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Spatiotemporal dynamics of food availability for juvenile Coho Salmon (*Oncorhynchus kisutch*) across a watershed habitat mosaic

Sheena Parsons[a,b], **Sean M. Naman**[b,c], **Carter Tsui**[b,d], **Douglas C. Braun**[b,e], **Daniella LoScerbo**[e], **Amanda M. Martens**[c], **and Chelsea J. Little**[a,d]

[a]Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada; [b]Aquatic Research Cooperative Institute, School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC, Canada; [c]Cultus Lake Salmon Research Laboratory, Fisheries and Oceans Canada, Cultus Lake, BC, Canada; [d]School of Environmental Science, Simon Fraser University, Burnaby, BC, Canada; [e]Fisheries and Oceans Canada, Science Branch, Freshwater Ecosystems, Simon Fraser University, Burnaby, BC, Canada

Corresponding author: **Sean Naman** (sean.naman@dfo-mpo.gc.ca)

Abstract

Variation in food availability can influence fish growth, survival, and life history diversity. Yet, relatively few studies have investigated spatiotemporal variation in food availability among fish-bearing habitats at the watershed scale. In this study, we described spatial and seasonal patterns of food availability (invertebrate prey abundance, quality, and accessibility) for juvenile (*Oncorhynchus kisutch*) in natal tributary streams and non-natal floodplain wetlands in the North Thompson watershed (British Columbia, Canada). We found striking seasonal differences between streams and wetlands for all dimensions of food availability. Notably, wetlands had up to 136 times greater prey abundance than streams throughout the rearing period. However, high prey abundance often coincided with high water temperature and low dissolved oxygen concentration that potentially limit prey accessibility in wetlands, suggesting that wetlands may be high-risk high-reward habitats. Comparatively low prey abundance in streams may be offset by more favourable abiotic conditions and higher-quality prey. Collectively, these results indicate that asynchrony in food availability generates a seasonally shifting portfolio of growth opportunities for juvenile salmon across a watershed habitat mosaic.

Key words: watershed, freshwater habitat, food availability, floodplains, Pacific Salmon

Introduction

Watersheds are heterogeneous landscapes comprising a mosaic of freshwater habitats that are dynamic in space and time (Stanford et al. 2005). Indeed, the spatial distribution of habitat patches on a landscape changes temporally (i.e., *shifting habitat mosaic*) due to hydrogeomorphic processes such as flooding, inundation, erosion, and deposition (Stanford et al. 2005). For instance, seasonal flooding of a mainstem river can generate off-channel floodplain habitats (e.g., ponds and wetlands) that expand and contract on the landscape with recurrent inundation. Tributary streams across river networks can also change through time with flow variation, which is driven by seasonal changes in climate and precipitation (Junk et al. 1989). In turn, abiotic and biotic conditions may be highly variable across these dynamic landscapes; for instance, seasonal regimes of water temperature, nutrient inputs, and biogeochemical processing rates often differ between stream and floodplain habitats (Wegener et al. 2017). Collectively, these dynamic spatiotemporal conditions across watersheds influence the performance and demographics of mobile consumers like fish, which may use a diversity of habitats across their life cycles (Schlosser 1991; Rossi et al. 2024).

Understanding spatial and seasonal variation in habitat conditions across watersheds is foundational for effective management of species that use freshwater habitats, including highly valued fishes like Pacific Salmon (*Oncorhynchus* spp.). Yet, while numerous studies have investigated the spatiotemporal dynamics of abiotic conditions like water temperature across watersheds (Steel et al. 2017), comparatively little is known about the biotic conditions that also determine aquatic consumer performance (Ouellet et al. 2024; Rossi et al. 2024). This knowledge gap hinders ecosystem management because, in addition to abiotic conditions (e.g., temperature or physical habitat), the growth and performance of consumers like fish are strongly influenced by biotic conditions like food availability (i.e., the food in a given habitat that is available for fish to consume). For instance, elevated water temperature increases fish metabolic demands, yet this can be offset to an extent by high food abundance, leading to increased fish growth

(Armstrong et al. 2010; Lusardi et al. 2020; Kiffney et al. 2025).

Variation in food availability through space and time across a watershed habitat mosaic has potential consequences for fish growth, survival, and life history diversity (Ebersole et al. 2006; Jeffres et al. 2020; Cordoleani et al. 2022; Rossi et al. 2022). For instance, asynchrony in food availability may generate a complex shifting portfolio of growth opportunities for fish (Bellmore et al. 2022; Rossi et al. 2022; Fellman et al. 2023). If fish can track food resources, this could lead to increased individual growth (Sethi et al. 2022) and population-level diversity (Rossi et al. 2022). Food availability (i.e., ration) is also a key input for bioenergetics models that predict fish growth regimes at the watershed scale (Fullerton et al. 2017; Armstrong et al. 2021; Kaylor et al. 2021). Yet, despite extensive conceptual development (Wipfli and Baxter 2010), there are limited empirical insights into spatiotemporal variation in food availability across watersheds (but see Cordoleani et al. 2022; Fellman et al. 2023). While studies focusing on seasonal or spatial patterns in isolation provide a solid foundation (Grosholz and Gallo 2006; Rine et al. 2016), integrating both spatial and temporal dimensions is a critical gap for predicting fish growth and performance across watershed habitat mosaics (Armstrong et al. 2021; Rossi et al. 2024).

Aquatic and terrestrial invertebrates are the primary food source for many fishes including salmonids, and there are several dimensions that define their availability (Wipfli and Baxter 2010; Ouellet et al. 2024). First, prey abundance describes the total amount of prey in a given habitat at a particular point in time (Ouellet et al. 2024), and this is determined by in situ invertebrate production, as well as terrestrial invertebrate subsidies (Wipfli and Baxter 2010). Second, prey quality refers to the energetic and nutritional value of invertebrate prey, as well as their digestibility (Ouellet et al. 2024). The energetic value of an invertebrate increases with body mass, so large prey (e.g., terrestrial invertebrates; Rosenfeld and Raeburn 2009) can be disproportionately valuable relative to their abundance (Dodrill et al. 2016), since prey size is often skewed towards small invertebrates (Solimini et al. 2001). Energetic value also increases with energy density, which declines with water content, leading to variable prey quality among taxa; for instance, adult aquatic and terrestrial insects can be relatively high quality for a given mass (Cummins and Wuycheck 1971). Finally, prey accessibility is defined as the capacity of a fish to encounter, capture, and consume prey (Ouellet et al. 2024). This may relate to habitat conditions being suitable for foraging (Walters and Juanes 1993); for instance, high water temperature and low dissolved oxygen concentration may limit cold-adapted fishes like salmonids from foraging in productive habitats. Anatomical constraints on prey ingestion may further constrain the prey that fish can capture and consume in a given habitat. This is determined by the body size of a fish consumer (i.e., gill raker spacing and jaw width) relative to that of its prey (Wańkowski 1979).

In this study, we focused on Pacific Salmon to understand how spatiotemporal dynamics of food availability may affect fish consumers across a watershed habitat mosaic. Salmonids have flexible diets (Rosenfeld and Raeburn 2009), rely on diverse habitats for rearing, and may track changes in food availability across large spatial and temporal scales (Hahlbeck et al. 2022). Further, many Pacific Salmon populations have experienced declines in recent decades (Price et al. 2019; Atlas et al. 2023), and are thus a main target of conservation efforts. Here, we focused on a threatened population of Interior Fraser Coho Salmon (*O. kisutch*) in the North Thompson watershed, British Columbia, Canada (COSEWIC 2016). We investigated spatial and temporal patterns of food availability for juvenile Coho Salmon among natal tributary streams and non-natal floodplain wetlands, which are their primary rearing habitats in the North Thompson watershed. Specifically, we characterized food availability for juvenile Coho Salmon in streams and wetlands by investigating spatiotemporal patterns of prey abundance (defined as invertebrate biomass concentration), prey quality (invertebrate size, and terrestrial vs. aquatic invertebrate subsidies), and prey accessibility (invertebrate size, and environmental conditions) throughout the juvenile rearing period. We also explored the relative influence of spatiotemporal versus environmental drivers underlying patterns of invertebrate prey abundance.

We hypothesized that streams and wetlands would offer contrasting foraging opportunities for juvenile Coho Salmon based on asynchronous spatiotemporal patterns and drivers of food abundance, quality, and accessibility. Based on prior work in the North Thompson watershed (Milner et al. 2025) and elsewhere (Jeffres et al. 2020), we specifically predicted that (1) floodplain wetlands would have higher yet more seasonally variable food abundance than streams; (2) variation in food abundance would be related to both broad spatial and temporal predictors as well as site-level conditions (e.g., temperature); and (3) streams would have higher quality and more accessible food than wetlands.

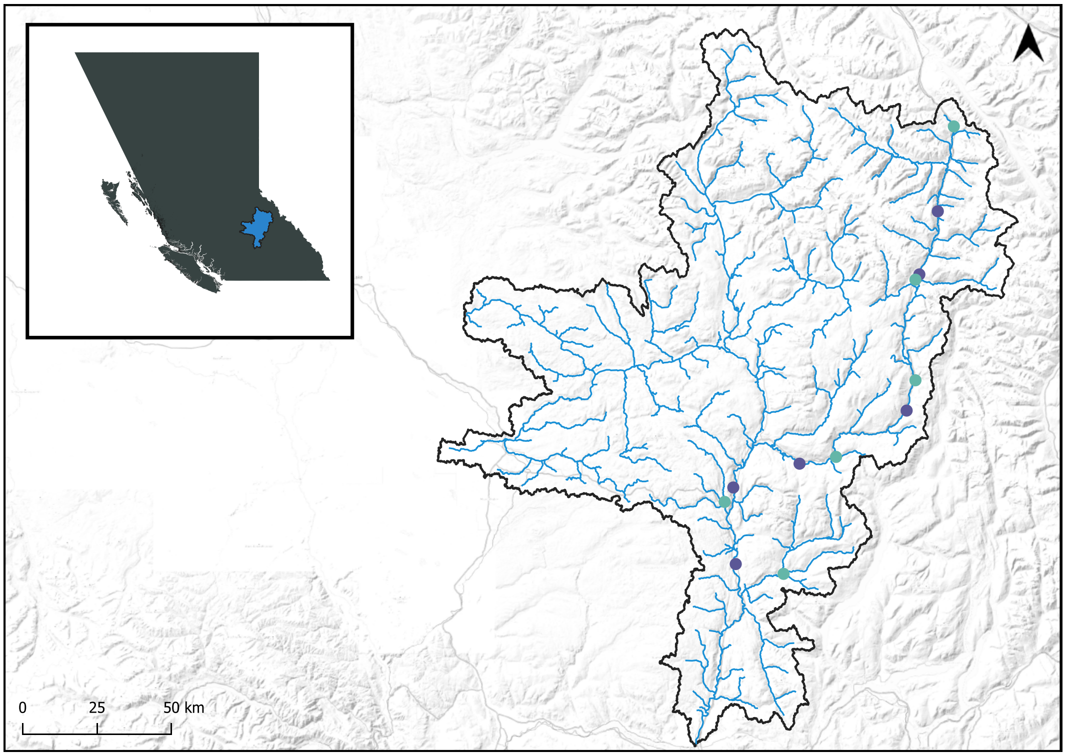
Materials and methods

Study system

The North Thompson watershed lies within Secwepemcúl̓ecw, Secwépemc, and Simpcw territory in the southeastern interior of British Columbia, Canada (Fig. 1). Its mainstem, the North Thompson River, is 365 km long and flows predominately north to south along a latitudinal gradient of climate and hydrology (see additional description in Milner et al. 2025). To examine broad-scale patterns of food availability, we selected six tributary streams and six floodplain wetlands of the North Thompson River that are known rearing habitats for juvenile Coho Salmon (Interior Fraser Recovery Team 2006), and that have a broad latitudinal distribution across the watershed. The study streams are low-gradient (0.47%–3.26%), higher order tributaries whose hydrologic regimes are influenced predominantly by snowmelt. The study wetlands have complex hydrology that is influenced by seasonal connectivity with the North Thompson River, groundwater inputs, as well as beaver activity at all sites (Milner et al. 2025).

This study was part of a larger research program that sought to understand watershed ecosystem dynamics, and the contribution of different habitats to Coho Salmon pro-

Fig. 1. Map of tributary stream (teal) and floodplain wetland (purple) locations across the North Thompson watershed, British Columbia. Note that stream sites are distinct tributaries in close proximity to the mainstem North Thompson. The topographic base layer was adapted from OpenTopoMap by QuickMapServices. Map data: © OpenStreetMap-Contributors, SRTM. Map representation: © OpenTopoMap (CC-BY-SA). The watershed boundary and river network were obtained from Global Watersheds (Heberger 2022). © Global Watersheds (CC-BY-4.0). The provincial boundary was adapted from Statistics Canada (2021). This does not constitute an endorsement by Statistics Canada of this product. This map uses the WGS-84 coordinate reference system.



ductivity. This program integrated physical habitat surveys (Cunningham et al. 2023), high resolution environmental monitoring, and fish surveys in stream and wetland habitats (Milner et al. 2025). For tractability, we restricted our focus in this study to juvenile Coho Salmon food availability (i.e., invertebrates) and its potential drivers. For further information on fish sampling methods, refer to Milner et al. (2025) and Fleming et al. (2026).

Sample collection and processing

To capture the range of prey resources that a single cohort of juvenile Coho Salmon would be exposed to during their freshwater rearing period, we collected invertebrate samples (3 or 4 samples) at each stream and wetland site monthly from July to October 2022, and in April 2023 (Table S1); at other times of year, sites were frozen or inaccessible. Further, we were unable to collect samples at some wetland sites in July and August 2022 due to low water levels, and we discarded two samples due to errors in the collection process.

In streams, we collected invertebrate samples using drift nets (250 μm mesh) that were positioned across multiple riffles, or in a cross section of a single riffle, depending on site characteristics. We set each net for a target of 30 min, but we reduced set times at sites with high flow to prevent net clogging, and extended set times at sites with low flow. We calculated the volume of water (m^3) filtered by each net as the product of the water velocity and the cross-sectional area of the net that was submerged. In wetlands, we collected invertebrate samples by performing horizontal tows from shore using a plankton net (250 μm mesh). We performed tows in different sections of each wetland to capture potential variation among open water and emergent vegetation microhabitats. Floats were fixed to the net circumference to ensure that a portion of the net opening was always above the surface of the water. We calculated the volume of water (m^3) filtered by each plankton tow using the tow length (m), net radius (m), and estimated proportion of net opening that was submersed:

$$\text{Volume} = \pi^{*}\ \text{net radius}^{2*}\ \text{tow length}^{*}\ \text{proportion submersed} \tag{1}$$

Following sample collection, we transferred sample material through a 250 μm mesh sieve and then preserved it in 95% ethanol. In the lab, we manually picked invertebrates from detritus using a dissecting microscope; however, samples with many invertebrates were subsampled (factor of 0.5, 0.25, or 0.125) using a Folsom splitter prior to sorting. We included all invertebrates that possessed (at least) a head filled with non-decomposing body tissue, with a few exceptions: (1) annelids and nematodes were included regardless of their state of decomposition or intactness; (2) molluscs were included if the shell was not empty; and (3) hydra were excluded as this taxon was not picked consistently. Further, a single gastropod was removed from one Little Fort Wetland July sample because it was considerably larger (2.4 cm) than what is possible for juvenile salmonids to consume.

Laboratory processing

We identified each invertebrate to Order (or to a coarser taxonomic resolution when this was not possible), and recorded its taxon, life stage, and habitat. Habitat (i.e., "aquatic" or "terrestrial") was assigned based on the environment that an invertebrate inhabits in its current life stage, and thus does not represent habitat of origin. We used a dissecting microscope (10–40× magnification) with a calibrated ocular micrometer (Manickam et al. 2019) to measure the body length (mm) of a random subset of whole-bodied individuals for each unique combination of taxon, life stage, and habitat per sample (average: 6.4 individuals; range: 1–135 individuals). This was intended to capture a representative range of invertebrate lengths across taxa and life stages. We measured body length from the anterior of the head to the posterior of the last abdominal segment, excluding appendages (Smock 1980). When the only invertebrate present in a sample for a given taxon, life stage, and habitat was not measurable (e.g., damaged), we assigned that invertebrate the average length of invertebrates in the same taxon, life stage, and habitat from another sample.

A subset of samples with high abundances of invertebrates were processed by professional taxonomists (Biologica Environmental Services Ltd.), who further subsampled some of these samples (factor of 0.5 or 0.25) prior to identification and length measurement, using a combination of dissecting (10–40×) and compound (100–1000×) microscopes. The taxonomists followed the same methods previously described; however, we adjusted some taxonomic and habitat classifications (i.e., "aquatic" and "terrestrial") to maintain consistency across datasets. Further, some terrestrial invertebrates ($n = 602$) from five stream samples (Tumtum Creek in July; Lemieux Creek in September and October) were mistakenly classified as "unknown", so we assigned these invertebrates to a specific taxon and life stage based on proportions of identified terrestrial taxa in their respective samples.

We estimated the dry mass (mg) of all measured invertebrates using taxon-specific length-mass regression coefficients (Table S2). We then performed the following steps for each sample, separately: (1) we grouped invertebrates of the same taxon, life stage, and habitat; (2) we determined the total invertebrate count for each group by multiplying the number of invertebrates in each group by the sample's subsample multiplication factor (Table S3); (3) we calculated average invertebrate biomass for each group; (4) we estimated "group-level" biomass by multiplying the average invertebrate biomass of each group by the corresponding total invertebrate count; and (5) we estimated "sample-level" biomass by summing all "group-level" biomass estimates. Following this, we summed "sample-level" biomass estimates to generate a single "site-level" biomass estimate, for each sampling month. We then standardized these "site-level" biomass estimates (mg) to invertebrate biomass concentration (IBC; $\text{mg}\cdot\text{m}^{-3}$) using the total volume of water (m^3) filtered at a given site, in a given sampling month.

Standardizing to a biomass concentration allows direct comparison of the different sampling methods used in each habitat, which reflect distinct foraging modes used by salmonids in lotic versus lentic environments. Salmonids in streams typically exhibit central place drift-feeding, while salmonids in wetlands exhibit search foraging to locate prey over a greater extent (Rosenfeld and Raeburn 2009; Harvey and Railsback 2014). In both cases, fish scan a given volume of water for prey; thus, standardizing prey measurements by the volume of water filtered allows comparison of both habitats using the prey concentration metric. Both sampling methods also captured the diversity of invertebrates in the water column and on the surface of the water—which are the primary prey sources for juvenile Coho Salmon—as well as generally matching the taxonomic composition of coho diets from the North Thompson (S. Naman unpublished data).

Habitat attributes

We collected physical, chemical, and hydrological information at each site to investigate the relative influence of site-level habitat features on food abundance (invertebrate biomass concentration). At all sites, we measured continuous water temperature (°C) and dissolved oxygen concentration ($\text{mg}\cdot\text{L}^{-1}$) using Onset HOBO U26 loggers (see Milner et al. 2025). We also recorded spot estimates using a YSI multiparameter probe. At each sampling event, we collected water ~10 cm below the surface in pre-washed 50 mL glass tubes for total phosphorous analysis, which followed the method of Murphy and Riley (1962). We calculated mean wetland canopy cover (%) using measurements collected in July 2024. Mean stream canopy cover (%) and mean stream fine sediment (%) were obtained from Cunningham et al. (2023). Although mean canopy cover does not account for seasonal changes during leaf-on and leaf-off, it does describe consistent differences among sites. Environmental conditions for streams and wetlands are shown in Table 1.

To characterize seasonal changes in hydrology, we used contrasting methods for flowing streams versus non-flowing wetlands. For streams, we estimated continuous discharge ($\text{m}^3\cdot\text{s}^{-1}$) for each site following methods described in Cunningham et al. (2023). Briefly, we estimated instantaneous discharge using the velocity-area method from cross-sectional velocity measurements that we collected at each stream site 3–5 times annually with a HACH FH950 velocity meter (accuracy ± 0.015 $\text{m}\cdot\text{s}^{-1}$). We then developed stage rating curves to estimate hourly discharge from water level measurements that were recorded hourly using Onset HOBO U20 L water level loggers (accuracy ± 0.004 m). Using these estimates, we calculated average daily discharge on the exact date that invertebrate samples were collected in 2022. To facilitate comparisons of discharge effects across streams

Table 1. Monthly mean and standard deviation (in brackets) of each habitat attribute, pooled across stream, and wetland sites.

		2022				2023
Habitat	Attribute	July	August	September	October	April
Stream	Canopy cover[a] (%)	64.26 (23.70)	64.26 (23.70)	64.26 (23.70)	64.26 (23.70)	64.26 (23.70)
	Fine sediment[a] (%)	32.99 (21.06)	32.99 (21.06)	32.99 (21.06)	32.99 (21.06)	32.99 (21.06)
	Total phosphorous (μg·L^{-1})	5.66 (2.07)	7.70 (2.82)	3.18 (1.94)	5.04 (2.75)	6.97 (1.96)
	Water temperature (°C)	12.63 (2.27)	14.37 (2.30)	7.88 (2.07)	6.52 (1.72)	3.03 (1.97)
	Discharge (m^3·s^{-1})	1.15 (1.35)	0.31 (0.28)	0.17 (0.17)	0.11 (0.13)	0.24 (0.19)
Wetland	Canopy cover[a] (%)	17.04 (33.22)	17.04 (33.22)	18.37 (36.96)	0.62 (1.07)	0.92 (1.31)
	Total phosphorous (μg·L^{-1})	13.29 (6.04)	17.08 (13.75)	10.75 (11.52)	10.62 (7.31)	13.70 (15.84)
	Water temperature (°C)	16.25 (4.50)	14.78 (3.75)	8.36 (2.21)	7.47 (1.10)	4.25 (1.91)

[a] Seasonal variation is not captured for these attributes.

of different sizes, we expressed measurements as a percentage of mean annual discharge (MAD), estimated across all sites from 2019 to 2024. Discharge for one site (Lemieux Creek; station 08LB078) was extracted from the Environment and Climate Change Canada Historical Hydrometric Data web site (https://wateroffice.ec.gc.ca/mainmenu/historical_data_index_e.html) on 12 February 2024.

In wetlands, we determined connectivity with the North Thompson River, which we interpreted to broadly represent contrasting periods of inundation (connected with larger wetted area) and disconnection (smaller wetted area). We followed the approach of Milner et al. (2025) and plotted the water level of each wetland site as a function of daily average North Thompson River (station 08LB047) discharge, which was extracted from the Environment and Climate Change Canada Historical Hydrometric Data web site (https://wateroffice.ec.gc.ca/mainmenu/historical_data_index_e.html) on 14 March 2024. We then visually identified the discharge threshold at which a wetland's water level started to change, which we considered an indication of connectivity. To account for uncertainty in the threshold estimates, we calculated a 20% range around each discharge threshold (threshold ± 10%). Based on this, we assigned *Connected*, *Possibly Connected*, or *Disconnected* to each wetland on the date that invertebrate samples were collected.

Statistical analyses

Prey abundance

To explore spatiotemporal patterns of prey abundance (invertebrate biomass concentration; mg·m^{-3}) in stream and wetland habitats, we developed a series of candidate statistical models including habitat type, month (categorical), and latitude as fixed effects (Tables S4). Further, we developed a series of candidate statistical models to assess the relative influence of environmental versus spatiotemporal variables on invertebrate biomass concentration. We analyzed streams and wetlands separately given distinct predictors (Table S5 and S6) and to limit model complexity. We used month (categorical) and latitude as spatiotemporal predictors of invertebrate biomass concentration for each habitat. Our environmental predictors for streams included discharge (m^3·s^{-1}), water temperature (°C), total phosphorous (μg·L^{-1}), canopy cover (% cover), and fine sediment (% cover). For wetlands, we used wetland connectivity (Connectivity), water temperature (Temperature; °C), total phosphorous (Phosphorous; μg·L^{-1}), and canopy cover (Canopy; % cover). In all models without month, we included site as a random intercept term to account for repeated measurements through time. Prior to fitting the models to the data, we centered all continuous explanatory variables and checked for collinearity. If two explanatory variables were highly correlated (i.e., Pearson correlation coefficient >0.60), we kept only the variable for which we had the strongest rationale. We used the *Performance* package (Lüdecke et al. 2021) to choose the appropriate distributional family for our invertebrate biomass concentration data (which are > 0, right-skewed, and have a non-normal sampling distribution). We fit generalized linear mixed effects models, or generalized linear models, with a Gamma error distribution and log link function. We used the *DHARMa* package (Hartig 2024) to check residual diagnostics (e.g., heteroscedasticity of simulated model residuals).

We fit each candidate mixed effects model using the *glmmTMB* function in the *glmmTMB* package (Brooks et al. 2017) and each candidate fixed effects model using the *glm* function in the *stats* package (R Core Team 2024). We used Akaike's Information Criterion corrected for small sample sizes (AICc) to identify the most parsimonious models (i.e., those with AICc < 2; Burnham and Anderson 2004). Each candidate model set also included an intercept only model. We used the *emmeans* package (Lenth 2024) to estimate the marginal mean and corresponding 95% confidence interval of each fixed effect group in the top-ranking models. We conducted a type II Analysis of variance (ANOVA) for each top-ranking model with fixed effects using the *Anova* function in the *car* package (Fox and Weisberg 2019), to assess the significance of additive and/or interactive fixed effects. We estimated the trigamma marginal R^2 for fixed effects, and the trigamma conditional R^2 for random and fixed effects combined using the *MuMIn* package (Bartón 2024). We ran all analyses in the R computing environment (version 4.4.2; R Core Team 2024).

Prey quality

We determined prey quality based on the proportion of total invertebrate biomass that was aquatic or terrestrial, as well as invertebrate size. We quantified the size of invertebrate prey in two ways. First, to explore differences in invertebrate size between habitats and through time, we fit a linear model to log-transformed invertebrate length data with habitat and month as categorical predictors, using the *stats* package (R Core Team 2024). We verified that assumptions of normality and homoscedasticity were met through visual assessments of model residuals. To account for imbalance in the number of length measurements across months and habitat types, we conducted a type III ANOVA using the *Anova* function in the *car* package (Fox and Weisberg 2019). We then estimated marginal mean invertebrate length for each combination of habitat and sampling month using the *emmeans* package (Lenth 2024).

We also investigated the skewness of prey size distributions to explore how the relative frequency of small- versus large-bodied invertebrates varied among habitats and through time. Skewness describes the asymmetry of a distribution; perfectly symmetrical distributions have zero skewness, whereas asymmetrical distributions with right tails (i.e., right-skewed distributions) have positive skewness and asymmetrical distributions with left tails (i.e., left-skewed distributions) have negative skewness (Brys et al. 2003). To estimate skewness, we fit a Gamma distribution to the invertebrate length data (separately for each combination of habitat and month), using the *fitdistrplus* package (Delignette-Muller and Dutang 2015). We then bootstrapped each gamma distribution (10 000 iterations) and used the resulting shape parameter estimates from each bootstrap to calculate skewness:

$$\text{skewness} = \frac{2}{\sqrt{\text{shape}}} \tag{2}$$

Finally, we obtained median skewness, as well as the 2.5% and 97.5% quantiles of skewness, for each habitat and month combination.

Prey accessibility

We determined the proportion of prey that were within anatomical constraints of consumption. Based on data from fish sampling in streams and floodplain wetlands across the North Thompson watershed (Milner et al. 2025; D. Braun unpublished data), we determined the approximate minimum, median, and maximum size of juvenile Coho Salmon (cm) for each sampling month, pooled across habitat types (Table 2). To constrain the focus of this analysis on contrasting invertebrate size distributions, we did not integrate site or habitat variation in juvenile Coho Salmon size (Milner et al. 2025). Consequently, this should be considered an analysis of *potential* accessibility constraints across the broader North Thompson Coho Salmon population rather than explicit site-level predictions.

Table 2. Fork length (cm) of juvenile Coho Salmon in each size class (minimum: 2.8–3.6 cm; median: 4.9–6.9 cm; and maximum: 10.9–13.5 cm), for each sampling month.

	Fork length		
Month	Minimum	Median	Maximum
July	2.9	5.2	10.9
August	2.8	4.9	12.4
September	3.1	5.6	13.5
October	3.5	5.6	11.4
April	3.6	6.9	11.5

We used fish size measurements to calculate the minimum and maximum invertebrate size (mm) that juvenile Coho Salmon of each size class (cm) could consume in a given sampling month, as per Wañkowski (1979) and Hayes et al. (2000):

$$\text{min invert length} = 0.115 * \text{fork length} \tag{3}$$

$$\text{max invert length} = 1.05 * \text{fork length} * 4.3 \tag{4}$$

For each invertebrate sample, we reduced its invertebrate count by the proportion of invertebrate length measurements in the sample that fall outside the invertebrate size thresholds of each fish size class. With these reduced counts, we estimated invertebrate biomass concentration that is theoretically consumable for each site and sampling month, using the biomass estimation methods previously described. We then determined what percentage of total invertebrate biomass would be theoretically consumable by juvenile Coho Salmon of each size class, for each combination of habitat and sampling month.

To explore how patterns of prey abundance may overlap with the occurrence of physiologically stressful environmental conditions, we plotted the relationship between maximum water temperature and minimum dissolved oxygen concentration (on the date of invertebrate sampling) with invertebrate biomass concentration for streams and wetlands. We considered abiotic conditions to be potentially stressful for Coho Salmon (thus limiting prey accessibility) when temperatures exceeded 20 °C or dissolved oxygen was below 5 $\text{mg}\cdot\text{L}^{-1}$. These values are associated with observed reductions in maximum consumption and growth for juvenile salmonids (Stewart and Ibarra 1991; Rosenfeld and Lee 2022), but should not be interpreted as acute mortality thresholds. Continuous dissolved oxygen concentration data were not available for two stream sites due to logger malfunction, so in these cases we used spot measurements.

Results

We collected and sorted 87 296 invertebrates across all samples, of which 86% were aquatic, 13% were terrestrial, and 1% were unknown. We measured the length of 13 011 individuals (15% of all invertebrates), which ranged in size from 0.04 to 24.4 mm. Across stream and wetland sites, monthly invertebrate biomass concentration varied from 0.06 to 10.35 $\text{mg}\cdot\text{m}^{-3}$ and from 1.01 to 572.75 $\text{mg}\cdot\text{m}^{-3}$, respectively.

Table 3. Estimated marginal mean invertebrate biomass concentration ($mg \cdot m^{-3}$) and 95% confidence intervals for streams and wetlands in each sampling month.

	Sampling month				
Habitat	July	August	September	October	April
Stream	2.37 [1.04, 5.40]	1.57 [0.69, 3.58]	2.43 [1.07, 5.54]	0.72 [0.31, 1.64]	2.35 [1.03, 5.37]
Wetland	259.43 [113.77, 591.58]	213.23 [93.51, 486.22]	127.01 [51.49, 313.33]	37.96 [11.83, 121.77]	2.54 [0.61, 10.60]

Table 4. Model selection results of candidate models for stream and wetland invertebrate biomass concentration (IBC).

Model	AICc[a]	ΔAICc[b]	Model weight	Log likelihood
IBC ∼ Habitat∗Month	369.61	0.00	0.84	− 170.51
IBC ∼ Habitat + Month	373.41	3.79	0.13	− 178.43
IBC ∼ Habitat + Month∗Latitude	376.56	6.95	0.03	− 172.28
IBC ∼ Habitat∗Latitude + Month	378.51	8.90	0.01	− 178.11
IBC ∼ 1 + (1|Site)	391.41	21.80	0.00	− 192.46
IBC ∼ 1	456.40	86.78	0.00	− 226.08

[a] Aikake's information criterion corrected for small sample size.
[b] Difference in AICc score between the given model and the most parsimonious model.

Prey abundance

The magnitude and the timing of invertebrate biomass concentration varied among tributary streams and floodplain wetlands. Consistent with predictions, wetlands had up to two orders of magnitude greater estimated marginal mean invertebrate biomass concentration than streams, depending on the season. Estimated marginal mean invertebrate biomass concentration in wetlands was 110 times greater than for streams in July, 136 times greater in August, 52 times greater in September, 53 times greater in October, and 1.1 times greater in April (Table 3). These observations were supported by statistical analysis (Table 4). Results of the ANOVA for the highest-ranked model include a significant effect of habitat type ($X^2_{(1,52)} = 126.99$, $p < 0.001$), month ($X^2_{(4,52)} = 10.11$, $p = 0.039$), and a significant habitat-month interaction ($X^2_{(4,52)} = 14.42$, $p = 0.006$; Fig. 2). These effects accounted for 76% of model variance (marginal $R^2 = 0.76$).

In streams, no predictor variables explained variation in invertebrate biomass concentration. We found a clear top-ranked model (ΔAICc > 2 to next-ranked model; Table 5) that included only a random effect of site, which explained 29% of the variance. Seasonal patterns of invertebrate biomass concentration varied among stream sites (Fig. 3). While some sites were relatively aseasonal (Cedar Creek and Haggard Creek), several sites showed unique temporal patterns, including decreasing invertebrate biomass concentration through time (Reg Christie Creek and Tumtum Creek) and distinct monthly peaks in invertebrate biomass concentration (Albreda River and Lemieux Creek).

In wetlands, there was a general trend of decreasing biomass concentration through time, although some sites exhibited more variable patterns (Fig. 4). There were two models with substantial support based on AIC_c model selection (Table 6). The top-ranked model included month and total phosphorous, whereas the second-ranked model included only month. The effect of month on wetland invertebrate biomass concentration was significant in both models ($X^2_{(4,52)} = 26.39$, $p < 0.001$; $X^2_{(4,52)} = 23.54$, $p < 0.001$), with invertebrate biomass concentration decreasing from July to April (Fig. 4). The effect of total phosphorous in the top ranked model was positive but not significant ($X^2_{(1,52)} = 3.45$, $p = 0.06$). The inclusion of total phosphorous marginally increased model parsimony and explained a greater proportion of the variation in invertebrate biomass concentration ($R^2 = 0.65$) relative to the second-ranked model ($R^2 = 0.60$). Notably, several wetland sites became dry between August and September, which persisted through the winter into April (Fig 4).

Prey quality

Prey size

Prey quality varied between tributary streams and floodplain wetlands. Invertebrate length varied significantly between habitats ($F_1 = 433.52$, $p < 0.001$), with stream invertebrates 1.3 times larger than wetland invertebrates. Size also varied through time but there was no clear trend, with larger average invertebrate length in July, August, and April relative to September and October ($F_4 = 26.69$, $p < 0.001$).

The distribution of invertebrate prey sizes was right-skewed for stream and wetland habitats across all sampling months, indicating that there were more small invertebrates relative to large invertebrates within each habitat (Fig. 5, Table S7). In particular, wetlands exhibited significantly greater right-skew (i.e., higher proportion of small invertebrates) relative to streams from July to September, but streams exhibited significantly greater right-skew relative to wetlands in April.

Fig. 2. Estimated marginal mean invertebrate biomass concentration (mg·m^{-3}) and corresponding 95% confidence interval in each sampling month for streams (teal) and wetlands (purple), from the highest-ranking model (top panel). Invertebrate biomass concentration in each sampling month is plotted for each stream (bottom left panel) and wetland (bottom right panel) sites. Note the different *Y*-axis scales for the bottom panels.

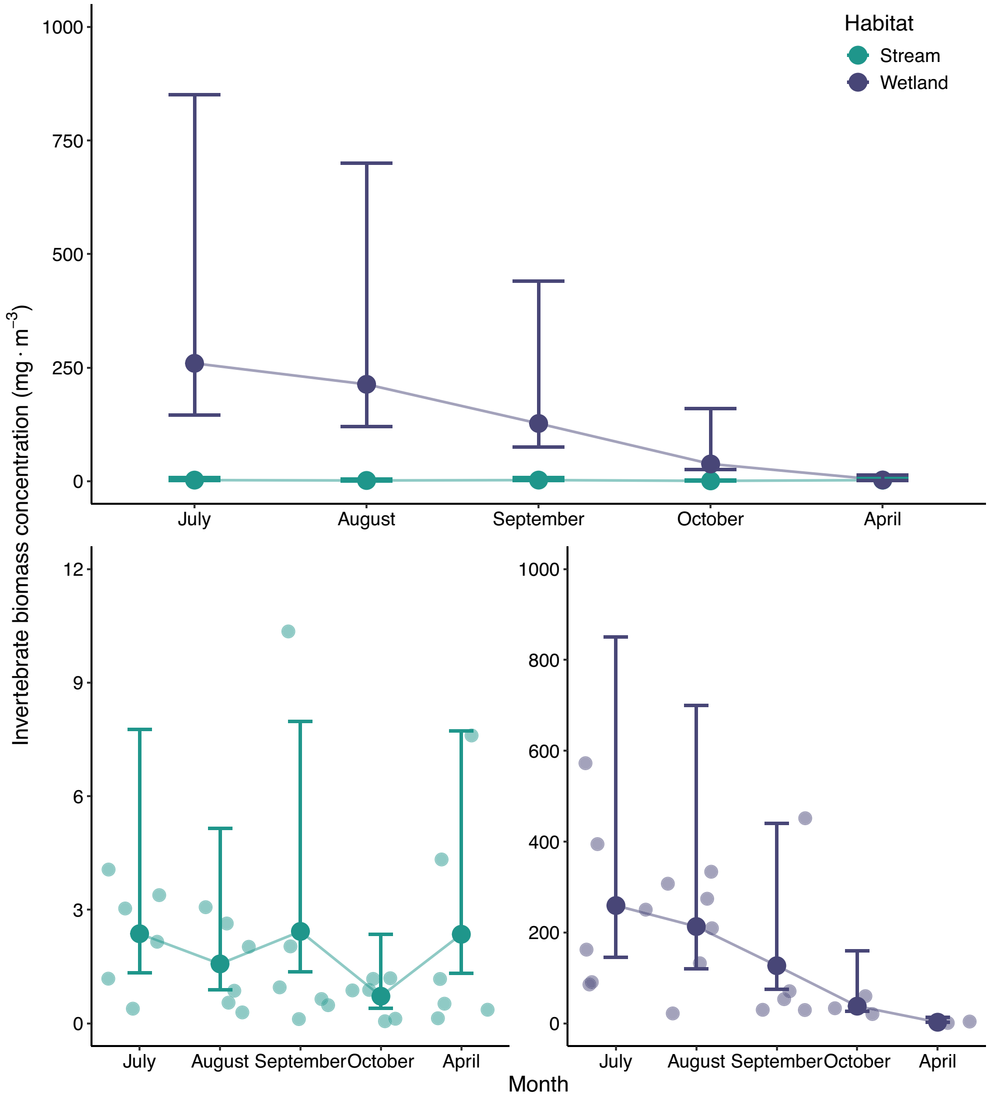


Table 5. Model selection results of candidate models for stream invertebrate biomass concentration (IBC).

Model	AICc[a]	ΔAICc[b]	Model weight	Log likelihood
$IBC_S \sim 1 + (1\|Site)$	99.61	0.00	0.70	−46.35
$IBC_S \sim 1$	102.77	3.16	0.15	−49.16
$IBC_S \sim Month + Canopy$	103.72	4.11	0.09	−42.32
$IBC_S \sim Month + Temperature$	104.89	5.28	0.05	−42.90
$IBC_S \sim Month$	108.75	9.13	0.01	−46.55
$IBC_S \sim Month + Phosphorous$	110.82	11.21	0.00	−45.87
$IBC_S \sim Month + Discharge$	112.09	12.47	0.00	−46.50
$IBC_S \sim Month + Sediment$	112.18	12.57	0.00	−46.55
$IBC_S \sim Latitude + Month$	112.18	12.57	0.00	−46.55

[a] Aikake's information criterion corrected for small sample size.
[b] Difference in AICc score between the given model and the most parsimonious model.

Fig. 3. Invertebrate biomass concentration (mg·m^{-3}) at each stream site, for each sampling month.

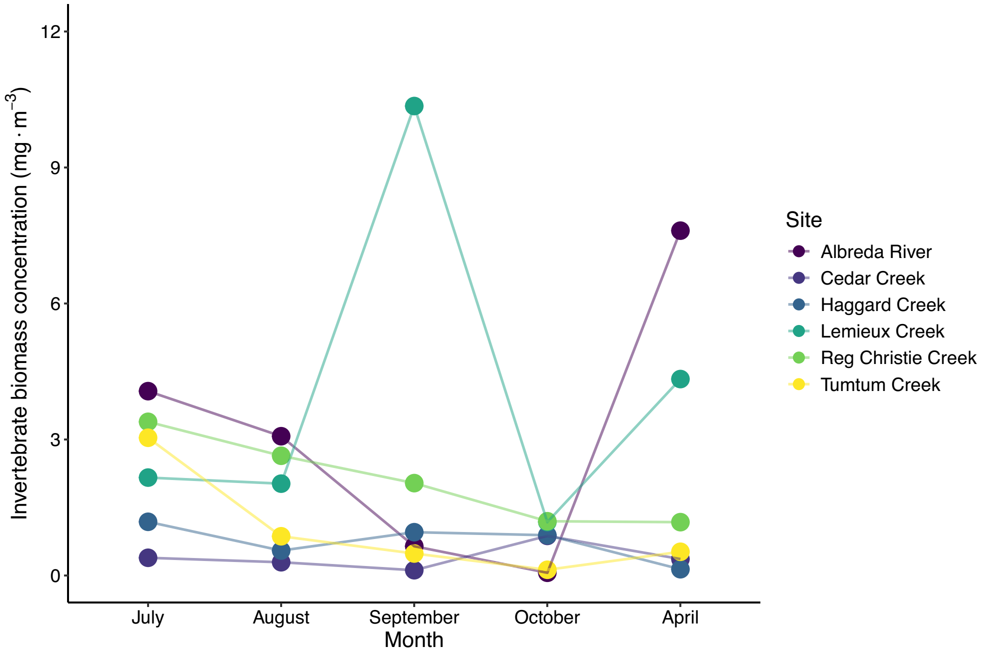
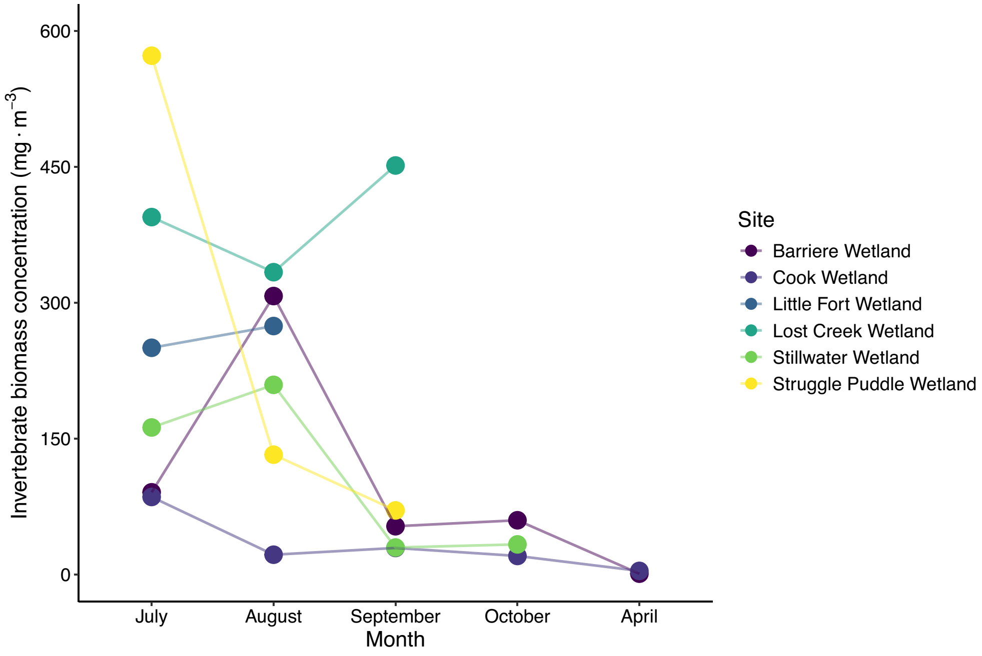


Fig. 4. Invertebrate biomass concentration (mg·m^{-3}) at each wetland site, for each sampling month. Discontinuities in points indicate that a site was dry or frozen.



Aquatic versus terrestrial invertebrates

Prey quality, as defined by terrestrial versus aquatic invertebrate contributions, varied between streams and wetlands (Fig. 6). In streams, terrestrial invertebrates made up a greater percentage of total biomass relative to aquatic invertebrates (terrestrial: 48%–88%, aquatic: 9%–50%) for all months except October when terrestrial and aquatic biomass were 48% and 50%, respectively. By contrast, aquatic invertebrates in wetlands made up a greater percentage of total biomass relative to terrestrial invertebrates (aquatic: 62%–100%, terrestrial: 0.05%–38%) across all sampling months. Notably, while percent terrestrial biomass was lowest for streams in Octo-

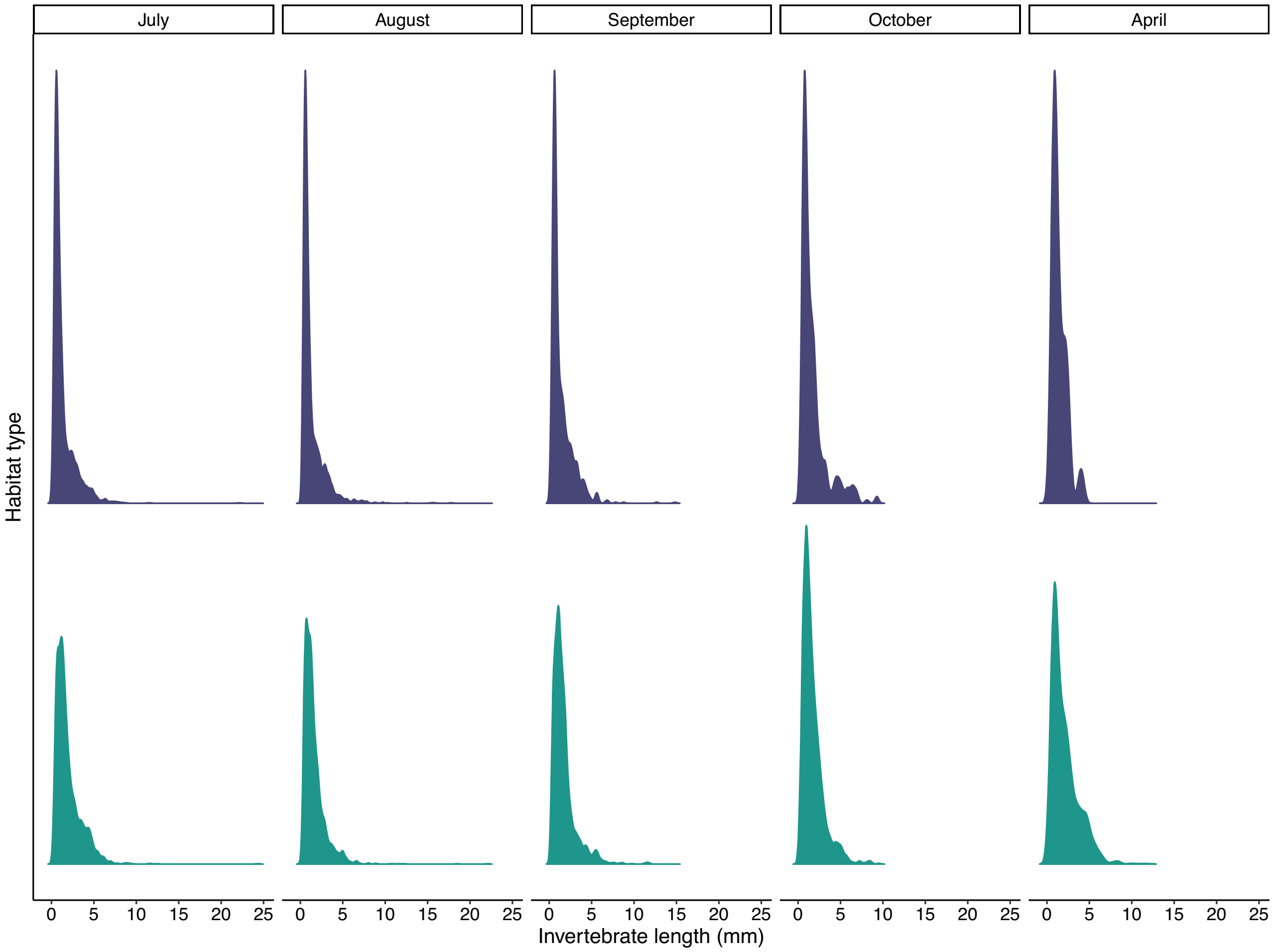
Table 6. Model selection results of candidate models for wetland invertebrate biomass concentration (IBC).

Model	AICc[a]	ΔAICc[b]	Model weight	Log likelihood
$IBC_W \sim Month + Phosphorous$	263.39	0.00	0.42	− 120.70
$IBC_W \sim Month$	263.42	0.02	0.41	− 122.91
$IBC_W \sim Latitude + Month$	267.20	3.81	0.06	− 122.60
$IBC_W \sim Month + Canopy$	267.47	4.08	0.05	− 122.73
$IBC_W \sim Month + Temperature$	267.78	4.38	0.05	− 122.89
$IBC_W \sim 1$	272.35	8.96	0.01	− 133.86
$IBC_W \sim Month + Connectivity$	272.42	9.03	0.01	− 122.67
$IBC_W \sim 1 + (1\|Site)$	272.85	9.46	0.00	− 132.76

[a] Aikake's information criterion corrected for small sample size.

[b] Difference in AICc score between the given model and the most parsimonious model.

Fig. 5. Probability densities of invertebrate length (mm) measurements in streams (teal, bottom) and wetlands (purple, top), for each sampling month.



ber, percent terrestrial biomass peaked for wetlands in this sampling month.

Prey accessibility

Anatomical constraints on prey consumption

The percentage of consumable prey for each size class of juvenile Coho Salmon varied seasonally between streams and wetlands (Table 7). Indeed, a greater (or equal) percentage of invertebrate biomass concentration was consumable in streams relative to wetlands for most sampling months, except for October. However, the percentage of consumable prey always exceeded 70% in wetlands, regardless of sampling month or Coho Salmon size class. For minimum-sized Coho Salmon in streams and wetlands, reductions in the percentage of consumable prey were due to the occurrence of inver-

Fig. 6. Percentage of invertebrate biomass consisting of invertebrates in an aquatic, terrestrial, or unknown life stage for streams and wetlands, across all sampling months. Instances when percent biomass is <2% are not depicted.

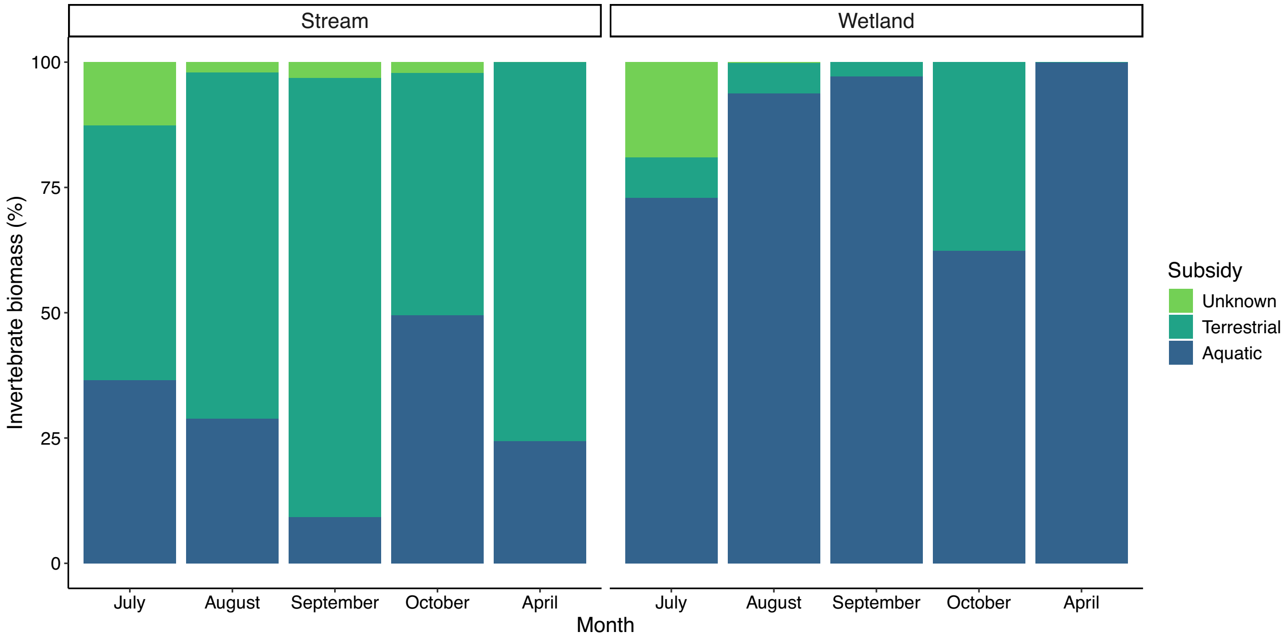


Table 7. Percentage of total invertebrate biomass concentration in streams and wetlands that is consumable by juvenile Coho Salmon of three size classes (minimum: 2.8–3.6 cm; median: 4.9–6.9 cm; and maximum: 10.9–13.5 cm), across all sampling months.

	Consumable IBC					
	Minimum		Median		Maximum	
Month	Stream	Wetland	Stream	Wetland	Stream	Wetland
July	99	89	98	93	89	73
August	96	81	99	96	76	74
September	100	78	99	99	89	84
October	100	100	97	99	74	82
April	100	100	99	94	96	87

tebrates that are too large for consumption. By contrast, reductions in the percentage of consumable prey for median- and maximum-sized Coho Salmon in both habitats is a result of invertebrates that are too small for these fish to consume, given anatomical constraints.

Abiotic habitat suitability

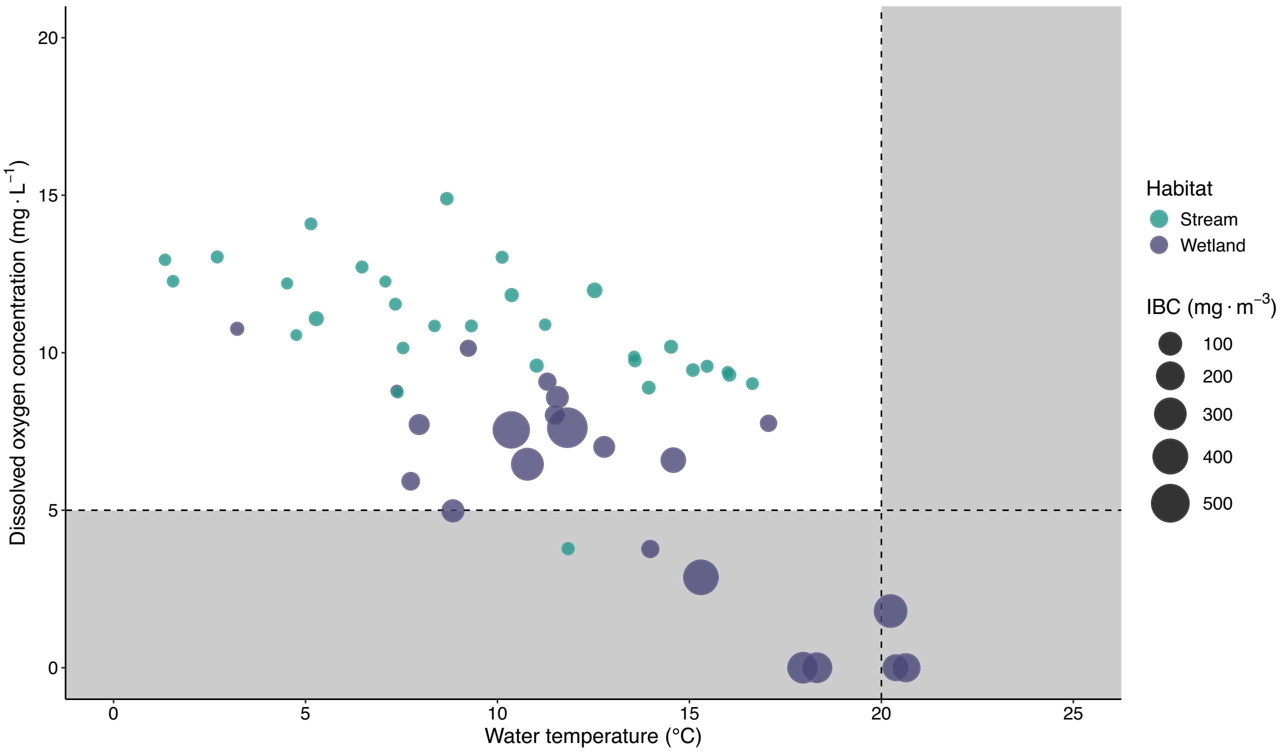
Wetlands were generally warmer and had lower dissolved oxygen concentration than streams in summer months; as a result, conditions at some wetland sites reached stressful levels (i.e., water temperature > 20 °C and/or dissolved oxygen concentration < 5 mg·L^{-1}) at multiple instances during the study period (Fig. 7). Notably, water temperature and dissolved oxygen concentration reached physiologically stressful levels at Stillwater Wetland in July, as well as at Stillwater Wetland and Lost Creek Wetland in August. Dissolved oxygen concentration also reached physiologically stressful levels at Little Fort Wetland, Lost Creek Wetland, and Barriere Wetland in July, at Little Fort Wetland and Lemieux Creek in August, as well as at Stillwater Wetland in September. In contrast to wetlands, water temperature and dissolved oxygen concentration in streams generally remained within a suitable range throughout the study period.

Elevated water temperature and low dissolved oxygen concentration coincided with periods of high relative prey abundance in wetlands, including at Lost Creek Wetland (August: 334 mg·m^{-3}) and Stillwater Wetland (July: 162 mg·m^{-3}; August: 210 mg·m^{-3}). Low dissolved oxygen concentration alone also coincided with high prey abundance, and occurred more frequently in wetlands, including at Little Fort Wetland (July: 250 mg·m^{-3}; August: 274 mg·m^{-3}), Lost Creek Wetland (July: 395 mg·m^{-3}), Stillwater Wetland (September: 30 mg·m^{-3}), and Barriere Wetland (July: 91 mg·m^{-3}).

Discussion

This study examined spatiotemporal patterns of food availability in tributary streams and floodplain wetlands across a large salmon-bearing watershed. We found striking dif-

Fig. 7. Water temperature (°C) and dissolved oxygen concentration (mg·L^{-1}) at each stream (teal) and wetland (purple) site, for each sampling month. Corresponding invertebrate biomass concentration (IBC; mg·m^{-3}) for a given site and sampling month is reflected by the size of the data point. The horizontal dotted line represents the lower dissolved oxygen concentration threshold for juvenile Coho Salmon (5 mg·L^{-1}). The vertical dotted line represents the upper water temperature threshold for juvenile Coho Salmon (20 °C). Physiologically sustainable environmental conditions fall within the white quadrat, whereas physiologically stressful environmental conditions are depicted by the light grey quadrats.



ferences between these habitats for multiple dimensions of food availability, which broadly support our hypothesis that streams and floodplain wetlands provide distinct and contrasting foraging environments for juvenile salmon. Many of our specific predictions were also supported, with the notable exception that variation in prey abundance was not consistently linked to spatial patterns (e.g., latitudinal gradients) and site-level predictors. Still, our collective results indicate that asynchronous dynamics in food availability contribute to a seasonally shifting portfolio of growth opportunities for juvenile Coho Salmon across the North Thompson watershed habitat mosaic.

Prey abundance

Streams and wetlands exhibited strikingly different seasonal patterns in prey abundance. In wetlands, average monthly prey abundance decreased through time, but remained 1.1–136 times greater than in streams throughout the rearing period, underscoring the importance of floodplain habitats as key sources of food for juvenile salmon. These estimates are consistent with other studies that have found substantially higher invertebrate abundance in floodplains relative to streams (10–100 times, Grosholz and Gallo 2006; 53 times, Jeffres et al. 2020; 10–100 times, Cordoleani et al. 2022). Comparatively low and aseasonal estimates of invertebrate biomass concentration at our streams (0.11–3.39 mg·m^{-3}) are similar to magnitudes and trends observed by other studies (e.g., 0.1– 1.06 mg·m^{-3}, Leung et al. 2009; 0.33–0.38 mg·m^{-3}, Fellman et al. 2023), except for Lemieux Creek and Albreda River (the two largest systems), whose estimates of invertebrate biomass concentration reached higher values (1.17–10.35 mg·m^{-3} and 0.06–7.60 mg·m^{-3}, respectively).

Patterns of prey abundance in streams and in wetlands were not explained by local predictors, with the exception of a weak positive effect of total phosphorous in wetlands. This conflicts with other studies that have found associations between invertebrates and abiotic habitat features (e.g., water temperature, Morin and Dumont 1994; and canopy cover, Hawkins et al. 1982). There are several possible explanations for this discrepancy. First, the effects of some predictors in our analysis (e.g., canopy cover and wetland connectivity) may be obscured by proximate, unmeasured drivers that have more direct influences on invertebrates (e.g., turbidity or primary productivity). Second, limited sample size precluded our ability to investigate nonlinear and interactive effects. Certain environmental predictors that were included in our analysis may not have a clear unidirectional effect on prey abundance; for example, stream flow can both increase invertebrate drift via passive entrainment or reduce it via dilution

(Rashidabadi et al. 2022). Similarly, patterns of invertebrate abundance may be driven by complex nonlinear or interactive effects among multiple predictors (Batzer 2013), which could not be directly tested.

Differences in invertebrate phenology between habitats and among sites likely contributed to the patterns of prey abundance that we observed. In particular, the timing of terrestrial invertebrate contributions may help to explain the observed seasonal variation in prey abundance among stream sites, which was unrelated to our predictors. Indeed, seasonal peaks in invertebrate abundance that occurred at some stream sites coincided with high subsidies of adult (terrestrial) insects. For instance, the September abundance peak at Lemieux Creek was driven by adult Hymenoptera, which comprised 77% of total biomass for that month. Similar late summer and fall peaks in terrestrial invertebrate inputs have also been observed in coastal salmon-bearing streams (Rundio and Lindley 2008; Li et al. 2016). This is also consistent with the suggestion that variation in prey phenology among streams can lead to asynchronous prey subsidies for salmonids (Nakano and Murakami 2001; Rossi et al. 2022). By contrast, greater proportions of small-bodied aquatic taxa with high turnover rates like zooplankton may underlie the more consistent seasonal trends across wetland sites. These inferences highlight the potential role of invertebrate diversity and phenology as it relates to salmon prey availability, but should be considered cautiously since our taxonomic classification was coarse (i.e., Order level).

Aspects of our methodology may have limited our ability to explain patterns in invertebrate abundance based on spatial and environmental drivers. In particular, while prey concentration is commonly used to describe foraging environments for fish, there are several caveats associated with this metric. First, prey concentration is a measure of invertebrate standing stock, and thus does not fully describe invertebrate production and potential energy flow to fish consumers (Benke 2018). Second, this metric also does not explicitly incorporate prey consumption by fish, which could theoretically depress invertebrate abundance and obscure results. In effect, high fish consumption could mask high invertebrate productivity. We contend that this is unlikely in streams since invertebrate drift is primarily produced locally in riffles that are not as accessible to fish (Lancaster et al. 2011; Naman et al. 2018), but it could occur in wetlands depending on fish density and consumption, as well as invertebrate turnover rates (Grosholz and Gallo 2006). Thus, accounting for fish consumption would, if anything, only amplify the patterns we observed.

Prey quality

Prey quality varied throughout the study period in relation to differences in prey composition between streams and wetlands, which highlight streams as key sources of energetically high-quality prey. Relative to wetlands, prey composition in streams was characterized by a greater proportion of larger invertebrates, based on average invertebrate length and invertebrate size distribution. Streams also had greater proportions of terrestrial invertebrates. By contrast, prey composition in wetlands was characterized by higher numbers of small invertebrates (primarily zooplankton) and mainly invertebrates of aquatic origin. Variation in prey size and composition between streams and wetlands translates into differences in prey quality because the total energy of a given prey item increases with size (Cummins and Wuycheck 1971), and terrestrial invertebrates are on average larger (Rosenfeld and Raeburn 2009) and have greater energy density than aquatic invertebrates (Koehler et al. 2006). These results are consistent with a study by Tiffan et al. (2014), who found that variation in prey composition between riverine and reservoir habitats was reflected in differences in the energy content of juvenile Chinook Salmon diets, with 11%–40% higher energy density in riverine diets resulting in significantly greater juvenile growth. While the metrics used here describe the energetic value of prey quality, we recognize that indicators of nutritional value may be similarly important dimensions of prey quality (Závorka et al. 2021), but were out of scope for this study.

Prey accessibility

Not all available prey in streams or wetlands were consumable by juvenile Coho Salmon, and the size class of the consumer determined its capacity to ingest invertebrates (Wañkowski 1979). For instance, minimum-sized Coho Salmon in wetlands were limited primarily by invertebrates that were too large for consumption, which were rare but comprised a large percentage of total invertebrate biomass concentration. In contrast, median- and maximum-sized Coho Salmon in both habitats were limited primarily by invertebrates that were too small for consumption. Size-dependent foraging constraints have been shown in other studies (e.g., Armstrong et al. 2010) and may have consequences for fish performance in different habitats and across seasons. However, the majority of invertebrates (>70%) in wetlands and in streams were accessible to juvenile Coho Salmon across all seasons, suggesting that these dynamics do not severely restrict prey consumption.

Environmental conditions varied between streams and wetlands throughout the study period, resulting in seasonal differences in prey accessibility when conditions became physiologically stressful for foraging. This occurred more frequently in wetlands, particularly in July and August as dissolved oxygen concentrations often declined beyond physiologically stressful limits and water temperature exceeded 20° C on several occasions. This is consistent with other observations of floodplain habitats, which exhibit greater variability and range in water temperature and dissolved oxygen concentration relative to streams (e.g., Cordoleani et al. 2022). This suggests the potential for a trade-off between high food abundance but challenging abiotic conditions in wetlands, versus lower food abundance but more favourable abiotic conditions in streams. While movements across streams and wetlands may be rare in the North Thompson watershed due to seasonal disconnection between these habitats (Milner et al. 2025), salmonids often exhibit behaviour and movements to track favourable conditions (e.g., Baldock et al. 2016). This may include using microhabitat patches of favourable conditions within wetland habitats as refugia (Woelfle-Erskine et al. 2017), which was not captured at the scale of our sampling. Thus, wetland habitats that experience physiologically stressful conditions should not be devalued, as they can play an important role in supporting fish growth (Armstrong et al. 2021).

Synthesis and implications

Collectively, our results suggest that streams and wetlands provide distinct foraging opportunities for juvenile Coho Salmon based on seasonal differences in prey abundance, quality, and accessibility. Most notably, prey abundance in wetlands was orders of magnitude greater than in streams throughout the majority of the rearing period. Greater prey abundance and increased assimilative capacity associated with warmer water temperatures near the thermal optimum implies that wetlands may provide juvenile coho with opportunities for higher growth (Sullivan et al. 2000). This has been observed in other studies and suggests that floodplain habitats are hot spots of fish production (e.g., Górski et al. 2013; Lusardi et al. 2020). However, our results also indicate that foraging in non-natal wetlands may be a high-risk high-reward strategy, as higher prey abundance often coincided with physiologically stressful conditions, such as such as low dissolved oxygen concentration (Milner et al. 2025). Comparatively low prey abundance in streams could potentially be offset, to an extent, by the consumption of higher-quality prey in this habitat, which has been shown to support increased fish growth (Tiffan et al. 2014). Further, environmental conditions in streams generally remained within a physiologically sustainable range throughout our study period; so, although prey abundance in streams was relatively low, foraging in this habitat may be a reliable low-risk strategy.

Our study offers several key insights for the management of Pacific Salmon and their watersheds. First, our findings support the importance of non-natal rearing habitats like floodplain wetlands for salmon populations. While this point has been made by other studies (e.g., Baker et al. 2025; Milner et al. 2025), our work highlights a specific mechanism (higher food availability) that potentially underlies the value that these habitats provide. Thus, despite being ephemerally wetted or connected—and often exhibiting stressful abiotic conditions—floodplain wetlands should be considered highly valuable salmon habitat. Second, our work supports a link between habitat diversity and asynchronous food availability for salmon, which may contribute to population resilience and stability (e.g., Bellmore et al. 2022). Therefore, management actions that maintain or improve habitat diversity and asynchrony (e.g., floodplain reconnection; Ciotti et al. 2021) should be prioritized. This is especially relevant in the context of a warming climate, which could have a homogenizing effect on watershed processes (Dunkle et al. 2025). Finally, this work underscores the importance of food availability as a key metric to evaluate fish habitat, and highlights the need to incorporate food web dynamics into the management and conservation of at-risk fish populations.

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Author information

Author ORCIDs

Sean M. Naman https://orcid.org/0000-0002-2113-8311
Douglas C. Braun https://orcid.org/0000-0002-4504-7035
Amanda M. Martens https://orcid.org/0000-0002-7838-3342

Author contributions

Conceptualization: SP, SMN, CJL
Data curation: SP, DCB, DL, AMM
Formal analysis: SP
Funding acquisition: SMN, DCB
Investigation: SP, SMN, CT, DCB, DL, AMM
Methodology: SP, SMN, CT
Project administration: SMN, CJL
Supervision: SMN, CJL
Visualization: SP
Writing – original draft: SP
Writing – review & editing: SP, SMN, CT, DCB, DL, AMM, CJL

Competing interests

The authors have no competing interests to declare.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2025-0364.

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