data available from a tow net survey in the reaches of the Fraser River near New Westminster but the feeding data are summarized at the reach level and only general taxa were given (Goodman, 1974). Most studies of juvenile Chinook salmon in rivers or streams elsewhere sampled nearshore habitats using beach seines and therefore the authors were not able to sample offshore habitats (e.g., Merz, 2001, Limm and Marchetti 2009-California: Muir 1996-Oregon). Exceptions are the mid channel purse seine data in the lower Columbia River by Bottom et al (1990) and recent studies with an offshore tow net, also in the lower Columbia River, Oregon (single transect close to shore; Weikamp et al 2022). Our study is based on a historical data set obtained by several of the authors 35 years ago when Chinook salmon were more abundant in the Fraser River (see Chalifour et al 2022 for information on declines in recent decades). However, the data are important as baseline information and are likely representative of the present-day feeding habits of the species, but are relative to any density-dependent effects. At the time of our study there were eleven Chinook salmon hatcheries in the watershed (see Whitehouse and Levings 1989) releasing smolts into the river so our catches of smolts were a mixture of wild and hatchery raised fish. Hatchery released Chinook salmon smolts substantially increased the number and biomass of the species over natural levels during our sampling.

2.0 STUDY AREA

The Fraser River is the largest river in British Columbia, Canada, with a length of 1,375 km and watershed area of 234,000 km^2 (Figure 1, inset). Our study area in Queens Reach, a six-km channel of the lower Fraser River, between approximately R-km 40 (River-km 40) upstream, as measured from Sandheads Light at the mouth, (49.10588 N, 123.30337 W) and R-km 46, is bordered by the City of Surrey on its south shore and the City of Coquitlam on the north bank (Figure 1). The Reach is located approximately between two highway bridges (the Pattullo and Port Mann bridges) and curves to the southwest in its downstream portion. Our sampling area was in the straight portion of the Reach, about one km downstream of the Port Mann bridge (49.21980 N, 122.81320 W). As shown on contemporary charts the river is about 500 metre (m) wide at the study area but recent modelling shows the width can vary from 500 m to 1000 m wide during freshet, with a narrower range (500-700 m) at low river discharge (Wu et al. 2022). The study area is well upstream of the area influenced by the salt wedge, which is known to penetrate to approximately R-km 30 at low river discharge (Ward, 1976). Two tributaries, the Coquitlam and Pitt Rivers enter the Reach a few kilometres above our study area, on the north shore (Figure 1).

Tide range at Port Mann at low flow is 1.2 m, and is reduced at high river discharge, although flow can be bi-directional even at freshet. Average channel flow velocity during flood tides can be 0.5 to 1 m s^{-1} (flow moving upstream), while ebb tides range from 1 to 1.5 m s^{-1}, with these velocities increasing during freshet. River discharge at Port Mann during the study period ranged from about 1500 $m^3 s^{-1}$ in March to 3000 $m^3 s^{-1}$ in August, with peak discharge of about 9000 $m^3 s^{-1}$ in early May.

The intertidal habitats of the Reach in 1988 were characterized by a mixture of vegetated and developed shorelines (Figure 1). Sediment types on shorelines and channel bottoms were dominated by sand and mud. Developments were mainly on the south shore and consisted of docks related to the forest industry, log storage and riprap for erosion protection.

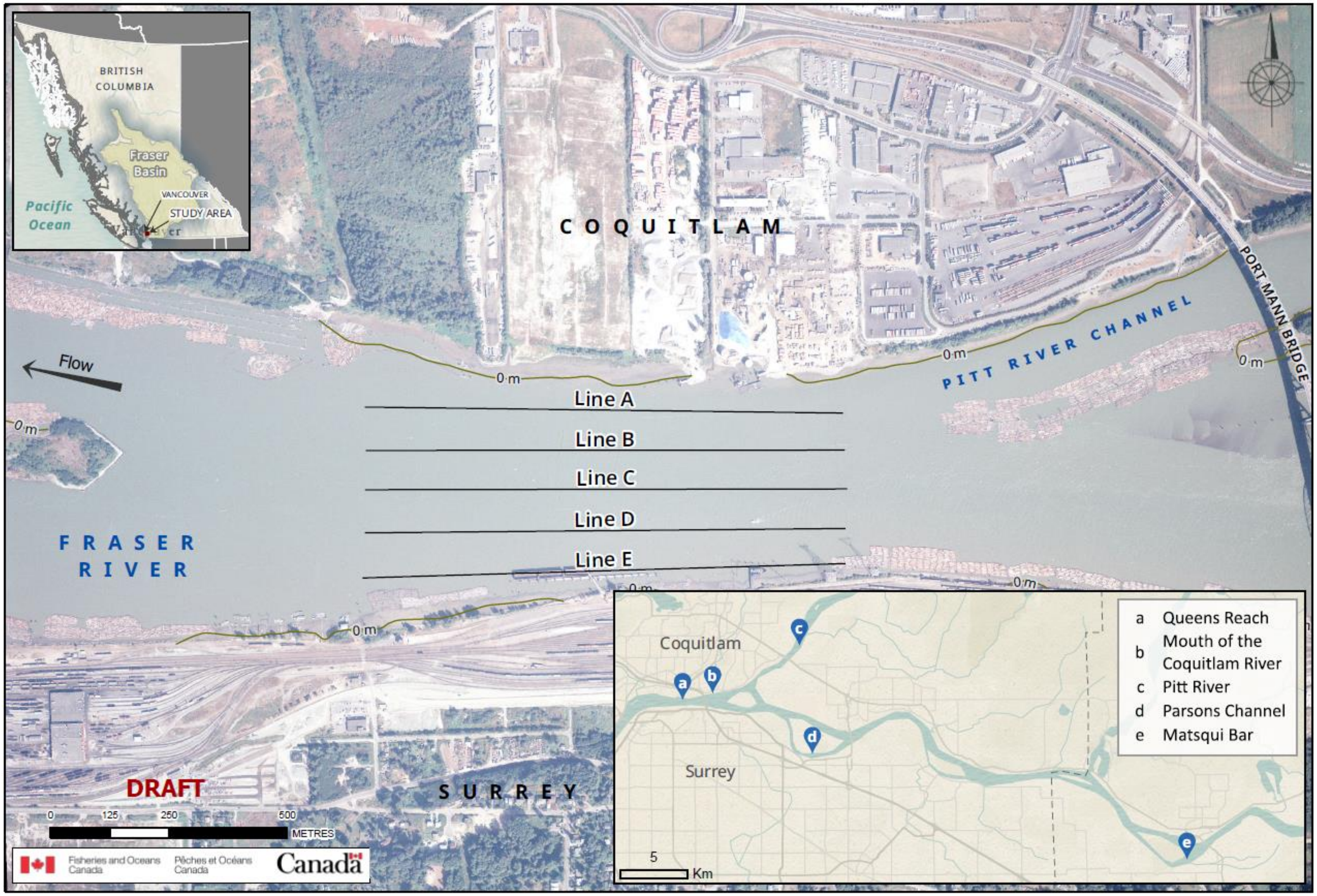

FIGURE 1: 1986 air photo (BCC534/80) of the study area on Queens Reach showing location of the sampling transects for surface trawls. Insets show lower Fraser River and the Fraser River watershed. Barges on Transect E were not present during the trawling in 1988

3.0 METHODS

3.1 SAMPLING TECHNIQUES

The surface trawl used for sampling was a square design with an effective opening of 4 m x 4 m and was held open by a pair of steel trawl doors. Mesh size in the cod-end was 0.5 cm. Complete details on the vessel and equipment used are given in Whitehouse and Levings (1989). Sampling was restricted to the slow water flow period associated with the daily higher high tide. This was the only period during which the trawl gear could be successfully fished without the boat being swept downstream. As a result, time of sampling varied from daylight to dark hours as the work had to be adjusted for tides and currents. Duration of the tows also varied, ranging from approximately 10 minutes (min) to 25 minutes. Towing speed ranged from 36 m min^{-1} to 66 m min^{-1} in an upstream direction.

Samples were obtained on five equally spaced transects from north to south shores, parallel to the shore (Figure 1). Line E on the south shore was about 50 m offshore. Lines D through A were approximately 100 m apart with Line E as a baseline. The transects were sampled weekly during January and February but no Chinook salmon were caught in those months. Sampling increased to one to three trips per week between March and August, when Chinook salmon were in the river. The net was towed approximately one km on each of five transects. Radar was used for positioning.

Subsamples of Chinook salmon were preserved in 10% formalin for stomach content analysis. Fish ≤ 55 mm length were classified as fry and fish ≥ 55 mm length were classified as smolt. The smolt category included an unknown portion of fish that were likely under-yearling migrants moving seaward in June to August. Stomach content data were obtained from 266 Chinook salmon fry, 32 adipose clip Chinook salmon smolts (hatchery production) and 252 unmarked Chinook salmon smolts (mixture of wild smolts and unmarked hatchery fish) (Nishimura et al. 1995). The sample size distributions by time and transect are a reflection of the catch patterns for Chinook fry and smolts. Fry were caught from early March to mid June and smolts from late March to mid August (Whitehouse and Levings, 1989). Most of the fry samples were from April catches (124) while most of the smolt samples were from May, June and July. Samples from across the five transects were fairly evenly distributed, with the number of fry samples ranging from 48 on transect B to 53 on transects A and C. For smolts, sample sizes ranged from 61 on transect A to 35 on transect E.

3.2 STOMACH CONTENT ANALYSIS

In the laboratory, fish preserved in 10% formaldehyde were rinsed in tap water for 24 hours. Fork length and weight of the preserved fish were measured and each specimen assigned a unique identification number. The stomach was removed from each chinook after an incision was made from its anus to the operculum. Food items or contents were analyzed and counted under a Wild Heerbrugg stereo microscope and identified, where possible, to order, family or genus.

3.3 DATA SETS

Most of the data analysis focused on fry and smolts and because not all hatchery reared Chinook are marked with a missing adipose fin our smolt data are from a mixture of wild and hatchery fish. The 32 marked fish we did sample were used for a specific analysis of inorganic items in the diet of wild vs hatchery fish and were included in the dominant prey data set described below

Two data sets were used in the statistical analysis for this report. The first one was a reduced data set accounting for about 85% of the dominant prey based on their numerical abundance (hereafter “Dominant prey data set” (Table 1).

A second data set was used for an analysis of potential food supply from various habitats (hereafter “Habitat Source Data Set”, Table 1). We assumed the following habitats were sources of production of some of the dominant food species in our analysis of the diet of juvenile Chinook salmon fry and smolt:

- **Marsh, mud and sand shorelines, shallow water** chironomid adults, chironomid pupae and larvae, Ephemeroptera
- **Riparian grass, shrubs and trees**: arboreal insects
- **River channel**: cladocerans (Crustacea)
- **Gravel reach** upstream: Plecopterans and Trichoptera

To aggregate data for the latter two taxa, several lower taxa units (e.g., families) were aggregated from the full data set (Table 1). These seven prey groups accounted for about 72% of the dominant food groups for fry and about 59% of the dominant food groups for smolts.

The entire database of the 550 juvenile Chinook salmon stomach contents, with all prey species uniquely coded, together with lengths, weights and biomass of food bolus of individual fish is presented in the open access file (https://publications.gc.ca/site/eng/450001/publication.html). The database also includes the biophysical data associated with each fish - date, transect, time of capture, river discharge, flow rate, and surface temperature.

3.4 HABITAT SOURCES MAPPING

Shorelines that include intertidal and near-shore riparian areas within the then-existing Fraser River Estuary Management Program (FREMP) (see Dorcey, 2004) were classified and colour-coded on the basis of the relative values of their habitat features in 1986. Examples of habitat features included mudflat, marsh, and bottomland forest. The classification system was based on an inventory of all habitat types in the estuary, and was used to estimate the area of the various habitats that we used in this study as local potential production sites for invertebrate prey for juvenile Chinook salmon. As well as including the specific shorelines inshore of our transects, this map also showed habitats approximately 1.5 km further up the Reach. Shoreline and channel habitats on Queens Reach, characterized by sand and mud substrates, are representative of a major portion of the river’s freshwater tidal habitat. The Fraser River is tidal approximately another 55 km upstream. Gravel substrates dominate shorelines upstream from R-km 90 (Rice and Church, 2010).

3.5 STATISTICAL METHODS

Violin plots (Hintze and Nelson, 1998) were developed to explore differences in habitat-sourced prey across the transects and seasonally. A trial was conducted on the use of Bayesian Inference for Beta Regression and Zero-or-One Inflated Beta Regression for further analyses.

4.0 RESULTS

4.1 DOMINANT PREY DATA SET

One hundred sixty-four taxa of invertebrates and two representatives of fish were found in the stomachs of the fry, smolts, and marked smolts. Representatives of four phyla were found in stomachs. Phylum Arthropoda accounted for most taxa, with Class Insecta dominating the diet along with Crustacea (cladocerans and amphipods) and Collembola. Representatives of Arachnida (spiders and mites) and few fish eggs and unidentifiable fry (Phylum Chordata) were also found. Nematodes (Phylum Nematoda) were also observed in the stomachs but some may have been parasites.

Inorganic items were present in 7.5% of fry stomachs and 7.9% of unmarked smolt stomachs and were noted as clay, sand, pieces of plastic or Styrofoam. More inorganic items were found in marked smolts (18.7%) (chi sq $p<0.05$).

The majority of food items in fry, smolts and marked smolts consisted of chironomid larvae, pupae and adults as these three taxa were among the top six ranked prey, along with unidentified Ephemeropteran nymphs, Heptageniid nymphs and Plecopteran nymphs. Cladocera, unidentified Homopteran adults and unidentified insects were also relatively highly ranked (Table 1). Differences in percent composition of the diet of the Chinook fry, smolts and marked smolts were not significant ($p>0.05$; Kruskal-Wallis).

4.2 TRANSECT AND SEASONAL TRENDS IN HABITAT-SOURCED PREY

Violin plots were prepared showing the distribution of the percent contribution of chironomid adults, chironomid pupae and larvae (Ephemeroptera, plecopterans, trichopterans, cladocerans and arboreal insects to juvenile Chinook fry and smolt stomach contents by transect and month of sampling (Figure 2 a, b, c, d). Mean percent abundance for each taxon was also calculated by month and transect (Table 2).

4.2.1 FRY

Transect analysis: The mean percent abundance of each of the six prey types found in fry stomachs did not vary significantly ($p>0.05$) across the transects. Chironomid pupae and larvae were the dominant prey the prey in Chinook salmon fry (mean percent abundance 68.6 %; standard error (se,) 0.02%)). Adult chironomids (12.2%, 0.01) and Ephemeroptera (13.6%, <0.01) were also important prey on each of the sampling lines. Plecopterans accounted for relatively low percentage (3.2%, .01) Cladocerans and arboreal insects were also prey on all transects but were fewer in fry stomachs (1.2%, 0.01 and 1.2%, 0.03) (Table 2a)

Seasonal analysis: Chironomid pupae and larvae were consistently important to fry through the sampling season, ranging from 71.0% of prey numbers in April to 41.5% in June. Chironomid adults accounted for a range of 8.9% to 18.2% over the season. Ephemeroptera were consumed mainly in May 19.6%, with other months ranging from <1.0% to 12.1%. Most Cladocerans were consumed in March (3.9%, later months < 1%). Plecopterans were eaten mainly in June (22.9%, range down to 1.5%). Arboreal insects were less important in June (5.8 %, range down to <1%). (Table 2b). Sample sizes were too small for statistical analyses of differences between months.

Median percentages for fry food items were calculated for each of the violin plots (Table 3). For both the transect and seasonal analysis all medians were zero, except for Chironomid larvae and pupae (0.75 for transect and 0.71 for seasonal). There no differences in medians across transect or seasons ($p>0.05$, sign test).

4.2.2 SMOLTS

Transect analysis: The mean percent abundance of each of the six most important (Chironomid pupae and larvae, Chironomid adults, Ephemeroptera, Plecoptera, Trichoptera and arboreal insects) prey types did not vary significantly in smolt stomachs sampled. across the transects (p>0.05). As with fry, chironomid larvae and pupae were the dominant prey for smolts (mean 38.6%, se <0.01) Mean chironomid adult importance was 21.9%, 0.03), followed by ephemeropterans (15.6 %). Mean abundance of arboreal insects was 9.7%, 0.01), followed by plecopterans (8.0%, 0.02)) and Trichopterans (5.9%, 0.01) (Table 2c).

Seasonal analysis: Chironomid larvae and pupae were dominant prey in April and May and were least important in June (54.1%-27.3%). Chironomid adult usage increased in summer and was lower in April and May (48.4%-4.9%). Ephemeropterans were also important in spring but decreased as prey in August (28.0% to <1%). Plecopterans were mainly eaten in June, with low contributions in other months (21.8% -<1%). Arboreal insects were consumed heavily in summer relative to spring (12.6 % in August-7.8% in April). Trichopteran usage ranged from 3.1% in August to 8.5 % in May. (Table 2d). Sample sizes were too small for statistical analyses of differences between months.

Median percentages for smolt food items were calculated for each of the violin plots (Table 3.). For both the transect and seasonal analysis all medians were zero, except for Chironomid larvae and pupae (0.33 for transect and 0.25 for seasonal). There no differences in medians across transect or seasons (p>0.05, sign test).

4.2.3 USE OF BAYESIAN INFERENCE FOR BETA REGRESSION AND ZERO-OR-ONE INFLATED BETA (ZOIB) REGRESSION FOR FURTHER ANALYSES

Using the parametric method described in the methods Section (page x) to test for differences in prey counts based on percentages in stomachs across transects and seasons and other characteristics of the data may be causing a type two error i.e. the error that occurs when one fails to reject a null hypothesis that is actually false). For this reason, a preliminary investigation of alternate statistical methods was conducted.

There are several challenging characteristics of the data: 1) its use of percentages (i.e. scaled data) restricts the data values between 0 & 1; 2) they are ‘zero-inflated’, but also '1-inflated’, with numerous zeros where no numbers of a particular prey was found in a stomach, but also cases where a single type of prey represented 100% of what was found in a given stomach; 3) unequal sample sizes, and in some cases a small or nil sample sizes, because sample size at any given time was dictated by the number of fish caught, and sometime few or no fish were caught on a given transect in a given month; 4) six different response variables (which correspond to the six prey type groups in each of the fry and smolt data sets) 5) a special case of ‘zero’ where fish were caught but no prey were found in their stomachs

A Bayesian approach called Zero-inflated Beta Regression (ZOIB) was tested (https://mvuorre.github.io/posts/2019-02-18-analyze-analog-scale-ratings-with-zero-one-inflated-beta-models/), which accommodates points 1 and 2. In the case of this paper, and in the worked example that follows, the general case of the ZOIB model (which usually allows for “zero or one”) is extended to allow for both zero and one inflation, a flexibility which makes this model even more appropriate.

For point 3 a suggested solution is to a) pool across months for analysis of the between-transect differences in abundance of each prey type, and b) to pool across transects for each month to look at temporal shifts in predation of particular prey types.

Point 4 manifests as a large number of pairwise comparisons required to test hypotheses, and thus elevated Type 1 statistical errors. With the case of, for example, six prey and two fish stages (smolt, fry), and two explanatory variable (Month, Transect) there will be 6 x 2 x 2 = 24 separate analyses. However, within the explanatory variables there are 6 levels for month and 5 levels for Transect), so it is more similar to 6 x 2 x 15 = 180 comparisons for the analysis of month-to-month differences (pooling across transects, and 6 x 2 x 10 = 120 comparisons for the analysis of differences across transects when pooling across month. This could result in a total of 300 pairwise comparisons but this does not consider multi-factor analysis to look at interactions.

Regarding point 5, a suggested approach is to use a zero for each instance where the fish had no food in its stomach. For this analysis we are not considering the ‘community’ of food in a given stomach, rather just the abundance of each prey type, and a zero is a zero for a given prey type regardless of whether there were other prey types found in a given stomach.

Two tests were completed using ZOIB and demonstrated that there was no difference in abundance of CHIR in stomachs from smolts caught on transect A compared to B. There was a difference in chironomid larvae and pupae abundance in stomachs from fish caught in May vs July (Figure 3).

4.2.4 HABITAT SOURCE ANALYSIS

Using measurements of potential prey source habitats from the FREMP map and a 1986 air photo, areal estimates of the various habitats were as follows: intertidal mud (10.1 ha), sand flats (0.4 ha), marsh (1.6) and shallow water (up to about one m depth at low tide 0.2 ha). Trees (6.2 ha) and riparian shrubs (4.4 ha) also accounted for a major portion of the shoreline habitat. The open, deep (over one m deep at low tide) water habitat of the main river channel at Queens Reach dominated the area (500 ha) (Table 1).

4.3 DATA TABLES

TABLE 1: Dominant prey data set showing percent that each taxon accounted for in all stomachs examined in Chinook salmon fry, smolts (mixture of hatchery and wild fish) and hatchery-reared smolts. Fourth column shows code used for taxa analysed in habitat source data set. When code is used in consecutive rows, data were aggregated. Fifth column shows the area of habitat sources: MSMS: intertidal mud/ intertidal sand/ marsh/ shallow water; T-S: trees and shrubs; CH: channel; CHIA: chironomid adults; CHIR: chironomid pupae and larvae; EPHE: Ephemeroptera; PLEC: plecopterans; TRIC: trichopterans; and ARBO: arboreal insects; Hectare (ha).

Type of invertebrate	Fry	Wild or Hatchery smolt	Hatchery smolt	Code for Habitat Source Data Set	Habitat Source/ Area (ha) In Reach
Unidentified adult dipterans	1.83	4.71	1.95		n.a.
Unidentified larval dipterans	1.7	1.31	0.31		n.a.
Chironomid larvae	41.27	17.02	8.77	CHIR	MSMS/12.3
Chironomid pupae	11.54	0	6.35	CHIR	MSMS/12.3
Chironomid adults	11.86	10.21	17.5	CHIA	MSMS/12.3
Ceratopogonid larvae	1.05	0	0.44		n.a.
Ceratopogonid adults	0.15	2.36	0.84		n.a.
Unidentified Emphemeroptera nymphs	1.94	13.87	1.38	EPHE	MSMS/12.3
Heptageniidae nymphs	3.05	0	2.06	EPHE	MSMS/12.3
Unidentified Homoptera adults	1.17	10.99	5.71	ARBO	T-S/10.4
Cicadellidae adult	0.24	0	1.83	ARBO	T-S/10.4
Psyllidae adult	0.27	0	3.57	ARBO	T-S/10.4
Hymenoptera adult	0.09	6.02	0.58	ARBO	T-S/10.4
Plecoptera nymphs	0.78	7.33	1.89	PLEC	Lotic (upstream gravel)
Plecoptera adults	0.18	1.83	0.29	PLEC	Lotic (upstream gravel)
Psocoptera adults	0	3.14	0.09	ARBO	T-S/10.4
Unidentified Trichoptera adults	0.09	4.97	0.12	TRIC	Lotic (upstream gravel)
Unidentified Hydropsychidae larvae	0.18	0	1.21	TRIC	Lotic (upstream gravel)
Collembola adults	1.91	0.79	0.32	ARBO	T-S/10.4
Cladocera	1.37	0	11.58	CLAD	CH/500.0
Arachnida	0.42	3.93	1.55	ARBO	T-S/10.4
Unidentified insecta	4.31	1.84	16.75		n.a.
Nematoda	0.06	1.31	1.54		n.a.
Coleoptera	0.03	1.05	0.97	ARBO	T-S/10.4
Hemiptera	0	0	2.23		n.a.

TABLE 2: Mean percentage of counts of seven prey groups in stomach contents of individual juvenile Chinook salmon, arrayed by transect and month. Table 2a,b: fry; Table 2c,d: smolts. See Figure 2 for prey abbreviations. CHIA: chironomid adults; CHIR: chironomid pupae and larvae; EPHE: Ephemeroptera; PLEC: plecopterans; TRIC: trichopterans; and ARBO: arboreal insects.

Table 2a

	CHIA	CHIR	EPHE	PLEC	CLAD	ARBO
A	0.117	0.735	0.102	0.015	0.022	0.008
B	0.114	0.732	0.116	0.010	0.013	0.016
C	0.153	0.607	0.163	0.056	0.000	0.021
D	0.115	0.664	0.176	0.027	0.011	0.006
E	0.108	0.693	0.122	0.054	0.014	0.009

Table 2b

	CHIA	CHIR	EPHE	PLEC	CLAD	ARBO
Mar	0.182	0.685	0.069	0.015	0.039	0.010
Apr	0.114	0.710	0.122	0.037	0.008	0.009
May	0.089	0.681	0.196	0.019	0.000	0.013
Jun	0.097	0.416	0.200	0.229	0.000	0.059

Table 2c

	CHIA	CHIR	EPHE	PLEC	ARBO	TRIC
A	0.275	0.403	0.114	0.073	0.105	0.030
B	0.169	0.407	0.159	0.072	0.117	0.076
C	0.276	0.372	0.145	0.063	0.088	0.056
D	0.201	0.357	0.205	0.050	0.129	0.057
E	0.176	0.395	0.159	0.143	0.049	0.077

Table 2d

	CHIA	CHIR	EPHE	PLEC	ARBO	TRIC
Apr	0.078	0.524	0.281	0.009	0.078	0.031
May	0.049	0.541	0.223	0.022	0.080	0.085
Jun	0.148	0.290	0.191	0.218	0.094	0.058
Jul	0.402	0.274	0.067	0.075	0.126	0.056
Aug	0.485	0.349	0.001	0.010	0.123	0.031

4.4 FIGURES

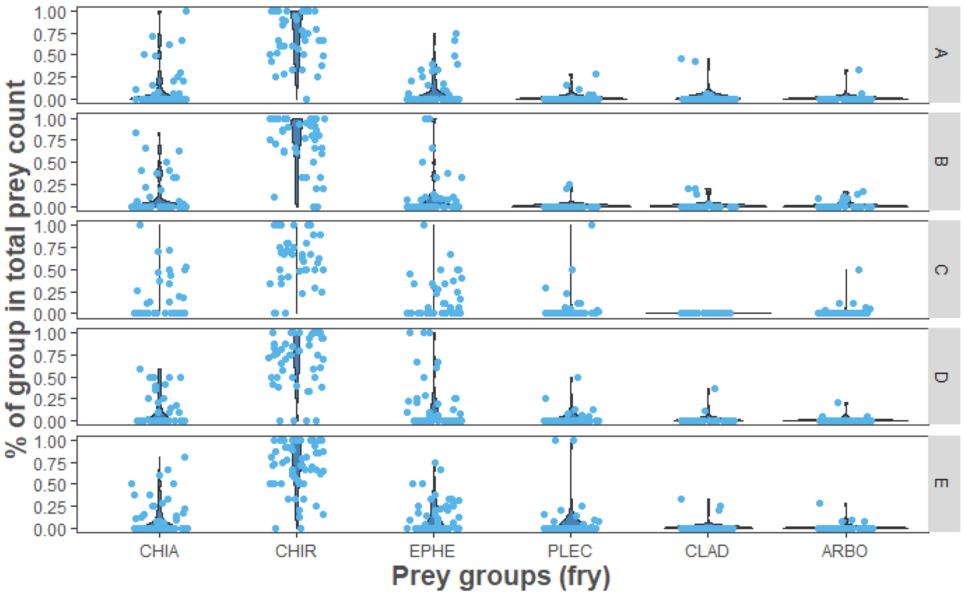

FIGURE 2a: Violin plots for percent composition of taxa in Chinook salmon fry stomach contents by transect. Wider sections of the violin plot represent a higher probability of observations taking a given value, the thinner sections correspond to a lower probability. Each dot represents the percent composition of prey in an individual fish and each half of the plot shows the frequency distribution. CHIA: chironomid adults; CHIR: chironomid pupae and larvae; EPHE:- Ephemeroptera; PLEC: plecopterans; CLAD: cladocerans; and ARBO: arboreal insects.

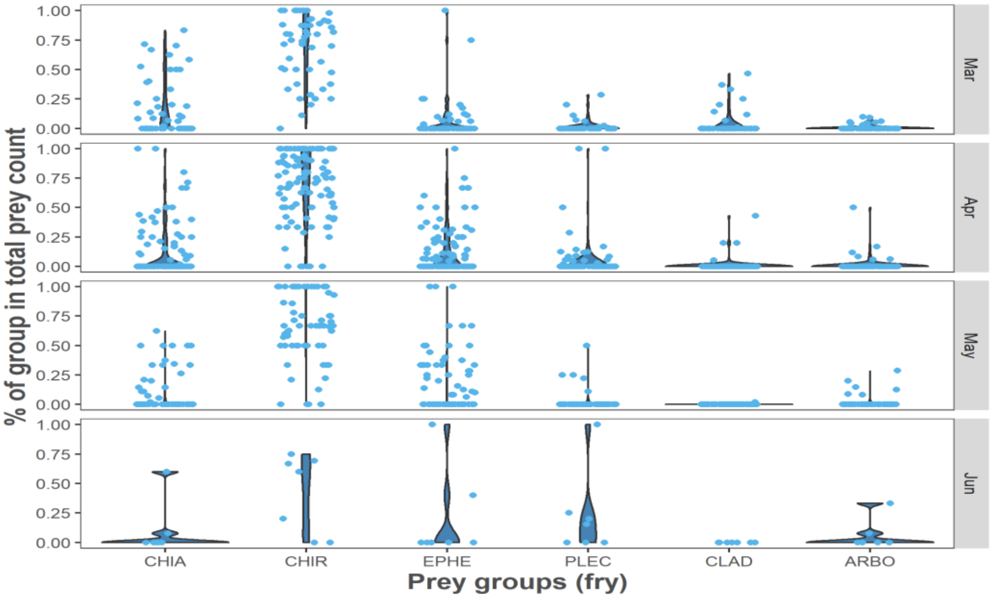

FIGURE 2b: Violin plot for percent composition of taxa in Chinook salmon fry stomach contents by month. CHIA: chironomid adults; CHIR: chironomid pupae and larvae; EPHE: Ephemeroptera; PLEC: plecopterans; CLAD: cladocerans; and ARBO: arboreal insects.

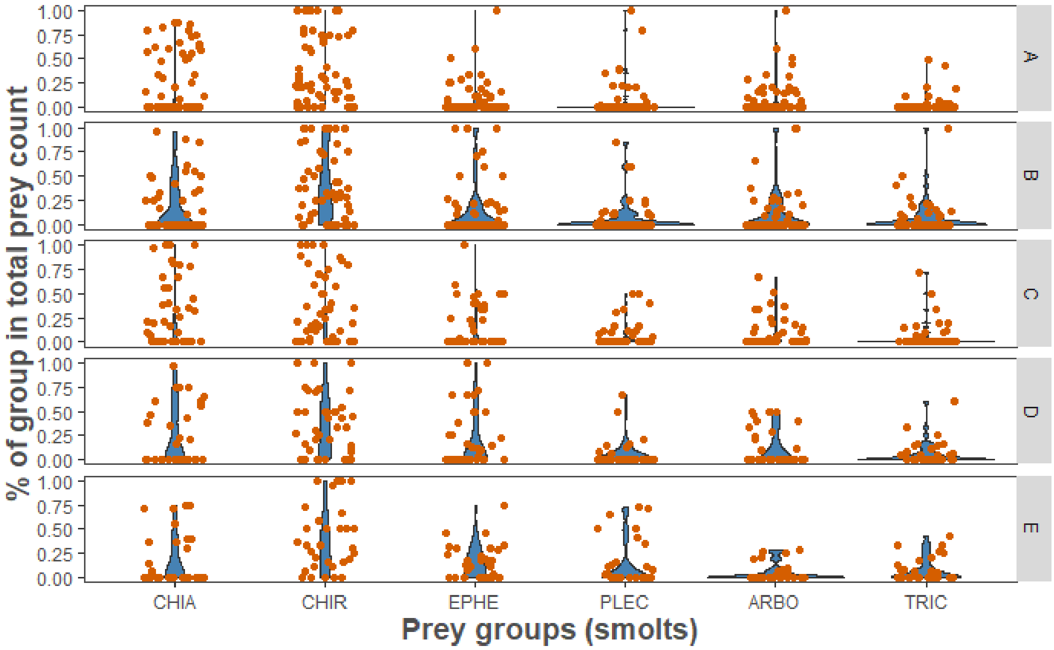

FIGURE 2c: Violin plot for percent composition of taxa in Chinook salmon smolt stomach contents by transect. CHIA: chironomid adults; CHIR: chironomid pupae and larvae; EPHE: Ephemeroptera; PLEC: plecopterans; TRIC:-trichopterans; and ARBO: arboreal insects.

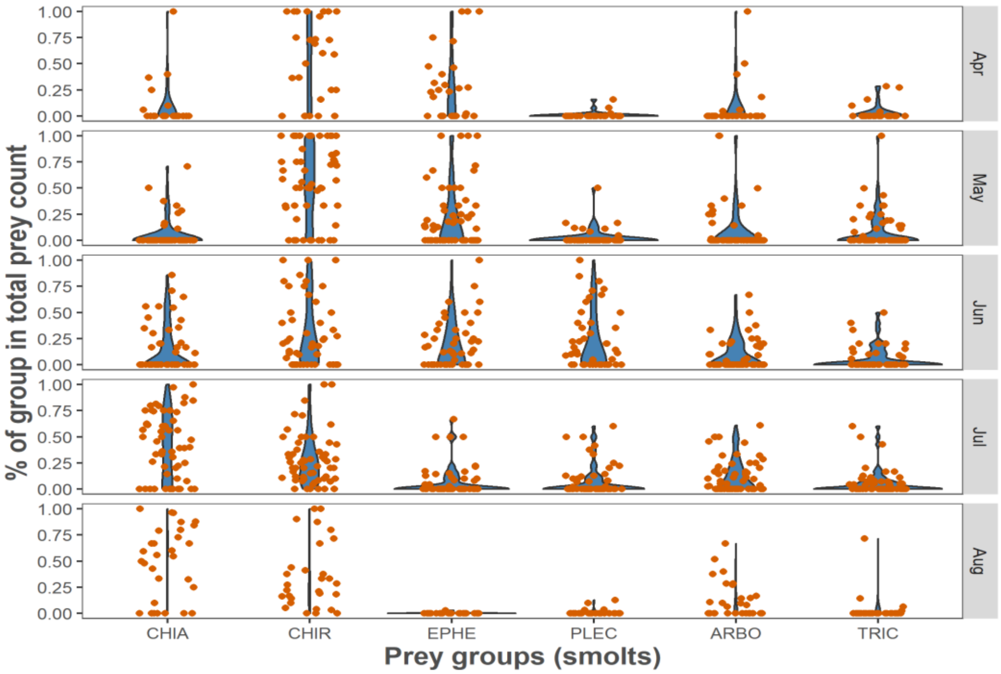

FIGURE 2d: Violin plot for percent composition of taxa in Chinook salmon smolt stomach contents by month by transect. CHIA: chironomid adults; CHIR: chironomid pupae and larvae; EPHE: Ephemeroptera; PLEC: plecopterans; TRIC: trichopterans; and ARBO: arboreal insects.

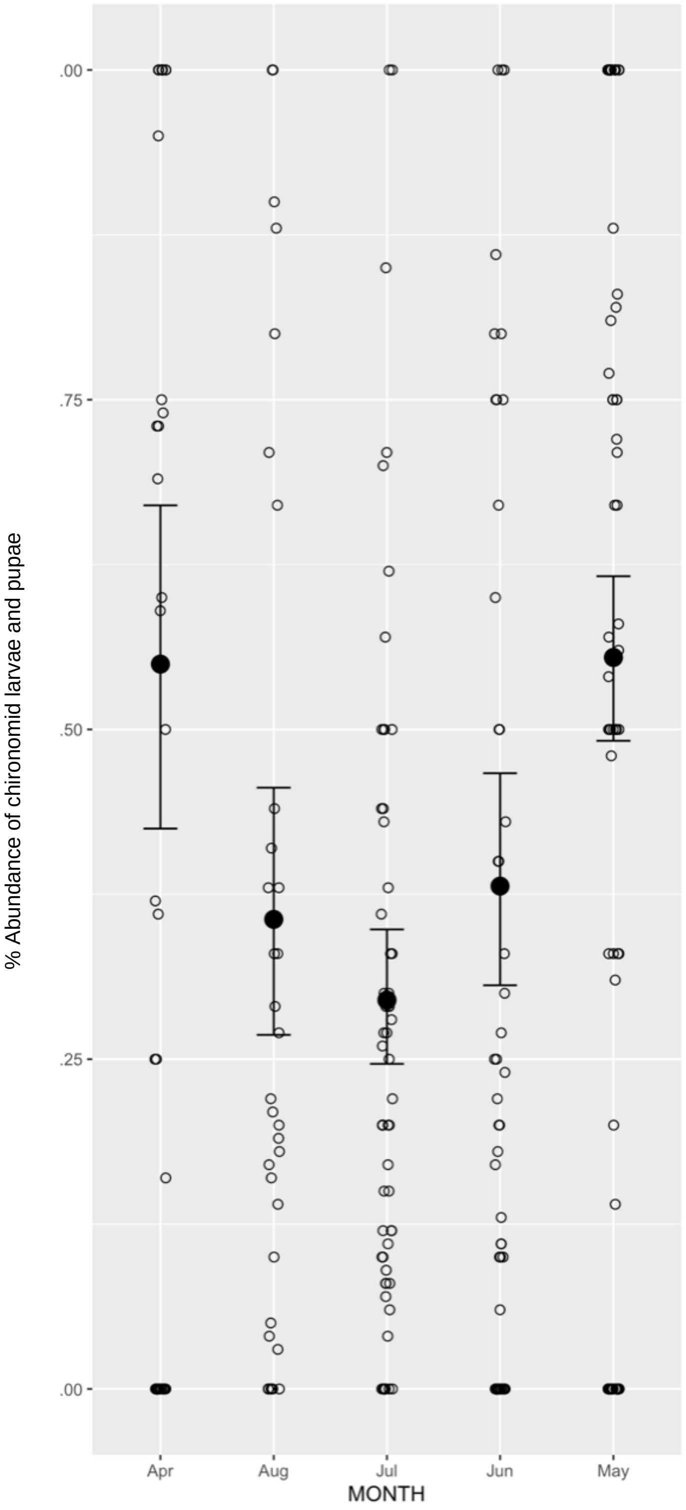

FIGURE 3: Results of Zero-inflated Beta Regression to test for differences in abundance of chironomid larvae and pupae between seasons (summarized over all transects). Apr = April; Aug = August; Jul = July; Jun = June.

5.0 DISCUSSION

5.1 COMPARISONS WITH PREVIOUS STUDIES

In general, the food spectrum of juvenile Chinook salmon was similar to that found in rivers in California (e.g., Merz, 2001), Oregon (Muir et al. 1996), Washington (McCain et al. 1990) and Alaska (Neuswanger et al. 2014). A wide variety of insects and crustaceans characterized stomach contents in these studies. As well, our findings on the diet composition of Chinook salmon fry and smolts are quite similar to those described by Northcote et al. (1979) from forty beach seines that caught juvenile Chinook salmon (32 fry and 8 smolts) in 1973 at in the lower mainstem Fraser, with some notable exceptions. These differences possibly can be attributed to differences in sampling methods and Chinook salmon populations sampled. Dipteran insects, possibly chironomids as we found, dominated the stomach contents for fry in the Northcote's (1979) work. We found cladocerans in fry stomach contents of fish caught by surface trawl but this taxon was not recorded in the beach seine study, possibly because the planktonic crustacea may have been more abundant further offshore in deeper water. Smolt stomachs from beach seining were also dominated by dipterans, as we found, but plecopterans and fish eggs and small fish were the second and third most abundant taxa, whereas in our trawl caught Chinook smolts, fish eggs and fish were rare. Insight into differences in availability of fish as prey for juvenile Chinook salmon might be facilitated by comparison of the fish communities present in 1973 (Northcote et al. 1978), in 1994 (Richardson et al. 2000) and our study in 1988 (Whitehouse and Levings, 1989). Although mysids were fairly numerous in the 1973 stomach samples, none were found in our study. Plecopterans were most abundant in fry and smolts caught by trawl in June and were found in uniform abundance across the transects. The differences in stomach content across transects may also be attributed to prey availability from both distal (outside of Queens Reach, likely upstream) and proximate (within Queens Reach, shoreline and channel) habitats, as described next.

5.2 PRODUCTION HABITAT SOURCE IN RELATION TO FOOD HABITS AND PREY DISPERSAL MECHANISMS

A variety of interacting factors such as abundance, size, behaviour, colour, and nutritional factors influence prey uptake by salmonids (see Levings, 2016). Using a habitat source analysis, we here discuss the possible relationship between habitat production area as a surrogate for prey abundance in our study area and consumption by juvenile Chinook salmon. We also comment on implications of habitat loss and climate change for juvenile Chinook salmon food sources.

Chironomids and ephemeropterans, some of the most important prey for Chinook fry and smolts, are produced on proximate habitats within Queens Reach (Table 1): intertidal mud (10.1 hectare (ha)), sand flats (0.4 ha) and marsh (1.6) as well as shallow water (0.2 ha). Chironomid larvae were about 10 times more abundant in shallow water grab samples relative to plecopterans, trichopterans and ephemeropterans at Parsons Channel (Northcote et al. 1976). Chironomid pupae and adults are clearly associated with emergent vegetation such as sedges (Whitehouse et al. 1993). Mid-river and nearshore abundance of daytime drift fauna in the lower mainstem area (Northcote et al. 1976) was about the same (25 organisms m^{-3}). Aerial dispersion of adult insects) produced on both north and south shores of the Queens Reach may have been moved by air currents across the Reach (Hardy and Milne, 1938; Bogan and Boersma, 2012). Chironomids and ephemeropterans were likely similarly available to juvenile Chinook salmon across the channel.

Weather, tides and currents affect dispersion of invertebrates within and into Queens Reach making associations between extent of various habitats and local prey availability complex. Surface drift invertebrates are also entering the Reach from upstream, although drift abundance was lower at the middle mainstem and upper mainstem sites studied by Northcote et al. (1976). The production of food invertebrates from intertidal mud, intertidal sand, marsh and shallow water in the study Reach is significant and the four habitats account for about 50% of the intertidal area available as source for these prey species. This “habitat budget” puts considerable weight on their importance as a local chironomid and Ephemeroptera resource for juvenile Chinook salmon.

Arboreal insects are associated with shoreline trees and shrubs. While trees (6.2 ha) and riparian shrubs (4.4 ha) accounted for a major portion of the habitat along the shorelines of our study reach, mean abundance of arboreal insects on the transects analysis for fry stomach content was low, about 1% consumed on any of the transects. However arboreal insects were particularly eaten by Chinook smolts in summer (up to 9 %), suggesting this taxon may be a supplemental food when the production of aquatic insects from the other intertidal habitat decreases.

The open water habitat of the main river channel at Queens Reach dominated the distal area (about 500 ha) of our study and the cladoceran crustaceans produced there or swept downstream into the reach (e.g., from connected Pitt Lake (Henderson et al. 1991) were important to Chinook salmon fry but not smolts. This may be owing to size differences as the small cladocerans may match prey dimensions for fry but not smolt, although the relatively large representation of cladocerans in hatchery smolts (Table 1) is an anomaly. Diurnal migration of the cladocerans may have reduced the availability to juvenile Chinook and as our samples were obtained in a mixture of day and night, further analyses are required. Cladocerans are likely abundant in the reach as Breckenridge (2022) reported their abundance was 50 individuals m^{-3} at a site 10 km downstream and were also found in midchannel tow net samples at Parsons Reach site (Northcote et al 1976). Thus, while the deep water is clearly important as rearing and migratory habitat, in situ-produced food availability appears to be limited. Juvenile Chinook fry using the channel receive a food subsidy from shoreline habitat production sites, notably those for dipteran insects.

The presence of gravel-dwelling plecopterans and trichopterans in stomachs indicate that Chinook salmon fry and smolts used distal food production sources upstream as sediments in Queens Reach are dominated by mud and sand. Chinook salmon smolts in the Queens Reach area and upstream were estimated to migrate at about 2.3 km · h^{-1} (Hvidsten et al. 1996) so with a travel time of about 20 h from the first major gravel habitat upstream at R-km 90 (Matsqui Bar, Rice and Church 2010) consumed plecopterans and trichopterans would be incompletely digested (Mock et al. 2022) when the fish were caught in our study. Plecopterans accounted for about 10% (numerical data) of the stomach contents of Chinook salmon fry and about 30 % of stomach contents of Chinook salmon smolts in the Northcote et al. (1979) study in the lower mainstem Fraser. As suggested by Northcote et al. (1979), it is likely the juvenile Chinook fed on plecopterans and trichopterans when they were migrating out of tributaries or through the extensive upstream gravel reaches of the river (approximately R-km (90km)) (Ashley, 2020; Rempel et al. 2000).

In summary the findings of food from proximate (local) and distal (upstream) habitats in juvenile Chinook salmon diets at Queens Reach support the idea of food continuum, with consecutive invertebrate communities (lotic insects such as plecopterans shifting to soft-sediment prey such as chironomids) as the fish migrate downstream. As well our results suggest that intertidal and shallow water habitats provide dipterans and other invertebrates swept across the Reach by air and water currents, providing a food subsidy (Richardson et al. 2010) for the deep channel rearing-migration corridor. It is important to maintain and restore these ecological conditions supporting Chinook salmon in the freshwater tidal reaches of the Fraser River.

Sea level rise and climate change could affect the integrity of intertidal mud, intertidal sand, marsh and shallow water habitats, for example by progressive deepening as river water levels increase. Another possible change might stem from lower flows in the river owing to climate change, resulting in increased penetration of the salt wedge in the lower river. This could result in the “estuarine squeeze” (Little et al. 2022) of the distinctive freshwater tidal zone of Queens Reach with its characteristic habitat and species. On the other hand, the salt wedge could bring brackish water species into Queens Reach such as calanoid copepods found further downstream (Levings, 1980, Breckenridge et al. 2020), possibly enhancing the potential food supply. However, there is a further risk that the salt wedge could bring larvae of invasive species found in the estuary proper (e.g., the bamboo worm, *Clymenella torquata*, Mach et al. 2012).

Ongoing foreshore development in the lower Fraser River, including from gravel removal, dredging, dyke modifications/upgrades, and log storage will continue to impact and reduce shallow water habitats, cause shoreline hardening, and transfer river energy downstream, which will result in further loss of these important nearshore shallow water habitats (Kehoe et al. 2021). These broad scale habitat changes as well as local losses from urban development could result in decreased productivity and abundance of key prey items for juvenile Chinook salmon. Results suggest that a broad scale, multi-reach approach is required to manage and conserve lower Fraser River juvenile Chinook salmon habitats. To further assist management knowledge of the habitat ecology of the lower Fraser River needs to be updated with new surveys and techniques to assess contemporary conditions.

6.0 ACKNOWLEDGEMENTS

Thanks are owing to field staff Suzanne Dionne and S. Doyle for assistance with the sampling and to Corrine Nidoy for preparation of Figure 1. Megan Francisco and Tolulope Amuwo assisted in data analysis. Dr. John Richardson kindly provided many useful comments on the manuscript. Mitchell Hoyle reviewed and formatted the report, Dr. Terri Sutherland helped edit the final manuscript and also helped in the field work when she was a student.

7.0 LITERATURE CITED

Ashley, K. (Ed). 2020. The Heart of the Fraser. BCIT Rivers Institute.

Bogan, M. T., and K. S. Boersma. 2012. Aerial dispersal of aquatic invertebrates along and away from arid-land streams. Fresh. Sci. 31(4): 1131-1144.

Bourret, S. L., C. C. Caudill, and M. L. Keefer. 2016. Diversity of juvenile Chinook salmon life history pathways. Rev. Fish Biol. Fish. 26(3): 375-403.

Breckenridge, J., E. Pakhomov, S. Emry, and N. Mahara. 2020. Copepod Assemblage Dynamics in a Snowmelt-Dominated Estuary. Est. Coast. 43: 1502–1518.

Breckenridge, J. 2022. Copepod dynamics of the Fraser River estuary. Ph.D. Thesis. Oceanography, University of British Columbia.

Chalifour, L., C. Holt, A. E. Camaclang, M. J. Bradford, R. Dixon, R. J. Finn, and T. G. Martin. 2022. Identifying a pathway towards recovery for depleted wild Pacific salmon populations in a large watershed under multiple stressors. J. Appl. Ecol. 59(9): 2212-2226.

Dorcey, A.H.J. 2004. The Evolution of Estuarine Governance in a Metropolitan Region: Collaborating for Sustainability in the Fraser River Estuary. *In* Fraser River Delta, British Columbia: Issues of an Urban Estuary. *Edited by* B.J. Groulx, D.C. Mosher, J.L. Luternauer, and D.E. Bilderback. Geol. Surv. Can. Bull. 567, 247-263.

Goodman, D. 1975. Fisheries Resources and Food Web Components of the Fraser River Estuary and on Assessment of the Impacts of Proposed Expansion of the Vancouver International Airport and Other Developments on These Resources. Dep. Environ., Fish. Mar. Serv. Vancouver, B.C.

Hardy, A. C., and P. S. Milne. 1938. Studies in the Distribution of Insects by Aerial Currents. J. Animal Ecol. *7*(2): 199–229.

Henderson, M.A., R.E. Diewert, J. Hume, K. Shortreed, D. Levy, and K. Morton. 1991. The carrying capacity of Pitt Lake for juvenile sockeye salmon (*Oncorhynchus nerka*). Can. Tech. Rep. Fish. Aquat. Sci. 1797.

Hintze, J. L., and R. D. Nelson. 1998. Violin plots: a box plot-density trace synergism*.* The Americ. Statist. 52(2): 181-184.

Hvidsten, N.A., C.D. Levings and J. Grout. 1996. A preliminary study of hatchery chinook salmon smolts migrating in the lower Fraser River, determined by radiotagging. Can. Tech. Rep. Fish. Aqua.t Sci. 2085. 9 p.

Kehoe, L. J., J. Lund, L. Chalifour, Y. Asadian, E. Balke, S. Boyd, and T. G. Martin. 2021. Conservation in heavily urbanized biodiverse regions requires urgent management action and attention to governance. Cons. Sci. Pract. 3(2): e310.

Levings, C.D. 1980. Vertical distribution and abundance of epibenthos and macro-zooplankton in the lower Fraser estuary. Can. Dat. Rep. Fish. Aquat. Sci. 241: 59 p.

Levings, C.D., K. Conlin, and B. Raymond. 1991. Intertidal habitats used by juvenile chinook (Oncorhynchus tshawytscha) rearing in the North Arm of the Fraser River estuary. Mar. Poll. Bull. 22: 20-26.

Levings, C. D., D. E. Boyle, and T. R. Whitehouse. 1995. Distribution and feeding of juvenile Pacific salmon in freshwater tidal creeks of the lower Fraser River, British Columbia. Fish. Manag. Ecol. 2(4): 299-308.

Levings, C.D. 2004. Knowledge of fish ecology and its application to habitat management. *In* Fraser River Delta, British Columbia: Issues of an Urban Estuary. *Edited by* B.J. Groulx, D.C. Mosher, J.L. Luternauer, and D. E. Bilderback. Geol. Surv. Can. Bull. 546: 213-236.

Levings, C.D. 2016. Ecology of salmonids in estuaries around the world. Adaptations, Habitats and Conservation. University of British Columbia Press. 388 pages and on-line supplemental material.

Limm, M. P., and M. P. Marchetti. 2009. Juvenile Chinook salmon (Oncorhynchus tshawytscha) growth in off-channel and main-channel habitats on the Sacramento River, CA using otolith increment widths. Env. Biol. Fish. 85(2): 141-151.

Little, S., J. P. Lewis, H. Pietkiewicz, and K. Mazik. 2022. Estuarine tidal freshwater zones in a changing climate: meeting the challenge of saline incursion and estuarine squeeze. P. 94-112 in J. Humphreys and S. Little. Challenges in estuarine and coastal science: Est. Coast. Sci. Assoc. 50th anniversary volume. Pelagic Publishing, pp.300.

Mach, M.E., C.D. Levings, K.M.A. Chan, and P.S. McDonald. 2012. An Atlantic infaunal engineer is established in the Northeast Pacific: Clymenella torquata (Polychaeta: Maldanidae) on the British Columbia and Washington coasts. Biol. Invas. 14: 503-507.

MacDonald, A. L. 1984. Seasonal use of nearshore intertidal habitats by juvenile pacific salmon on the Delta front of the Fraser River Estuary, British Columbia (Master's thesis). University of Victoria.

McCain, B. B., D. C. Malins, M. M. Krahn, D. W. Brown, W. D. Gronlund, L. K. Moore, and S. L. Chan. 1990. Uptake of aromatic and chlorinated hydrocarbons by juvenile chinook salmon (Oncorhynchus tshawytscha) in an urban estuary. Arch. Env Contamin. Toxicol. 19(1): 10-16.

Merz, J. E. 2001. Diet of juvenile fall-run Chinook salmon on the lower Mokelumne River, California. Cal. Fish Game. 97:102-114.

Muir, W.D. 1996. Diet of yearling chinook salmon and feeding success during downstream migration in the Snake and Columbia Rivers. Northwest Sci. 70(4).

Neuswanger, J., M. S. Wipfli, A. E. Rosenberger, and N. F. Hughes. 2014. Mechanisms of drift-feeding behavior in juvenile chinook salmon and the role of inedible debris in a clear-water Alaskan stream. Env. Biol. Fish. 97(5): 489-503.

Nishimura, D.J.H., C.D. Levings and T.R. Whitehouse. 1995. Stomach content data from juvenile chinook, Oncorhynchus tshawytscha, captured in surface trawl at Queens Reach, Lower Fraser River, March to August 1988. Can. Data. Rep. Fish. Aquat. Sci. 961: 71 p.

Northcote, T.G., N.T. Johnston, and K. Tsumura. 1976. Benthic, epibenthic and drift fauna of the lower Fraser River. Technical Report 11. Westwater Research Center, University of British Columbia, Vancouver: 227 pp.

Northcote, T.G., N.T. Johnston & K. Tsumura. 1978. A regional comparison of species distribution, abundance, size and other characteristics of lower Fraser River fishes. Westwater Research Centre Technical Report No.14, University of British Columbia, Vancouver: 38 pp.

Northcote, T.G., N.T. Johnston & K. Tsumura. 1979. Feeding relationships and food web structure of lower Fraser River fishes. Technical Report 16. Westwater Research Centre, University of British Columbia, Vancouver. 73 pp.

Rempel, L. L., J. S. Richardson, and M. C. Healey. 2000. Macroinvertebrate community structure along gradients of hydraulic and sedimentary conditions in a large gravel-bed river. Fresh. Biol. 45(1): 57-73.

Richardson, J. S., T. J. Lissimore, M. C. Healey, and T. G. Northcote. 2000. Fish communities of the lower Fraser River (Canada) and a 21-year contrast. Env. Biol. Fish. 59: 125-140.

Richardson, J. S., Y. Zhang, and L. B. Marczak. 2010. Resource subsidies across the land–freshwater interface and responses in recipient communities. Riv. Res. Applicat. 26(1): 55-66.

Ward, P.R.B. 1976. Seasonal salinity changes in the Fraser River Estuary. Can. J. Civil Eng. 3: 342–34.

Weitkamp, L. A., B. R. Beckman, D. M. Van Doornik, A. Munguia, M. Hunsicker, and M. Journey. 2022. Life in the fast lane: feeding and growth of juvenile steelhead and chinook salmon in main-stem habitats of the Columbia River estuary. Trans. Americ. Fish. Soc. 151(5): 587-610.

Whitehouse, T.R., and C.D. Levings. 1989. Surface trawl catch data from the lower Fraser River at Queens Reach during 1987 and 1988. Can. Data Rep. Fish. Aquat. Sci. 768: 53 pp.

Whitehouse, T.R., C.D. Levings, and J.S. Macdonald. 1993. Chironomid (*Diptera*) insects from natural and transplanted estuarine marshes in British Columbia. Leighton, D (Ed), *In* Proc: 1993 Canadian Coastal Conference, Vancouver, May 4-7 1993. Coastal Zone Engineering Program, National Research Council Canada, Building M-32, Montreal Road, Ottawa, Ontario K1A OR6. p. 500-524.